

Analysis of Scleractinian Distribution in Taiwan Indicating a Pattern Congruent with Sea Surface Temperatures and Currents: Examples from *Acropora* and Faviidae Corals

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(Accepted November 7, 1998)

Chaolun Allen Chen (1999) Analysis of scleractinian distribution in Taiwan indicating a pattern congruent with sea surface temperatures and currents: examples from *Acropora* and Faviidae corals. *Zoological Studies* **38**(2): 119-129. Taiwan, a continental island with several offshore islets, is located on the center or junction of the Philippine-Japan island arc. Approximately 300 species of scleractinian corals occur around Taiwan and its neighboring islets except on the west coast with its sandy or muddy habitats. I analyzed the distribution patterns of 104 species of 2 major groups of scleractinian corals, the genus *Acropora* and family Faviidae, from 8 regional databases using distance and parsimony methods. Distance analyses (neighbor-joining) indicate that southern Taiwan and Green Island possess similar scleractinian distributions for both *Acropora* and Faviidae corals, whereas northeastern Taiwan groups with other locations of Penghu. Parsimony analysis (exhaustive search) of *Acropora* shows a similar pattern of distance analysis, whereas parsimonious tree of Faviidae united northeastern Taiwan with Green Island and South Taiwan leaving Penghu as a single group. Combining both *Acropora* and Faviidae, parsimony analysis suggests 2 distinct provinces of scleractinian distributions which show a congruence with sea surface temperatures and currents around Taiwan.

Key words: Scleractinian corals, Tropical reef, Non-reefal community, Sea surface temperatures, Sea surface currents.

Reef-building corals, the scleractinians, are distributed throughout tropical and subtropical regions of the world. Distribution patterns of scleractinians are usually characterized in terms of numbers of families, genera, or species present in different regions. Veron (1995) summarized the global distribution and species diversity of scleractinians, suggesting that there is no Indo-Pacific center of diversity at the family level, with the Caribbean being almost as diverse as the Indo-Pacific. At the generic level, configuration of diversity is dominated by the Indo-Pacific center of diversity, with a relatively low diversity in the western Atlantic. Species diversity is also overwhelmingly high in the Indo-Pacific region with uniformity from the Red Sea to Fiji (Veron 1993 1995).

Regional (or latitudinal) distribution of scleractinians is presumably influenced by local physicalenvironmental constraints. Three major regions of the Indo-Pacific locations, including PhilippinesJapan, South Papua New Guinea-Eastern Australia, and Western Australia, have been the most comprehensively studied for their regional connections (Veron 1993, reviewed in Veron 1995). Among them, extensive oceanographic data were obtained providing the chance to study relationships between distribution patterns and physical-environmental factors in the Philippine-Japan island arc (Veron and Minchin 1992). The Kuroshio current originates in the northern Philippines, enters the East China Sea through a strait between Taiwan and the Yaeyama Islands, and flows northward to the west of the Ryukyu Islands (Veron and Minchin 1992, reviewed) in Veron 1995). This current in combination, with the effect of sea surface temperature limits, has divided scleractinian distribution along the Philippine-Japan Island arc into 3 groups: tropical reefs, temperate non-reefal communities, and high-latitude outlying populations (Veron 1992, Veron and Minchin 1992, Veron 1995). Taiwan, a continental island with several offshore islets, is located on the center or junction of the Philippine-Japan island arc (Fig. 1). The Taiwan Strait, situated to the west between Taiwan and mainland China, is a shallow channel with sandy or muddy habitats. To the east of Taiwan, the submarine topology drops steeply to 4000 m, and is close to the nearby Ryukyu Trench (Chu 1971). Despite habitat availability, occurrence of scleractinians is influenced by sea surface currents around Taiwan (Fig. 1). The strong Kuroshio current flows northward passing Orchid Island and Green Island; a weak side-branch flows to the Taiwan Strait up to Hsiaoliuchiu and southern Penghu in winter. This side-branch can penetrate across the Tropic of Cancer into more northern parts along the western shoreline during summertime (summarized in Shao et al. 1997, Fig. 1). In summer, the South China Sea Surface Current (SCSSC) driven by the southwestern monsoon flows northwards into the Taiwan Strait through the Penghu channel. On the contrary, the cold fresh China Coastal Water (CCW) driven by the northeast monsoon can enter the southern Taiwan Strait during winter (Fan 1979, Wang and Chern 1988 1992, Jan 1995).

Scleractinians have been reported from 7 major regions, including northeastern Taiwan, eastern Taiwan, southern Taiwan, the Penghu Islands, Hsiaoliuchiu, the Green Island, and Orchid Island (Fig. 1, reviewed in Dai 1997). Its high diversity of scleractinians and its central geographic position along the West Pacific island chain has led to the proposal that Taiwan might serve as a "steppingstone" for the northward and eastward dispersal of shallow water reef organisms (Dai 1989 1991). In the present study, I reviewed the distributions of 2 major groups of scleractinian corals, the genus *Acropora* and Family Faviidae, from a series of survey databases in Taiwan (Chang et al. 1991 1992 1993, Dai 1991, Chen et al. 1992, Fong et al. 1993, Dai et al. 1995). By applying distance and parsimony analyses, the distribution patterns of scleractinians can be divided into 2 clusters which reveal a congruence with sea surface temperatures and currents around Taiwan.

