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Spatial Patterns and Environmental Settings of Non-reefal Coral Communities Across the Tropic of Cancer in the Penghu Archipelago (Pescadores), Taiwan

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Hernyi Justin Hsieh, Colin Kou-Chang Wen, Yuan-Chao Huang, Kao-Sung Chen, Chang-Feng Dai, and Chaolun Allen Chen (2016) Non-reefal coral communities occurring at the edges of scleractinian coral distribution ranges normally show a sharp gradient in the composition of coral species. Environmental and biological factors such as sea surface temperature (SST), competition with other benthos, and human disturbances might play roles in shaping the structure of coral communities. The Penghu Archipelago is located on the east side of Taiwan Strait straddling the Tropic of Cancer and hosts non-reefal coral communities. In this study, benthic surveys throughout the Penghu Archipelago were conducted and potential environmental and biological factors that shape coral species distributions were inferred by multivariate analyses. A total of 103 species representing 28 genera of scleractinian corals were recorded. Three major ecological sectors (northeast, south, and inner) were defined based on a canonical analysis of the principal coordinates of scleractinian species composition. Correlation analyses showed that scleractinians in the south and northeast sectors were strongly influenced by SST-related variables. In contrast, the coral communities in inner sector were mainly affect by turbidity or nutrition, which supposed come from human activities. Distance-based redundancy analysis showed that benthos, except soft corals, hardly interacted with scleractinian coral distributions. Our study demonstrated a distinct coral species assemblage among different islands across the Tropic of Cancer in the Penghu Archipelago. Natural and human-derived environmental factors both showed a strong correlation with coral species distribution. It's clear that either natural and human-derived factors influenced coral composition in Penghu archipelago.

Key words: Non-reefal coral community, Penghu Archipelago, Environmental settings, Tropic of Cancer, Spatial pattern.

BACKGROUND

Scleractinian corals are normally associated with warm shallow waters ranging more or less between the Tropics of Cancer (23.5°N) and Capricorn (23.5°S), where coral reef formation is limited by environmental factors like temperature, light, and nutrients (reviewed in Veron 1995; Kleypas et al. 1999). Environmental settings within this geographic range have constantly warm sea surface temperatures (SST ~30°C), high irradiation, and low nutrient levels. Toward

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the Tropics of Cancer and Capricorn (*i.e.*, the Subtropics), fluctuations in SST and nutrients increases and irradiation decreases, creating dynamic subtropical environments compared to equatorial regions. Within the tropics, coral species richness is relatively high in general, and there is a trend in decreasing species diversity toward the borders of the subtropics (Veron 1995, 2000; Chen 1999; Jones et al. 2011; Dalton and Roff 2013). Beyond the subtropics, the development of coral reefs is significantly reduced due to lower SSTs (< 18°C) and other environmental and/or biological correlates, resulting in marginal “non-reefal” coral communities founded on rocky substrata and characterized by low coral diversity containing a combination of tropical, subtropical, and temperate species, with exceptions like Japan, Australia, and the Red Sea (Veron 1995; Kleypas et al. 1999, 2001; Denis et al. 2013). Coral distribution and geography from Philippines to Japan were clustered into tropical reefs, non-reefal communities and outlying populations, which are closely related to latitudinal and oceanographical gradients (Veron 1995). The definitions of “coral reef”, “coral reef community” and “coral community” have also been discussed. “Coral reef” is a sedimentary structure produced by a “coral reef community”. A “coral reef community” has the potential for reef construction, while a “coral community” does not have that potential (Buddemeier and Hopley 1988).

Coral community structures and environmental settings that modulate coral spatial patterns at the local scale across the tropics and the subtropics have been examined over the last few decades. For example, subtropical coral communities in eastern Australia show wide variations in range and latitude in species diversity and living coral cover at scales from 10 to 100 km (Harriott et al. 1994, 1995, 2002). *Acropora* corals generally are dominant at the Tropic of Capricorn (23.1-23.5°N; *e.g.*, Keppel Islands and Heron Reef) and then decrease in coverage toward higher latitudes (*e.g.*, Solitary Islands; Dalton and Roff 2013). Many environmental factors, such as water temperature, light availability, aragonite saturation, currents, larval dispersal, competition between corals and macroalgae, growth rate, and reproduction operate synergistically to create this latitudinal variation (reviewed in Harriott and Banks 2002). Therefore, corals in subtropical regions with histories of naturally fluctuating environmental factors (*e.g.*, temperature) are suspected to have greater resistance to elevated temperatures compared to tropical counterparts (Chen and Keshavmurthy 2009; Oliver and Palumbi 2011). In addition, marginal high-latitude regions might provide refuges for tropical corals in response to rising seawater temperatures (Hughes et al. 2010; Beger et al. 2011, Baird et al. 2012), although other environmental factors like low pH and high nutrient levels might confine this potential (Huang et al 2011). However, it is difficult to anticipate the possible shift of environmentally disturbed subtropical marginal corals without understanding the interactions between scleractinian coral composition and environmental settings.

The Penghu Archipelago (also known as the Pescadores), located at the eastern side of Taiwan Strait between Taiwan and China, is composed of 90 islands and islets extending 70 km in a north-south direction across the Tropic of Cancer (Fig. 1). The marine environment of the Penghu Archipelago is influenced by the seasonal changes in ocean currents around the western Pacific Ocean (reviewed in Chen 1999; Chen and Keshavmurthy 2009). In summer, the South China Sea Surface Current (SCSSC), driven by the warm southeastern monsoon, flows northward into Taiwan Strait. In winter, while southern Penghu is affected by a weak but warm branch of the Kuroshio Current, northern Penghu is influenced by cold, fresh China Coastal Water (CCW) driven by the northeastern monsoon (Wang and Chern 1998, 1992; reviewed in Chen and Keshavmurthy 2009). Qualitative surveys of coral distributions around Taiwan and Penghu show different compositions of *Acropora* and Faviidae corals between the southern and other parts of Penghu (Chen 1999). Most of corals in Penghu were also found attached to the bare substrates and were distinguished from coral reefs which are able to accumulate a build-up of calcium carbonate structure (Buddemeier and Smith 1999). These corals in Penghu were considered as non-reefal coral communities and can be interpreted as incoherent growths composed of only a single generation of potential framework builders that do not produce an interlocking framework (Halfar et al. 2005). In addition, this coral community is strongly influenced by human activities including oyster farming, marine cages, and sewage run-off from nearby urban areas, causing high sedimentation and eutrophication in the bay (Huang et al. 2011, 2012). Whether the impacts of regional environmental settings and localized human disturbances affect coral species composition across different islands remains unexplored.

Thus, full-scale surveys of corals/benthos and environmental settings were necessary in order to elucidate spatial variations in non-reefal coral communities and potential environmental drivers in the Penghu Archipelago.

In order to know the distribution of coral communities in Penghu, preliminary surveys were carried out before the sites selection. Besides, possible environment factors that might result in the community structure variations such as temperature, turbidity, sedimentation, water quality (organic content, Chl. *a* concentration), and biological interactions were also noticed, together with literature surveys, as possible quantitative

