



# Decadal phytoplankton dynamics in response to episodic climatic disturbances in a subtropical deep freshwater ecosystem



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## ABSTRACT

Information of the decadal timescale effects of episodic climatic disturbances (i.e., typhoons) on phytoplankton in freshwater ecosystems have received less attention and fewer seasonal evaluations partly due to the lack of long-term time-series monitoring data in typhoon prevailing areas. Through field observations of a total 36 typhoon cases in a subtropical deep freshwater ecosystem in the period of 2005–2014, we quantified phytoplankton biomass, production and growth rate in response to meteorological and hydrological changes in the weeks before, during and after typhoons between summer and autumn, and also investigated the effects of typhoon characteristics on the aforementioned phytoplankton responses. The results showed that phytoplankton exposed to typhoon disturbances generally exhibited an increasing trend over the weeks before, during and after typhoons in summer but varied in autumn. The correlations and multivariate regressions showed different contributions of meteorological and hydrological variables to individual phytoplankton responses before, during and after typhoons between seasons. The post-typhoon weeks (i.e., within two weeks after a typhoon had passed) were especially important for the timeline of phytoplankton increases and with a detectable seasonal variation that the chlorophyll *a* concentration significantly increased in autumn whereas both primary production and growth rate were associated with significant changes in summer. Additionally, phytoplankton responses during the post-typhoon weeks were significantly different between discrete or continuous types of typhoon events. Our work illustrated the fact that typhoons did influence phytoplankton responses in the subtropical deep freshwater ecosystem and typhoon passages in summer and autumn affected the phytoplankton dynamics differently. Nevertheless, sustained and systematic monitoring in order to advance our understanding of the role of typhoons between seasons in the modulation of phytoplankton productivity and functioning is required because such episodic climatic disturbances are projected to have intense magnitude and inconsistent frequency under 21st century climate change.

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## 1. Introduction

Typhoons, also referred to as tropical cyclones and hurricanes, are episodic climatic activities that are drawing world attention, serve as major forces in the disturbance of ecosystem structures

and functions, and increase the vulnerability of species in a community due to the high winds and heavy rainfall (Brokaw and Walker, 1991; Gardner et al., 2005; Flynn et al., 2010; Mumby et al., 2011; Das, 2012; IPCC, 2013). Worldwide, the highest numbers of major typhoon strikes have been recorded in the Pacific and North Atlantic regions over the past few decades (Giuliani and Peduzzi, 2011), simultaneously leading to large regional economic and ecosystem service losses (Das, 2012; Chiang et al., 2014). Based on current understanding and agreement in the 21st century projections, a decrease or unchanged global frequency of typhoon occurrences will occur concurrently with a likely increase in both global mean typhoon maximum wind speeds and heavy

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precipitation (IPCC, 2013), implying greater potential for ecosystem changes and the need for re-estimates of typhoon-driven ecosystem variation (Tsuchiya et al., 2013).

Phytoplankton are responsible for half of the Earth's biospheric primary production despite representing less than 1% of the photosynthetic biomass (Field et al., 1998), making them important to local and the global ecosystems. They are central to aquatic ecosystems' ecological and biogeochemical services, as they form the foundation of the food web and, in addition, are major drivers in the cycling of elements (Reynolds, 2006). Moreover, phytoplankton are considered a critical regulator of anthropogenic carbon dioxide (CO<sub>2</sub>) emissions under global warming (Raven and Falkowski, 1999; Rivero-Calle et al., 2015). Phytoplankton uptake atmospheric inorganic carbon and export organic carbon to the water interior (a mechanism known as the "biological pump"; Volk and Hoffert, 1985), which lowers the partial pressure of CO<sub>2</sub> in the water column and consequently facilitates the diffusive drawdown of atmospheric CO<sub>2</sub> levels, implying a positive feedback in the climate system. Recent findings further demonstrated that high CO<sub>2</sub> levels encourage the growth of single-cell coccolithophores, a group of tiny phytoplankton, suggesting that the phenomenon of phytoplankton abundance shift might mask global warming (Rivero-Calle et al., 2015). At present, the chlorophyll *a* (chl-*a*) concentration, primary production and growth rate are commonly measured as representations of phytoplankton dynamics, all of which play important roles in the process of material cycle and energy conversion in the aquatic ecological systems as indices of the productivity and trophic condition of fresh, coastal and oceanic waters (Sala et al., 2000).

Many studies have shown that the passage of typhoons cause physical disturbances and restructured stratification, promoting the phytoplankton and resulting in shifts of stoichiometric regulation of the aquatic ecosystem structure. When a typhoon passes over the waters, the recognized combined effects of upwelling and vertical mixing or terrestrial runoff and sediment resuspension supply nutrients to the euphotic layer and contribute significantly to the increase in the phytoplankton biomass and primary production (Zheng and Tang, 2007; Zhao et al., 2008; Hung and Gong, 2011; Lin, 2012; Tseng et al., 2014). A series of typhoons would create a pulse of biologically available nutrients such as phosphorus and nitrogen that could contribute to the different ratios, thereby providing specific species with a competitive advantage (Robarts et al., 1998; Findlay et al., 2001; Huisman et al., 2004; Streckler et al., 2004; Bopp et al., 2005; Tasi et al., 2008; Chen et al., 2009; Winder and Sommer, 2012; Tsuchiya et al., 2013). Moreover, when typhoon-induced water mixing accompanies seasonal forcing, it determines the extent to which aquatic ecosystems are carbon sinks or sources for the atmosphere because additional nutrients and dissolved organic carbon loading push the system towards autotrophy and heterotrophy, respectively (Fasham et al., 1990; Hanson et al., 2004; Tasi et al., 2008). However, typhoon-related studies mainly focus on a single or a few individual cases and/or the effects of a series of typhoon events on ecosystem changes and/or potential damage through remote sensing and image interpretation (Brokaw and Walker, 1991; Gardner et al., 2005; Zheng and Tang, 2007; Hung and Gong, 2011; Mumby et al., 2011; Tsuchiya et al., 2013). As far as our knowledge of the impacts of typhoons on phytoplankton, no studies have used long-term decadal monitoring and an extensive time series of field study tracking to explore the dynamics of aquatic ecosystems subject to disturbances from typhoons. Furthermore, the time lag in biological responses to either seasonal variation or extreme disturbances reflects the time-scale advection (Collos, 1986) that thus necessarily raises the topic of comparisons between phytoplankton responses and variations at the different periods associated with typhoons, e.g. during or after a

typhoon.

In addition, phytoplankton responses to the typhoon forcing also depend on the characteristics of a typhoon itself such as the intensity, translation speed and the level of induced-disturbance. Zhao et al. (2008) reported that a weak, slow-moving typhoon induced a higher phytoplankton biomass, whereas a strong, fast-moving typhoon induced blooms over a larger area in the South China Sea. Ko et al. (2016) found that a strong and long-duration typhoon was not strictly associated with the largest biological changes in a freshwater ecosystem and that no consistent correlations could be observed among phytoplankton biomass, production and turnover in comparison with typhoon disturbance ranking and length of a typhoon stay. However, unlike the impacts of single typhoons on aquatic ecosystems that have been previously evaluated, the ways in which continuous typhoon surges influence phytoplankton responses have not yet been reported and thus their relative effects on phytoplankton blooms remain to be investigated.

Taiwan is situated in the westbound belt of typhoon movement in the northwestern Pacific Ocean. This movement is primarily steered by the Pacific subtropical high-pressure circulation. Over the past decade (2005–2014), 57 typhoons have resulted in alerts being issued to Taiwanese citizens, and therefore, Taiwan has become a well-studied site for typhoon research in the (sub)tropics. The Fei-Tsui Reservoir located in the northern area of Taiwan is a critical water resource that provides water for the Taipei metropolitan and surrounding areas, and anthropogenic activities are limited within the entire watershed, which is covered mostly by secondary subtropical forests. A study of the watershed ecosystem and biogeochemistry of the Fei-Tsui Reservoir has been ongoing since the early 2000s due to the vulnerability of the island freshwater ecosystems to climate change (IPCC, 2013). Unlike areas of open-water ecosystems, in these areas, orographic effects have additionally played a crucial role in determining the climatic conditions and decreasing the transition speed and strength of typhoons in deep freshwater ecosystems (Hsu and Kuo, 2013), which limits wind-induced vertical mixing disturbance of the original stratification of the water column in Fei-Tsui. Therefore, although typhoons could enrich nutrients from entrainment in upstream land areas, prompting a subsurface with a significantly increased nutrient plume in mid-water (Tseng et al., 2010), we hypothesized that the phytoplankton growth in surface water might not be induced by the subsurface typhoon-driven nutrient pump in summer due to strong stratification and limited vertical mixing. In autumn, however, observations of phytoplankton blooms could be possible because of enhanced vertical mixing. Furthermore, according to the equal or even greater phytoplankton blooms resulting from the sustained influence of two or more typhoons in the previous Fei-Tsui study (Ko et al., 2016), we believed that similar results would be also observed in a long-term study.

