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Herbivorous fish rise as a destructive fishing practice falls in an Indonesian marine national park

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Abstract. Securing ecosystem functions is challenging, yet common priority in conservation efforts. While marine parks aim to meet this challenge by regulating fishing through zoning plans, their effectiveness hinges on compliance levels and may respond to changes in fishing practices. Here we use a speciose assemblage of nominally herbivorous reef fish in Karimunjawa National Park (zoned since 1989) to investigate whether areas subject to a restrictive management regime sustained higher biomass over seven years compared to areas where moderate and permissive regulations apply. Using a trait-based approach we characterize the functional space of the entire species pool and ask whether changes in biomass translate into changes in functional structure. We track changes in predator biomass, benthic community structure, and fishing practices that could influence herbivore trajectories. Overall herbivore biomass doubled in 2012 compared to 2006–2009 and remained high in 2013 across all management regimes. We found no evidence that this biomass build-up resulted from predator depletion or increased food availability but suggest it emerged in response to a park-wide cessation of fishing with large drive nets known as muroami. The biomass increase was accompanied by a modest increase in taxonomic richness and a slight decrease in community-scale rarity that did not alter functional redundancy levels. Subtle changes in both functional specialization and identity of assemblages emerged as generalist species with low intrinsic vulnerability to fishing recovered sooner than more vulnerable specialists. While this implies a recovery of mechanisms responsible for the grazing of algal turfs and detritus, restoring other facets of herbivory (e.g., macroalgal consumption) may require more time. An increase in the cost-benefit ratio per journey of muroami fishing facilitated a ban on muroami nets that met minimal resistance. Similar windows of opportunity may emerge elsewhere in which gear-based regulations can supplement zoning plans, especially when compliance is low. This does not advocate for implementing such regulations once a fishery has become unprofitable. Rather, it underlines their importance for breaking the cycle of resource depletion and low compliance to zoning, thus alleviating the resulting threats to food security and ecosystem integrity.

Key words: coral reefs; functional traits; herbivorous fishes; Indonesia; monitoring; muroami fishing; zoning.

INTRODUCTION

Securing ecosystem functions in the face of overexploitation and species loss is one of the greatest challenges of the Anthropocene. Establishing marine protected areas, zoning plans, and fishing regulations are central pathways to achieving this goal in the ocean, yet depend on public compliance and costly enforcement investments (Millennium Ecosystem Assessment 2005, Arias 2015). Effective zoning plans are most urgent and difficult to enforce in developing countries where societies are heavily reliant on fishing. These societies may be trapped in cycles of chronically low compliance and depleted resources leading to destructive exploitation practices with short-term returns (Stonich 1989, Cinner 2010, 2011). As declines in biomass and diversity of exploited resources may herald risks for food security and ecosystem function in these sensitive areas, tracking them across different management zones is crucial.

Coral reefs in Southeast Asia support the livelihoods of more than 138 million people through fisheries (Burke et al. 2011), with Indonesia being home to the largest

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number of coral reef fishers worldwide (1.7 million; Teh et al. 2013). Developing environmentally conscious, economically sound, and socially just fisheries is therefore a major governmental goal, and zoning plans including no-take and open-access areas are commonly developed with substantial stakeholder input throughout the region (Lucas 2009, Campbell et al. 2013, White et al. 2014). Prohibiting fishing in certain areas of the ocean can restore trophic structures, overall taxonomic richness, biomass of exploited resources, and key ecosystem processes (Russ and Alcala 1998, Micheli et al. 2004, McClanahan et al. 2009, Rasher et al. 2013, Topor et al. 2019). The extent to which different management regimes influence the trajectory of the functional structure of fish assemblages over time, thus reorganizing the make-up of ecosystem functions, is less clear.

Under escalating levels of stress, securing functions that facilitate ecosystem recovery is particularly important (Hoegh-Guldberg et al. 2008, Bellwood et al. 2019*a*). Herbivory is strongly linked to the integrity, stability, and resilience of coral reefs to disturbances (Burkepile and Hay 2008, Adam et al. 2011), and is primarily sustained by fishes. Insufficient herbivory can increase the probability of diverse coral-dominated reefs ecologically simplifying to persistent algal-dominated regimes stabilized by a new set of ecological feedbacks (McManus and Polsenberg 2004). Not surprisingly, sustaining biomass and diversity of nominally herbivorous fish is recognized as a critical step in managing reef futures (Graham et al. 2013).

As nominally herbivorous fish reach sizes in excess of 1 m, they are heavily harvested throughout the Indo-Pacific and Indonesia (Cinner et al. 2005, Campbell et al. 2014, Ford et al. 2016). Rarely are nominally herbivorous fishes afforded specific bans or catch limits, but they can be protected through spatially explicit fishery regulations (Williams et al. 2016). Such protection from fishing can, however, lead to increases in the abundance of predators, which may exert significant top-down pressure on herbivorous fish populations (Friedlander and DeMartini 2002, Houk and Musburger 2013). With some exceptions (Russ et al. 2018), the extent to which herbivore assemblages undergo different temporal trajectories in protected and open-access areas has been investigated at a coarse taxonomic level, or tangentially in meta-analyses including several fish families (Maliao et al. 2009, McClanahan et al. 2011, Edwards et al. 2014, Graham et al. 2015). However, species can respond differently to protection based on key life-history characteristics that determine their intrinsic vulnerability to exploitation (Jennings et al. 1998, Abesamis et al. 2014). Large-bodied long-lived parrotfishes and unicornfish, for instance, are highly vulnerable to exploitation, and thus tend to disappear rapidly along increasing fishing pressure gradients and recover slowly after cessation of fishing (Bellwood et al. 2012, Abesamis et al. 2014). Contrary patterns or no response to fishing or protection can be expected from short-lived, small-bodied, and fast-growing species. Damselfish biomass, for instance, tends to be highest in fished areas (Edwards et al. 2014), or insensitive to fishing pressure (Campbell and Pardede 2006). Tracing these contrasting trajectories may provide insight into potential changes in herbivory levels, and is therefore highly relevant to support coral reef management strategies.

Not only do nominally herbivorous fish vary in their intrinsic vulnerability to exploitation (Clua and Legendre 2008), but they are also functionally multifaceted. Nominally herbivorous species have been traditionally classified into a limited number of distinct functional feeding groups (e.g., grazers–detritivores, scrapers–small-excavators, and bioeroders–large-excavators, macroalgal browsers, and algal farmers; Green and Bellwood 2009). There are, however, important behavioral and functional differences among species within these groups (Fox and Bellwood 2013, Brandl and Bellwood 2014, Brandl et al. 2015, Streit et al. 2015, Burkepile et al. 2018). A functional trait-based approach that captures many of these differences may help to detect changes in trophic functional structure of speciose assemblages and the make-up of herbivory.

Monitoring changes in nominally herbivorous fish as both food and ecosystem function providers, and assessing the role of management in moderating these changes, calls for considering biomass together with several taxonomic and functional community metrics. Species richness should be examined in parallel with community-scale rarity, an underused yet useful metric tailored to capture changes in the distribution of abundance among species and the number of rare species, which consistently responds to protection (Soykan and Lewison 2015). A trait-based metric of functional redundancy (i.e., the capacity to functionally compensate the loss of others) may also indicate the susceptibility of herbivory to species loss (Mouillot et al. 2013*a*, Swenson 2014). Changes in other complementary trait-based community indices (e.g., functional specialization and identity) reveal important shifts in the distribution of species within niche space and may herald the homogenization of assemblages and their functions (Villéger et al. 2010, Ibarra and Martin 2015). Although changes in trait-based indices of fish faunas have been reported as a result of disturbances and non-native species introductions (Brandl et al. 2016, Toussaint et al. 2018), the capacity of management restrictions to buffer these changes through time remains largely untested.

Nominally herbivorous fish have been heavily exploited in Karimunjawa National Park (Campbell et al. 2014), and monitored with a high taxonomic resolution since 2006 (Pardede et al. 2016). Yet, temporal patterns of this key group have not been investigated throughout the full extent of the monitoring program. While compliance with the zoning has been sought through education and awareness-raising (Widyatmoko et al. 2012), drive nets, or muroami, have been used throughout the park, including restrictively managed areas, yielding large catches of herbivorous fishes (Campbell and Pardede 2006). Muroami is a large net (i.e., ~37 m long × 10 m deep), normally deployed by a fleet of several boats and operated in combination with divers (often supplied with compressed air from the surface) who walk on the reef converging towards the net while dragging ropes tied with stone weights. The muroami fishing practice appears to have changed over time, but quantitative data on these changes are fragmented (Marnane et al. 2004, Mukminin et al. 2006).

Here, we investigate the temporal changes within nominally herbivorous fish assemblages and their potential drivers between 2006 and 2013 in Karimunjawa National Park. Specifically, we assess changes in biomass, taxonomic richness, community-scale rarity, and in three trait-based metrics of community functional structure (i.e., functional redundancy, functional specialization, and functional identity) and relate them to three different management regimes, temporal trends in muroami fishing effort, and a set of environmental variables. In doing so, we highlight the role of spatially explicit fisheries management and gear-based restrictions in sustaining biodiversity and ecosystem function.

Materials and Methods

Study area

This study was conducted in the Karimunjawa archipelago, which is located 120 km north of Semarang in central Java (Indonesia) and comprises 27 islands (Fig. 1a, b). Spanning 22 of these islands and 111,625 ha, the Karimunjawa National Park is one of the largest marine parks in Indonesia. The park was first allocated a zoning plan in 1989 prohibiting all forms of fishing in certain areas, and allowing traditional fishing activities in others, but initial compliance was limited (Campbell and Pardede 2006). Revisions to the initial zoning were made with input from stakeholders in 2005 and 2012 yielding improved compliance with gear restrictions (Campbell et al. 2012, 2013; Fig. 1b; Appendix S1: Table S1). Data on fish and benthic assemblages were collected at relatively shallow (~7 m) forereef sites outside the park as well as within four different zones effective in 2012, namely core, protection, tourism, and traditional use zones (Fig. 1b). We classified sites in which fishing is prohibited (i.e., core and protection zones, $n = 22$) as subject to a restrictive management regime, where fishing requires a permit (i.e., tourism zones, $n = 7$) as moderately restrictive, and sites designated for traditional use or outside the park ($n = 13$) as permissive (Fig. 1). While 13 of our survey sites changed their original 2005 zoning designation during the 2012 rezoning (Appendix S1: Table S1), their management regime reflects the zone in which these remained for most years since 2005, rather than their corresponding zone in 2012.

