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RESEARCH ARTICLE

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Factors affecting macroalgal distribution in a eutrophic tropical lagoon in Taiwan

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Abstract Factors affecting distribution of macroalgal periphyton were examined during a complete seasonal cycle in Tapong Bay, a eutrophic tropical lagoon in southern Taiwan. Water residence time varied from a few days to weeks. Total biomass and species richness declined with increasing residence time. However, they appeared to exhibit a unimodal seasonal pattern across all study sites, with blooms and greater richness in winter and spring and lower values in summer and fall. Nonmetric multidimensional scaling ordination of macroalgal communities reveals a clear gradual continuum of changes in species composition along the flushing gradient, suggesting the communities were primarily structured by site, and secondarily by season. The fast-flushing region was dominated by the chlorophycean genus *Ulva*, which was replaced by *Enteromorpha intestinalis* at mid-flushing levels, while the cyanobacterium *Lyngbya majuscula* was the dominant species in the slow-flushing region. Tissue nitrogen, but not tissue phosphorus, of these dominant species increased with increasing nutrient availability as a result of slow flushing. Our results suggest that water motion was an important selective factor for the spatial dominance of macroalgal species in Tapong Bay. This study demonstrates that species-dependent ordination is more sensitive in discriminating between sites than are species-independent measures such as total biomass and nutrient content when monitoring coastal eutrophication in the tropics. However, more-sensitive ordination provides only an 'early warning' that a community is changing; less-sensitive measures are also required to indicate the magnitude and type of these environmental changes.

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Introduction

Eutrophication resulting from excessive nutrient enrichment is commonly recognized as an increasing pollution problem in coastal waters worldwide (Nixon 1995). Among the most threatened systems are shallow coastal lagoons, many of which have relatively low volume-to-surface ratios and very restricted connections with the sea. The eutrophication impact is expected to be greater in the tropics than at higher latitudes (Corredor et al. 1999; Downing et al. 1999).

The occurrence of macroalgal blooms in coastal waters is an increasing phenomenon worldwide (e.g. Lapointe 1997; Valiela et al. 1997). Although herbivory may be important in controlling the standing crops of macroalgae (Hughes et al. 1999), its effects apparently occur on limited temporal and spatial scales (Hatcher and Larkum 1983; Valiela et al. 1997). Considering that eutrophication associated with expanding human populations and aquaculture is a major mechanism altering coastal ecosystems worldwide (Lapointe 1997; Valiela et al. 1997; Kamer et al. 2001; Souchu et al. 2001; Thacker and Paul 2001), much research has emphasized the bottom-up control of macroalgae by increased nutrient supply (Wheeler and Björnsäter 1992; Lyngby and Mortensen 1994; Horrocks et al. 1995; Fong et al. 1998; Costanzo et al. 2000).

Despite this research, we still cannot clearly predict the responses of macroalgae to coastal eutrophication. The flushing times in coastal waters range from a few days to months (Nixon et al. 1996). Macroalgae generally have lower surface-to-volume ratios and have a lower capacity to harvest nutrients from water than microalgae (Hein et al. 1995). In slow-flushing waters, phytoplankton are hypothesized to become the

dominant producers because they have an advantage in nutrient uptake kinetics and sufficient time to allow the cell divisions needed to produce a well-developed phytoplankton population. Increased abundance of phytoplankton might shade macroalgae and lead to a decline in macroalgal abundance. On the other hand, fast flushing may remove nutrients and phytoplankton so rapidly that they cannot accumulate and thus affect the growth of macroalgae. In addition, the resulting turbulence may modify the boundary layer and the frictional shear force around macroalgae. The importance of flushing has been shown in its regulation of the responses of phytoplankton in lakes (Vollenweider 1976) and the responses of periphyton in streams (Horner and Welch 1981) to nutrient loading. While earlier studies (Smith 1984; Knoppers et al. 1991; Valiela et al. 1997) have noted the significance of flushing on phytoplankton, the effects of flushing on the responses of macroalgae to eutrophication have not been quantified. The purpose of this study was to examine factors affecting distribution of macroalgal periphyton by characterizing the biomass patterns, species composition, and tissue nutrient content in a eutrophic tropical lagoon during a complete seasonal cycle in regions with different flushing levels.

Materials and methods

Study site

This study was conducted in Tapong Bay, a choked tropical lagoon in southern Taiwan (22°27′N, 120°26′E), with only one inlet (1 km long, 138 m wide, 2 m deep) permanently connecting it to the sea. This inlet provides tidal flushing and seawater inputs (Fig. 1). Tapong Bay has a 4.44-km^2 surface area with a mean depth of 2.2 m at low tide. The depth ranges from 1–2 m in the outer region to 3–4 m in the middle region and is < 2 m in the inner region. The bay is primarily subjected to semidiurnal tides with a tidal range of 1.0 m. Hydrographic observations by both Jen (2002) and Chen (2002) showed that the water level fluctuations and spatial salinity distribution in the lagoon were controlled by tides. Thus, tidal flushing is the dominant cause for the mixing of seawater and lagoon water. The spatial distribution of sediment grain size demonstrated that physical energies were high at the inlet and decreased toward the inner region (Jen 2002). The water residence time was estimated to be 8–24 days (4–12% day^{-1}) in the inner region and 4–12 days (8–25% day^{-1}) in the outer region (Hung 2001).

The land surrounding the lagoon consists of mangrove swamps and a variety of aquaculture ponds producing fish, shrimp, and shellfish. No large river flows into the lagoon, but it receives waste discharges providing nutrient-rich water from two creeks draining the surrounding aquaculture ponds. Direct release of nutrients by reared oysters may also result in increases of nutrient concentrations in the water column. According to the stoichiometrically linked water–salt–nutrient budgets (Hung 2001), the loading rates of nitrogen (N) and phosphorus (P) in the lagoon were estimated to be 1.9 and 0.51 mol m^{-2} year^{-1}, respectively. The Lipan Creek in the inner region is the major source of nutrients into the lagoon (Hung 2001).

Tapong Bay is densely covered by thousands of oyster-culture pens. The surfaces of oyster pens, which are made of bamboo, provide large areas of substrata for colonization by periphyton. The pens are not routinely cleaned, and dense periphyton has become an abundant and ecologically important component in the lagoon.

