

Temporal Dynamics of Rocky-shore Macroalgal Assemblage Structures in Relation to Coastal Construction Threats in Orchard Island (Taiwan): Impacts of turbidity and nutrients on the blooms of *Galaxaura oblongata* and a red alga-sponge symbiose *Ceratodictyon/Haliclona*

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Abstract

Ecosystems in coastal areas of islands around Taiwan have faced construction threats in the past 10 years. A study was conducted from 2001-2004 to monitor the effects of disturbances on macroalgal assemblage structures on a nearshore rocky reef in Orchard Island (off southeastern Taiwan), where seashore road and jetty construction took place during 2002-2003. Outdoor laboratory experiments were used to confirm the factors responsible for changes of macroalgal compositions. Macroalgal cover and biomass increased markedly in 2002-2003 mainly due to the blooms of a red alga-sponge symbiose *Ceratodictyon/Haliclona* and a calcified rhodophyte *Galaxaura oblongata*. Hierarchical cluster analysis and non-metric multidimensional scaling ordination analysis of species similarities between different sampling times showed there are 3 clusters corresponding to 2001, 2002/2003, and 2004. The results of ANOSIM tests showed that species structure was different not only from year to year but also between seasons, and the results of SIMPER analysis showed that the blooms of *G. oblongata* and *Ceratodictyon/Haliclona* in 2002 and 2003, the decline of *Halimeda opuntia* in 2002-2004, and the appearance of *Amphiroa fragilissima* and *Gelidiopsis repens* in 2004 contribute to annual differences. Stepwise regression analysis indicates that temporal variations of *Ceratodictyon/Haliclona* biomass is negatively related to monthly maximum temperature and soluble-reactive phosphorus (SRP) concentrations but positively related to turbidity and DIN concentrations, while *Galaxaura oblongata* biomass is positively related to turbidity but negatively related to monthly minimum temperature and monthly cumulative precipitation. *Halimeda opuntia* biomass is negatively correlated with monthly maximum temperature but showed a positive relation to salinity and SRP concentrations. The comparison of macroalgal compositions with environmental variables shows that turbidity and SRP are the best combination of environment variables to explain the yearly changes in algal compositions. The data from outdoors laboratory culture experiments suggest that low SRP/high dissolved nitrogen (DIN) concentrations and reduced irradiance are the factors which led to the blooms of both *Ceratodictyon/Haliclona* and *Galaxaura oblongata* in 2002-2003. In conclusion, the coastal construction threats are reflected in increasing turbidity and high nitrogen/low phosphate loading, which result in the blooms of *Ceratodictyon/Haliclona* and *Galaxaura oblongata* and in turn, the modification of macroalgal assemblage structures around Orchard Island off southeastern Taiwan.

Keywords: assemblage, coastal construction, macroalgae, phosphate, seasonality, turbidity

Introduction

Coastal construction is known to seriously disturb Pacific coral reefs, in which turbidity and sediment

loads increase, thus in turn reducing light availability (Anthony and Fabricus 2000). Increasing sediment deposition effects on the distribution and diversity of macroalgal assemblage (Robles 1982, D'Antonio 1986,

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Santos 1993). In South Australia, the expansive covers of turf-forming algae on rocky shores have been shown to be associated with increased sediment loads together with high nutrient levels (Gorgula and Connell 2004). However, the effects of sediment on algal communities are controversial, for example algal diversity can be either decreased (Little and Smith 1980, Engledow and Bolton 1994) or increased (Littler *et al.* 1983, Airoidi and Cinelli 1997) by elevated sediment deposition and movement. Nutrient regenerated from sediments beneath thalli has an impact on the annual growth pattern of the green alga *Dictyosphaeria cavernosa* (Forskål) Børgesen from Kaneohe Bay, Hawaii (Stimson *et al.* 1996). Nutrient enrichment has been considered a factor leading to algal blooms. In the mid 1970s, studies on coral reefs in Kaneohe Bay, Hawaii 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 were studied worldwide, in such places as the coastal waters at Reunion Island, in the Indian Ocean (Cuet *et al.* 1988), the Caribbean and Florida regions (Lapointe and O'Connell 1989, Bell 1992, Lapointe *et al.* 1994), and southern Taiwan (Tsai *et al.* 2004, Hwang *et al.* 2004).

Coastal regions along Orchard Island (Fig. 1),



Fig. 1 The map of the sampling site

located 65 Km off the southeastern coast of Taiwan where the Kuroshio Current passes northward year round, faced increasing construction as well as tourism pressure over the past 10 years. Because seaweeds tend to integrate the effects of long-term exposure to adverse conditions, macroalgal assemblages are widely used to characterize and monitor benthic communities. Therefore, a 4-year quantitative investigation on the influence of natural and anthropogenic disturbances on

macroalgal abundance and species compositions along the coastal line of Orchard Island was conducted on a nearshore reef (GPS: 22°03'43''N; 121°33'92''E) at Dungching Bay in Orchard Island, where seashore road and jetty construction took place during 2002-2003. Our qualitative observations have shown that these activities not only affected coastal habitats (small rocks) but also altered water quality, increasing turbidity for example. The 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. 5 (Clarke and Warwick 1994). The comparison of temporal variations in macroalgal structure and environmental factors by BVSTEP analysis was made to extract the factors showing the best combination of environment variables to algal compositions. By using the similarity percentage breakdown procedure, SIMPER, the macroalgal species responsible for the difference in macroalgal assemblage structure from year to year were found to be the dominant species including a calcified rhodophyte *Galaxaura oblongata*, a red alga-sponge symbiose *Ceratodictyon/Haliclona*, and a calcified chlorophyte *Halimeda opuntia*. To identify the impact of these environmental factors on macroalgal assemblage structure, the growth responses of dominant algae to these variables were determined by use of an outdoor laboratory tank culture system. Stepwise regression analysis was used to determine the best multiple regression model to correlate the association of the areal wet weight biomass of *Ceratodictyon/Haliclona*, *Halimeda opuntia*, and *Galaxaura oblongata* with environmental parameters.

1. Materials and Methods

1) Study site and environmental characteristics

The study site has a horizontal width of 570 m with an intertidal region, approximately 5-35 m long and a subtidal macroalgal region, approximately 11-18 m long with a depth of 0-6 m (below MHWS) on a seaward gradient.

30-year climate records (1971-2000) 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 lowest (21.0°C) in January and highest (24.8°C) in July (Fig. 2). The annual mean relative humidity is 75% and the annual cumulative precipitation is 3081.3 mm which occurs mostly from May-September. Typhoons usually

