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Distribution of six taxa in the family Bosminidae Baird (Crustacea: Branchiopoda: Anomopoda) in the plankton of lakes and reservoirs within the continental United States, including expanded range of the invasive cladoceran *Bosmina* (*Eubosmina*) *coregoni* Baird

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Abstract

Updated range distributions in lakes and reservoirs of the continental United States are provided for six taxa in the family Bosminidae (*Bosmina* (*Bosmina*) cf. *longirostris* (Müller), *Bosmina* (*Eubosmina*) *coregoni* Baird, *Bosmina* cf. *longispina* Leydig, *Bosmina* (*Liederobosmina*) cf. *tubicen* Brehm, *Bosmina* (*Liederobosmina*) cf. *hagmanni* Stingelin, and *Bosminopsis deitersi* Richard), an ecologically important and taxonomically confusing group. This paper provides updated range distribution and information on the westward expansion of the invasive species *Bosmina* (*Eubosmina*) *coregoni*, which was first established in the Great Lakes in the late 1960's. Current survey data are compared with previous distribution records and discussed in the context of environmental variables.

Key words: Bosminidae, Cladocera, biogeography, distribution, *Bosmina* (*Eubosmina*) *coregoni*, invasive species

Introduction

Within North America, the family Bosminidae Baird is comprised of two genera, *Bosminopsis* Richard and *Bosmina* Baird. The genus *Bosmina* can be further divided into subgenera, four of which occur in North America (Kotov *et al*. 2009). Species within Bosminidae differ in terms of both their native and invaded geographical ranges. The Bosminidae are an ecologically important group of invertebrates, as they are ubiquitously distributed across most freshwater systems in the world (Goulden & Frey 1963; Lieder 1983), and often serve as a critical food-web link between primary producers and fish in aquatic systems. Since initial description of the genus *Bosmina* there have been several taxonomic revisions of the genus and much confusion over taxonomic distinctions and proper identification methods for species (Deevey & Deevey 1971; Nilssen & Larsson 1980; Lieder 1983; De Melo & Hebert 1994a; Taylor *et al*. 2002; Haney & Taylor 2003; Kotov *et al*. 2009; Faustová *et al.* 2010; Faustová *et al*. 2011).

Confusion and contradictions surrounding the taxonomic grouping of *Bosmina* is due in large part to cyclomorphological flexibility along seasonal and environmental quality gradients (Goulden & Frey 1963), particularly amongst female specimens, which tend to dominate samples collected in the field from natural habitats (as opposed to those raised in a laboratory setting). Additionally, predation by both fish and invertebrates has been shown to influence size and pigment characteristics of *Bosmina*, and has led to divergent phenotype distributions on a regional scale (Nilssen & Larsson 1980; Kerfoot 2006). Hybridization between presumable morpho-species of Bosminidae has likely also played a role in the difficulty surrounding identification of these taxa (Nilssen & Larsson 1980; Faustová *et al*. 2010). Faustová *et al*. (2010) concluded that the cyclic parthenogenic nature of bosminids (i.e. alternating parthenogenic and sexually reproductive lifestyle) can enhance the rate of speciation, contributing to the confusion over specific taxonomy. More recently, morphological distinctions between species have been coupled with genetic analyses (De Melo & Hebert 1994a; Taylor *et al.* 2002; Haney & Taylor 2003; Kotov *et al*. 2009; Faustová *et al*. 2010; Faustová *et al*. 2011), which have provided both confirmation and reorganization of previously delineated systematic relationships.

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Of the six Bosminidae taxa investigated in this study, the most significant to note is the invasive cladoceran, *Bosmina* (*Eubosmina*) *coregoni*. *Bosmina* (*E.*) *coregoni* is widespread across lakes and reservoirs in Europe and Asia (Lieder 1983). It is likely endemic to the Palearctic region of the globe, as a post-glacial species morph from ancestral Palearctic *B.* (*E.*) *longispina* (Faustová *et al*. 2010, Faustová *et al*. 2011). *Bosmina* (*Eubosmina*) *coregoni* was first reported in the U.S. in Lake Michigan in 1966 (Wells 1970), likely transported via ballast water in transoceanic freighters arriving from Europe (Lieder 1991; De Melo & Hebert 1994b). In the 1990's (30 years post-invasion), *B.* (*E.*) *coregoni* was reported to have expanded into inland lakes only within 100 km of the Great Lakes (De Melo & Hebert 1994b). A southern expansion of *B.* (*E.*) *coregoni* into reservoirs of southern Missouri was reported a few years later (Mabee 1998), and a westward expansion of *B.* (*E.*) *coregoni* into freshwater systems of the Pacific Northwest (Oregon/Washington) was reported between 2008–2012 by Smits *et al*. (2013). Mechanisms of expansion for *B.* (*E.*) *coregoni* into non-adjacent water bodies across the U.S. are unknown, however it was probably due to transport by recreational vessels and/or by migratory birds (Smits *et al*. 2013; Havel & Shurin 1994). Although it has been reported that the spread of *B.* (*E.*) *coregoni* may be limited by certain environmental factors such as its preference for hard water environments (Carter *et al*. 1980), establishment in new and distant lakes and reservoirs over the past half century has been steady and is likely to continue. This report adds to the record of expansion for *B.* (*E.*) *coregoni*, confirming its presence in additional lakes and reservoirs of the Pacific Northwest and elsewhere throughout the continental U.S., including the first reports of *B.* (*E.*) *coregoni* in Colorado, South Dakota, Nebraska and Kansas.

This study utilizes recent (2012) survey data of lakes and reservoirs from the continental U.S. to report updated and expanded geographical ranges for six Bosminidae taxa including *Bosmina* (*Bosmina*) cf. *longirostris*, *Bosmina* (*Eubosmina*) *coregoni*, *Bosmina* cf. *longispina*, *Bosmina* (*Liederobosmina*) cf. *tubicen*, *Bosmina* (*Liederobosmina*) cf. *hagmanni*, and *Bosminopsis deitersi*. The aim of this paper is to describe current range distributions within the continental U.S. for these common pelagic taxa. This study may be used as another resource, along with a multitude of existing taxonomic keys, for bench taxonomists making difficult identifications with limited samples. Range expansions were applied in the context of historical data and ecoregional specificity.

