

## Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models

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Received 8.6.1995      Accepted 18.2.1996

**Key words:** Patch reef, Spatial distribution, Island biogeography theory, Recruitment, Habitat-based model, Hierarchy theory, Habitat template

### Synopsis

One perspective emphasizing the importance of stochastic processes in determining coral reef fish assemblages implies that there is little organization in species richness, abundance structure, and spatial distribution. We examine the degree to which this perspective is correct by analyzing distribution of fishes on a collection of patch reefs (Discovery Bay, Jamaica). We ask the question whether these patches accumulate species and individuals in a manner consistent with stochastic expectations. To address this question we use two conceptual models, each permitting a different insight. One assumes that fish are distributed stochastically on patches while the other assumes presence of restrictions on fish distribution due to habitat structure. For each conceptual model we use two types of benchmark: we compare observed patterns to those predicted by theoretical models, and we also compare observed patterns to those obtained from a random reallocation of fish individuals to patches. We found that the conceptual model assuming stochastic processes appeared to provide weaker explanation of patterns than the conceptual model that includes restrictions due to habitat structure. Further, and more importantly, we found that (i) the community is shaped by a mixture of stochastic and non-stochastic mechanisms, and (ii) the stochastic assembly processes decrease in importance for species restricted to fewer microhabitat types and sites. Our study therefore indicates that patches do accumulate individuals and species in a manner consistent with stochastic expectations, however, this applies primarily to the habitat generalists (unrestricted species). By the same token, increased habitat specialization by some species imposes constraints on the stochastic model such that it eventually fails.

### Introduction

Assemblages of coral reef fish are systems exceptionally rich and highly variable in time and space. This has challenged ecologists to provide an explanation which has resulted in a number of models and perspectives (e.g. Sale 1980, Anderson et al. 1981). Of these, the stochastic perspective has gained considerable momentum and available evidence appears to support it. Specifically, fish compo-

sition and its variability on patch reefs is explained as a function of random events including (a) fish arrival, (b) creation of vacant sites via mortality and migration, and (c) establishment on or colonization of patches (Sale & Dybdahl 1978, Williams 1982, Victor 1983, Sale & Douglas 1984, Sale & Steel 1986, Doherty & Williams 1988, Bohnsack 1989, Robertson & Duke 1990). Some argue that any organization in reef fish assemblage reported by others may

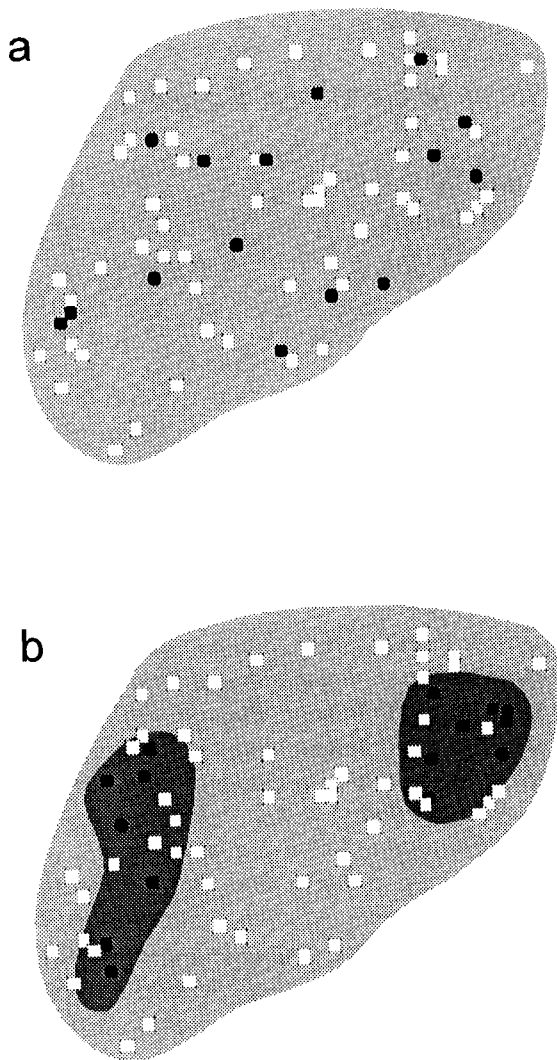


Fig. 1. Contrast between spatial patterns produced by unrestricted (a) and micro-habitat restricted fish distributions (b). For simplicity we use two species only and do not show individual patches. Both species (Species 1 '□',  $N_1 = 80$ ; Species 2 '●',  $N_2 = 20$ ) are placed randomly such that in Figure 1b Species 2 '●' is restricted to a micro-habitat (darker shading). This case would occur if the two species respond to two different levels of habitat structure with the Species 1, utilizing all micro-habitats (habitat generalist) and Species 2, restricted to one micro-habitat only (habitat specialist).

therefore be a function of biologically trivial factors such as sampling biases (e.g. Sale & Guy 1992).

This stochastic explanation, however, leads to the counter-intuitive conclusion that there is little organization in the coral reef fish assemblages. It does so despite a high number of interacting species and the

general expectation that complex systems are organized (e.g. Drake et al. 1996, Kauffman 1993). We suggest, therefore, that these assemblages may be more organized than the stochastic view implies. We also suggest that the failure to detect their organization is due, in part, to insufficient attention paid to proper scaling of observations and analyses. For example, if species within an assemblage perceive and therefore respond to the environmental template at more than one spatial and temporal scale (e.g. Hanski 1982, Kolasa 1989, Wiens 1989, Kotliar & Wiens 1990, Kareiva 1990, Milne 1991), then the distribution pattern may appear deterministic or stochastic depending on the scale of observation (Allen & Starr 1982, Maurer 1985, Collins & Glenn 1990). Such dependence on the method and approach is bound to produce alternative and sometimes conflicting explanations.

