Does nutrient enrichment alleviate stoichiometric constraint on plankton trophic structure?

Qiuqi Lin ⬤,* Lingli Liu, Zheng Gong, Liang Peng
Department of Ecology, Jinan University, Guangzhou, China

Abstract

Stoichiometric mismatch between phytoplankton and zooplankton has implication for trophic transfer efficiency. Phosphorus (P) enrichment is expected to lower phytoplankton carbon (C) to P ratio (C : P) and thereby either alleviate P deficiency or induce excess P for zooplankton. However, the generality of zooplankton facing excess P and its effect on plankton trophic structure in natural systems are poorly understood. We analyzed the stoichiometry of seston and zooplankton, and plankton trophic structure in 32 (sub)tropical Chinese reservoirs. Our results showed that (1) stoichiometric mismatch between seston and zooplankton involved P or/and nitrogen (N) deficits in low-nutrient reservoirs and P excess in high-nutrient reservoirs; (2) at given seston C and phytoplankton compositional food quality levels, zooplankton to phytoplankton biomass ratio (Zoo : Phyto) showed a two-segment piecewise relationship to seston N : P with a maximum at a breakpoint of 12.6 and strong reductions toward the extremes of seston N : P gradient; (3) increasing stoichiometric mismatch between seston and consumers reduced the contribution of cladocerans to zooplankton biomass and increased the trophic position of copepods; and (4) chlorophyll *a* (Chl *a*) to total phosphorus (TP) ratio (Chl *a* : TP) increased with decreasing Zoo : Phyto, and at a given Zoo : Phyto, it was higher in reservoirs with zooplankton dominated by copepods than in reservoirs with zooplankton dominated by cladocerans. These findings suggest that nutrient enrichment might improve stoichiometric constraint on plankton trophic structure in low-nutrient reservoirs, but enhance negative effect of excess P in high-nutrient reservoirs. Thus, negative impact of excess P on zooplankton may be a mechanism partly contributing to low Zoo : Phyto and high Chl *a* : TP in eutrophic reservoirs.

Eutrophication is one of the major aspects of environmental change in freshwaters with potentially large impact on trophic structure and ecosystem functioning (Alexander et al. 2017; Moody and Wilkinson 2019). Enrichment of aquatic ecosystems with nitrogen (N) and phosphorus (P) inevitably increases primary productivity. However, this increased primary productivity may not be efficiently transferred to the highest trophic levels, resulting in an accumulation of phytoplankton biomass (Kemp et al. 2001; Deininger et al. 2017). Zooplankton forms a central link in food webs, consuming organisms at lower trophic levels and transferring carbon up food chains. The capacity of zooplankton to utilize phytoplankton production is a crucial parameter in the regulation of food chain efficiency. However, the transfer of biomass across the phytoplankton–zooplankton interface is highly variable, and these two trophic levels can become partly uncoupled with eutrophication (Brett and Goldman 1997; Ger et al. 2014; Atkinson et al. 2021).

Nutrient enrichment may influence plankton trophic structure through both top-down and bottom-up processes (Ersoy et al. 2017). Fish play a key role in the trophic structure of aquatic ecosystems because they are efficient predators that can exert strong top-down effect on their prey (Schindler et al. 2001). Via trophic cascades, changes in fish community structure potentially have strong effect on the biomass accumulation of phytoplankton. Generally, with increasing primary productivity, there is a shift in fish community composition from dominance of piscivores to planktivores (Persson et al. 1991). In piscivore-dominated systems, piscivores reduce zooplanktivores, leading to the development of large-bodied zooplankton that effectively control phytoplankton biomass (Carpenter and Kitchell 1993). Thus, high grazing control may prevent the accumulation of phytoplankton biomass, allowing an inverted biomass pyramid to occur in plankton community (del Giorgio and Gasol 1995; Gasol et al. 1997). In contrast, in zooplanktivore-dominated systems, high fish predation shifts the zooplankton community composition from dominance of

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*Correspondence: tlinqq@jnu.edu.cn

large cladocerans to copepods and thereby reduces zooplankton grazing pressure below the level at which they can regulate phytoplankton biomass (Jeppesen et al. 2009). Accordingly, zooplanktivore-dominated systems are generally characterized by pyramidal plankton biomass structure. A large survey of temperate lakes showed a consistent pattern of reduced zooplankton to phytoplankton biomass ratio (Zoo : Phyto) with increased P, which was attributed to top-down effects from fish (Jeppesen et al. 2003).

Eutrophication caused changes in nutritional quality of phytoplankton is another mechanism regulating the shape of plankton biomass pyramid (Müller-Navarra et al. 2004; Dickman et al. 2008). Nutritional mismatch in phytoplankton supply and zooplankton demand may decrease the transfer efficiency from phytoplankton to zooplankton, which in turn reduce the zooplankton's capacity to suppress phytoplankton biomass (Müller-Navarra et al. 2000). In freshwater crustacean zooplankton, omega-3 highly unsaturated fatty acids (HUFA) such as eicosapentaenoid acid (EPA) and docosahexaenoic acid (DHA) are important for somatic growth and reproduction, but they cannot synthesize de novo EPA and DHA, and mostly accumulate them from phytoplankton (Twining et al. 2016). However, phytoplankton show enormous variation in fatty acid quality based on phylogeny. Eutrophication generally drives phytoplankton community from dominance of diatoms rich in essential HUFA to cyanobacteria poor in essential HUFA (Ahlgren et al. 1992; Watson et al. 1997; Galloway and Winder 2015). When essential HUFA levels in phytoplankton decrease to below what zooplankton require in their diets with eutrophication, there is a potential for an ecologically important mismatch between essential HUFA supply and demand. In a survey of US lakes covering a wide range of trophic state, Müller-Navarra et al. (2000, 2004) found that essential HUFA were negatively correlated with increased P notably due to an increased share of cyanobacteria, and attributed the reduced transfer efficiency to shifts in key HUFA with eutrophication.

In addition, phytoplankton may also show large variation in elemental composition based on phylogeny and environmental conditions (Quigg et al. 2003; Leonardos and Geider 2004). Though cyanobacteria and chlorophytes have elevated C : P and N : P ratios in comparison to diatoms, they may adjust their cell content of P to ambient nutrient concentration and lower C : P and N : P ratios under N or light limitation or nutrient replete conditions, resulting in potentially decreased C : P and N : P ratios of phytoplankton community with eutrophication (Sistla et al. 2015; Schulhof et al. 2019). In contrast, zooplankton are relatively more homeostatic in their C : N : P stoichiometry and are supposed to exist on a stoichiometric knife-edge (Plath and Boersma 2001; Boersma and Elser 2006). P-supplementation study by Zhou et al. (2018) showed that P-limitation of phytoplankton negatively affected zooplankton not only via reduced biochemical aspect of food quality, but also through reduced P availability. Similarly, Elser et al. (2001) showed that P enrichment of seston

from P limited lakes did not affect food abundance or concentrations and composition of essential fatty acids but dramatically lowered seston C : P and significantly stimulated *Daphnia* growth. In contrast, laboratory growth experiments showed that several species of *Daphnia*, copepods and rotifers may face excess P and reduce their performance under low food C : P conditions (Laspoumaderes et al. 2015; Elser et al. 2016; Zhou and Declerck 2019). Thus, flexible phytoplankton stoichiometry may induce mismatch between zooplankton's requirements and phytoplankton's nutrient contents, and thereby reduce the efficiency of carbon transfer through food chains (Sterner and Elser 2002). Different zooplankton taxa have different optimal biomass N : P ratios. Calanoids have higher N : P than cladocerans and cyclopoids and are supposed to be particularly sensitive to low N : P food with N in deficit or P in excess (McCarthy et al. 2006; Laspoumaderes et al. 2015). In contrast, cladocerans and cyclopoids with relatively high body P might be more sensitive to low P, high N : P food (Boersma and Elser 2006). Accordingly, in temperate freshwater systems, large generalist grazers, *Daphnia*, generally dominate zooplankton communities when seston C : P and N : P ratios are low, and calanoids dominate when seston C : P and N : P ratios are high (Hassett et al. 1997). Moderate P enrichment is expected to lower phytoplankton C : P and thereby reduce stoichiometric constraint on zooplankton with high body P, particularly *Daphnia* in nutrient-poor lakes (Elser et al. 2001). In contrast, P enrichment in high-nutrient lakes is likely to make zooplankton face phytoplankton with excess P (Zhou and Declerck 2019).

In (sub)tropical Chinese reservoirs, Zoo : Phyto decreased with increasing nutrient load due to increased filter-feeding fish predation and contribution of cyanobacteria to phytoplankton biomass (Lin et al. 2020, 2021, 2022). However, the biomass ratio also varied 10-fold within the same levels of fish and cyanobacteria biomass, suggesting there may be other phytoplankton quality parameters contributing to the scatter. Zooplankton was primarily dominated by cyclopoids which were omnivores to varying degrees in eutrophic reservoirs (Lin et al. 2014). Selective-feeding omnivores may overcome nutrient deficiency by predation on other animals when the nutrient contents of plant material mismatch their requirements (van der Lee et al. 2021). However, additional intermediate trophic levels may reduce the transfer efficiency of phytoplankton C to omnivores and the grazing pressure of omnivores on phytoplankton (Yoshida et al. 2001). As phytoplankton are capable of taking up and storing P in large amount whenever it becomes available (Solovchenko et al. 2019), it is possible that phytoplankton P content in some eutrophic reservoirs may be in excess of zooplankton's requirement, thereby favoring the dominance of omnivorous copepods. To gain a better understanding of stoichiometric effect of eutrophication on plankton trophic structure in (sub) tropical Chinese reservoirs, we surveyed the stoichiometry of seston and zooplankton, the trophic position of copepods and

plankton trophic structure in 32 reservoirs encompassing mesotrophic to hypertrophic conditions. We hypothesized that: (1) phytoplankton stoichiometric quality, together with compositional quality and fish predation mediate plankton trophic structure; (2) stoichiometric mismatch between phytoplankton and zooplankton may involve a deficit of P or N in low-nutrient reservoirs and an excess of P in eutrophic reservoirs; (3) copepods would shift their trophic position toward increased consumption of microzooplankton when the stoichiometry of phytoplankton is less comparable to their requirement than microzooplankton; and (4) increased stoichiometric mismatch would reduce Zoo : Phyto and the contribution of cladocerans to zooplankton biomass and, thereby, increase the yield of chlorophyll *a* (Chl *a*) per total phosphorus (TP).

