Zoological Studies **50**(1): 43-52 (2011)

Zoological Studies

Latitudinal Gradient of Morphological Variations in Zebra Coral *Oulastrea crispata* (Scleractinia: Faviidae) in the West Pacific

Kao-Song Chen[1,3], Hernyi Justin Hsieh[3], Shashank Keshavmurthy[1], Julia Ka Lai Leung[1,4], I-Ting Lien[5,6], Yoshikatsu Nakano[7], Sakanan Plathong[8], Hui Huang[9], Chaolun Allen Chen[1,2,10,*]

[1]Biodiversity Research Center, Academia Sinica, Nangang, Taipei 115, Taiwan
[2]Institute of Oceanography, National Taiwan University, Taipei 106, Taiwan
[3]Fisheries Research Institute, Council of Agriculture, Executive Yuan, Keelung 200, Taiwan
[4]Department of Life Science, National Taiwan Normal University, Taipei 106, Taiwan
[5]Graduate School of Agriculture, Kyoto University, Kyoto 605-8502, Japan
[6]Field Science Education and Research Center, Kyoto University, Wakayama 649-2211, Japan
[7]Sesoko Station, Tropical Biosphere Research Center, University of Ryukyus, Okinawa 905-0227, Japan
[8]Department of Biology, Prince of Songkla University, Songkla 90112, Thailand
[9]South China Sea Institute of Oceanology, Chinese Academics of Science, Guangzhong 510301, China
[10]ARC Center of Excellence for Coral Reef Studies, James Cook University, Townsville Q4810, Australia

(Accepted August 17, 2010)

Kao-Song Chen, Hernyi Justin Hsieh, Shashank Keshavmurthy, Julia Ka Lai Leung, I-Ting Lien, Yoshikatsu Nakano, Sakanan Plathong, Hui Huang, Chaolun Allen Chen (2011) Latitudinal gradient of morphological variations in zebra coral *Oulastrea crispata* (Scleractinia: Faviidae) in the West Pacific. *Zoological Studies* **50**(1): 43-52. Corals grow across latitudes throughout the tropics and subtropics where environmental factors, including the average annual temperature and seasonal changes in water clarity and temperature, substantially vary. These environmental factors could lead to latitudinal variations in coral skeletal morphology. In this study, morphometric variations of the zebra coral *Oulastrea crispata*, a small coral species with black and white septa and a colony diameter usually < 10 cm, were investigated. Previous studies reported that *O. crispata* can survive in extreme environmental conditions, such as low temperatures and turbid water. One hundred colonies of *O. crispata* were collected from sites spanning Thailand to Japan, across tropical, subtropical, and temperate regions. Five micro-characters of corallites were measured and examined using univariate and multivariate analyses. All micro-characters measured significantly differed among latitudinal regions (nested ANOVA, $p < 0.05$). A canonical discriminant analysis (CDA) indicated that corallite diameter was the most important character contributing to variations in *O. crispata* among the 3 latitudinal regions, although a plot of the 1st and 2nd canonical variables showed that *O. crispata* from different latitudinal regions could not be fully separated. Nevertheless, significant differences in the Mahalanobis distances between the CDA group centroids were detected, suggesting a latitudinal gradient of morphological variations in *O. crispata* in the West Pacific. http://zoolstud.sinica.edu.tw/Journals/50.1/43.pdf

Key words: Scleractinian, Morphometrics, Corallites, *Oulastrea crispata*, Latitudinal variation.

The coral reef environment is extremely heterogeneous and thus presents an adaptive challenge to sessile organisms that, beyond their larval stage, are incapable of escaping their surroundings. In order to improve fitness, many animals, especially scleractinian corals, have evolved diverse, environmentally relevant, morphologies (Wallace 1999, Veron 2000). Even within the same coral species, a striking degree of morphological variations along physical gradients

---

[*] To whom correspondence and reprint requests should be addressed. E-mail:cac@gate.sinica.edu.tw

and among geographic regions can be found (Veron 1981, Veron and Wallace 1984, Brown et al. 1985, Willis 1985, Willis and Ayre 1985, Wallace 1999). Defining boundaries between intraspecific and interspecific morphological variations in scleractinian corals continues to be a fundamental problem for all coral taxonomists and coral reef researchers, resulting in difficulties identifying cryptic or sibling species and leading to underestimates of reef biodiversity (Knowlton and Jackson 1994, Miller 1994, Stobart 2000, Stefani et al. 2008a b 2010).

Three main scales exist for morphological variations in adult corals: colony scale, corallite (the skeletal counterpart of the fleshy polyp) scale, and sub-corallite (micromorphological) scale. Morphological variations at the colony scale include colony growth forms such as branching, massive, encrusting etc., while corallites are characterized by features such as the septa number and arrangement, whereas sub-corallite features include septa teeth and granules (Veron 2000, Budd and Stolarski 2009). It is accepted that for colony and corallite scales at least, morphology is controlled by genetics (Amaral 1994, Knowlton and Jackson 1994, Miller and Benzie 1997) and/or external environmental factors such as wave action (Lesser et al. 1994, Bruno and Edmunds 1997) and light intensity (Muko et al. 2000, Todd et al. 2004b). Environmental influences on morphological characters are usually termed phenotypic plasticity and are documented in a wide range of coral species (Todd 2008). In ecological terms, morphological plasticity might enable corals to occupy a broad range of habitats and allow them to acclimatize to temporal changes in the environment (Bruno and Edmunds 1997). In taxonomic terms, such environmentally induced morphological changes can hinder accurate species identification.

