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# Roles of Temperature and Precipitation on Geographic Difference of Intertidal Macroalgal Abundance and Assemblage Structure along Taiwan's Coast

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## Abstract
Taiwan localizes between the subtropical and the tropical regions in Asia Pacific with the Kuroshio Current passing along its east side. The differences in the structure and abundance of coastal macroalgae in relation to environmental variables were investigated by determining the temporal dynamics (2001-2003) of intertidal macroalgal abundance and structure in northern (Hermei), southern (Nanwan) and southeastern (Taitung) Taiwan and the islands around Taiwan (Hsio-lu-chiu in the southwest, Penghu in the west, and Green Island and Lan-yu Island in the southeast of Taiwan). One hundred and seventy-one species have been identified with rhodophytes as abundant species. Species richness (number), diversity (H'), and evenness (J') showed site variation in the order of Nanwan = Hsio-lu-chiu > Green Island > Hermei > Taitung > Lan-yu Island > Penghu for species number and H', and Lan-yu Island >> Hermei > Hsio-liu-chiu > Green Island > Penghu > Taitung for J'. Dry weight biomass was higher in Hermei and Hsio-liu-chiu. The data from hierarchical cluster analysis and non-metric multidimensional scaling ordination of species similarities between different sampling times and the results of analysis of similarity (ANOSIM) showed that macroalgal assemblage is structured primarily by site and secondarily by year. There were three groups: 1. Hermei, 2. Hsio-liu-chiu and Green Island, and 3. Nanwan, Taitung, Lan-yu Island and Penghu. The species structure was different between 2001 and 2003, but similar between 2001 and 2002 and between 2002 and 2003. Less typhoon disturbance in 2002 may be one of the factors in explaining annual variability in intertidal macroalgal assemblage structure. The comparison of species compositions with environmental variables by BIO-ENV stepwise (BVSTEP) analysis shows that water temperature, salinity and precipitation are the abiotic variables which best explain the spatiotemporal dynamics of intertidal macroalgal abundance and structure around Taiwan. Cold winter temperature contributes to the distinction of Hermei (in the subtropical waters of northeastern Taiwan) from other sites localized in tropical waters. Precipitation and salinity are the factors affecting the seasonality of intertidal macroalgae in Taiwan. These results indicate that geographic difference in macroalgal assemblage structure in the intertidal regions around Taiwan can be attributable to temperature differences between subtropical and tropical waters in Taiwan. Salinity changes due to precipitation are considered as governing the seasonality of intertidal macroalgal assemblage structure in Taiwan.

## Introduction

Coral reefs are the most diverse marine ecosystems with the highest productivity on earth. Macroalgae, one of the components of the coral reef ecosystem, are usually inconspicuous on well developed reefs where nutrient concentrations are low and grazing pressure is high. In the past few years, several lines of evidence have shown that many coral reefs in tropical coastal waters of the western and central Pacific, Indian and western Atlantic Oceans have undergone shifts from coral to macroalgal dominance (Littler et al., 1992; Naim, 1993; Hughes, 1994; Lapointe, 1997). The shift of coral reefs to algal domination causes a dramatic decline in biodiversity in the reef ecosystem (Hughes, 1994; Andres and Witman, 1995). Thus, understanding the macroalgal abundance and the factors influencing species structure is an important aspect of the ecological, environmental, aesthetic and socio-economic value of reefs.

In the past 5 years, our laboratory has initiated a series of surveys on temporal and spatial changes of

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benthic macroalgal compositions around Taiwan and its adjunct islands, where anthropogenic activities in the coastal regions increased significantly over the past 10 years. We also plan to determine the factors affecting the macroalgal assemblage structure for the setup of marine protected areas (MPAs). Our studies on the coral reefs around Hengchun Peninsula in southern Taiwan have recently been published (Tsai *et al*., 2004; Hwang *et al*., 2005). It was found that temperature is a primary factor restricting macroalgal growth in Taiwan and the blooms of several macroalgae, such as *Gracilaria coronopifolia, Laurencia papillosa, Sargassum* spp., in coral reefs in southern Taiwan are attributable to high nutrient loading (Hwang *et al*., 2005). This reflects the impact of increasing anthropogenic activities on nearshore benthic communities. Similarly, the nearshore reefs of Du-Lang Bay in Taitung in southeastern Taiwan (Fig. 1) have faced increasing pressure from tourism over the past 10 years. Because macroalgae tend to integrate the effects of long-term exposure to adverse conditions, the macroalgal assemblages are widely used to characterize and monitor benthic communities. A 3-year quantitative investigation on the influences of natural and anthropogenic disturbances on macroalgal abundance and species compositions has been conducted on reefs along Taiwan during 2001-2003. The non-metric multidimensional scaling (nMDS) method and the analysis of similarity (ANOSIM) were used to compare the macroalgal assemblage compositions between sampling times using the Plymouth Routines in Multivariate Ecological Research (PRIMER) statistical software package, v. 6 (Clarke and Warwick, 1994). The comparison of temporal variations in macroalgal structure and environmental factors by using 'the forward selection backward elimination' algorithm (BVSTEP) was made to extract the factors showing the best combination of environment variables to algal compositions. The macroalgal species responsible for the difference in macroalgal assemblage structure between years and between seasons were identified by using the similarity percentage breakdown procedure (SIMPER).

## 1. Materials and Methods

### 1) Study site

Seven study sites in northern (Hermei), southern (Nanwan) and southeastern (Taitung) Taiwan and the islands around Taiwan (Hsio-lu-chiu in the southwest, Penghu in the west, and Green Island and Lan-yu Island in the southeast of Taiwan) have been chosen (Fig. 1).

