Macroalgal assemblage structure on a coral reef in Nanwan Bay in southern Taiwan

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Abstract

Four-season surveys of macroalgal assemblage structure on a coral reef in southern Taiwan were performed by transect investigation from October 1999 through August 2000. Species richness increased over time, and percentage cover and biomass peaked in April. Non-metric multidimensional scaling ordination analysis of species similarities between stations showed three distinct clusters corresponding to the upper reef flat, the lower reef flat and the reef slope. The macroalgal assemblage on the lower reef flat was further grouped into two clusters corresponding to the warmer months (October 1999 and August 2000) and the cooler months (January and April 2000), suggesting the macroalgal assemblage is structured primarily by zone and secondarily by season. Species richness, percentage cover, biomass, species diversity (H') and evenness (J') were highest on the lower reef flat, reflecting greater complexity in the macroalgal assemblage in this zone. However, species diversity and evenness on the lower reef flat and the reef slope did not show seasonal variations. Species diversity in the upper reef flat decreased in the warmer months due to the dominance of an unknown red alga in October 1999 and *Enteromorpha linza* in August 2000. The results of ANOSIM tests showed that species structure was different not only between zones but also between seasons, and the SIMPER analyses showed that, in the warmer months, *Gracilaria coronopifolia*, *Enteromorpha linza*, *Laurencia* spp. and *Hypnea charoides* were the species that separated the lower reef flat assemblage from other assemblages. In the same way, the unknown red alga (for

October 1999), *Enteromorpha linza* (for August 2000), *Halimeda* spp., *Mastophora rosea* and *Portieria hornemannii* were the species responsible for differences in structure between the upper reef flat and the reef slope. In the cooler months, the species responsible for differences in structures between the upper reef flat and the other two zones were *Sargassum* spp., *Gracilaria coronopifolia*, *Enteromorpha linza* and *Padina australis*, and those responsible for differences between the upper reef flat and the reef slope were *Hypnea charoides*, *Halimeda* spp., *Mastophora rosea*, *Enteromorpha linza* and *Portieria hornemannii*. The present investigation suggests that macroalgal abundance and structure on a coral reef in Nanwan Bay in southern Taiwan have marked spatial zonation and seasonal variations, and *Sargassum* on the lower reef flat has become the most abundant alga, as compared to 12 years ago.

Keywords: assemblage; macroalgae; seasonality; zonation.

Introduction

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

Coastal regions along Hengchuan Peninsula have the best developed coral reef ecosystem in southern Taiwan and face increasing pressure from expanded urban development and tourism. Most nearshore reefs in Hengchuan Peninsula are characterized by a high abundance of fleshy macroalgae and a low abundance of herbivorous fishes (Dai 1997). 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, Rodriguez-Prieto and Polo 1996). For example, increasing water-column nutrient concentrations seem to play a role in macroalgal blooming on Reunion Island, Indian Ocean (Cuet et al. 1988) and in the Caribbean and Florida coast-

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A. Map of study site

B. Sampling station (↓) on the transect

Figure 1 Map of Nanwan Bay in Hengchuan Peninsula in southern Taiwan with (A) location of the coral reef studied and (B) a sketch of sampling stations on each transect perpendicular to the shoreline [in a direction from shoreline (MHWS) to seaward].

al regions (Lapointe and O'Connell 1989, Bell 1992). Apparently, the growth of macroalgae out competes corals 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 addition, 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. Although qualitative observations have shown that the abundance of fleshy macroalgae in southern Taiwan has increased over the past ten years (Dai 1997), quantitative investigations on macroalgal abundance and species compositions have not been done on the reefs of this area. Hence, the present investigation [part of two collaborative coral reef conservation studies supported by the National Science Council (from 1995–1998 and from 1999–2000) and the Council of Agriculture (from 2002–2004), Taiwan, Republic of China] has been undertaken on a coral reef in Nanwan Bay in order to determine

the seasonal and spatial variations in macroalgal assemblage compositions in tropical Taiwan waters.

Materials and methods

Study site and environmental characteristics

The study site is a nearshore coral reef (GPS: 21°56'00"N; 120°50'10"E) in Nanwan Bay (Figure 1A), which is located on the western side of Hengchuan Peninsula surrounded by the Pacific Ocean to the east, the Bashi Channel to the south, and the Taiwan Straits to the west. This reef which is located beside the "Nanwan" sand beach on Nanwan Bay has a horizontal width of 1,200 m, comprising an intertidal region, approximately 50–130 m broad, and a subtidal macroalgal region, approximately 35–270 m broad and a depth gradient of 0–12 m [below mean high water springs (MHWS)] on a seaward gradient. In the upper intertidal region, there are two large intertidal pools of ca. 20–40 m width and 30–40 m length

Figure 2 Climate data for Hengchuan Peninsula from August 1999 to August 2000.

covered with fine sediments and seagrass [*Thalassia hemprichii* (Ehrenberg) Ascherson]. In the subtidal regions, there is a reef flat bordered by a sloping coralline rocky stretch ca. 80–90 m away from the coast line. Two drainage outlets are significant sewage sources in this reef, especially during the rainy period (from April to July).

The data obtained from the Central Weather Bureau of the Republic of China (1960–1990) show that the mean annual air temperature in Hengchuan Peninsula is 25°C; the mean monthly air temperature is low (20.3°C) in January and high (28.3°C) in July. The annual average relative humidity is 77%, maximum precipitation (mean annual precipitation is 1964.9 mm) and typhoons usually occur in May–September. The prevailing northeasterly winds occur during September–March, and during this monsoon period, the hydrological regimen is affected by strong dry winds from land to seaward. During September 1999–August 2000, the mean monthly air temperature was <25°C from November 1999 through March 2000, monthly cumulative precipitation was low from

November 1999 through June 2000 and irradiance was lower than 500 MJ/m² from September 1999 through February 2000 (Figure 2).