We therefore pose a question: Given a landscape of different size patches and an available species pool represented by  $n$  individuals, **does each patch accumulate individuals and species in a manner consistent with expectations of stochasticity?** Stated differently, is the presence of a species on a patch a probability function of patch size and number of individuals participating in the lottery, or is the presence of a species dependent on non-stochastic alternatives — the simplest involving restrictions on which patch a species may colonize and survive on? To answer this question we use data from a natural fish community to test two different conceptual models that emphasize different ecological mechanisms.

The first model borrows a combination of assumptions underlying both the 'island biogeography theory' (IBT, MacArthur & Wilson 1967) and variable recruitment in space and time (Sale 1980). Indeed, patches are not islands in the sense of MacArthur & Wilson (1967) because patch assemblages are not self maintaining populations, but aspects of IBT do apply to fragmented environments such as coral reef patches (Putman 1994). Thus, we use IBT only partially by borrowing one of its assumptions that the number of species on a patch is a function of the species immigration and emigration rates (or recruitment and subsequent removal of individuals). The assumption that these rates are influenced

by patch size is not unreasonable (Sale 1980, Anderson et al. 1981, Ogden & Ebersole 1981, Bohnsack 1983, Rahel et al. 1984, Clarke 1988, Sale & Steel 1989, Winemiller & Pianka 1990). In fact, similar assumptions are made in patch dynamic models in general.

The combined 'IBT-variable recruitment' conceptual model neither expects nor requires species to aggregate within the patch reefs system according to species specific criteria such as patch quality or presence of other species. The model thus evaluates assemblage patterns as a function of patch size and chance recruitment alone (Fig. 1a). Consequently, this model is insensitive to any habitat structure that might be perceived by species if other attributes of patches were relevant. For example, there might be two groups of patches, one with good hiding crevasses and the other without. Next, within each group of patches fish might discern those with predators to those without predators, and so on. The perception of such habitat subdivision by fish might result in their structured distributions. This aspect is best analyzed by the second model, the 'habitat-based model' (HBM; Kolasa & Strayer 1988, Kolasa 1989).

The 'habitat-based model' assumes nested patchiness of habitat space as a major force shaping species distribution and abundance. This means that species differ in their ability to use the habitat. For example, according to HBM, there will be species with broad ecological ranges (or habitat tolerances) which span the diverse and complete set of microhabitats (habitat generalists), and there will also be species restricted to a subset of microhabitats only (habitat specialists). Since ecological ranges and site distributions of specialists are largely nested within those of generalists (i.e. habitat specialists may be considered as operating at subdivisions or lower levels of habitat structure – Fig. 1b), we view the habitat and the associated community as being hierarchical. In such a hierarchy, specialists face a more fragmented environment than generalists which permits, given some additional assumptions, to calculate their expected relative abundances. This means that the colonization and extinction lottery is limited to varying degrees depending on the number and kind of patches the species are per-

mitted to use under the 'habitat-based model'. For example, species with special habitat requirements will be able to engage in the stochastic lottery on some patches only while species with few restrictions have the potential to colonize any patch.

The two alternative models, one with no restrictions on patch colonization and the other with species-specific restrictions, result in different expectations of community patterns. Such expected community patterns can be compared to those observed in a natural system. Differences in the relative fit of the expected (= theoretical) versus observed values indicate and contrast the relative importance of stochastic effects alone vis-à-vis habitat structure effects.

We wish to emphasize here that we are not interested in the merits of the models themselves but only in their ability to discriminate whether other mechanisms are involved that may, incidentally, produce an apparency of stochastic pattern. Unfortunately, patterns predicted by each model are not directly comparable (i.e., the first predicts richness, and the second predicts abundance). Thus, to gain and document insights into the mechanisms structuring fish community we take the additional steps: (i) divide the species pool into groups according to whether a species is a habitat specialist or generalist (cf. HBM Kolasa 1989), and (ii) apply the 'IBT-variable recruitment' model to each of the species groups.

This strategy permits mutual verification of results produced by the two conceptual models. Specifically, we hypothesize that if the HBM indicates strong effects of habitat structure, then IBT will apply well to broad range species only but fail with respect to narrow range species. The reason for this prediction is simple: as the restrictions as to which patch reefs can be effectively colonized increase in importance, a corresponding decline in importance of individual numbers and patch size is expected.

## Methods

### *Field*

Data on fish distributions were collected from

patch reefs in Discovery Bay, Jamaica, over three two-week periods (25.12.1990–10.1.1991, 25.12.1991–10.1.1992, and 25.12.1993–10.1.1994). All observations were conducted during daylight hours by direct visual census using SCUBA. We minimized weaknesses normally associated with this method (Diamond & May 1977, Rahel et al. 1984, Andrew & Mapstone 1987, Fowler 1987, Bellwood & Alcala 1988, Greene & Alevizon 1989) with the following procedures: (i) two divers settle simultaneously on opposite sides of a patch-reef, (ii) each diver records one half of the local species pool ( $S_{\text{total}} = 71$ ); the division determined by species daytime local migratory behaviour (e.g., Pomacentridae and Holocentridae versus Scaridae and Labridae), (iii) fish counting starts after a five minute habituation period, (iv) for the subsequent twenty minute observation all individuals within 1 m distance from the patch surface are recorded, such that, (v) the two divers complete a 360° rotation around the patch-reef in four five-minute 90° shifts.

After completing each assemblage enumeration, we recorded physical parameters for the patch (depth, X-Y-Z dimensions, and distance to surrounding patches). We measured depth as the perpendicular distance from the water surface to the base of the coral patch. Although other methods have been used to determine reef surface area (e.g., Risk 1972, Molles 1978), we approximated it by integrating the patch X-Y-Z dimensions into the equation for the surface area of a half ellipsoid. We chose this particular method because (a) we followed the assumption that in the back reef of Discovery Bay, Jamaica, large patches contain propor-

tionately the same habitat complexity relative to smaller patches (communiqué Risk), and (b) of its simplicity. Distances to nearby patches were measured by the shortest distance between the two patches.

