



# Functional shifts in lake zooplankton communities with hypereutrophication

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**Abstract**

1. Functional variation among consumer communities can alter ecosystem nutrient cycling. These impacts on ecosystem function can be specifically driven by interspecific variation in stoichiometric traits; thus, functional trait-based approaches can be used to explain the processes controlling ecosystem stoichiometry. However, eutrophication may reduce the functional importance of consumers in ecosystems by eliminating heterogeneity in nutrient recycling among taxa.
2. To test whether zooplankton functional diversity, i.e. aspects of the stoichiometric trait space occupied by zooplankton communities, varies over gradients in trophic state and nutrient stoichiometry, we examined functional and taxonomic variation in the zooplankton communities of 130 lakes in the agriculturally dominated state of Iowa (U.S.A.) over 7 years.
3. Stoichiometric functional dispersion decreased with trophic state index, supporting the trait abundance shift hypothesis that hypereutrophic lakes are characterised by different combinations of functional traits than their less eutrophic counterparts. Zooplankton communities became increasingly N-rich relative to P as TSI increased. Specifically, P-poor *Bosmina*, *Chydorus*, and cyclopoid copepods increased in abundance with eutrophication.
4. Stoichiometric trait distributions of zooplankton shift with eutrophication, which implies that the unique functioning of hypereutrophic lakes could be due in part to the consumers inhabiting them. As zooplankton N:P increased with trophic state while lake total nitrogen to total phosphorus ratio decreased with trophic state, P-poor zooplankton taxa may exacerbate excess P availability in these hypereutrophic systems by differentially recycling P at higher rates.

## 1 | INTRODUCTION

Eutrophication has large consequences for the structure and function of aquatic ecosystems (Carpenter et al., 1998; Smith, Tilman, & Nekola, 1999; Vitousek et al., 1997). In lakes, eutrophication can result in harmful algal blooms and diminish production at higher trophic levels (Filstrup, Hillebrand, Heathcote, Harpole, & Downing, 2014; Schindler, 1977; Smith, 1983). Hypereutrophic lakes, those that are extremely enriched in nutrients, are becoming increasingly prevalent around the globe (e.g. Downing & McCauley, 1992; Stoddard et al.,

2016). Research in hypereutrophic lakes has demonstrated that these ecosystems function in unique ways relative to oligotrophic and even eutrophic lakes (e.g. Filstrup & Downing, 2017; Jeppesen, Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000; McQueen, Johannes, Post, Stewart, & Lean, 1989; Paerl et al., 2011; Scheffer, Houser, Meijer, Moss, & Jeppesen, 1993; Song & Burgin, 2017). As a result, there is a growing need to understand how hypereutrophic lakes function in order to manage and mitigate the impacts of eutrophication.

Ecological stoichiometry provides a framework for predicting the consequences of increased eutrophication in the form of

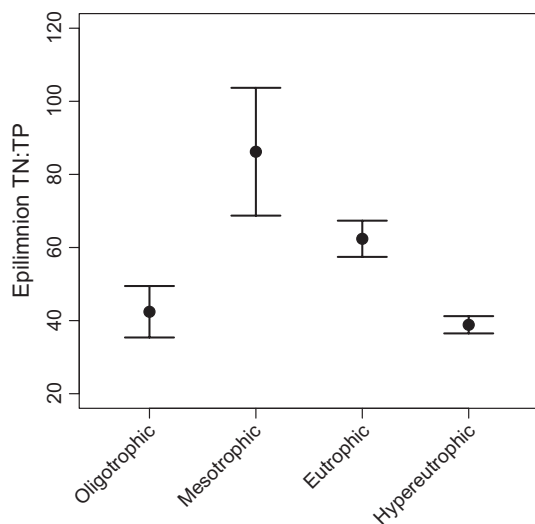
nitrogen (N) and phosphorus (P) loading (Elser, Sterner, Gorokhova, et al., 2000; Elser et al., 2010; Hessen, Ågren, Anderson, Elser, & De Ruiter, 2004). The relative supply of N and P can control nutrient limitation at the base of lake food webs (Elser et al., 2007), but grazing zooplankton can also control nutrient limitation of pelagic primary production in a top-down manner through the differential recycling of N and P. In particular, dominance of the zooplankton community by P-rich groups such as *Daphnia* can lead to reduced P recycling, elevated water column N:P ratios, and, ultimately, P-limited primary production (Elser, Elser, MacKay, & Carpenter, 1988; Schindler et al., 1993). However, zooplankton can also experience bottom-up growth limitation from imbalances in nutrient supply relative to their stoichiometric demand (Urabe, Clasen, & Sterner, 1997). Hypereutrophic lakes may function differently than oligotrophic lakes because the ratio of N:P supplied to lakes can still be above the threshold where primary production is P-limited while high P loading could shift zooplankton consumers below the threshold elemental ratio where excess P limits growth (Collins et al., 2017; Elser et al., 2016; Filstrup et al., 2014). Further, increased reliance on heterotrophic microbes in hypereutrophic systems may buffer taxa with flexible diets from these impacts (Christoffersen, Riemann, Hansen, Klysner, & Sørensen, 1990). As such, eutrophication may alter the functional role of zooplankton in lake ecosystems by selecting for different taxa as well as minimising the impact of nutrient recycling on lake stoichiometry.

