Conservation Biology

Contributed Paper

# Using community-level metrics to monitor the effects of marine protected areas on biodiversity

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**Abstract:** *Marine protected areas (MPAs) are used to protect species, communities, and their associated habitats, among other goals. Measuring MPA efficacy can be challenging, however, particularly when considering responses at the community level. We gathered 36 abundance and 14 biomass data sets on fish assemblages and used meta-analysis to evaluate the ability of 22 distinct community diversity metrics to detect differences in community structure between MPAs and nearby control sites. We also considered the effects of 6 covariates—MPA size and age, MPA size and age interaction, latitude, total species richness, and level of protection—on each metric. Some common metrics, such as species richness and Shannon diversity, did not differ consistently between MPA and control sites, whereas other metrics, such as total abundance and biomass, were consistently different across studies. Metric responses derived from the biomass data sets were more consistent than those based on the abundance data sets, suggesting that community-level biomass differs more predictably than abundance between MPA and control sites. Covariate analyses indicated that level of protection, latitude, MPA size, and the interaction between MPA size and age affect metric performance. These results highlight a handful of metrics, several of which are little known, that could be used to meet the increasing demand for community-level indicators of MPA effectiveness.*

**Keywords:** abundance, biomass, ecological indicator, monitoring, MPA, species diversity, species richness

Uso de Medidas a Nivel de Comunidad para Monitorear los Efectos de las Áreas Marinas Protegidas sobre la Biodiversidad

**Resumen:** *Las áreas marinas protegidas (AMP) son usadas para proteger especies, comunidades y sus hábitats asociados, además de tener otros objetivos. Sin embargo, medir la eficiencia de las AMP puede ser un reto, particularmente cuando se consideran las respuestas a nivel de comunidad. Reunimos conjuntos de datos sobre ensambles de peces, 36 conjuntos sobre abundancia y 14 sobre biomasa, y usamos un meta-análisis para evaluar la habilidad de detección de diferencias en la estructura de las comunidades entre las AMP y sitios cercanos de control de 22 medidas distintas de diversidad de comunidades. También consideramos los efectos de seis covarianzas en cada medida - tamaño y edad de la AMP, interacción entre el tamaño y la edad de la AMP, latitud, riqueza total de especies y nivel de protección. Algunas medidas comunes, como la riqueza de especies y la diversidad de Shannon, no difirieron consistentemente entre las AMP y los sitios de control, mientras que otras medidas, como la abundancia total y la biomasa, fueron diferentes de manera consistente en los estudios. Las respuestas de las medidas, derivadas de los conjuntos de datos sobre biomasa, fueron más consistentes que aquellas basadas en los conjuntos de datos sobre abundancia, lo que sugiere que la biomasa a nivel de comunidad entre las AMP y los sitios de control difiere de manera más predecible que la abundancia. Los análisis de covarianza indicaron que el nivel de protección, la latitud, el tamaño de la AMP y la interacción entre el tamaño y la edad de la AMP afectan el desempeño de las medidas. Estos resultados resaltan a un puñado de medidas, varias de las cuales son poco conocidas, que podrían usarse para satisfacer la demanda creciente de indicadores a nivel de comunidad de la efectividad de las AMP.*

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*Paper submitted September 27, 2013; revised manuscript accepted September 4, 2014.*



*Conservation Biology*, Volume 00, No. 0, 1–9

DOI: 10.1111/cobi.12445

**Palabras Clave:** abundancia, AMP, biomasa, diversidad de especies, indicador ecológico, monitoreo, riqueza de especies

## Introduction

Preserving biodiversity is often cited as a reason for establishing marine protected areas (MPAs) (Greenstreet 2008). Community-level metrics measure a distinct and important aspect of biodiversity, the number of different species, and their relative abundance; often these attributes are the focus of MPA designation. However, only recently, with the ascendance of ecosystem-based management and marine spatial planning, has management focus shifted from the population to the community and ecosystem level (e.g., Gaines et al. 2010; Halpern et al. 2010; Shin & Shannon 2010). With this shift comes a need to identify appropriate community-level indicators to support evaluation of MPA effectiveness (Pelletier et al. 2008).

