Community structure dynamics of the hermatypic corals on Luhuitou fringing reef, Hainan, China. II. species diversity^{*}

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Abstract : Patterns of community structure, in terms of total number of species, percentage of coral cover, species diversity and evenness, of the hermatypic corals on Luhuitou fringing reef were analyzed on the temporal scale of successional phases and the spatial scales of habitats. Temporal variation of species diversity in the mid- and the deep-zone declined during succession, while the shallow zone did not. There is no indication that coral assemblages in different habitats become more similar over time as corals grow; each successional period showed significant between-habitat variability in the pattern of species diversity.

Key words : community structure, dynamics, species diversity, hermatypic corals, Luhuitou fringing reef

Introduction

This is a subsequent paper of the study on the community structure of the hermatypic corals on Luhuitou fringing reef during succession. Sampling methods and data sets used have been described in a previous paper of this study.

Methods of data analysis

The selected data sets for each zone-successional period were characterized using the following variables:

- (1) total number of species;
- (2) percent coral cover;
- (3) species diversity, calculated as Shannon-Wiener index H (Magurran 1988, Ma Keping 1994):

$$H = - \sum_{i=1}^S P_i \ln P_i$$

where S is the total number of species and P_i is the proportion of total number of individuals belonging to the i th species;

- (4) species evenness, calculated as E for Shannon-Wiener index (Pielou 1975, Magurran 1988):

$$E = H / \ln S$$

where H and S are as defined above.

Values of these variables were examined in relation to successional phases using one-way ANOVA for each zone. A series of Tukey's Q -tests were subsequently performed to compare the means of these variables among successional phases for each zone, and the means of each zones in a successional phase. Differences in effects of successional phases and zone and their interactions with respect to these variables were also evaluated using a two-way ANOVA model. The treatments used in the analysis were successional phases (at five year's interval) and zones.

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Results

Habitat-specific temporal patterns of species diversity

The shallow zone. Age of the oldest colony found in this zone was 28 years ; thus sampled data for this zone were grouped into six successional phases at a five-year interval. All four community parameters , i.e. percent cover , number of species , species diversity indexes H and E showed no clear temporal pattern throughout these phases (see Fig. 1. a) . Statistic analysis detected no significant between- and among-successional phases differences in these variables , indicating that age of the community had no significant effect on the species diversity pattern in this zone (Tables 1 & 2) . In addition , compared with the mid- and deep-zone in the same successional phases , except evenness index E , the other three variables were significantly lower (see Fig. 1. a. & Table 2) .

Table 1 Summary of one-way ANOVA for the effects of successional phase on four variables of the three hermatypic coral zones on Luhuitou fringing reef. Successional phase was counted at five year 's interval from year 1 to 30 for the shallow zone and 1 to 65 for the intermediate and deep zone.

Zone	Variable	df	F value	Significance
Shallow	% cover	5	1.54	ns
	No. of species	5	2.03	ns
	H	5	2.36	ns
	E	5	0.98	ns
Mid	% cover	13	2.28	*
	No. of species	13	1.76	ns
	H	13	4.9	* *
	E	13	3.2	* *
Deep	% cover	13	2.15	*
	No. of species	13	21.3	* *
	H	13	32.2	* *
	E	13	26.6	* *

* = $F < F_{0.05}$; * * = $F < F_{0.01}$; ns = not significant.

The mid zone. In this zone , succession was found has significant effects on percent cover , H and E , but no significant effect on number of species (Table 1) although Q-tests revealed some significant between-period differences (Table 2) . Means of the four variables all were lowest in the earliest successional phase (1 ~ 5 years) and showed a generally similar increasing trend with succession time over earlier successional phases (1 ~ 20 years) , but their later variation patterns were different from one another (Fig. 1. b. & Table 1 , 2) .

Percent cover kept rapid increasing in periods 20 ~ 40 years , and remained at a maximum for the following successional phases. Comparison of means of percent cover shown no significant difference between these phases (> 45 years) (Table 2) . Number of species increases with succession time until periods 35 ~ 40 years. Unlike the percent cover , it declined slightly after it reached a peak at period 35 ~ 40 years ; however , differences among the means for these later periods were not statistically significant in most cases (Table 1) .

Species diversity measure H also increases with succession time before it arrives at a maximum in period 25 ~ 40 years ; but it decreases evidently during 35 ~ 45 years and remained no significant alteration over the following successional time (> 45 years) (Fig. 1. b. & Table 2) .

Temporal patterns of species evenness index E showed similar trends to H , except that the decreasing trend of E occurred earlier than that of H . This indicated that the decrease of H over later periods (35 ~ 45 years) was caused by a decrease of E , because species number did not

change much (Fig. 1. b. & Table 2).