The functional role of consumers can be altered by eutrophication, but this relationship depends on both the total quantities and the relative ratios of N and P (e.g. Spooner et al., 2013; Vanni et al., 2006). In a variety of moderately eutrophic lakes, increased P-rich *Daphnia* biomass does result in top-down increases in dissolved N:P ratios (van Egeren, Dodson, Torke, & Maxted, 2011; Elser, Sterner, Galford, et al., 2000; Paterson, Findlay, Salki, Hendzel, & Hesselein,

2002; Urabe, 1993; Urabe, Nakanishi, & Kawabata, 1995). However, in highly eutrophic systems where seston N:P is lower than zooplankton body N:P, low retention efficiency may reduce the impacts of functional diversity through uniformly low N:P recycling among all taxa (Elser, Gudex, Kyle, Ishikawa, & Urabe, 2001). As a result, we must understand both how functional diversity varies with eutrophication and how this variation relates to the relative availability of N and P. Therefore, general patterns in the functional role of zooplankton in eutrophic and hypereutrophic ecosystems may be informed by trait-based ecology.

Theory linking functional diversity to ecosystem structure and function has historically focused on functional diversity of primary producers (Litchman, Klausmeier, Schofield, & Falkowski, 2007; Tilman, 1999; Violle et al., 2007), but trait-based models have also been used effectively to predict responses to varying functional diversity at higher trophic levels (Barnett, Finlay, & Beisner, 2007; Hébert, Beisner, & Maranger, 2016a; Hulot, Lacroix, Lescher-Moutoué, & Loreau, 2000; Lefcheck & Duffy, 2015). Many stoichiometric traits vary predictably over biologically relevant environmental gradients, and the functional importance of these traits has been well-documented (Hébert, Beisner, & Maranger, 2016b); as a result, trait-based approaches offer a powerful link between organisms and ecosystem function (Carmona, de Bello, Mason, & Lepš, 2016; González, Dézerald, Marquet, Romero, & Srivastava, 2017; Meunier et al., 2017). While this approach has been used to examine nutrient acquisition traits (Frost, Evans-White, Finkel, Jensen, & Matzek, 2005), it has not been widely applied to study functional variation in consumer taxa among ecosystems.

In this study, we employ a trait-based framework to test how zooplankton functional diversity varies over a gradient in lake trophic state in an agriculturally dominated landscape. We use the graphical hypothesis framework of Boersma et al. (2016), which combines functional trait metrics developed for plant traits with approaches developed for stable isotope analysis (Laliberté & Legendre, 2010; Layman, Arrington, Montaña, & Post, 2007; Villéger, Mason, & Mouillot, 2008). In our analysis, we instead use zooplankton stoichiometric trait data to test whether functional diversity, the richness and evenness of functional trait combinations within a community, varies with lake trophic state index (TSI) and total nitrogen to total phosphorus ratio (TN:TP) among lakes in our dataset. Specifically, we test the hypothesis that eutrophication alters zooplankton functional diversity by shifting the relative abundance of functional traits among lake communities. Further, we hypothesise that this variation will lead to top-down effects on lake stoichiometry. We therefore predict that functional dispersion of zooplankton traits will vary with TSI and TN:TP among lakes.