The best-known and most common community-level indicator is species richness (Pillans et al. 2007; Lyashevska & Farnsworth 2012). Although easy to interpret and useful under certain circumstances, species richness has limited ability to detect changes in community composition (Russ 1985; Pillans et al. 2007; Lyashevska & Farnsworth 2012) in part because whether species richness increases or decreases in response to MPA establishment depends on the prior history of exploitation (Lester et al. 2009). Additionally, complex trophic interactions often mediate community-level responses to MPA establishment (Graham et al. 2003; Willis & Anderson 2003; Takashina et al. 2012), causing species richness to change in unexpected ways. Counter to expectations, numerous studies show that species often decline in response to MPA establishment, evidence of an indirect effect (i.e., increased predation or competition) due to protection (Micheli et al. 2004). Finally, species richness only describes one aspect of the ecological community, the total number of species, whereas alternate metrics address other aspects of community structure, such as the distribution of abundance among species (Rice 2000; Pillans et al. 2007; Pelletier et al. 2008).

Alternatives to species richness abound because dozens of metrics exist for measuring community structure (Magurran & McGill 2011; Lyashevska & Farnsworth 2012). However, surprisingly few studies have investigated the effectiveness of community-level metrics as ecological indicators in an MPA context. Herein we define *ecological indicators* as variables based on data collected in the field (or generated with a model) that can be linked to a management objective or research question (Pelletier et al. 2005).

Assessing MPA effectiveness is further complicated by the fact that local conditions may play an important role in determining the responses of a specific assemblage (Micheli et al. 2004). Although the relative importance of covariates such as MPA size and time since establishment, fishing pressure outside the MPA, level of protection, and latitude remains an active area of inquiry (e.g., Cote et al. 2001; Claudet et al. 2008; McClanahan et al. 2009; Edgar et al. 2011; Ainsworth et al. 2012), researchers agree on the importance of considering these—and other—covariates in studying MPA effectiveness. Guidetti and Sala (2007) conclude that MPAs and fished areas should not just be viewed as 2 treatments in ecological studies, rather these variables should be considered as factors that mediate assemblage response to protection.

We compared various diversity metrics between MPAs and adjacent control sites (assuming that the differences are a result of MPA establishment and not other factors [Discussion]). Our aim was to provide information on which community-level metrics are robust indicators of MPA response for management purposes. We also considered the influence of covariates on the performance of these metrics, thereby providing guidance on which conditions may favor the selection of certain metrics over others. Both objectives call for a synthetic approach that integrates results across studies. We therefore used meta-analysis to combine information from multiple MPAs in an objective, quantitative manner.

## Methods

Using McGill (2011) as a guide, we selected 13 community-level metrics that measure distinct aspects of community structure and have desirable statistical properties. We added 8 parametric (or semiparametric) metrics that have rarely been applied in the context of MPA research so as to evaluate their performance relative to more standard nonparametric metrics. These metrics are familiar to researchers studying species abundance distributions and have proven useful in other applied contexts (Gray et al. 1979; Ugland & Gray 1982). Given their ability to capture important aspects of community structure (using parameters that describe the shape and dispersion of a species abundance distribution), we considered their utility in detecting effects of MPA protection. We also added total biomass to our set because of its common usage in MPA studies. In total, we evaluated 22 metrics (Table 1).

