Seasonal growth dynamics of *Laurencia papillosa* and *Gracilaria coronopifolia* from a highly eutrophic reef in southern Taiwan: temperature limitation and nutrient availability

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**Abstract**

Both field and laboratory studies were used to investigate the effects of temperature limitation and nutrient availability on seasonal growth dynamics of *Laurencia papillosa* and *Gracilaria coronopifolia* from a nearshore coral reef in the southern tip of Taiwan during 1999–2000. *L. papillosa* was a summer blooming alga abundant in August–November and *G. coronopifolia* was abundant year round except April–May. *L. papillosa* blooms in the summer were attributed to its preference for high temperatures and highly sensitivity to low temperatures. A wider temperature range and a significant stimulation of growth by high N inputs can explain the appearance of *G. coronopifolia* year round and also its maximum growth in November–March. Levels of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) in water column were extremely high, but the growth of these two rhodophytes still suffered nutrient limitation that the type and severity of nutrient limitation were variable over time and also between two species. The growth of *L. papillosa* was limited by P in the early growth stage (August–September) as indicated by decreased tissue P contents, increased C/P and N/P molar ratios and increased alkaline phosphatase activity (APA) and in the later growth stage, it was subjected to N-limitation, evidenced by decreased tissue N contents and C/P and N/P molar ratios and increased tissue P contents. The growth of *G. coronopifolia* was also P-limited as indicated by increased tissue N contents and concomitantly decreased tissue P contents, while marked drops in tissue P contents below the subsistence level in mid September and December 1999 reveal severe P limitation, which was supported by increased alkaline phosphatase activity. Higher critical nutrient contents and nutrient thresholds for maximum growth of *G. coronopifolia* suggest that *G. coronopifolia* faced more frequent nutrient limitation compared to *L. papillosa*. In conclusion, the results from these laboratory and field studies provide evidence that the seasonal abundance of *L. papillosa* and *G. coronopifolia* from
southern Taiwan was determined by seasonal variations in seawater temperatures and nutrient concentrations as well as different physiological growth strategies. Seawater temperature and nutrient availability were important determinants of seasonal abundance of *L. papillosa* while the seasonal abundance of *G. coronopifolia* was influenced by nutrient availability.

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**Keywords:** Gracilaria coronopifolia; Laurencia papillosa; Nutrient; Temperature

### 1. Introduction

Coral reefs in many tropical coastal waters are now undergoing a phase shift from coral to algae-dominated reef (Littler et al., 1992; Naim, 1993; Hughes, 1994; Lapointe, 1997). Field and laboratory experiments have suggested that nutrient enrichment is a determinant of coral reef community structure (NRC, 2000). In the mid-1970s, the impact of anthropogenic nutrient inputs on macroalgal blooms was first reported for the case of a green alga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii (Banner, 1974; Smith et al., 1981). The role of increasing water-column nutrient concentrations on algal blooms has been suggested at Reunion Island, Indian Ocean (Cuet et al., 1988) and in the Caribbean and Florida coastal regions (Lapointe and O’Connell, 1989; Bell, 1992; Lapointe et al., 1994). Evidently, algal blooms on coral reefs are associated with enhanced nutrient availability. However, studies showed that nitrogen (N) and phosphorus (P) are nutrients limiting the productivity of macroalgae on coral reefs (Lapointe, 1987, 1997; Lapointe et al., 1987; Littler et al., 1991; Larned, 1998). The comparison of water-column inorganic nitrogen : phosphorus (N/P) ratios to algal tissue N/P ratios and the results of nutrient enrichment experiments indicate that the productivity of algae in Kaneohe Bay, Hawaii is limited by N instead of P (Larned, 1998). However, Lapointe (1997) showed primary P-limitation of macroalgal productivity on carbonate-rich reefs, Discovery Bay, Jamaican, that are enriched by submarine groundwater discharge of nitrate; in comparison, macroalgae were more N-limited on siliciclastic reefs of southeast Florida where the water column is more enriched in soluble reactive phosphorus (SRP). It is evident that the type and severity of nutrient limitation are variable among habitats, species, and time (Lapointe, 1987; Lapointe et al., 1987).

Coastal regions along Hengchuan Peninsula in the southern tip of Taiwan, which is the most developed coral reef ecosystems in Taiwan, have now faced increasing pressure from expanded urban development and tourism populations. Most nearshore reefs in Hengchuan Peninsula are characterized by high abundance in fleshy macroalgae and low abundance in herbivorous fishes (Dai, 1997). These algal blooms are often composed of opportunistic algae in the genera *Enteromorpha*, *Gracilaria*, *Laurencia*, and *Sargassum*. It is known that the shift of coral reefs to algae-dominated reefs generally causes a dramatic decline in fish stocks and biodiversity in coral reef ecosystems (NRC, 2000). Thus, the understanding of macroalgal abundance on southern Taiwan coral reefs is an important aspect of the ecological, environmental, aesthetic and socio-economic value of the reefs. The qualitative observations carried out in 1998 have showed that two rhodophytes *Laurencia papillosa* and *Gracilaria coronopifolia* abundant on Hengchuan Peninsula had different seasonality: *L. papillosa* was abundant in the summer months (July–October) while *G. coronopifolia* was abundant all the year except April–May (unpublished data). Both field and laboratory studies were conducted to determine whether the seasonal abundance of *L. papillosa* and *G. coronopifolia* from Hengchuan Peninsula was regulated by nutrient availability. In an effort to understand algal nutrient status and the type and severity of nutrient limitation over time, seasonal variations in seawater nutrient concentrations and algal tissue nutrient contents were analyzed and compared to the critical and subsistence nutrient contents. In addition, the determination of algal alkaline phosphatase activity (APA) as P deficiency indicator of coral reef algae (Lapointe, 1997) was included to assess the occurrence of P limitation. Because algal growth and morphology, distribution and seasonal abundance are affected by temperature
(Garbary, 1979; Lüning, 1984; Breeman, 1988; Pakker et al., 1994; Davison and Pearson, 1996; Lee et al., 1999), the growth temperature range and optima, and also the interactions of nutrient and temperature on algal growth were determined by an exposure of algae to varying temperatures ranging from 15–35 °C in continuous-flow seawater enriched with or without nutrients to elucidate the influences of temperature fluctuations and nutrient availability on seasonal variations of biomass abundance of L. papillosa and G. coronopifolia.