Corals grow and coral communities develop across latitudes throughout the tropics and subtropics where environmental factors including the average annual temperature and seasonal changes in water clarity and temperature substantially vary (Brown 2007). These environmental factors, along with ecological characteristics at the local scale, can significantly influence coral morphogenesis, resulting in latitudinal variations in their skeletal morphology. Although latitudinal variations in coral skeletal morphology were previously qualitatively described (Veron 1995, Wallace 1999), the quantitative examination of biogeographic skeletal variations remains unexplored.

In this study, we examined morphometric variations of skeletal characters of *Oulastrea crispata* collected from tropical reefs in the Andaman Sea, Thailand (< 10°N) to a high-latitudinal non-reefal coral community in Japan (> 35°N). *O. crispata* is an unusual coral species with a wide geographic distribution and habitat preferences (Veron 2000, Lam 2000b, Chen et al. 2003, Lien et al. 2007). *O. crispata* is found in the western Pacific between Japan in the north to the Great Barrier Reef in the south (Veron 2000). In Japan, it is usually distributed near the low tide mark, grows on bare boulder surfaces, and has relatively small colony sizes often of < 10 cm in diameter with an encrusting or massive growth form (Yajima et al. 1986). *O. crispata* was reported to occur near the low tide mark and on bare subtidal boulder surfaces in Hong Kong (Lam 2000a b), whereas around the Penghu Is., Taiwan, and within the Ryukyus Archipelago, Japan, *O. crispata* is common on shallow reef depressions and on turbid bay bedrock inhabited by only a few other corals (Nakano and Yamazato 1992, Chen et al. 2003). Several studies suggested that *O. crispata* is resistant to adverse environmental conditions (Yajima et al. 1986, Chen et al. 2003); for instance, it was recorded from the shores of the Noto Peninsula, Japan, where winter water temperatures are usually 7-10°C, and air temperatures are several degrees below freezing for about 20 d of the year (Yajima et al. 1986). These properties suggest that *O. crispata* can survive in extreme environmental conditions (Fig. 1), and we predict that its morphology varies among different latitudinal regions.

MATERIALS AND METHODS

Sampling sites and environmental data

In this study, 13 sites were surveyed across tropical, subtropical, and temperate regions in the West Pacific (Fig. 1, Table 1). Habitat types ranged from bedrock in high-latitudinal Japan, shallow reef depressions in subtropical reefs, to intertidal coral cays among tropical reefs. Samples collected from Sa-Tun, Thailand were from breaks in the mangrove area. An analysis of monthly mean sea surface temperatures (SSTs) clearly indicated a seasonal pattern of temperature fluctuations among the regions from a mean SST of 18.28°C at Okayama, Japan to 29.42°C in Sa-Tun (Lien et al. 2007). In high-latitude Japan, the lowest mean SST (11.86°C) was observed in Okayama in Feb., and SSTs of < 18°C can last for up to 5 mo. In contrast, SSTs in tropical reefs showed little fluctuation and were significantly higher than those in temperate and subtropical regions (Lien et al. 2007). In total, 100 colonies of *O. crispata* were collected, preserved in 85% ethanol, and shipped to the laboratory. Tissue samples were collected for molecular ecology studies (Chen et al. 2003, Lien et al. 2007). Skeletal samples were prepared by bleaching in 3% sodium hypochlorite

