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Marine reserves as linked social–ecological systems

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Marine reserves are increasingly recognized as having linked social and ecological dynamics. This study investigates how the ecological performance of 56 marine reserves throughout the Philippines, Caribbean, and Western Indian Ocean (WIO) is related to both reserve design features and the socioeconomic characteristics in associated coastal communities. Ecological performance was measured as fish biomass in the reserve relative to nearby areas. Of the socioeconomic variables considered, human population density and compliance with reserve rules had the strongest effects on fish biomass, but the effects of these variables were region specific. Relationships between population density and the reserve effect on fish biomass were negative in the Caribbean, positive in the WIO, and not detectable in the Philippines. Differing associations between population density and reserve effectiveness defy simple explanation but may depend on human migration to effective reserves, depletion of fish stocks outside reserves, or other social factors that change with population density. Higher levels of compliance reported by resource users was related to higher fish biomass in reserves compared with outside, but this relationship was only statistically significant in the Caribbean. A heuristic model based on correlations between social, cultural, political, economic, and other contextual conditions in 127 marine reserves showed that high levels of compliance with reserve rules were related to complex social interactions rather than simply to enforcement of reserve rules. Comparative research of this type is important for uncovering the complexities surrounding human dimensions of marine reserves and improving reserve management.

coral reef | human–environment interactions | socioeconomic | social-ecological system | marine protected area

Human influences on marine ecosystems are pervasive (1) and strong (2–5). Marine reserves, which prohibit extractive activities such as fishing, are one of the key management measures used to mitigate anthropogenic impacts on marine systems. Marine reserves vary considerably in design, maintenance, and performance, in part because they are at the interface of complex social and ecological linkages. Social, economic, cultural, and political conditions can have profound influences on the ways that societies organize to use and manage resources, including the development, placement, and implementation of nature reserves (6). Ecologically, marine reserves often are isolated islands of low human use within larger areas of extensive and often intense resource extraction and habitat modification. The complexity of these social–ecological interactions may produce site-specific and surprising responses but may also be driven by predictable resource needs along gradients of human population and development (7).

The success of marine reserves has both social and ecological dimensions, and recent multidisciplinary investigations are uncovering important roles for both (8–10). The empirical research that links social and ecological aspects of marine reserve performance is dominated by case studies, which are often of single sites. These case studies have provided important insights, but idiosyncratic approaches have made larger-scale comparisons difficult, consequently limiting their contribution to understanding general relationships between social and ecological aspects of marine reserve functioning (11). Comparative research on multiple reserves across gradients of socioeconomic conditions, however, can randomize the effects of unknown variables and uncover unexpected human and environmental forces influencing marine reserve performance (8–10).

Here, a comparative approach with data from marine reserves across the main coral reef regions of the world [the Caribbean, the Pacific (Philippines), and the Western Indian Ocean (WIO)] is used to explore the following research questions: "How is the ecological performance of marine reserves related to socioeconomic conditions in neighboring coastal communities?" and "What social, economic, and contextual factors are related to high levels of compliance with reserve rules?" We use socioeconomic and ecological data from 56 marine reserves to address the first question and socioeconomic data from 127 marine reserves to address the second question (see *SI Methods* for a description of the study sites).

Results and Discussion

Target reef fish biomass, defined as the biomass per unit area of demersal reef-associated fish that are commonly exploited by fishers, was used as the ecological response variable because it has been shown to be responsive to management and human use (7, 9). We chose a commonly used effect index, the logged response ratio ($\ln RR$), to measure the proportional response of fish to protection by the reserve: $\ln RR = \ln(inside/outside)$, where *inside* and *outside* are the mean biomass per unit area of reef fish inside and outside the reserve, respectively (12). Outside monitoring sites were always close to the reserve and in equivalent habitat. All regions had marine reserves with both negative and positive values of $\ln RR$, but in all three regions the trend was for higher fish biomass inside compared with outside reserves (mean $\ln RR \pm 95\%$ confidence limits for each region: Caribbean = 0.27 ± 0.07–0.46; WIO = 0.67 ± 0.18–1.17; Philippines = 0.59 ± -0.24–0.42).

Multiple linear regression models were used to identify relationships between the $\ln RR$ of target fish biomass and the following theoretically important socioeconomic characteristics of communities nearby the reserves: three multivariate indices of community-level socioeconomic development (which capture aspects of basic, advanced, and tourism-related development), compliance with reserve rules as reported by resource users and managers (what we refer to as *stated compliance*), human population density, and local participation in community-level

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decisions (democracy) (Tables S1 and S2). The following reserve characteristics were also included as independent variables: the presence of boundary markers, reserve size (log transformed), and reserve age (Table S1). All variables were initially tested for relationships separately for each region using stepwise regression.

