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Typhoon effects on phytoplankton responses in a semi-closed freshwater ecosystem

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Abstract. Analyses of past typhoons have suggested that global climate change may result in increases in the intensity of these episodic events and that the effects of typhoons on the biogeochemistry of aquatic ecosystems will also be strengthened. We collected a 2-year time series of phytoplankton responses, including chlorophyll-*a* concentration, primary production and turnover rate in the Fei-Tsui Reservoir, Taiwan, on the basis of five typhoons in 2011 and eight in 2012 (21 weeks affected). We found approximately a two-fold increase in phytoplankton responses during the typhoon period compared with the non-typhoon period. However, there were no consistent correlations between phytoplankton responses and typhoon disturbance and length of typhoon stay. Vertical distributions of phytoplankton responses indicated that the peak values of these responses occurred both during the typhoon periods and during the non-typhoon periods occurring between two typhoons. Moreover, the strongest correlations were found between euphotic depth-averaged phosphate and primary production and turnover rate. Combined effects on phytoplankton responses could explain at least 70% of the variability. The regulation of phytoplankton responses by multiple processes and interactions among factors that operate during each typhoon event may add complexity to the challenge of detecting typhoon-driven mechanisms in such ecosystems.

Additional keywords: chlorophyll-*a* concentration, primary production, turnover rate.

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Introduction

Global climate change in the 21st century is causing temperature increases worldwide. In addition, the frequency and severity of extreme weather and climatic events have increased around the world (IPCC 2007), altering environments of the Earth and producing stresses on ecosystems. Measuring and evaluating the physical, chemical and ecological impacts of such extreme weather and climatic events over short as well as long time scales has taken on new importance (Jennings *et al.* 2012; Klug *et al.* 2012). Typhoons, also termed tropical cyclones and hurricanes, particularly the increasing number of high-category typhoons is very likely to link to global climate change and extreme weather and climatic events (Kim *et al.* 2006; Lau *et al.* 2008; Hansen *et al.* 2012), are known to affect the structure and ecological function in both freshwater and marine ecosystems (Robarts *et al.* 1998; Shiah *et al.* 2000; Zheng and Tang 2007; Zhao *et al.* 2008; Siswanto *et al.* 2009; Sun *et al.* 2010; Tseng *et al.* 2010; Yang *et al.* 2010; Chung *et al.* 2012; Klug *et al.* 2012; Winder and Sommer 2012). They are accompanied by heavy rainfall, affecting nutrient runoff from terrestrial sources to the coastal zone and from the bottom layers of the water to the euphotic zone. The euphotic zone offers abundant light for photosynthesis, but it often lacks nutrients. However, assessment of the regional effects of such weather and climatic events on ecological processes has been generally limited to studies based on satellite imagery (for example, Millward *et al.* 2010; Lin 2012) or to the single biological response.

Phytoplankton is of global significance because of its role in the primary energy budget of the Earth and biogeochemical cycling. With less than 1% of the total phytosynthetic biomass, phytoplankton contributes nearly 50% of global net primary production (Field *et al.* 1998) and contributes to the largest active reservoir of organic carbon with every class of carbohydrate (Hedges 1992; Quinn and Bates 2011). Phytoplankton represents the channel by which energy is transmitted between the moving air and water. It plays an important role in the vertical transfer of atmospheric CO_2 to the bottom of the water column, especially under contemporary climate change (Winder and Sommer 2012). Through photosynthesis, phytoplankton absorbs CO_2 that enters the water from the atmosphere. CO_2 is then transformed into the organic compounds of which the cellular material of the phytoplankton is composed. By virtue of this unique ability, phytoplankton occupies a prominent place in the aquatic food web, because it serves as a food source for all aquatic organisms that do not perform photosynthesis. Moreover, vertical migrations, as well as the diversity, community structure and temporal dynamics of phytoplankton, are responsible for steep nutrient gradients across the thermocline.

Re-organisation of phytoplankton communities and dynamic changes in the behaviour of small-sized phytoplankton regulate trophic transfer and water quality. In addition, these processes regulate production by consumers (Winder and Sommer 2012). Like all other organisms, these microscopic autotrophic organisms influence the turnover times of both organic and inorganic elements. These elements are accumulated in the bodies of the organisms during their life.

To yield a better understanding of phytoplankton functions in the ecosystem, the fluctuations of phytoplankton populations can be expressed in terms of various quantitative parameters (e.g. chlorophyll-*a* (Chl-*a*) concentration, primary production and turnover rate; Cullen 1982; Marra 2002; Örnólfsdóttir *et al.* 2004; Boyer *et al.* 2009). Each parameter emphasises a certain characteristic of phytoplankton associations. Knowledge of these functions, characteristics and associations is needed to evaluate the importance of the role or roles played by phytoplankton in a particular ecosystem. Moreover, there is a long history of application of these three phytoplankton responses to index the productivity and trophic condition of aquatic ecosystems. The Chl-*a* concentration, as an indicator of photoautotrophic biomass, reflects the net result (standing stock) of processes involving growth and loss, such as grazing by microzooplankton in aquatic systems (Cullen 1982; Boyer *et al.* 2009). The Chl-*a* concentration has been viewed as the primary variable to be used as a trophic-state indicator. The primary production is the rate of accumulation of biomass and is critical to the examination of carbon-flow dynamics in the water environment (Marra 2002). The turnover (growth) rate is a physiological process (Örnólfsdóttir *et al.* 2004). Unlike Chl-*a* concentrations and primary production, which are affected by grazing, the turnover rate is often limited by temperature, nutrients or light. These aforementioned three quantitative phytoplankton responses were analysed in the present study.

