Factors governing phytoplankton biomass and production in tropical estuaries of western Taiwan

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ABSTRACT

Factors governing phytoplankton community composition and production in tropical estuaries remain mostly unknown. We aimed to quantify phytoplankton biomass, production, and community composition seasonally in 2 tropical estuaries with different levels of nutrient concentrations and turbidity, and we compared them with an offshore control site on the western coast of central Taiwan for two years. Phytoplankton biomass and production varied with season and site. Annual integrated primary production showed that these three sites were mesotrophic systems. Spearman rank correlations showed that phytoplankton biomass and production were positively correlated with water temperature, but negatively correlated with turbidity. The threshold of turbidity was 12 Nephelometric Turbidity Units (NTU), above which phytoplankton chlorophyll *a* concentrations were $< 0.5 \, \text{mg m}^{-3}$, and gross production rate was $< 100 \, \text{mg C m}^{-3} \, \text{d}^{-1}$. The results of nonmetric multidimensional scaling (MDS) showed that the community was primarily structured by season and secondarily by site. The functional traits further showed that turbidity, water temperature, and SiO_2 concentration were governing factors for the variations in the community. In summary, turbidity was the main factor governing phytoplankton biomass and production, whereas water temperature and SiO_2 concentration had both a direct effect on production and an indirect effect by changing community composition.

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1. Introduction

Coastal waters are highly productive ecosystems (Nixon et al., 1986). Although the volume of coastal waters occupies only 0.5% of the ocean, they can contribute up to 30% of primary production (Longhurst et al., 1995). However, a wide range of phytoplankton production from -692 to $1890 \, \text{g C m}^{-2} \, \text{yr}^{-1}$ was reported from 131 estuaries in the world (Cloern et al., 2014), indicating that influencing factors may differ remarkably among different estuaries. In addition, most of these studies were conducted in temperate waters. Studies are rarely conducted in tropical waters to quantify phytoplankton production and determine the influencing factors.

Irradiance and nutrients are generally considered as main factors governing phytoplankton production. Turbid water may constrain the photic zone to the surface layer and result in the mixed layer being much deeper than the photic depth, which can limit

phytoplankton production due to the lack of sufficient irradiance (Cloern, 1987). Moreover, irradiance may regulate the absorption and assimilation of nutrients of phytoplankton, which can affect primary production (Huppe and Turpin, 1994). In North San Francisco Bay, turbid water and lower irradiance were reported to result in a consistently low level of phytoplankton production, despite the high nutrient concentrations (Cloern, 1999). Suspended sediments in river flows (Wetsteyn and Kromkamp, 1994) and colored dissolved organic matter (Lawrenz et al., 2013) were indicated as the limiting factors of phytoplankton production. Resuspended sediments disturbed by tidal currents or strong winds in estuaries can reduce phytoplankton production by lowering the irradiance in the water column (Cloern, 1996; Schubel, 1968). In the northern Gulf of Carpentaria, Burford and Rothlisberg (1999) also noticed that the strong southeastern monsoon in winter could disturb the water column and lower the irradiance, which may reduce phytoplankton production to 60% of the summer level. Horizontal stratification, due to salinity, can help phytoplankton remain in the photic zone, which may increase the biomass (Cloern et al., 2014). However, tidal currents or strong winds can break the stratification and distribute phytoplankton evenly in the water column, which may reduce the irradiance

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conceived by phytoplankton (Koseff et al., 1993). On the contrary, such water mixing may reduce photoinhibition in the surface water and increase phytoplankton production (Mallin and Paerl, 1992).

Nutrients in estuaries are derived primarily from loadings of river flows and/or microbial detrital decomposition. In general, nitrogen (N) is the limiting factor in ocean and coastal waters (Elmgren and Larsson, 2001; Paerl et al., 1995). However, some estuaries highly influenced by river flows are phosphorus (P)-limited or co-limited by N and P due to the inputs of sewage containing more N (Sylvan et al., 2006). Silicon (Si) is an essential element for diatom growth and enters aquatic systems through the weathering of rocks and soil minerals in the catchment. Concentration of dissolved silica (SiO_2) in estuaries can be reduced by river eutrophication, and the enrichment of N and P in estuaries may increase the relative importance of SiO_2 (Howarth and Marino, 2006). Egge and Aksnes (1992) indicated that under the condition of $< 2 \mu M$ of SiO_2 concentration, phytoplankton may shift from a diatom-dominated to a flagellate-dominated community. Reduction of the relative importance of diatoms to phytoplankton production can further decrease overall production or biomass of phytoplankton (Butrón et al., 2009; Wu and Chou, 2003).

In addition to the effect on phytoplankton production, irradiance and nutrients may change the community composition. Ecological functional traits of phytoplankton have rarely been linked to environmental factors. Such approaches have the potential of increasing our ability to explain the composition of phytoplankton communities and predict their reorganizations under environmental change (Litchman and Klausmeier, 2008). Diatoms often occur in eutrophic and turbid coastal waters (Cloern and Dufford, 2005) due to the rapid growth rate (Smayda, 1997) and tolerance to low irradiance (Goldman and McGillicuddy, 2003). Moreover, most of them are centric diatoms, which can form resting spores and sink to the bottom during unfavorable conditions (Sugie and Kuma, 2008), thus revealing seasonal and spatial variations. Sarthou et al. (2005) indicated that absorption efficiency, nutrient capacity, and photon capture efficiency by diatoms depended upon the cell size. The growth rate of small-sized diatoms was faster due to the efficiency in nutrient absorption and photon capture. However, large-sized diatoms had higher nutrient capacity and often became the dominant species in coastal waters. Key et al. (2010) indicated that large-sized diatoms were relatively not affected by photoinhibition and adapted to the rapid change of irradiance in coastal waters.

In this study, we aimed to quantify phytoplankton biomass and production and characterize the community composition in 2 tropical estuaries with different levels of nutrient concentrations and turbidity, and we compared them with an offshore control site on the western coast of central Taiwan. We hypothesized that turbidity was the governing factor on phytoplankton biomass and production rather than nutrients. Despite the high nutrient concentrations, phytoplankton production and biomass were expected to be lower in the estuary with a high level of turbidity, and the community composition was dominated by the species adapting to a low level of irradiance.

2. Materials and methods

2.1. Study sites

The estuaries of Zhuoshui River (Ez) and the Xin Huwei River (Ex) are located in the coastal waters of western central Taiwan (Fig. 1). The shallow-sloped coast is characterized by muddy flats. The average water temperature over the year is 24.1 °C, with an annual rainfall of 2384 mm. The wet season is from April to September, and the dry season lasts from October to the next March. According to the water quality monitoring data of the Environmental Protection Agency of Taiwan (2012–2013), the mean suspended solid concentration at Ez reached 894.7 mg L^{-1} due to the high content of slate clay in the river. The mean concentrations of NH_4, NO_x ($NO_2 + NO_3$), and total phosphorus (TP) at Ez were 4.29 μM, 12.89 μM, and 5.24 μM, respectively. The mean suspended solid concentration was much lower (168.2 mg L^{-1}) at Ex, but the mean nutrient concentrations were higher (the concentrations of NH_4, NO_x, and TP were 219.6 μM, 96.5 μM, and 7.81 μM, respectively), due to the loading of piggery sewage in the catchment of Ex.

We set up 3 study sites in the coastal waters (Fig. 1). Ez and Ex were located at approximately 2 km outside of the Zhuoshui River Estuary (23°50′49.06″N, 120°11′18.26″E) and of the Xin Huwei
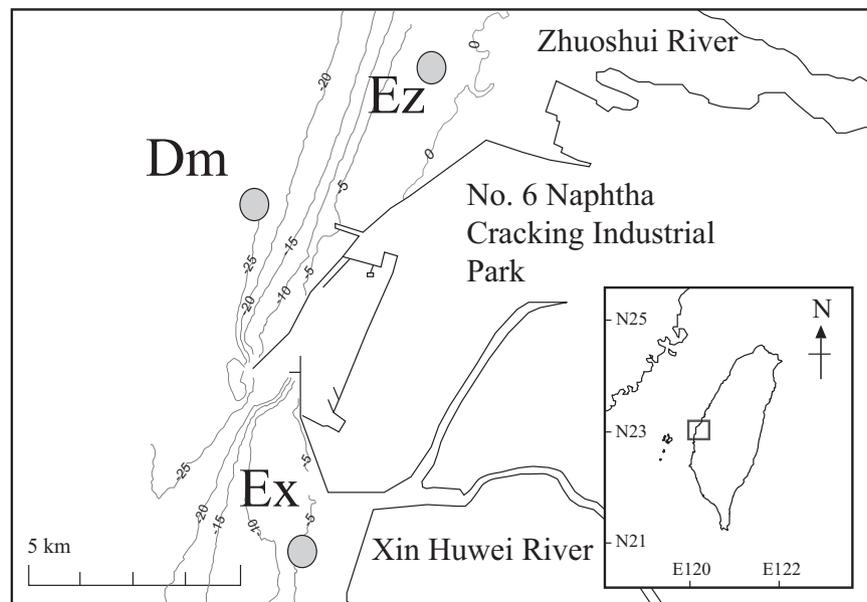

Fig. 1. The location of the three study sites (Ez, Dm, and Ex) in the coastal waters of western central Taiwan.