Significant associations were found between the ln*RR* of target fish biomass and stated compliance only in the Caribbean ($R^2 = 0.16$, $P = 0.016$) and population density in the Caribbean ($R^2 = 0.14$, $P = 0.021$) and WIO ($R^2 = 0.56$, $P = 0.0005$), but not in the Philippines. Relationships involving stated compliance and population density might, therefore, be region specific. Thus, when combining datasets, our starting model included the above independent variables, plus a term to test for differences between regions, and the interactions between region and population density and region and stated compliance (Table 1). The best stepwise model included region and its interactions with population density and stated compliance. Information-theoretic criteria (13) further indicated that this model was better supported by the data than other plausible but more complex models (Table 1).

Analysis of the "global" dataset thus confirmed that two socioeconomic variables, population density and stated compliance, were the best predictors of ln*RR* with important differences among regions. Specifically, the interaction between population density and region arose because increasing human population density was associated with decreasing ln*RR* in Caribbean and with increasing ln*RR* in WIO reserves (Fig. 1). In the Philippines sample, there was low variance in population density, making it difficult to discern potential relationships between population density and the response ratio of target fish biomass. Several past studies indicate negative impacts of dense human populations on reserve effectiveness and reef fish abundance (8, 9, 14, 15), but only our Caribbean result is in accord with these findings.

In light of previous studies and our Caribbean findings, the positive association between population density and the response ratio of fish biomass is intriguing. A previous study in the Philippines found a positive relationship between coral health, as measured by a mortality index, and fisher density and the rate of increase in population density (16). These findings were explained by human mobility: fishers simply migrating from damaged and over-fished reefs to more intact reefs with better fishing. One hypothesis to explain our WIO result is that the levels of resource exploitation may be very high outside reserves located in more densely populated areas, which may result in a high response ratio. A recent study in the WIO showed that reef fish biomass on fished reefs declined with increasing population density (7). In some cases, displaced fishing may be offset by the spillover effects of a reserve, particularly for settlement-limited fisheries (17). However, in an open-access fishery with high human migration, as in parts of the WIO, fishers might migrate to effective reserves that provide better fishing grounds (16, 18). Because methods of counting fish differed among regions, we could not test for separate effects on fish biomass outside and inside reserves. An alternative hypothesis is that high human population density may be related to other conditions that foster successful reserves, such as increased vigilance.

The interaction between region and stated compliance arose because high stated compliance was strongly associated with increased fish biomass in Caribbean reserves (relative to outside), but no relationship was detectable in the WIO and Philippines (Fig. 2). A previous study of Filipino reserves with a larger sample size (45 rather than 12) did find, however, a positive association between compliance and an ecological indicator of coral health in a reserve compared with outside (8). Additionally, our measure of stated compliance is based on responses from resource users. This indicator can be subject to cultural biases, especially where people in some cultural contexts may over-report compliance to "save face." Such a cultural bias may have occurred in Madagascar, where high levels of stated compliance by resources users did not correspond to expected response ratios of target reef fishes. When Madagascar is excluded from the WIO sample, stated compliance had a significant relationship with the response ratio of reef fishes ($F = 7.6$, df $= 10$, $P = 0.02$). Detailed knowledge of the local context is helpful when interpreting the results of cross-contextual studies such as this because of these types of cultural biases.

The effect of stated compliance on the response ratio of target fish biomass is simpler to interpret than human population density; better compliance means less fishing inside the reserve. The more interesting question is why the level of stated compliance varies. Theoretical and empirical studies suggest that a broad range of socioeconomic conditions can influence compliance with fisheries and other common-pool resource management institutions (10, 11, 19, 20). Heuristic models are used in some branches of the social sciences to allow the visualization of complex interactions between a set of interdependent variables (21). To lend insight into our second research question, socioeconomic data from 127 marine reserves in the three regions were used to develop a heuristic model of interrelationships between stated

Table 1. Results from candidate linear regression modeling of relationships between socioeconomic and reserve design variables and the effect of the reserve on fish biomass

Comments	Independent variables	r^2	AIC_c†
Starting model	Human population density + compliance + democracy + boundaries + size + age + basic dev. + advanced dev. + tourism dev. + region* + region × human population density* + region × compliance	0.46	152.0
Region removed	Human population density + compliance + democracy + boundaries + size + age + basic dev. + advanced dev. + tourism dev.	0.10	157.8
Final model‡	Region** + region × human population density*** + region × compliance*	0.39	127.7

dev., development.

$*P < 0.05$; $**P < 0.01$; $***P < 0.0001$.

†AIC_c indicates relative model fit (lower AIC_c values indicate better fit, and differences >2 indicate a reliable difference).

‡The final model was selected using a backward stepwise procedure from the starting model (criterion to drop a term, $P > 0.15$, minimum tolerance = 0.1). The final model is a better fit to the data than the other models based on comparison of AIC_c values.