Table 2 Summary of statistical analysis of spatio-temporal variations in percent cover, number of species, *H* and *E* on Luhuitou fringing reef. Shown are the mean $\pm$ SE of the data sets for each zone-successional phase, results of between-zone comparison (on the bottom of each variable successional phase block) and among successional phases comparisons for each zone (in the left column) using Turkey's *Q* tests (significance level : 95 %).

		Successional phase (year)			
		1 ~ 10 (P1)	11 ~ 20 (P2)	21 ~ 30 (P3)	31 ~ 40 (P4)
% cover	Shallow	1.16 $\pm$ 0.54	3.54 $\pm$ 0.85	3.41 $\pm$ 0.73	
	Mid	5.19 $\pm$ 0.40	7.07 $\pm$ 1.20	14.41 $\pm$ 2.11	35.88 $\pm$ 3.49
	Deep	5.64 $\pm$ 0.52	17.57 $\pm$ 2.23	43.92 $\pm$ 4.78	54.38 $\pm$ 5.35
		$S < I = D$	$S < I < D$	$S < I < D$	$I < D$
No. of species	Shallow	5.80 $\pm$ 0.94	6.20 $\pm$ 0.89	6.40 $\pm$ 1.04	
	Mid	7.20 $\pm$ 1.10	22.80 $\pm$ 2.44	31.60 $\pm$ 2.90	37.20 $\pm$ 3.51
	Deep	7.65 $\pm$ 1.11	24.00 $\pm$ 2.54	31.30 $\pm$ 3.29	30.00 $\pm$ 2.83
		$S < I = D$	$S < I = D$	$S < I = D$	$D < I$
<i>H</i>	Shallow	0.91 $\pm$ 0.11	1.03 $\pm$ 0.13	0.94 $\pm$ 0.10	
	Mid	1.33 $\pm$ 0.13	2.29 $\pm$ 0.20	2.56 $\pm$ 0.30	2.53 $\pm$ 0.20
	Deep	1.33 $\pm$ 0.12	2.37 $\pm$ 0.21	2.47 $\pm$ 0.26	2.23 $\pm$ 0.21
		$S < I = D$	$S < I = D$	$S < I = D$	$I > D$
		Successional phase (year)			Relationship
		41 ~ 50 (P5)	51 ~ 60 (P6)	> 60 (P7)	
% cover	Shallow				$P1 < P2 = P3$
	Mid	36.37 $\pm$ 3.82	36.37 $\pm$ 4.80	36.11 $\pm$ 4.81	$P1 < P2 < P3 < P4 = P5 = P6 = P7$
	Deep	56.37 $\pm$ 6.63	58.02 $\pm$ 6.53	58.11 $\pm$ 6.80	$P1 < P2 < P3 < P4 < P5 = P6 = P7$
		$I < D$	$I < D$	$I < D$	
No. of species	Shallow				$P1 = P2 = P3$
	Mid	38.00 $\pm$ 2.70	34.80 $\pm$ 2.87	36.00 $\pm$ 4.97	$P1 < P2 < P3 < P4 = P5 = P6 = P7$
	Deep	27.60 $\pm$ 3.32	26.80 $\pm$ 2.45	25.60 $\pm$ 2.75	$P1 < P2 < P3 = P4 > P5 = P6 = P7$
		$D < I$	$D < I$	$D < I$	
<i>H</i>	Shallow				$P1 = P2 = P3$
	Mid	2.17 $\pm$ 0.29	2.10 $\pm$ 0.18	2.14 $\pm$ 0.22	$P1 < P2 < P3 < P4 > P5 = P6 = P7$
	Deep	1.75 $\pm$ 0.17	1.63 $\pm$ 0.18	1.63 $\pm$ 0.13	$P1 < P2 < P3 = P4 > P5 = P6 = P7$
		$I > D$	$I > D$	$I > D$	

The deep zone. Compared with the mid zone, although variation patterns of the four variables over the earlier successional periods (1 ~ 20 year) resembled each other, their between-zone differences in the variation of these variables over following periods were remarkable. Although same as in the mid zone, means of these variables for the early periods were all significantly low than that of the later successional periods. The means for these variables showed much more dramatic changes and these changes lasted longer than that for the mid zone or the shallow zone (Fig. 1. b, c.). Further examination on the four variables in relation to both successional time and zone using two-way ANOVA and *Q*-test was also consistent with the above analysis (Table 2 & 3).

As succession advanced, the percent cover in deep zone rapidly increased (1 ~ 30 years) resulting in insignificant differences among the late time periods (> 30 years) (Fig. 1.c. & Table 2); while both early and late phases had significantly fewer species, lower *H* and *E* values than mid phases (20 ~ 30 years). This suggests that competition exclusions between coral species exerted great effect on the pattern of diversity in this zone.

Fig.1 Successional variations ($\bar{x} \pm SD$) of four parameter of community structure , i. e. coral coverage(%) , total number of species , species diversity H' and evenness E , of a. the shallow zone ; b. the mid zone , and c. the deep zone

Table 3 Summary of two way ANOVA for the effects of successional phase and distribution zone on four variables of the hermatypic coral community on Luhuitou fringing reef. Successional periods was counted at five year 's interval from year 1 to 65.

