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RESEARCH ARTICLE

Effects of consumer diversity on prey consumption are not influenced by omnivory

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In plant communities, higher levels of taxonomic richness are often shown to be more efficient at utilization of limiting resources due to resource partitioning among taxa. While resource partitioning is also thought to be important in consumer communities, consumers also exhibit more complex interactions like omnivory. Omnivory is generally thought to reduce the effects of consumer richness on the consumption of prey resources; however, empirical tests of this prediction are rare. Here, we report the results of 2 complementary studies to test the hypothesis that omnivory reduces the positive effects of consumer taxonomic richness on prey resource consumption. First, we analyzed data from a dataset consisting of 1,100 freshwater lakes across the continental United States. We show that the relationship between consumer taxonomic richness and the summed biomass of resource prey (phytoplankton) is independent of the proportion of zooplankton (consumers) that are omnivores. However, consumption rates were not explicitly measured in this dataset so that we conducted in situ feeding experiments in 37 lakes near Ann Arbor, MI, USA, to measure omnivorous consumption (Omni) as the amount of smaller microzooplankton (<200 μm) consumed by larger nonherbivorous mesozooplankton. We also measured the amount of phytoplankton consumption (G) across a gradient of zooplankton taxonomic richness (zpSR). We showed that there was a positive association between zpSR and G, suggesting that G was increased by zooplankton diversity. However, the effects of zooplankton diversity on the G are not altered by the level of Omni among zooplankton. Although omnivory does not influence the effects of consumer diversity on prey consumption, we do not negate the impacts of omnivory on other ecosystem functions in aquatic systems. We attempt to address a question that is of general interest to the field of ecology, especially of aquatic ecology, because omnivory is known to be common in aquatic systems.

Keywords: Omnivory, National Lake Assessment (NLA), Biodiversity-ecosystem functioning (BEF), Hierarchical model, Dilution experiment

1. Introduction

Many studies have shown that the consumption of prey resources increases with consumer diversity (Balvanera et al., 2006; Worm et al., 2006; Griffin et al., 2013). The positive effect of consumer diversity on the consumption of prey is often attributed to resource partitioning among consumers—either the utilization of different prey or the division of prey in space or time (Thébault and Loreau, 2003; Ives et al., 2005). Several empirical studies have directly demonstrated that resource partitioning allows consumer diversity to exert a strong influence on prey consumption (Duffy and Harvilicz, 2001; Duffy et al., 2003; Finke and Snyder, 2008; Straub and Snyder, 2008).

While resource partitioning is one of the primary mechanisms by which consumer diversity affects prey consumption and densities, several types of interspecific interactions among consumers can either reinforce or counteract this mechanism (Sih et al., 1998). Behavioral modifications of predator and prey (Sih et al., 1998), predator–predator facilitation (Losey and Denno, 1998; Losey and Denno, 1999), intraguild predation (IGP; Polis et al., 1989), or other forms of omnivory (Pimm and Lawton, 1978; Polis and Strong, 1996) all have potential to alter the effects of consumer diversity on prey consumption.

Among the interactions that can alter the effects of consumer diversity on prey consumption, omnivory is particularly common, occurring in 50% of all food webs (Arim and Marquet, 2004; Thompson et al., 2007). The modifying influence of omnivory on consumer diversity effects can be negative because consumers feed on each other rather than their resource prey (Finke and Denno, 2004; Schmitz, 2007). On the other hand, omnivory can

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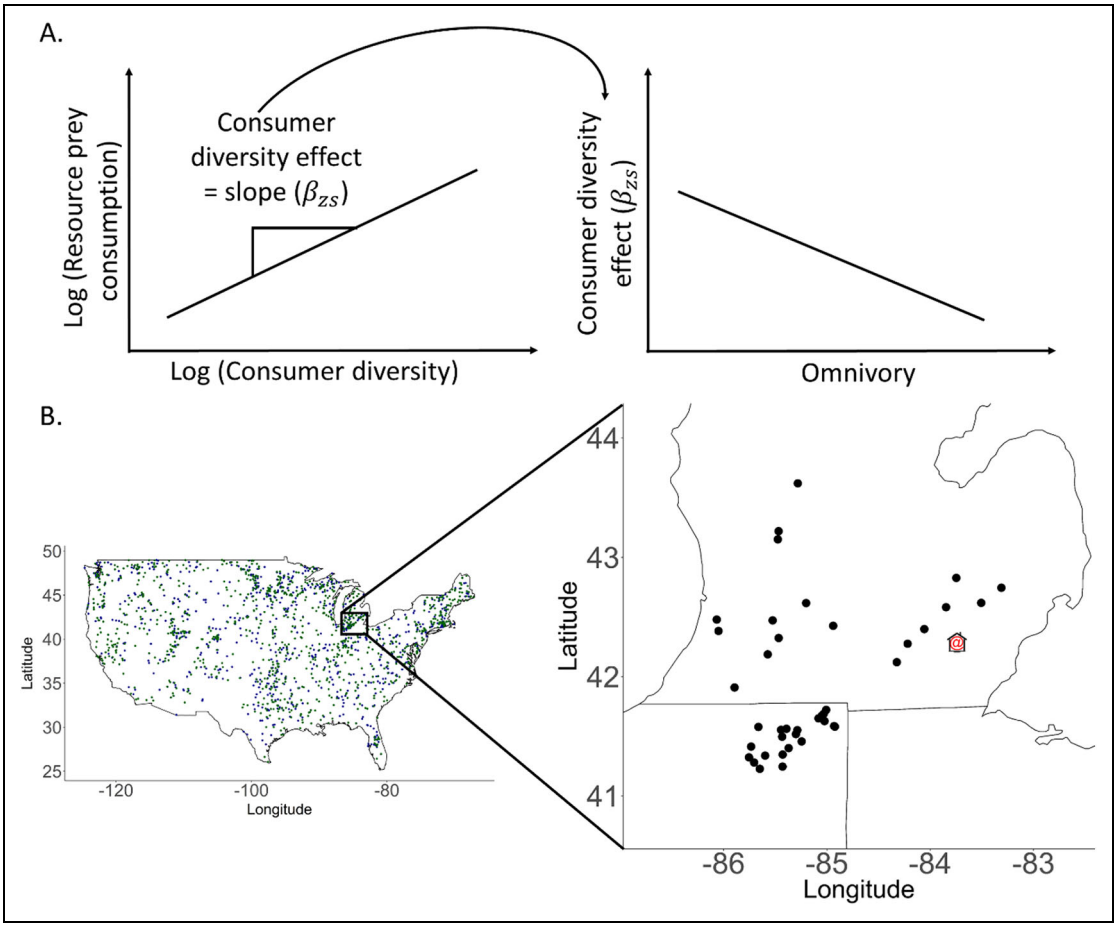