Data collection

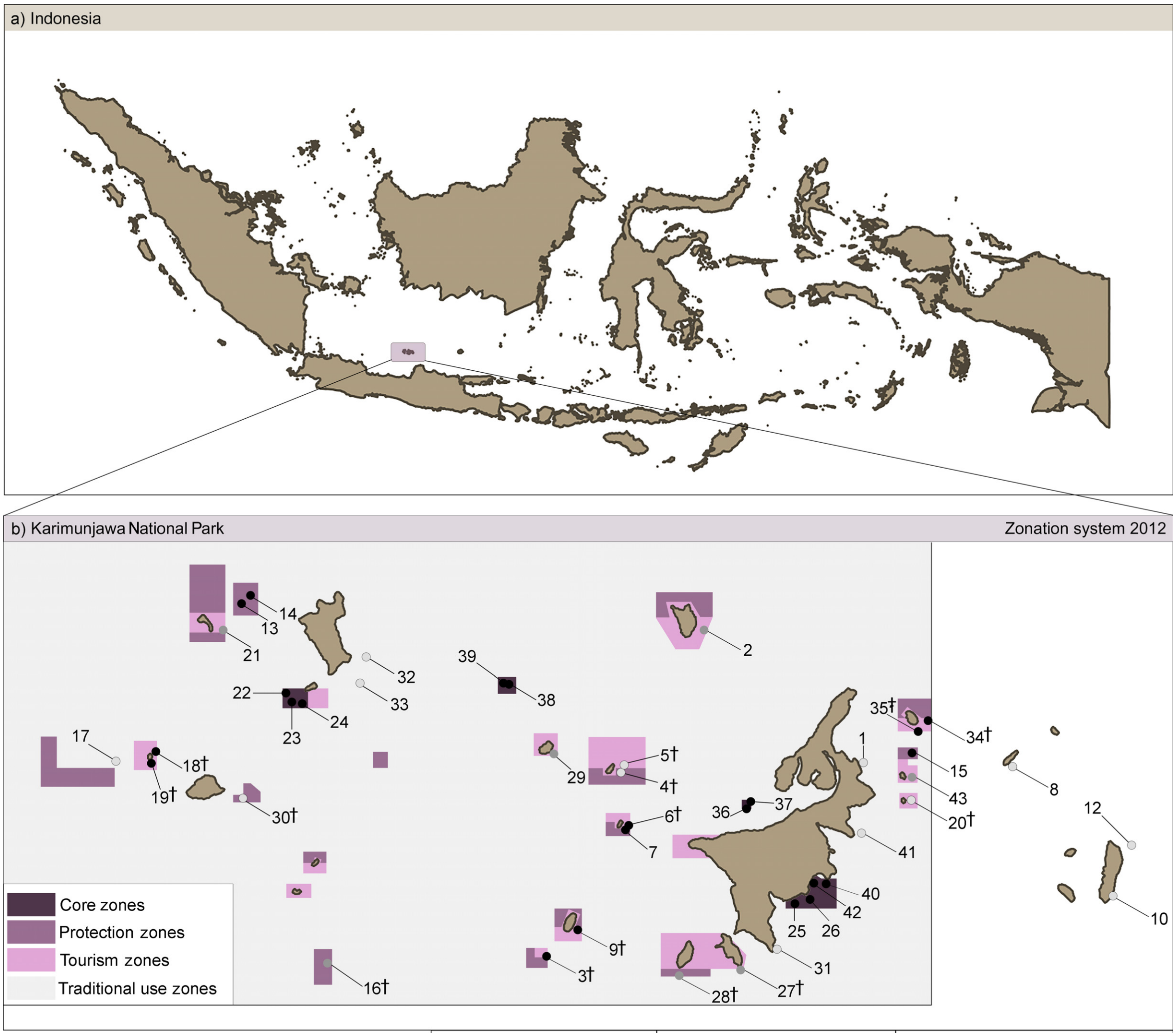
Fish and benthic data, as well as catch data analyzed here, were collected simultaneously under the Karimunjawa National Park Authority and Wildlife Conservation Society—Indonesia Programme. Underwater surveys were conducted in the same season (April–May) in 2006, 2007, 2009, 2012, and 2013. Fish catch surveys took place at landing sites on Karimunjawa Island. These were conducted yearly but sparsely on certain days of the year between 2003 and 2005, interrupted in January 2006 and reinitiated monthly for at least 15 d/month from November 2009 until December 2013. We focus our catch data analysis on the four years encompassing those months surveyed consistently and regularly (November 2009–October 2013).

Herbivore biomass, taxonomic richness, and community-scale rarity.—Abundance of nominally herbivorous fish was quantified using underwater visual censuses along 50 m belt transects. Each transect was surveyed in two passes to maximize accuracy when sampling highly diverse species assemblages (McClanahan 1994). Large fish (>10 cm in total length, TL) were counted in the first pass within 2.5 m either side of the observer (250 m^2), whereas small ($\leq$10 cm TL) site-attached fish were counted in the second pass within 1 m either side of the observer (100 m^2). Fish were identified to the species level and their total length was estimated to the nearest 5 cm. The number of replicate transects surveyed per site was consistent among sites within years, but ranged from 2 to 4 among years due to variable funding (Appendix S1: Table S2).

The present analysis focused on 77 species of nominally herbivorous fish (Appendix S1: Table S3) including surgeonfishes (Acanthuridae), batfishes (Ephippidae), chubs (Kyphosidae), parrotfishes (Labridae: Scarinae), rabbitfishes (Siganidae), and pomacanthids of the genus *Centropyge* (Green and Bellwood 2009). We also considered algal-farming damselfishes (Pomacentridae). Although these differ in functional importance from larger roving herbivores, they can preclude herbivory by other fishes, cause adult coral mortality, and substantially modify algal community structure (Potts 1977, Emslie et al. 2012, Casey et al. 2014).

To account for interspecific differences in life history characteristics related to potential vulnerability to fishing, we grouped species in five intrinsic vulnerability categories based on the ratio between their asymptotic length (L_∞) and body growth rate (k; Bejarano et al. 2013). Species-specific estimates of L_∞ and k were obtained using the FishBase life history tool (Froese and Pauly 2017; Appendix S1: Table S3).

Biomass was obtained by converting total length into mass data using published length–mass relationships (Kulbicki et al. 2005, Froese and Pauly 2017). Mean biomass per site and management regime (overall and per intrinsic vulnerability category) were computed by



c) Sites Stratified by Management Regime	● Restrictive		● Moderately restrictive	○ Permissive	
Uses	Core	Protection	Tourism	Traditional use	Open access
Fishing (all techniques)	X	X	p	✓	✓
Boat transit only	✓	✓	✓	✓	✓
Boat transit and anchoring	✓	✓	✓	✓	✓
Tourism	✓	✓	✓	p	✓
Traditional use	✓	✓	p	✓	✓

FIG. 1. (a) Location of the Karimunjawa National Park in Indonesia, (b) the zonation system of the park issued in 2012, and location of our 42 study sites. Sites are classified in restrictive, moderately restrictive, and permissive management regimes according to the zone in which they have remained for longest since 2005 (Appendix S1: Table S1) and (c) the uses allowed (✓), possible with a permit (p), or prohibited (X) within each zone. Sites remaining predominantly within core and protection zones are subject to a restrictive management regime (*n* = 22), tourism zones are subject to a moderately restrictive management regime (*n* = 7), and sites within traditional use and open access-zones are subject to a permissive management regime (*n* = 13). Note that sites marked with † shifted zones during the 2012 rezoning (Appendix S1: Table S1), yet their management regime reflects the zone in which these remained for most years since 2005, rather than their corresponding zone in 2012.

averaging transect values and site means, respectively. Mean taxonomic richness per year per management regime was obtained by averaging the total number of species recorded within the corresponding sites. Community-scale rarity was computed as the skewness of log-transformed biomass per site and year, and corresponding site means were averaged to obtain means per management regime and year (Soykan and Lewison 2015).

Trait-based characterization of nominally herbivorous fish trophic diversity.—Species were characterized using 13 morphological and ecological traits that relate to their foraging behavior and interaction with different components of the reef benthos (Appendix S1: Table S4). Traits were either continuous (i.e., 1, maximum total length; 2, breadth of depth range; and 3, snout angle), ordinal (i.e., 4, level of feeding territoriality; 5, home range; 6–10, level of interaction with detritus, algal turfs, upright macroalgae, calcareous reef matrix, and live corals), categorical (11, tooth morphology), or nominal multi-choice (i.e., 12, sociality and 13, types of macroalgae consumed). Species were ordered in a functional space using a Principal Coordinate Analysis (PCoA) based on a matrix containing an extension of the Gower's distance between all pairs of species developed to handle all trait types (Gower 1971, Pavoine et al. 2009). Further details on the compilation of these traits and the computation of the six-dimensional (6D) functional space are provided in the supplementary material (Appendix S1). In order to identify which traits contribute to the distribution of species along each axis in the 6D functional space, we computed the projections of traits onto this space and related them a posteriori to the axes using covariance values (for quantitative and ordinal traits) and fitted weighted class centroids with standard deviations (for categorical and nominal multi-choice traits; Legendre and Legendre 1998). To obtain a measure of the relative strength of the contribution among categorical and nominal multi-choice traits, we conducted ANOVAs comparing the scores of species grouped within factor levels or choices on the different axes.