Materials and methods

Study sites

The 32 reservoirs are located in South China ($20°21'$–$24°51'$N, $109°58'$–$116°46'$E), and stocked with *Hypophthalmichthys nobilis* and *Hypophthalmichthys molitrix* for fish production and water quality improvement (Supporting Information Fig. S1). Young-of-the-year (YOY) filter-feeding fish (200–2000 individuals ha^{-1}, depending on nutrient concentrations) are released into reservoirs after the selective harvesting of fish ≥ 1 kg individual^{-1} each year in late dry season. These reservoirs were selected to cover a wide range in nutrient concentrations, including one hypertrophic, 19 eutrophic and 12 mesotrophic reservoirs (Supporting Information Table S1).

Field sampling

Reservoirs were sampled during July to August (flood season) and November to December (dry season) in 2019. The temperature profile was taken at 1-m intervals in the central zone of each reservoir using a multiparameter probe (YSI6600). Mixing depth was defined at the depth of maximal temperature gradient in a thermally stratified water column. Then, integrated water samples for TP, total nitrogen (TN), total dissolved nitrogen (TDN), phytoplankton, Chl *a* and seston stoichiometry analyses were collected from the mixed layer with a 5-liter water sampler (UWITEC, Mondsee, Austria). We prefiltered water samples for seston analysis with 40-μm mesh to remove zooplankton and then filtered the remaining suspended materials onto pre-ashed 0.7-μm GF/F filters. Water subsamples for phytoplankton community analysis were preserved with 1% Lugol's. Zooplankton were collected from the surface to bottom at 1-m intervals with UWITEC water sampler. These samples were filtered through a 40-μm mesh, and zooplankton was preserved in 4% buffered formalin. Crustacean samples for stable nitrogen isotope and stoichiometry analyses were collected by hauling a net of mesh size 110-μm through the whole water column. Adult calanoids, cyclopoids, and cladocerans were picked from each

sample using a fine pipette. Separated zooplankton were maintained in filtered reservoir water for 24 h to allow gut evacuation. Sufficient individuals for each species (200–500 individuals depending on their size) were then collected and dried at 60°C for nutrient contents and stable isotope analysis.

Laboratory determinations

Water TDN and TN were determined as nitrate by the ultraviolet method after potassium persulfate digestion (Gross et al. 1999). Seston and crustacean P and water TP were measured after persulfate digestion through molybdate-blue ascorbic acid colorimetry and absorbance spectroscopy (Menzel and Corwin 1965). Seston and crustacean C and N contents were measured using an elemental analyzer (Vario EL III). We characterized the stoichiometry of the phytoplankton-crustacean interaction by calculating the elemental imbalance between seston and consumers ($C : P_I = Ln((C : P_{seston})/(C : P_{consumer}))$, $C : N_I = Ln((C : N_{seston})/(C : N_{consumer}))$ and $N : P_I = Ln((N : P_{seston})/(N : P_{consumer}))$, positive $C : P_I$ and $N : P_I$ indicate P deficit; negative $C : P_I$ and $N : P_I$ indicate P excess; negative $N : P_I$ coupled with positive $C : P_I$ and $C : N_I$ indicate N deficit).

Chl *a* was determined spectrophotometrically after extraction in acetone. Phytoplankton was counted using an Utermöhl chamber and inverted microscope and volumes estimated from geometrical shapes. Phytoplankton compositional food quality was calculated using an index based on the taxonomic quality of each phytoplankton taxon and its relative biomass after Dickman et al. (2008). Diatoms and cryptophytes were considered high-quality food and assigned a score of 2, cyanobacteria poor quality food (0), and chlorophytes and all other groups as medium quality food (1.24). All phytoplankton taxa with axial linear dimension $> 30 \mu$m were considered poor quality food and assigned a score of 0.

Crustacean δ^{15}N was analyzed using a Pyro Cube EA coupled with an Isoprime 100 continuous flow isotope ratio mass spectrometer. The average analytical error was normally within 0.2‰. We used dominant filter-feeding cladoceran in each reservoir as a baseline and assumed their trophic position to be 2. The trophic position of adult copepods in each reservoir was calculated using the formula in Post (2002): trophic position = $[(\delta^{15}N_{copepod} - \delta^{15}N_{cladoceran})/3.4] + 2$, where 3.4 is the assumed per trophic level increase in δ^{15}N. Zooplankton was counted and measured under a microscope. For rotifers, individual body volume was estimated from geometric shapes, and biomass for each species was obtained by assuming a specific gravity of 1. Crustacean biomass was estimated from length–weight relationship based on length measurements of 30 individuals of each species (Zhang and Huang 1991).

Statistical analyses

A paired *t*-test was conducted to test the differences in seston and crustacean stoichiometry, TP and TN between two seasons. Prior to paired *t*-test, Shapiro–Wilk tests were used to confirm the normality of the data. We used linear mixed

effects to test the effects of season and taxonomic group on crustacean stoichiometry. Mixed effects analyses were performed with the lmerTest package (Kuznetsova et al. 2020). Individual reservoirs were specified as random variable and, non-significant variables were removed from the fixed model component via the backward elimination procedure of the "step" function. Posh hoc comparisons between multifactorial combinations of the fixed model part were performed with the "ls_means" function. We performed reduced major axis regression to explore relationship between TP and TN with the lmodel2-package (Legendre 2018). To examine nutrient effects on phytoplankton biomass and compositional quality, we used multiple linear regression model with the model selection procedure using corrected Akaike's information criteria (AICc). The lm function was used to perform multiple regression analysis. For seston stoichiometry, we selected nutrients, phytoplankton composition and season as independent variables, and for Chl a : TP ratio, we selected Zoo : Phyto ratio and dominant zooplankton group (categorical variable) as independent variables. Each model assumed a Gaussian distribution. A model with the lowest AICc value and models with AICc not greater than 2 from the lowest AICc were selected as the best models (Burnham and Anderson 2004). AICc values were computed using the "aictab" function in the AICcmodavg package (Mazerolle 2020). Although some of the explanatory variables in the best models may be potentially related to each other, the variance inflation factors were < 1.5, indicating that collinearities among explanatory variables were not strong. We performed two-segment piecewise linear regression to relate seston stoichiometry to the trophic position of copepods, Zoo : Phyto and the relative biomass of three crustacean groups with the segmented package (Muggeo 2023). For the relative biomass of three crustacean groups and the trophic position of copepods, we fit the piecewise model with respect to N : P_I, and selected phytoplankton compositional quality as additional covariate. For Zoo : Phyto, the piecewise model was fit with respect to seston N : P, and seston C and phytoplankton compositional quality were selected as additional covariates. For all linear regressions, we ensured the normality and homoscedasticity of model residuals by plotting quantile-quantile plots and model residuals vs. fitted values plots. The relative biomass of phytoplankton and zooplankton were logit-transformed, and other variables were $\log_{10}$-transformed prior to analysis if necessary. All the statistical analyses were performed in R.

Results

Elemental stoichiometry

TP was significantly higher in the flood season than the dry season (paired *t*-test, $p = 0.01$), while TN showed no seasonal difference (paired *t*-test, $p = 0.80$). $\log_{10}$TN and $\log_{10}$TP were positively correlated, with scaling exponent < 1 in both seasons (N against P, all $p < 0.05$; Supporting Information

Fig. S2a). Thus, TN : TP tended to decrease overall with increased TP in both seasons (all $p < 0.05$; Supporting Information Fig. S2b), indicative of more extensive P than N enrichment in these reservoirs.

Seston C was positively related to TP ($p < 0.001$; Fig. 1a), and C : P spanned nearly one order of magnitude with 75% observations above Redfield ratio. Seston C : P was significantly higher in the dry season than the flood season (paired *t*-test, $p = 0.009$). Multiple regression revealed TP as the key determinant of C : P ($p < 0.001$; Fig. 1b; Supporting Information Table S3), while the relative biomass of cyanobacteria only had a weak positive relationship to the ratio ($p = 0.07$). Seston C : N exceeded Redfield ratio for 75% observations, and was significantly higher in the dry season than the flood season (paired *t*-test, $p < 0.001$). Multiple regression revealed that TN as the key determinant of C : N ($p < 0.001$; Fig. 1c; Supporting Information Table S3), and there also was a weak negative contribution from the relative biomass of diatoms ($p = 0.048$; Fig. 1d). The intercept was higher in the dry season than the flood season ($p < 0.001$). Seston N : P varied over a broad range and was significantly higher in the flood season than the dry season (Paired *t*-test, $p < 0.001$). There were 55% observations below Redfield ratio, and multiple regression revealed that it was negatively related to TP and the relative biomass of diatoms with a much higher intercept in the flood season than the dry season (all $p < 0.001$; Fig. 1e,f, Supporting Information Table S3).

