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# Tropical cyclone effects enhance limnetic plankton trophic-level relationships in a subtropical oligotrophic freshwater ecosystem

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## Abstract

1. Tropical cyclones (TCs), as natural extreme weather events, alter plankton and hydrological environments, affecting the stability of biological processes in freshwater ecosystems, and such TC effects vary with water depths. Previous studies have found increased phytoplankton biomass resulting from TC effects has been observed, leading to potential strong grazing of zooplankton and enhanced plankton trophic-level relationships. However, this remains understudied, particularly under in situ conditions.
2. Using a zooplankton to phytoplankton (ZB/PB) ratio to represent the plankton trophic-level relationship, we estimated the ZB/PB ratios at various depth intervals, including surface (2 m depth) and euphotic (depths between 0 and 20 m) depths and depth layer 0–50 m (depths between 0 and 50 m), in a subtropical deep oligotrophic freshwater ecosystem from 2012 to 2015 to understand how TC effects would influence changes in the ZB/PB ratio variations.
3. TCs affected the surface and euphotic ZB/PB ratios but not those at the depth layer 0–50 m. The TC durations had an initially negative and then positive impact on the surface ZB/PB ratio, indicating that slow-moving TCs might restructure surface plankton trophic-level relationships. The water temperature and nutrient dynamics during the TC weeks showed the highest correlations with the ZB/PB ratios at the surface and euphotic depths. The combined environmental effects influenced the ZB/PB ratios at the surface and euphotic depths during the TC weeks, with 65.1% and 72.2% of the total variations explained in the multivariate regressions, respectively.
4. There were greater impacts of TCs in shallow water (surface and euphotic depth) than in deep water. Aquatic food chains may be unexpectedly vulnerable to natural extreme weather events, such as TCs, and continuous assessments of food chain dynamics are necessary to better manage potential risks from natural extreme weather events in freshwater ecosystems.

KEYWORDS
aquatic food chain, biomass ratio, energy transfer efficiency, plankton, trophic-level relationship, tropical cyclone

  

## 1 | INTRODUCTION

Given that natural extreme weather events (large-scale and periodic abiotic disturbances) usually strongly impact species composition, ecological relationships, and resource use, an increasing number of studies have demonstrated their critical role in shaping ecosystem structure and dynamics (Chesson et al., 2004; Miriti et al., 2007; Paine & Trimble, 2004; Parmesan et al., 2020; Thibault & Brown, 2008). In terrestrial environments, phenology and vegetation structure were found to vary or lengthen due to extreme weather events (Allen & Breshears, 1998; Holmgren et al., 2001; Parmesan et al., 2020), whereas water quality, nutrient cycling, and population and community processes changed when experiencing weather perturbations in aquatic ecosystems (Lin et al., 2020; Lipp et al., 2001). Tropical cyclones (TCs), formed as a result of rising warm air buildup from ocean surface, can be regarded as natural extreme weather events and have been known to influence organisms and environments at different levels depending on their strength and passing tracks (Chen et al., 2020; Huang et al., 2022). TCs are additionally projected to increase in frequency and intensity, carry more rain, and become more widely distributed under climate change (Kossin, 2018; Lin et al., 2020; Mei et al., 2015; Ying et al., 2012).

As freshwater ecosystems are uniquely relatively isolated and physically fragmented within terrestrial landscapes but heavily exploited by humans, they are particularly vulnerable to TCs. The influences of TCs on organisms' biological processes, structure, and spatial distributions, as well as food web dynamics in the systems, are widely observed (Baek et al., 2020; Ko et al., 2016; Kossin, 2018; Stockwell et al., 2020; Vecchi & Soden, 2007; Ying et al., 2012). For example, phytoplankton responses to increased nutrient supplies during TC periods are widely observed compared with non-TC periods, despite TC passages in summer and autumn affecting phytoplankton dynamics differently (Ko et al., 2016, 2017; Zhao et al., 2008). After TCs, large amounts of dissolved nutrients frequently occur due to runoff and hydrological alteration, e.g., currents and upward mixing, are induced, which probably limit phytoplankton growth (Baleani et al., 2021; Havens et al., 2011; Jiang et al., 2022; Stockwell et al., 2020). Moreover, TCs show significant associations with gelatinous and carnivorous zooplankton at varying time intervals (López-López et al., 2012), but an understanding of how they affect a planktonic food chain is lacking because of limited plankton indices derived from a single trophic level, e.g., focusing merely on phytoplankton or zooplankton (Chai et al., 2021; Ko et al., 2016; López-López et al., 2012). Given that zooplankton feeding on phytoplankton plays a key role in energy transfer, TC effects on multiple aquatic species and trophic-level relationships must be further explored (Bode et al., 2018; Havens et al., 2011; Hunt et al., 2017). In addition, evidences have shown that TCs can affect aquatic ecosystems and their constituent species through their related attributes, such as lengths of stay and disturbance strength (Ko et al., 2016; Zhao et al., 2008, 2015). The responses to these TC-related attributes determine if the plankton community structure is stable to main its normal state or deviate from it, also reflecting resilience and resistance of an ecosystem to weather events (Byrnes et al., 2011; Chang et al., 2018).

The plankton trophic-level relationship, which can be simply expressed by a biomass ratio of zooplankton to phytoplankton, reflects a series of efficiencies in organism metabolism and trophic transferring, and usually varies with environmental changes and trophic status (Armengol et al., 2019; Calbet et al., 2014; Hessen et al., 2006). A high nutrient supply in eutrophic waters has influenced growth of inedible, large phytoplankton and has negatively affected the energy transfer from phytoplankton to upper trophic levels, weakening the plankton trophic-level relationships (Atkinson et al., 2020; Hart, 2011; Hoover et al., 2006; Irigoien et al., 2005). In contrast, oligotrophic waters have a highly varied biomass ratio of zooplankton to phytoplankton, which can be attributed to changes in plankton elements (e.g., carbon and nitrogen), biochemical compositions, and community structure (Billen et al., 1990; Calbet & Landry, 1999; Karpowicz et al., 2021; Yuan & Pollard, 2018). Water acidification also stimulates changes in phytoplankton's essential biomolecules and declines in plankton trophic-level relationships (Bermúdez et al., 2016; Cripps et al., 2016; Havens, 1992). Therefore, understanding trophic status has become increasingly essential to reveal carbon mass distributions and food chain dynamics in aquatic ecosystems (Barneche et al., 2021; Dalgren et al., 2010; Hessen et al., 2003).