The minimal number of patches to sample was determined by a requirement of the 'habitat-based model' (Kolasa 1989) that the ecological range covered by sampling exceeds that of the broadest species. This ensures that the scale of sampling is sufficient to measure all species adequately. Operationally, we define ecological range (ER) as a ratio of the number of patches a species is found on ( $n$ ) and the area of these patches ( $SA$ ) to the total habitat available ( $n_{\text{total}} * SA_{\text{total}}$ ). Ecological range is thus:

$$ER_i = \sqrt{(n_i - n_{\text{total}}) * (\sum SA_i / \sum SA_{\text{total}})}. \quad (1)$$

The measure scales from zero to one. Species with ER values close to zero are those species found on few and/or small patches. By contrast, species with ER values close to one are found on the majority of the patches, especially the larger patches. Although this measure of ecological range is arbitrary (other parameters such as consumable resource range or microhabitat requirements could be used instead) we believe that, given the nature of our tests, the above parameters are adequate. The biological interpretation of this measure is that the number of sites reflects, to some degree, the exposure of a species to different environmental conditions and, indeed, its ability to cope with them (cf. Brown 1984, Kolasa 1989). It also links the ecological range to the size of a patch by assuming that larger patches, not

Table 1. Summary of patch reef descriptors. Frequency distribution of surface areas is skewed towards the smaller patches ( $p < 0.05$ ).

Parameters	Sampling weeks		
	Season 1	Season 2	Season 3
Number of patches	35	40	39
Minimum surface area (m <sup>2</sup> )	0.20	0.30	1.10
Maximum surface area (m <sup>2</sup> )	19.5	33.1	30.9
Mean surface area (m <sup>2</sup> )	5.43	8.00	7.97
Standard deviation (m <sup>2</sup> )	4.55	8.42	6.70
Skewness	1.098	1.464	1.479
Total surface area (m <sup>2</sup> )	190.3	312.0	318.8

unlike larger islands, expose fish to a more diverse habitat (e.g. Risk 1972, Tonn & Magnuson 1982). We sampled 114 patch reefs from a 10 000 m<sup>2</sup> area of back reef from Discovery Bay, Jamaica. No patch was more than 15 m deep, nor were any patches closer than 2 m to their next nearest patch. Patch surface area ranged from 0.24 m<sup>2</sup> to 33 m<sup>2</sup> (with a higher frequency of smaller patches compared to larger patches: mean patch size is 7.2 m<sup>2</sup> and the S.D. equal to 6.86 m<sup>2</sup> – Table 1). Total patch surface area is 820 m<sup>2</sup> (8% of back reef habitat).

The first term in equation 1,  $n_i$ , is abundance of species  $i$  totaled for all patches. For some species (e.g., species of greater local mobility – Scaridae and Acanthuridae), species abundance could be overestimated if some individuals are counted several times on different patches. We reduced this source of error by weighing each species abundance by the mean time species were observed in association with patches. This was estimated by timing randomly selected individuals for five minutes (daylight hours,  $N_{\text{timed}} = 580$  fish). The number of individuals timed differed among species and may be a source of error.

We identified and included in the analysis 71 species of fish from 21 families (Table 3). Patch association ranged from 10% (*Inermia vittata*) to 100% (e.g., *Stegastes* sp.). Depending on the sampling season, single species abundance ranged from 0 (*Chro-*

*mis cyanea*) to 387 (*Scarus coeruleus*). Species abundance totals are 813, 1554, and 991 for the three seasons, respectively. The maximum patch richness observed was 25 species ( $S_{\text{minimum}} = 1$  species, mean = 10.0 species, and S.D. = 4.8 species).

### Theoretically expected and null community patterns

Recall that we posed the question of whether each patch accumulated individuals and species in a manner consistent with expectations of stochasticity. Statistical evaluation of the observed patterns calls two types of benchmark. We need to know what would be the patterns if each of the models were correct. We also need to know what patterns would emerge if most processes were stochastic. The approach we take to answer the question involves two steps. First, we search for the best fitting theoretical equations and, second, we create a 'null assemblage' (random reallocation of fish to patches) to test observed data for stochastic effects.

#### Step 1: Theoretical equations

The first step contrasts the relative fit between the expected (= theoretical) and observed patterns for both richness (IBT – variable recruitment) and abundance (HBM). Because we do not necessarily know what the expected patterns are, we evaluate a

Table 2. Fits (coefficients of determination,  $r^2$ ) among the predicted patch richness (S) and species abundance (N) and the observed data. The predicted values were obtained using the family of equations listed. We find that the equations that create the best correlations are equation no. 9 and no. 11 for the two models respectively (shown by an asterisk).

