Zoological Studies **62:**58 (2023)
doi:10.6620/ZS.2023.62-58

Zoological Studies

Open Access

Effects of Tropical Cyclone Passage on Plankton Community Respiration in a Phosphate-Limited Freshwater Ecosystem

Erica Silk P. dela Paz[1], Chao-Chen Lai[2], Fuh-Kwo Shiah[3], Chih-hao Hsieh[3,4,5], Chia-Ying Ko[1,5,*]

[1]*Institute of Fisheries Science, National Taiwan University, Taipei, 106 Taiwan. *Correspondence: E-mail: cyko235@ntu.edu.tw (Ko)*
E-mail: d07b45003@ntu.edu.tw (dela Paz)
[2]*Department of Science Education, National Taipei University of Education, Taipei 106, Taiwan. E-mail: ccjosephlai@mail.ntue.edu.tw (Lai)*
[3]*Research Center for Environmental Changes, Academia Sinica, Taipei 115, Taiwan. E-mail: fkshiah@gate.sinica.edu.tw (Shiah)*
[4]*Institute of Oceanography, National Taiwan University, Taipei 106, Taiwan. E-mail: chsieh@ntu.edu.tw (Hsieh)*
[5]*Master's Program in Biodiversity, Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, 106 Taiwan*

Received 22 August 2023 / Accepted 22 November 2023 / Published 29 December 2023
Communicated by Benny K.K. Chan

Plankton community respiration (CR) in aquatic ecosystems varies with environmental factors, which could be altered during tropical cyclones (TCs). A potential increase in CR resulting from the effects of TCs is generally understudied. Here, we examined the relationship between plankton CR and environmental factors, including during TC-affected periods, in a phosphate-limited freshwater ecosystem. We conducted an intensive *in situ* sampling in Fei-Tsui Reservoir (FTR) from January 2010 to December 2015 during TC periods and non-TC periods. Our results showed a consistent temporal pattern that plankton CR increased between March to October and declined between November to February. These changes in plankton CR, primarily supported by bacterial biomass, were positively influenced by euphotic depth-averaged temperature. The CR also significantly increased with euphotic depth-averaged NO_2^- concentrations and decreased with euphotic depth-averaged NO_3^- concentrations. These results indicated that these factors typically influenced CR dynamics in the FTR. During TC periods, plankton CR was increased further due to a higher and ideal euphotic depth-averaged temperature (23–27°C) and increased supply of limiting nutrient resources via stream runoff. Overall, this study showed that a TC positively influences plankton CR by creating favorable water conditions. Notably, with a higher frequency of intense TCs projected for the Western North Pacific in most climate change scenarios, the impact of TCs on CR may increase in the near future.

Key words: Bacterial biomass, Total community respiration, Oligotrophic lake, Plankton, Typhoon

BACKGROUND

Severe weather events (*e.g.*, storms, tornadoes, thunderstorms, heatwaves, droughts, wildfires) can cause considerable ecosystem challenges. Severe weather events impact some aquatic ecosystems, leading to noticeable negative effects on productivity, water quality, and biodiversity, among other indicators (Poff et al. 2002; Field et al. 2007). For instance, tropical cyclones (TCs), strong weather disturbances that develop as a result of warm air rising over the Pacific Ocean, are regularly observed in the Western North Pacific about 30 times each year (Emanuel 2005; Vecchi and Soden 2007; Ying et al. 2012; Chen et al. 2020). They are characterized by heavy precipitation and strong winds that influence terrestrial areas and have impacted various ecological relationships in lakes (Ko et al. 2016 2017; Huang et al. 2022). Yet, lakes have demonstrated

Citation: dela Paz ESP, Lai CC, Shiah FK, Hsieh Ch, Ko CY. 2023. Effects of tropical cyclone passage on plankton community respiration in a phosphate-limited freshwater ecosystem. Zool Stud **62:**58. doi:10.6620/ZS.2023.62-58.

varying degrees of resilience to TCs and have developed ways to cope with and recover (*i.e.*, nitrogen cycling) from the disturbance (Gao et al. 2021).

Although aquatic ecosystems may show resilience in the face of TCs, there is still variability in the subsequent impacts due to factors such as precipitation rate (Jansson et al. 2008; Ko et al. 2016). Precipitation associated with TCs increases water inflow into lakes, causing a rapid rise in water levels and increased sedimentation in the lake, which impacts the phytoplankton and zooplankton communities (Iavorivska et al. 2016; Hoover et al. 2006; López-López et al. 2012; Ko et al. 2016). Additionally, stream runoff from TCs can increase the phosphate (PO_4^{3-}) supply to a nutrient-limited system (Tseng et al. 2010). Furthermore, stronger precipitation has more dramatic effects on aquatic systems and can disrupt thermal stratification (Klug et al. 2012; Doubek et al. 2021; Lin et al. 2022). Thus, TCs accompanied by heavy precipitation have the potential to significantly impact aquatic ecosystems and their constituents (*e.g.*, species and water conditions).

Although other freshwater biological communities have been studied in the wake of a TC passage, the effects of TCs on plankton community respiration (CR) in this regard have not been studied. In aquatic ecosystems, plankton CR plays a critical role in carbon cycling, but is sensitive to changing environmental factors, particularly the limiting ones (Del Giorgio and Williams 2005). For example, warmer waters could reduce some enzymatic reactions, resulting in a higher respiration rate (Hall and Cotner 2007; Scofield et al. 2015), while more acidic water may increase cell membrane diffusion, which destabilizes the cell membrane of aquatic species (Russell 1992; Jin and Kirk 2018). Moreover, an increase in the concentrations of nitrogen compounds (*i.e.*, NO_2^- and NO_3^-), PO_4^{3-}, dissolved oxygen (DO), and dissolved organic carbon (DOC) increases CR (Bueno et al. 2012; Vikström and Wikner 2019). Additionally, CR is represented by the cumulative carbon consumption of constituents such as bacterioplankton, phytoplankton, planktonic protozoa, and zooplankton (Liu et al. 2000), contributing to some of the variability of CR. TCs, as a severe force, can rapidly alter plankton community and environmental conditions, potentially introducing limiting factors that can enhance CR. However, the effects of TCs on the relationship between species' biological activities and the environment are largely unexplored.

The aim of the present study was to examine the relationship between plankton CR and environmental factors, including in TC-affected periods, in the Fei-Tsui Reservoir (FTR), a phosphate-limited freshwater ecosystem. We hypothesized that (1) plankton CR dynamics resulted from environmental changes in the FTR and (2) TCs affect environmental factors that lead to an increase in plankton CR rate. To test these hypotheses, we analyzed a 6-year intensive *in situ* monitoring dataset from January 2010 to December 2015. Understanding how strong weather events affect this relationship involving plankton CR can help us better understand how nutrient-limited freshwater ecosystems are impacted, which is important for regulating and mitigating TC effects in lakes.

MATERIALS AND METHODS

Study site

Fei-Tsui Reservoir is a phosphate-limited freshwater reservoir in northern Taiwan (Tseng et al. 2010) (Fig. 1). The catchment area is approximately 303 km^2, and the water depth at the dam site is 90–120 m (Chow et al. 2017). It was created to provide drinking water to Taipei City and is surrounded by secondary forests and tea plantations (Ko et al. 2016; Chow et al. 2017). FTR flows to two adjacent streams: the upper stream of the Beishi River and the lower streams of the Xindian River and Nanshi River.

Study design

We used an intensive *in situ* monitoring dataset to investigate the TC effects on CR between the averaged depth of 0 to 20 m, *i.e.*, euphotic depth, in the FTR. Before noon, sampling was conducted at the dam site bi-weekly from January 2010 to December 2015, except (i) weekly sampling from July 2012 to September 2012 and July 2014, (ii) monthly sampling in August 2010, October 2010, February to July 2011, October 2011, April 2012, May 2013, October 2013, April 2014, and April 2015, and (iii) no sampling between November and December in 2010 and 2011. Our sampling involved collections of physical parameters (*i.e.*, temperature, pH), DO, bulk water samples for nutrients (NO_2^-, NO_3^-, and PO_4^{3-}), bacteria, chlorophyll-*a*, and DOC analyses, which were taken from 10 depth intervals (0, 2, 5, 10, 15, 20, 30, 50, 70, and 90 m) using 5 L Go bottles (General Oceanics, Miami, FL), and zooplankton samples. All these variables were analyzed as described in the following section.