The goal of this study was to investigate TC effects on the plankton trophic-level relationships at various depths in a subtropical deep oligotrophic freshwater ecosystem and to reveal environmental factors that influenced changes. Considering that phytoplankton often dominate within the euphotic layer due to light limitation, and zooplankton perform diel vertical migration and are more distributed along the water column than phytoplankton (Behrenfeld & Falkowski, 1997; Johnsen & Jakobsen, 1987; Leibold, 1990; Yacobi, 2006), we first hypothesised that different plankton trophic-level relationships would be observed at different depths. Because phytoplankton biomass was enhanced after TCs, potentially accompanied by a substantial increase in zooplankton grazing, we then hypothesised that TCs would highly stimulate effects on the plankton trophic-level relationships (Ko et al., 2016). A detailed understanding of TC effects on plankton trophic-level relationships and environmental factors across multiple water depths is fundamental for conserving freshwater ecosystems during future extreme weather events.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and sampling

Fei-Tsui Reservoir (FTR), with a catchment area of approximately 303 km$^2$, is a semi-enclosed oligotrophic protected catchment in northern Taiwan, and its dam has maximum depths of approximately

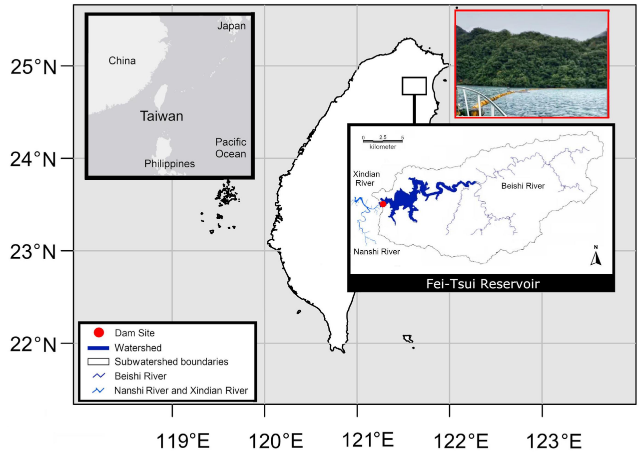


FIGURE 1 Map of the Fei-Tsui Reservoir in northern Taiwan. The dam site with a field photo is indicated by the red mark. The map was generated from R version 4.1.1 and GIMP 2.10 software.

90–120 m (Figure 1; Chow et al., 2017). FTR is mostly surrounded by a secondary subtropical forest and tea plantation along the mountain slope (Chow et al., 2017; Ko et al., 2016). The main FTR water input comes from the Beishi River, and the outflow goes to two tributaries, the Nanshi and Xindian rivers (Jurikova et al., 2016; Tung et al., 2006).

Sampling was before noon, and water samples were generally collected biweekly at the dam site from January 2012 to December 2015, except monthly sampling in April 2012, May 2013, October 2013, April 2014, and April 2015, and weekly sampling from July 2012 to September 2012 and July 2014. The water samples were taken from 10 depth levels, i.e., from surface down to the near bottom (0, 2, 5, 10, 15, 20, 30, 50, 70, and 90 m), using 5-L Go bottles (General Oceanics). Chemical and physical properties of the water column, including temperature, conductivity, depth, and pH, were measured using multiparameter sensor equipment (CTD, Idronaut), which was deployed in a free-fall collecting data file from the maximum depth up to the surface.

Zooplankton samples (1 L) were collected from 0 to 50 m depth using a 50-μm Norpac net with a net mouth radius of 0.225 m and an attached flowmeter (HYDRO-BIOS) to record the water volume passing through the net. Previous observations have indicated a low zooplankton density below a depth of 50 m, and an approximately 53% net hauling filtration efficiency has been estimated for the proportion of water passing through the net (Chang et al., 2014).

## 2.2 | Laboratory measurements and processing

The chlorophyll-a (Chl-a) concentration was used to represent phytoplankton biomass (PB), while nutrient concentrations, including $NO_2^-$ $NO_3^-$ and $PO_4^{3-}$ concentrations, were analysed to determine the resources availability for phytoplankton growth in this study. The water samples were filtered through Whatman GF/F glass microfiber filters (0.7 μm pore size, Whatman, GE Healthcare Life Sciences). The Chl-a concentration was then extracted using acetone and quantified by an in vitro fluorometer (TD-700 Laboratory Fluorometer, Turner Designs; Parsons et al., 1984). The PB was finally determined by multiplying the Chl-a concentration with a carbon conversion factor of 58 gC/g Chl-a (Eppley et al., 1992). The nutrient concentrations were measured and corrected using a fabricated flow injection analysis with a cadmium–copper column material, with detection limits of 0.05, 0.05, and 0.03 μM for $NO_2^-$, $NO_3^-$, and $PO_4^{3-}$ concentrations, respectively (Parsons et al., 1984).

Zooplankton biomass (ZB), representing zooplankton standing stocks governing the accumulation of biomass (Gonçalves et al., 2015; Guerrero & Rodríguez, 1997; Uye et al., 1998), was measured by direct estimation of organic carbon mass using taxon-specific dry weight. Each zooplankton sample was subjected to two subsamples, condensed to 120 ml with a $CO_2$ effervescing fixative agent, stored at 4°C for 1 hr, and preserved with a 2% formalin solution. We observed 300 zooplankton individuals per subsample using a stereomicroscope (Olympus SZX16 AnalSIS®) with an attached microscope charge-coupled device camera (OlympusDP71). Rotifera, Cladocera, and Copepoda had been observed to dominate zooplankton compositions in the FTR (Ho et al., 2016). Rotifera was identified using taxonomic keys by Li (2005) and Wang (1961). Cladocera were identified using keys from Chiang and Du (1979), Korovchinsky (2000), and Tuo and Young (2011, 2002). Copepoda were identified using a key by Shen et al. (1979). A CCD imaging system was then used to measure the length and width of Rotifera, the length of Cladocera, and the prosomal and urosomal length of Copepoda. To obtain taxon-specific dry weight, we converted the length and width of rotifer species to wet weight and then dry weight (Andersen & Hessen, 1991; Ejsmont-Karabin, 1998; Pace & Orcutt, 1981; Pauli, 1989; Ruttner-Kolisko, 1977), while the lengths of Cladocera and Copepoda were converted to dry weight (Andersen & Hessen, 1991; Bottrell, 1976; de Azevedo et al., 2012; Dumont et al., 1975; Michaloudi, 2005). The dry weights of individual taxa were converted to organic carbon of 0.48, and the ZB was finally counted after accumulating biomass from all taxa (Andersen & Hessen, 1991).