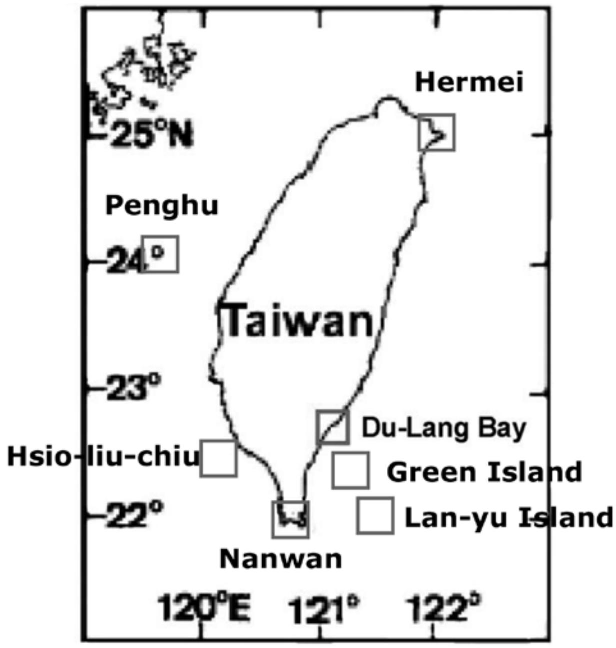


**Fig. 1 Map of sampling sites**

### 2) Estimation of macroalgal cover, biomass and species composition

To characterize the spatial changes in macroalgal assemblage compositions, two 10×10 $m^2$ blocks (as the effect of habitat) with a 10-m interval were set in the subtidal regions with 1-3 m water depth (MHWS) and at each block, 4 random stations were set for the estimation of species abundance in terms of percentage cover which was calculated as the sampling surface covered in vertical projection by the species using a 50×50 cm quadrat. Total macroalgal cover was the sum of all species cover. The macroalgal cover in different vegetation layers (erect layer, encrusting layer and turf) was recorded, and the total macroalgae in each 50×50 cm quadrat (there are 4 quadrats in each block with each quadrat as a replicated sample) were scraped for estimation of macroalgal compositions and biomass, and the species were identified using a microscope. Temporal changes in macroalgal cover and biomass and environmental variables were determined in winter, spring, summer, and autumn during 2001-2003 (Table 1).

### 3) Determination of seawater temperature, salinity, and nutrient concentrations

Seawater temperature, salinity, and seawater nutrient concentrations were determined randomly in 4 sampling stations for each block. Near-bottom (20 cm above the bottom) seawater samples were collected at each sampling station and transported to the laboratory at low temperature within 24 h. These water samples were

**Table 1. GPS and sampling time**

| | | Hermei | Nawan | Taitung | Penghu | Hsiao-liu-chiu | Green Island | Lan-yu Island |
|---|---|---|---|---|---|---|---|---|
| Abbreviation of sampling site | | N-Hm | S-Hw | SE-Dlb | SW-Ph | SW-Hlc | SE-G | SE-Ly |
| Time | GPS | 25°04'958"N 121°54'912"E | 21°56'000"N 120°51'010"E | 22°49'010"N 121°10'010"E | 23°39'014"N 119°53'010"E | 22° 20'34"N 120° 21'64"E | 22°38'147"N 121°30'204"E | 22°03'426"N 121°33'924"E |
| 2001 | Spring | 21-Apr | 30-Mar | 25-Apr | 28-Mar | 30-Mar | 27-Apr | 26-Apr |
| | Summer | 8-Jun | 27-May | 2-Jul | 2-Aug | 8-Aug | 20-Jul | 2-Aug |
| | Autumn | 27-Oct | 25-Oct | 19-Oct | 27-Oct | 25-Oct | 27-Oct | 20-Oct |
| 2002 | Winter | 22-Jan | 31-Dec | 23-Feb | 22-Feb | 22-Feb | 23-Feb | 23-Feb |
| | Spring | 2-Apr | 26-Mar | 5-May | 20-Apr | 13-Apr | 12-Apr | 4-May |
| | Summer | 27-Jun | 18-Jun | 31-Jul | 5-Jul | 25-Jul | 31-Jul | 31-Jul |
| | Autumn | 27-Oct | 5-Oct | 12-Oct | 10-Oct | 5-Oct | 12-Oct | 13-Oct |
| 2003 | Winter | 15-Jan | 19-Jan | 18-Jan | 31-Dec | 1-Jan | 18-Jan | 15-Feb |
| | Spring | 13-Apr | 5-Apr | 4-May | 12-Apr | 4-Apr | 4-May | 3-May |
| | Summer | 24-Jul | 3-Jul | 10-Jul | 9-Jul | 2-Jul | 10-Jul | 29-Jul |
| | Autumn | 2-Oct | 10-Oct | 27-Sep | 21-Sep | 13-Sep | 27-Sep | 27-Sep |

stored at -70°C until analysis. Before nutrient determination, frozen samples were thawed on ice in the dark. The determination of dissolved inorganic phosphorus (SRP) was modified from the method of Murphy et al. (1962). Colour reagent was prepared by mixing 1 ml of 3% ammonium molybdate solution and 0.75 ml of 5 N $H_2SO_4$ and after 10 min of incubation at room temperature, 0.9 ml of 1 M ascorbic acid (freshly prepared) and 0.08 ml of 2% potassium antimonyl-tartrate were added and held at room temperature for a further 10 min. Then, 50 µl of colour reagent was added in 0.5 ml of seawater and after 10 min of incubation at room temperature, the absorbance was read at 882 nm within 15 min by a Hitach spectrophotometer (model U-2000, Hitachi, Tokyo, Japan). The detection limit of SRP concentration was 0.02 µM.

Seawater $NO_2^-$ and $NO_3^-$ concentrations were determined according to Strickland and Parsons (1972) and $NH_4^+$ concentrations were determined according to Parsons et al. (1984). The detection limits for seawater $NO_2^-$, $NO_3^-$ and $NH_4^+$ concentrations were 0.2, 0.2 and 0.3 µM, respectively. The $NO_2^-$, $NO_3^-$, and $NH_4^+$ concentrations were summed as the concentration of dissolved inorganic nitrogen (DIN).

### 4) Data analysis

Statistical evaluation was performed using the SAS statistical software package v 8.0 (SAS Ltd., NC, USA). All summary statistics were expressed as mean and standard deviation (SD). The normality of environmental factors (mean monthly air temperature, mean monthly maximum air temperature, mean monthly minimum air temperature, annual cumulative precipitation, annual cumulative irradiance, temperature, salinity, and seawater nutrient concentrations) and biotic variables (total macroalgal cover, total macroalgal biomass (areal dry weight and species number) were analyzed by the Shapiro-Wilk W Test ($p > 0.05$). All parameters, which did not fit normality after data transformation, were subjected to non-parametrical analysis by Friedman's test for two-way (season and year changes) layout data (Siegel and Castellan, 1988). Homogeneity of variance was determined using the $F_{max}$ test (Sokal and Rohlf, 1981). Because all data did not show habitat difference ($p > 0.05$), only temporal (year and season) and site variations were tested.