Assessing trait-based metrics of the functional structure of herbivore assemblages.—The distribution of species and their abundances within the trait space was used as a proxy for their functional structure (Mouillot et al. 2013*b*, but see Bellwood et al. 2019*b*). Three metrics describing complementary facets of the functional structure of nominally herbivorous fish assemblages were computed per site and year in Karimunjawa, namely functional redundancy, functional specialization, and functional identity. Functional redundancy was taken as a property shared among the closest neighbors in functional space and thus computed as the mean abundance-weighted pairwise distance between every species in the assemblage and their nearest present neighbors (Mouillot et al. 2013*a*, Swenson 2014). Low values of this metric thus reflect the co-occurrence of functionally similar species (i.e., high functional redundancy), whereas high values indicate the co-occurrence of functionally dissimilar species (i.e., low functional redundancy; Swenson 2014). Functional specialization was computed as the mean abundance-weighted distance between every species in the assemblage and the centroid of all species in the assemblage (Mouillot et al. 2013*b*, Ibarra and Martin 2015). Functional identity was calculated as the average position of the assemblage along each of the PCoA axes (Mouillot et al. 2013*b*, Toussaint et al. 2018). Means per management regime and year were obtained averaging the values of the corresponding sites.

Reconstructing changes in muroami fishing.—As annual site-specific catch data are lacking, the total annual muroami fishing effort and volumetric catch per unit effort (CPUE) in Karimunjawa were computed for four years between November 2009 and October 2013. Annual fishing effort means were obtained averaging the mean number of daily muroami landings per month ($n = 12$). The volumetric CPUE comprised by nominally herbivorous fishes was computed per muroami landing using Eq. 1 and then averaged among the landings of each year to obtain an annual mean.

$$\text{CPUE} = \frac{W}{(T \times F)} \tag{1}$$

where W corresponds to total mass (kg) landed per trip, F to the total number of fishers per trip, and T to total fishing time of the fishing trip including travelling time.

By compiling government legislation bills and local reports we reconstructed all historical facts pertaining to the law on the use of muroami nets, as well as changes in fisher's perceptions and compliance.

Potential biological drivers of herbivore trajectories.—Biomass of strictly piscivorous fishes, which are known to have strong effects on herbivore behavior (Madin et al. 2012; Appendix S1: Table S5), was quantified in one pass along the same transects used for nominally herbivorous fishes. We focused on individuals larger than 10 cm in TL and thus capable of consuming the smallest of potential target prey species considered here (i.e., damselfish; Madin et al. 2012). Since nominally herbivorous fish track benthic characteristics and algal resources spatially (Russ et al. 2015, Tootell and Steele 2016), they could respond to temporal changes in benthic community structure and algal cover. Benthic community structure was therefore quantified by recording the presence of 21 broad benthic categories (Appendix S6: Table S6) every 50 cm along 50 m point-intercept transects ($n = 4$ per site). Along these transects, the percent cover of the most structurally complex coral forms (i.e., added cover of branching, digitate, tabulate, and foliose corals) and four algal types (i.e., algal turfs, articulated coralline algae, crustose coralline algae, and fleshy algae) were quantified separately.

Statistical analysis

To investigate whether herbivore assemblages changed over time, and if management regime influenced their temporal trajectory, we applied different statistical modeling approaches depending on the response variable and its distribution. In all cases, we fitted initial models including year (five levels), management regime (three levels), and their interaction, accounting for the lack of independence among repeated measures (i.e., fitting site as a random effect). Pearson residuals were plotted against the fitted values to check for homogeneity of variance, and against each explanatory variable to check for violations of independence (Zuur et al. 2007).

Modeling biomass, taxonomic richness, rarity, and functional structure metrics.—Mean herbivore biomass (overall and per intrinsic vulnerability category), community-scale rarity, and functional structure metrics were modeled using linear mixed-effects models (LMEs). Variance differed in some cases among management regimes, years, or the levels of the interaction term and heteroscedasticity was accounted for by using appropriate variance structure terms (Tables 1, 2; Zuur et al. 2009). Taxonomic richness was modeled using a generalized linear mixed-effects model (GLMM) with Poisson distribution verifying that the scale parameter φ was not significantly different from that assumed in a Poisson distribution (i.e., 1; Crawley 2007).

Modeling the probability of occurrence of the most uncommon and vulnerable herbivores.—The biomass of herbivores with the highest intrinsic vulnerability was heavily zero inflated (i.e., 85% of observations were 0s). We therefore refrained from applying models for zero-inflated continuous data (e.g., zero-inflated gamma models; Zuur and Ieno 2016) because these require a larger number of non-zero observations. Instead, a Bernoulli GLMM was fitted to the presence–absence of fishes within this group to gain an estimate of their probability of occurrence.

Table 1. Outputs of mixed-effects models fitted to test whether temporal trajectories of nominally herbivorous fish biomass differed among management regimes accounting for the correlation among repeated measures.

Metric and pairwise comparison	*P*
Overall biomass	
Year	**<0.0001**
varIdent(form = ~1| year × management regime)	
Management regime	0.170
Year × management regime	0.192
2009 < 2006	0.010
2012 > 2006, 2007, 2009	0.028, <0.001, <0.001
2013 > 2006, 2007, 2009	<0.001, <0.001, <0.001
Biomass (very low intrinsic vulnerability)	
Year	**0.0001**
varIdent(form = ~1| year × management regime)	
Management regime	0.129
Year × management regime	0.418
2012 > 2006, 2007, 2009	<0.001, <0.001, <0.001
2013 > 2006, 2007, 2009	<0.001, <0.001, <0.001
Biomass (low intrinsic vulnerability)	
Year	**0.0001**
varIdent(form = ~1| year × management regime)	
Management regime	0.572
Year × management regime	0.707
2009 < 2006, 2007	0.001, 0.002
2012 > 2006, 2007, 2009	0.007, 0.023, <0.001
2013 > 2006, 2007, 2009	0.004, 0.008, <0.001
Biomass (moderate intrinsic vulnerability)	
Year	**0.0001**
varIdent(form = ~1| year × management regime)	
Management regime	0.527
Year × management regime	0.357
2009 < 2006	0.004
2012 > 2007, 2009	0.011, <0.001
2013 > 2006, 2007, 2009	0.013, 0.002, <0.001
Biomass (high intrinsic vulnerability)	
Year	**0.0001**
varIdent(form = ~1| year × management regime)	
Management regime	0.760
Year × management regime	0.583
2013 > 2007, 2009	<0.001, <0.001
Probability of occurrence	
Year	**0.017**
(Very high intrinsic vulnerability)	
Management regime	0.738
(No variance structure required)	
Year × management regime	0.437
2007 > 2009, 2012	0.016, 0.029
2009 < 2013	0.038
2012 < 2007	0.029

Note: Significant terms are highlighted in boldface type and presented along with significantly different pairwise comparisons.

Assessing spatio-temporal trends of potential herbivore drivers.—Due to the lack of site-specific annual muroami effort and catch data, a quantitative evaluation of the strength and hierarchy of all potential drivers of herbivore change was not feasible. We therefore investigated whether temporal trends of the different drivers conformed to sound ecological hypotheses. Restrictive management regimes may enhance piscivore biomass, and piscivores can exert top-down influence over the abundance of prey fish, including small herbivores (Boaden and Kingsford 2015). We therefore asked whether trajectories of piscivore biomass were determined by management regimes using LMEs for small (10–25 cm TL) and medium-sized (26–40 cm TL) piscivores, and a Bernoulli GLMM for those larger than 40 cm TL. The variation in benthic community structure among sites and years was examined in a Principal Component Analysis (PCA) computed per management regime. PCAs were obtained from arcsine-transformed percent cover data as appropriate for percentages (Legendre and Legendre 1998). To test whether benthic community structure changed among years and whether trajectories differed among management regimes we applied principal

Table 2. Outputs of mixed-effects models fitted to test whether temporal trajectories of selected metrics of taxonomic and functional herbivore community structure differed among management regimes accounting for the correlation among repeated measures.

Metric and differences among years	*P*
Taxonomic richness (no variance structure required)	
Year	**0.0003**
Management regime	0.070
year × management regime	0.809
2012 > 2007	0.001
2013 > 2007	0.002
Community-scale rarity (no variance structure required)	
Year	**0.0017**
Management regime	**0.035**
Year × management regime	0.653
2012 < 2007, 2009	0.035, 0.011
2013 < 2009	0.020
Restrictive > moderately restrictive	0.037
Functional redundancy (no variance structure required)	
Year	0.373
Management regime	0.828
Year × management regime	0.941
Functional specialization (no variance structure required)	
Year	**<0.0001**
Management regime	0.918
Year × management regime	0.501
2013 < 2007, 2009	0.011, <0.001
Functional identity on PCo3 (no variance structure required)	
Year	**< 0.0001**
Management regime	0.738
Year × management regime	0.491
2012 > 2006, 2007	0.001, 0.015
2013 > 2006, 2007, 2009	<0.001, 0.004, 0.031
Functional identity on PCo5 (no variance structure required)	
Year	**0.0001**
Management regime	0.163
Year × management regime	0.258
2009 < 2006, 2007	0.001, 0.006
2013 < 2006, 2007	0.001, 0.006

Note: Significant terms are highlighted in boldface type and presented along with significantly different pairwise comparisons.

response curves, a special case of redundancy analysis that can include interactions among factors and account for repeated measures (Legendre and Legendre 1998). To investigate changes in food availability that could be mirrored by nominal herbivores, we modeled mean percent cover of structurally complex coral forms and benthic algal types as a function of year, management regime, and their interaction using LMEs. To determine whether significant changes in yearly muroami fishing effort and volumetric CPUE of nominal herbivores occurred from 2009 to 2013, we fitted one-way ANOVAs.

All steps involved in the construction of the 6D functional space, derivation of functional structure metrics, as well as all statistical analyses were implemented in the software R v. 3.2.3 (R Development Core Team 2019) (further detail in Appendix S1). LMEs were specified with the function lme of the nlme package (Pinheiro et al. 2017). Poisson GLMMs were fitted with the function glmer of the lme4 package (Zuur et al. 2013, Bates et al. 2014). Optimal LMEs and GLMMs were followed by post-hoc tests to investigate pairwise differences between significant factor levels. These tests were conducted using the glht function of the multcomp package, which generates multiplicity-adjusted *P*-values that can be directly compared with the significance level ($\alpha = 0.05$; Bretz et al. 2011). Bernoulli GLMMs were fitted using the function glmmTMB from the glmmTMB package (Brooks et al. 2017).

