

Nutrients, temperature, and salinity as primary factors influencing the temporal dynamics of macroalgal abundance and assemblage structure on a reef of Du-Lang Bay in Taitung in southeastern Taiwan

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ABSTRACT. Temporal dynamics (2001-2003) of macroalgal abundance and assemblage structure in relation to environmental variables were studied on a reef in Du-Lang Bay in southeastern Taiwan. Sixty-six species were identified, with rhodophytes as the abundant species. Both the areal wet weight and areal dry weight biomass of total macroalgae increased as time advanced and reached the maximum in the winter of 2003 mainly due to the blooms of *Gracilaria coronopifolia* and *Ceratodictyon/Haliclona*, a red alga-sponge symbiose. Macroalgal cover varied temporally, % cover in 2001 and 2002 was low in spring but high in summer while that in 2003 was high in winter, spring, and summer and low in autumn. Species richness (species number), diversity (H') and evenness (J') increased, peaked in the winter in 2001, stabilized in 2002, and then decreased in 2003. The data of hierarchical cluster analysis and non-metric multidimensional scaling ordination of species similarities between different sampling times and the results of an analysis of similarity (ANOSIM) showed that the macroalgal assemblage is structured primarily by year and secondarily by season. Although H' and J' showed fewer changes, the k -dominance curve and a decrease in species number as time advanced suggest a switch of species structure from a highly diversified community to a less diversified one. The similarity percentage breakdown procedure (SIMPER) analysis shows that *G. coronopifolia* and *Ceratodictyon/Haliclona* are the species contributing to year-over-year and seasonal differences in species structure. The comparison of macroalgal compositions with environmental variables indicates that decreasing soluble-reactive phosphorus (SRP) concentrations and increasing salinity are the best combination of environment variables to explain the yearly changes in algal compositions. Seasonal variations in species structure were associated with temporal variations in temperature, precipitation, salinity, and NH_4^+ . In conclusion, the nearshore macroalgal assemblage in Du-Lang Bay in Taitung in southeastern Taiwan during 2001-2003 became less diversified over time; the structure is modified yearly by increased nitrogen/phosphorus levels, and salinity and is also affected seasonally by fluctuating temperature and precipitation.

Keywords: Assemblage; Macroalgae; Nutrient; Salinity; Temperature; Temporal variation.

Abbreviation: ANOSIM, analysis of similarity; DIN, dissolved inorganic nitrogen; d. wt., dry weight; MDS, multidimensional scaling; SIMPER, similarity percentage breakdown procedure; SRP, soluble reactive phosphorus; w. wt, wet weight.

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 Ocean, the Indian Ocean, and the western Atlantic Ocean 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 the reef ecosystem's biodiversity (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.

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Nutrient enrichment is considered to be a factor behind macroalgal blooms. In the mid 1970s, several studies on coral reefs in Hawaii's Kaneohe Bay revealed the impact of anthropogenic nutrient inputs on the bloom of *Dictyosphaeria cavernosa* (Banner, 1974; Smith et al., 1981). After that, the effects of anthropogenic nutrient enrichment on macroalgal blooms have been studied worldwide, for example, in the coastal waters of Reunion Island in the Indian Ocean (Cuet et al., 1988) and the Caribbean and Florida regions (Lapointe and O'Connell, 1989; Bell, 1992; Lapointe et al., 1994). The changes in macroalgal assemblages are considered to be a consequence of habitat modification mediated by physical and/or anthropogenic disturbances (Banner, 1974; Smith et al., 1981). It has been suggested that increasing water column nutrient concentrations play a role in macroalgal blooming at Reunion Island (Cuet et al., 1988) and in the Caribbean and Florida coastal regions (Lapointe and O'Connell, 1989; Bell, 1992). Apparently, the growth of macroalgae overwhelms coral after changes driven by natural disturbance or human activities (McCook, 1999; Schaffelke, 1999; McCook et al., 2001), and highly abundant macroalgae, especially erect fleshy algae, are a sign of reef degradation (Done, 1992; Hughes, 1994).

In the past five years, our laboratory has initiated a series of surveys on temporal and spatial changes in benthic macroalgal compositions around Taiwan and its adjunct islands, where anthropogenic activities along the coastal regions have increased significantly over the past ten years. We also plan to determine the factors affecting the macroalgal assemblage structure for the setup of marine protected area (MPA). Our studies on the coral reefs in Hengchun Peninsula in southern Taiwan

have recently been published (Tsai et al., 2004; Hwang et al., 2004). It was found that temperature is a primary factor restricting macroalgal growth in Taiwan, and the blooms of macroalgae like *Gracilaria coronopifolia*, *Laurencia papillosa*, and *Sargassum* spp., in coral reefs in southern Taiwan are attributable to high nutrient loading (Hwang et al., 2004). It reflects the impact of increasing anthropogenic activities on the nearshore benthic community. Similarly, the nearshore reefs of Du-Lang Bay in Taitung in southeastern Taiwan (Figure 1) have faced increasing tourism pressure over the past ten 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 influence of natural and anthropogenic disturbances on macroalgal abundance and species compositions was conducted on a reef (GPS: 22°03'43" N; 121°32'18" E) of Du-Lang Bay over 2001-2003. A non-metric multidimensional scaling (nMDS) method and 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 a "forward selection backward elimination" algorithm (BVSTEP) was made to extract the factors showing the best combination of environmental variables to algal compositions. The macroalgal species responsible for differences in the macroalgal assemblage structure between years and between seasons were identified using the similarity percentage breakdown procedure (SIMPER).



Figure 1. The map of sampling site.

MATERIALS AND METHODS

Study site and environmental characteristics

The study site has a horizontal width of 652 m with an intertidal region approximately 20-435 m long, a subtidal macroalgal region approximately 17-28 m long, and a depth of 0-18 m (below MHWs) on a seaward gradient.

The 30-year climate records (1971-2000) of Taitung obtained from the Central Weather Bureau of the Republic of China show that the mean annual air temperature in Orchard is 22.6°C; the mean monthly air temperature is low (18.4°C) in January and high (26.2°C) in July (Figure 2). The annual mean relative humidity is 78% and the annual cumulative precipitation is 3081.3 mm, which mostly occurs in May-September. Typhoons usually occur in May-September, and the prevailing northeasterly winds occur in November-February.