Sampling and processing of macroalgal periphyton

Five study sites (A–E) along a transect across the lagoon were selected (Fig. 1). At each site, three oyster-culture pens were randomly sampled in June 2000 (summer, water temperature 26–31°C), October 2000 (fall, 25–26°C), January 2001 (winter, 22–25°C), and April 2001 (spring, 25–26°C). In southern Taiwan, spring and fall are transition periods between summer and winter and are relatively short (about 1–2 months). The submerged part of each oyster-culture pen, measuring 10×60 cm, was gently scraped. Macroalgal samples were kept in a cooler and brought back to the laboratory. Here they were gently swept to remove epiphytes, debris, mud, and animals. Macroalgal samples were then rinsed briefly with distilled water to remove salts, sorted by species, and weighed. They were then dried at 60°C and ground in mortar for tissue N and P analyses. Tissue N content was determined with a CHN-OS rapid element analyzer (Heraeus). Tissue P content was measured colorimetrically with a spectrophotometer following persulfate digestion of the sample (Solorzano and Sharp 1980).

Measurements of environmental variables

Environmental variables in the water column were measured at each site concurrently with sampling of periphyton, with the exception of water motion, which was studied once in April 2000 by means of the weight loss of plaster of Paris (about 40 g, $n = 5$) after 1 day of submersion in the water at each site following the method of Erftemeijer and Herman (1994). Water temperature and salinity were monitored in situ for 24 h at 10-min intervals using a YSI 600XLM multiparameter monitoring system. Light extinction coefficients in the water column for photosynthetically active radiation (PAR) were determined by light measurements using a Li-Cor Quantum Li-189 meter. Phytoplankton chlorophyll *a* was then determined with the spectrophotometeric method by immediately filtering water samples through Whatman GF/F filters in the field and then extracting in 90% aqueous acetone for 24 h at 4°C in the dark. Herbivorous fishes feeding on macroalgae were quantified monthly by electrofishing and gillnets. Electrofishing was conducted to quantify small fish in the night for 10 min at 12 V d.c. Gillnets (220 m long; 1.5 m high; mesh size 35 mm) were set to collect large fish in the night and lifted 1 h later.

Water samples for analyses of total dissolved nutrients and dissolved inorganic nutrients were collected in triplicate near the oyster-culture pens at each site and immediately placed on ice in a cooler. In the laboratory, each water sample was filtered through pre-combusted (at 450°C for 4 h) Whatman GF/F filters. Dissolved inorganic nitrogen (DIN: $NO_3 + NO_2 + NH_4$) and dissolved inorganic phosphorus (DIP: PO_4) were determined colorimetrically (Strickland and Parsons 1972) with a flow injection analysis method (Pai et al. 1990). Total dissolved nitrogen (DN) was measured with high-temperature oxidation and chemiluminescent detection (Antek N/S analyzer). Total dissolved phosphorus (DP) was measured with the UV-persulfate oxidation and colorimetric method (Ridal and Moore 1990). Dissolved organic phosphorus (DOP) and dissolved organic nitrogen (DON) were then determined from the differences between DP and DIP, and DN and DIN, respectively.

Data analysis

A two-way fixed analysis of variance (ANOVA) model was used to test whether differences in environmental variables and total macroalgal biomass depended on study sites (five levels) or seasons (four levels). Water motion was compared among sites (five levels) using a one-way fixed ANOVA model. The chi-square test for goodness of fit was used to compare the observed frequencies of herbivorous fish number with those of a random distribution across sites. Because of the limited samples for tissue nutrient analyses, macroalgal samples from summer and fall and from winter and

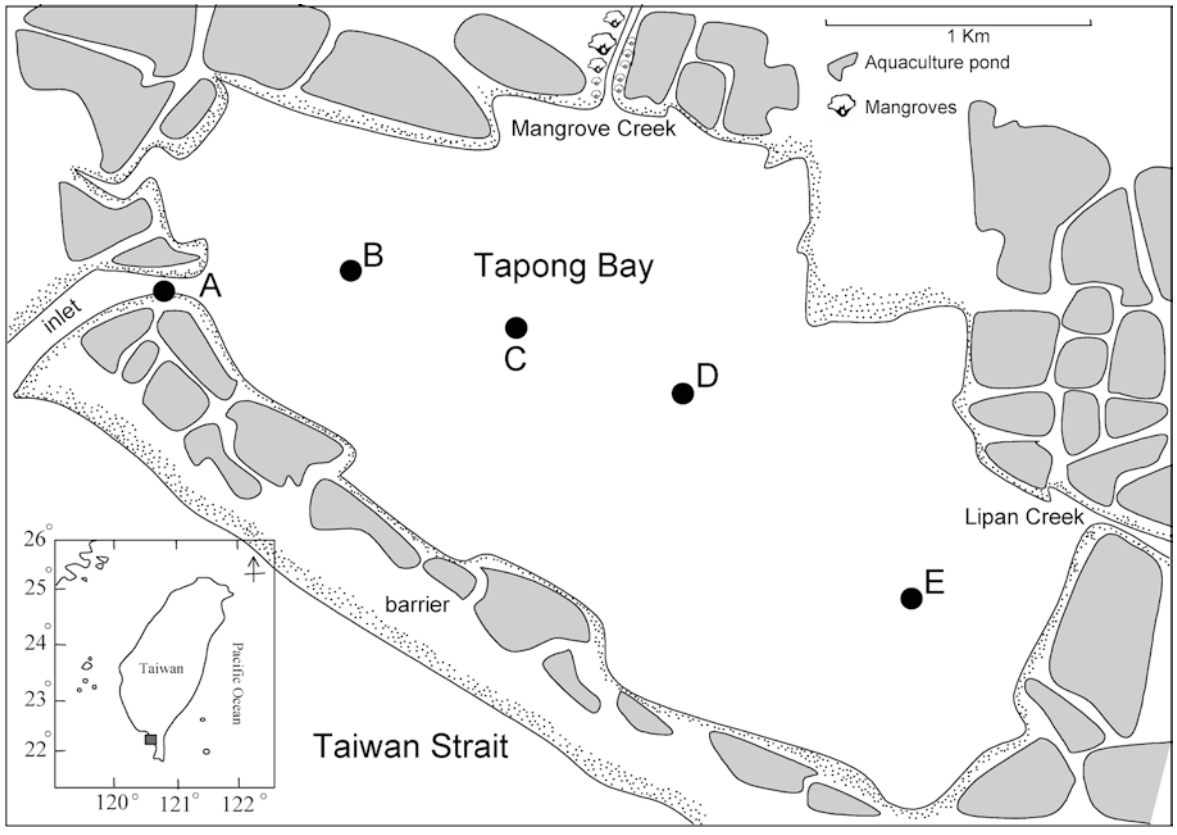

Fig. 1 Study sites (*A–E*) within the flushing gradient in Tapong Bay and surrounding land uses

spring were pooled for statistical analyses, respectively. A three-way fixed ANOVA model was used to evaluate whether tissue N and P and the tissue molar N:P ratio differed significantly among study sites (five levels), species (four levels), or times (two levels). Before the analyses, values of biomass, tissue N, and the tissue N:P ratio were 4th-root, square-root, and log transformed, respectively, using power transformations to conform to normality and homogeneity of variance assumptions (Clarke and Warwick 1994). If the results of ANOVA indicated significant main effects at the 0.05 probability level, then Fisher's protected least significant difference (LSD) test was used to determine which means significantly differed. The relationships between total macroalgal biomass and environmental variables and phytoplankton chlorophyll *a* were determined using Pearson correlations. These univariate statistical calculations were produced using the SAS system (vers. 8.1).

