

IDEA AND
PERSPECTIVE

Human impacts on the species–area relationship in reef fish assemblages

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Abstract

The relationship between species richness and area is one of the oldest, most recognized patterns in ecology. Here we provide empirical evidence for strong impacts of fisheries exploitation on the slope of the species–area relationship (SAR). Using comparative field surveys of fish on protected and exploited reefs in three oceans and the Mediterranean Sea, we show that exploitation consistently depresses the slope of the SAR for both power-law and exponential models. The magnitude of change appears to be proportional to fishing intensity. Results are independent of taxonomic resolution and robust across coral and rocky reefs, sampling protocols and statistical methods. Changes in species richness, relative abundance and patch occupancy all appear to contribute to this pattern. We conclude that exploitation pressure impacts the fundamental scaling of biodiversity as well as the species richness and spatial distribution patterns of reef fish. We propose that species–area curves can be sensitive indicators of community-level changes in biodiversity, and may be useful in quantifying the human imprint on reef biodiversity, and potentially elsewhere.

Keywords

Species abundance, coral, diversity, exploitation, fishing, macroecology, reef, species richness, scale, species–area.

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INTRODUCTION

The relationship between number of species (or higher taxa) and area is one of the most well-known macroecological patterns, and has been recognized since the middle of the 19th century (Rosenzweig 1995). Recently it has become the focus of much attention (e.g. Brose *et al.* 2004; Drakare *et al.* 2006; Martín & Goldenfeld 2006) as ecologists continue to develop underlying theory and synthesize empirical knowledge. Species–area relationships (SARs) are commonly (Drakare *et al.* 2006) described by the power function:

$$S = cA^z \quad (1)$$

where S is the number of species, A the area, c a fitted constant and z represents the slope in log–log space and hence the rate of accumulation of diversity with area. Although a number of other functional forms have been fitted to species–area data (Tjørve 2003), the power-law is the most frequently applied, and the slope parameter z has

been applied in terrestrial conservation to estimate extinction rates due to habitat loss (Pimm & Raven 2000) or climate change (Thomas *et al.* 2004). Here we provide evidence that the SAR in reef fish assemblages is sensitive to fisheries exploitation, and that the slope parameter may capture and quantify complex changes in community structure.

The effects of fishing on marine ecosystems worldwide have been well documented in terms of impacts upon populations and communities (e.g. Pauly *et al.* 2002; Myers & Worm 2003; Jennings & Blanchard 2004), yet general macroecological patterns in exploited marine ecosystems remain relatively unexplored (Fisher & Frank 2004). These population and community-level effects of exploitation may be captured in different ways by the numerous and various indices of biodiversity. Two of the most common measures of diversity are species richness and relative species abundance (Magurran 2004). Many other diversity indices represent some combination of these (e.g. Simpson's index, Shannon's index). However, such measures tend to be

insensitive to changes in spatial heterogeneity and patchiness that may occur independently of changes in richness and abundance. The SAR, however, is inherently affected by the spatial distribution of individuals and species (e.g. He & Legendre 2002). We examine the impacts of exploitation on SARs of reef fish assemblages.

Potential human impacts on the parameters of the SAR have, to the best of our knowledge, been little explored in the scientific literature. A recent meta-analysis of SARs does not include any papers that specifically examine this topic (Drakare *et al.* 2006). McClanahan (1994), Chittibabu & Parthasarathy (2000) and Reddy & Parthasarathy (2003) have presented data on changes in species richness with sampling area for protected (disturbed) and unprotected (less disturbed) sites – Kenyan coral reefs (also see McClanahan *et al.* 1999), tropical evergreen forest trees and tropical evergreen forest lianas, respectively. However as no model was fitted in any of these instances it is difficult to infer the magnitude, consistency and significance of any potential changes in the parameters of the SAR. Nonetheless, these studies raise important concerns about the potential for human impacts to affect the SAR. Flather (1996) fitted models to avian species-accumulation data and found that intensively used landscapes accumulated species less rapidly than landscapes with a greater proportion of natural habitats. Although it is not clear how the sampling scheme (particularly the temporal component of sample accumulation) would be converted to a classical species–area curve (Scheiner 2004; Adler *et al.* 2005), the results are again suggestive. Death (2000) fitted species–area models to benthic invertebrate data collected from two stream sites, one of which was more affected by anthropogenic disturbance resulting from changes in land-use. There was a significant difference in the power-law intercept $\log(\hat{z})$ between the two sites, but no change in the slope. As far as we are aware, therefore, there have been no studies that demonstrate a direct human impact on the slope parameter of the SAR. Here, we provide evidence for a consistent impact of exploitation on this scaling rate for multiple reef fish assemblages, and test for underlying changes in components of diversity that may be responsible for observed changes.

We used a series of comparative field surveys to examine SARs for coral reef fishes at sites located in three oceans (Glover's Atoll, Atlantic; Zanzibar Island, Indian; Line Islands, Pacific Ocean) and for rocky reef fishes in the Tuscan Archipelago (Mediterranean Sea). Using standardized protocols we compared protected to unprotected areas in order to observe the impact of fisheries exploitation. 'Protected areas' in the context of this paper are well enforced no-take zones where fishing is excluded; we cannot at present examine the effects of other disturbances that may occur. Mixed-effects models were fitted to test the

hypothesis that fishing, through the removal of particular species and changes in the abundance and spatial heterogeneity of those remaining, may affect the slope of the SAR. The SAR appears to consistently capture changes in these factors, and in some instances appears more sensitive than either species richness or relative species abundance as a measure of the effects of exploitation.

THEORY

Several mechanisms have been put forth to explain the highly robust pattern of SARs. Particularly prominent are the environmental heterogeneity hypothesis (i.e. larger areas contain more habitats) and the demographic process hypothesis (i.e. a dynamic balance of dispersal, colonization, speciation and extinction leads to the SAR; Drakare *et al.* 2006), though it has also been suggested that the SAR may be a sampling phenomenon (Connor & McCoy 1979). An experimental test of these three causes (Hoyle 2004) demonstrated that for a natural microecosystem the contribution of the metapopulation effect was roughly equivalent to the sum of the habitat-heterogeneity and sampling effects.