Figure 1. Figure shows the hypothesis (Panel A) and the resulting prediction tested in the study of National Lake Assessment dataset analyses as well as in the study of incubation experiments (panel). In Panel B, the map in the left-hand side shows the continental United States, and the dark blue and green dots represent the lakes included in the National Lake Assessment in year 2007 and 2012 respectively; the red symbol @ in the right-hand side represents the location of Ann Arbor, MI.

further increase consumer's diversity effects on prey consumption when the habitat is complex enough for some consumers to hide from predation or interferences from other consumers (Finke and Denno, 2006; Anderson and Semlitsch, 2016). More recently, studies have suggested that omnivory can enhance or weaken the effects of consumer diversity on prey consumption depending on the magnitude of omnivory (Chang et al., 2020; Chang and Cardinale, 2020). However, omnivory is still widely believed to reduce resource prey consumption either because some consumers are satiated by other consumers and not consuming the resource prey or because some consumers are not able to reach high enough density or biomass to capture resource prey efficiently (Ives et al., 2005; Casula et al., 2006; Duffy et al., 2007). Accordingly, we hypothesize omnivory to weaken the positive association between consumer diversity and resource prey consumption as depicted in **Figure 1A**.

To date, few empirical studies have tested the hypothesis that omnivory reduces the positive association between consumer diversity and resource prey consumption. Of the studies that do exist, they are restricted to investigations of the influence of the simplest case of omnivory, intraguild predation (IGP), on the consumption of resource prey. IGP occurs when one consumer species (the intraguild, IG predator) feeds on another (the intraguild, IG prey) with which it also competes for shared basal resources (Polis et al., 1989; Polis and Holt, 1992). Studies have shown that occurrence of IGP would decrease the consumption of resource prey (Finke and Denno, 2004; Finke and Denno, 2005; Sitvarin and Rypstra, 2014; Chang and Cardinale, 2020). However, these studies are restricted to a relatively simple and well controlled system. In more complex natural systems, where IGP can occur among consumer communities but not only species, it is still not clear whether IGP among consumer communities would also reduce the positive association between consumer diversity and resource prey consumption. The influences of omnivory as the form of IGP among consumer communities need to be studied if we are to better understand the relationship between consumer diversity and the consumption of resource prey.

Here, we report the results of 2 complementary studies used to test the hypothesis that omnivory diminishes the positive association between consumer diversity and prey

consumption. First, we analyzed the dataset encompassing measurements from approximately 1,100 natural lakes in the continental United States. This dataset was compiled by the U.S. Environmental Protection Agency's (EPA) National Lake Assessment (NLA). With this dataset, we examined whether the relationship between zooplankton species richness and standing stock biomass of phytoplankton varies as a function of the proportion of omnivorous zooplankton in the community. Because standing stock biomass is subject to the influences of many other factors and might not be a good proxy for consumption of phytoplankton, we conducted manipulative experiments in 37 lakes near Ann Arbor, MI, USA, to quantify the strength of omnivory among zooplankton and the amount of phytoplankton consumption (G) that occurs across a gradient of zooplankton taxonomic richness (zpSR). In the second study, we quantified the omnivorous consumption (Omni) among zooplankton as the amount of microzooplankton, which are smaller than 200 μm, consumed by larger nonherbivorous mesozooplankton. The Omni we measured can thus be regarded as IGP between the microzooplankton and the nonherbivorous mesozooplankton community. By studying the impacts of omnivory on consumer's diversity effects, our study contributes to the understanding of consumer diversity on ecosystem functioning.

2. Methods

2.1. Study 1—Observational data across natural lakes in the NLA dataset

The goal of the first study was to test the prediction that the proportion of omnivorous zooplankton would diminish the negative association between zpSR and the summed biomass of phytoplankton. Specifically, we analyzed data from the NLA dataset. The NLA dataset consisted of approximately 1,100 all natural or human-made freshwater lakes in the continental United States that have surface area greater than 10 acres (4 ha), depth greater than 1 m, and can be accessible by the sampling crew member. These 1,100 lakes were selected according to the Generalized Random Tessellation Stratified survey design (Stevens and Olsen, 2004) to ensure that the selected lakes were representative to the population of lakes in each ecological region—the geographic area in which soils, vegetation, and climate were similar.

2.1.1. NLA dataset overview

In each lake, chemical and biological variables were measured during May–September of year 2007 and 2012 (2 years the survey took place) following the same standardized protocols in all lakes. Chemical measurements included dissolved oxygen, nitrogen, phosphorus, silicate, conductivity, and dissolved organic carbon (DOC). These chemical measurements were conducted at the same laboratory under standard operating protocols administered by the U.S. EPA's Western Ecology Division. Biological measurements included zooplankton species composition and density as well as phytoplankton species composition and biomass. Zooplankton samples were collected by plankton nets (50 μm and 150 μm) from 5 m deep to the surface during the day and sent to 4 different laboratories around the country. The phytoplankton samples were collected by Poly bottle (2 L) at 0.3 m depth and processed at a single laboratory. Taxonomists in these laboratories then identified phytoplankton (300 individuals) and zooplankton (200–400 individuals) and measured their body size under microscope. All laboratories were subject to internal quality control on sorting and identification using the Integrated Taxonomic Information System and external quality control by independent taxonomists contracted to audit 10% of each laboratory's samples. These efforts were intended to ensure consistent taxonomic identification and enumeration. The NLA dataset along with the sampling and analysis protocols are publicly available at U.S. EPA's website (https://www.epa.gov/national-aquatic-resource-surveys/nla).