Sampling and laboratory analyses

Physical measurements

Physical properties of water, including vertical profiles of temperature, pH, and depth, were measured at the time of the collection from the surface to near bottom (90 m depth) by multiparameter sensor equipment (CTD, Idronaut, Brugherio (MB) Italy). Precipitation data, which is 7 days of accumulated precipitation before sampling, were obtained from the Taiwan Central Weather Bureau (CWB, https://www.cwb.gov.tw). These variables represented external factors that impact CR.

DOC concentrations

DOC was used to represent the energy source for heterotrophic organisms, usually derived from decomposing organic matter. Water samples of 300–500 ml were filtered in the laboratory through Whatman GF/F glass microfiber filters (0.7 µm pore size, Whatman, GE Healthcare Life Sciences, Little Chalfont, United Kingdom). DOC concentrations from the filtrates were determined by acidulating a 60 ml subsample with 0.5 ml of 80% H_3PO_4 and sprayed with 350 ml min^{-1} of CO_2-free O_2 for at least 10 minutes. Then, the concentration of DOC was analyzed by a Shimadzu TOC-5000 high-temperature catalytic oxidation analyzer.

Nutrients in the water

Dissolved inorganic nutrients such as NO_2^-, NO_3^-, and PO_4^{3-} were used to represent the resources available for the metabolic demands of plankton. Concentrations of NO_2^-, NO_3^- and PO_4^{3-} from a filtrate subsample of 60 ml were analyzed by a brucine sulfate method and a molybdenum blue method using a 10-cm detection cell in a fabricated flow injection analyzer (FIA) with a cadmium-copper column with material detection limits of the three nutrients (0.05 µM, 0.05 µM, and 0.03 µM, respectively) (Parsons et al. 1984).

Plankton community respiration

CR was determined using the DO method. We measured the initial DO concentrations from 2, 10, and 20 m depths using spectrophotometry with a precision ratio of 0.5 µM following the standard methods of Pai et al. (1993). Then, duplicate 350 ml subsamples were incubated in BOD bottles per depth for 24–48 hours in a dark chamber at *in situ* temperature (±1°C) (see

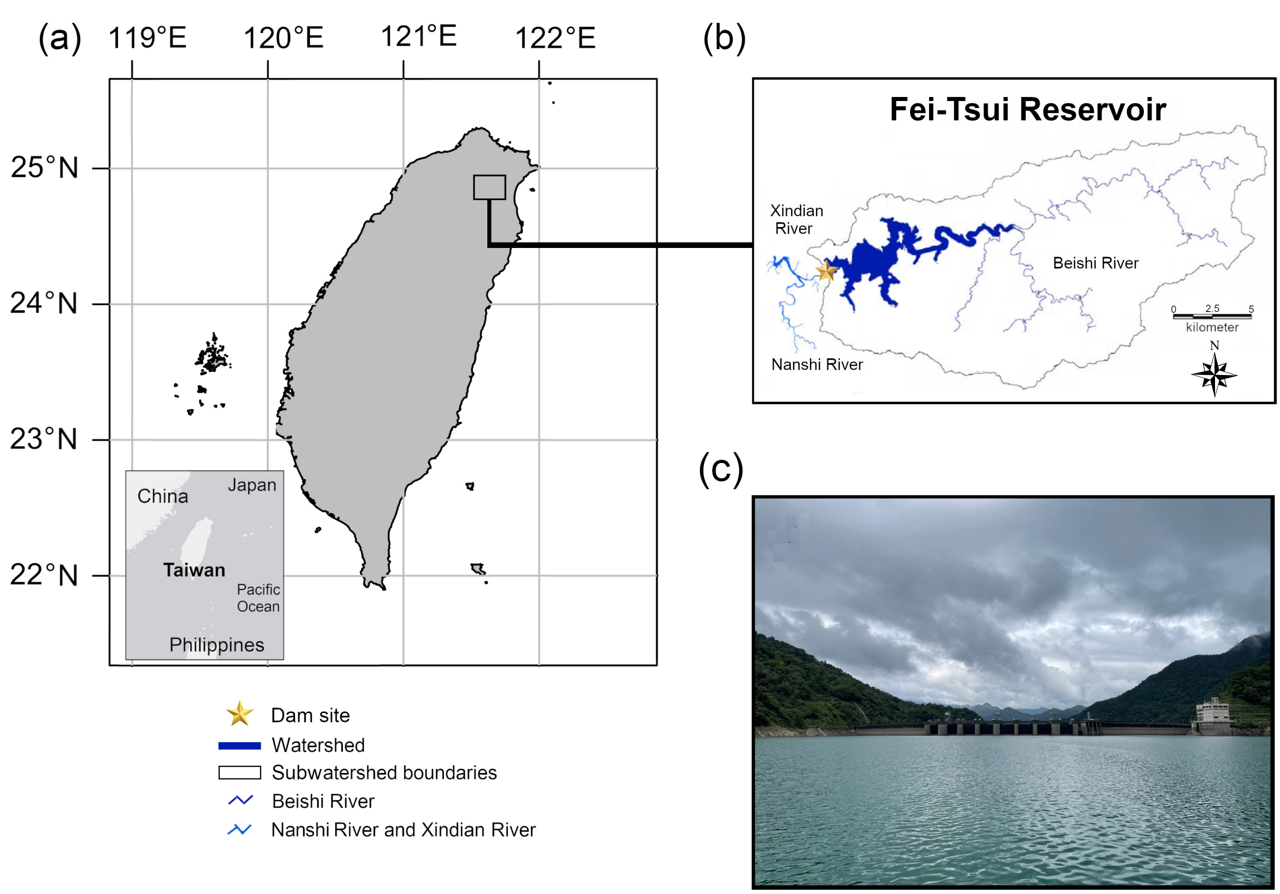

Fig. 1. Map of the study area, including (a) Taiwan's geographical location, (b) Fei-Tsui Reservoir, and (c) the dam site.

Chen et al. 2006). Next, 60 ml subsamples were taken to estimate DO concentrations (see Chen et al. 2007). Finally, CR was calculated from the difference between the initial DO and the DO concentrations treated in the dark chamber.

Bacterial biomass

Bacterial biomass was used to represent the abundance of microbial communities actively metabolizing and respiring in the FTR. Bacterial samples of approximately 100 ml were fixed with 0.1% glutaraldehyde and kept in a container at -80°C with liquid nitrogen. Then, samples were stained by SYBR-GREEN I and incubated at room temperature in the dark for 15 minutes. Stained samples were analyzed through a flow cytometer of CyFlow® Space (PARTEC) with < 1000 events sec^{-1} rate. To obtain bacterial biomass, bacterial cell count was transformed to carbon mass using a conversion factor of 20 fgC per cell (Ducklow and Carlson 1992).

Chlorophyll-*a* concentrations

Chlorophyll-*a* (Chl-*a*) served as an indicator of phytoplankton abundance and biomass in the FTR. The chl-*a* samples on the GF/F filter, collected from 300–500 ml filtered water samples, were extracted using acetone, and the concentrations were estimated using an *in vitro* fluorometer (TD-700 Laboratory Fluorometer, Turner Designs, Sunnyvale, CA, USA) following the standard protocols provided by Parson et al. (1984).

Zooplankton biomass

Zooplankton biomass was used to represent standing stocks of actively respiring and metabolizing zooplankton (Uye et al. 1998; Gonçalves et al. 2015). Zooplankton samples were collected by filtering approximately 1000 ml of depth-integrated samples between the surface and 50 m depth through a 50 µm Norpac net with a net mouth radius of 0.225 m and attached with a HYDRO-BIOS flowmeter with back-run stop, Model 438-115 (HYDRO-BIOS, Altenholz, Germany). A previous observation revealed that zooplankton density was significantly lower at depths less than 50 m. The results of net hauling indicated a filtration efficiency of 53% based on water volume (net opening area * hauling depth) (Chang et al. 2014).

In the laboratory, zooplankton samples were split, and each subsample was condensed to 120 ml with a CO_2 effervescing fixative agent, stored at 4°C for an hour, and preserved with a 2% formalin solution. Then, zooplankton samples were taxonomically identified, their lengths were measured, and their biomass was estimated. Using a stereomicroscope (Olympus SZX16 AnalSIS®) with an attached camera (OlympusDP71), we analyzed 300 zooplankton individuals per water sample. Species of zooplankton such as Rotifera, Cladocera, and Copepoda were identified using taxonomic keys by Li (2005), Wang (1961), Chiang and Du (1979), Korovchinsky (2000), Tuo and Young (2002 2011) and Shen et al. (1979). Subsequently, the length and width of Rotifera, the size of Cladocera, and the prosomal and urosomal length of Copepoda were measured using a charge-coupled device (CCD) imaging system. To obtain the biomass, each taxon-specific dry weight was calculated, and the resulting values were converted to organic carbon of 0.48 (Dumont et al. 1975; Bottrell 1976; Ruttner-Kolisko 1977; Pauli 1989; Pace and Orcutt 1981; Andersen and Hessen 1991; Ejsmont-Karabin 1998; Michaloudi 2005; de Azevedo et al. 2012). Finally, in this study, we used zooplankton biomass with a body size of < 177 µg (hereafter small zooplankton biomass) to better quantify the relationship of plankton CR with zooplankton.