**FIGURE 1** Variation in lake total nitrogen to total phosphorus ratio (TN:TP) of digested epilimnetic water with lake trophic state. Plot shows mean and standard error for each trophic state for ease of visual interpretation, but data were analysed with TSI as a continuous variable

## 2 | METHODS

### 2.1 | Study design

This study was conducted in the U.S. state of Iowa, where over 90% of land cover is under some form of agricultural production (Arbuckle

& Downing, 2001). Our dataset included 130 lakes across the state ranging in total P from <20 µg/L, where low P could limit P-rich zooplankton growth, to over 400 µg/L, where P may be in excess for many zooplankton (Boersma & Elser, 2006; Filstrup, Heathcote, Kendall, & Downing, 2016; Urabe et al., 1997). The data included in our analyses were collected annually between August and September during the years 2009–2015. The lakes sampled varied widely in physical and chemical characteristics over the study period (Table 1). Depth-integrated water chemistry samples were collected at the historical deep point in each lake from the upper mixed layer in stratified lakes or from 0.5 m above the maximum depth (up to 2 m) if no thermocline was present. Water chemistry samples were kept on ice in the field and stored at 4°C until analysis within 36 hr of collection. Zooplankton samples were preserved with a 10% formalin solution in the field. A detailed description of analytical methods is provided in Filstrup et al. (2016). Briefly, TP concentration was measured using the acid molybdate method following persulfate digestion, TN concentration was calculated as the sum of total Kjeldahl nitrogen, nitrate, and nitrite. Zooplankton samples were collected using a 63 µm Wisconsin net towed vertically from the thermocline or, if no thermocline was present, from 0.5 m above the lake bottom to the surface. Trophic state index was calculated from these individual sampling events based on chlorophyll-*a* to avoid direct dependence on TP using the equation of Carlson (1977).

Crustacean and rotifer zooplankton were identified to genus (with the exception of copepods, which were identified to order), and biomass was calculated using length-dry mass regressions (Filstrup et al., 2014). While variation among species within genera can be substantial, genus-level data provide a broad picture of how functional diversity varies among lakes. We then used biomass concentration data from zooplankton tows and average published body stoichiometry values for zooplankton taxa to define stoichiometric traits and estimate total nutrient storage by zooplankton communities per litre of lake volume (Hamre, 2016; Hébert, Beisner, & Maranger, 2016c; Hessen, Jensen, Kyle, & Elser, 2007). These traits are particularly well-suited to analyses that require fixed trait values as zooplankton generally exhibit strong stoichiometric homeostasis

(Persson et al., 2010) and intraspecific stoichiometric variation is relatively constrained among lakes (Prater, Wagner, & Frost, 2017) and experimental manipulations of food quality (Teurlincx et al., 2017). As the only rotifers for which we could find published body %N and %P data were *Brachionus* (Hamre, 2016; Hessen et al., 2007), we also calculated zooplankton P storage using the entire range of published rotifer values and excluding rotifers entirely to test for the robustness of our conclusions to this uncertainty. While the use of average trait values from an unrelated set of primarily oligotrophic lakes in our analyses may affect our results, the traits we chose are relatively phylogenetically constrained (Hébert et al., 2016c). Any deviation from these published values in our lakes is likely to be small in magnitude and relatively consistent among taxa (e.g. Prater et al., 2017; Teurlincx et al., 2017); for example, only two of 652 measurements of copepod %P in the dataset of Hébert et al. (2016c) exceed the lowest value of *Daphnia* %P. Therefore, our use of published averages is unlikely to substantially bias our conclusions. Total zooplankton N and P storage was calculated by multiplying %N and %P by zooplankton biomass for each taxon and summing these values for the entire community.