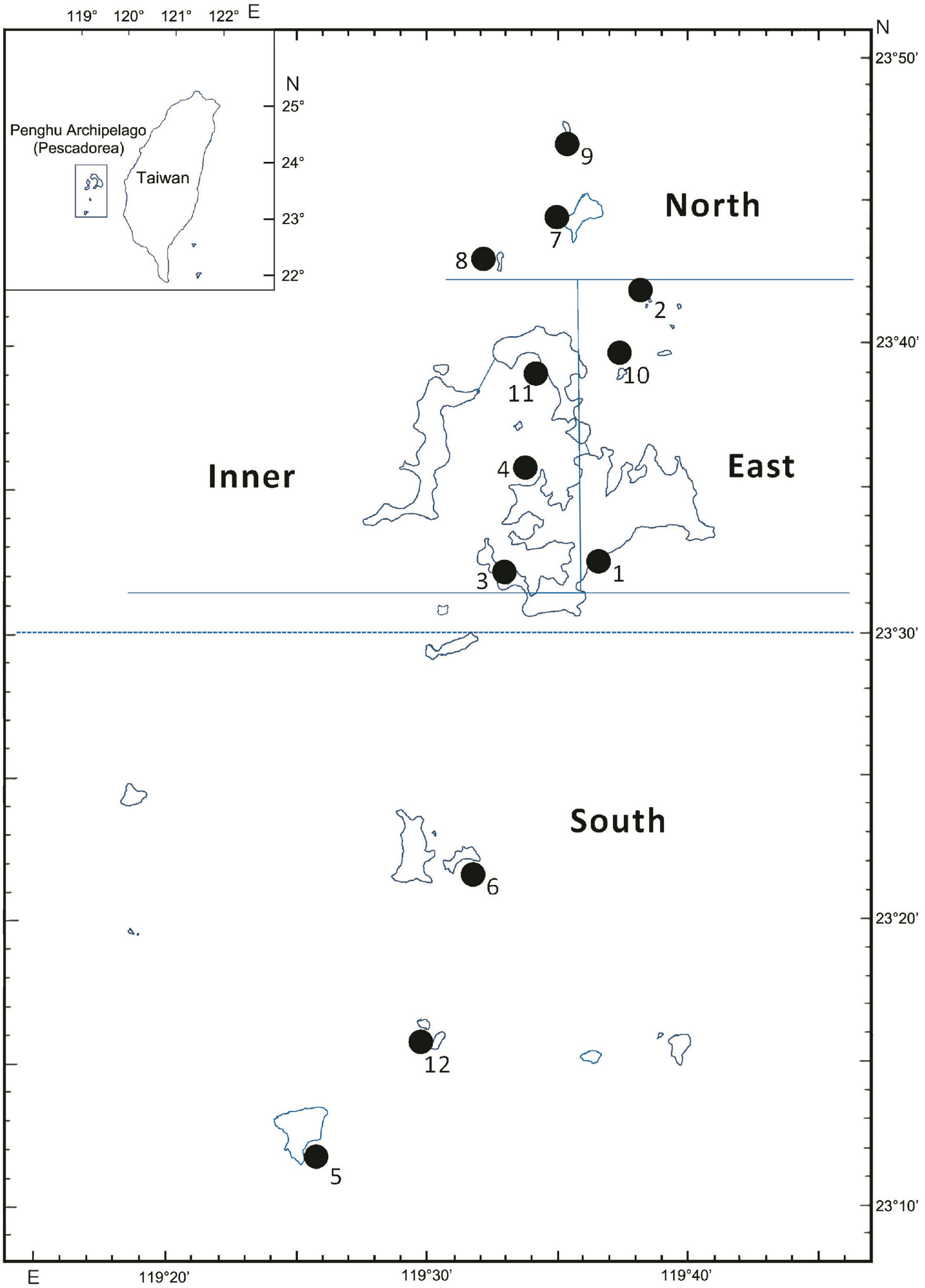

Fig. 1. Location of Penghu Archipelago (Pescadores) and 12 sampling sites. 1, Aimen; 2, Chudra; 3, Chinwan; 4, Chungkwang; 5, Chimei; 6, Dawen; 7, Gibei; 8, Gupo; 9, Mudo; 10, Ponpon; 11, Watung; 12, Yupin. Dotted line: Tropic of Cancer; solid lines delineate the four sampling site sectors.

environmental variables in this study. According to the results of preliminary surveys, a nested hierarchical design was adapted and quantitative surveys of benthic communities at 12 selected sites in 4 geographic sectors (3 sites in each sector) in the Penghu Archipelago were conducted. In addition, environmental data, including seawater temperature, turbidity, chlorophyll-*a*, and organic matter, as well as other benthic data, were collected and correlated with benthic composition to infer the factors that might drive scleractinian coral community patterns across the Tropic of Cancer in the Penghu Archipelago.

MATERIALS AND METHODS

Sampling sites

Surveys of benthic communities around the Penghu Archipelago were conducted in the summer of 2004. Three random sites were selected to represent four geographic sectors (North, East, South and Inner; Fig. 1) based on qualitative surveys using the manta-tow method from 1998 to 2003. The western sector was excluded due to the unsuitable pebble habitat for corals from pilot surveys. Coral communities of the Penghu Archipelago are limited to the upper 10 m of the water column at most of the studied sites due to its non-reefal characteristics (Hsieh 2008). Thus, six 20 m replicated transects were established to quantify community structure at two depth zones, 3-5 m (upper zone), 6-8 m (lower zone) at each site.

Benthic composition processing

An underwater digital video recorder (Sony TRV-950) was operated by scuba divers to record the images of benthic organisms within a distance of 0.5 m of each transect line. A total of 24 frames (25 cm × 25 cm) were randomly selected from the footages of each transect with iMovie software. Images were analyzed with CPCe (Coral Point Count with Excel extensions) for proportional coverage of benthos (Kohler and Gill 2006). Thirty points were randomly spread onto frames and codes were assigned that corresponded to objects (*i.e*. all live organisms and substrate types) identified in each frame. Scleractinian corals were identified to species and other benthic organisms to genus if possible. Scleractinian taxonomy followed Veron and Stafford-Smith (2000), Dai and Horng (2009a; 2009b), Budd et al. (2012), and Huang et al. (2014). A total of 144 transects were surveyed and 3456 frames were analyzed. Proportional coverage of scleractinian coral species and other benthic organisms were expressed as spreadsheet data files.

Environmental parameters

Loggers were set at a depth of 5 m at the studied sites to collect seawater temperature in one-hour intervals throughout the year. No significant vertical variations in temperature occur at these locations (Hsieh 2008). Several temperature parameters were generated to examine the environmental variables of the survey sites, including mean temperature ($_{\mathrm{mean}}$T), maximum/minimum daily temperature ($_{\mathrm{max}}$DT/$_{\mathrm{min}}$DT), maximum/minimum monthly temperature ($_{\mathrm{max}}$MT/$_{\mathrm{min}}$MT), and daily/monthly temperature differences ($_{\Delta}$DT and $_{\Delta}$MT). Three replicated water samples (1000 ml) from two depths were collected with metal-free Niskin bottles before conducting underwater surveys. Sampling equipment and processes followed Taiwan EPA quality assurance and quality control protocols (Huang et al. 2012). Water samples were stored at 4°C during transportation to the laboratory for analyses. Turbidity, particulate organic matter (POM), and chlorophyll-*a* were measured as proxies of human activity. Turbidity was measured with a nephelometer and then filtered through pre-weighted GF/C glass microfiber filters (0.45 μm; Whatman). Half of the collected solids were desalinated by washing with distilled deionized water then dried at 70°C in an oven to constant weights. Microfiber filters were ignited in a furnace at 450°C for 4 h to combust the organic matter, the residual compound representing POM. Planktonic chlorophyll-*a* was extracted from the remaining half of the filtered solids in 90% aqueous acetone for 24 hrs at 4°C, then measured with a spectrophotometer (Huang et al. 2012).