2. Materials and methods

2.1. Study site and environmental characters

The field experiments were performed during January 1999–August 2000 on a nearshore coral reef (GPS: 21°56' 00"N; 120°50' 10"E) from Nanwan Bay in southern Taiwan. Nanwan Bay is located at the western side of Hengchuan Peninsula, which is surrounded by the Pacific Ocean on the east coast, the Bashi Channel on the southern coast and the Taiwan Straits on the western coast (Fig. 1). This reef has a horizontal width of 1200 m, composed of an intertidal region, approximately 50–130 m long, and a subtidal region, approximately 35–270 m long and a depth of 1–12 m (MHWS) in a seaward gradient. Two drainage outlets carrying fertilizers and sewage from croplands and residential areas near the study site were significant nutrient pollutant sources in this reef and their effects were profound during the rainfall period (May–September). The monthly survey during 1999–2000 showed that the concentrations of DIN (NO$_3^-$ and NH$_4^+$ as the main component) and SRP in drainage outlets were 19.2–95.6 and 3.7–19.8 μM, respectively, with the peaks in June 1999 and May–June 2000, which correlated with the precipitation pattern.

![Fig. 1. Study site in southern Taiwan.](image-url)
The climate data (1960–1990) from the Central Weather Bureau of Taiwan of Republic of China showed that Hengchuan Peninsula has a warm tropical climate, the mean annual air temperature is 25 °C and the mean annual relative humidity is 77%. Mean monthly air temperature is low in January (20.3 °C) and high in July (28.3 °C). The mean annual precipitation is 1964.9 mm, mainly occurring during May–September with a peak in July–August. Typhoons often occur during May–November and the prevailing northeasterly winds occur during September–March, at this monsoon period the hydrological regime is affected by strong dry winds from land to seaward, leading to a weak ocean swell and a relatively clean water environment. One typhoon, MAGGIE, occurred in July of 1999 and two typhoons, KAI-TAK and BILIS, occurred in July and August 2000, respectively.

2.2. Estimation of algal biomass

Four line transects perpendicular to the shore were set at 100-m intervals and sampling stations on each line transect were set at 0, 25, 50, 75 and 100 m away from the average high tide mark towards the low tide mark (i.e. 0–5-m water depth (MHWS) in a seaward gradient). Because almost no macroalgae were found at the highest tidal region (i.e. 0-m sampling station), the data of 0-m sampling station were not included in this study. There were 16 replicates with each sampling stations. At each sampling station, algal %cover was estimated monthly using a 50×50-cm quadrat and thalli within the quadrats were collected and dried at 80 °C for the determination of areal biomass.

2.3. Determination of seawater nutrient concentrations and algal tissue nutrient contents

Near-bottom (20 cm above the bottom) seawater samples were collected at each sampling station and stored at 4 °C for transportation to the laboratory. Then, seawater was filtered through Whatman CF/G paper (0.45 μm) and immediately frozen in a −70 °C freezer until analysis. Before nutrient determination, frozen samples were thawed on ice in the dark. The determination of dissolved inorganic phosphorus (SRP) was modified from the method of Murphy and Riley (1962). Colour reagent was prepared by mixing 1 ml of 3% ammonium molybdate solution and 0.75 ml of 5 N 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 was added in 0.5 ml of seawater and after 10 min of incubation at room temperature, the absorbance was read at 882 nm within 15 min by a Hitachi spectrophotometer (model U-2000, Hitachi, Tokyo, Japan). The detection limit of SRP concentration was 0.02 μM. Seawater NO₃⁻ and NO₂⁻ concentrations were determined 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 powder sample of 5 mg dry weight (d. wt.) was put in 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 solution became clear, the digested samples were cooled at room temperature and made up to 5 ml with distilled H₂O. Tissue N and P contents were detected by colour 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 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.

2.4. Determination of APA

Algal APA was determined by modification of the method described by Lapointe et al. (1992). Apical thalli (0.48–0.58 g wet weight) were put in a capped
Pyrex test tube (25 ml) containing 5 mL of ambient seawater with 1 mM \( p \)-NPP (freshly prepared in distilled \( H_2O \)). To determine the interference of algal-released materials and auto-degraded \( p \)-NPP, two sets of controls were done. First set was the algal background by the incubation of algal materials without \( p \)-NPP (Sigma, USA). Second set was the seawater background carried out in two test tubes without algal materials: one was terminated by the addition of 1 M KOH before incubation and the other was terminated after incubation, the net absorbance value between the above two tubes was the seawater background. All tubes were capped and immersed in waters for in situ incubation. After 1 h, 1 ml of seawater was transferred to 1.5 ml plastic micro-centrifugation tube and 250 \( \mu l \) of 1 M KOH was added to terminate the reaction. Then, these tubes and algal materials were kept on ice in dark and then transferred to laboratory within 3 h. After centrifugation at 15,000 \( \times g \) for 10 min, the absorbance of supernatant was determined at 405 nm.

Algal samples were oven-dried at 80 °C to obtain algal dry weight. Average seawater background and algal background were obtained from three replicates. The obtained \( A_{405} \) value of algal sample minus both average seawater \( A_{405} \) values and average algal background \( A_{405} \) values was converted to enzymatic activity (nmol \( p \)-NP released h\(^{-1}\) g\(^{-1}\) d. wt.) by molar extinction coefficient of \( p \)-NP, 4.6 \( \times 10^3 \) M\(^{-1}\) cm\(^{-1}\).