Material and methods

National Lakes Assessment study sites. 1,038 lakes and reservoirs (hereinafter, lakes) selected from the USGS/USEPA National Hydrography Dataset (NHDPlus) (Simley & Carswell 2009) were comprehensively sampled throughout the continental U.S. in the spring and summer (May–September) of 2012 (USEPA 2012). Each lake was sampled for water quality, biological condition, habitat conditions, and recreational suitability. Lakes were selected without bias using probability-based selections and constituted a statistically valid representation of lakes in similar regions (USEPA 2012). Both man-made and natural lakes greater than one hectare in size (excluding the Great Lakes) were included, as well as some lakes sampled during the National Lakes Assessment in 2007. For the purposes of the National Lakes Assessment and other components of the USEPA's National Aquatic Resource Surveys (NARS), the 85 Level III ecoregions of the conterminous U.S. (Omernik 1987) were agglomerated into nine broader ecoregions (Herlihy *et al*. 2008), which were assessed on the basis of uniformity in reference-site quality and naturally occurring variation in stream macroinvertebrate assemblages. Hereinafter the term "ecoregion" will refer to the nine agglomerated ecoregions outlined by Herlihy *et al*. (2008).

Sample collection. Samples were taken near the deepest point of the water body. A 150 µm mesh plankton net was used for macrozooplankton samples. Each sample consisted of a 5 m vertical tow, and in situations where the water body was not deeper than 5 m, multiple tows were taken to get a cumulative tow of 5 m. Samples were preserved upon collection and stored in 70% ethanol before being shipped to BSA Environmental Services, Inc. (Beachwood, OH) for taxonomic identification.

Laboratory analyses. All zooplankton samples were analyzed at BSA Environmental Services, Inc. Each sample was identified by a trained taxonomist and organisms were identified to lowest possible taxonomic level, enumerated and measured for biomass estimates. Taxonomic sources used for the identification of Bosminidae included De Melo & Hebert (1994a), Dodson *et al*. (2010) and Taylor *et al*. (2002). Because the overwhelming majority of bosminid specimens were female, more recent taxonomic keys based on morphological characteristics of males (i.e. Kotov *et al*. 2009) were not appropriate for taxonomic determinations.

Prior to microscopic analysis, concentrated sample volume was measured and each sample was homogenized using a magnetic spinner at low speed. A subsample was taken using a wide-bore volumetric pipette and transferred into an Utermöhl chamber. Appropriate aliquots were examined at 100X magnification on Wilovert inverted microscopes. At least 400 organisms were counted in each sample excluding nauplii, rotifers and ostracods. For biomass estimates, 20 individuals were measured for dominant taxa (>40 individuals per sample). 10 measurements were taken for taxa encountered less than 40 times in a sample, and 5 measurements were taken for taxa encountered less than 20 times in a sample. Biomass estimates were based on established relationships between body length and dry weight (Dumont *et al.* 1975; McCauley 1984; Lawrence *et al.* 1987). Abundance (organisms per liter) was calculated for individual taxa using the following equation:

Taxon abundance = [(concentrated sample volume ÷ volume counted) ÷ tow volume] × abundance in sample

In accordance with McCauley (1984), biomass was computed for the appropriate number of individuals for each sample and the arithmetic mean biomass was multiplied by the taxon abundance to produce a taxon biomass for each sample. Out of the total 1,038 lakes sampled, 775 contained at least one Bosminidae taxon. Samples collected and identified from Wisconsin were not included in this study.

Nomenclature. The nomenclature used for initial determination of species at the time when specimens were counted primarily followed those outlined by Dodson *et al.* (2010), in which North American bosminid nomenclature was validated on the Integrated Taxonomic Information System (ITIS, itis.gov), as per the taxonomic requirements for the National Lakes Assessment. However, more detailed investigations using phylogenetic determinations have revealed discrepancies in that nomenclatural scheme (Taylor *et al.* 2002; Haney & Taylor 2003; Kotov *et al.* 2009; Faustová *et al.* 2010; Faustová *et al.* 2011). Accordingly, taxon names used in this manuscript are updated to reflect more recent nomenclature. Kotov *et al.* (2009) found phylogenetic and morphological features (of male specimens only) that justified breaking the genus *Bosmina* into several subgenera, four of which occur in North America: *Bosmina* (*Bosmina*), *Bosmina* (*Eubosmina*), *Bosmina* (*Liederobosmina*), and *Bosmina* (*Lunobosmina*). Data used in this article are available for download from the USEPA (https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys). Specimens initially identified as *Eubosmina coregoni* are referred to in this report as *Bosmina* (*Eubosmina*) *coregoni*. Specimens initially identified as *Bosmina longirostris* are referred to in this report as *Bosmina* (*Bosmina*) cf. *longirostris,* as several other North American species are morphologically indistinct from *B. longirostris.* Recent work, performed after the completion of this survey, suggests that *Bosmina* (*Liederobosmina*) *tubicen* (previously *Eubosmina tubicen*) and *Bosmina* (*Liederobosmina*) *hagmanni* (previously *Eubosmina hagmanni*) may not be distinct species but rather different morphotypes of the same species responding to different environmental conditions (A.A. Kotov, personal communication). As such, specimens initially identified as *Eubosmina tubicen* are referred to in this article as *Bosmina* (*Liederobosmina*) cf. *tubicen* and specimens initially identified as *Eubosmina hagmanni* are referred to in this article as *Bosmina* (*Liederobosmina*) cf. *hagmanni*.

Specimens initially identified as *Eubosmina longispina* are referred to in this article as *Bosmina* cf. *longispina*, due to the lack of phylogenetic proof of Nearctic specimens of this taxon belonging to the same species group as the previously described Palearctic population (Haney & Taylor 2003; Faustová *et al.* 2011). Furthermore, within North America there appears to be phylogenetic differentiation between Atlantic and Beringian populations of *B.* (*E.*) *longispina* (Haney & Taylor 2003), which we were not able to distinguish on a morphological basis alone. *Eubosmina longispina* is also absent from the most recent comprehensive key to North American cladocerans (Rogers 2016), published after this study was complete. As such, we felt it was necessary to add the "cf." designation (and no subgenus designation) when describing these organisms for this article. Descriptions of historical occurrences of the discussed taxa are also referred to using their modern nomenclatural designations in the context of this article, though they may have previously been described using taxonomic synonyms. For a more thorough record of taxonomic synonyms, see Kotov *et al.* (2009).