During the surveys (2001-2003), mean monthly air temperature was 23.9°C, annual precipitation was 3136.7 mm, and annual cumulative irradiance was 5881.9 MJ/m² (Figure 2). Temporal variations in mean monthly air temperature, mean monthly maximum air temperature,

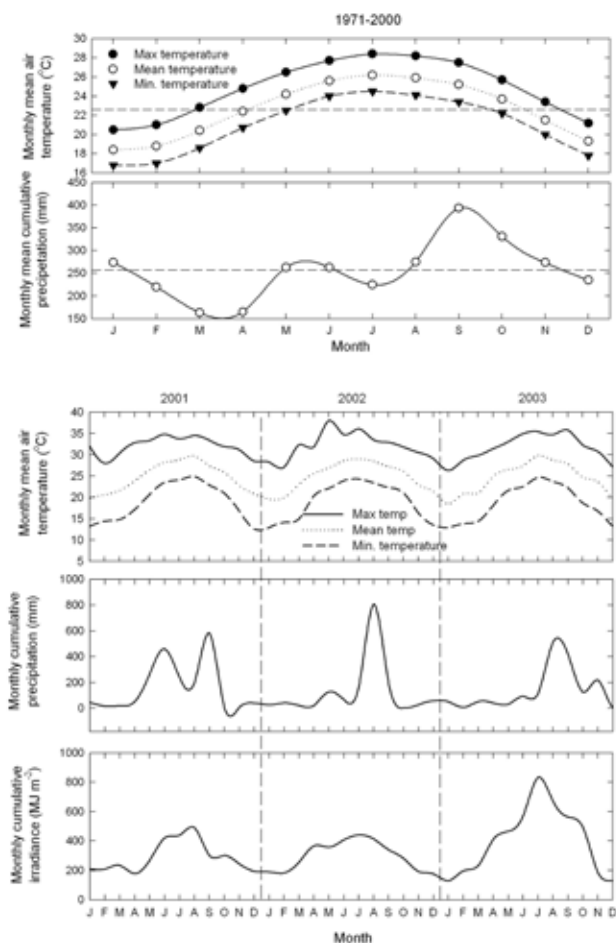


Figure 2. Climate data from 1971-2000 and during the survey (2001-2003).

mean monthly minimum air temperature, annual cumulative precipitation, and annual cumulative irradiance were significant (Friedman's test, $p < 0.001$); no year-to-year differences were found for these climate parameters, except that irradiance was highest in 2003. Precipitation not only showed seasonality with a low value in winter and high value in spring-autumn, but also showed year-to-year differences, such as being low in 2002 relative to 2001 and 2003. Four typhoons passed through Taitung in both 2001 and 2003, but none occurred in 2002.

Estimation of macroalgal cover, biomass and species composition

To characterize the spatial changes in macroalgal assemblage compositions, two 10×10 m² 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 four random stations were set up to estimate 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, and total macroalgal cover was the sum of all species cover values. The macroalgal cover in different vegetation layers (erect layer, encrusting layer and turf) was recorded,

and total macroalgae in each 50×50 cm quadrat (there were four 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 were determined in April, July, and October of 2001, in February, May, July, and October of 2002, and in January, May, July, and September of 2003 for the analysis of both year-to-year and seasonal (January-February as winter, April-May as spring, July as summer, and October-September as autumn) changes in macroalgal assemblage structure and their relationships to environmental variables.

Determination of turbidity, seawater temperature, salinity, and nutrient concentrations

Seawater temperature, salinity, and seawater nutrient concentrations were determined randomly in four sampling stations for each block. Near-bottom (20 cm above the bottom) seawater samples were collected at each sampling station, and one part was immediately subjected to sedimentation detection while another part was transported to the laboratory under low temperature within 24 h. These water samples were 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 and Riley (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 $0.02 \mu\text{M}$.

Seawater NO_2^- and NO_3^- concentrations were determined according to Strickland and Parsons (1972). 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_3^- , NO_2^- , and NH_4^+ concentrations were summed as the concentration of dissolved inorganic nitrogen (DIN).

Data analysis

Statistical evaluation was performed using 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 of biotic variables (total macroalgal cover, total macroalgal biomass (areal wet weight and areal dry weight), species number, and areal wet weight of *Ceratodictyon/Haliclona* association, and *Gracilaria coronopifolia*) was 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 (seasonal and year-to-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 variations (seasonal and year-to-year) 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.

A multivariate analysis was done to compare the macroalgal assemblage compositions between stations and between seasons using the Plymouth Routines in Multivariate Ecological Research (PRIMER) statistical software package (v. 5) (Clarke and Warwick, 1994). For each sampling time, the average data of eight replicates (the data collected on each quadrat) was used for analysis. 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 (Lambhead 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 that best explain the observed patterns of macroalgal assemblage structures.

RESULTS

Environmental factors

During the surveys, mean seawater temperature and salinity were $27.14 \pm 2.99^\circ\text{C}$ and 31.37 ± 4.77 psu, respectively (Figure 3). Seawater temperature showed

marked year-to-year (Friedman's test, $p < 0.0001$) (2003 > 2001, 2002) and seasonal ($F = 82.00$, $p < 0.0001$) (summer > spring > autumn > winter) variations and significant year-to-year and seasonal interaction ($F_{3,87} = 30.25$, $p < 0.0001$) (Table 1). Salinity did not show seasonal variations (Friedman's test, $F_{2,87} = 0.77$, $p = 0.5138$) (summer = autumn > spring > winter) but showed year-to-year variations ($F_{6,87} = 69.96$, $p < 0.0001$) (Table 1).