Statistical analysis

Coral community

Coral similarity among different geographical areas was examined by multivariate analysis under a three-factors design. Geographic factors - sector and zone were selected as fixed factors and site (nested in sector) was selected as a random factor. Present/absent data of scleractinian coral was reassembled according to taxonomic dissimilarity (Theta+; genus and species) prior to multivariate analysis (Clarke et al. 2006). Taxonomic dissimilarity was considered in this study due to these sampling sites across a large geographical region, and not many same species might be found among sites. In addition, the similarity of species from same genus or family might show similar environment preference and using this dissimilarity index to distinguish these sites around Penghu might be clearly differentiated from human or environmental influences. The 12 sites have been examined by different environmental processes and the difference can not easily be seen by unconstrained ordination method (*i.e.* MDS; Hsieh 2008). Therefore, a constrained ordination - canonical analysis of principal coordinates (CAP) with a prior hypothesis (factor-sector) was used to separate the sites based on geographical distribution of coral species around Penghu (Anderson and Willis 2003). A three-term model [sector, site (sector), and zone] was used to examine the significance levels of coral composition by permutational multivariate analysis of variance (Anderson 2001). The homogeneity of multivariate variances were verified for all model-terms [sector, site (sector), and zone] by using PERMDISP (permutational analysis of multivariate dispersions, $p > 0.05$; Anderson 2001). Type III (partial) sums of squares were used because it is more suitable for ecological data with unbalanced design and generate a probability distribution to calculate a p value for each factor. Pairwise tests were also conducted to determine the significant differences among each sector for both zones (upper and lower) to seek if there is an alternative sector based on coral composition besides our arbitrarily group based on geographical location. The scleractinian coral data matrix was analyzed and modeled by DistLM (Distance based Linear Model) for both zones separately to build a relationship model between coral distribution and environmental/benthos predictor variables (Anderson 2004). Environmental and benthos variables have been standardized transformation in prior to DistLM analysis. The significance level of each predictor variable was generated by a marginal test in DistLM. Akaike Information Criterion corrected (AICc) was used to chose the most parsimonious models from all the possible combinations of variables with *BEST* selection procedure (Anderson 2004). The parsimonious fitted model with only significant and correlated predictors (correlation > 0.2) was visualized by dbRDA (Distance-based redundancy analysis; McArdle and Anderson 2001). All multivariate analyses were conducted in Primer-e (v. 7; Anderson et al. 2008).

Model selection for coral distribution

GLMM (generalized linear mixed model) and GLM were used to examine the responses of each coral genus to geographic (sector, site, and zone) and environmental (abiota and biota) factors to understand which ones determine coral distribution. For geographic factors, sector and zone were selected as fixed factors and site (nested in sector) was selected as a random factor in GLMM. For GLM environmental factors, several temperature-related factors were generalized from temperature data prior to being analyzed with other environmental parameters. Such as mean temperature (${}_{\text{mean}}T$), maximum/minimum daily temperature (${}_{\text{max}}DT/{}_{\text{min}}DT$), maximum/minimum monthly temperature (${}_{\text{max}}MT/{}_{\text{min}}MT$), and daily/monthly temperature differences (${}_{\Delta}DT$ and ${}_{\Delta}MT$) as well as water quality parameters (turbidity, organic matter, and chlorophyll-*a*) were the variable ocean-physical parameters. Four different data distribution models (Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial) were used to determine the best goodness-of-fit of corals with all possible combination of factors. Four different models were tested due to the possible over-dispersion (high proportion of zeros) that is typical of ecological data and makes zero-inflated models more suitable. Poisson and negative binomial distribution components were chosen because of the possibility for larger variation in our data (Joseph et al. 2009). Factors were examined in a framework of four models using maximum likelihood to estimate parameters and a log-link function was chosen to approximate the above mentioned data distribution models. This approach was taken as no prior assumption of homogeneity was necessary (Adams et al. 2011). The null model (no factor) and alternative models (combination of different factors) were compared with Akaike's information criterion (AIC; Symonds and Moussalli 2011). Corrected AIC (AICc) was used in this study due to the small number of sample replicates. The model with lowest AICc was selected to represent the best goodness of fit and Akaike weight of models were also calculated for the likelihood (Wagenmakers and Farrell 2004). If there are more than two models with the same AICc value, the parsimony model should be selected due to the extra parameters being uninformative (Arnold 2010). GLMM and GLM modelling and AIC analyses were conducted in R (v. 3.2.2; R Core Team 2015).

RESULTS

A total of 103 species representing 28 genera of scleractinian corals were recorded in our study (Table 1). Coral species richness around Penghu ranged from 7 (upper zone of Watung (11)) to 37 species per site (upper zone of Chudra(2) (Fig. 2)). Acroporidae corals, including *Acropora* and *Montipora* were dominant at most sampling sites around Penghu, except Watung (11) which was dominant by *Goniopora*, *Coelastrea*, *Tubastrea*, and *Porites* (Table 1). The lower zones of Gupo (8) and Chudra (2) were dominated by non-Acroporidae genera like *Goniopora*, *Coelastrea*, *Turbinaria*, *Porites*, and *Echinopora* (Table 1). The south sector had a higher number of coral species (45) than East (29) and North sectors (34; Table 1). The Inner sector had the lowest species number (15) and medium live coral cover (LCC; 33%). The lowest LCC was found at the lower zone in Chungkwang (4)(15.84 ± 3.36%), whereas the lower zone in Chimei (5) had the highest LCC (75.53 ± 3.41%). On average, the South sector had a relatively higher LCC (59%) compared to the Inner sector (33%), East sector (31%), and North sector (32%).

Scleractinian coral communities

Scleractinian species composition was significantly different among sectors and sites (within sector), between depth zones, and interactions between zone and site (within sector) (P = 0.001), but there were no significant

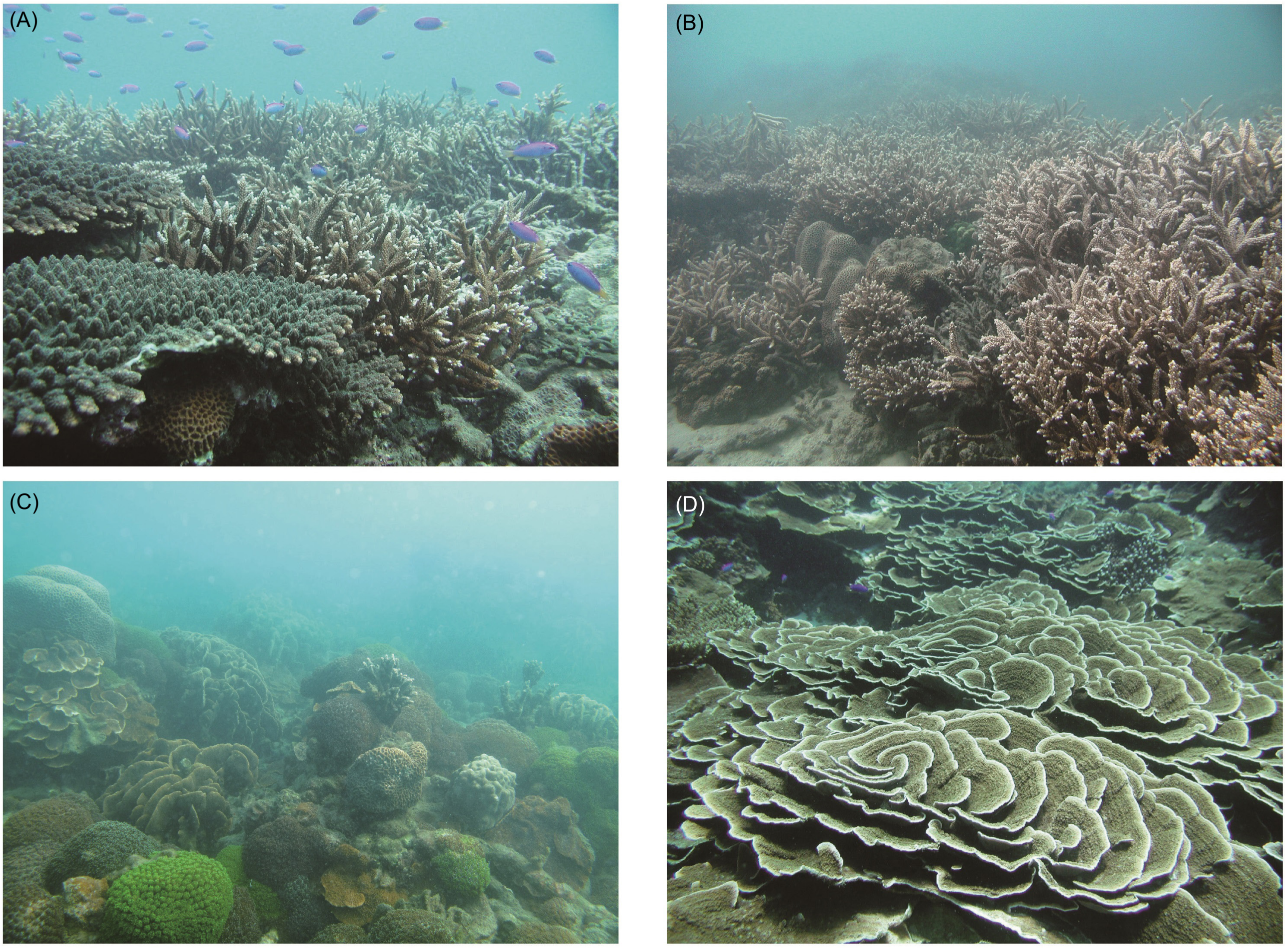

Fig. 2. Underwater images of the (A) north sector (Mudo), (B) east sector (Aimen), (C) inner sector (Chinwan), and (D) south sector (Chimei).