Mapping and statistical analyses. Data from the 2012 USEPA National Lakes Assessment were used for this study. The data were filtered to isolate the target taxa prior to analysis. For sites where more than one sample was taken during the course of the survey, mean biomass for a given taxon was calculated. Using the latitude and longitude for the sites and the biomass of the taxa, the data were then plotted on a map using Arc GIS® software.

Mean total biomass for all six bosminid taxa, as well as mean total bosminid biomass were computed and compared across the nine agglomerated ecoregions of the U.S. Relationships between bosminid biomass and environmental variables (Secchi depth (m), total nitrogen (mg L^{-1}), total phosphorus (µg L^{-1}), surface water temperature (°C) and chlorophyll-a (µg L^{-1})) were quantified using niche centroid analysis (ter Braak & Verdonschot, 1995). This analysis is used to determine the optimum value at which the maximal biomass may be observed. Niche centroid optima were calculated using:

$$u_k = \sum_{i=1}^{n} \frac{y_{ik}}{y_{+k}} x_i$$

where:

y_{ik} = the biomass of species k in the ith sample,

y_{+k} = the summed biomass of species k in all samples, and

x_i = the environmental variable in the ith sample.

179 crustacean zooplankton taxa identified from the 2012 National Lakes Assessment were used in Canonical Correlation Analyses (CCA) using PRIMER 6 (Clarke & Gorley, 2006). Samples with missing or unavailable water quality data were excluded from the analysis, resulting in 1,131 individual samples. The crustacean data set was standardized and a Bray-Curtis resemblance matrix of the standardized crustacean biomass data was used in a CCA (using the Canonical Analysis of Principal Coordinates (CAP) function of the PERMANOVA+ add-on in PRIMER 6) with a sample-matched, normalized matrix of seven water quality variables: water temperature (0-5 m mean), Secchi depth, total nitrogen, total phosphorus, chlorophyll-a, sample latitude and sample elevation. Following the CCA, samples were plotted on ordination diagrams using the first two CAP axes, and the biomass values of the six bosminid taxa found in this study were superimposed over the CCA plot.

A co-occurrence analysis was done to see if there was a correlation between taxon occurrence in lakes. The analysis was done in RStudio using the package *cooccur*. The package *cooccur* applies the probabilistic model of species co-occurrence (Veech 2013) to a set of taxa distributed among a set of survey or sampling sites (Griffith *et. al*. 2016).

Results

Taxa distributions. *Bosmina* (*Bosmina*) cf. *longirostris* O.F. Mueller was found to be ubiquitous throughout all regions of the continental U.S., occurring in all 47 states included in the survey (670 lakes; 86.5% of all lakes in which Bosminidae were present) (Figure 1A). *Bosmina* (*B.*) cf. *longirostris* was found in all nine ecoregions of the continental U.S., with highest mean biomass values in the Temperate Plains (34.61 µg d.w. L^{-1}), Southern Plains (29.85 µg d.w. L^{-1}) and Western Xeric (30.76 µg d.w. L^{-1}) ecoregions (Table 1). On average, *B.* (*B.*) cf. *longirostris* had higher biomass values than all other bosminid taxa.

Bosmina (*Eubosmina*) *coregoni* Baird was found in 39 lakes (5% of all lakes in which Bosminidae were present), and was primarily concentrated around the Great Lakes region (Ohio, Michigan, Indiana, Illinois, Pennsylvania and New York) (Fig. 1B). *Bosmina* (*E.*) *coregoni* was found in 13 of 47 states including Colorado, Illinois, Indiana, Kansas, Michigan, Minnesota, New York, Ohio, Oregon, Pennsylvania, South Dakota, Vermont and Washington. *Bosmina* (*E.*) *coregoni* was present in all nine ecoregions of the continental U.S., with highest mean biomass in the Coastal Plains (1.14 µg d.w. L^{-1}), Upper Midwest (1.94 µg d.w. L^{-1}) and Western Xeric (2.16 µg d.w. L^{-1}) regions.

Bosmina cf. *longispina* Leydig was found in 93 lakes (12% of all lakes in which Bosminidae were present), and ranged from the Atlantic and the Pacific coast (Fig. 2A). *Bosmina* cf. *longispina* occurred primarily in the northern portion of the U.S. The southernmost occurrence of *B.* cf. *longispina* was in Arizona at 35.12 °N. *Bosmina* cf. *longispina* was found in 25 out of 47 states including Arizona, California, Colorado, Connecticut, Iowa, Idaho, Indiana, Massachusetts, Maine, Michigan, Minnesota, Montana, North Carolina, North Dakota, New Hampshire, Nevada, New York, Oregon, Pennsylvania, Rhode Island, South Dakota, Utah, Vermont, Washington, and Wyoming. Highest mean biomass (1.09 µg d.w. L^{-1}) for *B.* cf. *longispina* was found in the Western Mountains region. *Bosmina* cf. *longispina* was not present in any samples in the Southern Plains.

Bosmina (*Liederobosmina*) cf. *tubicen* Brehm was found in 95 lakes (12.3% of all lakes in which Bosminidae were present), and occurred primarily in states along the Atlantic and Gulf coasts, including six lakes west of the Mississippi River (Fig. 2B). *Bosmina* (*L.*) cf. *tubicen* was found in 19 out of 47 states, including Alabama, Arkansas, Connecticut, Florida, Georgia, Kentucky, Louisiana, Massachusetts, Maine, Mississippi, North Carolina, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, South Carolina, Virginia and Vermont.

Bosmina (*L.*) cf. *tubicen* was present in only four out of the nine ecoregions of the continental U.S., and had highest biomass values in the Coastal Plains (3.46 µg d.w. L^{-1}) and Northern Appalachian (2.51 µg d.w. L^{-1}) regions.