Estimation of macroalgal cover, biomass and species composition

To characterize the spatial changes in macroalgal assemblage compositions, four transects (each transect was 130 m long) perpendicular to the shoreline were set at 100-m intervals and on each transect, sampling stations were marked at 5-m intervals running from the average high tide mark (MHWS) in a seaward direction; the 0 m station was made to coincide with the average high tide mark and 27 stations were set for each transect line (Figure 1B). At each station, species abundance, in terms of percentage cover, was calculated as the sampling surface covered in vertical projection by the species using a 50×50 cm quadrat, and the total macroalgal cover was the sum of all species cover. The macroalgal cover in different vegetation layers (erect layer, encrusting layer and turf) was recorded, and all seaweeds in a 50×50 cm quadrat were scraped free for estimation of macroalgal compositions and biomass. Species identification was determined using a microscope. Macroalgal cover and biomass were determined in October 1999, January 2000, April 2000 and August 2000 for the analysis of temporal changes in macroalgal assemblage structure.

Determination of seawater temperature, salinity, irradiance and nutrient concentrations

Our preliminary investigations in April and August 1999 indicated that three zones corresponding to different air exposure time can be found from the average high tide mark towards the low tide mark: an upper reef flat (0–20 m from MHWS) with average daily exposure time >10 h, a lower reef flat (25–80 m from MHWS) with average daily exposure time <6 h, and a reef slope (85–130 m from MHWS) without exposure to air. Envi-

Table 1 Changes in water temperature, salinity, irradiance, and DIN and SRP concentrations during surveys.

		Water temperature (°C)	Salinity (psu)	Irradiance (MJ/m ²)	DIN (μM)	SRP (μM)
Oct. 1999	Upper reef flat	27.08±0.66a	35.88±0.98a	988.17±125.85a	15.37±12.69a	0.88±2.16
	Lower reef flat	27.10±0.68a	38.13±3.60a	794.67±69.70ab	6.24±7.12a	0.00
	Reef slope	26.67±0.68a	36.04±3.20a	464.17±53.80c	8.33±4.32a	0.00
Jan. 2000	Upper reef flat	24.97±0.59a	36.25±2.96a	957.33±81.92a	2.95±1.08a	0.00
	Lower reef flat	23.83±0.98b	36.67±2.46a	796.67±108.97a	1.75±0.65a	0.00
	Reef slope	22.62±0.46c	36.04±1.66a	424.33±87.20b	1.15±0.39a	0.00
Apr. 2000	Upper reef flat	23.00±0.32a	37.50±0.00a	973.17±49.66a	8.87±1.94a	0.06±0.07a
	Lower reef flat	22.85±0.37a	37.71±0.51a	807.50±26.90b	8.76±3.05a	0.09±0.06a
	Reef slope	22.32±0.33b	37.50±0.00a	447.33±67.66c	8.67±3.30a	0.21±0.43a
Aug. 2000	Upper reef flat	31.33±0.75a	35.00±0.00a	842.17±105.82a	4.88±5.11a	0.00
	Lower reef flat	29.08±1.02b	33.33±4.08a	461.17±58.28b	0.93±1.20a	0.00
	Reef slope	27.17±0.78c	33.33±4.08a	265.83±46.65c	2.56±2.98a	0.00

Data are presented as means±SE (n=6) and different letters indicate significant differences at p<0.05 (Tukey's test). DIN=dissolved inorganic nitrogen (NO₃⁻+NO₂⁻+NH₄⁺); SRP=soluble reactive phosphorus.

ronmental factors including seawater temperature, salinity, irradiance (above the algal canopy) and seawater nutrient concentrations were determined randomly in 6 sampling stations for each zone (Table 1). The upper reef flat was 0–0.5 m deep (MHWS), the lower reef flat was approximately 1–2 m deep (MHWS), and the reef slope approximately 2.5–5 m deep. Collected seawater samples were immediately transported to the laboratory under low temperature and then stored at -70°C until analysis. After filtering through Whatman CF/G papers ($0.45\ \mu\text{m}$), seawater NO_2^- and NO_3^- concentrations were determined according to Strickland and Parsons (1972) and NH_4^+ concentrations were determined according to Parsons et al. (1984). Dissolved inorganic nitrogen (DIN) concentrations were the sum of $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$ concentrations. Soluble reactive phosphorus (SRP) concentrations were determined according to Murphy and Riley (1962). The detection limits for seawater NO_2^- , NO_3^- , NH_4^+ and SRP concentrations were 0.75, 0.5, 0.5 and 0.25 nm in 0.5 ml seawater, respectively.

Data analysis

Environmental factors including seawater temperature, salinity, irradiance and nutrient concentrations were tested for difference using two-way analysis of variance (ANOVA, SAS statistical software package v 8.0, SAS Ltd., NC, USA) with season and zone as fixed factors. Cochran's C-test was used to test heterogeneity of variance. The data for seawater temperature, salinity and SRP concentrations were $\log(x+1)$ -transformed. Tukey's test was used for multiple comparisons among means from significant ANOVA tests (Day and Quinn 1989).

Univariate indices and multivariate analysis were used 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 station, the average data of 4 replicates (the data collected on each line transect were treated as replicates) were used for analyses. The similarity matrix of species compositions (% cover 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 (MDS) analysis. Analysis of macroalgal assemblage structure was carried across the upper reef flat (5–20 m stations), the lower reef flat (30–80 m stations) and the reef slope (95–130 m stations). To measure attributes of community structure between seasons and between zones, 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 and tested for difference using two-way (season, zone) and one-way (zone) analysis of variance (ANOVA, SAS statistical software package v 8.0, SAS Ltd., NC, USA). Cochran's C-test was used to determine homogeneity of variance. Tukey's test was used for multiple comparisons among means from significant ANOVA tests (Day and Quinn 1989). Macroalgal assemblages were compared among stations by

means of hierarchical agglomerative cluster analysis and MDS (Kruskal and Wish 1978) of species % cover 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 differences in macroalgal assemblage structure between seasons and between zones was tested using two-way analysis of similarity (ANOSIM) (Clarke and Warwick 1994), and the species mainly responsible for differences between zones in each season were determined by the similarity percentage breakdown procedure (SIMPER) (Clarke 1993).