In this study, we described the effects of 36 typhoons that closely approached the Fei-Tsui in summer and autumn on the changes noted in phytoplankton blooms over a decade. The main objective of this study was to examine the long-term effects of typhoons on seasonal phytoplankton responses, including the chl-*a* concentration, primary production and growth rate before, during and after typhoon disturbances in the subtropical deep freshwater ecosystem using decadal time-series field observations. We also examined how seasonal phytoplankton bloom dynamics would be influenced with typhoon-related meteorological and hydrological environments. We finally identified the characteristics of typhoon disturbance events on the regulation of the dynamics of phytoplankton responses by seasons. This is the first study to explore multiple typhoons and biological interactions continuously and densely for this extended period.

## 2. Materials and methods

A decade (2005–2014) of water sampling was performed weekly (or biweekly due to a limitation of survey boats and the destruction of surrounding areas by typhoons) in the field at the dam site of the Fei-Tsui Reservoir, New Taipei City, Taiwan (24°54'N, 121°34'E) during the summer (June–August) and autumn (September–November) at ten different depths (0, 2, 5, 10, 15, 20, 30, 50, 70 and 90 m). Water samples for phytoplankton and dissolved nutrient supply analyses were collected with a 5 l Go-Flo bottle and stored in 300 ml bottles before noon. The laboratory analysis was performed immediately after sampling.

### 2.1. Determination of phytoplankton responses and dissolved nutrient concentrations

The chl-a concentration, primary production and growth rate were measured as representations of the phytoplankton dynamics in this study. The chl-a samples were filtered through Whatman GF/F filters and extracted with acetone. The chl-a concentration was determined fluorometrically using an *in vitro* fluorometer (TD-700 Laboratory Fluorometer, Turner Designs Inc., Sunnyvale, CA, U.S.A.) according to Parsons et al. (1984). Phytoplankton photosynthesis at each depth was determined via the <sup>14</sup>C assimilation method (Parsons et al., 1984). The assays were incubated under an instantaneous irradiance (artificial light source) of approximately 2000  $\mu\text{E m}^{-2} \text{s}^{-1}$  for 2 h by nine light levels corresponding to 0, 6, 12, 16, 23, 36, 44, 63 and 91% irradiance. After incubation, the samples were filtered through 0.2  $\mu\text{m}$  Millipore filters, decontaminated with 0.5 ml of 0.1 N HCl for 24 h, placed in scintillation vials with a scintillation cocktail (LSC-cocktail liquid, Ultima Cold, Packard BioScience B.V. Inc., Groningen, Netherlands) for an additional 24 h and counted with a liquid scintillation counter (Tri-Carb 2900 TR, PerkinElmer Inc., Waltham, MA, U.S.A.). Representations of primary production per unit time (i.e., photosynthetic rates) normalized to chl-a were constructed based on a photosynthesis-irradiance curve using the methods outlined by Gong et al. (1999). The phytoplankton growth rate was calculated as the primary production per unit chl-a with a phytoplankton carbon to chl-a (C:chl-a) ratio (58 g C g<sup>-1</sup> chl-a; Eppley et al., 1992) transformation.

The concentrations ( $\mu\text{M}$ ) of nitrite ( $\text{NO}_2^-$ ), nitrate ( $\text{NO}_3^-$ ) and phosphate ( $\text{PO}_4^{3-}$ ) were measured to analyze the dissolved inorganic nutrient supply. The samples for determination of the nutrients were first filtered through Whatman GF/F filters; the quantification of these nutrients was based on standard methods employed by Parsons et al. (1984) and modified using flow injection analysis (FIA).

Both the final phytoplankton responses and the nutrient concentrations for each individual week included in the subsequent analyses were integrated vertically from surface to the euphotic zone depth or to the 90 m depth using the trapezoidal rule (Hornbeck, 1975).

### 2.2. Meteorological and hydrological variables

Data on weekly mean local wind speed ( $\text{m s}^{-1}$ ), irradiance ( $\text{cal cm}^{-2}$ ), surface water temperature ( $^{\circ}\text{C}$ ), and weekly total runoff ( $\text{m}^3 \text{s}^{-1}$ ) at the dam site were collected from the Taipei Fei-Tsui Reservoir Administration and the Data Bank for Atmospheric Research, Taiwan (<https://dbar.ttfri.narl.org.tw/>). All weekly values were calculated according to daily values during the 7 day period prior to each sampling. A strong positive correlation existed between the weekly total runoff and weekly total precipitation ( $P < 0.01$ , data not shown). We used the runoff to represent the total water and nutrient input.

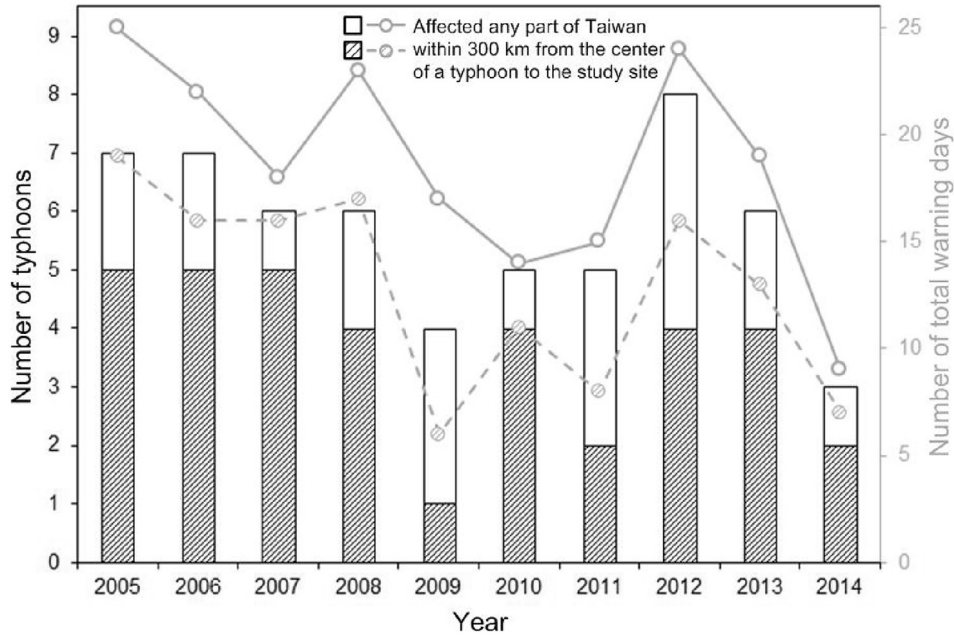
### 2.3. Typhoon records

Typhoon records were compiled from the Central Weather Bureau of Taiwan (<http://www.cwb.gov.tw/V7/>). A total of 36 typhoons (more than 63% of all recorded typhoons, i.e., 57, affecting Taiwan) that approached our study reservoir during the past decade had a <300 km distance from the center of the typhoon to the Fei-Tsui Reservoir (during the period between the first and last warnings issued by the Central Weather Bureau of Taiwan; Fig. 1, Table S1). The annual frequency of typhoons affecting the study site and surrounding areas showed a range of variability from 1 to 5, with a decadal average of 3.6 typhoons year<sup>-1</sup>; the number of total warning days was 6–19 days year<sup>-1</sup>. Of these typhoons, nine were intensity grade 3 typhoons (the maximum sustained wind speed near the center  $\geq 51.0 \text{ m s}^{-1}$ ), 15 were intensity grade 2 (32.7–50.9  $\text{m s}^{-1}$ ) and 12 were intensity grade 1 (17.2–32.6  $\text{m s}^{-1}$ ). The 2012 typhoon Tembin showed prolonged effects (i.e., warning days) that lasted for more than one week among these typhoons.