Equation	IBT-variable recruitment	$r^2$	Habitat based model	$r^2$
1	$S = SA$	0.335	$N = ER$	0.727
2	$S = SA \ln SA$	0.316	$N = ER \ln ER$	0.157
3	$S = SA^{1.5}$	0.307	$N = ER^{1.5}$	0.790
4	$S = SA^2$	0.276	$N = ER^2$	0.816
5	$S = SA^2 \ln SA$	0.257	$N = ER^2 \ln ER$	0.562
6	$S = SA^{2.5}$	0.248	$N = ER^{2.5}$	0.825
7	$S = SA^3$	0.226	$N = ER^3$	0.827
8	$S = e^{SA}$	0.064	$N = e^{ER}$	0.774
9	$S = SA^{0.5} \ln SA$	0.339*	$N = ER^{0.5} \ln ER$	0.150
10	$S = (\ln SA)^2$	0.314	$N = (\ln ER)^2$	0.212
11	$S = SA (\ln SA)^{-1}$	0.002	$N = ER (\ln ER)^{-1}$	0.852*
12	$S = \ln SA (SA)^{-1}$	0.005	$N = \ln ER (ER)^{-1}$	0.071
13	$S = \ln SA (SA)^{-2}$	0.038	$N = \ln ER (ER)^{-2}$	0.037

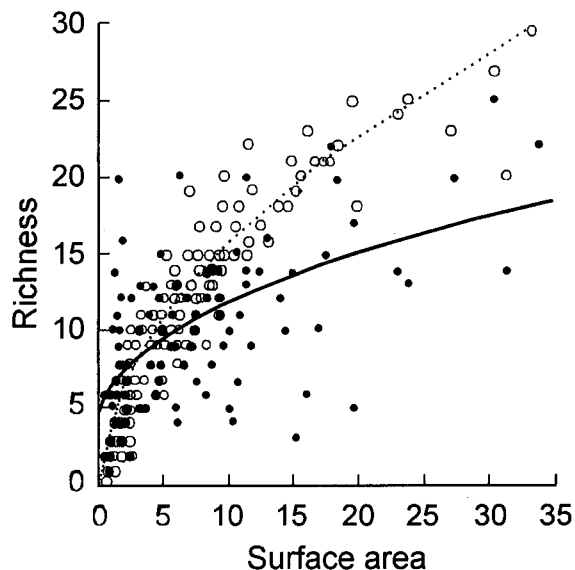


Fig. 2. Patch richness as a function of patch size for the null (open circles, dashed line) and observed (closed circles, continuous line) assemblages. Both relationships are best described ( $r^2_{\text{null}} = 0.886$ ,  $p < 0.001$ ,  $r^2_{\text{observed}} = 0.343$ ,  $p < 0.001$ ) by the nonlinear equation:  $S = \beta_0 + \beta_1 (SA)^{0.5}$ . Beta coefficients differ significantly between the two curves.

family of related equations to choose one that best describes the observed data (Table 2). Once an equation is selected, we interpret its coefficient of determination as an indirect measure of importance of processes reflected in the assumptions of each model.

As a direct comparison of the two models does not permit a definitive answer as to whether stochastic processes dominate the community structure (primarily because the models predict different parameters — richness and abundance), we attempt to combine insights from each of the two models by the following procedure.

#### Step 2: Null assemblage

We grouped species according to species-specific criteria and then compared patterns obtained within each species group to 'null patterns' produced by stochastic processes alone. We then chose the ratio of 'coefficient of determinations' between observed and null richness for each species group as an index of pattern consistency with stochastic expectations. Specifically, (i) we created a null (= stochastic) assemblage by random allocation of individual fish

species onto patch reefs with probability of colonizing a particular patch proportional to the total abundance of that species and surface area of the patch. This simplification ignores other factors such as patch proximity to other patches, competitive and opportunistic adult and predator-prey interactions and others, but this appears to be an acceptable strategy to generate stochastic assemblages suitable for our tests (Sale 1980, Anderson et al. 1981, Ogden & Ebersole 1981, Bohnsack 1983, Rachel et al. 1984, Clarke 1988, Sale & Steel 1989, Wine-miller & Pianka 1990). We verified this assumption, for patch richness only, by showing that the relationships in so generated assemblages approximate those in the observed assemblage. Specifically, we find that the regression model that maximizes the correlations (see Appendix) between patch richness and patch surface area is the same for both the observed and null (= stochastic) assemblages. This model assumes the form:  $S = \beta_0 + \beta_1 (SA)^{0.5}$ , where  $S$  is patch richness, and  $SA$  is patch surface area ( $r^2_{\text{observed}} = 0.343$ , and  $r^2_{\text{null assemblage}} = 0.886$ ,  $p_{\text{null}}$  and  $p_{\text{observed}} < 0.001$ ). The significant difference between the respective regression models lies in the values of the beta coefficients. This difference leads to a prediction of a higher patch richness for the null assemblage (paired t-test mean difference = 1.553,  $p = 0.005$ ) (Fig. 2). (ii) we allocate each species in the species pool to species groups based on the principles of the 'habitat-based model' (for both null and observed assemblages). We use the 'habitat-based model' specifically because it groups species by similarities in how they perceive and respond to a template of diverse microhabitats. The model clusters species according to similarities in their ecological range and abundance. The assumption made is that the fewer microhabitat types a species perceives to be suitable, the more restricted and, possibly, patchy its range becomes. This results in a cost (e.g., finding mates, shelter from predation, foraging) which is measurable in terms of the species abundance and distribution. The two variables, ecological range and abundance, can then be used to group species on the premise that such grouping will reflect major differences in how species relate to their habitat. We use a cluster analysis with Euclidean distance and average linkage on species ecological

Table 3. Fish community from the back reef of Discovery Bay, Jamaica. 'Time' refers to the species percent time associated with patch reefs; 'Abundance' shows species abundances for each of the three sampling seasons; 'Patches' is the number of patch reefs the species was observed during a corresponding season (maximum possible: season 1 – 35 patches, season 2 – 39 patches, and season 3 – 40 patches); 'Total surface area' is the area of patch habitat a species was observed (maximum possible: season 1 – 190 m<sup>2</sup>, season 2 – 312 m<sup>2</sup>, and season 3 – 319 m<sup>2</sup>); 'Gp' is the 'habitat-based model' group designation number.