## 2.3 | Tropical cyclone-related attributes

To better quantify TC effects on the FTR, only the TCs with their centres hitting Taiwan's offshores were considered. The TC records from 2012 to 2015 were obtained from Ventusky meteorological data (https://www.ventusky.com) provided by the Der Deutscher Wetterdienst under Germany's National Meteorological Service and the National Oceanic and Atmospheric Administration, USA, and the individual lengths of TC stays were calculated separately. The minimum centre pressures and maximum sustained wind speeds of individual TCs were acquired from the Japan Meteorological Agency (https://www.jma.go.jp). We defined a TC week if the sampling was within 7 days after the TC hit the study area because TC delay effects on plankton had been recognised and were usually accompanied by a weekly time-lag nutrient supply by the TC (Arteaga et al., 2020; Collos, 1986). Precipitation was acquired from the Central Meteorological Bureau Weather Warning List by the Central Weather Bureau (https://www.cwb.gov.tw), and accumulated precipitation throughout the sampling of the TC week, i.e., 7 days before the sampling day, was used for further analyses. The combination of wind speeds and accumulated precipitation was then calculated for the TC disturbance ranking (Ko et al., 2016):

$$\text{Disturbance ranking} = \frac{(10 \times \text{Accumulated precipitation during the TC week})}{\text{Maximum sustained wind speed}}$$

## 2.4 | Data analyses

Except for values at the surface (2 m) depth, a trapezoidal rule was used to calculate specific depth-averaged values (i.e., 0–20 and 0–50 m), including environments of the water column, PB, and nutrient concentrations, to consistently compare changes across depths (Hornbeck, 1975). The trophic-level relationship in this study was represented as the ratio of zooplankton biomass to phytoplankton biomass (ZB/PB). Student *t* test was used to identify changes in PB, ZB, and ZB/PB between the TC and non-TC weeks at different depths. Relationships between PB and ZB were estimated using log-log simple linear regressions considering all data or excluding outliers. A *z* score of ±1.65 on the basis of a 90% confidence interval was used to identify outliers.

The Shapiro–Wilko normality and Levene tests were first used to assess the normality and equality of variances of all environmental factors, respectively (Table S1). The autocorrelations of environmental factors either during the TC weeks or during the non-TC weeks were then examined, and only the environmental factors with correlation coefficients less than 0.6 were selected for further analyses (Tables S2 and S3). To examine relationships between the ZB/PB ratios and TC-related attributes, Spearman correlations or polynomial regressions were used. Spearman correlations were additionally used to examine relationships between the ZB/PB ratios and individual environmental factors during the TC weeks. Multivariate regressions with stepwise backward elimination were developed to investigate combined effects of environmental factors on the ZB/PB ratios at different depths during both TC and non-TC weeks. All statistical analyses in this study were performed using R version 4.1.1 (R Development Core Team, 2021).

# 3 | RESULTS

## 3.1 | Responses of ZB/PB ratios to TCs

A total of 21 TCs, including eight regarded as intense, seven as moderate, and six as minor, affected the FTR and northern Taiwan from 2012 to 2015, with TCs staying from 1 to 5 days and accumulated precipitation up to 388.6 mm (Table 1). TC Tembin unusually approached twice and was classified separately in this study. The TC weeks mostly occurred in specific months, including warmer months from June to August and cooler months from September to November. TC Saola in 2012 had the longest length of stay and the greatest disturbance ranking, while TC Hagibis in 2014 and Soudelor in 2015 had the strongest minimum centre pressure and maximum sustained wind speed and accumulated precipitation during the TC weeks, respectively.

When considering individual indices of PB at varying depths and ZB at the depth layer 0–50 m, different responses to TCs were observed (Figure 2). Both surface (2 m) and euphotic (0–20 m) PB increased during the TC weeks, but only the surface PB showed significance ($p < 0.05$). In contrast, both PB and ZB at the depth layer 0–50 m were slightly higher during the non-TC weeks than during the TC weeks, but no significant changes were detected (both $p > 0.05$). These results not only indicated that the PB near the surface might be more affected by TCs than that at deeper depths but also implied that using a single index or considering changes at one depth in the water column might cause limited understandings when estimating TC effects on plankton.

When further considering synergistic relationships between PB and ZB, the TC effects on the ZB/PB ratios varied largely at different depths, and the ZB/PB ratios showed significant decreases, particularly at the surface and euphotic depths, during the TC weeks (both $p < 0.05$, Figure 3). During the TC weeks, the ZB/PB ratios ranged from 0.03% to 1.62% at the surface depth, from 0.07% to 1.78% at the euphotic depth, and from 7.6% to 187.11% at the depth layer 0–50 m, whereas during the non-TC weeks, the ZB/PB ratio varied from 0.03% to 10.51% at the surface depth, from 0.03% to 9.44% at the euphotic depth, and from 2.98% to 800.06% at the depth layer 0–50 m. These results indicated that TCs could highly affect the ZB/PB ratios in the FTR by promoting phytoplankton growth, especially in the upper water column, and lead to low ZB/PB ratios. Notably, such decreased ZB/PB ratios during the TC weeks existed with different underlying mechanisms. With increasing PB, ZB decreased at the surface depth but increased at the euphotic and deep depths, although in situ observations in this study exhibited limited statistical significance (Figure 4). To better explore TC effects on the plankton trophic-level relationships, the surface and euphotic ZB/PB ratios were used in the following analyses.