interactions between zone and sector (*P* = 0.16, PERMANOVA). Canonical analysis of principal coordinates (CAP) showed that significant differences between sectors (*P* = 0.001, Fig. 3). Three sites in the South sector were grouped into one cluster, three sites from the Inner sector were scattered, and sites from the North and East sectors generally overlapped (Fig. 3). CAP results were consistent with *post hoc* pairwise tests in that no significant differences were found between North and East sectors at both depth zones (Table 2). Thereafter, North and East sectors were grouped as a single ecological sector, the Northeast sector, for the analyses. Nevertheless, there was no consistent pattern in coral composition differences between depth zones among other sectors. We separated scleractinian coral composition into upper and lower zones in order to reveal which corals drove the differences in depth zones among sites and sectors. Fewer coral species were driving coral composition differences in the upper zone compared to the lower zone in the dbRDA analysis (Fig. 4). In the upper zone (Fig. 4A), *Goniopora dijiboutiensis* was dominant at Watung (11) and Chiwan (3) (inner sector), while *Acropora intermedia*, *Echinopora gemmacea*, and *Montipora stellata* were common in most South sector transects. *Acropora valida* and *Acropora hyacinthus* were the main contributors to the scleractinian coral community in the Northeast sector. In contrast, the composition of lower-zone corals were more scattered and not consistent with ecological sectors (Fig. 4B). The lower zone of the Inner sector had more *Acropora humilis*, *Montipora cactus*, *Lithophyllon undulatum*, and *Cyphastrea chalcidicum.* The South sector and Gibei (7) and Mudo (9) of the Northeast sector had abundant *Montipora aequituberculata*, *Acropora hyacinthus*, and *Echinopora lamellosa*. Many other scleractinian coral species, such as *Turbinaria peltata*, *Tubinaria mesenterina*, *Platygyra sinensis*, *Porites lutea*, *Dipsastraea maxima*, and *Coelastrea aspera*, lead the different groups in the Northeast sector into different directions.

Scleractinian coral composition correlated with environmental parameters

Environmental parameters from four geographic sectors around Penghu are listed in Table S1. The mean temperature around Penghu is from 23.12°C in the Inner sector to 23.82°C in the East and South sectors. Significance and correlations of coral composition and environ-

Table 1. Coral cover and coral species number of each site around Penghu Archipelago

Site	Region based on geographic locality	Depth zone	No. of coral species	Live coral cover (%)	Top 2 dominant coral species (coverage %)		Region based on coral species composition
Watung	Inner	U	7	19.63 ± 1.50	*Goniopora djiboutiensis* (18.45%)	*Goniopora favulus* (0.51%)	Inner
	Inner	L	13	28.76 ± 4.45	*Turbinaria frondens* (7.10%)	*Porites lutea* (5.91%)	Inner
Chungkwang	Inner	U	14	47.66 ± 2.59	*Acropora muricata* (18.68%)	*Montipora cactus* (13.62%)	Inner
	Inner	L	10	15.84 ± 3.36	*Montipora cactus* (3.28%)	*Acropora muricata* (2.32%)	Inner
Chinwan	Inner	U	15	53.40 ± 2.96	*Acropora muricata* (20.42%)	*Montipora cactus* (10.07%)	Inner
	Inner	L	8	32.48 ± 4.32	*Acropora humilis* (15.63%)	*Montipora cactus* (6.50%)	Inner
Gibei	North	U	17	37.82 ± 6.40	*Acropora muricata* (25.79%)	*Pocillopora damicornis* (2.75%)	Northeast
	North	L	18	17.75 ± 3.89	*Acropora muricata* (8.22%)	*Acropora hyacinthus* (2.29%)	Northeast
Gupo	North	U	34	61.97 ± 1.99	*Acropora muricata* (17.31%)	*Montipora efflorescens* (11.39%)	Northeast
	North	L	30	35.90 ± 2.45	*Turbinaria mesenterina* (5.73%)	*Acropora solitaryensis* (5.01%)	Northeast
Mudo	North	U	20	26.99 ± 3.35	*Acropora muricata* (10.74%)	*Acropora monticulosa* (6.57%)	Northeast
	North	L	18	40.66 ± 3.40	*Acropora muricata* (11.89%)	*Acropora hyacinthus* (8.45%)	Northeast
Aimen	East	U	18	48.77 ± 4.44	*Acropora muricata* (32.29%)	*Acropora hyacinthus* (11.48%)	Northeast
	East	L	26	22.48 ± 2.78	*Turbinaria mesenterina* (6.37%)	*Porites solida* (2.94%)	Northeast
Chudra	East	U	37	19.86 ± 4.98	*Acropora hyacinthus* (7.64%)	*Acropora muricata* (2.99%)	Northeast
	East	L	29	16.27 ± 1.94	*Echinopora lamellosa* (2.48%)	*Turbinaria mesenterina* (2.20%)	Northeast
Ponpon	East	U	19	58.43 ± 2.39	*Acropora muricata* (27.50%)	*Acropora hyacinthus* (23.75%)	Northeast
	East	L	8	22.80 ± 4.06	*Acropora muricata* (7.73%)	*Acropora valida* (4.06%)	Northeast
Chimei	South	U	14	75.39 ± 3.09	*Acropora intermedia* (21.99%)	*Acrpora muricata* (18.84%)	South
	South	L	25	75.53 ± 3.41	*Montipora efflorescens* (16.62%)	*Echinopora gemmacea* (15.05%)	South
Dawen	South	U	11	62.07 ± 10.17	*Acropora muricata* (25.03%)	*Acropora aspera* (10.95%)	South
	South	L	22	41.83 ± 5.63	*Acropora intermedia* (14.03%)	*Echinopora lamellosa* (9.14%)	South
Yupin	South	U	17	52.25 ± 5.66	*Acropora intermedia* (17.06%)	*Acropora muricata* (16.71%)	South
	South	L	22	47.92 ± 8.52	*Acropora hyacinthus* (16.57%)	*Acropora muricata* (12.22%)	South

mental factors among sites were examined based on the Distance-based Linear Model (DistLM; Table 3).

Scleractinian composition in upper zones significantly correlated with temperature-related variables, including $_{Mean}$T, $_{MAX}$DT, $_{min}$MT, $_{MAX}$MT, $_{\Delta}$DT, $_{\Delta}$MT and water quality such as turbidity and chlorophyll *a* (Table 3a). $_{\Delta}$MT was higher with corals of inner sector $_{min}$MT was higher with most corals in the Northeast sector except Ponpon (10) and Gupo (8) (Fig. 5A). Other temperature factors such as $_{Mean}$T, $_{MAX}$DT, $_{MAX}$MT, $_{\Delta}$DT were all higher with corals of south sector which is also low latitude. Higher chlorophyll-*a* was with corals in the Inner sector and higher turbidity with the Northeast sector, especially at Ponpon (10). In lower zone of reefs, all the temperature and water environmental factors were significant with coral distribution (Table 3a). The temperature correlations were similar to those in upper zones, except that $_{Mean}$T were higher in Aimen (1) and Chudra (2) in the Northeast sector (Fig. 5B). Water quality factors - chlorophyll-*a* and turbidity were higher at most sites in the Inner sector. Overall, temperature parameters were consistent with the latitudinal distribution of sites in the archipelago, except that temperature variations