Tropical cyclones

To accurately measure TC effects on FTR, only TCs with their centers impacting the Taiwan region were considered in this study. Considering the period of time for phytoplankton and bacteria to respond to an abrupt nutrient injection by TCs (Collos 1986; Arteaga et al. 2020), a TC period is defined in this study as the day the TC entered the Taiwan region up to 7 days after the last day the TC was over Taiwan. FTR was impacted by 24 TCs between 2010 and 2015, considering TC Tembin as two independent TCs as its track crossed twice into the Taiwan region (Table 1). TC residence time was determined based on the days or duration of stay of TCs within Taiwan, and data were obtained from Ventusky Meteorological (https://www.ventusky.com), supported by Deutscher Wetterdienst (DWD) and National Oceanic and Atmospheric Administration (NOAA). The minimum center pressures and maximum sustained wind speeds of individual TCs were acquired from the CWB. TC intensity was determined based on maximum sustained wind speed classified as minor, 17.2–32.6 m s^{-1}; moderate, 32.7–50.9 m s^{-1}; or intense ≥ 51.0 m s^{-1} (Ko et al. 2016).

Statistical analyses

A trapezoidal rule was used to calculate averaged euphotic depth-integrated values (*i.e.*, 0–20 m depth-averaged) to allow comparisons between each variable of the water column, including temperature, DO, DOC concentrations, nutrient concentrations, plankton CR, bacterial biomass concentrations, and chl-*a* concentrations (Hornbeck 1975). Small zooplankton biomass was set to the depth-averaged values between 0–50 m.

Data were tested for equal variances and normality using Levene's and Shapiro-Wilk tests, respectively (Table S1). Factors were analyzed for autocorrelation and a 0.6 threshold estimation was used to select factors for this study (Table S2). After autocorrelation tests, the selected variables were euphotic depth-averaged temperature, DOC, DO, NO_2^-, NO_3^-, PO_4^{3-}, chl-*a*, and 0–50 m depth-averaged small zooplankton.

To test Hypotheses 1, which provides a baseline connection between CR and environmental factors in the FTR, we examined significant relationships between the factors and CR using simple linear regression. Also, to estimate which biological factors greatly contributed most to the plankton CR, the relationships of bacterial biomass, chl-*a*, and small zooplankton biomass concentration versus plankton CR were tested using Pearson's correlation test. To test Hypothesis 2, we analyzed the relationship between the factors and CR using simple linear regression during TC and non-TC periods and compared their change of rate using slope values. To accurately identify the impact of TCs on resource availability, we compared the factors during TC and non-TC periods using the data within May–November. In all hypothesis testing procedures, the 5% significance level (based on $a = 0.05$) was used.

RESULTS

Time-series pattern and variation of plankton CR in the Fei-Tsui Reservoir

Plankton CR gradually increased between March–October and decreased between November–February (Fig. 2). Moreover, using all datasets, CR had significantly increased in TC periods (2.28 ± 1.03 mM/d) compared to non-TC periods (1.69 ± 1.07 mM/d) ($p = 0.01$, Fig. 2). But, CR dynamics analyzed using only the May–November dataset showed no significant difference between TC and non-TC periods ($p > 0.05$, Fig. S1). The results revealed the complex dynamics of plankton CR in the context of TCs and highlighted the need for further analysis to explore the underlying mechanisms.

Table 1. List of Pacific tropical cyclones that hit Taiwan from 2010 to 2015 and their characteristics

Year	Name	Residence time	Minimum center pressure (hPa)	Maximum sustained wind speed (m/s)	Intensity grade*
2010	Fanapi	1 (19 September)	940	45	Moderate
	Megi	2 (22–23 October)	935	48	Moderate
2011	Nanmadol	1 (28 August)	920	53	Intense
2012	Talim	3 (19–21 June)	985	26.7	Minor
	Doksuri	2 (28–29 June)	992	20.1	Minor
	Saola	5 (30 July–3 August)	960	37.9	Moderate
	Haikui	2 (6–7 August)	965	33.5	Moderate
	Kai-Tak	2 (14–15 August)	970	33.5	Minor
	Tembin	5 (21–25 August)	945	45	Moderate
	Tembin	3 (27–28 August)	965	35	Moderate
	Jelawat	2 (27–28 September)	910	55.9	Intense
2013	Soulik	2 (12–13 July)	925	51.4	Intense
	Usagi	2 (21–23 September)	910	55.9	Intense
	Fitow	2 (5–6 October)	960	37.9	Moderate
	Krosa	3 (1–3 November)	970	37.9	Moderate
2014	Hagibis	3 (13–15 June)	996	20.1	Minor
	Matmo	2 (22–23 July)	965	35.8	Moderate
	Fung-wong	3 (20–22 September)	985	22.4	Minor
2015	Noul	1 (11 May)	920	55.9	Intense
	Linfa	2 (10–11 July)	980	26.8	Minor
	Soudelor	2 (7–8 August)	900	58	Intense
	Goni	2 (22–23 August)	930	51.4	Intense
	Dujuan	3 (27–29 September)	925	55.9	Intense
	Koppu	3 (19–21 October)	925	51.4	Intense

*The intensity grade was based on the maximum sustained wind speed near the center: minor, < 32.7 m/s; moderate, 32.7–50.9 m/s; intense, > 50.9 m/s.

Relationship between plankton CR and environmental factors

Simple linear regression analysis showed that euphotic depth-averaged temperature had a strong positive influence on CR in FTR ($p < 0.001$, Fig. 3a). Euphotic depth-averaged DO and DOC did not show a significant influence on CR (both $p > 0.05$, Fig. 3b–c). Euphotic depth-averaged NO_2^- and NO_3^- strongly influenced CR; the former had a positive influence, and the latter had a negative influence (both $p < 0.001$, Fig. 3d–e). Euphotic depth-averaged PO_4^{3-} did not show a significant influence on CR ($p = 0.10$, Fig. 3f). These results indicated that CR variability in the FTR was primarily influenced by euphotic depth-averaged temperature and nutrients (NO_2^- and NO_3^-), among other environmental variables.

The different planktonic components' contributions to CR are shown in figure 4. CR was highly positively correlated with bacterial biomass ($p < 0.001$, Fig. 4a), while it was weakly correlated with chlorophyll *a* ($p = 0.09$, Fig. 4b) and small zooplankton biomass ($p = 0.37$, Fig. 4c). Thus, plankton CR was supported by bacterial biomass in the FTR.

Relationship of environmental factors and plankton CR in TC and non-TC periods

Temperature substantially influenced CR during the TC and non-TC periods (Fig. 5), complementing the findings above. An increasing euphotic depth-averaged temperature enhanced CR rate in TC periods and in non-TC periods using all datasets and the May–November dataset (all $p < 0.05$, Fig. 5a); however, a higher value of regression slope was found in TC periods ($b = 0.48$, Fig. 5a) compared to non-TC periods (both $b = 0.15$, Fig. 5a). Accumulated precipitation during the TC periods had no direct effect on CR ($p = 0.59$, Fig. 5b).

Changes in environmental factors between TC and non-TC periods

Accumulated precipitation was significantly higher during TC periods than non-TC periods, confirming that TCs were accompanied by heavy precipitation ($p = 0.002$, Fig. 6a, Fig. S2a). Euphotic depth-averaged DOC concentration was higher during the TC period, but this change was not significant ($p = 0.28$, Fig. 6b, Fig. S2d). Euphotic depth-averaged NO_2^- and NO_3^- did not significantly change between TC and non-TC periods ($p = 0.26$ and $p = 0.42$, Fig. 6c–d, Fig. S2e–f). Euphotic depth-averaged PO_4^{3-} concentration was limited and did not significantly change between TC and non-TC periods ($p = 0.35$, Fig. 6e, Fig. S2g).

DISCUSSION

We examined how plankton CR is affected by environmental factors, particularly during periods when TCs are impacting FTR, a phosphate-limited freshwater ecosystem. Plankton CR was typically affected by euphotic depth-averaged temperature, NO_2^-, and NO_3^- in the FTR, supporting Hypothesis 1. It was found that bacteria significantly contribute to CR, among other biological factors. Moreover, during TC periods, the increase in plankton CR was higher than usual, attributed to a higher and ideal euphotic depth-averaged temperature, supporting Hypothesis 2. Furthermore, the concentration of limiting nutrient factors was supplied by the indirect effect of precipitation and ultimately increased the CR. These findings show that plankton CR in the FTR alters due to environmental changes. With the TC effects, CR tends to increase as the water conditions during TC periods are favorable. This implies that strong weather events indirectly affect biological activities in nutrient-limited freshwater ecosystems.