Previous studies have demonstrated the sensitivity of phytoplankton to climate and the enhancement of phytoplankton responses by typhoons (Zheng and Tang 2007; Zhao *et al.* 2008; Lin 2012; Winder and Sommer 2012). These processes affect phytoplankton both directly, through physiology, and indirectly, by changing water-column stratification and resource availability, primarily the availability of nutrients and light, or by producing intensified grazing by heterotrophs. Generally, a temperature increase usually leads to greater phytoplankton growth rates and biomass accumulation if it is accompanied by an adequate resource supply (Zheng and Tang 2007; Lin 2012). However, these changes are also accompanied by an increase in the metabolism of heterotrophic organisms (Winder and Sommer 2012). This effect strengthens top-down control over primary production, by increasing grazing rates. The seasonal cycle or abrupt changes in heat-exchange processes and wind action create two opposing tendencies, the tendency to stratify and suppress mixing and the tendency for inputs of turbulent kinetic energy to promote mixing, which further balance water column environments (Wetzel 2001; Winder and Sommer 2012). The results include phenomena such as turbulence and phytoplankton responses such as cell sedimentation. Specifically, typhoon winds, rain and induced currents and rainwater runoff trigger a series of ecological offshore and nearshore phytoplankton consequences through both vertical mixing and upwelling (Zheng and Tang 2007; Zhao *et al.* 2008; Tseng *et al.* 2010; Chung *et al.* 2012; Lin 2012). A strong and slow-moving typhoon appears to have the strongest effects on phytoplankton blooms (Bender *et al.* 1993). Strong typhoons produce strong surface cyclonic wind-stress curls over a large surface area in aquatic systems, producing strong vertical mixing and upwelling and bringing cold and nutrient-rich water to the euphotic zone. Additionally, slow-moving typhoons enhance cooling of the surface mixing layer.

However, most geochemical estimates of phytoplankton responses and typhoons have been based on studies in oceanic and coastal ecosystems. There is little direct evidence linking time series of typhoon events to changes in phytoplankton responses in freshwater ecosystems. Taiwan is located along typhoon tracks because the Pacific Ocean is often subject to high pressure systems in the summer. The north–east trade winds contribute to the formation of typhoons. The formation of typhoons is generally followed by movement to the west and the north-west, following clockwise circulation patterns. Taiwan, therefore, is frequently influenced by typhoons during the summer months. In the present study, we investigate whether the types of phytoplankton responses expected in oceanic and coastal ecosystems are found as a result of typhoons in a semi-closed freshwater ecosystem. We also ask how these phytoplankton responses vary vertically and whether there are characteristic correlations and interactions between phytoplankton responses and typhoons.

Materials and methods

Study site and field sampling

Fei-Tsui Reservoir (24°54′N, 121°34′E), located on the downstream of the Pei-Shi River in the northern Taiwan (Fig. 1), is the major water supply to the Taipei metropolitan area. The reservoir was constructed in 1987 and has been protected from human activities since then. Therefore, the Fei-Tsui Reservoir behaves as a natural semi-closed freshwater ecosystem. The Fei-Tsui Reservoir has a watershed catchment area of 303 km^2 with an altitude from 450 m above sea level (ASL) to 1170 m ASL, and that is covered mostly by secondary subtropical forests. It has a basin area of 10.24 km^2 and a designed total water capacity of 4.06×10^8 m^3 at its normal maximum surface elevation of 170 m ASL. The average slope of the reservoir bed is 0.3%, the mean depth of the reservoir is 39.4 m and the maximum depth of the reservoir is 113.5 m at the dam. The water level fluctuates from 144 to 168 m ASL and the surface temperature ranges from 17 to 31°C. The average residence time of the reservoir is 115 day (Chen *et al.* 2006). According to the long-term records of the Carlson's trophic state index, the Fei-Tsui Reservoir is classified as a mesotrophic lake (Chou *et al.* 2007).

Samples were collected at the dam site weekly (but biweekly in March and April, owing to limitation of survey-boat resources) during the warm season (i.e. when the mixing layer depth $<$ the photic depth) from the following 10 different depths: 0, 2, 5, 10, 15, 20, 30, 50, 70 and 90 m. Water samples were collected with a 5-L Go-Flo bottle and placed in 100–300-mL bottles for the following phytoplankton response experiment.