### 2.4. Statistical analyses

To explore changes of phytoplankton responses through time, we first categorized the sampling data into three groups: pre-typhoon, typhoon and post-typhoon weeks. The samples from the weeks before the first typhoon approached every year ( $N = 59$ ) were used to represent the phytoplankton responses during the pre-typhoon period as baseline values. When any day(s) of the warning periods of individual typhoons was(were) within the 7 day period prior to sampling, we regarded the samples ( $N = 41$ ) as the phytoplankton responses of the typhoon weeks, which therefore resulted in slightly different numbers between typhoons and so-called typhoon weeks in the study. Those samples ( $N = 37$ ) collected within 2 weeks (due to the weekly or biweekly sampling limitation) after the typhoon weeks were used to represent the post-typhoon period. We then compared the changes occurring before, during and after the typhoons. Nonparametric statistical comparisons for phytoplankton responses and environmental changes (including nutrient supply and meteorological and hydrological variables) were conducted using the Kruskal-Wallis test and Mann-Whitney  $U$  test to detect whether medians among pre-typhoon, typhoon and post-typhoon weeks and between any two of the aforementioned weeks, respectively, are different. The Pearson correlation test was applied to assess the quantitative relations between phytoplankton responses and environmental variables. Multivariate linear regression models using stepwise backward elimination were built to quantify the mechanisms of how phytoplankton responses are associated with the environments. The contribution of environmental variables was determined by model selection based on Akaike's information criterion (AIC). The model with the lowest AIC score ( $\text{AIC}_{\min}$ ) and models with AIC differences ( $\Delta\text{AIC} = \text{AIC}_i - \text{AIC}_{\min}$  for model  $i$ ) less than 2 ( $\Delta\text{AIC} \leq 2$ ) were considered to be the best-supported models (Burnham and Anderson, 2002). The environmental variables were  $\log_{10}$  transformed as needed to fulfill the assumptions of normality and homogeneity of variance.

To further analyze the effects of different characteristics of the typhoon disturbances, individual typhoon events were classified into categories: discrete and continuous. A discrete typhoon event was at least one month apart from the last warning date of the previous typhoon event, whereas a continuous typhoon event approached the study site within one month after the previous typhoon passed. The Kruskal-Wallis test and Mann-Whitney  $U$  test was also used to compare two types of typhoon disturbances between seasons. To quantify the mechanisms and impacts of the different types of typhoon disturbances, we additionally conducted



**Fig. 1.** The number of typhoons and total warning days affecting any part of Taiwan (open circle and bar) and within 300 km from the center of a typhoon to the subtropical deep freshwater ecosystem of the Fei-Tsui Reservoir (slash-pattern circle and bar) for the period from 2005 to 2014.

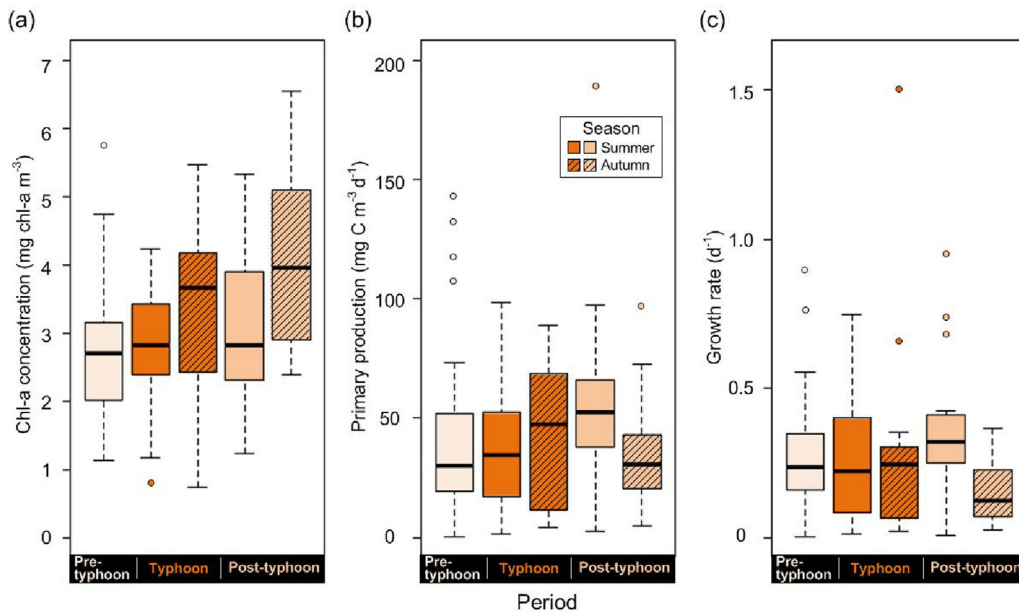
a relationship analysis to assess the typhoon event variability of the typhoon-related property values, including typhoon intensity, numbers of warning days and the typhoon-disturbance index (see detailed calculations in Table S1), grouped by season and typhoon type in this study. The typhoon-related property values for a discrete typhoon event were based on its original records while those values intended to represent a continuous typhoon event were the sum of the values from the current and previous typhoon events. Notably, we here only included the effects caused by two typhoons continuously visiting the study site. If three typhoons had approached within a short time frame, we did not consider the potential effects of the first typhoon on the third one. All statistical

analyses were conducted with R 3.0.2 for Windows (R Core Team, 2014).

**3. Results**

*3.1. Phytoplankton dynamics before, during and after typhoons between summer and autumn*

Phytoplankton exposed to typhoons generally showed an increasing trend before, during and after typhoons in summer but not in autumn (Fig. 2). Before typhoon disturbances (i.e., the pre-typhoon weeks), the weekly decadal median euphotic depth-



**Fig. 2.** Box plots of phytoplankton responses, including the chlorophyll *a* (chl-*a*) concentration (a), primary production (b) and growth rate (c), during the pre-typhoon, typhoon and post-typhoon weeks in the summer and autumn seasons in the subtropical deep freshwater ecosystem of the Fei-Tsui Reservoir for the period from 2005 to 2014. The boxes represent the 25th and 75th percentiles, the lines inside the boxes are the medians, the whiskers represent values within the 1.5 interquartile range of the 25th and 75th percentiles, and the circles represent outliers.