2.5. Estimation of critical and subsistence nutrient contents and growth temperature ranges

A continuous-flow culture was used for the estimation of the critical and subsistence nutrient contents and also the growth temperature ranges and optima. Apical thalli were sampled in August 2003 and then incubated for 7 days in a 60-l outdoor polyethylene tank containing 50 l seawater aerated by air for recovery of wounding. Healthy thalli of 1 g wet weight (w. wt.) were cultured in a 1000-ml glass culture flask fitted with a tube for aeration in a flow rate of 20 ml min\(^{-1}\) and two tubes for inflowing and outflowing culture seawater, which was pumped from a 60-l polyethylene tank (nutrient tank) to the culture flask in the speed of 5 ml min\(^{-1}\) with a peristaltic pump. Seawater was collected from Nanwan Bay in 4–5-m depth and 20 km offshore to insure DIN <0.1 \( \mu M \) and SRP <0.01 \( \mu M \). After collection, seawater was immediately filtered through 5-\( \mu M \) filter papers and stored at 4 °C in the dark before use. Seawater in the nutrient tank was changed every day and the flasks were shaded to obtain approximately 60% of full sun to mimic the light levels (250–830 \( \mu E \) m\(^{-2}\) s\(^{-1}\) between 8:00 am and 4:00 pm determined during August–September 1999) on the surface of these two rhodophytes in the field. Six flasks were linked to a nutrient tank and five replicate flasks were randomly sampled from a nutrient tank and their averaged value was the value of a nutrient tank. In this study, three replicate nutrient tanks were used for each nutrient or temperature treatment and the daily specific growth rate and algal tissue nutrient contents determined in the outdoor culture experiments were mean±S.E.M. (\( n=3 \)).

For the determination of critical and subsistence nutrient levels, the water temperatures of nutrient tanks were maintained in a range of 24–26 °C by cooler and heater. According to monthly surveys of seawater nutrient concentrations during 1996–1998 at the present study site that the average \( NH_4^+ \), NO\(_3^-\), and PO\(_4^{3-}\) concentrations were 3.04, 6.58 and 0.43 \( \mu M \), respectively, and to simulate seawater nutrient status at the present study site, NO\(_3^-\) and NH\(_4^+\) were applied together as nitrogen source and PO\(_4^{3-}\) was used as SRP source that the levels of NO\(_3^-/NH_4^+\)/PO\(_4^{3-}\) for the determination of critical nutrient contents were set at 0:0:0, 0.4:0.2:0.03, 0.8:0.4:0.06, 1:0.5:0.075, 1.3:0.67:0.1, 1.6:0.8:0.12, 2:1:0.15, 4:2:0.3, 8:4:0.6, 16:8:0.6, and 24:12:1.8 (\( \mu M \)) for \( L. papillosa \), and 0:0:0, 1:0.5:0.075, 1.6:0.8:0.12, 2:1:0.15, 3:1:0.225, 4:2:0.3, 6:3:0.45, 10:5:0.75, 16:8:1.2, 30:15:2.25, 40:20:3, 60:30:4.5, and 90:30:6 (\( \mu M \)) for \( G. coronopifolia \). NO\(_3^-\) was not used due to trace NO\(_2^-\) amount detected during 1996–1998 (the average concentration was 0.03±0.05 \( \mu M \)). Although there have several reports that NH\(_4^+\) reduces NO\(_3^-\) uptake of several macroalgae (Haines and Wheeler, 1978; D’Elia and DeBoer, 1978; Thomas and Harrison, 1987), and it has been recently shown that NO\(_3^-\) uptake was suppressed by 38% in the presence of NH\(_4^+\)>5 \( \mu M \) in the rhodophyte \( Gracilaria \) (Smit, 2002), the combined application of NH\(_4^+\) and NO\(_3^-\) was to estimate the responses to seawater nutrient compositions at the present study site. Nutrient-enriched seawater in the nutrient tank was changed every day. To check the nutrient concen-
trations in the flasks, the seawater nutrient concentrations in the flasks were selectively determined after 1 day of culture in “1:0:5:0.075 (NO$_3^-$/NH$_4^+$/PO$_4^{3-}$) µM”, “4:2:0.3 µM”, “16:8:1.2 µM”, and 60:30:4.5, treatments along the culture period. Average concentrations of NO$_3^-$, NH$_4^+$, and PO$_4^{3-}$ were 0.98±0.06 (means±S.D., n=36), 0.49±0.03, and 0.07±0.005 µM for “1:0:5:0.075 (NO$_3^-$/NH$_4^+$/PO$_4^{3-}$) µM” treatment, 3.96±0.09, 2.06±0.03, and 0.31±0.04 µM (n=36) for “4:2:0.3 µM” treatment, 15.73±0.11, 8.12±0.08, 1.18±0.03 µM (n=36) for “16:8:1.2 µM” treatment, and 59.33±0.96, 31.26±0.29, and 4.36±0.11 µM (n=18) for “60:30:4.5 µM” treatment. These data indicate that the nutrient concentrations remained almost unchanged after culture. Algal wet weight was determined at the start and after 16 days of incubation for the calculation of daily specific growth rate (% day$^{-1}$): (W$_{16}$−W$_0$)/W$_0$/16×100% (W$_0$=wet weight at day 0, W$_{16}$=wet weight at day 16). Then, sampled thalli were dried at 80 °C and ground to powder for tissue nutrient content analysis. Tissue nutrient contents in algae whose specific growth rate is zero are subsistence N and P levels (Fujita et al., 1989). Subsistence contents were determined by incubation of algae in ambient seawater without nutrient pulse and tissue N and P contents in algae whose growth rate is zero are subsistence N and P levels (Fujita et al., 1989).

For the determination of growth temperature ranges and optimum, seven temperature levels (15, 20, 22.5, 25, 27.5, 30 and 35 °C) (±1.0 °C) were set in different nutrient tanks and algal thalli were cultured in 1000-ml glass flasks for 16 days in seawater enriched with or without nutrients (NO$_3^-$/NH$_4^+$/PO$_4^{3-}$=5:2.5:0.375 (µM)). For each temperature treatment, six replicate flasks were supplied by a nutrient tank and five flasks were randomly sampled from used and the daily specific growth rate was determined after 16 days as the following equation: % day$^{-1}$=(W$_{16}$−W$_0$)/W$_0$/16×100% (W$_0$=wet weight at day 0, W$_{16}$=wet weight at day 16). During the 16-day culture period, daily seawater samples in the flasks were taken for nutrient concentration determination. The average concentrations of NO$_3^-$, NH$_4^+$, and PO$_4^{3-}$ for 5:2.5:0.375 µM treatment were 4.95±0.21, 2.43±0.23, and 0.377±0.009 µM (means±S.D., n=672), respectively. Thus, seawater nutrient concentrations did not change after 1-day culture. The growth temperature range was defined on the basis of positive specific growth rate.