2.1.2. Variable selection

The following variables were used to test the prediction that the proportion of omnivorous zooplankton would diminish the relationship between zpSR and the standing stock biomass of phytoplankton: (1) the standing stock phyB was taken to be the summed biovolume of all phytoplankton in a sample (μm^3/L); (2) zpSR was used to represent the zooplankton diversity (species level for zooplankton and lowest possible taxonomic level for nauplii, which is usually genus); (3) the proportion of omnivorous zooplankton in the lake zooplankton community was taken to represent omnivory (Omnip). To identify the omnivorous zooplankton, we followed the functional feeding group of each zooplankton taxon labeled by the expert who identify the species. However, the functional feeding group labeling was only applied to adult zooplankton. The functional feeding group included herbivore, omnivore, and predator. Of the 141 and 516 species encountered in 2007 and 2012, respectively, 64 and 308 species were herbivore, 35 and 125 species were omnivores, and 15 and 44 species were predators. Omnip was calculated as the density of omnivorous zooplankton divided by the density of all zooplankton.

Because many factors other than zooplankton richness (zpSR) or omnivory (Omnip) can influence the standing stock biomass of phytoplankton (phySR), we statistically controlled for as many other covariates as were available in the NLA dataset. Our analyses included 11 additional variables, including phytoplankton taxonomic richness (phySR), TN and TP (μg/L), zooplankton community density, water temperature (Temp; °C), water pH (pH), silica (Si; μg/L), DOC (μg/L), growing days (Lat), and light (Sol). Among these variables, water pH was hypothesized to affect algal growth rates by mediating nutrient availability and nutrient uptake of algal species (Tilman et al., 1982). Silica was critical to the growth and ecology of diatoms and it could be the third limiting nutrient following nitrogen and phosphorus in freshwater systems (Martin-Jézéquel et al., 2000; Evans et al., 2011). DOC was shown to increase shading in freshwater systems and thus negatively correlated with primary production (Carpenter et al., 1998; Seekell et al., 2015). Note that the growing days are represented by the latitude of the lake as the

latitude was frequently used to measure growing period, or in the case of phytoplankton, ice-off period (Weyhenmeyer et al., 2013). Also, because light was not explicitly measured in the NLA dataset, we obtained data on the total solar radiation incident given the coordinate of each lake from the NASA Prediction Of Worldwide Energy Resources. We then calculated the mean of total solar radiation from May to September, when the NLA dataset was collected, as an estimate for light intensity.

Finally, the NLA dataset encompassed a large spatial extent. To account for this inherent spatial heterogeneity, we included the Type III ecoregion that each lake was located in (ECO3) as a random effect in our analyses. The Type III ecoregion was derived from Omernik (1987), which classified North American into areas of similar biotic, abiotic, terrestrial, and aquatic ecosystem (Omernik, 1987; 1995). A total of 105 Type III ecoregions were identified in the continental United States, with 81 represented in the NLA dataset. We included ECO3 information to statistically control for some macroecological differences among lakes such as soils, vegetation, and climate.

2.1.3. Data processing

Estimates of taxonomic richness are heavily dependent on sampling intensity and the number of organisms captured in a sample. Therefore, to compare taxonomic richness across lakes, we used the vegan package (Oksanen et al., 2018) in R to rarefy samples from the NLA dataset to the minimal density (66 individual/mL for zooplankton and 6,625 individual/mL for phytoplankton) in order to obtain estimates of taxonomic richness for comparable sampling efforts (i.e., organismal densities). In addition, variables except Lat and pH were log-transformed to improve the normality of the distributions (Figures S1 and S2 in Supplement 1). Finally, all variables were standardized to have a mean of 0, and a standard deviation of 1 in order to facilitate computation (described next), and to make the coefficients of statistical directly comparable.

2.1.4. Model analyses

To test the prediction, we built hierarchical models with the standing stock of phytoplankton (phyB) as the response variable and proportion of omnivorous zooplankton (Omnip) as well as zpSR as the independent variables. Besides Omnip and zpSR, we also included other variables that were significantly associated with phyB in the model as covariates to statistically control for those variables (Supplement 1). To account for the large-scale spatial heterogeneity, we built a hierarchical structure to make the associations of all variables dependent on the level III ecoregion (ECO3) to which the lake was affiliated. Doing so was essentially making ECO3 as a random effect so that each variable can have difference relationships with phyB in different level III ecoregions. Finally, we included an interaction term between zpSR and Omnip to examine if the association between zpSR and phyB would be linearly reduced by Omnip. If the interaction term was not significantly smaller than zero, we rejected the prediction. To select the most important variables, we manually performed forward stepwise model selection based on the the leave-one-out cross-validation method (Tables S1 and S2 in Supplement 1; Vehtari et al., 2017). All above analyses were performed with R ver. 3.5.3 (R Core Team, 2018). The hierarchical model analyses were performed with the brms and rstan package in R (Carpenter et al., 2017; Bürkner, 2017; 2018; Stan Development Team, 2018).

2.2. Study 2—In situ incubation experiments

In the second study, we conducted in situ 24-h incubation experiments in 37 natural lakes near Ann Arbor, MI (red colored @ in **Figure 2**), to measure the actual amount of omnivory occurring in a planktonic food-web (Omni, i.e., consumption of microzooplankton by nonherbivorous mesozooplankton) and the actual consumption of phytoplankton by the entire zooplankton community (G, resource prey consumption). We then examined if the Omni altered the relationship between zpSR and consumption of phytoplankton across lakes. The experimental design was a combination of an exclusion feeding experiment (bottom left box in **Figure 2**) and a "dilution experiment" (bottom right box in **Figure 2**). The design of the exclusion experiment is based on the observation that 20 of 21 nonherbivorous mesozooplankton taxa in the study lakes are larger than 200 μm (Table S3 in Supplement 2). As such, we used a screen mesh with 200 μm opening to separate nonherbivorous mesozooplankton from microzooplankton. The exclusion feeding experiment was thus implemented to estimate Omni, which was calculated as the differences between the microzooplankton density changes in the presence and absence of nonherbivorous mesozooplankton. However, similar body size of phytoplankton and zooplankton, especially microzooplankton (Landry and Hassett, 1982), hinders our ability to measure the consumption of phytoplankton by zooplankton (G) by conducting exclusion feeding experiment. We thus adopted the idea of the "dilution experiment" to estimate zooplankton-free growth rate of phytoplankton, which was then used to calculate phytoplankotn biovolume changes in the absence of zooplankton. By calculating the difference between phytoplankotn biovolume changes in the absence and presence of entire zooplankton, we finally obtained the consumption of phytoplankton by the presence of entire zooplankton community (G).