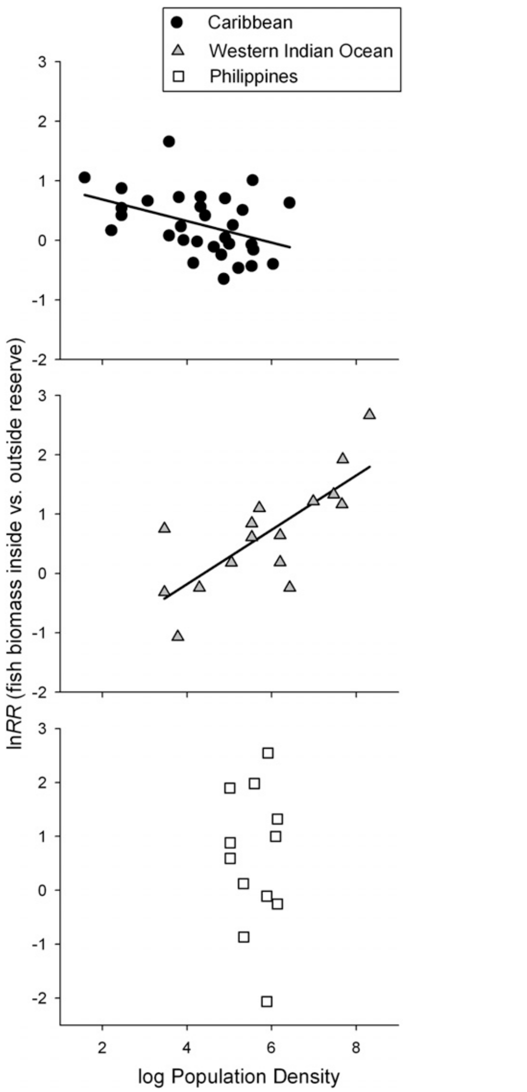

Fig. 1. Relationships between human population density and fish biomass inside marine reserves (relative to outside). Lines are fit using linear regression for statistically significant relationships ($P < 0.05$). $n = 31$ in Caribbean, 16 in WIO, and 11 in Philippines.

compliance with marine reserve rules and 28 variables related to the socioeconomic context. Patterns of relationships in a correlation matrix of these variables were used to develop the model (*SI Methods*).

The socioeconomic indicators directly related to stated compliance included the presence of marine reserve features (which include marker buoys, management plans, and signs), ecological monitoring by both advisors and the community, training (capacity formation), and a formal consultation process with the community (Fig. 3). Findings are consistent with socioeconomic theories of compliance and common property theory, which predict that perceived legitimacy of processes, effective resource monitoring, and clearly defined boundaries can influence levels of compliance with common-pool resource institutions (10, 19, 20). Interestingly, enforcement and adaptive management were not directly related to compliance in this analysis but rather were indirectly related through correlations with other variables, including the presence of ecological monitoring, ongoing training, and marine reserve features. This suggests that compliance is related to a range of contextual conditions and processes, rather

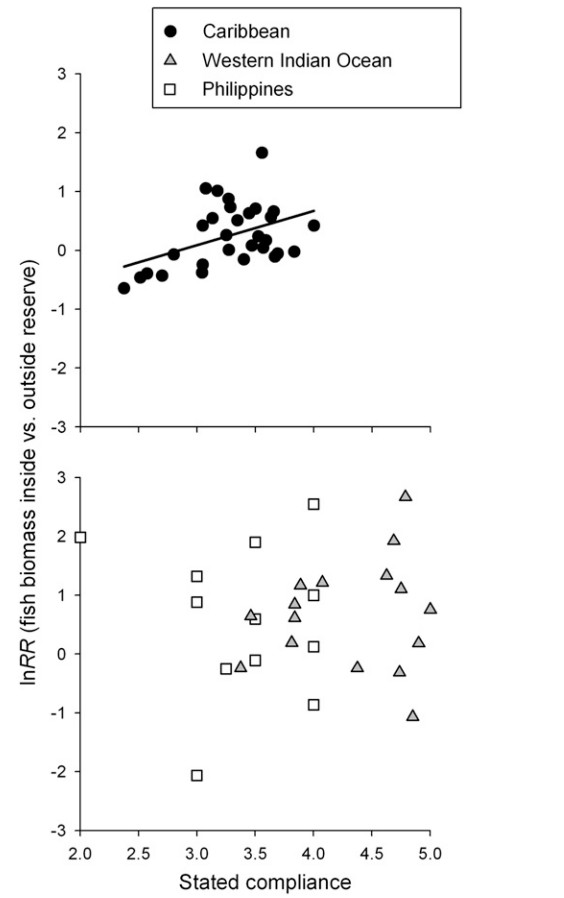

Fig. 2. Relationships between compliance with marine reserve rules and fish biomass inside marine reserves (relative to outside). Lines are fit using linear regression for statistically significant relationships ($P < 0.05$). $n = 31$ in Caribbean, 16 in WIO, and 11 in Philippines.

than just the level of enforcement (10, 20). Marine reserve managers, donors, and governments should consider investments in the processes and conditions that foster compliance a key priority for both existing and planned marine reserves.

