ORIGINAL ARTICLE

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The effect of patch reef size on fish species richness in a shallow coral reef shore zone where territorial herbivores are abundant

Abstract Small patch reefs can harbor many reef fishes because most fishes have a drifting larval phase to randomly disperse over patchy habitats. We examined the species–area relationship (SAR) of damselfish (Pomacentridae) assemblages over 84 small patch reefs (0.05–45.4 m^2) using an enlarged section of a high-resolution color aerial photograph as a field map (1/2500) in a shallow coral reef shore zone (<2 m deep, 3.6 ha, Shiraho Reef, Ishigaki Island, Japan). This study confirmed that the logarithmic function is better than other functions (including the power function) to explain the SAR in this scale. Actual species richness (24) over the entire study site was much higher than the species richness (15.4) extrapolated from the regression line in semi-log space. Better estimates were obtained using random placement models and computer simulations. These results suggest that several small patch reefs are likely to have higher species richness than a single large reef of equivalent area at the study site. The total number of individuals of the four most abundant territorial herbivores increased almost linearly with patch reef area, but that of other species roughly increased with the square root of the area. While no territorial species were found in the smallest reefs, the large territorial herbivore, *Hemiglyphidodon plagiometopon*, was abundant and had negative effects on species richness in large reefs. Although the well-known single-large-or-several-small (SLOSS) debate has largely been settled, this dichotomy

can be important in places where territorial herbivores do not occupy the smallest reefs.

Introduction

Patchy habitats often enhance species coexistence and population abundance of species (Tilman and Kareiva 1997; Turner et al. 2001). A transition area between terrestrial and marine environments often produces several types of patchy habitat, such as rocky reefs and seagrass beds in the shallow subtidal shore zone (Irlandi et al. 1995; Pittman et al. 2004; Grober-Dunsmore et al. 2007). Accordingly, nearshore habitats are often characterized by high species diversity with complex seascapes (Robbins and Bell 1994; Mumby and Harborne 2006). Patchy habitats have various sizes and shapes, and their total area is a crucial determinant of total species richness (Rosenzweig 1995, 2004).

The species–area relationship (SAR) is one of the most important tools for conservation biology and landscape ecology (Rosenzweig 1995, 2004; Tjørve 2003; Dengler 2009). While there are several variants of SAR that involve different patterns of sampling, which has often been a subject of intense debate (Scheiner 2003, 2004), the SAR data of the present study can be analyzed with confidence. This is because the present SAR data on species richness are classified into "non-nested" and "isolates", which are not a subject of debate (Dengler 2009). Habitat patches, such as patch reefs, are non-nested and isolates.

A single large habitat patch is often better in terms of habitability than several small fragmented habitats of equivalent area, because it usually has a greater diversity of microhabitats. Moreover, larger habitats can also harbor larger populations for which the probability of species extinction is lower (Connor and McCoy 1979;

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Pullin 2002). However, in places where the microhabitat diversity does not differ greatly between patches and where the mobility of target species is not low, small patches are essentially equivalent to a single large habitat of equivalent area with regard to species richness, as suggested by random placement models (Lomolino 1994; Rosenzweig 1995, 2004). Thus, the well-known SLOSS controversy (i.e., a single-large or several-small debate on terrestrial reserve design; see Primack 2004) has largely been settled: the total area of habitat is important (Lomolino 1994; Rosenzweig 2004). On very fine scales, however, small patchy habitats often enhance species coexistence because of edge effects (Simberloff and Gotelli 1984; Primack 2004) and metapopulation dynamics (Tilman and Kareiva 1997; Turner et al. 2001; Hattori 2002). Rosenzweig (2004) implies that the SLOSS dichotomy might be important in very fine scales providing information on the underlying biological processes that influence the SAR. For example, if species richness observed at an entire study site exceeds the expected species richness calculated from the regression line or curve with the total area of the patchy habitats, small patches could be better with regard to species richness than a single large habitat of equivalent total area (Rosenzweig 2004). This suggests that edge effects and/or metapopulation dynamics are important in the study site. In contrast, if the species richness is lower, a single large habitat would be better (Rosenzweig 2004). This suggests that the diversity of microhabitat is greater in larger habitats. Methodologies including extrapolation in a relatively narrow range have been developed for analysis of SARs (Turner et al. 2000; Rosenzweig 2004).

Coral reefs that have developed on tropical or subtropical shore zones are among the richest animal communities in nature (Lowe-McConnell 1987; Sale 1991). As most marine animals have a drifting larval phase, the presence of a number of patchy habitats allows larvae to disperse over and connect up metapopulations and metacommunities (Hughes et al. 2005). Thus, small patch reefs may play an important role in sustaining overall meta-populations and -communities. SARs have often been studied on coral reefs (e.g., McGuinness 1984; McClanahan 1994; Ault and Johnson 1998; Tittensor et al. 2007), but rarely on patch reefs (Sale and Steel 1986; Chittaro 2002; Belmaker et al. 2007). It can be difficult for field workers to measure the total area of patches, since ordinary line transects or quadrats cannot cover the areas of patches of various sizes and shapes. It is also difficult for high-tech remote sensors, such as those in satellites and aircraft, to quantify the species richness of small fishes and invertebrates. Several authors who managed to examine SARs for coral reef fishes stressed that in places where there are no marked differences in habitat heterogeneity between patches, several small patches do not differ in species richness from a continuous large reef of equivalent area, which can be attributed to random recruitment systems (Sale and Steel 1986; McClanahan 1994;

Chittaro 2002; Belmaker et al. 2007). However, it should be noted that these studies were not conducted in very shallow shore zones, where territorial herbivores, such as *Stegastes nigricans*, are predominant in a large portion of the reef substratum. Ceccarelli et al. (2001) suggested that territorial herbivores have large effects on benthic community structures including reef fishes. Spatial distribution patterns of species may be uneven among habitat patches (He and Legendre 2002), because territorial herbivores can exclude some reef fishes from their territories (Ceccarelli 2007). More empirical studies on SARs are needed in marine environments (Neigel 2003), and more convenient methods are needed for studies on SARs in these habitats.

Hattori and Kobayashi (2007, 2009) developed a simple technique to incorporate the fine-scale seascape composition in very fine scales, including areas of habitat patches and habitat use by marine animals in a shallow coral reef shore zone. In their study, an enlarged section of a high-resolution color aerial photograph (less than 0.1 m) was used to produce a seascape map (equivalent to 1/2500 scale or more). Each individual animal was located directly in the field map and image-analysis software was used to quantify the surrounding abundance of individual habitat patches. We applied their methodology to collect data on SARs on a fine scale at a nearshore habitat and analyzed the results using conventional methods including computer simulations.

