



FEATURE ARTICLE

Responses of phytoplankton and periphyton to system-scale removal of oyster-culture racks from a eutrophic tropical lagoon

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ABSTRACT: There is great concern about the ecological impacts and benefits of oyster culture on estuaries and coastal waters. To examine the effects of the system-scale removal of oyster culture racks on phytoplankton and periphyton in a eutrophic tropical lagoon, a long-term study was conducted at 2 to 3 mo intervals from June 2000 to June 2004 (includes the time of complete oyster culture removal from Tapong Bay, southwestern Taiwan in June 2002). The abundances, productivities, and community structures of the inner (poorly flushed) and outer (well flushed) regions were compared before and after rack removal. Tidal flushing was an important factor regulating the responses of phytoplankton. After rack removal, mean chlorophyll *a* and maximum gross production (GP_{max}) rate of phytoplankton increased 4-fold in the inner region, but remained unchanged in the outer region and at the control site. Phytoplankton communities in both regions and at the control site were dominated by Bacillariophyta alone before rack removal, but shifted to a co-dominance of Bacillariophyta, Dinophyta, and Cyanobacteria after rack removal. When GP_{max} rate was normalized to chl *a* (P_{max}^B) and expressed as maximum photosynthetic intensity, no significant difference was detected before and after rack removal in either region. Chl *a* accumulation rate, GP_{max} rate, P_{max}^B , and dominant species of periphyton did not differ significantly before and after rack removal in either region. Our results suggest the effectiveness of top-down control of phytoplankton abundances and a reduction in community diversity by cultured oysters in this eutrophic lagoon.

KEY WORDS: Tapong Bay · Abundance · Productivity · Community structure · Top-down control · Flushing

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Suspended culture of the Pacific oyster *Crassostrea gigas* in Tapong Bay, Taiwan

Photo: Teng-Chung Wang

INTRODUCTION

Aquaculture is a rapidly expanding industry in coastal waters worldwide. Oyster production ranks second in the world among the top ten aquaculture species (Food and Agriculture Organization 2004). There is great concern about the ecological impacts and benefits of oyster culture on estuaries and coastal waters. Cultured oysters and biofouling communities on suspended oyster cultures reduce phytoplankton abundances (Officer et al. 1982, Newell 1988, Souchu et al. 2001) and cause shifts in the dominant species (Baker et al. 1998, Dupuy et al. 2000, Souchu et al.

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2001, Pietros & Rice 2003). Oyster restoration has been proposed as an ecological tool for top-down control of phytoplankton blooms and to reverse cultural eutrophication in estuaries and coastal waters (Coen et al. 2007), although this ecosystem service is currently controversial (Pomeroy et al. 2006, Fulford et al. 2007), indicating that ecosystem effects of oyster culture in coastal waters have been poorly quantified.

Previous studies on effects of cultured bivalves in coastal ecosystems were mostly conducted by comparing nutrient concentrations and phytoplankton communities between bivalve-culture zones and adjacent areas (e.g. Baudinet et al. 1990, Mazouni et al. 2001, Souchu et al. 2001). Restoration and sustainable management of coastal ecosystems for bivalve culture require ecosystem-scale (rather than population- or community-scales) knowledge of the feedback interactions between bivalves and biological and abiotic factors (Prins et al. 1997). Understanding the response of natural systems to removal or modifications of perturbations may become increasingly important for effective environmental management and successful restoration of impacted ecosystems. There have been few studies on responses of communities in impacted coastal waters to system-scale removal of bivalve culture, an exception being the study by Dame et al. (2002) in which oysters were completely removed from tidal creeks subject to rapid tidal flushing. However, they (op. cit.) were unable to determine whether there was a significant increase in phytoplankton abundance after culture removal.

Tapong Bay ($22^{\circ} 27' \text{N}$, $120^{\circ} 26' \text{E}$) is a eutrophic, poorly flushed tropical lagoon in southwestern Taiwan; it has only one tidal inlet (1 km long, 138 m wide, 2 m deep) connecting it to the sea (Fig. 1). Until recently, the lagoon was an important site for culturing the oyster *Crassostrea gigas*. Almost all lagoon area was devoted to oyster culture, and the density reached as high as $2932 \text{ racks km}^{-2}$ (Lin et al. 2006). Phytoplankton and periphyton on the oyster culture racks and rocks along the coast were the dominant autotrophs in the lagoon. In 1997, this lagoon was designated a National Scenic Area, and oyster culture was prohibited. All of the oyster culture racks were removed from Tapong Bay at the same time in June 2002. This provided an opportunity (similar to a manipulation experiment) for an integrated study within the framework of LOICZ (Land-Ocean Interactions in the Coastal Zone) (Pernetta & Milliman 1995) to examine responses of an entire lagoon to ecosystem-scale removal of oyster cultures. The purposes of this study were to charac-

terize changes in abundances, productivity levels, and community structures of phytoplankton and periphyton before and after the complete removal of oyster culture racks. We hypothesized that removing the oyster culture racks would release top-down control of phytoplankton abundances and cause a shift in the dominant phytoplankton species, but we predicted no equivalent changes in lagoon periphyton.

MATERIALS AND METHODS

Study site. Tapong Bay has a surface area of 4.44 km^2 and a mean depth of 2.2 m at low tide (Fig. 1). It is surrounded by a variety of aquaculture ponds producing fish and shrimp and receives nutrient-rich waste discharges averaging $172 \times 10^3 \text{ m}^3 \text{ d}^{-1}$ from 2 mangrove-lined creeks that drain the surrounding aquaculture ponds. Loading rates of N and P in the lagoon reach $1.87 \text{ and } 0.51 \text{ mol m}^{-2} \text{ yr}^{-1}$, respectively (Hung & Hung 2003). Consequently, while concentrations of dissolved oxygen in the surface water are $>5.4 \text{ mg l}^{-1}$, the bottom water in the inner region may become hypoxic (2 mg l^{-1}) in summer when the water is partially stratified. No rooted macrophytes are normally observed in the lagoon.