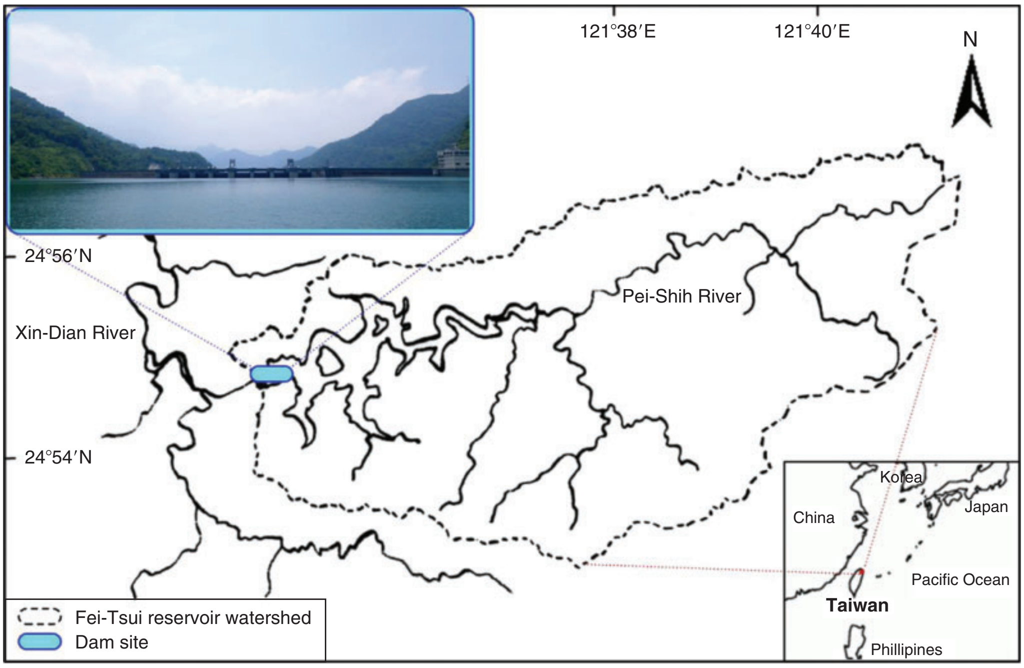

Fig. 1. Location of the Fei-Tsui Reservoir and its dam site, where the maximum depth is 113.5 m, surrounded by mountains with mostly secondary subtropical forests in Taiwan.

Phytoplankton responses

In the present study, the Chl-*a* concentrations were determined by filtration of the water samples through Whatman GF/F glass microfibre filters, extraction with acetone, and measurement with an *in vitro* fluorometer (TD-700 Laboratory Fluorometer, Turner Designs, Sunnyvale, CA, USA; Parsons *et al.* 1984). The primary production was measured by the ^{14}C assimilation method (Parsons *et al.* 1984). The water samples were incubated under an instantaneous irradiance (artificial light source) of $\sim$2000 μE $m^{-2} s^{-1}$ for 2 h with night density filters (ARRI filters, ARRI GB Ltd, Heston, Middlesex , UK, 0, 6, 12, 16, 23, 36, 44, 63 and 91%), then filtered. To remove excess $H^{14}CO_3^-$, 0.1 N hydrochloric acid (HCl) was added, and the sample was left at room temperature for 24 h. A treatment with LSC-cocktail liquid (Ultima Cold, Packard BioScience BV, Groningen, Netherlands) was applied for an additional 24 h. A liquid scintillation analyser (Tri-Carb 2900TR, PerkinElmer, Waltham, MA, USA) was then used to count biological radioactivity, which was then expressed as the primary production per unit time. The turnover rate was calculated as:

$$\text{Primary production} \div (\text{Chl-}a \text{ concentration} \times \text{CCF})$$

The carbon conversion factor (CCF) is a conversion ratio of phytoplankton biomass carbon to the Chl-*a* concentration, with a value of 58 g C g^{-1} Chl-*a* (Eppley *et al.* 1992).

Typhoon records and impacts

We compiled historical typhoon records and parameters of typhoons (including length of typhoon stay, intensity grade, maximum sustained wind speed, minimum centre pressure and radius of over 15 m s^{-1} winds) from the Central Weather Bureau, Taiwan (http://www.cwb.gov.tw, accessed 9 May 2014). In addition, we evaluated a synthetic typhoon disturbance using a typhoon-disturbance index (Tseng *et al.* 2010; Merritt-Takeuchi and Chiao 2013) calculated as:

$$(10 \times \text{the accumulated precipitation over the watershed during the typhoon stay}) \div \text{the maximum sustained wind speed}$$

Because of time-lag effects of typhoons, i.e. a response time of the phytoplankton population to a sudden nutrient injection by typhoons (Zheng and Tang 2007), we defined the sampling day within 6 days after a typhoon hit as the typhoon week (i.e. the week when affected by a typhoon).

Typhoon-related hydrological and climatic factors

We selected six hydrological and climatic factors, including runoff, depth-averaged phosphate in the euphotic zone, phosphate content integrated to a depth of 90 m, local wind speed, light irradiation and temperature. On the basis of a variety of aquatic ecosystem and meteorological studies, these factors are considered to be biologically important for phytoplankton activity and representative of typhoon-induced hydrological and climatic changes. Factors with daily values, except for euphotic depth-averaged phosphate and integrated phosphate to a depth of 90 m , were obtained from the Taipei Fei-Tsui Reservoir Administration and the Data Bank for Atmospheric Research (https://dbar.ttfri.narl.org.tw, accessed 7 January 2014), Taiwan. To obtain meteorological conditions that represented values close to those occurring during the weekly

Table 1. List of typhoons affecting Taiwan in 2011 and 2012

The intensity grade of a typhoon was evaluated by the maximum sustained wind speed near the centre: minor, 17.2–32.6 m s^{-1}; moderate, 32.7–50.9 m s^{-1}; intense, ≥51.0 m s^{-1}

Year	Name	Length of stay (days) (period)	Intensity grade	Maximum sustained wind speed (m s^{-1})	Minimum centre pressure (hPa)	Radius of over 15 m s^{-1} winds (km)	Disturbance ranking
2011	Aere	2 (9–10 May)	Minor	23	990	150	0.23
	Songda	2 (27–28 May)	Intense	55	920	220	776.60
	Meari	3 (23–25 June)	Minor	28	982	200	458.36
	Muifa	3 (4–6 August)	Moderate	43	945	280	68.37
	Nanmadol	5 (27–31 August)	Intense	53	920	180	1492.48
2012	Talim	3 (19–21 June)	Minor	25	985	150	115.50
	Doksuri	2 (28–29 June)	Minor	23	995	120	23.92
	Saola	5 (30 July–3 August)	Moderate	38	960	220	2767.92
	Haikui	2 (6–7 August)	Moderate	35	960	180	35.35
	Kai-Tak	2 (14–15 August)	Minor	20	995	150	20.40
	Tembin	5 (21–25 August)	Moderate	45	945	180	395.55
	Tembin	3 (26–28 August)	Moderate	35	965	180	257.95
	Jelawat	2 (27–28 September)	Intense	55	910	250	756.25