2.2.1. Study sites

Lakes selected for this study were chosen on the basis of 3 criteria: (1) lakes were selected within a 200 km radius of Ann Arbor, MI, to allow for samples to be returned to the lab for processing after a 2-day trip, (2) selected lakes must have been included in either the 2007 or 2012 NLA sampling efforts, and (3) lakes were in the 56 level-III ecoregion (Eastern Corn Belt Plains), which is characterized by the similar underlying geology, soils, vegetation, and climate (Omernik, 1987; 1995). This led to a sample size of 37 lakes near Ann Arbor, MI (see **Figure 1B**). We conducted in situ incubation experiments in these 37 lakes in June and July of 2017 and June 2018.

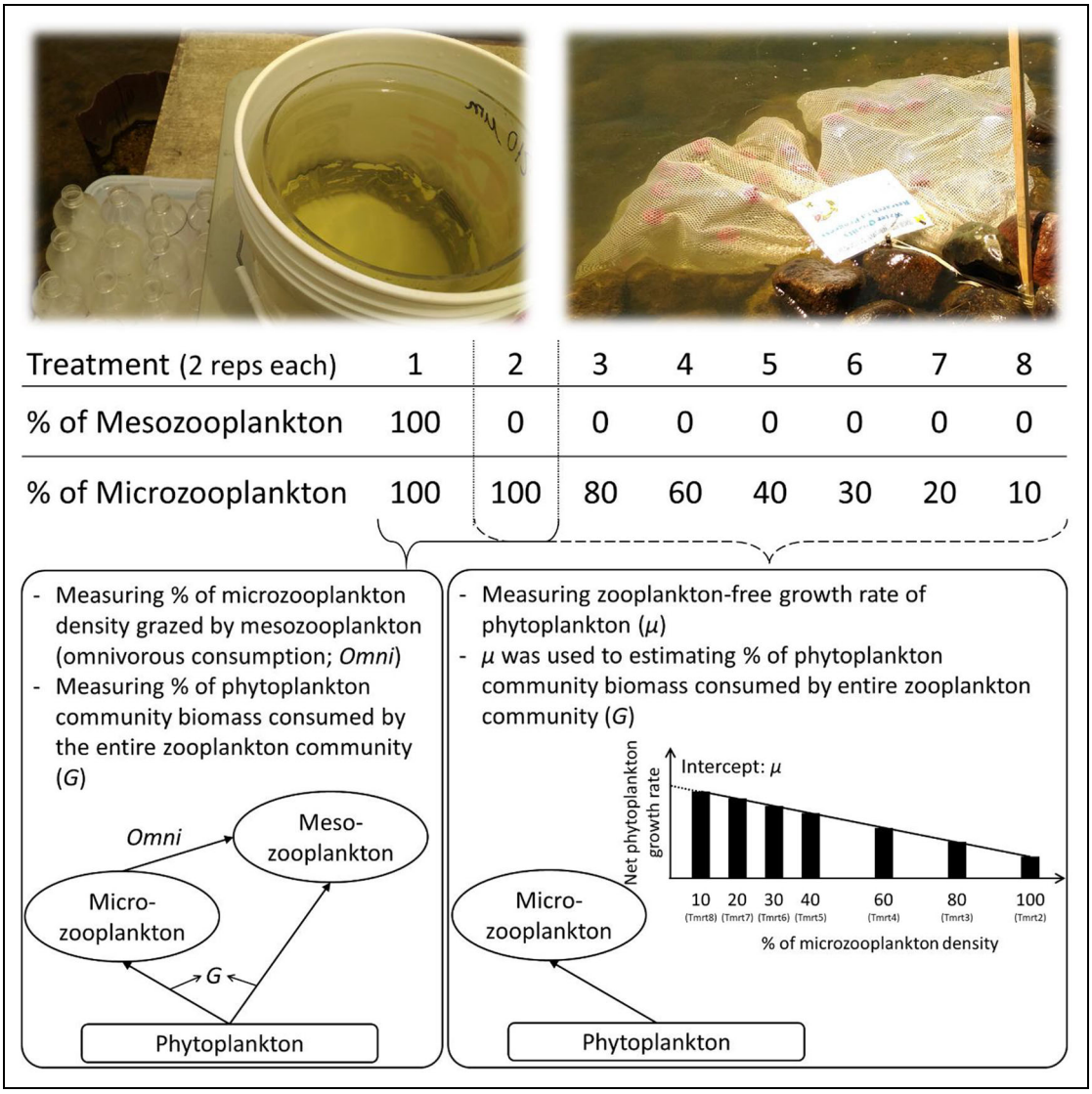

Figure 2. Schematic plot explaining the purpose and experimental design of the treatments in the incubation experiments (Study 2). The 2 pictures above are taken from the experiments.

2.2.2. Experimental units

Experimental units for the incubation experiments were Corning Costar® 1 L Traditional Style Polystyrene Storage Bottles (the actual volume was 1.25 L). These bottles were acid rinsed one day before conducting the experiment and rinsed with the lake water that was filtered through 0.2 μm filter right before the experiment. All bottles were put in a 32″ × 36″ nylon mesh equipment bag (item model number: LR-AK3R-VPUA), which was then tied on a 1 m steel bar. The steel bar was then anchored in the lake near the lake bank so that all the bottles can float in the lake to receive ambient environmental conditions like light and temperature. The incubation lasted 24 h.