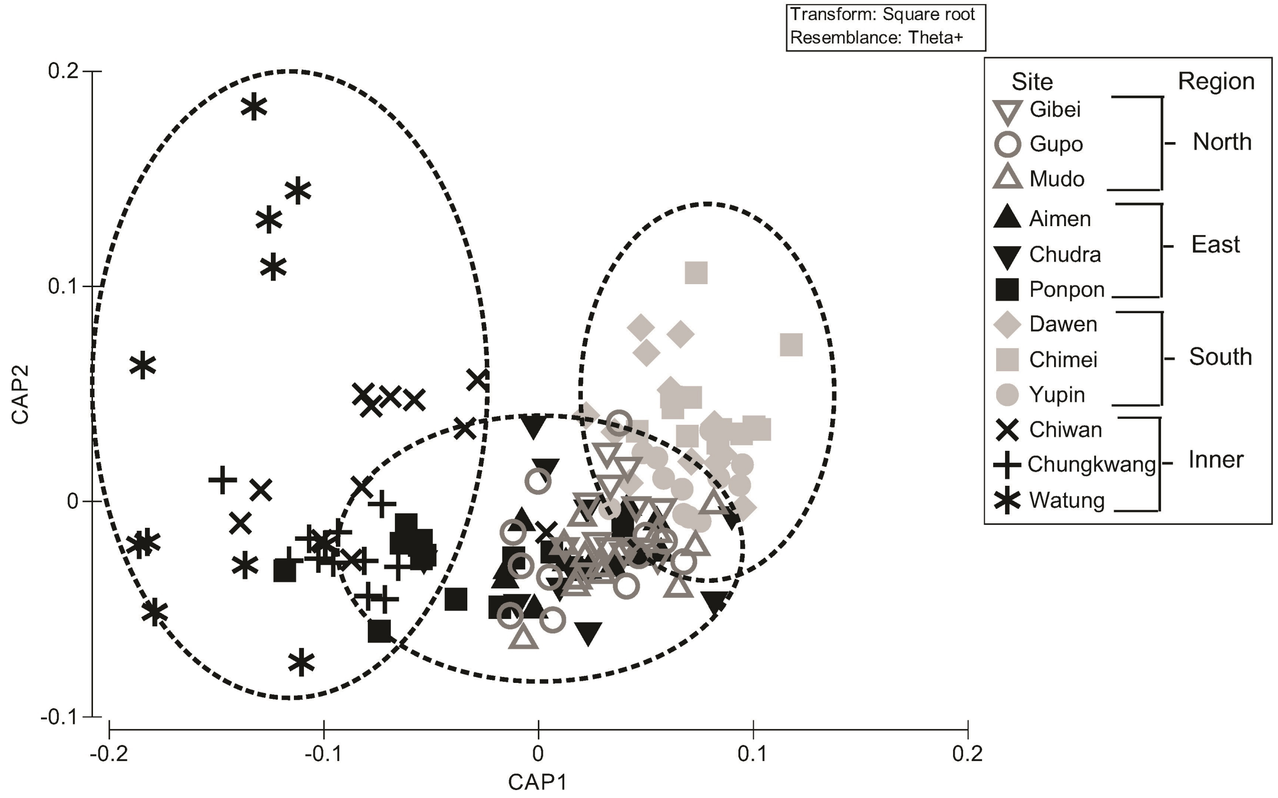

Fig. 3. Canonical analysis of principal coordinates (CAP) with a prior hypothesis (four different sectors: inner, north, east, and south) for coral communities among Penghu (Eigenvalues of correlation: 1 = 0.9284, 2 = 0.7247; Permutation test: $P = 0.001$). The dash circles indicated the significant differences from PERMANOVA pairwise tests.

Table 2. Post hoc pairwise PERMANOVA test and average similarity distances results of coral composition at both upper zone (lower-left triangle) and lower zone (upper-right triangle) among sectors

	East	Inner	South	North
East		63.917$^{n.s.}$	62.934*	52.916$^{n.s.}$
Inner	65.346*		74.746*	65.558$^{n.s.}$
South	58.961*	72.443*		57.269*
North	49.988$^{n.s.}$	65.976*	53.38$^{n.s.}$	

*: $p < 0.05$, n.s.: not significant.

at some sites in the Inner and Northeast sectors were higher. Meanwhile, turbidity and chlorophyll-*a* (nutrients) were consistently higher in the Inner sector and higher turbidity in upper zone or northwest sites (Fig. 5B).

Correlation of scleractinians with other benthos

Only a couple benthos and abiota, such as soft corals and dead coral with algae, at both zones were significantly correlated with corals around

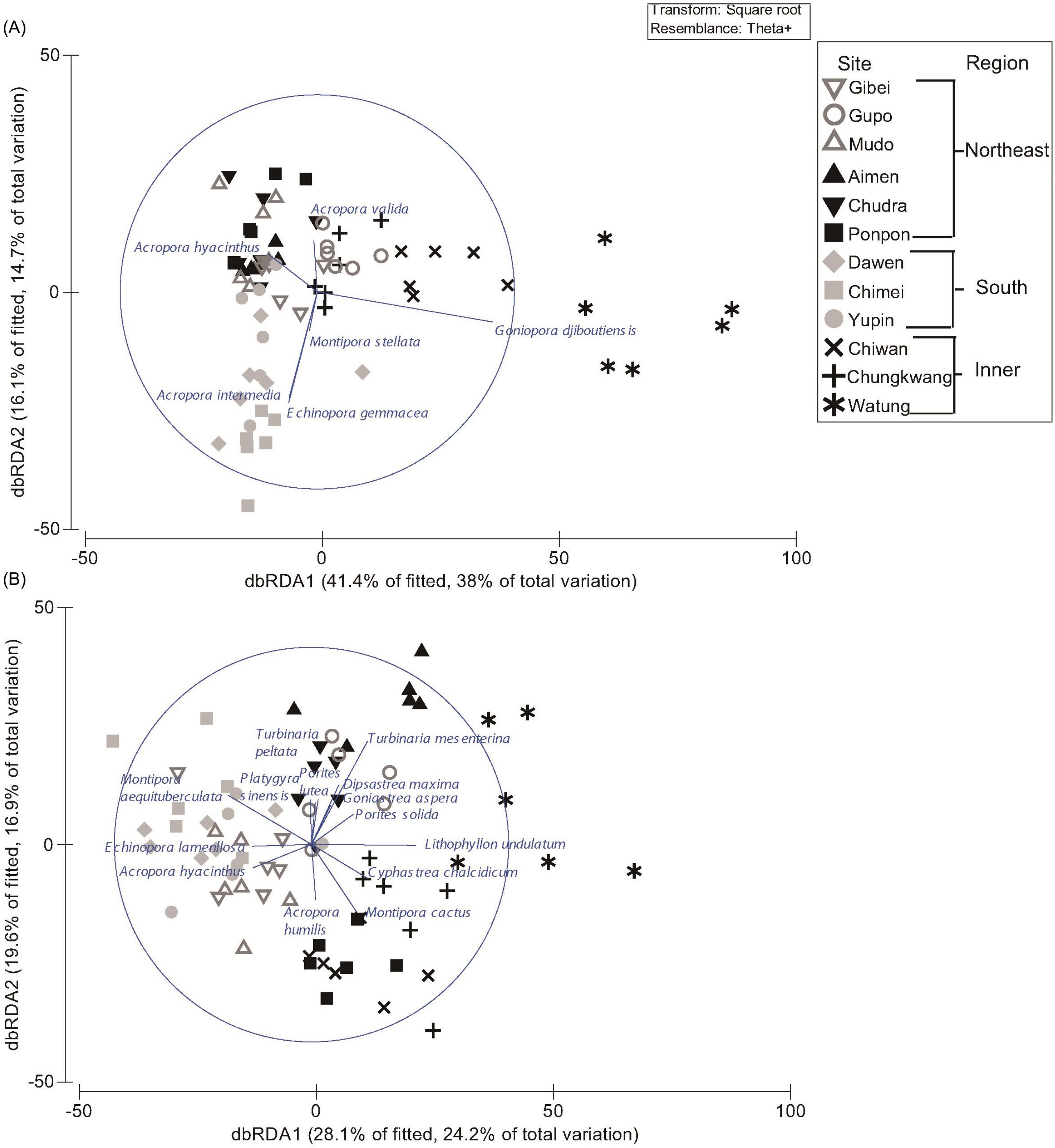

Fig. 4. Distance-based redundancy analysis (dbRDA) of coral communities with coral species as variables at (A) upper and (B) lower zones among three different sectors at Penghu. Only significantly related coral species with correlations > 0.2 are included on the plot.

the Penghu archipelago (Table 3b). In addition, coralline algae coverage were significantly higher with the corals in the upper zone, other benthos including polychaetes, bryozoans, echinoderms, bivalves, anemones, and gastropods, were significantly more abundant in the lower zones (Table 3b). The dbRDA showed similar pattern that soft corals had higher coverage significantly in the south sector and dead coral were more abundant in other sectors in upper zone (Fig 6A). Higher coralline algae coverage was more abundant in few places only, such as Ponpon (10), Mudo (9), and Yupin (12). Contrarily, soft corals were more abundant in lower zone of Chudra (2), Mudo (9), and Gibei (7) in the Northeast sector (Fig. 6B). Other benthos were more abundant in South sector, while dead corals were consistently abundant in both zones of the Inner and in upper zone of Northeast sector.