Results

Environmental factors

Environmental factors had zonation and seasonal variations (Table 1). Seawater temperature [$\log(x+1)$ -transformed] showed seasonal (ANOVA; $F_{3,60}=355.28$, $p<0.0001$) and zonation ($F_{2,60}=47.22$, $p<0.0001$) variations; seawater temperatures in October 1999 and August 2000 were higher than those in January and April 2000 (Tukey, $p<0.05$) while in August 2000, seawater temperature in the upper reef flat was higher than those in both the lower reef flat and the reef slope (Tukey, $p<0.05$). Salinity [$\log(x+1)$ -transformed] showed seasonal variations ($F_{3,60}=6.67$, $p=0.0006$) but did not show zonation variations (ANOVA; $F_{3,60}=0.43$, $p=0.6538$); salinity was low in August 2000 (Tukey, $p<0.05$). Irradiance showed seasonal (ANOVA; $F_{3,60}=46.02$, $p<0.0001$) and zonation ($F_{2,60}=297.31$, $p<0.0001$) variations; irradiance was low in August 2000 (Tukey, $p<0.05$) and irradiance in the reef slope was significantly lower than that in the upper reef flat (Tukey, $p<0.05$). DIN concentrations showed seasonal variations (ANOVA; $F_{3,60}=22.61$, $p<0.0001$) with higher concentrations in October 1999 and April 2000 (Tukey, $p<0.05$). Although DIN concentrations did not show zonation variation (ANOVA; $F_{2,60}=2.96$, $p=0.0595$), average DIN concentrations in the upper reef flat were higher than those in other zones. Soluble reactive phosphorus concentrations did not show seasonal (ANOVA; $F_{3,60}=0.59$, $p=0.5582$) or zonation ($F_{2,60}=1.08$, $p=0.3648$) variations. The above data together with the climate data from the Central Weather Bureau of the Republic of China (Figure 2) show that October 1999 and August 2000 were the warmer months and January and April 2000 were the cooler months, and the upper reef flat had higher irradiance and higher temperature, especially in the warmer months.

Macroalgal assemblage structure

Fifty-eight species were recorded during the surveys (Table 2), 19 Chlorophyta, 10 Phaeophyta, 27 Rhodophyta and 2 Cyanophyta. There were 36 species recorded in October 1999 and January 2000, 45 species in April 2000 and 53 species in August 2000. Erect algae were more abundant than encrusting and turf algae. *Enteromorpha linza* and *Hypnea charoides* were the common algae on the upper reef flat, *Ulva lactuca*, *Sargassum* spp., *Gra-*

Table 2 Macroalgae recorded on a nearshore reef at Nanwan Bay in southern Taiwan during October 1999–August 2000.

			Oct. 1999	Jan. 2000	Apr. 2000	Aug. 2000
Chlorophyta						
Ulvales	Ulvaceae	<i>Enteromorpha linza</i> (Linnaeus) J. Agardh	+	+	+	+
		<i>Ulva lactuca</i> Linnaeus	+	+	+	+
		<i>Ulva reticulata</i> Forsskål		+	+	+
Dasycladales	Dasycladaceae	<i>Bornetella nitida</i> Sonder		+	+	+
		<i>Bornetella sphaerica</i> (Zanardini) Solms-Laubach	+	+		+
		<i>Neomeris annulata</i> Dickie		+	+	+
		<i>Neomeris van-bosseae</i> M.A. Howe	+		+	+
Cladophorales	Cladophoraceae	<i>Chaetomorpha linum</i> (O.F. Müller) Kützinger	+		+	+
		<i>Cladophora</i> sp.	+	+	+	+
Siphonocladales	Valoniaceae	<i>Valoniopsis pachynema</i> (G. Martens) Børgesen	+	+		+
		<i>Dictyosphaeria cavernosa</i> (Forsskål) Børgesen	+		+	+
	Boodleaceae	<i>Boodlea composita</i> (Harvey) F. Brand	+		+	+
Bryopsidales	Siphonocladaceae	<i>Boergesenia forbesii</i> (Harvey) Feldmann				+
	Anadyomenaceae	<i>Anadyomene wrightii</i> Harvey ex J.E. Gray	+		+	+
	Caulerpaceae	<i>Caulerpa brachypus</i> f. <i>parvifolia</i> (Harvey) Cribb				+
	Halimedaceae	<i>Halimeda macroloba</i> Decaisne	+	+	+	+
		<i>Halimeda opuntia</i> (Linnaeus) Lamouroux	+	+	+	+
	Udoteaceae	<i>Chlorodesmis caespitosa</i> J. Agardh			+	+
		<i>Chlorodesmis fastigiata</i> (C. Agardh) Ducker	+	+	+	+
Phaeophyta						
Dictyotales	Dictyotaceae	<i>Dictyota cervicornis</i> Kützinger		+	+	+
		<i>Padina australis</i> Hauck	+	+	+	+
Scytosiphonales	Scytosiphonaceae	<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès et Solier		+		
		<i>Hydroclathrus clathratus</i> (C. Agardh) Howe		+		
Fucales	Sargassaceae	<i>Sargassum berberifolium</i> J. Agardh	+	+	+	+
		<i>Sargassum glaucescens</i> J. Agardh		+	+	
		<i>Sargassum polycystum</i> C. Agardh	+	+	+	+
		<i>Sargassum sandei</i> Reinbold			+	+
		<i>Sargassum siliculosum</i> J. Agardh	+	+	+	+
		<i>Turbinaria ornata</i> (Turner) J. Agardh	+			+
Rhodophyta						
Nemaliales	Galaxauraceae	<i>Galaxaura marginata</i> (Ellis et Solander) J.V. Lamouroux	+	+	+	+
		<i>Scinaia pseudojaponica</i> Yamada et Tanaka		+	+	+
	Liagoraceae	<i>Helminthocladia australis</i> Harvey		+	+	+
		<i>Liagora orientalis</i> J. Agardh			+	+
Gracilariales	Gracilariaceae	<i>Yamadaella caenomyce</i> (Decaisne) I.A. Abbott		+	+	+
		<i>Gracilaria arcuata</i> Zanardini			+	+
		<i>Gracilaria chorda</i> Holmes				
		<i>Gracilaria coronopifolia</i> J. Agardh	+	+	+	+
		<i>Gracilaria sordida</i> W.A. Nelson	+	+	+	+
		<i>Gracilaria</i> sp.	+	+	+	+
Corallinales	Corallinaceae	<i>Tricleocarpa fragilis</i> (Linnaeus) Huisman et Townsend		+	+	
		<i>Jania adhaerens</i> Lamouroux	+	+	+	+
Gigartinales	Gigartinaceae	<i>Mastophora rosea</i> (C. Agardh) Setchell	+	+	+	+
		<i>Chondrus ocellatus</i> Holmes	+			+
Hypneaceae	Hypneaceae	<i>Hypnea cervicornis</i> J. Agardh			+	+
		<i>Hypnea charoides</i> J.V. Lamouroux	+	+	+	+
		<i>Hypnea pannosa</i> J. Agardh	+		+	+
	Sarcodiaceae	<i>Sarcodia montagneana</i> (J.D. Hooker et Harvey) J. Agardh		+	+	+
	Solieriaceae	<i>Eucheuma serra</i> (J. Agardh) J. Agardh		+	+	+
	Rhizophyllidaceae	<i>Portieria hornemannii</i> (Lyngbye) P.C. Silva	+	+	+	+
Rhodomeniales	Champiaceae	<i>Champia bifida</i> Okamura				+
Ceramilales	Rhodomelaceae	<i>Acanthophora spicifera</i> (M. Vahl) Børgesen	+	+	+	+
		<i>Acrocystis nana</i> Zanardini	+			+
		<i>Bostrychia tenella</i> (J.V. Lamouroux) J. Agardh	+			+
		<i>Laurencia intermedia</i> Yamada	+	+	+	+
		<i>Laurencia papillosa</i> (C. Agardh) Greville	+	+	+	+
		<i>Melanamansia glomerata</i> (C. Agardh) R.E. Norris		+	+	+
		<i>Vidalia obtusiloba</i> (Merten ex C. Agardh) J. Agardh	+		+	+
Unknown red alga			+	+	+	+
Cyanophyta						
Oscillatoriales	Oscillatoriaceae	<i>Symploca hydroides</i> (Harvey) Kützinger	+		+	+
	Stigonemataceae	<i>Brachytrichia quoyi</i> (C. Agardh) Bornet et Flahault				+