To measure attributes of community structure between sampling times, several univariate indices including the number of species, the Shannon-Wiener species diversity index, H' (Shannon and Weaver, 1949) (by log *e* in the calculation) and evenness, Pielou's J' (Pielou, 1975) (by log *e* in the calculation), were calculated.

The multivariate analysis were used to compare the macroalgal assemblage compositions between stations and between seasons by the Plymouth Routines in Multivariate Ecological Research (PRIMER) statistical software package (v. 6) (Clarke and Warwick, 1994). For each sampling time, the average data of 8 replicates (the data collected on each quadrat) were used for analyses. The similarity matrix of species compositions (areal wet weight without data transformation) was classified by hierarchical agglomerative clustering using the unweighted pair group mean arithmetic (UPGMA) linkage method and was ordinated using non-metric multidimensional scaling (nMDS) analysis. Macroalgal assemblages were compared among stations by means of hierarchical agglomerative cluster analysis and MDS (Kruskal and Wish, 1978) of species areal wet weight using the Bray-Curtis similarity measure (Bray and

Curtis, 1957). Diversity profiles were also drawn using k-dominance curves to extract information on patterns of relative species abundance and dominance (Lambshead et al., 1983). The difference of macroalgal assemblage structure between seasons and between years was tested using ANOSIM (analysis of similarity) (Clarke and Warwick, 1994), and the species mainly responsible for differences between years were determined by the similarity percentage breakdown procedure, SIMPER (Clarke, 1993). The 'forward selection backward elimination' algorithm analysis (BVSTEP) was used to determine the environmental factors which best explained the observed patterns of macroalgal assemblage structures.

## 2. Results and Discussion

### 1) Environmental factors and habitat characteristics

The 30-year climate records (1971-2000) including air temperature, precipitation, and irradiance were obtained from the Central Weather Bureau of the Republic of China (data not shown). Typhoons frequently occurred in summer in 2001 and 2003, but no significant typhoon struck Taiwan in 2002 (data not shown). During the surveys, temporal changes in seawater temperature, salinity, and DIN, $NO_3^-$, $NO_2^-$, $NH_4^+$, and SRP concentrations in each study site were significant ($P < 0.01$) (data not shown). Winter temperature was lower, around 12°C in Hermei in northeastern Taiwan, and higher toward southern Taiwan, around 24°C for Nanwan, Taitung, Hsio-lu-chiu, Green Island, Lan-yu Island. The winter temperature for Penghu was around 16°C.

The study sites for Nanwan (N-Hm), Hsio-lu-chiu (SW-Hlc), and Green Island (SE-G) belong to bicarbonate reefs while those for Hermei (N-Hm), Taitung (SE-Dlb), Lan-yu Island (SW-Hlc), and Penghu (SW-Ph) belong to rocky reefs.

### 2) Macroalgal abundance and species structure

One hundred and seventy-one species have been identified during the survey with rhodophytes as an abundant species. Species richness (number per $m^2$) showed significant temporal (2002 > 2003 > 2001, Winter > Autumn, Spring, Summer) and site (S-Nw > SW-Hlc > SW-Dlb, SE-G, N-Hm > SE-Ly > SW-Ph) variations. These results demonstrate that species abundance in Taiwan was higher in carbonate reefs and relatively low in rocky reefs.

The dry weight biomass was temporally (2001 > 2002 > 2003, Summer > Spring, Winter, Autumn) and spatially (SE-Dlb > N-Hm, SW-Hlc, SE-G, S-Nw > SE-Ly, SW-Ph) variable ($P < 0.05$) (Table 2 and Fig. 2). Algal biomass was highest in southeastern Taiwan (Taitung) and lowest in Lan-yu Island in southeastern Taiwan and Penghu in southweastern Taiwan (Fig. 2). The %cover also showed temporal (2001 > 2002 > 2003, Summer > Spring, Winter, Autumn) and spatial (SE-Dlb > N-Hm, SW-Hlc, SE-G, S-Nw > SE-Ly, SW-Ph) variations ($P < 0.05$) (Fig. 3 and Table 2). The spatial difference in %cover exhibited a similar pattern as the dry weight biomass. The habitat of Taitung (SE-Dlb) was characterized by heavy sedimentation, which allowed the growth of a few algae, for example, the rhodophytes *Gracilaria coronopifolia* and *Ceratodictyon/Haliclona*. In addition, the data over 2001-2003 showed that there was a linear decrease in macroalgal abundance as the years advanced.

The univariate indices, Shannon-Wiener species diversity index, H', did not show temporal variations, but evenness, Pielou's J', showed significant temporal variations (2003 > 2002, 2001, Spring > Summer > Autumn > Winter). Besides, H' and evenness J' showed site variations in the order of Nanwan (S-Nw) = Hsio-lu-chiu (SW-Hlc) > Green Island (SE-G) > Hermei (N-Hm) > Taitung (SE-Dlb) > Lan-yu Island (SW-Hlc) > Penghu (SW-Ph) for H', and SE-Ly > N-Hm, SW-Hlc, SE-G, S-Nw > SW-Ph > SW-Dlb for J' (Table 2 and Fig. 4). The *k*-dominance curves showed that species dominance was highest for SE-Dlb, SE-Ly, and SW-Ph assemblages and lowest for SE-G assemblage (Fig. 5). The Green Island showed relatively high species diversity while Taitung in southeastern Taiwan, Lan-yu Island, an island in southeastern Taiwan, and Penghu, an island in the southwest, all containing rocky reefs, showed lowest species diversity.

Two-way cross ANOSIM testing showed that macroalgal assemblage was yearly ($R = 0.037$, $p = 0.036$) and spatially ($R = 0.561$, $p = 0.001$) significant (Table 3). Based on the value of each block, the results from cluster analysis and MDS ordination analysis of species areal dry weight (without data transformation) using the Bray Curtis similarity measures showed that two groups were discerned corresponding to 2001-2002 and 2002-2003 groups (Fig. 6). The assemblage structure of N-Hm was different than at other sites. The structures of N-Nm, SE-Dlb, SE-Ly, and SW-Ph assemblages were the same, while the structure of SW-Hlc was the same as that of SE-G. Therefore, macroalgal assemblage is primarily structured by site and secondarily by year (group 2001-2002, group 2002-2003). However, no seasonal difference in macroalgal assemblage structure can be observed ($R = 0.059$, $p = 0.142$).