Coral genus distribution based on abiotic/biotic factors

Each genus was modeled with geographic factors as well as coverage of other biotic and abiotic data. The distribution of all coral genera seemed to be affected by three factors: site (nested in sector), sector, and depth, except *Euphyllia* and *Stylocoeniella* (Table 4). In addition, 16 of 25 genera in our survey showed a preference of either the upper zone or bottom zone of the reefs at Penghu. Few genera, such as *Acanthastrea*, *Echinopora*, *Dipsastraea*, *Favites*, *Hydnophora*, *Pocillopora*, *Stylophora* were equally abundant in both depth zones with some preference of certain collecting site around Penghu.

Most coral genera showed a negative trend (negative coefficient in the model) with most benthos in the GLM model (Table 5). No

Table 3. Results of variables from marginal test of DistLM on (a) environmental parameters and (b) benthos (biota and abiota) of both upper and lower zones

(a)

	Upper zone		Lower zone	
Variable	Pseudo-F	*p*	Pseudo-F	*p*
${}_{\mathrm{Mean}}\mathrm{T}$	6.1974	0.001*	8.8863	0.001*
${}_{\mathrm{min}}\mathrm{DT}$	1.867	0.102	3.6444	0.003*
${}_{\mathrm{MAX}}\mathrm{DT}$	4.8569	0.002*	5.2645	0.001*
${}_{\mathrm{min}}\mathrm{MT}$	13.117	0.001*	14.534	0.001*
${}_{\mathrm{MAX}}\mathrm{MT}$	7.2105	0.001*	3.2051	0.002*
${}_{\Delta}\mathrm{DT}$	8.5159	0.001*	6.3117	0.001*
${}_{\Delta}\mathrm{MT}$	10.989	0.001*	8.0842	0.001*
Turbidity	4.5505	0.003*	13.342	0.001*
Organic matter	1.4266	0.178	2.8982	0.016*
Chlorophyll *a*	18.651	0.001*	17.662	0.001*

(b)

	Upper zone		Lower zone	
Variable	Pseudo-F	*p*	Pseudo-F	*p*
Soft corals	4.0614	0.005*	2.9484	0.008*
Sponges	1.2298	0.252	1.5485	0.166
Zoanthids	1.3335	0.182	2.033	0.054
Macroalgae	0.7591	0.523	1.0681	0.391
Other benthos	1.4544	0.183	2.2112	0.033*
Dead coral (with algae)	9.1123	0.001*	5.84	0.001*
Coralline algae	2.3246	0.039*	0.51965	0.880
Diseased corals	No test		0.77924	0.675
Abiota (sand, pavement, rubble)	1.4306	0.187	1.5178	0.159

*symbol indicates the significant correlation of factors among sampling sites, $p < 0.05$.

responses in abiota and diseased corals were detected relative to all scleractinian genera. Several scleractinian genera, such as *Pocillopora*, *Galaxea*, *Euphyllia*, and *Coscinaraea*, had neither positive nor negative responses to all benthic substrata. Dead coral with algae showed half

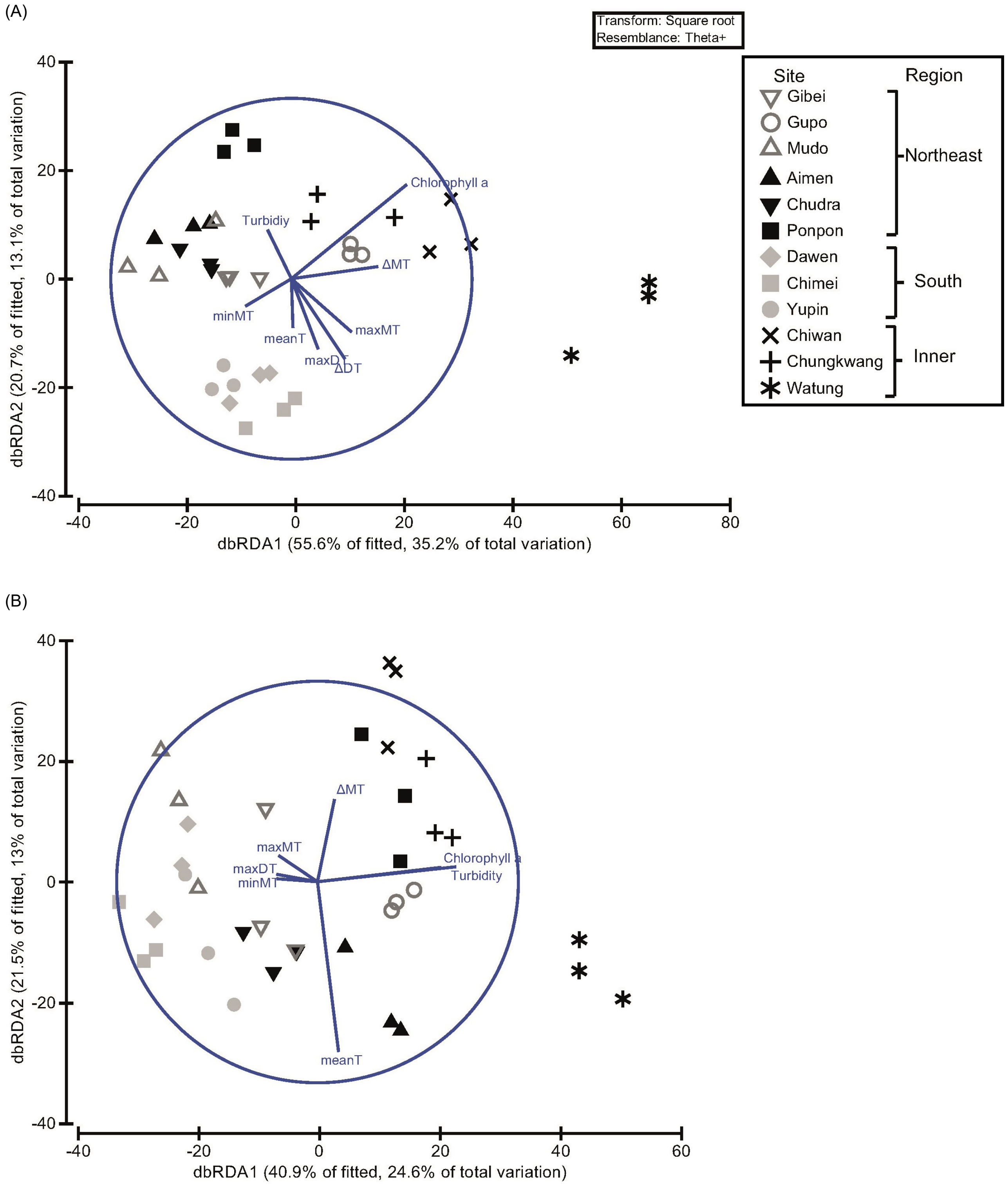

Fig. 5. dbRDA of coral communities with environmental variables at (A) upper and (B) lower zones among three different sectors at Penghu. Only significantly related environmental variables with correlations > 0.2 are included on the plot.

negative and half positive responses to many coral genera (15/28). There were only a very few positive responses occurring for *Acropora* vs. coralline algae, *Goniopora* vs. macroalgae, and *Stylocoeniella* vs. other benthos.