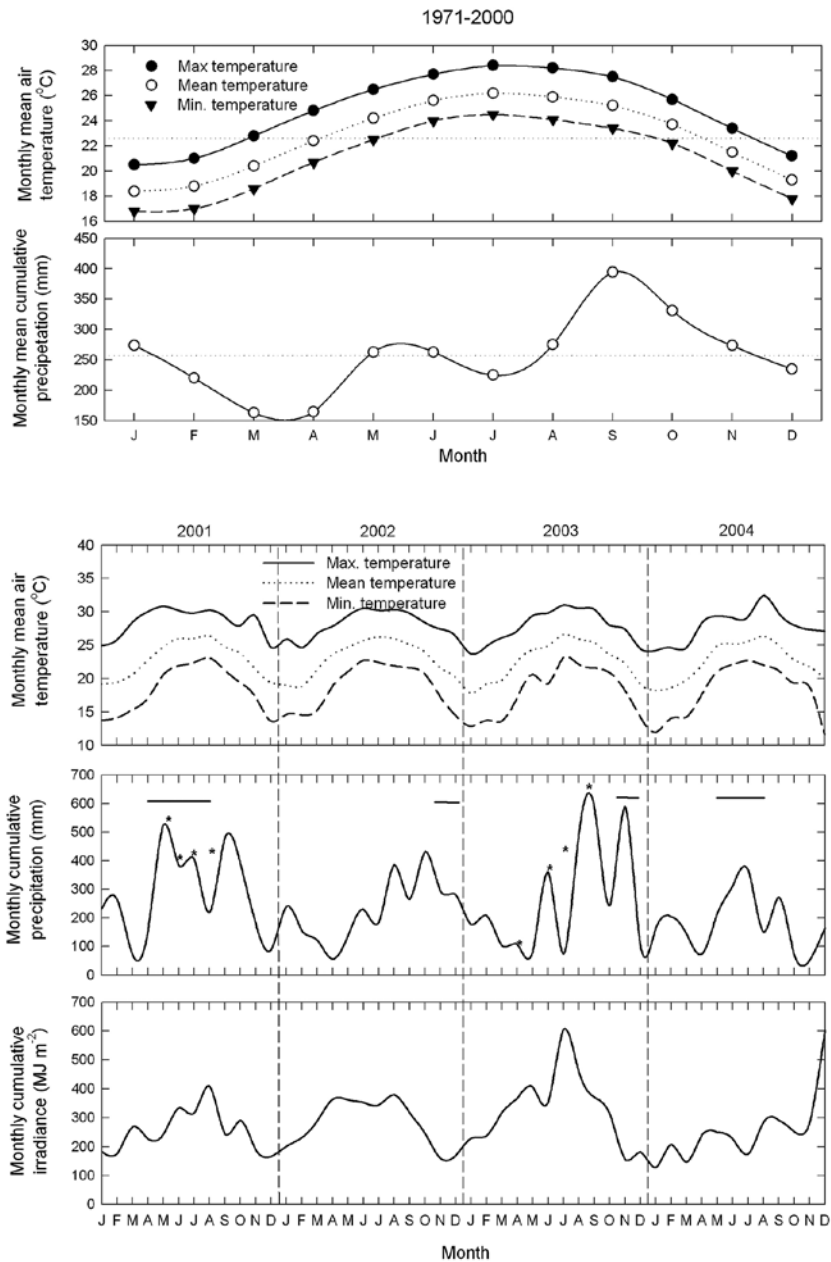


Fig. 2 Climate data for Orchard Island from 1971-2000 and during the survey (2001- 2004)

occur in May-September and the prevailing northeasterly winds occur in November-February.

During the surveys (2001-2004), mean monthly air temperature was 22.9°C, annual precipitation was 3097.0 mm and annual cumulative irradiance was 3391.0 MJ/m² (Fig. 2). Temporal variations in mean monthly air temperature, mean monthly maximum air temperature, mean monthly minimum air temperature, annual cumulative precipitation, and annual cumulative irradiance were significant (Friedman's test, $p < 0.001$); no difference between years was found for these climate parameters except irradiance which was highest in 2003. Precipitation not only showed significant seasonality

with low values in winter and high values in spring-autumn but also exhibited annual differences, and was low in 2002 in contrast to 2001 and 2003. There were 4, 4, and 2 typhoons passing Orchard Island in 2001, 2003, and 2004, respectively, while no typhoons occurred in 2002.

2) 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) at 10-m intervals were set in the subtidal regions with 1-3 m water depth (MHS) and at each

block, 4 random stations were set up 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, and total macroalgal cover was calculated as the sum of all species cover. 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 are 4 quadrats in each block with each quadrat acting as a replicated sample) was scraped for the estimation of macroalgal compositions and biomass, and species identification was determined using a microscope. Temporal changes in macroalgal cover and biomass were determined in April, August, October of 2001, February, May, July and October of 2002, February, May, July and September of 2003, and February, July, and September of 2004 for the analysis of both annual and seasonal (February as winter, April-May as spring, July-August as summer, and October-September as autumn) changes in macroalgal assemblage structure and its relationships to environmental variables.

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

Environmental factors including seawater turbidity (Nephelometric Turbidity Units (NTU) used as a surrogate measurement of suspended sediments), seawater temperature, salinity, and seawater nutrient concentrations were determined randomly at 4 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 and 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 *et al.* (1962). Colour reagent was prepared by mixing 1 ml of 3% ammonium molybdate solution and 0.75 ml of 5 N H₂SO₄ 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 were 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 Hitachi spectrophotometer (model U-2000, Hitachi, Tokyo, Japan). The detection limit of SRP concentration was 0.02 µM.

Seawater NO₂⁻ and NO₃⁻ concentrations were deter-

mined according to Strickland and Parsons (1972) and NH₄⁺ concentrations were determined according to Parsons *et al.* (1984). The detection limits for seawater NO₂⁻, NO₃⁻ and NH₄⁺ concentrations were 0.2, 0.2 and 0.3 µM, respectively. The NO₃⁻, NO₂⁻, and NH₄⁺ concentrations were summed as the concentration of dissolved inorganic nitrogen (DIN).

For the determination of tissue N and P contents, dried thalli were ground to powder and a powder sample of 5 mg dry weight (d. wt.) was put in a 10 ml test tube, then 0.05 g of catalyst A (HgO : K₂SO₄=1 : 20 (w/w)) and 0.025 g of catalyst B (Na₂S₂O₃) were added. After the addition of 1 ml conc. H₂SO₄ containing 5% salicylic acid, thallus samples together with catalysts were digested at high temperature (400°C). When the solution became clear, the digested samples were cooled at room temperature and volume was increased to 5 ml with distilled H₂O. Tissue N and P contents were detected by color development of H₂SO₄-digested samples in the dark according to Smith (1980) (phenol-nitroprusside method) and Lanzetta *et al.* (1979), respectively. Tissue C contents were determined by the titrimetric dichromate redox method (Tiessen and Moir 1993). Algal tissue C and N contents were confirmed by elemental analyzer analysis (Perkin-Elmer 2400 (II) CHN analyzer). Algal tissue nutrient contents were expressed as the percentage (%) of g d. wt.

4) Outdoor laboratory culture of *Galaxaura oblongata* in continuous flow seawater tanks

A continuous-flow culture was used for determining the interaction of light, nutrient, and temperature on the growth of *Galaxaura oblongata*. The plants of *Galaxaura oblongata* were sampled in June 2005 from the study site and transferred to our laboratory in National Sun Yat-sen University at Kaohsiung for a 7-day incubation period in a 60-l outdoor polyethylene tank containing 50 l seawater aerated by air. After the 7-day incubation period for the recovery from wounding, healthy thalli of 1 g wet weight were cultured in a 1000-ml glass culture flask which was fitted with a tube for aeration with a flow rate of 20 ml/min and 2 tubes for inflowing and outflowing culture seawater, which was pumped from a 60-l polyethylene tank (nutrient tank) to the culture flask at a speed of 5 ml/min with a peristaltic pump. Seawater used in the laboratory culture was collected from Nanwan Bay in southern Taiwan at 4-5 m depth and 20 km offshore. The nutrient concentrations of seawater were determined to ensure seawater used in this study has low DIN (< 0.1 µM) and SRP (< 0.01 µM) concentrations.

Because high turbidity will reduce light availability,

glass culture flasks were shaded to obtain low (270-290 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ detected between am 10:00-pm 2:00 in June 2002) and high (853-1050 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ detected between am 10:00-pm 2:00 June 2004) light intensities on the surface of these two rhodophytes in the field. According to the present investigation, there were two nutrient states, low N/high P and high N/low P. Therefore, two nutrient combinations, 0.4 μM HN_4Cl and 1 μM K_2HPO_4 (low N/high P) and 4 μM HN_4Cl and 0.1 μM K_2HPO_4 (high N/low P), were used for each light intensity. To test growth responses to seasonal temperature variations, five temperatures (15, 20, 25, 30, and 35°C) were employed for each nutrient combination. Overall, there were 20 treatments for the combination of light, nutrient and temperature. For each combination, six flasks were linked to a nutrient tank and 5 replication flasks were randomly sampled from a nutrient tank and their averaged value was taken as the value of each treatment. The seawater nutrient concentrations in the flasks were determined daily for adjusting the nutrient concentrations during the culture period. Temperatures in the nutrient tank were controlled by heater and cooler for adjusted differential growth temperatures. In this study, 3 replication nutrient tanks were used for each treatment. Algal wet weight (w. wt.) was determined both at the start and after 16 days of incubation for the calculation of daily specific growth rate (%/d): $(w. wt._{16} - w. wt._0) / w. wt._0 / 16 \times 100\%$ ($w. wt._0$ = wet weight at day 0, $w. wt._{16}$ = wet weight at day 16), and the data were shown as mean \pm standard error of mean (SEM, (n=3)).