2.2.3. Experimental treatments

In each lake we conducted one incubation experiment. In each incubation experiment, 25 L of lake water was collected with a Van Dorn water sampler (6.2 L PVC Vertical Beta™ Bottle) from 1-meter deep to prepare 8 treatments composed of 2 replicates each. The first and the second treatment were the exclusion feeding experiment (bottom left box in **Figure 2**), which was designed to measure Omni. The first treatment was the untreated lake water that contained 100% of the ambient meso- and microzooplankton density. The second treatment was created by passing the lake water through a screen mesh with 200 μm mesh size to remove larger nonherbivorous mesozooplankton but retain the smaller microzooplankton. The second treatment thus contained 100% of the ambient microzooplankton density but 0% of mesozooplankton density.

Treatments 2–8 were the dilution experiment designed to estimate zooplankton-free growth rate of phytoplankton (μ; the intercept of the figure in bottom right box in **Figure 2**), which was then used to calculate the consumption of phytoplankton by the entire zooplankton community (G). Treatments 2–8 had no mesozooplankton but had 100%, 80%, 60%, 40%, 30%, 20%, and 10% of ambient microzooplankton density. The gradient of microzooplankton density was created by gently combining lake water

passed through a 200 μm screen mesh, which removed mesozooplankton, with lake water passed through a 0.2 μm filter that removed all particles in the lake water.

2.2.4. Sample processing

To measure microzooplankton density and phytoplankton biovolume before incubation, we subsampled 3 replicates of 50 mL water samples from the 25 L lake water taken by the Van Dorn sampler and preserved them with formalin (final concentration 0.5%). After a 24-h incubation period, 50 mL of water sample from each incubation bottle was preserved with formalin (final concentration 0.5%). These preserved samples were then processed with a Flow Cytometer And Microscope (FlowCAM) to estimate the summed biovolume of phytoplankton in each treatment. The FlowCAM is an automated sampling device that has been shown to exhibit high accuracy and efficiency in measuring phytoplankton body size and density in grazing experiments (Ide et al., 2008; Alvarez et al., 2011). Specifically, we used the 4× objective with the 300 μm flowcell to capture the images of all particle ranging from 4 to 200 μm equivalent spherical diameter in 5 mL of the sample (or until the 80,000-particle limit was reached to avoid producing files that were too heavy). All samples were processed in around 5 min. We then manually removed images of debris and detritus to avoid overestimating the summed biovolume of phytoplankton. The summed biovolume of phytoplankton (μm^3/L) in all treatments were then used to calculate consumption of phytoplankton by the entire zooplankton community (G).

To estimate microzooplankton density change, 30 mL of the preserved samples from the first and second treatments were processed with FlowCAM. When processing with FlowCAM, the same objective, flowcells, and size limits were applied for microzooplankton. We specifically looked for rotifers, ciliates, dinoflagellates, and the nauplii of crustaceans (see Figure S4 in Supplement 2 for examples of microzooplankton images). At least 100 microzooplankton images were captured in each sample for further analyses.

In addition, we concentrated zooplankton by passing lake water of the first treatment (untreated lake water) through an 80 μm screen mesh and preserved all zooplankton in formalin (final concentration 0.5%). From the preserved sample of each lake, we then counted and identified 300 individual mesozooplankton to genus level with a dissecting microscope to estimate the taxonomic richness (zpSR). The density of entire zooplankton community (*zpD*; ind./L) was the sum of microzooplankton density estimated by the FlowCAM and the density of mesozooplankton counted by the dissecting microscope.

In addition to the phytoplankton and zooplankton, we measured the following abiotic covariates in each lake: water temperature (Temp; °C) and conductivity (Cond; μS/cm) were measured in situ using the YSI Model 85 Handheld Dissolved Oxygen, Conductivity, Salinity and Temperature System, which was calibrated before visiting the lakes. Lake water pH (pH) was measured with the Eutech Waterproof pHTestr20, which was also calibrated before each visit. To measure light intensity, we used the original Apogee Instruments Quantum sensors to measure the photosynthetically active radiation (PAR; mol/m^2 s) at the surface and at 1-m depth to calculate % PAR at 1-m depth, where water was collected for experiments. To measure TN (μmol/L) and TP (μmol/L), 80 mL out of 25 L of lake water was distributed into 2 Falcon™ 50 mL Conical Polypropylene Centrifuge Tubes (one for TN and one for TP). The two 40-mL water samples were immediately frozen and sent to the Biological Station of University of Michigan for TN and TP measurements.

2.2.5. Variable calculation

In our study, the Omni was measured as differences between the microzooplankton density change after incubation in the presence (Treatment 1) and absence of nonherbivorous mesozooplankton (Treatment 2). This difference was then divided by the initial microzooplankton density as a standardization to obtain the % of initial microzooplankton density that was grazed by nonherbivorous mesozooplankton over the 24-h incubation period. Specifically, we used the following equation to calculate Omni.

$$\mathrm{Omni} = \left(\mathrm{mzpD}_{T0,2} - \mathrm{mzpD}_{T24,2}\right) - \left(\mathrm{mzpD}_{T0,1} - \mathrm{mzpD}_{T24,1}\right) / \mathrm{mzpD}_{T0,2},$$

where $\mathrm{mzpD}_{T0,\,i}$ and $\mathrm{mzpD}_{T24,\,i}$ were the density of microzooplankton before and after incubation in treatment *i*.

The consumption of phytoplankton (G) is measured as the difference between phytoplankton biovolume with and without the presence of by the entire zooplankton community after incubation. The phytoplankton biovolume with the presence of zooplankton was the phytoplankton biovolume in Treatment 1 (the untreated lake water) after incubation ($\mathrm{phy}_{T24,1}$). The phytoplankton biovolume with the absence of entire zooplankton community was calculated from the zooplankton-free growth rate of phytoplankton (μ), which was estimated from Treatments 2 to 8. Specifically, we used the gradient of microzooplankton density in treatments 2–8 to represent the grazing pressure exerted by the microzooplankton on the phytoplankton community. When net growth rates of phytoplankton (*r*) were regressed on the corresponding percentage of ambient microzooplankton density, the intercept of the regression was used to obtain the phytoplankton growth rate in the absence of any grazing by zooplankton (μ; the intercept of the figure in the bottom right box in **Figure 2**).