The mixed effects model indicated that cyclopoids tended to have higher C : P than cladocerans but lower value than calanoids (all $p < 0.001$; Fig. 2a; Supporting Information Table S2). Calanoids had higher C : P in the flood season than the dry season (paired *t*-test, $p < 0.001$), while cyclopoids and cladocerans showed no significant seasonal difference in C : P (paired *t*-test, both $p > 0.1$). C : P_I for calanoids, cyclopoids, and cladocerans varied between -1.1 to 0.5, -0.7 to 1.2, and -0.3 to 1.3, respectively (Fig. 3), and decreased with increased TP (all $p < 0.001$). C : P_I was generally negative for calanoids in reservoirs with TP $> 20 \, \mu g \, L^{-1}$, and negative for cyclopoids and cladocerans in reservoirs with TP $> 40 \, \mu g \, L^{-1}$. For C : N, three crustacean groups all had higher values in the dry season than the flood season (paired *t*-test, all $p < 0.001$), and both calanoids and cyclopoids had lower C : N than cladocerans (all $p < 0.001$; Fig. 2b; Supporting Information Table S2). C : N_I for calanoids, cyclopoids, and cladocerans varied between -0.05 to 1.5, -0.12 to 1.4 and -0.1 to 1.3, respectively (Fig. 3), and decreased with increased TN (all $p < 0.001$). For three crustacean groups, C : N_I was ≥ 0 for the majority of observations and was only slightly lower than zero when the values were negative. For N : P, it was higher in copepods than cladocerans, and lower in cyclopoids than calanoids (all $p < 0.001$; Fig. 2c; Supporting Information Table S2). N : P_I for calanoids (-1.4 to 0.4) was negative for 45 of the 48 observations, and decreased with increased TP ($p < 0.001$). Similarly, N : P_I for cyclopoids (-1.5 to 1.0) and cladocerans (-0.6 to 1.2)
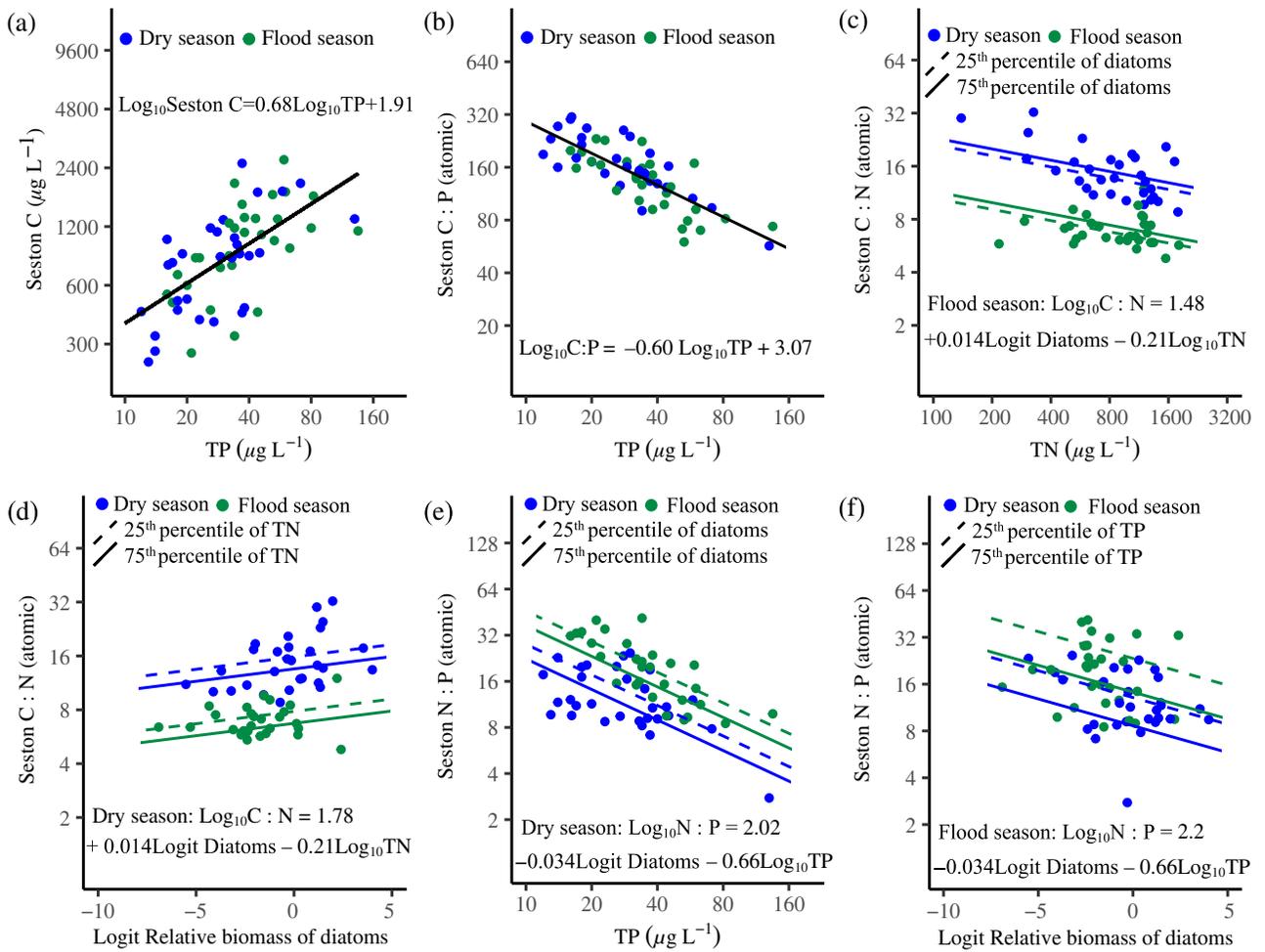
Fig. 1. Seston C (**a**) and C : P (**b**) vs. TP, seston C : N vs. TN (**c**) and the relative biomass of diatoms (**d**), and seston N : P vs. TP (**e**), and the relative biomass of diatoms (**f**).
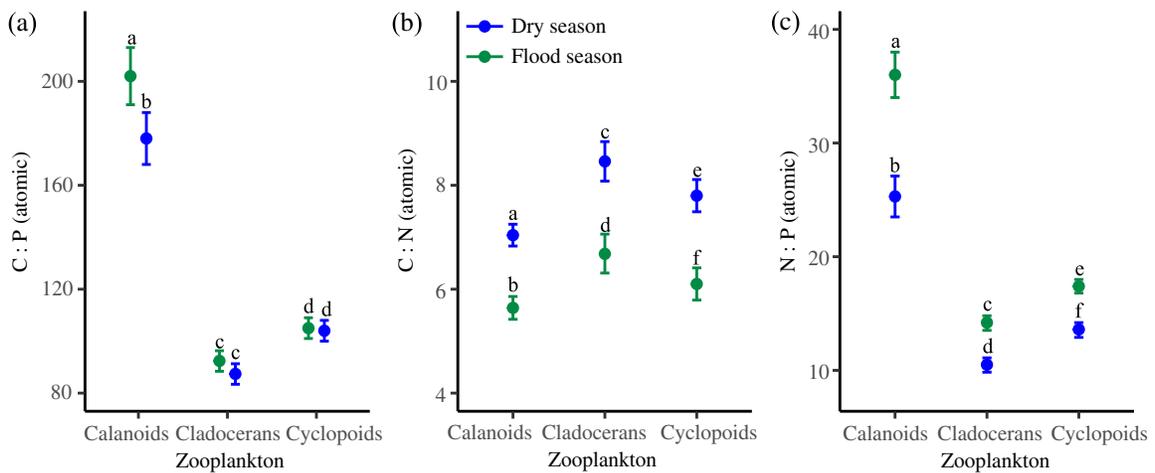
Fig. 2. The averages and 95% confidence intervals of C : P (**a**), C : N (**b**), and N : P (**c**) ratios for three zooplankton groups. Letters denote significant differences among three zooplankton groups and between dry and flood seasons based on post hoc comparisons.
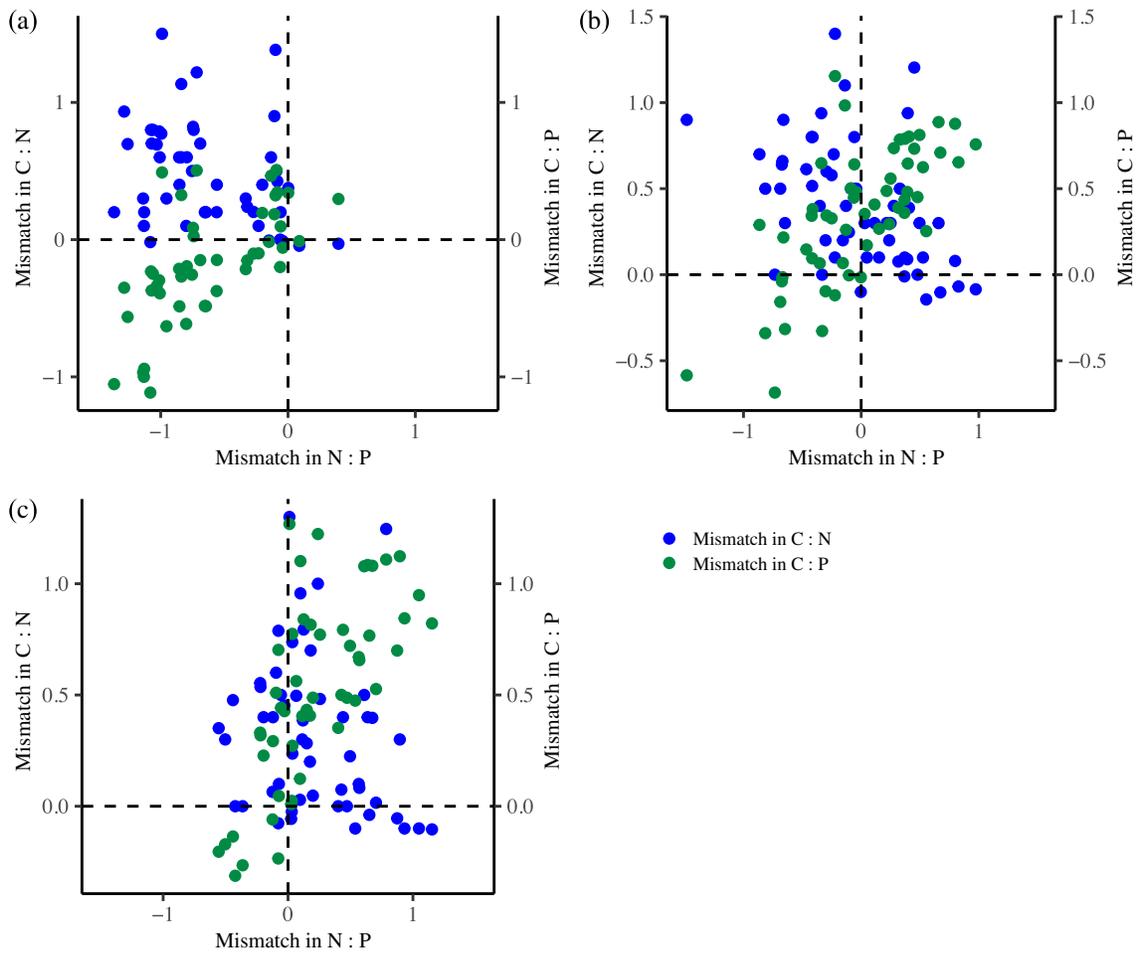
Fig. 3. Mismatches in C : N and C : P vs. mismatch in N : P between seston and three crustacean groups (**a**: calanoids, **b**: cyclopoids, **c**: cladocerans).