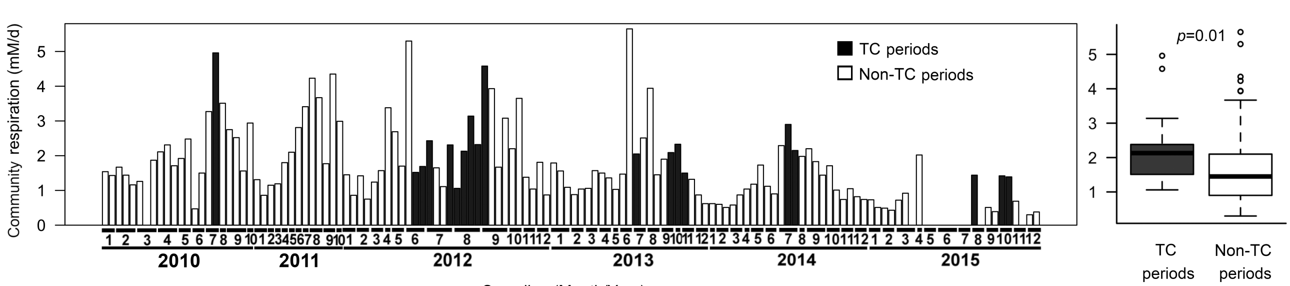

Fig. 2. Timeseries and boxplot displaying differences in euphotic depth-averaged plankton community respiration in tropical cyclone (TC) and non-TC periods in the Fei-Tsui Reservoir from January 2010 to December 2015. The euphotic depth spans from 0–20 m on average. Each bar represents individual sampling. Different bar colors indicate the TC and Non-TC periods. periods. The *p*-value estimated by the Mann-Whitney *U* test is shown.

Factors affecting plankton CR dynamics

Euphotic depth-averaged water temperature is a significant environmental factor in regulating plankton CR in the FTR, supporting Hypothesis 1. We find that euphotic depth-averaged water temperature positively influenced the seasonal variation of CR, which is consistent with many studies (Hall and Cotner 2007; Scofield et al. 2015; Pace et al. 2021; García et al. 2023). This information has significant implications for how biological activities respond to increasing global warming. Additionally, our study further

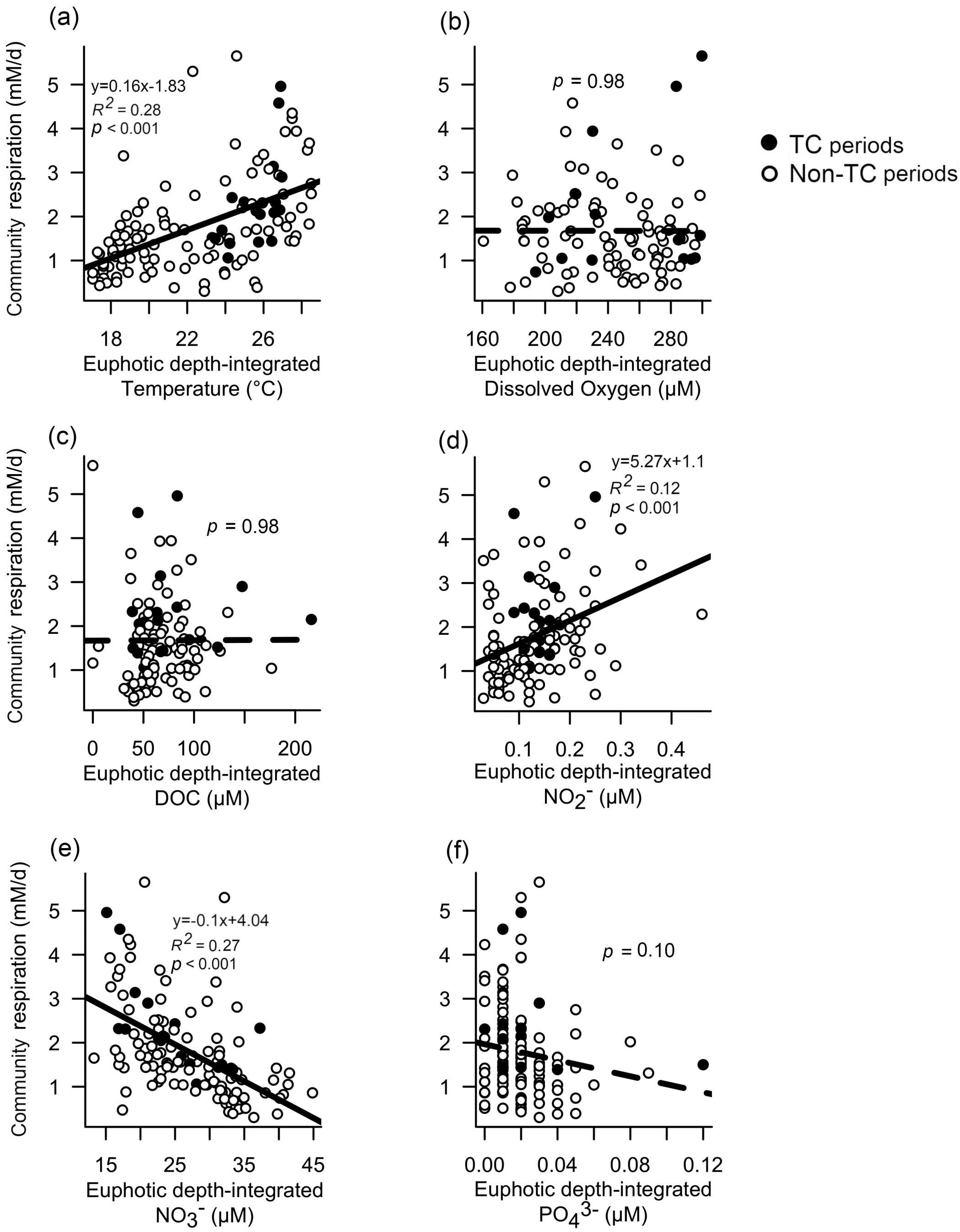

Fig. 3. Relationships between euphotic depth-averaged plankton community respiration versus (a) euphotic depth-averaged temperature, (b) dissolved oxygen (DO), (c) dissolved organic carbon (DOC), (d) NO_2^-, (e) NO_3^-, and (f) PO_4^{3-} concentrations in the Fei-Tsui Reservoir from January 2010 to December 2015. The euphotic depth spans from 0–20 m on average. Black and white circles represent tropical cyclone (TC) and non-TC periods, respectively. Estimated R^2 and p-values by simple linear regression analysis are shown. The solid line indicates a significant relationship ($p \leq 0.001$) and the broken line indicates no significant relationship ($p > 0.05$).