MATERIALS AND METHODS

Data acquisition

As indicated by Veron and Minchin (1992), the study of distribution patterns of scleractinian corals requires 2 separate data sets: detailed records of the coral fauna throughout the distribution range, and high quality oceanographic data with which these distributions may be correlated. For coral distribution, I reviewed the species occurrence of Taiwanese scleractinians from the available literature (for references, see Table 1). Studies of taxonomy and distribution of scleractinians in Taiwan could be traced back as early as the 1930s (Hayasaka 1935, Hilasaka 1935, Kawaguti 1942 1943 1953, Jones et



Fig. 1. Map of Taiwan and neighboring islets showing reef localities and current systems around the island. #: reef database used in this study; bold line () indicates the known scleractinian distributions around Taiwan. Sea surface currents and their directions are indicated as different arrow patterns: () Kuroshio current and its branch; () South China Sea surface current; () China coastal water.

Location	No. species	Reference			
Southern Taiwan (KT)	230	Dai (1991)			
Northeastern Taiwan (NE)	153	Jeng et al. (1997)			
Eastern Taiwan ^a	32	Chang and Jeng (1990)			
Green Island (GI)	168	Chang et al. (1992)			
Orchid Island ^a	45	Chang et al. (1989)			
Hsiaoliuchiu ^a	200	Yang et al. (1976)			
Tongsha (TS)	101	Dai et al. (1995)			
Penghu					
Southern (SP)	101	Fang et al. (1993)			
Northern (NP)	96	Chang et al. (1992)			
Eastern (EP)	95	Chang et al. (1993)			
Inner (IP)	76	Shao et al. (1992)			

Table 1. Number of scleractinian corals recorded from different localities of Taiwan

^adata were not used in the present study.

al. 1972, Yang et al. 1976). However, reliable scleractinian taxonomy was not settled until the 1990s after major revision was completed (Dai 1991). Therefore, I used data exclusively published after 1991. For this study, scleractinian abundance from 2 major locations of Taiwan, southern Taiwan (KT) and northeastern Taiwan (NE) and 2 adjacent islands, Green Island (GI) and Penghu Islands, were utilized (Fig. 1). The Penghu Islands were divided into southern (SP), northern (NP), eastern (EP) and inner (IP) according to the reports (Chang et al. 1991 1992 1993, Chen et al. 1992, Fong et al. 1993). Data from eastern Taiwan, Orchid Island and Hsiaoliuchiu, though available in the literature (Table 1), were not used in this study due to the taxonomic confusion mentioned above. Tungsha (Pratas Island, Dai et al. 1995), an atoll located at the northern edge of the South China Sea, was used as a geographical outgroup in the following analyses (Fig. 1). Generally accepted sea surface current patterns around Taiwan (Chu 1963, Fan and Yu 1981; Fig. 1) were used to infer their relationships with scleractinian distribution, although detailed oceanographic data around Taiwan are still equivocal (Fan 1979, Wang and Chern 1988 1992, Jan 1995).

Data transformation

I analyzed the distribution patterns of *Acropora* and Faviidae. *Acropora* is the largest extant coral genus and the review of this genus in Taiwan was recently initiated (Veron and Wallace 1984, Wells 1987, Wallace et al. 1991, Wallace and Dai 1997). Faviidae is the largest family in terms of number of genera, and ranks next to the Acroporidae in number of species and overall abundance in most reef biotopes throughout the Indo-Pacific (Veron et al. 1977).

These 2 groups are also the most abundant groups of scleractinians (> 30%) in Taiwan (Fig. 2). In the literature, scleractinian distributions were surveyed from different sites within a location (e.g., 8 sites at Tungsha, Dai et al. 1995). The abundance of scleractinians was usually recorded qualitatively, i.e., as not recorded, rare, occasional, common, or abundant (Chang et al. 1991 1992 1993, Dai 1991, Chen et al. 1992, Fong et al. 1993, Dai et al. 1995). To transform the datasets into quantitative analyses, 2 approaches were applied. First, ranks (0, 1, 2, 3, 4) were given to the 5 categories of qualitative abundance for each site within the location. Average abundance index (AAI) of each location was obtained by the following transformation:



Fig. 2. Percentage of *Acropora* and Faviidae corals from each locality used in the present study. Abbreviations of localities are referenced in table 1.

Therefore, AAI matrices were constructed for *Acropora* and Faviidae, respectively (Tables 2, 3). Secondly, a 2-state matrix (1, 0) was constructed based on the AAI matrix: 1 corresponded to the presence of a species in the location and 0 corresponded to its absence.