Climatic data derived from the weather station at Donggang during 1999 to 2003 (Climatological Data Annual Report, Central Weather Bureau of Taiwan) show that in winter (the dry season, October to April) the mean monthly rainfall normally does not exceed 40 mm, and that in summer (the wet season, May to September) the average monthly rainfall frequently exceeds 200 mm. Since no large river flows into the lagoon, its small volume makes salinity responsive to

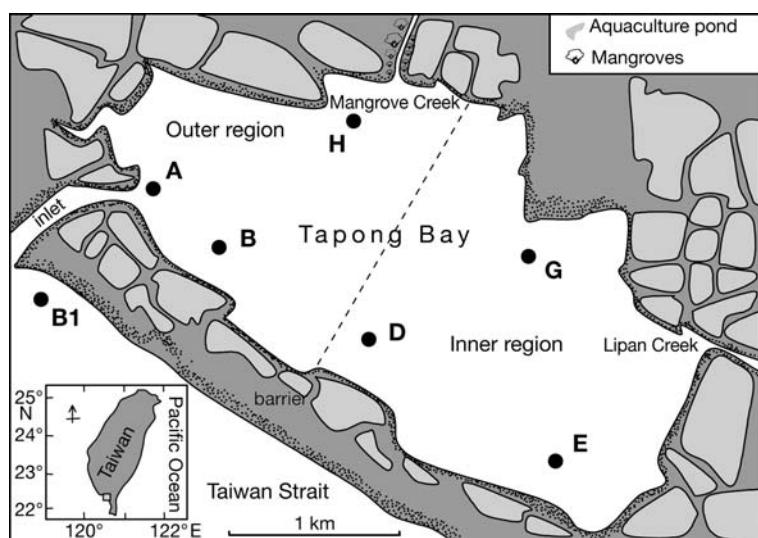


Fig. 1. Outer and inner regions of Tapong Bay, showing sampling locations (A, B, D, E, G, H) and the control site (B1)

changes in rainfall inputs and evaporative losses. Consequently, salinities are lower in summer (about 25.4 psu) and higher in winter (about 33.9 psu), with a mean value of 31.8 psu. Water temperatures range from about 32°C in summer to about 22°C in winter.

Tapong Bay primarily experiences semidiurnal tides, with a tidal range of about 1.0 m. Tidal pumping is the mixing agent between the open sea and the lagoon. There are 2 anti-directional circulation eddies that meet in the middle area of the lagoon (Chen 2002). Such a circulation pattern remained after the removal of oyster culture racks (J. C. S. Yu, pers. comm.). Tidal flushing is thus the most important factor spatially separating abundances and species compositions of phytoplankton (Su et al. 2004) and periphyton (Lin & Hung 2004) between inner and outer regions of the lagoon. Su et al. (2004) found that the abundance and productivity of phytoplankton were greater at sites D, E, and G in the inner region, which are subject to poor flushing (Fig. 1). Lin & Hung (2004), however, found that abundance and species richness of periphyton on oyster culture racks were greater at sites A, B, and H in the well-flushed region near the tidal inlet. In order to examine the effects of flushing on the responses of phytoplankton and periphyton to rack removal, measurements were made at 6 study sites in the 2 regions of the lagoon and at site B1 outside the lagoon in the Taiwan Strait (as a control).

Water flows. The box model (Gordon et al. 1995) was applied to construct water and salt budgets for comparing water flows across the boundaries of Tapong Bay. Budgets were constructed every 2 to 3 mo from August 1999 to December 2001 (before rack removal) and from February 2003 to September 2004 (after rack removal) in the 2 lagoon regions. Assuming that the water volume in Tapong Bay remains constant, the water budget can be expressed as:

$$V_O + (V_P - V_E) + V_G + V_{in} - V_{out} = 0 \quad (1)$$

where V_O , V_P , V_E , V_G , V_{in} , and V_{out} are mean flow rates of terrestrial water (wastewater), precipitation, evaporation, groundwater, advective inflow, and advective outflow of water from the lagoon (box), respectively. Eq. (1) can be rearranged as follows:

$$V_R = V_{out} - V_{in} = V_O + (V_P - V_E) + V_G \quad (2)$$

where V_R denotes the residual flow, and V_P and V_E are calculated from the lagoon area and the precipitation and evaporation rates reported by the weather station at Donggang. V_O was determined from measured flow velocities and channel cross-sectional areas in Lipan Creek and Mangrove Creek. V_G is relatively small and negligible in this calculation because of over-extraction of groundwater for aquaculture in the surrounding area. Taking salinity as zero for fresh-

water (V_P and V_E), and a salinity S_O for wastewater (V_O), the salt budget in the lagoon, therefore, can be derived:

$$(S_2 - S_1)V_X = S_R V_R - S_O V_O \quad (3)$$

where V_X is seawater exchange flow from the Taiwan Strait, and $S_R = (S_1 + S_2)/2$; S_1 and S_2 are mean values of salinity in the lagoon and Taiwan Strait, respectively. Consequently, $V_X = (S_R V_R - S_O V_O)/(S_2 - S_1)$. The total water exchange time (τ) of lagoon water was estimated from the ratio $V_{syst}/(|V_R| + V_X)$, where V_{syst} is the volume of the lagoon.

Changes in the relative water motion in the respective regions of Tapong Bay were studied in April 2000 before rack removal and in March 2004 after rack removal by means of plaster of Paris weight loss (about 40 g, $n = 5$) after 1 d of submersion in the water at spring tide (following the method of Erftemeijer & Herman 1994).

Environmental variables. Environmental variables in the water column were monitored (at times closely matching the times of abundance determinations and productivity incubations at the 6 sites in the 2 regions) every 2 to 3 mo from June 2000 to June 2004 (spanning the time of removal of oyster culture racks in June 2002). On each occasion, water temperature, pH, and salinity were continually monitored *in situ* for 24 h at 10 min intervals using YSI 600XLM multiparameter monitoring sensors. The light extinction coefficient (k) in the water column for photosynthetically active radiation (PAR) was determined by light measurements using a Li-Cor Quantum Li-189 meter at low tide.

Water samples for analyses of total dissolved nutrients and dissolved inorganic nutrients were collected at a depth of 30 cm at low tide at the 6 sites in the 2 regions. 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: $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) and dissolved inorganic phosphorus (DIP: PO_4^{3-}) were determined colorimetrically (Strickland & Parsons 1972) by a flow injection analytical method (Pai et al. 1990). Total dissolved nitrogen (DN) was measured by high-temperature oxidation and chemiluminescent detection (Antek N/S analyzer). Total dissolved phosphorus (DP) was measured by UV-persulfate oxidation and a colorimetric method (Ridal & Moore 1990). Dissolved organic phosphorus (DOP) and dissolved organic nitrogen (DON) were determined from the differences between DP and DIP and DN and DIN, respectively. The loading rates of N and P in Tapong Bay were derived by multiplying the waste discharge (V_O) from the 2 creeks by the DN and DP concentrations.