	Zone (df = 2)		Successional phase (df = 12)		Zone x Period (df = 24)	
	<i>F</i>	Sig. of <i>F</i>	<i>F</i>	Sig. of <i>F</i>	<i>F</i>	Sig. of <i>F</i>
% cover	8.39	* *	1.35	ns	6.34	* *
No. species	5.83	*	1.72	ns	1.82	*
<i>H</i>	9.61	* *	18.43	* *	2.80	* *
<i>E</i>	8.95	* *	16.26	* *	2.42	* *

* = $P < 0.05$; * * = $P < 0.01$; ns = not significant.

Effects of succession on and habitat type on species diversity

From the above descriptions of successional changes of each zone, we could get the impression that difference in the effects of succession time and habitat type on species diversity was remarkable. Analysis of variance revealed significant influences of both successional phase and zone on these variables (Table 3). Between-zone differences were statistically significant in nearly all successional phases (Table 1 & 2). There were also significant interactions between zone and successional phase (Table 3) on all four variables, which were resulted from the among-zone differences in these variables and their distinct temporal patterns.

Temporal variation in the mid- and the deep-zone seems to decline during succession, while the shallow does not. The later successional phases in the deep- and the mid-zone, in accordance with theory, appear to be more stable than earlier phases. This form of variation is likely to represent, at least in part, resistance of the community to disturbance from external sources, and therefore may be interpreted as a measure of structure stability. There is, however, no indication in this study that coral assemblages in these zones become more similar over time as the corals grow. Each of the successional phases shows significant among- and between-zone variability in the four variables being analyzed (Table 1). Spatial variability therefore does not appear to decline during succession. On the contrary, coral zonations became more distinct along succession.

Discussion

Temporal patterns of species diversity and the environmental conditions

The temporal pattern of species diversity is closely correlated with the predictability of environment (Putman & Wratten, 1984). Species patterns may be highly deterministic in stable, or predictable (e.g. the deep zone on the study reef) environmental conditions. This is because, in such an environment, especially in late successional phases, species diversity patterns are maintained mainly by reef-building corals themselves through species-specific interaction. On the contrary, stochastic variations of species diversity over time are more likely to be found in unpredictable environments.

Results in this study reiterate that, it may be always unlikely that an entire community on a reef could be categorized as belonging to a single successional stage. Thus, comparison between different habitat types for reef corals at various scales is critical for further understanding succession.

Spatial subdivision plays a key role in controlling species dynamics and species diversity of the coral community on a given habitat. For example, the superior competitor *Acropora* spp. displaced most of the seral species from the less divided habitat (the deep zone), while competing species could coexist in spatial subdivided habitat in the mid zone. Another example is that, rare species may be extremely specialized on physical characteristics of the environment in the mid zone

on this reef, where environment heterogeneity is the highest among the three zones. As it has been pointed out, specialization results in fewer encounters between species and hence with fewer competitors. Where competition with neighboring species occurs the species with the greater specialization will have an advantage.

On the evaluation of the relative importance of different ecological factors in controlling species diversity patterns

Actual community trajectories are influenced by many factors, both physico-chemical and biotic (Done et al. 1991). Ecologists now appreciate that many factors concurrently influence distribution and abundance and that single factor analyses are insufficient to understand how populations, groups of species and, ultimately, communities are structured (Polis 1994).

At the same time, different types of ecological factors and processes operate on different temporal and spatial scales; In other word, physical and biological processes exhibit different patterns of distribution along the spatial and/or temporal dimension. Reliable conclusions on controls on species diversity can be reached only when both spatial and temporal scales are considered; e. g. that the appearance of a coral colony of a given species depends on the previous conditions arising in the environment, that disturbances can both reduce and increase diversity depending on history, and that physico-chemical conditions and inter-species competition are of different importance between environments and between times in a given environment, etc. Therefore, convincing evaluations of the relative importance of different ecological factors and processes in determining the spatio-temporal patterns of species diversity of reef-building corals will require detailed and simultaneous investigation by applying both multi-factorial and scaling approaches.

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海南鹿回头岸礁造礁石珊瑚群落结构动态 . 物种多样性

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摘 要 根据石珊瑚物种的总数、石珊瑚覆盖的百分率、物种多样性和均匀度,对鹿回头岸礁造礁石珊瑚群落结构类型所处演替阶段的时间状态和生境的空间状态进行分析。在中等和深水区物种多样性的时间变异,随演替的发展而有所下降;浅水区不随演替而变化。在不同生境区珊瑚生长的聚群上,与时间的发展无关;每个演替时期,物种多样性的类型与生境的变化有关。

关键词 群落结构动态,物种多样性,造礁石珊瑚,鹿回头岸礁