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Invasive and toxic cyanobacteria regulate allochthonous resource use and community niche width of reservoir zooplankton

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Abstract

1. Cyanobacterial dominance or blooms can influence ecosystem structure in reservoirs, yet there are only few studies of its effect on the resource use and trophic structure of zooplankton. We hypothesised that zooplankton traits would exhibit a strong response to the increase of invasive and toxic cyanobacteria.

2. We investigated the effect of an invasive bloom-forming cyanobacterium *Raphidiopsis raciborskii* (formerly *Cylindrospermopsis raciborskii*) on zooplankton functional traits (e.g., growth, reproduction, allochthonous resource use and realised niche) through laboratory experiments and 3-year field investigations in two subtropical reservoirs. The realised niche (i.e., resource and habitat use) was quantified using stable isotopes (termed isotopic niches).

3. We fed the cladoceran zooplankton *Moina* sp. with *Scenedesmus obliquus* (chlorophyte), *R. raciborskii*, and a mixture of *S. obliquus* and *R. raciborskii* in laboratory experiments. A diet of *R. raciborskii* alone depressed the growth and reproduction of *Moina* sp. compared to a diet of *S. obliquus* alone, but a mixture of *S. obliquus* and *R. raciborskii* greatly alleviated the inhibition effects caused by cyanobacteria.

4. Under natural field conditions, we did not find a strong inhibition effect of *R. raciborskii* dominance on the zooplankton, but a high biomass of *R. raciborskii* was associated with an increase (17%) in the relative allochthonous resource (terrestrially derived organic matter) use by cladocerans (but not for copepods), even though the chlorophyll-*a* concentration increased from 17 μg/L in the non-bloom period to 28 μg/L during periods of *R. raciborskii* dominance or blooms. Furthermore, a high biomass of *R. raciborskii* increased the contribution of inter-taxa variation (taxa sorting) to the expanded isotopic niches of the zooplankton community.

5. Our study helps to clarify cyanobacteria-zooplankton interactions and highlights the importance of cyanobacterial dominance or blooms in regulating

cross-ecosystem resource use and biogeochemical cycling mediated by zooplankton in aquatic ecosystems.

1 | INTRODUCTION

Cyanobacterial blooms are an increasing threat to human health and ecosystem sustainability globally (Huisman et al., 2018; Paerl et al., 2019; Paerl & Paul, 2012). Blooms can influence aquatic ecosystems through changes in physicochemical conditions, such as by generating toxins, increasing turbidity, and causing oxygen depletion (Huisman et al., 2018). Such environmental changes have led to major shifts in zooplankton community composition as well as changes in their functional traits (e.g., growth and reproduction) (Ger et al., 2016; Hansson et al., 2007; Huisman et al., 2018; Paerl & Paul, 2012). Despite the low food quality, cyanobacteria can still provide amino acids and proteins for zooplankton (Wilk-Woźniak, 2020). As zooplankton are the critical link between phytoplankton and higher trophic levels (Carpenter et al., 1985; Gao et al., 2019; Ger et al., 2016; Jeppesen et al., 2011) in pelagic ecosystems and may play key roles in controlling biogeochemical cycles in aquatic ecosystems (Brierley, 2014; Houghton et al., 2018), it is important to understand how cyanobacterial blooms will influence zooplankton community structure and traits. The complexity of cyanobacteria–zooplankton interactions makes it difficult to predict the effects of cyanobacterial blooms on zooplankton communities (Ger et al., 2016; Huisman et al., 2018; Wilk-Woźniak, 2020; Wilk-Woźniak et al., 2016).

Raphidiopsis raciborskii (formerly *Cylindrospermopsis raciborskii*) is a widespread cyanobacterial species, which has gained considerable attention in inland waters due to its toxicity, bloom formation, and strong invasiveness (Antunes et al., 2015; Paerl, 2018; Sidelev et al., 2020; Wilk-Woźniak et al., 2016). Apart from competing with other phytoplankton species, *R. raciborskii* dominance can cause a cascade of changes in zooplankton communities in numerous ways (Liu et al., 2019). Firstly, this bloom-forming cyanobacterium typically lacks the essential nutrients (e.g., poor sterols) for zooplankton (dos Santos Severiano et al., 2018; Martin-Creuzburg et al., 2008); secondly, the morphology and chemical characteristics (e.g., chlorophyll-*a* and stoichiometry) of cyanobacteria can influence zooplankton fitness (Bednarska et al., 2014; Ferrão-Filho et al., 2019; Müller-Navarra et al., 2000); thirdly, cyanobacterial secondary metabolites (i.e., cylindrospermopsins) may reduce zooplankton fitness (Agasild et al., 2019; Burford et al., 2016). The influence of cyanobacteria on zooplankton has been documented under laboratory (da Costa et al., 2013; Gebrehiwot et al., 2019; Panosso & Lürling, 2010) and natural conditions (Schaffner et al., 2019). The majority of laboratory studies were conducted only at species or

population levels, while investigations of the influence of cyanobacteria on plankton under natural conditions generally focus on the community level (Josué et al., 2019; Pinheiro-Silva et al., 2020; Work & Havens, 2003). Nonetheless, the influence of toxic *R. raciborskii* on zooplankton communities and their specific functional traits (e.g., growth, reproduction, and grazing behaviour) remain largely unexplored in natural waters, including subtropical reservoirs.

Functional traits are defined as any morphological, physiological, or behavioural traits that determine interspecific and species-environment interactions (Violle et al., 2007). Functional traits such as body size, grazing behaviour, and habitat preference play key roles in regulating nutrient cycling, respiration, and assimilation efficiencies as well as determining the strength of cascading effects on phytoplankton and water quality (Gao et al., 2019; Hébert et al., 2016; Josué et al., 2019). However, these traits can change rapidly in response to environmental changes, including cyanobacterial dominance or blooms (Hairston et al., 2001).

Knowledge of the grazing behaviour of zooplankton can be obtained by tracking their carbon sources (Cole et al., 2011; Sommer & Sommer, 2006). Aquatic ecosystems receive both autochthonous and allochthonous organic material (Gao et al., 2021; Ndayishimiye et al., 2020; Tanentzap et al., 2017). Freshwater zooplankton obtain autochthonous resources via grazing on phytoplankton, but they can also assimilate allochthonous resources through grazing on microbes that have consumed allochthonous organic matter (Emery et al., 2015; Karlsson et al., 2003) or through direct ingestion of allochthonous organic matter (Taipale et al., 2014). The relative allochthonous resource use by freshwater zooplankton typically varies greatly from 0% to >90% (Cole et al., 2011; Emery et al., 2015; Grosbois et al., 2017). An important question is how the allochthonous resource use will change in the increasingly human-modified world (Tanentzap et al., 2017). For example, when autochthonous phytoplankton production is high, it can be the dominant source of organic matter available to zooplankton and thus lead to low relative allochthonous resource use, especially when there is a high-quality and preferred autochthonous resource (e.g., chlorophyte) (Tanentzap et al., 2017). However, filamentous and colonial cyanobacteria are often difficult for zooplankton to capture and ingest, they are of poor nutritional quality and may potentially be toxic, resulting in reduced grazing (Hairston et al., 2001; Paerl & Paul, 2012; Schaffner et al., 2019). Therefore, the relative allochthonous resource use by zooplankton may depend on the proportion of cyanobacteria to other autochthonous (such as easily grazed phytoplankton) and allochthonous inputs. So far, few studies have addressed how

allochthonous resource use by zooplankton responds to dominance or blooms of *R. raciborskii* in inland waters.