A number of studies have elucidated the linkages between diversity, range size, aggregation and SARs. For example, Leitner & Rosenzweig (1997) noted that, under an assumption that range size and abundance are positively correlated and a log-normal distribution of abundance, it was possible to derive a relation connecting point diversity, range size and provincial species diversity. Ney-Nifle & Mangel (1999) assumed characteristic patterns of geographic range and occupancy and ascertained that the main features of the SAR depended on these characteristics (along with patch census method). He & Legendre (2002) examined how changes in the species-abundance distribution and intraspecific spatial aggregation affected the number of species found within a censused region. They derived models combining evenness, aggregation and area, and determined that an increase in evenness caused a correspondent increase in species richness within a sampling area, and that an increase in intraspecific aggregation caused a decrease in species richness. Changes resulting from one factor could be counterbalanced by changes in the other. Picard *et al.* (2004) derived a model addressing the effect of the spatial distribution of species on the SAR, and found that it could be as important as the species-abundance distribution in modifying the SAR. Harte *et al.* (2005) generated a model based on the assumption of equal spatial allocation probabilities for individuals of a species at every scale under consideration, and from this were able to uniquely determine the shape of the SAR from the species-abundance distribution. All of the above models demonstrate that changes in species richness, evenness and spatial distribution can affect the SAR.

He & Legendre (2002) also provided a useful two-level conceptual model in which the ultimate drivers of the relationship between species and area (environmental and biotic factors) generated patterns of species-abundance and spatial distribution: the proximate, observable factors influencing the shape of SAR. We might expect that exploitation could be added to the list of ultimate drivers of the SAR, since it can have substantial effects on species diversity (e.g. Worm *et al.* 2005), ecosystem structure (e.g. Roberts 1995) and habitat (e.g. Coleman & Williams 2002). But how might such changes manifest in the parameters of a SAR? We can envision such effects both from the models above and from a simple graphical example to help conceptualize connections between species diversity and the power-law SAR. Figure 1a shows the power-law SAR that would arise from a particular arrangement of species in a set of nested sampling quadrats. Changes such as a decrease in species richness (Fig. 1b) or an increase in average patch occupancy per species (Fig. 1c) can affect both parameters of the power-law SAR. Thus, we hypothesize that the complex interplay of changes in species richness, spatial distribution and relative species abundance caused by exploitation may affect the SAR. We used replicated field surveys to test whether such effects are indeed visible, consistent, and whether they can be generalized across different reef habitats.

MATERIALS AND METHODS

Fish data collection

To gather empirical evidence for testing the effects of exploitation on SARs in the field, we conducted replicated underwater surveys on coral reef sites in the Atlantic, Indian and Pacific Oceans, and on rocky reef sites in the Mediterranean Sea. Data were collected using standardized scientific SCUBA surveys, at both protected and exploited sites, using either transect lines or point censuses.

Atlantic Ocean

Data were gathered during April 2005 from Glover's Reef, a 260 km² atoll (16°42.5' to 16°56'N, 87°53.5' to 87°40.5'W) located *c.* 30 km offshore from Belize (McClanahan & Muthiga 1998). No longlining, netting or traps are permitted anywhere within the atoll; fisheries are mainly artisanal. A triangular section in the southern half of the atoll has been designated a fully protected reserve since 1993, with no extractive activities permitted. Eight 100 m transects were surveyed in the protected area and eight within the fished region of the atoll. All sites were located on the forereef slope and very similar in terms of habitat features and exposure. Four transects in each section were surveyed at 5 m depth and four at 10 m. All sites were selected at random within the stratified design. The transects were divided into 20 intervals of 5 m length, and presence/

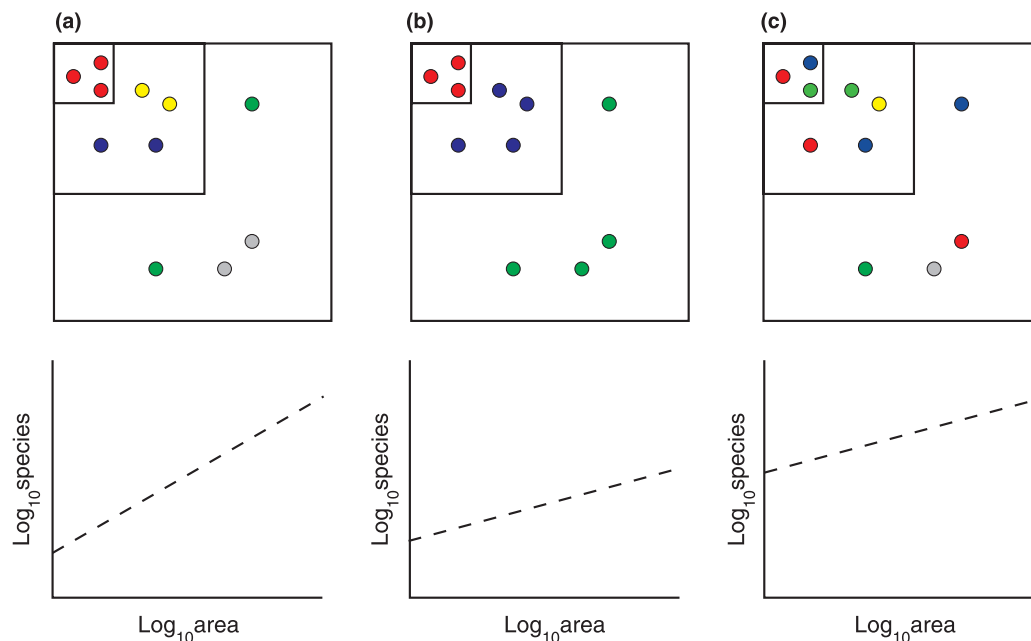


Figure 1 Conceptual diagram depicting an example of changes in the species–area relationship (SAR; a) with (b) a decrease in species richness and (c) an increase in mean species patch occupancy for a set of nested sampling units. The top row represents the distribution of species within units, with colours representing different species. The bottom row represents the SAR derived from such a distribution.

absence for all fish species recorded within 1 m on each side of the transect, for a total area of 200 m² per transect. After laying the transect and giving fish time to settle, one observer slowly swam the transect and recorded free-swimming pelagic species from 0 to 15 m ahead. The second observer followed and recorded demersal and benthic species. This order of censusing aimed to reduce error from fish avoiding human presence.