To reveal spatial and seasonal patterns of macroalgal communities in Tapong Bay, changes in species composition were studied using multivariate analyses in the PRIMER (vers. 5.2) computer package (Clarke and Gorley 2001). The Bray–Curtis coefficient was used to produce a dissimilarity matrix of species composition between any 2 samples according to the relative abundance of each species. The data matrix consisted of a total of 60 samples with 17 species.

The dissimilarity matrix was first classified by hierarchical agglomerative clustering using the unweighted pair group mean arithmetic (UPGMA) linking method and was then ordinated using nonmetric multidimensional scaling (MDS) techniques. Stress values < 0.2 indicate that a two-dimensional MDS plot gives a usable summary of sample relationships (Clarke and Warwick 1994). A two-way crossed ANOSIM (analysis of similarities) was used to determine whether the effects of site and season on species composition were significant by comparing the observed statistic to its permutation distribution for the absence of differences (Clarke and Warwick 1994). ANOSIM is a nonparametric analog of a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. If the results indicated significant main effects at the 0.05 probability level, pairwise comparisons and the Bonferroni correction for the significance level were used to determine which levels differed. Similarity of percentages (SIMPER) was employed to reveal the most common species for the replicate samples at each site in each season. The BIOENV analysis was used to examine which environmental variables best explained the observed patterns of species composition.

Results

Environmental variables

No significant differences in water temperature were observed among the study sites in Tapong Bay (Table 1, ANOVA, $P > 0.05$). However, light extinction showed a significant interaction between site and season (ANOVA, $P = 0.004$). At site E, light extinction was higher in summer when phytoplankton bloomed. However, water motion was significantly faster at site A and slower at sites D and E (ANOVA, $P < 0.001$, Fisher's LSD test). The spatial pattern in water motion corresponded well with the estimated water residence time (Hung 2001) and with the spatial sediment grain-size distribution pattern (Jen 2002) in Tapong Bay. As a result, salinity was significantly greater at site A and lower at site E (ANOVA, $P < 0.001$, Fisher's LSD). However, since no large river flowed into the lagoon, salinity remained high (> 17 psu) across all study sites with a small decrease from mean values of 32 psu at site A to 27 psu at site

Table 1 Environmental variables (mean ± SD, $n = 12$) measured and total number of herbivorous fish ($n = 11$) caught by electrofishing and gillnets at five study sites along the flushing gradient in Tapong Bay from June 2000 to April 2001 except water motion, which was studied in April 2000 by means of the weight loss of plaster of Paris in water (mean ± SD, $n = 5$)

Site	Location	Water motion (g day^{-1})	Temperature (°C)	Salinity (psu)	Light extinction coefficient (m^{-1})	Total number of herbivorous fish
A	22°27′5″N120°27′4″E	15 ± 3	25.8 ± 2.2	32.1 ± 3.7	1.11 ± 0.34	145
B	22°27′7″N120°27′15″E	7.4 ± 0.8	26.0 ± 2.1	29.6 ± 6.9	0.96 ± 0.47	81
C	22°26′59″N120°27′38″E	6.5 ± 0.5	25.9 ± 2.5	30.7 ± 5.7	0.75 ± 0.18	84
D	22°26′50″N120°27′59″E	5.2 ± 0.1	25.9 ± 2.4	29.0 ± 7.3	0.92 ± 0.21	152
E	22°26′45″N120°28′30″E	5.3 ± 0.6	25.8 ± 2.9	27.0 ± 7.0	0.90 ± 0.26	14

E. In contrast to the seasonal pattern of water temperature, salinity was greater in winter and lower in summer (ANOVA, $P < 0.001$, Fisher's LSD test). Higher numbers of herbivorous fish were caught at sites A and D, and lower numbers were caught at site E (the chi-square test for goodness of fit, $P < 0.0001$).

Water column nutrient concentrations (Fig. 2) and phytoplankton chlorophyll *a* (Fig. 3) also showed clear spatial and seasonal patterns. DIN and DIP in the water column and phytoplankton chlorophyll *a* were significantly higher at site E, which is subjected to poor flushing, and lower at site A, which is subjected to better flushing (ANOVA, $P < 0.05$, Fisher's LSD test). Despite a lack of statistical significance, DON and DOP in the water column were also higher at sites D and E and lower at site A. Changes in concentrations of DIN, DON, and DOP, but not DIP, were also significant among seasons (ANOVA, $P = 0.01$, Fisher's LSD test). DIN and DON in the water column were higher in winter and lower in summer and fall, but DOP was higher in fall and lower in winter. Phytoplankton chlorophyll *a* peaked in summer across all study sites.

Total biomass

Total macroalgal biomass was not stimulated by increased nutrient concentrations in the water column as a result of poor flushing (Fig. 4). Biomass values at sites A, B, and C were significantly greater than those at sites D and E, and the biomass at site D was also significantly greater than that at site E (ANOVA, $P < 0.001$, LSD test). The maximum reached 465–732 g wet weight m^{-2} at sites A, B, and C, compared to 137 g wet weight m^{-2} at site E. Total biomass appeared to exhibit a unimodal seasonal pattern across all study sites, with macroalgal blooms in winter or spring and lower biomass in summer or fall (ANOVA, $P < 0.001$, LSD test). At site E, however, not only was the duration of blooms shorter, but the amplitude was also smaller. While blooms began earlier in winter and continued throughout spring at site A, biomass was greater only in spring at site E.

Pearson correlations indicated that salinity correlated positively ($r = 0.55$, $P = 0.01$), and DP ($r = -0.43$, $P = 0.05$) and phytoplankton chlorophyll a ($r = -0.48$, $P = 0.03$) negatively with total macroalgal biomass.