5) Data analysis

Statistical evaluation was performed using the SAS statistical software package v 8.0 (SAS Ltd., NC, USA). With the exception of the growth rate (mean \pm standard error of mean (SEM)) of outdoor laboratory cultured *Galaxaura oblongata*, all summary statistics were expressed as mean and standard deviation (SD). The growth rate of *Galaxaura oblongata* in response to light, nutrient, and temperature treatments was tested by 3-way ANOVA. 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, seawater turbidity (NTU), temperature, salinity, and seawater nutrient concentrations) and 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, *Halimeda opuntia*, and *Galaxaura oblongata*) was analyzed by the Shapiro-Wilk W Test ($p > 0.05$).

DIN, areal total macroalgal wet weight, and dry weight fit normality following root square-transformation, while other parameters did not fit normality after data transformation. Root square-transformed DIN, root square-transformed total areal macroalgal wet weight, and root square-transformed total areal macroalgal dry weight were tested by two-way ANOVA with season and year as factors and then Tukey's test was used for multiple comparisons among means from significant ANOVA tests ($p < 0.05$) (Day and Quinn 1989). Other data which did not fit normality were subjected to nonparametrical tests by Kruskal-Wallis analysis and Friedman's test for one-way (temporal changes) and two-way (seasonal and annual changes) layout data, respectively (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 ($p > 0.05$), habitat was not considered a factor for statistical analysis and only temporal variations (year and season) were tested.

Multivariate analyses were used to compare the macroalgal assemblage compositions between stations and between seasons by the Plymouth Routines in the Multivariate Ecological Research (PRIMER) statistical software package (v. 5) (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 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 differences of macroalgal assemblage structure between seasons and between years were tested using ANOSIM (analysis of similarity) (Clarke and Warwick 1994), and the species mainly responsible for differences between years were determined by similarity percentage breakdown procedure, SIMPER (Clarke 1993). BVSTEP analysis was used to determine the environmental factors best explaining the observed patterns of macroalgal assemblage structures.

Stepwise regression analysis was used to determine the best multiple regression model to correlate the areal wet weight biomass of *Ceratodictyon/Haliclona* associa-

tion, *Halimeda opuntia*, and *Galaxaura oblongata* with environmental parameters. Parameters entered into the model for each sampling time were monthly mean air temperature, monthly maximum temperature, monthly minimum temperature, monthly cumulative irradiance, monthly cumulative precipitation, seawater turbidity, seawater temperature, salinity, seawater DIN, NO_2^- , NO_3^- and NH_4^+ concentrations, and seawater SRP concentrations. Seawater DIN concentrations were root-transformed (expressed as $\sqrt{\text{DIN}}$) and turbidity was arcsine-transformed to fit normality. Other data which did not show normality underwent $\log(x+1)$ -transformation prior to analysis when it was necessary to obtain a linear relationship between the variables. Significance was set at the 0.05 level.

2. Results

1) Environmental factors

Seawater temperature, salinity, and turbidity showed temporal variations (Kruskal-Wallis test, $p < 0.0001$). Mean seawater temperature and salinity during the surveys were $27.4 \pm 2.53^\circ\text{C}$ and 31.59 ± 5.25 psu, respectively (Fig. 3). Seawater temperature showed annual (Friedman's test, $p < 0.0001$) ($2003 > 2002 > 2001, 2004$) and seasonal ($p < 0.001$) (summer $>$ autumn $>$ spring $>$ winter) variations and significant annual and seasonal interaction ($F_{9,112} = 13.45$, $p < 0.0001$). Salinity showed seasonal variations (Friedman's test, $p = 0.0175$) (summer = autumn $>$ spring $>$ winter) but did not show annual ($p = 0.0893$) variations. Turbidity showed annual varia-

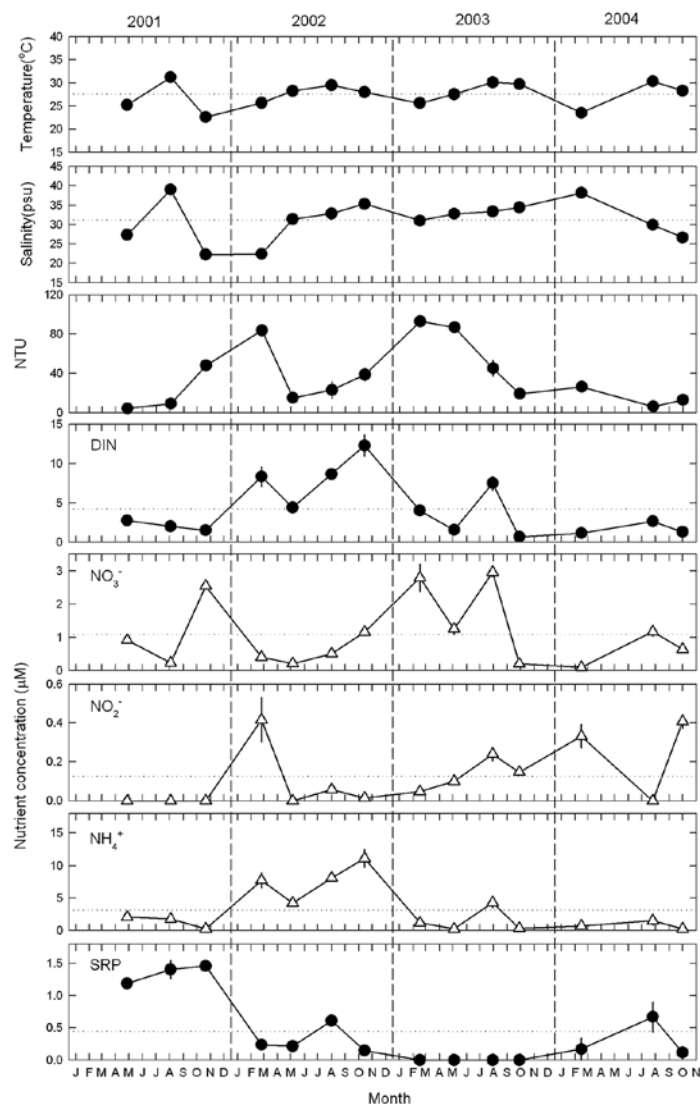


Fig. 3 Variations of seawater temperature, salinity, turbidity, and concentrations of DIN, NO_3^- , NO_2^- , NH_4^+ , and SRP from 2001-2004. Data are presented as mean \pm SD ($n=8$)

tions (Friedman's test, $p < 0.001$) (2002 = 2003 > 2001 = 2004) but did not show seasonal variations ($p = 0.5089$). When jetty and coastal road construction began in the winter of 2001, turbidity increased concomitantly and this increase continued until the autumn of 2003 (Fig. 3).

Mean DIN, NO_3^- , NO_2^- , NH_4^+ , and SRP concentrations during the survey were 4.91 ± 4.05 , 1.12 ± 1.06 , 0.09 ± 0.13 , 3.73 ± 4.03 , and 0.53 ± 0.59 μM , respectively (Fig. 3). DIN concentrations showed temporal variations (root square-transformed, ANOVA, $F_{14,112} = 57.73$, $p < 0.0001$) that were annually ($F_{3,112} = 26.92$, $p < 0.0001$) (2002 = 2003 > 2001 = 2004) and seasonally ($F_{3,112} = 8.75$, $p < 0.0001$) (summer > winter = autumn = spring) variable and the interaction of year and season was significant ($F_{9,112} = 17.07$, $p < 0.0001$). DIN concentrations were high in 2002 and 2003 (Fig. 3). NO_3^- and NH_4^+ concentrations during the survey also showed temporal variations (Kruskal-Wallis test, $p < 0.001$) but NO_2^- con-

centrations did not show temporal variations ($p = 0.0639$). NO_3^- concentrations had seasonal variations (Friedman's test, $p < 0.0001$) (summer = autumn > winter > spring) but did not have annual variations ($p = 0.132$). NH_4^+ concentrations showed both annual (Friedman's test, $p < 0.0001$) (2002 > 2001 = 2003 = 2004) and seasonal ($p < 0.0001$) (summer > winter > autumn > spring) variations. SRP concentrations only exhibited annual variations (Friedman's test, $p < 0.0001$) (2001 > 2004 > 2002 > 2003), in which SRP concentrations were high in 2001, then dropped gradually year by year, even dropping below the detection limit (0.2 μM) in 2003, and in 2004, recovering to levels similar to 2002.