2.6. Statistical analysis

SAS program (SAS, NC, USA) was used to analyze the field and experimental data. One-way analysis of variance (ANOVA) was used to compare means of areal dry weight biomass, seawater nutrient concentrations, algal tissue nutrient contents and algal APA with a factor of time. Two-way ANOVA was used for temperature experiments with factors of temperature and nutrient. Tukey’s test was used for multiple comparisons among means from significant ANOVA tests (P<0.05) (Day and Quinn, 1989). Homogeneity of variance was determined using the F$_{max}$ test (Sokal and Rohlf, 1981).

The stepwise regression analysis was used to determine the best multiple regression model to correlate the areal dry weight biomass of both L. papillosa and G. coronopifolia with environmental parameters. Parameters entered into the model for each sampling time were seawater temperature, surface irradiance, seawater DIN, NO$_2^-$, NO$_3^-$ and NH$_4^+$ concentrations, and seawater SRP concentrations. To normalize data, the areal dry weight biomass of L. papillosa and seawater NO$_2^-$ concentrations, seawater NH$_4^+$ concentrations were double root (i.e. 4th root)-transformed (expressed as $\sqrt[4]{\cdot}$), and seawater SRP concentrations were root-transformed (expressed as $\sqrt[3]{\cdot}$). Significance was set at the 0.05 level.

3. Results

3.1. Climate data and seawater nutrient concentrations

The climate data of Hengchuan Peninsula during 1999–2000 were obtained from the Central Weather Bureau of Taiwan of Republic of China. Monthly mean air temperature showed significant temporal variations (P=0.0001) that were high in May–October and low in December–April, and seawater temperatures showed a similar trend; mean air and seawater temperatures were 25.14 and 24.97 °C, respectively (Fig. 2). During the survey, monthly
cumulative photosynthetic photon flux density (PPFD) had a range from 1403 to 2605 mol m$^{-2}$ month$^{-1}$, except 441–1121 mol m$^{-2}$ month$^{-1}$ in April–June 1999 (Fig. 2). Monthly cumulative precipitation was high during May–October (Fig. 2). This suggests that the climate of Hengchuan Peninsula can be grouped into the warmer and wet months (May–October) and the cooler and dry months (November–April).

Seawater nutrient concentrations (DIN, NO$_3^-$, NO$_2^-$, NH$_4^+$, and SRP) were extremely high and varied seasonally during the survey ($P=0.0001$) (Fig. 3). DIN concentrations, ranging from 0.07 to 18.80 μM, peaked in July and December 1999 and mid April 2000, respectively. NO$_3^-$ concentrations, ranging from 0–12.33 μM, increased in July 1999 and in April–May 2000, NO$_2^-$ concentrations, ranging from 0 to 1.33 μM, increased in January and April 2000, and NH$_4^+$ concentrations, ranging from 0 to 12.45 μM, increased in November 1999–January 2000. Mean DIN, NO$_3^-$, NO$_2^-$ and NH$_4^+$ concentrations during the survey were 6.40±5.01, 4.10±3.04, 0.22±0.34 and 2.08±3.59 μM, respectively. SRP concentrations, ranging from 0 to 3.47 μM, peaked in July 2000 and had the mean concentration was 0.71±0.23 μM during the survey. DIN/SRP molar ratio increased in December 1999–May 2000.

Fig. 2. Mean monthly air and seawater temperatures, monthly cumulative precipitation, and monthly cumulative irradiance during 1999–2000.
3.2. Algal biomass and stepwise multiple regression analysis

During the survey, the percentage total line biotic cover was high in March (72.37–82.50%) and low in July (47.43–51.23%). Macroalgae were the dominant component that %cover was 59.08–67.26% in March and 34.19–36.48% in July; Padina spp., Gracilaria spp., Laurencia spp., Halimeda spp. and Sargassum spp. were the dominant species. Gracilaria spp. and

Fig. 3. Seasonal variations in seawater nutrient concentrations during 1999–2000. Data are means (n=16) with 95% confidence limits.
Laurencia spp. were widely distributed at 25-, 50- and 75-m sampling stations. Coral cover ranged from 8.06% to 15.60%; Favia spp. and Platygyra spp. were the dominant species mainly distributed at 75- and 100-m sampling stations. Low coral cover and high algal cover can be interpreted to indicate coral reef decline in southern Taiwan.

The areal dry weight biomass of both *L. papillosa* and *G. coronopifolia* varied seasonally according to species (*P*=0.0001) (Fig. 4). The areal biomass of *L. papillosa* started to increase in August and reached the maximum in mid August–September following a significant decrease after mid November. *G. coronopifolia* was abundant year around except April–May; its areal biomass significantly decreased in May 1999 following an increase in August 1999–February 2000, and then again a decline in mid April–mid May 2000.

The multiple regression analysis was used to elucidate the relationship between environments (seawater temperature, irradiance, and seawater nutrient concentrations) and macroalgal biomass. The results indicated that seasonal variations in areal biomass of *L. papillosa* were positively correlated with seawater temperature but negatively correlated with seawater NO$_2^-$ and NO$_3^-$ concentrations: $\Delta \sqrt{(\text{biomass})} = 0.0895$ (seawater temperature)−0.8519 (Δ √ (seawater NO$_2^-$ concentration))−0.0773 (seawater NO$_3^-$ concentration) (Table 1). The correlation coefficients (*R* value) for seawater temperature, √(seawater NO$_2^-$ concentration) and seawater NO$_3^-$ concentration were 0.2030, 0.4932 and 0.5411, respectively. Seasonal variations in monthly cumulative irradiance and seawater DIN and SRP concentrations were not correlated with areal biomass of *L. papillosa* (*P*>0.05). Areal biomass of *G. coronopifolia* was negatively correlated with seawater NO$_3^-$ concentrations: (biomass) = 15.1163 − 1.7718 (seawater NO$_3^-$ concentration), and the correlation coefficient (*R* value) for NO$_3^-$ concentration was 0.1215 (Table 1). Seasonal variations in monthly cumulative irradiance and seawater DIN, NO$_2^-$, and SRP concentrations were not correlated with *G. coronopifolia* biomass (*P*>0.05).