The present study was performed to examine SARs on a very fine scale for assessment of quality, in terms of species richness, of small patch reefs at a shallow coral reef shore zone where territorial herbivores are abundant, and to determine whether the SLOSS dichotomy influences the total species richness on this scale. Damselfishes (Pomacentridae) were selected as the target taxon because they are abundant, basically resident and conspicuous, and so observation bias is expected to be very low. They also show a variety of feeding habits, including territorial defense for attached algae (Allen 1991). Null hypotheses were tested as follows: (1) any regression curves or lines including the power function and the logarithmic function on SAR cannot be used to predict species richness in a patch reef; (2) the edge length of the patch reef cannot be used to predict species richness in a patch reef; (3) a single large reef has equivalent species richness to several small reefs of equal area; (4) the SAR cannot be explained by a random placement model; (5) the number of individuals of particular species, such as the territorial species *Stegastes nigricans*, is irrelevant to species richness in a patch reef. As coral cover often makes a substantial contribution to species richness (Bell and Galzin 1984; Sale and Steel 1986; Chittaro 2002; Belmaker et al. 2007), another null hypothesis was also tested: (6) coral cover does not contribute to SARs. These hypotheses do not exclude each other (Turner and Tjørve 2005). To test the hypotheses, we counted the number of individuals and species in patch reefs and measured the area of patch

reefs, as well as that of coral cover. We applied computer simulations (Simberloff and Gotelli 1984) to test hypotheses 3 and 4.

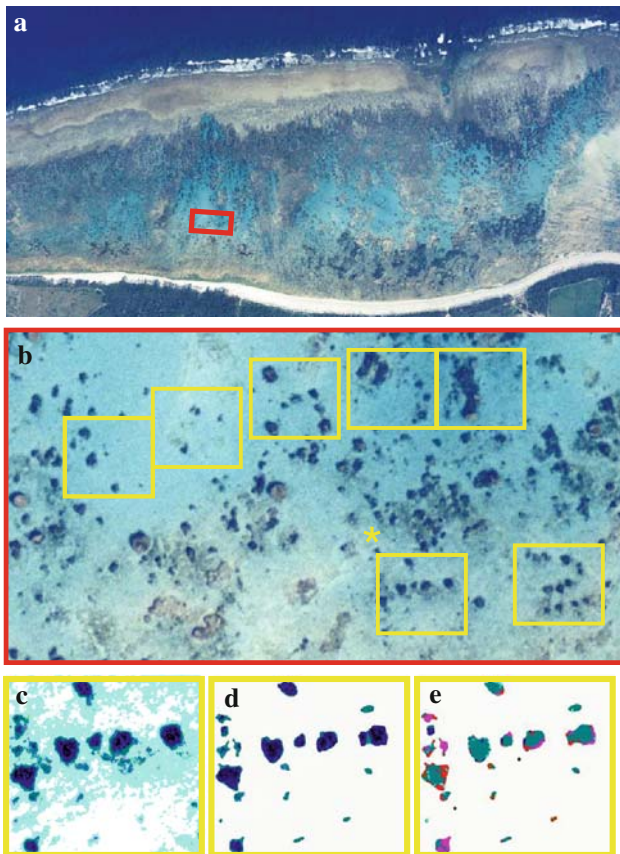## Materials and methods

Study site and observational map

The field study was conducted between June and September 2007 at Shiraho Reef, Ishigaki Island (24°22′18.22N, 124°15′13.82E), Okinawa, Japan (Kobayashi and Hattori 2006; Hattori and Kobayashi 2007, 2009; Tamura et al. 2007). The study site was located in the shallow sandy shore zone (1.5–2 m in

Fig. 1 a Location of the study site (*red square*, 129.9 × 68.2 m²) of the back reef (0–3 m deep) of Shiraho Reef, Ishigaki Island, Okinawa, Japan (original color aerial photograph: OKC-94-13, 1/10000, 95 Ishigaki C15-34, Geographical Survey Institute, Ministry of Land, Infrastructure and Transport, Japan). **b** The magnification of the study site and the seven observation sites (*yellow squares*). The *asterisk* indicates an observation site for **c**–**e**. **c** Magnification of an observation site after applying the posterization function with image-analysis software. **d** The modification of the observation site after underwater measurements were conducted. **e** The completed map of the observation site after coral cover was sketched on patch reefs. Different types of coral are indicated by *different colors*: *brown*, massive coral; *pink*, branching coral; *red*, pillar coral; *light green*, digitate coral; *indigo*, encrusting coral; and *green*, no coral. *Yellow squares* are equivalent to 20.94 m width × 19.12 m height

depth) of the back reef (Fig. 1a) where there were numerous small patch reefs of various sizes. In this study, patch reefs were defined as small natural reefs that were at least 0.25 m wide and 0.35 m tall, with a live and/or dead coral skeleton: e.g., coral patches, coral bommies, and micro-atolls. To make field maps of the patch reefs, we used a large aerial photograph (92 × 92 cm²), which was enlarged from the original negative of the aerial photograph of Shiraho Reef (23 × 23 cm², OKC-94-13, 1/10000, 95 Ishigaki C15-34, taken in 1995 by the Geographical Survey Institute, Ministry of Land, Infrastructure and Transport, Japan, Fig. 1b, 129.9 × 68.2 m², maximum depth = 2 m at spring low tide). Part of the photograph was converted to a digitized image (Windows BMP format, 1832 × 961 pixels) with a scanner at a resolution of 720 dpi. The seven observation sites were selected in the study site so as not to transect the edges of patch reefs (Fig. 1b, each area = 587 × 536 pixels, 20.94 × 19.12 m).

As the boundaries of small patch reefs were often unclear, even in the enlarged photograph (see Fig. 1b), we used the posterization function of image-analysis software (Adobe Photoshop CS) and simplified the photographic map (Fig. 1c, see Hattori and Kobayashi 2009). One snorkeler examined each patch reef and corrected the configuration of the patch reefs on the printed maps, measuring the diameters of reefs and distances between them in situ: several reefs had been moved (about 1 m) or broken probably as a result of major typhoons. Patch reef maps were redrawn on a computer using image-analysis software (Fig. 1d). There were 84 patch reefs in the seven observation sites (Fig. 1b). Coral cover was also sketched on each patch reef identifying types of coral (digitate, massive, branching, pillar, or encrusting coral) using the new maps (Fig. 1e). Distances between several benthic landmarks were measured in the field: a distance of 28.032 pixels on the digitized maps was equivalent to 1 m, and one pixel was much smaller than the smallest patch reef inhabited by damselfishes.

