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Genetic structure of a scleractinian coral, *Mycedium elephantotus*, in Taiwan

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Abstract The genetic structure of *Mycedium elephantotus* (Pallas, 1766) populations from three regions around Taiwan was examined using allozyme electrophoresis. Eight loci were scored from seven enzyme systems. Seven loci were polymorphic under the 95% criterion. The high ratio of observed to expected genotypic diversities at the collection sites ($G_O:G_E=0.8$ to 1.0) indicate that *M. elephantotus* propagates predominantly by sexual reproduction. Allele frequencies of *M. elephantotus* differed significantly among regions ($D=0.024$ to 0.256, $F_{ST}=0.032$ to 0.218, $p < 0.001$), while populations among collection sites within each region were homogeneous ($D=0.000$ to 0.015, $F_{ST}=0.010$ to 0.022, $p > 0.05$). Genetic differentiation between populations from southern Taiwan and the Penghu Islands is greater than that between southern and northern Taiwan populations, although the former two regions are much closer geographically. The UPGMA dendrogram based on Nei's unbiased genetic distance showed a clear subdivision of populations into two groupings, northern Taiwan/Penghu Islands and southern Taiwan. A higher level of gene flow was found between *M. elephantotus* populations in northern Taiwan and the Penghu Islands ($N_m=7.56$) than that between populations in southern Taiwan and other regions ($N_m=0.90$ to 1.72). The pattern of genetic subdivision among regions is consistent with the pattern of ocean currents, indicating that genetic differentiation is likely driven by surface circulation vicariance.

Introduction

Population genetic studies of marine species have often shown that species with high dispersal potential have little genetic differentiation over large geographic scales (Benzie and Williams 1992; Burnett et al. 1995; Hellberg 1996). These results suggest high levels of gene flow between marine populations, but there may often be limits to the actual dispersal of marine species with high dispersal potential (Stoddart 1984; Edmands et al. 1996; Benzie and Williams 1997; Palumbi et al. 1997). These limits vary widely with species, habitat, local ocean conditions, and recent history, and they may create sufficient opportunity for genetic divergence (Palumbi 1992, 1994; Benzie et al. 1995; Palumbi et al. 1997). Although such limits may seldom create absolute barriers to gene flow, they may often constrain gene flow in some directions or at some times (Edmands et al. 1996; Benzie and Williams 1997). Thus partially isolated populations may occur quite commonly in marine systems.

The complex oceanic circulation patterns, both in the past and at present, set the biogeographic boundaries that define the limits of biogeographic provinces (Veron 1995). Ocean currents may act as barriers to dispersion or vehicles of transport, and genetic divergence of marine populations is often driven by surface circulation vicariance (Veron 1995). On the other hand, ocean currents are sometimes able to carry larvae far from their parents. The distance that a larva can be transported by currents depends on its duration of planktonic stage and its sources of energy (Strathmann 1986). The type of embryonic and larval development affects dispersal and hence gene flow in species with sedentary adults (Hedgecock 1986). However, even if larvae were simply passive planktonic particles and drifting passively in ocean currents, gene flow across the ocean would be neither continuous nor random (Billingham and Ayre 1996; Palumbi et al. 1997). There may be a limit to gene flow even in species with larvae that

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can disperse long distances. In addition, marine species may not realize their greatest dispersal potential because behavioral mechanisms or planktonic transport may pose hazards (Edmands et al. 1996). Effective dispersal may also be limited by physical processes, including large-scale current patterns (Incze et al. 1990) and smaller-scale eddies and upwelling zones (Ebert and Russell 1988). If most planktonic dispersal follows the ocean current, then movement from one current regime or water mass to the others might be infrequent (Palumbi 1994; Veron 1995). Since the world ocean is composed of many current systems, even the open ocean is a fragmented habitat. Although few data exist on the influence of ocean current on population genetic structure, gene flow across the oceans is probably constrained or directed by such circulation patterns (Ayre et al. 1991; Billingham and Ayre 1996; Edmands et al. 1996).