Using the regression intercept to represent the zooplankton-free growth rate of phytoplankton (μ) is based on the rationale of the "dilution experiment" (Landry and Hassett, 1982; Landry et al., 1995; Li et al., 2017). The rationale of the dilution experiment is to measure the change of phytoplankton net growth rate in response to a gradient of grazing pressure, which is created by diluting the water containing zooplankton with zooplankton-free water in a series. Assuming phytoplankton instantaneous growth rate is not affected by grazing pressure and the dilution processes (i.e., density dependence is negligible in the short incubation time), then

phytoplankton net growth rate can be regarded as the instantaneous growth rate minus the grazing rate from microzooplankton. The expected phytoplankton net growth rate when there is zero grazing pressure, that is, the regression intercept, thus represent the zooplankton-free growth rate of phytoplankton (μ).

With the zooplankton-free growth rate (μ), we used the following equation to calculate the maximum biovolume that the phytoplankton community could achieve after 24 h of incubation without the presence of zooplankton (phyE).

$$\mathrm{phyE} = \mathrm{phy}_0 e^{\mu t},$$

where phy_0 is the initial phytoplankton biomass and t is 24 h. Note that phyE was calculated based on the exponential growth assumption, which we were unable to verify, so the G could be systematically overestimated in our experiments. With phyE, we then used the following equation to calculate G as the difference between phytoplankton biovolume with ($\mathrm{phy}_{T24,1}$) and without (phyE) the presence of by the entire zooplankton community. The difference was then standardized by the initial phytoplankon biovolume phy_0.

$$\mathrm{G} = \left(\mathrm{phyE} - \mathrm{phy}_{T24,1}\right)/\mathrm{phy}_0.$$

Through the above calculations, we were able to obtain Omni and consumption of phytoplankton (G) independently for each lake. Along with the zooplankton richness (zpSR), we performed the following data processing and analyses to test the hypothesis that omnivory would diminish the positive association between consumer diversity and prey consumption.

2.2.6. Data processing and analyses

As a first step in data analyses, the distribution of all variables was screened for linearity, normality, and correlations (Figures S5 and S6 in Supplement 2). Variables were log-transformed when necessary to improve the normality of distributions, and all variables were standardized to a mean of 0 and standard deviation of 1 to make the scale of variables comparable. To reduce the dimensionality of the dataset, we used principal component (PC) analysis to reduce the 6 abiotic variables into a smaller number of axes of environmental variation (Figure S6 in Supplement 2). The first 3 PCs of this analyses represented a combined 68% of the environmental variance; these PCs were used in the subsequent analyses to statistically control for the abiotic variation among lakes.

We performed 2 types of analyses to test the prediction that Omni alters the relationship between zpSR and the consumption of phytoplankton by the entire zooplankton community (G). First, we built a multiple linear model (first row of **Table 1**) to examine whether zpSR and Omni interact to influence G. Second, because correlations between certain explanatory variables were high (e.g., *zpD*

Table 1. Table summarizing the results from the incubation experiments in 37 natural lakes (Study 2)

Model		zpSR	zpSR: Omni	zpD	phyB	Omni
Multiple linear model (LM):						
G ∼	zpSR × Omni + phySR + zpD + phyB + Envi_PC1 + Envi_PC2 + Envi_PC3	**0.41 (0.1, 0.73)**; $P = 0.02$	0.22 (–0.16, 0.6)	0 (–0.31, 0.31)	0.15 (–0.39, 0.6)	–0.34 (–0.91, 0.24)
Structural equation modeling (SEM):						
G ∼	zpSR × Omni + phySR + zpD + phyB	**0.46 (0.19, 0.74)**; $P < 0.01$	0.16 (–0.15, 0.47)	–0.03 (–0.24, 0.31)	0.04 (–0.35, 0.43)	–0.14 (–0.53, 0.25)
zpSR ∼	Envi_PC1 + Envi_PC2 + Envi_PC3					
phySR ∼	Envi_PC1 + Envi_PC2 + Envi_PC3					
zpD ∼	Envi_PC1 + Envi_PC2 + Envi_PC3					
phyB ∼	Envi_PC1 + Envi_PC2 + Envi_PC3					
covariates:						
phyB ∼∼	phySR					
phyB ∼∼	zpD					
phySR ∼∼	zpD					
phyB ∼∼	zpSR					

Each column shows the standardized effect and the 95% confidence interval of the variable on the consumption of phytoplankton by the entire zooplankton community (G). Results from the multiple linear model (LM) and the structural equation modeling (SEM) analyses are listed in the first and second row. The significant coefficients are bolded.

and phyB; Figure S5 in Supplement 2), we used structural equation modeling (SEM) to test the same prediction while controlling for covariance among independent variables (second row of **Table 1**). In the SEM, we also included an interaction term between zpSR and Omni to test the prediction. Because the experiments were conducted in 2 consecutive years, year was included as a random effect in all above analyses.

Finally, we examined whether the interaction between zpSR and Omni was significantly different than zero. More specifically, our a priori prediction was that the interaction term would be significantly smaller than zero, indicating that the Omni decreases the effects of consumer (zooplankton) diversity (zpSR) on resource prey (phytoplankton) consumption (G). All analyses were performed with R ver. 3.5.3 (R Core Team, 2018). The structure equation modeling was performed with the lavaan package in R (Rosseel, 2012).

3. Results

Both studies failed to support the prediction that omnivory alters the relationship between consumer diversity and resource prey consumption. For the NLA dataset, there was no significant interaction between the proportion of omnivores in the zooplankton community (Omnip) and zooplankton taxonomic diversity (zpSR) on phyB in either 2007 or 2012 (**Table 2**). Unexpectedly, the relationship between zpSR and phyB was positive but not significant in year 2007 (first row of **Table 2**), but positive and significant in 2012 (second row of **Table 2**).

In the second study, we found no support for the prediction that Omni alters the relationship between zpSR and G. In both the multiple linear model (model LM in **Table 1**) and the structural equation model (model SEM in **Table 1**), the consumption of phytoplankton by the entire zooplankton community (G) was positively related to zpSR. But the relationship between zpSR and G was not altered by the Omni among zooplankton.