Data collection and analyses

Two snorkelers recorded the number of individuals and their species names in each patch reef, identifying the size of individuals (smaller than 2 cm in total length, or large), over a week between late June and early July: the first and second observers recorded data for all patch reefs twice and four times, respectively. Small individuals do not mean early settlers. To avoid stranding and to easily observe sheltered fishes, we collected data when the sea level was around the mean sea level of Tokyo Bay between 9.00 and 16.00 hours. One hour was spent completing a census, with the exception of one site where there were only three small reefs (see Fig. 1b). Food habits and territoriality of each fish species observed were classified on the basis of published data (Masuda et al. 1984; Allen 1991). Here, the term "algal feeders"

Table 1 Average total number of individuals ($\pm$ SD) of each species in a census ($n = 6$), and correlation coefficient between the number of individuals and the area of patch reef

Scientific name	Total number of individuals	r-value	P	Coefficient of variation (%)	Food habit	Territoriality
Chrysiptera cyanea	715.7 $\pm$ 75.3	0.643	< 0.001	10.5	P	
Dascyllus aruanus	545.2 $\pm$ 36.4	0.109	NS	6.7	P	
Chromis viridis	321.3 $\pm$ 111.5	0.023	NS	34.7	P	
Pomacentrus adelus	264.2 $\pm$ 40.5	0.728	< 0.001	15.3	A	
Pomacentrus moluccensis	151.2 $\pm$ 11.1	0.616	< 0.001	7.4	A	
Amblyglyphidodon curacao	149.7 $\pm$ 34.9	0.347	0.001	23.3	P	
Stegastes nigricans	133.8 $\pm$ 16.9	0.666	< 0.001	12.6	AA	x
Stegastes lividus	70.8 $\pm$ 9.4	0.957	< 0.001	13.3	AA	x
Cheiloprion labiatus	40.8 $\pm$ 7.0	0.407	< 0.001	17.2	C	
Amphiprion frenatus	32.2 $\pm$ 2.0	0.599	< 0.001	6.3	A	x
Abudefduf sexfasciatus	27.0 $\pm$ 12.0	0.643	< 0.001	44.3	P	
Pomacentrus amboinensis	19.2 $\pm$ 4.0	0.008	NS	20.7	A	
Dischistodus prosopotaenia	19.2 $\pm$ 2.0	0.040	NS	10.3	AA	
Hemiglyphidodon plagiometopon	10.0 $\pm$ 2.4	0.922	< 0.001	24.5	AA	x
Pomacentrus chrysurus	9.7 $\pm$ 1.9	−0.048	NS	20.1	AA	x
Amblyglyphidodon leucogaster	6.7 $\pm$ 5.4	0.066	NS	80.9	P	
Neoglyphidodon melas	3.3 $\pm$ 1.2	0.180	NS	36.3	A	
Amphiprion ocellaris	3.0 $\pm$ 0.6	0.861	< 0.001	21.1	A	
Neoglyphidodon nigroris	2.8 $\pm$ 0.8	0.405	< 0.001	26.6	A	
Chrysiptera rex	2.3 $\pm$ 0.8	0.783	< 0.001	35.0	A	
Chrysiptera biocellata	1.0 $\pm$ 0.0	−0.034	NS	0	A	
Abudefduf vaigiensis	0.8 $\pm$ 0.4	−0.010	NS	49.0	P	
Pomacentrus bankanensis	0.8 $\pm$ 0.4	−0.015	NS	49.0	A	
Plectroglyphidodon dickii	0.5 $\pm$ 0.5	0.066	NS	109.5	A	
24 species	2531.2 $\pm$ 260.3	0.718	< 0.001	10.3		

NS not significant. Coefficient of variation, food habit, and territoriality are also shown. *P* mainly feed on plankton; *AA* feed on algae; *A* feed on algae and others; *C* feed on coral polyps

includes omnivorous species that often feed on algae (see Table 1), such as several anemonefishes (Allen 1975).

The area of patch reef and the area of coral cover were calculated on a computer using the public domain software Image J 1.33 (see Rasband, W.S. Image J, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/, 1997–2007). The edge length of the patch reef was also measured.

Several possible mathematical models were applied to our SAR data in arithmetic space to select a best-fitting model as suggested by Dengler (2009): the power function, the logarithmic function, the Lomolino function, and the cumulative Weibull function were fitted to the data as the isolate-type (see Fig. 2). The non-linear function of R 2.4.1 (R Development Core Team 2006) was used, and the best-fitting model was selected on the basis of the Akaike Information Criteria (AIC). The relationship between species richness in the patch reef and the total number of individuals of all species was also analyzed using extrapolation methods to fit the data into the following equation (Function 5 in Turner et al. 2000; Rosenzweig 2004: $S_{\mathrm{obs}} = a^{(1-N^{(-bN^b)})}$), where a is the asymptote, b is the coefficient of curvature, and N is the number of individuals in the patch reef. The asymptote indicates the estimated true number of species that would appear in the entire study site (Turner et al. 2000; Rosenzweig 2004).

The relationship between the total number of individuals of each species in the patch reef and the area of patch reef was also analyzed to select the best-fitting

models. The relationship between species richness in the patch reef and the number of individuals of each species was also analyzed. Stepwise regression analysis was performed to determine the important species, removing the less valuable species so as to minimize the AIC value (using the "step" function of R 2.4.1). Before this analysis, the regression line between species richness and the number of individuals was examined in each species, and the species of which linear regression was significant ($p < 0.05$) was used for the stepwise analysis. Generalized linear models with Gaussian distributions were applied to the "count" data because of the use of the average values.