In benthic marine invertebrates, the dispersal of larvae constitutes the primary source of continuing gene flow (Hedgecock 1986; Hellberg 1995). Broad dispersal should genetically homogenize populations, as immigrants originate in widely different environments. In contrast, geographically restricted gene flow enhances differentiation among populations, as the relatively few immigrants arriving from nearby populations tend to resemble residents genetically. Species with high larval dispersal capabilities such as broadcast spawners have been associated with lower levels of genetic subdivision and wider geographical ranges than those with low dispersal capabilities such as brooders (Buroker 1985; Benzie et al. 1995; Hellberg 1996).

Mycedium elephantotus is a widely distributed scleractinian on many Indo-Pacific reefs, where it may form large assemblages and dominate certain reef areas (Veron 1993). *M. elephantotus* has been considered one of the dominant species in coral communities around Taiwan (Yang and Dai 1982; Dai 1993). It is a broadcast spawner and has an annual reproductive cycle (Fan 1996). Its life history characteristics suggest that high levels of gene flow and limited genetic differentiation among populations could be expected. Dai et al. (1992) reported that spawning of *M. elephantotus* populations in southern Taiwan populations took place primarily in April and May, while that in northern Taiwan occurred in July and August. In addition, complex circulation patterns around Taiwan have been reported by several authors (e.g. Wang and Chern 1988, 1996; Chern and Wang 1989, 1992). Such temporal isolation of reproduction and the complex circulation patterns, either alone or together, may have important influences on population structures. In the present study we used an electrophoretic survey at eight allozyme loci to quantify levels of variation among *M. elephantotus* populations from three regions in Taiwan.

Materials and methods

Field collections

Specimens of *Mycedium elephantotus* (Pallas, 1766) were collected from three regions in Taiwan: northern Taiwan, Penghu Islands, and southern Taiwan (Fig. 1) between 1995 and 1996. Within each region, samples were collected at two or three separate reef sites at a distance of more than 5 km apart, and samples from each reef site were considered as a population. Each population consisted of fragments (approximately $3 \times 3 \text{ cm}^2$) from 18 to 34 individual colonies. Fragments were collected haphazardly from each reef site within apparently uniform habitats. Care was taken not to include replicate fragments from colonies (within a few centimeters of the periphery) that had apparently undergone recent colony fragmentation due to sedimentation pollution. After removing epiphytic organisms, chips from a given colony were placed in liquid nitrogen within 2 h of collection, transported to the laboratory, and stored at -70°C .

Laboratory analysis

The coral tissues were scraped off and ground in two drops of indicator extractant (Stoddart 1983) and then homogenized in half of the sample volumes of indicator extractant using a sonicator. Homogenates were centrifuged at $17000 \times g$ for 40 min at 4°C , and the supernatants were then stored at -70°C until electrophoresis.

Horizontal electrophoresis with 12% starch gel was performed at 4°C under different buffer systems and electrical conditions. The following eight enzyme systems were used: malate dehydrogenase (MDH, EC 1.1.1.37); esterase (EST, EC 3.1.1.-); phosphoglucomutase (PGM, EC 5.4.2.2); dipeptidase using glycyl-leucine as a substrate (PEPA, EC 3.4.-.-); mannose-6-phosphate isomerase (MPI, EC 5.3.1.8); malic enzyme (NADP^+) (MEP, EC 1.1.1.40); and tri-peptide aminopeptidase using leucyl-glycyl-glycine as a substrate (PEPB, EC 3.4.-.-). MDH, EST and PGM were run using a Tris EDTA citrate pH 7.0 (TEC 7.0) buffer (modified buffer of TEC 7.9 in Benzie et al. 1995); PEPA, MPI, and MEP were run using a Tris citrate pH 8.0 buffer; and PEPB was run using a Tris citrate borate LiOH buffer (Redfield and Salini 1980). Alleles were assigned a value based on the ratio of their electrophoretic mobility relative to that of the most common allele.

Statistical analysis

Gene frequencies, basic measures of genetic variability, analyses of heterogeneity among populations, genetic distances and cluster analyses were done using programs in BIOSYS-1 (Release 1.7, Swofford and Selander 1989). The hypotheses that each population is in Hardy-Weinberg equilibrium was tested with χ^2 tests. When more than two alleles are observed at a locus, BIOSYS-1 pools genotypes into three classes and repeats the tests. This is accomplished by considering all alleles except the most common one as a single allele.