Abundance determinations. Abundances of phytoplankton and periphyton were determined every 2 to

3 mo from June 2000 to June 2004. On each occasion, water samples for phytoplankton abundance were collected at a depth of 30 cm at low tide at the 6 sites in the 2 regions. At the control site, samples were collected in triplicate at low tide every 3 mo from August 2001 to March 2003 to quantify phytoplankton abundance, productivity, and community structure. We made no periphyton measurements at the control site. Chl *a* concentration was determined in a spectrophotometer by immediately filtering water samples through Whatman GF/F filters in the field and extracting them in 90% acetone in the dark for 24 h at 4°C.

Periphyton abundance largely depends upon the submersion time and type of substratum (Lin & Shao 2002). Bamboo was the material used for oyster culture racks in the lagoon. For comparisons before and after removal of oyster culture racks, periphyton abundances were determined by submerging plates of bamboo in the water column for periphyton colonization, and the results were standardized by submersion time. At each site, a row of 20 plates of bamboo, each measuring 10 × 20 cm and 1 cm thick, was vertically attached to a projecting structure on the shore at a depth of 30 cm 3 wk before the productivity incubations were conducted. All plates were positioned toward the sun to avoid shading. After submersion for 3 wk, all the space on the plates was covered by representative periphyton species at natural field density (Lin & Hung 2004). After the productivity incubations, the periphyton was gently scraped from the surfaces of randomly selected bamboo plates ($n = 6$) and mixed using a mixer. The chl *a* content was determined and expressed as the chl *a* accumulation rate ($\text{mg chl } a \text{ m}^{-2} \text{ d}^{-1}$).

Productivity incubations. Production rates of periphyton and phytoplankton were determined as changes in dissolved oxygen concentrations in microcosm incubations every 2 to 3 mo from June 2000 to June 2004 in the 2 lagoon regions (Lin et al. 2005); measurements were made for the water column only and for periphyton + water column ($n = 6$ for each treatment) in outdoor tanks with flow-through seawater. At the control site, phytoplankton productivity was determined by changes in dissolved oxygen concentrations in light and dark (300 ml) BOD bottles incubated in outdoor flowing seawater tanks ($n = 3$ for each treatment). The water column microcosm was used both to determine the production rates of phytoplankton and to correct the dissolved oxygen measurements in the periphyton + water column microcosm. Periphyton added to the periphyton + water column microcosm was obtained by submerging the plates of bamboo in the water column in each region on each occasion for periphyton colonization. Water for the microcosms was directly pumped from the same depth at dawn when the submerged plates with periphyton were taken for produc-

tivity incubations, and when the dissolved oxygen in the water column was low. Sampling was timed to correspond with low tides.

Each microcosm consisted of a 3.75 l (10 cm wide × 25 cm long × 15 cm deep) transparent chamber with a propeller attached to the clear acrylic top. The propeller was used to disrupt vertical gradients in oxygen concentrations in the water column. When conducting the microcosm incubations, 6 microcosms were arranged in a row within an acrylic tank, and the distance between the microcosms was at least 10 cm to avoid shading caused by neighboring microcosms. Three replicate microcosms within each tank in random order were incubated for the water column only, while the other 3 were for the periphyton/water column. Flowing seawater outside the microcosms was used to maintain temperatures at ambient levels, and it did not mix with the water inside the microcosms. The flowing-seawater system was constructed by arranging 5 tanks at different heights side by side in cascading order, so that seawater pumped from the lagoon could flow by gravity from the top to the bottom tank. The incubations were conducted beside Tapong Bay from 10:00 to 14:00 h when the irradiance was saturating for photosynthesis. During this period, incident photon irradiance remained at around $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in spring and winter and $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in summer and fall. On each occasion in each region, each tank was exposed to the same photon irradiance of about $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ by interposing screens with different mesh sizes. At this intensity, the relationships between production rates and irradiance levels (the *P-I* curve) described by the hyperbolic tangent function suggested by Jassby & Platt (1976) in different seasons in the 2 regions showed that production rates of periphyton and phytoplankton in the lagoon had generally reached asymptotic values near the maximum rates (Lin et al. 2005). Dark microcosms with 100% shading were tightly wrapped in aluminum foil for complete exclusion of light for determination of respiration rates.

Water samples were collected using a peristaltic pump at the start of the incubations and then at the end of the 1 to 2 h incubations. Maximum net production and respiration rates of periphyton ($\text{mmol O}_2 \text{ m}^{-2} \text{ substratum } h^{-1}$) and phytoplankton ($\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$) were derived from changes in dissolved oxygen concentrations over time in illuminated and darkened incubation microcosms, respectively. Measurements of net production and respiration rates reflected the oxygen turnover of the entire community, including photoautotrophic and heterotrophic activities. Therefore, respiration refers to community respiration, and the term 'net production' (NP) was used instead of 'net primary production'. Dissolved oxygen concentrations were monitored using a DO meter (model 52, YSI)

immediately after sampling. The maximum gross production (GP_{max}) was calculated as the sum of the respiration and maximum NP.

Community structure. One aliquot of water sample for determinations of phytoplankton abundance and productivity was fixed with Lugol's solution immediately after filtering through a 200 μm net (Parson et al. 1984). After settlement, the upper clear water was siphoned off, and the concentrated sample of 10 to 20 ml was stored in a small bottle. Identification and counting of taxa were accomplished after sedimentation on a scaled slide using a light microscope under phase- and DIC-contrast at 400 \times . A volume of 0.5 ml of the concentrated sample in duplicate was scanned. Identification was carried out according to Drebes (1974), Council of Agriculture (1991), and Tomas (1997).

Periphyton biovolume was determined for major groups using standard formulae for the solid geometric shape which the cells most closely approximated.

Data analyses. Since our primary concern was to detect differences before and after removal of oyster culture racks, 1-way analysis of variance (ANOVA) was used to evaluate whether environmental factors and abundances and productivities of phytoplankton and periphyton differed between the 2 yr before and after the removal in the outer and inner regions and at the control site. Before analyses, values of P^B_{max} were 4th root-transformed (Clarke & Warwick 1994) to fit the data to assumptions of normality and variance homogeneity. The relationships between abundances and productivities of phytoplankton and periphyton and environmental variables were determined using Spearman rank correlations. A chi-square test was

used to determine differences in the phytoplankton community before and after the oyster removal in the 2 lagoon regions and at the control site.

RESULTS

Water flows

Before removal of oyster culture racks from Tapong Bay, the water budget showed a clear spatial pattern (Table 1). The residual outflow and seawater exchange rates were higher in the outer region than in the inner region. After rack removal, there were no significant differences in residual outflow or net inputs of freshwater and wastewater in either region. However, the seawater exchange rate significantly increased in both regions after rack removal; the mean lagoon water exchange times were 11.1 d and 6.1 d before and after rack removal, respectively.

