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Determinants of the steep species–area relationship of coral reef fishes

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Abstract The increase in species richness with area is known as the species–area relationship (SPAR). Although several mutually non-exclusive processes may produce the SPAR, the null, often ignored, hypothesis states that a SPAR can be generated by random placement alone. The log–log-transformed SPAR of coral reef fishes on small patch-reefs revealed a steep slope of 0.55. However, this slope was dependent on the cumulative area of the reef examined and was therefore affected by random placement. After statistically removing the contribution of random placement from the SPAR, the slope was estimated to be 0.21. This is consistent with estimates from other, mostly terrestrial, systems. Furthermore, a randomization procedure, where the probability of fishes to reach a patch was proportional to reef area, showed that the field measured SPAR did not differ from random placement. In addition, fish assemblages on species poor reefs did not form subsets of species rich reefs (i.e., no nestedness) beyond that expected from random placement. Steep log–log-transformed SPARs can be formed by random placement alone, indicating that caution should be used when assigning an ecological meaning to SPARs generated from small spatial scales.

Keywords Spatial distribution · Scale · SPAR · Nested subset · Red Sea

Introduction

It has long been recognized that species richness increases with area, a phenomenon commonly known as the species–area relationship (SPAR). The most familiar pattern of this relationship is the one described by a power function (Arrhenius 1921). This can be linearized by logarithmic transformation of both axes, with a slope typically symbolized by the letter z (i.e., $\log S = z \log A + c$; where S represents the species number, A is area, and c is a fitted constant; Preston 1962a, b). A linear relationship between $\log S$ and $\log A$ has been demonstrated in many taxa (e.g., Connor and McCoy 1979; Rosenzweig 1995, and references within).

The SPAR has been used as a conservation tool to estimate the effect of fragmentation and habitat loss on species diversity and to estimate local species richness (see Neigel 2003 for a review of the use of SPARs in conservation of marine environments). The value of z is also often used to infer the extent of isolation (or connectivity) between patches from the point of view of the organism, where steeper slopes imply greater isolation between patches (Strong and Levin 1975; Rosenzweig 1995). This range of uses highlights the need to distinguish among mechanisms that generate the SPAR. As summarized by Tjørve (2003): “With the prevalent emphasis on fitting an equation to the SPAR, it has been frequently forgotten to examine its biological mechanisms.”

Studies of SPAR for fish on coral reefs find steep slopes: in the Caribbean, Chittaro (2002) found z values ranging between 0.43 on continuous reefs and 0.24 on patch reefs, while in the Great Barrier Reef Ault and Johnson (1998a) revealed an approximate (presented on an arithmetic scale and not on a logarithmic scale) slope of $z = 0.67$ for patch reefs and $z = 0.54$ for continuous

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reefs. Therefore, the steep slopes of the SPAR for fishes on coral reefs appear to be a wide-ranging phenomenon. The range of slopes found for reef fishes contrasts with that found in many other systems, where z values are typically much shallower (Rosenzweig 1995).

What causes such steep SPARs on coral reefs? Several mutually non-exclusive hypotheses are possible. Area is highly correlated with habitat diversity, so steep SPARs can be produced if habitat diversity increases exceptionally quickly on coral reefs. Likewise, species-specific behavioral avoidance of, or high local extinctions on, small patches will result in minimum area requirements that produce a positive SPAR (Turner and Tjørve 2005). Another explanation is that the steep SPAR may be produced by the unique three dimensionality of the reef system, where many fish use both the water above the reef and the reef itself (Chittaro 2002). Similarly, on patch reefs, fish abundance might be in direct proportion to patch volume causing the SPAR to be steeper than in intrinsically two-dimensional systems. This mechanism might apply to other reef-associated taxa that use the intricate reef matrix for food and shelter. In such taxa, it is likely that abundance would be strongly affected by reef volume and less by reef surface area.

Random processes may affect species diversity patterns independently of any directed biological process. Therefore, non-experimental studies of SPARs must distinguish ecological mechanisms from random processes by having an explicit model that describes the expected pattern in the absence of known biological processes. In the case of the SPAR, the null hypothesis states that a SPAR can be generated by random placement alone, such that larger areas form larger targets, accumulate higher number of individuals, which in turn correlate with high numbers of species (Coleman 1981). Random placement as a mechanism underlying SPARs should not be confused with SPARs generated from incomplete surveying. While the former has biological significance, the latter is a sampling artifact (Turner and Tjørve 2005). The suitability of random placement to explain the SPAR for coral reef fish has not been previously addressed, although this mechanism has been suggested to operate at these small scales (Chittaro 2002).

This study aimed to examine determinants of the steep slope of a coral reef fish SPAR. Empirical data on fish from coral reef patches in the Red Sea were compared to the pattern generated from randomization models to determine whether the SPAR could be explained by random placement alone. Data were explored to determine whether species-poor reefs formed a proper subset of species-rich reefs (i.e., whether they were “nested”). To reveal the role of habitat in producing the observed SPAR, the relationship between species richness and various habitat variables was also examined. It is argued that it is vital to explicitly test for the contribution of random placement before drawing ecological inference from empirical SPARs.