## 2.2 | Data analysis

For these analyses, we treated each lake-year as an independent replicate because biological conditions are somewhat independent from summer-to-summer following ice-off. However, this assumption is not entirely realistic as winter conditions often influence dynamics in the following summer (Hampton et al., 2017). To test whether the severity of this temporal dependence could impact our conclusions, we calculated partial autocorrelation coefficients for each variable at all possible time lags using the *pacf* function in the *forecast* package in R (Hyndman, 2017). We determined whether temporal autocorrelation was a significant concern if a larger number of time-lagged correlation coefficients were significantly different from zero than expected by random chance alone. We did not find a significant proportion of autocorrelation coefficients that were different from zero for any variables at any time lags (Supporting Information Table S1), supporting our assumption of independence of lake-years for our study responses.

We employed the graphical hypothesis framework of Boersma et al. (2016) to test hypotheses of how stoichiometric traits vary among zooplankton communities with trophic state. This framework tests hypotheses using functional diversity metrics based on the functional centroid, i.e. the central tendency of the functional trait space occupied by a community, as well as other metrics based on the area of trait space occupied. This functional framework is similar to the concept of the stoichiometric niche (González et al., 2017; Peñuelas, Sardans, Ogaya, & Estiarte, 2008), but unlike that framework, we explicitly examine both trait space occupied and changes in relative abundance of traits in communities. We calculated four metrics of functional diversity for comparisons among lakes: (1) functional dispersion, i.e. the mean distance between individual taxa and the respective functional centroid for their community, to test

**TABLE 1** Descriptive table of environmental variables measured in 130 study lakes in Iowa between 2009 and 2015

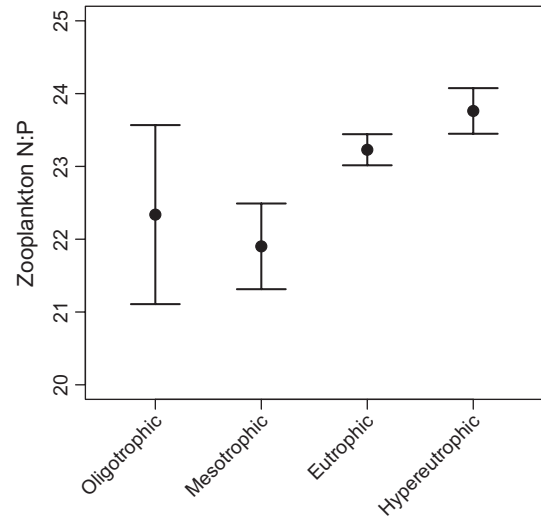
Variable	Min	Max	Average
Alkalinity (mg/L)	47	305	135.88
Chlorophyll- <i>a</i> (µg/L)	1	417	45.65
Dissolved oxygen (% saturation)	19	297	99.38
Maximum depth (m)	0.7	40.9	6.17
Secchi depth (m)	0.1	6.2	0.87
Total nitrogen (TN; mg/L)	0.08	17.52	2.04
Total phosphorus (TP; µg/L)	5	918.5	129.70
TN:TP (molar)	2.29	1319.53	57.66
pH	6.7	10.4	8.38

the trait abundance shift hypothesis that the relative abundance of certain trait combinations shifts with lake trophic state (Laliberté & Legendre, 2010); (2) functional richness, i.e. the total area of trait space occupied by each community, to test the convergence/divergence hypothesis that zooplankton communities share no trait combinations among trophic states in spite of having a similar trait centroid location (Villéger et al., 2008); and (3) total biomass to test the equal impact hypothesis that the change in abundance with trophic state is equal among trait combinations. Finally, we tested the null hypothesis that stoichiometric functional diversity does not vary with TSI or TN:TP. Variation in these metrics can be tested using similar approaches because they all have lower bounds at zero with no upper bounds.