Two measures were used to assess the possible effects of asexually derived recruits on the genotypic diversity of collections. First, each colony was assigned a multilocus ("clonal") genotype. The number of multilocus genotypes detected (N_G) is thus an estimate of the minimum number of clones that are present within a population; and the ratio N_G/N_I (number of collected individual colonies) provides the simple index of the effects of asexual reproduction on genotypic diversity. Second, the ratio of observed multilocus genotypic diversity (G_O) to that expected under conditions of sexual reproduction (G_E) was calculated following Stoddart and Taylor (1988). Departure of G_O/G_E from unity provides an index of the combined effects of departures from single-locus Hardy-Weinberg equilibrium and multilocus linkage disequilibrium.

Fig. 1 Map of Taiwan showing three study regions with detailed collection sites indicated by stars (MO Mao-ao; YL Yeh-liu; JY Jin-yu; GPY Gu-po-yu; HCW Hsiang-chiao-wan; HC Hung-chai; TS Tiao-shi). Arrows indicate the current flows in spring and summer

um. A genetically variable population with high levels of asexual recruitment should display a low ratio of observed to expected genotypic diversity.

F-statistics use departures from levels of heterozygosity expected under complete panmixia to partition total inbreeding (F_{IT}) into components due to inbreeding within subpopulations (F_{IS}) and subdivision among populations (F_{ST}). The significance of F_{ST} , a measure of genetic differentiation among populations, and of F_{IS} , a measure of genetic variation within populations, was calculated using equations given in Waples (1987). Gene flow (N_m), the average number of genetically effective migrants exchanged between populations each generation, can be estimated from F_{ST} using the approximation $N_m = [(1/F_{ST}) - 1]/4$. This provides an unbiased estimate of gene flow that is insensitive to moderate levels of selection (Slatkin and Barton 1989).

Results

The mean number of alleles per locus (N_a) were 2.9, 2.4 to 2.5, and 3.0 to 3.1 in northern Taiwan, Penghu and

southern Taiwan populations, respectively (Table 1). Percentages of polymorphic loci were greater than 50% (ranging from 50% to 75%). The observed heterozygosities, ranging from 0.155 to 0.251, were generally lower than expected under Hardy–Weinberg equilibrium (Table 1).

The ratios of the number of observed genotypes (N_G) to the number of individuals sampled (N_I) were close to one (0.917 to 1.000), indicating that almost as many genotypes as individuals were found in all the *Mycedium elephantotus* populations (Table 2). The ratios of $G_O:G_E$ among collection sites were high (0.8 to 1.0), suggesting high degrees of sexual reproduction.

Allele frequencies of *Mycedium elephantotus* populations were markedly different among the three regions (Table 3). The *MDH-1*85*, *MDH-2*90*, and *PEPA*83* appeared only in southern Taiwan populations. The frequencies of *EST*100*, *PEPA*100* and *PGM*93* were higher, and those of *MPI*100* lower, in Penghu and northern Taiwan populations. For *EST*, all colonies from Penghu populations had the allele *100, while those from southern Taiwan populations had the allele

Table 1 *Mycedium elephantotus*. Genetic variability in seven populations, with standard errors in parentheses. Locality abbreviations as in Fig. 1

	Northern Taiwan		Penghu		Southern Taiwan		
	MO	YL	JY	GPY	HCW	HC	TS
Mean no. of alleles/locus	2.9 (0.6)	2.9 (0.6)	2.5 (0.6)	2.4 (0.5)	3.0 (0.7)	3.1 (0.6)	3.1 (0.7)
Polymorphic loci (%)	62.5	62.5	50.0	50.0	75.0	75.0	75.0
Observed heterozygosity	0.219 (0.078)	0.230 (0.079)	0.155 (0.071)	0.224 (0.094)	0.251 (0.078)	0.251 (0.078)	0.233 (0.072)
Expected heterozygosity	0.340 (0.108)	0.383 (0.110)	0.267 (0.113)	0.283 (0.112)	0.341 (0.110)	0.350 (0.107)	0.315 (0.097)

*97. However, there were no distinct differences in allele frequencies among populations within each region.