River Estuary (23°44′53.66″N, 120°9′38.09″E), respectively. The water depth was 7–8 m. The offshore control site (Dm, 23°49′11.14″N, 120° 9′27.96″E) was located between the two estuaries and 3 km outside of No. 6 Naphtha Cracking Industrial Park, with a water depth of 21 m, for comparisons with the 2 estuaries.

This study was conducted from March 2012 (winter) to November 2013 (fall) for two cycles of seasonality. According to the long-term record of water temperature in the coastal waters (1998–2014, the Central Weather Bureau of Taiwan) (http://www.cwb.gov.tw/V7/climate/marine_stat/wtmp.htm), we conducted sampling during December and March ($< 20\ °C$) for winter, April and May (from $20\ °C$ to $28\ °C$) for spring, June and September ($> 28\ °C$) for summer, and October and November (from $28\ °C$ to $20\ °C$) for fall. In the tropical zone, spring and fall are the transition periods between summer and winter and are relatively short (1 to 2 months). In total, we conducted 8 sampling occasions for phytoplankton variables and environmental factors, with the exception of nutrient data that were collected from summer 2012 to fall 2013.

2.2. Phytoplankton biomass

During each sampling event, phytoplankton samples were collected at low tide in the early morning in triplicate at each site to quantify biomass and productivity and to examine community composition. While we realize that these samples may not be representative of each area, this sampling design was performed simply for the purpose of exploring site and seasonal patterns in the data. Phytoplankton biomass, in terms of chlorophyll a concentration (CHL a, corrected for phaeopigment), was determined on a Turner fluorometer (Trilogy, Turner Design, USA) by immediately filtering water samples through 0.7 μm GF-75 filters (AdvanTec, Japan) in the field and then extracting the filters in 90% acetone for 24 h at $4\ °C$ in the dark (Arar and Collins, 1997).

2.3. Phytoplankton productivity

Phytoplankton productivity was determined using a DO method, modified from Parsons et al. (1984), by incubation in 300-mL BOD bottles in outdoor flowing seawater tanks (n=3 for each light irradiance per site). Flowing seawater outside the bottles was used to maintain temperatures at ambient levels and did not mix with the water inside the bottles. Incubations were conducted in situ on the coast next to Ez on a sunny day under ambient light from 10:00 h to 14:00 h, when irradiance was at a saturation level for photosynthesis. The incident irradiance remained at approximately 1500 μmol photons m^{-2} s^{-1} in spring and winter and 2000 μmol photons m^{-2} s^{-1} in summer and fall.

The BOD bottles were exposed in the field to five different irradiances of 0%, 30%, 50%, 70%, and 100% shading by interposing screens with different mesh sizes. Net production (NP) rate under various irradiances and respiration rates (100% shading or dark bottles) were derived from changes in dissolved oxygen (DO) concentrations over time measured by a DO meter (Model 52, 5909 probe, YSI, USA). Gross production (GP) was then calculated as the sum of respiration and NP. To incorporate variations in respiration during nighttime periods, a ratio of 1.48 between respiration rates during daytime and nighttime periods, derived from Lee et al. (2011), was used to estimate nighttime respiration rates.

Daily GP rates of phytoplankton were calculated by integrating the interpolated GP rates under various irradiances in reference to the relationships between irradiances and GP rates (P-E curve) for each incubation occasion at each site. On each occasion, incident photosynthetically active radiation (PAR) was continuously measured in situ at 5 min intervals with a Li-1400 meter (LI-COR, USA),

from early morning (07:00 h) until after sunset (19:00 h).

Each P-E curve on each occasion at each site was described by Eq. (1) of Jassby and Platt (1976) as.

$$GP^B = GP^B_m \tanh\left(\alpha E/GP^B_m\right) \qquad (1)$$

where GP^B refers to the GP rate normalized to CHL a concentration, GP^B_m is the maximum GP rate normalized to CHL a concentration in the absence of photoinhibition under optimal light, α is the initial slope of the P-E curve when GP rate is assumed to be proportional to photon density, and E is the irradiance measured as PAR in μmol photons m^{-2} s^{-1}. GP^B_m can also be interpreted as the photosynthetic capacity. The parameter, α, also indicates the efficiency with which incident irradiance is converted into photosynthetic production by phytoplankton. The light-saturation onset parameter (E_K) refers to the irradiance in time when GP rate reaches maximum capacity (i.e., GP^B_m). We used SigmaPlot (v. 8.02, SPSS) for nonlinear regression fitting and considered the results acceptable when the fit was significant ($p < 0.05$) and the power of the performed test was > 0.80. We used a photosynthetic quotient of 1.2 to convert O_2 fluxes into CO_2 fluxes for daily integration and literature comparisons (Meyercordt et al., 1999).

2.4. Phytoplankton community composition

Phytoplankton community composition was examined from fall 2012 to fall 2013 for at least a cycle of seasonality. In northern South China Sea, while picoplankton ($< 3\ \mu$m) dominated phytoplankton biomass in the offshore, microplankton ($> 20\ \mu$m) dominated in the coast and contributed 70% of total CHL a concentration due to the influence of nutrient-rich discharge of Pearl River (Liu et al., 2011). Similarly, the variation of microplankton accounted for most of the variability of CHL a concentration (42%) and primary productivity (71%) in the nutrient-rich waters of southern East China Sea (Lee Chen, 2000). Since the coastal waters of western central Taiwan were influenced by river flows, we focused on community composition of microplankton. One aliquot of a phytoplankton sample for productivity determination was fixed in 5% formaldehyde immediately after filtering through a 20-μm plankton net (Wildco, Buffalo, USA). After settlement, the upper clear water was siphoned out and the concentrated sample of 10–20 mL was stored in a small bottle. Identification and counting of taxa were accomplished using a light microscope under phase and Differential Interference Contrast (DIC) (ZEISS, Germany) at $400 \times$ after sedimentation on a scaled slide. A volume of 0.5 mL of the concentrated sample in triplicate was scanned and at least 300 cells per slide were examined. Identification was carried out according to Cupp (1943) and Tomas (1997). Filamentous algae were enumerated based on counting the unit amount of homogenized fragments.

2.5. Environmental factors

Surface water temperature, pH, DO, and salinity were continuously monitored at low tide at 1-min intervals in situ for 10 min using multi-parameter monitoring sensors (Model 600XLM, YSI, USA) concurrently with sampling for phytoplankton. Turbidity measured in Nephelometric Turbidity Units (NTU) in the water column was also determined using a turbidimeter (Model 2020e, LaMotte, USA). On each sampling occasion, these measurements were determined in 5 replicates at each site.

Surface water samples for analyses of total dissolved inorganic nutrients were also collected at low tide in triplicate in acid-washed 100 mL sample bottles at each site and immediately placed on ice in a cooler. In the laboratory, each water sample was filtered through 0.45 μm Millipore filters to remove the suspended and

particulate matter prior to laboratory analysis. Nutrient concentrations were determined colorimetrically (NO$_3$: Goldman and Jacobs, 1961; NO$_2$: Parsons et al., 1984; Pai et al., 1990; NH$_4$: Parsons et al., 1984; Pai et al., 2001; PO$_4$: Murphy and Riley, 1962; SiO$_2$: Method 4500 APHA, 1995).