Here, we tested whether zooplankton traits (e.g., growth and reproduction) were influenced by dominance of the cyanobacterium *R. raciborskii* under laboratory conditions. We studied the response of functional traits (e.g., allochthonous resource use and habitat preference) and interspecific competition among zooplankton to different degrees of *R. raciborskii* dominance over a 3-year field investigation (from 2016 to 2018) in two subtropical reservoirs (Shidou and Tingxi reservoirs) in southeast China. *Raphidiopsis raciborskii* frequently dominates Shidou Reservoir, and it is therefore a suitable site for the study of the effects of *R. raciborskii* on zooplankton (Tan et al., 2021). In contrast, a very low biomass of *R. raciborskii* (<0.04 mg/L) was found in all samples from Tingxi Reservoir (Figure 1), which therefore served as a control (Yang et al., 2021). Environmental disturbances may alter isotopic niches of animals

(Magioli et al., 2019), but whether this is also true for zooplankton is unclear. Therefore, we also studied the ecological niche space of the zooplankton community using stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes, thereby obtaining quantitative information on both resource and habitat use (termed isotopic niches) (Gao et al., 2019; Layman et al., 2007; Lemmens et al., 2017).

The aim of our laboratory experiments was to assess the influence of *R. raciborskii* on zooplankton growth and reproduction. The aims of the field investigations were to assess: (1) the degree of allochthonous resource use by zooplankton in response to *R. raciborskii* dominance; and (2) the variation in isotopic niches of the zooplankton community influenced by *R. raciborskii*. Our hypotheses were: (1) *R. raciborskii* would depress the growth and reproduction of the cladoceran zooplankton *Moina* sp. under laboratory condition; (2) high-density of *R. raciborskii* would force cladocerans to graze more on allochthonous resources under natural conditions; and (3)
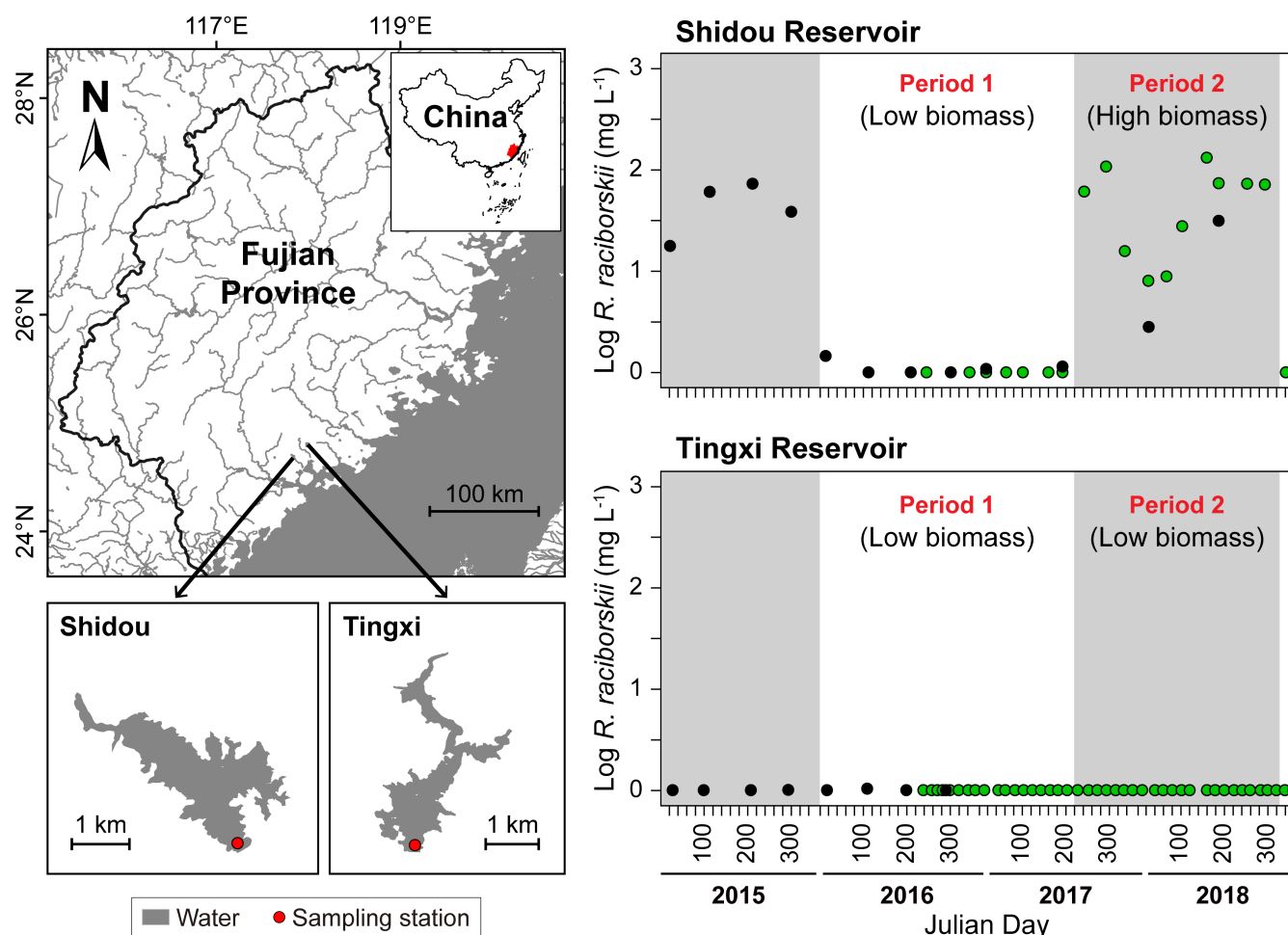

FIGURE 1 Location of sampling sites in Fujian province, southeast China (left), and the biomass of invasive and toxic *Raphidiopsis raciborskii* (right) in Shidou and Tingxi reservoirs, showing the *R. raciborskii* dominance or bloom in 2015 and 2018 in Shidou Reservoir. In Shidou Reservoir, zooplankton were sampled from January 2016 to December 2018, and the sampling days were artificially divided into period 1 (January 2016 to August 2017) with low *R. raciborskii* biomass (<0.5 mg/L) and period 2 (September 2017 to November 2018) with high *R. raciborskii* biomass (>7 mg/L), respectively. The two-period definition was extended to data on Tingxi Reservoir for comparison even though *R. raciborskii* biomass here was always lower than 0.04 mg/L in all samples. We focused on the data from January 2016 to November 2018 in the following data analyses. The black and green dots (right) represent the *R. raciborskii* data from microscopy and flow cytometry methods, respectively, from 2015 to 2018

the zooplankton community would adapt to the high *R. raciborskii* biomass by changing their isotopic niches.