## 3.2 | Influences of TC-related attributes on ZB/PB ratios

We found that limited TC-related attributes had relationships with the ZB/PB ratios at different depths (Figure 5). The disturbance ranking of TCs was not correlated with the ZB/PB ratios at either surface or euphotic depth (both $p > 0.05$). A short and moderate TC stay, i.e., 1–3 days, was associated with a declining surface ZB/PB ratio, and a long length of TC stay increased the surface ZB/PB ratios ($p = 0.02$), but no such significant pattern was observed for the

TABLE 1 List of tropical cyclones (TCs) that hit northern Taiwan from 2012 to 2015.

| Year | Name | Length of stay (day) | Minimum centre pressure (hPa) | Maximum sustained wind speed (m/s) | Intensity grade[a] | Accumulated precipitation during the TC week (mm) | Disturbance ranking |
|---|---|---|---|---|---|---|---|
| 2012 | Talim | 3 (19–21 June) | 985 | 26.7 | Minor | 84 | 31 |
| | Doksuri | 2 (28–29 June) | 992 | 20.1 | Minor | 4.4 | 2 |
| | Saola | 5 (30 July 3 August) | 960 | 37.9 | Moderate | 344.6 | 91 |
| | Haikui | 2 (6–7 August) | 965 | 33.5 | Moderate | 117.3 | 35 |
| | Kai-Tak | 2 (14–15 August) | 970 | 33.5 | Minor | 30.8 | 9 |
| | Tembin | 5 (21–25 August) | 945 | 45 | Moderate | 130 | 29 |
| | Tembin | 3 (27–28 August) | 965 | 35 | Moderate | 93.8 | 27 |
| | Jelawat | 2 (27–28 September) | 910 | 55.9 | Intense | 19.5 | 3 |
| 2013 | Soulik | 2 (12–13 July) | 925 | 51.4 | Intense | 103.5 | 20 |
| | Usagi | 2 (21–23 September) | 910 | 55.9 | Intense | 69.7 | 12 |
| | Fitow | 2 (5–6 October) | 960 | 37.9 | Moderate | 79.5 | 21 |
| | Krosa | 3 (1–3 November) | 970 | 37.9 | Moderate | 9.5 | 3 |
| 2014 | Hagibis | 3 (13–15 June) | 996 | 20.1 | Minor | 45.7 | 23 |
| | Matmo | 2 (22–23 July) | 965 | 35.8 | Moderate | 130.1 | 36 |
| | Fung-wong | 3 (20–22 September) | 985 | 22.4 | Minor | 193.5 | 86 |
| 2015 | Noul | 1 (11 May) | 920 | 55.9 | Intense | 62.8 | 11 |
| | Linfa | 2 (10–11 July) | 980 | 26.8 | Minor | 105.6 | 39 |
| | Soudelor | 2 (7–8 August) | 900 | 58 | Intense | 388.6 | 67 |
| | Goni | 2 (22–23 August) | 930 | 51.4 | Intense | 212.5 | 41 |
| | Dujuan | 3 (27–29 September) | 925 | 55.9 | Intense | 287.7 | 51 |
| | Koppu | 3 (19–21 October) | 925 | 51.4 | Intense | 24.6 | 5 |

[a]The intensity grade was defined based on the maximum sustained wind speed near the centre: minor, <32.7 m/s; moderate, 32.7–50.9 m/s; intense, >50.9 m/s.

euphotic ZB/PB ratios ($p>0.05$). The results suggested that the TC-related attributes might have greater influences on the surface than on the euphotic ZB/PB ratios.

### 3.3 | Influences of environmental factors on ZB/PB ratios

The surface water temperature and/or nutrient dynamics during the TC weeks showed the highest correlations with the ZB/PB ratios at the surface and euphotic depths (Table 2). During the TC weeks, the surface ZB/PB ratios were significantly positively correlated with surface water temperature ($\rho=0.49$, $p=0.02$) and $NO_2^-$ concentration ($\rho=0.66$, $p=0.001$), while the euphotic ZB/PB ratios were significantly positively correlated with the euphotic depth-averaged $NO_2^-$ concentration ($\rho=0.61$, $p=0.003$). The different combined environmental effects affected the ZB/PB ratios at the surface and euphotic depths during the TC weeks (Table 3). The surface ZB/PB ratios increased when a TC rapidly moved, i.e., a short stay, the surface euphotic depth-averaged $NO_2^-$ concentrations increased, and the 0–90 m depth-averaged $NO_3^-$ concentration decreased. However, the euphotic ZB/PB ratios were enhanced when there were increased euphotic depth-averaged $NO_2^-$ concentrations and decreased 0–90 m depth-averaged $NO_3^-$ concentrations. The above final models, based on multivariate regressions with stepwise backward selection, explained 65.1% and 72.2% of the total variations in the surface and euphotic ZB/PB ratios, respectively. Unlike the high explanatory power of environmental factors during the TC weeks, combined environmental effects on the ZB/PB ratios merely explained 13.1% and 11.5% of the total variations at the surface and euphotic depths, respectively, during the non-TC weeks (Table 4). This revealed that stronger plankton trophic-level relationships were prompted during the TC weeks than during the non-TC weeks, and TCs could significantly enhance plankton trophic-level relationships through altering environmental conditions in the subtropical oligotrophic freshwater ecosystem, such as the FTR.

## 4 | DISCUSSION

We showed that the impacts of TCs on the plankton trophic-level relationships in deep subtropical oligotrophic freshwater varied