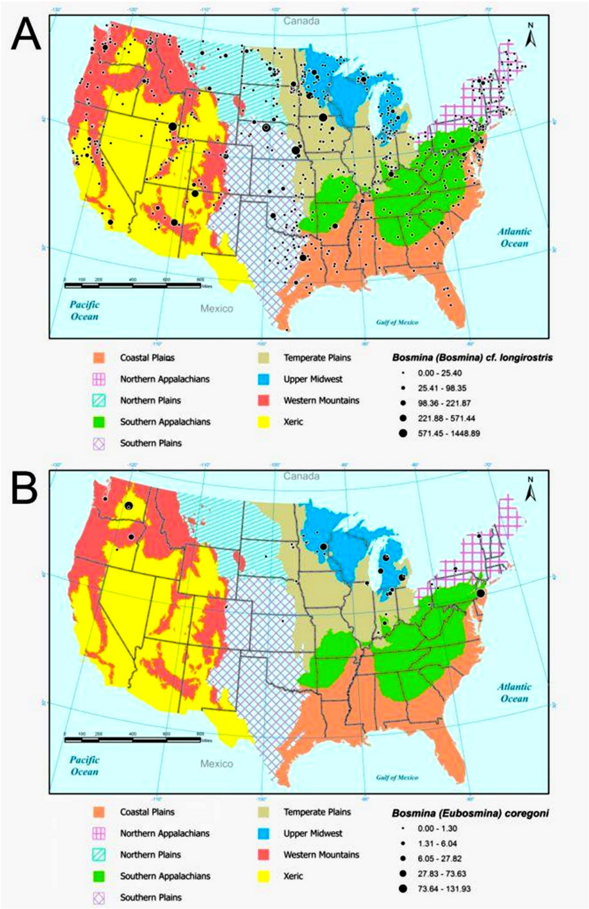

FIGURE 1. Distribution of *Bosmina* (*Bosmina*) cf. *longirostris* (A) and *Bosmina* (*Eubosmina*) *coregoni* (B) in the continental United States. Each circle represents one sample; circle size represents total biomass (µg d.w. L^{-1}) in a sample.

Bosmina (*Liederobosmina*) cf. *hagmanni* Stingelin was found in 18 lakes (2.3% of all lakes in which Bosminidae were present), and occurred only in states west of the Mississippi River (Fig. 3A). *Bosmina* (*L.*) cf. *hagmanni* was found in 6 out of 47 states including Kansas, Montana, Nebraska, New Mexico, Oklahoma and Washington. *Bosmina* (*L.*) cf. *hagmanni* was present in five out of the nine ecoregions of the continental U.S., and had highest biomass values in the Southern Plains (2.04 µg d.w. L^{-1}) and Temperate Plains (1.56 µg d.w. L^{-1}) regions.

Bosminopsis deitersi Richard was found in 17 lakes (2.2% of all lakes in which Bosminidae were present), and occurred only in the Southeast portion of the U.S. (Fig. 3B). Biomass for *B. deitersi* was always relatively low (<9 µg d.w. L^{-1}) compared to other bosminid taxa. *Bosminopsis deitersi* was found in 7 out of 47 states including Alabama, Arkansas, Florida, Georgia, Mississippi, North Carolina and South Carolina. *Bosminopsis deitersi* was present only in the Coastal Plains and Southern Appalachians ecoregions, and had relatively low mean biomass (0.16 and 0.003 µg d.w. L^{-1}, respectfully) in both regions.

Co-occurrence of bosminid taxa. No positive correlations of co-occurrence were found between any of the five Bosminidae taxa analyzed (Fig. 7). *Bosmina* (*B.*) cf. *longirostris* showed negative correlations with all other bosminid taxa, indicating that *B.* (*B.*) cf. *longirostris* rarely co-occurs with other bosminid taxa and that it is often the only bosminid taxon present in a single lake. *Bosmina* (*L.*) cf. *tubicen* showed a negative correlation with both *Bosmina* (*E.*) *coregoni* and *Bosmina* cf. *longispina*. This result is in spite of the fact that the geographical ranges of these taxa overlap in the northeastern region of the country (Figs. 1B, 2A and 2B). All other taxon pair combinations showed no significant negative or positive co-occurrence correlations, meaning that instances where any of the other taxon-pairs occur together is due to random chance and is not ecologically significant.

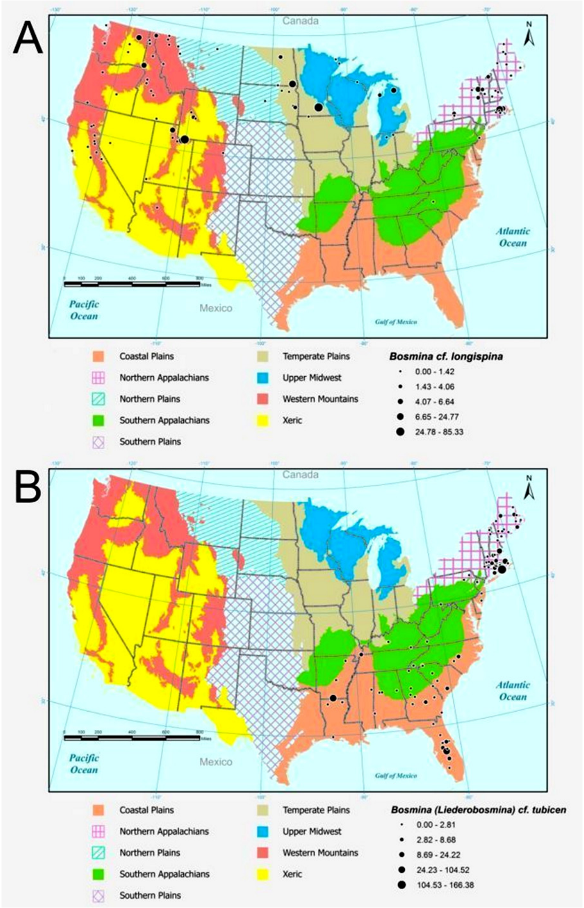

FIGURE 2. Distribution of *Bosmina* cf. *longispina* (A) and *Bosmina* (*Liederobosmina*) cf. *tubicen* (B) in the continental United States. Each circle represents one sample; circle size represents total biomass (µg d.w. L^{-1}) in a sample.