2 | METHODS

2.1 | Study area and sampling design

Field sampling was conducted in the lacustrine area near the dam-walls of Shidou (24°42′N, 118°00′E) and Tingxi (24°48′N, 118°08′E) reservoirs situated near Xiamen city, Fujian province, southeast China (Figure 1). The main functions of these reservoirs are flood control, irrigation, and water supply. Both reservoirs have well-forested catchments and are almost devoid of macrophytes as they are deep and subjected to major water level fluctuations (Yang et al., 2021). Details of the general characteristics of the reservoirs and climatic conditions are given in Yang et al. (2012), Yang et al. (2017), and Gao et al. (2019). Water samples were collected from a subsurface layer (depth 0.5 m), the hypoxic boundary (depth 4–29 m), and a sub-bottom layer (2 m above the bottom sediments) at one location per reservoir, depending on thermal stratification and water depth (Gao et al., 2019; Nyirabuhoro et al., 2020) every 45 days in Shidou Reservoir and every 20 days in Tingxi Reservoir from 2016 to 2018 (Figure S1).

2.2 | Laboratory experiment

We isolated a cylindrospermopsin-producing strain (XM1) of the cyanobacterium *R. raciborskii* from Shidou Reservoir in 2018 (Tan et al., 2021). Cladoceran cultures were established in the laboratory experiment. We used a clone of the cladoceran *Moina* sp. to evaluate the influence of *R. raciborskii* on zooplankton. *Moina* sp. has a short life span with a generation time of approximately 3 days and is easy to culture. Thus, it is a suitable taxon for testing the effect of *R. raciborskii* on survival and reproduction-related traits because of its coexistence with potentially toxic bloom-forming cyanobacteria (Jiang et al., 2017; Kâ et al., 2012), and it is often abundant in subtropical waters (Jiang et al., 2017). The clone was isolated from the water near Shidou Reservoir. It was raised in the laboratory for at least four generations prior to the experiment. The water used for the experiment was taken from the reservoir and filtered through 0.2 μm pore-size polycarbonate filters (47 mm diameter; Millipore, Billerica, MA, U.S.A.) to remove all particles and plankton. Ten newborn *Moina* individuals of the same clone with similar body size were placed in 12 replicated glass vials (250 ml) containing 200 ml of the filtered water. The experimental set-up consisted of four treatments with three replicates run at a constant temperature of 25°C in 12 hr/12 hr light/dark cycle: the first treatment was blank (only zooplankton) to determine the survival time without food; in the second treatment, the zooplankton were fed 4×10^7 individuals of *S. obliquus* (chlorophyte) per litre; in the third treatment, the zooplankton were fed 4×10^7 individuals of *R. raciborskii* per litre; and in the fourth treatment, the zooplankton were fed 4×10^7 individuals per litre of a 1:1 mixture

of *S. obliquus* and *R. raciborskii*. The phytoplankton was cultured in BG11 medium under the same conditions before the experiment. Then, the phytoplankton was maintained in the treatments until the end of the culture experiment. Chlorophyll-*a* concentrations and zooplankton number and size were measured every day. We randomly took 10 specimens to measure the size of zooplankton from every vial. We manually agitated the glass vials three times every day to avoid sedimentation. All culture units were maintained for 7 days.

For statistical analyses, we separately compared the density and body size of *Moina* sp. among the four treatments each day based on Kruskal–Wallis tests with Dunn's post hoc test using Bonferroni corrected *p* values. Chlorophyll-*a* concentrations were compared between treatments with and without *Moina* sp. using nonparametric Mann–Whitney *U* test.

2.3 | Field investigation on environmental data

Water depth was measured with a Speedtech SM-5 Depthmate portable sounder (Speedtech Instruments, Great Falls, VA, U.S.A.). Water transparency was measured with a 30 cm diameter Secchi disk. Euphotic depth (Z_{eu}) was estimated as 2.7 times the Secchi depth. Water temperature, pH, dissolved oxygen, and electrical conductivity were measured in situ at 0.5-m intervals using a multiparameter water quality analyser (Hydrolab DS5, Hach company, Loveland, CO, U.S.A.). Total carbon, total organic carbon, total nitrogen, ammonium nitrogen, the sum of nitrate and nitrite nitrogen, total phosphorus, and phosphate phosphorus were measured according to methods described in Gao et al. (2021). Chlorophyll-*a* was measured with a PHYTO-PAM Phytoplankton Analyzer (Heinz Walz GmbH, Effeltrich, Germany). Water level, water storage, and precipitation data were provided by Xiamen Water Resources Agency, China. The comprehensive trophic state index was calculated using chlorophyll-*a* (μg/L), transparency (m), and total phosphorus (μg/L) following Yang et al. (2012).

2.4 | Field investigation on plankton

For the field investigation, zooplankton were sampled with a plankton net (mesh size 112 μm) that was hauled vertically from the bottom (2 m above the sediments) to surface waters 20 times in each sampling. In total, 23 and 55 zooplankton samples were collected from Shidou and Tingxi reservoirs, respectively. All zooplankton taxonomic groups were counted on a Nikon SMZ800 stereo microscope (Nikon Corporation, Tokyo, Japan) and classified into six dominant taxonomic groups based on taxonomy and size (Gao et al., 2019): *Bosmina*, *Bosminopsis*, other Cladocera, small cyclopoida (200–450 μm), large cyclopoida (≥450 μm), and Diaptomidae. Dry weight (μg/ind) and biomass were recorded after drying in an oven at 60°C for 48 hr. Dry weight was considered as the body size of zooplankton following our previous study (Gao et al., 2019).

Phytoplankton (autochthonous resources) were collected by scraping off the sediment traps that were placed 1 m beneath the

water surface. The phytoplankton from surface waters (0.5 m) were counted using a flow cytometer (FlowSight, Amnis, Merck Millipore, Darmstadt, Germany) equipped with blue-green (488 nm, 60 mV) and sideward scatter (785 nm, 12 mV) solid-state lasers at high image resolution (20× magnification) from 2016 to 2018. The analyses were performed with Amnis IDEAS software (version 6.2). Red autofluorescence of photosynthetic pigments and sideward scatter were used to distinguish *R. raciborskii*, other phytoplankton, and detritus (Figure S2). Furthermore, a microscope was used to identify *R. raciborskii* and estimate the biomass of cyanobacteria (Figure 1) following our previous approaches (Yang et al., 2017). The community composition of phytoplankton from Shidou and Tingxi reservoirs was described in Yang et al. (2021). The flow cytometry can help us to determine the phytoplankton biomass with high frequency, while the microscopy approach not only provided the phytoplankton biomass data but also the detailed taxonomic composition. In this study, the flow cytometry and microscopy results on *R. raciborskii* population dynamics were similar, thus corroborating the accuracy of the biomass determination of phytoplankton (Figure 1).