Distribution pattern analyses

Species distribution could be plotted for every location after the presence/absence frequency of each species was calculated. "Widely-distributed" species was defined as those species that occurred

Table 2. Average abundance index calculated from the literature for *Acropora*. See text for locality abbreviations. "*n*" is the number of sites surveyed in that locality

Species	КТ	TS	NP	IP	SP	EP	NE	GI
	(<i>n</i> = 7)	(<i>n</i> = 8)	(<i>n</i> = 10)	(<i>n</i> = 12)	(<i>n</i> = 15)	(<i>n</i> = 7)	(<i>n</i> = 9)	(<i>n</i> = 6)
Acropora palifera	1.43	0.5	0	0	0.07	0.29	0.33	2.83
A. bruggemanni	0	0.25	1.5	0.42	0	0.29	0	0
A. cuneata	1	0	0	0	0	0	0	0.5
A. humilis	2.57	0.88	1.20	1.08	0	1.43	0.11	1.33
A. gemmifera	0.43	0.13	0	0	0	0	0	0.83
A. monticulosa	1.86	0.13	2	0	0.07	0	0	1.50
A. digitifera	2.29	0.25	1.5	1.33	0.47	0	0.22	1.17
A. glauca	0.86	0	0	0	0	0	0	1.67
A. robusta	1.29	0.38	0	0	0.47	0	0	0.83
A. palmerae	1.14	0	0	0	0	0	0.56	1.33
A. noblis	1.57	1.25	1.5	0.25	0.4	1.29	0	0
A. grandis	1.86	0.63	0	0	0.07	0	0	0.67
A. formosa	2.29	1.63	0	1.17	0	0.86	0	1
A. valenceinnesi	1.29	0	0	0	0	0.14	0	0
A. microphthalma	1.86	0.5	0	0	0	0	0	0
A. aspera	1	1.5	0	0	0.2	0	0	1
A. pulchra	1.43	0	0	0	0	1.00	0	0
A. millepora	0.71	0.25	0	0	0.07	0.14	0	0
A tenuis	0.43	1 13	15	0	0.73	0.71	0	0.67
A dendrum	1 14	0	0	0	0	0.29	0	0
A selano	2	Ő	Ő	õ	0 07	0	0	0 67
A cytherea	1 14	0 75	17	0	0	0 71	0	1 67
A microclados	1.57	0	0	Õ	0.67	0	0	0
A hvacinthus	3 14	0.63	Õ	0.83	0.80	1 43	1	15
Δ anthoceris	0.86	0.00	0	0.00	0.00	0	0	0.83
Δ latistella	1.86	0	0	0	0.47	0	0 11	0.00
A studeri	0.20	0	0	0	0.47	0	0.11	0.00
A nana	0.23	0	13	0	0	0 86	0 44	0
A. nana A. oustoro	0.14	0	1.5	0	0	0.00	0.44	0
A. austera A. coroalis	2.14	0	0	0	0	0	0 89	083
A. Cerealis A. donoi	2.14	0 13	0	0	0	0	0.89	0.03
Λ pacuta	1 20	0.15	0	0	033	0	0	0
A. nasula A. cocolo	0.20	0.25	0	0	0.55	0	0	0
A. secale	0.29	0.3	0	0	0	0	0	0
A. calulus	0 96	0.25	16	0 22	0 27	0 57	0 11	0
A. vallua	0.00	0.5	1.0	0.33	0.27	0.57	0.44	1.00
A. Claimala	0.29	0	0.7	0	0	0	0	1.03
A. Ulvallcala	1.00	0.25	0.7	0	0 07	0	0	0.5
A. IIOIIUA	0.29	0.25	1.5	0	0.07	0	0	0.5
A. SUDYIADIA	0	0.13	0	0	0	0	0	0.17
A. DUSNYENSIS	0	0	0	0.67	0	0	0	0
A. sarmentosa	0	0	0	1	0	0	0	0
A. elseyl	0	0	0	0.33	0	0	0	0
A. spicitera	0	0	0	0	0	1.29	0	0
A. verweyi	0	0	0	0	0	0.14	0	0
A. samoensis	U	0	U	U	U	0.14	0	0
A. clathrata	0	0	U	U	0	0	0.33	0
A. solitaryensis	0	0	0	U	0.13	0	0.11	0
A. specifera	0	0	2.1	0	0	0	0.33	1
A. syringodes	0	0	0	0	0	0	0.44	0
A. echinata	0	0	0	0	0	0	0	0.5