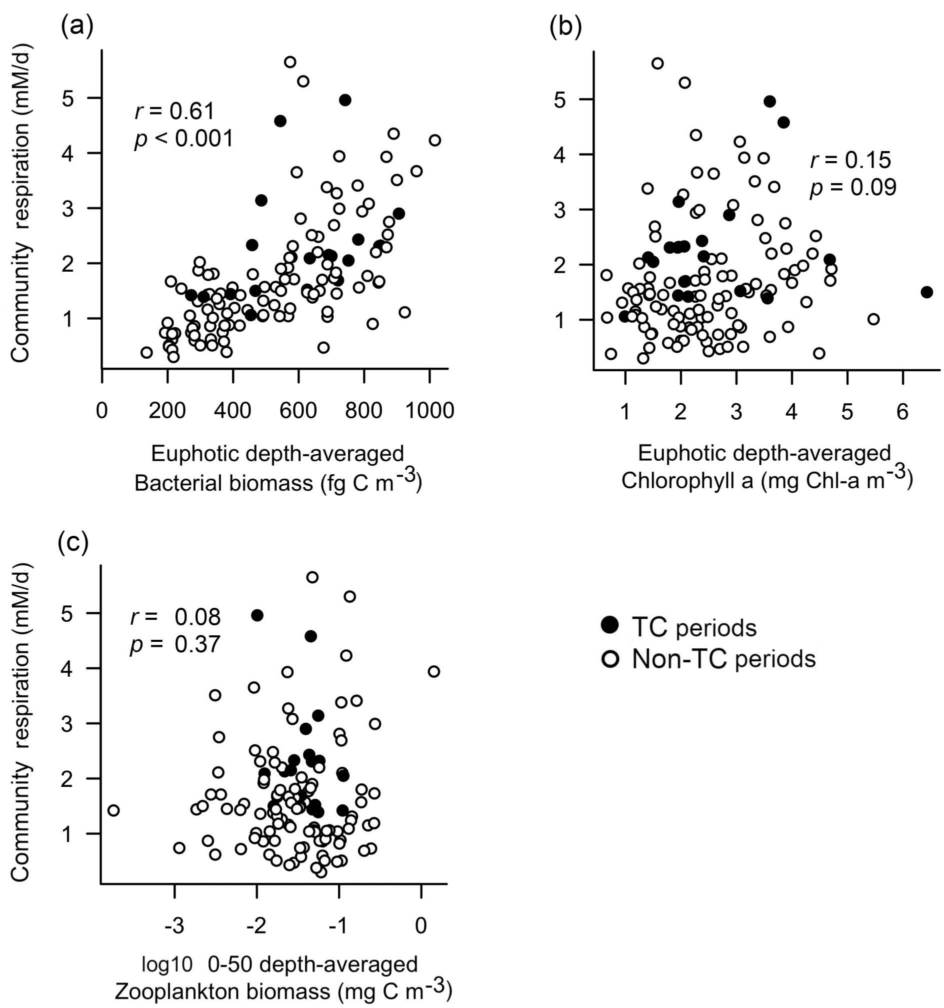

Fig. 4. Relationships between euphotic depth-averaged plankton community respiration versus (a) euphotic depth-averaged bacterial biomass, (b) chlorophyll a, and (c) $\log_{10}$ 0–50 m depth-averaged small zooplankton biomass in the Fei-Tsui Reservoir from January 2010 to December 2015. The euphotic depth spans from 0–20 m on average. Black and white circles represent tropical cyclone (TC) and non-TC periods, respectively. The correlation coefficient (*r*) and *p*-values estimated by Pearson's correlation test are shown.

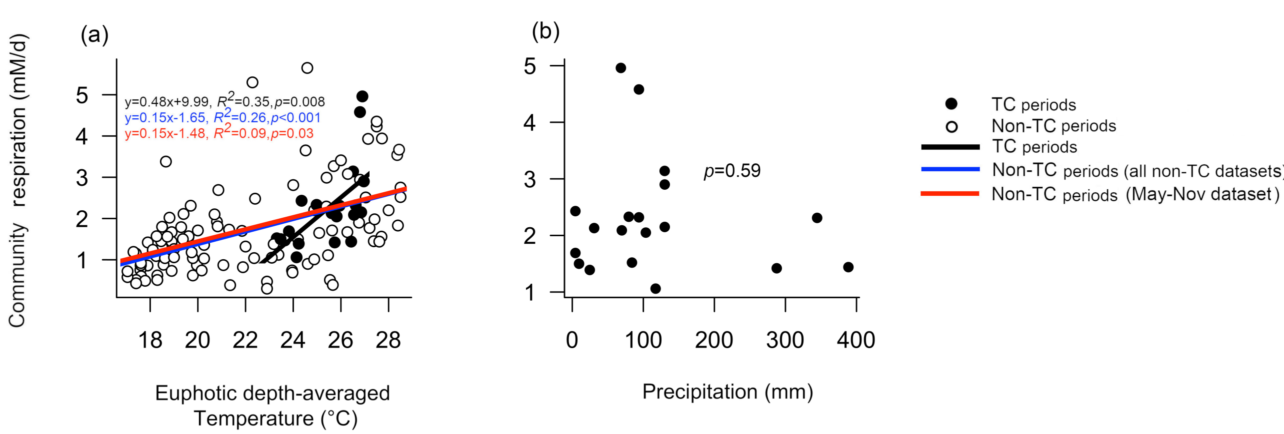

Fig. 5. Relationships between euphotic depth-averaged plankton community respiration versus (a) euphotic depth-averaged temperature during tropical cyclone (TC) periods and non-TC periods (all datasets and May–November dataset) and (b) precipitation during TC periods in the Fei-Tsui Reservoir. The euphotic depth spans from 0–20 m on average. Black and white circles represent TC and non-TC periods, respectively. Estimated R^2 and *p*-values by simple linear regression analysis are shown. The solid line indicates a significant relationship ($p \leq 0.05$).

demonstrated that plankton CR may be enhanced during TC passages. Previous findings showed that TCs from the Pacific Ocean typically crossed and/or hit Taiwan between May and November (Ko et al. 2017), with increased euphotic depth water temperatures during this period; this explains a higher plankton CR. Given the significant relationship of temperature with plankton CR, understanding the dynamics of these factors is crucial for predicting CR variability during TC periods. Therefore, additional analyses were conducted to examine the interactions between CR and water temperature and their implications for ecosystem

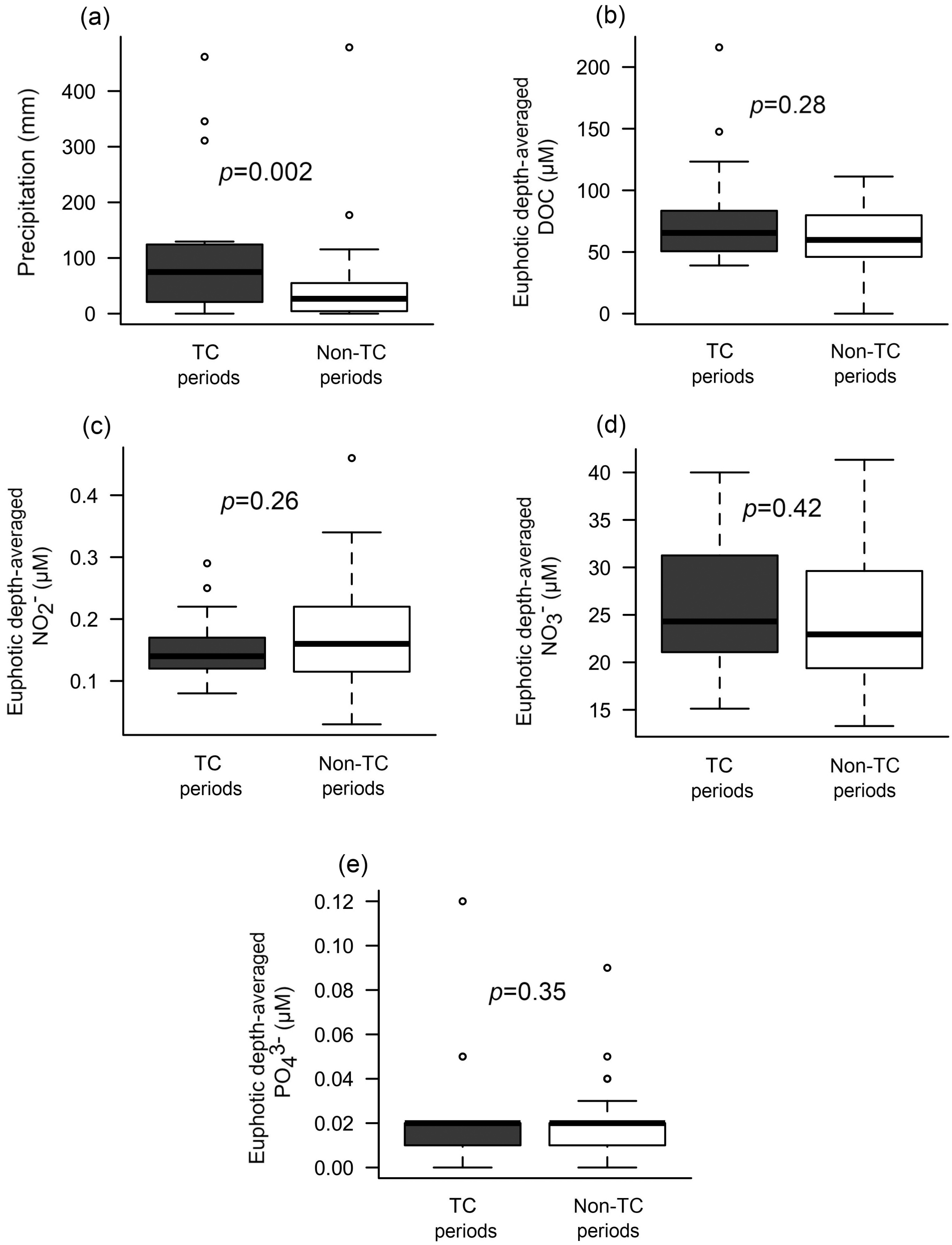

Fig. 6. Boxplots comparing (a) precipitation, (b) euphotic depth-averaged dissolved organic carbon (DOC), (c) NO_2^-, (d) NO_3^-, (e) PO_4^{3-} concentrations between tropical cyclone (TC) periods and non-TC periods using the May–November dataset. The euphotic depth spans from 0–20 m on average. Estimated *p*-values by the Mann-Whitney *U* test are shown.

functioning while being impacted by TCs.