The terrestrial (allochthonous) materials, consisting of different types of floating leaves on the water surface or fallen leaves near the shore, were sampled to get enough biomass for the isotopic analysis once every 3 months to explore their seasonal shifts. Three replicates were obtained for each sample.

2.5 | Stable isotope analysis of field samples

About 50 copepods (e.g., Cyclopoida and Diaptomidae) and 200 cladocerans (e.g., *Bosmina* and *Bosminopsis*) from each replicate were used to obtain a sufficient mass. Different zooplankton taxonomic groups were directly put into pressed tin capsules and dried in an oven at 60°C for 48 hr prior to the isotopic analyses. The allochthonous and phytoplankton (autochthonous) samples were freeze-dried at −80°C. Then about 0.5–1.0 mg allochthonous and phytoplankton materials were transferred to the pressed tin capsules for isotopic analyses. Stable isotopic ratios were measured using a Thermo Electron Flash EA 2000 elemental analyser coupled to a Delta V isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, U.S.A.). Both carbon and nitrogen stable isotope ratios were presented as $\delta^{13}C$ and $\delta^{15}N$ relative to the Vienna Pee Dee Belemnite carbonate and atmospheric N_2 isotope, respectively (Fry, 2006). Note that we did not acidify the samples before analysis since this has a major influence on $\delta^{15}N$ determination (Schlacher & Connolly, 2014). The carbon content and the carbon-to-nitrogen ratio were used to correct the $\delta^{13}C$ of zooplankton for lipid bias (Syväranta & Rautio, 2010).

2.6 | Data analysis of field samples

For comparative study, we artificially defined January 2016 to August 2017 as period 1 with low *R. raciborskii* biomass (<0.5 mg/L)

and September 2017 to November 2018 as period 2 with high *R. raciborskii* biomass (>7 mg/L), respectively (Figure 1), since zooplankton samples were only available from January 2016 to December 2018 (Figure S1). The two periods were extended to Tingxi Reservoir data for comparison despite the fact that *R. raciborskii* biomass was always lower than 0.04 mg/L in all samples in Tingxi Reservoir. We focused on the data from 2016 to 2018 in the following data analyses. During period 2, a high abundance of *R. raciborskii* was found in Shidou Reservoir, which is, therefore, a suitable site for the study of the effect of *R. raciborskii* on zooplankton community. In contrast, a very low biomass of *R. raciborskii* (<0.04 mg/L) was found in all samples from Tingxi Reservoir (Figure 1), which therefore served as a control (Yang et al., 2021). The different results between the two reservoirs will provide more evidence for the effect of *R. raciborskii* on zooplankton. Comparison of environmental parameters between two periods was performed based on nonparametric Mann–Whitney *U* test for Shidou and Tingxi reservoirs, respectively. The difference in body size (dry weight), $\delta^{13}C$, and $\delta^{15}N$ of zooplankton between two periods was determined by nonparametric Mann–Whitney *U* test with significant difference at $p < 0.05$.

Bayesian stable isotope mixing models (Parnell & Inger, 2016) were applied to estimate the relative autochthonous and allochthonous resource use by different zooplankton taxonomic groups using $\delta^{13}C$ and $\delta^{15}N$ of phytoplankton and terrestrial samples, respectively. The Bayesian mixing models were run for 10,000 iterations, 1000 burn-in, and a thinning interval of 10 based on the result of convergence diagnostics (Parnell & Inger, 2016). The analyses were conducted using the *simmr* package (version 0.3, Parnell & Inger, 2016) in the R environment, version 4.0.3 (R Core Team, 2019). Trophic fractionation factors of 0.5‰ ($SD = 0.17‰$) and 2.2‰ ($SD = 0.30‰$) were used for $\delta^{13}C$ of unacidified samples (McCutchan et al., 2003).

We used community isotopic niche breadth to evaluate resource and habitat use by the zooplankton community using $\delta^{13}C$ and $\delta^{15}N$ values (Layman et al., 2007). The classical Layman's mean nearest neighbour distance (MNND) was calculated for each zooplankton taxonomic group to investigate the intra-taxonomic group competition, lower MNND values indicate stronger intra-taxonomic group competition (Gao et al., 2019; Layman et al., 2007). We further calculated standard ellipse area (SEA), which is an equivalent of total area in $\delta^{13}C$–$\delta^{15}N$ bi-plot space (Layman et al., 2007) and indicates the total amount of isotopic niche space occupied (Jackson et al., 2011), applying the *SIBER* package (version 2.1.3, Jackson et al., 2011) in R environment (R Core Team, 2019). Because the food web topology and SEA are independent from any difference in the isotopic baseline, we did not perform the correction for possible baseline shifts following previous studies (Bas et al., 2019; Magioli et al., 2019). Bayesian SEAs (SEA_B) were calculated for the comparison of isotopic niches of the zooplankton community between two periods as they are not affected by bias associated with the number of community members. The niche overlap was expressed as the proportion of niche space with which one group was overlapped by another group.

The observed changes in SEA_B of zooplankton community from period 1 to period 2 were partitioned into taxa sorting (TS) and

intra-taxonomic group variation (ITGV), corresponding to species sorting and intraspecific trait variation (Gao et al., 2019; Lemmens et al., 2017). In this partitioning, TS indicates a community change due to a shift in the relative abundances of different taxonomic groups and mediated by environmental factors, while ITGV represents the community change due to within-taxa changes, encompassing shifts in species abundance, evolutionary change, environmental responses (e.g., phenotypic plasticity), or ontogenetic changes (Govaert et al., 2016; Teurlincx et al., 2017; Violle et al., 2012).

3 | RESULTS

3.1 | Influence of *R. raciborskii* on zooplankton traits

Raphidiopsis raciborskii influenced the growth (body size) and reproduction of cultured *Moina* sp. (cladoceran) in the laboratory experiment (Figure 2a,b). All *Moina* individuals were dead after 5 days in the treatment without phytoplankton (food; Figure 2a), although their size exhibited a slow increase (Figure 2b). The density of *Moina* individuals fed with *S. obliquus* was higher than that fed with *R. raciborskii* only (Kruskal–Wallis with Dunn's post hoc test, Bonferroni corrected $p < 0.05$) on and after the fourth day of cultivation. The density of *Moina* individuals fed with a mixture of *S. obliquus*/*R. raciborskii* (average density = 150 ind/L) was higher than that fed with *R. raciborskii* only (average density = 45 ind/L) on the fourth day of cultivation, although the difference was not significant during the first 3 days of the laboratory experiment (Kruskal–Wallis with Dunn's post hoc test, Bonferroni corrected $p > 0.05$). Furthermore, the body size of *Moina* sp. cultured with *S. obliquus* and *S. obliquus*/*R. raciborskii* was larger than those cultured with *R. raciborskii* only (Kruskal–Wallis with Dunn's post hoc test, Bonferroni corrected $p < 0.01$)

on the second and third days of cultivation. Chlorophyll-*a* concentrations of *R. raciborskii* and *S. obliquus*/*R. raciborskii* cultured with *Moina* sp. were lower than those without *Moina* sp. after 7 days of culture (Mann–Whitney *U* test, $p < 0.05$), indicating the grazing effect of *Moina* on phytoplankton (Figure 2c).