Relative water motion measurements corresponded well to the spatial patterns determined by the water exchange time. After rack removal, the relative water motion became significantly faster in both regions.

Environmental variables

There were no significant changes in water temperature, salinity, or pH in either lagoon region after removal of oyster culture racks (Table 1). Light extinction remained low in the outer region, but significantly increased in the inner region after rack removal (Table 1).

Table 1. Water flows and environmental variables (mean \pm SE) measured in the outer and inner regions of Tapong Bay. Environmental variables were measured ($n = 3$ in each region) from August 1999 to September 2004, before and after complete oyster culture rack removal (June 2002). Relative water motion was measured ($n = 5$ in each region) in April 2000 before rack removal and in March 2004 after rack removal. DIN: dissolved inorganic nitrogen; DON: dissolved organic nitrogen; DIP: dissolved inorganic phosphorus; DOP: dissolved organic phosphorus. Asterisks indicate significant differences (1-way ANOVA) after complete removal of oyster culture racks at * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$

Region	Outer region		Inner region	
	Before	After	Before	After
No. of sampling occasions	9	6	9	6
Residual outflow ($10^3 \text{ m}^3 \text{ d}^{-1}$)	191 \pm 40	167 \pm 33	182 \pm 34	159 \pm 28
Seawater exchange rate ($10^3 \text{ m}^3 \text{ d}^{-1}$)	606 \pm 111	932 \pm 167*	413 \pm 58	621 \pm 93*
Water exchange time (d)	8.71 \pm 1.62	6.13 \pm 0.73*	11.6 \pm 2.17	8.18 \pm 0.98*
Relative water motion (g d^{-1}) ($n = 1$)	15.0 \pm 1.0	20.5 \pm 0.5**	5.3 \pm 0.3	11.8 \pm 0.3***
Water temperature ($^{\circ}\text{C}$) ($n = 11$)	26.1 \pm 0.6	27.0 \pm 0.7	26.2 \pm 1.0	26.7 \pm 0.9
Salinity (psu) ($n = 11$)	34.4 \pm 0.4	34.0 \pm 0.5	31.3 \pm 0.7	29.9 \pm 0.8
pH ($n = 11$)	8.28 \pm 0.05	8.25 \pm 0.08	8.08 \pm 0.06	8.15 \pm 0.06
Light extinction (m^{-1}) ($n = 11$)	1.19 \pm 0.23	1.09 \pm 0.14	1.55 \pm 0.15	2.42 \pm 0.33*
Water column nutrients (μM)				
DIN ($n = 11$)	9.51 \pm 4.10	5.80 \pm 1.27	32.9 \pm 6.81	30.7 \pm 7.85
DON ($n = 6$)	19.9 \pm 5.26	26.0 \pm 4.03	26.9 \pm 4.91	36.1 \pm 7.27
DIP ($n = 11$ before, 12 after)	2.26 \pm 0.72	0.48 \pm 0.08**	10.5 \pm 1.61	7.40 \pm 2.30*
DOP ($n = 6$)	1.13 \pm 0.25	0.72 \pm 0.22	3.76 \pm 1.67	1.01 \pm 0.30*

Water column nutrient concentrations in Tapong Bay also showed clear spatial patterns (Table 1). They were higher in the inner region, which is subject to poor flushing and closer to anthropogenic nutrient sources, than in the outer region, which is better flushed. After removal of oyster culture racks, the loading rate of N in the lagoon more than doubled to $4.26 \text{ mol m}^{-2} \text{ yr}^{-1}$, but that of P remained constant at $0.46 \text{ mol m}^{-2} \text{ yr}^{-1}$. Consequently, DIN concentrations tended to be lower, but DON concentrations tended to be higher, although the changes were not statistically significant due to high temporal variations (Fig. 2). DIP concentrations were significantly lowered in both regions after rack removal (Table 1). DOP concentrations also decreased significantly in the inner region (Table 1). Despite the more rapid water exchange after rack removal in the outer region, the mean concentrations of DIN and DIP were still higher than those at the control site ($2.33 \mu\text{M}$ and $0.36 \mu\text{M}$, respectively). Patterns of temporal variations in concentrations of DIN and DIP also changed. Lower concentrations of DIN and DIP in fall/winter before rack removal shifted to summer/fall after rack removal.

Phytoplankton response

Before removal of oyster culture racks, phytoplankton chl *a* showed a clear spatial pattern (Fig. 3a). Mean values were 14.1 mg m^{-3} in the inner region, 3.35 mg m^{-3} in the outer region and 0.23 mg m^{-3} at the control site outside the lagoon (Table 2). After rack removal, values of phytoplankton chl *a* remained low in the outer region and at the control site but increased significantly in the inner region to 64.0 mg m^{-3} (Table 2). Moreover, the spring maximum chl *a* values in the inner region greatly increased from $29–33$ to $127–154 \text{ mg m}^{-3}$ after rack removal. In the second year after rack removal, the maximum value shifted from spring to early winter (tracking the shift in nutrient concentrations).

Phytoplankton GP_{max} rate also showed a clear spatial pattern (Fig. 3b). The mean value was $16.8 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ in the inner region, $5.49 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ in the outer region and $3.43 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ at the control site (Table 2). The phytoplankton GP_{max} rate response to removal of oyster culture racks generally followed the temporal trend of chl *a*. However, when the GP_{max} rate was normalized to chl *a* (P^B_{\max}) and expressed as the maximum photosynthetic rate, there were no significant differences between

before and after rack removal values in either region (Table 2). Nevertheless, P^B_{\max} responded to the removal more quickly than chl *a* and GP_{max} rate, and the P^B_{\max} values were also greater than those before rack removal in the inner region (Fig. 3c).

DIN, DIP, and light extinction were positively correlated with phytoplankton chl *a* and GP_{max}, while salinity and pH were negatively correlated with these parameters (Table 3). However, only light extinction was found to be significantly and positively correlated with the P^B_{\max} rate.