Random placement simulation

To estimate the species richness on a local scale under a random placement model, we conducted a computer simulation using R 2.4.1 with abundance data. In the absence of marked differences in habitat heterogeneity between patches and competition at each reef, larger reefs would randomly accumulate large numbers of settling individuals. Accordingly, greater species richness would be observed at larger reefs (Coleman 1981; Simberloff and Gotelli 1984; Belmaker et al. 2007). In the computer simulation, an individual of a species was reshuffled among the 84 patch reefs such that the probability of settling on each patch was proportional to its relative area: an individual of a species is assumed to settle simply

Fig. 2 a Species–area relationship in arithmetic space. *Open circles* indicate average species richness in patch reefs. The several non-linear regression curves with AIC values are also shown. **b** Species–area relationship of the regression line in semi-log space. The *open triangle* with *dotted line* and the *solid triangle* indicate the extrapolated species richness in the virtual reef of an area equal to that of all patch reefs and the actual species richness, respectively. **c** Relationship between the number of individuals of all species and species richness in patch reefs. The best-fit regression curve and the estimated species richness (*horizontal line*) are shown
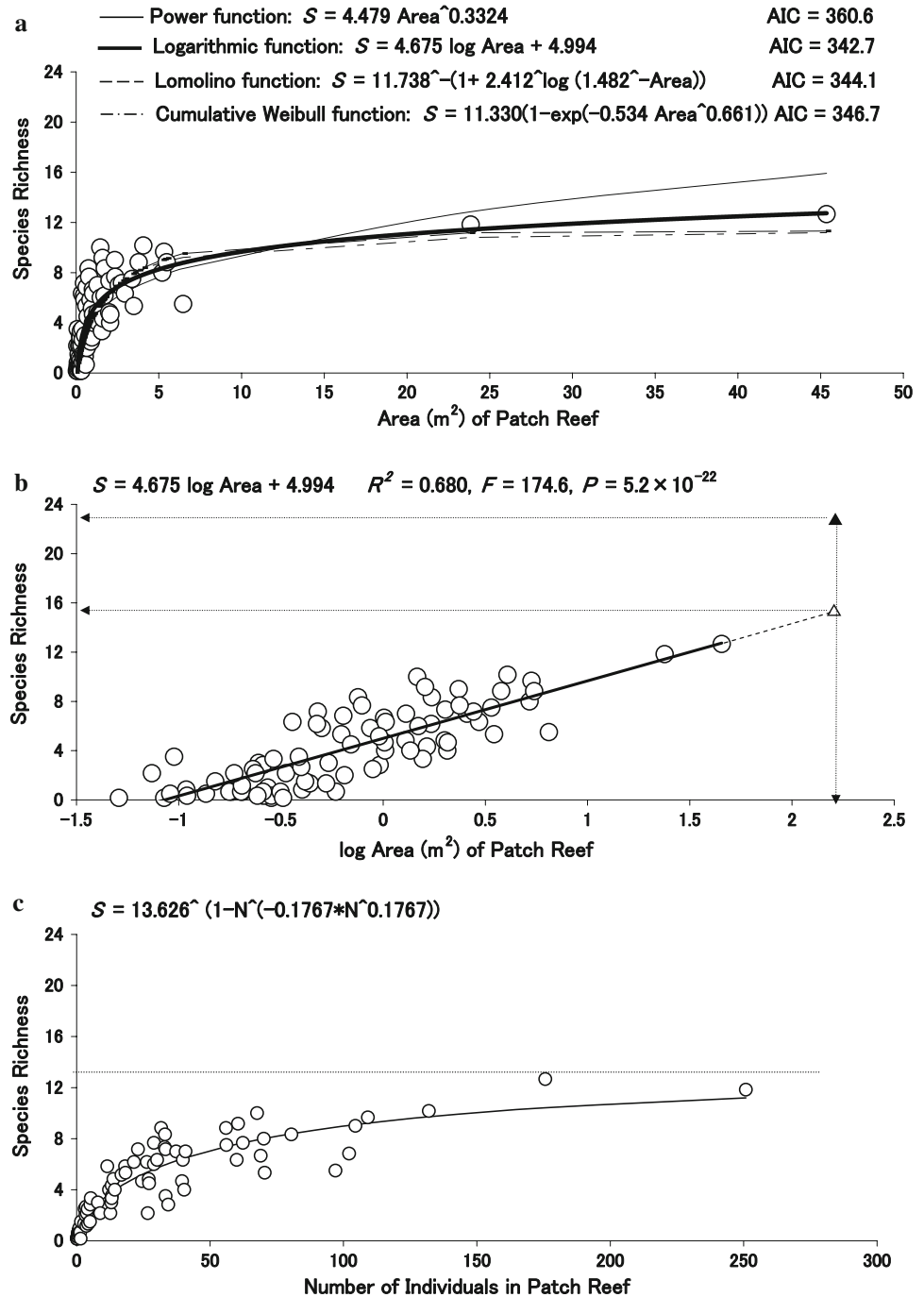
from an external pool without any interactions or competition. We repeated this procedure with the total number of individuals in each species and counted the number of species at each patch reef. This simulation was repeated 10000 times, and the average species richness and its standard deviation were calculated. Results obtained were compared with the observed SAR.

We also used a computer application developed by Turner et al. (2000) to predict species richness by extrapolation on a relatively narrow scale. The total number of individuals of all species at all patch reefs was input into the program, and the above-mentioned equation

(Function 5 in Turner et al. 2000; Rosenzweig 2004) was used. The application randomly combined patch reefs to produce 84 virtual reefs and calculated the average asymptote after this procedure was repeated 10000 times.

Results

Species–area relationship

On average ($n = 6$), a total of 2531.2 individuals (37.2% of them were small individuals), comprising 23.2 species,

were recorded in the 84 patch reefs (0.05–45.4 m^2). Figure 2a shows the SAR in arithmetic space: the logarithmic function was statistically better than the other non-linear functions to explain the SAR (logarithmic: AIC = 342.7; Lomolino: AIC = 344.1; cumulative Weibull: AIC = 346.7; power: AIC = 360.6). The plot of the semi-log SAR was very linear (R^2 = 0.680, F = 174.6, $p < 0.001$), and the slope and intercept of the line were both highly significant (Fig. 2b, slope: F = 174.6, $p < 0.001$; intercept: F = 588.3, $p < 0.001$). The relationship between the species richness of small individuals and log area of patch reef was also linear and significant (S_{obs} = 4.083 + 3.488 log area, R^2 = 0.487, F = 77.8, $p < 0.001$). Overall, 24 species were found in the patch reefs (166.028 m^2). Species richness extrapolated from the total area of patch reefs (15.4 species) using the logarithmic function was much lower than the average total species richness (Fig. 2b), indicating that small patch reefs have higher species richness than the virtual single large reef of equivalent total area. The relationship between species richness and the total number of individuals in the patch reef showed a good fit to the equation (Fig. 2c): $S_{obs} = a^{(1-N^{(-bN^b)})}$. The parameters a (estimated species richness) and b were both highly significant (a = 13.626: t = 5.98, $p < 0.001$; b = 0.177: t = 11.26, $p < 0.001$, AIC = 281.6). The estimated species richness was also much lower than the

actual species richness. There was no statistically significant correlation between edge length of the patch reef and species richness (r = 0.182, t = 1.678, p = 0.097, n = 84).