In the field, zooplankton traits (e.g., allochthonous resource use based on stable isotopes, body size, and biomass) in both reservoirs differed between periods 1 and 2 for some but not all zooplankton taxonomic groups (Figure 3). In Shidou Reservoir, a higher density of *R. raciborskii* was found in period 2 (from September 2017 to November 2018) than period 1 (from January 2016 to August 2017). Most environmental factors exhibited similar seasonal variation in both Shidou and Tingxi reservoirs (Figures S3, S4). In Shidou Reservoir, the $\delta^{13}C$ values of *Bosmina* and other Cladocera decreased significantly (Mann–Whitney *U* test, $p < 0.05$) from periods 1 to 2, while no significant differences were found for the other zooplankton taxonomic groups. In Tingxi Reservoir, the difference in $\delta^{13}C$ between periods 1 and 2 was not significant for any of the groups ($p > 0.05$). No significant difference in $\delta^{15}N$ and body size between the two periods was found for any of the zooplankton groups ($p > 0.05$) in either reservoir except that *Bosmina* showed an increasing body size from periods 1 to 2 in Tingxi Reservoir. In Shidou Reservoir, the biomass of large cyclopoida (≥450 μm) increased significantly from 25.3 μg C/L in period 1 to 72.3 μg C/L in period 2 ($p < 0.05$). For other zooplankton taxonomic groups, biomass tended to be higher in period 2 than in period 1, although not significantly so. In Tingxi Reservoir, the biomass of *Bosmina* and all copepods increased significantly from periods 1 to 2 ($p < 0.05$), while no significant difference was found for *Bosminopsis* and other Cladocera. In Shidou Reservoir, the ratio of zooplankton biomass to chlorophyll-*a* increased from 19 in period 1 to 27 in period 2 ($p > 0.05$; Figure S5). In Tingxi Reservoir, the ratio increased significantly from 19 in period 1 to 39 in period 2 ($p < 0.01$).
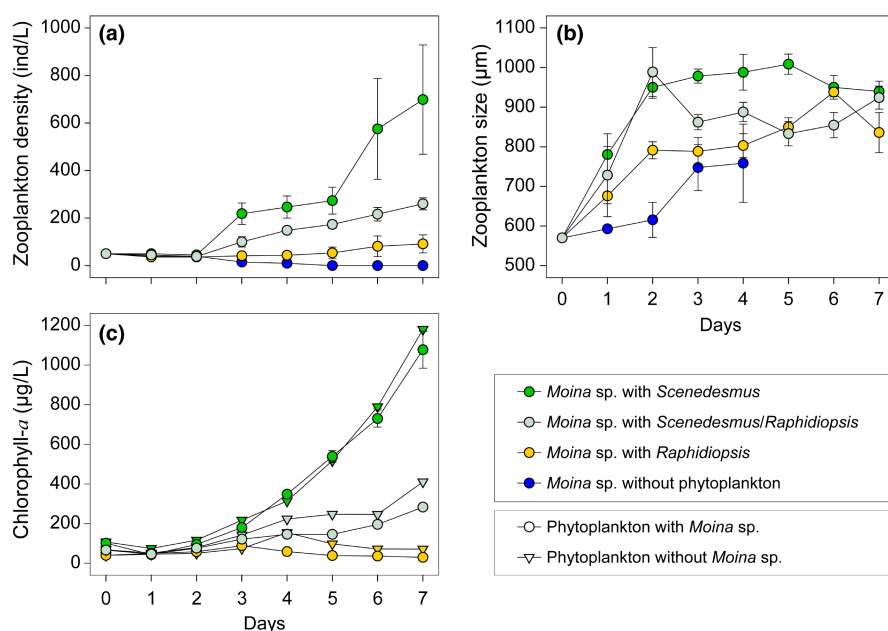

FIGURE 2 Temporal dynamics of zooplankton density (a), adult zooplankton size (b), and chlorophyll-*a* concentration (c) in laboratory culture experiments in different treatments with *Raphidiopsis raciborskii* (cyanobacteria) and *Scenedesmus obliquus* (chlorophyte). Data are mean ± 1*SE*
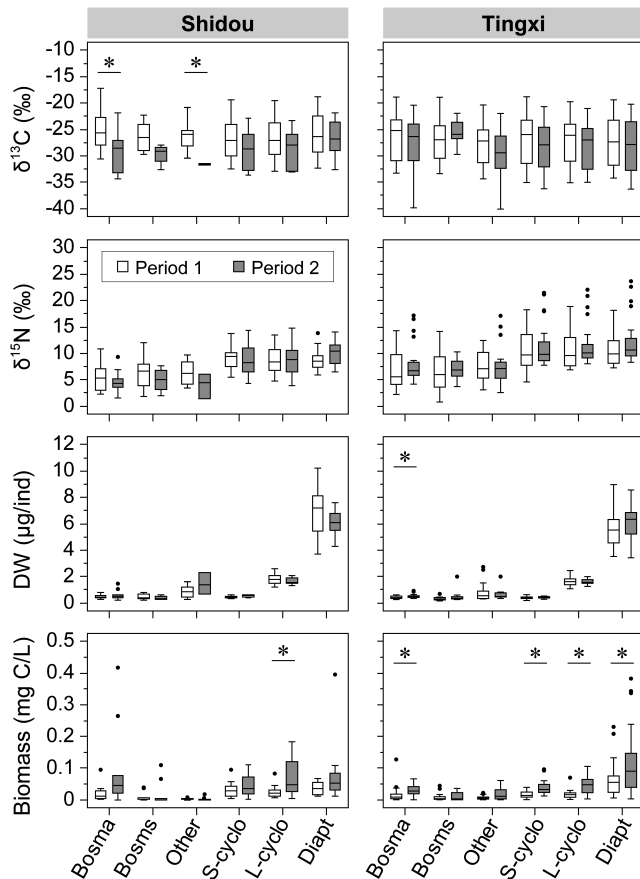
FIGURE 3 Comparison of the traits of different taxonomic groups of zooplankton between the two periods in Shidou and Tingxi reservoirs, respectively, from January 2016 to November 2018. Bosma, *Bosmina*; Bosms, *Bosminopsis*; Other, other Cladocera; S-cyclo, small cyclopoida (200–450 μm); L-cyclo, large cyclopoida (≥450 μm); Diapt, Diaptomidae. DW, dry weight (body size) of the individual zooplankton. Note that the genus *Moina* belongs to the group of other Cladocera. Statistical analysis is nonparametric Mann–Whitney *U* test, *$p < 0.05$. Boxes and error bars indicate the 25th/75th and 5th/95th percentiles, respectively; middle line of the boxes is the median