Before removal of oyster culture racks, the spatial pattern of phytoplankton cell density corresponded well to the chl *a* pattern, with greatest density in the inner region and the lowest at the control site (Table 4). Community composition did not significantly differ ($p > 0.05$) among the outer and inner regions and the control site, which was dominated by Bacillariophyta (diatoms) alone. The diatoms *Skeletonema costatum*, *Chaetoceros* sp., *Cylindrotheca closterium*, and *Nitzschia* sp., the cyanobacterium *Oscillatoria* sp., and the dinoflagellate *Protoperidinium* sp. were the most frequently observed

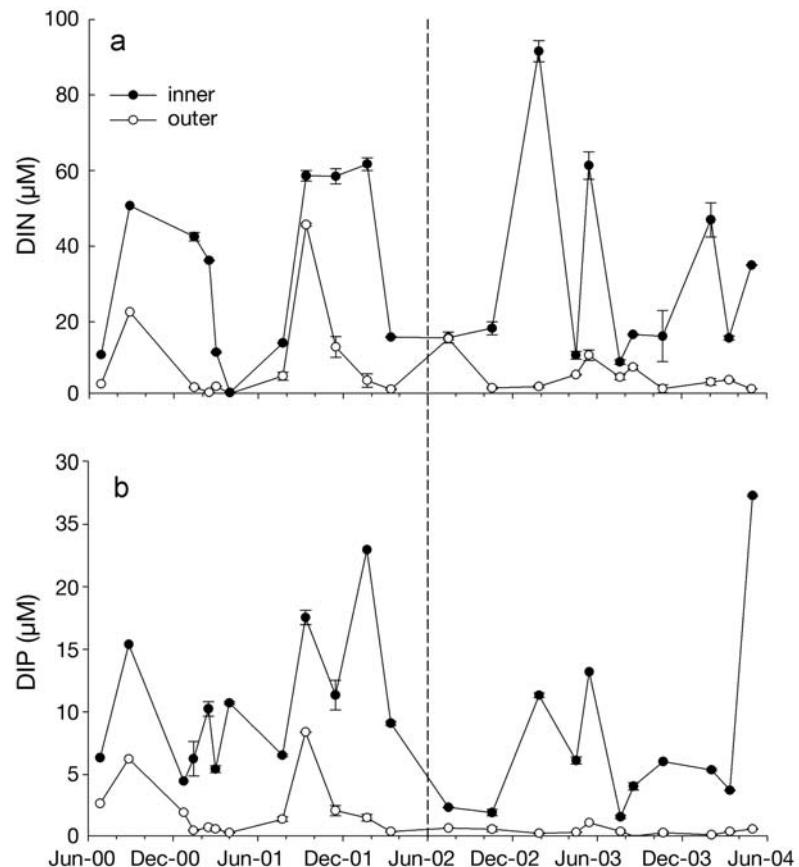


Fig. 2. Temporal variation (mean \pm SE, $n = 3$ sites in each region) in (a) dissolved inorganic nitrogen (DIN) and (b) dissolved inorganic phosphorus (DIP) in the water column of the outer and inner regions of Tapong Bay before and after the complete removal of oyster culture racks in June 2002 (dashed line)

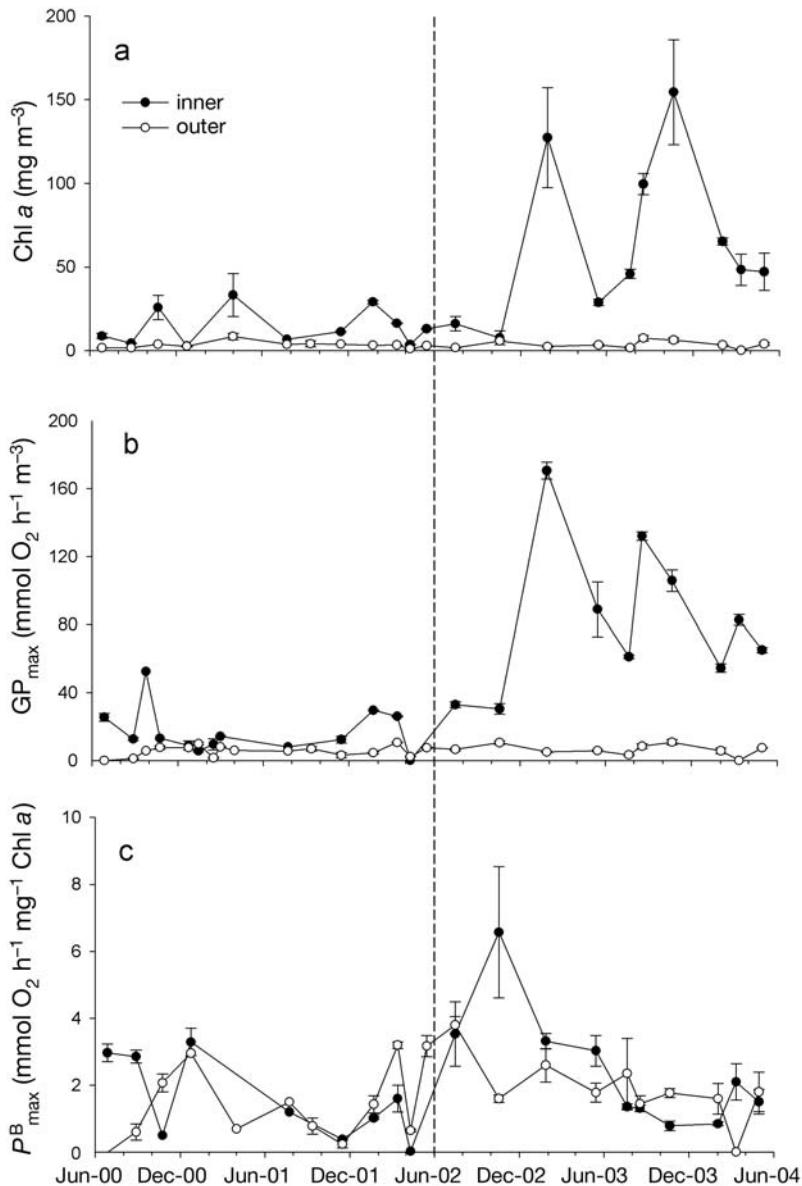


Fig. 3. Temporal variation (means \pm SE, n = 3 sites in each region) in phytoplankton (a) chl a , (b) maximum gross production (GP_{\max}) rate, and (c) chl a -normalized net production (P_{\max}^B) in the outer and inner regions of Tapong Bay before and after the complete removal of oyster culture racks in June 2002 (dashed line)

species. After rack removal, phytoplankton cell numbers remained low at the control site, but were significantly greater in both regions of the bay. The dominant phytoplankton community phyla in both regions shifted to a co-dominance of Bacillariophyta, Dinophyta (dinoflagellates), and Cyanobacteria, but not at the control site. The relative abundances of Cryptophyta and Euglenophyta also increased after rack removal in both bay regions. Consequently, the diversity of the phytoplankton community tended to increase after rack removal in both bay regions, although tests for statistical significance were not possible because of the small number of samples.