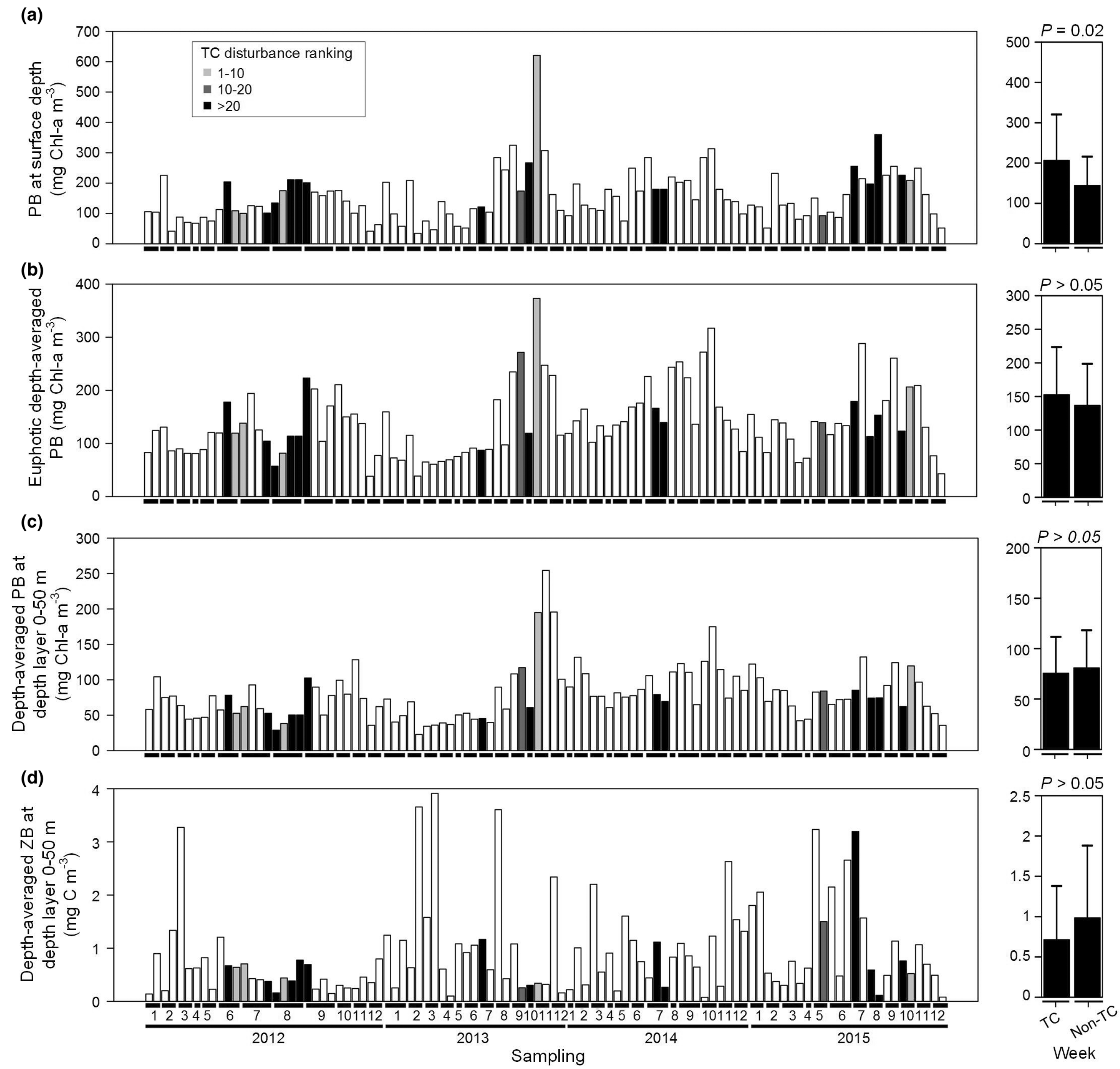


**FIGURE 2** Monthly patterns and averages (±*SD*) of (a) phytoplankton biomass (PB) at a surface depth of 2 m, and depth-averaged PB at (b) euphotic depths of 0–20 m and (c) a depth layer 0–50 m, and (d) depth-averaged zooplankton biomass (ZB) at a depth layer 0–50 m in the Fei-Tsui Reservoir from 2012 to 2015. Each bar represents individual sampling. Different bar colours indicate disturbance ranking of tropical cyclones (TCs). *p* values estimated by Student *t* test are shown.

among different depths that were differently driven by TC disturbance mechanisms and TC-related environments. Despite aquatic systems and depths being demonstrated their responses after TCs in many previous studies (Chai et al., 2021; Hoover et al., 2006; Ko et al., 2016), our results clearly provided such responses in certain depths in water column, e.g., significantly high ZB/PB ratios at the surface (2 m) and euphotic (0–20 m) depths but not at the depth layer 0–50 m. The TC-induced disturbance created depth-dependent environments for phytoplankton growth, leading to low PB responses and limited trophic-level relationships in deep water layers. Therefore, depth should not be ignored when analysing potential TC effects on biological processes in aquatic ecosystems. In addition, compared to the plankton trophic-level relationships, individual trophic indices, such as PB and ZB, showed poor responses to TCs throughout the water column except values at the surface depth, showing that caution is needed because of the limitations of using indices of individual trophic levels to investigate the TC effects on aquatic food chains. Our results also indicated that the TC-related attributes, particularly the TC duration, had a stronger effect on the plankton trophic-level relationships at the surface depth than that at the deeper depths, and the plankton trophic-level relationships were highly correlated with environmental factors both at the surface