Mean DIN, NO_3^- , NO_2^- , NH_4^+ , and SRP concentrations during the survey were 4.35 ± 3.52 , 2.05 ± 3.39 , 0.06 ± 0.10 , 2.37 ± 1.88 , and $0.47 \pm 0.48 \mu\text{M}$, respectively (Figure 3). DIN concentrations showed year-to-year ($F_{2,87} = 3.21$, $p = 0.0468$) (2002 = 2003 > 2001) and seasonal ($F_{3,87} = 14.88$, $p < 0.0001$) (winter > summer = spring > autumn) variations and the year-to-year and seasonal interaction was significant ($F_{6,87} = 17.07$, $p < 0.0001$) (Table 1). NO_3^- concentrations did not show seasonal variations (Friedman's test, $F_{2,87} = 2.26$, $p = 0.0570$) but did show year-to-year variations ($F_{2,87} = 15.27$, $p < 0.0001$) and the year-to-year and seasonal interaction was significant ($F_{6,87} = 17.67$, $p < 0.0001$). NO_2^- concentrations showed seasonal (Friedman's test, $F_{3,87} = 9.19$, $p < 0.0001$) and year ($F_{2,87} = 117.25$, $p < 0.0001$) variations, and the year and season interaction was significant ($F_{6,87} = 3.33$, $p = 0.0096$) (Table 1). NH_4^+ concentrations showed both seasonal ($F_{3,87} = 6.49$, $p = 0.0006$) (spring = summer > winter > autumn)

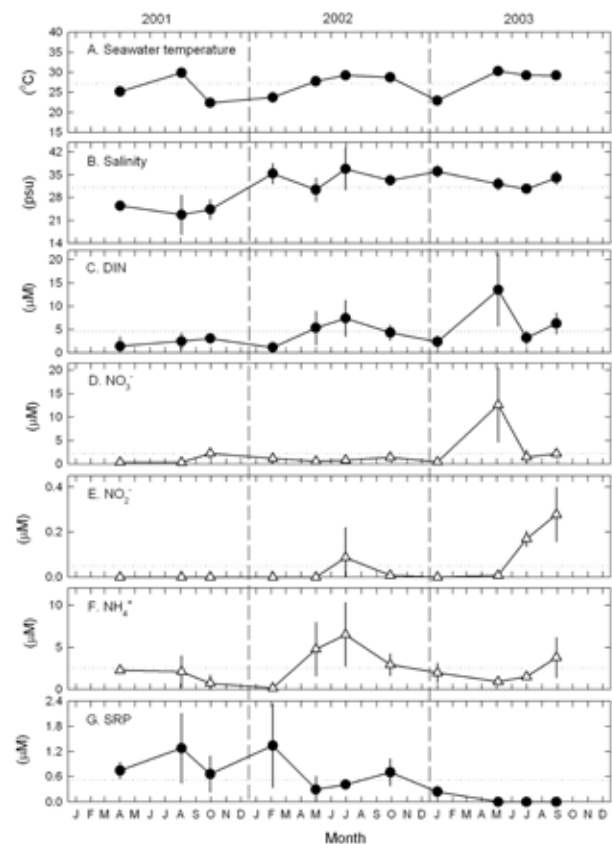


Figure 3. Variations of seawater temperature, salinity, DIN, NO_3^- , NO_2^- , NH_4^+ , and SRP from 2001-2003. Data are present as mean \pm SD ($n=8$).

and year (Friedman's test, $F_{2,87} = 11.30$, $p < 0.0001$) (2002 > 2001 = 2003) variations but the year and season interaction was not significant ($F_{6,87} = 1.80$, $p = 0.1241$) (Table 1). SRP concentrations also showed seasonal ($F_{3,87} = 14.54$, $p < 0.0001$) (summer > autumn > spring > winter) and year variations (Friedman's test, $F_{2,87} = 129.26$, $p < 0.0001$) (2001 > 2002 > 2003) (Table 1), in which SRP concentrations were $\geq 0.6 \mu\text{M}$ in 2001 and February of 2002, and then decreased gradually as time advanced, even below the detection limit ($0.2 \mu\text{M}$) in 2003.

Table 1. Friedman test for environment factors.

	F	p	Tukey's test ¹
NH₄⁺			
Season	6.49	0.0006	Spr ^{2a} = Sum ^a > Win ^{ab} > Aut ^b
Year	11.3	<0.0001	2002 ^a > 2003 ^b = 2001 ^b
Season*year	1.8	0.1241	
NO₂⁻			
Season	9.19	<0.0001	Spr ^a > Sum ^{ab} > Win ^b = Aut ^b
Year	117.25	<0.0001	2003 ^a > 2002 ^b = 2001 ^b
Season*year	3.33	0.0096	
NO₃⁻			
Season	2.63	0.057	
Year	15.27	<0.0001	2003 ^a > 2001 ^b = 2002 ^b
Season*year	17.67	<0.0001	
DIN			
Season	14.88	<0.0001	Win ^a > Sum ^b = Spr ^b > Aut ^c
Year	3.21	0.0468	2003 ^a = 2002 ^a > 2001 ^b
Season*year	6.73	<0.0001	
SRP			
Season	14.54	<0.0001	Sum ^a > Aut ^{ab} > Spr ^{bc} > Win ^c
Year	129.26	<0.0001	2001 ^a > 2002 ^b > 2003 ^c
Season*year	2.17	0.0675	
Seawater temperature			
Season	82	<0.0001	Sum ^a > Spr ^b > Aut ^c > Win ^d
Year	23.26	<0.0001	2003 ^a > 2002 ^b = 2001 ^b
Season*year	30.25	<0.0001	
Salinity			
Season	0.77	0.5138	
Year	69.96	<0.0001	2002 ^a = 2003 ^a > 2001 ^b
Season*year	3.45	0.0079	

¹Different symbol indicates significance at $p < 0.05$.

²Spr, spring; Sum, summer; Aut, autumn; Win, winter.

Macroalgal abundance

Sixty-six species were recorded during the surveys: 21 Chlorophyta, 8 Phaeophyta, and 39 Rhodophyta (Table 2). Because the data did not show habitat difference, the data of eight sampling stations from two blocks (four random samples from each block) were pooled and averaged for analysis to give the overall picture of seasonal changes in macroalgal abundance (Figure 4). Mean species numbers per m² were affected by season (Friedman's test, $F_{3,87} = 11.30$, $p = 0.0003$) (winter > spring > autumn > summer) and year ($F_{2,87} = 11.26$, $p < 0.0001$) (2002 > 2001 = 2003), and the interaction of year and season was significant ($F_{6,87} = 5.33$, $p = 0.0004$ and Table 3). Mean species numbers per m² were highest in October 2001 mainly due to the appearance of several chlorophytes and rhodophytes. During the survey, erect algae were more abundant than encrusting and turf algae.

