Community Structure Dynamics of the Hermatypic Corals on Luhuitou Fringing Reef, Hainan, China. I. Species Composition and Abundance *

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ABSTRACT

The existing hermatypic coral community is composed of localities in different successional ages. Data sets were selected from original sampling data to deduce the trajectory of community structure in this and subsequent papers. Patterns of species composition and abundance distribution during community succession in the scope of different habitats were described in this paper. It is found that the effect of succession on community structure is closely correlated with the environmental conditions. Each coral assemblage in different habitat has its own distinguishing temporal pattern of species composition and abundance distribution.

Key words Luhuitou fringing reef, hermatypic corals, community structure

1 Introduction

Study on coral community succession, especially the recovery of disturbed coral communities, has received a great deal of theoretical and empirical attention in the last two decades (e.g. Connell 1978; Grigg 1983; Fitzhardinge 1985; Hughes 1985, 1989; Hughes and Jackson 1985; Sammarco 1985; Wallace 1985a, b; Colgan 1987; Done et al. 1988, 1991; Phongsuwan 1991, etc). However, most studies of hermatypic coral succession have been concentrated on only a portion of a community and covered a much shorter time period compared with the time taken for a coral community succession process. Some of these investigations primarily concern only whether or not damaged reef returns to coral dominance. There are limited data on the community structure dynamics from various aspects and among different hermatypic coral habitats.

Since in 1992, the research project entitled "Structure, Function and Recovery Mechanisms of Coral-Reef Ecosystems" has been carried out by the authors. The dynamics of the community structure of hermatypic corals during succession is a main subject in this research. Luhuitou fringing reef, the study site, is a typical fringing reef in South China Sea, and was declared as a protected reef of the first National Coral Reef Reserve in China in 1990. However, the reef had long been disturbed intermittently mainly by local people through direct

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uprooting of corals and dredging up of the substrata (for making lime and building material), and the way of using explosive and trawl in fishing. These man-induced disturbances provided primary space on which corals and/or other organisms can resettle. Recovery, or secondary successions thus initiated continuously on those disturbed sites. The existing coral community is composed of patches in different successional ages. Under these special circumstances, it is possible to depict the recovery trajectory of hermatypic corals on this reef by putting together the investigation data of sites in different succession phrases.

Theoretically and strictly speaking, study of coral community dynamics should be based on long-term observation. However, even if there is an opportunity, such an approach would last too long a time to have much practical value in providing scientific basis for coral-reef conservation. This approach as adopted in our study may serve to certain extent as an alternative to the long-term monitoring in investigating some processes of the secondary succession (or recovery) of a hermatypic coral community both on finer spatial scales and over longer temporal scales. These results in our study may have marked a beginning for a more complete understanding of the temporal and spatial variation in the community structure of hermatypic coral communities.

Succession and dynamics of species diversity of the hermatypic corals at the community level on this reef has been described by us recently. This paper reports the results of the study on the spatio-temporal patterns of species composition and distribution of abundance during community succession. Due to limited space, the detailed discussion will be presented in subsequent papers.

2 *Materials and methods*

Luhuitou fringing reef (109°28'E, 18°13'N) is located on Luhuitou Peninsula, at the south end of the Hainan Island, China (Fig. 1). Tides in Sanya Bay are irregularly diurnal. The reef is from 400 to 500 m wide measured from the shore to the outer edge of the reef slope and is divided into 2 morphological units: a reef flat and a seaward slope separated by shingle rampart. Detailed descriptions of the morphology of this reef are available in previous studies (Zou Renlin et al. 1966, Huang Jinshen et al. 1975).

The zonation patterns of hermatypic corals on Luhuitou fringing reef also have been described (Zou Renlin et al. 1966, Zou Renlin and Yu Dengpan 1993). The three reef coral zonations found were referred to as *Goniasterea*-zone, *Montipora*-zone and *Acropora*-zone according to the dominant genus inhabited on each zone in that investigation time (Zou Renlin et al. 1966). It is also found in this study that the reef-building corals revealed depth-related zonations on this reef, which are defined in this study as "shallow-zone", "mid-zone" and "deep-zone" with depth ranges: 0.0~1.5 m, 2.0~3.0 m and 3.0~8.0 m below mean high water respectively. These three major zones were always distinct in nearly all successional stages, but the dominant taxa on a zone may exchange during succession.