Materials and methods

Fish census and reef parameters

The study took place along the Israeli coast of the Gulf of Aqaba, Red Sea, in the northern part of the Coral Beach Nature Reserve (29°31'N, 34°55'E; Fig. 1). The surveyed area ranged in depth between 4 and 8 m and had numerous patch reefs (i.e., isolated, usually circular reef patches) of various sizes, situated on a sandy bottom in front of a narrow fringing reef (i.e., a coral reef that forms near the shoreline). The average distance to the fringing reef was 38 m (range 2–100 m). All reefs in this area were sampled, providing they were at least 1 m wide and 0.8 m tall and separated from their nearest neighbor by more than 3 m of open sand. In total, 39 patch reefs were examined, ranging in size between 3.55 and 190 m². The patches were variable in appearance, with live coral cover ranging between 17 and 80% (see Table 1 for a summary of the physical characteristics of the patch reefs).

Fish were visually surveyed using SCUBA by a single diver (N.B.M.) to reduce observer bias. First, large fish that swam up to 1.5 m from the reef were recorded, from a distance of several meters. Next, smaller fish were documented while swimming closer to the reef. Finally, holes, crevices and the area within corals were examined and all species that were not previously counted were recorded. Only presence–absence of each species was recorded, since we were concerned of potential inaccuracies in visual abundance counts of whole reefs that could occur in this system (Thompson and Mapstone 2002). A complete list of species surveyed is presented in the Appendix. Semi-pelagic fish and fish that are not

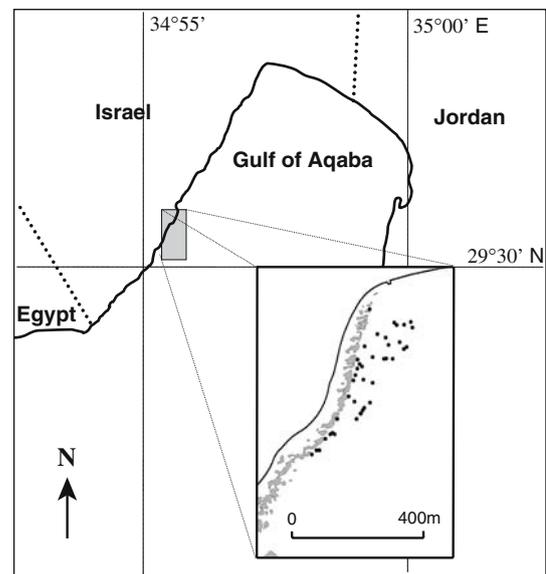


Fig. 1 Map of the northern Gulf of Aqaba, with the study site in the Coral Beach Nature Reserve enlarged. Each point depicts a coral patch reef examined in the study

Table 1 Summary statistics of the habitat variables characterizing the patch reefs examined

Variable	Transformation	Mean (\pm SD) of untransformed data
Reef area	\log_{10}	24.25 (\pm 34) m ²
Reef volume	\log_{10}	16 (\pm 26.08) m ³
Substrate diversity (Shannon index)	None	1.43 (\pm 0.32)
Proportion of live substrate	Angular	0.44 (\pm 0.18)
Distance from fringing reef	\log_{10}	37.6 (\pm 32.5) m
Topographic complexity (contour vs. linear length)	Angular	0.29 (\pm 0.12)

Prior to regression analysis most variables were transformed in order to promote normality

usually associated with coral reefs were not counted. Based on a preliminary survey, five additional species that are small and cryptic and therefore subject to strong sampling bias were excluded. These species are found on patch reefs of all sizes, and therefore their exclusion is not expected to substantially alter the results.

To estimate the reef surface-area two orthogonal photographs of each reef were taken. Each image had a scale bar in it. Using J-Image software, the face surface-area and maximum reef height was calculated from the photograph. The sum of the two orthogonal faces was multiplied by 2 and the base area (calculated from the circumference at the reef base considering the reef to be circular; Sale and Douglas 1984) was added to give the final surface-area estimate. Based on the cylindrical shape of the patch reefs examined reef volume was estimated by multiplying its base area by its height.

A number of habitat variables were collected for each patch reef to examine their contribution to the SPAR. Microhabitat cover was estimated using the line-intercept method (Loya 1972). Three line transects were placed across each reef at 60° angles running through the middle of the patch (Sale and Douglas 1984), and reef substrate along each line was recorded to the nearest centimeter and assigned to 1 of 15 categories (Table 2). These categories were later reduced using principle component analysis (see below). In addition, the following variables were calculated: (1) substrate diversity estimate, using the Shannon index (Ault and Johnson 1998a), (2) proportion of live substrate, (3) distance from the edge of the fringing reef, and (4) surface topographical complexity, using the contour-versus-linear-length method (McCormick 1994; Ault and Johnson 1998b), calculated as the average of the three transects.