Family	Species	Common name	Time	Abundance			Patches			Total surface area			Gp
				1	2	3	1	2	3	1	2	3	
Acanthuridae	<i>Acanthurus bahianus</i>	Surgeon	0.3	0	0	17	0	0	10	0.0	0.0	121.1	3
	<i>A. chirurgus</i>	Doctofish	0.3	17	26	42	7	11	18	46.0	126.9	148.5	1
	<i>A. coeruleus</i>	Blue tang	0.3	10	9	1	5	8	1	38.9	123.4	5.9	2
Apogonidae	<i>Apogon binotatus</i>	Barred cardinal	1.0	6	31	19	4	14	12	15.2	100.6	83.9	2
	<i>A. towrsendi</i>	Belted cardinal	1.0	0	8	1	0	5	1	0.0	72.4	10.6	3
	<i>Phaeoptyx pigmentaria</i>	Dusky cardinal	1.0	0	0	8	0	0	5	0.0	0.0	55.3	3
Aulostomidae	<i>Aulostomus maculatus</i>	Trumpet	1.0	0	2	0	0	2	0	0.0	40.7	0.0	3
	<i>Paradiplogrammus bairdi</i>	Lancer dragonet	1.0	0	1	0	0	1	0	0.0	1.6	0.0	3
Chaetodontidae	<i>Chaetodon capistratus</i>	Foureye butterfly	0.4	8	17	2	6	8	2	51.1	110.8	22.0	2
	<i>Amblycirrhitus pinos</i>	Red spotted hawkfish	1.0	0	0	1	0	0	1	0.0	0.0	2.0	3
Diodontidae	<i>Diodon holocanthus</i>	Balloon	1.0	0	3	0	0	3	0	0.0	16.7	0.0	3
	<i>Gerres cinereus</i>	Yellowfin mojarra	0.2	0	0	15	0	0	9	0.0	0.0	60.8	3
Holocentridae	<i>Holocentrus adscensionis</i>	Squirrel	1.0	26	40	0	14	17	0	80.3	204.4	0.0	2
	<i>H. rufus</i>	Longspine squirrel	1.0	1	8	22	1	7	15	8.5	67.5	186.6	2
	<i>Myripristis jacobus</i>	Black squirrel	1.0	1	1	0	1	1	0	1.0	4.5	0.0	2
Inermiidae	<i>Neoniphon marianus</i>	Longjaw squirrel	1.0	3	6	4	3	5	4	22.5	57.1	44.3	2
	<i>Sargocentron coruscus</i>	Reef squirrel	1.0	11	20	5	4	12	5	34.4	120.6	57.4	2
	<i>S. vexillarius</i>	Dusky squirrel	1.0	2	0	1	2	0	1	20.5	0.0	5.3	2
Labridae	<i>Inermia vittata</i>	Boga	0.1	0	0	1	0	0	1	0.0	0.0	7.2	3
	<i>Bodianus rufus</i>	Spanish hogfish	0.7	0	2	0	0	2	0	0.0	40.7	0.0	3
	<i>Halichoeres bivittatus</i>	Slippery wrasse	0.7	21	3	5	5	1	4	40.5	2.8	35.3	2
	<i>H. garnoti</i>	Yellowhead wrasse	0.7	18	0	1	9	0	1	55.3	0.0	12.6	3

Table 3. Continued.

Family	Species	Common name	Time	Abundance			Patches			Total surface area			Gp
				1	2	3	1	2	3	1	2	3	
	<i>H. maculopinna</i>	Clown wrasse	0.7	44	0	0	11	0	0	75.1	0.0	0.0	3
	<i>Thalassoma bifasciatum</i>	Bluehead wrasse	0.7	10	36	12	4	11	10	22.0	122.8	85.9	2
	<i>Xyrichtys martinicensis</i>	Rosy razor wrasse	0.7	0	0	1	0	0	1	0.0	0.0	4.0	3
Lutjanidae	<i>Ocyurus chrysurus</i>	Yellowtail snapper	0.3	0	1	3	0	1	3	0.0	1.6	35.0	3
Monacanthidae	<i>Cantherhines pullus</i>	Orange spotted filefish	0.4	1	0	0	1	0	0	2.3	0.0	0.0	3
	<i>Monacanthus tockeri</i>	Slender filefish	0.3	2	0	0	1	0	0	2.3	0.0	0.0	3
Mullidae	<i>Mulloidichthys martinicus</i>	Yellowtail goatfish	0.3	1	0	0	1	0	0	7.4	0.0	0.0	3
	<i>Pseudupeneus maculatus</i>	Spotted goatfish	0.3	3	0	7	3	0	6	19.9	0.0	57.4	2
Pomacanthidae	<i>Holacanthus bermudensis</i>	Blue angel	0.7	2	3	11	2	3	2	12.3	34.3	7.9	2
Pomadasyidae	<i>Haemulon aurolineatum</i>	Tomtate grunt	1.0	0	61	18	0	2	12	0.0	1.8	92.3	3
	<i>H. flavolineatum</i>	French grunt	1.0	12	15	11	4	8	7	34.8	111.2	74.5	2
	<i>H. macrostomum</i>	Spanish grunt	1.0	0	0	1	0	0	1	0.0	0.0	10.0	3
	<i>H. striatum</i>	Striped grunt	1.0	0	4	14	0	3	7	0.0	57.7	85.0	2
Promacetrinae	<i>Abudefduf saxatilis</i>	Sergeant major	1.0	2	0	5	2	0	2	21.2	0.0	20.9	2
	<i>Microspathodon chrysurus</i>	Yellowtail damselfish	1.0	0	0	3	0	0	3	0.0	0.0	21.7	3
	<i>Stegastes diencaeus</i>	Longfin damselfish	1.0	29	11	12	15	6	9	87.8	76.3	137.7	1
	<i>S. fuscus</i>	Dusky damselfish	1.0	18	102	4	8	29	4	45.0	248.1	31.1	2
	<i>S. leucostictus</i>	Beaugregory damselfish	1.0	115	151	10	29	37	10	161.7	300.9	107.4	1
	<i>S. partitus</i>	Bicolor damselfish	1.0	4	17	21	4	11	16	22.1	77.6	129.7	2
	<i>S. planifrons</i>	Threespot damselfish	1.0	89	120	151	22	22	34	134.5	259.0	300.7	1
	<i>S. variabilis</i>	Cocoa damselfish	1.0	16	60	17	6	23	9	23.6	246.6	112.6	2
	<i>Chromis cyanea</i>	Blue chromis	1.0	0	7	10	0	4	2	0.0	33.2	24.5	2
Scaridae	<i>Scarus coeruleus</i>	Blue parrot	0.4	0	1	0	0	1	0	0.0	1.1	0.0	3
	<i>S. iserti</i>	Striped parrot	0.4	103	387	93	13	22	26	91.5	241.8	249.4	1
	<i>S. taeniopterus</i>	Princess parrot	0.4	140	203	138	18	24	34	98.3	249.6	292.1	1
	<i>Sparisoma atomarium</i>	Greenblotch parrot	0.4	1	1	3	1	1	3	1.5	33.1	34.5	2
	<i>S. aurofrenatum</i>	Redband parrot	0.4	10	35	73	6	15	28	29.8	177.2	265.1	2
	<i>S. chrysopteron</i>	Redtail parrot	0.4	2	2	23	2	2	15	12.1	43.7	121.6	2
	<i>S. radians</i>	Bucktooth parrot	0.4	0	1	0	0	1	0	0.0	1.1	0.0	3
	<i>S. rubripinne</i>	Yellowtail parrot	0.4	0	0	2	0	0	1	0.0	0.0	1.1	3
	<i>S. viride</i>	Stoptight parrot	0.4	19	40	31	7	22	17	49.5	228.1	202.7	1
Serranidae	<i>Cephalopholis cruentata</i>	Graysby	1.0	0	0	1	0	0	1	0.0	0.0	7.2	3
	<i>C. fulvus</i>	Coney	1.0	0	0	4	0	0	3	0.0	0.0	19.6	3
	<i>Epinephelus guttatus</i>	Red hind bass	1.0	0	0	1	0	0	1	0.0	0.0	17.3	3
	<i>Hypoplectrus aberrans</i>	Yellowbelly hamlet	1.0	4	1	1	3	1	1	19.8	22.7	4.7	2