Results

Herbivore biomass, taxonomic richness, and community-scale rarity

Management regime had no effect on the temporal trajectory of the biomass of nominally herbivorous fish. Overall herbivore biomass was at least twice as high in 2012 and 2013 compared to all earlier years (2006–2009) irrespective of management regime (Fig. 2a, Table 1). This trend reflects mainly an increase in species of very low to moderate intrinsic vulnerability to fishing (e.g., small- and medium-sized parrotfishes and surgeonfishes, rabbitfishes, damselfishes; Table 1; Appendix S1: Fig. S1a–c). The biomass of species with high intrinsic vulnerability (e.g., large-bodied parrotfishes and *Naso unicornis*) was stable from 2007 through to 2012 but higher in 2013 compared to 2007–2009 (Table 1; Appendix S1: Fig. S1d). The probability of occurrence of the largest and most vulnerable species (e.g., *Bolbometopon muricatum*, *Hipposcarus harid*) remained relatively low throughout the study with moderate peaks in 2007 and 2013 (Table 1; Appendix S1: Fig. S1e).

Differences in taxonomic richness and community-scale rarity between the 2006–2009 and 2012–2013 periods were less pronounced than those observed for biomass. In 2012 and 2013 mean taxonomic richness values were 30% higher than in 2007 but indistinguishable from other years (Fig. 2b, Table 2). In 2012 community-scale rarity was modestly but significantly lower (and thus biomass less skewed among species) compared to 2007 and 2009, and in 2013 it persisted significantly lower than in 2009 (Fig. 2c, Table 2). Although the temporal trajectory of community-scale rarity was uninfluenced by management regime, it was on average slightly higher under restrictive than moderately restrictive regimes (Fig. 2c, Table 2).

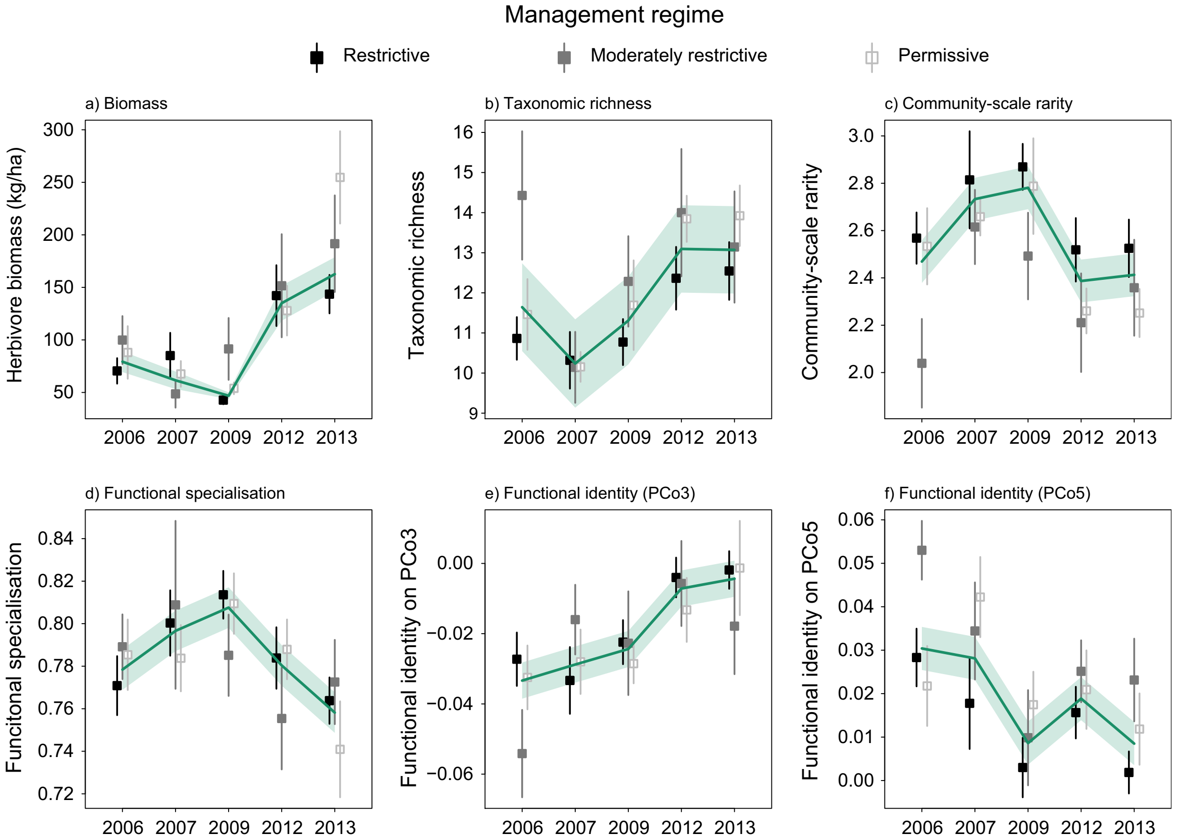


FIG. 2. (a) Biomass of all nominally herbivorous fish, (b) taxonomic richness, (c) community-scale rarity, (d) functional specialization, (e) functional identity on principal coordinate 3 (PCo3), and (f) functional identity on PCo5. Dots represent observed means per year and management regime (±SE) whereas colored lines and ribbons mark the means and SEs fitted by the optimal mixed-effects models, respectively.

Trait space for trophic diversity of the entire species pool

The majority of herbivorous fish species surveyed within Karimunjawa congregated towards the extremes of the functional space when represented by the first two axes, with only a few generalists occurring near the center (Fig. 3). These first two axes accounted for 54% of the total functional variance. The segregation of species along the first two axes reflects mainly their distribution along gradients of (1) maximum total length increasing right to left, (2) breadth of depth range widening from the top right to the bottom left corner, and (3) snout-angle increasing from the bottom left to the top right corner limiting species with most pronounced snouts to the lower half of the ordination space (Fig. 4a, Table 3). Parrotfishes and damselfishes conformed relatively compact and distinct groups along these axes indicating some taxonomic basis for the observed functional groupings. Ordinal traits had a weaker yet noticeable influence on the species' distribution within the ordination space. The level of interaction with algal turfs, for instance, contributed to the separation of parrotfishes (i.e., algal turf removers) from a mixed group of surgeonfishes, rabbitfishes, batfishes, and chubs that either crop turfs or have minimum interaction with them, and from turf farming damselfishes (Fig. 4b, Table 3). The level of interaction with upright macroalgae and the types consumed contributed to some extent to the distribution of species along the first two axes. A small group of macroalgal browsers consuming the fleshy foliose, terete corticated, and leathery types was confined to the bottom of the functional space, separated from others that occasionally feed on calcareous articulated macroalgae (i.e., mainly parrotfishes), or have no interaction with upright macroalgae (Fig. 4, Table 3; Appendix S1: Fig. S5). Tooth morphology contributed consistently to segregate species in small groups along all axes (Fig. 4c, Table 3). Both species and families tended to be more regularly distributed within the functional space when represented by axes three to six (Appendix S1: Figs. S2–S4).

Trait-based community metrics of functional structure over time

Management regime did not influence any of the community metrics of functional structure or their temporal trajectories. Despite the increase observed in biomass

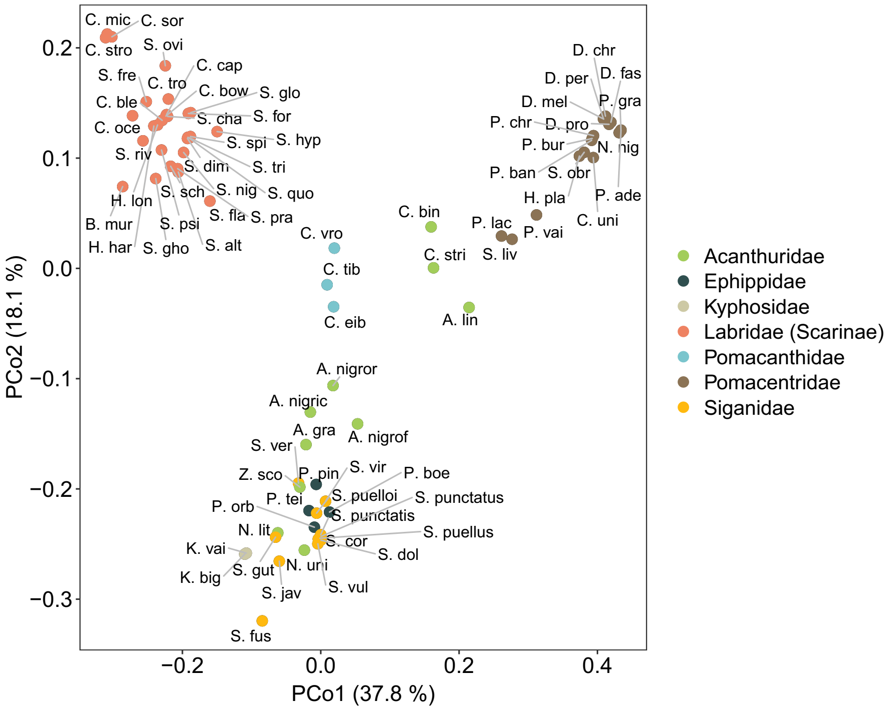


FIG. 3. Principal Coordinate Analysis (PCoA) representing the trait space for nominally herbivorous reef fishes. The first two axes account for 54% of the total functional variance. Species names are abbreviated to the first letter of the genus and first three of the species, with some acronyms disambiguated (see Table S3 for full species names).

and species richness, functional redundancy of species assemblages remained unchanged throughout the study (Table 2; Appendix S1: Fig. S6). Functional specialization was slightly but significantly lower in 2013 compared to 2007 and 2009, reflecting a more even ratio between the biomass of specialists and generalists within species assemblages (Figs. 2d, 5a–e, Table 2). In line with the changes in biomass, there was a small shift (10%) in the average position of species assemblages in the functional space (i.e., functional identity) along PCo3 in 2012 and 2013 compared to previous years (Figs. 2e, 5f–j, Table 2) and along PCo5 in 2009 compared to 2006 and 2007 (Figs. 2f, 5f–j, Table 2). Although subtle, these shifts in average position within the functional space reflect (1) the addition of a few species with more pronounced snouts (i.e., lower snout angle), slightly smaller sizes and slightly broader depth ranges in 2012 and 2013 compared to species present in previous years, (2) the replacement of some species that interact minimally with algal turfs by those that interact