![Fig. 4. Seasonal variations in areal biomass of *L. papillosa* and *G. coronopifolia*. Data are means (n=16) with 95% confidence limits.](image-url)
3.3. Algal tissue nutrient contents

Tissue nutrient contents and tissue C/N, C/P and N/P molar ratios of _L. papillosa_ varied seasonally \((P=0.0001)\) (Fig. 5). Tissue C contents were low \((16.62–18.75\%)\) during April–July and high \((19.57–26.08\%)\) during August–March, tissue N contents were low \((0.74–1.72\%)\) during February–June and high \((1.16–3.87\%)\) during July–January, and tissue P contents were ranged from 0.03% to 0.04% during February–March that were relatively low as compared to 0.04–0.14% during May–February. Tissue C/N molar ratios were high \((18–30)\) during February–June and low \((7–21)\) during July–January and in contrast, tissue N/P molar ratios were low \((13–74)\) during February–June and high \((33–240)\) during July–January. During the growing period (June–November), tissue C/P molar ratios were low \((682–837)\) during the emergence of young plants (June–July 2001) and then increased to a peak in mid September 2001 following a sharp drop.

Tissue nutrient contents and tissue C/N, C/P and N/P molar ratios of _G. coronopifolia_ also varied seasonally \((P=0.0001)\) (Fig. 6) Tissue C contents were low \((16.8–25.6\%)\) during April–August and high

### Table 1

Results of stepwise multiple regression analysis for _L. papillosa_ and _G. coronopifolia_ areal dry weight biomass

<table>
<thead>
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<th>Variable</th>
<th>Coefficient</th>
<th>S.E.</th>
<th>(F)</th>
<th>(P)</th>
<th>(R)</th>
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<td></td>
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<tr>
<td>Seawater temperature</td>
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</table>

\(^a\) Double root-transformed.

![Fig. 5.](image-url) Seasonal variations in tissue C, N and P contents and C/N, C/P, and N/P molar ratios in _L. papillosa_. Data are means \((n=16)\) with 95% confidence limits. The upper and lower dash lines indicate the critical and subsistence nutrient contents, respectively.
(26.9–31.6%) during September–March. Tissue N contents were low (0.86–1.94%) during February–July and high (1.98–4.73%) during September–January with peaks in mid September 1999, January 2000 and September 2000, respectively. In contrast, tissue P contents were low (0.04–0.14%) during September–March and relatively high (0.10–0.18%) during April–August. Tissue C/N molar ratios peaked during mid February–May while tissue C/P and N/P molar ratios peaked during September–March.

### 3.4. Algal APA

The APA of both *L. papillosa* and *G. coronopifolia* indicated significant seasonal variations (ANOVA, P<0.05) (Fig. 7). During the survey, the APA of *L. papillosa* increased in August 1999 and also in January–mid February 2000; the magnitude of APA increase in January–mid February 2000 was higher than that in August 1999. In comparison with *L. papillosa*, *G. coronopifolia* showed more frequent increase in APA during the survey. The APA of *G. coronopifolia* increased in February–April 1999, in October 1999, and in December 1999–January 2000; the magnitude of APA increase in December 1999–January 2000 was relatively higher as comparing to those in both February–April 1999 and October 1999.

### 3.5. Critical and subsistence nutrient contents

Changes in daily specific growth rate and tissue N and P contents of *L. papillosa* in response to varying nutrient concentrations were determined to estimate the critical nutrient contents (Fig. 8A). As nutrient concentrations increased, daily specific growth rate increased and reached the maximum when $\text{NO}_3^- / \text{NH}_4^+ / \text{PO}_4^{3-}$ were ≥2:1:0.15 μM. Tissue N and P contents increased as nutrient concentrations increased. Critical N and P contents were estimated as 2.06% and 0.078%, respectively.
The subsistence nutrient contents were estimated from the time-course changes in daily specific growth rate and tissue N and P contents of *L. papillosa* grown in seawater without nutrient enrichment (Fig. 8B). Daily specific growth rate decreased gradually after exposure to nutrient starvation and became negative after 20 days, and tissue N and P contents also decreased over time. The subsistence N and P contents were 0.81% and 0.042%, respectively.

The changes of daily specific growth rate and tissue N and P contents in *G. coronopifolia* in response to varying nutrient concentrations showed that daily specific growth rate increased as NO₃⁻/NH₄⁺/PO₄³⁻ increased from 0:0:0 to 16:8:1.2 A (Fig. 9A). Both tissue N and P contents increased as nutrient concentrations increased. The critical N and P contents of *G. coronopifolia* were 3.20% and 0.27%, respectively. When exposed to nutrient-starved conditions, both daily specific growth rate and tissue N and P contents of *G. coronopifolia* decreased over time (Fig. 9B), and according to the comparison of tissue nutrient contents and daily specific growth rate, the subsistence N and P contents of *G. coronopifolia* were estimated as 0.94% and 0.045%, respectively.

3.6. Effects of temperature on daily specific growth rate

The responses of algal growth to varying temperatures were carried out in continuous-flow seawater enriched with or without nutrients. The daily specific growth rates of both *L. papillosa* and *G. coronopifolia* were affected by temperature (*P*=0.0001) and nutrient enrichment (*P*=0.0001), and the interaction between temperature and nutrient was significant (*P*=0.0001 for *L. papillosa* and *P*=0.0001 for *G. coronopifolia*) (Fig. 10).

When cultured in nutrient-enriched seawater, the daily specific growth rate of *L. papillosa* was positive in a range from 25 to 35 °C and reached the maximum at 30–32.5 °C, while that of *G. coronopifolia* was positive in a range from 15 to 35 °C and reached the maximum at 30 °C. When incubated in seawater...
without nutrient enrichment, the daily specific growth rate of *L. papillosa* was positive in a range from 25 to 35 °C and reached the maximum at 30–35 °C, while that of *G. coronopifolia* was positive in a range from 20 to 35 °C and reached the maximum at 30 °C.