**Table 2. ANOVA analysis of abiotic variable**

| Variable | *d.f.* | F | *p* | Separation[1] |
|---|---|---|---|---|
| Species number | 148 | 6.774 | <0.001 ** | |
| Site | 5 | 66.186 | <0.001 ** | S-Nw[a] > SW-Hlc[b] > SW-Dlb[c], SE-G[c], N-Hm[c] > SE-Ly[d] > SW-Ph[e] |
| Year | 4 | 18.17 | <0.001 ** | 2002[a] > 2003[ab] > 2001[b] |
| Season | 3 | 14.817 | <0.001 ** | Win[a] > Aut[b], Spr[b], Sum[b] |
| Site*Year | 10 | 7.94 | <0.001 ** | |
| Site*Season | 15 | 4.289 | <0.001 ** | |
| Year*Season | 10 | 5.776 | <0.001 ** | |
| Site*Year*season | 23 | 5.826 | <0.001 ** | |
| Evenness (J') | 141 | 2.533 | <0.001 ** | |
| Site | 5 | 6.864 | <0.001 ** | SE-Ly[a] > N-Hm[b], SW-Hlc[b], SE-G[b], S-Nw[b] > SW-Ph[c] > SW-Dlb[c] |
| Year | 4 | 11.119 | <0.001 ** | 2003[a] > 2002[b], 2001[b] |
| Season | 3 | 9.48 | <0.001 ** | Spr[a] > Sum[ab] > Aut[bc] > Win[c] |
| Site*Year | 10 | 1.809 | 0.058 | |
| Site*Season | 15 | 3.9 | <0.001 ** | |
| Year*Season | 10 | 2.958 | 0.001 ** | |
| Site*Year*season | 21 | 2.149 | 0.003 * | |
| Diversity (H') | 148 | 4.393 | <0.001 ** | |
| Site | 5 | 43.787 | <0.001 ** | S-Nw[a], SW-Hlc[a] > SE-G[b] > N-Hm[bc] > |
| Year | 4 | 1.819 | 0.124 | |
| Season | 3 | 0.494 | 0.687 | |
| Site*Year | 10 | 4.574 | <0.001 ** | |
| Site*Season | 15 | 2.476 | 0.002 * | |
| Year*Season | 10 | 3.155 | 0.001 ** | |
| Site*Year*season | 23 | 4.175 | <0.001 ** | |
| Cover (%) | 151 | 5.84 | <0.001 ** | |
| Site | 5 | 18.015 | <0.001 ** | SE-Dlb[a] > N-Hm[b], SW-Hlc[b], SE-G[b], S-Nw[b] > SE-Ly[c], SW-Ph[c] |
| Year | 4 | 10.148 | <0.001 ** | 2001[a] > 2002[ab] > 2003[b] |
| Season | 3 | 8.338 | <0.001 ** | Sum[a] > Spr[b], Win[b], Aut[b] |
| Site*Year | 10 | 3.58 | <0.001 ** | |
| Site*Season | 15 | 12.252 | <0.001 ** | |
| Year*Season | 10 | 8.084 | <0.001 ** | |
| Site*Year*season | 23 | 8.501 | <0.001 ** | |
| Dry weight (g/m2) | 149 | 6.029 | <0.001 ** | |
| Site | 5 | 22.012 | <0.001 ** | N-Hm[a] > SW-Hlc[b], SE-Ly[b] > SE-Dlb[c], S-Nw[c], SE-G[c], SW-Ph[c] |
| Year | 4 | 2.565 | 0.038 * | 2002[a] > 2001[b], 2003[b] |
| Season | 3 | 5.859 | <0.001 ** | Spr[a] > Aut[ab] > Win[bc] > Sum[c] |
| Site*Year | 10 | 12.136 | <0.001 ** | |
| Site*Season | 15 | 9.432 | <0.001 ** | |
| Year*Season | 10 | 15.325 | <0.001 ** | |
| Site*Year*season | 23 | 10.281 | <0.001 ** | |