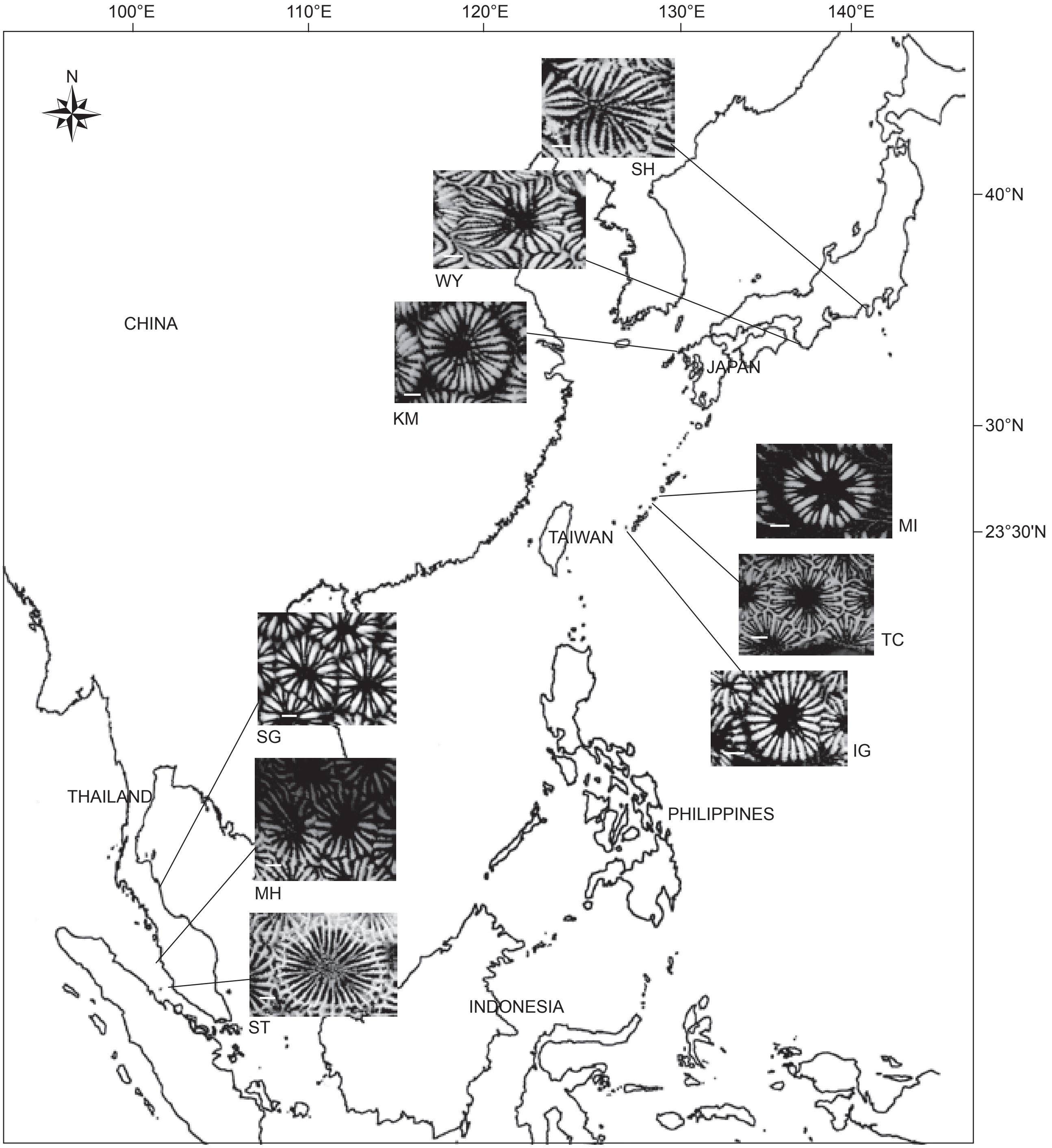

Fig. 1. Map of the collecting localities and images of the skeleton of *Oulastrea crispata* from each locality. Scale bars in the photo indicate 1 mm.

to remove residual tissues. Skeletons were air-dried before the morphometric data were extracted. All skeletal samples were deposited at the Biodiversity Research Museum, Academia Sinica, Taipei, Taiwan. Monthly mean SST (1948-2010) and chlorophyll *a* records (2002-2009) were acquired from NOAA Earth System Research Laboratory NCEP/NCAR data (http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl; downloaded 14 Mar. 2010), and chlorophyll *a* records (2002-2009) adjacent to the sampling localities were acquired from the Giovanni online data system (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi? instance_id=ocean_month; downloaded 14 Mar. 2010), which was developed and is maintained by the NASA Goddard Earth Sciences (GES) Data and Information Services Center (DISC), MD, USA. Chlorophyll *a* is utilized as an indicator of light penetration in the water around the coral reef areas (Lesser et al. 1990, Lesser 1996).

Morphometric measurements

A digital camera (Olympus C5050, Olympus Corporation, Tokyo, Japan) connected to a stereo-microscope (Olympus SZ-40) was used to take images of corallites with a standard scale. Five corallites (Fig. 2) were randomly chosen from every colony to measure 5 characters: corallite diameter (CD), the spacing of corallites (CS), columella width (CW), the length of the 1st cycle septa (LS), and the thickness of the 1st cycle septa (TS). These characters are frequently used in scleractinian morphometrics (Miller 1994, Stobart 2000, Stefani et al. 2008a b). Images were imported into an Intel-based Macintosh computer, and characters were measured with ImageJ vers. 1.43 (http://rsbweb.nih.gov/ij/).

Table 1. Locality, numbers of corallites, and measurements of 5 skeletal characters of *Oulastrea crispata* used in analysis (mean ± S.D., mm). Five corallites were measured for each colony

Latitudinal region/Locality			Habitat	Character	CD	CS	CW	L1S	T1S
			type	No. of colonies					
Temperate									
SH	140°17'E	35°38'N	bedrock	8	5.35 ± 0.78	2.72 ± 0.37	2.10 ± 0.50	1.73 ± 0.22	0.30 ± 0.03
OY	133°48'E	34°56'N	bedrock	7	6.23 ± 0.56	3.34 ± 0.35	2.43 ± 0.39	1.83 ± 0.26	0.29 ± 0.05
WY	134°22'E	34°01'N	bedrock	11	5.43 ± 0.53	2.85 ± 0.26	2.10 ± 0.50	1.85 ± 0.20	0.37 ± 0.06
KM	130°48'E	32°03'N	bedrock	7	5.84 ± 0.42	3.00 ± 0.32	2.31 ± 0.30	1.80 ± 0.15	0.38 ± 0.06
Subtropical									
MI	127°03'E	25°29'N	Shallow reef depression	9	5.18 ± 0.58	3.19 ± 0.43	1.71 ± 0.19	1.79 ± 0.27	0.36 ± 0.02
TC_1	127°03'E	25°29'N	Shallow reef depression	4	5.37 ± 0.43	2.85 ± 0.18	2.15 ± 0.15	1.67 ± 0.17	0.33 ± 0.04
TC_2	127°03'E	25°29'N	Shallow reef depression	10	5.10 ± 0.75	2.69 ± 0.43	1.92 ± 0.42	1.72 ± 0.18	0.31 ± 0.03
IG	124°01'E	24°22'N	Shallow reef depression	8	4.42 ± 0.62	2.87 ± 0.41	1.55 ± 0.14	1.47 ± 0.27	0.31 ± 0.05
Tropical									
WJ	109°15'E	21°10'N	Intertidal coral cay	6	5.49 ± 0.78	2.77 ± 0.47	2.32 ± 0.33	1.74 ± 0.15	0.35 ± 0.04
HN	110°19'E	20°05'N	Intertidal coral cay	5	4.61 ± 0.55	2.27 ± 0.39	1.65 ± 0.27	1.46 ± 0.24	0.36 ± 0.06
SC	100°51'E	13°08'N	Intertidal coral cay	12	3.97 ± 0.40	2.42 ± 0.31	1.49 ± 0.27	1.28 ± 0.12	0.34 ± 0.05
MH	98°30'E	07°50'N	Intertidal coral cay	4	4.03 ± 0.54	2.13 ± 0.34	1.52 ± 0.35	1.34 ± 0.11	0.32 ± 0.05
ST	100°04'E	06°43'N	Mangroves	9	5.01 ± 0.60	2.57 ± 0.46	2.07 ± 0.38	1.55 ± 0.17	0.33 ± 0.03

CD, corallite diameter; CS, spacing of the corallites; CW, columella width; L1S, length of the 1st cycle septa; T1S, thickness of the 1st cycle septa. Abbreviations of localities are defined in figure 1.