2.6. Statistical analysis

A two-way fixed-factor analysis of variance (ANOVA) model was used to determine whether phytoplankton variables and environmental factors differed among the 3 study sites (Sites Ez, Dm, and Ex) and 4 seasons (spring, summer, fall, and winter). Before the analysis, CHL a concentrations and turbidity values were fourth root transformed, and salinity values were log transformed to conform to the normality and homogeneity of variance assumptions (Clarke and Warwick, 1994). If the results of the ANOVA indicated significant main effects at the 0.05 probability level, then Tukey's studentized range (HSD) test was used to determine which means significantly differed. Relationships of phytoplankton variables with environmental factors were determined using Spearman rank correlations. ANOVA, HSD test, and Spearman rank correlations were conducted using SigmaPlot v12.5 (Systat Software, Inc, Richmond, CA).

Changes in community composition were studied using multivariate analyses in the PRIMER (v6.0) computer package (Clarke and Gorley, 2006) to reveal site and seasonal patterns of phytoplankton communities. The Bray-Curtis coefficient was used to produce a similarity matrix of taxon composition between any two samples according to the cell number of each taxon. The data matrix consisted of a total of 45 samples with 37 taxa. The similarity matrix was fourth root-transformed, cluster-analyzed, and then ordinated using nonmetric multidimensional scaling (MDS) techniques to visualize the similarity matrix and to illustrate latent patterns in community composition. A two-way crossed analysis of similarities (ANOSIM) was used to determine whether the effects of site and season on community composition were significant by comparing the observed statistic to its permutation distribution for the absence of differences (Clarke and Warwick, 1994). If the results indicated significance at the 0.05 probability level, pairwise comparisons and the Bonferroni correction for the significance level were used to determine which levels differed. The significance level was calculated by comparing the observed statistic (R, reflecting observed differences between treatments contrasted with differences among replicates within a treatment) to its permutation distribution. If the results of the global test indicated significance at the 5% probability level, pairwise R values were used to determine their separation. Communities could be clearly separated when $R > 0.5$, but barely separable at all when $R < 0.25$. Similarity of percentages (SIMPER) was employed to reveal the most-common taxa in replicate samples for each community. The relationship of phytoplankton composition and environmental factors was analyzed using distance-based redundancy analysis (dbRDA). The significance level was set at 0.05 for all of the statistical analysis.

3. Results

3.1. Phytoplankton biomass

Phytoplankton CHL a concentrations ranged from 0.26 to 4.35 mg m^{-3} (Fig. 2) and showed a significant interaction between site and season (Table 1). In spring 2012, CHL a concentrations were much higher at Ex than the other two sites; whereas in winter 2012 and summer 2013, the concentrations were higher at Ez, followed by Ex. In summer 2012, fall 2012, and fall 2013, CHL a
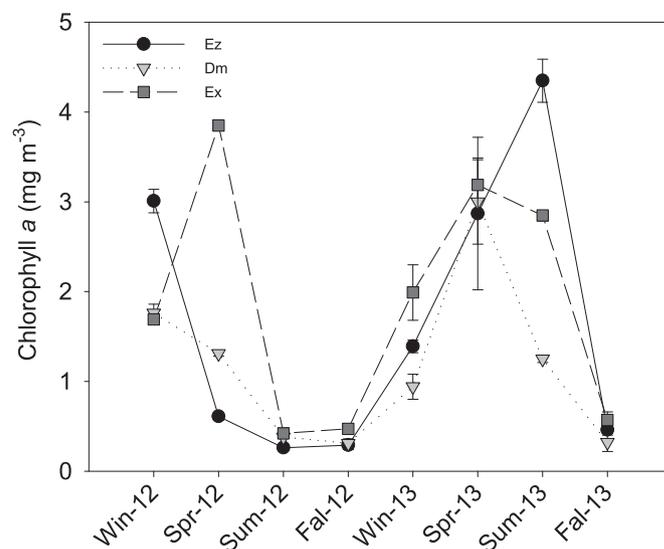

Fig. 2. Changes (mean ± SD, n = 3) in phytoplankton CHL a concentration (mg m^{-3}) at the three sites in four seasons from 2012 to 2013 in the coastal waters of western central Taiwan.

concentrations were consistently < 0.6 mg m^{-3} at all 3 sites. The spatial variation patterns were not consistent between the two consecutive years.

3.2. Phytoplankton productivity

The P-E curves of phytoplankton obtained at the 3 sites in March 2012 (winter) are shown as examples (Fig. 3). The derived GP$_m^B$ ranged from 0.4 to 3.0 mmol O$_2$ mg chl a^{-1} h^{-1}, with an exceptionally high value at Dm in fall 2013 (Table 2). In general, the higher values occurred in summer 2012, fall 2012, and spring 2013. The higher values in summer 2012 and fall 2012 were attributed to the lower CHL a concentrations at those times. The derived α showed similar spatial and seasonal patterns as the patterns of GP$_m^B$. In general, the derived E$_k$ were higher at Dm than the other 2 estuarine sites, with the maximum values in winter 2012 and the minimum values in fall 2013.

Phytoplankton daily GP rates ranged from 13.01 to 789.77 mg C m^{-3} d^{-1} (Fig. 4a). The spatial and seasonal patterns were similar to those of phytoplankton biomass, with higher values in spring and lower values in summer 2012 and fall 2013. The variation patterns of daily respiration rates (Fig. 4b) differed slightly from those of daily GP rates. In general, higher daily respiration rates occurred at Ez and Dm in winter 2013, reaching 771.7 mg C m^{-3} d^{-1} and 412.3 mg C m^{-3} d^{-1}, respectively. Daily respiration rates were also higher at Ez in summer 2013 and at Dm in spring 2012 and fall 2013. Daily NP rates ranged from $-$596.4 mg C m^{-3} d^{-1} to 617.54 mg C m^{-3} d^{-1} (Fig. 4c). Like GP rates, the higher values also occurred in spring or at Ex. In winter 2013, daily NP rates became largely negative at Ez and Dm due to the very high respiration rates.

Taking into account the seasonal variation in daily GP rate and integrating through the euphotic zone (1.5–2.5 m) at the 3 sites, the annual integrated primary production (IPP) was estimated to be 113.7 g C m^{-2} yr^{-1}, 106.4 g C m^{-2} yr^{-1}, and 127.0 g C m^{-2} yr^{-1} for Ez, Dm, and Ex, respectively. These 3 sites can be classified as mesotrophic systems (100–300 g C m^{-2} yr^{-1}) based on Nixon (1995).

3.3. Phytoplankton community composition

In total, 30 diatom genera and 2 dinoflagellate genera were identified. The MDS results showed that the community could be

Table 1
Results of two-way ANOVA of concentrations of nutrient and phytoplankton CHL *a* among six seasons and three sites in the coastal waters of western central Taiwan. Different letters adjacent to groups denote post-hoc differences ($p < 0.05$) when an overall difference was detected.

|		df	F	P	Tukey's studentized range test					
NO_X	Season	5	85.0	< 0.001	Sum-12[b]	Fal-12[c]	Win-13[ab]	Spr-13[a]	Sum-13[ab]	Fal-13[d]
	Site	2	1.7	0.194						
	Season x site	10	1.4	0.233						
NH_4	Season	5	32.9	< 0.001						
	Site	2	28.4	< 0.001						
	Season x site	10	17.1	< 0.001						
PO_4	Season	5	110.2	< 0.001						
	Site	2	320.9	< 0.001						
	Season x site	10	187.2	< 0.001						
SiO_2	Season	5	9.7	< 0.001	Sum-12[bc]	Fal-12[ab]	Win-13[ab]	Spr-13[a]	Sum-13[c]	Fal-13[ab]
	Site	2	11.4	< 0.001	Ex[b]	Dm[a]	Ex[b]			
	Season x site	10	1.4	0.208						
CHL *a*	Season	7	134.7	< 0.001						
	Site	2	28.7	< 0.001						
	Season x site	14	13.0	< 0.001						

NO_X: $NO_2 + NO_3$.
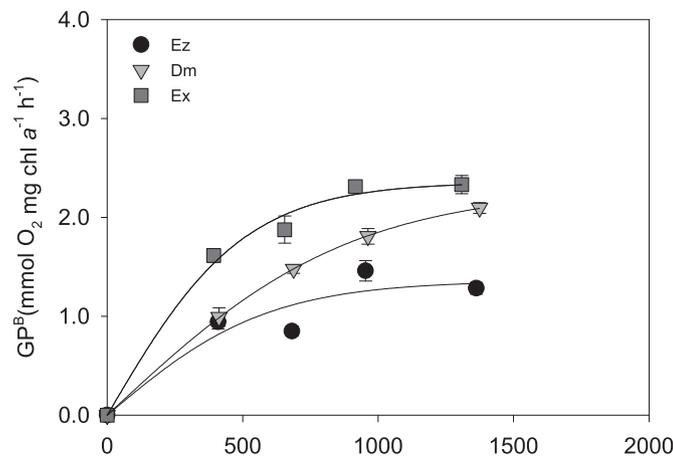
Fig. 3. Phytoplankton photosynthesis-irradiance (P-E) curves in March (winter) 2012 at the three sites in the coastal waters of western central Taiwan.