Table 3. Continued.

Family	Species	Common name	Time	Abundance			Patches			Total surface area			Gp		
				1	2	3	1	2	3	1	2	3			
	<i>H. chlorurus</i>	Yellowtail hamlet	1.0	0	0	8	8	0	0	0	0	0	0	69.5	3
	<i>H. guttavarius</i>	Shy hamlet	0.8	0	0	2	0	0	0	0	0	0	0	30.4	3
	<i>H. indigo</i>	Indigo hamlet	1.0	13	13	2	2	9	11	1	67.6	137.6	2.0	2	2
	<i>H. nigricans</i>	Black hamlet	1.0	0	8	8	8	0	8	8	0	117.7	77.7	2	2
	<i>H. puella</i>	Barred hamlet	0.9	24	29	58	58	14	18	33	78.0	172.0	273.0	1	1
	<i>H. unicolor</i>	Butter hamlet	0.5	3	8	2	2	3	5	2	23.1	62.8	5.5	2	2
	<i>Hypoplectrus</i> sp.	Masked hamlet	1.0	0	3	0	0	0	2	0	0.0	41.9	0.0	3	3
	<i>Liopropoma rubre</i>	Peppermint bass	1.0	0	1	0	0	0	1	0	0.0	29.9	0.0	3	3
	<i>Mycteroperca tigris</i>	Tiger grouper	1.0	0	0	1	1	0	0	1	0.0	0.0	17.3	3	3
	<i>Serranus tabacarius</i>	Tobaccofish	1.0	0	0	1	1	0	0	1	0.0	0.0	5.8	3	3
	<i>S. tigrinus</i>	Harlequin bass	1.0	0	5	0	0	0	4	0	0.0	37.1	0.0	3	3
Synodontidae	<i>Synodus saurus</i>	Bluestriped lizardfish	0.5	0	0	7	7	0	0	0	0.0	0.0	44.8	3	3
Tetraodontidae	<i>Canthigaster rostrata</i>	Sharpnose puffer	0.7	22	47	74	74	11	22	31	54.0	226.7	288.4	1	1
	<i>Sphoeroides spengleri</i>	Bandtail puffer	0.7	0	4	2	2	0	2	2	0.0	2.8	26.4	2	2

range and abundance to identify three such groups. (iii) the coefficients of determination for the area- richness relationship obtained for the entire observed and null (stochastic) assemblages differ in magnitude ( $r^2_{\text{observed}} = 0.343$ ,  $r^2_{\text{null assemblage}} = 0.886$ ). The coefficients of determination for the three species groups identified by the cluster analysis are obtained via an equation selection process that involves several decision steps (see Appendix for more details). In order to assess how different species groups contribute to the overall explanation of 34% and 89% of variance obtained for the entire assemblages, respectively, we express values obtained for the three species groups in relative terms (i.e. group coefficient/assemblage coefficient). These relative values are directly comparable between the observed and null data sets by generating a ratio, an 'index of stochasticity', of the observed to null coefficients of determination. A ratio value close to 1.0 means that the observed patterns is similar to the null one and, consequently, that a particular species group is distributed over the landscape of patches in a manner consistent with the stochastic mechanisms. A ratio value smaller than 1.0 means that members of the group respond to some other mechanisms.