Niche centroids. Niche centroid analysis revealed differences in environmental optima amongst bosminid taxa (Table 2), although the calculation of weighted standard deviation (ter Braak & Verdonschot 1995) showed a high degree of spread within the environmental data. *Bosmina (B.)* cf. *longirostris* and *Bosmina* (*L.*) cf. *hagmanni* exhibited higher biomass in sites with elevated trophic conditions, as indicated by high optimum niche centroid values for total nitrogen (2.9 and 2.5 mg L^{-1} respectively), total phosphorus (266.9 and 245.8 µg L^{-1} respectively), and chlorophyll-a (89.9 and 59.7 µg L^{-1} respectively), and relatively low values for Secchi depth (reduced water clarity, 1.1 and 0.2 m respectively). Contrastingly, *Bosminopsis deitersi* and *Bosmina* (*L.*) cf. *tubicen* achieved highest biomass under more oligotrophic conditions. Optima for those two taxa in terms of total nitrogen (0.4 and 0.5 mg L^{-1} respectively), total phosphorus (49.5 and 31.1 µg L^{-1} respectively) and chlorophyll-a (16.0 and 10.0 µg L^{-1} respectively) were comparatively lower. *Bosmina* (*E.*) *coregoni* and *Bosmina* cf. *longispina* showed highest biomass under intermediate nutrient and chlorophyll-a conditions, compared with the other bosminid taxa found in this study. Temperature optima also varied for bosminid taxa, and generally aligned with observed latitudinal distributions. The lowest temperature optimum was seen for *B.* cf. *longispina* (18.3 °C), while the highest temperature optimum was observed for *B. deitersi* (28.8 °C).

Canonical Correlation Analysis. Canonical correlation analysis (CCA) compared 179 crustacean zooplankton taxa and seven water quality variables, producing two canonical axes with strong correlations. Axes one and two explained 74% and 52% of the total variance, respectively. Elevation and latitude exhibited strong negative correlations with the first axis (-0.667 and -0.683 respectively). Secchi depth displayed a moderate positive correlation with the second axis (0.501), while chlorophyll and total phosphorus displayed moderate negative correlations with the second axis (-0.466 and -0.496 respectively). Temperature and total nitrogen were weakly correlated with both axes.

TABLE 1. Mean biomass (µg d.w. L^{-1}, ±standard error) by ecoregion for the six bosminid taxa, and mean total bosminid biomass (µg d.w. L^{-1}) by ecoregion.

	Bosmina* (*Bosmina*) cf. *longirostris	***Bosminopsis deitersi***	***Bosmina* (*Eubosmina*) *coregoni***	***Bosmina* (*Liederobosmina*) cf. *hagmanni***	***Bosmina* cf. *longispina***	***Bosmina* (*Liederobosmina*) cf. *tubicen***	**Total Bosminidae**
Northern Appalachians	3.97 *(±1.57)*	0	0.06 *(±0.04)*	0	0.51 *(±0.25)*	2.51 *(±1.48)*	7.05 *(±2.13)*
Southern Appalachians	5.56 *(±1.92)*	0.003 *(±0.002)*	0.05 *(±0.04)*	0	0.00004 *(±0.0004)*	0.05 *(±0.03)*	5.66 *(±1.91)*
Coastal Plains	8.88 *(±3.85)*	0.16 *(±0.08)*	1.14 *(±1.14)*	0	0.01 *(±0.009)*	3.46 *(±2.10)*	13.65 *(±4.45)*
Temperate Plains	34.61 *(±16.51)*	0	0.04 *(±0.02)*	1.56 *(±1.15)*	0.24 *(±0.18)*	0.0002 *(±0.0002)*	36.45 *(±16.52)*
Northern Plains	11 *(±3.26)*	0	0.005 *(±0.005)*	0.0003 *(±0.0003)*	0.02 *(±0.008)*	0	11.02 *(±3.25)*
Southern Plains	29.85 *(±14.18)*	0	0.02 *(±0.02)*	2.04 *(±1.66)*	0	0	31.90 *(±14.21)*
Upper Midwest	5.35 *(±1.89)*	0	1.94 *(±0.97)*	0	0.57 *(±0.49)*	0	7.86 *(±2.14)*
Western Mountains	11.29 *(±3.88)*	0	0.3 *(±0.25)*	0.56 *(±0.56)*	1.09 *(±0.78)*	0	13.24 *(±3.98)*
Western Xeric	30.76 *(±19.96)*	0	2.16 *(±2.15)*	0.0003 *(±0.0003)*	0.1 *(±0.09)*	0	33.03 *(±20.01)*

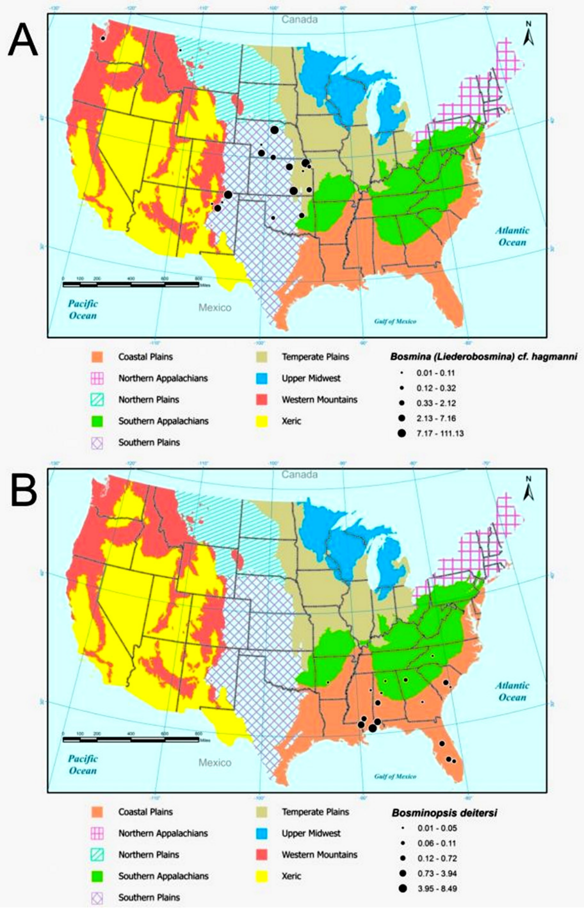

FIGURE 3. Distribution of *Bosmina* (*Liederobosmina*) cf. *hagmanni* (A) and *Bosminopsis deitersi* (B) in the continental United States. Each circle represents one sample; circle size represents total biomass (µg d.w. L^{-1}) in a sample.