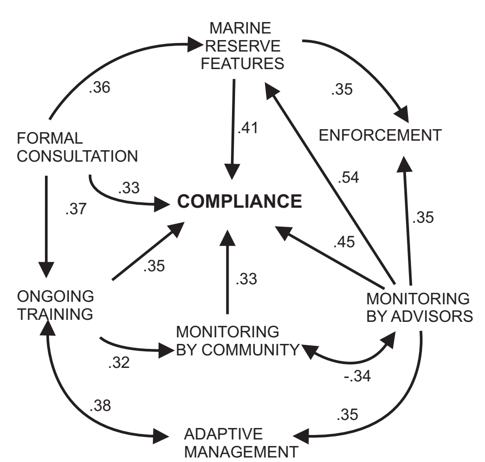

Fig. 3. Heuristic model of relationships between socioeconomic conditions and compliance with marine reserves. The N in each correlation ranges from 45 to 127, with most >90. Arrows indicate the proposed direction of the relationship, based on empirical and theoretical research. Numbers are the Spearman's rho correlation coefficient.

Conclusions

Relationships between social systems and responses of target fish biomass in reserves were strong enough to be detectable using our sample of 56 reserves, whereas influences of other commonly studied reserve properties (reserve size and age) were not. Links between social and ecological systems can be complex, and sometimes even counterintuitive, forcing a reconsideration of generally held notions. This study provided such a finding, with different study regions showing positive and negative associations between human population density and the response ratio of target fish. Empirical support for the widely held view that better compliance improves reserve performance was found, but there may be cultural biases in reporting this metric. Levels of compliance with reserve rules were, however, related to complex social dynamics, rather than simply enforcement (9, 10). Multidisciplinary research that examines reserves as part of linked social–ecological systems, as illustrated here, are required to uncover and understand these complexities and may help inform better design and management of marine reserves.

Methods

Comparable socioeconomic and ecological data were collected from 56 marine reserves across the Caribbean, WIO, and Pacific. Comparable socioeconomic data were also collected from communities adjacent to an additional 71 marine reserves. All of the marine reserves in this study prohibit fishing, and some are part of a larger protected area where a variety of activities are restricted or prohibited.

We tested nine independent variables as predictors of an index of the effect of marine reserve implementation on reef fish biomass per unit area (ln*RR*). Seven independent variables were theoretically important socioeconomic characteristics of human communities using reserves: local participation in community-level decisions (democracy), human population density, the presence of boundary markers, stated compliance with reserve rules, and three multivariate indices of community-level socioeconomic development that capture aspects of basic human development, tourism development, and technological development (Tables S1 and S2). The remaining two independent variables, reserve age and reserve size, are potentially important reserve design criteria that have had mixed results in empirical tests for their effect on fish biomass (12, 22). For example, the effect of reserve size seems to be quite complex, with some studies showing a strong effect of reserve size (12) and others showing no effect at all (15, 22).

Initially, relationships between ln*RR* and the nine independent variables were tested separately for each region using stepwise linear regression. Both forward and backward stepping routines were used to identify significant independent variables and produced identical results. Checks were made to ensure the data conformed to the assumptions of the regression model and confirm a lack of collinearity between the independent variables. Because the results indicated that relationships involving stated compliance and population density were region specific, when combining datasets, our starting model included the above independent variables, plus a term to test for differences between regions, and the interactions between region and population density and region and stated compliance (Table 1). We again used stepwise procedures to identify independent variables that should be included in the final model. We also checked whether the final model was better supported by the data than the starting model, plus one other plausible but more complex model (Table 1). We used the small sample version of Akaike's Information Criterion (AIC_c) to measure the relative fit of the three models (6) (see *SI Methods* for further details).

Additionally, a heuristic model was developed to assess direct and indirect interrelationships between a range of social, cultural, political, and economic conditions and stated compliance (*SI Methods*). Besides the 56 marine reserves used in the regression analysis, additional social, cultural, political, and economic data were available from another 71 reserves that lacked fish biomass data (n = 127 total). Data on 27 relevant independent variables were available, and although not all variables were recorded at all sites, there was an overlap for more than 80 sites (Table S1). On the basis of a correlation matrix, we traced interrelationships among all of the independent variables that had correlation coefficients above rho 0.3 (for detailed methods, see *SI Methods*).

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