We gathered data sets on fish assemblage structure in MPAs and nearby control sites with 2 separate methods. First, we extracted studies included in Micheli et al. (2004), which yielded 15 data sets containing information

**Table 1. Classification of community-level metrics included in a study of indicator responses to marine protected area establishment.[a]**

| *Metric* | *Description* | *Formula* |
|---|---|---|
| Biomass[b] | | |
| total biomass | total biomass of individuals sampled | $B$ |
| Abundance[c] | | |
| total abundance | total number of individuals sampled | $N$ |
| $\gamma$ scale | $\beta$ represents the scale parameter for the gamma distribution | $\frac{\beta^\alpha}{\Gamma(\alpha)} x^{\alpha-1} e^{-\beta x}$ |
| log normal $\mu$ | mean of the lognormal distribution | $\frac{1}{x\sigma\sqrt{2\pi}} e^{-\frac{(\ln x = \mu)^2}{2\sigma^2}}$ |
| log normal $\sigma$ | standard deviation of the lognormal distribution | |
| log series $c$ | estimated from the iterative solution of the equation to the right | $S/_N = \left(\frac{1-c}{c}\right)(-\ln(1-c))$ |
| Dominance[d] | | |
| relative | number of individuals in the most abundant species divided by the total number of individuals in the sample (also referred to as Berger-Parker dominance) | $\frac{n_1}{N}$ |
| McNaughton | number of individuals in the 2 most abundant species divided by the total number of individuals in the sample | $\frac{n_1+n_2}{N}$ |
| Zipf-Mandelbrot $c$ | scale parameter for the Zipf-Mandelbrot distribution | $\frac{1/(i+b)^c}{\sum_{i=1}^{N}(i+b)^c}$ |
| Evenness[e] | | |
| Gambin $\alpha$ | calculated using a gamma distribution with the scale parameter, $\beta$, set to 1 over the interval 0–0.99 | $\frac{1}{\Gamma(\alpha)} x^{\alpha-1} e^{-x}$ |
| eCDF slope | slope of a line fit to the cumulative distribution function[i] for a community | |
| eCDF inflection | inflection point of the line fit to the cumulative distribution function for a community | |
| $\gamma$ shape | $\alpha$ represents the shape parameter for the gamma distribution | $\frac{\beta^\alpha}{\Gamma(\alpha)} x^{\alpha-1} e^{-\beta x}$ |
| Shannon evenness | Shannon diversity metric standardized by the number of species | $\frac{H'}{\ln S}$ |
| Rarity[f] | | |
| log skew | skew of the log-transformed data | |
| percentage rare $N/S$ | percentage of species whose abundance is less than the average abundance of species in the sample | |
| Richness[g] | | |
| species richness | number of species sampled | $S$ |
| Margalef diversity | species richness standardized by the number of individuals sampled | $\frac{S-1}{\ln N}$ |
| Log series $\alpha$ | log series index | $\alpha = \frac{N(1-c)}{c}$ |
| Diversity[h] | | |
| Shannon diversity | diversity metric based on information theory | $H' = -\sum p_i \ln p_i$[j] |
| Simpson diversity | probability that any 2 individuals drawn at random belong to the same species | $\frac{\sum n_i(n_{i-1})}{\sum N(N-1)}$[k] |
| Zipf-Mandelbrot $b$ | shape parameter for the Zipf-Mandelbrot Distribution | $\frac{1/(i+b)^c}{\sum_{i=1}^{N}(i+b)^c}$ |

[a] *This framework is based on the one described in McGill (2011), although we treat his subgroups as distinct groups for simplicity. There are 7 main categories.*
[b] *Includes only 1 metric, total biomass, which measures the total biomass of all individuals in the community.*
[c] *Includes 5 metrics related to the total number of individuals in the community.*
[d] *Includes 3 metrics related to the relative abundance of the most abundant individuals in the community.*
[e] *Includes 5 metrics related to the distribution of abundance among species.*
[f] *Includes 2 metrics related to the relative abundance of the rarest species in the community.*
[g] *Includes 3 metrics related to the total number of species in the community.*
[h] *Includes 3 metrics related to both species richness and evenness.*
[i] *A standardized plot of the proportion of points with a value (here abundance) less than a given value.*
[j] *The $p_i$ is the proportion of individuals in the ith species.*
[k] *The $n_i$ is the number of individuals of species i. [Correction added after online publication on January 8, 2015: Formatting of table corrected.]*