The deviation of gene frequencies between the southern Taiwan population and other regions was also reflected in the greater genetic distance between the southern Taiwan population and other populations ($D=0.103$ to 0.293 , Table 4). These values were an order of magnitude greater than those between populations from northern Taiwan and Penghu Islands ($D=0.020$ to 0.037). Genetic distance between populations from southern Taiwan and Penghu Islands is greater ($D=0.241$ to 0.293) than that between southern and northern Taiwan populations ($D=0.103$ to 0.229), although the former two regions are much closer geographically. The grouping of the seven populations on a UPGMA (unweighted pair-group method using arithmetic averages) dendrogram based on Nei's unbiased genetic distance (Nei 1978) also reflects the differentiation among regions and homogeneity among populations within each region (Fig. 2). The dendrogram revealed a clear subdivision of populations into one group including populations from Penghu and northern Taiwan, and another group containing populations from southern Taiwan.

Deviations from Hardy–Weinberg equilibrium were found in five out of seven polymorphic loci (Table 5). F_{IT} displayed positive values for all loci except *MDH-1** and *MDH-2**, indicating a general deficiency of heterozygotes. The highest values of F_{IT} were recorded for *EST**. Estimates of the inbreeding coefficient, F_{IS} , deviated from zero for four out of seven polymorphic loci and were consistent with heterozygote deficits, suggesting that these populations may not have fully random mating.

Significant values of F_{ST} were detected among all populations and among regions for all loci except *MEP** (Table 6). However, there was no significant difference among populations within each region for all loci except *EST** within northern Taiwan populations, and *PEPA** and *MPI** within southern Taiwan populations (Table 6). Paired comparisons between regions showed

Table 2 *Mycedium elephantotus*. Effects of asexual reproduction on genotypes within samples of individual (N_I) coral colonies collected from seven populations. Level of multilocus genotypic variation within each population was expressed as number of multilocus genotypes (N_G). Relative contribution of asexual reproduction was estimated both by ratio of $N_G:N_I$ and ratio of observed genotypic diversity (G_O) to that expected (G_E). Locality abbreviations as in Fig. 1

Population	N_I	N_G	$N_G:N_I$	G_O	G_E	$G_O:G_E$
MO	29	29	1.000	29.00	29.00	1.000
YL	25	25	1.000	25.00	25.00	1.000
JY	25	23	0.920	20.16	25.00	0.806
GPY	24	22	0.917	19.20	24.00	0.800
HCW	18	18	1.000	18.00	18.00	1.000
HC	19	19	1.000	19.00	19.00	1.000
TS	34	33	0.971	31.24	34.00	0.919

Table 3 *Mycedium elephantotus*. Allele frequencies for seven populations collected from seven reef sites in three regions. Locality abbreviations as in Fig. 1 (n number of individual samples)