2) Macroalgal abundance and assemblage structure

Eighty species were recorded during the surveys: 17 Chlorophyta, 9 Phaeophyta, and 54 Rhodophyta (Table 1). Because the data did not show habitat difference,

Table 1. Macroalgae recorded near Orchard Island near southeastern Taiwan during 2001-2004

Taxa	2001			2002			2003			2004				
	Apr	Aug	Oct	Feb	May	Jul	Oct	Feb	May	Jul	Sept	Feb	Jul	Sept
CHLOROPHYTA (species number)	2	3	4	6	5	2	3	6	2	5	3	4	0	2
<i>Ulothrix flacca</i> (Dillwyn) Thurer in Le Jolis				+										
<i>Ulva lactuca</i> Linnaeus												+		
<i>Anadymene wrightii</i> Harvey ex Gray				+	+			+						
<i>Valoniopsis pachynema</i> (Martens) Børgesen		+	+											
<i>Chaetomorpha linum</i> (Müller) Kützinger													+	
<i>Cladophora catenata</i> (Linnaeus) Kützinger										+				
<i>Cladophora fascicularis</i> (Mertens ex C. Agardh) Kützinger												+		
<i>Cladophora</i> sp.						+								
<i>Boergesenia forbesii</i> (Harvey) Feldmann				+										
<i>Cladophoropsis zollingeri</i> (Kützinger) Reinbold								+						
<i>Boodlea composita</i> (Harvey et Hooker) Brand				+				+		+				
<i>Caulerpa serrulata</i> v. <i>serrulata</i> f. <i>lata</i> (W.-v. Bosse) Tseng			+							+				
<i>Chlorodesmis caespitosa</i> J. Agardh	+	+	+		+	+		+		+		+		
<i>Chlorodesmis fastigiata</i> (C. Agardh) Ducker				+	+		+	+	+		+			
<i>Halimeda macroloba</i> Decaisne					+			+						
<i>Halimeda opuntia</i> (Linnaeus) Lamouroux	+	+	+	+	+		+	+	+	+	+	+		+
<i>Udotea orientalis</i> A. Gepp et E.S. Gepp														+
PHAEOPHYTA (species number)	0	2	3	4	3	2	1	1	1	2	0	2	0	0
<i>Ectocarpus confervoides</i> Le Jolis				+										
<i>Dictyopteris repens</i> (Okamura) Børgesen		+										+		
<i>Dictyota cervicornis</i> Kützinger			+	+										
<i>Lobophora variegata</i> (Lamouroux) Womersley				+										
<i>Padina australis</i> Hauck			+		+	+								
<i>Sargassum crassifolium</i> J. Agardh					+									
<i>Sargassum polycystum</i> C. Agardh										+				
<i>Turbinaria conoides</i> (Turner) J. Agardh					+	+	+					+		
<i>Turbinaria ornata</i> (Turner) J. Agardh		+	+	+				+	+	+				

Temporal dynamics of rocky-shore macroalgal assemblage structures

Taxa	2001			2002			2003			2004				
	Apr	Aug	Oct	Feb	May	Jul	Oct	Feb	May	Jul	Sept	Feb	Jul	Sept
RHODOPHYTA (species number)	5	13	17	18	9	4	12	8	5	6	10	9	9	15
<i>Dermonema virens</i> (J. Agardh) Pedroche & Vila Orth					+		+					+		
<i>Actinotrichia fragilis</i> (Forsskål) Børgesen				+		+								
<i>Galaxaura filamentosa</i> R. Chou in W.R. Taylor							+	+			+			
<i>Galaxaura marginata</i> (Ellis et Solander) Lamouroux	+	+	+		+									+
<i>Galaxaura oblongata</i> (Solander) Lamouroux	+			+	+	+	+	+	+	+	+			+
<i>Galaxaura obtusata</i> (Ellis and Solander) Lamouroux												+	+	
<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman et Townsend					+									
<i>Helminthocladia australia</i> Harvey		+	+											
<i>Gelidiella acerosa</i> (Forsskål) Feldmann et Hamel										+		+	+	+
<i>Gloiopeltis tenax</i> (Turner) Decaisne				+										
<i>Chondrus ocellatus</i> Holmes		+	+											
<i>Gigartinale tenella</i> Harvey				+										
<i>Grateloupia filicina</i> (Wulfen) C. Agardh		+	+	+			+							
<i>Halymenia floresia</i> (Clemente) C. Agardh												+		
<i>Hypnea cervicornis</i> J. Agardh					+									
<i>Hypnea charoides</i> Lamouroux							+	+					+	
<i>Hypnea japonica</i> Tanaka				+									+	
<i>Hypnea pannosa</i> J. Agardh											+			
<i>Peyssonnelia caulifera</i> Okamura				+										
<i>Peyssonnelia conchicola</i> Piccone et Grunow in Piccone							+							
<i>Peyssonnelia distenta</i> (Harvey) Yamada										+				
<i>Ahnfeltiopsis flabelliformis</i> (Harvey) Masuda									+					
<i>Plocamium telfairiae</i> (Hooker et Harvey) Harvey ex Kützing									+	+				
<i>Portieria hornemannii</i> (Lyngbye) P.C. Silva	+	+	+	+	+		+	+			+	+		
<i>Eucheuma denticulatum</i> (Burman) Collins et Harvey														+
<i>Eucheuma serra</i> J. Agardh				+										+
<i>Amphiroa foliacea</i> Lamouroux							+							
<i>Amphiroa fragilissima</i> (Linnaeus) Lamouroux				+							+	+		+
<i>Amphiroa valonioides</i> Yendo				+										
<i>Bossiella cretacea</i> (Postels & Ruprecht) Johansen		+	+											
<i>Cheilosporum acutilobum</i> (Decaisne) Piccone		+	+								+	+		
<i>Corallina squamata</i> Linnaeus				+										
Dermatolithon tumidulum (Foslie) Foslie		+	+											
<i>Jania adhaerens</i> Lamouroux		+	+	+	+			+	+				+	
<i>Jania unguata</i> (Yendo) Yendo							+			+				
<i>Mastophora rosea</i> (C. Agardh) Setchell	+	+	+	+			+	+			+	+		+
<i>Mesophyllum mesomorphum</i> (Foslie) Adey				+										
<i>Mesophyllum simulans</i> (Foslie) Lemoine											+			+
<i>Gracilaria chorda</i> Holmes													+	
<i>Gracilaria coronopifolia</i> J. Agardh													+	
<i>Gracilaria sordica</i> (Suringar) Hariot				+										
<i>Champia parvula</i> (C. Agardh) Harvey														+
<i>Ceratodictyon spongiosum</i> Zanardini				+	+	+	+	+	+	+	+	+	+	
<i>Gelidiopsis repens</i> (Kützing) Schmitz		+	+											+
<i>Centroceras clavulatum</i> (C. Agardh) Montagne														+
<i>Dasyphila plumarioides</i> Yendo														+
<i>Acanthophora spicifera</i> (Vahl) Børgesen													+	

Taxa	2001		2002			2003			2004			
	Apr	Aug	Oct	Feb	May	Jul	Oct	Feb	May	Jul	Sept	
<i>Chondria crassicaulis</i> Harvey						+						+
<i>Laurencia grevilleana</i> Harvey			+	+								
<i>Laurencia papillosa</i> (C. Agardh) Greville												+
<i>Melanamansia glomerata</i> (C. Agardh) Norris		+	+	+				+				+
<i>Vidalia obtusiloba</i> (Merten ex C. Agardh) J. Aagaedh							+				+	
<i>Callophyllis japonica</i> Okamura	+											
unknown rhodophyte		+	+	+	+							
Total macroalgal species number	7	18	24	28	17	8	16	15	8	13	13	15
												9
												17

the data of 8 sampling stations from 2 blocks (4 random samples from each block) were pooled and averaged for analysis to give an overall picture of seasonal changes in macroalgal abundance (Fig. 4). Mean species number per m² showed temporal variations (Kruskal-Wallis test, $p = 0.0042$). Mean species numbers per m² were varied by year (Friedman's test, $p = 0.0352$) (2002 = 2004 > 2003 > 2001) and season ($p = 0.0156$) (winter = autumn > spring > summer) but the interaction of year and season was not significant. Mean species numbers per m² were highest in both February 2002, mainly due to the appearance of several chlorophyte and rhodophytes, and also in October 2004 due to the appearance of rhodophytes. During the survey, erect algae were more abundant than encrusting and turf algae. The *Ceratodictyon/Halictona*

association was most abundant, especially in 2002 and 2003. The calcified chlorophyte *Halimeda opuntia* and the calcified rhodophyte *Galaxaura oblongata* were also the common algae appearing in winter and spring, while *Jania adhaerens* was the common turf algae which was abundant in autumn and winter.