and biweekly sampling, we calculated the values of these factors from the sampling day to 1 week previous to the sampling day. Local wind speed, light irradiation and temperature were expressed as mean values per week. Runoff was shown as average weekly values. Because land areas may capture rainwater directly and nutrients can be carried from tributaries to the dam, we used runoff instead of precipitation, to represent the total amount of water input and nutrient supply. Note that wind speed was estimated locally at the dam site and, therefore, differed from the sustained wind speed of the typhoons themselves. Phosphate concentrations were determined with weekly and biweekly *in situ* measurements performed with a custom-made flow-injection analyser with a 10-cm detection cell (Parsons *et al.* 1984). The concentration values of euphotic depth-averaged phosphate and integrated phosphate to a depth of 90 m were used to represent consumption of nutrient in the system. However, because the Fei-Tsui Reservoir is a phosphate-limited system, often resulting in rapid nutrient (phosphate) use (Tseng *et al.* 2010), the value of euphotic depth-averaged phosphate may not be detectable.

Statistical analysis

In the present study, we used the trapezoid method (Hornbeck 1975) to calculate the depth-integrated values of phytoplankton responses, and we computed averages based on the depth of the euphotic layer. We used a Mann–Whitney U-test to evaluate the differences in phytoplankton responses between typhoon and non-typhoon periods. To quantify the mechanisms and impacts of typhoons, we applied a Pearson correlation analysis or a polynomial regression to the typhoon-disturbance index, length of typhoon stay and individual typhoon-related hydrological and climatic factors from each typhoon. To construct a good-fit model for the multiple effects of aforementioned eight factors on phytoplankton responses, all factors were first involved into the model and key factors defined as significant at 10% level were then preceded in the multivariate regressions using stepwise backward elimination, with individual phytoplankton response as the dependent variable. The final models were selected when the adjusted R^2 peaked. All statistical analyses were performed in R 3.0 (R Development Core Team 2013).

Results

Thirteen typhoons hit Taiwan, five in 2011 and eight in 2012, with an average duration of 3 days (Table 1). Twenty-one sampling weeks (of a total of 40), especially in August, were affected by typhoons. The strongest of these typhoons were Songda and Jelawat. At peak intensity, the sustained winds were 55 m s^{-1}, the central pressure was 910–920 hPa, and the average radius of typhoon-force winds was 220–250 km. Typhoons Nanmadol and Saola most affected the Fei-Tsui Reservoir semi-closed freshwater ecosystem, showing the longest stay and the highest typhoon disturbance. Average weekly runoff from typhoons showed a strong variation, ranging from 3.85×10^5 m^3 day^{-1} to 2.87×10^7 m^3 day^{-1}. Despite episodic high runoffs during the typhoon period, the weekly runoff patterns during the typhoon (mean = 4.03×10^6 m^3 day^{-1}, s.e. = 1.41×10^6, $n = 21$) and non-typhoon (mean = 2.84×10^6 m^3 day^{-1}, s.e. = 6.24×10^5, $n = 19$) periods were not significant ($P = 0.788$, Fig. 2*a*).

A large variety of weekly patterns of phytoplankton responses was found, and these responses during the typhoon period were highly significant (all $P < 0.05$, Fig. 2*b–d*). Approximately a two-fold variability of mean phytoplankton responses was found between the typhoon and non-typhoon periods. During the typhoon period, the mean annual Chl-*a* concentration was 3.14 mg Chl-*a* m^{-3}, primary production was 75.44 mg C m^{-3} day^{-1} and turnover rate was 0.43 day^{-1}. During the non-typhoon period, these corresponding values were 2.45 mg Chl-*a* m^{-3}, 36.36 mg C m^{-3} day^{-1} and 0.27 day^{-1}. Moreover, the phytoplankton responses at the individual sampling times were highly variable from typhoon to typhoon. For example, the Chl-*a* concentration ranged from 1.75 mg Chl-*a* m^{-3} to 5.61 mg Chl-*a* m^{-3}, the primary production ranged from 24.87 mg C m^{-3} day^{-1} to 220.92 mg C m^{-3} day^{-1} and the