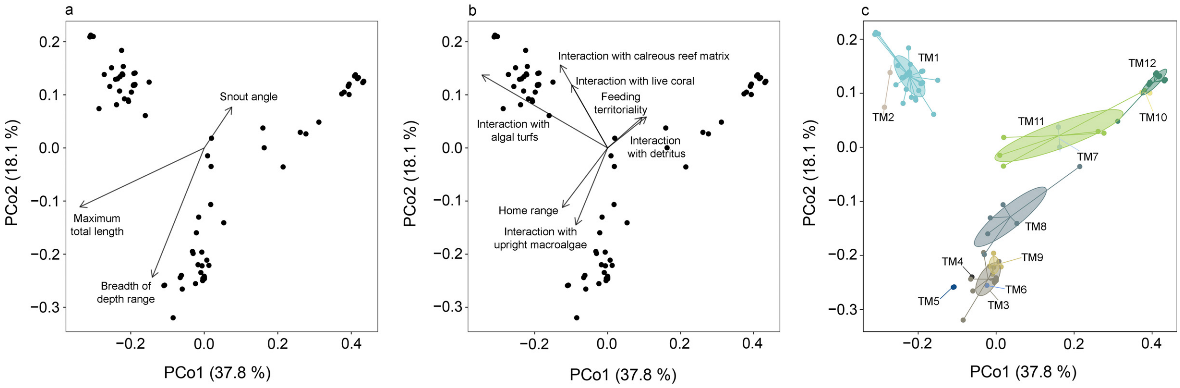


FIG. 4. Principal Coordinate Analysis (PCoA) representing the trait-space for nominally herbivorous reef fishes on PCo1 and PCo2 with the projection of (a) continuous functional traits and (b) ordinal functional traits, and (c) the tooth morphology type. Arrows represent the covariance values with axes and are scaled differently (arbitrarily) for illustration clarity. Color-coded lines mark the position of the fitted weighted class centroids per tooth morphology type and ellipses represent the standard deviation.

TABLE 3. Traits that contribute primarily to the species distribution along each axis of the six dimensional functional space, based on the (a) covariance values between each axis and vectors for quantitative and ordinal traits and (b) R^2 of ANOVAs comparing the mean position per level for categorical and nominal multi-choice traits (Legendre and Legendre 1998).

Functional traits	Dim1	Dim2	Dim3	Dim4	Dim5	Dim6
Quantitative						
1. Maximum total length	−67.7	−22.2	−41.8	−51.2	14.6	74.0
2. Breadth of depth range	−28.3	−48.7	−22.8	−10.8	−114.8	−17.9
3. Snout angle	15.0	15.4	−69.4	−46.8	28.4	−22.7
Ordinal						
4. Feeding territoriality	1.6	0.9	0.0	−0.2	0.6	−0.4
5. Home range	−1.9	−1.7	−0.5	−2.7	1.7	1.2
6. Interaction with upright macroalgae	−1.3	−2.2	0.2	−0.8	0.0	0.7
7. Interaction with algal turfs	−5.2	2.1	5.1	6.0	−1.6	2.5
8. Interaction with detritus	1.4	0.9	0.1	−0.5	−0.4	1.9
9. Interaction with calcareous matrix	−1.9	2.3	−0.2	−0.1	0.8	1.1
10. Interaction with live corals	−1.5	1.8	−5.0	3.3	2.4	3.4
Categorical						
11. Tooth morphology	0.93	0.95	0.53	0.65	0.44	0.65
Nominal multi-choice						
12. Sociality						
Solitary	−0.002	0.13	0.02	−0.001	0.02	−0.01
Paired	−0.01	0.35	0.04	0.11	0.002	0.04
Groups	0.20	−0.01	0.12	0.06	0.38	0.01
Schools	0.03	0.06	0.05	0.01	0.03	−0.01
13. Types of upright macroalgae consumed						
Calcareous articulated	0.43	0.71	−0.02	−0.003	0.03	−0.01
Fleshy foliose	0.36	0.38	0.13	0.16	0.02	−0.02
Terete corticated	0.40	0.43	0.07	0.11	0.13	−0.02
Leathery	0.08	0.12	0.13	0.28	−0.01	0.04

Notes: For functional traits 1–10, values are covariance values with each axis. For functional traits 11–13 values are R^2 of ANOVAs. Underlined R^2 values indicate significant differences based on a Bonferroni adjusted P value (i.e., $P < 0.0009$).

strongly with algal turfs, and (3) the increase in biomass of certain turf feeding species observed all years in 2012 and 2013 (Fig. 5).

Changes in muroami fishing over time

Important changes occurred during the study period in the muroami fishing practice. These changes pertained not only to the fishing effort and the volumetric CPUE of nominally herbivorous fishes (Fig. 6), but also to fishers' perceptions about muroami fishing, and the laws regulating their use (Fig. 7). There was a rapid increase in the number of muroami fleets in Karimunjawa in the early 2000s and by 2003–2005 muroami nets accounted for 56% of fish catches, much of which was comprised by nominally herbivorous fish (Fig. 7e). Large catches came, however, at the cost of fishers' decompression accidents, and the physical destruction of benthic habitats, which interfered with other traditional fishing practices (Fig. 7d). Muroami fishing effort decreased threefold in the year starting in November 2010 compared to the previous year and ceased from November 2011 onwards ($P < 0.0002$, Fig. 6a), due in part to poor catch rates (Fig. 7b). In 2009 and 2010 the volumetric CPUE of nominally herbivorous fishes for muroami fishing was <1% of the highest CPUE ever recorded (i.e., during irregular catch surveys in 2005: 3.56 $\text{kg}\cdot\text{fisher}^{-1}\cdot\text{trip}^{-1}$), and became null in the year starting in November 2011 (Fig. 6b). Based on the fishing effort and CPUE reported here, the yearly biomass of herbivorous fish taken through muroami fisheries was approximated to 356 kg (in November 2009–October 2010) and 185 kg (in November 2010–October 2011). No regulation other than a minimum mesh size existed for muroami nets until 2015, when a national law prohibited the use of all nets in Indonesian waters, and a decree to improve surveillance and enforcement was registered at the provincial, district, and national park levels (Fig. 7a, b). It is noteworthy that, while practiced, muro-ami fishing took place indiscriminately throughout the park except in some restrictively managed areas with high compliance (i.e., the smallest core zones; Campbell et al. 2014).

Changes in potential biological drivers of herbivore assemblages

The effect of year and management regime on piscivorous fish biomass differed among size classes. The biomass of small piscivores was significantly higher in 2012

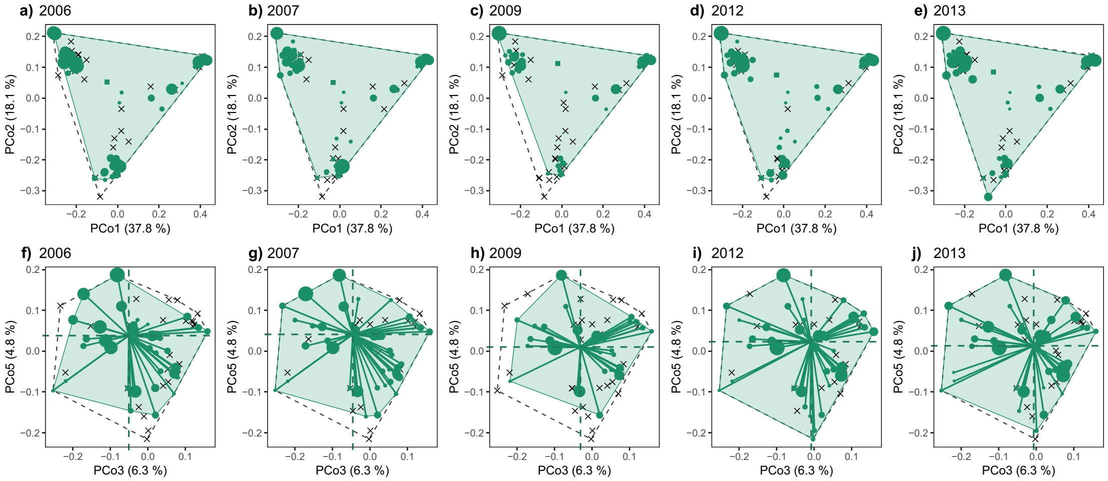


FIG. 5. Subtle changes in functional specialization and functional identity of nominally herbivorous fish assemblages represented along axes PCo1, PCo2, PCo3, and PCo5. Species are ordered within each plot based on their trait values. Gray crosses delimited by the dashed black line represent the 77 species from the Karimunjawa species pool. Green dots delimited by the green convex hull indicate species present per year. Dot size represents the mean relative biomass per species and year. Plots a–e represent the significant decrease in functional specialization in 2013 compared to 2007 and 2009. Plots f–j illustrate the shift in functional identity along PCo3 and PCo5 marked by the dotted green lines crossing each axis.