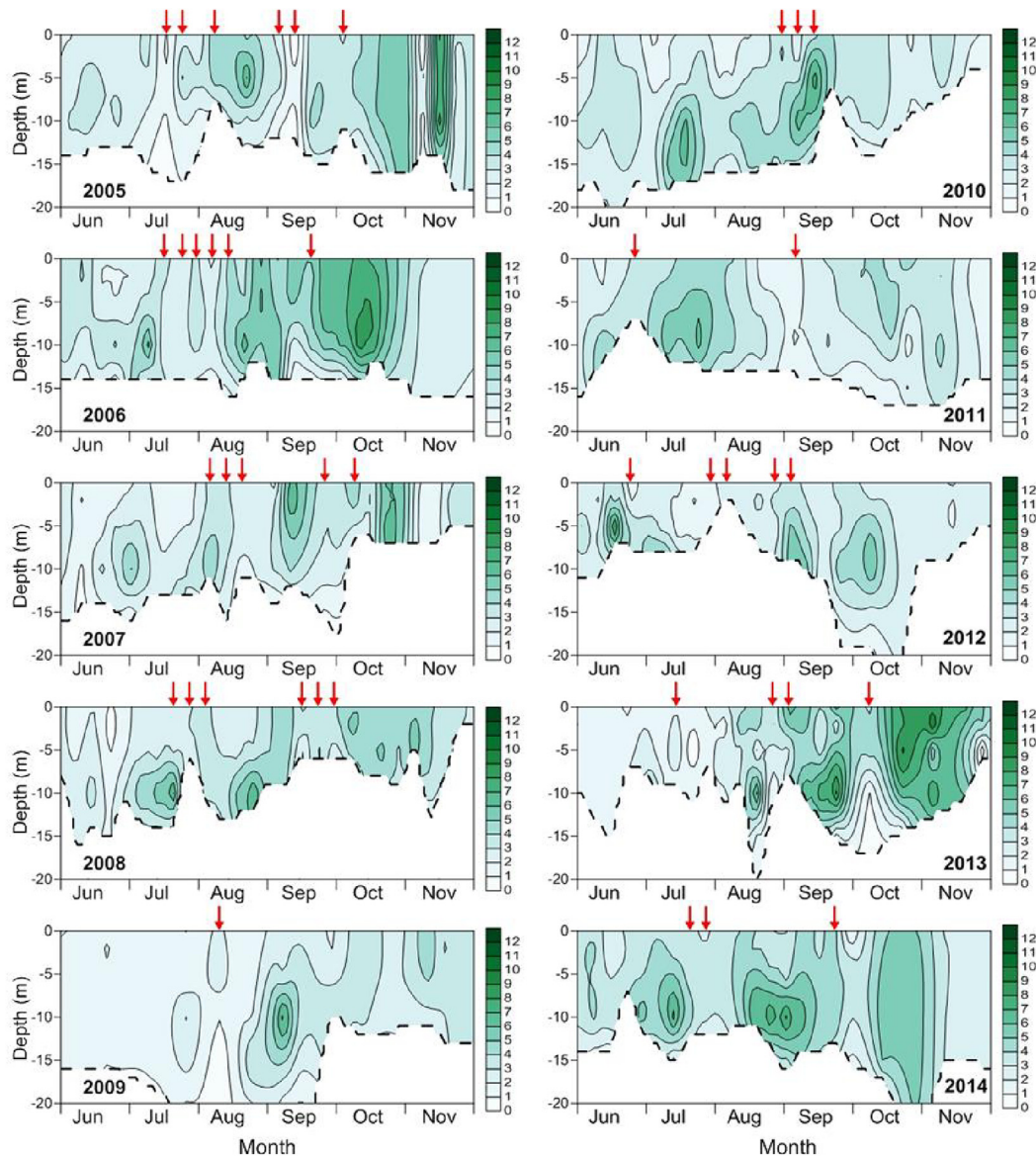


averaged chl-a concentration, primary production and growth rate were  $2.71 \text{ mg chl-a m}^{-3}$ ,  $30.19 \text{ mg C m}^{-3} \text{ d}^{-1}$  and  $0.24 \text{ d}^{-1}$ , respectively. In summer, no significant differences were observed in the chl-a concentrations among the pre-typhoon, typhoon (median  $2.82 \text{ mg chl-a m}^{-3}$ ) and post-typhoon (median  $2.81 \text{ mg chl-a m}^{-3}$ ) weeks (Fig. 2a,  $P > 0.05$ ), whereas the primary production and growth rate showed significant differences among weeks (both  $P < 0.05$ ). Both primary production and the growth rate remained constant when the typhoons approached, with medians of  $34.55 \text{ mg C m}^{-3} \text{ d}^{-1}$  and  $0.22 \text{ d}^{-1}$ , respectively, but significantly increased after typhoons (medians  $52.52 \text{ mg C m}^{-3} \text{ day}^{-1}$  and  $0.32 \text{ d}^{-1}$ , respectively; Fig. 2b and c, both  $P < 0.05$ ). In autumn, there was a significant difference in the medians of chl-a concentration among weeks ( $P < 0.01$ ). A significant increase of approximately 1.4-fold in the chl-a concentration was observed during and after typhoons (medians  $3.66$  and  $3.80 \text{ mg chl-a m}^{-3}$ , respectively; Fig. 2a, both  $P < 0.05$ ) compared with the pre-typhoon weeks, whereas the primary production and growth rate were

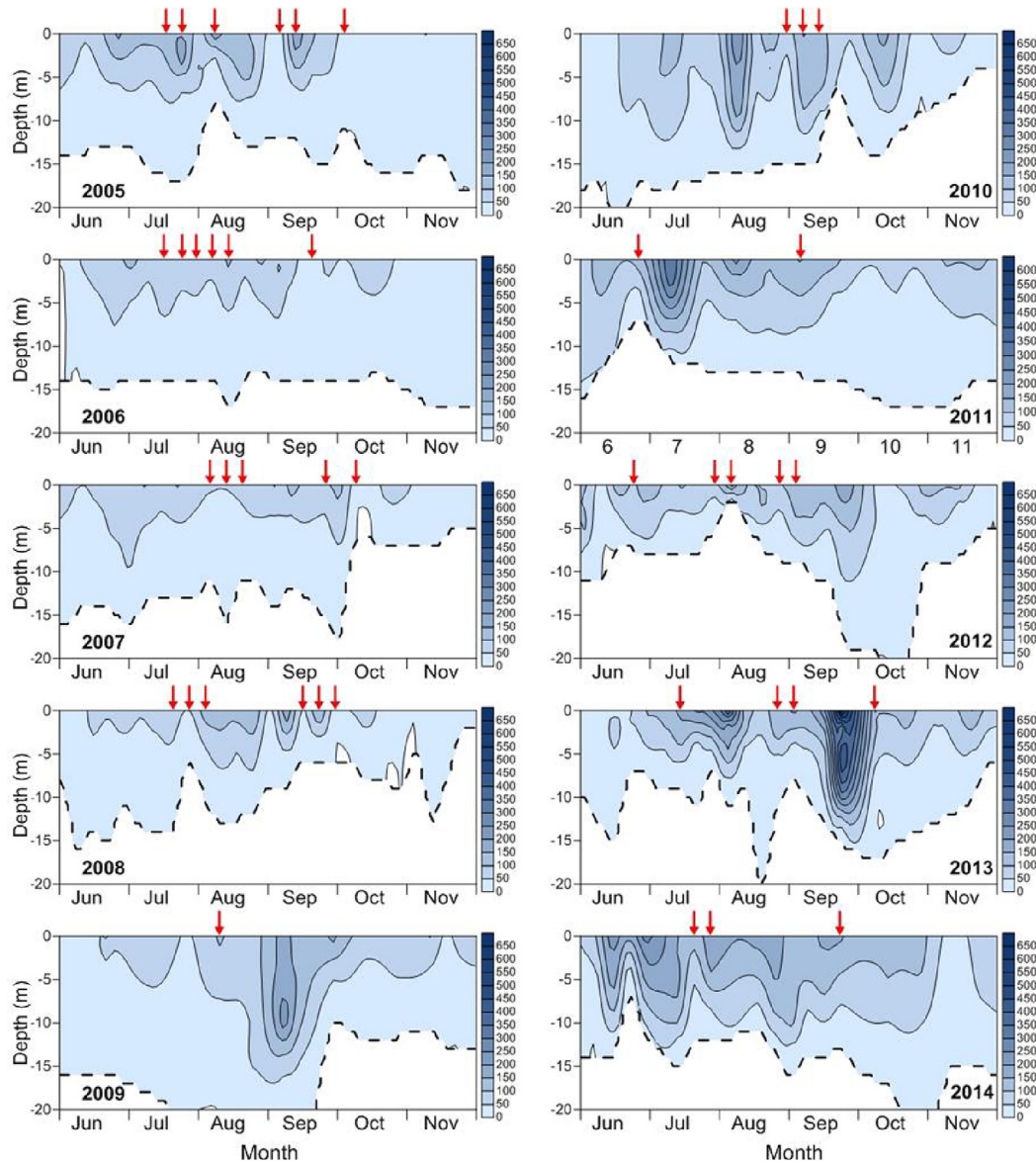
associated with no significant changes in the different weeks (medians of primary production and growth rate during and after typhoons:  $47.68$  and  $32.07 \text{ mg C m}^{-3} \text{ day}^{-1}$  and  $0.24$  and  $0.12 \text{ d}^{-1}$ , respectively; Fig. 2b and c,  $P > 0.05$ ).

The vertical profiles of chl-a concentration revealed that great subsurface plumes occasionally occurred at depths of 10 m but occurred at shallower depths ( $\leq 5 \text{ m}$ ) with typhoons (Fig. 3). A more uniform gradient of the chl-a concentration was observed in most typhoon weeks. The primary production and growth rate were usually higher in the surface and decreased with depth (Figs. 4 and 5).