on fish abundance and 5 data sets containing information on fish biomass inside and outside MPAs. Second, we did a Web of Science search for the search terms *Marine Protected Area** or *MPA** or *Marine Reserve** and *biodiversity* or *diversity* or *richness* or *biomass* that resulted in 4989 articles as of April 2011. We identified articles that contained data on fish abundance or biomass both inside and outside of a MPA and found an additional 21 abundance and 9 biomass data sets. Thus, we had a total of 36 abundance and 14 biomass data sets (Supporting Information). Given the modest number of studies, we were unable to run separate analyses on subsets of studies that employed distinct sampling designs. This may have introduced additional heterogeneity into our results, which could make it more difficult to detect a pattern.

For each locale, replicate samples from within the MPA were pooled, as were replicate samples from outside the MPA. This resulted in 50 data sets from within the MPAs and 50 from outside the MPAs (36 abundance and 14 biomass). The data sets were analyzed with MatLab software written to calculate the 22 species diversity metrics used for this study and available upon request from B.J. McGill) (Supporting Information). The abundance-based and biomass-based data sets were kept separate for all subsequent analyses.

To assess indicator response to MPA establishment across studies, we used a modern meta-analysis (hereafter, meta-analysis), defined as a statistical technique that combines the measures of effects from individual studies into an estimate of the overall strength of the effect and then uses this to determine significance (Rosenberg et al. 2000). Meta-analysis has become the preferred method for combining data across studies in order to draw general conclusions (Stewart 2009). Its advantages include the ability to make use of sample size information from the individual studies, the ability to quantify the overall magnitude of the effect being studied, and the ability to assess the overall agreement (homogeneity) or lack thereof among studies (Rosenberg et al. 2000).

Following Cote et al. (2001), we used response ratio (RR) as a measure of effect size for the meta-analysis because it can be calculated without knowledge of sample variances (Rosenberg et al. 2000). The RR is defined as the ratio of the means measured in experimental and control areas (i.e., in the present study, indicator values inside and outside each MPA). We used the natural logarithm of the RR (Rosenberg et al. 2000), defined as $\ln \mathrm{RR} = \ln[(X^{I})(X^{O})^{-1}]$, where $X^{I}$ and $X^{O}$ are the indicator values in the experimental (inside MPA) and control (outside MPA) areas.

To account for variation among studies in sampling effort, we used a weighting scheme based on the total area censused in each study, following Cote et al. (2001). Each indicator estimate was weighted by the natural logarithm of the total area covered by the census from which the estimate was obtained. Separate meta-analyses were carried out for each indicator-response variable combination to quantify the overall effect of protection (e.g., a separate meta-analysis of Shannon diversity was done for both the abundance and biomass data sets). This resulted in 44 meta-analyses. All mean effect sizes, a measure of the effect of protection across studies, are presented as back-transformed values so that they can be interpreted easily as the ratio of densities inside to outside the MPAs. Effect sizes were considered significantly different from 1 when the 95% CI did not include 1 after back-transformation. Analyses were conducted using the metafor package in R (Viechtbauer 2010; R Development Core Team 2014).

We assessed the sensitivity of our results to influential studies using leave-one-out regression, also with the metafor package in R. Leave-one-out regression, as its name implies, involves sequentially dropping each data point, refitting the model, and comparing the new models to the full model developed using every data point (Belsley et al. 1980). It indicates the sensitivity of the results to individual data points and draws attention to the relative influence of each.

For each indicator, to test whether all MPAs showed homogeneous responses to protection, the heterogeneity statistic was calculated and compared with a chi-square distribution with $n - 1$ df (where $n$ is the number of MPAs included in the analysis) (Supporting Information). Because numerous indicators had heterogeneous responses to protection, we used random-effects models for all meta-analyses. This maintains comparability of results across indicators while assuring that the results obtained are conservative. Random-effects models account for the fact that, in addition to sampling error, there is a true random component of variation in effect sizes among studies (Rosenberg et al. 2000).