Table 2
Phytoplankton photosynthetic capacity GP_m^B (mmol O_2 mg chl a^{-1} h^{-1}), photosynthetic efficiency α (mmol O_2 mg chl a^{-1} h^{-1} µmol photons m^{-2} s^{-1}), and saturation irradiance E_K (µmol photons m^{-2} s^{-1}) in four seasons from 2012 to 2013 at the three sites in the coastal waters of western central Taiwan.

Season	Site	GP_m^B		α		E_K	
		2012	2013	2012	2013	2012	2013
Winter	Ez	1.36	1.53	0.0023	0.0039	590.3	392.9
	Dm	2.30	2.41	0.0026	0.0043	884.8	561.4
	Ex	2.36	0.87	0.0047	0.0014	501.5	642.1
Spring	Ez	0.93	2.64	0.0019	0.0061	486.6	432.0
	Dm	1.69	3.04	0.0033	0.0048	511.2	632.6
	Ex	1.46	2.00	0.0032	0.0070	453.3	285.2
Summer	Ez	3.69	1.28	0.0127	0.0026	290.6	492.3
	Dm	3.36	0.69	0.0053	0.0010	637.3	692.3
	Ex	2.23	1.38	0.0043	0.0022	517.7	627.3
Fall	Ez	3.69	0.40	0.0118	0.0008	465.2	523.0
	Dm	4.34	14.91	0.0046	0.0950	541.1	157.0
	Ex	6.27	1.80	0.0053	0.0049	493.8	366.0

separated into 5 major groups by season and 2 minor groups by site (Ex vs. Ez and Dm) in winter 2013 (Fig. 5), indicating that the community was primarily structured by season and secondarily structured by site. The community composition in fall 2012 was generally similar to that in fall 2013, but the relative abundance differed (Fig. 6). The community composition at Ex in winter 2013
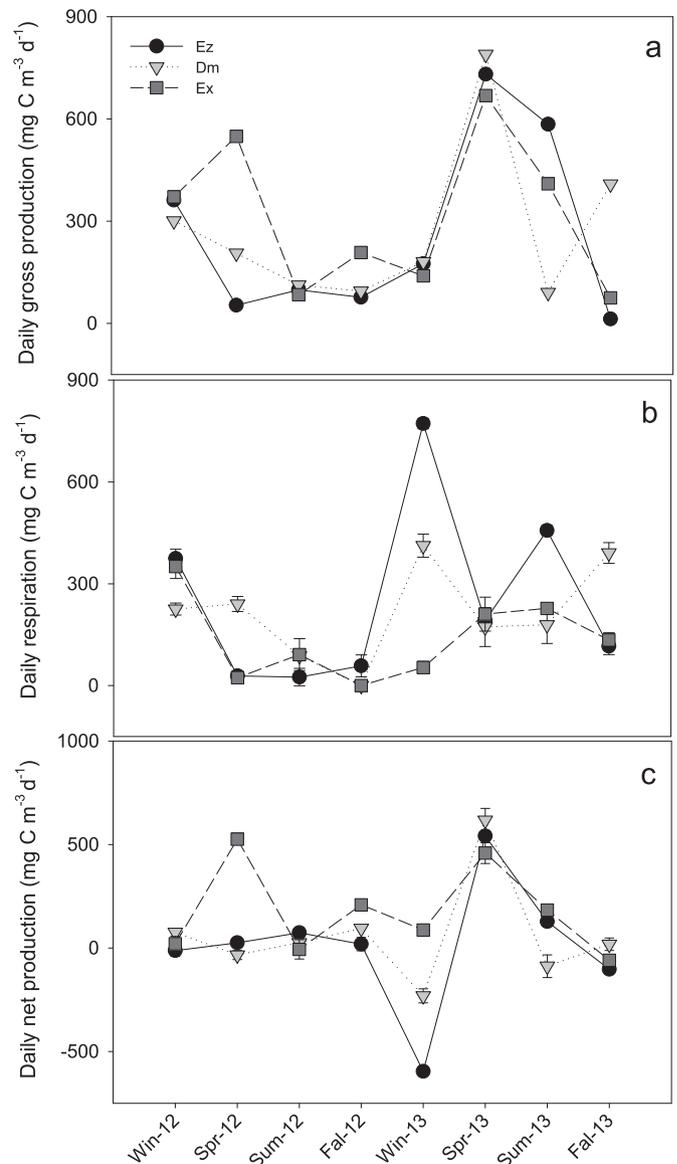

Fig. 4. Daily rates of gross production (a), respiration (b), and net production (c) by phytoplankton in four seasons from 2012 to 2013 at the three sites in the coastal waters of western central Taiwan.
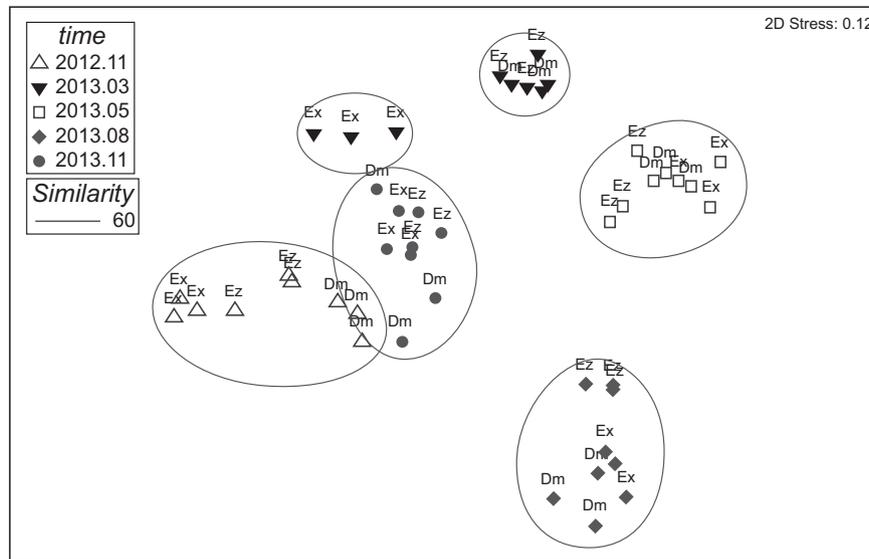
Fig. 5. Clustering and MDS ordination of Bray-Curtis similarities from fourth root-transformed cell numbers for each taxon of phytoplankton communities collected from fall 2012 to fall 2013 at the three sites in the coastal waters of western central Taiwan.
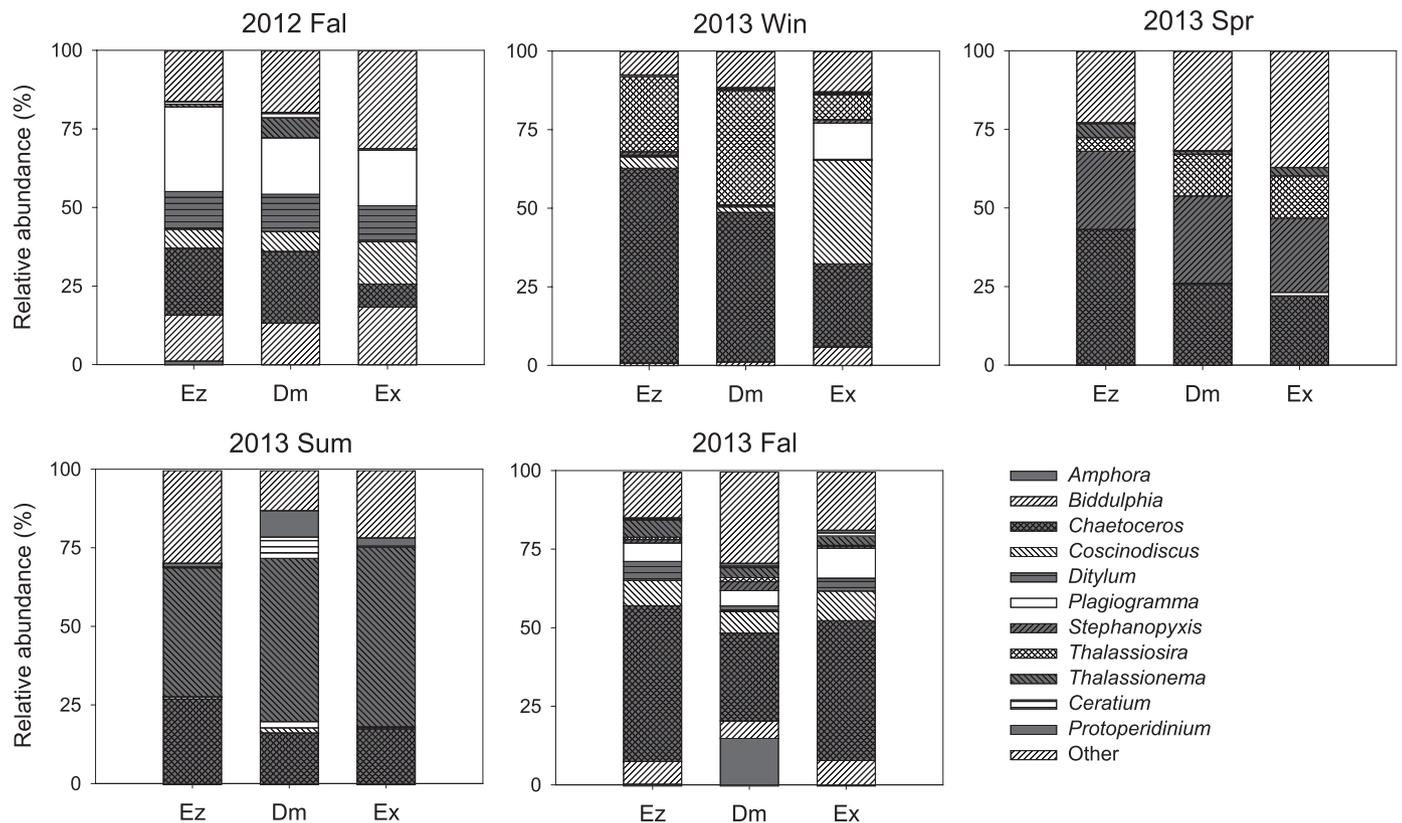