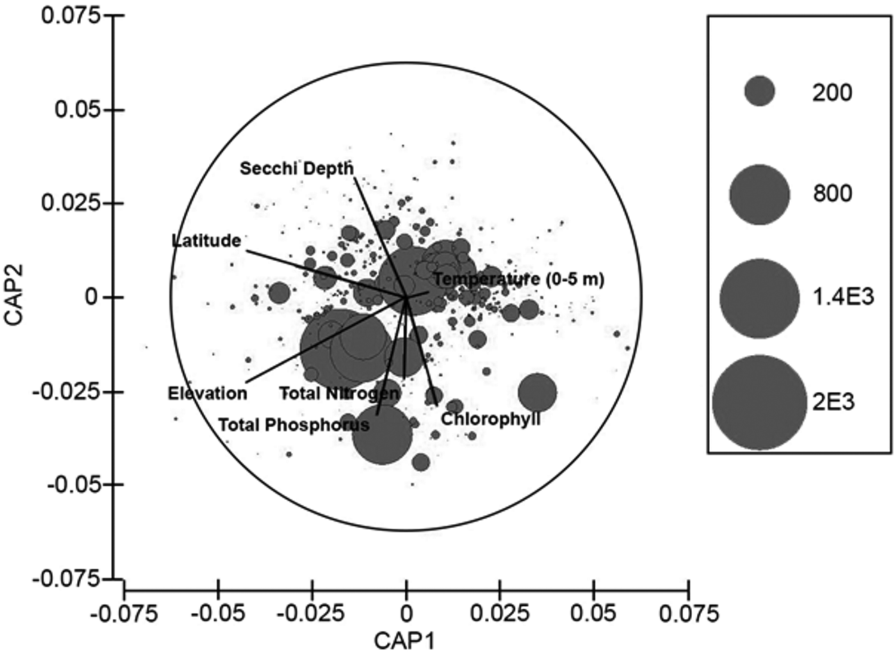

FIGURE 4. CCA ordination bubble diagram for *Bosmina* (*Bosmina*) cf. *longirostris.* Individual bubbles represent the biomass (µg d.w. L^{-1}) in one sample. Individual bubble size represents the magnitude of biomass (see scale).

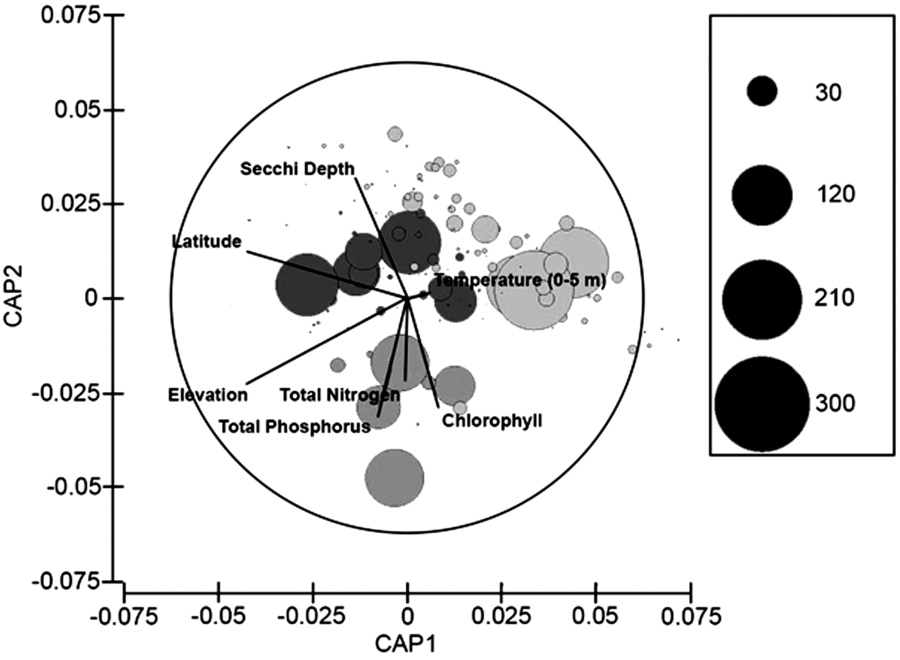

FIGURE 5. CCA ordination bubble diagram for *Bosmina* (*Eubosmina*) *coregoni* (darkest gray bubbles), *Bosmina* (*Liederobosmina*) cf. *hagmanni* (medium gray bubbles) and *Bosmina* (*Liederobosmina*) cf. *tubicen* (lightest gray bubbles). Individual bubbles represent the biomass (µg d.w. L^{-1}) in one sample. Individual bubble size represents the magnitude of biomass (see scale).

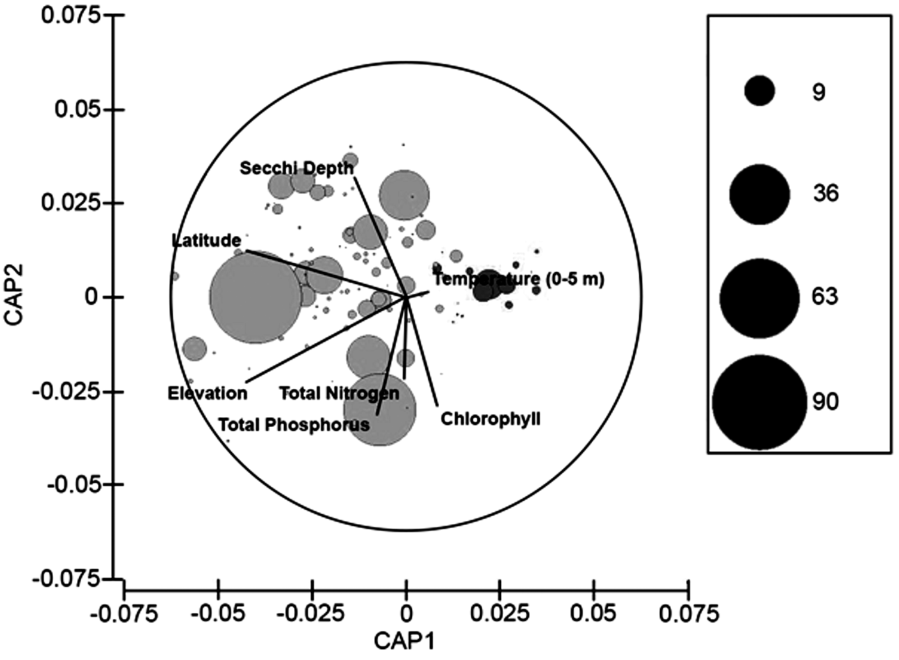

FIGURE 6. CCA ordination bubble diagram for *Bosmina* cf. *longispina* (light gray bubbles) and *Bosminopsis deitersi* (dark gray bubbles). Individual bubbles represent the biomass (µg d.w. L^{-1}) in one sample. Individual bubble size represents the magnitude of biomass (see scale).