Statistical analysis

To examine morphometric measurements of *O. crispata* with the following procedure, normality and homogeneity of variance were first examined using SAS 9.1 (pro GLM) (SAS Institute Inc., Cary, NC, USA). Most of the characters were normally distributed; hence all analyses were applied to raw data. A nested analysis of variance (ANOVA) and Bonferroni tests were conducted to analyze each character among colonies and sites. In order to examine the combined effects of skeletal characters, a multivariate ANOVA (MANOVA) was performed using the corallite variables measured among different sites, and a canonical discriminant analysis (CDA) was used to visually examine morphological differences. Last, Mahalanobis distances, a measure of distance between different CDA groups based on the means, variances, and covariances, were calculated. All statistical analyses were carried out using Aabel 2.4 (www.gigamiz.com), SAS 9.1, and PAST (http://folk.uio.no/ohammer/past/).

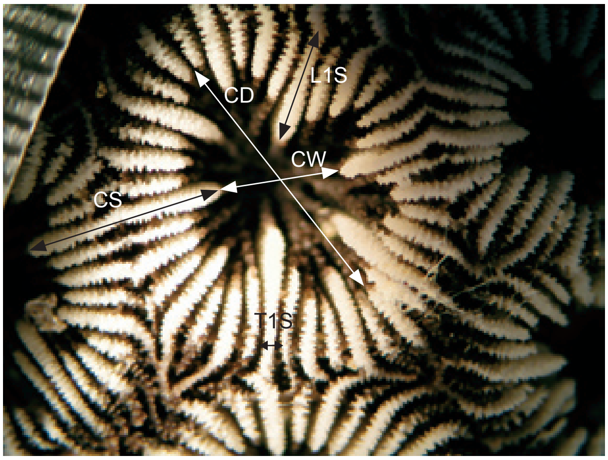

Fig. 2. Photograph of corallites indicating skeletal measurements taken on colonies of *Oulastrea crispata*. List of micro-characters measured: CD: Corallites diameter; CS: Spacing of corallites; CW: Columella width; L1S: Length of 1st cycle septa; T1S: Thickness of 1st cycle septa.

RESULTS

The SST ranged from a mean of 18.28°C at Okayama, Japan to 29.42°C at Sa-Tun, Thailand (Fig. 3A). In high-latitude Japan, the lowest mean SST (11.86°C) was observed at Okayama in Feb., and SSTs of < 18°C could last for up to 5 mo.

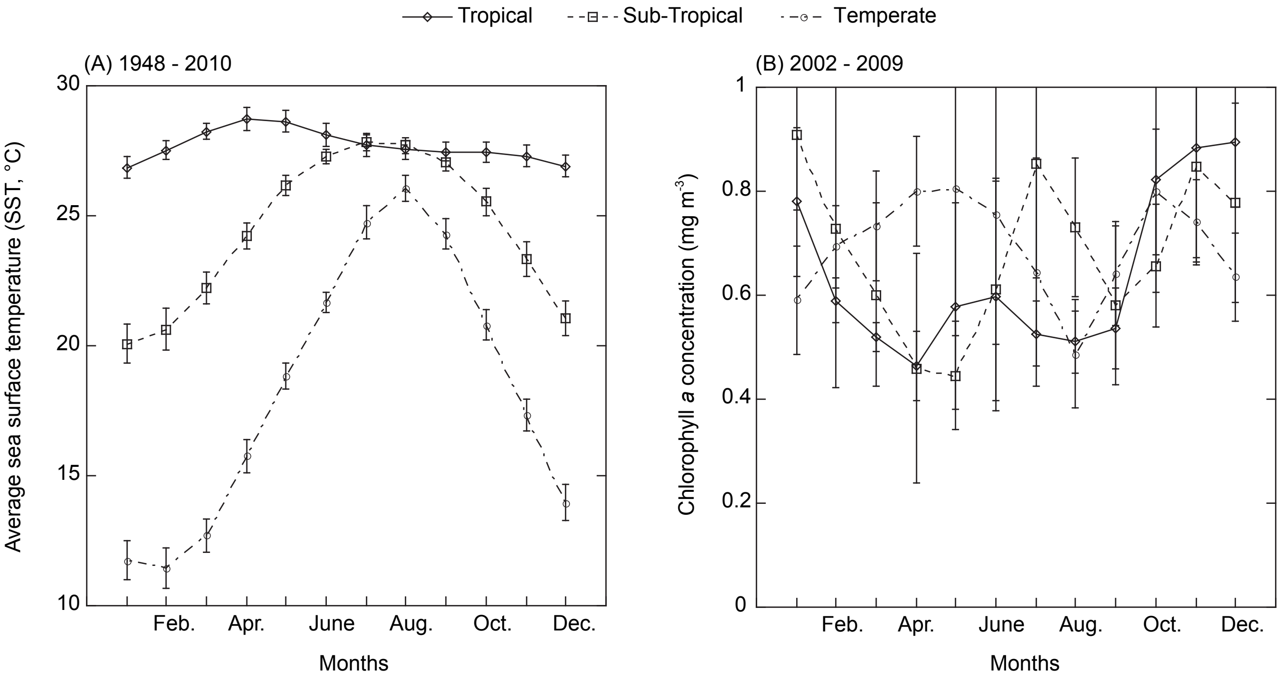

Fig. 3. (A) Monthly averages of sea surface temperatures (SST) and (B) seasonal patterns of chlorophyll *a* concentrations for the temperate, subtropical, and tropical regions. The average monthly sea surface temperature (SST) from Jan. 1948 to Dec. 2010, and chlorophyll *a* from Jan. 2002 to Dec. 2009 were acquired from a database retrieved from NOAA Earth System Research Laboratory NCEP/NCAR data (http://www.esrl.noaa.gov). Each point represents the monthly average ± S.D.