The intensity of both observed local wind speed and total runoff was found to vary considerably and was significantly different between the pre-typhoon and typhoon weeks in both the summer and autumn seasons (Table 1). The local wind speed was persistently significantly higher after typhoons than before typhoons in the two seasons. Two extremes occurred (Table S1): the first in 2008 (typhoon Sinlaku with 6 warning days, a total runoff of



**Fig. 3.** Chlorophyll *a* concentration ( $\text{mg chl-a m}^{-3}$ ) profiles in the summer and autumn seasons for the period from 2005 to 2014. All panels are in the same color scale. Dashed lines indicate the euphotic depth. Red arrows indicate the weeks in which a typhoon occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



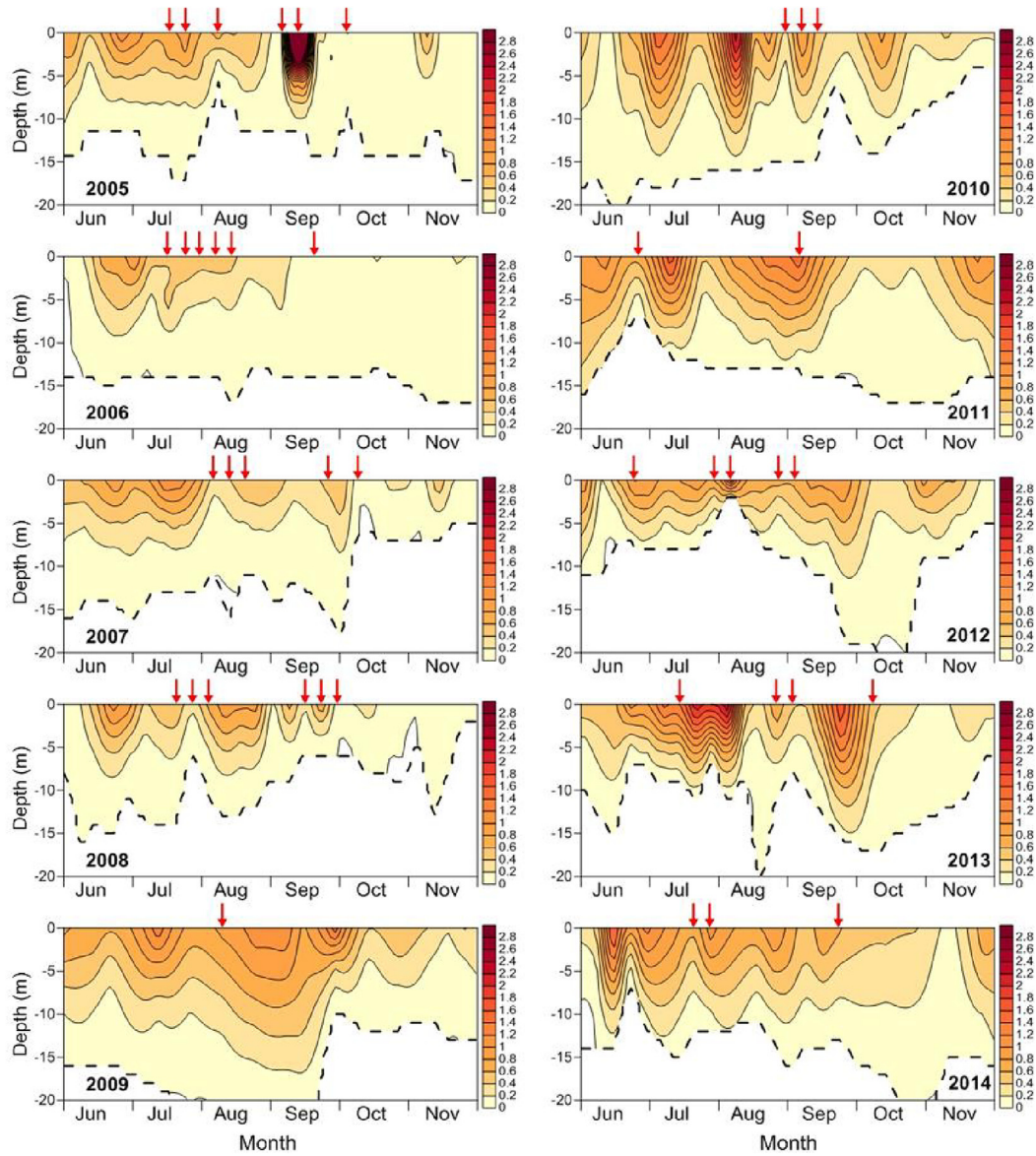
**Fig. 4.** Primary production ( $\text{mg C m}^{-3} \text{d}^{-1}$ ) profiles in the summer and autumn seasons for the period from 2005 to 2014. All panels are in the same color scale. Dashed lines indicate the euphotic depth. Red arrows indicate the weeks in which a typhoon occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$786.3 \text{ m}^3 \text{ s}^{-1}$  and a level of disturbance of 154.18) and the second in 2012 (typhoon Saola with 5 warning days, a total runoff of  $728.4 \text{ m}^3 \text{ s}^{-1}$  and a highest level of disturbance of 191.68). In contrast, the 2010 typhoon Meranti induced the lowest total runoff ( $8.1 \text{ m}^3 \text{ s}^{-1}$ ) over the 2 warning days. Moreover, the observed local wind speeds were much lower than the maximum sustained wind typhoon speeds, suggesting that the mountains surrounding the Fei-Tsui Reservoir might reduce typhoon-induced forces as a natural barrier. The majority of the nutrient supply variables were not significantly different between the pre-typhoon and typhoon weeks and between the pre-typhoon and post-typhoon weeks except for the typhoon-week euphotic depth-averaged  $\text{NO}_3^-$  concentration and the typhoon-week euphotic depth-averaged  $\text{NO}_2^-$  concentration in summer and in autumn, respectively (both  $P < 0.05$ ), implying that rapid consumption of nutrients (especially phosphate) might be occurring in the system.

The correlation and multivariate regression analyses showed the relative contributions of the different environmental variables

to the observed phytoplankton variability in the subtropical Fei-Tsui Reservoir deep freshwater ecosystem (Table 2, Table 3 and Table S2). The Pearson correlation matrix between these variables and the phytoplankton responses was provided in Table 2. Unlike the primary production and growth rate, which were significantly negatively correlated with the euphotic depth-averaged  $\text{NO}_3^-$  concentration ( $r = -0.282$  and  $-0.298$ , respectively; both  $P < 0.05$ ) and significantly positively correlated with irradiance and surface water temperature (all  $r > 0.3$  and  $P < 0.05$ ), the chl-a concentrations showed no correlation with any individual environmental variables before the typhoons. These results implied that the physical and chemical environments might not individually explain the phytoplankton biomass variability in this deep freshwater ecosystem. However, the chl-a concentrations were significantly positively correlated with the euphotic depth-averaged  $\text{NO}_2^-$  concentration when typhoons approached in summer, whereas the primary production and growth rate were significantly positively correlated with the total runoff. After typhoons, irradiance showed a





**Fig. 5.** Phytoplankton growth rate ( $d^{-1}$ ) profiles in the summer and autumn seasons for the period from 2005 to 2014. All panels are in the same color scale. Dashed lines indicate the euphotic depth. Red arrows indicate the weeks in which a typhoon occurred. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significantly negative effect on the chl-a concentrations but showed a significantly positive effect on the growth rate. In autumn, no significant correlations were observed between the variables and the chl-a concentrations and growth rate during the typhoon

weeks, whereas high correlations were found between the variables and primary production (all  $r > 0.4$ ). Overall, irradiance and surface water temperature were the two key variables driving the observed changes in phytoplankton responses during the post-

**Table 1**

Mean (standard deviation) of environmental variables measured before, during and after typhoons in the summer and autumn seasons from 2005 to 2014. The asterisks indicate significant differences between the pre-typhoon weeks and the typhoon or post-typhoon weeks (\* $P < 0.05$ ; \*\* $P < 0.01$ ).

Week	Pre-typhoon	Typhoon		Post-typhoon	
		Summer	Autumn	Summer	Autumn
Environmental variable/Season					
Euphotic depth-averaged $NO_2^-$	0.270 (0.171)	0.334 (0.307)	0.193 (0.093)*	0.516 (0.769)	0.234 (0.121)
Euphotic depth-averaged $NO_3^-$	25.165 (10.468)	21.085 (11.230)*	25.573 (11.255)	21.656 (10.929)	24.291 (11.993)
Euphotic depth-averaged $PO_4^{3-}$	0.027 (0.025)	0.027 (0.024)	0.023 (0.017)	0.019 (0.020)	0.025 (0.024)
90 m-depth integrated $PO_4^{3-}$	2.836 (2.438)	2.842 (2.588)	4.308 (2.925)	2.660 (1.517)	3.555 (2.938)
Local wind speed	0.803 (0.348)	1.406 (0.567)**	1.585 (0.561)**	1.066 (0.495)*	1.293 (0.687)**
Irradiance	375.248 (126.139)	364.059 (173.373)	326.440 (147.138)	424.202 (102.745)	348.776 (150.579)
Surface water temperature	26.727 (1.862)	27.306 (0.818)	26.115 (1.451)	27.665 (0.995)	24.999 (2.521)**
Total runoff	193.789 (212.654)	466.198 (527.420)**	748.658 (801.095)**	126.259 (93.586)	260.810 (192.878)

**Table 2**

Pearson correlation coefficients among the chlorophyll *a* concentration, primary production and growth rate before, during and after typhoons in the summer and autumn seasons from 2005 to 2014. The asterisks indicate significant correlations between the phytoplankton responses and variables (\* $P < 0.05$ ; \*\* $P < 0.01$ ).