Species composition

In total, 17 species were collected on the surfaces of oyster-culture pens in Tapong Bay during the study period (Table 2). Species richness declined from the outer to the inner region. Site E subject to slow flushing had the lowest species richness (5 species). Here only the cyanobacterium *Lyngbya majuscula* and the chlorophyte *Enteromorpha intestinalis* were frequently observed. The highest species richness was observed at site B, subject to fast flushing (15 species).

The maximum species richness was found in winter (15 species), followed by spring (13 species), summer (8 species), and fall (7 species). The Chlorophyta displayed the greatest species richness (9 species) followed by the Rhodophyta (7 species) and Cyanobacteria (1 species; Table 3). *E. intestinalis*, *Ulva lactuca*, and *L. majuscula* occurred in large numbers all year round. Rhodophytes occurred mostly in winter.

Community ordination

Since the stress value is low (< 0.1), an MDS ordination of multivariate analyses is a more useful representation than is a cluster analysis (Clarke and Warwick 1994), and thus only results of MDS ordination are shown here. MDS ordination of the macroalgal communities corresponded well to the gradient determined by water residence time and revealed a clear gradual continuum of changes in species composition along the gradient in Tapong Bay (Fig. 5). Generally, communities from each site are placed close to their true locations in the lagoon with site A at the upper left, site E at the lower right, and sites B, C, and D scattering in the center. Communities collected at sites D and E were more seasonally dispersed than others. At both sites, the communities collected in winter and spring when species richness was higher moved toward those collected at sites B and C.

Two-way crossed ANOSIM analyses demonstrate that communities differed significantly among sites and among seasons (Table 4). The pairwise comparisons show that the communities collected at site A were well separated from the others. The communities from site E were also distinct from those collected at site B or C. However, the communities collected at sites B, C, and D,

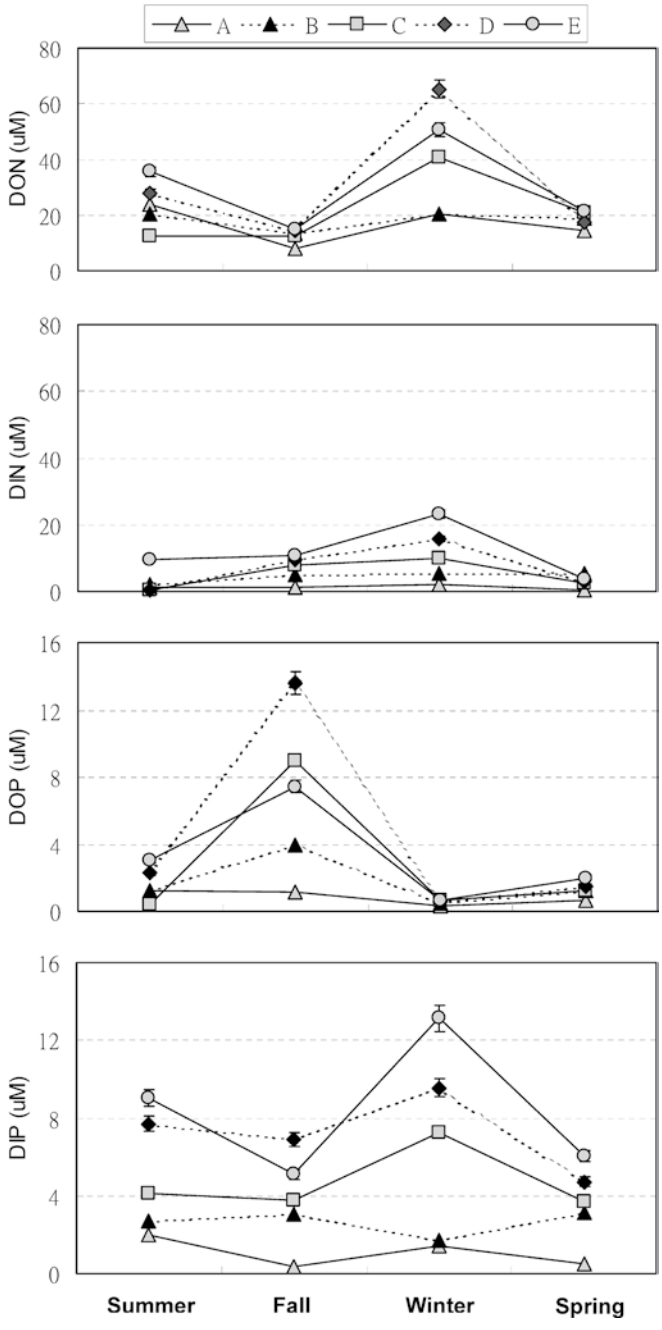

Fig. 2 Seasonal variations of dissolved organic and inorganic nitrogen (*DON* and *DIN*) and dissolved organic and inorganic phosphorus (*DOP* and *DIP*) at five study sites (*A–E*) along the flushing gradient in Tapong Bay

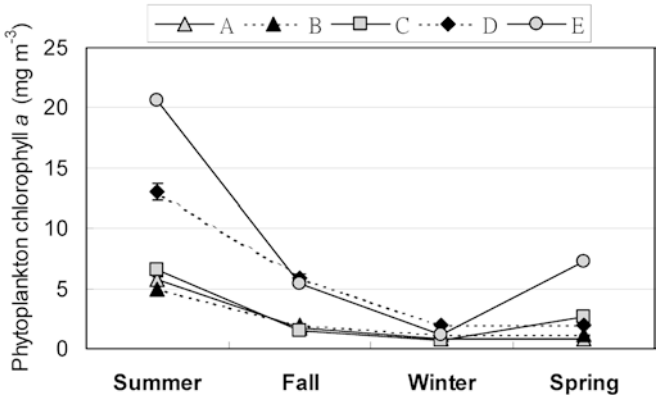

Fig. 3 Seasonal variations of phytoplankton chlorophyll *a* at five study sites (*A–E*) along the flushing gradient in Tapong Bay