[1]Different symbol indicate significant difference between treatments

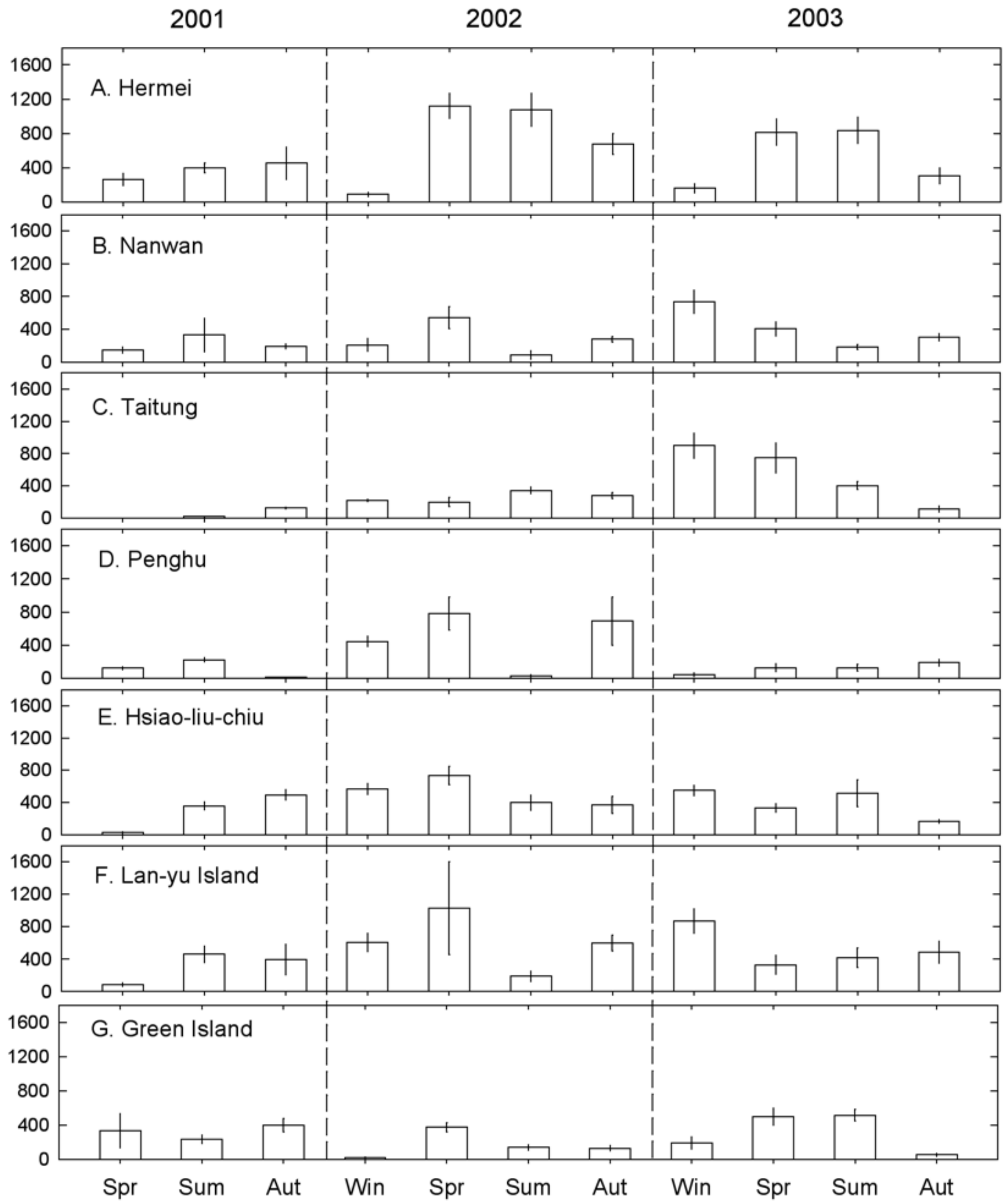


**Fig. 2 Dry weight biomass in sampling sites over 2001-2003. Data are present as mean ± SD (n=8).**

The coral reef islands, Hsio-Liu-Chiu and Green Island, exhibited the same species structure. Taitung in southeastern Taiwan, Lan-yu Island, an island in southeastern Taiwan, and Penghu, an island in the southwest, all containing to rocky reefs, had the same species structure. These results reflect that the substrate property is possibly a factor in determining the species for recruitment and growth, and consequently, the pattern of algal species and abundance. For example, the SIMPER analysis of species contributing to year difference showed that the species responsible for difference in the structure of Hermei to other sites was *Pterocladiella capillacea*. This rhodophyte can tolerate low salinities and low temperatures, but can not tolerate high temperatures. It explains why this red alga could bloom in northeastern Taiwan but was not abundant in southern Taiwan with relatively high temperatures all year round.

### 3) Environmental factors determining structure difference

To elucidate environmental factors in regulating temporal variations in macroalgal assemblage, the BVSTP analysis was used for determination of the best combinations of the 11 environment variables (mean monthly air temperature, mean monthly maximum air temperature, mean monthly minimum air temperature,