Total macroalgal % cover showed seasonal (Friedman's test, $F_{3,87} = 10.35$, $p < 0.0001$) (summer = winter > autumn > spring) and year ($F_{2,87} = 4.22$, $p = 0.0189$) (2003 > 2002 > 2001) variations, and the interaction of year and season was significant ($F_{6,87} = 4.43$, $p = 0.0015$) (Figure 4 and Table 3). Total macroalgal wet weight biomass showed seasonal (Friedman's test, $F_{3,87} = 9.48$, $p < 0.0001$) (winter > summer > spring > autumn) and year ($F_{2,87} = 19.84$, $p < 0.0001$) (2003 > 2002 > 2001) variations, and the interaction of year and season was significant ($F_{6,87} = 3.34$, $p = 0.0093$) (Figure 4 and Table 3). Total macroalgal dry

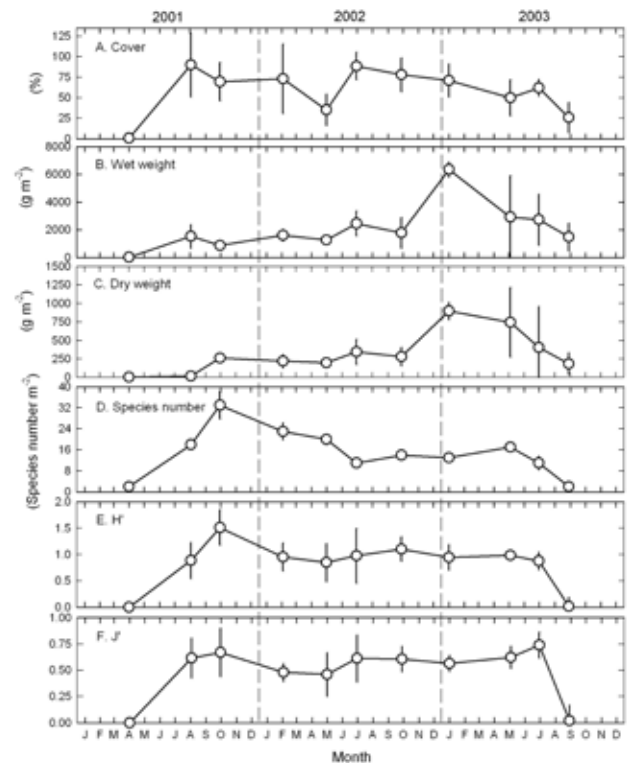


Figure 4. Total macroalgal cover (A), areal wet weight (B), areal dry weight (C), species number (D), H' (E), and J' (F). Data are present as mean \pm SD (n=8).

Table 2. (Continued.)

Family	Species	2001			2002			2003				
		Spr ¹	Sum	Aut	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut
Hypneaceae	<i>Hypnea cervicornis</i> J. Agardh			+								
	<i>Hypnea charoides</i> Lamouroux		+	+	+	+	+	+	+	+	+	+
	<i>Hypnea pannosa</i> J. Agardh											
Phylloporaceae	<i>Ahnfeltia plicata</i> (Hudson) Fries			+								
	<i>Ahnfeltiopsis flabelliformis</i> (Harvey) Masuda		+									
Rhizophyllidaceae	<i>Portieria hornemannii</i> (Lyngbye) P.C. Silva		+	+								
Sarcodiaceae	<i>Sarcodia montagneana</i> (Hooker et Harvey) J. Agardh										+	
Solieriaceae	<i>Eucheuma serra</i> J. Agardh									+	+	
Corallinaceae	<i>Amphiroa fragilissima</i> (Linnaeus) Lamouroux											+
	<i>Jania adhaerens</i> Lamouroux		+	+	+	+				+	+	
	<i>Jania ngulate</i> (Yendo) Yendo										+	
	<i>Mastophora rosea</i> (C. Agardh) Setchell		+			+						
	<i>Gracilaria arcuata</i> Zanardini											+
Gracilariaceae	<i>Gracilaria coronopifolia</i> J. Agardh		+									
	<i>Gracilaria eucheumoides</i> Harvey		+	+	+		+	+	+	+	+	+
	<i>Gracilaria sordica</i> (Suringar) Hariot			+								
	<i>Gracilaria</i> sp.						+					
	<i>Ceratodictyon spongiosum</i> Zanardini	+	+		+	+	+	+	+	+	+	+
Rhodymeniaceae	<i>Gelidiopsis repens</i> (Kützting) Weber-van Bosse						+					
Ceramiales	<i>Ceramium</i> sp.											
Rhodomelaceae	<i>Acanthophora spicifera</i> (Vahl) Børgesen										+	+
	<i>Acrocystis nana</i> Zanardini										+	
	<i>Bostrychia tenella</i> (Lamouroux) J. Agardh										+	+
	<i>Laurencia brongniartii</i> J. Agardh										+	
	<i>Laurencia intermedia</i> Yamada										+	
	<i>Laurencia okamurae</i> Yamada										+	
	<i>Laurencia pinnata</i> Yamada		+			+						
	<i>Laurencia papillosa</i> (C. Agardh) Greville		+	+	+	+	+	+	+	+	+	+
<i>Melanamansia glomerata</i> (C. Agardh) Norris		+										

¹Spr, spring; Sum, summer; Aut, autumn; Win, winter.

weight biomass showed seasonal ($F_{3,87} = 81.26$, $p < 0.0001$) (winter > spring > summer > autumn) and year ($F_{2,87} = 59.18$, $p < 0.0001$) (2003 > 2002 > 2001) variations, and the interaction of year and season was significant ($F_{6,87} = 7.94$, $p < 0.0001$) (Figure 4 and Table 3). Macroalgal biomass increased gradually as time advanced and peaked in January 2003 while macroalgal % cover only showed a drop, with cover < 50% in April 2001, May 2002, and September 2003.