We found that Omni was not significantly correlated with zpSR (**Figure 3A**) and G (**Figure 3B**). Instead, we found that Omni positively covaried with the proportion of zooplankton in family *Cyclopidae* (**Figure 4A**; $P = 0.05$) and negatively covaried with the proportion of zooplankton in family Daphniidae (**Figure 4B**; $P = 0.05$). Many species in the *Cyclopidae* family have been reported to be omnivorous (Strickler and Bal, 1973), while *Daphniidae* was shown to be herbivores (Gliwicz, 2003; Ebert, 2005). These results suggest that Omni is driven by the compositional change in the zooplankton community but not the taxonomic richness per se. In addition, neither the proportion of *Cyclopidae* zooplankton nor *Daphniidae* zooplankton were related to either zpSR ($P = 0.6$ and $P = 0.15$, respectively) or G ($P = 0.69$ and $P = 0.74$, respectively). These relationships suggest that increasing Omni is possibly driven by the increase of the proportion certain nonherbivores taxa and the decrease of the proportion of certain herbivorous taxa in the zooplankton community. The compositional change of zooplankton community is not associated with either zpSR or G.

4. Discussion

Results of both studies presented in this article did not support the hypothesis that omnivory would alter the relationship between zooplankton diversity and G or standing stock. In the first study where we analyzed the NLA dataset, we found that the summed biomass of phytoplankton was positively related to phytoplankton taxonomic richness, as well as to the concentrations of nitrogen and phosphorous. These results are consistent with prior studies of this dataset (Zimmerman and Cardinale, 2014). However, we found no evidence that phytoplankton biomass was negatively related to zpSR (in fact, the trend was the opposite in 2012), and no evidence that the proportion of omnivores altered any relationship between the zooplankton (consumer) taxonomic richness and the summed biomass of phytoplankton.

In the incubation experiments presented in the second study, we found a positive relationship between zpSR and G, which is consistent with our a priori expectation. However, the positive relationship between zooplankton richness and G was not altered by Omni, that is, the amount of smaller microzooplankton consumed by larger nonherbivorous mesozooplankton. The positive relationship between consumer diversity and consumption or prey have been documented in numerous other studies (Duffy and Harvilicz, 2001; Duffy et al., 2003; Gamfeldt et al., 2005; Griffin et al., 2009; Whalen et al., 2013; Duffy et al., 2015; Gamfeldt et al., 2015; Whalen et al., 2016). In addition, the effects size of consumer diversity on resource prey consumption found in our study (approximately 0.4) is similar to that reported in previous meta-analyses (Balvanera et al., 2006; Griffin et al., 2013). As

Table 2. Table summarizing the results from the analyses of National Lake Assessment dataset (Study 1)

Year	zpSR	zpSR: Omnip	Omnip	phySR	TN	TP	R^2
2007	0.04 (–0.02, 0.1)	0.01 (–0.05, 0.06)	0.03 (–0.03, 0.08)	**0.3 (0.22, 0.39)**	**0.18 (0.08, 0.29)**	**0.21 (0.09, 0.34)**	0.51
2012	**0.12 (0.06, 0.18)**	–0.01 (–0.05, 0.04)	0.01 (–0.05, 0.06)	**0.15 (0.09, 0.21)**	**0.44 (0.35, 0.52)**	**0.29 (0.2, 0.38)**	0.59

The second to eighth columns show the standardized coefficients of each variable on the phytoplankton community biomass (phyB). The significant coefficients are bolded. The number in the bracket is the 95% credible interval. The last column shows the R^2 of the model.

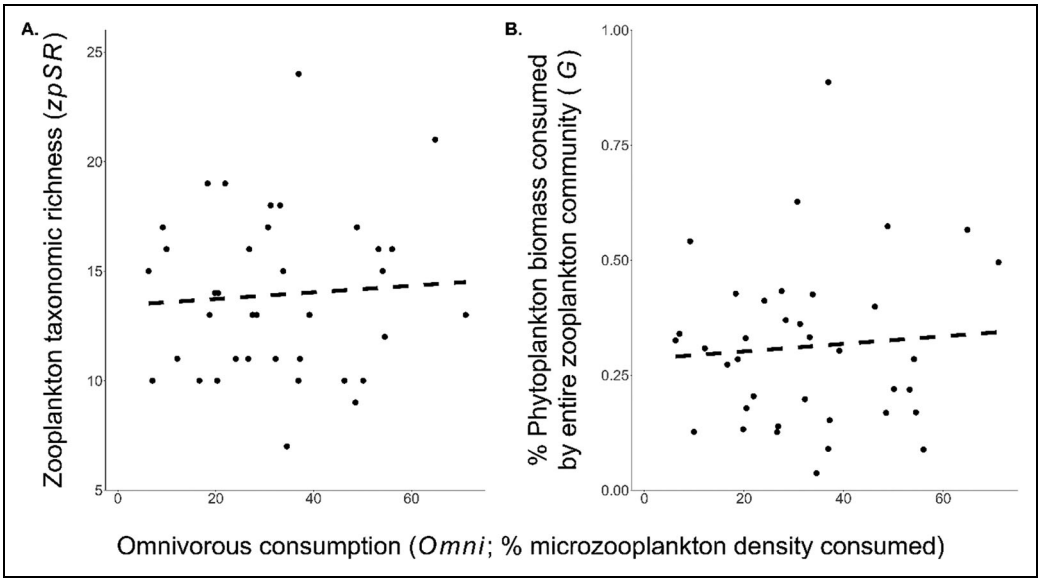

Figure 3. Relationships between omnivorous consumption (Omni) and zooplankton taxonomic richness (zpSR; Panel A) as well as between Omni and the consumption of phytoplankton by the entire zooplankton community (G; Panel B). Both relationships are not statistically significant as indicated by the dashed line.