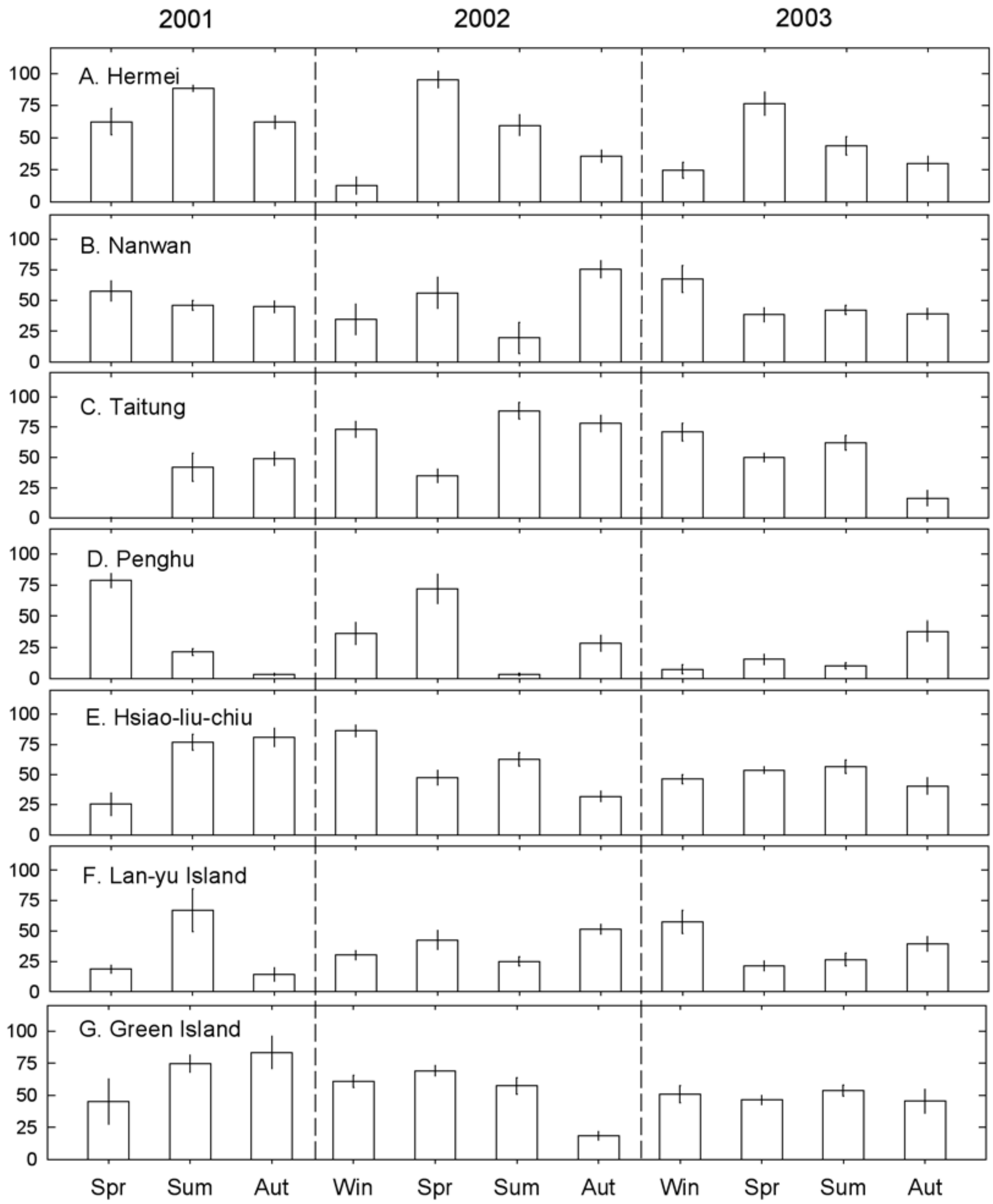


**Fig. 3 % cover in sampling sites over 2001-2003. Data are present as mean ± SD (n=8).**

monthly cumulative irradiance, monthly cumulative precipitation, seawater temperature, salinity, and DIN, $NO_3^-$+$NO_2^-$, $NH_4^+$, and SRP concentrations) producing the largest matches of changes in macroalgal structure and environment variables over the period 2001-2003. Water temperature, salinity and precipitation are the abiotic variables which best explain the spatiotemporal dynamics of intertidal macroalgal abundance and structure around Taiwan (Table 4).

Present evidence has suggested that temperature is a primary factor influencing geographic variations of macroalgal assemblage structure around Taiwan. Cold winter temperature contributes to the distinction of Hermei (in the subtropical waters of northeastern Taiwan) from other sites localized in tropical waters. Temperature has been recognized as the principal ecological factor affecting macroalgal growth and morphology, geographical distribution and seasonal changes in growth patterns (Garbary, 1979; Lüning, 1984; van den Hoek, 1984; Breeman, 1988; Pakker et al., 1994; Davison and Pearson, 1996; Lee *et al*., 1999). Studies carried out on lagoons and nearshore waters in the Gulf of Mexico showed that seawater temperature is critical for seasonality in benthic algae in tropical waters (Conover, 1964; Earle, 1969). It is also found that temperature can influence the seasonality in vegetation growth and reproduc-

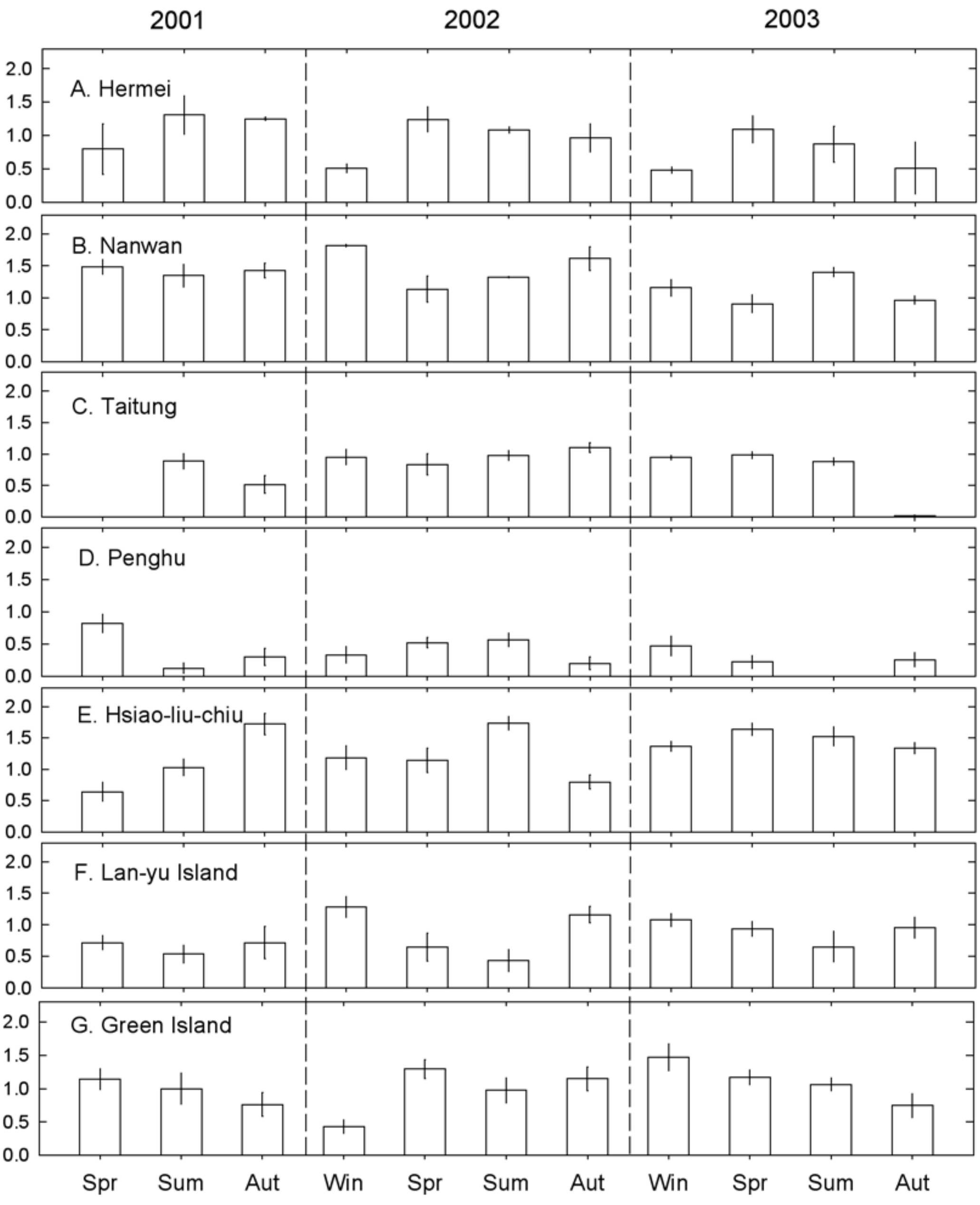


**Fig. 4 H' (A) and J' (B) values in sampling sites over 2001-2003. Data are present as mean ± SD (n=8).**

tion of *Sargassum* in Hawaii (De Wreede, 1976) and the British Isles (Jephson and Gray, 1977). In Currimao, Ilocos Norte, Northern Philippines, slight seasonal variations of seawater temperature were positively correlated with biomass of *Sargassum* from subtidal zones (Hurtado and Ragaza, 1999). Our previous studies have identified the impact of temperature on the growth of *Gracilaria tenuistipitata* in Taiwan (Lee *et al*., 1999). In these studies, laboratory and field experiments have shown that the seasonal abundance of *Gracilaria coronopifolia* from southern Taiwan was determined by seasonal variations in seawater temperatures and nutrient concentrations as well as different physiological growth strategies (Hwang *et al*., 2004). So, the seasonality of biomass of *Gracilaria coronopifolia* from Du-Lang Bay in Taitung in southeastern Taiwan was influenced by temperature fluctuations, especially in 2001 and 2003. However, the response of *Ceratodictyon*/*Haliclona* growth to temperature fluctuations is still not clear.