Fig. 6. Relative abundance of phytoplankton genera collected from fall 2012 to fall 2013 at the three sites in the coastal waters of western central Taiwan.

differed from that at Ez and Dm in the same season, but was more similar to that at Ex in fall 2013.

The results of SIMPER showed the shift of dominant taxa in the community followed a clear seasonal pattern (Fig. 6). The dominant genera in fall 2012 were *Plagiogramma*, *Biddulphia*, and *Ditylum*, shifted to *Chaetoceros* and *Thalassiosira* in winter 2013, and then followed by *Stephanopyxis* and *Thalassionema* in spring and summer 2013, respectively. The community composition in fall 2013 was similar to that in the same season in 2012, but the relative abundance of *Chaetoceros* was higher, and the abundance of *Plagiogramma*, *Biddulphia*, and *Ditylum* was lower.

The results of SIMPER also showed spatial variation in the community within each season (Fig. 6). In winter 2013, the communities at Ez and Dm were dominated by *Chaetoceros* and *Thalassiosira*, but the community at Ex was dominated by *Coscinodiscus*, *Plagiogramma*, and *Biddulphia*, which was more similar to the community at the same site in fall 2013. In summer 2013, the relative abundance of *Thalassionema* was >40% at all of the sites, but the abundance of *Chaetoceros* and *Hemiaulus* was remarkably higher at Ez. The dinoflagellates *Protoperidinium* and *Ceratium* were more abundant at Dm. *Streptotheca* was more abundant at Ex. In fall 2013, the dominant genera were similar between the
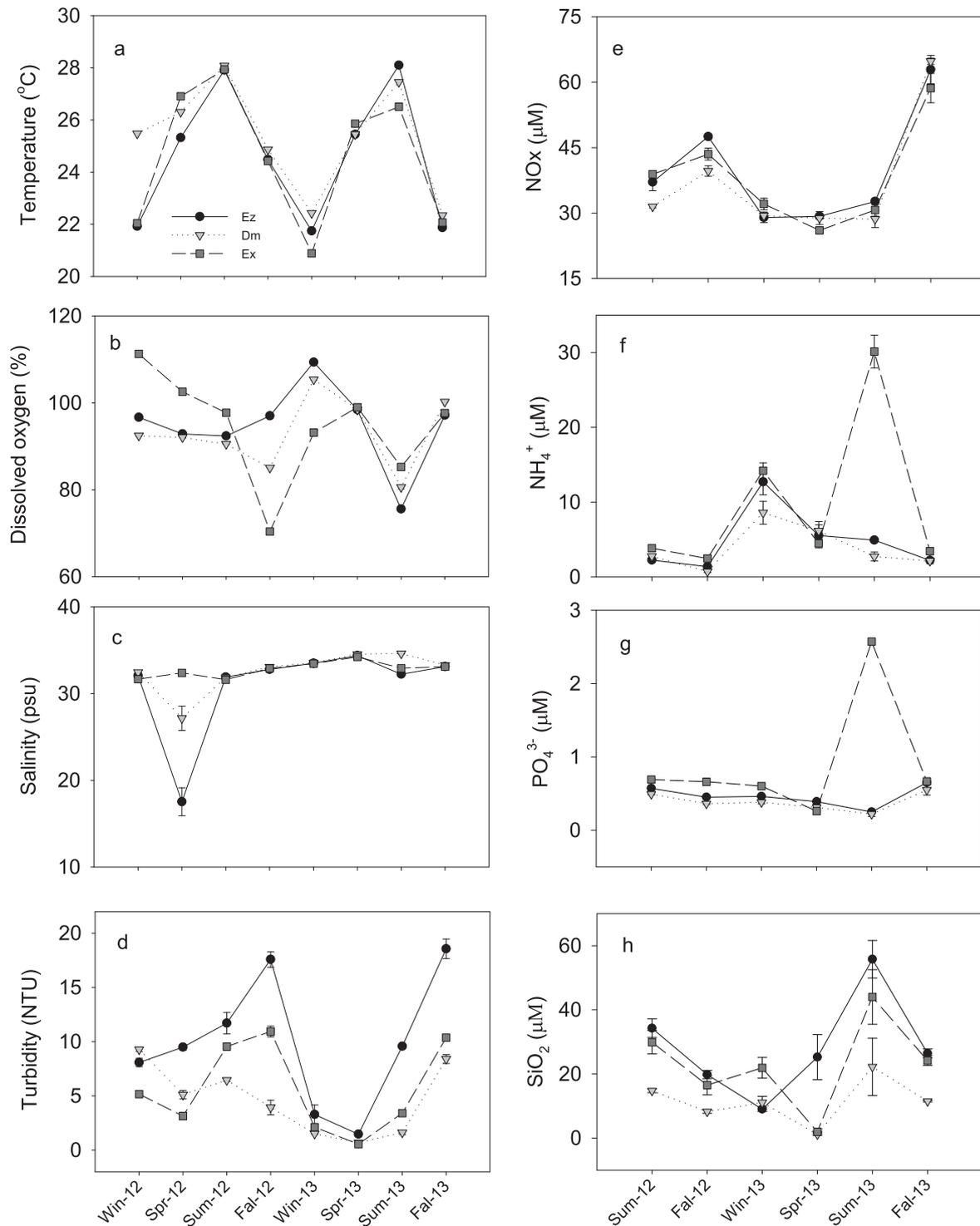
Fig. 7. Environmental factors ((a) Water temperature, (b) Dissolved oxygen (in % saturation), (c) Salinity, (d) Turbidity, (e) $NO_2^- + NO_3^-$, (f) NH_4^+, (g) PO_4^{-3}, (h) SiO_2) in four seasons from 2012 to 2013 at the three sites in the coastal waters of western central Taiwan.

communities at Ez and Ex. *Chaetoceros* and *Plagiogramma* were more abundant at the 2 estuarine sites, whereas the abundances of *Amphora* and *Grammatophora* were higher at Dm.