Figure 3 Dendrograms for hierarchical clustering of macroalgal assemblage (similarity threshold at 35%) based on Bray Curtis similarities and multidimensional scaling (MDS) ordination. Number indicates the sampling station, for example, 0 represents the 0-m station.

Figure 4 Species richness, percentage cover and biomasses of each station along each transect. Data are presented as means $\pm$ SD ($n=4$).

cilaria coronopifolia and *Laurencia papillosa* were abundant on the lower reef flat and *Halimeda* spp., *Portiera hornemannii* and *Mastophora rosea* were abundant on the reef slope. *Jania adhaerens*, the common turf alga

observed in this study coral reef, was abundant on the lower reef flat.

The results from cluster analysis and MDS ordination analysis of species cover (%) (without data transforma-

Table 3 Seasonal changes in species richness (species number/m²), cover (%) and biomass (g WW/m²) of total macroalgae and abundant macroalgae.

		Oct. 1999	Jan. 2000	Apr. 2000	Aug. 2000	F	P
Total macroalgae	Species richness	12.77±6.91a	14.73±5.79a	13.32±5.38a	14.91±7.78a	1.05	0.6192
	Cover	31.92±9.4b	23.74±3.38ab	36.28±9.26a	23.44±6.87ab	6.85	0.0061
	Biomass	359.34±100.95b	434.27±50.82b	948.49±160.84a	341.31±98.82b	3.67	0.0438
<i>Enteromorpha linza</i>	Cover	2.47±4.17ab	1.78±2.16b	1.44±2.75b	4.13±5.02a	4.07	0.0072
	Biomass	64.08±4.43a	43.95±2.20a	37.46±2.94a	107.85±5.21a	2.15	0.0933
<i>Ulva lactuca</i>	Cover	1.24±1.54ab	0.87±1.09b	0.45±0.96b	2.11±2.89a	5.30	0.0014
	Biomass	30.35±1.59a	19.44±1.08a	12.26±1.03a	54.24±3.04a	0.19	0.9040
<i>Halimeda macroloba</i>	Cover	0.39±0.49a	0.99±0.76a	0.63±1.64a	0.34±0.74a	0.83	0.7530
	Biomass	9.83±0.51b	20.76±0.75a	8.72±1.32b	8.09±0.79b	17.05	0.0008
<i>Halimeda opuntia</i>	Cover	0.31±0.40a	0.22±0.48a	0.61±1.04a	0.66±1.08a	0.82	0.6807
	Biomass	6.66±0.39c	4.81±0.49c	13.16±1.07b	16.80±1.15a	15.30	0.0092
<i>Padina australis</i>	Cover	0.03±0.07a	0.17±0.37a	1.89±3.05a	0.03±0.11a	0.18	0.6279
	Biomass	0.22±0.71ab	3.23±7.41ab	31.02±51.79a	1.34±3.87ab	0.99	0.0491
<i>Sargassum berberifolium</i>	Cover	0.99±1.40b	3.76±7.39b	11.47±12.54a	0.06±0.14b	17.49	0.0001
	Biomass	25.86±1.47b	101.63±7.84b	294.88±13.07a	1.61±0.15b	19.80	0.0001
<i>Sargassum polycystum</i>	Cover	0.03±0.07b	5.10±7.65a	3.74±4.82a	0.07±0.25b	16.37	0.0001
	Biomass	0.56±0.07c	128.66±8.04a	100.33±4.98b	2.00±0.27c	14.47	0.0001
<i>Sargassum siliculosum</i>	Cover	0.02±0.10b	0.05±0.24b	3.40±4.35a	0.36±0.67b	16.43	0.0001
	Biomass	0.50±0.10b	1.38±0.26b	91.00±4.49a	9.57±0.71b	10.73	0.0001
<i>Gracilaria coronopifolia</i>	Cover	3.72±4.91a	2.28±2.74ab	0.91±1.16b	2.08±2.75b	7.32	0.0001
	Biomass	97.83±5.12a	61.43±2.79a	23.63±1.21b	55.02±2.87a	5.51	0.0010
<i>Mastophora rosea</i>	Cover	0.23±0.37a	0.23±0.42a	0.22±0.41a	0.37±0.51a	0.69	0.8152
	Biomass	4.94±0.37b	5.94±0.45b	5.23±0.43b	9.90±0.53a	2.92	0.0496
<i>Laurencia intermedia</i>	Cover	2.98±3.81a	0.03±0.11ab	0.34±0.56ab	1.37±2.21a	1.05	0.0435
	Biomass	75.55±3.95a	0.89±0.11d	8.80±0.59c	35.12±2.34b	19.32	0.0001
<i>Laurencia papillosa</i>	Cover	1.83±2.29a	1.17±1.72ab	0.46±0.55b	2.30±3.65a	4.66	0.0032
	Biomass	47.53±2.39a	30.86±1.81b	11.81±0.57c	56.06±3.89a	10.78	0.0001
<i>Hypnea charoides</i>	Cover	1.67±2.46ab	2.47±2.33ab	1.40±1.89b	3.24±4.11a	2.86	0.0365
	Biomass	41.37±2.61b	60.69±2.45b	36.41±1.98ab	81.85±4.37a	6.12	0.0004
<i>Portieria hornemannii</i>	Cover	0.13±0.29b	0.17±0.36b	0.63±0.96a	0.53±1.04ab	2.02	0.0465
	Biomass	1.90±0.17c	3.41±0.35c	11.53±0.81a	9.12±0.87b	8.71	0.0098