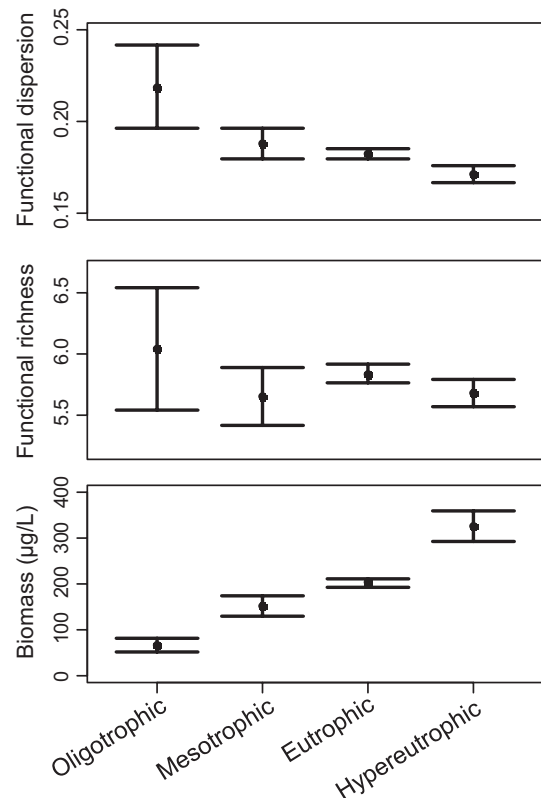
We used mixed-effects models to test differences in functional diversity metrics with TSI, TN:TP, and their interaction as fixed effects with lake as a random effect (Bates, Maechler, Bolker, & Walker, 2015). To assess potential collinearity, we also examined the relationship of TN:TP with TSI using a similar mixed-effect model with lake as a random effect. We performed these analyses with and without rotifer taxa included due to the uncertainty in rotifer stoichiometry based solely on data from one genus. Finally, to assess which zooplankton taxa contributed to functional shifts among lakes, we also calculated Spearman rank correlation coefficients between each taxon and both TSI and TN:TP among lake-years. All analyses were performed using the statistical software R version 3.4.0 with the *FD*, *forecast*, and *lme4* packages (Bates et al., 2015; Hyndman, 2017; Laliberté, Legendre, & Shipley, 2014; R Core Team, 2017).

### 3 | RESULTS

We first examined how zooplankton community stoichiometry varied with lake TSI and TN:TP. Among lake-years, TN:TP decreased with TSI ( $F_{1,750} = 14.21$ ,  $p < 0.001$ ) but still varied somewhat within trophic states (Figure 1). Due to this variation and the reasonably low correlation between TN:TP and TSI ( $r = -0.228$ ), we included both variables in models of zooplankton functional diversity metrics. We found that zooplankton N:P increased with TSI ( $F_{1,748} = 5.37$ ,  $p = 0.021$ ; Figure 2), but did not vary with lake TN:TP ( $F_{1,748} = 1.66$ ,  $p = 0.198$ ) or its interaction with TSI ( $F_{1,748} = 0.83$ ,  $p = 0.362$ ). We then calculated functional diversity metrics to test our alternate hypotheses explaining variation in stoichiometric functional diversity with TSI (Figure 3). Supporting the trait abundance shift hypothesis, we found that functional dispersion decreased with TSI ( $F_{1,748} = 5.56$ ,  $p = 0.019$ ) while total zooplankton biomass increased with TSI ( $F_{1,748} = 10.47$ ,  $p = 0.001$ ). Neither functional dispersion ( $F_{1,748} = 2.30$ ,  $p = 0.130$ ) nor total biomass ( $F_{1,748} = 0.88$ ,  $p = 0.347$ ) varied with TN:TP, and neither exhibited a significant interacting effect of TSI and TN:TP. Further, functional richness did not vary with TSI ( $F_{1,748} = 1.14$ ,  $p = 0.287$ ), TN:TP ( $F_{1,748} = 2.60$ ,  $p = 0.107$ ), or their interaction ( $F_{1,748} = 0.37$ ,  $p = 0.541$ ). Functional diversity metric data are presented in Supporting Information Table S2.



**FIGURE 2** Variation in zooplankton community N:P with lake trophic state. Plot shows mean and standard error for each trophic state for ease of visual interpretation, but data were analysed with TSI as a continuous variable



**FIGURE 3** Zooplankton community functional metrics among lake trophic states determined by the trophic state index (TSI) based on chlorophyll-*a* concentrations. Plots show mean and standard error for each trophic state for ease of visual interpretation, but data were analysed with TSI as a continuous variable

To account for uncertainty in rotifer stoichiometry from using only data from a single genus to represent all genera, we also examined these patterns for only crustacean zooplankton. We found

no qualitative differences in our conclusions when excluding rotifers from the analyses, indicating that variation in crustacean zooplankton taxa may be more important to these lake ecosystems. Rotifers comprised only 6.6% of total zooplankton biomass on average.