### 4. Discussion

The seasonal patterns of two frondose rhodophytes *L. papillosa* and *G. coronopifolia* from a southern Taiwan coral reef were different that *L. papillosa* was a summer blooming alga abundant in August–September while *G. coronopifolia* appeared year round except April. The present results indicated that both seawater temperature and nutrient availability were important determinants influencing the seasonal growth of *L. papillosa* and nutrient availability was the main factor influencing the seasonal growth of *G. coronopifolia*. Our recent experiments have also provided multiple lines of evidence suggesting that nutrient enrichment and temperature limitation both play a role on the seasonal growth of *Sargassum* populations from the same coral reef of Nanwan Bay at Hengchuan Peninsula (Hwang et al., 2004).

All the results suggest a preference of *L. papillosa* for high temperatures. Based on the outdoor laboratory experiments, the occurrence of the maximum growth of *L. papillosa* at 30–32.5 °C gives a good explanation for the mass production of *L. papillosa* in the hot summer months that seawater temperatures ranged from 28.4 to 33.3 °C during July–September.

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**Fig. 8.** Changes in daily specific growth rate and tissue N and P contents of *L. papillosa* in response to varying nutrient concentrations (A) or starvation treatment (B). Data are means (n=3) with S.E.M.
Because seawater temperatures during November–March were smaller than the lower growth temperature limit (22.5 °C) of *L. papillosa*, it can be suggested that the low abundance of *L. papillosa* in the cold months was due to the limitation of growth by extreme low temperatures. The results of the stepwise multiple regression analysis of field data also showed that seawater temperature was positively correlated with *L. papillosa* biomass. It is not surprising for this red alga inhabited in the tropical waters of Taiwan that it tends to become more abundant in the hot summer months.

Seasonal variations in seawater temperature did not account for biomass variations of *G. coronopifolia*.

Because nutrient-enriched *G. coronopifolia* showed a more wider growth temperature range from 15 to 35 °C with the maximum at 30 °C, its appearance year round except April in southern Taiwan can be expected. This was ascertained by the results of regression analysis that *G. coronopifolia* biomass did not correlate with seawater temperatures. The present data that seawater water temperatures were around 30 °C in the summer months also suggest that the growth of *G. coronopifolia* from southern Taiwan was not limited by high temperatures in the summer. Several studies have shown that the growth and physiological performance of *Gracilaria* from tropical waters is optimal at 25 °C. The best temperature for

Fig. 9. Changes in daily specific growth rate and tissue N and P contents of *G. coronopifolia* in response to varying nutrient concentrations (A) or starvation treatment (B). Data are means (n=3) with S.E.M.
the growth of *G. tikvahiae*, a tropical alga from Florida, USA, was 25 °C (Lapointe et al., 1984b). The data from flask culture showed that thalli of tetrasporophytes of *G. verrucosa* from Bacoor, Cavite, Philippines, had the maximal growth rate at 25 °C for apical segments and 30 °C for mid and basal segments (Hurtado-Ponce and Umezaki, 1987). The higher optimal temperature for southern Taiwan *G. coronopifolia* may be indicative of the adaptation to high temperature conditions. However, high temperatures in the hot summer months limit *Gracilaria* growth in the tropical waters. The field survey reported that *G. cf. verrucosa* in Shantou District, Guangdong, in mainland China disappeared from intertidal zones when water temperature >30 °C (Wang et al., 1984). Other studies provide evidence that not only high temperature but also low temperature limit the growth of *Gracilaria* in the field. The survey carried out in Israel has shown that the growth of *G. conferta* declined in the winter months and reached the maximum in the summer months, mainly due to extreme seawater temperatures during these seasons: 13 and 31 °C, respectively (Friedlander et al., 1987). The study of Lapointe et al. (1984a) suggests that temperature will become a limiting factor for *G. tikvahiae* sampled from shallow water in the Indian River of Florida, USA, when temperatures were <15 °C during November and March in
Florida, explaining their occurrence in summer months in north temperate waters. This study found that in southern Taiwan, seawater temperatures (>20 °C) in November–March were near the lower growth temperature limit (15 °C for nutrient-enriched seawater and 20 °C for nutrient-unriched seawater) of *G. coronopifolia*, suggesting that the limitation of growth of *G. coronopifolia* in the cold months. However, *G. coronopifolia* still exhibited high biomass during November 1999–February 2000, suggesting that there are factors interacting with temperature and thus alleviates the restriction of growth in low temperatures. Here, we found that nutrient enrichment can shift the lower growth temperature limit in *G. coronopifolia* from 20 °C to 15 °C, but did not alter the growth temperature range of *L. papillosa*. The results from the outdoor laboratory culture that the growth of *G. coronopifolia* can be markedly stimulated by nutrient enrichment in low temperature ranges (20–22.5 °C) and its growth temperature range was extended from 20–35 to 15–35 °C by nutrient enrichment suggest that the significant biomass of *G. coronopifolia* during November 1999–January 2000 may be indicative of enhanced growth by highly enriched DIN concentrations in the water column. It has been shown that *G. gracilis* displayed a higher affinity for NH₄⁺ than NO₃⁻ at low temperatures (Smits, 2002). Although it was not the same species, the marked input of DIN, especially NH₄⁺, in November 1999–January 2000 may explain the significant growth of southern Taiwan *G. coronopifolia* in the cold months. All the field and experimental data together with the results of regression analysis indicate that the growth responses of *G. coronopifolia* to varying temperatures were influenced by nutrient availability, and temperature may be not one of factors affecting seasonal variations in areal biomass of *G. coronopifolia* from a coral reef of southern Taiwan.

Temperature may influence several physiological processes leading to enhance nutrient availability in algae; for example, temperature will influence the rate of diffusion and carrier-mediated uptake of nutrients. In *Gracilaria tikvahiae*, NO₃⁻ uptake rates increased with increasing temperatures (Lapointe et al., 1984b). Our data showed that tissue N contents of *G. coronopifolia* increased up to the amounts near the critical N contents in August–September 1999, although seawater DIN concentrations were low during this high-temperature period. It is possible that high temperatures during summer months may stimulate the uptake rates of DIN in *G. coronopifolia*, and thus the enhancement of algal growth and the accumulation of tissue N even when seawater DIN concentrations were low in this period. This might also occur in *L. papillosa* in the summer. We thus hypothesize that the nutrient uptake of these two rhodophytes increased with increasing temperatures in southern Taiwan and thus alleviated N shortage due to growth stimulation by high temperatures in the summer months.