The SPAR and random placement

Larger targets may randomly accumulate high numbers of individuals, which in turn correlate with high numbers of species (Coleman 1981). Therefore, a SPAR may form simply from the higher number of individuals on

Table 2 Summary of the 15 habitat categories recorded during the line-intercept transects and their correlation with the first four principal components (PC)

Habitat variable	PC1	PC2	PC3	PC4
Live coral from the following genera				
1. <i>Acropora</i> spp.	0.36	0.11	-0.28	-0.04
2. <i>Porites</i> spp.	-0.21	-0.20	0.12	-0.29
3. <i>Stylophora</i> spp.	-0.22	0.38	0.30	0.18
4. <i>Pocillopora</i> spp.	0.12	0.20	0.34	0.41
Corals from the following growth forms				
5. Massive coral	-0.04	-0.54	0.11	0.23
6. Encrusting coral	0.28	-0.01	-0.36	-0.33
7. Tabular coral	0.30	0.12	0.08	0.38
Other live substrate categories				
8. Sea anemones	0.45	-0.11	0.21	-0.23
9. Sponges	-0.24	0.07	0.08	-0.13
10. Soft coral	0.14	0.23	0.17	-0.36
11. Other live substrate	-0.04	-0.09	-0.33	0.20
Dead substrate				
12. Coral rubble	0.17	0.15	-0.40	0.36
13. Dead branching coral	-0.45	0.28	-0.22	-0.08
14. Rock (pavement)	-0.03	-0.51	0.12	0.11
15. Holes (Diameter narrower than depth)	0.27	0.16	0.37	-0.13

These variables were also used to calculate the Shannon index, a measure of substrate complexity and the proportion of live cover. Correlations $> |0.3|$ are in bold

larger patches. The conceptually similar sampling artifact caused by incomplete surveying may also form a positive SPAR (Turner and Tjørve 2005). However, since whole patch reefs were surveyed exhaustively rather than sampled, incomplete surveying is probably of minor importance to the SPAR in the present study. To estimate whether random placement is responsible for the observed SPAR, the slope of the log-log-transformed SPAR as a function of cumulative patch area was examined (Rosenzweig 2004). To do this, patches were added up, in a random order, and the corresponding cumulative number of species recorded. For example, point number 1 was calculated as the average number of species on a patch; point 2 as the average number of species on two randomly selected patches, etc. This was done over 1,000 iterations to obtain an average SPAR, where each point represents the average number of species and the average area of an increasingly larger number of aggregated patches. Next, the slope, z , of the new SPAR at each point was evaluated by calculating the slope from a particular point to the next one, which was formed by an addition of one more patch. If z does not change when patches are added, random placement does not produce the SPAR. In contrast, if z forms a decreasing function of cumulative area, random placement is clearly one of the mechanisms producing the SPAR. Furthermore, the asymptotical value of z represents the “true” slope of the log-log-transformed SPAR without the effect of random placement (Rosenzweig 2004).

A simulation model was constructed to estimate numerically the expected species richness on each reef patch under random placement. Two versions of this null model were considered. In the first, randomizations were based on patch volume, testing whether the steep SPAR can be produced by the three-dimensionality of coral reefs. In the second model, randomizations were based on patch area, testing the more conventional null hypothesis that SPAR is produced by random placement according to area.

This was done following the procedure described by Simberloff and Gotelli (1984) and Gotelli and Graves (1996) for incidence data. The new analytical method described by Colwell et al. (2004) could not be used as the sample units differed in size. In each simulation the observed species incidences were reshuffled among patches such that the probability to reach each patch was proportional to its size. Therefore, if A_j is the size (area or volume) of patch j and n is the total number of patches examined, the probability of a certain species incidence to reach a patch is given by $A_j / \sum_{j=1}^n A_j$. Since the observed species incidence function was retained, there was no need to assume any specific underlying species abundance distribution. This procedure was repeated 1,000 times, and empirical data was then compared with the range of values produced from the simulation. This simulated a scenario of random colonization from an external pool in which species arrive completely independent of one another (i.e., no interspecific interactions).

To evaluate whether the SPAR was compatible with that obtained from the simulations, empirical regression parameters were compared with the distribution of these parameters values obtained from the simulations. However, the parameters of the linear log-transformed SPAR could not be directly compared with the simulation model since the computer-generated random placement curve was not linear. Consequently, a polynomial regression was used (i.e., $\log S = B_0 + B_1 \times \log A + B_2 \times (\log A)^2$, where B_0 , B_1 and B_2 are fitted parameters) since it provided the best fit with the random placement curve (minimized the Akaike Information Criterion; Hilborn and Mangel 1997). In addition, a linear relationship is nested within a polynomial one; therefore a polynomial model can be reduced to a linear one if necessary without biasing the results. This non-linearity in the random placement curve is anticipated since the log-log random placement curve is frequently non-linear (McGuinness 1984; Gotelli and Graves 1996; see also Fig. 2b). An observed parameter was considered significantly different than the null model when it was <2.5 or >97.5% of the simulated values.