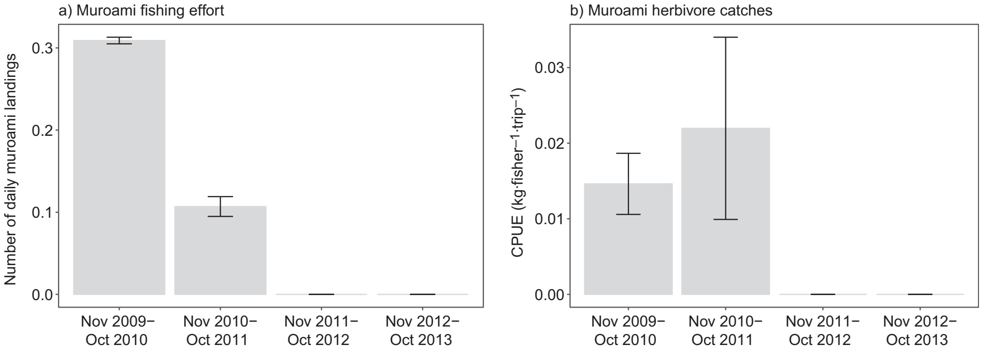
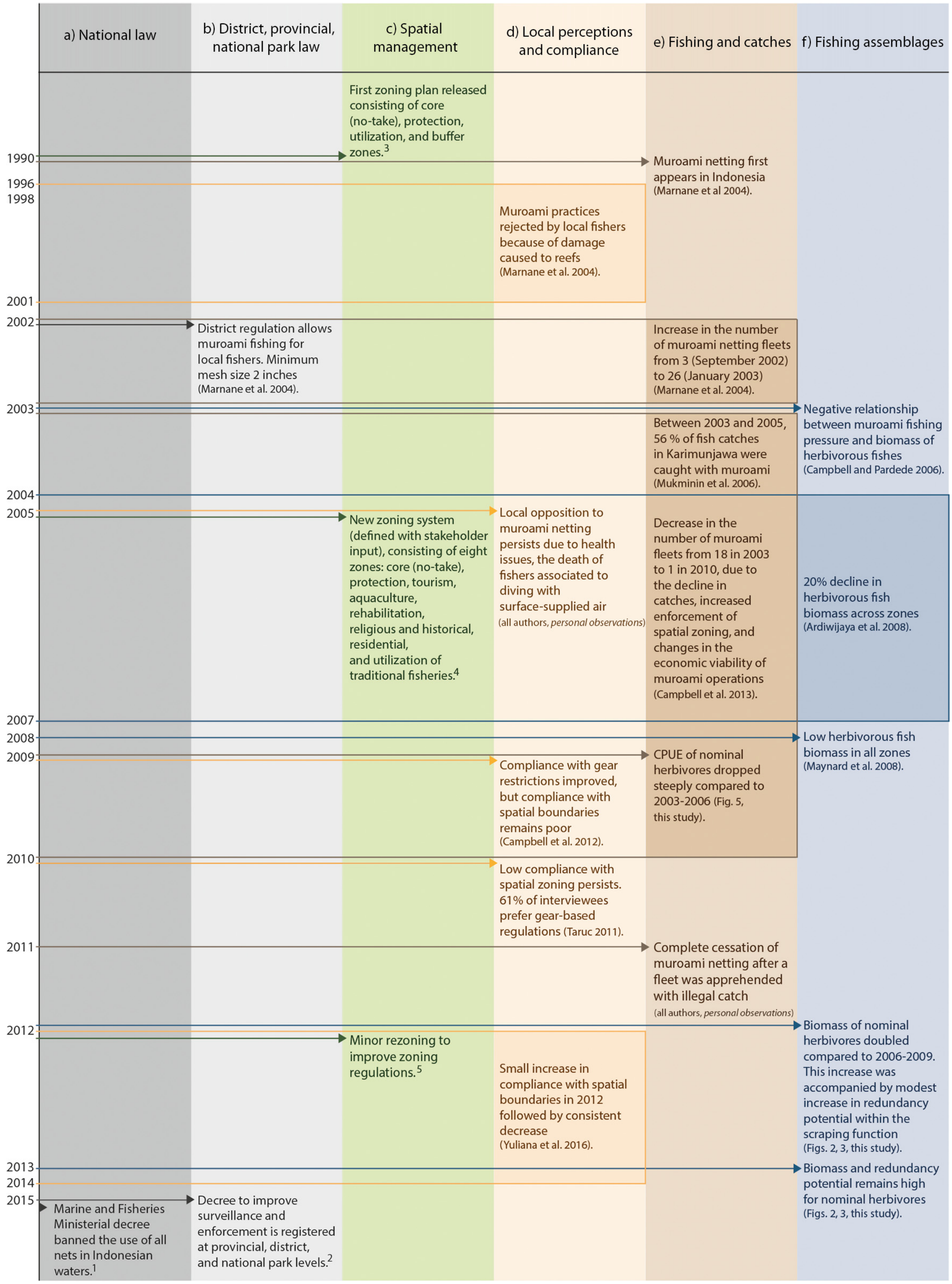


FIG. 6. (a) Muroami fishing effort throughout the Karimunjawa National Park expressed as the mean number of daily muroami landings per year (±SE), and (b) volumetric catch per unit effort (CPUE) of nominal herbivores for muroami fishing (mean ± SE).

and 2013 compared to 2009 but was unaffected by management regime. Localized increases in medium-sized piscivores occurred in 2013 only at sites subject to permissive management regimes, and large piscivores were consistently uncommon throughout Karimunjawa (Fig. 8; Appendix S1: Table S7). Benthic assemblage structure, defined by the percent cover of 21 benthic categories, did not change significantly over time or differ among management regimes (Fig. S8). However, the percent cover of structurally complex coral forms increased in 2013 compared to all other years regardless of management regime (Fig. 9; Appendix S1: Table S8). Percent algal cover changed over time with trajectories being unaffected by management regime (Fig. 10). Algal turfs, the dominant algal category, decreased significantly by ~33% in 2009 compared to 2006, but remained at a stable ~30% from 2009 to 2013 (Fig. 10a; Appendix S1: Table S8). The cover of articulated and crustose coralline algae, as well as fleshy algae, varied between 0% and 1.7% and was generally lowest during 2012 and 2013 across management regimes (Fig. 10b–d; Appendix S1: Table S8).

DISCUSSION

Reconciling the growing demand for resources while sustaining ecosystem functioning and resilience is one of the greatest challenges of the Anthropocene. Determining whether management interventions can influence the trajectory of ecosystems is a fundamental step in meeting this challenge. Here we find that in one of the main reef fishing grounds in the Java Sea, biomass of



	a) National law	b) District, provincial, national park law	c) Spatial management	d) Local perceptions and compliance	e) Fishing and catches	f) Fishing assemblages
1990			First zoning plan released consisting of core (no-take), protection, utilization, and buffer zones.^{3}		Muroami netting first appears in Indonesia (Marnane et al 2004).	
1996				Muroami practices rejected by local fishers because of damage caused to reefs (Marnane et al. 2004).		
1998						
2001						
2002		District regulation allows muroami fishing for local fishers. Minimum mesh size 2 inches (Marnane et al. 2004).			Increase in the number of muroami netting fleets from 3 (September 2002) to 26 (January 2003) (Marnane et al. 2004).	
2003					Between 2003 and 2005, 56 % of fish catches in Karimunjawa were caught with muroami (Mukminin et al. 2006).	Negative relationship between muroami fishing pressure and biomass of herbivorous fishes (Campbell and Pardede 2006).
2004						20% decline in herbivorous fish biomass across zones (Ardiwijaya et al. 2008).
2005			New zoning system (defined with stakeholder input), consisting of eight zones: core (no-take), protection, tourism, aquaculture, rehabilitation, religious and historical, residential, and utilization of traditional fisheries.^{4}	Local opposition to muroami netting persists due to health issues, the death of fishers associated to diving with surface-supplied air (all authors, *personal observations*)	Decrease in the number of muroami fleets from 18 in 2003 to 1 in 2010, due to the decline in catches, increased enforcement of spatial zoning, and changes in the economic viability of muroami operations (Campbell et al. 2013).	
2007						
2008						Low herbivorous fish biomass in all zones (Maynard et al. 2008).
2009				Compliance with gear restrictions improved, but compliance with spatial boundaries remains poor (Campbell et al. 2012).	CPUE of nominal herbivores dropped steeply compared to 2003-2006 (Fig. 5, this study).	
2010				Low compliance with spatial zoning persists. 61% of interviewees prefer gear-based regulations (Taruc 2011).		
2011					Complete cessation of muroami netting after a fleet was apprehended with illegal catch (all authors, *personal observations*)	
2012			Minor rezoning to improve zoning regulations.^{5}	Small increase in compliance with spatial boundaries in 2012 followed by consistent decrease (Yuliana et al. 2016).		Biomass of nominal herbivores doubled compared to 2006-2009. This increase was accompanied by modest increase in redundancy potential within the scraping function (Figs. 2, 3, this study).
2013						Biomass and redundancy potential remains high for nominal herbivores (Figs. 2, 3, this study).
2014						
2015	Marine and Fisheries Ministerial decree banned the use of all nets in Indonesian waters.^{1}	Decree to improve surveillance and enforcement is registered at provincial, district, and national park levels.^{2}				

FIG. 7. Chronology of muroami fishing and the zoning plan in the Karimunjawa National Park. Changes pertain to (a, b) national and local legislation regarding the use of muroami nets, (c) the zoning system, and (d) compliance levels. Changes documented here and in previous studies in (e) muroami catch levels, and (f) nominal herbivore assemblages are presented in parallel.

(FIG. 7. *Continued*)

Changes occurring within one year are indicated by colored arrows, whereas multiyear changes are indicated with colored brackets and boxes within the corresponding column. [1]National Marine and Fisheries Ministerial Decree No. 02/2015, [2]Central Java Provincial MFA Decree No. 523/2487/X/2014 registered at the provincial (No. 562.2/2222/IX/2014), district (No. 523/1642/IX/2014), and KNPA (No. 75/BTNKJ -1.6/2014) governance levels, [3]Director General of PHKA Decree no. 127/Kpts/DJ-VI/1989, [4]Director General of PHKA, Decree no. 79/IV/Set-3/2005, [5]Director General of PHKA, Decree no. 28/IV/Set/2012 on 6 March 2012.