Species	KT	TS	NP	IP	SP	EP	NE	GI
	(n = 7)	(n = 8)	(n = 10)	(n = 12)	(n = 15)	(n = 7)	(n = 9)	(n = 6)
Cyphastrea chalicidicum	2	0.63	11	1.08	0	0	0.78	1 17
C microphthalma	2 57	0.5	22	0.83	0	0	0.56	2 17
C. serailia	0.29	0.13	2.3	0.92	0.67	0	0.56	1.67
Caulastrea furcata	0.57	0.13	0	0	0	0.29	0.11	0
Diploastrea helipora	2.14	0.13	0	0	0.13	0	0	1.83
Echinopora lamellosa	2.43	0.25	1.6	0.33	0.47	1.14	1.22	1.67
E. gemmacea	0	0	0.7	0	0	0	0	0
Favia favus	2.29	0.13	1.4	1.17	0	1.14	1.22	0.33
F. pallida	1.14	0.38	2.5	1.25	0.07	0	0.67	1.33
F. rotumana	1.14	0.13	0.5	0	0	0.29	0.22	0
F. speciosa	2.43	0.63	2.3	1.75	0.53	0.57	1.33	1.83
F. stelligera	2.29	0.5	0	0	0	0	0.11	2.17
F. laxa	0.71	0.63	1.3	0.17	0	0.29	0.78	0.83
F. maxima	1.14	0	0.4	0.75	0.07	0	0	0
F. maritima	0	0	1.1	0	0.40	0.14	0.11	1.17
F. matthaii	0	0	0	0	0	0.71	0	0
F. veroni	0	0	0	0	0.27	0	0	0
F. lizardensis	0	0	0	0	0.07	0	0	0
F. helianthoides	0	0	0	0	0.07	0	0	0
Favites abdita	2.43	1	2.8	1.92	0	0.29	0.33	2
F. chinensis	0.57	0.25	0	0	0.6	0	0.11	1
F. complanata	1.71	0	1.2	0	0	0	0.78	1.17
F. rotundata	0.57	0	0	0	0.13	0	0	0
F. flexuosa	1.29	0.25	1.7	1.17	0.07	0.86	0.22	1.33
F. halicora	0.43	0	1.5	0	0	0	0.22	0
F. russelli	0	0.13	0.6	0.92	0	0	0.11	0
F. pentagona	1.86	0.13	1.5	1.17	0	0	0.22	1.5
Barabattoia amicorum	0.29	0	0.7	0	0	0	0	0
Montastrea valenciennesi	1.57	0	1.3	0.25	0.07	0.14	0.67	1
M. curta	0.57	0.38	1.8	0	0.13	0.29	0.33	0.67
M. annuligera	0	0	0.8	0	0	0	0	0
M. magnistellata	0	0	0.8	0	0	0.14	0.22	0
Goniastrea australiensis	1.71	0.88	0.8	0	0.13	0.29	0.11	0
G. edwardsi	0.14	0	1.6	3.25	0.6	0.29	0.11	1.67
G. aspera	2.57	0	1.8	3.08	0	0.14	1.11	1.67
G. pectinata	0.71	0.13	2.1	1.58	0.13	0.29	0.11	1.5
G. retiformis	1.43	0.38	0.7	0.83	0.93	0.57	0.11	1.67
G. favulus	0	0	0	0	0	0.14	0.11	0
Hydnophora exesa	2.29	0	0	0	0.67	0	0.56	0
H. microconos	1.57	0	0	0	0	0	0.22	0
H. rigida	0.86	0	0	0	0	0	0.22	0
Leptoria phrygia	2.14	0.5	0	0	0	0	1	2
Oulphyllia crispa	0.71	0	0	0	0	0	0.33	0.83
Leptastrea purpurea	0	0	0.6	0	0	0	0.22	0.83
L. transversa	0	0	0.4	0	0	0	0.33	0.5
Platygyra astreiformis	0.29	0	0	0	0	0	0	0
P. pini	1.43	0	1.6	1.58	0.33	0	0	1.33
P. lamellina	2.43	0.25	1.3	1.75	0	0.29	0.67	2
r. aaeaalea	2.14	0.63	U	U	0.27	0.57	0.56	1.33
P. sinensis	1.14	0.25	U	1.33	0.2	0.29	0.67	1.33
P. ryukyuensis	U	0	U	1.5	U	0	U	U
r. verweyl	0	0	U	0 47	U	0.29	0.00	U
Piesiasirea versipora	1.29	0	0.3	0.17	0.07	0.57	0.89	U
Ouiastrea crispata	U	0	U	1.42	0.27	U	U	U

Table 3. Average abundance index calculated from the literature for Faviidae. See text for locality abbreviation. "*n*" is the number of sites surveyed in that locality

in 7 or 8 locations; "commonly-distributed" for those that occurred in 3 to 6 locations and "restrictivelydistributed" for those only found in 1 or 2 locations. The Neighbor-Joining (NJ) method was used to cluster the 8 location data after average taxonomic distance coefficients (Sneath and Sokal 1973) were calculated for the AAI matrices using NTSYS-PC 1.8 (Rohlf 1992). For the analyses of 2-state matrices using the parsimony method, the exhaustive search option in PAUP 3.1.1 (Swofford 1993) was used. In all analyses, Tungsha was used as an outgroup.

RESULTS

The highest diversity of scleractinians was found at the southern tip of Taiwan with 230 species recorded in 1991 (Table 1). Numbers of species for other locations ranged from 76 at IP to 168 at GI. Totally 50 species of Acropora and 54 species of Faviidae were extracted from the 8 regional databases (Tables 2, 3). Among the Acropora, A. valida, recorded in 8 locations, was the most widely-distributed species; A. humilis, A. digitifera, and A. hyacinthus occurred in 7 locations (Table 2). Of Acropora species, 42% were commonly distributed. Surprisingly, 50% of *Acropora* were restricted to only 1 or 2 locations (Fig. 3). Plotting the species distribution indicated that most locations possessed several restrictively-distributed Acropora except NP. IP had the highest percentage (30%) of restrictively-distributed species (Fig. 4a).