## Results

### Step 1: Theoretical equations

The equation  $S = SA^{0.5} \ln SA$  ( $S$  = richness, and  $SA$  = patch surface area) optimized the fit between the expected (theoretical) and observed richness pattern (Table 2,  $r^2_{\text{IBT - variable recruitment}} = 0.339$ ). Similarly, the equation,  $N = ER (\ln ER)^{-1}$  ( $N$  = species abundance,  $ER$  = ecological range) optimized the fit between the expected (= theoretical) and observed abundance patterns ( $r^2_{\text{habitat-based model}} = 0.852$ ). Of the two coefficients of determination, the one obtained for 'HBM' is significantly higher than that for 'IBT - variable recruitment'. This implies that significant constraints are in place on how the stochastic processes are allowed to operate. A quantitative evaluation of this aspect follows.

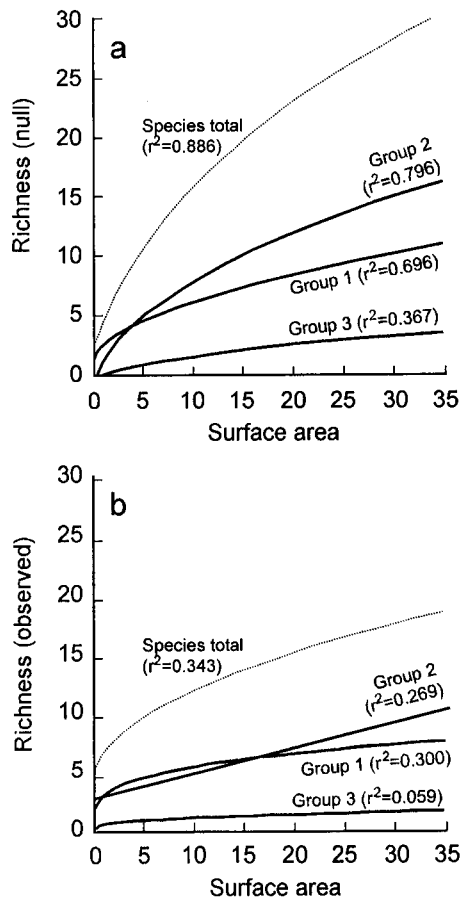


Fig. 3. Patch richness explained as a function of patch size for three groups of species: Group 1 – habitat generalists, Group 2 – intermediate species, and Group 3 – habitat specialists. The null assemblage (a) exhibits substantially stronger relationships than the observed assemblage (b) but the trends associated within the groups are similar. The uppermost line (dotted) is the fit line for the whole assemblage (as in Fig. 2).

#### Step 2: Null assemblage

We identified three species groups using cluster analysis on ecological range and abundance of species. The three groups differ significantly in their mean ecological range and abundance (ANOVA Tukey HSD matrix of pairwise comparison probabilities all  $p < 0.001$ ). Group 1 ( $S_{\text{Group1}} = 9$  species) is best characterized by species that are highly abundant and found throughout most of the habitat range for each of the three sampling seasons. Group 3 ( $S_{\text{Group3}} = 34$  species) comprises species having low abundance (possibly even zero for one or two sam-

pling seasons) and found on few patch reefs only. Group 2 ( $S_{\text{Group2}} = 28$  species) shows intermediate characteristics between Group 1 and Group 3 (Table 3).

‘IBT – variable recruitment’ models for species Group 1, 2, and 3 differ in the proportion of variance they explain between the observed and null data sets (Fig. 3, Table 4). Specifically, the ‘index of stochasticity’ decreases from habitat generalists (Group 1) to habitat specialists (Group 3). These results suggest that the stochastic assembly processes decrease in importance for species groups restricted to fewer microhabitat types and sites. They do so even despite the high richness found in species Group 3.

#### Discussion

A preliminary comparison of the two models (as outlined in Step 1 of the Results section) leads to somewhat contradictory conclusions, and to difficulties with a meaningful quantitative interpretation. On one hand, the ‘IBT – variable recruitment’ model points to significant stochastic processes as governing the distribution of fish species on patch reefs. On the other hand, the ‘habitat-based model’ clearly points to non-stochastic factors as governing fish distributions. To add to this apparent contradiction each model describes a different pattern (richness vs. abundance), and therefore a direct quantitative comparison is not immediately informative (34% vs. 85% of variance explained, respectively).

The analysis performed in Step 2 removes this apparent contradiction and quantitative limitation as to whether stochastic or non-stochastic factors structure the fish assemblage. This analysis shows: (i) that the community is shaped by a mixture of stochastic and non-stochastic mechanisms, and that (ii) there is a shift in predominance from stochastic to non-stochastic processes along the generalist-to-specialist species gradient.

We thus conclude that the two models are in fact consistent; according to the ‘IBT – variable recruitment’ model habitat generalists are distributed according to stochastic expectations. According to the ‘habitat-based model’ constraints apply to the hab-

itat specialists, and this is precisely where the ‘IBT – variable recruitment’ model should fail and does fail.

In summary, our analysis indicates that patches do accumulate individuals and species in a manner consistent with stochastic expectations (‘IBT – variable recruitment’ model). However, this applies to the habitat generalists only. The analysis further indicates that increasing habitat specialization by some species imposes constraints on the stochastic model such that, at the opposite extreme (that of the habitat specialists), the stochastic model fails. This is not surprising if we assume habitat specialists are restricted to a specific set of patches within the template of patch reefs. Thus, a lottery approach to their distribution is unlikely to show a pattern of species accumulation that parallels the distribution pattern of habitat generalists.

By contrast, the ‘habitat-based model’ performs well because it predicts species abundance as a function of landscape fragmentation. The model requires that habitat specialists be restricted to some patches only and be not permitted to use other patches. The model has a good fit to the data because some, but not all, species are subject to such spatial restrictions.