SSTs at tropical reefs showed little fluctuation through the seasons and were higher than those of temperate and subtropical regions. Mean values of monthly chlorophyll *a* were shown to largely differ between temperate regions and those of subtropical and tropical regions from Mar. to Aug. (Fig. 3B).

Univariate statistics of each character measurement of *O. crispata* collected from the 13 sites are summarized in tables 1 and 2. A population of *O. crispata* with larger corallites was found in Okayama with a mean CD) of 6.23 ± 0.56 mm, whereas in Si-Chiang, corallites were significantly smaller with a mean CD of 3.97 ± 0.40 mm (Table 1). All 5 characters of CD, CS, CW, LS, and TS significantly differed among sites (nested ANOVA, $p < 0.01$, Table 2). *O. crispata* corallites from temperate regions were significantly larger in diameter than those of subtropical and tropical regions. Overall, corallites of tropical *O. crispata* were significantly smaller than those from subtropical and temperate regions based on the 5 skeletal characters measured (nested ANOVA, Bonferroni test, $p < 0.05$, Fig. 4).

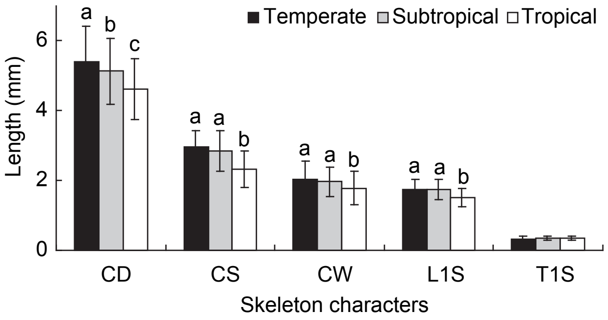

Fig. 4. Bonferroni test of 5 skeletal characters grouped by latitudinal regions. The length (mean ± S.D., mm) of the skeletal characters grouped by the same letter indicates a non-significant difference ($p > 0.05$) between regions.

The MANOVA based on 5 skeletal characters of 100 colonies was significant (Hotelling-Lawley test, $p < 0.01$). The CDA showed that 94.92% of the variation among tropical, subtropical, and temperate groups was explained by the 1st 3 canonical variables. The 1st axis accounted for 64.45% of the variation, and the 2nd axis only accounted for 18.93% (Table 3). Although a plot of the 1st 2 canonical variables could not fully separate *O. crispata* in accordance with the latitudinal regions, most tropical colonies fell into the 2nd and 3rd quadrants, while most subtropical colonies fell into the 1st and 2nd quadrants, and most temperate individuals fell into the 1st and 4th quadrants, thus providing a visually demonstrative trend that separated tropical and temperate populations (Fig. 5). Canonical discriminant coefficients of each character to the 1st axis were characterized by positive loadings (eigenvectors) for CD, L1S, and CS. The 2nd canonical discriminant axis was characterized by positive loadings (eigenvectors) for CS, CW, and L1S (Table 4). Mahalanobis distances between the CDA groups (latitudinal regions) significantly differed: 2.96

Table 2. One-way ANOVA of 5 skeletal characters among sites and colonies

Characters	Effect	Sum of squares	*d.f.*	Meansquare	*F*	*p*
CD	Sites	40.70	12	3.39	9.68	< 0.01
CS	Sites	9.22	12	0.77	5.51	< 0.01
CW	Sites	9.29	12	0.77	7.00	< 0.01
L1S	Sites	3.68	12	0.31	7.46	< 0.01
T1S	Sites	0.08	12	0.01	3.35	< 0.01

Skeletal characters are defined in the footnotes to table 1.

Table 3. Eigenvalues, percent (%) of variance, and cumulative percent (%) of variance accounted for by the 1st 3 canonical discriminative analysis axes

Axis	Eigenvalue	Percent of variance	Cumulative percent of variance
1	3.22	64.45	64.45
2	0.95	18.93	83.38
3	0.58	11.54	94.92

between tropical and temperate regions, 2.15 between tropical and subtropical regions, and 1.53 between subtropical and temperate regions; and the Mahalanobis distances between all paired CDA groups significantly differed (*F*-test, $p < 0.05$).

DISCUSSION

With the aid of morphometric measurements and multivariate analyses of skeletal characters, we demonstrated latitudinal variations of corallites in the stress-resistant coral, *O. crispata*, collected from tropical coral reefs in Thailand to non-reefal coral communities in high-latitudinal Japan. Temperate *O. crispata* had larger corallites, while corallites of *O. crispata* in tropical coral reefs tended to be the smallest.