Mediterranean Sea

Stationary point counts were conducted at the Mediterranean islands of Capraia and Giannutri, part of the Tuscan Archipelago off the north-western coast of Italy. Capraia has a coastline of 27 km, Giannutri 11 km. Both islands have rocky reefs with protected and exploited regions. Point counts were conducted in circles of 5 m radius at 10 m depth. Twelve sites (six protected, six unprotected) were sampled at Giannutri and nine (three protected, six unprotected) at Capraia, with sites on both sides of each island. Eight replicate censuses were conducted at each site, and three complete sets of these surveys were conducted. Point counts were conducted by two divers for 5 min, followed by an additional minute of searching for benthic species within the 5 m radius circle. Methods are fully described in Micheli *et al.* (2005).

Pacific Ocean

Christmas Island, Fanning Island and Palmyra Island are three atolls in the central Pacific Line Islands chain. They experience varying degrees of fishing pressure but similar oceanic conditions. Christmas Island has been inhabited for *c.* 2000 years, and currently supports 7000–8000 inhabitants engaged in commercial, subsistence and localized sport fisheries. Fanning Island's population recently increased to *c.* 3500; historically, however, the island sustained a much smaller population. At both of these islands local fishermen use gill nets and hook and line to catch reef sharks for Asian markets. Nets, lines, traps and spears are used to catch reef fishes for local consumption and for the aquarium trade. Palmyra Atoll has been privately owned for 100 years and was purchased by The Nature Conservancy in 2000. It is now under the jurisdiction of the US Fish and Wildlife Service and protected as a National Wildlife Refuge. With its minimal historical and present population, Palmyra has not had an extensive fishery at any time. Visual fish surveys were conducted in May 2005. Three to seven randomly placed 4 × 50 m belt transects were surveyed between 2 and 10 m depth at sites on outer-lagoon reefs located along the leeward side of each island. Three sites were surveyed at Christmas and Fanning Islands, and four at Palmyra (GPS coordinates in Table S4). In total, 15 transects were surveyed at Christmas Island, 14 at Fanning Island and 20 at Palmyra Atoll. Two observers surveyed each transect: one recorded the abundance of apex predators – jacks (Carang-

idae), snappers (Lutjanidae), sharks (Carcharhinidae) and groupers (Serranidae) – along the transect, while the other observer estimated the abundance of every other demersal fish larger than 5 cm, by family. Methods are fully described in Stevenson *et al.* (2007).

Indian Ocean

Five sites (Bawe, Changuu, Chumbe, Nyange and Pange; GPS coordinates in Table S4) near the island of Zanzibar, Tanzania were surveyed using transect sampling. All reefs were similar in physical structure; fringing small islands or sandbanks stretching from the water surface down to the bottom at *c.* 10 m depth. Four of the sites – Nyange, Changuu, Bawe and Pange – are open to fisheries, whereas Chumbe Island Coral Park has been a well-protected no-take marine reserve since 1994. Nyange is located 8 km from the shore of Zanzibar and is accessible by larger fishing boats, whereas Changuu (5 km), Bawe (5 km) and Pange (3 km) are within day-range of smaller fishing vessels such as dugout canoes (*mtumbwi*) and hence experience visibly increased fishing effort. Chumbe is located 3 km from shore. Species diversity, abundance and size (to the nearest 5 cm) of fish were surveyed using 5 × 50 m belt transects placed randomly between 3 and 8 m depth parallel to the reef crest (*n* = 10 per site). Due to the difficulty of identifying very small fishes to species level, only individuals ≥ 5 cm were included in the study. The transects were further subdivided into 1, 10 and 25 m nested sections from the beginning of each transect, and fish data recorded separately for each of these sections.

Habitat data collection

Habitat differences between fished and unfished regions may have potentially confounding influences upon SARs. Furthermore, fishing may alter habitat as well as affecting fish communities directly. For this reason, we collected habitat data at three of four regions surveyed (Indian Ocean, Pacific Ocean and the Mediterranean Sea) to quantify whether there was a difference between protected and unprotected regions. Habitat data were not collected for the Atlantic Ocean; transects were situated in areas with qualitatively similar percentages of live coral cover at both depths in fished and protected areas.

Indian Ocean

Data were collected on percentage live coral cover, algae, rubble and dead coral cover, and 'other' habitat types. The benthic community structure was surveyed using 50 m (*n* = 10 per reef) transects placed randomly at depths between 3 and 8 m and parallel to the reef crest, using the line-intercept transect method described by English *et al.* (1997).

Pacific Ocean

Habitat data were collected using 33 replicate 0.25 m² quadrats at each site. Percentage algal cover and live coral cover were averaged for each site on each island.

Mediterranean Sea

Thirty 0.5 m² quadrats were sampled at each site on each island. Percentage encrusting (coralline) algae, bare rock and cover by other algae and invertebrates were measured. Replicate quadrats were averaged for each site.

Calculating species–area relationships

Though there has been some debate over the most appropriate model for the SAR (Tjørve 2003), the power-law function typically provides the best fit at intermediate spatial scales such as those of this study (He & Legendre 1996). In a previous study on coral reef SARs (Chittaro 2002), the power-law provided the best fit of the models tested in most cases. To ensure that it was indeed an appropriate model, we empirically tested seven functional forms for modelling the data using a least-squares framework: the power-law, exponential model, untransformed model, log(species) vs. area, breakpoint regression (both power-law and exponential) and the cumulative Weibull distribution, a nonlinear sigmoidal model [all models described in Tjørve (2003); methods fully described in Appendix S1]. Two of the linear models were consistently among the best-fitting models in all regions (the power-law and the exponential model; Table S1), and so we used both functions to fit the data in our mixed-effects model analysis. The power-law function is described in eqn 1. The exponential model is:

$$S = d + e \log(A) \quad (2)$$

where S is the number of species, A area, d the intercept and e the slope in log-linear space. For all spatial levels we calculated log(species + 1) for the power-law model to prevent taking logs of zero. In the Pacific we calculated family–area relationships, according to the taxonomic resolution of the data. Species–area relationships were constructed for the different regions as follows.