Random placement simulation

The results of the random placement model (see "Materials and methods") are shown in Fig. 3. The logarithmic function was statistically better than the power function to explain the results (Fig. 3a, logarithmic: AIC = 120.4; power: AIC = 244.5). In small reefs, the logarithmic curve or line calculated from the observed species richness was within 2 SD of the simulation results. However, in large reefs, it was not within 2 SD (Fig. 3). The extrapolated species richness (21.0 species) was close to the average total species richness (Fig. 3b). The computer application produced by Turner et al. (2000) also yielded a very good estimate (23.002 species).

Species composition and species richness

Four common planktivores, *Chrysiptera cyanea*, *Dascyllus aruanus*, *Chromis viridis*, and *Amblyglyphidodon curacao*, were conspicuous and very abundant, but

Fig. 3 a The results of the random placement model simulation (n = 10000) in arithmetic space. *Solid circles* with *vertical lines* indicate average species richness in patch reefs with ±2 SD (standard deviation) shown by the simulation. The two non-linear regression curves with AIC values are shown. The actual species–area relationship (*large open circles*) and the regression curve are also shown. **b** The same results in semi-log space. *Two open squares* with *broken lines* indicate the extrapolated species richness in the virtual reef of an area equal to that of all the patch reefs and the *solid square* indicates the actual species richness
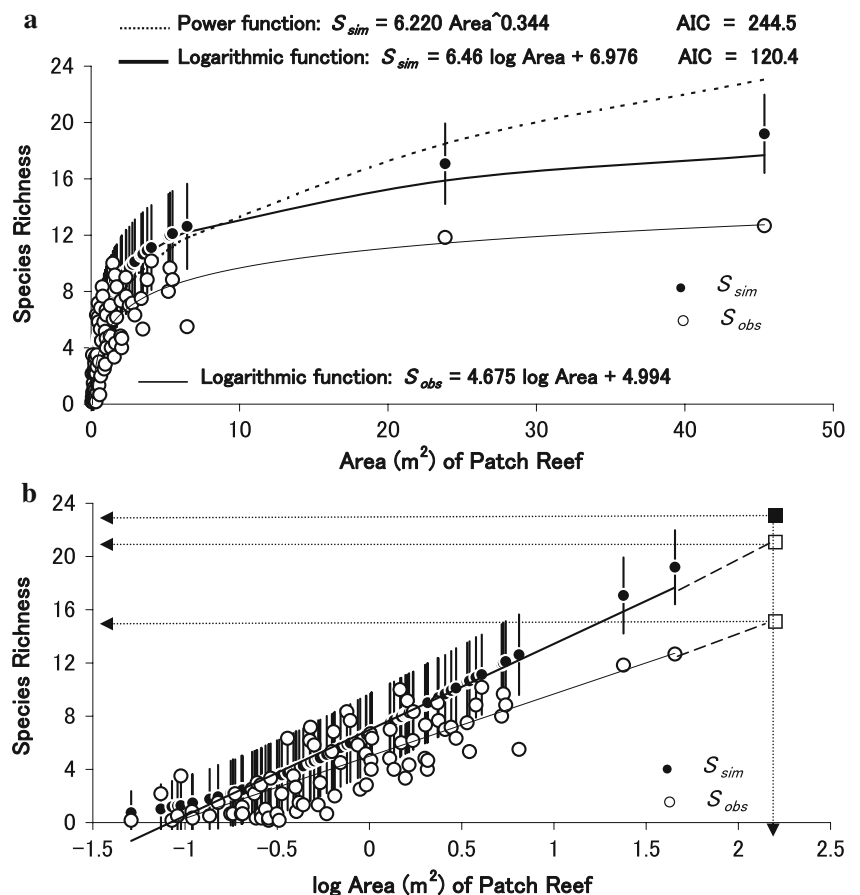
herbivores were also common and abundant (Table 1). In total, seven species (29.2%) were planktivores and 16 (66.7%) were algal feeders: feeding on algae or on algae and others. In the most abundant 14 species, of which more than ten individuals were observed in a survey, eight species (57%) were algal feeders and five (36%) were planktivores. Six of the algal feeders (*Pomacentrus adelus*, *P. moluccensis*, *Stegastes nigricans*, *S. lividus*, *Amphiprion frenatus*, and *Hemiglyphidodon plagiometopon*) and only two of the planktivores (*C. cyanea* and *Abudefduf sexfasciatus*) showed highly significant large correlation coefficients ($r \geq 0.599$) between the number of individuals in the patch reef and the area of patch reef (Table 1).

Among the six most abundant algal feeders, four species showed territoriality. The total number of individuals of the four territorial herbivores was very highly correlated with the area of the patch reef ($r = 0.959$, $t = 30.7$, $p < 0.001$, $n = 84$). Although there was almost no difference in AIC values, the power function was slightly better than the linear function to explain the relationship between the total number of individuals of the four territorial herbivores and patch reef area; the total number of the individuals increased almost linearly with patch reef area (Fig. 4a). Accordingly, no territorial herbivores (< 1 individual) were expected in the smallest reefs less than 0.6 m²; in fact, there were almost no territorial herbivores in the smallest reefs (0.27 individuals on average ± 0.62 SD, $n = 41$). In contrast, the total number of individuals of the other 20 species was less significantly correlated with the area of patch reef ($r = 0.632$, $t = 7.39$, $p < 0.001$, $n = 84$): the total number of the individuals roughly increased with the

square root of the patch reef area (Fig. 4b, $N_{obs} = 27.619$ Area$^{0.507}$). There were expected to be 21 individuals in the small patch reef of 0.6 m², and there were 6.6 individuals on average in the smaller reefs (± 9.62 SD, $n = 41$). The relationship between the number of each territorial herbivore and the patch reef area is shown in Fig. 4c–f. The number of *Hemiglyphidodon plagiometopon* increased almost linearly, but the number of *Stegastes nigricans* did not increase linearly with patch reef area. The other two territorial species showed a similar tendency to that of *H. plagiometopon*.