Morphometrics were used to illustrate phenotypic plasticity of skeletal variations in scleractinians on clonal population structures (Willis 1985, Willis and Ayre 1985) and species diagnosis (Miller 1994, Stobart 2000, Stefani et al. 2008a b 2010). In combination with field experiments, morphometrics are applied to understand responses of coral colonies to specific physical environmental factors, such as wave action, light intensity, and sediments (Lesser et al. 1994, Bruno and Edmunds 1997 1998, Todd et al. 2001). A photographic technique was used to examine morphological differences in living polyps of Singaporean *Favia speciosa*, showing that corals with large polyps close to the main island of Singapore are possibly a plastic response or selection for high sediment levels (Todd et al. 2001).

The influences of environmental factors, such as the average annual temperature and seasonal changes in water clarity and temperature on skeletal morphology, are not restricted to the local scale, but can also operate across the biogeographic scale (Veron 1995, Wallace 1999). Qualitative descriptions of colony morphology or corallite variation of corals from different biogeographic regions were previously reported (Veron 1995 2000, Wallace 1999). Our study; however, provides quantitative evidence of morphometric variations of corallites in the same scleractinian species across biogeographic regions. *O. crispata* is a peculiar coral species that has a latitudinal distribution restricted to the West Pacific with a range from Japan in the north to the Great Barrier Reef in the south (Veron 1993). Within this range, environmental factors, such

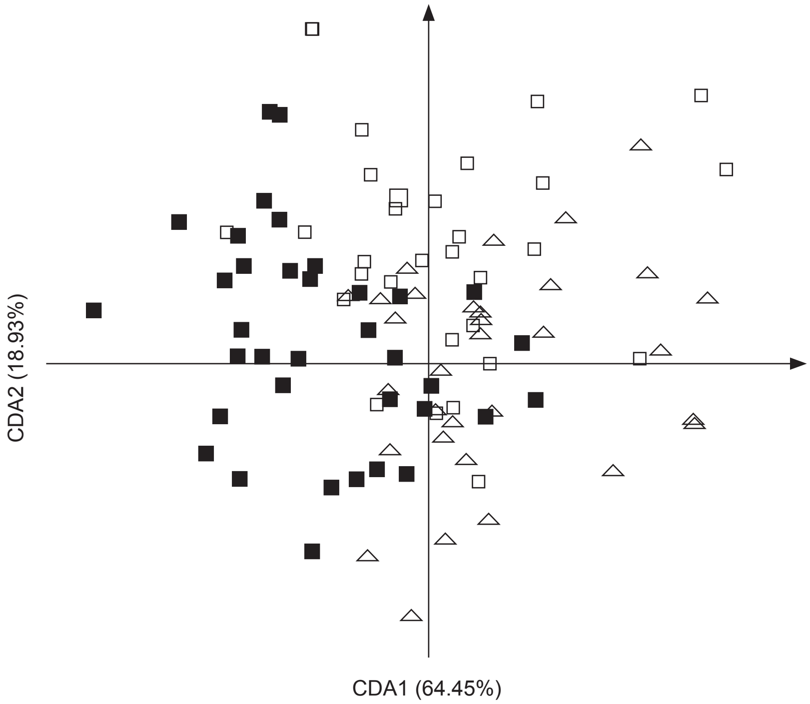

Fig. 5. Results from canonical discriminant analysis of all *Oulastrea crispata* colonies. Plot of the 1st 2 canonical variates, △: temperate; □: subtropical; ■: tropical.

as temperature, light, and turbidity, can fluctuate on a seasonal basis (Fig. 2), and might influence corallite and colony growth, asexual budding, and mortality of *O. crispata*. However, tank experiments with controlled factors (Todd et al. 2004a) need to be done to confirm this hypothesis.

Seawater temperature is one of the major factors limiting coral distributions throughout different latitudinal regions, with temperatures of 18-28°C usually required for coral survival (Veron 1995). SSTs can be as low as 11°C in winter and below 18°C for over 5 mo, yet *O. crispata* is capable of persisting at these extremely low temperatures (Yajima et al. 1986, Chen et al. 2003). Our data show that temperate *O. crispata* colonies have larger corallites than those of tropical and subtropical ones. Although *O. crispata* tends to grow more slowly at higher temperatures and vice versa in winter (Lam 2000b), the relationship between temperature and corallite size in this species is not clear.

As with other species (Caras et al. 2008), light may be an important factor influencing corallite size in *O. crispata*. Photosynthetic optimization by corallite size was also found in *F. speciosa* at the Wakatobi Marine National Park, Indonesia (Caras et al. 2008). Tank experiments that controlled flow, sediment, and light on Singaporean *F. speciosa* and *Dilpoastrea heliopora* showed a relationship between corallite morphology and light, but no consistent pattern was detected for fragments kept in the tank (Todd et al. 2004a), confirming that light plays an important role in shaping the corallite size of corals.

Differences in colony morphology are largely genetically determined, although environmental gradients undoubtedly modify colony morphologies (Ayre and Willis 1988, Willis and Ayre 1985). Transplantation of distinct genotypes of *Madracis mirabilis* between 2 populations in Jamaica, in the Caribbean Sea, showed that many of the acquired phenotypes in transplants conformed to the morphology of conspecifics residing in their original sites in each treatment environment, suggesting that both genotypes tended to maintain similarly different growth rates under diverse environmental conditions (Bruno and Edmunds 1997). Transplanting Singaporean *F. speciosa* and *D. heliopora* along a depth cline (i.e., light) and turbidity gradient treatment showed that morphological changes were more pronounced in the former than the latter treatment, suggesting that environmental interactions play as important a role as genotype in the phenotypes of these 2 species (Todd et al. 2004b). Similar tank experiments need to be conducted to examine the influences of light and genotype × environmental interactions on *O. crispata* from different geographic localities.