2.1 *Methodologies of field survey and data sets selection*

The original data come from two field investigations. The first investigation was conducted from March 1993 to January 1994. Systematic quadrat sampling method (Greig-Smith 1952, Lu Yang 1986) was adopted. Four underwater transects were set up. Each transect started from the high-water mark and ended at the outer edge of the reef slope (Fig. 1). A 1×1 m steel frame was used to conduct the survey. A quadrat sampling was made a-

long each transect at 1 m interval. The second investigation was conducted from April to August 1994 adopting contiguous grid sampling method. Twenty 10×10 m sampling stations were randomly defined along each of the four transects set up in the first investigation, and divided into 1×1 m quadrats. Samples were then taken in the quadrats.

Fig. 1 Locations of study reef and of sampled transects on the reef

In both investigations, each colony was counted as a single individual. Maximum length, width and height were measured for each colony. If a coral colony was more or less circular in shape, then the cover area of such a coral colony was calculated as the area of circle. In case of an irregularly shaped coral, cover area was calculated based on the assumption that the coral colony was elliptical.

The age of each coral colony was estimated according to its maximum width (W), length (L) and height (H), and the linear growth rate (L_{GR}) of this species follows:

$$\text{Age} = (W + L + H) / 3 (L_{GR})$$

L_{GR} s of 32 coral species on the study reef were measured *in-situ* from March 1993 to April 1994, data on L_{GR} s of the rest 26 species were adopted from Ma TYH (1937, 1959). The age of the oldest coral colony in a quadrat was counted as the successional time of the locality in this quadrat. The method of identifying the size of patches (Greig-Smith 1952, see also Ver Hoef and Glenn-Lewin 1989, Kotliar and Wiens 1990) was used in pooling the quadrat samples into zone-successional period groups, with successional time of each quadrat sample and the zone it located in used as parameters. Successional time period was counted at 5 a and 10 a interval respectively.

Through statistic analyses on these original data, we have found that both the size and position of a patch have significant effects on coral recruitment pattern. However, when only larger patches ($> 10 \text{ m}^2$) were compared, effects resulting from patch size become insignificant (due to limited space, details to be reported separately). Therefore, quadrat samples in a patch less than 10 m^2 were not chosen, to insure that the difference in effects of size on coral recovery could be neglected. Totally, 2380 quadrat samples were selected from all samples collected. It is essential that same sample size be used in the comparison of the parameters of community structure among zones and successional periods. To this end, 30 quadrats were randomly selected for 10 times from all the quadrat samples identified to be of a zone-

successional period; the 30 quadrats selected each time were treated as one data set in this and subsequent papers.

2.2 Data analysis

Relative abundance of each species was measured in percentage importance value (IV%) for each data set of each zone-successional period. The among successional period variations of relative abundance of common species in each zone were examined adopting Tukey's Q-tests to decide whether a given species was more abundant at one period than another. Species being tested for each zone-successional period group are present at abundance level of importance value (IV) > 10.

Distribution of species abundance was analyzed by comparing the data set of a given zone-successional period with four main conventional models, i. e. the geometric series, the log normal distribution, the logarithmic series and MacArthur's broken stick model. Because the importance values of some rare species are less than 0.001, the parameter for species relative abundance we adopted in this study is 10 times IV%, ranging from 1 to 1000 (instead of the number of individuals as in many other studies). The procedure for fitting a model is to calculate the number of species expected in each abundance class and compare that with the IV% of species actually observed using an X^2 -test (for details see Magurran 1988). In calculating X^2 value for last three models, $\log_2$ was used in expressing the species abundance class, or octave in this study.

3 Results

3.1 The shallow-zone

The age of the oldest colony found in this zone was 28 a; thus sampled data for this zone could only be grouped into 6 successional periods at 5 a interval. Species richness in this zone was constantly low, and showed no marked change during succession. Species abundance distributions in all three periods on this zone fitted the geometric series pattern (Fig. 3. a, Table 1). Difference among these models was due to the fact that the K values showed slight decrease with successional time, indicating that the relative abundance of dominant species was slightly higher in the initial successional period than later period.

3.2 The mid-zone

As shown in Fig. 2. b. and Fig. 3. b., several patterns of species abundance and composition are evident on mid-zone. *Porites lutea* decreased during succession whereas *Montipora* spp. and *Favia speciosa* increased their abundance. Dominance of *P. lutea* was gradually replaced after 5 a when *Montipora* spp. became the dominant species. *Montipora rostrata*, *M. sinensis*, *Acropora corymbosa*, *F. speciosa* and *Platygyra crosslandi* all showed rapid increases in relative abundance over early successional periods (1~30 a), while mid and late periods (>21 a) supported approximately the same abundance levels. *Montipora* spp. contributed the most important part of the community biomass in later successional phases (>20 a) (Fig. 2. b.).