Week Environmental variable/Season	Pre-typhoon	Typhoon		Post-typhoon	
		Summer	Autumn	Summer	Autumn
<b>Chlorophyll <i>a</i> concentration</b>					
Euphotic depth-averaged NO <sub>2</sub> <sup>-</sup>	-0.098	0.422*	-0.042	0.660*	-0.045
Euphotic depth-averaged NO <sub>3</sub> <sup>-</sup>	-0.115	0.052	-0.420	-0.026	0.197
Euphotic depth-averaged PO <sub>4</sub> <sup>3-</sup>	-0.088	-0.086	-0.310	-0.121	-0.074
90 m depth-integrated PO <sub>4</sub> <sup>3-</sup>	0.011	-0.038	-0.308	-0.341	0.192
Local wind speed	-0.086	0.031	0.010	-0.276	-0.078
Irradiance	0.032	0.143	0.181	-0.623*	-0.263
Surface water temperature	0.058	0.038	0.440	-0.220	-0.530*
Total runoff	0.255	-0.322	-0.250	0.243	-0.381
<b>Primary production</b>					
Euphotic depth-averaged NO <sub>2</sub> <sup>-</sup>	-0.142	-0.206	-0.599*	-0.398	-0.249
Euphotic depth-averaged NO <sub>3</sub> <sup>-</sup>	-0.282*	0.219	-0.559*	-0.061	-0.372
Euphotic depth-averaged PO <sub>4</sub> <sup>3-</sup>	-0.129	-0.291	-0.401	-0.248	-0.418
90 m depth-integrated PO <sub>4</sub> <sup>3-</sup>	-0.107	-0.066	-0.613*	-0.104	-0.481
Local wind speed	-0.021	-0.251	-0.406	0.204	0.137
Irradiance	0.507**	0.348	0.694**	0.503	0.592**
Surface water temperature	0.321*	-0.367	0.554*	0.171	0.454*
Total runoff	0.054	0.450*	-0.727**	-0.255	-0.521*
<b>Growth rate</b>					
Euphotic depth-averaged NO <sub>2</sub> <sup>-</sup>	-0.094	-0.324	-0.494	-0.512	-0.234
Euphotic depth-averaged NO <sub>3</sub> <sup>-</sup>	-0.298*	0.233	-0.395	-0.172	-0.450
Euphotic depth-averaged PO <sub>4</sub> <sup>3-</sup>	-0.116	-0.252	-0.099	-0.152	-0.395
90 m depth-integrated PO <sub>4</sub> <sup>3-</sup>	-0.152	-0.120	-0.497	0.233	-0.567*
Local wind speed	0.081	-0.242	-0.321	0.260	0.230
Irradiance	0.511**	0.194	0.361	0.633*	0.563*
Surface water temperature	0.314*	-0.307	0.080	0.252	0.631**
Total runoff	-0.076	0.574**	-0.380	-0.479	-0.355

typhoon weeks. The multivariate regression models providing the best fit to the phytoplankton responses over different weeks between seasons were listed in Table 3 and Table S2. During and after typhoons, the combined effects of the environmental variables could explain at least 42% of the variation in changes of individual phytoplankton responses. The euphotic depth-averaged PO<sub>4</sub><sup>3-</sup> concentration variable appeared most frequently in the best models.

### 3.2. Impacts of typhoon types

The aforementioned observations showed that the post-typhoon weeks were important for the timeline of phytoplankton blooms following disturbances. We therefore analyzed the effects of discrete and continuous typhoon events over the past decade using the data collected after the typhoons.

Significant differences were observed in all phytoplankton responses among seasons and typhoon types (Kruskal-Wallis one-way ANOVA  $P = 0.048, 0.045$  and  $0.0012$  on the chl-*a* concentration, primary production and growth rate, respectively). Among comparisons, the phytoplankton responses induced by the discrete typhoon events in summer were significantly different (Fig. 6). Lower chl-*a* concentrations in summer and slightly higher chl-*a* concentrations in autumn were observed after the discrete typhoon events compared to the continuous typhoon events. In contrast, the primary production and growth rate were higher for the discrete typhoon events than for the continuous typhoon events in summer but lower in autumn.

Because phytoplankton responses for the continuous typhoon events were not different but those for the discrete typhoon events were different between the summer and autumn seasons (see Fig. 6), the data available for the continuous typhoon events was combined whereas only summer-discrete typhoon events were used when estimating correlations between phytoplankton responses and typhoon-related property values. For the type of

summer-discrete typhoons, the phytoplankton responses were generally negatively correlated with typhoon intensity and length of typhoon warning days, except for the growth rate versus typhoon intensity (Fig. 7a–f), showing that minor and shorter discrete typhoon events produced stronger effects on phytoplankton biomass and production. However, for the continuous typhoon events, the accumulated typhoon intensity and accumulated number of warning days showed significant variability in relation to three phytoplankton responses (Fig. 7a–f). The chl-*a* concentrations showed an inverse bell phenomenon that reached the lowest values when the level of accumulated typhoon intensity was 4–5 and the accumulated number of warning days was 7–8. In contrast, a bell-shaped relationship was produced by the continuous typhoon events in the growth rate. Primary production was negatively correlated with the accumulated typhoon intensity but positively correlated with the accumulated numbers of typhoon warning days, suggesting that high phytoplankton production was supported by smaller and longer lasting typhoon events. There were no significant relationships observed between the (accumulated) typhoon disturbances and phytoplankton responses (Fig. 7g–i).

## 4. Discussion

For the weekly, time-series, field observations of phytoplankton responses collected over a decade, the measured typhoon characteristics (i.e., intensity, number of warning days and disturbance index) and the phytoplankton changes suggested that typhoons played an integral role in the dynamics and ecology of the subtropical deep freshwater ecosystem of the Fei-Tsui Reservoir. The typhoon effects showed a seasonal difference although only changes of the chl-*a* concentrations agreed with our hypothesis, increasing more in autumn than in summer. Instead the primary production and growth rate changed less in autumn, especially after the typhoons. In this study, the lowest phytoplankton



**Table 3**  
Multivariate regression analysis using Akaike Information Criteria (AIC) to assess variables that may explain phytoplankton response patterns. A positive estimate for a model variable indicates a positive correlation between the phytoplankton responses and that model variable, whereas a negative estimate indicates a negative correlation between the phytoplankton responses and that model variable. The asterisks indicate significant correlations between the phytoplankton responses and the variable (\* $P < 0.05$ ; \*\* $P < 0.01$ ).