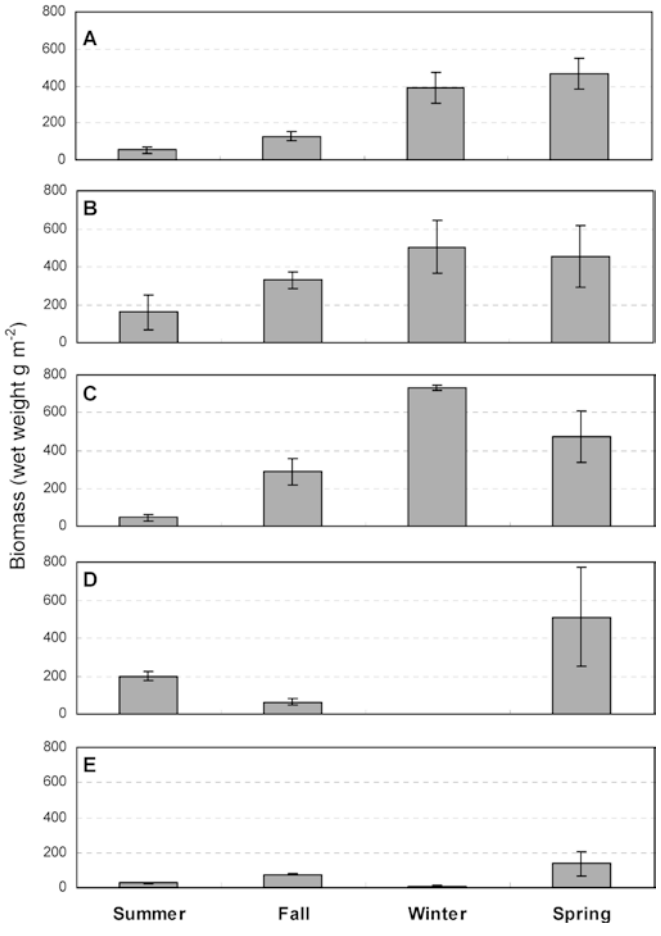

Fig. 4 Seasonal variations of total macroalgal biomass in terms of wet weight collected at five study sites (*A–E*) along the flushing gradient in Tapong Bay

and the communities from sites D and E were barely separable at all. The pairwise comparisons also indicate that communities collected in winter or spring were well separated from those collected in summer or fall, but those from summer and fall did not significantly differ. Overall, the grouping patterns of MDS ordination were primarily determined by site, and secondarily by season, suggesting that spatial effects are more important than temporal effects in structuring the macroalgal periphyton in Tapong Bay. Among the examined environmental factors, the BIOENV analyses (Table 5) also showed that the combination of water motion (a spatial effect) and water temperature (a temporal effect) best explained the patterns of changes in the macroalgal community in the lagoon (weighted Spearman's rank correlation, $\rho_w = 0.59$).

Table 2 Macroalgal periphyton on oyster-culture pens identified at five study sites along the flushing gradient in Tapong Bay

Species	Site				
	A	B	C	D	E
Cyanobacteria					
Lyngbya majuscula (Dillwyn) Harvey	+	+	+	+	+
Chlorophyta					
Boodlea composita (Harvey) Brand		+			
Bryopsis harveyana J. Agardh	+	+	+		
Chaetomorpha crassa (C. Agardh) Kützing	+	+	+	+	
C. antennina (Bory) Kützing		+		+	+
Chlorodesmis fastigiata (C. Agardh) Ducker	+	+			
Cladophora sakaii Abbott	+	+	+		
Enteromorpha intestinalis (Linnaeus) Nees	+	+	+	+	+
Ulva fasciata Delile	+				
U. lactuca Linnaeus	+	+	+	+	+
Rhodophyta					
Acanthophora spicifera (Vahl) Børgesen	+	+		+	
Centroceras clavulatum (C. Agardh) Montagne	+	+			
Ceramium cimbricum H. Petersen in Rosenvinge	+	+		+	
C. flaccidium (Kützing) Ardissone	+	+	+	+	+
Gracilaria chorda Holmes	+				
Hypnea charoides Lamouroux	+	+			
Polysiphonia sp.		+			
Number of species	14	15	7	8	5
Shannon–Wiener diversity	0.21	0.30	0.20	0.15	0.08

Table 3 Seasons of occurrence of macroalgal periphyton on oyster-culture pens identified in Tapong Bay

Species	2000		2001	
	Summer	Fall	Winter	Spring
Cyanobacteria				
Lyngbya majuscula (Dillwyn) Harvey	+	+	+	+
Chlorophyta				
Boodlea composita (Harvey) Brand				+
Bryopsis harveyana J. Agardh			+	+
Chaetomorpha crassa (C. Agardh) Kützing	+	+	+	+
C. antennina (Bory) Kützing				+
Chlorodesmis fastigiata (C. Agardh) Ducker			+	+
Cladophora sakaii Abbott	+	+	+	+
Enteromorpha intestinalis (Linnaeus) Nees	+	+	+	+
Ulva fasciata Delile			+	+
U. lactuca Linnaeus	+	+	+	+
Rhodophyta				
Acanthophora spicifera (Vahl) Børgesen	+	+	+	+
Centroceras clavulatum (C. Agardh) Montagne	+		+	
Ceramium cimbricum H. Petersen in Rosenvinge			+	+
C. flaccidium (Kützing) Ardissone	+		+	+
Gracilaria chorda Holmes		+	+	
Hypnea charoides Lamouroux			+	
Polysiphonia sp.			+	
Number of species	8	7	15	13
Shannon–Wiener diversity	0.04	0.08	0.35	0.16

The SIMPER analyses (Table 6) showed that seasonal variations in the macroalgal community at sites A, B, and C (with a mean similarity of 66–69%) were smaller than those at sites D (41%) and E (50%). The most dominant and frequently observed species at site A was *U. fasciata*. At sites B and C, *U. lactuca* became the dominant and most frequently collected species. The relative abundance and collecting frequency of *E. intestinalis* increased at site D. At the most poor-flushing site E, *L. majuscula* was the most frequently observed species colonizing the surfaces of oyster-culture pens.

Tissue nutrients

Changes in macroalgal communities in Tapong Bay can be fully realized by shifts in the abundances of these four macroalgal species because the sum of contributions to similarity at each site is >98% (Table 6). For this rea-

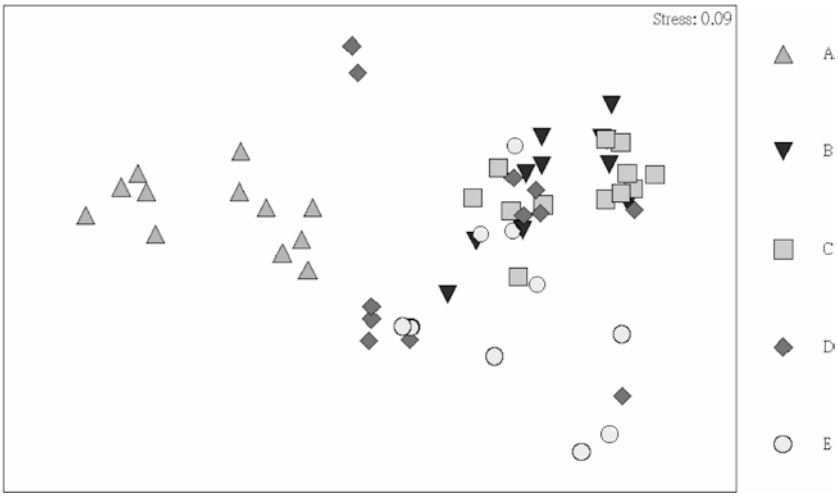

Fig. 5 MDS ordination of Bray–Curtis similarities between macroalgal communities on oyster-culture pens collected at five study sites (*A–E*) along the flushing gradient in Tapong Bay