Data are presented as means±SD (n=108). Different letters indicate significant differences at $p<0.05$ (Tukey).

tion) using Bray Curtis similarity measures discerned three groups corresponding to three zones similar to our preliminary investigations in April and August 1999: an upper reef flat (5–20 m from MHWS), a lower reef flat (30–80 m from MHWS) and a reef slope (95–130 m from MHWS) (Figure 3). The 0 m, 25 m, 85 m and 90 m stations were not included to avoid marginal effects. The data on total macroalgal biomass and percentage cover and species richness (i.e., species number per m²) also showed three zones similar to the above patterns (Figure 4).

The data for 108 sampling stations were pooled and averaged for analysis to give an overall picture of seasonal changes in macroalgal abundance: species richness did not show seasonal variations (ANOVA, $F_{3,78}=1.05$, $p=0.6192$) but total macroalgal cover (ANOVA, $F_{3,78}=6.85$, $p=0.0061$) and biomass (ANOVA, $F_{3,78}=3.67$, $p=0.0001$) were temporally variable, with a peak in April 2000 (Tukey, $p<0.05$) (Table 3). Percentage cover and/or biomasses of abundant macroalgae also showed seasonal variations (Table 3).

Apart from significant seasonal variations, species richness (ANOVA, $F_{2,78}=161.82$, $p<0.0001$), percentage cover (ANOVA, $F_{2,78}=215.18$, $p<0.0001$) and biomass (ANOVA, $F_{2,78}=261.33$, $p<0.0001$) also show zone variations (Figure 5). Species richness, percentage cover and biomass were highest in the lower reef flat. The percentage cover and biomass of common species also showed

zoned variation. *Enteromorpha linza*, *Gracilaria coronopifolia*, *Hypnea charoides* and an unknown red alga were common in the upper reef flat, while *Ulva lactuca*, *Sargassum* spp. (especially in the stations of 45–70 m) and *Laurencia* spp. were abundant in the lower reef flat. We found that *Halimeda macroloba* bloomed in the upper reef flat in January 2000. The most abundant alga, *Sargassum*, bloomed in the cooler months and we have identified 5 species in this survey: *S. berberifolium*, *S. polycystum* and *S. siliculosum* were abundant and *S. glaucescens* and *S. sandei* were less abundant. The calcified algae *Halimeda* spp. and *Mastophora rosea* were abundant on the reef slope.

Evenness (J') showed zonation variations (ANOVA, $F_{2,78}=23.34$, $p<0.0001$) but did not show seasonal variations (ANOVA, $F_{3,78}=2.28$, $p=0.1112$) (Figure 5). Species diversity (H') showed zonation (ANOVA, $F_{2,78}=102.81$, $p<0.0001$) and seasonal (ANOVA, $F_{3,78}=4.43$, $p=0.0063$) variations (Figure 5). Evenness and species diversity in the upper reef flat showed seasonal variations while those in the lower reef flat and reef slope did not show seasonal variations. In the upper reef flat, evenness and diversity in October 1999 and August 2000 were lower than those in January and April 2000 (Figure 5). The k -dominance curves also showed that species diversity was higher in both the lower reef flat and the reef slope than in the upper reef flat, reflecting higher species number on the lower reef flat and the reef slope (Figure 6).

Figure 5 Species richness, percentage cover, biomass, evenness (J') and species diversity (H') on the upper reef flat, the lower reef flat and the reef slope.

Means are indicated and different symbols indicate significant differences at $p < 0.05$ (Tukey).

Figure 6 k -dominance curves for macroalgal species abundance in three zones and four seasons.

On the upper reef flat, species diversity in October 1999 and August 2000 was lower than in January and April 2000; this was due to the dominance of the unknown red alga in October 1999 and *Enteromorpha linza* in August 2000 (Figure 6). It is evident that the macroalgal assemblage is more structured in the lower reef flat compared to the upper reef flat.

The MDS analysis of three zones (the upper reef flat, the lower reef flat and the reef slope) showed that the

macroalgal assemblage in the lower reef flat can be grouped into 2 clusters corresponding to the warmer months (October 1999 and August 2000) and the cooler months (January 2000 and April 2000) (Figure 7). It is clear that the macroalgal assemblage is primarily structured by zone and secondarily by season.

The results of ANOSIM tests showed that the species structure was significantly different not only between zones but also between seasons ($p < 0.05$) (Table 4). The Global R value for structure difference between October 1999 and August 2000 was lower than for other comparisons, indicating that the difference between October 1999 and August 2000 was relatively small as compared to other seasons (Table 4).