3.2 | Allochthonous resource use by zooplankton in reservoirs

In the field, the δ^{13}C signatures for terrestrial organic matter were much lower than those for phytoplankton in all seasons (Figure S6). Zooplankton showed distinct δ^{13}C signatures from their basal food resources (i.e., phytoplankton and terrestrial end members) in both reservoirs. In Shidou Reservoir, the average relative allochthonous resource use by *Bosmina* changed from 51% in period 1 to 62% in period 2 (Mann–Whitney *U* test, $p > 0.05$; Figure 4a). The relative allochthonous resource use by *Bosminopsis* and other Cladocera was lower in period 1 (<56%) than in period 2 (>79%; Mann–Whitney *U* test, $p < 0.05$). The relative allochthonous resource use by all cladocerans (including all datasets for *Bosmina*, *Bosminopsis*, and other Cladocera) was significantly lower in period 1 (54%) than in period 2 (71%; Figure 4b, $p < 0.01$). No significant difference was found

between the two periods for all copepod groups (e.g., small cyclopoida, large cyclopoida, and Diaptomidae; Figure 4a,b, $p > 0.05$). In Tingxi Reservoir without strong pressure from *R. raciborskii*, the relative allochthonous resource use by cladocerans and copepods did not differ between the two periods (Figure 4c,d, $p > 0.05$). There is almost a 10‰ increase in δ^{15}N from allochthonous organic matter to zooplankton taxonomic groups despite the high use of allochthonous resources, indicating that zooplankton may have assimilated allochthonous resources through grazing on microbes that have consumed allochthonous organic matter. Furthermore, high abundance of *R. raciborskii* reduced the difference among different seasons in Shidou Reservoir compared to Tingxi Reservoir (Figure S7).

3.3 | Zooplankton community isotopic niches in reservoirs

In Shidou Reservoir, the mean niche overlap among the different taxonomic groups decreased significantly from 74% in period 1 to 57% in period 2 (paired *t*-test, $T_5 = 10.647$, $p < 0.01$; Figure S8). In Tingxi Reservoir, the mean niche overlap among taxonomic groups did not differ between the two periods (paired *t*-test, $T_5 = 0.555$, $p = 0.603$).

The community isotopic niche width (SEA$_B$) of zooplankton increased from period 1 to period 2 in both reservoirs (Figure 5b). The TS and ITGV contributed 38.0% and 62.0% to the observed changes in the community isotopic niche from period 1 to period 2 in Shidou Reservoir, while the contributions of TS and ITGV were 20.4% and 79.6% in Tingxi Reservoir, respectively (Figure 5a). In Shidou Reservoir, higher MNND values (lower intra-taxonomic group competition) of all zooplankton taxonomic groups were observed in period 2 than in period 1 (Figure S9). In Tingxi Reservoir, higher MNND values of *Bosmina*, *Bosminopsis*, other Cladocera, small cyclopoida (200–450 μm), and Diaptomidae were observed in period 2, while the reverse pattern was observed for large cyclopoida (≥450 μm). In Shidou Reservoir, intra-taxonomic competition was significantly lower in period 2 than in period 1 (paired *t*-test, $T_5 = -4.959$, $p = 0.004$), while in Tingxi Reservoir, the difference was not significant between the two periods.

4 | DISCUSSION

4.1 | Effect of *R. raciborskii* on zooplankton growth and reproduction

In our laboratory experiments, *R. raciborskii* depressed the growth rate and reproduction of *Moina* sp., but the negative effects were mitigated by adding a high-quality food item such as chlorophytes (e.g., *S. obliquus*). Bloom-forming cyanobacteria are believed to be consumed less often by zooplankton than chlorophytes (Agasild et al., 2019; Major et al., 2017). However, our study showed that *Moina* sp. survived and exhibited slow net growth in the toxic
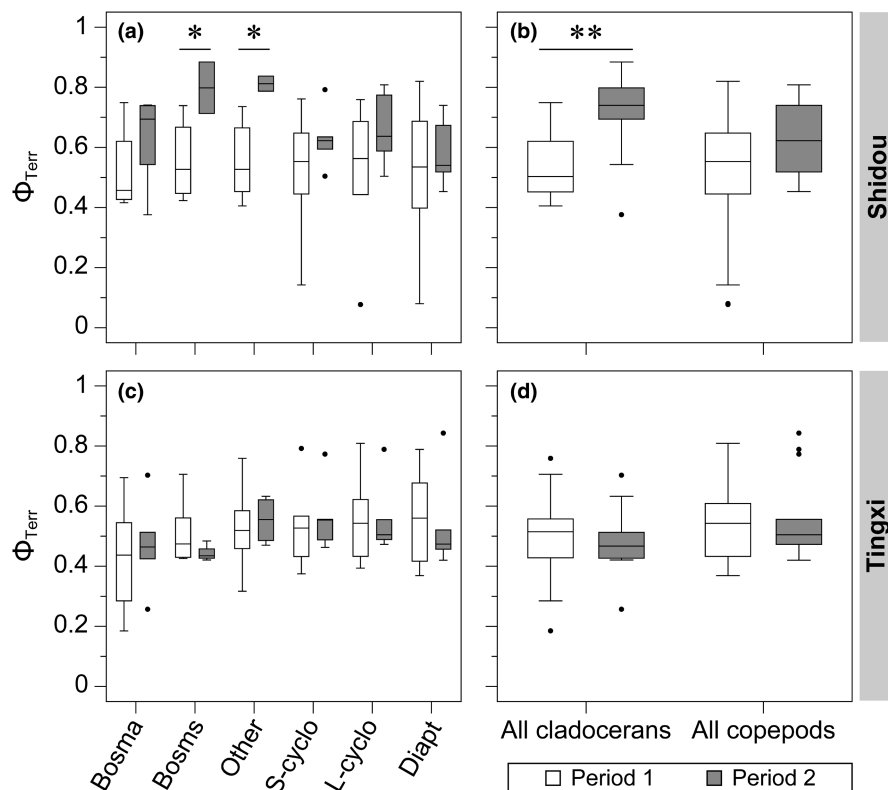
FIGURE 4 Comparison of allochthonous resource use by zooplankton taxonomic groups in Shidou (a and b) and Tingxi (c and d) reservoirs between period 1 (January 2016 to August 2017) and period 2 (September 2017 to November 2018), respectively. Bosma, *Bosmina*; Bosms, *Bosminopsis*; Other, other Cladocera; S-cyclo, small cyclopoida (200–450 μm); L-cyclo, large cyclopoida (≥450 μm); Diapt, Diaptomidae. Φ_{Terr}, allochthonous (terrestrial) resource use by zooplankton. Statistical analysis is nonparametric Mann–Whitney *U* test, $*p < 0.05$, $**p < 0.01$. Boxes and error bars indicate the 25th/75th and 5th/95th percentiles, respectively; middle line of the boxes is the median