Total macroalgal cover (Kruskal-Wallis test, $p = 0.0027$) and areal biomass (ANOVA, $F_{14,112} = 4.77$, $p < 0.0001$ for areal wet weight (square root-transformed) and $F_{14,112} = 3.24$, $p < 0.0001$ for areal dry weight (square root-transformed)) were temporally variable. The percentage cover (2002 > 2003 > 2001 > 2004) and biomass (2002 = 2003 > 2001 = 2004) were annually variable ($p < 0.05$) but did not show seasonal variations ($p > 0.05$) (Fig. 4); the marked increase in macroalgal cover and

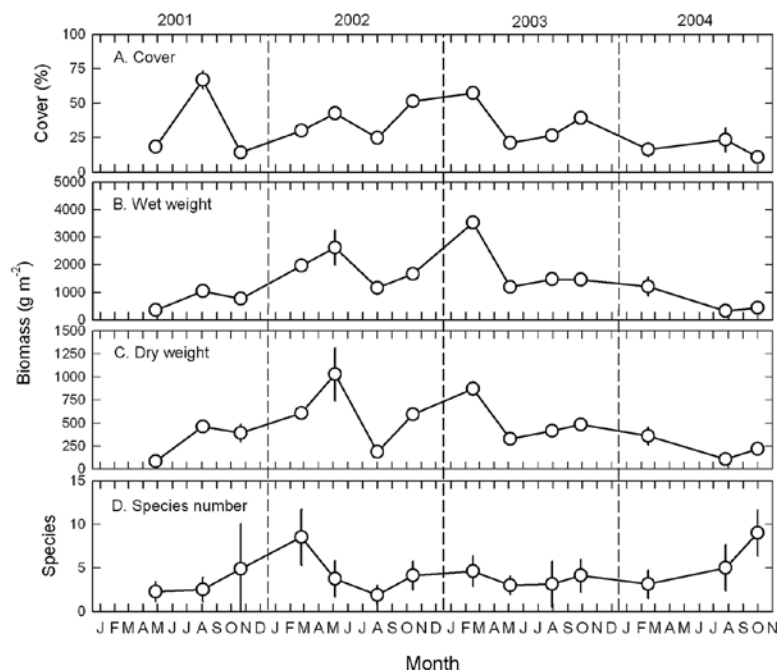


Fig. 4 Total macroalgal cover (A), areal wet weight (B), areal dry weight (C), and species number (D). Data are presented as mean \pm SD ($n=8$)

biomass in 2002-2003 was attributable to the abundance of *Ceratodictyon/Haliclona* association and *Galaxaura oblongata*. Macroalgal cover and biomass showed significant seasonality with peaks in August, 2001, May, 2002 and February, 2003, while seasonality was not marked in 2004 (Fig. 4).

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 3 groups were discerned: a 2001-dominated group, a 2002/2003-dominated group, and a 2004-dominated group (Fig. 5). The k-dominance curves showed that spe-

cies diversity was lower in 2001 as compared to other years (Fig. 6), mainly due to the abundance of the calcified chlorophyte *Halimeda opuntia* in 2001 (Fig. 6). The *k*-dominance curves also revealed that species diversity was lower in the summer period in 2001, 2002, and 2003, which was dominated by *Halimeda opuntia* in 2001, and by *Ceratodictyon/Haliclona* association in both 2002 and 2003.

It was found that macroalgal assemblage is primarily structured by year (group 2001, group 2002/2003, and group 2004) and secondarily by season. One-way ANOSIM testing showed that annual difference in macroalgal assemblage was significant ($R = 0.212$, $p =$

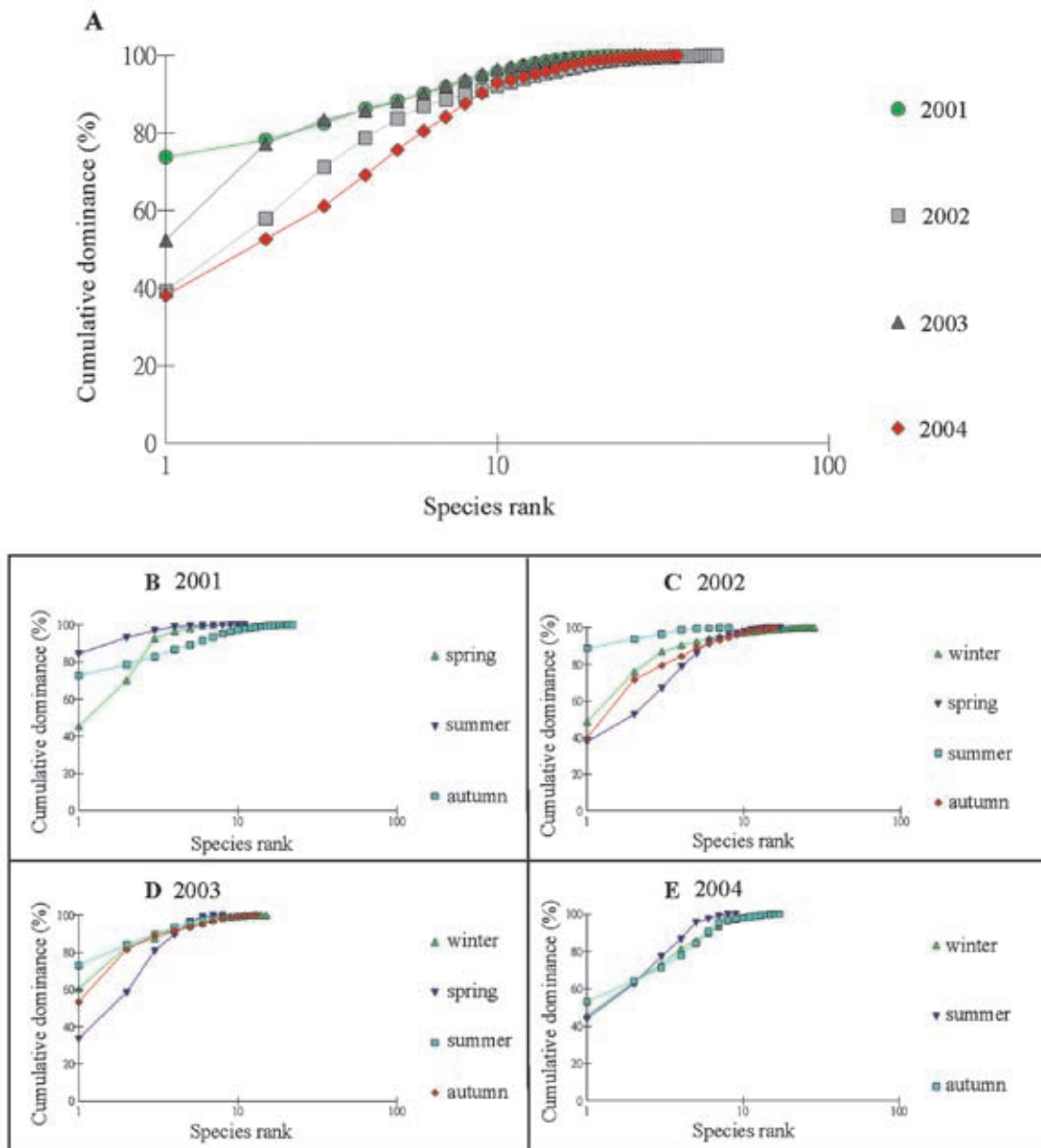


Fig. 5 Clustering group (A) and multidimensional scaling (MDS) ordination (B) of samples taken at each sampling time during 2001-2004