Macroalgal assemblage structure

The univariate indices—the Shannon-Wiener species diversity index, the H' and evenness, and Pielou's J' —showed significant temporal variations that H' values had

year-over-year variations (Friedman's test, $F_{2,87} = 3.15$, $p = 0.0491$) while J' values showed seasonal variations ($F_{3,87} = 4.83$, $p = 0.0042$) (Figure 4 and Table 3).

Based on the value of each block, the results from cluster analysis and MDS ordination analysis of species areal wet weight (without data transformation) using the Bray Curtis similarity measures showed that three groups were discerned to correspond to 2001, 2002, and 2003 groups (Figure 5A and B). The k -dominance curves showed that species diversity was lower in 2002 and 2003 as compared to 2001 (Figure 5C), and this is mainly due to the high abundance of the rhodophyte *Gracilaria coronopifolia* and *Ceratodictyon/Haliclona* association in 2001 (Figure 6).

Table 3. Friedman test for macroalgal abundance, H' , and J' .

	F	p	Tukey's test ¹
Wet weight biomass			
Season	9.48	<0.0001	Win ^{2a} > Sum ^{ab} > Spr ^{bc} > Aut ^c
Year	19.84	<0.0001	2003 ^a > 2002 ^b > 2001 ^c
Season*Year	3.34	0.0093	
Dry weight biomass			
Season	9.83	<0.0001	Win ^a > Spr ^{ab} > Sum ^{bc} > Aut ^c
Year	59.18	<0.0001	2003 ^a > 2002 ^b > 2001 ^c
Season*Year	7.94	<0.0001	
% Cover			
Season	10.35	<0.0001	Win ^a =Sum ^a > Aut ^{ab} > Spr ^b
Year	4.22	0.0189	2003 ^a > 2002 ^b > 2001 ^c
Season*Year	4.43	0.0015	
Species number			
Season	7.27	0.0003	Win ^a > Spr ^{ab} > Sum ^b =Aut ^b
Year	11.26	<0.0001	2002 ^a > 2001 ^b =2003 ^b
Season*Year	5.33	0.0004	
H'			
Season	0.85	0.4696	
Year	3.15	0.0491	2002 ^a > 2001 ^{ab} =2003 ^{ab}
Season*Year	4.15	0.0024	
J'			
Season	0.57	0.5691	
Year	4.83	0.0042	2002 ^a > 2001 ^b =2003 ^b
Season*Year	5.45	0.0003	

¹Different symbol indicates significance at $p < 0.05$; ²Spr, spring; Sum, summer; Aut, autumn; Win, winter.

Table 4. Two-way ANOSIM of macroalgal assemblage.

	R statistic	Significance level	Permutation
Year	0.569	0.001**	999
2001-2002	0.603	0.001**	999
2001-2003	0.908	0.001**	999
2002-2003	0.532	0.001**	999
Season	0.495	0.001**	999
Spring-Summer	0.451	0.001**	999
Spring-Autumn	0.589	0.002**	999
Spring-Winter	0.581	0.001**	999
Summer-Autumn	0.556	0.007**	999
Summer-Winter	0.411	0.001**	999
Autumn-Winter	0.440	0.001**	999

** $p < 0.01$.

Macroalgal assemblage is primarily structured by year (group 2001, group 2002, and group 2003) and secondarily by season. A two-way cross ANOSIM test showed that macroalgal assemblage was yearly ($R = 0.569$, $p = 0.001$) and seasonally ($R = 0.469$, $p = 0.001$) significant (Table 4). The SIMPER analysis of species contributing to year-over-year difference showed that the species responsible for differences in structures between years was *Gracilaria coronopifolia*, the *Ceratodictyon/Haliclona* association, *Gracilaria* sp., *Gracilaria euchemoides*, and *Hypnea charoides* (Table 5). *Gracilaria coronopifolia* and *Ceratodictyon/Haliclona* association were the main species corresponding to the difference in macroalgal assemblage structure between 2001 and 2002, between 2001 and 2003, and also between 2002 and 2003. *Gracilaria coronopifolia* biomass increased gradually from a low level in 2001 (areal wet weight was 159.36 g w. wt./m²) to 786.39 g w. wt./m² in 2002 and further to 1577.83 g w. wt./m² in 2003 (Figure 6 and Table 5). The red alga/sponge *Galaxaura oblongata* showed a

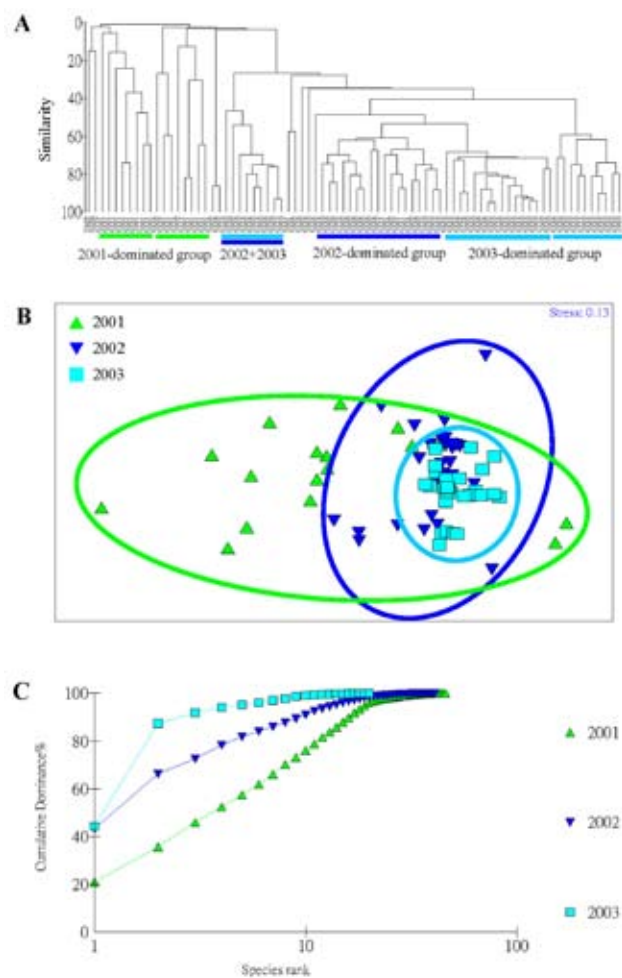


Figure 5. Clustering group (A), multidimensional scaling (MDS) ordination (B) and k -dominance curve (C) of samples taken on each sampling time during 2001-2003.