decreased with increased TP (both $p < 0.001$; Fig. 3) and were generally negative in reservoirs with TP > 40 μg L^{-1}.

Plankton and trophic structure

Multiple regression revealed that phytoplankton biomass was related positively to TN and negatively to TDN : TP (Fig. 4a,c; Supporting Information Table S3). Phytoplankton were dominated by either diatoms or cyanobacteria or chlorophytes. Diatoms contributed 0.1–98.2% to phytoplankton biomass, and was related negatively to TN and positively to TDN : TP (all $p < 0.001$; Supporting Information Table S3; Fig. S3a,d). In contrast, the proportion of cyanobacteria was related positively to TN and negatively to TDN : TP (all $p < 0.001$; Supporting Information Table S3; Fig. S3b,e), while the relative biomass of chlorophytes was related neither to TN nor to TDN : TP (all $p > 0.1$; Supporting Information Fig. S3c, f). Thus, phytoplankton compositional food quality varied from 0 to 2, and was related negatively to TN and positively to TDN : TP in a multiple linear regression analysis (all $p < 0.001$; Fig. 4b,d; Supporting Information Table S3).

Zooplankton biomass increased with increased TP ($p < 0.001$), and was primarily contributed by small cladocerans (e.g., *Bosmina fatalis* and *Diaphanosoma orghidani*) or copepods (e.g., *Phyllodiaptomus tunguidus* and *Mesocyclops thermocyclopoides*). Cladocerans contributed 3–86% to zooplankton biomass, and its relative biomass was positively related to phytoplankton compositional food quality and showed a two-segment linear relationship with N : P$_{\text{I}}$ (all $p < 0.001$; Fig. 5a,d; Supporting Information Table S3). The breakpoint was situated at an imbalance value of −0.15 (± 0.08 SE) which did not differ significantly from zero. At a given compositional food quality level, the relative biomass showed a maximum at the breakpoint and strong reductions toward the extremes of the imbalance gradient. Unlike cladocerans, the relative biomass of calanoids and cyclopoids were related neither to N : P$_{\text{I}}$ nor to phytoplankton compositional food quality (all $p > 0.1$; Fig. 5). The trophic position of calanoids and cyclopoids varied from 2.05 to 3.33 and 2.01 to 3.59, respectively, and both increased with decreased phytoplankton compositional food quality and showed a two-segment linear relationship with
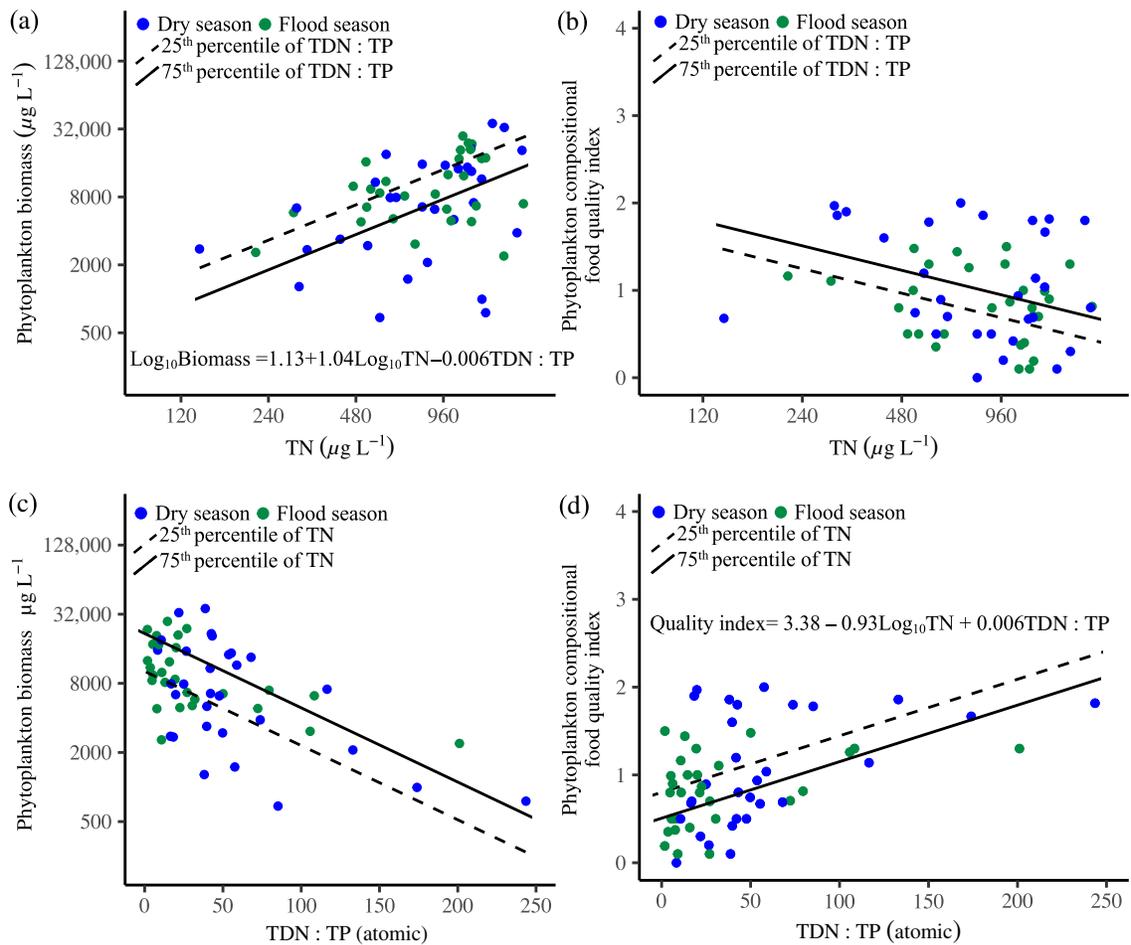
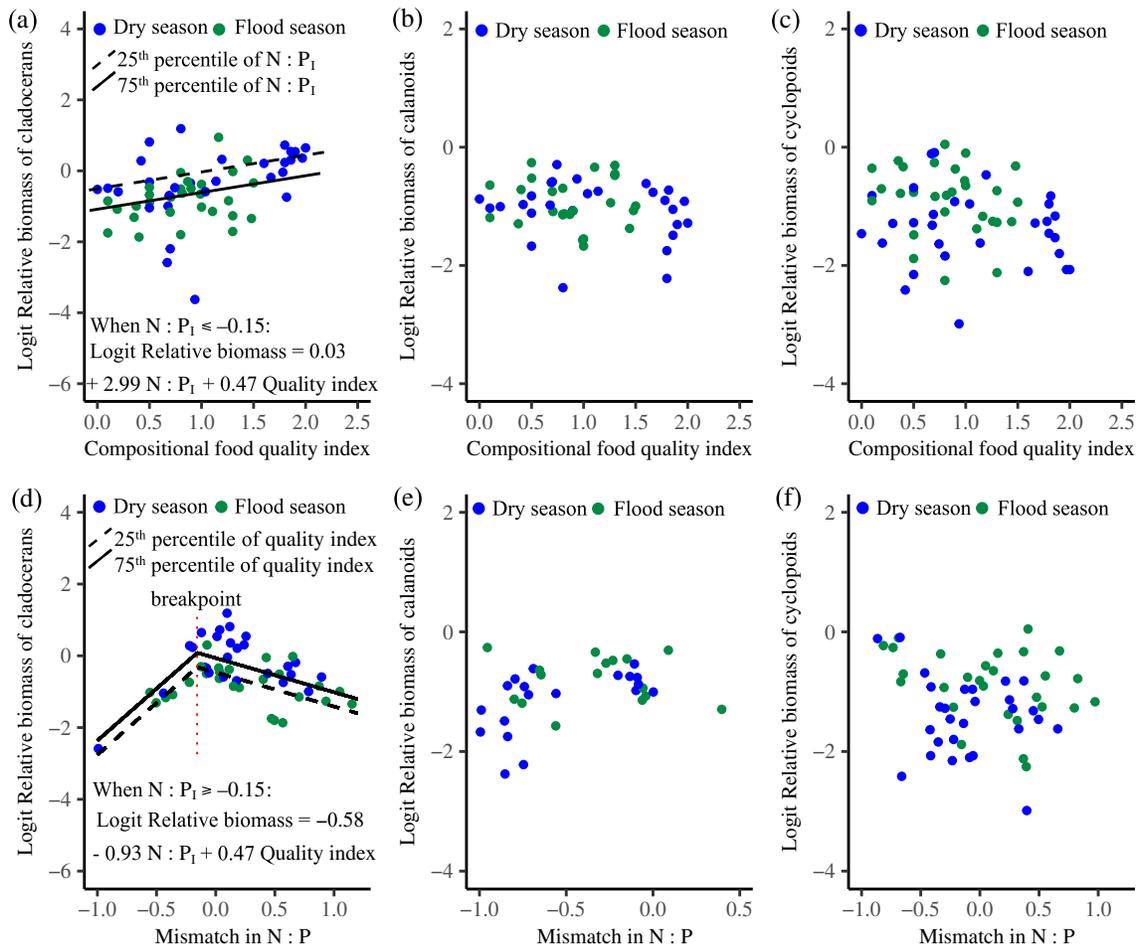**Fig. 4.** Phytoplankton biomass and compositional food quality index vs. TN (**a**, **b**) and TDN : TP (**c**, **d**).