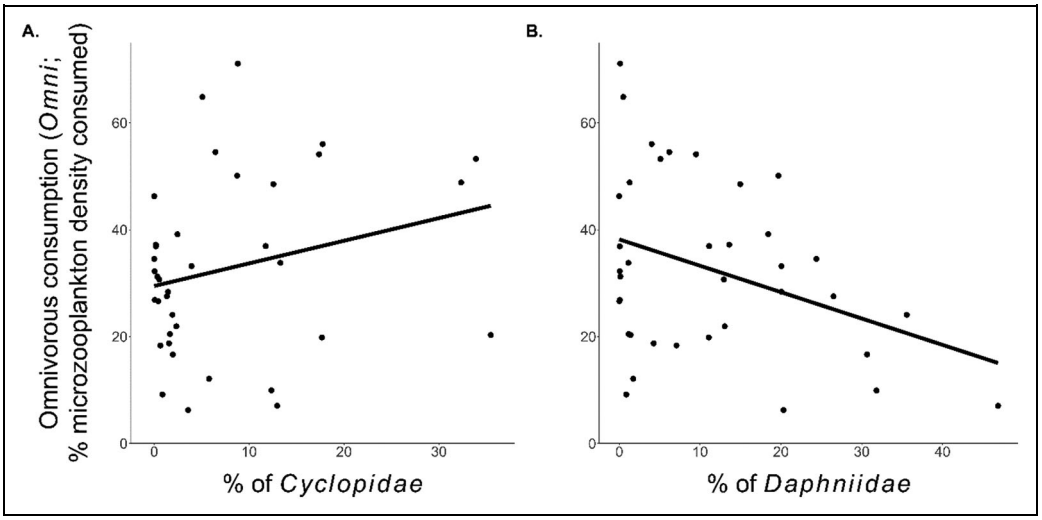

Figure 4. Relationship between omnivorous consumption (Omni) and the proportion of zooplankton in the *Cyclopidae* family (nonherbivore; Panel A) and in the *Daphniidae* family (herbivore; Panel B). Solid lines indicate significant correlations ($P = 0.05$ in both panels).

such, our study adds another line of evidence to support the positive effects of consumer diversity on the consumption of resource prey.

Our incubation experiments provide no evidence of any significant influence of Omni on the relationship between zpSR and G. This result runs counter to the belief that Omni should reduce the effects of consumer diversity on prey consumption either because it alters consumer diversity or because it outweighs other interspecific interactions among consumers like resource partitioning (Ives et al., 2005). We also showed that Omni was not related to either zpSR (**Figure 3A**) or G (**Figure 3B**). Therefore, we argue that Omni in zooplankton community does not influence the effects of zooplankton diversity on the consumption of resource prey. Our study suggests that Omni is associated with taxonomic compositional changes of zooplankton community. Among the most abundant zooplankton taxa (Figure S7 in Supplement 2), we show that Omni is positively associated with dominance of predatory *Cyclopoidae* and negatively associated with dominance by largely herbivorous *Daphniidae* (**Figure 4**). The zooplankton compositional changes are not related to zpSR and G. This implies that Omni in zooplankton community was possibly the function of zooplankton taxonomic compositional changes. However, neither the Omni nor the taxonomic compositional changes alter the relationship between zpSR and phytoplankotn consumption. We argue that the nonsignificant effects in our study

are some mix of omnivory reducing and increasing consumption and that cannot be detected at the scale of our study. Although we do not find significant impacts of omnivory on prey consumption, we do not negate the importance of omnivory in other ecosystem functioning, like the stability of predator and/or prey community biomass (e.g., McCann and Hastings, 1997). The roles of omnivory in aquatic systems deserve further research to elucidate.

There are 2 major caveats in the incubation experiments (the second study). First, although the dilution technique has been applied to measure the consumption of phytoplankton in the field, especially in marine systems (e.g., Calbet and Landry, 2004), the dilution technique is not free from criticism (Dolan and McKeon, 2005). The caveats of dilution technique include the nonlinear functional responses of zooplankton (Chen et al., 2014; Li et al., 2017), feeding behavior change due to dilution (Landry et al., 1995; Dolan et al., 2000), and trophic cascades occurring in the incubation bottles (Calbet and Saiz, 2013). Despite these limitations, the dilution grazing experiment is still the most widely used method to estimate grazing rate in planktonic systems as there are few alternatives (Schmoker et al., 2013).

A second caveat of the incubation experiments is that body size of zooplankton is an imperfect proxy for trophic interaction, and this may affect the quantitative estimates of omnivory. For example, some large zooplankters eliminated by our screening were herbivores (e.g., *Daphnia*), and excluding these mesozooplankton could have influence estimations of Omni. We did, however, show that the 200 μm screen mesh was effective at excluding 20 of 21 nonherbivorous mesozooplankton taxa (Table S3 in Supplement 2), and that changes in microzooplankton density after incubation decreased monotonically with the amount of nonherbivorous mesozooplankton in the incubation bottles (Figure S3 in Supplement 2). These results provide assurance that our results and conclusions are qualitatively robust even if the measures of omnivory are slightly inaccurate due to imperfect manipulation of the omnivorous fraction of zooplankton.

In conclusion, we show that the positive association between consumer diversity and the consumption of resource prey was not altered by omnivory. Instead, omnivory is possibly the function of taxonomic changes in consumer community. However, given the fact that consumer species diversity and species composition are not explicitly controlled in our studies, we cannot quantify the impacts of the consumer compositional change as well as the impacts of omnivory in influencing the association between consumer diversity and consumption of resource prey. We urge more studies to focus on the relative importance between omnivory and compositional change in consumer community to better understand the functional role of consumer diversity on the consumption of resource prey.

Data accessibility statement

The NLA dataset is publicly available on the EPA National Aquatic Resource Surveys website (https://www.epa.gov/national-aquatic-resource-surveys). The data of manipulative experiment and the code are now publicly available at DOI:10.5281/zenodo.4347422.

Supplemental files

The supplemental files for this article can be found as follows:

Supplements 1 and 2. Figures S1–S7. Tables S1–S3. Docx

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Competing interests

The authors declare that they have no conflict of interest.

Author contributions

Conceived the study: FHC, BJC.

Conducted the study and analyzed the data: FHC.

Wrote the manuscript with substantial contribution from BJC: FHC.

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