In order to unravel latitudinal differences in genotype × environmental interactions, the genetic information of a species across the biogeographic range can be retrieved from a phylogeographic analysis, and compared to morphological variations. In the Pacific, a phylogeographic analysis of a widespread coral, *Plesiastrea versipora*, showed strong geographical associations among populations along the southeastern coast of Australia (Rodriguez-Lanetty and Hoegh-Guldberg 2002). Colony morphology of *P. versipora* ranges from encrusting to massive forms (Veron 1974). But a distinct geographic subspecies at high latitudes so differed in color and morphology, that it was previously described as a distinct ecomorph (Wijsman-Best 1977), and later considered a separate species (Veron 1995). On the other hand, phylogeographic and morphometric analyses of a branching octocoral, *Pseudopterogorgia elisabethae*, from the Bahamas, Florida Keys, and western Caribbean showed that despite both genetic and morphological variations among certain populations of *P. elisabethae* at these sites, these variations did not correspond to each other, suggesting that local environmental components might be a stronger determinant of branching morphology than the biogeography (Gutiérrez-Rodríguez et al. 2009). In *O. crispata*, growth forms at the colony scale did very vary as it always appeared as encrusting or massive colonies, which tended to grow more slowly in summer and faster in winter (Lam 2000b). A slower growth rate might be a trade-off for better acclimatization at higher temperatures (Gates and Edmunds 1999). However, the relationship between the colony growth rate and corallite size is uncertain. A further phylogeographic analysis is currently underway to illustrate genetic variations

Table 4. Canonical discriminant coefficients of 5 skeletal characters that contribute to the 1st and 2nd canonical discriminant axes

Axis	CD	CS	CW	L1S	T1S
1	0.85	0.2	-0.52	0.65	-0.42
2	-2.46	1.17	0.27	1.05	-0.25

Skeletal characters are defined in the footnotes to table 1.

and possible interactions of corallite size and environment factors in *O. crispata* across the West Pacific region (Lien et al. unpubl. data).

Acknowledgments: Many thanks go to members of the Coral Reef Evolutionary Ecology and Genetics Laboratory, Biodiversity Research Center, Academia Sinica (BRCAS) and 2 anonymous referees for constructive comments. CAC is the recipient of the Australian Endeavour Award (2010-2011) and the National Science Council (NSC)-Australian Academy of Science fellowship (2010). KS is the recipient of a post-doctoral fellowship (2008-2010) from the NSC and a post-doctoral fellowship (2010-2011) from Academia Sinica, Taiwan. This study was supported by an NSC grant and Academia Sinica Thematic Grants (2002-2004, 2005-2007) to C.A.C. This is the Coral Reef Evolutionary Ecology and Genetics Group, BRCAS contribution no. 64.

REFERENCES

Amaral FD. 1994. Morphological variation in the reef building coral *Montastrea cavernosa* in Brazil. Coral Reefs **13:** 113-117.

Ayre DJ, BL Willis. 1988. Population structure in the coral *Pavona cactus*: clonal genotypes show little phenotypic plasticity. Mar. Biol. **99:** 495-505.

Brown BE. 2007. Coral reefs of the Andaman Sea: an integrated perspective. Ocean Mar. Biol. **45:** 173-194.

Brown BE, L Syarani, MDL Tissier. 1985. Skeleton form and growth in *Acropora aspera* from the Pulau, Seribu, Indonesia. J. Exp. Mar. Biol. Ecol. **86:** 139-150.

Bruno JF, PJ Edmunds. 1997. Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. Ecology **78:** 2177-2190.

Bruno JF, PJ Edmunds. 1998. Metabolic consequences of phenotypic plasticity in the coral *Madracis mirabilis* (Duchassaing and Michelotti): the effect of morphology and water flow on aggregate respiration. J. Exp. Mar. Biol. Ecol. **229:** 187-195

Budd AF, J Stolarski. 2009. Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. Acta Zool. **90:** 142-165.

Caras T, A Bachar, Z Pasrernak. 2008. Morphological variation in the oral disc of the scleractinian coral *Favia speciosa* (Dana) at Indonesia. Comp. Biol. Chem. **32:** 345-348.

Chen CA, KK Lam, Y Nakano, WS Tsai. 2003. A stable association of the stress-tolerant zooxanthellae, *Symbiodinium* clade D, with the low-temperature-tolerant coral, *Oulastrea crispata* (Scleractinia: Faviidae) in subtropical non-reefal coral communities. Zool Stud **42:** 545-550.

Crabbe MJ, DJ Smith. 2006. Modelling variations in corallite morphology of *Galaxea fascicularis* coral colonies with depth and light on coastal fringing reefs in Wakatobi Marine National Park (S. E. Sulawesi, Indonesia). Compar. Biol. Chem. **30:** 155-159.

Gates RD, PJ Edmunds. 1999. The physiological mechanisms of acclimatization in tropical reef corals. Am. Zool. **39:** 30-43.

Graus RR, IG Macintyre. 1982. Variation in the growth forms of the reef coral *Montastrea annularis* (Ellis and Solander): a quantitative examination of growth response to light distribution using computer simulation. Smithson. Contrib. Mar. Sci. **12:** 441-464.

Gutiérrez-Rodríguez C, M Barbeitos, J Sánchez, HR Lasker. 2009. Phylogeography and morphological variation of the branching octocoral *Pseudopterogorgia elisabethae*. Mol. Phylogenet. Evol. **50:** 1-15.

Knowlton N, JBC Jackson. 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some. TREE **9:** 7-9.

Lam KK. 2000a. Sexual reproduction of a low temperature tolerant coral, *Oulastrea crispata*, in Hong Kong, China. Mar. Ecol. Progr. Ser. **205:** 101-111.