Except the impact of seasonally variable temperatures, variations in nutrient availability were also involved in the seasonality of southern Taiwan rhodophytes. Seawater DIN and SRP concentrations at the present study site were extremely high compared to coral reefs in Caribbean area, the Great Barrier Reef (Australia) and Hawaii (Lapointe and O’Connell, 1989; Lapointe, 1997; Larned, 1998; Schaffelke and Klumpp, 1998). This might be due to significantly expanded urban development and tourism in Hengchuan Peninsula in recent 10 years and we also found that the sewage waters were directly released to this southern Taiwan coral reef without treatments before January 2001. The riverine inputs by two large drainage outlets were an important nutrient source in this coral reef. Our investigations have shown that water nutrient concentrations were high in these two drainages and there were two peaks of nutrient concentrations occurring in June 1999 and May–June 2000, respectively, mainly caused by heavy precipitation (the data were described in Materials and methods). This was consistent with the temporal pattern of seawater nutrient concentration fluctuations that there were two peaks of seawater NO₃⁻ concentrations in July 1999 and May–June 2000, respectively, and one peak of seawater SRP concentrations in July 1999. It strongly supports that nutrient (NO₃⁻ and SRP) was imported into this coral reef mainly by raining and riverine input, especially during the rainfall period (May–September). Evidently the coastal regions in the southern tip of Taiwan have become a highly eutrophic coral reef during 1999–2000. However, most seawater DIN and SRP concentrations during the survey were still lower than the nutrient thresholds for the maximum growth of *G. coronopifolia* (16:8:1.2 µM of NO₃⁻/NH₄⁺/
PO₄³⁻), indicating that the growth of *G. coronopifolia* was nutrient-limited during the survey. On the other hand, it may also imply that *G. coronopifolia* biomass will increase if more nutrients are input in this system. This may be also occurred to *L. papillosa* that seawater nutrient concentrations were lower than the nutrient threshold in August–September, i.e. the early growth period of this rhodophyte, reflecting the nutrient limitation for *L. papillosa* growth in the hot summer months. However, the growth of *L. papillosa* at certain time of the year may suffer high nutrient injury, for example, NH₄⁺ toxicity. The data showed that decreased growth rate of *L. papillosa* was found in response to nutrient concentrations higher than 8:4:0.6 μM (NO₃⁻/NH₄⁺/PO₄³⁻). In the cold months, NH₄⁺ concentrations increased to approximately 4 μM in mid November 1999 and reached a peak of 15 μM in January 2000. It has been known that higher NH₄⁺ level was toxic to algal growth (Haines and Wheeler, 1978) and the uptake of NO₃⁻ by algal cells can be inhibited by NH₄⁺ (Haines and Wheeler, 1978; D’Elia and DeBoer, 1978; Thomas and Harrison, 1987; Smit, 2002). We suggest that high NH₄⁺ concentrations (>4 μM) in the cold months may suppress the growth of *L. papillosa*. In this period, high APA indicated P deficit of *L. papillosa*. It is likely that the combination of low temperature, toxic DIN concentration and limited P availability accounted for the low abundance of *L. papillosa* during November–January. These two rhodophytes from southern Taiwan displayed higher nutrient thresholds compared to 0.5–1.0 μM DIN and 0.1 μM SRP for most macroalgae from tropical coral reefs (Bell, 1992; Lapointe, 1997, 1999). A phaeophyte *Sargassum baccularia* from nearshore coral reefs in the Great Barrier Reef, Australia, also showed a higher nutrient threshold (5 μM NH₄⁺ and 0.5 μM SRP) (Schaffelke and Klumpp, 1998). It is possibly the consequence of the adaptation of algal metabolisms to extra high N and P flux in southern Taiwan waters. On the other hand, the nutrient threshold may be over-estimated by the use of “NO₃⁻+NH₄⁺” combination possibly due to the inhibition of NO₃⁻ uptake by NH₄⁺, which reduces internal N pool and thus the following assimilation processes and growth. The nutrient thresholds for the maximum growth of *G. coronopifolia* were determined in this study as 16:8:1.2 μM for NO₃⁻/NH₄⁺/PO₄³⁻. Because a recent examination by *G. gracilis* has shown that the uptake of NO₃⁻ can be suppressed up to 38% by NH₄⁺ at concentrations above 5 μM (Smit, 2002), it is likely that at the concentration for maximum growth (16:8:1.2 μM for NO₃⁻/NH₄⁺/PO₄³⁻), the utilization of oxidized N (NO₃⁻) was inhibited by 8 μM NH₄⁺. This interaction of NO₃⁻ and NH₄⁺ may be also observed in *L. papillosa*. Here, the use of NO₃⁻ and NH₄⁺ in the present study was to simulate the actual DIN composition in southern Taiwan coral reef waters and the nutrient thresholds determined under mixed N conditions represent the situation of rhodophytes grown in this highly eutrophic southern Taiwan coral reef.

It has been known that most macroalgae can rapidly remove pulsed nutrient inputs from water columns before they can be detected (Fong et al., 1998), and algal tissue nutrient contents are thus used to infer limitation of either N or P (Wheeler and Björnsäter, 1992). So, algal tissue nutrient contents were analyzed in this study and compared to the critical and subsistence nutrient contents to comprehending seasonal variations in nutrient status of both algae. During the growing season, the comparison of tissue nutrient contents to critical and subsistence nutrient contents suggests that the severity of nutrient limitation was different between *L. papillosa* and *G. coronopifolia*. During the survey, most tissue N and P contents in *G. coronopifolia* were low and close to the subsistence levels, but half of tissue N and P contents in *L. papillosa* were ≥ the critical levels, indicating that *L. papillosa* has luxury N and P stores comparing to *G. coronopifolia*. This indicates that *G. coronopifolia* faced more severe nutrient limitation than *L. papillosa* on southern Taiwan. The above view is also supported by the higher nutrient thresholds of *G. coronopifolia* than those of *L. papillosa* obtained from the measurement of growth responses of macroalgae to nutrient enrichment of varying magnitude.