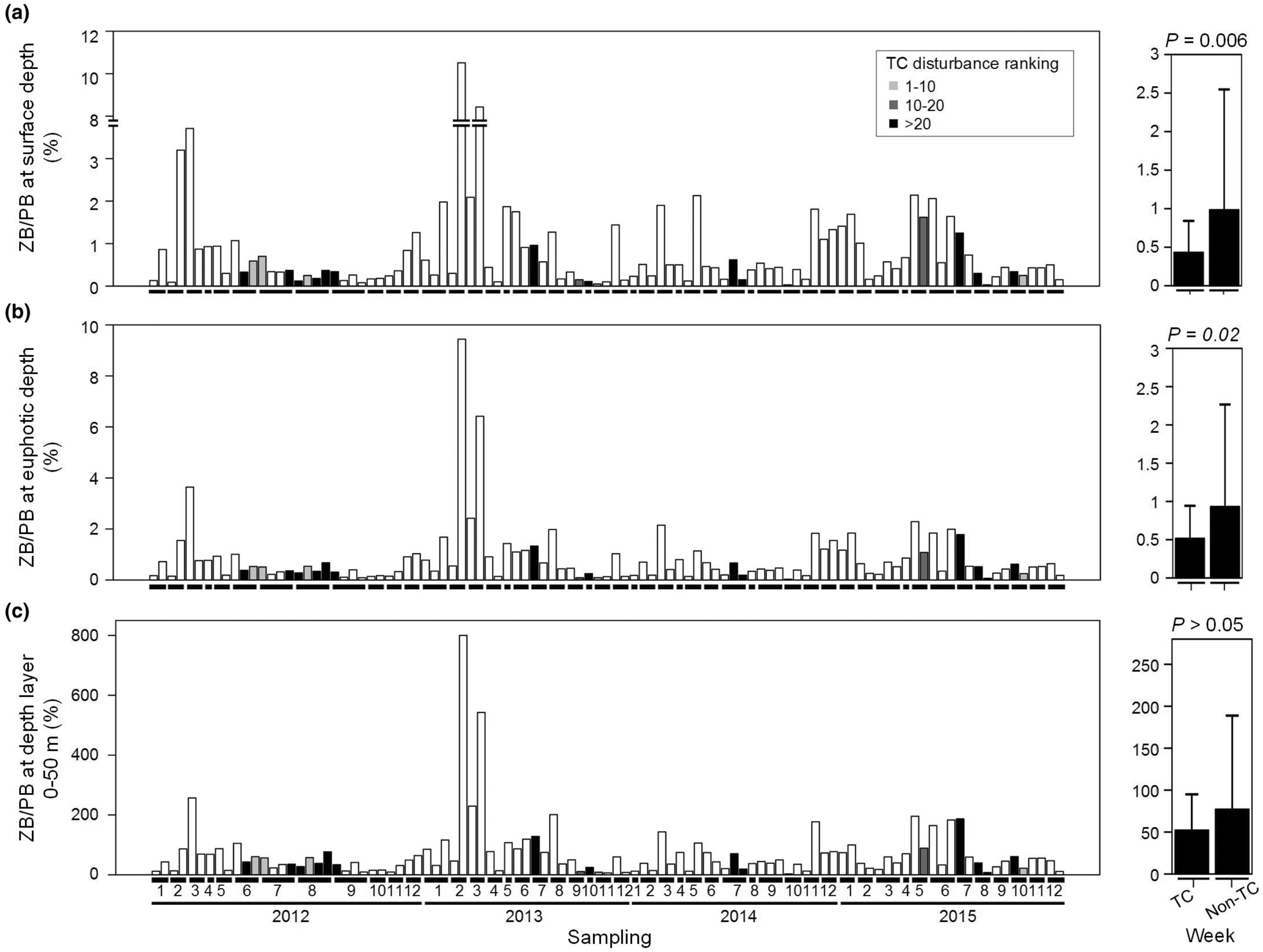


FIGURE 3 Monthly patterns and averages (±*SD*) for ratios of zooplankton biomass to phytoplankton biomass (ZB/PB) (a) at a surface depth of 2 m, (b) euphotic depths of 0–20 m, and (c) at a depth layer 0–50 m in the Fei-Tsui Reservoir from 2012 to 2015. Except for the PB values at the depth of 2 m, other PB and ZB values are depth-averaged. Each bar represents individual sampling. Different bar colours indicate disturbance ranking of tropical cyclones (TCs). *p* values estimated by Student *t* test are shown.

and euphotic depths wherein nutrients were important for ZB/PB ratio dynamics during the TC weeks. Considering ongoing changes in TC frequency and strength under climate change, exploring how TCs would affect variance of plankton trophic-level relationships in freshwater ecosystems becomes increasingly important and requires more understandings (Hessen et al., 2003).

Plankton often play a central role in maintain strong trophic links in aquatic ecosystems, both as links between primary-producing phytoplankton and zooplankton and as important carbon transfer target, but more and more studies have shown that TCs have potentials to change these links, particularly TCs with long stays (Armengol et al., 2019; Barneche et al., 2021; Calbet et al., 2014; Cripps et al., 2016; Hoover et al., 2006; Ko et al., 2016, 2017; Zhao et al., 2008). For example, the strong TC disturbance decreased Chl-a concentrations but moderate TC disturbance highly favoured autotrophs' growth in the northern Taiwan (Ko et al., 2016, 2017). The weak, slow-moving TCs promoted phytoplankton blooms over a large area in the South China Sea (Zhao et al., 2008). After a strong TC passed, nutrient-rich runoff rapidly affected dynamics of phytoplankton and zooplankton population and structure by changing grazing pressure in southern Kaneohe Bay, Hawaii (Hoover et al., 2006). Notably, in this study, a moderate TC duration significantly weakened the plankton trophic-level relationships at the surface depth, which might pose challenges for plankton to recover quickly. We thus speculated that the weak associations between plankton trophic-level relationships and TC disturbance ranking in this study might be additionally caused by orographic effects, which mountain slopes that surround the FTR might modulate TC effects on the reservoir catchment (Lentink et al., 2018; Minamide & Yoshimura, 2014; Whitford & Duval, 2020). Moreover, TCs can promote trophic-level relationships both through bottom-up and top-down controls in plankton communities (Byrnes et al., 2011; Chen et al., 2020; Hoover et al., 2006). Given the increased phytoplankton density observed during TC weeks, substantial bottom-up control might exist in the FTR system.