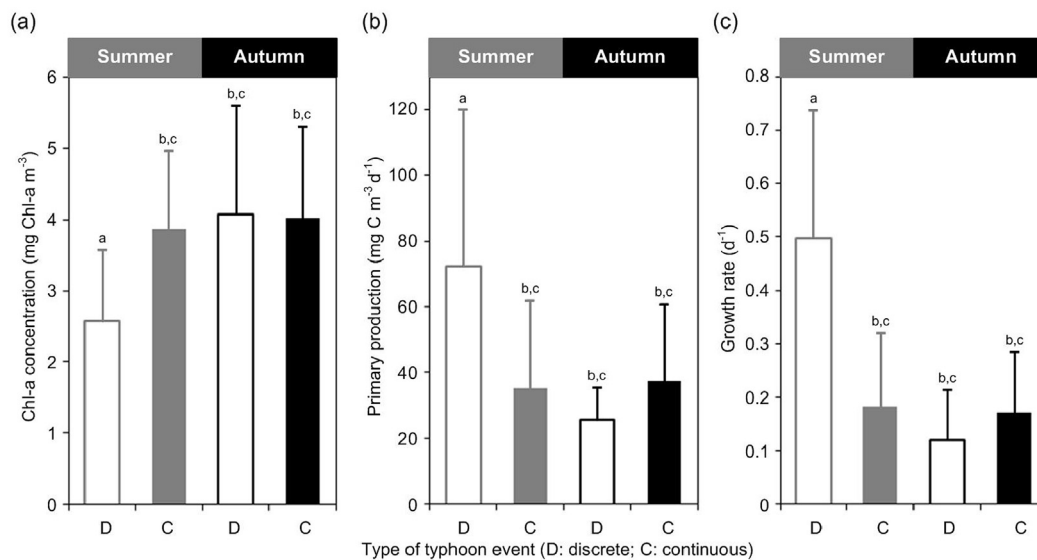
Phytoplankton response	Week	Season	Model (estimate)	AIC	R <sup>2</sup>
Chlorophyll <i>a</i> concentration	Pre-typhoon		$\text{NO}_2^-(-0.50)+\log_{10}\text{NO}_3^-(1.30)+\text{PO}_4^{3-}(-9.51)+\text{sPO}_4^{3-}(0.07)+\text{WS}(-0.45)+\text{T}(0.09)+\log_{10}\text{R}(1.21^{**})$	119.60	0.32
	Typhoon	Summer	$\text{NO}_2^-(1.25^{**})+\log_{10}\text{NO}_3^-(1.28^*)+\text{PO}_4^{3-}(-2.32)+\log_{10}\text{R}(-0.84^{**})$	28.54	0.63
		Autumn	$\text{NO}_2^-(12.66^*)+\log_{10}\text{NO}_3^-(8.37)+\text{PO}_4^{3-}(-78.81)+\text{sPO}_4^{3-}(0.63)+\text{WS}(0.88)+\log_{10}\text{I}(5.68)+\text{T}(-1.47)$	24.42	0.86
	Post-typhoon	Summer	$\text{NO}_2^-(1.38^*)+\text{PO}_4^{3-}(-31.25^*)+\text{WS}(-1.07^*)+\log_{10}\text{I}(6.57)+\text{T}(-0.41)+\log_{10}\text{R}(1.54^{**})$	18.44	0.94
Autumn		$\text{PO}_4^{3-}(-25.67)+\text{sPO}_4^{3-}(0.02)+\text{WS}(1.51)+\log_{10}\text{I}(-0.59)+\text{T}(-0.53^*)+\log_{10}\text{R}(-1.53^*)$	37.79	0.84	
Primary production	Pre-typhoon		$\text{NO}_2^-(-0.18)+\log_{10}\text{NO}_3^-(0.82^{**})+\text{PO}_4^{3-}(-5.38)+\text{sPO}_4^{3-}(0.06)+\log_{10}\text{I}(0.74^{**})+\log_{10}\text{R}(0.23^*)$	15.12	0.40
	Typhoon	Summer	$\log_{10}\text{NO}_3^-(0.82^*)+\text{PO}_4^{3-}(0.43)+\text{WS}(-0.36^*)+\log_{10}\text{I}(1.24^*)+\log_{10}\text{R}(0.50^*)$	19.89	0.75
		Autumn	$\text{NO}_2^-(-1.34)+\log_{10}\text{I}(0.76^*)+\log_{10}\text{R}(-0.39^*)$	6.64	0.79
	Post-typhoon	Summer	$\log_{10}\text{NO}_3^-(0.60^{**})+\text{PO}_4^{3-}(-30.66^{**})+\text{sPO}_4^{3-}(0.15^{**})+\text{WS}(-0.34^{**})+\log_{10}\text{I}(2.27^{**})$	-22.00	0.98
Autumn		$\text{NO}_2^-(-0.62)+\log_{10}\text{NO}_3^-(0.44)+\text{PO}_4^{3-}(-9.87)+\text{sPO}_4^{3-}(0.07)+\log_{10}\text{I}(0.20)+\log_{10}\text{R}(-0.42^*)$	-3.70	0.88	
Growth rate	Pre-typhoon		$\log_{10}\text{NO}_3^-(0.38^*)+\text{PO}_4^{3-}(-1.62)+\log_{10}\text{I}(0.31^*)$	-39.52	0.25
	Typhoon	Summer	$\log_{10}\text{NO}_3^-(0.45^*)+\text{PO}_4^{3-}(-2.59)+\log_{10}\text{I}(0.97^{**})+\text{T}(-0.24^{**})+\log_{10}\text{R}(0.19^*)$	-15.25	0.75
		Autumn	$\text{NO}_2^-(-0.74)+\text{PO}_4^{3-}(1.72)+\text{WS}(-0.16^*)+\log_{10}\text{I}(0.29)$	-11.57	0.66
	Post-typhoon	Summer	$\log_{10}\text{NO}_3^-(0.11)+\text{PO}_4^{3-}(-11.15)+\text{sPO}_4^{3-}(0.08^*)+\log_{10}\text{I}(0.40)+\log_{10}\text{R}(-0.46^{**})$	-9.91	0.89
Autumn		$\log_{10}\text{NO}_3^-(0.20)+\text{PO}_4^{3-}(1.44)+\log_{10}\text{I}(0.29)$	-27.42	0.42	

Abbreviation:  $\text{NO}_2^-$ , euphotic depth-averaged  $\text{NO}_2^-$ ;  $\text{NO}_3^-$ , euphotic depth-averaged  $\text{NO}_3^-$ ;  $\text{PO}_4^{3-}$ , euphotic depth-averaged  $\text{PO}_4^{3-}$ ;  $\text{sPO}_4^{3-}$ , 90 m depth-integrated  $\text{PO}_4^{3-}$ ; WS, local wind speed; I, irradiance; T, surface water temperature; R, total runoff.

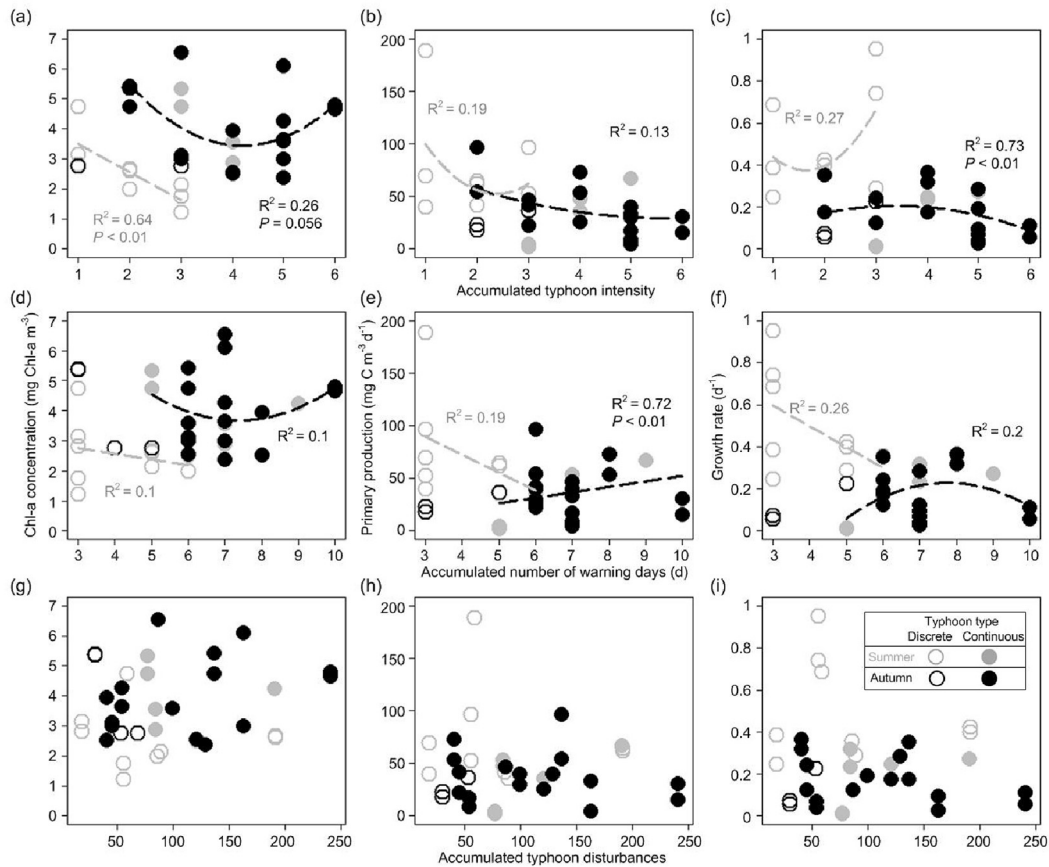
responses primarily occurred in the weeks before typhoons, except for the growth rate. In summer, the highest values for the integrated chl-*a* concentrations, primary production and growth rate were all observed in the weeks after the typhoons. In autumn, the highest values for the integrated chl-*a* concentrations were still obtained in the weeks after the typhoons, but not even a slight decrease occurred in the primary production and growth rate. Overall, the post-typhoon weeks demonstrated the importance of the timeline of a disturbance on the ability of the phytoplankton blooms to absorb, resist or persist (maintain). Notably, only the closer strikes by typhoons experienced by northern Taiwan were examined here; thus, the actual total impacts of typhoon disturbances on phytoplankton are probably greater. Global climate models project an increase in extreme meteorological events and a change in their timing (IPCC, 2013), whereas regional climate models project a lower frequency of the typhoon pattern but strong wind and heavy precipitation in the future (Lin and Chan, 2015). In

both of these models, typhoon disturbances would lead to strong altered availability of resources in freshwater ecosystems that would direct the spatial and temporal dynamics of the phytoplankton. These responses would lead to unusual behavior of the phytoplankton community that contradicts the expectations under climatic change.