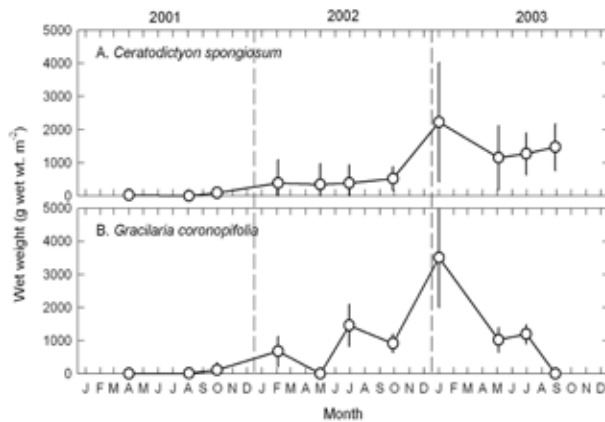


Figure 6. Temporal variations in areal wet weight of dominant algae during 2001-2003. Data are present as mean \pm SD (n=8).

similar pattern in that the biomass increased from 2.82 g w. wt./m² in 2001 to 421.02 and 1536.73 g w. wt./m² in 2002 and 2003, respectively (Figure 6 and Table 5). The biomass of *Hypnea charoides* showed an approximately 4-fold increase in 2002 over 2001 (Table 5). In contrast, the biomass of *Gracilaria eucheumoides* disappeared in 2002 (Table 5). Shown in table 5, the SIMPER analysis of species contributing to seasonal difference revealed that *Gracilaria coronopifolia* and the *Ceratodictyon/Haliclona* association, the most important species separating winter assemblages and other assemblages in spring, summer, and autumn, was abundant in winter with 2088.55 and 1305.87g w. wt./m², respectively.

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 eleven environmental variables (mean monthly air temperature, mean monthly maximum air temperature, mean monthly minimum air temperature, monthly cumulative irradiance, monthly cumulative precipitation, seawater temperature, salinity, and DIN, NO₃⁻+NO₂⁻, NH₄⁺, and SRP concentrations) producing the largest matches of changes in macroalgal structure and environmental variables over 2001-2003. SRP and salinity were the best variable combination responsible for year variations in macroalgal assemblage, its Spearman rank correlation (ρ) was 0.484 (Table 6). The best combination of environmental variables producing the largest matches of seasonal changes in macroalgal structure and environment variables in each year was also analyzed. As can be seen in Table 6, temperature, irradiance, and precipitation were the factors determining the seasonality in 2001 and 2003 while seasonal variations in species structure in 2002 were attributable to variations in NH₄⁺ concentrations and salinity.

DISCUSSION

Temporal variations in macroalgal assemblage compositions in Du-Lang Bay have been monitored in 2001-2003. Sixty-six species have been identified, in which erect algae were more abundant than encrusting and turf algae. The red alga *Gracilaria coronopifolia* and the *Ceratodictyon/Haliclona* association are the dominant algae, with yearly biomass advances which peaked in 2003. Total macroalgal wet weight and dry weight biomass also increased as time advanced due to the blooms of the *Ceratodictyon/Haliclona* association and *Gracilaria coronopifolia*.

The macroalgal assemblage structure showed year-over-year variation. *k*-Dominance curve analysis demonstrates a continuous decrease in species diversity from 2001 to 2003, and also shows a shift of macroalgal assemblage compositions after 2001, in which the 2001 assemblage with less abundant *Ceratodictyon/Haliclona* and *Gracilaria coronopifolia* changes to a assemblage dominated by them in 2002/2003. The shift of macroalgal assemblage structure from 2001 to 2002 is also reflected by decreased *Gracilaria eucheumoides* abundance in 2002. The blooms of *Gracilaria coronopifolia* and identified *Gracilaria* species were accompanied by reduction in *Gracilaria eucheumoides*. *Gracilaria coronopifolia* and an identified *Gracilaria* species seem to compete with it. After 2002, the dominance of *Ceratodictyon/Haliclona* and *Gracilaria coronopifolia* further increased and caused a shift of macroalgal compositions to an assemblage of low diversity in 2003. MDS analysis confirms this change in the macroalgal community, in which 2003 samples in the MDS plot were closer to each other than to those of 2002, and samples in 2002 were closer to each other than to those of 2001.

Low DIN/SRP ratios in 2001 and then increasing DIN/SRP ratios as time advanced indicate N limitation during 2001 and P limitation during 2002 and 2003 in Du-Lang Bay. The type and severity of nutrient limitation vary among habitats, species, and time (Lapointe, 1987; Lapointe et al., 1987). In a nearshore coral reef in the southern tip of Taiwan (Nanwan Bay), the growth of *G. coronopifolia* was P-limited as indicated by decreased tissue P contents, a marked drop in tissue P contents below the subsistence level, and increased alkaline phosphatase activity in mid-September and December 1999 (Tsai et al., 2005). The P-limitation of macroalgal productivity was also demonstrated by Lapointe (1997) on carbonate-rich reefs in Discovery Bay, Jamaica, that are enriched by nitrate in the submarine groundwater. However, Lapointe (1997) found that macroalgae were more N-limited on the siliclastic reefs of southeast Florida, where the water column was more enriched in soluble reactive phosphorus (SRP). The data from the comparison of water-column inorganic nitrogen:phosphorus (N:P) ratios to algal tissue N:P ratios and the results of nutrient enrichment experiments also indicate that the productivity of algae

Table 5. Result of SIMPER test on percentage contributions of species.