We hypothesize that precipitation and salinity are the factors affecting the seasonality of intertidal macroalgae in Taiwan. Because salinity has been know as a factor affecting macroalgal growth, it can be expected that macroalgal composition and growth are influenced by a change of salinity in the studied reef in response to precipitation. The effects of salinity on macroalgal

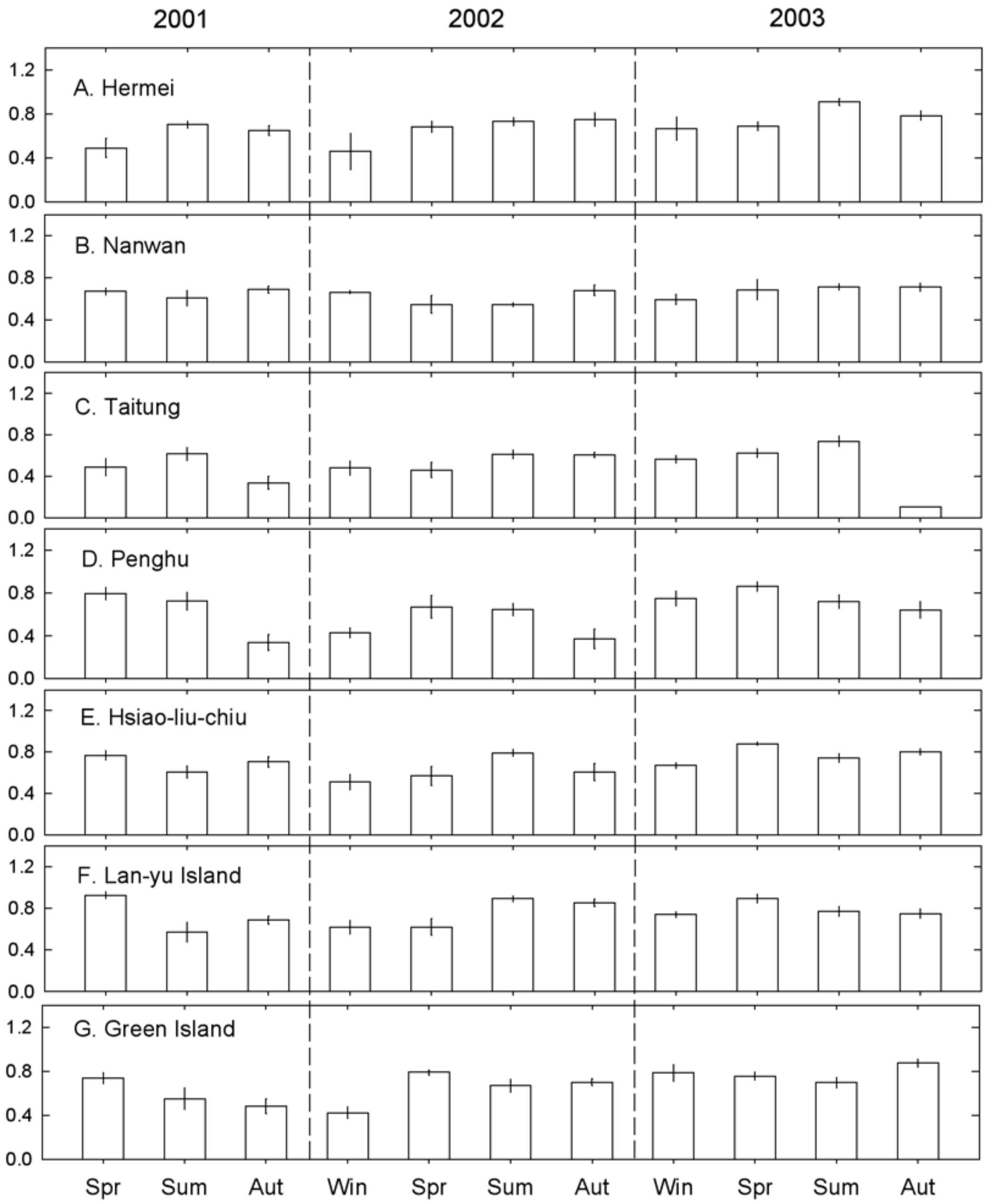


**Fig. 4 continued.**

growth have been documented in many studies (Dawes *et al*., 1998; Eriksson and Bergstrom, 2005; Israel *et al*., 1999; Larsen and Sand-Jensen, 2006). Kramer and Fong (2000) demonstrated that the populations of *E. intestinalis* in coastal estuaries may suffer from freshwater inputs if salinity conditions are persistently reduced. Thus, it makes sense that salinity changes due to precipitation are involved in governing seasonality of intertidal macroalgal assemblage structure in Taiwan.

Ecosystems in coastal areas of Taiwan and the islands around Taiwan have faced threats in the past 10 years. We have observed that there were significant urban sewage wastes releasing into these studied reefs. Our previous studies on coastal areas show the impact of nutrient and its interaction with temperature on the blooms of macroalgae (Tsai *et al*., 2004; Hwang *et al*., 2005). However, the present paper does not show the role of nutrient on macroalgal abundance and structure.