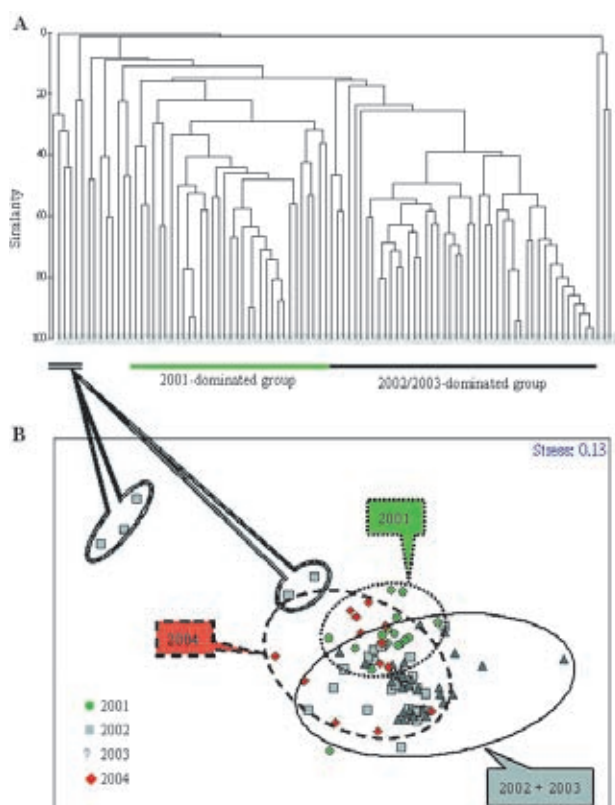


Fig. 6 *k*-dominance curves of macroalgal abundance for 2001-2004 and for seasons in each of those years

0.001); species structure was different between 2001 and 2002, between 2001 and 2003, between 2001 and 2004, and between 2002 and 2004 ($p < 0.05$), whilst species structure was not different between 2002 and 2003 ($R = 0.023$, $p = 0.094$) (Table 2). Results shown in Table 3 indicate that the species responsible for difference in structures between years was *Ceratodictyon/Haliclona* association, *Halimeda opuntia*, and *Galaxaura oblongata*. *Ceratodictyon/Haliclona* biomass was low in 2001 (areal wet weight was 7.55 g w. wt./m²), then significantly increased to 726.59 and 1034.95 g w. wt./m² for 2002 and 2003, respectively, and dropped to 73.99 g w. wt./m² in 2004. *Galaxaura oblongata* showed a similar pattern with the biomass increasing from 38.52 g w. wt./m² in 2001 to 138.08 and 122.44 g w. wt./m² in 2002 and 2003, respectively, and then decreasing to 7.37 g w. wt./m² in 2004. In contrast, the biomass of *H. opuntia* decreased from 674.50 g w. wt./m² in 2001 to 346.27-489.08 g w. wt./m² in 2002-2004. The SIMPER analysis of species contributing to seasonal difference showed that *Ceratodictyon/Haliclona*, the most important taxa separating summer/winter assemblages and other assemblages in spring and autumn, was abundant in summer and winter, while *Halimeda opuntia* was the most important taxa separating the autumn assemblages and other

Table 2. Results of 1-way ANOSIM

A. One-way ANOSIM of macroalgal assemblage between years.

Year	R statistic	Significance level	Permutation
Year	0.212	0.001**	999
2001 - 2002	0.232	0.001**	999
2001 - 2003	0.393	0.001**	999
2001 - 2004	0.244	0.004**	999
2002 - 2003	0.023	0.094	999
2002 - 2004	0.168	0.023*	999
2003 - 2004	0.369	0.001**	999

B. One-way ANOSIM of macroalgal assemblage between seasons for each year.

Year	R statistic	Significance level	Permutation
2001	0.345	0.001**	999
Spring - Summer	0.275	0.008**	999
Spring - Autumn	0.204	0.103	999
Summer - Autumn	0.107	0.228	999
2002	0.140	0.005**	999
Spring - Summer	0.165	0.055	999
Spring - Autumn	0.134	0.055	999
Spring - Winter	0.215	0.004**	999
Summer - Autumn	0.203	0.037*	999
Summer - Winter	0.183	0.017*	999
Autumn - Winter	0.013	0.436	999
2003	0.226	0.001**	999
Spring - Summer	0.113	0.094	999
Spring - Autumn	0.183	0.021*	999
Spring - Winter	0.298	0.003**	999
Summer - Autumn	0.308	0.004**	999
Summer - Winter	0.147	0.079	999
Autumn - Winter	0.344	0.005**	999
2004	0.415	0.008**	999
Winter - Summer	0.397	0.033*	999
Winter - Autumn	0.333	0.075	999
Summer - Autumn	0.889	0.100	999

** 0.05 < P < 0.01

* P < 0.05

assemblages in spring, summer and winter. *Galaxaura oblongata* abundant in spring was the species responsible for differences in assemblage structure between spring and other seasons. Overall, the most dominant species in both 2001 and 2004 was *Halimeda opuntia* and the most dominant species in both 2002 and 2003 was *Ceratodictyon/Haliclona* association.

To elucidate environmental factors in regulating temporal variations in macroalgal assemblage, BVSTP analysis was applied to determine the best combinations of the thirteen environment variables (mean monthly air temperature, mean monthly maximum air temperature, mean monthly minimum air temperature, monthly cumulative irradiance, monthly cumulative precipitation, seawater temperature, salinity, turbidity, and DIN, NO₃⁻, NO₂⁻, NH₄⁺, and SRP concentrations) producing the largest matches of changes in macroalgal structure and environment variables from 2001-2004. It was found

that SRP and turbidity were the factors responsible for the best variable combination and its Spearman rank correlation (ρ) was 0.465 (Table 4). We also examined the best combinations of environment variables producing

the largest matches of seasonal changes in macroalgal structure and environment variables in each year. As can be seen in Table 4, nutrient availability was one of the factors determining seasonality; DIN and irradiance were

Table 3. Result of SIMPER test on percentage contributions of species to determine significant differences between years

Species	Mean abundance (g wet wt./m ²)		Contribution (%)	Cumulative contribution (%)
	2001	2002		
<i>Halimeda opuntia</i>	674.50	346.27	33.11	33.11
<i>Ceratodictyon/Haliclona</i>	7.55	726.59	28.48	61.58
<i>Galaxaura oblongata</i>	38.52	138.08	6.72	68.30
<i>Jania adhaerens</i>	13.28	93.16	3.09	71.39
	2001	2003		
<i>Ceratodictyon/Haliclona</i>	7.55	1034.95	35.55	35.55
<i>Halimeda opuntia</i>	674.50	489.08	31.09	66.64
<i>Galaxaura oblongata</i>	38.52	122.44	6.51	73.16
	2001	2004		
<i>Halimeda opuntia</i>	674.50	350.57	40.30	40.30
<i>Ceratodictyon/Haliclona</i>	7.55	73.99	6.62	46.93
<i>Amphiroa fragilissima</i>	0.00	60.25	6.01	52.94
<i>Gelidiopsis repens</i>	0.00	77.86	5.24	58.17
<i>Galaxaura oblongata</i>	38.52	7.37	4.73	62.90
<i>Galaxaura marginata</i>	34.31	6.51	4.08	66.98
	2002	2004		
<i>Ceratodictyon/Haliclona</i>	726.59	73.99	29.12	29.12
<i>Halimeda opuntia</i>	346.27	350.57	21.93	51.05
<i>Galaxaura oblongata</i>	138.08	7.37	4.71	55.87
<i>Amphiroa fragilissima</i>	8.25	60.25	4.82	60.58
	2003	2004		
<i>Ceratodictyon/Haliclona</i>	1034.95	73.99	34.28	34.28
<i>Halimeda opuntia</i>	489.08	350.57	22.56	56.84
<i>Galaxaura oblongata</i>	122.44	7.37	4.90	61.74
<i>Amphiroa fragilissima</i>	6.69	60.25	3.79	65.53

Table 4. The best combinations of 13 environment variables (monthly mean air temperature, monthly maximum air temperature, monthly minimum air temperature, monthly cumulative irradiance, monthly cumulative precipitation, seawater temperature, salinity, turbidity, DIN, SRP, NO₃⁻, NO₂⁻, and NH₄⁺) producing the largest matches of changes in macroalgal assemblage and environmental variables over 2001-2004

A. years (2001-2004)		
Number of variable	Spearman rank correlation (ρ)	Best variable combination
2	0.465	Turbidity, SRP
B. seasons of each year		
Number of variable	Spearman rank correlation (ρ)	Best variable combination
2001		
2	0.347	DIN, monthly mean air temperature
2	0.341	DIN, irradiance
2002		
3	0.510	SRP, turbidity, irradiance
2003		
4	0.579	NO ₃ ⁻ , DIN, turbidity, precipitation
3	0.491	NO ₃ ⁻ , turbidity, seawater temperature, precipitation
2004		
3	0.526	NO ₂ ⁻ , DIN, irradiance

factors involving in the seasonal variations of macroalgal assemblage in 2001, 2003 and 2004 while SRP influenced the seasonality of 2002 macroalgal assemblage.