Locus	Northern Taiwan		Penghu		Southern Taiwan		
	MO	YL	JY	GPY	HCW	HC	TS
<i>MDH-1*</i>							
100	1.000	1.000	1.000	1.000	0.944	0.867	0.912
85	0.000	0.000	0.000	0.000	0.056	0.133	0.088
<i>MDH-2*</i>							
108	0.034	0.040	0.000	0.000	0.139	0.031	0.059
100	0.966	0.960	1.000	1.000	0.861	0.938	0.926
90	0.000	0.000	0.000	0.000	0.000	0.031	0.015
<i>EST*</i>							
100	0.845	0.580	1.000	1.000	0.000	0.000	0.000
97	0.155	0.420	0.000	0.000	1.000	1.000	1.000
<i>PEPA*</i>							
112	0.034	0.000	0.000	0.000	0.000	0.000	0.015
110	0.000	0.100	0.020	0.000	0.028	0.026	0.029
105	0.310	0.300	0.520	0.333	0.361	0.342	0.221
100	0.586	0.560	0.420	0.542	0.222	0.158	0.088
95	0.000	0.020	0.000	0.063	0.056	0.026	0.074
91	0.069	0.020	0.040	0.063	0.083	0.053	0.044
83	0.000	0.000	0.000	0.000	0.250	0.395	0.529
<i>MPI*</i>							
105	0.038	0.000	0.040	0.000	0.056	0.029	0.000
100	0.346	0.280	0.240	0.292	0.500	0.588	0.714
94	0.327	0.240	0.200	0.146	0.361	0.294	0.107
88	0.115	0.100	0.040	0.042	0.028	0.000	0.089
82	0.173	0.380	0.480	0.521	0.056	0.088	0.089
<i>PGM*</i>							
115	0.000	0.000	0.000	0.000	0.000	0.029	0.000
112	0.143	0.022	0.040	0.021	0.167	0.118	0.121
105	0.089	0.239	0.420	0.354	0.278	0.235	0.364
100	0.482	0.413	0.360	0.417	0.472	0.500	0.439
93	0.214	0.239	0.180	0.208	0.083	0.118	0.076
85	0.071	0.087	0.000	0.000	0.000	0.000	0.000
<i>MEP*</i>							
103	0.121	0.120	0.020	0.063	0.036	0.167	0.156
100	0.776	0.720	0.880	0.792	0.821	0.700	0.734
96	0.103	0.160	0.100	0.146	0.143	0.133	0.109
<i>PEPB*</i>							
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000
(n)	(29)	(25)	(25)	(24)	(18)	(19)	(34)

significant genetic differentiation for most of the loci. Higher genetic differentiation was found between coral populations from southern Taiwan and other regions, while that between Penghu and northern Taiwan populations was lower. The level of gene flow was high be-

Table 4 *Mycedium elephantotus*. Nei's unbiased genetic distance (below diagonal) and unbiased genetic similarity (above diagonal) (Nei 1978) between populations. Locality abbreviations as in Fig. 1

Population	Northern Taiwan		Penghu		Southern Taiwan		
	MO	YL	JY	GPY	HCW	HC	TS
MO		0.986	0.972	0.980	0.844	0.828	0.796
YL	0.014		0.964	0.972	0.902	0.889	0.861
JY	0.028	0.037		1.000	0.786	0.768	0.746
GPY	0.020	0.028	0.000		0.779	0.765	0.746
HCW	0.170	0.103	0.241	0.250		1.000	0.985
HC	0.189	0.118	0.264	0.268	0.000		1.000
TS	0.229	0.150	0.293	0.293	0.015	0.000

Fig. 2 UPGMA dendrogram showing relationships among populations based on Nei's unbiased genetic distances (D) in Table 2. Locality abbreviations as in Fig. 1

tween northern Taiwan and Penghu populations ($N_m = 7.56$), low between southern and northern Taiwan populations ($N_m = 1.72$), and very low between southern Taiwan and Penghu populations ($N_m = 0.90$). However, estimated gene flows among populations within each region were very high ($N_m = 11.11$ for northern and southern Taiwan populations, 24.75 for Penghu populations).

Discussion

Allozyme analyses revealed that populations of *Mycedium elephantotus* differed significantly among regions. Furthermore, the UPGMA dendrogram based on Nei's unbiased genetic distance showed a clear subdivision of populations into two groupings, northern Taiwan/Penghu Islands and southern Taiwan. This suggests that genetic differentiation for species with high dispersal potential may occur on a fine geographic scale of less than 200 km apart, and the genetic differentiation is not related to geographic distance but is instead due to other factors. Recent studies have also shown the non-equilibrium nature of population genetic structures and the fine-scale genetic differentiation in marine species with high dispersal potential (Benzie and Williams 1997; Palumbi et al. 1997).