Lam KK. 2000b. Early growth of a pioneer recruited coral *Oulastrea crispata* on PFA-concrete blocks in a marine park in Hong Kong, China. Mar. Ecol. Progr. Ser. **205:** 113-121.

Lesser MP. 1996. Elevated of ambient levels of solar ultraviolet radiation on zooxanthellae and photosynthesis of the reef coral *Montipora verrucosa*. Mar. Biol. **116:** 319-327.

Lesser MP, WR Stochaj, DW Tapley, JM Shick. 1990. Bleaching in coral reef anthozoans: effect of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs **8:** 225-232.

Lesser MP, VM Weis, P Patterson, PL Jokiel. 1994. Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. J. Exp. Mar. Biol. Ecol. **178:** 153-179.

Lien YT, Y Nakano, S Plathong, H Fukami, JT Wang, CA Chen. 2007. Occurrence of the putatively heat-tolerant *Symbiodinoium* phylotype D in high-latitudinal outlying coral communities. Coral Reefs **26:** 35-44.

Miller KJ. 1994. Morphological variation in the coral genus *Platygyra*-Environmental influences and taxonomic implications. Marine Ecology-Progress Series. **110:** 19-28.

Miiler KJ, JAH Benzie. 1997. No clear genetic distinction between morphological species within coral genus *Platygyra*. Bull. Mar. Sci. **61:** 907-917.

Muko S, K Kawasaki, K Sakai, F Takasu, N Shigesada. 2000. Morphological plasticity in the coral *Porites sillimaniani* and its adaptive significance. Bull. Mar. Sci. **66:** 225-239.

Nakano YKY. 1992. Ecological study of reproduction of *Oulastrea crispata* in Okinawa. Zool. Sci. **9:** 1292

Rodriguez-Lanetty M, O Hoegh-Guldberg. 2002. The phylogeography and connectivity of the latitudinally widespread scleractinian coral *Plesiastrea versipora* in the Western Pacific. Mol. Ecol. **11:** 1177-1189.

Stefani F, F Benzoni, M Pichon, C Cancelliere, P Galli. 2008a. A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). Zool. Script. **37:** 71-91.

Stefani F, F Benzoni, M Pichon, G Mitta, P Galli. 2008b. Genetic and morphometric evidence for unresolved species boundaries in the coral genus *Psammocora* (Cnidaria; Scleractinia). Hydrobiology **596:** 153-172.

Stefani F, F Benzoni, SY Yang, M Pichon, P Galli, CA Chen. 2010. The genus *Stylophora* (Cnidaria, Scleractinia) in the Gulf of Aden, Yemen: an integrated systematics and evolutionary study. Coral Reefs. (submitted)

Stobart B. 2000. A taxonomic reappraisal of *Montipora digitata* based on genetic and morphological evidence. Zool. Stud. **39:** 179-190.

Todd PA. 2008. Morphological plasticity in scleractinian corals. Biol. Rev. **83:** 315-337.

Todd PA, RJ Ladle, NJI Lewin-Koh, LM Chou. 2004b. Genotype x environment interactions in transplanted clones of the massive corals *Favia speciosa* and *Diploastrea heliopora*. Mar. Ecol. Progr. Ser. **271:** 167-182.

Todd PA, PG Sanderson, LM Chou. 2001. Morphological variation in the polyps of the scleractinian coral *Favia speciosa* (Dana) around Singapore. Hydrobiology **444:** 227-235.

Todd PA, RC Sidle, NJI Lewin-Koh. 2004a. An aquarium experiment for identifying the physical factors inducing morphological change in two massive scleractinian corals. J. Exp. Mar. Biol. Ecol. **299:** 97-113.

Veron J. 2000. Corals of the world. Townsville, Australia: Australian Institute of Marine Sciences.

Veron JEN. 1974. Southern geographic limits to the distribution of Great Barrier Reef hermatypic corals. Proc. 2nd Int. Coral Reef Symp. **2:** 465-473.

Veron JEN. 1981. The species concept in “Scleractinia of Eastern Australia”. Proc. 4th Int. Coral Reef Symp. **1:** 18-22.

Veron JEN. 1993. Coral of Australia and the Indo-Pacific. Honolulu: Univ. of Hawaii Press.

Veron JEN. 1995. Corals in space and time: the biogeography and evolution of the Scleractinia. Ithaca, NY and London: Cornell Univ. Press.

Veron JEN, CC Wallace. 1984. Scleractinia of eastern Australia, Part. 5 Family Acroporidae. Townsville, Australia: Australian Institute of Marine Sciences, pp. 1-485.

Wallace CC. 1999. Staghorn corals of the world: a revision of the coral genus *Acropora* (Scleractinia; Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology, phylogeny and biogeography. Collingwood, Australia: CSIRO Publishing.

Wijsman-Best M. 1977. Indo-Pacific coral species belonging to the subfamily Montastreinae (Vaughan and Wells 1943). Part 1: the genera *Montastrea* and *Plesiastrea*. Zool. Meded. **52:** 81-97.

Willis BL. 1985. Phenotypic plasticity versus phenotypic stability in the reef corals *Turbinarian mesenterina* and *Pavna cactus*. Proc. 5th Int. Coral Reef Symp. **6:** 107-112.

Willis BL, DJ Ayre. 1985. Asexual reproduction and genetic determination of growth form in the coral *Pavona cactus*: biochemical genetic and immunogenic evidence. Oecologia **65:** 516-525.

Yajima T, O Sano, T Okamoto, Y Shirai, T Shinya, M Matada. 1986. Ecological distribution of the reef coral, *Oulastrea crispata* (Lamarck) at the shore region in the vicinity of Tukumo Bay. Bull. Jpn. Sea Res. Inst. **18:** 21-36.