The distribution pattern of Faviidae was significantly different from that of *Acropora* (Fig. 3, χ^2 -test,



Fig. 3. Plotted distribution frequency of *Acropora* and Faviidae in each locality. Towards the "left-ended" X-axis indicates species with the wide distributions (i.e., occurring in 7 or 8 localities) and towards the "right-ended" X-axis are the species with restrictive distributions (only recorded in 1 or 2 localities).

p < 0.001). Echinopora lamellosa, Favia speciosa, Favites flexuosa, Goniastrea pectinata, and G. retiformis were found in 8 locations; 18.5% of Faviidae occurred in 7 locations; over 46% of Faviidae was commonly distributed and only 27% was restrictively-distributed (Fig. 3). Plotting the species distribution showed similar patterns among locations, i.e., most Faviidae species were widelydistributed (Fig. 4b).

Using Tungsha as the outgroup, NJ analysis of AAI indicated that KT and GI possess similar scleractinian distributions, whereas NE assembled with other locations of Penghu (Fig. 5a, b). An exhaustive search of parsimony analysis on the presence/absence matrix of *Acropora* showed a similar pattern of the NJ tree (Fig. 6). On the other hand, the parsimony tree of Faviidae clustered NE with GI/ KT and left Penghu as a single group (Fig. 6). This is probably due to the higher similarities of distribution patterns among locations for Faviidae corals. Combining both *Acropora* and Faviidae, parsimony analysis suggested 2 provinces of scleractinian distributions in Taiwan (Fig. 7).

DISCUSSION

Reef environments and coral communities have been comprehensively investigated in coral reefs of Taiwan (Dai 1991 1993, Dai et al. 1995, for review, see Dai 1997). In summary, approximately 300 species of scleractinians have been recorded in Taiwan (reviewed in Dai 1997), which is comparable to those of the Ryukyu Islands and the Philippines (Veron and Minchin 1992). Nevertheless, the distribution patterns are variable among localities within Taiwan in terms of number of species. Higher diversities were found at the southern tip of Taiwan, Green Island, and probably Hsiaoliuchiu where communities can be categorized as "tropical reefs" according to Veron (1995). On the other hand, Penghu and northeastern Taiwan were clustered into "non-reefal communities" (Fig. 7, sensu Veron 1995). Though only 2 families with 104 species of scleractinians were analyzed in this study, the pattern still showed the congruence with those documented for the reef fishes around Taiwan, i.e., "Kuroshio-affected zone" and "southwestern monsoon-affected zone" could be clearly defined (sensu Shao et al. 1994 1997). Although the island of Taiwan is not long, only 450 km in length, these 2 distinct provinces of scleractinian distribution in Taiwan are relatively unique comparing to those of South Paupa New Guinea-Eastern Australia, Western Australia or the Ryukyu arc where



Fig. 4. Distribution patterns of Acropora and Faviidae corals in 8 localities. The X-axis is the same scale as in figure 3; the Y-axis is the percentage of occurrence in that category.

different coral communities expand over 1000 km (Veron and Marsh 1988, Veron and Minchin 1992, Veron 1993, reviewed in Veron 1995).

Temperature is one of the major environmental parameters showing significant correlation with scleractinian species distribution at the latitudinal scale (Veron and Minchin 1992, Veron 1995). The annual variation of monthly mean water temperature in southern Taiwan ranges from 20.1 °C in winter to 28.2 °C in summer, indicating a suitable environment for coral growth (Fang 1989, Dai 1991, Lin et al. 1998). On the contrary, minimums of 16.5 °C and 16 °C recorded for winter temperature at Penghu and northeastern Taiwan, respectively, (Lin et al. 1998) are below the minimum temperature (18 °C) for coral survival (reviewed in Veron 1995). This low temperature restricts some species distributed to Penghu and northeastern Taiwan, however, maintaining the low-temperature-tolerant species is a characteristic feature of these regions. For example, Oulastrea crispata, a zooxanthellate species that can tolerate temperature as low as 0 °C (Yajima 1986) has only been recorded from southern and inner Penghu (Table 2).

Sea surface currents are a reflection of physical/ environmental factors (e.g., temperature, salinity,



(b) Faviidae



Fig. 5. Neighbor-Joining tree based on the average taxonomic distance (NT-SYS 1.8) calculated from the indices of tables 2 and 3. Abbreviations of localities are referenced in table 1.