Nested subset analysis

Nested-subset patterns occur when species-poor samples form a proper subset of species-rich samples. Both the

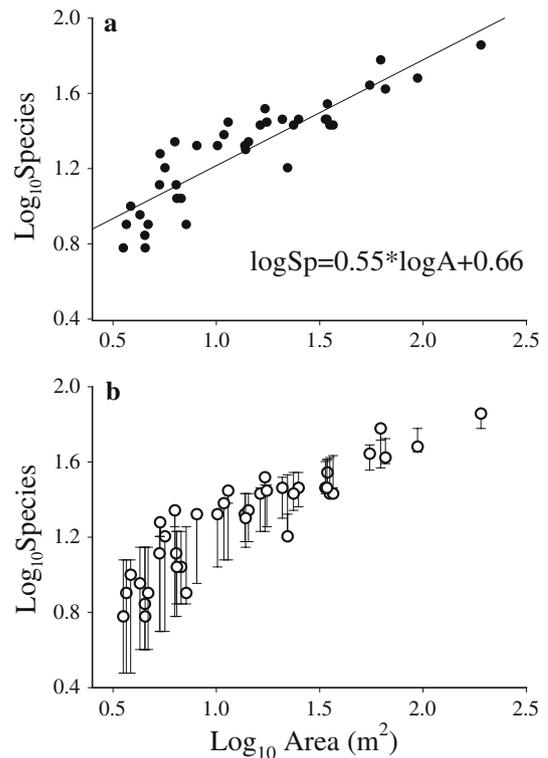


Fig. 2 Species richness versus area of fishes residing on patch reefs. Data points represent empirical data. **a** Ordinary least-square regression ($R^2 = 0.8$, $P < 0.001$). **b** Observed species richness (O) compared to expected species richness from random placement by area. Lines enclose 95% of the randomization model results. The model randomized incidences between patches, such that the probability of reaching a patch was proportional to its area

habitat diversity hypothesis and the minimum area effect (differential immigration/extinction) predict species poor sites to be nested within species rich sites (Turner and Tjørve 2005). To examine whether the patch reefs are indeed nested, the nestedness “temperature” calculator was used (Atmar and Patterson 1993). However, because small patches are less likely to sample rare species than large patches, a nested pattern may be produced solely as a consequence of random placement (Fischer and Lindenmayer 2002). To test this possibility the previously described null model was used to construct random data sets and thereafter calculated the simulated data’s temperature. One hundred repetitions allowed comparing the “temperature” of the empirical data with the distribution of “temperatures” expected from random placement (compare with McAbendroth et al. 2005).

Statistics

Multiple linear regressions were performed to analyze the contribution of habitat diversity to the observed SPAR. To choose the best model out of the large number of possible combinations of independent

variables the “all possible subset” method was used (Graham 2003). Initially, the combination of independent variables that yields the highest coefficient of determination for each number of parameters was found. Of these models, the one that minimized the Akaike Information Criterion was selected (Hilborn and Mangel 1997).

First, a simple analysis was performed with log species richness as the dependent variable and the measured habitat variables as the independent variables. However, this does not standardize species richness to the variable size of the patches. Therefore, to compare species richness among different size patches, while accounting for the statistical contribution of random placement, another regression analysis was performed in which the expected species richness from the random placement model was added as an independent variable. This allowed comparing the relative contribution of habitat variables and purely size-related effects caused by random placement to the SPAR.

The large number of microhabitat categories (15) was reduced by performing a principal component analysis (PCA). Prior to analysis, microhabitat categories were converted from length units to proportions and transformed (angular transformation). The first four principal components (PC1 to PC4) explained 52% of the total variance and were subsequently used as independent variables in the regression analysis. The contribution of the various microhabitat categories to each of the principal components is shown in Table 2. Other independent variables included (after transformation to insure normality): topographic complexity (angular transformation), distance from fringing reef (log transformed), proportion of live substrate (angular transformation), and the Shannon index of substrate diversity (Table 1).

Results

An empirical positive linear SPAR was found between species and area on a log-log scale ($R^2 = 0.8$, $P < 0.001$; Fig. 2a). Least-squares regression estimated the slope of the log-based SPAR, z , to be 0.55 (± 0.05 SE), and the intercept, c , to be 0.66 (± 0.06 SE). A semi-log SPAR gave very similar qualitative results. However, the log-log equation was preferred as it can be directly compared with the relevant literature.

The slope of the log-log-transformed SPAR decreased as a function of cumulative patch area (Fig. 3), suggesting that random placement is accountable, at least partly, for the observed SPAR. Non-linear regression techniques were used to estimate the asymptotic value of z . Only regression models that yield an asymptotic value were compared since it is a priori assumed that a constant value of z would ultimately be reached. Of these models, the one that minimized the Akaike Information Criterion (Hilborn and Mangel

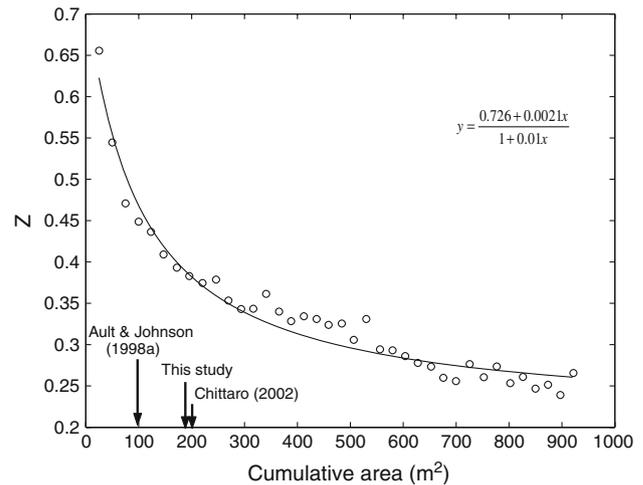


Fig. 3 The slope of the log-log SPAR (z) as a function of cumulative reef area. Cumulative area and z are means over 1,000 iterations. Patches were added up, at a random order, and the corresponding cumulative number of species recorded. This produces a SPAR, where each point represents the number of species and the area of an increasingly larger number of aggregated patches. The slope, z , of the new SPAR at each point was evaluated by calculating the slope from one particular point to the next, which was formed by an addition of one more patch (see text for details). Although the initial slope is high, it decreases rapidly when additional patches are added. A rational non-linear regression was fitted to the data ($R^2 = 0.96$, $P < 0.001$). The maximum area of the reefs examined in several other studies is indicated with an arrow