Atlantic Ocean

Data from each transect were accumulated in (spatially consecutive) 10, 20, 50, 100 and 200 m² sections; in all cases, we used all sections from each transect at every spatial level in the calculations.

Mediterranean Sea

Stationary observation circles of 5 m radius were combined using every possible combination for each sampling repetition at each site (consisting of eight circles), as there

was no obvious spatial ordering; thus, each SAR consisted of eight 5 m radius circles, 28 sets of two 5 m circles, 70 sets of four 5 m circles and one set of eight 5 m circles. Data from each survey was used to construct separate SARs; thus we had three sets of SARs for each site.

Pacific Ocean

Each site consisted of three to seven transects with no obvious spatial ordering. The spatial combinations used to form each SAR depended upon the number of transects in each site (details in Table S3).

Indian Ocean

Nested belt transect subdivisions of sizes 5 m, 50 m, 125 m and 250 m² (one of each level on each transect) were used to construct SARs. There were 10 transects for each site.

Mixed-effects models

Primary statistical analyses of the SAR data for all regions were conducted using linear mixed-effects models (Pinheiro & Bates 2000). This approach allowed us to construct the SAR and conduct statistical analyses within a single modelling framework. Moreover, mixed-effects models explicitly incorporate the effects of autocorrelation between spatial scales within each random effect unit (Pinheiro & Bates 2000), an important consideration with nested data. We allowed the intercept of each transect or observation circle to vary as a random effect. The effects of area and protection were included as fixed-effects for all regions; the interaction between these terms is the effect of protection on the slope of the SAR. Region-specific fixed-effects were depth (Atlantic), live coral cover, algal cover, rubble and dead coral, and other habitat (Indian), live coral cover and algal cover (Pacific), and island (Capraia or Giannutri), encrusting (coralline) algae, bare rock, and algal and invertebrate cover (Mediterranean). Full models included all first-order interactions and all linear terms. Two models, one containing coral cover and one algal cover, were used to assess habitat effects in the Pacific as a single model would not converge due to limited degrees of freedom. Equations for the mixed-effects models are given in Appendix S3. Data were converted from abundance to presence/absence where necessary. Habitat percentage cover data were arcsine square-root transformed before being incorporated in the mixed-effects models.

Mixed-effects models were fitted by the method of restricted maximum-likelihood in *S-PLUS 7* (Insightful Inc., Seattle, WA, USA). Use of likelihood ratio tests for assessing fixed-effect terms is not recommended for mixed-effects models (Pinheiro & Bates 2000); model selection and simplification were therefore carried out using backwards stepwise regression from the full model, removing the least

significant fixed-effect term (assessed with marginal F -tests) at each step until only terms with a significance level of $P < 0.05$ remained (Pinheiro & Bates 2000). We used conditional t -tests to assess the marginal significance of fixed-effect coefficients in the final minimal adequate models (Pinheiro & Bates 2000). Insignificant linear terms were retained when they were involved in a significant interaction effect.

Results for the power-law model are presented in the text; full exponential model results are available in the Supplementary Material (Table S2). Further tests of statistical robustness were also carried out using more traditional methods such as ANOVA and nonparametric tests (see Appendix S2 in the Supplementary Material).

RESULTS

Figure 2 depicts the mean fitted power-law SARs for each region, and Fig. 3 illustrates the mean slope parameters z with standard errors. Table 1 gives results for the minimal adequate models. In all regions, protected (unfished) locations showed a higher mean species–area slope than exploited (fished) regions. In the Atlantic this effect was significant ($P < 0.0001$) for both depths (shallower and deeper forereef slope). In the Indian Ocean the mean slope decreased proportionally to the accessibility (and thus visible fishing pressure) of the reef (Fig. 3). The difference was significant between the protected area (Chumbe) and the most accessible exploited region (Pange, $P < 0.0001$), as

well as one of the two next-most accessible regions (Bawe, $P = 0.025$). In the Pacific the effect of exploitation on the mean species–area slope was significant between the protected area, Palmyra, and both unprotected areas, Christmas Island ($P = 0.011$) and Fanning Island ($P = 0.0098$). Both full models in the Pacific resulted in the same minimal adequate model. In the Mediterranean the difference in mean slope between fished and unfished sites was significant for both islands ($P < 0.0001$). We focus on changes in mean slope z as the value of the intercept $\log(\varrho)$ is dependent upon the units of areal measurement, and changes in intercepts may only be assessed if the slopes are not significantly different. Habitat effects and their interaction terms were not significant for any of the three regions tested, and none of the minimal adequate models retained habitat as a factor. Thus we found no evidence of significant habitat differences between protected and unprotected areas in these regions, nor of habitat effects on the parameters of the power-law SAR.

Results for the exponential SAR model were very similar, with statistically significant ($P < 0.05$) decreases in slope with exploitation for all four regions (Table S2). In the Indian Ocean, the effect was significant at an additional site, Changuu ($P < 0.0001$), roughly the same distance from shore as Bawe. The most notable difference between the power-law and exponential models was that in the Mediterranean the minimal adequate exponential model retained interaction effects between area and encrusting algae, and area and algal/invertebrate cover, indicating that the