Periphyton response

Before removal of oyster culture racks, the periphyton chl a accumulation rate was generally higher in the inner region, but the GP_{\max} rate and P_{\max}^B were greater in the outer region (Fig. 4). Periphyton mainly comprised macroalgae, diatoms, and heterotrophic organisms, but the biovolume contribution of macroalgae exceeded 80%. Species richness of macroalgal periphyton was lower in the inner region than in the outer region. The dominant species in the outer region were the chlorophytes *Ulva fasciata* and *U. lactuca*, but shifted to the cyanobacterium *Lyngbya majuscula* in the inner region. These species retained dominance after rack removal.

After rack removal, there were no significant changes in periphyton chl a accumulation rate, GP_{\max} , or P_{\max}^B in either region (Table 2). In the outer region, however, the mean periphyton chl a accumulation rate was about double that before rack removal, although this was not statistically significant due to high temporal variations (Fig. 4a).

Salinity was positively correlated with periphyton GP_{\max} , while water temperature and light extinction were negatively correlated with this parameter (Table 3). Only light extinction was found to be significantly and negatively correlated with periphyton P_{\max}^B rate.

DISCUSSION

Before removal of oyster culture racks from Tapong Bay, phytoplankton and periphyton were the dominant autotrophs. Although periphyton contributed <6% to daily system gross production,

periphyton biomass may have exceeded that of phytoplankton in the well-flushed outer region where there was a large number of oyster farms available for periphyton colonization (Lin et al. 2005). Joint analyses of stomach contents and stable isotopes showed that periphyton was the most important assimilated food for the dominant detritivorous fish (e.g. *Liza macrolepis*) in the lagoon (Lin et al. 2007). After rack removal, neither periphyton chl a accumulation rate nor GP_{\max} significantly increased, but the periphyton proportion of total system biomass was greatly reduced by the loss of available substrata for colonization. On the other hand,

Table 2. Abundances and productivities of phytoplankton and periphyton (mean \pm SE) determined at the 3 sites in the outer and inner regions of Tapong Bay from June 2000 to June 2004, before and after complete removal of oyster culture racks in June 2002. At the control site, only phytoplankton parameters were determined from August 2001 to March 2003. GP: gross production; P^B : chlorophyll *a*-normalized net production. Asterisks indicate significant differences (1-way ANOVA) after the complete removal of oyster culture racks at * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$

	Outer region		Inner region		Control site	
	Before	After	Before	After	Before	After
Phytoplankton						
No. of sampling occasions	12	10	11	10	3	3
Chl <i>a</i> (mg m ⁻³)	3.35 \pm 0.54	3.61 \pm 0.72	14.1 \pm 3.24	64.0 \pm 15.2**	0.23 \pm 0.02	0.19 \pm 0.07
GP _{max} (mmol O ₂ h ⁻¹ m ⁻³)	5.49 \pm 0.78	6.34 \pm 1.02	16.8 \pm 3.80	82.4 \pm 13.9***	3.43 \pm 0.83	1.76 \pm 1.01
P^B_{max} (mmol O ₂ h ⁻¹ mg ⁻¹ chl <i>a</i>)	1.45 \pm 0.33	1.89 \pm 0.30	1.54 \pm 0.40	2.44 \pm 0.55	13.1 \pm 4.05	9.27 \pm 1.93
Periphyton						
No. of sampling occasions	12	9	11	10		
Chl <i>a</i> accumulation (mg m ⁻² d ⁻¹)	3.92 \pm 0.72	7.26 \pm 2.57	9.02 \pm 3.21	9.06 \pm 4.44		
GP _{max} (mmol O ₂ h ⁻¹ m ⁻²)	13.2 \pm 1.89	17.5 \pm 3.92	10.1 \pm 2.50	11.5 \pm 4.84		
P^B_{max} (mmol O ₂ h ⁻¹ mg ⁻¹ chl <i>a</i>)	0.38 \pm 0.14	0.26 \pm 0.06	0.23 \pm 0.10	0.17 \pm 0.06		

Table 3. Spearman rank correlation coefficients relating abundances and productivities of phytoplankton and environmental variables in Tapong Bay. DIN: dissolved inorganic nitrogen; DON: dissolved organic nitrogen; DIP: dissolved inorganic phosphorus; DOP: dissolved organic phosphorus; GP_{max}: maximum gross production. Significant correlations in **bold**

		Phytoplankton			Periphyton		
		Chl <i>a</i>	GP _{max} rate	P^B_{max}	Chl <i>a</i> accumulation rate	GP _{max} rate	P^B_{max}
Water temperature	r	-0.003	0.03	-0.12	-0.17	-0.33	-0.18
	p	0.98	0.82	0.48	0.28	0.03	0.28
Salinity	r	-0.55	-0.59	-0.22	0.12	0.38	0.29
	p	<0.001	<0.001	0.19	0.46	0.01	0.07
pH	r	-0.41	-0.39	-0.21	-0.28	0.01	0.40
	p	0.03	0.04	0.32	0.25	0.95	0.07
Light extinction	r	0.41	0.54	0.34	-0.08	-0.54	-0.34
	p	0.01	<0.001	0.04	0.66	0.001	0.05
DIN	r	0.47	0.50	0.01	0.17	-0.03	-0.24
	p	0.004	<0.001	0.94	0.30	0.88	0.15
DON	r	0.28	0.34	0.26	0.27	-0.17	-0.38
	p	0.21	0.12	0.27	0.33	0.49	0.15
DIP	r	0.51	0.47	-0.08	-0.05	-0.27	-0.23
	p	0.001	0.002	0.66	0.75	0.10	0.16
DOP	r	-0.04	0.14	0.15	-0.08	-0.01	-0.07
	p	0.85	0.53	0.52	0.77	0.95	0.79

Table 4. Changes in phytoplankton cell density, species diversity (mean \pm SE) and phylum composition at 3 sites in the outer and inner regions of Tapong Bay before and after the complete removal of oyster culture racks in June 2002. Phylum composition is presented as percentage of mean total cell number in each region from June 2000 to June 2004 and at the control site from August 2001 to March 2003. *Significant differences after complete removal of oyster culture racks

	Outer region		Inner region		Control site	
	Before	After	Before	After	Before	After
No. of sampling occasions	7	7	7	7	3	3
Cell number (L ⁻¹)	12477 \pm 3217	62328 \pm 19144*	48486 \pm 24836	201320 \pm 92937*	2089 \pm 79	1530 \pm 538
Shannon-Wiener diversity	1.60 \pm 0.19	1.94 \pm 0.32	1.49 \pm 0.17	1.66 \pm 0.42	2.59 \pm 0.38	2.71 \pm 0.29
Phylum composition (%)						
Cyanobacteria (%)	5.43	16.24	19.90	28.92	1.00	3.33
Euglenophyta (%)	0.00	2.69	0.00	3.41	1.00	0.00
Cryptophyta (%)	0.12	10.32	0.53	8.21	0.00	0.67
Dinophyta (%)	13.30	21.88	17.92	21.37	7.33	4.00
Bacillariophyta (%)	72.63	40.39	50.91	28.19	83.3	89.0
Raphidophyta (%)	1.28	0.22	0.00	2.20	0.00	0.00
Chlorophyta (%)	7.24	8.30	10.77	7.41	7.33	3.00