1997) was a rational function in the form of $y = \frac{a+bx}{1+cx}$. This yielded a highly significant regression ($P < 0.001$, $R^2 = 0.96$; Fig. 3). Parameter values estimated by the regression were: $a = 0.726$ (± 0.031 SE), $b = 0.0021$ (± 0.0004 SE) and $c = 0.01$ (± 0.001 SE). These values correspond to an asymptote at $z = 0.21$.

Using the randomization model (see [Materials and methods](#)) for the volume of the reef, little agreement was found between the observed data and the SPAR expected from random placement. Only 11 out of 39 reefs were within the 95% confidence intervals of the model. Furthermore, since residuals were negatively correlated with reef volume (Spearman's rank correlation, $r = -0.66$, $P < 0.001$), richness was underestimated by random placement on reefs of small volume but overestimated on reefs of large volume, indicating a biased fit to the empirical data. Moreover, two out of three parameters of the polynomial regression were outside the 95% confidence intervals obtained from the random placement simulation.

However, the second randomization model, where the probability to reach a patch reef was proportional to its area, fitted the empirical data well (Fig. 2b). Species richness in 30 out of 39 reefs was within the 95% confidence intervals of the simulations (Fig. 2b). Residuals were not correlated with patch size (Spearman's rank correlation, $r = -0.24$, $P = 0.14$), implying that there was no consistent size bias in the random placement estimate. Furthermore, all three parameters of the

polynomial regression were within the model's confidence intervals.

Multiple linear regressions were used to estimate the contribution of habitat diversity to species richness (Table 3). Habitat variables explained 58% of the variation in species richness among reefs (Table 3, top). This value is similar to the values obtained by Chittaro (2002) using similar methods on patch reefs (54% of variation explained by habitat variables). Significant habitat variables included topographic complexity, PC1 and PC3 (see Table 2 for the description of the principle components). However, this analysis did not explicitly take into account the effect of area; therefore, estimated species richness was not standardized among different sized reefs. Even after including all significant habitat variables, the model fit was greatly improved by the addition of the expected species richness from the random placement model as an independent variable (Table 3, middle).

To standardize species richness among different-sized reefs, or in other words to account for the statistical contribution of random placement, the expected species richness from the random placement model was used as another independent variable. The new model explained 91% of the variation in species richness among reefs (Table 3, bottom). Of this 82% can be attributed to the effect of random placement and 9% to all other habitat variables examined combined. Habitat variables that were found to significantly affect species richness included topographic complexity, PC3, PC4 and PC1.

Finally, fish assemblages were examined to see whether species poor reefs were nested subsets of assemblages on species rich reefs. Initially, the reefs seemed to be highly nested (Matrix "temperature" = 12.89, $P < 0.001$). However, simulations showed that this was not different than the values expected from random placement ($P_{\text{one tail}} = 0.29$).

Discussion

The steep slope of the log-log SPAR found in this study (i.e., $z = 0.55$) is usually associated with insular habitats with limited dispersal (Rosenzweig 1995). This slope is similar to those found by other studies examining SPARs for coral reef fish in the Caribbean (Chittaro 2002) and the Great Barrier Reef (Ault and Johnson 1998a). Direct comparisons of the intercepts are problematic as they are scale dependent (Rosenzweig 1995) and sampling was inevitably dissimilar, due, for example, to different sampling intensity.

Several lines of evidence point to the importance of random placement in producing the observed SPAR. The decreasing slope of the log-log-transformed SPAR as a function of cumulative patch area (Fig. 3) suggests that random placement cannot be dismissed as a determinant of the empirical SPAR. Moreover, the asymptotic value of z , which corresponds to the slope of the SPAR in this system after excluding the effect of random placement, was estimated to be around 0.21. This value is well in agreement with the z values in other, mostly terrestrial, systems (Rosenzweig 1995). Consequently, the steep slopes of the log-log-transformed SPARs for fishes on coral reefs do not seem to represent an intrinsic, biologically based, unique character of reef fishes. This notion is reinforced by the good fit between empirical data and the random placement randomization model, with probabilities proportional to area. Hence, in this system the steep SPAR can be parsimoniously explained by random placement, where larger patch reefs form larger targets and consequently accumulate more species.