Having identified changes in the abundance of stoichiometric traits among zooplankton communities, we lastly examined which taxa specifically varied in biomass with TSI using Spearman correlation tests. Among crustacean taxa, biomass of the relatively P-poor *Bosmina*, *Chydorus*, and cyclopoid copepods was positively correlated with TSI (Table 2, Figure 4). As with cyclopoids, nauplii biomass was also positively correlated with TSI. Among rotifers, biomass of several taxa including *Anuraeopsis*, *Brachionus*, *Filinia*, *Keratella*, *Pompholyx*, and *Trichocerca* all increased with TSI while *Ascomorpha*, *Conochilus*, and *Gastropus* all decreased in biomass with TSI (Table 2).

**TABLE 2** Spearman correlation coefficients between individual zooplankton taxa and trophic state index

Group	Taxon	<i>r</i>	<i>p</i>	<i>n</i>
Cladocera	<i>Bosmina</i>	0.099	0.003	304
Cladocera	<i>Ceriodaphnia</i>	0.014	0.673	336
Cladocera	<i>Chydorus</i>	0.139	<0.001	227
Cladocera	<i>Daphnia</i>	-0.047	0.160	618
Cladocera	<i>Diaphanosoma</i>	0.041	0.219	108
Cladocera	<i>Moina</i>	0.01	0.757	7
Copepoda	Calanoida	0.048	0.159	589
Copepoda	Cyclopoida	0.238	<0.001	810
Copepoda	Nauplii	0.172	<0.001	875
Rotifera	<i>Anuraeopsis</i>	0.118	<0.001	26
Rotifera	<i>Ascomorpha</i>	-0.134	<0.001	92
Rotifera	<i>Asplanchna</i>	0.001	0.997	198
Rotifera	<i>Brachionus</i>	0.15	<0.001	409
Rotifera	<i>Conochilus</i>	-0.088	0.009	326
Rotifera	<i>Euchlanis</i>	-0.024	0.474	8
Rotifera	<i>Filinia</i>	0.22	<0.001	248
Rotifera	<i>Gastropus</i>	-0.077	0.022	14
Rotifera	<i>Hexarthra</i>	-0.038	0.258	50
Rotifera	<i>Kellicottia</i>	-0.009	0.782	112
Rotifera	<i>Keratella</i>	0.105	0.002	787
Rotifera	<i>Lecane</i>	-0.015	0.656	22
Rotifera	<i>Monostyla</i>	0.037	0.277	24
Rotifera	<i>Platyias</i>	-0.023	0.492	3
Rotifera	<i>Polyarthra</i>	-0.055	0.103	598
Rotifera	<i>Pompholyx</i>	0.113	<0.001	328
Rotifera	<i>Synchaeta</i>	-0.048	0.154	48
Rotifera	<i>Testudinella</i>	-0.039	0.247	5
Rotifera	<i>Trichocerca</i>	0.109	0.001	191