The species richness in later successional periods was similar. In addition, between-period fluctuations in species richness of the rare species in this zone were less than in the deep-zone (Fig. 3. b~c.). The mid-zone harbored more rare species than either of the other two zones.

Fig. 2 Species composition and relative abundance of the hermatypic corals in: a. the shallow-zone, b. the mid-zone and c. the deep-zone in the process of succession. Shown are the percentage importance value (IV%) for each species that has IV > 5

Abbreviations of species names in Fig. 2a ~ c: Ac = *Acropora corymbosa* (Quelch); Af = *A. formosa* (Dana); Ah = *A. humilis* (Dana); Ap = *A. prostrata* (Dana); Cs = *Cyphastrea serailia* (Forsk.); Fa = *Favites abdita* (Ellis & Solander); Fs = *Favia speciosa* (Dana); Ga = *Goniastrea aspera* Verrill; Gp = *G. pectinata* (Ehrenberg); Gr = *G. retiformis* (Lamarck); Gd = *Gonipora duofasciata* Thiel; Gf = *Galaxea fascicularis* (Linnaeus); Gl = *G. larmarcki* Milne-Edwards & Haime; Mh = *Montipora hispida* (Dana); Mr = *M. ramosa* Bernard; Ms = *M. sinensis* Bernard; Pa = *Porites andrewsi* Vaughan; Pl = *P. lutea* Milne-Edwards & Haime; Pb = *Pocillopora brevicornis* Lamarck; Pd = *P. damicornis* (Linnaeus); Pc = *Platygyra crosslandi* (Matthai); Pg = *P. gracilis* (Dana); Pr = *P. rustica* (Dana)

The comparative rarity and persistence of rare species in the mid-zone during succession may imply that these species are slow to settle into this habitat, but once having done so, they

are quite persistent.

Table 1 Fit model of species abundance distribution for each zone-successional period (at 10 a interval)

Zone	Suc. time (a)	Fitted model	χ^2	df	P-value	Parameters in equation
Shallow	1~10	GM	4.92	5	$0.30 < P < 0.50$	$K = 0.5709$
	11~20	GM	3.50	6	$0.70 < P < 0.80$	$K = 0.4438$
	21~30	GM	1.50	6	$0.95 < P < 0.98$	$K = 0.4056$
Mid	1~10	GM	12.42	11	$0.30 < P < 0.50$	$K = 0.1876$
		BS	3.73	3	$0.20 < P < 0.30$	$S = 12; N = 1000$
	11~20	BS	3.84	7	$0.70 < P < 0.80$	$S = 32; N = 1000$
		LN	8.05	7	$0.30 < P < 0.50$	$\alpha = 0.21241; R_0 = 8; S_0 = 4.66$
		GM	43.58	31	$0.05 < P < 0.10$	$K = 0.1610$
	21~30	LN	5.71	10	$0.80 < P < 0.90$	$\alpha = 0.21337; R_0 = 7; S_0 = 5.86$
	31~40	LN	6.36	9	$0.70 < P < 0.80$	$\alpha = 0.22035; R_0 = 6; S_0 = 7.42$
	41~50	LN	7.12	9	$0.50 < P < 0.70$	$\alpha = 0.2425; R_0 = 7; S_0 = 7.35$
	51~60	LN	10.26	10	$0.30 < P < 0.50$	$\alpha = 0.2651; R_0 = 7; S_0 = 7.28$
	>60	LN	8.93	10	$0.50 < P < 0.70$	$\alpha = 0.2672; R_0 = 6; S_0 = 7.46$
Deep	1~10	GM	2.81	10	$0.98 < P < 0.99$	$K = 0.2477$
		BS	3.06	4	$0.50 < P < 0.70$	$S = 11; N = 1000$
	11~20	GM	32.26	31	$0.30 < P < 0.50$	$K = 0.1461$
	21~30	LN	5.07	10	$0.80 < P < 0.90$	$\alpha = 0.2315; R_0 = 7; S_0 = 6.51$
	31~40	LN	9.52	11	$0.30 < P < 0.50$	$\alpha = 0.2251; R_0 = 6; S_0 = 7.5$
	41~50	LS	8.18	8	$0.30 < P < 0.50$	$\alpha = 6.8091; x = 0.9993196$
		GM	37.67	48	$0.30 < P < 0.50$	$K = 0.1256$
	51~60	LS	3.31	11	$0.98 < P < 0.99$	$\alpha = 5.9067; x = 0.9994097$
		GM	32.81	43	$0.50 < P < 0.70$	$K = 0.1573$
	>60	LS	7.49	11	$0.70 < P < 0.80$	$\alpha = 5.3728; x = 0.9994630$