The results of SIMPER analyses showed that in the warmer months (October 1999 and August 2000), *Gracilaria coronopifolia*, *Enteromorpha linza*, *Laurencia* spp. and *Hypnea charoides* were the most important taxa separating the lower reef flat assemblage and assemblages in two other zones, and *Enteromorpha linza* (for August 2000), *Halimeda* spp., *Mastophora rosea*, *Portieria hornemannii* and the unknown red alga (for October 1999) were the species mostly responsible for differences in assemblage structure between the upper reef flat and the reef slope (Table 5). The data from Table 5 and the percentage cover (Table 6) and biomass (Table 7) showed that in October 1999 and August 2000, *Gracilaria coro-*

Figure 7 Multidimensional scaling (MDS) ordination of samples taken on the upper reef flat (○), the lower reef flat (□) and the reef slope (△).

Table 4 Global R values of two-way (sampling time and zone) crossed ANOSIM tests.

Global R value for structure difference			
Between sampling times	zones		
Oct. 1999–Jan. 2000	0.676*	Upper reef flat–lower reef flat	0.979*
Oct. 1999–Apr. 2000	0.798*	Upper reef flat–reef slope	0.978*
Oct. 1999–Aug. 2000	0.412*	Lower reef flat–reef slope	0.994*
Jan. 2000–Apr. 2000	0.611*		
Jan. 2000–Aug. 2000	0.704*		
Apr. 2000–Aug. 2000	0.723*		

*Significance level <5%.

nopifolia, *Enteromorpha linza*, *Laurencia* spp. and *Hypnea charoides* were abundant in the lower reef flat (Tukey, $p < 0.05$), and *Halimeda* spp., *Mastophora rosea* and *Portiera hornemannii* were abundant in the reef slope (Tukey, $p < 0.05$).

In the cooler months (January and April 2000), the results of SIMPER analyses indicate that the species responsible for difference in structures between the upper reef flat and two zones were *Sargassum* spp., *Gracilaria coronopifolia*, *Enteromorpha linza* and *Padina australis*, and those responsible for difference between the upper reef flat and the reef slope were *Hypnea charoides*, *Halimeda* spp., *Mastophora rosea*, *Enteromorpha linza* and *Portiera hornemannii* (Table 5). Tables 6 and 7 show that in the cooler months, *Sargassum* spp., *Gracilaria coronopifolia* and *Padina australis* had higher percentage cover and biomass in the lower reef flat, while *Halimeda* spp., *Mastophora rosea* and *Portiera hornemannii* had higher percentage cover and biomass in the reef slope (Tukey, $p < 0.05$).

Discussion

The present study shows that macroalgae are highly abundant on a tropical nearshore coral reef in Nanwan Bay in southern Taiwan. Macroalgal biomass appeared to follow a distinct seasonal pattern with blooms in spring (April) and a decline in the warmer months. As compared to a previous study (carried out by random sampling in the lower reef flat at the same site) showing that macroalgal cover and biomass in April of 1987 ranged from 30–70% and 20–160 g wet weight (WW)/m², respectively (Chiang and Wang 1988), the present results obtained from transect surveys indicate a significant increase in macroalgal biomass over the past 12 years. In April of 2000, macroalgal cover in the lower reef flat ranged from 28.79–88.51% and biomass ranged from 184.60–770.82 g WW/m². Further, the 4-season survey (during 1987–1988) by Wang and Chiang (1988) reported that the most dominant alga at the lower reef flat in this coral reef was a rhodophyte *Hydroclathrus clathratus* (32.16% coverage in April) and there was one *Sargassum* species (*Sargassum polycystum*) recorded with a percentage cover of 18.38% in April of 1987. However, their survey in 1994 at the same site showed that *Sargassum* had become the most dominant species in Hengchuan Peninsula (Wang and Chiang 1994). The present study (1999–2000) also found that *Sargassum* populations had large standing stocks on this coral reef in Nanwan Bay, with maximum percentage cover and biomass of 18.61%

and 486.21 g WW/m² (64.53% and 63.68% of total macroalgal cover and biomass, respectively) in April 2000. So, the spread of *Sargassum* is evident on a coral reef of Nanwan Bay over the past few years.

The patterns of macroalgal assemblage in Nanwan Bay appeared markedly different across water depths and seasons. Erect algae were the dominant component on this coral reef, and their composition and abundance varied significantly between zones and seasons. The lower reef flat assemblage exhibited higher species number, evenness and diversity as compared to the upper reef flat and the reef slope. Most of the abundant species such as *Sargassum* spp., *Gracilaria coronopifolia*, *Laurencia* spp. and *Hypnea charoides* occurred largely on the lower reef flat. The *Sargassum* population in the lower reef flat showed a marked seasonal fluctuation with the maximum abundance in April, with only holdfasts and/or plants with small shoots remaining in the hot summer months.

It is known that the growth and distribution of macroalgae are influenced by physical factors such as temperature, light, salinity and water movements (Lüning 1993, Andrew and Viejo 1998), and increased nutrient concentrations in water columns should also be considered. Our recent investigation provides several lines of evidence showing that increased nutrient input is one of the factors leading to the overgrowth by *Sargassum* in Nanwan Bay (Hwang et al. 2004). The impact of seawater temperature on *Sargassum* seasonality has also been shown in Hawaii (DeWreede 1976), the British Isles (Jephson and Gray 1977) and Northern Philippines (Hurtado and Ragaza 1999). Using canonical correlation analysis ($p < 0.05$), temperature was extracted to correlate with primary cover of *Sargassum* from reefs at Balibago, Luzon, Philippines (Ang 1986). It is also suggested in our recent study that *Sargassum* seasonality in Nanwan Bay is linked to temporal variations in seawater temperature (Hwang et al. 2004). Possibly, temperature and nutrients interact to affect *Sargassum* growth in southern Taiwan.

The upper reef flat had lower species number, evenness and diversity; in this zone, *Enteromorpha linza* was the most common taxon in all seasons, possibly due to its high tolerance to long air exposure times and higher temperature in the upper regions of the intertidal zone. This agrees with the view that *Enteromorpha* is one of the most stress resistant macroalgae (Littler and Littler 1980). Further, the data on seasonal changes in evenness and species diversity values and k -dominance curves in the upper reef flat reveal that the upper reef flat assemblage in the warmer months was less diverse than that in the cooler months, and this is mainly due to the dis-

Table 5 Results of SIMPER test on percentage contributions of species for significant ANOSIM contrasts.