3.4. Environmental factors

During the study period, water temperature (interaction, $F = 792.2$, $p < 0.001$), DO saturation (interaction, $F = 1047.9$, $p < 0.001$), DO (interaction, $F = 153.4$, $p < 0.001$), pH (interaction, $F = 223.2$, $p < 0.001$), salinity (interaction, $F = 149.2$, $p < 0.001$), and

turbidity (interaction, $F = 30.7$, $p < 0.001$) showed significant interactions between site and season. The mean water temperatures at the 3 sites ranged from 20.9 to 28.1 °C (Fig. 7a), which coincided with the local long-term record (1998–2014) of the Central Weather Bureau of Taiwan (http://www.cwb.gov.tw/V7/climate/marine_stat/wtmp.htm). The mean DO values at the 3 sites remained between 5.45 mg L^{-1} and 7.56 mg L^{-1} (Fig. 7b) (in % saturation, 70.4–111.3%), and the seasonal pattern reversed to the pattern of water temperature. The pH at the 3 sites remained between 7.90 and 8.15. The mean salinity remained between 32

and 34, but were remarkably lower at Ez and Dm in spring 2012 and slightly lower at Ez and Ex in summer 2013 (Fig. 7c). There was a large variation in turbidity, ranging from 0.66 NTU to 18.56 NTU (Fig. 7d). For the 3 sites, higher turbidity values occurred in summer 2012, fall 2012, and fall 2013 and lower values occurred in winter 2013 and spring 2013. In general, the mean values and variation were highest at Ez and lowest at Dm.

NO_x concentrations ranged from 26.1 μM to 62.9 μM (Fig. 7e). There was no significant difference among the 3 sites, but there was a clear seasonal variation, with higher values in fall 2013 and lower values in summer 2012 (Table 1). There were significant interactions between site and season on NH_4 and PO_4 concentrations (Table 1). NH_4 concentrations were lower in fall and higher in winter (Fig. 7f). In general, NH_4 concentrations were higher at Ex, reaching an extreme value of 30.1 μM in summer 2013. The spatial variation in PO_4 concentration was similar to that of NH_4 concentration (Fig. 7g). In general, PO_4 concentrations were also higher at Ex, reaching an extreme value of 2.57 μM in summer 2013. There were significant site and seasonal effects on SiO_2 concentration (Table 1), ranging from 0.07 μM to 3.40 μM. SiO_2 concentrations were higher in summer than in the other seasons and higher at the 2 estuaries than at the control site (Dm) (Fig. 7h).

3.5. Correlations between phytoplankton variables and environmental factors

The results of Spearman rank correlations showed that phytoplankton biomass was positively correlated with water temperature and NH_4 concentration, but negatively correlated with turbidity, NO_x and PO_4 concentration (Table 3). The results also showed that daily GP rate was positively correlated with phytoplankton biomass, but negatively correlated with turbidity. Daily respiration rate was positively correlated with phytoplankton biomass and NH_4 concentration. Daily NP rate was also positively correlated with water temperature and phytoplankton biomass, but negatively correlated with turbidity and NO_x concentration. However, there was no significant correlation between daily rates of GP, R, and NP normalized to CHL a concentration and environmental factors, suggesting that phytoplankton biomass was mostly responsible for the observed correlation. Among the environmental factors, turbidity and nutrient concentrations were negatively correlated with salinity (Table 3), indicating that turbidity

and nutrient concentrations were greatly affected by river discharge in the coastal waters.

The results of dbRDA showed that the first two axes accounted for a total of 55% of the variation. The first axis correlated more with water temperature ($r=0.78$), NO_x concentration ($r=-0.67$), and turbidity ($r=-0.61$) (Fig. 8a). The second axis correlated more with salinity ($r=0.55$) and SiO_2 concentration ($r=-0.49$). In fall, with higher turbidity and NO_x concentrations, the dominant genera were *Biddulphia*, *Plagiogramma*, *Ditylum*, and *Nitzschia* (Fig. 8b). In winter, with lower water temperature and SiO_2 concentration, the dominant genera were *Chaetoceros*, *Thalassiosira*, and *Schroederella*. In spring, when turbidity decreased, the abundance of *Stephanopyxis*, *Cerataulina*, *Hemiaulus*, and *Rhizosolenia* increased. In summer, when water temperature and SiO_2 concentration increased, the dominant genera were *Thalassionema* and *Lauderia*. *Ceratium* and *Protoperidinium* also appeared at this time. Turbidity, water temperature, and SiO_2 concentration were the governing factors for the spatial and seasonal variation of the phytoplankton community.

4. Discussion

The present study showed that turbidity was the main factor governing the seasonal and spatial variations in phytoplankton biomass and production, as there were highly negative correlations between turbidity and CHL a concentrations and daily GP rate. Suspended solids and resuspended sediments in the river flows of estuaries can absorb and/or disperse irradiance in the water column and constrain phytoplankton production (Cloern, 1987). In estuaries with turbid water and high nutrient concentrations, the peaks of phytoplankton biomass and production often occurred in spring and summer, when irradiance was higher (Gameiro et al., 2011).

The relationships between turbidity and phytoplankton CHL a concentration in the coastal waters of western central Taiwan further demonstrated that the threshold of turbidity was 12 NTU, above which phytoplankton CHL a concentrations were < 0.5 mg m^{-3} (Fig. 9a). The higher turbidity in fall more likely resulted from the sediment resuspension caused by the onset of the northeastern monsoons (Climatological Data Report, Central Weather Bureau of Taiwan, 1980–2010), which may have restricted the irradiance

Table 3
Spearman rank correlation coefficients relating phytoplankton CHL a concentration and daily rates of gross production, net production and respiration and environmental factors during the study period at the three sites in the coastal waters of western central Taiwan. CHL a: chlorophyll a; DGP: daily gross production; DR: daily respiration; DNP: daily net production; DGP^B: DGP normalized to CHL a; DR^B: DR normalized to CHL a; DNP^B: DNP normalized to CHL a; TEMP: water temperature; DO%: dissolved oxygen in % saturation; SAL: salinity; TUR: turbidity; and NO_x: $NO_2^- + NO_3^-$.

	CHL a	TEMP	DO%	pH	SAL	TUR	NO_x	NH_4	PO_4	SiO_2
DGP	0.74[***]	0.43	0.22	−0.14	0.13	−0.51[*]	−0.50	0.45	−0.31	−0.21
DR	0.32[*]	−0.01	0.34	0.12	−0.02	−0.08	−0.20	0.43[**]	−0.17	0.08
DNP	0.41[***]	0.40[**]	−0.17	−0.18	0.12	−0.35[**]	−0.30[*]	0.01	−0.16	−0.16
DGP^B	−0.42[*]	0.23	0.00	−0.32	−0.05	0.07	0.25	−0.47	−0.02	−0.30
DR^B	−0.33	−0.20	0.39	0.01	0.01	0.23	0.24	−0.08	0.15	0.08
DNP^B	−0.05	0.30	−0.27	−0.25	0.02	−0.09	0.00	−0.28	−0.09	−0.18
CHL a	–	0.37[**]	0.15	0.22	−0.02	−0.48[***]	−0.70[***]	0.67[***]	−0.29[*]	0.05
TEMP	–	–	−0.44[***]	0.30[*]	−0.34[**]	−0.02	−0.29[*]	−0.09	−0.26	0.27[*]
DO%	–	–	–	−0.33[**]	0.22	−0.31[**]	−0.12	0.23	−0.06	−0.40[**]
pH	–	–	–	–	−0.07	−0.25	0.36	0.07[**]	0.49	−0.01[***]
SAL	–	–	–	–	–	−0.56[***]	−0.46[***]	0.23	−0.48[***]	−0.51[***]
TUR	–	–	–	–	–	–	0.79[***]	−0.46[***]	0.51[***]	0.49[***]
NO_x	–	–	–	–	–	–	–	−0.47[***]	0.51[***]	0.35[*]
NH_4	–	–	–	–	–	–	–	–	0.12	0.08
PO_4	–	–	–	–	–	–	–	–	–	0.38[**]