Additionally, plankton CR in the FTR shows varying responses to euphotic depth-averaged DO, DOC, NO_2^-, and NO_3^-, which are attributed to many external influences (Rajesh and Rehana 2022; Walter et al. 2023). Weak responses of plankton CR with DO and DOC dynamics indicated that other factors may have a greater impact on CR. For example, temperature, limiting resources, and predation pressure can all affect plankton metabolism and respiration rates (García et al. 2023). Moreover, our study further showed that NO_2^- is a valuable resource for enhancing CR levels. As precipitation increases, it intensifies NO_2^--leaching from deep soils (Mastrocicco et al. 2019), increasing its concentration within the system (Fig. S2) and positively influencing plankton CR. At the same time, despite the supply of NO_3^- and its importance as a resource for plankton CR, its abundance with increased precipitation does not improve CR, but their relationship reflects seasonal fluctuations (Hermansson et al. 2001; Smith and Prairie 2004). Seasonal NO_3^- fluctuations have been observed in the FTR, coinciding with the seasonal patterns of summer stratification (March–October) and winter mixing (November–February) (Itoh et al. 2015). Decreased euphotic depth-averaged NO_3^- concentration during summer stratification results from strong nutrient uptake by plankton (*e.g.*, bacteria and phytoplankton), whereas accumulated euphotic depth-averaged NO_3^- concentration during winter mixing is due to the effects of upwelling and reduced phytoplankton production (Itoh et al. 2015; Ko et al. 2017). In contrast, PO_4^{3-} concentration in the FTR is poor, and species compete for such resources; thus, we failed to observe its dynamics in the system. Nonetheless, these findings indicate that although environmental factors may play a role, they are overshadowed by stronger external factors that impact the relationship with plankton CR.

In addition to abiotic factors, plankton CR has a highly significant link to bacterial biomass, but it has a weak association with chlorophyll-*a* and small zooplankton biomass. Increased CR is associated with higher phytoplankton abundance in many aquatic ecosystems, such as estuaries, coastal areas, and marine waters (Jensen et al. 1990; Smith and Kemp 1995; Chen et al. 2003), but our findings demonstrate that in the FTR, plankton CR is supported by bacterial communities. Bacterial respiration rate is closely associated with temperature and is also increased by DOC or indirectly by zooplankton sloppy eating and excretion (Hall and Cotner 2007; García et al. 2023). However, these findings suggest that high temperature enhances microbial activities and majorly contributes to total CR in the FTR.

Plankton CR responses to environmental factors during TC periods

Plankton CR increases one-fold during TC periods, in contrast to non-TC periods, although this effect was less pronounced in 2013. To further elucidate the CR increase, it is essential to consider the environmental factors and mechanisms at play during TC periods. Moreover, in July 2013, moderate precipitation (ca. 103.5 mm) led to anthropogenic discharge from the reservoir, which could have diluted plankton concentrations (Ko et al. 2016), leading to a less evident plankton CR increase. Conversely, between September and November 2013, the time-series pattern shows that plankton CR increased marginally during TC periods compared to non-TC periods. This trend of increasing CR during TC periods is consistent in other years, suggesting that TC passages enhanced plankton CR.

Plankton CR increases during TC periods due to a higher euphotic depth-averaged water temperature, an ideal temperature for species metabolism and respiration, supporting Hypothesis 2. The euphotic depth-averaged temperature rises to 23–27°C during TC periods. The relationship between euphotic depth-averaged temperature and CR displays a higher rate of positive change, represented by the regression slope, during the TC periods; this indicates a greater likelihood for plankton CR to increase during TC periods compared to non-TC periods. It is also important to note that during TCs, there may be supplies of limiting resources for plankton CR in addition to the increased euphotic depth-averaged water temperature leading to higher CR rates.

Limiting nutrient factors that positively influence plankton CR during TC periods may be supplied by the precipitation, revealing an indirect influence on plankton CR (Hoover et al. 2006). In this study, accumulated precipitation significantly increased during TC periods, introducing limiting resources for bacteria, zooplankton, and phytoplankton (Hoover et al. 2006; Tornevi et al. 2014; Ko et al. 2016). Previous studies have identified that tributary discharge into the dam site and the mixing of subsurface water were two major sources of limiting resources in the FTR (Chou et al. 2006; Itoh et al. 2015). However, an intense stream runoff resulting from moderate (80–120 mm) to heavy precipitation (> 300 mm) suggests natural dilution in the dam (Ko et al. 2017). Although there is a supply of resources, the increase in NO_2^-, NO_3^-, and PO_4^{3-} concentrations remains unnoticed for the following reasons. Nutrient injections through stream runoff were lower at the euphotic layer (*i.e.*, 0–20 m depth) and then increased with depth (Tseng et al. 2010). Additionally, species (*e.g.*, phytoplankton and bacteria) rapidly assimilated the limited concentration of supplied nutrients, especially PO_4^{3-}, in the euphotic layer (Ko et al. 2016). Lastly, FTR may perform an operating scheme regarding reservoir release depending on the water level, which could impact nutrient levels (Chou et al. 2006).

Given that our study focused on TC effects on plankton CR in a deep and phosphate-limited freshwater ecosystem, further research is warranted to explore the TC effects on the relationship of CR and environmental factors in different aquatic ecosystems (*e.g.*, shallow lakes, eutrophic lakes). It is important to emphasize that with a higher frequency of intense TCs projected for the Western North Pacific in most climate change scenarios and the influence on TC attributes still unknown, impacts on CR from TCs may be expected to increase in the near future (IPCC 2021; Utsumi and Kim 2022).

CONCLUSIONS

This study revealed that plankton CR tends to increase during TC periods as the water conditions become ideal. Plankton CR in FTR is typically associated with euphotic depth-averaged temperature and nutrient resources, and is primarily supported by bacterial biomass; this information has implications for the species' responses under increasing global warming conditions. Furthermore, it has been observed that during TC periods, there is an increase in plankton CR due to a rise in euphotic depth-averaged temperature and the supply of limiting nutrient factors through stream runoff in the dam. Understanding the plankton CR response to TCs provides insight into how extreme weather events have significantly impacted biological activities in nutrient-limited freshwater ecosystems. With the expected increase in the frequency of TCs with future climate change, TC effects on aquatic ecosystems are expected to become more pronounced and significant in the long term.

List of Abbreviations

BOD: Biochemical Oxygen Demand.
CCD: Charge-coupled device.
Chl-*a*: Chlorophyll-*a*.
CO_2: Carbon dioxide.
CR: Community respiration.
CTD: Conductivity, Temperature, Depth.
CWB: Central Weather Bureau.
DO: Dissolved oxygen.
DOC: Dissolved organic carbon.
DWD: Deutscher Wetterdienst.
FIA: Fabricated Flow Injection Analyzer.
FTR: Fei-Tsui Reservoir.
H_3PO_4: Phosphoric acid.
NOAA: National Oceanic and Atmospheric Administration.
Non-TC periods: Non-Tropical Cyclone periods.
NO_2^-: Nitrite.
NO_3^-: Nitrate.
O_2: Oxygen.
PO_4^3: Phosphate.
TC: Tropical cyclone.
TC periods: Tropical Cyclone periods.

Acknowledgments: The authors thank all the researchers and the Taipei Fei-Tsui Reservoir Administration for their assistance during the fieldwork at the study site. We also thank Stephen Griffith for his helpful comments on writing.

Authors' contributions: ESPDP, CCL, and CYK conceptualized the study. CCL and FKS conducted the plankton CR, bacterial biomass, phytoplankton, and nutrient metrics. CHH conducted zooplankton metrics. ESPDP analyzed and wrote a first draft of the manuscript with contributions from CCL. All the authors approved the final manuscript.

Competing interests: ESPDP, CCL, and CHH declare no conflict of interest. FKS has received a research grant from Academia Sinica, Taiwan (AS-SS-111-04-4). CYK has received research grants from the MOST, Taiwan (NSTC110-2636-B-002-019-, NSTC111-2636-B-002-022-, NSTC112-2636-B-002-013-).