etc.). Even as sea surface temperature plays an important role in scaling scleractinian distribution, sea surface currents may still account for the scleractinian distribution patterns around Taiwan for their mechanical dispersion. Although the dispersal ability of corals is recognized to be sufficiently great to not limit intra-regional dispersion, there are still some local proximity effects (Veron and Minchin 1992, Veron 1995). Broadcasting scleractinians in both the Philippines and the southern Taiwan are known to spawn between late April to early May (Bermas et al. 1992, Dai et al. 1992). The northernmost island of the Philippine arc, Batan Island, is about 90 km from the southern Taiwan. The speed of the Kuroshio current was measured at less than 0.9 m.s⁻¹ (summarized in Veron and Minchin 1992), indicating that transportation could easily occur from the northern Philippines to southern Taiwan by Kuroshio branch in less than 2 d. A minimum planktonic development period of approximately 4 to 6 d is required before externally developed planulae of many gamete-spawning corals are capable of settlement and metamorphosis (reviewed in Harrison and Wallace 1990). It is apparent that the Kuroshio branch could connect southern Taiwan to the center of scleractinian diversity in the northern Philippines by larval dispersion. This connection reaches Hsiaoliuchiu, a reefal island off southwest Taiwan, during later winter and early spring. In combination with Orchid Island and Green Island, these reefs form the richest scleractinian fauna around Taiwan (for review, see Dai 1997). On the other hand, although scleractinian corals spawn between late April and early May in southern Taiwan,



Fig. 6. Parsimonious trees derived from the presence/ absence matrices examined by the exhaustive option of PAUP 3.1.1. Abbreviations of localities are referenced in table 1.



Fig. 7. Plotting the geographic localities and minimum winter temperatures to the parsimonious tree derived from the combined presence/absence matrices of *Acropora* and Faviidae examined by the exhaustive option of PAUP 3.1.1. Abbreviations of localities are referenced in table 1.

the cold fresh China coastal water might still retard scleractinian larvae distribute to the Penghu Islands and northern Taiwan due to the exchange period of the current systems (from CCW to SCSSC) in the Taiwan Strait (Jan 1995).

Glacio-eustatic changes and consequent changes in the Kuroshio current in the East China Sea may have impacted on the origin and growth of coral reefs around Taiwan. Eighteen thousand years ago, sea levels were approximately 120 to 135 m below those of the present (Grigg and Epp 1989). Taiwan was still part of the Asian continent and the South China Sea was partly landlocked (Veron 1995). Southern Taiwan retained its present status despite the fluctuations of sea-level changes. Penghu and northeastern Taiwan were still part of the land bridge between the mainland Asian continent and the Ryukyu Island archipelago (Kimura 1991, reviewed in Veron 1995). The ancient Kuroshio current flowed further eastwards than its present pathway (Kimura 1991). About 9000 to 6000 yr ago, modern reefs began growing, and the maximum sea level was about 6 m higher than the present during the last inter-glacial period (Veron 1995). In an analyses of the planktonic foraminifera fauna composition, coarse fraction measurement and detailed C-14 dating indicate that the ancient Kuroshio current changed to its present position, including the side branch turning to the South China

Sea, at about 7500 yr ago (Shieh and Chen 1995). However, the Penghu Islands were still a residual landbridge between Taiwan and the mainland, indicating that the formation of coral communities at Penghu Islands and northeastern Taiwan were geologically quite recent event.

In conclusion, this preliminary analysis of *Acropora* and Faviidae databases indicates a characteristic pattern of zoogeographic distribution of reef corals around Taiwan. A comparable study of reef fishes also shows a similar pattern (Shao et al. 1994 1997). This consensus implies that the distribution of other reefal organisms in Taiwan may also show a correlation with sea surface temperatures and currents around the island and neigbhoring islets. Further investigation of other taxa of marine invertebrates or algae may clarify the comprehensive pattern of marine biogeography in Taiwan.

Acknowledgments: I would like to extend my gratitude to K.-T. Shao and 3 anonymous reviewers for their comments on the methodological corrections. I am greatly indebted to C.-F. Dai and M.-S. Jeng for providing survey databases of coral reefs in Taiwan. Many thanks to H.-W. Gauo, C.-F. Weng, and the members of Evolution and Ecology Group, Institute of Zoology, Academia Sinica for constructive comments. This is the Evolution and Ecology Group Contribution No. 1. Financial support was provided by an infrastructure grant of the Institute of Zoology, Academia Sinica.