There was no significant linear relationship between population density (number of individuals/m²) of the four most abundant territorial herbivores and patch reef area ($r = -0.017$, $t = 0.150$, $p = 0.881$, $n = 84$). The best-fitting model was the power function, but the parameter b was not significant ($D_{obs} = a$ Area^b, $a = 1.596$: $t = 5.098$, $p < 0.001$; $b = 0.049$: $t = 0.338$, $p = 0.736$). However, the density was statistically higher in larger patch reefs (Spearman's correlation analysis: $rs = 0.504$, $z = 4.590$, $p < 0.001$, $n = 84$). The population density of the other 20 species was inversely proportional to patch reef area ($D_{obs} = a/$Area $+ b$, $a = 3.857$: $t = 2.46$, $p = 0.016$; $b = 15.67$: $t = 2.68$, $p = 0.009$): so, the density was 15.67 individuals/1 m² in larger reefs. Over the entire study site, the density was not lower in larger patch reefs ($rs = 0.149$, $z = 1.36$, $p = 0.175$, $n = 84$). However, when ignoring small reefs less than 1 m², the population density of the 20 species was statistically lower in larger patch reefs ($rs = -0.394$, $z = 2.23$, $p = 0.026$, $n = 33$).

Stepwise regression analysis of the relationship between species richness in patch reefs and the number

Fig. 4 Relationship between the total number of individuals of species and patch reef area. **a** The four most abundant territorial herbivores, *Stegastes nigricans*, *S. lividus*, *Amphiprion frenatus*, and *Hemiglyphidodon plagiometopon*. **b** The other 20 species. **c** *H. plagiometopon*. **d** *S. lividus*. **e** *S. nigricans*. **f** *A. frenatus*
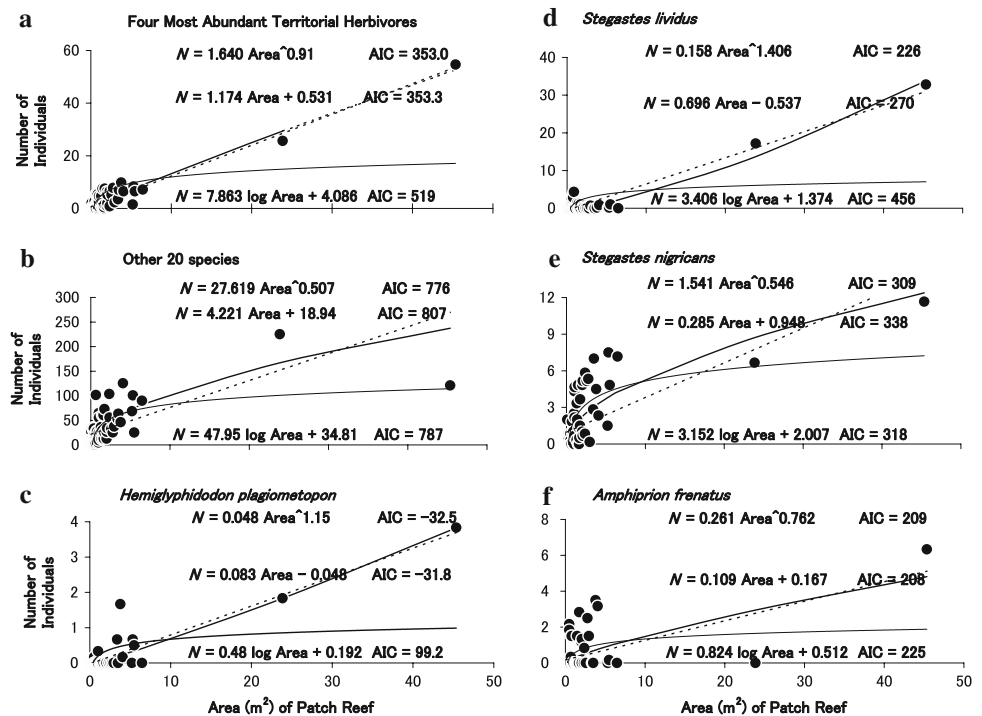
of individuals (#) of species revealed a best-fitting model, which consisted of eight species (AIC = 307.6, all coefficients were significant, $p < 0.05$): $S_{obs} = 1.532 + 0.085$ # *Dascyllus aruanus* $+ 0.380$ # *Pomacentrus moluccensis* $+ 0.262$ # *Stegastes nigricans* $+ 0.418$ # *P. adelus* $+ 1.001$ # *Amphiprion frenatus* $- 0.031$ # *Chrysiptera cyanea* $- 0.436$ # *Abudefduf sexfasciatus* $- 1.816$ # *Hemiglyphidodon plagiometopon*. They were eight of the most abundant species. The two territorial species, *H. plagiometopon* and *A. frenatus*, had the largest negative or positive effects on species richness.

Coral cover and species–area relationship

The total area of coral cover was largest in the largest two reefs (Fig. 5, Reefs 1 and 2), although coral cover percentage was not the highest in these reefs (Reef 1, 32.7%; Reef 2, 37.3%). The coral cover percentage in patch reefs was on average only 33.1% (± 24.5 SD, $n = 84$, Fig. 5). Species richness in patch reefs was significantly correlated with the total area of coral cover in the patch reef ($r = 0.526$, $t = 5.60$, $p < 0.001$, $n = 84$) but was not correlated with coral cover percentage ($r = 0.071$, $t = 0.647$, $p = 0.520$, $n = 84$). Using log area as the first independent variable, coral cover (%) as the second independent variable, and the interaction term of the two variables, a highly significant model was found to explain the observed species richness in patch reefs ($R^2 = 0.730$, $F = 75.7$, $p < 0.001$, AIC = 329.5): $S_{obs} = 3.806 + 3.335$ log area $+ 0.040$ coral cover (%) $+ 0.047$ log area $\times$ coral cover (%). The interaction term was significant ($F = 7.05$, $p < 0.01$). The coefficient of determination of the equation increased by 4.96–73.0% over the semi-log SAR without coral cover percentage (68.04%, see Fig. 2b).

Discussion

Species–area relationship on a very fine scale

SARs on broader scales are scale-dependent (Crawley and Harral 2001; Turner and Tjørve 2005; Drakare et al.