[***] Significance level: $p < 0.001$
[**] Significance level: $p < 0.01$
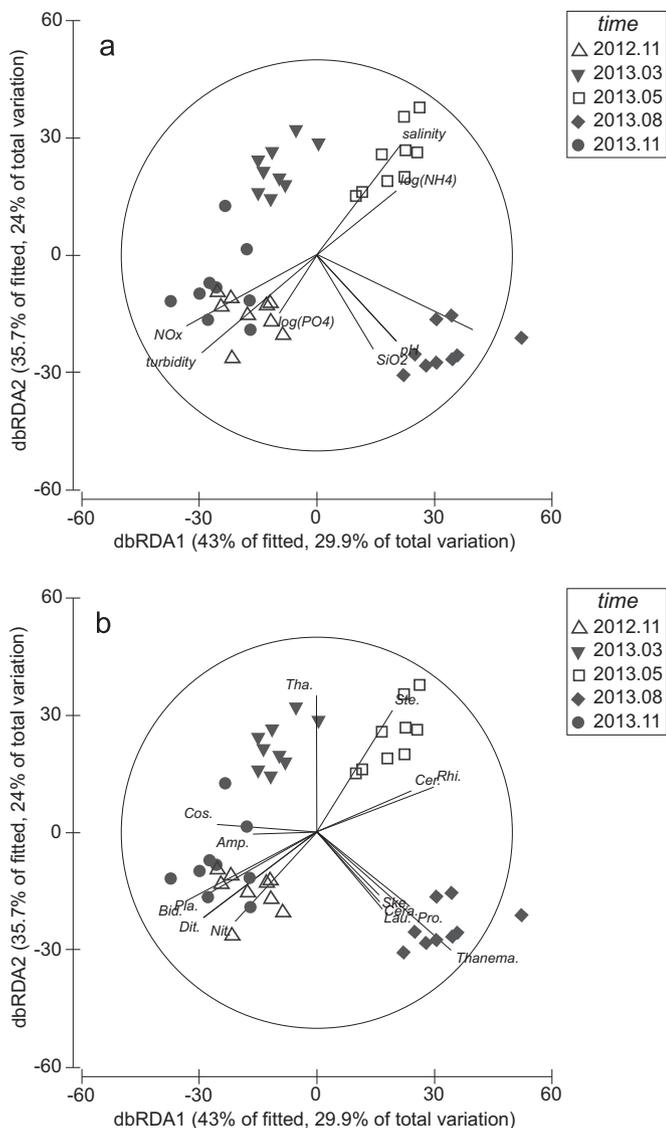[*] Significance level: $p < 0.05$.

Fig. 8. Distance-based Redundancy analysis (dbRDA) of relationships between (a) environmental factors and (b) phytoplankton composition from fall 2012 to fall 2013 at the three sites in the coastal waters of western central Taiwan. Amp: *Amphora*; Bid: *Biddulphia*; Cer: *Cerataulina*; Cera: *Ceratium*; Cos: *Coscinodiscus*; Dit: *Ditylum*; Lau: *Lauderia*; Nit: *Nitzschia*; Pla: *Plagiogramma*; Pro: *Protoperidinium*; Rhi: *Rhizosolenia*; Ske: *Skeletonema*; Ste: *Stephanopyxis*; Thanema: *Thalassionema*; and Tha: *Thalassiosira*.

Fig. 9. The relationships between (a) phytoplankton CHL *a* concentration and (b) daily gross production rate with turbidity during the study period at the three sites in the coastal waters of western central Taiwan.

reaching phytoplankton and evenly dispersed phytoplankton in the water column caused by vertical mixing (Burford and Rothlisberg, 1999) or reduce the residence time of phytoplankton in the euphotic zone (Diehl et al., 2002). In the Pearl Estuary, China, phytoplankton biomass was also limited by irradiance in fall, when strong vertical mixing occurred (Ho et al., 2010). In the Godavari Estuary, India, phytoplankton biomass started to increase only when turbidity decreased to 75% (Sarma et al., 2009).

There was also a negative relationship between turbidity and phytoplankton daily GP rate (Fig. 9b). Daily GP rate was higher in spring 2013 when turbidity was lowest, but daily GP rate was lower in the fall of both years when turbidity reached the highest. Consistent with our hypothesis, the higher turbidity at Ez also resulted in the spatial variation in phytoplankton production, with lower levels at Ez than the other 2 sites. The turbidity threshold of 12 NTU can also be applied to phytoplankton production, because there were highly positive correlations between CHL *a* concentrations and daily GP, respiration, and NP rates. The higher turbidity > 12 NTU in
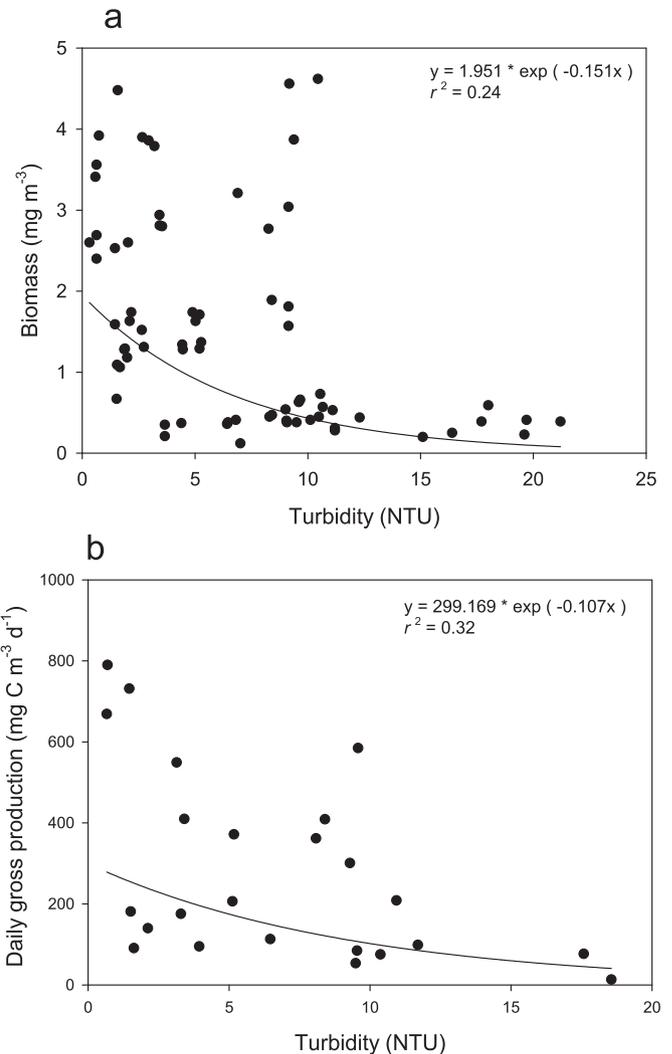
summer 2012 and fall in both years also resulted in daily GP rates < 100 mg C m^{-3} d^{-1}. Similarly, although nutrient loading increased in the wet season in some estuaries, increased turbidity may result in the irradiance limitation of phytoplankton biomass and production (Cloern, 1999; Domingues et al., 2011).

However, turbidity did not appear to be the main limiting factor in summer 2013. Phytoplankton production was highest at Ez and lowest at Dm in summer 2013, when turbidity was highest at Ez and lowest at Dm. These results suggested that other factors may be involved in the growth of phytoplankton in summer in the coastal waters. In summer 2013, the most dominant genera was *Thalassionema*, the relative abundance reaching 41–57%. The averaged Si:N ratio of 27 diatom species was 1.05, but the ratio of *Thalassionema nitzschioides* was 4 times the average (Brzezinski, 1985), indicating a relatively larger requirement of Si by *Thalassionema*. In this study, *Thalassionema* occurred only in summer when SiO_2 concentration was higher. In addition, the spatial variation in phytoplankton production matched well with the spatial variation of SiO_2 concentration in summer 2013. This suggested that SiO_2 concentration became a main regulating factor for phytoplankton production in summer (Fig. 10).