Species	Mean abundance	Mean abundance	Contribution (%)	Cumulative contribution (%)
Oct. 1999				
	Upper reef flat	Lower reef flat		
<i>Gracilaria coronopifolia</i>	0.00	8.15	20.52	20.52
<i>Laurencia intermedia</i>	0.00	6.29	16.36	36.88
<i>Enteromorpha linza</i>	0.49	5.26	12.19	49.08
<i>Laurencia papillosa</i>	0.00	3.96	10.78	59.86
	Upper reef flat	Reef slope		
Unknown red alga	4.50	0.00	60.43	60.43
<i>Halimeda macroloba</i>	0.00	0.90	11.27	71.69
<i>Mastophora rosea</i>	0.00	0.53	6.88	78.58
<i>Halimeda opuntia</i>	0.00	0.52	6.54	85.12
	Lower reef flat	Reef slope		
<i>Gracilaria coronopifolia</i>	8.15	0.00	21.14	21.14
<i>Laurencia intermedia</i>	6.29	0.00	16.88	38.02
<i>Enteromorpha linza</i>	5.26	0.00	12.83	50.85
<i>Laurencia papillosa</i>	3.96	0.00	11.16	62.01
Jan. 2000				
	Upper reef flat	Lower reef flat		
<i>Sargassum polycystum</i>	0.00	10.42	25.61	25.61
<i>Sargassum berberifolium</i>	0.00	8.47	18.96	44.57
<i>Gracilaria coronopifolia</i>	0.08	5.09	12.64	57.22
<i>Enteromorpha linza</i>	0.73	3.48	7.89	65.10
	Upper reef flat	Reef slope		
<i>Hypnea charoides</i>	2.63	0.00	29.90	29.90
<i>Halimeda macroloba</i>	2.21	0.49	19.65	49.55
<i>Mastophora rosea</i>	0.00	0.74	7.82	57.37
<i>Enteromorpha linza</i>	0.73	0.00	6.47	63.84
	Lower reef flat	Reef slope		
<i>Sargassum polycystum</i>	10.42	0.45	22.54	22.54
<i>Sargassum berberifolium</i>	8.47	0.00	17.21	39.76
<i>Gracilaria coronopifolia</i>	5.09	0.02	11.73	51.48
<i>Hypnea charoides</i>	4.40	0.00	9.72	61.20
Apr. 2000				
	Upper reef flat	Lower reef flat		
<i>Sargassum berberifolium</i>	0.00	24.11	42.95	42.95
<i>Sargassum polycystum</i>	0.00	8.05	14.01	56.96
<i>Sargassum siliculosum</i>	0.00	7.56	13.17	70.13
<i>Padina australis</i>	0.00	4.14	6.79	76.92
	Upper reef flat	Reef slope		
<i>Halimeda opuntia</i>	0.00	1.50	20.13	20.13
<i>Enteromorpha linza</i>	0.88	0.00	14.91	35.04
<i>Portieria hornemannii</i>	0.00	1.08	11.70	46.74
<i>Mastophora rosea</i>	0.00	0.65	10.22	56.96
	Lower reef flat	Reef slope		
<i>Sargassum berberifolium</i>	24.11	0.69	39.69	39.69
<i>Sargassum polycystum</i>	8.05	0.47	12.66	52.35
<i>Sargassum siliculosum</i>	7.56	0.03	12.46	64.81
<i>Padina australis</i>	4.14	0.00	6.48	71.29
Aug. 2000				
	Upper reef flat	Lower reef flat		
<i>Enteromorpha linza</i>	1.38	8.64	21.40	21.40
<i>Hypnea charoides</i>	0.13	6.79	18.26	39.67
<i>Gracilaria coronopifolia</i>	0.00	4.58	12.54	52.21
<i>Laurencia papillosa</i>	0.00	4.67	12.47	64.68
	Upper reef flat	Reef slope		
<i>Enteromorpha linza</i>	1.38	0.00	14.42	14.42
<i>Halimeda macroloba</i>	0.00	0.95	13.65	28.07
<i>Mastophora rosea</i>	0.00	0.76	11.35	39.42
<i>Portieria hornemannii</i>	0.00	0.88	9.81	49.23
	Lower reef flat	Reef slope		
<i>Enteromorpha linza</i>	8.64	0.00	20.95	20.95
<i>Hypnea charoides</i>	6.79	0.00	15.97	36.92
<i>Gracilaria coronopifolia</i>	4.58	0.00	10.77	47.70
<i>Laurencia papillosa</i>	4.67	0.00	10.75	58.44

Table 6 Cover (%) (means $\pm$ SD, n=6) of macroalgal species from SIMPER test.