A decoupling of trends in the integrated chl-*a* concentrations, primary production and growth rate during the pre-typhoon, typhoon and post-typhoon weeks between summer and autumn could result from both pronounced effects of light limitation on phytoplankton succession and tight predator-prey forcing (i.e., grazing), which has been suggested by several studies to be the key factors regulating the variations in phytoplankton (Marra and Barber, 2005; Behrenfeld, 2010; Winder and Sommer, 2012; Chen et al., 2013). When disturbances occur (i.e., a typhoon or winter surface cooling), the surface water within the euphotic zone experiences natural dilution. In summer, grazer biomass and the



**Fig. 6.** Decadal mean ( $\pm$ SD) of the chlorophyll *a* (chl-*a*) concentration (a), primary production (b) and growth rate (c) in relation to discrete and continuous typhoon events during the post-typhoon weeks in the summer and autumn seasons for the period from 2005 to 2014. Columns bearing the same letter are not significantly different (Dunn post hoc comparison test,  $P < 0.05$ ).



**Fig. 7.** Scatter plots of the chlorophyll *a* concentration, primary production and growth rate in relation to the accumulated typhoon intensity (a–c), accumulated number of warning days (d–f), and accumulated typhoon disturbances (g–i) during the post-typhoon weeks in the summer and autumn seasons for the period from 2005 to 2014. Regression lines (dashed lines), values of regression ( $R^2$ ) and significant  $P$ -values shown in the figures were calculated based on values for the discrete typhoon events in summer (gray) and the continuous typhoon events (black) in summer and autumn.

impacts of grazing on phytoplankton increase; consequently, an accumulation of the phytoplankton biomass does not occur, although the production and growth rate of the phytoplankton become positive. Conversely, with the limitation of less irradiance in autumn, the primary production and growth rate do not increase but phytoplankton biomass (i.e., chl-*a* concentrations) accumulates synchronously with the low grazing pressure.

Terrestrial areas of upstream catchments are always important suppliers of nutrients and affect the quantity and quality of the dissolved matter in the watersheds (Fellman et al., 2009; Williams et al., 2010). Typhoons result in fluctuations in the dissolved ion concentrations in freshwater water on a weekly scale and exhibit high variability (Chang et al., 2013; Ko et al., 2016). The dissolved nutrient contents delivered through the water current with the force of physical and vertical mixing often stimulate biological cycles such as phytoplankton blooms. According to our decadal field observations and the results of Tseng et al. (2010), typhoon-induced dissolved nutrient concentrations were greatly increased at depths >50 m in deep water. Without the combined impact of strong winds and the vertical mixing disturbance of the original stratification of the water column, we found that a phytoplankton bloom could not be induced even under intense typhoon disturbances. Unlike many studies reporting phytoplankton blooms induced by typhoons in nearshore and offshore regions and shallow lakes (Shiah et al., 2000; Lin et al., 2003; Zheng and Tang, 2007; James et al., 2008; Ding et al., 2012; Lin, 2012), our study suggested that nutrient enrichment due to wind-driven mixing and rainwater-

supplied terrestrial runoff is critical for phytoplankton growth in the deep freshwater ecosystem; furthermore, these induced actions must occur simultaneously. We also suggested that our observed phytoplankton blooms were in fact induced by the dissolved nutrients that were directly contributed from the surrounding land areas of the dam site, which were immediately consumed by organisms in this system. Thus, almost no changes in the dissolved nutrients were observed among the three typhoon-associated periods.

Interestingly, our data indicated that discrete typhoon disturbances in summer highly contributed to the strong enhancement of phytoplankton primary production and growth rate. Unlike the simulations of typhoon–ocean interactions (Bender et al., 1993) and analyses of short-term typhoon effects (Ko et al., 2016) showing that a moderate disturbance and slow-moving typhoon had the strongest effects on phytoplankton blooms, typhoons with low intensity grade and few warning days appeared to highly impact phytoplankton blooms in the long-term observations. Although continuous typhoon disturbances might damage the ecosystem, the phytoplankton increased in biomass when exposed to a typhoon of longer duration and greater intensity, potentially due to the more abundant nutrient intake. Additionally, many studies have reported that climatic disturbances, such as typhoons and global warming, provide a species-specific competitive advantage in a disturbed environment (Robarts et al., 1998; Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004; Bopp et al., 2005; Winder and Sommer, 2012; Tsuchiya et al., 2013). For example, the

nitro-fixing cyanobacteria *Anabaena* was triggered in biological conditions of low nitrogen availability relative to phosphorus in Lake Biwa after a series of typhoons (Robarts et al., 1998). Buoyant species and flagellates are threatened in an environment where turbulence is not present to resuspend the planktonic species that have relatively low net sinking velocities, but these plankton are also highly motile and capable of selecting an environment with appreciable light and nutrients in the water column (Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004). These shifts in species compositions and size structures can have cascading ecosystem effects and consequently alter important ecosystem functions, including biogeochemical cycling and energy transfer through the food web (Winder and Sommer, 2012). The complex phytoplankton community differences that exist between discrete and continuous typhoon disturbances require further investigation.

Because successful short-term control is not capable of ensuring the long-term maturation of the ecosystem, long-term observations and ecological science experiments substantially contribute to our basic knowledge of ecological interactions and our ability to forecast change, test ecological theories and ensure the Earth's future. Moreover, these studies provide valuable perspectives and help solve many of the crucial environmental problems faced by society today (Müller et al., 2010; Robertson et al., 2012). We found different levels of significance in the correlations and contributions of environments to phytoplankton changes between the 2-year (i.e., short-term; Ko et al., 2016) and 10-year (i.e., long-term; this study) observations. For example, the dissolved nutrients, nitrogen and phosphorus, showed important long-term and short-term effects on individuals as well as separate successive and cumulative environmental changes in the phytoplankton responses. In specific typhoon-related periods and/or seasons (e.g., the typhoon weeks in autumn), meteorological factors played a critical role in phytoplankton regulation and weather patterns. Therefore, we infer that a nutrient co-limitation condition, where two or more nutrients have simultaneously been reduced to levels where the addition of both (or in some cases either) is required to stimulate biological growth, will also strongly influence the hierarchy of the different scales of biological and ecological complexity from the single cell to the biosphere (Moore et al., 2013). These conditions may potentially operate in the subtropical Fei-Tsui Reservoir deep freshwater ecosystem.

## 5. Conclusions

Disturbance has been regarded as a key component of all ecosystems (Fraterrigo and Rusak, 2008). Disturbance affects every level of biological organisms and spans a broad range of spatial and temporal scales (Fraterrigo and Rusak, 2008). Its non-uniform effects with both benefits and damage to the ecosystems result in wide variation in ecosystem responses. Results from decadal continuous and dense field monitoring show that typhoons do influence phytoplankton responses in the subtropical deep freshwater ecosystem. Accordingly, during typhoon disturbances, phytoplankton dynamics determined more than 70% of the increase in the disturbance and even reached 200% during the stratification period (i.e., summer) in the subtropical deep freshwater. Moreover, the post-typhoon weeks are especially important for the timeline of phytoplankton increases and with a detectable seasonal variation that the chl-a concentration significantly increased in autumn whereas both primary production and growth rate were associated with significant changes in summer. Besides, episodic climatic events belonging to the type of discrete or continuous disturbance can generate a dynamic change in the ecosystem and affect its recovery time and resilience. A moderate but less intense disturbance is usually and generally beneficial to

ecosystems when regarding the effects occurring with a few years, whereas in the long term, typhoon disturbance causes varied biological responses that show both increases and decreases. Finally, long-term observations have been performed separately in terrestrial and aquatic ecosystems, which are closely associated (especially in the assessment of nutrient dynamics). We suggest that future studies should focus not only on typhoon disturbances on aquatic ecosystems themselves but should also explore different ecosystems linked to one another to determine if the entire ecosystem is at risk, especially when the ecosystems are vulnerable.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.watres.2016.11.011>.

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