R. raciborskii alone treatment, and the concentration of chlorophyll-*a* increased more in the absence of *Moina* sp., suggesting that cladocerans can survive by grazing on *R. raciborskii*. Correspondingly, Work and Havens (2003) found colonies of filamentous cyanobacteria in the guts of zooplankton in subtropical lakes. In our experiment, *R. raciborskii* was a food item of poor quality as we observed a smaller body size and a lower biomass of *Moina* sp. in the *R. raciborskii*-only treatment compared to the *Scenedesmus* treatments. The negative effects probably reflect the absence of essential nutrients (e.g., sterol) in cyanobacteria, which constrains the efficiency of carbon transfer from cyanobacteria to zooplankton (e.g., *Daphnia*) (Martin-Creuzburg et al., 2008). However, addition of high-quality phytoplankton (e.g., *Scenedesmus obliquus*) to *R. raciborskii* increased the growth, either because it was used as an alternative food source by zooplankton or as a supplement to *R. raciborskii*, thereby compensating for the absence of essential nutrient in the cyanobacteria (Gebrehiwot et al., 2019; Martin-Creuzburg et al., 2008).

In the field, a more complex plankton community typically provides *network buffering* to mitigate the inhibition effect of *R. raciborskii* on zooplankton (Ger et al., 2016; Josué et al., 2019; Konopka et al., 2015) compared to our more controlled laboratory experiment. Moreover, predation by fish and predatory invertebrates may have strong effects on the zooplankton (DeMott et al., 2001; Jeppesen et al., 2010, 2011). In our field investigation, we found an increase in the zooplankton biomass: chlorophyll-*a* ratio from period 1 to period 2 in Tingxi Reservoir but only an insignificant increase for Shidou Reservoir, and the average biomass of cladocerans increased from 10.3 μg C/L in period 1 to 39.2 μg C/L in period 2 in Shidou Reservoir and from 10.2 to 19.7 μg C/L, respectively, in

Tingxi Reservoir. These results are indicative of higher fish predation on zooplankton (Jeppesen et al., 2011) when the biomass of *R. raciborskii* was high and eliminated the difference between the two periods in Shidou Reservoir compared to that in Tingxi Reservoir. Similar seasonal patterns have been found in other subtropical reservoirs in China (Lin et al., 2014). Since the seasonal response pattern that the ratio of zooplankton biomass to chlorophyll-*a* and the average biomass of cladocerans in Shidou and Tingxi reservoirs were similar, we assume that variations in fish predation cannot explain the below described differences in zooplankton use of allochthonous matter and their habitat selection in the two reservoirs.

4.2 | Allochthonous resource use by zooplankton

We found that the relative allochthonous resource use by zooplankton ranged from 1% to 88%, which is in agreement with previous studies (Cole et al., 2011; Emery et al., 2015; Grosbois et al., 2017). The relative allochthonous resource use by cladocerans increased significantly from 54% to 71% when the biomass of *R. raciborskii* rose despite an increase in the total chlorophyll-*a* concentration from 17.2 to 28.3 μg/L (65%) in Shidou Reservoir; in contrast, no differences were found for any of the zooplankton taxonomic groups between the two periods in Tingxi Reservoir where the abundance of *R. raciborskii* was always low in both periods. No difference between the two periods was found for copepods in the two reservoirs. Our findings suggest that the dominance of cyanobacterium *R. raciborskii* led to an increase in the relative contribution of allochthonous organic matter in the diet of zooplankton, although this varied among the
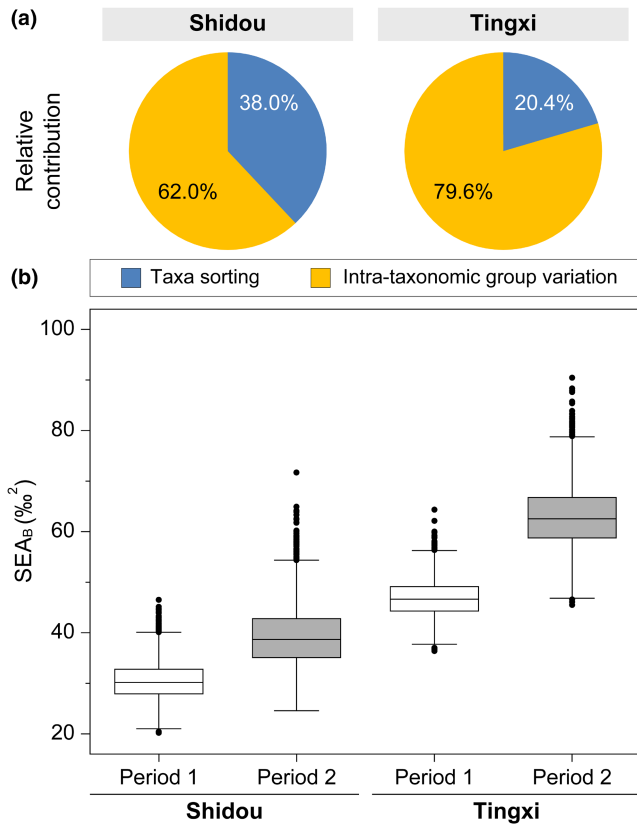
FIGURE 5 Relative contribution of taxa sorting (inter-taxonomic group variation) and intra-taxonomic group variation (a) to the changes in resource and habitat use (isotopic niches) of the zooplankton community (b) in Shidou and Tingxi reservoirs, respectively. The values in the pie chart (a) indicate the relative contribution of taxa sorting (blue) and intra-taxonomic group variation (yellow) to the isotopic niche width of the zooplankton community from period 1 (January 2016 to August 2017) to period 2 (September 2017 to November 2018). Boxplot (b) represents the isotopic niche width (standard Bayesian ellipse areas, SEA$_B$) of the zooplankton community. Boxes and error bars indicate the 25th/75th and 5th/95th percentiles, respectively; middle line of the boxes is the median

different taxonomic groups. A stronger effect of *R. raciborskii* on the grazing behaviour of cladocerans has also been observed in another study (Bouvy et al., 2001). Several explanations can be put forward. Firstly, cladocerans are filter feeders that typically are non-selective but whose prey depends on size, and will consume higher proportion of allochthonous organic matter when the phytoplankton is dominated by filamentous and colonial cyanobacteria that are often difficult to capture (Sommer & Sommer, 2006). Secondly, copepods have the ability to avoid toxic or chemically undesired phytoplankton or terrestrial source materials even when they are of optimal size (Hong et al., 2013; Sommer & Sommer, 2006). Nevertheless, we found that δ^{13}C of *Bosmina* and other Cladocera decreased significantly from period 1 to period 2, coinciding with a shift to *R. raciborskii* dominance in Shidou Reservoir, while no changes were found for all zooplankton taxonomic groups between the two periods in Tingxi Reservoir where the abundance of *R. raciborskii* was always

low in both periods. These results indicate that the resource use by cladocerans in reservoirs was regulated by blooming or dominance of the cyanobacterium *R. raciborskii*.