In addition, the type and severity of nutrient limitation of *L. papillosa* and *G. coronopifolia* were variable over time. The results that seawater SRP concentrations in 1999 were mostly higher than the threshold SRP concentration of *L. papillosa* and those in 2000 were near zero suggest that *L. papillosa* suffered more serious P limitation in 2000 than in 1999. During the growing season (June–November), *L. papillosa* was first P-limitation (the start of biomass increase) as supported by decreased tissue P contents.
and increased in C/P and N/P molar ratios before biomass reached the maximum, and during the period when the biomass started to decrease), it became N-limited as suggested by a drop in tissue N contents, a rise in tissue P contents and a decrease in C/P and N/P molar ratios. Increased APA as the biomass reached the maximum in mid August also supported the primary P limitation of L. papillosa.

The growth of G. coronopifolia during the period of biomass increase (August 1999–January 2000) was also P-limited, as indicated by increased tissue N contents but concomitantly decreased tissue P contents. However, the severity of P limitation for G. coronopifolia growth was temporally variable during the period of biomass increase. There were marked drops in tissue P contents below the subsistence level in both mid September and December 1999, showing relatively serious P limitation at these 2 periods. Significantly increased APA of G. coronopifolia supports P limitation in the two periods. Because a marked increase in tissue N contents was found when serious P limitation occurred, it is possible that the growth limitation of G. coronopifolia by P at these two periods was caused by enhanced N availability. A significant increase of seawater DIN concentrations accompanied by increased biomass of G. coronopifolia seems to suggest that increased N input in December 1999 leads to enhanced growth and increased tissue N contents in G. coronopifolia, and thus, a relative P deficiency occurred in cold months when seawater SRP concentrations only showed a relatively small increase. The production of algae from eutrophic waters of carbonate-rich Jamaican reef was also limited by P (Lapointe, 1997). Littler et al. (1991) have concluded from the investigation of algal tissue nutrient contents and water-column nutrient concentrations among different geological systems in tropical waters of Republic of Seychelles that P is limited for algal production in carbonate-rich reefs. P limitation was also observed in other oligotrophic waters (Lapointe et al., 1987, 1992, 1993). However, N limitation has been recorded for several coral reefs (Lapointe et al., 1987; Littler et al., 1991; Larned, 1998). It is apparent that the type of nutrient limitation depends on the interactions between macroalgal species, environments, and season.

The present study shows that L. papillosa and G. coronopifolia from southern Taiwan had a relative high APA as compared to macroalgae from other places in the world (Lapointe et al., 1992; Schaffelke, 2001). It has been suggested that those algae with high APA and other mechanisms to acquire a range of nutrient are likely benefit from an increased nutrient supply caused by increased human activities (Schaffelke, 2001). The study of Schaffelke (2001) showed that high APA could compensate the relative P-limitation of macroalgae in response to significant N-inputs in inshore reefs of the Great Barrier Reefs, Australia. Thus, these two opportunistic rhodophytes with high APA tend to bloom in nearshore reefs with extra high nutrient inputs in southern Taiwan.

Multiple factors involve in macroalgal seasonality. Factors such as light intensity may also influence the seasonal abundance of these 2 rhodophytes. Light is considered a primary factor affecting algal growth. It has been identified that the seasonal growth rates of Florida G. tikvahiae are correlated with seasonal variations in light intensity (Lapointe and Ryther, 1978). In this work, a sharp decrease in light intensity (1000 mol m⁻² month⁻¹, only 50 % of the normal level) may be a cause for the sudden drop of G. coronopifolia biomass in April–July 1999. However, there was a decline of G. coronopifolia biomass occurring early in mid March–mid April 2000 even the light intensity remained around 2000 mol m⁻² month⁻¹, suggesting factors other than light leading to this biomass decline. The results of multiple regression analysis of field data have also shown that seasonal variations in monthly cumulative irradiance in the southern tip of Taiwan did not correlate with biomass abundance of both G. coronopifolia and L. papillosa. It is therefore suggested that light intensity might be not a factor influencing the seasonality of these two rhodophytes in southern Taiwan.

Our unpublished data showed that the abundance in grazers on reefs of Nanwan Bay of Hengchuan Peninsula (including sea urchins, Tripneustes gratilla (Linnaeus), Toxopneustes pileolus (Lamarck), Echinothrix spp. and herbivorous reef fishes Abudedefduf spp., Dascyllus spp., Chaetodon spp.) significantly decreased in recent 5 years (1996–2000). A previous investigation on the temporal changes in population dynamics, diet and recovery of sea urchins (Tripneustes gratilla) in Hengchuan Peninsula from 1996 to 1997 reported that this sea urchin can consume the amount of algae (especially G. coronopifolia) up to 1/
of its body weight per day but its population density was only 0.0016 times that of 1984 caused by the human harvest of sea urchin gonad (Chao, unpublished data). Evidently the herbivorous pressure on coral reefs of Nanwan Bay in Hengchuan Peninsula decreased over the past decade. A recent study by Lapointe et al. (2004) suggests that bottom-up control via nutrient enrichment is a primary factor regulating macroalgal biomass and taxonomic assemblages on coral reef, whereas grazing is more important in controlling relative species composition via dietary preferences. However, the seasonal variations in herbivorous pressure have not been determined at the present site and its relation to macroalgal abundance and composition and to nutrient enrichment-mediated macroalgal blooms is thus not clear.

In conclusion, the results of present investigation suggest that the coastal regions in the southern tip of Taiwan were already a highly eutrophic coral reef during the survey, and the differences in nutrient utilization strategy and temperature-dependent growth responses were responsible for variations in temporal abundance dynamics between L. papillosa and G. coronopifolia from a highly eutrophic coral reef in southern Taiwan. Our data showed that macroalgal blooms, especially G. coronopifolia, might increase if more nutrients are input in this system. Because macroalgal blooms on tropical waters are attributed to interactions among eutrophication, reduced herbivores (Lapointe, 1999; Lapointe et al., 2004) and other environmental parameters (Hughes and Connell, 1999), the role of temporal variations in herbivorous pressure and its interactions with other factors on the standing crops of both L. papillosa and G. coronopifolia still need to be addressed in the near future.

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References