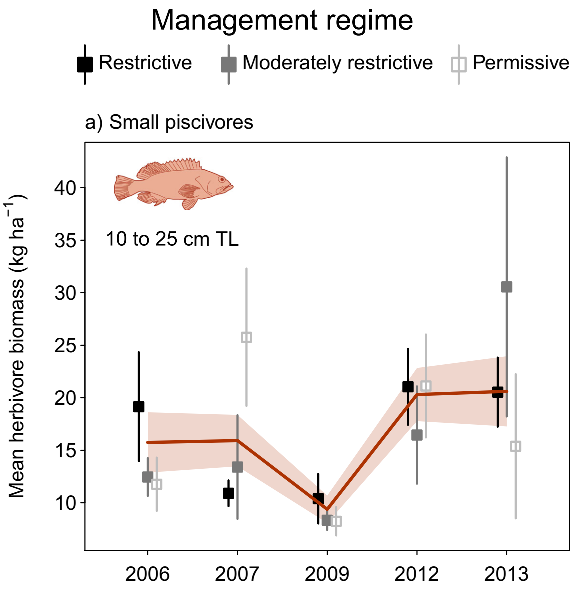
nominally herbivorous fishes doubled in 2012 and 2013 compared to previous years (i.e., 2006–2009) regardless of management regime. These changes in biomass were accompanied by a smaller increase in taxonomic richness and a decrease in community-scale rarity. Our findings suggest these changes emerged in response to the cessation of muroami fishing throughout the Karimunjawa National Park in 2011, as opposed to predator depletion or increased food availability. These changes were accompanied by a subtle decrease in functional specialization and a modest shift in functional identity but no change in functional redundancy. These changes reflect increases in small-bodied generalists located closer to the center of the functional space concurrent with more functionally distinct species located on the periphery of the functional space remaining relatively stable. Collectively, these changes imply that following the cessation of a destructive fishing practice, the capacity of assemblages to remove algal turfs and access cryptic spaces tends to be restored faster than other key facets of herbivory (e.g., macroalgal removal and bioerosion), which are underpinned by some of the species most vulnerable to fishing. In Karimunjawa, fishers stopped using muro-ami nets due to an increase in the cost-to-benefit ratio per fishing journey and led to high levels of voluntary compliance for the effective ban of muro-ami nets established by the national and local governments in 2015. We argue that similar windows of opportunity may emerge in other marine parks to implement gear-based regulations that can supplement spatial zoning plans in areas with low compliance. This does, however, not advocate for introducing gear-based regulations only once a fishery has become unprofitable. Rather, it underlines the importance of these regulations for breaking cycles of resource depletion, habitat destruction, and low compliance to zoning, thus alleviating threats to food security and ecosystem integrity.

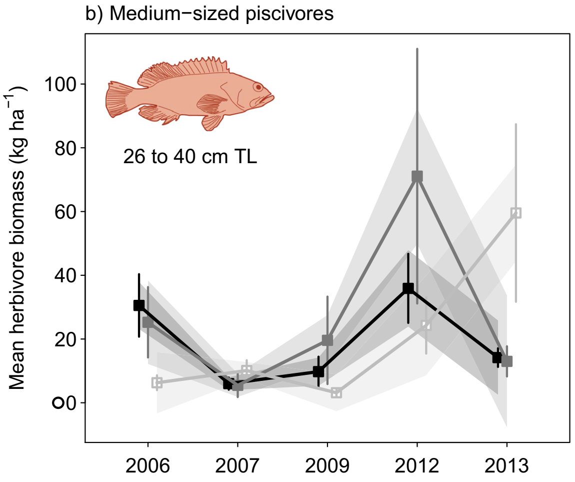
Herbivore biomass rises as muroami ceases across management regimes

A reasonable stakeholder expectation is that areas closed to fishing will sustain higher levels of fish biomass and ecosystem function (Topor et al. 2019). The temporal trajectories of fish community structure metrics in certain no-take reserves have indeed diverged from those observed in nearby fished areas (Micheli et al. 2004, Aburto-Oropeza et al. 2011, Graham et al. 2015). In Karimunjawa, our study revealed similar trajectories of herbivorous fish communities in areas subject to restrictive, moderately restrictive, and permissive management regimes over 7 yr. A positive effect of protection may not always be detectable due to insufficient time since protection and/or poor compliance (Noble et al. 2013). No-take zones in Karimunjawa were first designated in 1989, with compliance being initially (pre-2005) low (Campbell et al. 2012). Even after the participatory rezoning of the Park in 2012 and subsequent increase in the awareness of fishing restrictions (Campbell et al. 2012), levels of compliance may have remained low and hence zoning may not reflect the spatial distribution of fishing pressure throughout the Park (Campbell and Pardede 2006, Campbell et al. 2014).

The rapid accumulation of biomass of nominally herbivorous fish between 2009 and 2012 appears most likely related to the park-wide cessation of muroami fishing. We found no evidence that this increase in biomass resulted from predator depletion or increased food availability. A negative relationship between muroami fishing pressure and biomass of herbivorous fishes had been previously detected (Campbell and Pardede 2006). Here, the complete cessation of muroami fishing in 2011 coincided with a 62% increase in the biomass of nominal herbivores from 2009 to 2012. Because nominal herbivores are also important targets of spear and trap fishers in Karimunjawa (Campbell and Pardede 2006, Campbell et al. 2012), it could be argued that temporal changes in these fishing practices may have contributed to the observed biomass increase. However, the fishing effort of spearfishers declined significantly and steadily from ~3 to 1 landings per day between November 2009 and October 2012 ($P < 0.001$; Appendix S1: Fig. S7). This decrease is contrary to expectations given that muroami fishing involves a patron–client relationship, and we anticipated its cessation would result in an increased number of self-employed fishers shifting to more traditional gears (e.g., spears; Campbell et al. 2014). In our case, economic drivers (e.g., elevated fuel price) may have prevented an increase in spearfishing landings (all authors, *personal observation*). Interestingly, the CPUE of spearfishers more than doubled from 2012 to 2013 despite no change in effort, likely as a consequence of the surplus of herbivore biomass generated by the cessation of muroami fishing.

After the cessation of muroami it might reasonably be expected that the biomass of nominally herbivorous fish would increase most rapidly in restrictively managed areas. This was, however, not the case. While it could be argued that two years may have been insufficient for temporal trends of herbivore biomass to diverge among management regimes, persistent issues of non-compliance with the zoning and/or legacy effects of the





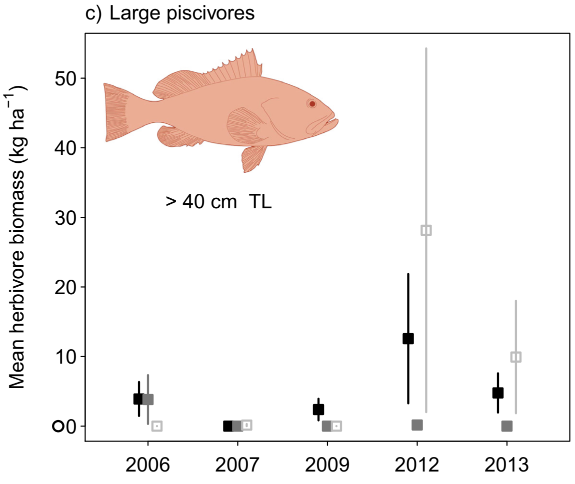


FIG. 8. Biomass of (a) small (10–25 cm total length [TL]),

destructive muroami nets may be precluding the rate at which fish populations recover after the cessation. Legacy effects of fishing practices have, in some cases, persisted for 20 yr after cessation (Parravicini et al. 2010). Given the destructive nature of muroami nets, legacy effects (e.g., destruction of branching corals) are likely throughout the Karimunjawa National Park. Such effects could have also played a role in the persistent lack of an effect of management regime in herbivore biomass. In our case, the cover of the most structurally complex coral forms was also unaffected by management regime but increased significantly by 10% in 2013 compared to all previous years (Fig. 9) likely increasing the availability physical refugia for fishes.

Asynchronous responses of herbivores to muroami cessation reflect life-history strategies

The clearest and steepest biomass build-up occurred for species classified here as having very low to moderate intrinsic vulnerability to fishing (e.g., small-bodied and fast-growing surgeonfishes, parrotfishes, and rabbitfishes) commonly caught by muroami fishers. Biomass of these groups had increased between 85% and 132% the year after the muroami cessation (i.e., 2011). Although previous studies have emphasized the importance of recruitment in replenishing fish stocks and sustaining reef resilience (Graham et al. 2006, Ledlie et al. 2007), the rapid accumulation of biomass in Karimunjawa appeared related to a combination of recruitment and growth of existing individuals. This was evidenced by the increases in small (6–10 cm TL) and medium-sized (21–25 cm TL) parrotfishes, and medium-sized (16–30 cm TL) surgeonfishes and rabbitfishes (Appendix S1: Fig. S9). Our findings are consistent with previous studies documenting a rapid recovery of small-bodied parrotfishes and surgeonfishes within the first three to five years of reserve establishment (Stockwell et al. 2009, Abesamis et al. 2014), facilitated by their short life spans and rapid turnover rates (Choat et al. 1996, Taylor et al. 2014). Species classified here as highly vulnerable (e.g., large *Chlorurus* spp., *Cetoscarus ocellatus*, *Naso unicornis*) did not reach significantly higher biomasses compared to the muroami fishing years until 2013 (two years after cessation), whereas the very highly vulnerable species (e.g., *Bolbometopon muricatum*) remained uncommon throughout the study.

The increase in biomass of algal farmers following the muroami cessation was unexpected given the marked increase in piscivores and potential competitors, and

(FIG. 8. *Continued*)
(b) medium-sized (26–40 cm TL), and (c) large (>40 cm TL) piscivorous fish, which reportedly pose the risk of predation for juvenile and adult nominally herbivorous fish. Dots represent observed means per year per management regime (±SE) whereas colored lines and ribbons mark the means and SEs fitted by the optimal mixed-effects models, respectively.

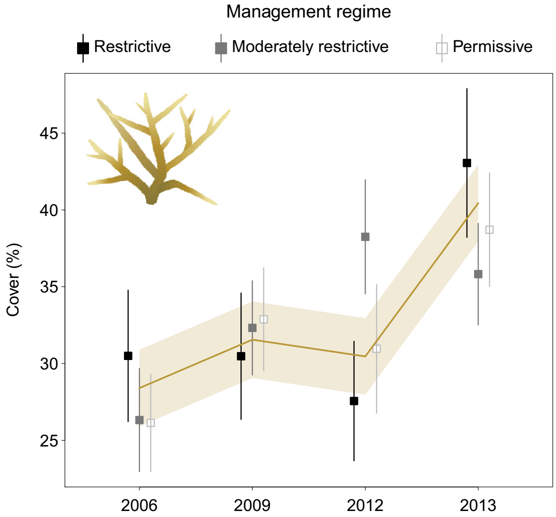


FIG. 9. Percent cover of the most structurally complex coral forms (i.e., branching, digitate, tabulate, and foliose). Dots represent observed means per year per management regime (±SE) whereas the colored line and ribbon, respectively, mark the mean and SE predicted by the optimal mixed-effects model.

considering their low vulnerability to capture by muroami nets (Campbell and Pardede 2006). Algal farming damselfishes can be extensive, intensive, or indeterminate in their farming and territory defense behaviors, and hence their impact on benthic assemblages (Emslie et al. 2012). The increase in the biomass of algal famers in the present study was driven mainly by a significant increase in indeterminate farming species ($P < 0.001$; Appendix S1: Fig. S10). On the Great Barrier Reef, the abundance of indeterminate has been shown to be positively related to topographic complexity (Emslie et al. 2012). As such, the observed increase in indeterminate farmers in our study may be related to the increase in structurally complex coral forms following the cessation of muroami fishing (Fig. 9).