REFERENCES

- Bermas NA, PM Alino, MP Atrigenio, A Uychiaoco. 1992. Observations on the reproduction of scleractinian and soft corals in the Philippines. Proc. 7th Coral Reef Symp. 2: 443-447.
- Chang KH, SC Chang, Y Su, CE Chang, YS Lin, L Liu, PS Yang. 1989. Investigation and evaluation of natural resources of the Lanyu (Orchid Island) National Park. Bureau of Construction, Ministry of Interior, R.O.C. (in Chinese).
- Chang KH, YM Chiang, CH Chen, RQ Jan, CF Dai, MS Jeng. 1992. Marine biological resources in the north sea of Penghu. Penghu Scenic Area Administration, Bureau of Tourism, Ministry of Communication, R.O.C. (in Chinese).
- Chang KH, RQ Jan, CF Dai, RC Tseng, MS Jeng, Y Su. 1991. Investigation and conservation studies on marine biological resources of the Green Island. East Coast Scenic Area Administration, Bureau of Tourism, Ministry of Communication. (in Chinese).
- Chang KH, MS Jeng. 1990. Marine ecological and scenery resources of the East Coast Scenic Area. Bureau of Housing and Urban Development, Taiwan Provincial Government. (in Chinese).
- Chang KH, HN Yang, CH Chen, RQ Jan, CF Dai, MS Jeng. 1993. Marine biological resources of the enclosed sea of Penghu. Penghu Scenic Area Administration, Bureau of Tourism, Ministry of Communication, R.O.C. (in Chinese).
- Chen CC, KT Shao, J Lewis, HP Yu, JS Huang. 1992. Marine biological resources of the east sea of Penghu. Penghu Scenic Area Administration, Bureau of Tourism, Ministry of Communication, R.O.C. (in Chinese).
- Chu TY. 1963. The oceanography of the surrounding waters of Taiwan. Report Inst. Fishery Biol., Natl. Taiwan Univ. 1: 29-44. (in Chinese).
- Chu TY. 1971. Environmental study of the surrounding waters of Taiwan. Sino-American Science Cooperation Colloquium on Ocean Resources. Vol. II.
- Dai CF. 1989. Scleractinia of Taiwan. I. Families Astrocoeniidae and Pocilloporidae. Acta Oceanogr. Taiwanica 22: 83-101.
- Dai CF. 1991. Reef environment and coral fauna of southern Taiwan. Atoll Res. Bull. **354:** 1-28.
- Dai CF. 1993. Patterns of coral distribution and benthic space partitioning on the fringing reefs of southern Taiwan. P.S.Z. N.I: Mar. Ecol. **42:** 185-204.
- Dai CF. 1997. Assessment of the present health of coral reefs in Taiwan. *In* RW Grigg, C Birkeland, eds. Status of coral reefs in the Pacific. Honolulu: Univ. of Hawaii, pp. 123-131.
- Dai CF, TY Fan, CS Wu. 1995. Coral fauna of Tungsha Tao (Pratas Island). Acta Oceanogr. Taiwanica **34:** 1-16.
- Dai CF, K Soong, TY Fan. 1992. Sexual reproduction of corals in northern and southern Taiwan. Proc. 7th Coral Reef Symp. 2: 448-455.
- Fan KL. 1979. On upwelling off the Peng-hu Islands. Acta Oceanogr. Taiwanica **9:** 50-57.
- Fan KL, CY Yu. 1981. A study of water mass in the seas of southmost Taiwan. Acta Oceanogr. Taiwanica 12: 94-111.
- Fang LS. 1989. Coral biology. Taipei: Lee-Ming Publ. Press. (in Chinese).
- Fong HC, HK Mok, HY Chen, K Soong, LL Liu. 1993. Marine biological resources of the south sea of Penghu. Penghu

Scenic Area Administration, Bureau of Tourism, Ministry of Communication, R.O.C. (in Chinese).

- Grigg RW, D Epp. 1989. Critical depth for the survival of coral islands: effect on the Hawaiian Archipelago. Science **243**: 638-641.
- Harrison PL, CC Wallace. 1990. Reproduction, dispersal and recruitment of scleractinian corals. *In* Z Dubinsky, ed. Ecosystems of the world. vol. 25. Coral Reef. Amsterdam: Elsevier Sci. Publ., pp. 133-207.
- Hayasaka I. 1935. Glance of the reef corals in Shu-Gwao Bay. Taiwan Geol. Report **3:** 5-8. (in Japanese).
- Hilasaka Y. 1935. Scleractinia of Taiwan. Japanese Acad. Assoc. Report. (in Japanese).
- Jan S. 1995. Current systems of Taiwan Strait. PhD thesis, Natl. Taiwan Univ., Taipei, Taiwan.
- Jeng MS, RQ Jan, CS Tzeng, FL Feng. 1997. Survey and monitoring of natural ecological resources in the Northeast Coast National Scenic Area (III) Northeast Coast National Scenic Area Administration, Bureau of Tourism, Ministry of Communication, R.O.C. (in Chinese).
- Jones RS, RH Randall, YM Cheng, HT Kami, SM Mak. 1972. A marine biological survey of southern Taiwan with emphasis on corals and fishes. Inst. Oceanog. Coll. Sci. Natl. Taiwan Univ. Spec. Publ. **1:** 1-93.
- Kawaguti S. 1942. Coral fauna of the Taiwan waters. Kagaku no Taiwan **11:** 1-6.
- Kawaguti S. 1943. Coral fauna of Garampi. Formosa Nat. Hist. Soc. **33:** 258-259.
- Kawaguti S. 1953. Coral fauna from Botel Tobago, Formosa, with a list of corals from the Formosa waters. Biol. J. Okayama Univ. 1: 185-201.
- Kimura M. 1991. Quaternary land bridges of the Ryukyu Arc detected on seismic reflecting profiles. Spec. Vol. Univ. Tohoku 35: 109-117.
- Lin CY, CT Tseng, CZ Shyu. 1998. NOAA-satellite derived SST report surrounding Taiwan. Available from http:// www.tfrin. gov.tw/D-FI/lab.satrs.
- Rohlf FJ. 1992. NTSYS-PC, Numerical taxonomy and multivariate analysis system, version 1.80. New York: Exeter Software.
- Shao KT, JP Chen, LT Ho, CP Lin, PH Kao, PL Lin, LS Chen. 1994. Checklist and distributional patterns of the fishes of the Pescadores Islands. Proc. 4th Indo-Pacific Fish Conf. Bangkok, Thailand: Kasetart Univ., pp. 267-280.
- Shao KT, JP Chen, SC Wang. 1997. Distribution and database of marine fishes in Taiwan waters. Proc. 7th Indo-Pacific Fish Conf. New Caledonia. Sybium. (in press).
- Shieh YT, MP Chen. 1995. The ancient Kuroshio current in the Okinawa trough during the Holocene. Acta Oceangr. Taiwanica **34:** 73-80.
- Sneath PHA, RR Sokal. 1973. Numerical taxonomy. San Francisco: W. H. Freeman.
- Swofford DL. 1993. PAUP: Phylogenetic analysis using parsimony. Champaign, IL: Illinois Nat. Hist. Survey.
- Veron JEN. 1992. Hermatypic corals of Japan. Aust. Inst. Mar. Sci. Monogr. Series 8.
- Veron JEN. 1993. A biogeographic database of hermatypic corals; species of the central Indo-Pacific, general of the world. Aust. Inst. Mar. Sci. Monogr. Series **9**.
- Veron JEN. 1995. Corals in space and time. Sydney: Univ. of New South Wales Press.
- Veron JEN, LM Marsh. 1988. Records and annotated check list of the hermatypic coral of the Western Australia. Rec. Western Aust. Mus. Suppl. **29**.
- Veron JEN, PR Minchin. 1992. Correlations between sea surface