The exact shape of the random placement curve is dependent on the underlying species-abundance distribution but is seldom truly linear on a log-log space

Table 3 Summary of multiple regressions relating species richness (\log_{10} transformed) to habitat variables

Model			R^2	df model	df error	F ratio	P
a. Habitat variables alone			0.58	5	33	9.1	< 0.001
Independent variable	Coefficient	F ratio	P				
Topographic complexity	1.13	14.3	< 0.001				
PC3	0.74	12.2	< 0.001				
PC1	-0.36	4.7	< 0.05				
Distance from fringing reef	-0.11	2.4	NS				
PC2	-0.24	1.8	NS				
Above habitat variables with the expected richness from the random placement model			0.90	6	32	46.9	< 0.001
b. All variables			0.91	5	33	69.9	< 0.001
Independent variable	Coefficient	F ratio	P				
Expected from random placement	0.77	143.4	< 0.001				
PC3	0.42	21	< 0.001				
PC4	-0.26	6.1	< 0.05				
PC1	-0.23	8.5	< 0.01				
Topographic complexity	0.33	5	< 0.05				

Partial regression coefficients of each of the variables selected are shown below the summary statistics for the full model. Variables are listed in the order they were entered into the regression

(McGuinness 1984; Gotelli and Graves 1996). Therefore, small spatial scales present a level of discrepancy between the SPAR and the linear log–log relationship (Rosenzweig 1995). When jointly examining small and large scales (where small and large are terms relevant only to the system under consideration) a SPAR may not perfectly fit a log–log linear equation (Fig. 3 in Chittaro 2002; Fig. 2). Another expression of this discrepancy is that small spatial scales may present steeper slopes, i.e., higher z values, than larger scales when using a linear log–log relationship (Preston 1962a, b; Chittaro 2002; Fig. 3). However, the random-placement curve fitted empirical data from reefs across the entire size range available well (Fig. 2b).

These results show that random placement is an important determinant of the SPAR slope in this system. However, alternative mechanisms must also be considered. The highly complex structure of coral reef has been proposed as a possible cause for the steep SPAR on reefs (Chittaro 2002). On patch reefs, fish abundance might be in direct proportion to patch volume causing the SPAR to be steeper than in intrinsically two-dimensional systems. The lack of fit between the simulation model and the observed data when random placement was proportional to volume, as well as the high fit when proportional to area, does not seem to favor this hypothesis. Nevertheless, this model may provide a better fit for cryptic species, which were excluded, as well as for other more strongly reef-associated taxa.

Nestedness of fish assemblages according to area is a prediction shared by the habitat availability and differential colonization/extinction hypotheses. If habitat availability limits the number of species on small reefs, it would be expected that small reefs would be nested within large reefs that contain diverse habitats. Similarly, if small reefs contain few species due to differential colonization/extinction, large reefs should contain the species found in small patches as well as a new set of species that only appear on patches above a certain size. While nestedness is a common feature of most natural communities (Wright et al. 1998), this might not always be true for coral reef fishes (Acosta and Robertson 2002; but see McLain and Pratt 1999 examining fringing reefs at a larger spatial scale). Although nestedness was found in fish assemblages in this study, assemblages were not nested beyond that expected from random placement. This seems to refute both habitat heterogeneity and minimum area requirements as the main explanations for the observed SPAR.

To further quantify the effect of habitat diversity on the SPAR the contribution of habitat variables to species richness was examined through regression analysis. Without taking area or random placement into account, habitat variables explained 58% of the total variability in species richness (Table 3, top). However, accounting for random placement significantly improved the model's fit, with the new model explaining 91% of the total variability in species richness (Table 3, bottom). Of this, 82% can be attributed

directly to random placement, while 9% is explained by habitat variables. Hence, while habitat characteristics do play an important role in determining the number of species on patch reefs, area per se, through the mechanism of random placement, is the major determinant of the observed SPAR.

So why are steep SPARs for fishes on coral reefs found? A commonality of studies examining SPARs on coral patch reefs is the relatively small size of the reefs examined, ranging from a minimum of 0.64 m² to a maximum of 200 m² (Chittaro 2002). Scale dependence of z was already realized by Preston (1962a, b). However, with the increased use of SPARs, this scale dependence was often neglected. Recent theoretical (Williams 1995; He and Legendre 1996) and empirical (Condit et al. 1996; Crawley and Hurrall 2001) evidence re-emphasize this scale dependence. At small spatial scales, patches do not contain all species in a given community, but merely a sub-sample of it. Consequently, at small spatial scales, random placement may provide the most appropriate explanation for the SPAR. However, at larger spatial scales, where the number of individuals persisting in a patch is much larger, other mechanisms are more likely to create the SPAR and the importance of random placement is expected to diminish (Turner and Tjørve 2005).

This view is consistent with previous studies that found fish assemblages on small patch reefs to be highly variable, both spatially and temporally, with little response to habitat variables (Sale and Douglas 1984; Sale et al. 1994; Ault and Johnson 1998b; Chittaro and Sale 2003, cf. Caley and St John 1996; Syms and Jones 2000). Nevertheless, this does not mean habitat is unimportant to reef fish. First, habitat variables do account for a significant amount of the variation in species richness among patches (9% in this study). Second, random placement as the major determinant of the SPAR does not imply fish are distributed completely at random. It only means that the SPAR is influenced by random processes that can override the effect of deterministic processes that may nevertheless also be significant. Third, habitat may be relatively evenly distributed among patches. Under this scenario, a direct effect of habitat on species richness will not be observed, not because an effect is absent but because it has a similar effect across all patches. This is more likely when sampling takes place within a relatively small or homogeneous location. In this study, there was a considerable heterogeneity in the physical appearance of the reefs with living cover ranging from 17 to 80%. Therefore, it seems unlikely that habitat was equally distributed among patches in this case. Nevertheless, studies that compared species diversity across several reef zones or have sampled at larger spatial scales usually found fish assemblages to be relatively predictable (e.g., Ogden and Ebersole 1981; Khalaf and Kochzius 2002; Bouchon-Navaro et al. 2005). Therefore, at small spatial scales, even if fishes respond to habitat gradients, the major small-scale determinant of species richness might be

random processes that dominate the ecological signal. This emphasizes the importance of explicit reference to scale and heterogeneity when interpreting ecological results.