Several factors might contribute to the spatial pattern of genetic variation of *Mycedium elephantotus*; these include the effects of temporal differences in reproduction, selection due to environmental differences, or the separation of surface ocean current. There are no temporal differences in reproduction for coral populations in southern Taiwan and the Penghu Islands, because

Table 5 *Mycedium elephantotus*. Estimates of deviations from Hardy–Weinberg proportions, and F -statistics (Nei 1977) of seven populations. F -statistics indicate deviations from Hardy–Weinberg proportions within the total population (F_{IT}), within populations (F_{IS}) and among populations (F_{ST}). Locality abbreviations as in Fig. 1

Population	<i>MDH-1</i> *	<i>MDH-2</i> *	<i>EST</i> *	<i>PEPA</i> *	<i>MPI</i> *	<i>PGM</i> *	<i>MEP</i> *
MO	–	–0.036	0.868***	0.067	0.419	0.325	0.352
YL	–	–0.042	0.918***	0.180	0.324	0.324	0.366
JY	–	–	–	0.202	0.581*	0.333*	0.628*
GPY	–	–	–	–0.134	0.396**	0.239	0.282
HCW	–0.059	–0.161	–	0.182	0.365	0.582**	0.059
HC	–0.154	–0.049	–	0.095	0.684**	0.382	0.139
TS	–0.097	–0.066	–	0.281*	0.614***	0.166	0.190
F_{IT}	–0.041	–0.046	0.979	0.238	0.472	0.356	0.281
F_{IS}	–0.115	–0.092	0.901***	0.128	0.527***	0.336***	0.268***
F_{ST}	0.066***	0.042**	0.786***	0.125***	0.103***	0.030*	0.018

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 6 *Mycedium elephantotus*. Genetic differentiation (F_{ST} values), and estimates of gene flow (N_m , average number of migrants per generation) within and among regions. Statistical significance of F_{ST} values was determined using equations given in Waples (1987)

	F_{ST}								N_m
	<i>MDH-1</i> *	<i>MDH-2</i> *	<i>EST</i> *	<i>PEPA</i> *	<i>MPI</i> *	<i>PGM</i> *	<i>MEP</i> *	Mean	
Population-total	0.066***	0.042*	0.786***	0.125***	0.103***	0.030*	0.018	0.188***	1.08
Region-total	0.062***	0.028***	0.727***	0.112***	0.081***	0.024***	0.009	0.167***	1.25
Paired comparisons between regions									
N Taiwan vs Penghu	–	0.019*	0.161***	0.011	0.025***	0.024***	0.010	0.032***	7.56
N Taiwan vs S Taiwan	0.047***	0.009	0.565***	0.126***	0.051***	0.018***	0.000	0.127***	1.72
Penghu vs S Taiwan	0.047***	0.039***	1.000***	0.108***	0.113***	0.012*	0.012	0.218***	0.90
Comparisons among populations within regions									
N Taiwan	–	0.000	0.086**	0.006	0.019	0.015	0.004	0.022	11.11
Penghu	–	–	–	0.023	0.003	0.007	0.010	0.010	24.75
S Taiwan	0.012	0.020	–	0.029*	0.038*	0.007	0.016	0.022	11.11

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

mass spawning of corals occurs in the same period in the two regions. Furthermore, selection on an environmental basis is not likely because the marine environments in southern Taiwan and the Penghu Islands are more similar due to their closer geographic locations while the genetic distance between populations from these two regions is greater. Although the F_{ST} values for EST^* are one to two orders of magnitude greater than the other loci, implying that selection may act on esterase. However, the allele frequencies of EST^* are more similar between northern and southern Taiwan populations than those between southern Taiwan and the Penghu Islands. The lack of distinct relationship between EST^* variations and environmental conditions, along with the general concordance of the level of inter-population differences (F_{ST}) for most of the loci, suggest that the effect of restricted gene flow is more prevailing than that of selection.

The pattern of genetic variation observed in *Mycedium elephantotus* is consistent with the pattern of surface ocean currents around Taiwan. The marine environment around Taiwan is influenced mainly by two major water masses, the Kuroshio and the South China Sea warm water (Fig. 1 present study; Wang and Chern 1988; Chern and Wang 1992). The main stream of the Kuroshio Current flows steadily northward along the east coast of Taiwan. Along the west coast, there is also a persistent northward flow through the Taiwan Strait. In wintertime, a branch of the Kuroshio splits near the southern tip of Taiwan and flows into the Taiwan Strait (Wang and Chern 1988). However, during summertime, when southwest monsoons prevail, the South China Sea surface warm water flushes into the Taiwan Strait and the Kuroshio water is prohibited from entering the Taiwan Strait (Wang and Chern 1988).