A fit model was chosen using χ^2 -test (significance level: 95%). GM=geometric series; BS=broken stick; LN=log normal; LS=log series

3.3 The deep zone

The deep zone stood apart from the others on the aspects of patterns of species composition and abundance distribution (Fig.2, Fig.3 and Table 1). It included the highest proportion of Acroporidae, and the lowest proportion of both Faviidae and massive Porites. Besides, colonies of the *Acropora* spp. in the deep-zone were generally larger than those in the mid-zone.

The characteristic species in the deep-zone in the late successional phrases were *A. formosa*, *A. corymbosa*, and *A. humilis*. Percent cover of these fast-growing species increased rapidly with succession during periods 11~30 a (Fig. 2. c., Fig. 3. c.). They were rather commonly overgrown many of the massive and encrusting corals formerly occupying this zone.

Fig. 3 Rank abundance plots showing species abundance distribution of the community and each zone in different successional periods (at 10 a interval)

Data are mean IV% of each species for 10 data sets of each successional period (see text for details)

4 Discussion

4.1 Habitat-specific patterns of species composition and abundance

In the shallow zone, species were always scarce in any of the successional periods. Altogether only 7 species (*Goniastrea aspera*, *G. yamanarii*, *G. retiformis*, *Porites lutea*, *Platygyra rustica*, *Favia speciosa*, and *Acropora pulchra*) were recorded in this zone for all three 10 a periods (Fig. 2. a). These species, especially *P. lutea*, *G. aspera* and *A. pulchra*, exhibited general distribution pattern on this reef. These species also inhabited in elsewhere in the mid- and the deep-zone and was more abundant in mid-zone in 1 ~ 20 a period (Fig. 2. b, c). The geometric series patterns of species abundance were found primarily in species-poor (and often harsh) environments or in the very early successional stages. The shallow-zone on Luhuitou fringing reef was obviously an unsuitable habitat for most hermatypic corals.

Analysis of variance for the mid zone revealed significant interactions between successional stages and sample dates for the species richness and density of nearly all taxa at the family level.

All rare species ($IV < 10$) in this zone showed fluctuations in relative abundance although no common pattern was found. Most rare species was more abundant at this zone and species richness in later successional periods was similar (Fig. 3. b). This phenomenon indicated that the environmental conditions in the mid-zone were the most complicated among the three kinds of habitats on the study reef.

In the deep zone, initial coral recovery occurred mainly as the result of coral larval resettlement, while space competition among corals played the most important role in later successional stages. Decreases of species diversity in the middle successional periods were apparently due to space limitation and competitive exclusion by dominant species. A few species were quite common and the rest were rather rare in those late successional periods (Fig. 2. c). Only 6 species' IV% were greater than 1 after the period 31~40 a, IV% of the other species in these periods were between 0.016 and 1 (Fig. 3. c).

Patterns of species composition and abundance reflected the difference in environmental conditions. Results showed that the proportionate population densities of the component species occurred in a distinct pattern in each habitat type, and this pattern was clearly apparent at almost any sufficiently extensive site in each zone. We suggest that these phenomena are a direct result of the existence and maintenance of different population densities in different zones by most component species. This also clearly demonstrates that these three zones can be distinguished as different habitats for reef corals.

4.2 Mechanism responsible for the variation of species composition and abundance

From the aspect of hermatypic corals themselves, the mechanism responsible for the variation of species composition and abundance appears to involve both habitat-selection and competitive exclusion, with the former playing more important role in structuring these coral assemblages in the earlier successional stages, while the later being more important in the late successional stages.

Our study also suggests that spatial heterogeneity is an essential factor controlling the species composition and abundance of a hermatypic coral community. The habitat-associated differences might be attributable to the combined effect of recruitment pattern, competition exclusion and spatial heterogeneity. For example, the superior competitor *Acropora* spp. displaced most of the serial species from the less divided habitat (the deep zone), while competing species could coexist in spatially subdivided habitat in the mid zone. Rare coral species may be extremely specialized on physical characteristics of the environment in the mid zone on this reef, where the environment heterogeneity is the highest among the three zones. These findings may therefore re-initiate the potential importance of spatial heterogeneity.

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