temperature, circulation patterns and the distribution of hermatypic corals of Japan. Continental Shelf Res. **12:** 835-857.

- Veron JEN, M Pichon, M Wijsman-Best. 1977. Scleractinia of East Australia. Part II. Family Faviidae and Trachyphylliidae. Aust. Inst. Mar. Sci. Monogr. 3.
- Veron JEN, CC Wallace. 1984. Scleractinia of East Australia. Part V. Family Acroporidae. Aust. Inst. Mar. Sci. Monogr. 6.
- Wallace CC, CF Dai. 1997. Scleractinia of Taiwan (IV): review of the coral genus Acropora from Taiwan. Zool. Stud. 36: 288-324.
- Wallace CC, JM Pandolfi, A Young, J Wolstenholme. 1991. Indo-Pacific coral biogeography: a case study from the *Acropora selago* group. Aust. Syst. Bot. 4: 199-210.
- Wang J, CS Chern. 1988. On the Kuroshio branch in the Taiwan Strait during wintertime. Prog. Oceanogr. 21: 469-491.

- Wang J, CS Chern. 1992. On the distribution of the bottom cold waters in the Taiwan Strait during wintertime. La mer 30: 213-221.
- Wells JW. 1987. Note on Indo-Pacific Scleractinian corals. Part II. A new species of *Acropora* from Australia. Pacif. Sci. 39: 338-339.
- Yajima T. 1986. Ecological distribution of the reef coral crispata (Lamarck) at the shore region in the vicinity of Tsukumo Bay. Bull. Jpn. Sea Res. Inst., Kanazawa Univ. **18:** 21-36. (in Japanese).
- Yang RT, CC Huang, CH Wang, SZ Yeh, YF Jan, SL Liu, CH Chen, SJ Chen, LF Chang, CL Sun, W Huang, TF Tsai. 1976. A marine biological data acquisition program in the Nan-wan Bay area. Phase I. A preliminary reconnaissance survey. Inst. Oceanogr. Nat. Taiwan. Univ. Spec. Publ. 11: 1-133.

臺灣造礁珊瑚之分布與海水表面溫度及海流之一致性:

以軸孔珊瑚與菊石珊瑚分析為例

陳昭倫1

臺灣是一個大陸性的島嶼,和周圍幾個小島位處於菲律賓一日本島弧的中心交界上。除了西部沙岸 或泥岸之外,大約有三百種造礁珊瑚分布在臺灣及周圍的小島。以距離法及儉約法分析八個珊瑚礁生態 調查資料庫中,包括軸孔珊瑚屬及菊珊瑚科一百零四種造礁珊瑚的分布形式。鄰聚分析皆顯示軸孔珊瑚 和菊珊瑚在南臺灣和綠島的分布種類相似,而東北角則和澎湖相似。儉約分析軸孔珊瑚地理分群和由鄰 聚分析所得結果一致,但是,儉約分析菊珊瑚則顯現東北角與南臺灣和綠島形成一個群集。以儉約法分 析合併軸孔珊瑚和菊珊瑚的分布資料,支持臺灣周圍的造礁珊瑚分布可分成兩大組群,而這兩大組群與 海水表面溫度及海流流向呈現一致性。

關鍵詞:造礁珊瑚,熱帶珊瑚礁,非珊瑚礁群聚,海水表面溫度,洋流。

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