We then used the metaphor package in R (Viechtbauer 2010; R Development Core Team 2014) to analyze the relationship between MPA effect size and the 6 covariates which characterized each MPA: latitude, ln(MPA size), MPA age at the time of the census, an interaction term for MPA size and age (ln[size*age]), total fish species richness surveyed (both inside and outside the MPA), and level of protection (partial vs. full). We used multiple linear regression to reduce the number of statistical analyses and to allow for the effect of one covariate to influence the effect of the others. Separate analyses were performed for each indicator-response variable combination, resulting in 44 multiple regressions (22 for each of the 2 response variables, abundance and biomass; see the Supporting Information for further methodological details).

## Results

Of the 21 indicators considered for the abundance data sets, 3 had effect sizes that differed significantly from 1 at an alpha level of 0.05 (Fig. 1; Supporting

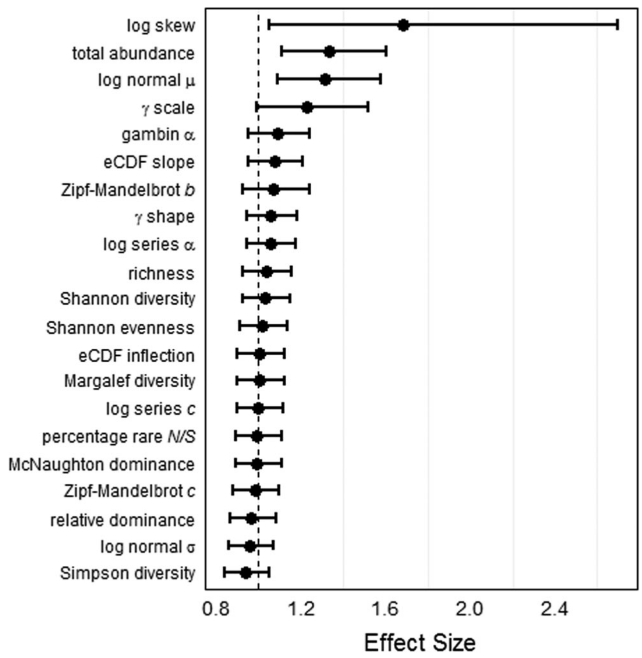


*Figure 1. Mean effect size and 95% confidence intervals for the 21 metrics used on the fish abundance data sets. See Table 1 for metric definitions. The mean values and associated confidence intervals are the result of back-transformation of mean values and intervals calculated for log-transformed data. An effect size >1 means metric values in marine protected areas (MPAs) are greater than at control sites, whereas effect sizes <1 mean the opposite. Metrics whose confidence intervals do not include 1 differ significantly between MPA and control sites across studies (at alpha 0.05).*

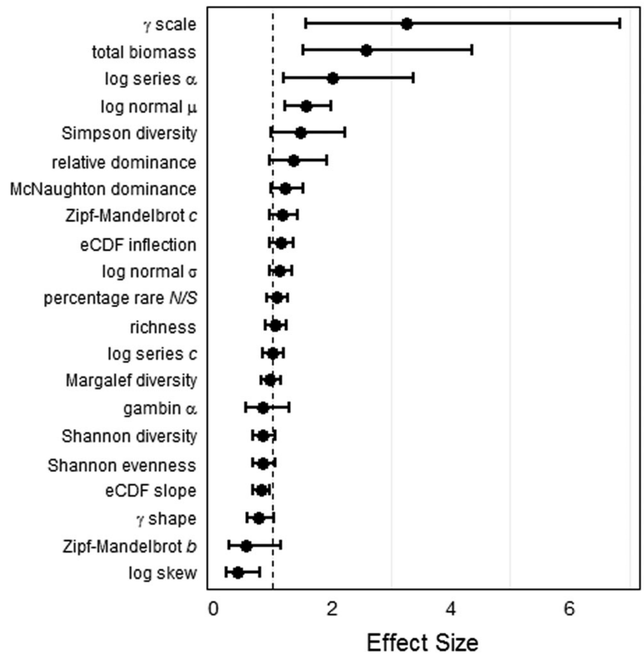


*Figure 2. Mean effect size and 95% confidence intervals for the 21 metrics used on the fish biomass data sets. See Table 1 for metric definitions. The mean values and associated confidence intervals are the result of back-transformation of mean values and intervals calculated for log-transformed data. An effect size >1 means metric values in marine protected areas (MPAs) are greater than at control sites, whereas effect sizes <1 mean the opposite. Metrics whose confidence intervals do not include 1 differ significantly between MPA and control sites across studies (at alpha 0.05).*