DISCUSSION

Two main biogeographic distribution patterns were found in corals at Penghu Archipelago. One was a latitudinal distribution pattern from

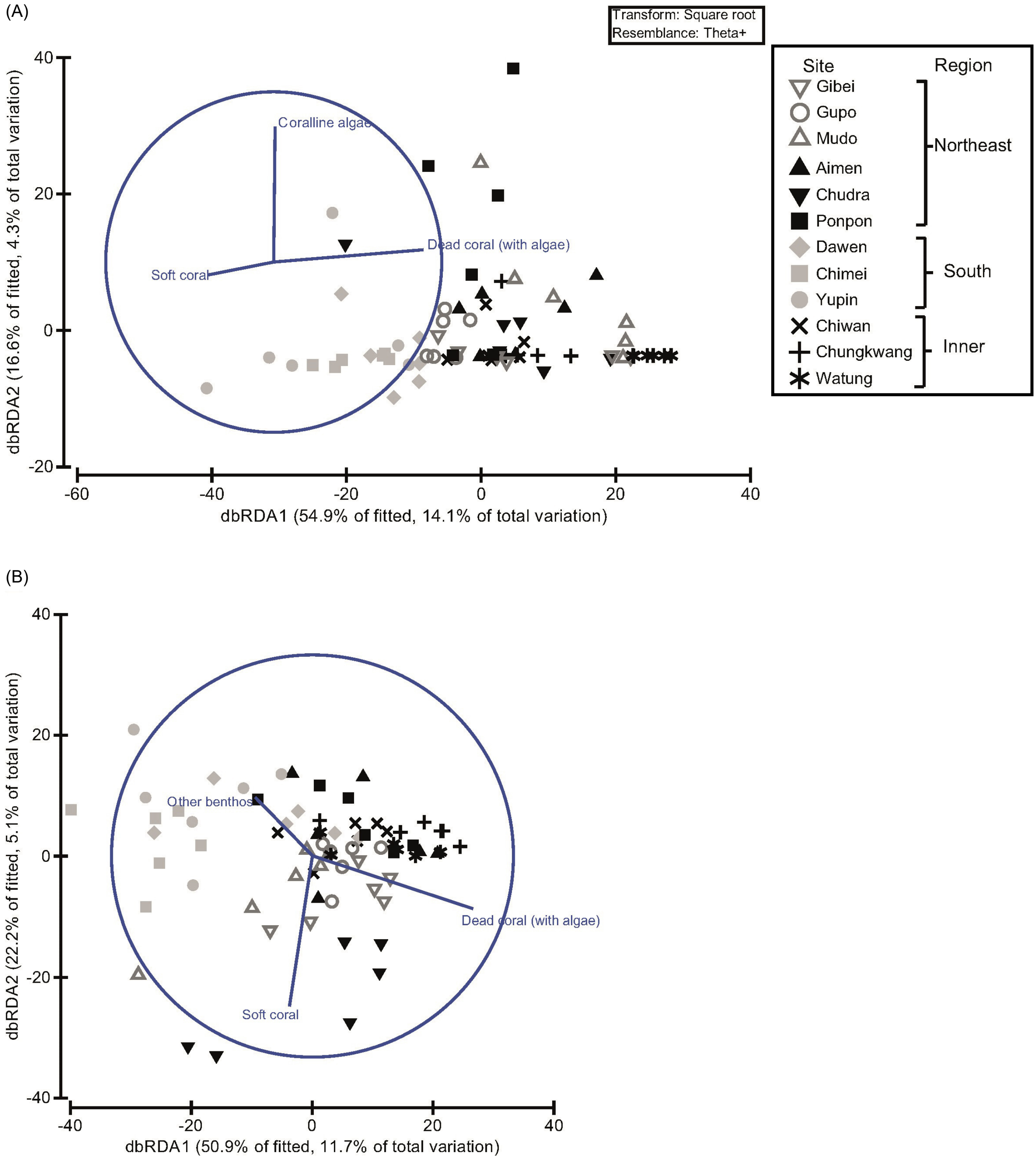

Fig. 6. dbRDA of coral communities with benthos/abiota variables at (A) upper and (B) lower zones among three different sectors at Penghu. Only significantly related benthos/abiota with correlations > 0.2 are included on the plot.

the south sector to the east sector to the north sector, which was related to seawater temperature and sea currents connecting Penghu to nearby island groups. Another distribution pattern was the differences among the Inner and other sectors, which correlated with natural/human disturbances and water circulation within the Inner sector. In addition, we did not detect a strong interaction between corals and other benthic invertebrates and substrata from our data. Only a few benthos were consistent with the biogeographic distributions of corals at Penghu.

Latitudinal distribution of corals and environmental settings

Coral coverage and coral species number around Penghu were generally consistent with latitude. Coral coverage and species number decreased from tropical (south sector) to subtropical areas (north and east sectors) at Penghu. Compared to other places in Taiwan, numbers of coral species within 70 km of Penghu (103 species) were higher than in subtropical northern Taiwan (~60 species) but lower than in tropical southern Taiwan (~300 species; Dai 1991; Hsieh 2008). Compared to other islands around the northwestern Pacific Ocean, Penghu has lower richness than the Yaeyama Islands (368 species) and Miyako Islands (249 species) of the Okinawa Archipelago (Kayanne et al. 2012). Similar latitudes in the southern hemisphere and in the southern Great Barrier Reef of Australia (400 km) have about 144 coral species in inshore reefs (De Vantier et al. 2006) and 244 species in whole region. However, the Great Keppel Island group (23°S) at the edge of the tropical zone has only 40+ coral species (Sweatman et al. 2007). The latitudinal decrease in coral species number from southern Taiwan, Penghu, and northern

Table 4. Summary of GLMM/GLM selection for coral genera distribution with geographic factors. The best goodness-of-fit models were selected from lowest Akaike Information Criterion correction(AICc) among all the geographic factors combination (Site(nested in Sector), Zone and Sector). Akaike weight indicates the likelihood of given model as best goodness-of-fit model. Total coral cover of each genus showed the contribution of each genus in Penghu coral reefs. $^{\#}$indicates the best model also has factor "sector" but with same AICc and Akaike weight

Genera	Model structure	AICc	Akaike weight	(%) of total coral cover
Acanthastrea	Coral cover ~Site(Sector)$^{\#}$	365.11	0.385	0.88
Acropora	Coral cover ~Site(Sector)+Zone$^{\#}$	1611.93	0.500	56.37
Coscinaraea	Coral cover ~Site(Sector)+Zone$^{\#}$	62.26	0.476	0.03
Cyphastrea	Coral cover ~Site(Sector)+Zone	411.74	0.489	0.79
Echinophyllia	Coral cover ~Site(Sector)+Zone$^{\#}$	348.01	0.303	0.78
Echinopora	Coral cover ~Site(Sector) $^{\#}$	571.71	0.386	4.98
Euphyllia	Coral cover ~NULL	143.65	1.000	0.28
Dipsastraea	Coral cover ~Site(Sector) $^{\#}$	448.43	0.382	0.88
Favites	Coral cover ~Site(Sector) $^{\#}$	667.95	0.386	2.19
Galaxea	Coral cover ~Site(Sector)+Zone$^{\#}$	316.23	0.312	0.49
Goniastrea	Coral cover ~Site(Sector)+Zone$^{\#}$	583.93	0.296	1.48
Goniopora	Coral cover ~Site(Sector)+Zone$^{\#}$	320.98	0.500	2.79
Hydnophora	Coral cover ~Sector	196.60	0.397	0.43
Lithophyllon	Coral cover ~Site(Sector)+Zone$^{\#}$	240.09	0.477	0.68
Phymastrea	Coral cover ~Zone	109.73	0.698	0.13
Montipora	Coral cover ~Site(Sector)+Zone$^{\#}$	1078.83	0.256	13.50
Mycedium	Coral cover ~Site(Sector)+Zone$^{\#}$	293.50	0.500	0.69
Pavona	Coral cover ~Site(Sector)+Zone$^{\#}$	415.80	0.415	0.95
Platygyra	Coral cover ~Site(Sector)+Zone$^{\#}$	466.93	0.268	0.97
Pocillopora	Coral cover ~Site(Sector)$^{\#}$	789.90	0.387	2.71
Porites	Coral cover ~Zone	799.42	0.365	3.47
Psammocora	Coral cover ~Zone	70.08	0.716	0.89
Stylocoeniella	Coral cover ~NULL	44.61	0.998	0.02
Stylophora	Coral cover ~Sector	246.48	0.462	0.86
Turbinaria	Coral cover ~Site(Sector)+Zone$^{\#}$	55.99	0.499	3.53