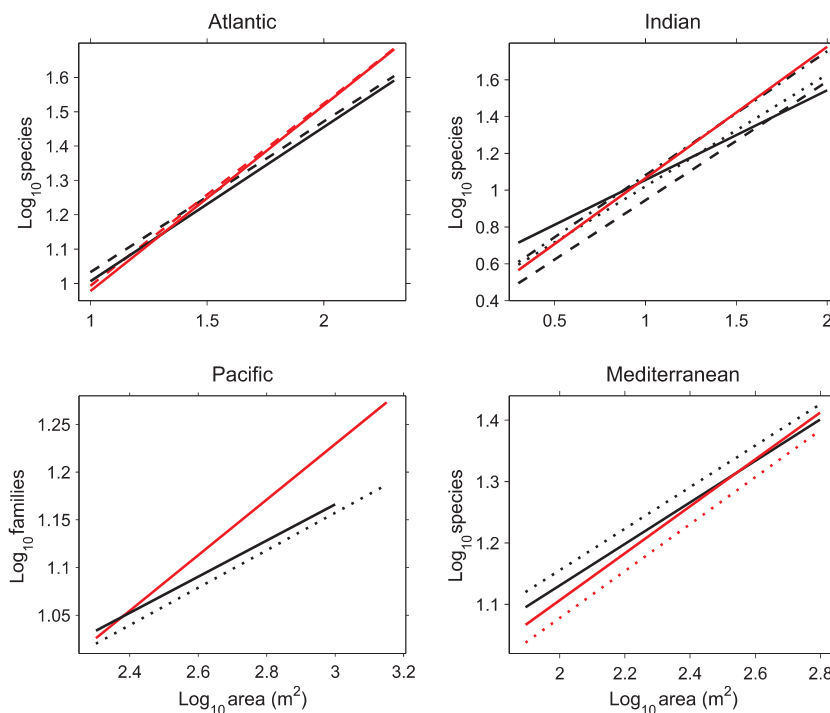


Figure 2 Mean fitted power-law species–area relationships for each region, from minimal adequate mixed-effects models except Atlantic (includes depth) and Mediterranean (includes island). Red lines represent protected regions. Atlantic: solid lines are shallow transects, dashed lines deep. Indian: solid red line is Chumbe, solid black Pange, dash-dot Nyange, dashed Changuu, dotted Bawe. Pacific: solid red line is Palmyra, solid black Fanning, dotted line Christmas. Mediterranean: solid lines are Giannutri, dotted lines Capraia. Note the different scaling on each axis.

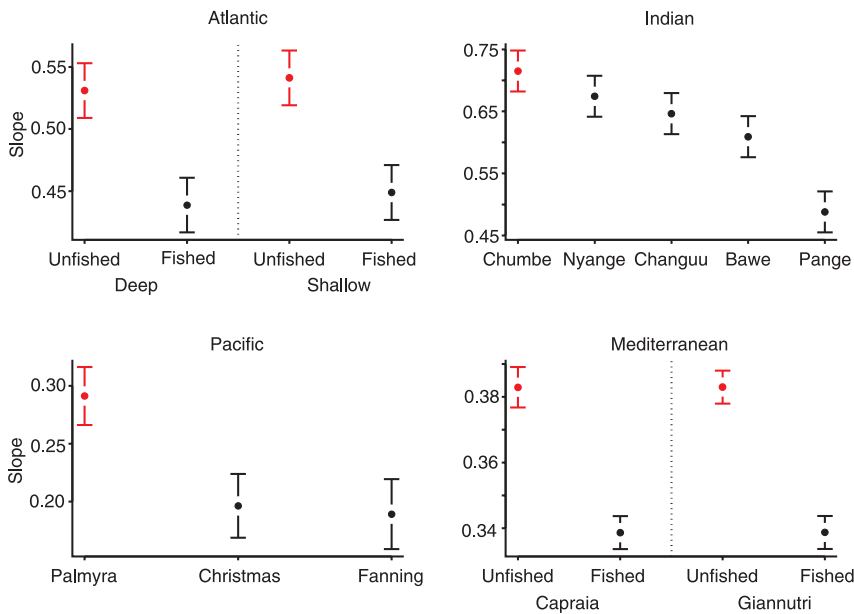


Figure 3 The effects of fishing on the species–area slope of the power-law model. Mean fitted slopes with standard errors are shown as calculated from minimal mixed-effects models except Atlantic (includes depth) and Mediterranean (includes island). Red indicates a protected area, black exploited (with increasing fishing pressure from left to right in the Indian Ocean).

relationship between species richness and area was sensitive to the amount of algal cover and encrusting algae. There was no evidence, however, for significant differences in these habitat variables between protected and unprotected sites, indicating that habitat differences were not responsible for observed changes.

Power-law results were tested for robustness using ANOVA and nonparametric tests (Appendix S1); for all tests in all regions the effects of exploitation were statistically significant at $P < 0.05$, though in some cases the level of significance changed depending on the model used.

The factors responsible for the observed changes in the slope parameter ζ appeared to depend upon the region. Table 2 shows a breakdown of changes in species richness, relative abundance and mean patch occupancy per species, all of which can contribute to changes in the SAR slope (see Theory section). Mean patch occupancy was lower in protected sites, while the other measures varied in both magnitude and direction between regions. In the Atlantic, the decrease in species–area slope appears to be a function of increased richness at larger sampled scales in protected areas, together with changes in relative species abundance (both significant at $P < 0.01$), although we cannot rule out habitat effects from our qualitative measures of habitat similarity. In the Indian Ocean, for three of four fished sites there was a significant increase in species richness at larger scales, and significant differences in relative species abundance in comparison to the protected site. Two exploited sites also had significantly higher mean spatial patch occupancy per species (Table 2). In the Mediterranean, the only statistically significant difference was increased mean

species richness at the smallest spatial scales in unprotected areas. In the Pacific, none of these indices was statistically significant individually, though the change in SAR slope was. This may indicate either that a combination of changes in species richness, evenness and spatial patchiness were important, or that unmeasured parameters were responsible for the observed changes.

Figure 4 shows relative species abundance (derived from presence/absence data in the Atlantic; family abundance for the Pacific) plots for all study locations on a log–log scale, with significance assessed in Table 2. In three regions (Atlantic, Indian, Pacific) the protected area distribution showed a longer tail of rare species. In the fourth region (Mediterranean) the species rank-abundance distributions for the protected areas had a tail of rare species that was either the same length as (Giannutri Island) or shorter than (Capraia Island) that for unprotected areas; thus, species richness was actually equal or lower in the protected areas. In exploited regions relative abundance was clearly more uneven at some sites in the Indian Ocean (Fig. 4), but the pattern was less clear in other regions (Fig. 4; Table 2).