Information). These were total abundance, lognormal $\mu$, and log skew (see Table 1 for definitions of all metrics used in this study). One other metric, $\gamma$ scale, had an effect size that differed from 1 at an alpha level of 0.1 (Supporting Information).

Of the 21 indicators considered for the biomass data sets, 5 had effect sizes that differed significantly from 1 at an alpha level of 0.05, including total biomass, eCDF slope, lognormal $\mu$, log series $\alpha$, and log skew (Fig. 2; Supporting Information). An additional 7 metrics had effect sizes that differed from 1 at an alpha level of 0.1 (Supporting Information). These were $\gamma$ scale, $\gamma$ shape, McNaughton dominance, relative dominance, Shannon diversity, Shannon evenness, and Simpson diversity.

Leave-one-out regression results suggested that these results were robust to influential data points (see Supporting Information for details).

Latitude had the most influence on metric performance for the abundance data sets; for the biomass data sets it was level of protection (Supporting Information). For the abundance data sets, increasing latitude had a significant negative effect on abundance. MPA size, age, and the interaction between size and age had significant effects on log skew (the effects of size and age were negative, whereas the effect of the interaction was positive). With the biomass data sets, full protection had a significant negative effect on McNaughton dominance, Simpson diversity, and Zipf-Mandelbrot *c*, and a significant positive effect on $\gamma$ shape, Shannon diversity, Shannon evenness, and Zipf-Mandelbrot *b* (Supporting Information). Other covariates with significant effects on metric performance for the biomass data sets included the interaction between MPA size and age (negative effect on biomass) and latitude (positive effect on $\gamma$ shape).

## Discussion

Although the use of MPAs as a spatial management instrument has spread around the world, our ability to evaluate

**Table 2. Indicators of community-level response to marine protected area establishment recommended for use by managers.**

| *Category* | *metric (s)* |
|---|---|
| Biomass | total biomass |
| Abundance | total abundance & log normal $\mu$ |
| Dominance | McNaughton & relative dominance |
| Evenness | eCDF slope |
| Rarity | log skew |
| Richness | log series $\alpha$ |
| Diversity | Shannon & Simpson diversity |

the effects of MPA protection is nascent, and for the community level, robust metrics have not been identified. The variation in metric responses we found draws attention to the importance of indicator selection for the evaluation of MPA effectiveness. Some commonly used metrics, such as species richness and Shannon diversity, did not respond consistently across MPAs, suggesting that they are not very useful for assessment purposes. However, other common metrics, such as total abundance and total biomass, performed quite well, which supports their use as indicators of MPA effectiveness. Importantly, several little-used metrics, such as log skew and lognormal $\mu$, were also consistently able to capture MPA effects (see Table 2 for a full list of recommended metrics).

The disparity in metric performance between biomass- and abundance-based data sets supports the assertion that biomass provides a more robust measure of community response to MPA establishment than abundance (García-Charton et al. 2008; Lester et al. 2009). More than 50% of biomass metrics responded significantly to MPA establishment at an alpha level of 0.1, whereas <25% of abundance-data metrics responded comparably. This discrepancy likely reflects the fact that fish size increases following MPA establishment (Halpern 2003; Pillans et al. 2007; Lester et al. 2009). However, this difference may also result from the complex trophic interactions that accompany an increase in large predatory fishes (e.g., Graham et al. 2003; Harborne et al. 2008; Takashina et al. 2012). These results support the growing call for reporting of biomass (and more specifically body size) data in MPA effects studies (Lester et al. 2009).