Species	Mean abundance (g wet wt./m ²)		Contribution (%)	Cumulative contribution (%)
A. between years				
	2001	2002		
<i>Gracilaria coronopifolia</i>	159.36	786.39	28.80	28.80
<i>Ceratodictyon spongiosum</i>	2.82	421.02	14.86	43.66
<i>Gracilaria</i> sp.	0	114.92	8.19	51.85
<i>Gracilaria euclideanoides</i>	298.31	0	5.72	57.57
<i>Hypnea charoides</i>	26.86	104.08	4.59	62.16
	2001	2003		
<i>Ceratodictyon spongiosum</i>	2.82	1536.73	37.51	37.51
<i>Gracilaria coronopifolia</i>	159.36	1577.83	30.85	68.36
	2002	2003		
<i>Ceratodictyon spongiosum</i>	421.02	1536.73	37.48	37.48
<i>Gracilaria coronopifolia</i>	786.39	1577.83	32.45	69.93
Species	Mean abundance		Contribution (%)	Cumulative
B. between seasons				
	Spr ¹	Sum		
<i>Gracilaria coronopifolia</i>	480.55	888.74	26.39	26.39
<i>Ceratodictyon spongiosum</i>	704.15	553.59	23.84	50.23
<i>Gracilaria</i> sp.	209.56	0	7.59	57.81
<i>Gracilaria euclideanoides</i>	0	223.73	7.53	65.34
	Spr	Aut		
<i>Ceratodictyon spongiosum</i>	704.15	548.43	31.99	31.99
<i>Gracilaria coronopifolia</i>	480.55	480.36	24.99	56.99
<i>Gracilaria</i> sp.	209.56	0	9.89	66.88
	Spr	Win		
<i>Gracilaria coronopifolia</i>	480.55	2088.55	38.37	38.37
<i>Ceratodictyon spongiosum</i>	704.15	1305.87	27.12	65.48
<i>Gracilaria</i> sp.	209.56	0	6.22	71.71
	Sum	Aut		
<i>Gracilaria coronopifolia</i>	888.74	480.36	28.60	28.60
<i>Ceratodictyon spongiosum</i>	553.59	548.43	26.04	54.64
<i>Gracilaria euclideanoides</i>	223.73	0	8.44	63.08
	Sum	Win		
<i>Gracilaria coronopifolia</i>	888.74	2088.55	34.91	34.91
<i>Ceratodictyon spongiosum</i>	553.59	1305.87	26.27	61.18
<i>Gracilaria euclideanoides</i>	223.73	0	6.05	67.23
	Aut	Win		
<i>Gracilaria coronopifolia</i>	480.36	2088.55	40.28	40.28
<i>Ceratodictyon spongiosum</i>	548.43	1305.87	30.14	70.43

¹Spr, spring; Sum, summer; Aut, autumn; Win, winter.

Table 6. The best combinations of 11 environmental variables producing the largest matches of changes in macroalgal assemblages and environmental variables over 2001-2003. Environmental variables are monthly mean temperature, monthly maximum temperature, monthly minimum temperature, monthly cumulative irradiance, monthly cumulative precipitation, seawater temperature, salinity, DIN, SRP, $\text{NO}_3^- + \text{NO}_2^-$, and NH_4^+ .

Number of variable	Spearman rank correlation (ρ)	Best variable combination
A. 2001-2003		
2	0.484	SRP, Salinity
B. each year		
2001		
2	0.757	Seawater temperature, Monthly cumulative irradiance
1	0.701	Monthly minimum temperature
2002		
2	0.295	NH_4^+ , Salinity
1	0.288	Monthly maximum temperature
2003		
3	0.451	Seawater temperature, Monthly cumulative precipitation, Monthly cumulative irradiance
1	0.440	Monthly maximum temperature
1	0.419	Seawater temperature

in Kaneohe Bay, Hawaii is limited by N instead of P (Larned, 1998). Evidently, the type and severity of nutrient limitation are variable among habitats, species, and time (Lapointe, 1987; Lapointe et al., 1987). It is clear that the nutrient status in the nearshore reefs of Du-Lang Bay in Taitung shifts over the 2001-2003 period, with a change toward P limitation after 2001.

Nutrients are linked to the temporal variations in macroalgal abundance and assemblage structure. Because *Gracilaria* is known as the species that could accumulate high N and P reserves in response to high nutrient environments (DeBoer et al., 1978; Costanzo et al., 2000), the blooming of *Gracilaria coronopifolia* in Du-Lang Bay can be considered a sign of eutrophication. Although algal blooms on coral reefs are associated with enhanced nutrient availability (Bell, 1992; Tsai et al., 2004; Hwang et al., 2004; Tsai et al., 2005), the productivity of macroalgae on coral reefs is still limited by nitrogen (N) and/or phosphorus (P) (Lapointe, 1987; Lapointe et al., 1987; Littler et al., 1991; Lapointe, 1997; Larned, 1998). Our previous study using a continuous flow-through outdoor laboratory tank culture system showed that the nutrient threshold for the maximum growth of *Gracilaria coronopifolia* is 16/8/1.2 μM $\text{NO}_3^-/\text{NH}_4^+/\text{PO}_4^{3-}$ (Tsai et al., 2005). The seawater nutrient concentrations were below the threshold. It is therefore clear that the growth of *Gracilaria coronopifolia* was still under nutrient limitation. If nutrient concentrations increase further, the biomass of *Gracilaria coronopifolia* will increase. The type and

severity of nutrient limitation still need to be determined.

A positive correlation between *Ceratodictyon/Haliclona* biomass and decreased SRP concentrations suggests that the blooms of *Ceratodictyon/Haliclona* are associated with decreased P availability. By tracing the stable isotope of ^{15}N and feeding experiments, it is proposed that N sources from grazing on ultraplankton by the sponge partner of *Ceratodictyon/Haliclona* symbioses (Pile et al., 2003) and subsequent waste ammonium excretion to the rhodophyte partner (Davy et al., 2002) are essential for the growth of *Ceratodictyon* in the nutrient-poor waters of the Great Barrier Reef. However, a positive correlation of *Ceratodictyon/Haliclona* biomass with seawater DIN concentrations reflects that the blooming of *Ceratodictyon/Haliclona* in Du-Lang Bay might not be due to the need to meet the N requirement of an algal partner. We propose that the association of *Ceratodictyon* with *Haliclona* enables the alga to obtain P from *Haliclona* under P-limited conditions (2002 and 2003). However, the role of P status on regulating the growth of the *Ceratodictyon/Haliclona* association needs further work. A study carried out in One Tree Lagoon in the southern Great Barrier Reef of Australia has shown that *Ceratodictyon/Haliclona* is absent in regions that lack hard substrata for attachment of propagules or fragments (Trautman et al., 2000, 2003). The habitats in the present study site are changing.