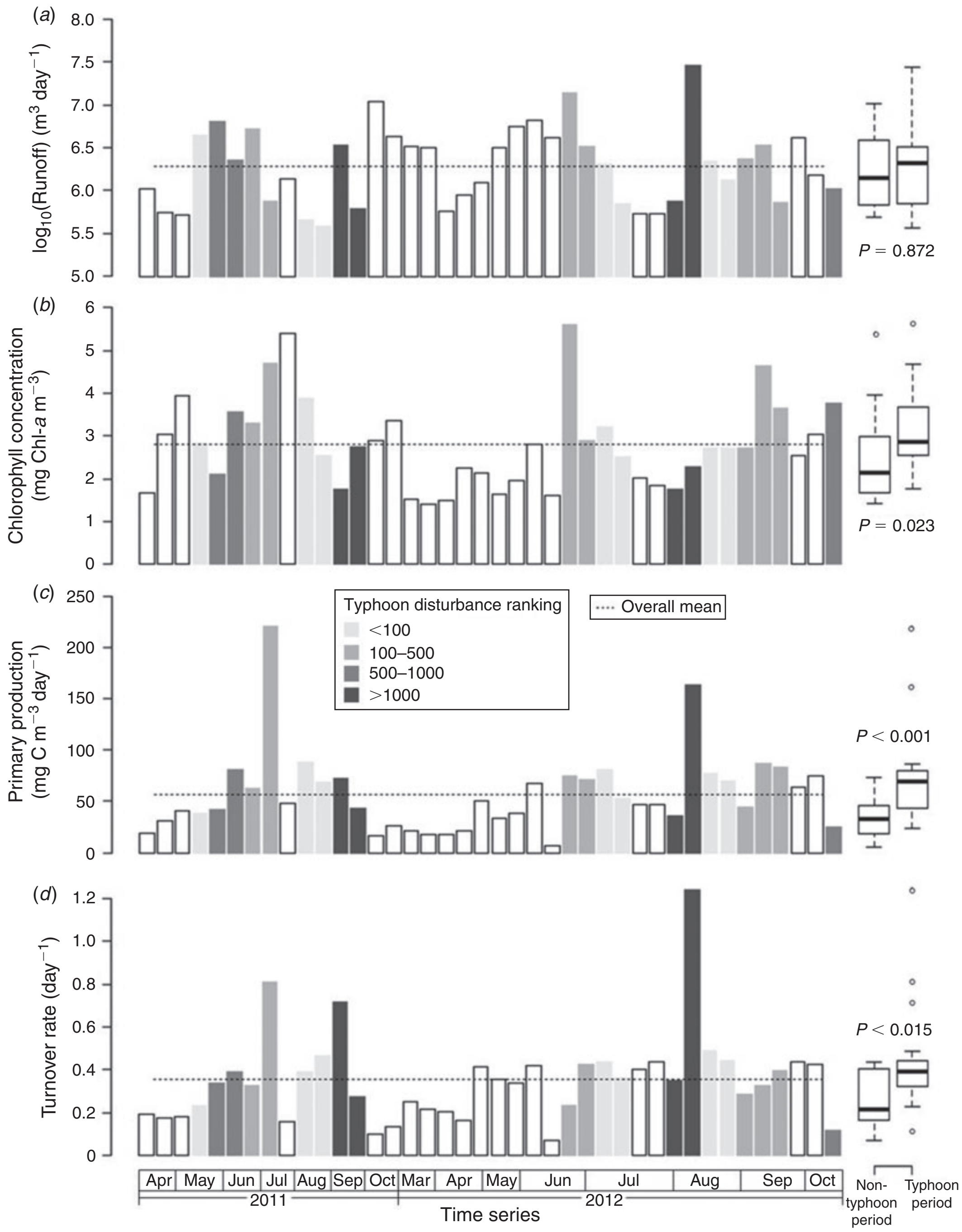

Fig. 2. Weekly patterns and boxplots of (*a*) averaged runoff ($\log_{10}$ transformation, m^3 day^{-1}), (*b*) chlorophyll-*a* concentration, (*c*) primary production and (*d*) turnover rate in the Fei-Tsui Reservoir, a semi-closed freshwater ecosystem in Taiwan, in 2011–2012.

turnover rate ranged from 0.11 day^{-1} to 1.24 day^{-1} during the 2011–2012 typhoon period.

However, there were no consistent correlations between phytoplankton responses and typhoon disturbance or length of typhoon stay (Fig. 3). The Chl-*a* concentration was negatively correlated with typhoon disturbance ($r = -0.45$, $P < 0.05$), showing that minor typhoon events produced stronger effects on phytoplankton biomass than did moderate and intense typhoon events. However, a moderate length of typhoon stay (i.e. 3 days in the present study) caused a significantly higher Chl-*a* concentration ($R^2 = 0.46$, $P < 0.01$) than did a short or long length of typhoon stay, producing a dome-shaped relationship. In contrast, positive correlations between the turnover rate and typhoon disturbance ($r = 0.44$) and between the turnover