Bosminid taxa biomass was superimposed onto the ordination diagrams to illustrate associations with the water quality variables. *Bosmina* (*B.*) cf. *longirostris* was well distributed on the ordination diagram, indicating that the chosen environmental variables have little effect on distribution of this taxon (Figure 4). *Bosmina* (*E.*) *coregoni* showed highest biomass in samples on the positive side of the CAP2 axis, indicating an association with samples having higher Secchi depths (greater water clarity) and lower nutrient concentrations, while *B.* (*L.*) cf. *hagmanni* showed highest biomass on the negative side of the CAP2 axis, indicating an association with samples having lower water clarity and higher nutrient concentrations (Figure 5). Highest biomass for *B.* (*L.*) cf. *tubicen* was seen on the positive side of the CAP1 axis, indicating an association with higher water temperatures and lower latitude and elevation (Figure 5). *Bosmina* cf. *longispina* displayed highest biomass values on the negative side of the CAP1 axis, indicating an association with samples at higher latitudes and elevations regardless of water clarity and nutrient concentrations, while *B. deitersi* was found only on the positive side of the CAP1 axis in association with lower latitudes and elevations and higher water temperatures (Figure 6).

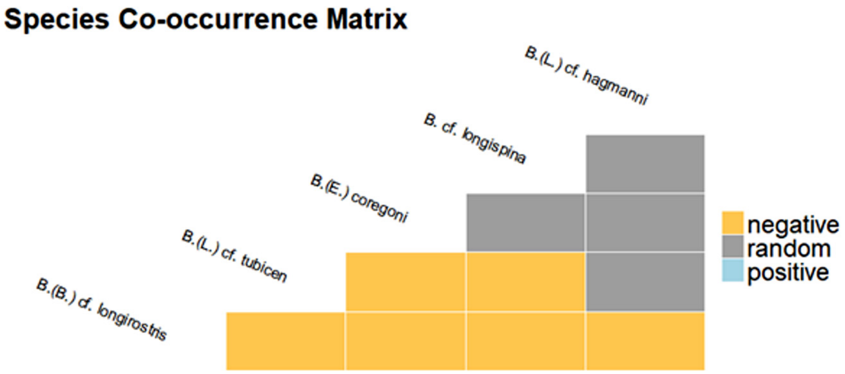

FIGURE 7. Co-occurrence matrix for five Bosminidae taxa: *Bosmina* (*Bosmina*) cf. *longirostris Bosmina* (*Liederobosmina*) cf. *tubicen*, *Bosmina* (*Eubosmina*) *coregoni*, *Bosmina* cf. *longispina* and *Bosmina* (*Liederobosmina*) cf. *hagmanni*.

TABLE 2. Locations of niche centroids (± weighted standard deviation, terBraak & Verdonschot 1995) showing the relationship between individual taxa biomass and five environmental variables: Secchi depth (m), total nitrogen (mg L^{-1}), total phosphorus (mg L^{-1}), surface water temperature (top 5 meters of the water column, °C) and chlorophyll-a (µg L^{-1}).

	Secchi Depth (m)	Total Nitrogen (mg L^{-1})	Total Phosphorus (µg L^{-1})	Temperature 0-5 m (°C)	Chlorophyll-a (µg L^{-1})
Bosmina (Bosmina) cf. *longirostris*	1.10 (±3.40)	2.87 (±2.34)	266.92 (±217.42)	25.81 (±14.85)	89.91 (±86.10)
Bosminopsis deitersi	1.01 (±0.67)	0.44 (±0.18)	49.49 (±20.10)	28.81 (±1.03)	16.00 (±9.55)
Bosmina (Eubosmina) coregoni	1.88 (±1.28)	0.67 (±0.27)	58.19 (±37.73)	23.25 (±2.06)	21.34 (±20.93)
Bosmina (Liederobosmina) cf. *hagmanni*	0.19 (±0.15)	2.46 (±2.08)	245.80 (±102.93)	20.91 (±3.35)	59.65 (±42.32)
Bosmina cf. *longispina*	1.98 (±2.01)	1.15 (±0.97)	108.45 (±127.47)	18.29 (±5.53)	21.75 (±36.24)
Bosmina (Liederobosmina) cf. *tubicen*	1.67 (±0.88)	0.54 (±0.35)	31.08 (±43.54)	27.59 (±3.43)	10.02 (±13.02)

Discussion

Comparison to historical distributions. *Bosmina* (*Bosmina*) cf. *longirostris.* The broad geographical range of *B.* (*B.*) cf. *longirostris* found in this study supports previous work that has described it as a cosmopolitan taxon with a wide geographical range and ability to tolerate a range of environmental conditions (Deevey & Deevey 1971; Lieder 1983). Similar to its wide geographical range in the U.S., *B.* (*B.*) cf. *longirostris* has been reported throughout Canada, from the Atlantic to the Pacific coast (Andre 2011). Within the U.S., *B.* (*B.*) cf. *longirostris* has been reported in lakes from across the country including lakes in Kansas, Montana, Louisiana and Wisconsin (Goulden & Frey 1963) and in California (De Melo & Hebert 1994a). Carter *et al.* (1980) reported instances of *B.* (*B.*) cf. *longirostris* throughout glaciated eastern North America (Canada and the U.S.). Subfossil remains of *B.* (*B.*) cf. *longirostris* were found in lake sediments in Connecticut and Indiana (Goulden & Frey 1963).