In summer 2013, the mixotrophic dinoflagellate *Ceratium* (Tomas, 1997) and heterotrophic dinoflagellate *Protoperidinium* (Jeong et al., 2004) were more abundant at the offshore site (Dm), where
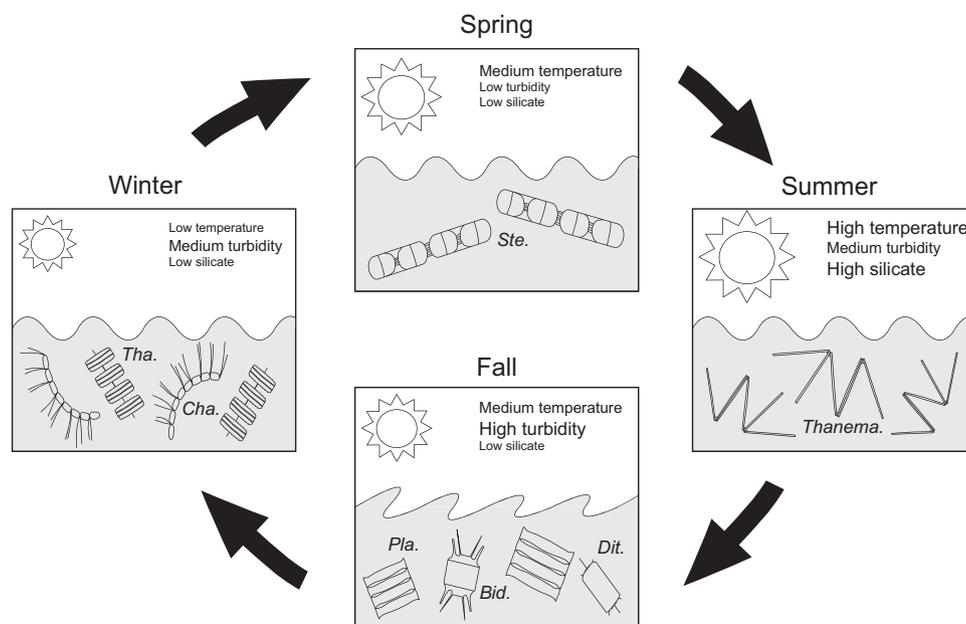
Fig. 10. Conceptual diagram synthesizing the role of different limiting factors over four seasons and the dominance of different phytoplankton taxa in the coastal waters of western central Taiwan. *Bid: Biddulphia; Cha: Chaetoceros; Dit: Ditylum; Pla: Plagiogramma; Ste: Stephanopyxis; Thanema: Thalassionema; Tha: Thalassiosira.*

the water was relatively less enriched when compared to the estuarine sites. Dinoflagellates were less sensitive to nutrients than diatoms (Baek et al., 2008) because they can obtain required elements by consuming other algae (Olseng et al., 2002), which leads to dinoflagellates becoming more dominant in more oligotrophic waters (Baek et al., 2011). They are diatom-feeders, and their herbivory on diatoms may be the reasons for the low phytoplankton biomass and production at Dm in summer.

Surprisingly, there was high phytoplankton production at the offshore site (Dm) in fall 2013 when the water was turbid. The results of SIMPER showed that the benthic diatoms *Amphora* and *Grammatophora* were the most common genera at Dm at this time, accounting for 15% and 14%, respectively, of the total abundance. This suggested that a large proportion of phytoplankton taxa was derived from sediment resuspension caused by strong wave action in the fall. The saturation irradiance for benthic microalgae was low, ranging from 66 to 185 µmol photons $m^{-1} s^{-1}$ (Guarini et al., 2002; Serôdio et al., 2012). The growth condition was still good for *Grammatophora marina* when cultured under 180 µmol photons $m^{-1} s^{-1}$ (Affan et al., 2006). In this study, the P-E curves showed that the E_k for phytoplankton at Dm in fall 2013 was 157 µmol photons $m^{-1} s^{-1}$. This supported our deduction that the high phytoplankton production at Dm in fall 2013, when the water was turbid, was mainly contributed by the benthic diatoms *Amphora* and *Grammatophora*.

Ecological functional traits can be further used to explore the potential influencing factors for phytoplankton production. The results of dbRDA showed that there was a clear seasonal variation in phytoplankton community composition, but it was not so clear for the spatial variation. In fall, when the water was most turbid, phytoplankton production was the lowest (Fig. 10). The dominance of the benthic diatoms *Plagiogramma* and *Nitzschia* at this time reflected the strong mixing of the water column. In addition, the dominant genera *Biddulphia* and *Ditylum* were also the microalgae growing in the bottom layer of water column (Gallegos et al., 1990). *Ditylum brightwellii* preferred the environment under very low irradiance (Richardson et al., 1983) and could sink to prevent the injury by high irradiance (Rijstenbil, 2001). The phytoplankton community in fall, when the water was most turbid, was mainly comprised of low-irradiance algal taxa.

In winter, when water column became more calm and turbidity remarkably decreased, phytoplankton production was still low. This suggested that the low temperature became a main limiting factor for phytoplankton production in winter (Fig. 10). At this time, the phytoplankton community was dominated by *Thalassiosira*, *Chaetoceros*, and *Schroederella*. The combined contribution by *Thalassiosira* and *Chaetoceros* to the total abundance reached 68%. *Thalassiosira rotula* and *Chaetoceros curvisetus* were reported to bloom in spring at < 4 °C (Lewandowska and Sommer, 2010), indicating they can grow in low-temperature environments.

Phytoplankton production reached a peak in spring, when water turbidity remained low and temperature increased (Fig. 10). The relative abundance of *Stephanopyxis*, *Hemiaulus*, *Cerataulina*, and *Rhizosolenia* in the community increased. Among these genera, *Stephanopyxis* occurred only in spring. In summer, when water turbidity increased, phytoplankton production was slightly lower than that in spring and the dominance shifted to *Thalassionema*. In the Tagus Estuary, Portugal, *Stephanopyxis* was observed outside of the estuary in high salinity and low turbid water, whereas *Thalassionema* was widely distributed in the estuary (Gameiro et al., 2004), suggesting that there were some differences between these 2 genera in their adaptation to salinity and turbidity. Culture experiments also showed that elongated light duration and higher irradiance stimulated the growth of *Stephanopyxis* (Sommer, 1994). However, elevated temperature and reduced irradiance did not affect the abundance and biomass of *Thalassionema* in mesocosm experiments (Lewandowska and Sommer, 2010). It appeared that *Stephanopyxis* preferred more clear water and occurred only in spring, whereas *Thalassionema* appeared only in summer when SiO_2 loading was higher, although the adaptation to irradiance was larger. Si was also reported as the limiting nutrient for phytoplankton abundance in the largest estuary of northern Taiwan (Wu and Chou, 2003). In this study, it was clear that turbidity was the main factor governing phytoplankton production, whereas temperature and SiO_2 concentration affected community composition and then regulated the production.

When compared with phytoplankton gross production determined at other sites in nearby seas and estuaries (Table 4), the spring production at our 3 sites in the coastal waters ranked the highest, followed by the measurements at the Pearl River Estuary.

Table 4
Comparisons of mean daily gross production (mg C m^{-3} d^{-1}) of phytoplankton determined at the three sites in the coastal waters of western central Taiwan with the measurements reported in nearby seas and estuaries in spring and summer.

Study site	Location	Spring	Summer	Citation
East China Sea	30°23′10″N 123°25′53″E	13.3	83.5	Gong et al. (2003)
South China Sea (D1)	23°30′20″N 117°36′53″E		91.0	Liu et al. (2011)
South China Sea (S1)	22°56′08″N 116°38′55″E		239.8	Liu et al. (2011)
South China Sea (A3)	21°49′31″N 114°19′35″E		473.2	Liu et al. (2011)
Daya Bay	22°28′35″N 114°24′55″E	38.5	106.5	Song et al. (2004)
Pearl River Estuary (western)	22°17′37″N 114°03′11″E	500.0	600.0	Ho et al. (2010)
Pearl River Estuary (southern)	22°10′56″N 114°05′12″E	510.0	2000.0	Ho et al. (2010)
Danshuei Estuary	25°09′03″N 121°26′54″E	211.8	755.7	Li (2014)
Tsengwen Estuary	23°03′06″N 120°03′09″E	492.2	705.2	Liu (2014)
Ez	23°50′49″N 120°11′18″E	53.5–731.3	584.6	This study
Dm	23°49′11″N 120°09′27″E	206.2–789.8	90.9	This study
Ex	23°44′53″N 120°09′38″E	549.1–668.7	409.8	This study

However, the summer production ranks behind the Pearl River Estuary, the Danshuei River Estuary, and the Tsengwen Stream Estuary. Most of the measurements showed that the summer daily GP rate was higher than the spring rate (Table 4). The summer production rate determined in the western Pearl River Estuary was similar to our summer rates. Ho et al. (2010) indicated that turbidity (4–17 NTU) was higher in the western Pearl River Estuary, which constrained the phytoplankton production in summer. In this study, turbidity at Ex was consistently > 10 NTU, which likely constrained phytoplankton production. On the contrary, SiO_2 concentrations in the East China Sea, the Daya Bay, and the southern Pearl River Estuary were much higher (> 8 µM) than at our 3 sites, suggesting the low SiO_2 concentrations in the coastal waters of western Central Taiwan could also be a limiting factor for the summer phytoplankton production.

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