Considering all four seasons, we found that *R. raciborskii* alleviated the difference in the allochthonous resource use by zooplankton among different seasons. For example, in Shidou Reservoir with frequent occurrences of *R. raciborskii* dominance, the relative allochthonous resource use exhibited no difference among different seasons for any of the zooplankton taxonomic groups. In contrast, in Tingxi Reservoir with low *R. raciborskii* pressure, the relative allochthonous resource use by all copepod groups was different among different seasons. These results demonstrate the effect of *R. raciborskii* on the seasonal patterns of zooplankton feeding behaviour, and this can vary even among different taxa of cladocerans as demonstrated also by Pagano (2008) and da Costa et al. (2013). Furthermore, the relatively low use of allochthonous organic matter in Tingxi Reservoir compared to Shidou Reservoir may reflect high phytoplankton production in summer (Yang et al., 2017), providing a high abundance of high-quality food resource (e.g., chlorophyte) for the zooplankton, while *R. raciborskii* forces the zooplankton assimilate more allochthonous organic matter despite the high phytoplankton production in summer and autumn in Shidou Reservoir.

4.3 | Changes in resource and habitat uses of zooplankton

The observed larger isotopic niche width is generally representative of a higher degree of feeding plasticity (Gao et al., 2019; Layman et al., 2007; Yeakel et al., 2016). Although the changes in isotopic niche width exhibited the same pattern in Shidou and Tingxi reservoirs, the changes in niche width were driven more by taxa sorting in Shidou than in Tingxi reservoirs, which reflects a community change due to a shift in the relative abundances of different taxonomic groups (Gao et al., 2019; Lemmens et al., 2017) and mediated by environmental factors along a *R. raciborskii* biomass gradient. These results are closely related to the changes in the biomass of *R. raciborskii* in Shidou Reservoir. In addition, the decreased competition within and among different zooplankton taxonomic groups in Shidou Reservoir can be attributed to the expanded niche width of the zooplankton community driven by the poor nutritional quality of *R. raciborskii*, reflecting the adaptive evolution of zooplankton in response to the changing diet (Schaffner et al., 2019). These results indicate that the high environmental selection driven by *R. raciborskii* played a key role in shaping the zooplankton community structure (Schaffner et al., 2019; Teurlincx et al., 2017). Since environmental selection can allow for populations to adapt and change, the taxa sorting exhibited a high contribution to the changes in the niche width of the zooplankton community in Shidou Reservoir when *R. raciborskii* biomass became high. In contrast, the intra-taxonomic group variation contributed more to the changes in the zooplankton community in Tingxi Reservoir where the pressure of *R. raciborskii*
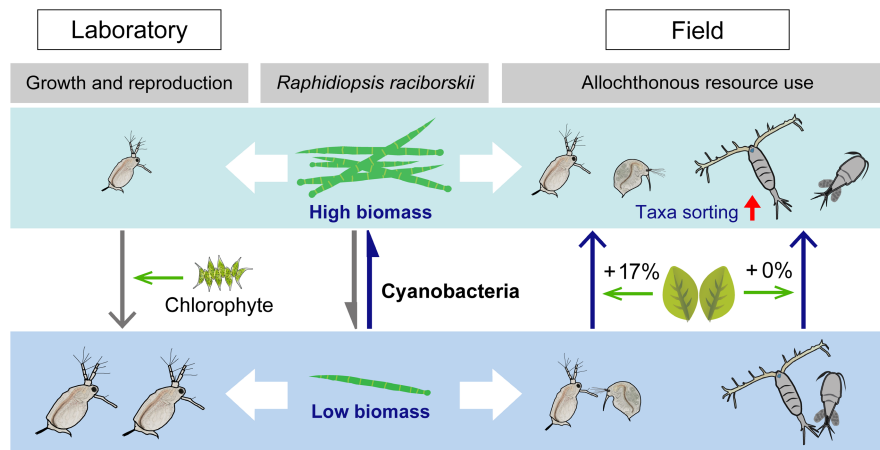
FIGURE 6 A conceptual paradigm showing the responses of zooplankton traits (i.e., growth, reproduction, allochthonous resource use, interspecific competition, and niche width) to a bloom-forming, invasive, and toxic cyanobacterium (*Raphidiopsis raciborskii*) based on both laboratory experiments and field observations. The high- and low-biomass periods of *R. raciborskii* in laboratory experiments correspond to the bloom and non-bloom periods of *R. raciborskii* in Shidou Reservoir, respectively. The values (e.g., +17%) in the right panel represent the changes in the allochthonous resource use from non-bloom to bloom periods of *R. raciborskii*. The red arrow in the right panel indicates the increase in the contribution of taxa sorting (inter-taxonomic group variation) to the changes in the niche width of the zooplankton community from non-bloom to bloom periods of *R. raciborskii*. The grey and blue arrows indicate the transition between the *R. raciborskii* bloom and non-bloom periods

was not strong. This is supported by previous studies on intra- and interspecific variation without the high-biomass *R. raciborskii* pressure (Bolnick et al., 2011; Gao et al., 2019; Lemmens et al., 2017). These results indicated that *R. raciborskii* dominance may increase the contribution of taxa sorting to the expanded isotopic niches of the zooplankton community. Functional traits (e.g., resource use) have been proved to be important for the response of zooplankton functional groups to changing cyanobacterial biomass in temperate reservoirs (Krztoń & Kosiba, 2020). We further quantified the functional traits (e.g., resource use) of zooplankton and discovered that bloom-forming cyanobacterium (*R. raciborskii*) changed the resource and habitat uses of the zooplankton community through intra- and inter-taxonomic group variations in subtropical reservoirs.

5 | CONCLUSION

This study evaluates the responses of zooplankton traits (i.e., growth, reproduction, allochthonous resource use, interspecific competition, and habitat preference) to a toxic bloom-forming cyanobacterium (*R. raciborskii*) in subtropical reservoirs based on both laboratory experiments and field observations over a 3-year period (Figure 6). Our results revealed that *R. raciborskii* depressed the growth and reproduction of the cladoceran zooplankton *Moina* sp., but in laboratory culture experiments the addition of other high-quality phytoplankton (e.g., chlorophyte) provided a buffer that counteracted the inhibition effect of *R. raciborskii*. Under natural conditions, such an inhibition effect of *R. raciborskii* was not observed, but high relative use of allochthonous resources by cladocerans and broad resource and habitat uses (i.e., broad isotopic niches) of the zooplankton community were observed in the presence of high biomasses of

R. raciborskii. Cladocerans were more sensitive to the influence of *R. raciborskii* than copepods. The high biomass of *R. raciborskii* increased the contribution of inter-taxonomic group variation (taxa sorting) to the expanded isotopic niches of the zooplankton community. This study brings insight into cyanobacteria–zooplankton interactions in subtropical reservoirs and provides key information about cross-ecosystem resource use in a changing environment. Future studies should integrate both environmental changes and different zooplankton functional traits in illustrating the influence of cyanobacterial dominance or bloom on zooplankton resource use in aquatic ecosystems.

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