Table 4 Two-way crossed ANOSIM (analysis of similarities: site×season) of macroalgal communities on oyster-culture pens at five study sites from four seasons in Tapong Bay. The significance level was calculated by comparing the observed statistic (*r*, sample relationship) to its permutation distribution. Tests were significant at the level of 5% except where indicated by NS. The Bonferroni correction for pairwise comparisons when $\alpha = 0.05$ is $\alpha' = 0.05/10 = 0.005$ for the site effect and $\alpha' = 0.05/6 = 0.0083$ for the season effect

Factor	Observed*r*	Permutations used	Number≥ observed *r*	Significance level
Site effect	0.61	999	0	0.1%
Pairwise comparisons				
A vs B	0.94	999	0	0.1%
A vs C	1.0	999	1	0.2%
A vs D	0.82	999	0	0.1%
A vs E	1.0	999	0	0.1%
B vs C	−0.06	999	709	71% (NS)
B vs D	0.24	999	79	8% (NS)
B vs E	0.70	999	0	0.1%
C vs D	0.44	999	9	1% (NS)
C vs E	0.88	999	0	0.1%
D vs E	0.23	999	53	5% (NS)
Season effect	0.49	999	0	0.1%
Pairwise comparisons				
Spring vs summer	0.58	999	0	0.1%
Spring vs fall	0.55	999	1	0.2%
Spring vs winter	0.33	999	2	0.3%
Summer vs fall	0.35	999	20	2%(NS)
Summer vs winter	0.61	999	1	0.2%
Fall vs winter	0.39	999	1	0.2%

son, only results of the four most dominant and frequent species are shown here. Tissue N, but not tissue P, of *L. majuscula* and *E. intestinalis* increased with increasing nutrient availability as a result of slow flushing, and this pattern was clearer in summer and fall (Tables 7 and 8). However, the increased pattern in tissue N of *U. lactuca* was not so clear as that of *L. majuscula* and *E. intestinalis*. Tissue N and P of the four most-common species in the lagoon ranged from 2.28–7.04% to 0.09–0.34% dry weight, respectively. The tissue N:P ratio ranged from 31 to 132. Tissue N and the N:P ratio, but not tissue P, significantly differed among sites, among species, and between times (Table 9). Generally, tissue N and the N:P ratio were highest at sites D and E and lowest at site A. Significantly higher tissue N and the N:P ratio occurred in summer and fall than in winter and spring. Of the four species, *L. majuscula*, the most dominant and frequent species at site E, had the highest tissue N and N:P ratio.

Discussion

The appearance of dense canopies of macroalgae is a common phenomenon in eutrophic coastal waters worldwide. Harlin (1995) hypothesized that shallow marine systems shift toward massive growths of macroalgae with increasing nutrient input. In Tapong Bay, however, total macroalgal biomass did not increase with increasing nutrient concentrations as a result of slow flushing. In contrast to the results of earlier studies in temperate shallow waters (Borum 1985; Valiela et al. 1997; Costanzo et al. 2000; Kamer et al. 2001), biomass values at the nutrient-rich site E were lower than those at the relatively nutrient-poor site A. The mean biomass was in the range of 53–465 g wet weight m^{-2} at site A, which is within the same order of magnitude of macroalgae collected from rock or mud in other systems (Lowthion et al. 1985; Pregnall and Rudy 1985; Her-

Table 5 The best ten combinations of the nine environmental variables producing the largest matches of changes in macroalgal communities and environmental variables in Tapong Bay, as measured by weighted Spearman rank correlation (ρ_w); *Phy* phytoplankton chlorophyll *a*; *Motion* water motion; *T* temperature; *Sal* salinity; *K* light extinction; *DIN* dissolved inorganic nitrogen; *DIP* dissolved inorganic phosphorus; *DON* dissolved organic nitrogen; *DOP* dissolved organic phosphorus

Number of variables	Weighted Spearman rank correlation (ρ_w)	Best variable combinations
2	0.593	Motion, T
3	0.574	Motion, T, DIP
4	0.567	Motion, T, K, DIP
3	0.557	Motion, T, K
4	0.540	Motion, T, DIP, DOP
5	0.536	Motion, T, K, DIP, DOP
5	0.529	Motion, T, K, DIN, DIP
4	0.528	Motion, T, DIN, DIP
5	0.514	Motion, T, DIN, DIP, DOP
5	0.510	Motion, T, Phy, K, DIP

nández et al. 1997; Valiela et al. 1997; Kamer et al. 2001; Naldi and Viaroli 2002). While water residence time increased from a few days at site A to weeks at site E, the mean biomass decreased to 8–137 g wet weight m^{-2}, corresponding to 15–30% of those collected at site A. On the other hand, the mean phytoplankton chlorophyll *a* increased about threefold at site E. Valiela et al. (1997) noted modifying effects of water residence time on the relative contribution of primary production by macroalgae and phytoplankton in response to increasing nitrogen loading. This study clearly demonstrates the modifying effects of flushing on macroalgal biomass in response to nutrient enrichment in shallow coastal waters. It is also clear that increased nutrient availability in the water column did not result in greater macroalgal biomass, and thus, changes in algal biomass are not necessarily a good indicator of nutrient availability or eutrophication as found by Lin et al. (1996) and Fong et al. (1998).