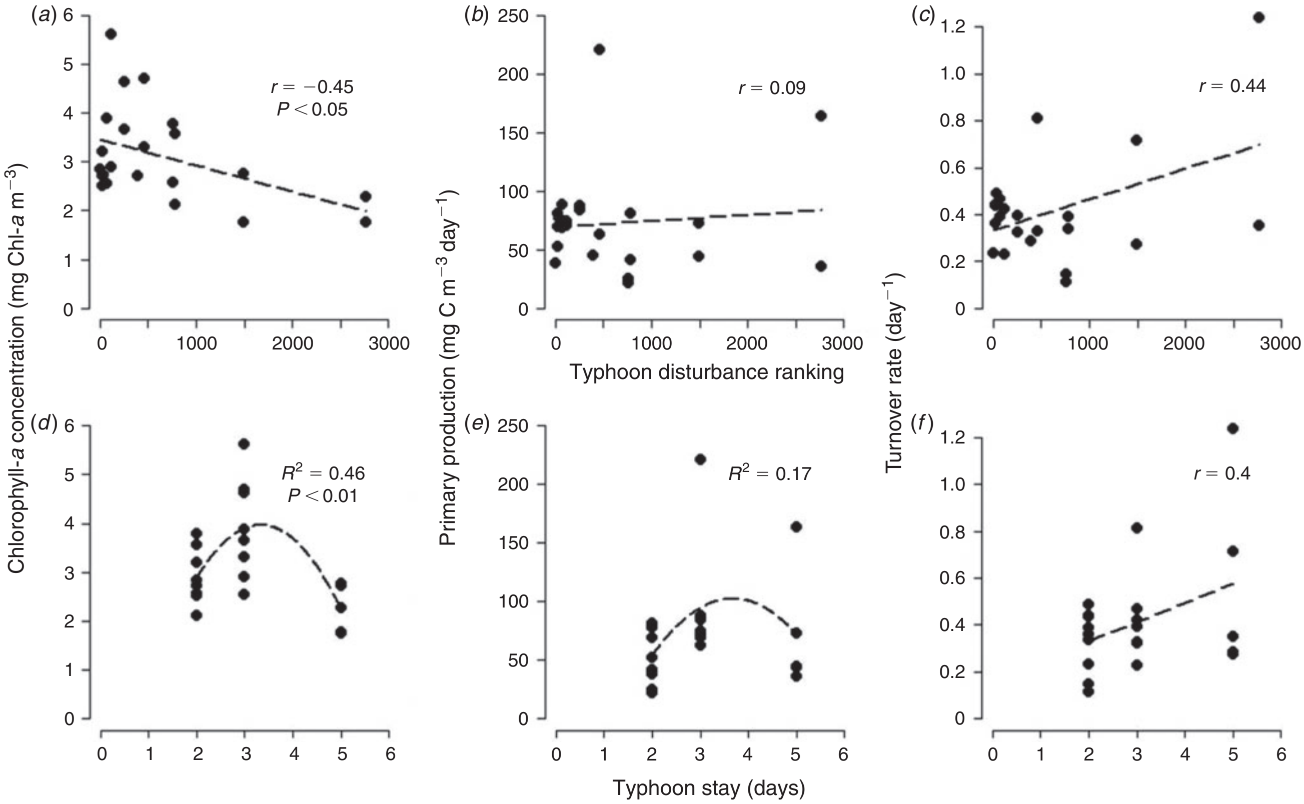

Fig. 3. Scatter plots of chlorophyll *a* concentration, primary production and turnover rate in relation to (*a–c*) typhoon-disturbance ranking and (*d–f*) days of typhoon stay in the Fei-Tsui Reservoir, a semi-closed freshwater ecosystem in Taiwan, in 2011–2012. Pearson correlation coefficients (r) or values of polynomial regression (R^2) and significant P-values for the respective correlations or R^2-values are indicated in the figures.

rate and length of typhoon stay ($r = 0.4$) suggested that a lower turnover rate was associated with a small typhoon disturbance and a short typhoon stay. The primary production was not correlated with typhoon disturbance ($r = 0.09$) or length of typhoon stay ($R^2 = 0.17$), implying that the dynamics of primary production might be influenced by not only typhoons but also other biological effects such as community composition in the system.

The spatial distributions of phytoplankton responses indicated that the peak values occurred during the typhoon periods and during the non-typhoon periods between two typhoon periods (Fig. 4). Moreover, the depth at which the peaks in the Chl-*a* concentration, primary production and turnover rate were observed (usually 5–10 m for the Chl-*a* concentration and <5 m for the primary production and turnover rate) was not consistent even at a single sampling time. These implied that different mechanisms may separately influence the dynamics of these responses and that the magnitude of the typhoon time-lag effect might differ among these responses.

The estimated correlations between phytoplankton responses and individual typhoon-related hydrological and climatic factors during the typhoon period appeared to differ for the Chl-*a* concentration, primary production and turnover rate (Table 2). The Chl-*a* concentration was generally weakly correlated with all factors. Both primary production and turnover rate showed the strongest negative correlations with euphotic depth-averaged phosphate ($P < 0.05$ in the primary production). Among the factors, only runoff showed a consistent positive correlation with the three phytoplankton responses. Moreover, multivariate regression analysis showed that different sets of factors played dominate roles in explaining individual phytoplankton responses to typhoons, and the final models explained 73.9, 69.7 and 94.2% of the variability of the Chl-*a* concentration, primary production and turnover rate respectively ($R^2 = 0.739$, 0.697 and 0.942 respectively, Table 3). The Chl-*a* concentrations with less typhoon disturbance ($P = 0.002$), lower integrated phosphate to a depth of 90 m ($P = 0.014$) and lower temperature ($P = 0.004$) were significantly higher than those with the weather and climatic events with severe typhoon disturbance, high integrated phosphate to a depth of 90 m and high temperature. The effects of interactions between the length of typhoon stay and euphotic depth-averaged phosphate on the primary production showed a highly significant but opposite relationship ($P = 0.05$ and 0.002 respectively). Moreover, a significant relationship was registered for the turnover rate and the length of typhoon stay, euphotic depth-averaged phosphate, integrated phosphate to a depth of 90 m, local wind speed and light irradiation (all $P < 0.05$).

Discussion

We showed that typhoons significantly affected phytoplankton blooms (i.e. high Chl-*a* concentration, primary production and