Availability of data and materials: The data are available from CYK upon reasonable request.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Andersen T, Hessen D. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnol Oceanogr **36(4):**807–814. doi:10.4319/lo.1991.36.4.0807.
Arteaga LA, Boss E, Behrenfeld MJ, Westberry TK, Sarmiento JL. 2020. Seasonal modulation of phytoplankton biomass in the Southern Ocean. Nat Commun **11:**5364. doi:10.1038/s41467-020-19157-2.
Bueno E, Mesa S, Bedmar EJ, Richardson DJ, Delgado MJ. 2012. Bacterial adaptation of respiration from oxic to microoxic and anoxic conditions: redox control. Antioxid Redox Signal **16(8):**819–852. doi:10.1089/ars.2011.4051.

Bottrell H. 1976. A review of some problems in zooplankton production studies. North-West J Zool **24:**419–456.

Chang CW, Shiah FK, Wu JT, Miki T, Hsieh Ch. 2014. The role of food availability and phytoplankton community dynamics in the seasonal succession of zooplankton community in a subtropical reservoir. Limnologica **46:**131–138. doi:10.1016/j.limno.2014.01.002.

Chen CC, Shiah FK, Gong GC, Chiang KP. 2003. Planktonic community respiration in the East China Sea: importance of microbial consumption of organic carbon. Deep-Sea Res II **50:**1311–1325. doi:10.1016/S0967-0645(03)00025-0.

Chen CC, Chiang KP, Gong GC, Shiah FK, Tseng CM, Liu KK. 2006. Importance of planktonic community respiration on the carbon balance of the East China Sea in summer. Glob Biogeochem Cycles **20:**1–14. doi:10.1029/2005GB002647.

Chen CC, Gong GC, Shiah FK. 2007. Hypoxia in the East China Sea: One of the largest coastal low-oxygen areas in the world. Mar Environ Res **64:**399–408. doi:10.1016/j.marenvres.2007.01.007.

Chen J, Wang Z, Tam CY, Lau NC, Lau DSD, Mok HY. 2020. Impacts of climate change on tropical cyclones and induced storm surges in the Pearl River Delta region using pseudo-global-warming method. Sci Rep **10:**1965. doi:10.1038/s41598-020-58824-8.

Chiang SC, Du NS. 1979. Fauna sinica; crustacean: freshwater Cladocera. Freshwater Cladocera. Available at: http://agris.fao.org/agris-search/search.do?recordID=XF2015041144.

Chou WS, Lee TC, Lin JY, Yu SL. 2006. Phosphorus Load Reduction Goals for Feitsui Reservoir Watershed, Taiwan. Environ. Monit Assess **131:**395–408. doi:10.1007/s10661-006-9485-1.

Chow MF, Lai CC, Kuo HY, Lin CH, Chen TY, Shiah FK. 2017. Long Term Trends and Dynamics of Dissolved Organic Carbon (DOC) in a Subtropical Reservoir Basin. Water **9(545):**1–14. doi:10.3390/w9070545.

Collos Y. 1986. Time-lag algal growth dynamics: biological constraints primary production in aquatic environments. Mar Ecol Prog Ser **33:**193–206. doi:10.3354/meps033193.

de Azevedo F, Dias JD, de Souza Magalhães Braghin L, Bonecker CC. 2012. Length-weight regressions of the microcrustacean species from a tropical floodplain. Acta Limnol Bras **24(1):**1–11. doi:10.1590/s2179-975x2012005000021.

Del Giorgio PA, Williams PJB. 2005. Respiration in aquatic ecosystems: history and background. *In*: Del Giorgio PA, Williams PJB (eds) Respiration in aquatic ecosystems, New York: Oxford Univ Press, pp. 1–17.

Doubek JP, Anneville O, Dur G, Lewandowska AM, Patil VP, Rusak JA, Salmaso N, Seltmann, CT, Straile D, Urrutia-Cordero P, Venail P, Adrian R, Alfonso MB, DeGasperi CL, de Eyto E, Feuchtmayr H, Gaiser EE, Girdner SF, Graham JL, Grossart HP, Hejzlar J, Jacquet S, Kirillin G, Llames ME, Matsuzaki SIS, Nodine ER, Piccolo MC, Pierson DC, Rimmer A, Rudstam LG, Sadro S, Swain HM, Thackeray SJ, Thiery W, Verburg P, Zohary T, Stockwell JD. 2021. The extent and variability of storm-induced temperature changes in lakes measured with long-term and high-frequency data. Limnol Oceanogr **66:**1979–1992. doi:10.1002/lno.11739.

Ducklow HW, Carlson CA. 1992. Oceanic Bacterial Production. *In*: Advances in Microbial Ecology, Volume 12. Springer: Berlin/Heidelberg, Germany, pp. 113–181.

Dumont HJ, Velde I, Dumont S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia **19(1):**75–97. doi:10.1007/BF00377592.

Emanuel KA. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature **436:**686–688. doi:10.1038/nature03906.

Ejsmont-Karabin J. 1998. Empirical equations for biomass calculation of planktonic rotifers. Polskie Archiwum Hydrobiologii/Polish Archives of Hydrobiology **45(4):**513–522.

Field CB, Mortsch LD, Brklacich M, Forbes DL, Kovacs P, Patz JA, Running SW, Scott MJ. 2007. North America. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Cambridge University Press, Cambridge, UK, pp. 617–652.

Gao X, Chen H, Gu B, Jeppesen E, Xue Y, Yang J. 2021. Particulate organic matter as causative factor to eutrophication of subtropical deep freshwater: Role of typhoon (tropical cyclone) in the nutrient cycling. Water Res **188:**116470. doi:10.1016/j.watres.2020.116470.

García FC, Clegg T, O'Neill DB, Warfield R, Pawar S, Yvon-Durocher G. 2023. The temperature dependence of microbial community respiration is amplified by changes in species interactions. Nat Microbiol **8:**272–283. doi:10.1038/s41564-022-01283-w.

Gonçalves DA, Marques SC, Primo AL, Marthino F, Bordalo MDB, Pardal MÂ. 2015. Mesozooplankton biomass and copepod estimated production in a temperate estuary (Mondego estuary): effects of processes operating at different timescales. Zool Stud **54:**57. doi:10.1186/s40555-015-0135-6.

Hall EK, Cotner JB. 2007. Interactive effect of temperature and resources on carbon cycling by freshwater bacterioplankton communities. Aquat Microb Ecol **49:**35–45. doi:10.3354/ame01124.

Hermansson M, Lindgren PE, Rosen P. 2001. Effects of the nitrate supply mode on denitrifying populations in activated sludge. FEMS Microbiol Ecol **36(3):**173–180.

Hoover RS, Hoover D, Miller M, Landry MR, DeCarlo EH, Mackenzie FT. 2006. Zooplankton response to storm runoff in a tropical estuary: bottom-up ad top-down controls. Mar Ecol Prog Ser **318:**187–201. doi:10.3354/meps318187.

Hornbeck RW. 1975. Numerical Methods. Prentice-Hall, Englewood Cliffs. NJ, USA.

Huang S, Du Y, Yi J, Liang F, Qian J, Wang N, Tu W. 2022. Understanding human activities in response to typhoon Hato from multi-source geospatial big data: A case study in Guangdong, China. Remote Sensing **14:**1269. doi:10.3390/rs14051269.

Iavorivska L, Boyer EW, DeWalle, DR. 2016. Atmospheric deposition of organic carbon via precipitation. Atmos Environ **146:**153–163. doi:10.1016/j.atmosenv.2016.06.006.

IPCC. 2021. Summary for Policymakers. *In*: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI, Huang M, Leitzell K, Lonnoy E, Matthews JBR, Maycock TK, Waterfield T, Yelekçi O, Yu R, Zhou B (eds) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 3–32. doi:10.1017/9781009157896.001.

Itoh M, Kobayashi Y, Chen TY, Tokida T, Fukui M, Kojima H, Miki T, Tayasu I, Shiah FK, Okuda N. 2015. Effect of interannual variation in winter vertical mixing on CH_4 dynamics in a subtropical reservoir. J Geophys Res Biogeosci **120:**1–16. doi:10.1002/2015JG002972.

Jansson M, Hickler T, Jonsson A, Karlsson J. 2008. Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in Subarctic Sweden. Ecosystem **11:**367–276. doi:10.1007/s10021-008-9127-2.

Jensen LM, Sand-Jenson K, Marcher S, Hansen M. 1990. Plankton community respiration along a nutrient gradient in a shallow

Danish estuary. Mar Ecol Prog Ser **61:**75–85.

Jin Q, Kirk MF. 2018. pH as a Primary Control in Environmental Microbiology: 1. Thermodynamic Perspective. Front Environ Sci **6:**21. doi:10.3389/fenvs.2018.00021.