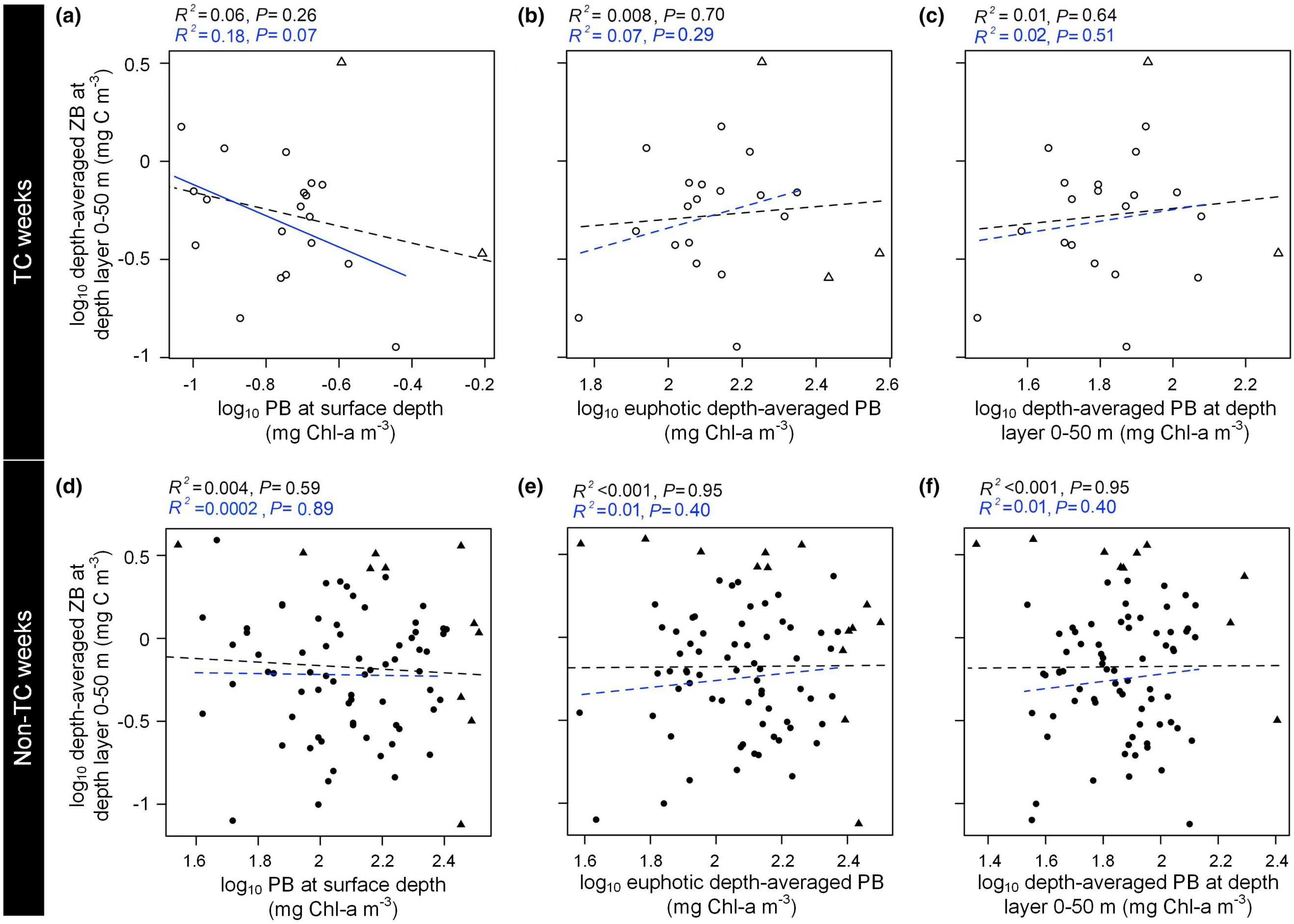


**FIGURE 4** Relationships between phytoplankton biomass (PB), depth-averaged PB and zooplankton biomass (ZB) at surface (a depth of 2 m) and euphotic (depths between 0 and 20 m) depths, and a depth layer 0–50 m in the Fei-Tsui Reservoir during tropical cyclone (TC) weeks (a–c) and non-TC weeks (d–f). White and black triangles represent outliers during the TC and non-TC weeks, respectively. Black lines represent models with all data, while blue lines represent models with data excluding outliers, i.e., data not within a 90% confidence interval. The solid line indicates a marginally significant relationship ($p$ = 0.07), while the dashed line indicates no significance ($p$ > 0.05).

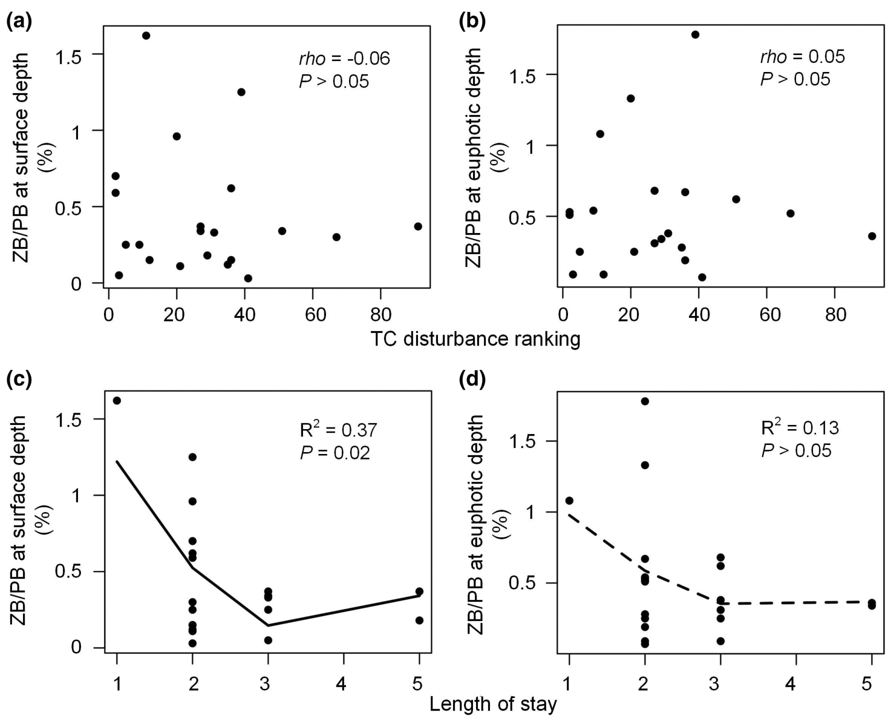


**FIGURE 5** Relationships between (a, b) disturbance ranking and (c, d) tropical cyclone (TC) duration and zooplankton biomass to phytoplankton biomass (ZB/PB) ratios at surface (a depth of 2 m) and euphotic (at depths between 0 and 20 m) depths, respectively, in the Fei-Tsui Reservoir from 2012 to 2015. The $r^2$ and $p$ values are shown. The solid line indicates a significant relationship ($p \leq 0.05$), while the dashed line indicates no significance ($p$ > 0.05).

**TABLE 2** Correlations between environmental factors and ratios of phytoplankton biomass (PB) and depth-averaged zooplankton biomass (ZB) at a depth of 2 m, i.e., surface depth, and depth-averaged ZB/PB at depths between 0 and 20 m, i.e., euphotic depth, during the weeks when tropical cycles approached the study area.

| | Surface ZB/PB | | Euphotic ZB/PB | |
|---|---|---|---|---|
| Environmental factors | *ρ* | *p* | *ρ* | *p* |
| 2 m depth temperature (°C) | 0.49 | 0.02* | – | – |
| Euphotic depth-averaged temperature (°C) | – | – | 0.12 | 0.61 |
| 2 m depth $NO_2^-$ (μM) | 0.66 | 0.001*** | – | – |
| Euphotic depth-averaged $NO_2^-$ (μM) | – | – | 0.61 | 0.003** |
| 0–90 m depth-averaged $NO_2^-$ (μM) | 0.21 | 0.36 | 0.28 | 0.23 |
| 0–90 m depth-averaged $NO_3^-$ (μM) | −0.38 | 0.09 | −0.34 | 0.13 |
| 2 m depth $PO_4^{3-}$ (μM) | 0.15 | 0.51 | – | – |
| Euphotic depth-averaged $PO_4^{3-}$ (μM) | – | – | 0.04 | 0.85 |

*Note*: Asterisks indicate significant *p* values: a single asterisk (*) for $p \le 0.05$, double asterisks (**) for $p \le 0.01$ and triple asterisks (***) for $p \le 0.001$. A hyphen (–) indicates that a particular factor was not applicable to the ZB/PB ratio at a specific depth.