$N : P_I$ (all $p < 0.001$; Fig. 6; Supporting Information Table S3). Their breakpoints were situated at imbalance values of -0.01 (± 0.07) and 0.07 (± 0.07), both of which did not differ significantly from zero. Meanwhile, at a given compositional food quality level, their trophic position showed a minimum at the breakpoint and strong increases toward the extremes of the imbalance gradient.

The zooplankton to phytoplankton biomass ratio (Zoo : Phyto) decreased from 0.261 to 0.005 with increased seston C and decreased phytoplankton compositional food quality, and showed a two-segment linear relationship with seston $N : P$ (all $p < 0.001$; Fig. 7a–c; Supporting Information Table S3). At given seston C and compositional food quality levels, Zoo : Phyto showed a maximum at a breakpoint of 12.6 (± 1.6) and strong reductions toward the extremes of the seston $N : P$ gradient. The chlorophyll a to TP ratio (Chl a : TP) ranged from 0.09 to 1.53, and was negatively related to Zoo : Phyto with a much higher intercept in reservoirs with zooplankton dominated by copepods than reservoirs with zooplankton dominated by cladocerans (all $p < 0.001$; Fig. 7d; Supporting Information Table S3).

Discussion

Effects of seston stoichiometric quality on zooplankton

We found that seston C : N, C : P, and N : P ratios decreased greatly along a eutrophication gradient in (sub)tropical Chinese reservoirs, which is a common finding of many studies in the field of ecological stoichiometry (Hessen et al. 2003; Hessen 2006). For three crustacean groups, their body stoichiometry changed at a much smaller scale than seston along a eutrophication gradient. Thus, stoichiometric mismatch between seston and three crustacean groups changed with eutrophication. Following from the Liebig minimum principle, positive $C : N_I$ and $C : P_I$ associated with negative $N : P_I$ for calanoids suggested that they might face N-deficit phytoplankton in low-nutrient reservoirs. For cyclopoids and cladocerans, positive $C : P_I$ and $C : N_I$ associated with either positive or negative $N : P_I$ indicated that they may face phytoplankton with either P or N in deficit in low-nutrient reservoirs. *Daphnia* have the highest P requirements as well as the lowest C : P among the crustacean zooplankton, and may face excess P when food C : P is < 120 (Hessen 1990; Elser et al. 2016).
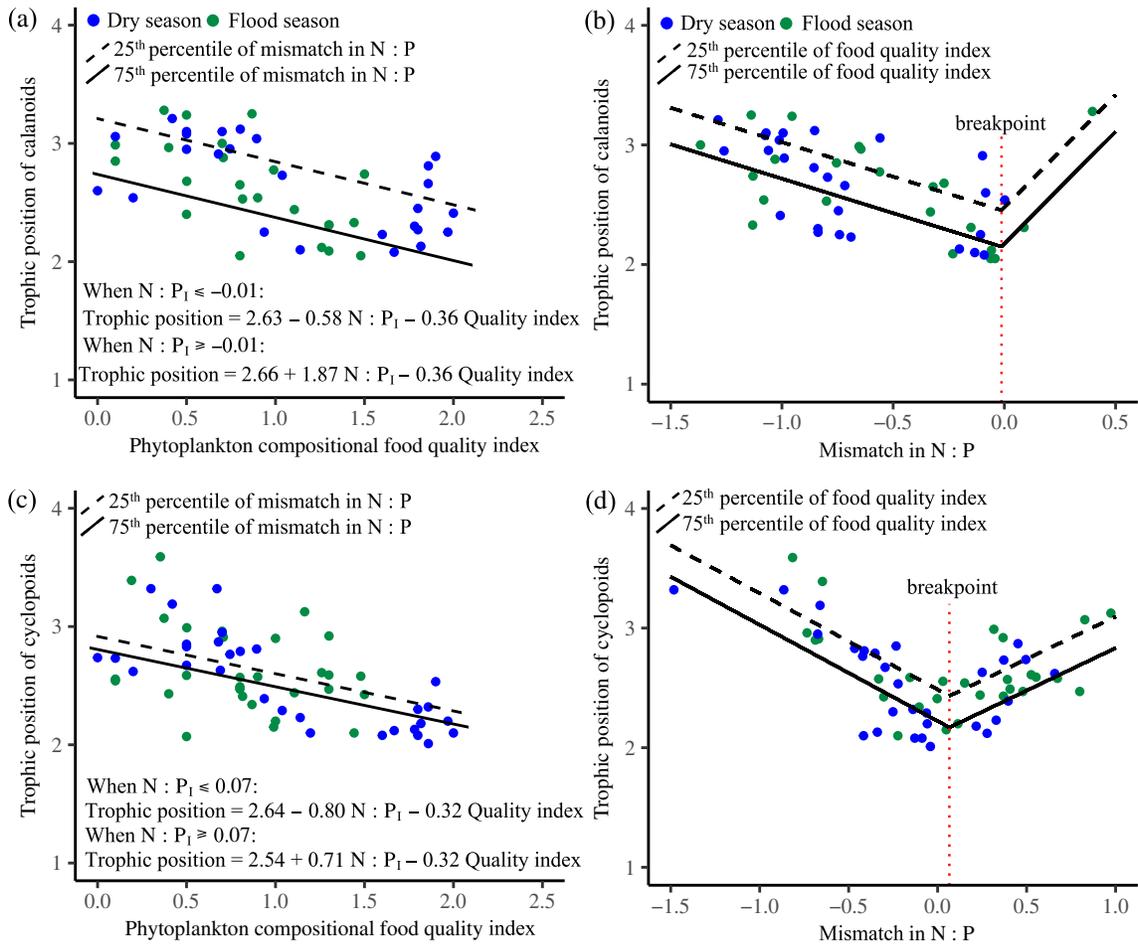
Fig. 5. The relative biomass of cladocerans, calanoids, and cyclopoids vs. phytoplankton compositional food quality index (**a–c**) and mismatch in N : P between seston and their body tissue (**d–f**).

Non-*Daphnia* zooplankton may be less able to cope with excess P due to limited internal sinks to accommodate extra P (Elser et al. 2003), and growth experiments by Laspoumaderes et al. (2015) and Zhou et al. (2018) showed that C : P thresholds for copepod *Parabroteas sarsi* and rotifer *Brachionus calyciflorus* facing excess P were > 120. Thus, negative $C:P_I$ and $N:P_I$ coupled with seston C : P < 100 suggested that three crustacean groups might face phytoplankton with excess P in reservoirs with TP > 40 μg l^{-1}. As seston C : N and C : P ratios tended to decrease with eutrophication, it seems likely that moderate nutrient enrichment might improve the stoichiometric quality of phytoplankton for crustacean zooplankton in low-nutrient reservoirs, but reduce it in high-nutrient reservoirs.

Zooplankton were dominated either by small cladocerans or by copepods irrespectively of TP. This pattern is consistent with earlier studies by Lin et al. (2014, 2020), which reported that high filter-feeding fish predation accounted for the absence/rarity of *Daphnia* in (sub)tropical Chinese reservoirs. Meanwhile, we also found that cladocerans only dominated

in reservoirs with high phytoplankton compositional food quality and low N : P mismatch degree between seston and their requirement. Moreover, seston stoichiometric quality explained a higher amount of variance (33.2%) in the relative biomass of cladocerans than phytoplankton compositional food quality (23.8%). Cladocerans are generally expected to have a competitive advantage over copepods in a situation of high phytoplankton food quality, due to their greater efficiency in food collection and faster metabolic rates than animals of a similar size (Sommer and Stibor 2002). However, as they are relatively nonselective filter feeders that tend to ingest particles in the same ratio as they are encountered, they may reduce their performance and lose their competitive advantage when bulk phytoplankton quality is poor (Richman and Dodson 1983; Plath and Boersma 2001). Thus, in low-nutrient reservoirs, the relative biomass of cladocerans tended to decrease with increasing seston C : P, which is consistent with the findings in Norwegian lakes and Wolf Lake (Hessen 2006; Prater et al. 2018). In contrast, in high-nutrient reservoirs with seston C : P < 100, cladocerans was likely to

Fig. 6. The trophic position of adult calanoids and cyclopoids vs. phytoplankton compositional food quality index (**a**, **c**) and mismatch in N : P between seston and their body tissue (**b**, **d**).

face phytoplankton with P in excess, and their relative biomass tended to decrease with decreasing seston C : P.