DISCUSSION

Our results indicate that exploited reefs had systematically lower values of the species–area slope parameters ζ (power-law) and ϵ (exponential function) in comparison with adjacent sites that experienced less or no fishing. This pattern was surprisingly consistent across all regions studied, irrespective of local species composition, habitat type, depth or hydrographic factors. It is possible that human impacts

Table 1 Results for minimal adequate mixed-effects models (power-law)

Parameter	Estimate	SE	<i>t</i>	<i>P</i> -value
<i>Atlantic Ocean</i>				
Intercept	0.449	0.036	12.313	< 0.0001
Log(area)	0.536	0.018	29.817	< 0.0001
Unprotected	0.127	0.052	2.458	0.028
Log(area)*unprotected	-0.092	0.025	-3.628	< 0.0001
<i>Indian Ocean</i>				
Intercept	0.350	0.047	7.492	< 0.0001
Log(area)	0.715	0.033	21.615	< 0.0001
Bawe	0.062	0.066	0.935	0.36
Changuu	-0.051	0.066	-0.766	0.45
Nyange	0.057	0.066	0.869	0.39
Pange	0.218	0.066	3.301	0.0020
Log(area)*Bawe	-0.106	0.047	-2.263	0.025
Log(area)*Changuu	-0.069	0.047	-1.470	0.14
Log(area)*Nyange	-0.041	0.047	-0.870	0.39
Log(area)*Pange	-0.227	0.047	-4.857	< 0.0001
<i>Pacific Ocean</i>				
Intercept	0.356	0.068	5.239	< 0.0001
Log(area)	0.291	0.025	11.643	< 0.0001
Christmas Island	0.213	0.102	2.091	0.075
Fanning Island	0.243	0.106	2.283	0.056
Log(area)*Christmas Island	-0.095	0.037	-2.547	0.011
Log(area)*Fanning Island	-0.102	0.039	-2.602	0.0098
<i>Mediterranean Sea</i>				
Intercept	0.331	0.016	20.359	< 0.0001
Log(area)	0.383	0.005	83.396	< 0.0001
Unprotected	0.135	0.022	6.263	< 0.0001
Log(area)*unprotected	-0.044	0.006	-7.288	< 0.0001

Atlantic: Intercept and log(area) are intercept and slope for the protected sites. Unprotected is the difference between protected and unprotected site intercepts. Log(area)*unprotected is the difference between protected and unprotected site slopes. Indian, Pacific, the Mediterranean: results are presented in a similar manner; named sites are exploited. Non-significant coefficients retained only when overall term is significant or involved in an interaction term.

other than fishing may affect the scaling of diversity with area; however, we could not test for such effects in this analysis.

Changes in species richness, relative species abundance and mean patch occupancy all appeared to contribute to the observed changes in SAR slope, conforming to theoretical work that has demonstrated the importance of these factors (e.g. He & Legendre 2002; Picard *et al.* 2004). However, none were statistically significant for all regions. This suggests that the SAR may be a sensitive measure of the effects of exploitation, as it appeared to detect changes when some of the other indices did not. Only patch occupancy showed a consistent direction of change across all regions. It is interesting to note, however, that all

protected regions exhibited one or both of an increase in species richness at the largest scale, or a decline in species richness at the smallest scale. We might anticipate either of these to lead to an increase in slope.

The effects of relative species abundance on species richness have been analysed by He & Legendre (2002), who found that an increase in species evenness should also correspondingly increase species richness in a sampling area. This relationship appears to hold for the Indian Ocean reefs, in that the three exploited sites with significantly lower evenness than the protected site also have significantly lower species richness at larger scales (Table 2).

Our data suggest that protected areas tend to have higher overall diversity, and increased spatial heterogeneity at smaller scales (Table 2), along with the observed higher values of the SAR slope parameters ζ (power-law) and e (exponential function). Species diversity can therefore be expected to be higher in protected areas at larger spatial scales (Worm *et al.* 2006). Why these changes are generally not reflected at smaller spatial scales is unknown. We speculate that higher diversity may intensify interspecies competition for both physical and niche space, resulting in lower occupancy per unit area for each individual species. Additionally, in unexploited regions there are likely to be higher number of predators (Roberts 1995; Micheli *et al.* 2004), which could have an effect on the aggregation behaviour of smaller species.

Although habitat structure can exert a powerful effect on fish diversity, the inclusion of habitat data in the mixed-effects models allowed for the partitioning of habitat and exploitation effects in our analysis. At the locations for which we had such data there was no evidence that systematic habitat changes between exploited and protected areas may have confounded the effects of fishing. The only habitat effects retained in any minimal adequate mixed model were those of algal/invertebrate and encrusting algal cover and their interaction with area in the exponential model for the Mediterranean. This model, however, did not include any terms that suggested a significant difference in habitat between protected and unprotected regions. Though we can exclude habitat effects at the scale of measurement, there are other potential caveats. In particular, we must consider the possibility that observed changes in diversity may be sampling artefacts.

Firstly, the behaviour of fish, particularly large predatory fish that tend to be targeted by exploitation, may vary between protected and unprotected areas (Kulbicki 1998). This can lead to a change in detectability driven by attraction to or repulsion from divers, biasing estimates of abundance in comparison to unexploited systems. We note, however, that of families present in two or more regions, only 15 of 30 (50%) show a consistent pattern of decline or increase in average abundance under exploitation within