Although macroalgal biomass differed significantly among the study sites, the biomasses across all study sites appeared to follow a distinct seasonal pattern with blooms in winter or spring and lower biomasses in summer or fall. The same pattern has been documented in southwestern (Huang 1990) and northeastern (Huang 1999) Taiwan, in Hong Kong (Kaehler and Williams 1996), and in southern California (Peters et al. 1985). This seasonal pattern may be typical of macroalgae in tropical and subtropical waters. On the other hand, the seasonal pattern in temperate waters exhibits a maximum in summer or fall and lower biomasses in winter or spring (Lowthion et al. 1985; Pregnall and Rudy 1985; Hernández et al. 1997; Kamer et al. 2001; Naldi and Viaroli 2002). Discrepancies in the timing of macroalgal blooms between tropical and temperate waters suggest that controlling factors for the temporal dynamics differ. In temperate waters, the sparse macroalgae in winter can be attributed to light and/or winter temperature limitations (Kamer et al. 2001). In Tapong Bay, the occurrence of bleaching macroalgae in summer (H.-J. Lin, personal observations) as observed in Hong Kong (Kaehler and Williams 1996) suggests that the intense illumination (>2000 μmol photons m^{-2} s^{-1}) was likely to be a limiting factor on the growth of the noncalcified macroalgae on oyster-culture pens. This was supported by the decline in species richness and by the observation that only cyanobacteria, *Ulva*, and *Enteromorpha* occurred in summer (Table 3). These genera are widely recognized as among the most stress resistant macroalgae (Littler and Littler 1980). Water temperature was one of the environmental factors that best explained the observed changes in macroalgal communities and is likely their largest source of stress.

The cause of the sparse macroalgae in the inner region of Tapong Bay was not clear. Despite the greater phytoplankton chlorophyll *a* at sites D and E, subject to longer residence time, the macroalgae were unlikely to be light limited, because they were positioned just below

Table 6 Average biomass (g wet weight m^{-2}), contribution (%), and variation (similarity/SD) of the four dominant species to the average similarity of macroalgal communities at five study sites along the flushing gradient in Tapong Bay

Species	Site				
	A	B	C	D	E
Average community similarity	66%	68%	69%	41%	50%
Lyngbya majuscula					
Average biomass		0.7	0.5	1.0	6.7
Contribution to the average similarity		2%	7%	8%	46%
Variation of contribution		0.4	0.7	0.4	1.2
Enteromorpha intestinalis					
Average biomass	11	17	3.8	32	29
Contribution to the average similarity	11%	9%	6%	67%	37%
Variation of contribution	0.6	0.4	0.4	1.1	0.8
Ulva fasciata					
Average biomass	245				
Contribution to the average similarity	88%				
Variation of contribution	4.2				
U. lactuca					
Average biomass		343	378	160	31
Contribution to the average similarity		88%	85%	24%	17%
Variation of contribution		2.5	3.7	0.4	0.5
Sum of contributions to similarity	99%	99%	98%	99%	100%

Table 7 Tissue nitrogen (*N*), phosphorus (*P*), and the molar N:P ratio of the dominant species on oyster-culture pens collected in winter and spring at five study sites along the flushing gradient in Tapong Bay (mean ± SD). *NA* The species were absent or too few to analyze the tissue nutrients

Species	Site				
	A	B	C	D	E
Lyngbya majuscula					
N (% dry weight)	NA	2.32	4.92 ± 1.07	5.57 ± 0.77	6.33 ± 0.42
P (% dry weight)		0.13	0.09 ± 0.01	0.13 ± 0.01	0.15 ± 0.05
Mean N:P		31	122	101	103
Number of replicates		1	5	5	5
Enteromorpha intestinalis					
N (% dry weight)	2.73 ± 0.69	4.16	2.28 ± 0.97	4.30 ± 0.11	3.92 ± 0.79
P (% dry weight)	0.21 ± 0.01	0.19	0.10 ± 0.01	0.12 ± 0.03	0.12 ± 0.01
Mean N:P	31	48	52	79	72
Number of replicates	4	1	4	5	7
Ulva fasciata					
N (% dry weight)	4.27 ± 0.50	NA	NA	NA	NA
P (% dry weight)	0.21 ± 0.02				
Mean N:P	45				
Number of replicates	4				
U. lactuca					
N (% dry weight)	NA	4.12 ± 0.46	4.42 ± 0.39	3.86 ± 0.20	4.08 ± 0.05
P (% dry weight)		0.13 ± 0.07	0.22 ± 0.07	0.15 ± 0.08	0.14 ± 0.01
Mean N:P		83	50	66	64
Number of replicates		4	6	4	3

Table 8 Tissue nitrogen (*N*), phosphorus (*P*), and the molar N:P ratio of the dominant species on oyster-culture pens collected in summer and fall at five study sites along the flushing gradient in Tapong Bay (mean ± SD). *NA* The species were absent or too few to analyze the tissue nutrients

Species	Site				
	A	B	C	D	E
Lyngbya majuscula					
N (% dry weight)	NA	5.53	NA	NA	7.04 ± 0.08
P (% dry weight)		0.10			0.12 ± 0.01
Mean N:P		122			132
Number of replicates		1			2
Enteromorpha intestinalis					
N (% dry weight)	3.68 ± 0.43	5.09	3.98 ± 0.67	4.31 ± 0.69	5.43
P (% dry weight)	0.17 ± 0.02	0.11	0.22 ± 0.04	0.14 ± 0.02	0.20
Mean N:P	54	101	51	70	59
Number of replicates	6	1	4	4	1
Ulva fasciata					
N (% dry weight)	4.82 ± 0.44	NA	NA	NA	NA
P (% dry weight)	0.20 ± 0.02				
Mean N:P	57				
Number of replicates	4				
U. lactuca					
N (% dry weight)	NA	3.97 ± 0.90	3.82 ± 1.11	NA	NA
P (% dry weight)		0.19 ± 0.07	0.09 ± 0.01		
Mean N:P		52	94		
Number of replicates		2	2		

the water surface, and the light extinction coefficients were no lower than those at sites A, B, and C (Table 1). Quantitative observations of herbivorous fishes also suggest that grazer density in the inner region was not greater than in the outer region. Although salinity correlated positively with overall macroalgal biomass, salinity was unlikely a limiting factor for the growth of macroalgae. At sites D and E, salinity remained high (> 20 psu) throughout the study period. The dominant species *E. intestinalis* has been shown to have significantly slower growth rates only at salinities lower than 5 psu (Martins et al. 1999). The sparse macroalgae in the inner region were apparently due to the decline in species richness, which led to large decreases in total biomass. Although the biomass values of *E. intestinalis* and *L. majuscula* increased at sites D and E, the increased biomasses were apparently unable to compensate for decreases in biomass by *U. lactuca* (Table 6) and other species (Table 2). Therefore, it is not surprising that total biomass correlated negatively with concentrations of TP and phytoplankton chlorophyll *a*, because higher concentrations of TP and phytoplankton chlorophyll *a* are indicative of slower flushing.