Taxonomic and functional structure of herbivore assemblages following muroami cessation

Given that fisheries typically cause declines in biomass rather than local extinctions, the weaker response of taxonomic richness (i.e., 30% increase) and community-scale rarity (i.e., 15% decrease) to the cessation of fishing may be expected (Lester et al. 2009, Soykan and

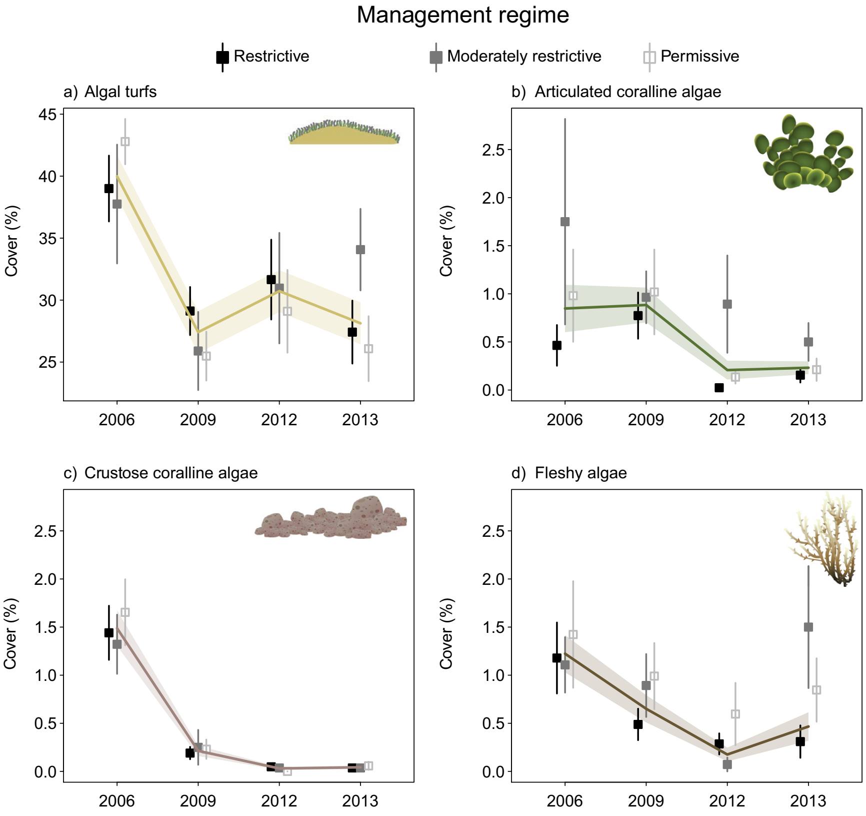


FIG. 10. Percent cover (mean ± SE) of (a) algal turfs, (b) articulated coralline algae, (c) crustose coralline algae, and (d) fleshy algae calculated among sites subject to restrictive, moderately restrictive, and permissive management regimes. Dots represent observed means per year per management regime (±SE) whereas colored lines and ribbons mark the means and SEs fitted by the optimal mixed-effects models, respectively.

Lewison 2015). While biomass doubled rapidly following muroami cessation, taxonomic richness increased by 30%. In line with the weak changes in taxonomic richness and rarity that followed the muroami cessation, we found no change in the functional redundancy of assemblages. In other words, species additions following the cessation of muroami fishing did not increase the co-occurrence of functionally similar species. Ancillary analyses of our data showed that neither functional redundancy computed following Ricotta et al. (2016) nor functional originality, taken as the inverse proxy for functional redundancy, changed after muroami cessation. This may seem particularly counterintuitive for a pool of species within the same trophic guild (i.e., herbivorous), but may be inherent to an approach based on multiple fine-scale functional traits. Substantial changes in functional redundancy were found in fish assemblages following natural and anthropogenic disturbances when indices were computed for larger pools of species and using smaller sets of coarser functional traits (Brandl et al. 2016, Oliveira et al. 2018, Richardson et al. 2018). Functional redundancy is paramount for the stability of ecosystems and their resilience to species loss (Elmqvist et al. 2012). While adding species to speciose communities is more like to increase redundancy rather than complementarity (Halpern and Floeter 2008), our findings reinforce that conserving species richness does not necessarily equate to preserving functional redundancy (Villéger et al. 2010). This applies particularly when functional redundancy is estimated conservatively using multiple fine-scale traits and in mega-diverse systems.

Functional specialization is projected to decrease following a disturbance as specialists are often more sensitive to reductions in a particular resource (e.g., dietary or habitat) than generalist species (Leitão et al. 2016). We report a decrease in the functional specialization of herbivorous fish communities two years after the cessation of muroami fishing, despite a 30% increase in species richness. This suggests that functional specialization is not only sensitive to the loss of specialists through habitat degradation, but also to interspecific rates of recovery after a chronic perturbation has ceased. A decrease in functional specialization can thus herald the biotic homogenization of ecosystem functions (Ibarra and Martin 2015), but also be an early sign of asynchronous recovery of different facets of ecosystem functions. We therefore argue that the duration of protective measures should encompass sufficient time to allow for the preservation of distinct facets of herbivory.

Functional identity of assemblages can change over time, substantially influencing ecosystem processes while other facets of functional diversity remain unchanged (Mouillot et al. 2011, Weigel et al. 2016). Changes in functional identity generally reflect the influx of species with higher values of certain traits compared to previously occurring species (Leitão et al. 2018, Toussaint et al. 2018). The changes in functional identity (on PCo3 and PCo5) that accompanied the increase in biomass following muroami cessation were less pronounced than those observed in stream fish assemblages as a result of deforestation or introduction of nonnative species (Leitão et al. 2018, Toussaint et al. 2018). Such disturbances had strong environmental filtering effects thus causing a larger displacement of the assemblage across the functional space. PCo3 and PCo5 collectively explain only 11% of the functional variability among species, and hence the changes in functional identity along these axes likely reflect minor modifications of the make-up of herbivory. These changes do, however, reflect an increased prevalence of pronounced snouts characteristic of rabbitfishes (Siganidae), smaller body sizes and broader depth ranges, and a moderate increase in the capacity of assemblages to remove algal turfs.

Ecological consequences of changes in herbivore assemblages

We discuss four potential ecological implications of our findings, which can guide future management policies in Karimunjawa and elsewhere. First, throughout the archipelago, mechanisms to remove algal turfs, detritus, and light sediment loads are largely unaffected by management regime/zoning. Second, the cessation of muroami fishing led to a moderate increase in the capacity of fish assemblages to remove algal turfs and access cryptic spaces through pronounced snouts (Brandl and Bellwood 2013). This indicates that at least some level of functional complementarity, by means of which a variety of microhabitats can be grazed, began to be restored. Third, although indeterminate algal-farmers have the lowest rates of territorial aggression and weakest effect on benthic communities among damselfishes, their potential contribution to the propagation of thick algal turfs and lower abundance of juvenile corals should not be underestimated (Casey et al. 2015). The increase observed here may therefore pose a mild risk to a key mechanism of resilience (i.e., coral recruitment). This reinforces the importance of sustaining high biomass of piscivores as potential sources of population control, as well as continued protection of turf croppers and removers. Fourth, although extensive macroalgal stands are unlikely to develop when algal turf removal mechanisms are in place (Hughes et al. 2007), sufficiently strong perturbations leading to extensive coral mortality may increase macroalgal cover and dilute the feeding impact of herbivores (McClanahan et al. 2001). The persistent paucity of key regime-shift reversing species (e.g., macroalgal browsers; Hoey and Bellwood 2009) implies that precarious situations might emerge if extensive coral mortality occurs and the capacity of algal turf grazers to maintain turfs in a cropped state is compromised. The cessation of muroami fishing may lead to increases in catch levels of permitted gears, such as spears. The maintenance of key ecosystem functions (e.g., macroalgal removal), may rest on the selectivity of some of these gears to divert fishing pressure away from functionally critical and highly vulnerable species (e.g., *Naso unicornis*). Consideration should, in our opinion, be given to post-disturbance protection of macroalgal browsers to boost the systems' potential to recover at vulnerable times (McClanahan et al. 2011, Graham et al. 2013).

Weak compliance is a common ailment of most MPAs in the developing world (Steneck et al. 2009, Green et al. 2011, White et al. 2014), and may worsen with increased poverty (Cinner 2011). Contingencies such as gear modifications or restrictions are known to supplement MPAs in meeting conservation targets (Vaughan and Carmichael 2002, Cinner et al. 2009). Focusing on megadiverse coral reefs, and tracking trajectories of herbivorous fish over a modest temporal scale (i.e., 7 yr), we find that the cessation of a destructive fishing practice facilitated a rapid build-up of herbivore stocks. However, more time may be needed to help reinstate functional specialization and redundancy, as well as the biomass of key groups (e.g., macroalgal browsers). The continuity of this positive trajectory is uncertain, and will depend on natural processes emerging from species interactions, and patterns of fish larvae recruitment (Sale 2004). Compliance with the ban might remain high given fishers' current perceptions, but may require vigilance. Excessive herbivore catches with permitted gears must be prevented if key mechanisms required for benthic post-disturbance recovery processes are to be maintained. We anticipate that continued compliance with the ban on muroami fishing, together with a preventive management approach may further enhance the recovery of herbivore assemblages and the systems' capacity to rebound from disturbances.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1981/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.655j692