All analyses in this manuscript were based on presence–absence data alone. The additional use of accurate abundance data could have refined the conclusions in several important ways. The basic premise of the random placement hypothesis is that larger reefs form larger targets and therefore accumulate larger numbers of individuals. This can be directly tested with abundance data. Moreover, abundance data would have allowed us to examine the response of individual species or the community (in a univariate or a multivariate approach, respectively) to habitat variables. A strong and positive response of most species to reef size may provide support to the present conclusion. In addition, using abundance data more sophisticated and elaborate null models may be used. Nevertheless, it is important to realize that models that assume random distribution of individuals among reefs may not provide an appropriate model for fish assemblages. This is because these models assume no intraspecific aggregation, i.e., all individuals are distributed independently. Independent distribution of individual is probably not appropriate for reef fish, where many species form intraspecific aggregations. Indeed, a poor fit with the data was found when using models that applied complete randomization of individuals (Sale and Steel 1986; Ault and Johnson 1998a).

It is shown here that steep SPARs for fish on patch reefs can be generated by random processes over small spatial scales. It remains to be seen whether similar mechanisms can produce steep SPARs on continuous reefs. Random placement as the major determinant of the SPAR implies scale dependence, since the resulting curve is almost always curvilinear on a log–log scale. Therefore, it is stressed that ecologists should not use small-scale SPARs to estimate the effect of fragmentation on species diversity without explicit reference to random placement. Testing empirical data using the method outline here, examining the change in z as area is increased by randomly summing up the observed patches, is recommended. Only when random placement does not contribute to the SPAR, should the empirical slope be used for biological inference and conservation.

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Appendix

Table 4

Table 4 All 121 reef-associated fish species sited on the patch reefs and used for the analysis

Acanthuridae
<i>Acanthurus nigrofuscus</i> (Forsskål, 1775)
<i>Zebrasoma veliferum</i> (Bloch, 1795)
<i>Zebrasoma xanthurum</i> (Blyth, 1852)
Apogonidae
<i>Apogon cyanosoma</i> (Bleeker, 1853)
<i>Apogon exostigma</i> (Jordan & Starks, 1906)
<i>Apogon fleurieu</i> (Lacepède, 1802)
<i>Apogon nigrofasciatus</i> (Lachner, 1953)
<i>Apogon</i> sp.
<i>Archamia fucata</i> (Cantor, 1849)
<i>Cheilodipterus macrodon</i> (Lacepède, 1802)
<i>Cheilodipterus novemstriatus</i> (Rüppell, 1838)
<i>Cheilodipterus quinquelineatus</i> (Cuvier, 1828)
Balistidae
<i>Balistapus undulatus</i> (Park, 1797)
<i>Rhinecanthus assasi</i> (Forsskål, 1775)
<i>Sufflamen albicaudatus</i> (Rüppell, 1829)
Blenniidae
<i>Atrosalaria fuscus</i> (Rüppell, 1838)
<i>Ecsenius aroni</i> (Springer, 1971)
<i>Ecsenius frontalis</i> (Valenciennes, 1836)
<i>Ecsenius gravieri</i> (Pellegrin, 1906)
<i>Ecsenius nalolo</i> (Smith, 1959)
<i>Meiacanthus nigrolineatus</i> (Smith-Vaniz, 1969)
<i>Plagiotremus rhinorhynchus</i> (Bleeker, 1852)
<i>Plagiotremus tapeinosoma</i> (Bleeker, 1857)
<i>Plagiotremus townsendi</i> (Regan, 1905)
Casionidae
<i>Caesio</i> sp.
Chaetodontidae
<i>Chaetodon auriga</i> (Forsskål, 1775)
<i>Chaetodon austriacus</i> (Rüppell, 1836)
<i>Chaetodon fasciatus</i> (Forsskål, 1775)
<i>Chaetodon paucifasciatus</i> (Ahl, 1923)
<i>Chaetodon trifascialis</i> (Quoy & Gaimard, 1825)
<i>Heniochus intermedius</i> (Steindachner, 1893)
Cirrhitidae
<i>Cirrhitichthys oxycephalus</i> (Bleeker, 1855)
<i>Paracirrhites forsteri</i> (Schneider, 1801)
Diodontidae
<i>Cylichthys spilostylus</i> (Leis & Randall, 1982)
<i>Diodon hystrix</i> (Linnaeus, 1758)
Gobiidae
<i>Gobiodon citrinus</i> (Rüppell, 1838)
<i>Lotilia graciliosa</i> (Klausewitz, 1960)
<i>Pleurosicya micheli</i> (Fourmanoir, 1971)
<i>Trimma avidori</i> (Goren, 1978)
Holocentridae
<i>Myripristis murdjan</i> (Forsskål, 1775)
<i>Sargocentron diadema</i> (Lacepède, 1802)
Labridae
<i>Anampses lineatus</i> (Randall, 1972)
<i>Anampses meleagridesb</i> (Valenciennes, 1840)
<i>Anampses twistii</i> (Bleeker, 1856)
<i>Bodianus anthioides</i> (Bennett, 1832)
<i>Bodianus axillaris</i> (Bennett, 1832)
<i>Bodianus diana</i> (Lacepède, 1801)
<i>Cheilinus lunulatus</i> (Forsskål, 1775)
<i>Cheilinus trilobatus</i> (Lacepède, 1801)
<i>Cheilinus undulatus</i> (Rüppell, 1835)
<i>Cirrhilabrus rubriventralis</i> (Springer & Randall, 1974)
<i>Coris aygula</i> (Lacepède, 1801)
<i>Coris caudimacula</i> (Quoy & Gaimard, 1834)
<i>Gomphosus caeruleus</i> (Lacepède, 1801)
<i>Hemigymnus fasciatus</i> (Bloch, 1792)
<i>Labroides dimidiatus</i> (Valenciennes, 1839)
<i>Larabicus quadrilineatus</i> (Rüppell, 1835)