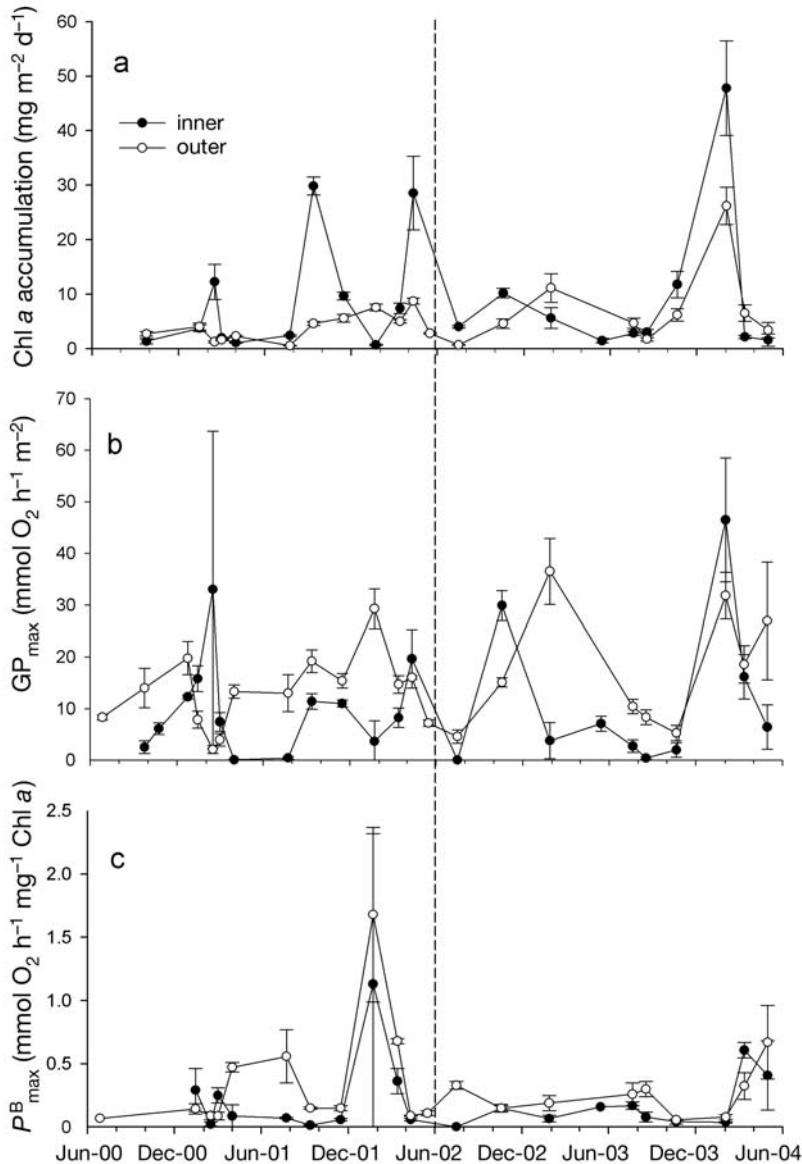


Fig. 4. Temporal variations (mean \pm SE, $n = 3$ sites in each region) in periphyton (a) chl a accumulation rate, (b) maximum gross production (GP_{\max}) rate, and (c) chl a -normalized net production (P^B_{\max}) in the outer and inner regions of Tapong Bay before and after the complete removal of oyster culture racks in June 2002 (dashed line)

phytoplankton chl a and GP_{\max} remained at similar levels (after rack removal) in the outer region, but increased 5-fold in the inner region. Bioavailable POM (particulate organic matter) derived from internal phytoplankton production was expected to become the dominant food supply to the food web after rack removal. Moreover, removal of oyster culture racks might have caused a loss of shelter for lagoon reef fish (Powers et al. 2007), which declined by 23%; pelagic or planktivorous fish increased by 268% after rack removal (H. J. Lin et al., unpubl. data). It is likely that

the decline in periphyton-grazing reef fish in the lagoon resulted in a higher periphyton maximum chl a accumulation rate and GP_{\max} in February 2003 immediately after rack removal. In contrast to the shift in the food chain caused by the introduction of oyster culture (Leguerrier et al. 2004), a reverse shift from periphyton-grazing to phytoplankton-grazing organisms likely occurred in the lagoon after rack removal.

Responses of phytoplankton to oyster culture rack removal from Tapong Bay were significant. However, tidal flushing might have played an important role in regulating the responses of phytoplankton after rack removal. After being released from filtration pressure by cultured oysters, phytoplankton chl a and GP_{\max} dramatically increased in the inner region, which is poorly flushed. These parameters remained low in the outer region, which is subjected to faster flushing, as is the control site. Before removal of oyster culture racks, Chen (2002) reported that the current velocity was up to 200 cm s^{-1} in the outer region during ebb tide. Removal of oyster culture racks further increased the seawater exchange rate and relative water motion (Table 1), and reduced the mean exchange time from 8.71 d ($11.5\% \text{ d}^{-1}$) to 6.13 d ($16.3\% \text{ d}^{-1}$), which may have reduced light penetration into the water column as a result of greater turbulence and the flushing out of nutrients and phytoplankton populations. Consequently, it is difficult to single out the causes of depressed phytoplankton abundance and production in the outer region. Light limitation likely did not occur in this shallow lagoon, because light extinction remained low (1.09 m^{-1}). After rack removal, Tapong Bay still received nutrient-rich discharges from 2 mangrove-lined creeks.

Therefore, the decreased concentrations of DIN and DIP in the water column might have resulted from faster flushing and/or reduced excretion and remineralization of feces and pseudofeces by cultured oysters.