2006), but species richness often increases linearly with habitat area in log–log space on relatively narrow scales (Rosenzweig 2004; Tittensor et al. 2007; Tjørve and Tjørve 2008). In the present study, the logarithmic function fitted our SAR data better than the power function, suggesting that SAR is scale-dependent in this very fine and narrow scale (0.05–45.4 m²). It is suggested that non-linear SAR in log–log plots, especially upward-convex species–area curves, are attributable to sampling artifacts, which are often caused by sampling bias or small sample size (Rosenzweig 2004; Turner and Tjørve 2005; Belmaker et al. 2007). In the present study, however, 84 reefs were exhaustively surveyed six times over a week rather than sampled, and target species (damselfishes) were all resident and very conspicuous (see Allen 1991). Therefore, incomplete surveying was probably of minor importance to the SAR in the present study.

Recent studies suggest that several possible mathematical models, including the power function and the logarithmic function, should be applied to empirical SAR data and a best-fitting model should be selected based on AIC or other related values when shapes and functions of species–area curves are analyzed (Tjørve 2003; Dengler 2009). At the present study site, the logarithmic function was the best-fitting model, and SAR in semi-log space showed very good linearity (Fig. 2b). This indicates that the regression line could be used to predict species richness in a patch reef by interpolation in a semi-log plot. In contrast, species richness very slightly extrapolated from the total area of the patch reefs (15.4 species in 166.0 m²) was much lower than the average species richness over the entire study site (23.2 species). It should be noted that the area of the virtual reef (166.0 m²) was only less than four times the area of the largest reef (45.4 m²). These results suggest that a group of 84 small single reefs are more likely to have higher species richness than a virtual single large reef of equivalent area at the present study site. Several authors suggested that on very fine scales, several small habitat patches can accommodate more diverse species than a single large habitat, which is probably because of edge effects or metapopulation dynamics (Simberloff and Gotelli 1984; Tilman and Kareiva 1997; Turner et al. 2001; Rosenzweig 2004). In the present study, the edge

Fig. 5 Relationship between patch reef area, coral cover, and species richness. The 84 patch reefs are ranked in terms of area
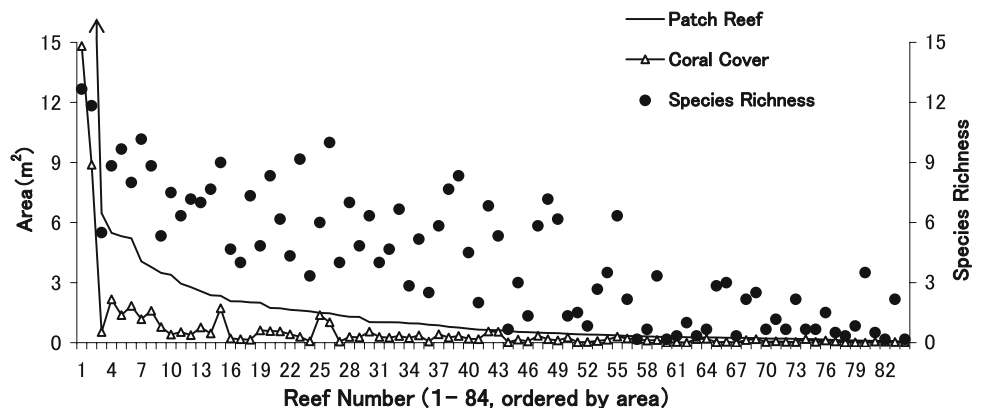
length of patch reefs was not significantly correlated with species richness. Thus, metapopulation dynamics might be relevant to the results obtained. By adding coral cover (%) to log area of patch reef, a slightly better regression was found to explain the observed species richness in patch reefs. If the virtual single large reef had 83% of coral cover, species richness in the virtual reef could be predicted to 23.2. However, the coral cover percentage was not so high in large reefs. A single large reef may not provide more microhabitats than several smaller patch reefs at the present study site.

Species–area relationship under the random recruitment system

Coral reef fishes have a drifting larval phase to randomly disperse over patchy habitats (Planes et al. 2009; Saenz-Agudelo et al. 2009), and several authors suggest that in places where there are no marked differences in habitat heterogeneity between patches, small reefs do not differ in species richness from a continuous large reef of equivalent area, because of the random recruitment system (Sale and Steel 1986; McClanahan 1994; Chittaro 2002; Belmaker et al. 2007). In the present study, the random placement model indicated a highly significant regression line in semi-log space, and the species richness calculated from the total area of the patch reefs (21.0 species in 166.0 m^2) was close to the actual species richness in the study sites (23.2 species). In this simulation, species were accumulated randomly so that the probability of an individual settling on each reef was simply proportional to its area. Accordingly, the species richness in the entire study site can be determined primarily by the random recruitment system. However, species richness in the actual largest reefs was much lower than that calculated from the regression line (Fig. 3). The random placement model assumes no major differences in habitat heterogeneity (Simberloff and Gotelli 1984, Rosenzweig 2004). Indeed, there were no marked differences in coral cover percentage between reefs: the contribution of coral cover percentage to explain species richness in patch reefs was only 4.96%, and the average coral cover percentage in patch reefs was only 33%. The random placement model also assumes no competition (Simberloff and Gotelli 1984, Rosenzweig 2004). However, interspecific competition may be severe in the largest reefs, because territorial herbivores were abundant in the largest reefs at the present study site.

Territorial herbivore, unoccupied patch, and species–area relationship

Territorial herbivorous damselfishes often occupy a large area of hard substratum in shallow subtidal zones of coral reefs and have direct or indirect effects on the benthic community structure including fishes (Ceccarelli et al. 2001; Ceccarelli 2007). At the present study site, the total number of individuals of eight species in the patch reef had positive or negative effects on species richness, and three of these were territorial herbivores, i.e., *Hemiglyphidodon plagiometopon*, *Amphiprion frenatus*, and *Stegastes nigricans*. This means that benthic community structure can be influenced by the number of individuals of the territorial herbivores, as well as the size of the patch reef. The establishment of a territory is dependent on the benefits obtained from the defended food source and the costs of defense against adjacent competitors, and territory size usually becomes small with an increasing number of adjacent competitors (Norman and Jones 1984; Ceccarelli et al. 2001). In areas with abundant food sources, territory size is substantially determined by the number of competitors alone (Norman and Jones 1984). In very small reefs, however, the amount of food must be limited simply because of the small surface area. Minimal territories may not support territorial herbivores in small reefs. Although our data include small juveniles, small reefs of less than 0.6 m^2 were unoccupied by territorial herbivores. In other words, superior competitors (i.e., the territorial herbivores) occupy some spaces in the large reefs, but they do not occupy the smallest reefs. Our computer simulations also indicate that the SAR can be well explained in small reefs by random placement alone (Fig. 3). As many damselfishes, including juveniles, can move between neighboring reefs (Abelson and Shlesinger 2002; Hattori 2002; Hattori and Shibuno, pers. obs.), small patches can play an important role in the coexistence of competing species as temporal refuges.