In conclusion, this study indicates that nearshore macroalgal assemblage in Taiwan is grouped into the low temperature group, the coral-reef island group, and the high temperature/rocky reef group. Temperature is not only a factor influencing structure seasonality, but also the main factor for geographic difference in assemblage structure along Taiwanese coasts. The different responses of macroalgal structure and growth to

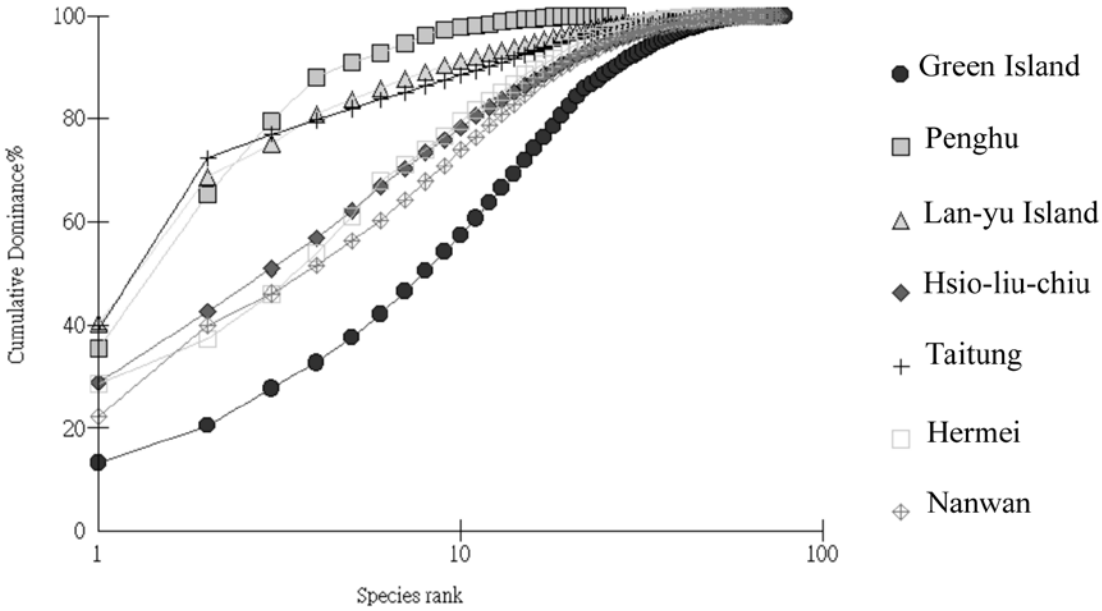


**Fig. 5 k-Dominance curve.**

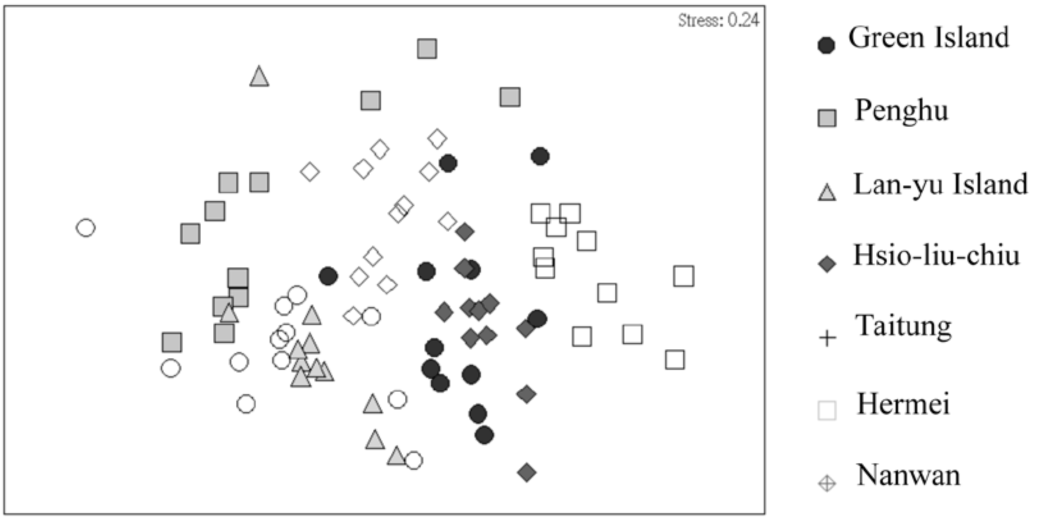


**Fig. 6 MDS plot.**

**Table 4. The best combination of the nine environment variables producing the largest matches of changes in macroalgal assemblage and environmental variables among 7 sites over 2001-2003.**

| Number of variable | Spearman rank correlation (ϱ) | Best variable combination |
|---|---|---|
| 3 | 0.396 | Seawater temperature, Salinity, Precipitation |

temperature provide the way for the proper management of benthic communities on nearshore reefs in Taiwan. However, the relative importance of abiotic and biotic (such as herbivores) factors affecting the growth of macroalgae needs to be further ascertained in the near future.

## Acknowledgements

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Breeman, A.M. 1988. Relative importance of tempera-

**Table 3A. Two-way cross ANOSIM analysis.**

| | R statistic | Significance level |
|---|---|---|
| Site | 0.561 | 0.001** |
| SE-G - SW-Ph | 0.599 | 0.002* |
| SE-G - SE-Ly | 0.599 | 0.002* |
| SE-G - SW-Hlc | 0.301 | 0.013 |
| SE-G - SE-Dlb | 0.598 | 0.001** |
| SE-G - N-Hm | 0.861 | 0.002* |
| SE-G - S-Nw | 0.575 | 0.004* |
| SW-Ph - SE-Ly | 0.310 | 0.017 |
| SW-Ph - SW-Hlc | 0.731 | 0.001** |
| SW-Ph - SE-Dlb | 0.111 | 0.185 |
| SW-Ph - N-Hm | 0.712 | 0.002* |
| SW-Ph - S-Nw | 0.273 | 0.016 |
| SE-Ly - SW-Hlc | 0.731 | 0.001** |
| SE-Ly - SE-Dlb | 0.259 | 0.032 |
| SE-Ly - N-Hm | 0.834 | 0.001** |
| SE-Ly - S-Nw | 0.291 | 0.054 |
| SW-Hlc - SE-Dlb | 0.666 | 0.001** |
| SW-Hlc - N-Hm | 0.899 | 0.002* |
| SW-Hlc - S-Nw | 0.766 | 0.003* |
| SE-Dlb - N-Hm | 0.762 | 0.001** |
| SE-Dlb - S-Nw | 0.430 | 0.012 |
| N-Hm - S-Nw | 0.897 | 0.001** |
| Season | 0.059 | 0.142 |

**Table 3B. One-way ANOSIM analysis.**

| | R statistic | Significance level |
|---|---|---|
| Year | 0.037 | 0.036** |
| 2001-2002 | 0.049 | 0.058 |
| 2001-2003 | 0.077 | 0.011* |
| 2002-2003 | 0.019 | 0.746 |


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