During the study period, there was no significant difference in phytoplankton P^B_{\max} before and after rack removal in the outer region (Table 2). Moreover, there was no significant positive correlation between phytoplankton P^B_{\max} and nutrient concentrations in the water column (Table 3). The higher phytoplankton

P^B_{\max} at the control site may be attributable to the lower chl *a* outside the lagoon. After rack removal, concentrations of DN and DP in the water column (DIN < 1.0 μM and DIP < 0.1 μM) were still much greater than critical levels for potential phytoplankton limitation (Perry & Eppley 1981, Justic et al. 1995). Dissolved silicate (DSi) concentrations (5.94 μM , Hung 2002) were also higher than critical levels (< 2.0 μM) for potential phytoplankton limitation (Nelson & Brzezinski 1990). In our view, the low phytoplankton chl *a* and GP_{max} in the outer region resulted simply from the flushing-out of phytoplankton communities. This might also be the reason that Dame et al. (2002) failed to determine a significant increase in phytoplankton abundance after removal of oysters from tidal creeks (because the fast flushing rate might have reduced the time oysters needed to exert top-down control of phytoplankton through filtration).

In the inner region, the direct influence of tidal flushing on phytoplankton responses to removal of oyster culture racks appeared to be minor, although the mean water exchange time was reduced from 11.6 (8.60% d^{-1}) to 8.18 d (12.2% d^{-1}). Phytoplankton chl *a* and GP_{max} dramatically increased in response to rack removal. The distinct responses in the 2 regions were unlikely to have resulted from different species compositions (Table 4) because spatial variations in phytoplankton community structure are small (due to horizontal mixing by the tidal circulation, Su et al. 2004). Phytoplankton P^B_{\max} in the inner region tended to be stimulated by increased water motion (as found by Traaen & Lindstrøm 1983); a slow current velocity of <10 cm s^{-1} before rack removal (Chen 2002) was thought to thicken the boundary layer around phytoplankton and decrease P^B_{\max} (Su et al. 2004).

Filter feeding by bivalves is known to control phytoplankton abundances in estuaries (Officer et al. 1982, Newell 1988, Souchu et al. 2001). Oysters are active suspension feeders with a high filtering efficiency. Newell (1988) estimated that the entire water body in Chesapeake Bay could have been completely filtered in <3–6 d before 1870 when oyster stocks were still high, although Pomeroy et al. (2006) argued that the filtration rate was overestimated. Before removal in June 2002, almost all of Tapong Bay contained a high density of oyster culture racks (Lin et al. 2006). It seems that oysters would have had no difficulty in accessing all of the lagoon's water.

Fluxes of N (1.87 mol $\text{m}^{-2} \text{yr}^{-1}$) and P (0.51 mol $\text{m}^{-2} \text{yr}^{-1}$) into Tapong Bay are higher than those of most Mexican tropical lagoons (Smith et al. 1997). In particular, the N flux is about 10-fold higher than in Mexican lagoons. Nevertheless, phytoplankton chl *a* concentrations in the inner region were low to moderate when compared to those recorded in non-eutrophic Mexican

lagoons, including Terminos Lagoon (Manickchand-Heileman et al. 1998), Tampamachoco Lagoon (Rosado-Solórzano & Guzmán del Prío 1998), Celestun Lagoon (Vega-Cendejas & Arreguín-Sánchez 2001), and Hui-zache-Caimanero Lagoon (Zetina-Rejón et al. 2003). Our values are also comparable to those of treatment with oysters in a mesocosm study conducted to determine the effects of cultured oysters on phytoplankton abundances (Pietros & Rice 2003). After rack removal, the rapid and dramatic increase in phytoplankton chl *a* (127 to 154 mg m^{-3}) in the inner region was much greater than values reported in most estuaries and coastal lagoons (Boynton et al. 1982). However, no significant changes in phytoplankton chl *a* occurred at the control site after rack removal. It is clear that the dramatic increases in phytoplankton chl *a* and GP_{max} were caused by the release from cultured oyster and associated mussel (*Mytilopsis sallei*, Lin et al. 2006) filtration pressure.

The release from filtration pressure was also evidenced by increases in the cell number and changes in phytoplankton community structure. Langdon & Newell (1990) indicated that oyster particle retention is a function of cell size, with efficiency declining sharply for particles <2 μm . Similarly, Dupuy et al. (2000) found that the oyster *Crassostrea gigas* cannot retain picoparticles <5 μm , and concluded that microphytoplankton, particularly diatoms, were the main food source. Accordingly, the cause of changes in the phytoplankton community may be attributable to the size-class composition of the planktonic community that oyster gills can retain. Cell numbers of Bacillariophyta (diatoms) did increase remarkably, but the relative dominance of this phylum decreased after removal of oyster culture racks. Nevertheless, the relative dominances of *Cyanobacteria*, Euglenophyta, Cryptophyta, and Dinophyta increased in both regions, but not at the control site. Our results suggest that oysters not only control phytoplankton abundances but also reduce the diversity of the phytoplankton community.

Unlike phytoplankton, periphyton chl *a* accumulation rate and GP_{max} did not significantly change in either region with removal of oyster culture racks. It may be that periphyton communities growing on bamboo substrata were not flushed out despite the faster flushing in the outer region. Moreover, there is little evidence that periphyton P^B_{\max} was limited by the high DIN and DIP concentrations in either region after rack removal. Indeed, water motion has been suggested as an important selective factor for the spatial dominance and occurrence of periphyton species in Tapong Bay (Lin & Hung 2004). The divided blades of *Ulva fasciata*, which was restricted to the fast-flushing outer region, have a higher surface area to volume ratio, which may promote rapid uptake of nutrients at low concentra-

tions when current velocities are high (Littler & Littler 1980). In the inner region of Tapong Bay, reduced flow velocity resulting from poor flushing would have thickened the boundary layer around benthic algal cells. The nonheterocystous filamentous cyanobacterium *Lyngbya majuscula* can fix molecular N (Paerl et al. 1996). 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 factors likely assure the success of *L. majuscula* in slowly moving water with a very low DIN:DIP ratio (3.1) in the inner region (resulting from a significant decreases in DIP concentrations after rack removal).

In conclusion, phytoplankton and periphyton responded differently to the complete removal of oyster culture racks from Tapong Bay. Tidal flushing played an important role in regulating the responses of phytoplankton after rack removal. Removal of oyster culture racks resulted in phytoplankton blooms only in the inner region, which is subject to poor flushing. The blooms may be attributable to phytoplankton release from bivalve filtration pressure after rack removal. Nevertheless, periphyton chl *a* accumulation rate and GP_{max} did not significantly change in either region with the complete removal of culture racks. While there is speculation that overharvesting oyster stocks may be a factor contributing to declines in water quality and shifts in dominant species (e.g. Ulanowicz & Tuttle 1992, Prins et al. 1997), our results suggest that cultured oysters in this eutrophic lagoon have effective top-down control of phytoplankton abundances and that they are responsible for reductions in the planktonic community diversity.

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