The effects of the largest territorial damselfishes on benthic community structure have been well documented, and they are known to exclude other algal feeders and coral from their territory (Ceccarelli et al. 2001). In the present study site, one of the largest territorial herbivores, *H. plagiometopon*, increased in number almost linearly with patch reef area (Fig. 4c): it was most abundant in the larger reefs, while it was not found in the smallest reefs. Furthermore, the number of individuals of this species had only negative effects on species richness of other damselfishes in patch reefs. Algal biomass within its territory is usually much larger than that outside its territory, and is much larger than that inside the territories of other damselfishes (Ceccarelli et al. 2001). However, algal species richness inside its territory is often lower than that outside its territory (Ceccarelli et al. 2001) because *H. plagiometopon* does not feed on the alga itself but instead feeds mainly on detritus, which degrades species richness (Wilson and Bellwood 1997; Ceccarelli 2007). The presence of a number of small reefs where *H. plagiometopon* is not present may enhance species coexistence of fishes in shallow coral reef shore zones.

Other smaller territorial herbivores were also abundant in large reefs (Fig. 4a) but they had no negative effects on species richness. *S. nigricans* is also one of the largest territorial damselfishes and is well known for

strong interspecific territoriality (Ceccarelli et al. 2001). However, it had slightly positive effects on species richness. Unlike *H. plagiometopon*, this species is less dependent on detritus in algal turf (Wilson and Bellwood 1997) and frequently weeds out unpalatable algae to feed on more suitable algae (Hata and Kato 2002, 2006). This weeding behavior may provide other fishes with additional food, such as detached pieces of algae. Furthermore, *S. nigricans* forms large colonies in large reefs, unlike *H. plagiometopon*, and its territorial borders are often complicated. As a result, these colonies may provide other non-herbivores with a variety of food sources at the borders. *A. frenatus* had positive and relatively large effects on species richness. *A. frenatus* is essentially omnivorous, although it feeds on algae, and it does not show strong territoriality (Allen 1975). It also forms larger colonies in larger reefs, which are usually taller three-dimensional reefs with large vertical walls, and larger reefs inhabited by *A. frenatus* provide refuge for other damselfishes (Hattori and Kobayashi 2007). Shibuno (unpublished data) also observed that *A. frenatus* was almost always found in sites where the species richness of other damselfishes is very high in shallow back reef habitats. Although *S. lividus* showed territoriality and formed large colonies, it had no significant effects on species richness in patch reefs. The direct or indirect effects of territorial herbivores on other damselfishes in patch reefs of different areas are now under investigation.

Density–area relationship and interspecific competition

The relationship between the total number of individuals of all species and species richness (Fig. 2c) indicated that the expected species richness was much lower than the actual species richness. However, the computer application produced by Turner et al. (2000), which uses the total number of individuals of a randomly combined large reef and the species list in the group, yielded a very good estimate. These findings suggest that the density of individuals is lower in larger reefs. In fact, the population density of the four most abundant territorial herbivores was slightly higher in larger patch reefs, but that of the other 20 species was inversely proportional to the patch reef area. The total number of individuals of the territorial herbivores increased linearly with patch reef area, but that of other 20 species roughly increased with the square root of the area. Large reefs with relatively small population density, which is attributable to the presence of territorial herbivores, could not harbor high species richness in comparison with several small reefs of equivalent area.

Conclusion

While surface topography or habitat complexity have been shown to have large effects on species richness of coral reef fishes (e.g., Luckhurst and Luckhurst 1978; Bell and Galzin 1984; McCormick 1994; Chabanet et al. 1997), the effect of patch reef size on fish species richness has not been studied extensively (see Sale and Steel 1986; Chittaro 2002; Belmaker et al. 2007). The present study demonstrated that species richness in a patch reef can be predicted by the area of the patch reef. By adding data on live coral cover to the area of patch reef, a better regression was obtained to explain the observed SAR. However, information on SAR without coral cover will still be useful, as corals are usually less abundant in shallow coral reef shore zones. When applying to broader scales, extrapolation methods are problematic: in addition, smaller patches are usually more abundant in a natural environment. However, these methods are often useful for predicting species richness in habitat island patches slightly larger than the observed largest patch (Rosenzweig 1995, 2004); especially, a better estimate on species richness in the whole study site could be obtained, using random placement models and computer simulations with abundance data (Turner et al. 2000; this study). In contrast to the area of patch reef, the edge length could not predict species richness of damselfish assemblages in the patch reef.

The present study also demonstrated that the SLOSS dichotomy can provide important information on biological processes that influence the SAR, although we only focused on damselfish assemblages. In the present study, the group of 84 single reefs are better with likely to have higher species richness than the virtual single large reef of equivalent area. This result can be attributed to the fact that the largest territorial herbivore was more abundant in larger reefs. As a result, species richness in a patch reef could be explained by the total number of individuals of particular species involving some territorial herbivores. While interspecific interactions seemed to influence the species richness in large reefs, the observed SAR in small reefs was within the results of random placement, as Belmaker et al. (2007) suggested. At small spatial scales, each patch cannot have a large number of individuals and consequently contain a small sample of all species of a given community; at larger scales, where the number of individuals inhabiting a patch can be influenced by several factors involving habitat complexity and competition, other mechanisms are more likely to create the SAR and the importance of random placement is expected to diminish (Turner and Tjørve 2005; Belmaker et al. 2007). However, we did not discriminate early setters from residents. Further empirical studies are necessary to examine isolate-type SAR in relation to recruitment and post-recruitment processes. Our new visual census techniques applied in the present study, using enlarged aerial photographs (the resolution should be less than 10 cm on the ground surface) and image-analysis software to produce a photographic map, can be used widely in shallow water seascapes (up to a depth of 2 m with high water transparency). These techniques incorporate the area of habitat patches into the data analysis and can

cover wider area continuously than that with ordinary belt-transects or quadrats, which are usually separately and sparsely set in the field.

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