**TABLE 3** Relationships between environmental factors and ratios of phytoplankton biomass (PB) and depth-averaged zooplankton biomass (ZB) at a depth of 2 m, i.e., surface depth, and depth-averaged ZB/PB at depths between 0 and 20 m, i.e., euphotic depth, based on final models estimated by multivariate regressions with backward selection during the weeks when tropical cycles approached the study area.

| | Surface ZB/PB | | | Euphotic ZB/PB | | |
|---|---|---|---|---|---|---|
| Environmental factors | Coefficient | *SE* | *p* | Coefficient | *SE* | *p* |
| Disturbance ranking | | | | | | |
| Length of stay (day) | −0.199 | 0.068 | 0.009** | | | |
| 2 m depth temperature (°C) | | | | – | – | – |
| Euphotic depth-averaged temperature (°C) | – | – | – | | | |
| 2 m depth $NO_2^-$ (μM) | 3.122 | 0.864 | 0.002** | – | – | – |
| Euphotic depth-averaged $NO_2^-$ (μM) | – | – | – | 7.257 | 1.141 | $<0.001$*** |
| 0–90 m depth-averaged $NO_2^-$ (μM) | 4.523 | 2.377 | 0.075 | | | |
| 0–90 m depth-averaged $NO_3^-$ (μM) | −0.050 | 0.018 | 0.01** | −0.024 | 0.014 | 0.11 |
| 2 m depth $PO_4^{3-}$ (μM) | | | | – | – | - |
| Euphotic depth-averaged $PO_4^{3-}$ (μM) | – | – | – | | | |
| Intercept | 1.644 | | | 0.267 | | |
| $r^2$ | 0.651 | | | 0.722 | | |

*Note*: Asterisks indicate significant *p* values: double asterisks (**) for $p \le 0.01$ and triple asterisks (***) for $p \le 0.001$. A hyphen (–) indicates that a particular factor was not applicable to the ZB/PB ratio at a specific depth.

Regarding the environmental factors influencing trophic-level relationships among phytoplankton, increased $NO_2^-$ concentrations during the TC weeks may be essential for shaping plankton trophic-level relationships, particularly in semi-enclosed oligotrophic freshwater ecosystems. In the FTR, the dynamics of $NO_2^-$ concentrations were highly positively correlated with plankton trophic-level relationships at both surface and euphotic depths during the TC weeks. That is, increasing $NO_2^-$ concentrations with increasingly strong plankton trophic-level relationships. However, our results differed for eutrophic lakes with excessive nutrients (high $NO_2^-$ and $NO_3^-$ concentrations) because these usually decouple phytoplankton and zooplankton relationships (Calbet et al., 2014; Havens et al., 2011; Yuan & Pollard, 2018). Moreover, synergic effects of $NO_2^-$ concentrations and water temperature during the TC weeks can enhance plankton trophic-level relationships and interactively affect phytoplankton in freshwater ecosystems. For example, changes of biomass, production and turnover in phytoplankton lead to different relationships between phytoplankton and other organisms (Ko et al., 2016, 2017). In this study, we found that there were greater TC influences on the surface (2 m depth) plankton trophic-level relationships in warmer environments (water temperature >28.1°C in July and August in summer) than those in cool environments, revealing that the effect of $NO_2^-$ concentration might increase with temperature. Therefore, when TCs occur in tropical and subtropical oligotrophic freshwater ecosystems in different seasons, nutrient fluctuation and plankton trophic-level relationships may respond differently, which may cause unpredictable food-chain consequences and be worth exploring for

TABLE 4 Relationships between environmental factors and ratios of phytoplankton biomass (PB) and depth-averaged zooplankton biomass (ZB) at a depth of 2 m, i.e., surface depth, and depth-averaged ZB/PB at depths between 0 and 20 m, i.e., euphotic depth, based on final models estimated by multivariate regressions with backward selection during the non-tropical cycle weeks.

| | Surface ZB/PB | | | Euphotic ZB/PB | | |
|---|---|---|---|---|---|---|
| Environmental factors | Coefficient | *SE* | *p* | Coefficient | *SE* | *p* |
| 2 m depth temperature (°C) | −0.162 | 0.054 | 0.004*** | – | – | – |
| Euphotic depth-averaged temperature (°C) | – | – | – | −0.126 | 0.047 | 0.009*** |
| 2 m depth pH | 0.356 | 0.204 | 0.09 | – | – | – |
| Euphotic depth-averaged pH | – | – | | | | |
| 0–50 m depth-averaged $NO_2^-$ (μM) | 12.591 | 6.628 | 0.06 | 8.235 | 5.046 | 0.107 |
| 0–90 m depth-averaged $NO_2^-$ (μM) | −7.665 | 4.955 | 0.13 | −7.495 | 3.813 | 0.053 |
| 0–90 m depth-averaged $NO_3^-$ (μM) | | | | | | |
| 2 m depth $PO_4^{3-}$ (μM) | | | | – | – | – |
| 0–90 m depth-averaged $PO_4^{3-}$ (μM) | | | | | | |
| Intercept | 1.794 | | | 3.616 | | |
| $r^2$ | 0.131 | | | 0.115 | | |

*Note*: Asterisks indicate significant *p* values: triple asterisks (***) for $p \le 0.001$. A hyphen (–) indicates that a particular factor was not applicable to the specific depth ZB/PB and was not included in the multivariate analysis.

future work. Overall, the combined effects of TC-related attributes and environmental factors account for the correlations and interdependence between planktonic organisms and environments, and the regression methods applied in this study effectively evaluate the responses of plankton trophic-level relationships to TCs.

Our findings based on the analyses of in situ field PB and ZB observations clearly demonstrated how TCs affected the plankton trophic-level relationships at various depths in the subtropical oligotrophic FTR freshwater ecosystem, and greater impacts of TCs were observed in shallow water (at the surface and euphotic depths) than in deep water (at the depth layer 0–50 m). It is conceivable that the aforementioned effects observed in the shallow, euphotic zone would have substantial consequences for the key trophic processes in this ecosystem. In conclusion, aquatic food chains may be unexpectedly vulnerable to natural extreme weather events, such as TCs, and continuous assessments of food chain dynamics are necessary to better manage potential risks from the occurrence of natural extreme weather events in freshwater ecosystems.

## AUTHOR CONTRIBUTIONS

Conceptualisation: E.S.P.d.P., C.-h.H., F.-K.S., C.-Y.K. Conducting the research: E.S.P.d.P., F.-S.L., C.-h.H., F.-K.S., C.-Y.K. Developing methods: E.S.P.d.P., F.-S.L. Data analysis: E.S.P.d.P., C.-Y.K. Data interpretation: C.-W.C., C.-h.H., P.-F.L., F.-K.S. Preparation of figures and tables: E.S.P.d.P., C.-Y.K. Writing: E.S.P.d.P., F.-S.L., C.-W.C., C.-h.H., P.-F.L., F.-K.S., C.-Y.K.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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