If we are correct, one can view the assemblage structure as hierarchical, with groups of species characterized by different habitat resolutions and different densities. In such a hierarchical structure stochastic factors may be important at any single

level (species group), but in different proportions and with different implications for generic models such as ‘IBT – variable recruitment’ and habitat partitioning models such as the ‘habitat-based model’.

### Acknowledgements

We thank for help in data collecting P. Allen, R. Allen, K. Barnes, J. Beecker, S. Connor, S. LaFlair, K. Lankester, T. Lunn, T. Kaczanowski, K. Sebalj and S. Varieur. Further we extend our appreciation to S. Collins, D. Rollo, S. Glenn and two reviewers for commenting on drafts of this manuscript. Special thanks go to J. Woodley, M. Haley and the staff at the Discovery Bay Marine Laboratory for their continuous help and support. Funding was provided by NSERC to J. Kolasa, and Sigma Xi to N. Waltho.

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*Table 4.* Proportion of variance explained by correlation between the observed and null (= stochastic) data sets. We show for each species group (a) the regression model that maximizes the fit between patch richness and patch surface, (b) the respective coefficients of determination ( $r_i^2$ ), (c)  $r^2$  relative to one obtained for the whole assemblage (i.e., observed  $r^2 = 0.343$ , and null  $r^2 = 0.886$ ), and (d) ‘index of stochasticity’ (this is the ratio between the  $r^2$  obtained from the observed data and those for the null [stochastic] models).

	(a) Regression model	p	(b) $r_i^2$	(c) Relative $r_i^2$	(d) ‘Index of stochasticity’
Observed data					
Group 1 <sub>obs.</sub>	$S = b_0 SA^{b_1}$	< 0.001	0.300	0.874	1.113
Group 2 <sub>obs.</sub>	$S = b_0 + b_1 SA$	< 0.001	0.269	0.784	0.871
Group 3 <sub>obs.</sub>	$S = b_0 + b_1 SA^{0.5}$	< 0.05	0.059	0.172	0.415
Null assemblage					
Group 1 <sub>null</sub>	$S = b_0 + b_1 SA^{0.5}$	< 0.001	0.696	0.785	n/a
Group 2 <sub>null</sub>	$S = b_0 + b_1 SA^{0.5}$	< 0.001	0.797	0.900	n/a
Group 3 <sub>null</sub>	$S = b_0 + b_1 SA^{0.5}$	< 0.001	0.367	0.414	n/a

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## Appendix

We use a family of simple curvilinear and polynomial regression models to optimize the fit between patch richness and patch surface area for (a) entire null and observed assemblages, and (b) null and observed species groups (Table Curve 2D – Jandel 1994). We use the following steps and criteria to choose the most optimal equation: (i) the regression model is statistically significant, (ii) the beta coefficient for the highest ordered term must be statistically significant, (iii) once an equation meets the above criteria we compare its F statistic with the F statistic for the next equation that also meets these criteria but has one less ordered term. We choose the model with the higher F statistic, (iv) iterate

the above process (steps i to iii) for equations with consecutively fewer terms, (v) if no curvilinear or polynomial equation is accepted, we chose the simple linear regression model (equation no. 41) to describe the relationship (assuming it has not already been chosen through the iterative process).

Simple curvilinear and polynomial equations (maximum 4th order polynomial) used: 1  $\ln y = a + bx + cx^2 + dx^3$ ; 2  $y^2 = a + bx + cx^2 + dx^3$ ; 3  $y^{0.5} = a + bx + cx^2 + dx^3$ ; 4  $y^{-1} = a + bx + cx^2 + dx^3$ ; 5  $y = a + b(\ln x)^{-1} + c(\ln x)^{-2} + d(\ln x)^{-3}$ ; 6  $y = a + b(x)^{-1} + c(x)^{-2} + d(x)^{-3}$ ; 7  $y = a + b \ln x + c(\ln x)^2 + d(\ln x)^3$ ; 8  $y = a + b(\ln x)^2 + c \ln x + d(\ln x)^{-1}$ ; 9  $y = a + bx + cx^2 + d(x)^{-1}$ ; 10  $y = a + bx + cx^2 + dx^3$ ; 11  $\ln y = a + bx + cx^2$ ; 12  $y^2 = a + bx + cx^2$ ; 13  $y^{0.5} = a + bx + cx^2$ ; 14  $y = a + b(\ln x)^{-1} + c(\ln x)^{-2}$ ; 15  $y = a + b(x)^{-1} + c(x)^{-2}$ ; 16  $y = a + b \ln x + c(\ln x)^{-1}$ ; 17  $y = a + b(\ln x)^2 + c \ln x$ ; 18  $y = a + bx + c(x)^{-1}$ ; 19  $y = a + bx + cx^2$ ; 20  $\ln y = a + bx$ ; 21  $y = a + be^{-x}$ ; 22  $y = a + b(x)^{-2}$ ; 23  $y = a + b \ln x(x)^{-2}$ ; 24  $y = a + b(x)^{-1.5}$ ; 25  $y = a + b(x)^{-1}$ ; 26  $y = a + b \ln x(x)^{-1}$ ; 27  $y = a + b(x)^{-0.5}$ ; 28  $y = a + b(\ln x)^{-1}$ ; 29  $y = a + b \ln x$ ; 30  $y = a + bx^{0.5}$ ; 31  $y = a + bx(\ln x)^{-1}$ ; 32  $y = a + b(\ln x)^2$ ; 33  $y = a + bx^{0.5} \ln x$ ; 34  $y = a + be^x$ ; 35  $y = a + bx^3$ ; 36  $y = a + bx^{2.5}$ ; 37  $y = a + bx^2 \ln x$ ; 38  $y = a + bx^2$ ; 39  $y = a + bx^{1.5}$ ; 40  $y = a + b \ln x$ ; 41  $y = a + bx$ .