Klug JL, Richardson DC, Ewing HA, Hargreaves BR, Samal NR, Vachon D, Pierson DC, Lindsey AM, O'Donnell DM, Effler SW, Weathers KC. 2012. Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. Environ Sci Technol **46(21):**11693–11701. doi:10.1021/es302063v.

Ko CY, Lai CC, Chen TY, Hsu HH, Shiah FK. 2016. Typhoon effects on phytoplankton responses in a semi-closed freshwater ecosystem. Mar Freshw Res **67:**546–555. doi:10.1071/MF14294.

Ko CY, Lai CC, Hsu HH, Shiah FK. 2017. Decadal phytoplankton dynamics in response to episodic climatic disturbances in a subtropical deep freshwater ecosystem. Water Res **109:**102–113. doi:10.1016/j.watres.2016.11.011.

Korovchinsky NM. 2000. Redescription of *Diaphanosoma dubium* Manuilova, 1964 (Branchiopoda: Ctenopoda: Sididae), and description of a new, related species. Hydrobiologia **441:**73–92. doi:10.1023/A:1017574921558.

Li CH. 2005. A taxonomic study of freshwater rotifers, Brachionina in Taiwan. National Hsinchu University of Education, Hsinchu, Taiwan.

Lin HC, Tsai JW, Tada K, Matsumoto H, Chiu CY, Nakayama K. 2022. The impacts of the hydraulic retention effect and typhoon disturbance on the carbon flux in shallow subtropical mountain lakes. Sci Total Environ **803:**150044. doi:10.1016/j.scitotenv.2021.150044.

Liu KK, Iseki K, Chao SY. 2000. Continental margin carbon fluxes. *In*: Hanson RB, Ducklow HW, Field JG. (eds) The changing ocean carbon cycle: A midterm synthesis of the Joint Global Ocean Flux Study. Cambridge University Press, Cambridge, pp. 187–239.

López-López L, Molinero JC, Tseng LC, Chen QC, Houng JW, Hwang JS. 2012. Effects of typhoons on gelatinous carnivore zooplankton off Northern Taiwan. Cah Biol Mar **53:**349–355.

Michaloudi E. 2005. Dry weights of the zooplankton of Lake Mikri Prespa (Macedonia, Greece). Belg J Zool **135(2):**223–227.

Mastrocicco M, Colombani N, Soana E, Vincenzi F, Castaldelli G. 2019. Intense rainfalls trigger nitrite leaching in agricultural soils depleted in organic matter. Sci Total Environ **665:**80–90. doi:10.1016/j.scitotenv.2019.01.306.

Pace ML, Orcutt JD. 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnol Oceanogr **26(5):**822–830. doi:10.4319/lo.1981.26.5.0822.

Pace ML, Buelo CD, Carpenter SR. 2021. Phytoplankton biomass, dissolved organic matter, and temperature drive respiration in whole lake nutrient additions. Limnol Oceanogr **66:**2174–2186. doi:10.1002/lno.11738.

Pai SC, Gong GC, Liu KK. 1993. Determination of dissolved oxygen in seawater by direct spectrophotometry of total iodine. Mar Chem **41:**343–351. doi:10.1016/0304-4203(93)90266-Q.

Parsons TR, Maita Y, Lalli CM. 1984. A Manual of Chemical and Biological Methods for Sea Water Analysis. Pergamon, New York, USA.

Pauli HR. 1989. A new method to estimate individual dry weights of rotifers. Hydrobiol **186–187(1):**355–361. doi:10.1007/BF00048932.

Poff NL, Brinson MM, Day JWJ. 2002. Aquatic ecosystems and Global climate change: Potential Impacts on Inland Freshwater and Coastal Wetland Ecosystems in the United States. 2002. Available from: www.pewclimate.org. Retrieved 26 June 2019.

Rajesh M, Rehana S. 2022. Impact of climate change on river water temperature and dissolved oxygen: Indian riverine thermal regimes. Sci Rep **12:**9222. doi:10.1038/s41598-022-12996-7.

Russell JB. 1992. Another explanation for the toxicity of fermentation acids at low pH: anion accumulation versus uncoupling. J Appl Bacteriol **73:**363–370. doi:10.1111/j.1365-2672.1992.tb04990.x.

Ruttner-Kolisko A. 1977. Suggestions for biomass calculations of planktonic rotifers. Archiv fur Hydrobiologie Beihefte **21:**71–76.

Scofield V, Jacques SMS, Guimarães JRD, Farjalla VF. 2015. Potential changes in bacterial metabolism associated with increased water temperature and nutrient inputs in tropical humic lagoons. Front Microbiol **6:**310. doi:10.3389/fmicb.2015.00310.

Shen JR, Tai AY, Zhang CZ, Li ZY, Song DX, Chen G. 1979. Fauna sinica, crustacean, freshwater copepod. Institute of zoology, Academia Sinica, Beijing, China. (in Chinese)

Smith EM, Kemp WM. 1995. Seasonal and regional variations in plankton community respiration for Chesapeake Bay. Mar Ecol Prog Ser **116:**217–231.

Smith EM, Prairie YT. 2004. Seasonal changes in the contributions of different microbial groups to the carbon flow from submerged macrophytes to bacterioplankton in a clear-water eutrophic lake. FEMS Microbiol Ecol **48(1):**1–11.

Tornevi A, Bergstedt O, Forsberg B. 2014. Precipitation Effects on Microbial Pollution in a River: Lag Structures and Seasonal Effect Modification. PLoS ONE **9(5):**e98546. doi:10.1371/journal.pone.0098546.

Tseng YF, Hsu TC, Chen YL, Kao SJ, Wu JT, Lu JC, Lai CC, Kuo HY, Lin CH, Yamamoto Y, Xiao T, Shiah FK. 2010. Typhoon effects on DOC dynamics in a phosphate-limited reservoir. Aquat Microb Ecol **60:**247–260. doi:10.3354/ame01423.

Tuo YH, Young SS. 2002. Freshwater Cladocera (Crustacea: Branchiopoda: Cladocera) of Taiwan (Master's Thesis). National Hsinchu Teachers College, Hsinchu, Taiwan.

Tuo YH, Young SS. 2011. Taxonomy of Chydoridae (Crustacea: Branchiopoda: Cladocera) from Taiwan. TW J of Biodivers **13(3):**18–212. doi:10.7064/TJB.201107.0183.

Utsumi N, Kim H. 2022. Observed influence of anthropogenic climate change on tropical cyclone heavy rainfall. Nat Clim Chang **12:**436–440. doi:10.1038/s41558-022-01344-2.

Uye SI, Nagano N, Shimazu T. 1998. Biomass, production and trophic roles of micro- and net-zooplankton in Dokai Inlet, heavily eutrophic inlet, in summer. Plankton Biol Ecol **45:**171–182.

Vecchi GA, Soden BJ. 2007. Effect of remote sea surface temperature change on tropical cyclone potential intensity. Nature **450:**1066–1070. doi:10.1038/nature06423.

Vikström K, Wikner J. 2019. Importance of Bacterial Maintenance Respiration in a Subarctic Estuary: a Proof of Concept from the Field. Microb Ecol **77(3):**574–586. doi:10.1007/s00248-018-1244-7.

Walter JA, Coombs NJ, Pace ML. 2023. Synchronous variation of dissolved organic carbon in Adirondack lakes at multiple timescales. Limnol Oceanogr Lett **8:**649–656. doi:10.1002/lol2.10328.

Wang J. 1961. Fauna of the freshwater Rotifera of China. Academia Sinica.

Ying M, Knutson TR, Kamahori H, Lee TC. 2012. Impacts of climate change on tropical cyclones in the western North Pacific basin. Part II: Late twenty-first century projections. Trop Cyclone Res Rev 1 **2:**231–241. doi:10.6057/2012TCRR02.09.

Supplementary Materials

Fig. S1. Boxplots comparing euphotic depth-averaged plankton community respiration between tropical cyclone (TC) and non-TC periods using data from May to November of each year's study period. The euphotic depth spans from 0–20 m on average. The *p*-value estimated by the Mann-Whitney *U* test is shown. (download)

Fig. S2. Time series pattern of (a) precipitation, (b) euphotic depth-averaged temperature, (c) dissolved oxygen (DO), (d) dissolved organic carbon (DOC), (e) NO_2^-, (f) NO_3^-, (g) PO_4^{3-} concentrations. The euphotic depth spans from 0-20 m on average. (download)

Table S1. Results of Levene's test for equal variances and Shapiro-Wilk normality test. (download)

Table S2. Autocorrelation tests of factors during tropical cyclone (TC) periods and Non-TC periods. (download)