3) Temporal variations in abundance of *Ceratodictyon/Haliclona*, *Galaxaura oblongata*, and *Halimeda opuntia* and their relationships to environmental variables

The areal wet weight of *Ceratodictyon/Haliclona* symbiotic association showed temporal variations (Kruskal-Wallis test, $p < 0.0001$), in which the fluctuation of *Ceratodictyon/Haliclona* biomass varied yearly (Friedman's test, $p < 0.0001$) and seasonally ($p = 0.0027$); the wet weight biomass in 2002 and 2003 was higher than that in 2001 and 2004, and winter biomass was higher than summer and autumn biomass (Fig. 7). The areal wet weight of *Galaxaura oblongata* was also higher in 2002 and 2003 ($p = 0.0315$), in which their biomass peaked in spring (Friedman's test, $p = 0.0260$). The results of stepwise regression analysis showed that temporal variations of *Ceratodictyon/Haliclona* biomass appeared in a negative relation with monthly maximum temperature and SRP concentrations but in a positive relation with turbidity and DIN concentrations ($\log(\text{biomass} + 1) = 22.691 + 31.932 \arcsin(\text{turbidity}) -$

$19.461 \log(\text{monthly maximum temperature} + 1) - 2.481 \log(\text{SRP} + 1) + 0.323 \sqrt{\text{DIN}}$, $R = 0.639$). *Galaxaura oblongata* biomass was positively related to turbidity but negatively related to monthly minimum temperature and monthly cumulative precipitation ($\log(\text{biomass} + 1) = 3.815 + 26.528 \arcsin(\text{turbidity}) - 2.698 \log(\text{monthly minimum temperature} + 1) - 0.335 \log(\text{monthly cumulative precipitation} + 1)$, $R = 0.518$).

The areal wet weight of *Halimeda opuntia* showed temporal variation (Kruskal-Wallis test, $p = 0.003$) that showed annual variations (Friedman's test, $P = 0.0438$) and significant annual and seasonal interaction ($p < 0.0001$) but did not show seasonal variations ($p = 0.1865$), reflecting that the temporal fluctuation of *Halimeda opuntia* wet weight biomass did not follow the spring-summer-autumn-winter pattern from 2001-2004 (Fig. 7). The biomass pattern was similar in 2002 and 2003, a V-shape with the valley occurring in August-September (Fig. 7). But, *Halimeda biomass* in 2001 peaked at August, and in 2004 remained low until late October, that is, *Halimeda biomass* did not recover in winter 2004 as had been seen in other years (Fig. 7). The results of stepwise regression analysis showed that temporal variations of *Halimeda opuntia* biomass are negatively correlated with monthly maximum temperature but showed

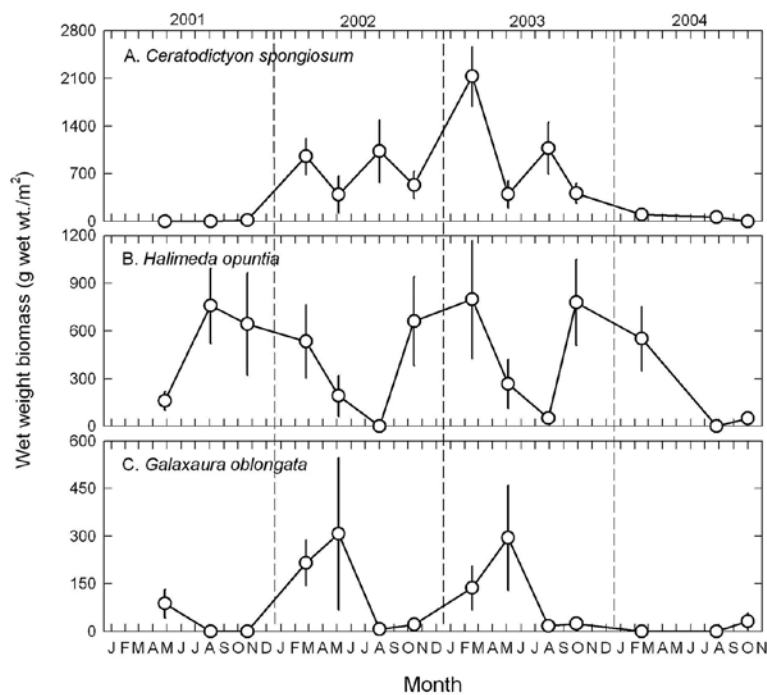


Fig. 7 Temporal variations in areal wet weight of dominant algae during 2001-2004. Data are presented as mean \pm SD (n=8)

a positive relation to salinity and SRP concentrations ($\log(\text{biomass} + 1) = 15.783 + 0.730 \log(\text{salinity} + 1) - 10.679 \log(\text{monthly maximum temperature} + 1) + 2.010 \log(\text{SRP} + 1)$, $R = 0.433$).

4) Growth response of *Galaxaura oblongata* to various light, nutrient and temperature levels

According to the analysis of field data by BVSTEP and stepwise regression, it is hypothesized that turbidity and nutrient levels are the factors affecting algal growth, which in turn, changes algal assemblage structure. *Ceratodictyon/Haliclona* and *Galaxaura oblongata* were selected in this study to test this hypothesis. Because

the culture of *Ceratodictyon/Haliclona* did not succeed, only the results of experiments relating to *Galaxaura oblongata* were available. The growth rate of *Galaxaura oblongata* was affected by light, nutrient, and temperature ($p < 0.05$) and the interactions of light and temperature, nutrient and temperature, and light, nutrient and temperature on growth rate were also significant ($p < 0.0001$) (Table 5). The interaction of light and nutrient on growth rate was not significant ($p = 0.1488$). The growth rate in low P/high N conditions was significantly higher than that in high P/low N conditions ($p < 0.05$), and the growth rate was maximal at 20–25°C in both low P/high N and high P/low N conditions ($p < 0.05$). High tempera-

Table 5. Changes in the growth rate (%/d) of *Galaxaura oblongata* in response to varying light levels, nutrient levels, and temperature treatments

A. Growth rate (%/d) of *Galaxaura oblongata*.

Data are shown as means \pm SEM (n=3) and different symbols indicate significant difference at $P < 0.05$ (Tukey's test).

		Temperature (°C)				
		15	20	25	30	35
Low light	Low P/high N	0.96 \pm 0.07	2.94 \pm 0.25	3.07 \pm 0.16	0.60 \pm 0.05	-4.37 \pm 0.59
	High P/low N	0.74 \pm 0.16	1.28 \pm 0.26	1.87 \pm 0.22	-0.92 \pm 0.12	-5.23 \pm 0.40
High light	Low P/high N	0.65 \pm 0.08	1.89 \pm 0.12	2.08 \pm 0.21	0.55 \pm 0.11	-5.91 \pm 0.53
	High P/low N	-0.01 \pm 0.19	0.37 \pm 0.13	0.95 \pm 0.07	-2.11 \pm 0.17	-6.47 \pm 0.64

B. Results of ANOVA analysis of light, nutrient, and temperature treatments on the growth rate (%/d) of *Galaxaura oblongata*.

	Sun of Squares	DF	Mean Square	F	P
Light	12.0064	1	12.0064	148.78	<0.0001*
Nutrient	21.6240	1	21.6240	267.88	<0.0001*
Temperature	440.6903	4	110.1762	1364.48	<0.0001*
Light x Nutrient	0.1750	1	0.1750	2.17	0.1488
Light x Temperature	1.3858	4	0.3465	4.29	0.0055
Nutrient x Temperature	5.3019	4	1.3255	16.42	<0.0001*
Light x Nutrient x Temperature	1.0363	4	0.2591	3.21	0.0224*

* < 0.05

ture inhibited growth rates whereby the growth rate was negative when temperature was higher than 30°C. The growth was greater in low light conditions as compared to high light conditions ($p < 0.05$).