Similar to cladocerans, copepods would reduce their performance on food with either excess P or N or P in deficit (Bullejos et al. 2014; Laspoumaderes et al. 2015; Mathews et al. 2018). However, copepods are selective feeders, and can feed discriminately based on food nutrient status (Butler et al. 1989), which may confer a competitive advantage to copepods over cladocerans in conditions of low phytoplankton nutritional quality. Selective feeding experiment by Meunier et al. (2015) showed that nauplii of *Acartia tonsa* characterized by a low body N : P selected for P-rich food, while older copepodite stages with higher body N : P selected for nitrogen-rich food. In oligotrophic Patagonian lakes, the trophic position of *Boeckella gracilipes* was positively related to seston C : N (Trochine et al. 2019). Similarly, nitrogen stable isotope analysis indicated that both calanoids and cyclopoids were omnivorous to varying degrees in (sub)tropical Chinese reservoirs. Moreover, their trophic position increased with decreased phytoplankton compositional food quality and

increased stoichiometric mismatch degree between phytoplankton and their requirement, suggesting that they may shift their trophic position toward carnivory when the stoichiometric and compositional food quality of phytoplankton were low. Copepods are exposed to a mixture of phytoplankton taxa that may vary in elemental and biochemical composition in natural systems and on which they may also feed selectively to cope with nutritional mismatches (Ahlgren et al. 1992; Quigg et al. 2003; Meunier et al. 2015). However, our results suggested that copepods might avoid nutritional mismatches primarily via positive prey selection for animal material offering the right balances of nutrients. Moreover, the amount of variation in the trophic position of copepods explained by phytoplankton stoichiometric quality (36.7–39.2%) was comparable to the amount explained by compositional food quality (34.5–39.0%). Thus, our results suggested that phytoplankton stoichiometric quality together with biochemical quality mediated zooplankton community structure and the trophic position of copepods, and low phytoplankton nutritional quality may favor copepods over other zooplankton
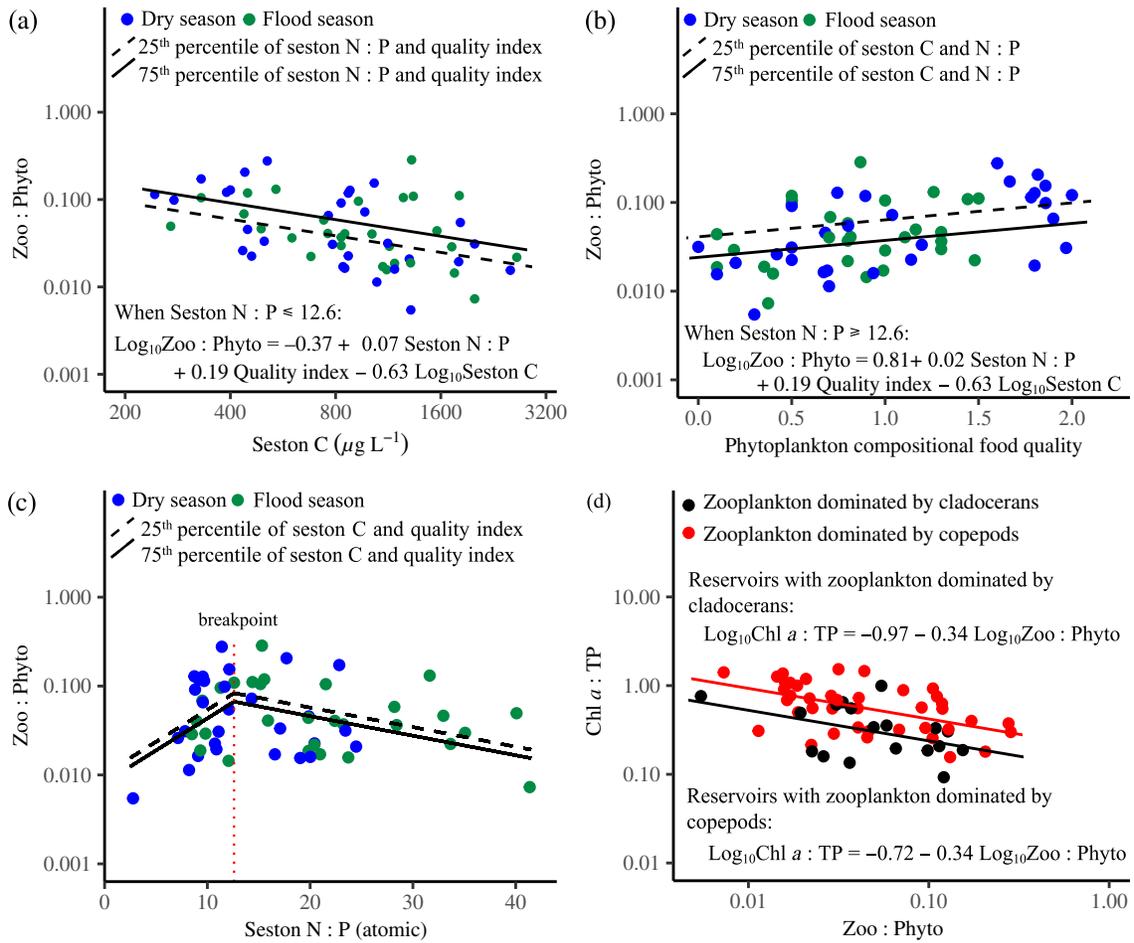
Fig. 7. Zoo : Phyto vs. seston C (**a**), phytoplankton compositional food quality index (**b**) and seston N : P (**c**). Also shown is relationship between Chl *a* : TP and Zoo : Phyto ratios (**d**).

in (sub)tropical Chinese reservoirs. However, a further research is needed to unravel how phytoplankton stoichiometric and biochemical quality mediate copepod's feeding selection between animal material and phytoplankton.

Effects of seston stoichiometric quality on trophic structure

In (sub)tropical Chinese reservoirs, TP concentration increased faster than TN and thereby decreased TDN : TP with eutrophication. The fact that phytoplankton biomass increased with increased TN and decreased TDN : TP suggested a prevailing co-limitation by N and P. Thus, phytoplankton biomass increased rapidly with eutrophication. Though zooplankton biomass also increased with reservoir productivity, it increased less rapidly than phytoplankton biomass, resulting in decreased Zoo : Phyto along the eutrophication gradient. These observations are consistent with patterns documented in temperate lakes (Jeppesen et al. 2003; Hessen et al. 2006). The decrease in Zoo : Phyto with increased productivity has been linked mainly to either an increased planktivorous fish predation or a reduced phytoplankton quality or both in

temperate lakes (Jeppesen et al. 2003; Müller-Navarra et al. 2004; Hessen et al. 2006). YOY filter-feeding fish were released into (sub)tropical Chinese reservoirs for fish production, and stock fish biomass increased with reservoir productivity. Thus, filter-feeding fish predation pressure increased with reservoir productivity, thereby partly accounting for reduced Zoo : Phyto with increased seston C. However, the ratio also varied 10-fold within the same level of productivity, indicating that there were other factors together with fish predation accounting for the scatter. As algal species differ phylogenetically in biochemical composition, an increasing share of cyanobacteria may decrease biochemical quality of phytoplankton, and thereby reduce Zoo : Phyto (Müller-Navarra et al. 2004). As expected, phytoplankton compositional food quality decreased overall with eutrophication, and was positively related to Zoo : Phyto in (sub)tropical Chinese reservoirs. Moreover, phytoplankton was dominated either by green algae or by cyanobacteria in eutrophic reservoirs, leading to considerable variation in phytoplankton compositional food quality within the same level of TP, thereby partly accounting for the scatter in Zoo : Phyto. Meanwhile, at given

seston C and phytoplankton compositional food quality levels, Zoo : Phyto showed a maximum at intermediate seston N : P and strong reductions toward the extremes of the seston N : P gradient. Moreover, seston stoichiometric quality explained a higher amount of variation (14.7%) in Zoo : Phyto than phytoplankton compositional food quality (10.7%). Thus, our result suggested that phyoplankton stoichiometric quality together with biochemical quality and fish predation mediated the biomass ratio.

Our results aligned with findings from Thomas et al.'s (2022) meta-analysis using > 100 experimental studies, which reported that co-limitation among elements, fatty acids and sterols may be strong in zooplankton. Moreover, enclosure experiment in a low nutrient lake also showed that shading alone may increase zooplankton production and thereby increase Zoo : Phyto by decreasing seston C : P (Urabe et al. 2002). However, field data relating excess P to zooplankton production and Zoo : Phyto are sparse. Present evidences for excess P effect on zooplankton are primarily obtained in well-defined laboratory experiments which focused on the response of a single consumer to elemental mismatch with one producer (Laspoumaderes et al. 2015; Elser et al. 2016; Zhou et al. 2018). Growth experiment by Currier and Elser (2017) showed that lowering lake seston C : P below 110 by P enrichment may reduce *Daphnia magna* growth, supporting the existence of the "excess P" side of the "stoichiometric knife edge" under field conditions. However, field study by Prater et al. (2018) suggested that food quality effects on daphnid biomass production were likely to act along a continuum controlled by dietary elemental stoichiometry in oligotrophic systems and switching to biochemical regulation under more eutrophic conditions. In natural systems, zooplankton communities not only consist of multiple species that may differ from each other in their response to nutritional mismatch (Currier and Elser 2017), but also are exposed to a mixture of food source types that may vary in elemental and biochemical composition and on which they may feed selectively. Further field work is necessary to examine the effects of excess P on zooplankton community and unravel whether excess P and biochemical limitation may effect zooplankton production and Zoo : Phyto in conjunction or in a mutually exclusive manner in eutrophic systems.