Table 2 Indices of diversity for protected and exploited sites

Ocean	Site	Mean species richness smallest sample unit	Significance vs. protected† (<i>P</i> -value)	Mean species richness largest sample unit	Significance vs. protected† (<i>P</i> -value)	Total species richness	Relative species abundance, significance vs. protected (<i>P</i> -value)§	Patch occupancy smallest sampling unit¶	Significance vs. protected† (<i>P</i> -value)
Atlantic	Unprotected	9.3 ± 0.9	0.88	34.9 ± 3.1	0.0017	67	< 0.0001	0.18 ± 0.21	0.19
	Protected	9.2 ± 2.7	–	41.4 ± 3.1	–	83	–	0.16 ± 0.15	–
Indian	Pange	3.8 ± 1.6	0.0068	32.9 ± 4.1	0.0002	84	< 0.0001	0.15 ± 0.13	0.080
	Bawe	2.3 ± 0.8	0.68	38.7 ± 4.4	0.0002	94	0.0001	0.16 ± 0.12	0.050
	Changuu	1.6 ± 1.0	0.22	33.3 ± 2.9	0.0002	121	< 0.0001	0.16 ± 0.07	0.040
	Nyange	2.3 ± 1.0	0.66	49.2 ± 5.7	0.058	133	0.25	0.14 ± 0.07	0.095
	Chumbe*	2.1 ± 0.7	–	55.2 ± 6.6	–	154	–	0.11 ± 0.02	–
Mediterranean	Capraia unprotected	12.0 ± 2.8	< 0.0001	23.8 ± 4.0	0.10	37.5‡	0.95	0.40 ± 0.25‡	0.34
	Capraia protected	10.0 ± 2.5	–	22.0 ± 2.7	–	34	–	0.37 ± 0.28	–
	Giannutri unprotected	11.4 ± 2.7	0.017	22.7 ± 3.1	0.71	43	0.83	0.38 ± 0.24	0.34
	Giannutri protected	10.6 ± 2.5	–	23.3 ± 3.3	–	43	–	0.34 ± 0.24	–
Pacific	Christmas	9.5 ± 1.5	0.87	12.3 ± 1.5	0.17	14‡	0.50	0.73 ± 0.25‡	0.20
	Fanning	9.5 ± 1.4	0.83	13.7 ± 2.1	0.63	16	0.97	0.67 ± 0.27	0.57
	Palmyra*	9.7 ± 2.0	–	15.0 ± 2.2	–	18.3‡	–	0.60 ± 0.30‡	–

Significant differences from protected sites are expressed in bold. Pacific are family data.

*Protected.

†Significance assessed using Wilcoxon rank sum test.

‡Corrected for unequal sampling effort by resampling equal numbers of transects 10 000 times and taking the mean.

§Mean relative species abundance per largest sampling unit. Atlantic data presence/absence only; Pacific is relative family abundance. Significance assessed using Kolmogorov–Smirnov test.

¶Within each large sampling unit in which a species had non-zero abundance (i.e. for which species was used to construct SAR).

each region, dropping to four of 30 (13%) across all exploited sites in all regions (see Figure S1 and Table S6). Thus, fully half of these families, under identical exploitation pressure, showed both declines and increases among exploited sites within at least one region. This suggests that behaviour is likely not of overriding importance, since we would anticipate similar responses within families should this be the case.

Secondly, when species are less abundant (as is likely in fished regions) the likelihood of encounter is reduced, thus leading to another potential sampling artefact. However, in the Mediterranean, species richness was higher or equal for exploited areas on both islands, yet still the SAR slope declined. In the Pacific, family-level grouping should reduce the effect of such an artefact upon our results. Thus, it seems unlikely that this factor is playing a strong role in observed differences.

Thirdly, though typical for similar reef studies, the scale of the sampling units may be too small to capture the full impacts of fishing on the abundances of large, highly mobile species. Nevertheless, the scale and replication of our study

was sufficient to detect significant differences in the SAR between exploited and unexploited sites in all regions. We do not suggest that this study is a full census of these reef regions, nor are we trying to extrapolate to larger scales; we detect differences in patterns of spatial distribution, richness and abundance of species within a finite sampling area. Within each region our sampling and statistical methods were entirely consistent between fished and unfished sites, so any bias in the methodology should equally affect both treatments, and be unlikely to introduce systematic variation. Thus, although we cannot rule out the effects of sampling on our study, given the consistency of results across diverse regions, the most likely explanation remains that of impacts on diversity patterns caused by exploitation.

Fourthly, although we included habitat as a variable in our mixed-effects analysis, differences between exploited and protected systems at less than the grain of the habitat measurements would not be captured by our surveys. Reefs can be highly complex habitats, and such fine-scale complexity could potentially have an effect on our results. Although the mixed-effects analysis suggests coarse habitat

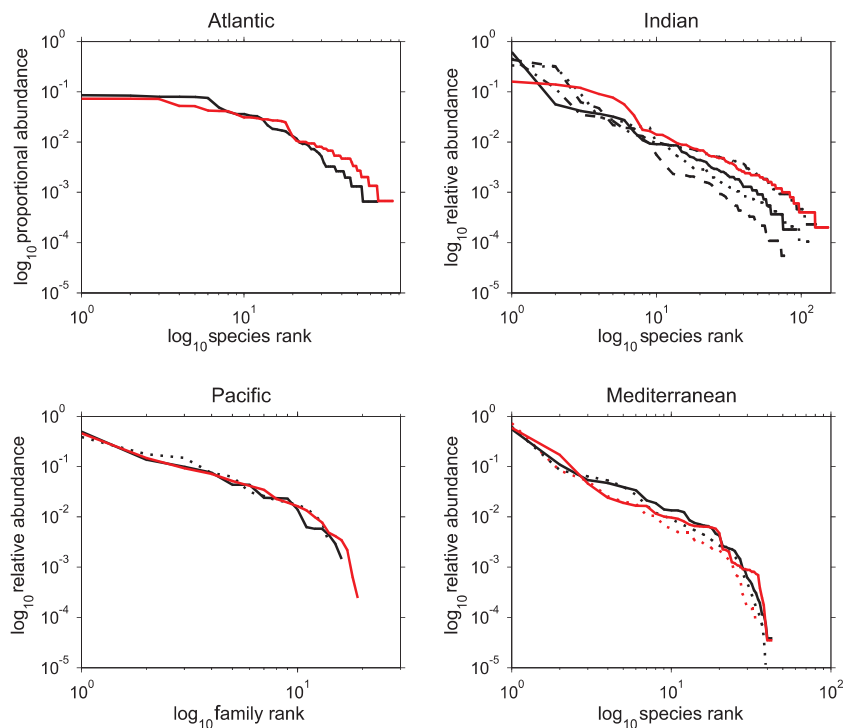


Figure 4 Patterns of rarity under fishing pressure. Shown are rank-abundance curves for species (Atlantic, Indian, the Mediterranean) and families (Pacific) on a log–log scale. Red lines represent protected areas, black fished areas. Pacific: Solid red line is Palmyra Atoll, solid black line Fanning Island, dotted black line Christmas Island. Indian: Solid red line is Chumbe, solid black line Pange, dotted black line Bawe, dashed line Changuu, dash-dot line Nyange. Mediterranean: dotted line is Capraia Island, solid line Giannutri Island. Data are corrected for sampling effort by subsampling 10 000 times and taking the mean. Atlantic curves based on presence/absence data.

differences are not apparent between our protected and exploited sites, further investigation of fine-scale differences would be prudent before fully excluding it as a confounding factor.