	Upper reef flat	Lower reef flat	Reef slope
	Oct. 1999		
<i>Enteromorpha linza</i>	2.78 $\pm$ 4.82	5.26 $\pm$ 5.02	0.00
<i>Halimeda macroloba</i>	0.00	0.22 $\pm$ 0.24	0.90 $\pm$ 0.56
<i>Halimeda opuntia</i>	0.00	0.21 $\pm$ 0.36	0.52 $\pm$ 0.41
<i>Gracilaria coronopifolia</i>	0.00	8.15 $\pm$ 4.22	0.00
<i>Mastophora rosea</i>	0.00	0.06 $\pm$ 0.10	0.53 $\pm$ 0.49
<i>Laurencia intermedia</i>	0.00	6.29 $\pm$ 3.26	0.00 $\pm$ 0.01
<i>Laurencia papillosa</i>	0.00	3.96 $\pm$ 1.80	0.00 $\pm$ 0.01
Unkown red alga	2.29 $\pm$ 2.19	1.11 $\pm$ 1.80	0.00
	Jan. 2000		
<i>Enteromorpha linza</i>	9.24 $\pm$ 16.00	3.48 $\pm$ 1.93	0.00
<i>Halimeda macroloba</i>	0.00	0.85 $\pm$ 0.64	0.49 $\pm$ 0.42
<i>Sargassum berberifolium</i>	0.00	8.47 $\pm$ 9.25	0.00 $\pm$ 0.00
<i>Sargassum polycystum</i>	0.00	10.42 $\pm$ 8.70	0.45 $\pm$ 0.77
<i>Gracilaria coronopifolia</i>	0.18 $\pm$ 0.31	5.09 $\pm$ 1.50	0.02 $\pm$ 0.04
<i>Hypnea charoides</i>	4.20 $\pm$ 5.89	4.40 $\pm$ 1.89	0.00
<i>Mastophora rosea</i>	0.00	0.00	0.74 $\pm$ 0.48
	Apr. 2000		
<i>Enteromorpha linza</i>	0.25 $\pm$ 0.30	2.98 $\pm$ 3.60	0.00
<i>Halimeda opuntia</i>	0.00	0.09 $\pm$ 0.24	1.50 $\pm$ 1.41
<i>Padina australis</i>	0.00	4.14 $\pm$ 3.45	0.00 $\pm$ 0.01
<i>Sargassum berberifolium</i>	0.00	24.11 $\pm$ 7.06	0.69 $\pm$ 1.20
<i>Sargassum polycystum</i>	0.00	8.05 $\pm$ 4.24	0.47 $\pm$ 0.93
<i>Sargassum siliguosum</i>	0.00	7.56 $\pm$ 3.27	0.03 $\pm$ 0.09
<i>Portieria hornemannii</i>	0.00	0.24 $\pm$ 0.46	1.08 $\pm$ 1.05
<i>Mastophora rosea</i>	0.00	0.00 $\pm$ 0.00	0.65 $\pm$ 0.52
	Aug. 2000		
<i>Enteromorpha linza</i>	0.15 $\pm$ 0.21	8.64 $\pm$ 4.16	0.00
<i>Gracilaria coronopifolia</i>	0.00	4.58 $\pm$ 2.34	0.00
<i>Hypnea charoides</i>	0.00	6.79 $\pm$ 3.78	0.00
<i>Portieria hornemannii</i>	0.00	0.04 $\pm$ 0.07	0.95 $\pm$ 1.15
<i>Mastophora rosea</i>	0.00	0.32 $\pm$ 0.45	0.76 $\pm$ 0.60
<i>Laurencia papillosa</i>	0.00	4.67 $\pm$ 4.34	0.00

appearance of several algae in October and August, such as *Halimeda macroloba*, *Hydroclathrus clathratus*, *Hypnea cervicornis*, *Hypnea charoides* and *Vidalia obtusiloba*. In the upper reef flat, the occurrence of *Enteromorpha linza* might be also considered as the result of eutrophication. However, the impacts of air-exposure, high temperature and high irradiance can be more profound than the effects of nutrient enrichment for the growth of *Enteromorpha linza* in the upper reef flat.

The reef slope zone, a subtidal reef flat bordered by a sloping coralline rocky stretch that has a strong undertow is characterized by *Halimeda* spp. and *Mastophora rosea* in all seasons and *Portieria hornemannii* in April and August 2000. Grazing, irradiance and wave action are considered the factors governing the structure of benthic macroalgal assemblages on the reef slope (Lobban and Harrison 1997).

In conclusion, this study provides evidence that Nanwan coral reefs in southern Taiwan are now characterized by abundant macroalgae, and MDS analyses show the assemblage to be structured primarily by zone and secondarily by season. Although macroalgae are important as primary producers in coral reef systems, overgrowing macroalgae can compete for both space and light with corals and cause adverse effects on the growth of corals

in Nanwan Bay. To provide the proper management of benthic communities on southern Taiwan coral reefs, there is need to ascertain the relative importance of abiotic and biotic (such as herbivores) factors affecting the growth of macroalgae.

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Table 7 Biomass (g WW/m²) of macroalgal species from SIMPER test.

	Upper reef flat	Lower reef flat	Reef slope
Oct. 1999			
<i>Enteromorpha linza</i>	2.78±4.82	126.87±163.68	0.00
<i>Halimeda macroloba</i>	0.00	2.56±3.09	3.05±2.42
<i>Halimeda opuntia</i>	0.00	0.29±0.70	2.06±1.05
<i>Gracilaria coronopifolia</i>	0.00	49.58±25.73	0.00
<i>Mastophora rosea</i>	0.00	0.24±0.48	2.00±1.79
<i>Laurencia intermedia</i>	0.00	95.28±66.10	0.10±0.29
<i>Laurencia papillosa</i>	0.00	13.53±8.42	0.01±0.02
Unkown red alga	2.29±2.19	3.07±4.64	0.00
Jan. 2000			
<i>Enteromorpha linza</i>	9.24±16.00	54.62±49.53	0.00
<i>Halimeda macroloba</i>	0.00	25.30±23.30	15.14±14.76
<i>Sargassum berberifolium</i>	0.00	102.26±115.84	0.00
<i>Sargassum polycystum</i>	0.00	411.98±405.19	1.34±2.14
<i>Gracilaria coronopifolia</i>	0.18±0.31	41.56±29.12	0.25±0.71
<i>Hypnea charoides</i>	4.20±5.89	62.47±30.31	0.00
<i>Mastophora rosea</i>	0.00	0.00	13.55±9.40
Apr. 2000			
<i>Enteromorpha linza</i>	0.25±0.30	30.72±41.52	0.00
<i>Halimeda opuntia</i>	0.00	3.11±8.91	91.29±98.62
<i>Padina australis</i>	0.00	65.13±61.65	0.12±0.33
<i>Sargassum berberifolium</i>	0.00	537.16±263.60	15.63±29.05
<i>Sargassum polycystum</i>	0.00	218.75±139.33	9.09±17.89
<i>Sargassum siliculosum</i>	0.00	302.07±190.39	0.65±1.85
<i>Portieria hornemannii</i>	0.00	11.48±32.82	63.09±91.80
<i>Mastophora rosea</i>	0.00	0.00	30.53±30.33
Aug. 2000			
<i>Enteromorpha linza</i>	0.15±0.21	41.99±29.90	0.00
<i>Gracilaria coronopifolia</i>	0.00	36.33±20.02	0.00
<i>Hypnea charoides</i>	0.00	167.66±109.03	3.75±10.61
<i>Portieria hornemannii</i>	0.00	0.36±0.95	50.93±94.50
<i>Mastophora rosea</i>	0.00	3.31±5.27	41.43±51.80
<i>Laurencia papillosa</i>	0.00	12.41±10.72	0.39±1.11

Data are presented as means±SE (n=6).

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