Table 5. Summary of GLM for coral genera distribution with abiotic and biotic benthos. Symbols – and + indicates the best fitting model structure with given biota or abiota factors and either with negative coefficient and positive coefficient in the selected model. X in NULL column indicated no factor was detected in the best goodness-of-fit model. Akaike weight indicates the likelihood of given model as best goodness-of-fit model

Genera	Soft coral	Sponge	Zoanthids	Macroalgae	Other benthos	Dead coral with algae	Coralline algae	Diseased coral	Abiota	NULL	AICc	Akaike weight	(%) of total coral cover
Acropora						−	+				1145.77	0.195	56.37
Montipora					−	−	−				718.12	0.251	13.50
Echinopora						−					403.35	0.206	4.98
Turbinaria			−			+	−				359.27	0.106	3.53
Porites							−				426.08	0.093	3.47
Goniopora				+	−	−					232.75	0.070	2.79
Pocillopora										X	408.20	0.063	2.71
Favites			−			−	−				357.13	0.148	2.19
Goniastrea							−				596.99	0.079	1.48
Platygyra			−			−	−				230.89	0.120	0.97
Pavona						+	−				227.64	0.055	0.95
Psammocora						-					35.60	0.097	0.89
Acanthastrea				−	−	−	−				207.35	0.081	0.88
Favia				−			−				215.16	0.078	0.88
Stylophora						−					164.62	0.154	0.86
Cyphastrea		−	−	−		+					195.07	0.095	0.79
Echinophyllia			−	−							184.09	0.060	0.78
Mycedium		−				+					152.08	0.103	0.69
Lithophyllon		−				+					136.34	0.063	0.68
Galaxea										X	145.35	0.080	0.49
Hydnophora						−					106.96	0.142	0.43
Euphyllia										X	82.61	0.079	0.28
Montastrea						+					58.68	0.037	0.13
Coscinaraea										X	13.97	0.075	0.03
Stylocoeniella					+						12.97	0.087	0.02

Taiwan is comparable to eastern Australia and the southwestern Pacific Ocean (Harriott and Banks 2002), even though the distance between north and south Taiwan is significantly shorter than that of east Australia. Oceanographical variations such as convergence of Kuroshio Current and China coastal current as well as seasonal monsoon are the possible major factors (Jan et al. 2002) which result in a sharp temperature changes and coral distributions in Penghu. In addition, coral coverage around Penghu is compatible to marginal corals of Australia (30-60%) suggested the possible consistency of marginal coral communities at western Pacific region. (Harriott and Banks 2002; De Vantier et al. 2006; Sweatman et al. 2007).

The coral community in the south sector of Penghu is separated from the northeast sector because corals in the south sector are normally associated with warm, clear water and less temperature fluctuation. For example, *Stylophora pistillata*, *Pocillopora eydouxi*, *P. meandrina*, and *Acropora intermedia*, which are typical tropical species strongly associated with clear and warm waters, were only found in the south sector. Conversely, the coral community of the upper northeast sector was dominated by subtropical species such as *Turbinaria mesenterina*, *T. frondens*, *Mycedium elephantotus*, and *Echinopora lamellosa*, which are cup-shaped or encrusting morphs that have the advantages of increased sediment removal efficiency and increased surface area for light absorption (Riegl et al. 1996). Other dominant species in the Northeast region have relatively robust structures (*Acropora solitaryensis* and *A. monticulosa*) or massive and encrusting growth forms (*Montipora efflorscens*, *Favites halicora*) for protection against the physical impacts of seasonal monsoons. In addition, fast-growing species like *A. muricata*, *A. hyacinthus*, and *A. valida* can recruit to available spaces between disturbances. The rapidly changing environments between the northeast and south sectors are related to geological location, ocean-physical conditions, and topography. The Penghu Archipelago is located at the intersection of three sea currents, which are the CCW, SCSSC, and a branch of the Kuroshio Current (Chen 1999). CCW brings cold water to the northeastern region of Penghu, while the SCSSC and the Kuroshio branch bring warm waters from tropical areas. These currents probably also connect the coral communities of Penghu with Japan, South China, and Philippines as well as Taiwan (reviewed Chen and Keshavmurthy 2009). Further investigations of genetic connectivity across island groups will help to reveal the patterns in this area.

Human disturbances to corals in the Inner sector

The Inner sector had the lowest coral species number and living coral coverage compared to other sectors (South and Northeast). Marginal tests with the Distance-based Linear Model suggested that the highest temperature and high variations in temperature, turbidity, and nutrients might affect coral species composition in the Inner sector, which is surrounded by three major islands and characterized by shallow water (depth mostly < 15 m) and limited circulation with outside bay waters (Fig. 1). Coastal urbanization plus industrial scale oyster farming and marine cage culture stretching from the intertidal zone to deeper waters in the Inner sector has resulted in the discharge of sewage, modification of benthic fauna, and eutrophication derived from feed debris and feces of cultivated fish (Huang et al. 2011). These may account for the high levels of turbidity, sedimentation, and nutrients in the seawater of the Inner sector (Huang et al. 2011; 2012). Consequently, only coral genera like *Galaxea*, *Goniopora*, *Cyphastrea*, and *Montipora* that can tolerate these stressors colonize the limited substructure of the Inner sector. These genera can either remove the sediments efficiently by secreting mucus (Brown and Bythell 2005) and polyp sweeping (Stafford-Smith 1993), or may benefit from the dissolved or suspended inorganic/organic nutrient loads (Bongiorni et al. 2003).

Relationship between corals and other marine organisms on coral reefs

We did not see many benthic invertebrates or abiota substrata relating to coral distribution around Penghu except for soft corals, which were consistently correlated with hard corals in both zones. Soft corals (alcyonacean) are quite abundant in tropical/subtropical areas around Taiwan (Dai 1991). Interactions and competition between soft and hard corals are diverse and depend on the species involved (Dai 1990; Maida et al. 2001). The differing competitive hierarchy of each hard and soft coral species might also determine the distribution of both coral types around Penghu (Dai 1993). However, the limited ability to identify soft corals at Penghu (but see Benayahu et al. 2012), especially from photo images, makes it difficult to understand the possible interactions of hard and soft corals in this area. Macroalgae is quite common as a benthos driver for coral distribution in most tropical and subtropical areas (McCook 1999; Hoey et al. 2011), especially eutrophic environments (McCook et al. 2001) like the Inner sector in the present study. Surprisingly, we did not see macroalgae as a significant driver of coral distribution around Penghu, which might be due to fish herbivory. Macroalgae plays an important role in the competition between coral and algae (Ceccarelli et al. 2005; Wismer et al. 2009). It is necessary to include reef-associated fish surveys in the future to understand the interactions among corals, macroalgae, and herbivorous fishes.

In conclusion, spatial variation in coral species diversity and assemblages was detected between the Penghu Archipelago and other islands distributed along a 70 km transect oriented north-to-south across the Tropic of Cancer in Taiwan Strait. Environmental factors such as sea surface temperature, turbidity, and nutrients showed significant correlations with coral species distribution in different sectors, suggesting that these environmental factors might account for the formation of coral assemblage patterns at Penghu. Considering the increasing threats from local disturbances (Hsieh et al. 2011) and rising global sea surface temperatures, our study provides an important baseline for the management and conservation of the unique non-reefal coral communities of Taiwan.

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