In contrast to the responses of total biomass, tissue N increased with increasing nutrient availability as a result of slow flushing. For the three widespread and dominant macroalgal species in the lagoon (Tables 7 and 8), mean tissue N increased from 3.3–4.0% dry weight at the fast-

Table 9 Three-way ANOVA (site×species×season) of tissue nitrogen (*N*), phosphorus (*P*), and the molar N:P ratio of the four dominant species on oyster-culture pens at five study sites in Tapong Bay. If the results of ANOVA indicated significant treatment effects at the 0.05 probability level (*p*), then Fisher's protected LSD test was used to determine which means significantly differed. Means with the same letter are not significantly different; *df* degree of freedom; *Ly Lyngbya majuscula*; *Uf Ulva fasciata*; *Ul U. lactuca*; *Ei Enteromorpha intestinalis*

Source	*df*	*F* value	$p > F$	Separation
Tissue N				
Site	4	4.62	0.002	E^{a} D^{ab} C^{bc} B^{c} A^{c}
Species	3	10.09	< 0.001	Ly^{a} Uf^{b} Ul^{bc} Ei^{c}
Season	1	9.73	0.003	Summer and fall > winter and spring
Site×Species	6	5.11	0.002	
Site×Season	4	1.96	0.11	
Species×Season	3	4.96	0.004	
Site×Species×Season	2	1.92	0.15	
Tissue P				
Site	4	0.87	0.49	
Species	3	2.08	0.11	
Season	1	2.81	0.10	
Site×Species	6	0.51	0.80	
Site×Season	4	1.25	0.30	
Species×Season	3	0.56	0.64	
Site×Species×Season	2	11.30	< 0.001	
N:P ratio				
Site	4	3.09	0.02	E^{a} D^{ab} C^{b} B^{b} A^{c}
Species	3	3.94	0.01	Ly^{a} Ul^{b} $Ei^{b}Uf^{b}$
Season	1	9.22	0.003	Summer and fall > winter and spring
Site×Species	6	5.72	0.001	
Site×Season	4	1.49	0.21	
Species×Season	3	2.25	0.09	
Site×Species×Season	2	6.48	0.003	

flushing site A or B to 4.1–6.5% dry weight at the slow-flushing site E. These N values are comparable to values of similar taxa found in other studies under enriched and unenriched conditions (Björnsäter and Wheeler 1990; Fong et al. 1998; Kamer et al. 2001; Naldi and Viaroli 2002). However, mean tissue P was restricted to the range of 0.10–0.20% dry weight across the study sites and there were no significant differences among sites. These P values were also similar to those of similar taxa found in other field studies (Kamer et al. 2001) but lower than those reported in laboratory experiments (Björnsäter and Wheeler 1990, 0.30–0.56% dry weight). Although the molar DIN:DIP ratios in the water column remained low (0.94–1.81) and suggested N limitation, this was not matched by the tissue N:P ratios of macroalgae (31–132). It suggests that there was another source of N for macroalgal growth, for example high DON recycling from the excretion of the reared oysters, and/or release of DIN from the sediment, due to the effect on sediment metabolism of the deposition of feces and pseudofeces. In addition, variations in tissue nutrients of macroalgae were much smaller than variations (DIN: 0.46–23.2 μM, DIP: 0.35–13.1 μM) in nutrient concentrations in the water column. These results support the suggestions of previous studies (Björnsäter and Wheeler 1990; Lyngby and Mortensen 1994; Fong et al. 1998) that tissue nutrient content of macroalgae is a more useful monitoring tool than traditional water chemistry for evaluating in situ nutrient status.

Despite the taxonomically diverse species in Tapong Bay, only relatively small numbers of species of cyanobacteria and chlorophytes were observed all year round (Table 3). In addition to their stress resistance in summer, *Lyngbya*, *Ulva,* and *Enteromorpha*, having simple thalli with large surface-to-volume ratios, are capable of rapid growth (Littler and Littler 1980) and are characteristic of systems subject to large inputs of nutrients (Valiela et al. 1997; Kuffner and Paul 2001). The dominance of these opportunistic species in Tapong Bay is indicative of a eutrophic system. Among these tropical species, blooms of *L. majuscula* at the most poor-flushing site E give cause for great concern, because it has been shown to have chemical-based toxic effects on ecosystems and human health (Osborne et al. 2001).

The modifying effect of flushing was most evident on the spatial changes in macroalgal communities. Our results suggest that water motion was an important selective factor for the spatial dominance and occurrence of macroalgal species in Tapong Bay. Any increase in water motion or turbulence would reduce the thickness of the boundary layer around macroalgae. In contrast, the increase added to the frictional shear force of the passing flow. Current velocity has been shown to influence community structure of periphyton in streams (McIntire 1966). Horner and Welch (1981) indicated velocity in streams increased to a level well above 50 cm s^{-1} increases friction to the point that advantage of improved nutrient delivery was overcome. Traaen and Lindstrøm (1983) also found that many macroalgal colonies exhibited better development at velocities > 20 cm s^{-1}, while few thrived at velocities > 100 cm s^{-1}. In Tapong Bay, Chen (2002) observed that current velocity increased up to 200 cm s^{-1} at the fast-flushing site A when ebbing, but was maintained at < 10 cm s^{-1}at the slow-flushing site E. The nonheterocystous filamentous cyanobacterium, *L. majuscula*, can fix N (Paerl et al. 1996). Kuffner and Paul (2001) showed that *L. majuscula* has more efficient growth and/or nutrient uptake mechanisms compared to other species on

Guam's coral reefs. Diaz et al. (1990) found an opportunistic strategy of N utilization by *L. majuscula,* whereby molecular N is primarily consumed only in the absence of alternate inorganic N sources. These likely assure the success of *L. majuscula* in slowly moving water in the inner region and were evident in the significantly greater tissue N of *L. majuscula* than others (Table 9). On the other hand, the divided blades of *U fasciata*, which was restricted to the fast-flushing site A, have a higher surface-to-volume ratio and may be appropriate for rapid uptake of low nutrient concentrations at high current velocities (Littler and Littler 1980).

The results of this study can be used to address the question of whether total biomass, community structure, and tissue nutrient content behave the same or differently, and which are the most sensitive tools for monitoring coastal eutrophication in the tropics. It is clear that MDS ordination of community changes was much better at discriminating between sites than were total biomass measures, because sites with similar biomasses did not cluster together on the MDS ordination. Tissue nutrient measures are only valid for the widespread and stress-resistant species. The more sensitive ordination of community changes can be used for detecting differences in species composition between sites to monitor coastal eutrophication. However, ordination can only give an 'early warning' that community changes are occurring, while less sensitive measures such as biomass and tissue nutrient content are also required to indicate the magnitude and direction of these changes.

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