Biomass and abundance behave in fundamentally different ways following MPA establishment. Variation in abundance among species decreases (i.e., the evenness of the community increases) as target species populations rebound and prey species abundances decline (due to top–down control by increasingly abundant predators). In contrast, variation in biomass among species increases as target species, which generally include larger-bodied taxa, have an opportunity to grow to full size. In our study, abundance-data metrics which measured evenness, rarity, and dominance such as log skew, eCDF slope, and relative dominance followed patterns that were the opposite of those for biomass-data metrics. If measuring abundance, evenness increased whereas rarity and dominance decreased following MPA establishment; for biomass the pattern was inverted.

Encouragingly, of the 7 categories of indicators tested, 5 (biomass, abundance, evenness, rarity, and richness) had at least 1 metric that detected a significant difference at an alpha level of 0.05, whereas all 7 groups had at least 1 metric that detected a significant difference at an alpha level of 0.1. This suggests that the different aspects of species diversity these metrics measure all respond to MPA establishment and can be used to monitor MPAs effectively. Each of these indicator categories has relevance to management, reflecting different aspects of community composition that might be the target of MPA protection (Table 3). Total biomass reflects both the size of individuals and their abundance. Increasing both is often a core goal of MPA protection, as is increasing the total number of species. Evenness, dominance, and rarity reflect the distribution of abundances and biomass among species. Disturbed communities are often dominated by one or a handful of species that tolerate human activity, whereas species that would normally be present are uncommon (Dornelas et al. 2011). Such communities are less stable and provide fewer ecosystem services (Worm et al. 2006). Thus, these community properties fit into the larger goals of ecosystem-based management, making it important for managers to monitor how metrics that measure these properties change in response to MPA establishment. Finally, species heterogeneity integrates the number of species and their relative abundance. Metrics that measure heterogeneity, such as Shannon and Simpson diversity, are among the most commonly used in biodiversity studies, making their measurement and monitoring useful for comparative purposes.

Overall, relatively few of the regression models identified statistically significant covariates. For the abundance data sets, total abundance responded to latitude, with the RR declining as latitude increased. In other words, MPA protection had a greater effect on total abundance in more tropical locales. Log skew was influenced by MPA size, age, and the interaction between size and age. The negative effects of size and age on log skew were consistent with expectations that older and larger MPAs will have fewer rare species. A positive coefficient for the interaction term likely accounted for some large, old MPAs having more rare species than expected, perhaps due to poor enforcement or high fishing pressure outside the reserve.

For the biomass-based data sets, numerous metrics responded to level of protection; the most responsive metrics were those that measured dominance (McNaughton dominance and Zipf-Mandelbrot *c*), evenness (Shannon evenness and $\gamma$ shape), and heterogeneity (Shannon diversity, Simpson diversity, and Zipf-Mandelbrot *b*). The coefficient values all suggested that the metrics responded as expected to decreases in fishing pressure in no-take MPAs (Supporting Information). The influence of

**Table 3. Management relevance of the community-level metrics that measure the effects of marine protected area establishment included in this study.[a]**

| *Metric* | *Management relevance*[b] | *Expected response to MPA establishment* |
|---|---|---|
| Biomass | 1, 2, 3 | increases |
| Abundance | 3 | usually increases, but may decrease if species composition shifts from small to large-bodied species |
| Dominance | 4 | usually decreases if counting number of species; may increase if counting biomass of species |
| Evenness | 5 | usually increases if counting number of species; may decrease if counting biomass of species |
| Rarity | 6 | similar to dominance |
| Richness | 3, 7 | usually increases; may decline or not change depending on level of fishing pressure prior to MPA establishment or due to altered trophic interactions within the MPA |
| Heterogeneity | 3, 7 | similar to richness |