Meanwhile, impaired zooplankton performance induced by low phytoplankton nutritional quality may reduce their grazing pressure, which in turn promote the accumulation of phytoplankton biomass. Thus, Chl *a* : TP tended to increase with decreased Zoo : Phyto. Moreover, cladocerans have faster metabolic rates than copepods of a similar size, and zooplankton compositional shift from a cladoceran assemblage to a copepod assemblage is expected to reduce zooplankton grazing pressure on phytoplankton (Sommer and Stibor 2002; Persaud and Dillon 2011). Thus, stoichiometric mismatch might reduce zooplankton grazing pressure on phytoplankton by decreasing contribution of cladocerans to zooplankton

biomass. Meanwhile, copepods shifted their trophic position toward increased consumption of animal material when the stoichiometry of phytoplankton became less comparable to their requirement, leading to a greater proportion of phytoplankton C transferring to copepods with additional intermediate trophic levels, and thereby reducing the trophic transfer efficiency. Thus, at a given Zoo : Phyto, Chl *a* : TP tended to be higher in reservoirs with zooplankton dominated by copepods than reservoirs with zooplankton dominated by cladocerans. Moreover, copepod grazing can occur via three food chains with two to four levels and different grazing pressure on phytoplankton. Two-level chain implies a negative effect on phytoplankton, three-level chain a positive effect, and four-level chain may have variable results (Yoshida et al. 2001; Sommer and Sommer 2006). It is not clear whether the net effect of copepods on phytoplankton biomass would change with their trophic position, thereby partly accounting for the scatter in Chl *a* : TP in copepods-dominated systems. A further research is needed to unravel how phytoplankton stoichiometric quality and copepods omnivory regulate planktonic trophic interactions.

Conclusions

We observed decreases in seston C : P, C : N, and N : P ratios and zooplankton to phytoplankton biomass ratio, coupled with an increase in the yield of Chl *a* per TP along the eutrophication gradient in (sub)tropical Chinese reservoirs. Zooplankton may face phytoplankton with P or/and N in deficit of their demands in low-nutrient reservoirs and P in excess in eutrophic to highly eutrophic reservoirs, facilitating the dominance of copepods which can overcome this nutrient deficiency or excess by predation on microzooplankton. Therefore, it seems that the greater stoichiometric mismatch between phytoplankton and zooplankton might induce a much lower Zoo : Phyto associated with a much higher Chl *a* : TP. Eutrophication is generally expected to result in reduced trophic efficiency and accumulation of phytoplankton biomass via the promotion of toxic or inedible cyanobacterial blooms or/and the enhancement of planktivorous fish stocks. Our results suggest that negative impact of excess P on zooplankton may be another mechanism partly contributing to the low trophic transfer efficiency in eutrophic (sub)tropical Chinese reservoirs.

Data availability statement

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

References

Ahlgren, G., I. B. Gustafsson, and M. Boberg. 1992. Fatty acid content and chemical composition of freshwater microalgae. J. Phycol. **28**: 37–50. doi:10.1111/j.0022-3646.1992.00037.x

Alexander, T. J., P. Vonlanthen, and O. Seehausen. 2017. Does eutrophication-driven evolution change aquatic ecosystems? Philos. Trans. R. Soc. B **372**: 20160041. doi:10.1098/rstb.2016.0041

Atkinson, A., and others. 2021. Increasing nutrient stress reduces the efficiency of energy transfer through planktonic size spectra. Limnol. Oceanogr. **66**: 422–437. doi:10.1002/lno.11613

Boersma, M., and J. J. Elser. 2006. Too much of a good thing: On stoichiometrically balanced diets and maximal growth. Ecology **87**: 1325–1330. doi:10.1890/0012-9658(2006)87[1325:TMOAGT]2.0.CO;2

Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. Science **275**: 384–386. doi:10.1126/science.275.5298.384

Bullejos, F. J., P. Carrillo, E. Gorokhova, J. M. Medina-Sánchez, E. G. Balseiro, and M. Villar-Argaiz. 2014. Shifts in food quality for herbivorous consumer growth: Multiple golden means in the life history. Ecology **95**: 1272–1284. doi:10.1890/13-0410.1

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. **33**: 261–304. doi:10.1177/0049124104268644

Butler, N. M., C. A. Suttle, and W. E. Neill. 1989. Discrimination by freshwater zooplankton between single algal cells differing in nutritional status. Oecologia **78**: 368–372. doi:10.1007/BF00379111

Carpenter, S. R., and J. F. Kitchell. 1993. The trophic cascade in lakes. Cambridge Univ. Press.

Currier, C. M., and J. J. Elser. 2017. Beyond monoculture stoichiometry studies: Assessing growth, respiration, and feeding responses of three *Daphnia* species to P-enriched, low C:P lake seston. Inland Waters **7**: 348–357. doi:10.1080/20442041.2017.1319180

Deininger, A., C. L. Faithfull, J. Karlsson, M. Klaus, and A.-K. Bergström. 2017. Pelagic food web response to whole lake N fertilization. Limnol. Oceanogr. **62**: 1498–1511. doi:10.1002/lno.10513

del Giorgio, P. A., and J. M. Gasol. 1995. Biomass distribution in freshwater plankton communities. Am. Nat. **146**: 135–152. doi:10.1086/285790

Dickman, E. M., J. M. Newell, M. J. González, and M. J. Vanni. 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. Proc. Natl. Acad. Sci. USA **105**: 18408–18412. doi:10.1073/pnas.0805566105

Elser, J. J., K. Hayakawa, and J. Urabe. 2001. Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. Ecology **82**: 898–903. doi:10.1890/0012-9658(2001)082[0898:NLRFQF]2.0.CO;2

Elser, J. J., and others. 2003. Growth rate-stoichiometry couplings in diverse biota. Ecol. Lett. **6**: 936–943. doi:10.1046/j.1461-0248.2003.00518.x

Elser, J. J., M. Kyle, J. Learned, M. L. McCrackin, A. Peace, and L. Steger. 2016. Life on the stoichiometric knife-edge: Effects of high and low food C:P ratio on growth, feeding, and respiration in three *Daphnia* species. Inland Waters **6**: 136–146. doi:10.5268/IW-6.2.908

Ersoy, Z., and others. 2017. Size-based interactions and trophic transfer efficiency are modified by fish predation and cyanobacteria blooms in Lake Mývatn, Iceland. Freshw. Biol. **62**: 1942–1952. doi:10.1111/fwb.13039

Galloway, A. W. E., and M. Winder. 2015. Partitioning the relative importance of phylogeny and environmental conditions on phytoplankton fatty acids. PLoS One **10**: e0130053. doi:10.1371/journal.pone.0130053

Gasol, J. M., P. A. del Giorgio, and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. Limnol. Oceanogr. **42**: 1353–1363. doi:10.4319/lo.1997.42.6.1353

Ger, K. A., L.-A. Hansson, and M. Lürling. 2014. Understanding cyanobacteria-zooplankton interactions in a more eutrophic world. Freshw. Biol. **59**: 1783–1798. doi:10.1111/fwb.12393

Gross, A., C. E. Boyd, and J. Seo. 1999. Evaluation of the ultraviolet spectrophotometric method for the measurement of total nitrogen in water. J. World Aquacult. Soc. **30**: 388–393. doi:10.1111/j.1749-7345.1999.tb00690.x

Hassett, R. P., B. Cardinale, L. B. Stabler, and J. J. Elser. 1997. Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton–phytoplankton interaction. Limnol. Oceanogr. **42**: 648–662. doi:10.4319/lo.1997.42.4.0648

Hessen, D. O. 1990. Carbon, nitrogen and phosphorus status in *Daphnia* at varying food conditions. J. Plankton Res. **12**: 1239–1249. doi:10.1093/plankt/12.6.1239

Hessen, D. O. 2006. Determinants of seston C:P-ratio in lakes. Freshw. Biol. **51**: 1560–1569. doi:10.1111/j.1365-2427.2006.01594.x

Hessen, D. O., T. Andersen, P. Brettum, and B. A. Faafeng. 2003. Phytoplankton contribution to sestonic mass and elemental ratios in lakes: Implications for zooplankton nutrition. Limnol. Oceanogr. **48**: 1289–1296. doi:10.4319/lo.2003.48.3.1289

Hessen, D. O., B. A. Faafeng, P. Brettum, and T. Andersen. 2006. Nutrient enrichment and planktonic biomass ratios in lakes. Ecosystems **9**: 516–527. doi:10.1007/s10021-005-0114-6

Jeppesen, E., and others. 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: A study of 466 lakes from the Temperate zone to the Arctic. Ecosystems **6**: 313–325. doi:10.1007/PL00021503

Jeppesen, E., and others. 2009. Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. J. Environ. Qual. **38**: 1930–1941. doi:10.2134/jeq2008.0113