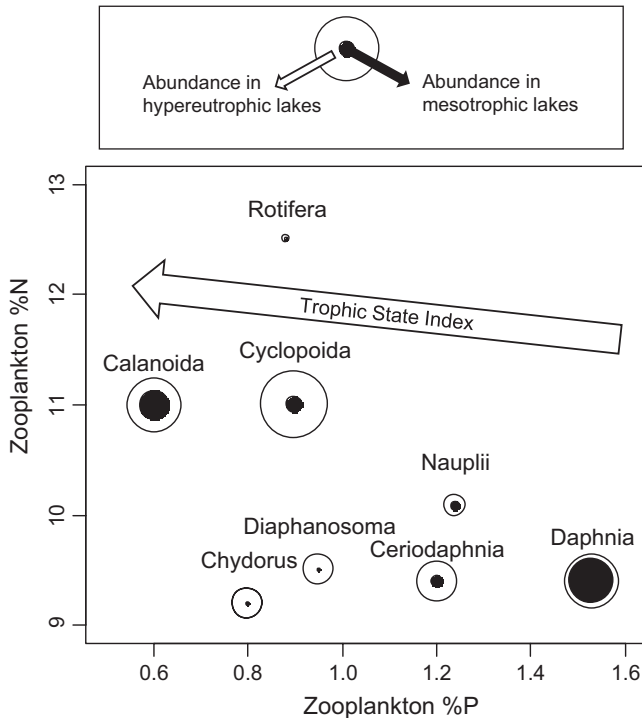
## 4 | DISCUSSION

Zooplankton play an important functional role in lake ecosystems by differentially storing and recycling key nutrients such as N and P, but it is not clear how this role changes in highly eutrophic lakes. We found that stoichiometric trait abundance shifted with TSI such that zooplankton communities in hypereutrophic lakes occupied a different region of trait space than those from oligotrophic lakes (Figure 3). Specifically, zooplankton community N:P increased with TSI as hypereutrophic lakes were increasingly dominated by P-poor cyclopoid copepods, *Bosmina*, and *Chydorus* (Figures 2 and 4, Table 2). This shift towards small-bodied, P-poor taxa has been observed in other studies of the impacts of eutrophication on zooplankton communities (e.g. van Egeren et al., 2011; Korosi, Paterson, & Desellas, 2008; Nevalainen & Luoto, 2017). As these P-poor zooplankton communities exist in increasingly P-rich (i.e. low N:P) hypereutrophic lakes, our results suggest that the functional role of zooplankton in mediating nutrient availability also shifts with TSI.

Shifts in the zooplankton community composition explained the functional trait abundance shift with TSI. Relatively P-poor taxa such as *Bosmina*, *Chydorus*, and cyclopoid copepods dominated hypereutrophic lake communities; thus, the zooplankton community N:P increased in these lakes. We also observed shifts in the rotifer community with TSI, indicating that some rotifer taxa such as *Filinia*, *Brachionus*, *Anuraeopsis*, and *Pompholyx* perform better in hypereutrophic systems than others (Table 2). However, the low rotifer biomass observed in our study lakes suggests that rotifers may have a diminished functional role relative to crustacean zooplankton. Rotifers can play an important role in the transfer of microbial production to higher trophic levels (i.e. the microbial loop) by consuming protozoans and recycling food and nutrients to the microbial community (Arndt, 1993). In hypereutrophic lakes where the phytoplankton community is dominated by cyanobacteria, the microbial loop can be an important process supporting crustacean zooplankton biomass (Christoffersen et al., 1990; Ger et al., 2016). As this process involves several intermediate steps in transferring energy from phytoplankton to zooplankton, it may contribute to reduced trophic transfer efficiency in hypereutrophic lakes (Filstrup et al., 2014). As a result, the high turnover in rotifer populations (e.g. Gaedke, 1993) suggests that the low standing biomass we typically observed is likely to be an underestimate of the true functional importance of rotifers in these lakes across the year. In particular, this may explain why some crustacean taxa did not vary in biomass with TSI.

Surprisingly, the keystone P-rich cladoceran grazer *Daphnia* did not vary with TSI despite multitudes of evidence that *Daphnia* can both affect lake stoichiometry (e.g. Elser et al., 1988; Sterner, Elser, & Hessen, 1992) as well as experience P-limited growth (Elser et al., 2010; Urabe et al., 1997). This observed invariance could represent the increased role of heterotrophic bacteria in supporting *Daphnia* biomass in hypereutrophic lakes (Ger et al., 2016) or the presence of a stoichiometric knife-edge, i.e. a narrow optimal range of P concentrations supporting *Daphnia* growth (Boersma & Elser, 2006;





**FIGURE 4** Graphical representation of how zooplankton functional traits vary with trophic state. Point sizes are scaled to the mean biomass of each taxon in mesotrophic (black circles) and hypereutrophic (white circles) lakes. While all taxa increased in biomass in hypereutrophic lakes, P-poor taxa such as copepods, *Diaphanosoma*, and *Chydorus* increased most dramatically

Currier & Elser, 2017). Alternatively, *Daphnia* growth may switch from P-limitation to fatty acid-limitation in hypereutrophic lakes, where high cyanobacteria biomass leads to low availability of unsaturated fatty acids (Müller-Navarra et al., 2004). Further, variation in *Daphnia* traits among lakes may promote population viability under a wide range of conditions (Frisch et al., 2014; Prater et al., 2017). These results highlight gaps in our understanding of how individual zooplankton taxa respond to increasing eutrophication, but suggest that a diversity of response strategies may be present among them.