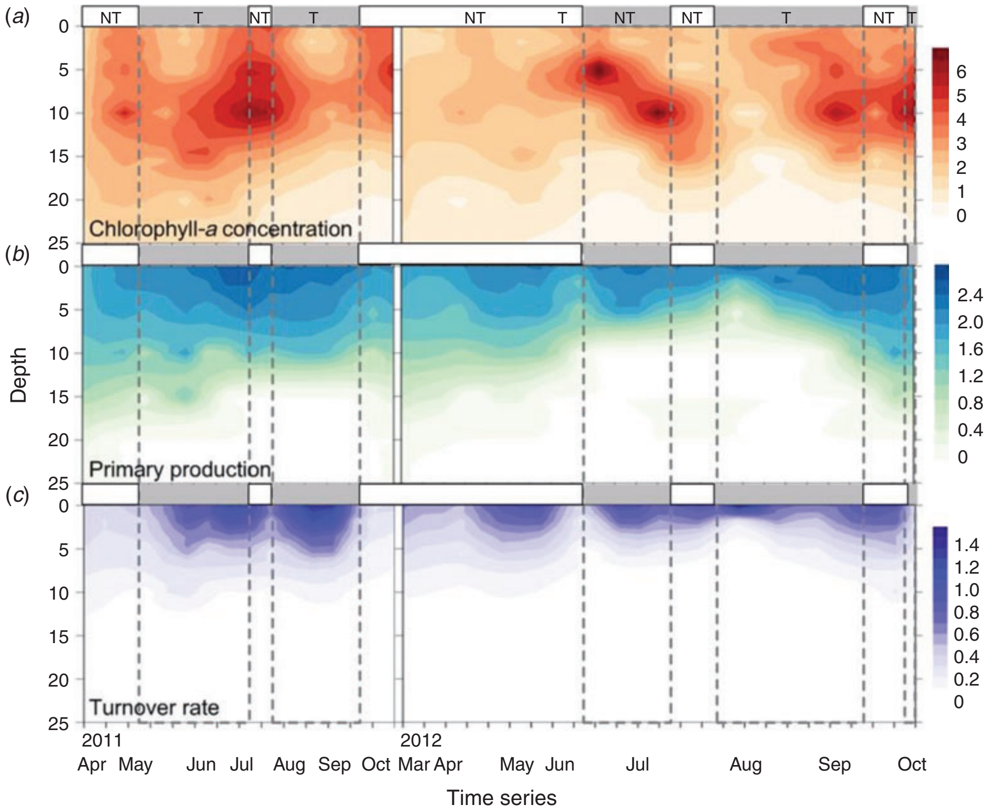

Fig. 4. Vertical distributions of (*a*) chlorophyll-*a* concentration (mg Chl-*a* m^{-3}), (*b*) primary production (log_{10} transformation, mg C m^{-3} day^{-1}) and (*c*) turnover rate (day^{-1}) patterns in 2011–2012. T, typhoon period; NT, non-typhoon period.

Table 2. Correlations among chlorophyll-*a* concentration, primary production and turnover rate and typhoon-related hydrological and climatic factors

Pearson correlation coefficients are given for all correlations. Asterisks represent significant ($P < 0.05$) correlations between values

Factor	Chlorophyll-*a* concentration	Primary production	Turnover rate
Hydrological			
Runoff (m^3 day^{-1})	0.05	0.13	0.31
Euphotic depth-averaged phosphate (μM)	−0.14	−0.65*	−0.44
90-m depth integrated phosphate (μM)	−0.02	−0.28	−0.23
Climatic			
Local wind speed (m s^{-1})	−0.23	−0.13	−0.13
Light irradiation (W cm^{-2})	−0.11	0.08	−0.04
Temperature (°C)	−0.04	0.30	0.23

turnover rate) in the semi-closed reservoir freshwater ecosystem. The stronger phytoplankton responses for the warm-season typhoon period suggest that without typhoons, annual freshwater phytoplankton production and growth in Taiwan may be limited and less productive. An approximately two-fold enhancement in phytoplankton responses associated with typhoon crossings relative to the annual and warm-season background phytoplankton responses at the surface were found in the present study, which can be also observed in various aquatic ecosystems, including open-sea ecosystems (e.g. South China Sea), shelf ecosystems and freshwater ecosystems (e.g. Shiah *et al.* 2000; Bauer and Waniek 2013), although the magnitude of the enhancement varies with time and space. Moreover, given that phytoplankton plays an important role in assimilating CO_2 and contributes to the sinking of atmospheric CO_2 to the bottom of the water column (Winder and Sommer 2012), typhoon-induced phytoplankton blooms in Taiwan may additionally serve to mitigate local and regional warming under climate change.

It is widely known that the sustained wind speed and translation speed of typhoons (i.e. length of typhoon stay used in the present study), the two factors that are critical components of typhoon forcing, may potentially increase nutrient concentrations in the surface water and fuel phytoplankton blooms by inducing strong upwelling and vertical mixing in the wake of a typhoon (Zhao *et al.* 2008; Siswanto *et al.* 2009; Sun *et al.* 2010; Yang *et al.* 2010; Lin 2012). However, such associations of typhoon events with phytoplankton responses have been debated. Zhao *et al.* (2008) found that a weak and slow-moving typhoon induced phytoplankton blooms with a higher Chl-*a* concentration, whereas a strong and rapidly moving typhoon induced phytoplankton blooms with higher primary production over

Table 3. Final models using multivariate regression analysis for three phytoplankton responses, namely, chlorophyll-*a* concentration, primary production and turnover rate, during the typhoon period

Factor	Phytoplankton response								
	Chlorophyll-*a* concentration			Primary production			Turnover rate		
	Regression coefficient	Standard error	*P*	Regression coefficient	Standard error	*P*	Regression coefficient	Standard error	*P*
Typhoon disturbance ranking	−0.002	0.0003	0.002				0.0002	0.0001	0.099
Typhoon stay				18.447	8.638	0.050	0.1407	0.055	0.043
Runoff							0.00	0.001	0.083
Euphotic depth-averaged phosphate	−21.120	43.470	0.640	−6432.678	1583.009	0.002	−42.84	7.541	0.001
90-m depth integrated phosphate	−0.741	0.235	0.014	−7.956	7.470	0.312	0.124	0.040	0.021
Local wind speed	1.317	0.723	0.106				−0.411	0.121	0.014
Light irradiation							0.002	0.001	0.028
Temperature	−0.941	0.235	0.004						
Intercept	30.46			124.158			−0.1775		
R^2	0.739			0.697			0.942		

a larger area. Siswanto *et al.* (2009) showed that the primary production in the southern East China Sea tended to be higher if typhoons traversed slowly with trajectories that allowed strong southerly winds to prevail over Yonaguni Island. Yang *et al.* (2010) indicated that a weak and rapidly moving typhoon had few effects on the upper ocean. Note that in the present study, we used a combination of the characteristics of typhoons (i.e. typhoon-disturbance index, including precipitation and maximum sustained wind speed) to represent the strength of typhoons. In contrast to the findings cited above, we generally found that stronger typhoons produced a lower Chl-*a* concentration but a higher turnover rate, whereas a moderate speed of typhoon movement (i.e. a moderate length of typhoon stay) was fairly favourable for phytoplankton blooms. We suggest that the causes of this inconsistent trend found for the phytoplankton responses include the following. First, orographic screening effects change the typhoon circulation and the further influence of typhoons in freshwater ecosystems (Hsu and Kuo 2013). As a result of decreases in the translational speed of typhoon movement and large amounts of rainfall occurring after landfall, phytoplankton responses showed a dome-shaped relationship with the length of typhoon stay. Second, a long-term analysis and an analysis of multiple typhoon events may provide different but reasonably integrated trends, in contrast with comparisons involving a few typhoons or a single typhoon event. Third, a typhoon that occurs not long after the previous typhoon or a continuous period of multiple typhoon events without sufficient time for ecosystem recovery may enhance or reduce the effects of typhoons on phytoplankton responses. For example, if the stay of a typhoon is long enough to establish a strong upwelling, the induction of significant upper phytoplankton responses can be expected (see additional discussion below; Sun *et al.* 2010).