Table 4 (Contd.)

Macropharyngodon bipartitus (Smith, 1957)
Paracheilinus octotaenia (Fourmanoir, 1955)
Stethojulis albavittata (Bonnaterre, 1788)
Stethojulis interrupta (Bleeker, 1851)
Thalassoma lunare (Linnaeus, 1758)
Thalassoma rueppelli (Klunzinger, 1871)
Thalassoma sp.
 Monacanthidae
Cantherhines dumerilii (Hollard, 1854)
Pervagor randalli (Hutchins, 1986)
 Mullidae
Parupeneus cyclostomus (Lacepède, 1801)
Parupeneus forsskali (Fourmanoir & Guézé, 1976)
Parupeneus macronema (Lacepède, 1801)
 Muraenidae
Gymnothorax johnsoni (Smith, 1962)
Gymnothorax griseus (Lacepède, 1803)
Gymnothorax sp.
 Nemipteridae
Scopelogadus ghanam (Forsskål, 1775)
 Ostraciidae
Ostracion cubicus (Linnaeus, 1758)
 Pempheridae
Parapriacanthus ransonneti (Steindachner, 1870)
Pempheris vanicolensis (Cuvier, 1831)
 Pinguipedidae
Parapercis hexophthalma (Cuvier, 1829)
 Pomacanthidae
Apolemichthys xanthurus (Fraser-Brunner, 1950)
Pomacanthus imperator (Bloch, 1787)
Pomacanthus maculosus (Forsskål, 1775)
 Pomacentridae
Abudefduf sexfasciatus (Linnaeus, 1758)
Abudefduf vaigiensis (Quoy & Gaimard, 1825)
Amblyglyphidodon leucogaster (Bleeker, 1847)
Amphiprion bicinctus (Rüppell, 1830)
Chromis dimidiata (Klunzinger, 1871)
Chromis flavaxilla (Randall, 1994)
Chromis viridis (Cuvier, 1830)
Dascyllus aruanus (Linnaeus, 1758)
Dascyllus marginatus (Rüppell, 1829)
Dascyllus trimaculatus (Rüppell, 1829)
Neopomacentrus miryae (Dor & Allen, 1977)
Plectroglyphidodon laeymatus (Quoy & Gaimard, 1825)
Pomacentrus sulfureus (Klunzinger, 1871)
Pomacentrus trichourus (Günther, 1867)
 Pseudochromidae
Haliophis guttatus (Forsskål, 1775)
Pseudochromis fridmani (Klausewitz, 1968)
Pseudochromis springeri (Lubbock, 1975)
 Scaridae
Chlorurus gibbus (Rüppell, 1829)
Scarus ghobban (Forsskål, 1775)
Scarus niger (Forsskål, 1775)
Scarus sp.
 Scorpaenidae
Pterois miles (Bennett, 1828)
Pterois radiata (Cuvier, 1829)
 Serranidae
Cephalopholis argus (Bloch & Schneider, 1801)
Cephalopholis miniata (Forsskål, 1775)
Epinephelus fasciatus (Forsskål, 1775)
Epinephelus tauvina (Forsskål, 1775)
Pseudanthias squamipinnis (Peters, 1855)
Pseudanthias taeniatus (Klunzinger, 1884)
Variola louti (Forsskål, 1775)
 Siganidae
Siganus luridus (Rüppell, 1829)
 Syngnathidae

Table 4 (Contd.)

Corythoichthys flavofasciatus (Rüppell, 1838)
Corythoichthys schultzi (Herald, 1953)
Doryrhamphus dactylophorus (Bleeker, 1853)
Trachyrhamphus bicoarctatus (Bleeker, 1857)
 Synodontidae
Saurida gracilis (Quoy & Gaimard, 1824)
 Tripterygiidae
Enneapterygius pusillus (Rüppell, 1835)
 Others
 Unidentified species 1
 Unidentified species 2
 Unidentified species 3
 Unidentified species 4

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