Given this functional trait abundance shift, it is important to understand what drives variation in the zooplankton community or covaries with it to inform management of these lakes. Zooplankton community changes are often thought to be driven by planktivorous fish biomass, as planktivores preferentially prey on and reduce the biomass of large-bodied, P-rich taxa such as *Daphnia* (Brooks & Dodson, 1965; Carpenter, Kitchell, & Hodgson, 1985; Elser et al., 1988). However, in our study lakes, this variation was caused primarily by increased abundance of N-rich taxa rather than decreased abundance of P-rich taxa. It is less clear why small-bodied, N-rich taxa such as cyclopoid copepods and *Bosmina* should increase in biomass if large-bodied taxa such as *Daphnia* do not vary. One hypothesis is that, at least in Cladocerans, smaller-bodied taxa are more efficient at consuming filamentous cyanobacteria, which frequently dominate the phytoplankton biomass of our hypereutrophic

study lakes during the time of year from which our samples were collected (mid-August to September; Gliwicz, 1977; Filstrup et al., 2016). Indeed, the dominance by cyanobacteria in hypereutrophic lakes is likely to play a large role in driving functional shifts in zooplankton communities (Josué et al., 2018). As a result, the functional role of zooplankton in controlling or mitigating harmful algal blooms has been identified as an important topic for future research (Ger et al., 2016).

While our results support the functional trait abundance shift hypothesis, our data do not provide an explicit test of the functional implications of this shift. In particular, we assumed that body stoichiometry did not vary within taxa among lakes. Although intraspecific variation in body stoichiometry is increasingly being recognised as important (Jeyasingh, Cothran, & Tobler, 2014), several studies of lake zooplankton have found little to no systematic intraspecific variation in these traits with trophic status (e.g. Prater et al., 2017; Teurlincx et al., 2017). However, some stoichiometric variation among lakes nonetheless is likely, and more explicitly considering this variation would strengthen our ability to draw inferences on functional variation with hypereutrophication. This is particularly true of rotifers, whose body stoichiometry is poorly studied but probably more variable than that of crustacean taxa (Hessen et al., 2007). Further, consideration of additional stoichiometric traits will provide a more complete understanding of functional variation. For example, variation in nutrient assimilation efficiency can have stronger effects on functions such as food consumption and nutrient recycling even when body stoichiometry does vary (Moody et al., 2018; Sherman, Roy, Baker, Weider, & Jeyasingh, 2017). Future work explicitly examining variation in these traits and their influence on trophic transfer efficiency and nutrient recycling will illuminate the true extent of the impacts of functional shifts in zooplankton communities with increased eutrophication.

Despite these caveats, the trait shifts we observed probably have significant impacts on how hypereutrophic lakes function given the functional importance of zooplankton in lake ecosystems. The functional importance of consumers can be diminished in eutrophic systems (Elser et al., 2001; Spooner et al., 2013), but pelagic consumers can still play an important functional role even in hypereutrophic lakes. Among our study lakes, zooplankton community N:P increased with TSI while TN:TP decreased (Figures 1 and 2), indicating that N-rich zooplankton could recycle more P into hypereutrophic lakes and exacerbate excess P availability. Our work illustrates the utility of functional trait-based approaches in testing stoichiometric hypotheses. Further, our results expand on prior findings from a limited set of moderately eutrophic lakes (Elser, Sterner, Galford, et al., 2000; Elser et al., 2001; Paterson et al., 2002; Urabe et al., 1995) by supporting the top-down functional importance of the zooplankton community even in highly nutrient-enriched systems. Future work on the feedbacks between zooplankton and nutrient cycling in hypereutrophic lakes is needed to understand how these systems function and how to manage their potential for developing harmful algal blooms.

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## CONFLICT OF INTEREST

We declare no conflict of interest.

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## SUPPORTING INFORMATION

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