Mycedium elephantotus is a broadcast spawner and spawning occurs annually from late spring to summer (Dai et al. 1992). During the spawning season, the South China Sea warm water dominates the Taiwan Strait and provides a northbound gene flow from the Penghu Islands to northern Taiwan. While gametes and larvae released from southern Taiwan populations are prohibited from entering the Taiwan Strait and are unable to reach the Penghu Islands. The level of gene flow between coral populations of the Penghu Islands and northern Taiwan is thus much higher ($N_m = 7.56$) than that between the Penghu Islands and southern Taiwan populations ($N_m = 0.90$). Therefore, genetic subdivision of *M. elephantotus* populations in Taiwan is likely driven by isolation of ocean current. Chen (1996) also reported a similar pattern on a group of reef fish, Apogoniidae, by analyzing faunal data and mitochondrial DNA sequences. These data indicate that the separation by surface ocean currents plays an important role in genetic differentiation among populations of marine organisms.

The population differentiation, expressed in genetic distance and F_{ST} , between populations from southern Taiwan and the Penghu Islands is greater than those between southern and northern Taiwan populations, although the former two regions are much closer geographically and more similar environmentally. This further supports the view that the population differentiation of *Mycedium elephantotus* in Taiwan might be promoted by surface circulation vicariance. While running through northeastern Taiwan, a branch of the Kuroshio Current may enter the coastal area in northern Taiwan (Chern and Wang 1989, 1992), and a higher level of gene flow between northern and southern populations could be expected. However, due to the considerable distance between these two regions, it is possible that only few larvae from southern Taiwan could reach northern Taiwan and that the gene flow is therefore relatively low ($N_m = 1.72$).

The significant deviations from Hardy–Weinberg expectations were primarily due to heterozygote deficits which may reflect the effects of inbreeding or the stochastic error of small sample sizes. Inbreeding or interspecies hybridization may not be infrequent in broadcasting corals (Richmond and Hunter 1990). The high ratios of observed and expected genotype diversity ($G_O:G_E > 0.8$) and the fact that most genotypes were observed only once ($N_G:N_I = 1$) suggest that *Mycedium elephantotus* propagates mainly by sexual reproduction. Previous studies on scleractinians and other cnidarians have often revealed clonal genotypes within populations (Stoddart 1984; Ayre and Willis 1988; Ayre et al. 1991; Benzie et al. 1995; Burnett et al. 1995; Billingham and Ayre 1996). For each of these species, asexual reproduction appears to play a primary role in the maintenance of local populations, although sexual reproduction may be the primary source of rare or episodically successful colonizing larvae (Stoddart 1984; Ayre and Willis 1988). Only few studies have shown the consistency and range of dispersal and recruitment of sexually produced larvae on coral populations (Ayre and Dufty 1994; Brazeau and Harvell 1994; Burnett et al. 1994). In the present study, the majority of individual colonies displayed unique multilocus genotypes within most populations (Table 2). Exceptions were confined largely to those collections that had little allelic variation and hence few detectable genotypes. These data suggest that *M. elephantotus* populations receive little input from asexual reproduction via fragmentation. This might be due to the restriction of its colony morphology. Colonies of *M. elephantotus* usually appear in foliaceous or encrusting forms. The asexually produced fragments often remain attached to the substrate and would be difficult to disperse.

The high level of genotypic diversity of *Mycedium elephantotus* might also be related to habitat-disturbance history. Moderate disturbances are considered to favor genotypic diversity in coral communities (Hunter

1993), especially if initial colonization is via sexually generated larvae (Ayre and Dufty 1994). The reefs sampled in this study are under the influences of frequent typhoon disturbances and northeast monsoons (Dai 1991). These disturbance events may occur often enough across and within populations, relative to a species' generation time, to prevent domination of space by locally adapted clonal genotypes. These factors may act alone, or in conjunction, to allow the coexistence of several clones and maintain high genotypic diversity in this species.

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