Kemp, W. M., M. T. Brooks, and R. R. Hood. 2001. Nutrient enrichment, habitat variability and trophic transfer

efficiency in simple models of pelagic ecosystems. Mar. Ecol. Prog. Ser. **223**: 73–87. doi:10.3354/meps223073

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2020. lmerTest: tests in linear mixed effects models. Available from http://cran.r-project.org/package=lmerTest

Laspoumaderes, C., B. Modenutti, J. J. Elser, and E. Balseiro. 2015. Does the stoichiometric carbon:phosphorus knife edge apply for predaceous copepods? Oecologia **178**: 557–569. doi:10.1007/s00442-014-3155-8

Legendre, P. 2018. lmodel2: Model II Regression. R package version 1.7-3. Available from https://cran.r-project.org/packages=lmodel2. doi:10.1684/ejd.2018.3451

Leonardos, N., and R. J. Geider. 2004. Effects of nitrate : phosphate supply ratio and irradiance on the C : N : P stoichiometry of *Chaetoceros muelleri*. Eur. J. Phycol. **39**: 173–180. doi:10.1080/0967026042000201867

Lin, Q., X. Jiang, B.-P. Han, and E. Jeppesen. 2014. Does stocking of filter-feeding fish for production have a cascading effect on zooplankton and ecological state? A study of fourteen (sub)tropical Chinese reservoirs with contrasting nutrient concentrations. Hydrobiologia **736**: 115–125. doi:10.1007/s10750-014-1896-3

Lin, Q., Q. Chen, L. Peng, L. Xiao, L. Lei, and E. Jeppesen. 2020. Do bigheaded carp act as a phosphorus source for phytoplankton in (sub)tropical Chinese reservoirs? Water Res. **180**: 115841. doi:10.1016/j.watres.2020.115841

Lin, Q., D. Zeng, T. Guo, and L. Peng. 2021. Filter-feeding fish (*Hypophthalmichthys molitrix*) mediated phosphorus recycling versus grazing pressure as drivers of the trophic cascade in large enclosures subsidized by allochthonous detritus. Water Res. **204**: 117579. doi:10.1016/j.watres.2021.117579

Lin, Q., Y. Liao, Q. Xia, and L. Peng. 2022. Body size mediates the trophic cascade effect of filter-feeding fish [*Hypophthalmichthys molitrix* (Val.)] on phytoplankton in large enclosures. Hydrobiologia **849**: 4707–4724. doi:10.1007/s10750-022-05009-1

Mathews, L., C. L. Faithfull, P. H. Lenz, and C. E. Nelson. 2018. The effects of food stoichiometry and temperature on copepods are mediated by ontogeny. Oecologia **188**: 75–84. doi:10.1007/s00442-018-4183-6

Mazerolle, M. J. 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). Available from https://cran.r-project.org/package=AICcmodavg. doi:10.1002/cl2.1111

McCarthy, V., I. Donohue, and K. Irvine. 2006. Field evidence for stoichiometric relationships between zooplankton and N and P availability in a shallow calcareous lake. Freshw. Biol. **51**: 1589–1604. doi:10.1111/j.1365-2427.2006.01599.x

Menzel, D. W., and N. Corwin. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. **10**: 280–282. doi:10.4319/lo.1965.10.2.0280

Meunier, C. L., M. Boersma, K. H. Wiltshire, and A. M. Malzahn. 2015. Zooplankton eat what they need: Copepod selective feeding and potential consequences for marine systems. Oikos **125**: 50–58.

Moody, E. K., and G. M. Wilkinson. 2019. Functional shifts in lake zooplankton communities with hypereutrophication. Freshw. Biol. **64**: 608–616. doi:10.1111/fwb.13246

Muggeo, V. M. 2023. segmented: Regression models with break-pints/change-points (with possibly random effects) Estimation. Available from https://cran.r-project.org/packages=segmented. doi:10.3390/cancers15092554

Müller-Navarra, D. C., M. T. Brett, A. M. Liston, and C. R. Goldman. 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. Nature **403**: 74–77. doi:10.1038/47469

Müller-Navarra, D. C., M. T. Brett, S. Park, S. Chandra, A. P. Ballantyne, E. Zorita, and C. R. Goldman. 2004. Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. Nature **427**: 69–72. doi:10.1038/nature02210

Persaud, A. D., and P. J. Dillon. 2011. Differences in zooplankton feeding rates and isotopic signatures from three temperate lakes. Aquat. Sci. **73**: 261–273. doi:10.1007/s00027-010-0174-3

Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1991. Shifts in fish communities along the productivity gradient of temperate lakes-patterns and the importance of size-structure interactions. J. Fish Biol. **38**: 281–293. doi:10.1111/j.1095-8649.1991.tb03114.x

Plath, K., and M. Boersma. 2001. Mineral limitation of zooplankton: Stoichiometric constraints and optimal foraging. Ecology **82**: 1260–1269. doi:10.1890/0012-9658(2001)082[1260:MLOZSC]2.0.CO;2

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology **83**: 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Prater, C., N. D. Wagner, and P. C. Frost. 2018. Seasonal effects of food quality and temperature on body stoichiometry, biochemistry, and biomass production in *Daphnia* populations. Limnol. Oceanogr. **63**: 1727–1740. doi:10.1002/lno.10803

Quigg, A., and others. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature **425**: 291–294. doi:10.1038/nature01953

Richman, S., and S. I. Dodson. 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. Limnol. Oceanogr. **28**: 948–956. doi:10.4319/lo.1983.28.5.0948

Schindler, D. E., R. A. Knapp, and P. R. Leavitt. 2001. Alteration of nutrient cycles and algal production resulting from

fish introductions into mountain lakes. Ecosystems **4**: 308–321. doi:10.1007/s10021-001-0013-4

Schulhof, M. A., J. B. Shurin, S. A. J. Declerck, and D. B. van de Waal. 2019. Phytoplankton growth and stoichiometric responses to warming, nutrient addition and grazing dependent on lake productivity and cell size. Global Change Biol. **25**: 2751–2762. doi:10.1111/gcb.14660

Sistla, S. A., A. P. Appling, A. M. Lewandowska, B. N. Taylor, and A. A. Wolf. 2015. Stoichiometry flexibility in response to fertilization along gradients of environmental and organismal nutrient richness. Oikos **124**: 949–959. doi:10.1111/oik.02385

Solovchenko, A. E., and others. 2019. Luxury phosphorus uptake in microalgae. J. Appl. Phycol. **31**: 2755–2770. doi:10.1007/s10811-019-01831-8

Sommer, U., and H. Stibor. 2002. Copepoda—Cladocera—Tunicata: The role of three major mesozooplankton groups in pelagic food webs. Ecol. Res. **17**: 161–174. doi:10.1046/j.1440-1703.2002.00476.x

Sommer, U., and F. Sommer. 2006. Cladocerans versus copepods: The cause of contrasting top-down controls on freshwater and marine phytoplankton. Oecologia **147**: 183–194. doi:10.1007/s00442-005-0320-0

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: The biology of elements from molecules to the biosphere. Princeton Univ. Press.

Thomas, P. K., C. Kunze, D. B. van de Waal, H. Hillebrand, and M. Striebel. 2022. Elemental and biochemical nutrient limitation of zooplankton: A meta-analysis. Ecol. Lett. **25**: 2776–2792. doi:10.1111/ele.14125

Trochine, C., V. D. Villanueva, E. Balseiro, and B. Modenutti. 2019. Nutritional stress by means of high C:N ratios in the diet and starvation affects nitrogen isotope ratios and trophic fractionation of omnivorous copepods. Oecologia **190**: 547–557. doi:10.1007/s00442-019-04438-5

Twining, C. W., J. T. Brenna Jr., N. G. Hairston, and A. S. Flecker. 2016. Highly unsaturated fatty acids in nature: What we know and what we need to learn. Oikos **125**: 749–760. doi:10.1111/oik.02910

Urabe, J., M. Kyle, W. Makino, T. Yoshida, T. Andersen, and J. J. Elser. 2002. Reduced light increases herbivore production due to stoichiometric effects of light/nutrient balance. Ecology **83**: 619–627. doi:10.1890/0012-9658 (2002)083[0619:RLIHPD]2.0.CO;2

van der Lee, G. H., J. A. Vonk, R. C. M. Verdonschot, M. H. S. Kraak, P. F. M. Verdonschot, and J. Huisman. 2021. Eutrophication induces shifts in the trophic position of invertebrates in aquatic food webs. Ecology **102**: e03275. doi:10.1002/ecy.3275

Watson, S. B., E. McCauley, and J. A. Downing. 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. Limnol. Oceanogr. **42**: 487–495. doi:10.4319/lo.1997.42.3.0487

Yoshida, T., T. Gurung, M. Kagami, and J. Urabe. 2001. Contrasting effects of a cladoceran (*Daphnia galeata*) and a calanoid copepod (*Eodiaptomus japonicus*) on algal and microbial plankton in a Japanese lake, Lake Biwa. Oecologia **129**: 602–610. doi:10.1007/s004420100766

Zhang, Z., and X. Huang. 1991. Research methods of freshwater plankton. Science Press.

Zhou, L., K. D. Lemmen, W. Zhang, and S. A. J. Declerck. 2018. Direct and indirect effects of resource P-limitation differentially impact population growth, life history and body elemental composition of a zooplankton consumer. Front. Microbiol. **9**: 172.

Zhou, L., and S. A. J. Declerck. 2019. Herbivore consumers face different challenges along opposite sides of the stoichiometric knife-edge. Ecol. Lett. **22**: 2018–2027. doi:10.1111/ele.13386

Acknowledgments

Conflict of Interest

None declared.