The generality of our results across different reef ecosystems, together with the fact that they capture relatively subtle gradients in fishing pressure, leads us to propose that SAR slopes may be useful as a complement to existing metrics of biodiversity for gauging the impacts of human exploitation upon reefs. There are a number of unresolved questions, however, that need to be addressed before the usefulness of such a method can be fully ascertained. For one, it is possible for changes in one aspect of diversity (e.g. spatial heterogeneity) to offset another (e.g. relative species abundances) in their effect on the parameters of the SAR (He & Legendre 2002). This would reduce the sensitivity of the SAR at detecting a combined set of changes. For this reason, the consistency of the direction of underlying trends in diversity on reefs needs to be confirmed before such a method can be applied. Moreover, the theoretical basis for SARs, while developing rapidly (e.g. He & Legendre 2002; Picard *et al.* 2004; Harte *et al.* 2005; Martín & Goldenfeld 2006) is complex, and a more complete model of observed changes under exploitation needs to be integrated within this framework.

Limitations of the method include that it is not possible to disentangle the underlying effects responsible for changes in the SAR without the use of other indices (such as those in

Table 2). Comparisons should only be conducted between geographically adjacent and environmentally comparable reefs, due to regional differences in SAR slopes (as seen in Fig. 3). The method may not be easily applied at larger spatial sampling scales, especially given that the slope of the SAR can vary with spatial scale (e.g. Crawley & Hurrell 2001; Fridley *et al.* 2005). We caution that the robustness and sensitivity of this pattern across different sampling scales needs to be quantified. We chose to examine a similar spatial extent for all study regions to avoid the confounding effects of scale among studies, and to operate on scales commonly used for the assessment of reef diversity. Finally, this study was carried out on nested sampling units; the results may be different when isolates are used to construct the SAR.

These difficulties, however, are offset by a number of advantages. Unlike conventional indices, SARs appear to be sensitive to changes in spatial heterogeneity, relative species abundance and species richness at multiple scales. As exploitation could potentially alter any or all of these facets of diversity, an index that is responsive to all of these could prove useful, and sensitive to combinations of changes in these parameters in a manner that other indices are not (as in our results). SARs appear to condense the numerous effects of exploitation pressure on fish assemblages into a concise, easily comparable value (the slope parameter; z for the power-law, e for the exponential model, though we caution that the c parameter also affects the slope of the power-law model in linear space). The effects of exploitation

on the SAR slope appear robust to changes in survey methodology, statistical analysis and taxonomic resolution. Only presence/absence data are required to construct SARs, and as they do not require measurement of abundance or body size they are a relatively practical and inexpensive survey tool. The apparent sensitivity at higher taxonomic levels could also be useful when taxonomic expertise is limited (for instance, when identification to species level is not possible). Given these multiple practical considerations, and that SARs can be calculated from rapid and simple SCUBA surveys, we believe that the usefulness of SARs as a method for ascertaining human impacts on coral reef deserves further investigation. We speculate that it might be possible to use temporal changes in the SAR to monitor recovery rates of newly protected areas and trends in diversity under exploitation over time. We further suggest that evidence of anthropogenic changes upon the SAR could be visible in other marine, freshwater and perhaps terrestrial environments, though there are likely to be substantial differences between habitats (e.g. Death 2000).

CONCLUSION

We have provided evidence for fisheries impacts on one of the oldest known general laws in ecology, the SAR. The slope parameter of the SAR, and thus the scaling of diversity on reefs, is consistently altered by exploitation. Our results suggest that the slope parameter of the SAR can in some instances be more sensitive to the effects of exploitation on marine biodiversity than species richness, relative species abundance or patch occupancy alone. The changes in scaling of diversity on shallow-water reefs we have described are robust irrespective of geographical location, depth, method of analysis, model function fitted and even taxonomic resolution. Such effects may be driven by changes in species richness, relative species abundance and average patch occupancy. Our results are generally consistent with theoretical work on the effects of these changes on the slope of the SAR. We propose exploration of the potential use of SARs in addition to other indices for quantifying anthropogenic impacts on reefs. While human impacts on point measures of marine biodiversity such as species richness are well recognized (e.g. Worm *et al.* 2005), alteration of the underlying scaling laws of diversity hints at a deeper raft of ecosystem changes. Fish species diversity scales closely with the diversity of functional traits (Micheli & Halpern 2005); thus changes in spatial species richness may have functional ecosystem consequences (Nyström & Folke 2001). That the effects of exploitation on the SAR slope are clearly visible even at the relatively low intensities of artisanal fishing as seen on Glovers Atoll and Zanzibar

Island provides further evidence that our impacts are not limited to industrialized fisheries.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Word doc. A file consisting of the following:

- **Appendix S1** Testing functional forms for the species-area model.
- **Appendix S2** Tests of statistical robustness.
- **Appendix S3** Mixed-effects model equations.
- **Figure S1** Normalised change in family abundance relative to protected areas.
- **Table S1** Mean adjusted *r*-squared values for the seven least-squares regression models fit to species-area data.
- **Table S2** Results for minimal adequate mixed-effects models (exponential model).
- **Table S3** Spatial combinations of transects used to calculate SARs in the Pacific.
- **Table S4** GPS coordinates for Pacific and Indian sites.
- **Table S5** Family names for Figure S1.
- **Table S6** Species list for all study locations.

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