Discussion

The temporal variations in macroalgal assemblage compositions near a coastal shore experiencing the dangers of coastal construction were monitored in 2001–2004 around Orchard Island off southeastern Taiwan. Eighty species have been identified, in which erect algae were more abundant than encrusting and turf algae. The *Ceratodictyon/Haliclona* association and calcified algae *Halimeda opuntia* and *Galaxaura* spp. are the dominant algae. However, their temporal variations in biomass showed different patterns. The *Ceratodictyon/Haliclona*

association was the most abundant species with a marked increase of biomass in 2002 and 2003. Although these 2 calcified algae appeared in winter and spring, *Galaxaura oblongata* was abundant in 2002 and 2003, while *Halimeda opuntia* biomass decreased slightly after 2001.

The present results suggest there is an association between coastal construction and the modification of nearshore benthic macroalgal compositions in Orchard Island. Total macroalgal wet weight and dry weight biomass significantly increased during the construction period (2002–2003) mainly due to the blooms of *Ceratodictyon/Haliclona* association and *Galaxaura oblongata*. In contrast, the biomass of *Halimeda opuntia* decreased after construction. Evidence from *k*-dominance curve analysis shows that there is a shift of macroalgal assemblage compositions after 2001; the 2001 assemblage with less *Ceratodictyon/Haliclona*

but high *Halimeda opuntia* became a *Ceratodictyon/Haliclona*-dominated assemblage in 2002/2003. The effects of coastal construction could also be reflected in a change in macroalgal assemblage structure. The 2002 and 2003 communities are grouped as the same macroalgal assemblage structure in contrast to the 2001 and 2004 communities. We have found that the dominant algae *Ceratodictyon/Haliclona* association, *Halimeda opuntia* and *Galaxaura oblongata* are the species leading to annual differences in macroalgal structure. *Ceratodictyon/Haliclona* is the main species contributing to annual differences in macroalgal assemblage structure, in which this red alga/sponge association was highly abundant in 2002 and 2003. The blooms of *Ceratodictyon/Haliclona* and *Galaxaura oblongata* are accompanied by a decline in *Halimeda opuntia* abundance, suggesting that the *Ceratodictyon/Haliclona* and *Galaxaura oblongata* may compete with *Halimeda opuntia*. After construction finished, macroalgal compositions became a relatively high-diversified assemblage in 2004 with a marked drop in the abundance of *Ceratodictyon/Haliclona* and *Halimeda opuntia* and the appearance of several species such as *Amphiroa fragilissima* and *Gelidiopsis repens*. The results of ANOSIM testing also show the 2001 and 2004 communities are different. It is evident that the macroalgal assemblage structure did not recover soon after construction or it can be assumed that the macroalgal compositions have been without recovery post construction probably due to a change in habitats from large rocks to small rocks.

The results of BVSTEP analysis of the correlation between macroalgal assemblage and environment variables suggest that SRP and turbidity are the main factors influencing structure alterations through their impact on the growth of abundant algal species. During the survey, the nutrient status in seawater was shifted from high SRP/low DIN in 2001 to low SRP/high DIN in 2002-2003, and then returned to high SRP/low DIN in 2004, reflecting that low SRP/high DIN is caused by coastal construction. Possibly, a decrease in P availability would lead to *Ceratodictyon/Haliclona* blooms. By tracing ^{15}N stable isotope 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, the results of regression analysis and field surveys showed a positive correlation of *Ceratodictyon/Haliclona* biomass with seawater DIN concentrations, reflecting that the blooming

of *Ceratodictyon/Haliclona* near Orchard Island off southeastern Taiwan might not be due to meeting the N requirement of algal partner. Instead, we propose that the association of *Ceratodictyon* with *Haliclona* enables the alga to obtain P from *Haliclona* under P-limited conditions (2002 and 2003). The regulation of *Ceratodictyon/Haliclona* association by P status requires further investigation.

A positive correlation of turbidity with *Ceratodictyon/Haliclona* abundance suggests the association of turbidity with the formation of *Ceratodictyon/Haliclona* symbioses. Turbidity was increased by construction as indicated by a match of turbidity increase and construction time. Increased turbidity will reduce light availability for photosynthesis. Presumably, the association of *Ceratodictyon/Haliclona* is to overcome the reduction of metabolisms driven by photosynthesis. Additionally, intact reefs and corals in the present study site were broken up during 2002-2003. The study in One Tree Lagoon in the southern Great Barrier Reef of Australia has shown that *Ceratodictyon/Haliclona* is particularly abundant in the reefs where the substratum consists of dead coral rubbles (Trautman *et al.* 2000, 2003); its biomass can reach 270 g wet weight per m² (Trautman *et al.* 2000). These results suggest that *Ceratodictyon/Haliclona* blooms in response to changing environments caused by human activities in Orchard Island.

A positive correlation of turbidity and DIN but a negative correlation of SRP with *Galaxaura oblongata* biomass and the results of outdoor laboratory culture experiments identify the preference of *Galaxaura oblongata* under conditions of low irradiance and low P/high N as well. It is likely that an increase in *Galaxaura oblongata* abundance in 2002 and 2003 also reflects environmental changes caused by construction. In addition, the seasonality of *Galaxaura oblongata* in 2002 and 2003 is negatively regulated by temperature as suggested by the results of stepwise regression analysis. Disappearance of the calcified red alga in hot summer months can be explained by high temperature inhibition of *Galaxaura oblongata* growth shown in outdoor laboratory culture experiments. Additionally, high summer irradiance may cause photoinhibition. A role for temperature on the regulation of macroalgal growth in southern Taiwan has been suggested by our recent study that Sargassum seasonality in Nanwan Bay on the southern tip of Taiwan is linked to temporal variations in seawater temperature, Sargassum growth is generally inhibited by high temperatures in summer months (Hwang *et al.* 2004). Besides, a negative correlation of *Galaxaura oblongata* abundance with precipitation may explain the blooms of this red

alga in 2002-2003, when precipitation was relatively light compared to 2001 and 2004. Precipitation not only decreased salinity but also increased nutrient loading via enhanced run-off. Because the growth of *Galaxaura oblongata* is favored in low nutrient conditions, it could be expected that *Galaxaura oblongata* would tend to bloom under low precipitation conditions. Evidently, *Galaxaura oblongata* biomass is influenced by construction threats and natural disturbances as well.

Using multiple regression analysis, *Halimeda opuntia* biomass appeared to be in positive correlation with annual variations in SRP concentrations but shows a negative relationship with seasonal temperature fluctuation (monthly maximum temperature). Its relationship to temperatures is in contrast to *Halimeda opuntia* from the Hengchun Peninsula on the southern tip of Taiwan in that its abundance is low in autumn-winter and high in spring-summer (Tsai *et al.* 2005). Because we did not check the growth responses of *Halimeda opuntia* to environmental factors in outdoor laboratory culture experiments, the factors governing the seasonality of *Halimeda opuntia* during 2001-2004 are not clear.

In conclusion, this study provides evidence showing that irradiance and nutrient levels are considered the factors governing the structure and abundance of benthic macroalgal assemblages in tropical Taiwan in areas undergoing coastal construction. The macroalgal assemblage in Orchard Island is structured primarily by year and secondarily by season. The change in Orchard Island macroalgal assemblage due to the blooms of *Ceratodictyon/Haliclona* and *Galaxaura oblongata* during 2002-2003 is associated with anthropogenic threats caused by coastal construction, especially decreased P availability and increased turbidity. Because macroalgae tend to integrate the effects of long-term exposure to adverse conditions, macroalgal assemblages are widely used to characterize and monitor benthic communities. Construction threats on Orchard Island can be seen in by a shift of macroalgal assemblage from *Halimeda opuntia* as the dominant species before construction to highly abundant *Ceratodictyon/Haliclona* and *Galaxaura oblongata* during construction, which then shows high algal diversity after the construction has ceased.

Abbreviation

ANOSIM, analysis of similarity; DIN, dissolved inorganic nitrogen; d. wt., dry weight; MDS, multi-dimensional scaling; SIMPER, similarity percentage breakdown procedure; SRP, soluble reactive phosphorus;

w. wt, wet weight.

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This work is dedicated to the memory of Prof. Chung-Sin Chen (Department of Aquaculture, National Taiwan Ocean University, Keelung, Taiwan, Republic of China).

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