[a]*Ideally estimates of these metrics in the MPA should be considered relative to 3 reference points: the area encompassed by the MPA prior to protection; nearby unprotected areas; and large MPAs or unfished sites (e.g., around remote islands) in the same biogeographic province. Values for these sites provide information on the state of the fish community in the MPA and its trajectory relative to the past, currently fished sites, and unfished (or lightly fished) baseline endpoints. If these reference points are unavailable, managers can examine the change in the metric over time to determine if it is following the expected trajectory described above. Together these categories of indicators provide complementary information on the state of the fish community.*
[b]*Definitions: 1, fisheries spillover (i.e., bolster the fish stock for surrounding fisheries); 2, correlated with other metrics of interest to managers (e.g., maximum body length, growth rate, lifespan [McClanahan et al. 2014]); 3, mandated by legislation, often listed as a goal of MPA establishment; 4, indicator of disturbance; 5, enhanced ecosystem function and services; 6, rare species often the focus of conservation efforts; 7, commonly used (enables comparisons with other MPAs). [Correction added after online publication on January 8, 2015: "Letter definitions" in note b changed to "Definitions".]*

level of protection on so many metrics supports previous assertions that partial versus no-take MPAs have different effects on ecological communities (Lester & Halpern 2008; Edgar et al. 2011). The effect of the interaction between MPA size and age was negative for biomass, but each covariate on its own had a positive, albeit not significant, coefficient (perhaps for the same reasons elaborated above for log skew).

Just as most MPA effects studies have significant shortcomings (Harborne et al. 2008), so too will the syntheses based on those studies. For example, Edgar and Stuart-Smith's (2009) results suggest that MPAs are situated in areas with few fishery resources, biasing comparisons between them and adjacent fished sites (which generally had greater total biomass and total abundance than the newly established MPAs). Any study without an appropriate before–after, control-impact sampling design may risk confounding MPA effects with natural variability (Underwood 1994). These are important considerations during sampling design (Fraschetti et al. 2002), but they cannot be incorporated into meta-analyses until sufficient studies using the appropriate design have been conducted and their results published (along with detailed data on species abundance and biomass in protected and control sites).

We did not have information on a number of other covariates that influence MPA effectiveness, including human population density, habitat variables, landscape-level factors, and fishing pressure outside the MPA (Cote et al. 2001; Edgar & Stuart-Smith 2009; Pollnac et al. 2010). Including these and other factors in the analysis would likely reduce the heterogeneity among studies and produce more statistically significant results. Nevertheless, we doubt that it would fundamentally alter the conclusions of our study.

A final caveat to consider is that species diversity metrics, even the broad range presented herein, measure only certain aspects of biodiversity (Lyashevska & Farnsworth 2012). It is therefore essential that managers decide a priori what the most relevant biological variables to depict MPA effects are (Amand et al. 2004). Other indices, such as those that measure biological originality, trait or functional diversity, or phylogenetic diversity exist and are worthy of consideration (Dornelas et al. 2011).

Our results provide important guidance to managers interested in monitoring biodiversity at the community level. The metrics highlighted in Table 2 are robust to the heterogeneity that is unavoidable in meta-analytic studies and should be well situated to handle the task of comparing control and MPA samples from a single locale. Moreover, these metrics are easily calculated using routinely collected data (e.g., number and relative abundance of the species detected during surveys [see Supporting Information for details on how to obtain the software used to calculate the metrics discussed herein]) and can readily be incorporated into a monitoring framework. With the increasing need to evaluate community-level effects of MPAs, we suggest that conservation managers familiarize themselves with the various metrics that exist, selecting those that perform well in a specific MPA context and are aligned with management objectives.

## Acknowledgments

This work was supported by a grant from the Gordon and Betty Moore Foundation. Many thanks to B. McGill for making the MatLab code available and to NCEAS and the members of the working group on Species Abundance Distributions for help in developing these ideas.

## Supporting Information

A map of the study locations (Appendix S1), supplementary tables describing the studies included in our meta-analyses, heterogeneity results for the meta-analyses, meta-analysis results for each metric, and multiple regression results for both abundance and biomass data sets (Appendix S2), information on the software used in this study (Appendix S3), methodological details (Appendix S4), and leave-one-out regression results (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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