In addition, anthropogenic reservoir management might also explain the observation that the phytoplankton response initially increased with the typhoon stay, peaked at a stay of approximately 3 days and then decreased with further increases in typhoon stay, reaching minimum values at the longest typhoon stay. Short-stay typhoons (i.e. a 2-day stay) have a limited effect on all phytoplankton responses because of the limited nutrient input associated with these events. In contrast, although long-stay typhoons (i.e. a 5-day stay) bring rich nutrient inputs, phytoplankton concentrations may be diluted as a result of the anthropogenic discharge of water from the reservoir. As a result, a phytoplankton bloom would not occur. Therefore, a moderate typhoon stay would produce accumulated precipitation, such that more and more nutrient input occurred both from the upper tributaries and the surrounding land areas of the dam site, but without strong reservoir dilution. In this case, the strongest phytoplankton responses could be induced.

Importantly and interestingly, we found that the contrast between continuous and discrete patterns of typhoon events would be a key factor in the regulation of phytoplankton responses. Thus, an equal or even greater phytoplankton response was found between two typhoon periods occurring during the non-typhoon periods. In this case, the original enhancement of the phytoplankton response was initiated when a typhoon approached. Then, the phytoplankton response was prolonged until the next typhoon(s), with the strongest blooms occurring after the end of the final typhoon event. This finding implies that the impact of typhoons on surface phytoplankton responses as a result of the sustained influence of two or more typhoons could be much stronger than the previously known effects (Sun *et al.* 2010; Yang *et al.* 2010; Lin 2012).

Compared with typhoon disturbance and forcing time, individual typhoon-related hydrological and climatic effects on water-column stability appear not to play a direct, primary role in typhoon-period phytoplankton growth in the Fei-Tsui Reservoir system. Local meteorological forcing has been noted as the most important factor for the formation of the vertical distribution of temperature in the water column and for further phytoplankton responses (Bauer and Waniek 2013). We have found a significant association of local meteorological forcing with annual non-typhoon period phytoplankton responses in the Fei-Tsui Reservoir (data not shown). Stable high values with less variation in temperature and low-level light irradiation during the typhoon periods might be the reason for the less marked contribution of the typhoon periods to phytoplankton responses. Moreover, our results did not support the importance of local wind forcing as a factor influencing phytoplankton growth, as observed in the central Beibu Gulf as well as the Arabian Sea (Bauer *et al.* 1991; Bauer and Waniek 2013). Both typhoon and non-typhoon periods showed a low correlation or even no correlation between local wind forcing and phytoplankton responses. Both a decrease in local wind forcing as a result of orographic screening effects and the tendency of the natural morphology of the basin of the Fei-Tsui Reservoir to block the wind might produce fewer wind disturbances on the surface and in the upper water column. Finally, the growth and propagation of phytoplankton depends vitally on nutrients in the water column, especially on the source of phosphate at this study site (Tseng *et al.* 2010). A sequence of processes involving phosphate is expected to occur at the site. Bound phosphate would be released as dissolved phosphate in a reducing environment and transported upward to the euphotic zone (Robarts *et al.* 1998; Chen *et al.* 2006; Tseng *et al.* 2010). In the present study, positive correlations were found between phytoplankton responses and runoff. These correlations corresponded to an excess of nutrients during the typhoon periods. However, negative correlations were found between phytoplankton responses and euphotic depth-averaged phosphate and 90-m depth integrated phosphate, which showed rapid consumption of phosphate in the system.

Combined factors showing clear effects on phytoplankton responses revealed that successive and cumulative environmental changes may result from the additive effects of individual factors or the interactive effects of multiple factors of an ecosystem, i.e. the attributes of typhoon impacts and typhoon-related hydrological and climatic factors used in the present study were not mutually exclusive but, rather, highly interdependent. Their interaction generated the complexity inherent in typhoon-induced cumulative environmental changes in a semi-closed freshwater ecosystem such as the Fei-Tsui Reservoir. Although different phytoplankton responses were associated with different sets of key factors, the high R^2-values indicated the importance of these factors in exploring the influence of a typhoon on ecological functions. However, the research focussing on the extreme weather and climatic events (such as typhoons) and the ecological responses is very limited. More studies are necessarily needed to evaluate the risks and vulnerabilities that the extreme weather and climatic events would impose on the aquatic ecosystems.

Overall, on the basis of the 2-year time series of typhoons analysed in the present study, typhoons significantly increased phytoplankton responses in the semi-closed freshwater ecosystem. But the effects of the strength and the speed of movement of typhoons in this ecosystem may not be linearly associated. Accordingly, further studies should include considerations of the continuity of successive typhoon events. Moreover, the phytoplankton responses to typhoons are not closely related with their individual hydrological and climatic conditions induced by the typhoons, and combined effects from multiple factors need to be considered. We also infer that the regulation of phytoplankton responses by multiple processes such as time lags and biological bottom-up or top-down effects operating at each typhoon event may additionally add complexity to the challenge of detecting typhoon-driven mechanisms in semi-closed freshwater ecosystems.

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