Ecosystems in coastal areas of islands around Taiwan have faced threats in the past ten years. We observed the release of significant urban sewage wastes into this studied

reef in 2001. The sampling site in this study is shallow, 1-3 m deep, which explains why the salinities in the upper regions of the subtidal reef at the study site (1-3 m depth) are low in 2001, and the concentrations of nutrient, especially P, are high in 2001. However, we observed that the release of urban sewage was reduced after June 2002, allowing the salinities to recover. Because salinity is known to affect macroalgal growth, one could expect a shift of salinity to influence macroalgal compositions and their growth in the studied reef in southeastern Taiwan.

The effects of salinity on macroalgal growth have been documented in many studies (Dawes et al., 1998; Israel et al., 1999; Eriksson and Bergstrom, 2005; 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. This work shows an increase of both *Gracilaria coronopifolia* and *Ceratodictyon/Haliclona* biomass after salinity increased to normal levels (35 psu) in 2002 and 2003, and this suggests that the growth of both species might be inhibited under low salinity conditions. The growth of *Gracilaria* spp. (Gracilariales, Rhodophyta) from Japan, Malaysia, and India was optimal at a normal seawater salinity, 35 psu (Raikar et al., 2001). Possibly the growth of *Gracilaria coronopifolia* at the reef in Du-Lang Bay was restricted by low salinities in 2001. However, as we know, the responses of *Ceratodictyon/Haliclona* to salinity fluctuations have not been reported, and its response to decreasing salinity is unclear.

Present evidence has suggested that temperature was a primary factor influencing the seasonal variations of the macroalgal assemblage structure in both 2001 and 2003. Temperature has been recognized as principal ecological factor affecting macroalgal growth and morphology, geographical distribution, and seasonal changes in growth pattern (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 have shown that seawater temperature is pivotal in the seasonality of benthic algae in tropical waters (Conover, 1964; Earle, 1969). Temperature has also been found to influence the seasonality in vegetation growth and reproduction of *Sargassum* in Hawaii (De Wreede, 1976) and the British Isles (Jephson and Gray, 1977). In Currimao, Ilocos Norte, in the northern Philippines, slight seasonal variations of seawater temperature were positively correlated with the 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). Laboratory and field experiments from those studies also showed that the seasonal abundance of *Gracilaria coronopifolia* from southern Taiwan was determined by seasonal variations in seawater temperatures and nutrient concentrations as well as by 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 remains unclear.

In conclusion, this study indicates that the nearshore macroalgal assemblage in Du-Lang Bay in southeastern Taiwan is structured primarily by year and secondarily by season and the blooms of *Ceratodictyon/Haliclona* and *Gracilaria coronopifolia* in 2002-2003 contribute to year-over-year variations of the algal assemblage structure. Nutrients and salinity are the factors governing the year-over-year variations in the structure and abundance of tropical benthic macroalgal assemblages in southeastern Taiwan. Temperature is a factor influencing seasonality. To provide the proper management of benthic communities on coral reefs in southeastern Taiwan, it will be necessary to ascertain the relative importance of abiotic and biotic (such as herbivores) factors affecting the growth of macroalgae.

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營養鹽、溫度及鹽度是影響東南台灣之台東都蘭灣大型海藻豐度及群聚時間變化的重要因子

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本研究進行位於東南台灣之台東都蘭灣大型海藻豐度及群聚時間（2001-2003）變化與環境因子關係的調查重要因子。共紀錄 66 種海藻，紅藻為優勢種類。藻類單位面積濕重及乾重隨時間增加而增加，於 2003 年冬季達最高值，主要是因為傘房龍須菜（*Gracilaria coronpifolia*）及紅藻與海綿共生之角網藻（*Ceratodictyon/Haliclona*）大量生長所致。藻類單位面積覆蓋率隨時間而明顯變異，2001 及 2002 年在春季低而夏季高，2003 年則在秋季低而在冬、春及夏季高。種類數豐度、歧異度（ H' ）及均勻度（ J' ）隨時間增加而增加，於 2001 年底的冬季達最高值後於 2002 年保持不變，2003 年下降。不同取樣時間種類相似度之群集分析及無母數多變量向量分析與 ANOSIM（analysis of similarity）分析指出都蘭灣大型海藻群聚主要因年而分群，次為受季節影響而分群，所以海藻群聚在 2001 至 2003 年間有極大之變動。雖然 H' 及 J' 無明顯隨時間增加而增加或減少的趨勢， k -Dominance curve 結果及隨時間增加而降低之種類數則指出台東都蘭灣大型海藻種類結構由 2001 年較高歧異度逐漸轉為 2003 年較低歧異度之群聚。Similarity percentage breakdown procedure (SIMPER) 分析證明傘房龍須菜及角網藻是造成群聚年與季節變動的主要海藻種類。群聚與環境因子的比較分析指出可溶性無機磷（soluble-reactive phosphorus; SRP）濃度降低及鹽度升高群聚年變動的主因而影響群聚季節變動的主因則為溫度、降雨、鹽度、及氨態氮。本研究結果指出東南台灣之台東都蘭灣大型海藻群聚之時間（2001-2003）變化不但受隨時間增加而增加之 N/P 營養鹽比率及增高之鹽度而有年度變動，也受到季節性溫度及降雨變動而有季節性變動，其群聚結構由 2001 年較高歧異度逐漸轉為 2003 年較低歧異度狀態。

關鍵詞：群聚；大型海藻；營養鹽；鹽度；溫度；時間變異。