Bosmina (*Eubosmina*) *coregoni* was first established in the U.S. in Lake Michigan in 1966, as reported by

Wells (1970). This is despite the reporting of *B.* (*E.*) *coregoni* in the U.S. from Goulden & Frey (1963), in which it was observed from three lakes in North Carolina. Unfortunately, because of the complexity and confusion surrounding identification of Bosminidae and the ontogenetic nature of many distinguishing morphological features, it is impossible to verify those earliest reports. Between 1969 and 1978, *B.* (*E.*) *coregoni* was found in 15 inland lakes within 100 km of the Great Lakes (including lakes in Canada) by Carter *et al.* (1980). By the early 1990's, *B.* (*E.*) *coregoni* was found in four out of five of the Great Lakes (Erie, Huron, Ontario and Michigan) and had spread to 23 inland lakes within 100 km of the Great Lakes (De Melo & Hebert 1994b). The first report of *B.* (*E.*) *coregoni* beyond the Great Lakes region in the U.S. was by Mabee (1998), who found *B.* (*E.*) *coregoni* in three reservoirs in southern Missouri. Smits *et al.* (2013) then reported observations of *B.* (*E.*) *coregoni* in four freshwater systems in the Pacific Northwest (the Lower Columbia River Estuary, Lake Washington, Pothole Reservoir and Moses Lake) between 2008 and 2012. The reports of *B.* (*E.*) *coregoni* in the Pacific Northwest were concurrent with the findings of this study, in which we observed *B.* (*E.*) *coregoni* in three lakes in Oregon and two lakes in Washington during the summer of 2012. This study is the first known reporting of the spread of *B.* (*E.*) *coregoni* across the entire continental U.S. (including first reports from Colorado, South Dakota, Nebraska and Kansas), and showcases the detailed expansion of the invasive species both southward and westward from the Great Lakes region.

Bosmina cf. *longispina.* In the northern half of the U.S., *Bosmina* cf. *longispina* is also widespread from coast-to-coast in Canada, and has been found as far north as Baffin Island (Andre 2011). Previous records agree with our findings that *B.* cf. *longispina* is primarily a northern latitude taxon. It was previously observed as having a southern limit of Connecticut/Rhode Island (Deevey & Deevey 1971), and as being abundant and well-distributed in glaciated eastern North America (Carter *et al.* 1980; De Melo & Hebert 1994a). However the current survey found *B.* cf. *longispina* in lakes further south than previously noted for the U.S., including South Carolina, Colorado, Utah, California and Arizona. Thus, this study reports an expanded southern range for *B.* cf. *longispina* within North America. Historical records (including subfossil remains from lake sediments) indicate that *B.* cf. *longispina* may be limited by warmer waters near the Neotropical region, as well as by increasing eutrophication (Nilssen & Larsson 1980). Haney & Taylor (2003) analyzed *B.* cf. *longispina* from the Atlantic to the Pacific coast of North America and determined that Atlantic populations were genetically divergent from Beringian populations, indicating that occurrences of this taxon in this study may represent two separate species with distinct establishment histories.

Bosmina (*Liederobosmina*) cf. *tubicen.* The literature record indicates that this taxon has a broad latitudinal range; it was first described by Brehm (1953) from lakes in Venezuela, and has since been documented as far north as Ontario and New Brunswick (De Melo & Hebert 1994a; Carter *et al.* 1980). Deevey & Deevey (1971) describe *B.* (*L.*) cf. *tubicen* as "clearly Neotropical", however they also report instances of finding *B.* (*L.*) cf. *tubicen* in lakes in New England (Connecticut) and in the far temperate zone of eastern North America, into Nova Scotia. The western range for *B.* (*L.*) cf. *tubicen* in the U.S. is less well clarified in the literature, although it has been found previously in Arkansas (Post *et al.* 1995); this record, along with the findings of this study suggest that states bordering the Mississippi River to the west likely represent the current western limit in the U.S. for *B.* (*L.*) cf. *tubicen*.

Bosmina (*Liederobosmina*) cf. *hagmanni.* Although this taxon was first described from samples in South America (De Melo & Hebert 1994a), Deevey & Deevey (1971) described it was "widespread and variable, probably confined to the Americas". Deevey & Deevey (1971) also made a note about difficulty of identification of *B.* (*L.*) cf. *hagmanni* in the absence of a male specimen. *Bosmina* (*L.*) cf. *hagmanni* has previously been recorded across many parts of the southern and western U.S. including North Carolina, Indiana (Goulden & Frey 1963), Kansas, Texas, Arizona, the Rocky Mountains and the Pacific Northwest (Deevey & Deevey 1971). These records largely agree with the findings of this study, which suggest that *B.* (*L.*) cf. *hagmanni* is confined to the western U.S. However, sparse records of *B.* (*L.*) cf. *hagmanni* from the temperate northeast region of North America have been reported, including isolated instances from New England (Massachusetts and Connecticut, De Melo & Hebert 1994a), and a single record in eastern Ontario (Carter *et al.* 1980).

Bosminopsis deitersi is largely considered to be a tropical species, common in the Amazon floodplain (Junk & Roberts 1997) and in South and Central America (Dumont & Tundisi 1984). In the U.S., *B. deitersi* has been recorded in lakes of south Florida (Pinto-Coelho *et al.* 2005) and Oklahoma (Jones 1958), which is well within the geographical range found in this study.

Factors potentially determining Bosminidae biomass and distribution. Previous studies have concluded that high Bosminidae biomass is usually found under highly enriched nutrient conditions typical of eutrophic lakes (Bays & Crisman 1983; Havens *et al*. 2015). Food web structures in productive lakes differ fundamentally from lakes with lower nutrient concentrations and are characterized by higher concentrations of cyanobacteria and more intense predation pressure on larger crustacean zooplankton by planktivorous fish (Carpenter *et al*. 1985; Carpenter & Kitchell 1996). Bosminidae are among the smallest crustacean zooplankton in lakes and are less impacted by predation by planktivorous fish. This, combined with superior ability to utilize less nutritious and often toxic phytoplankton (e.g., Jiang *et al.* 2013), affords Bosminidae a distinct competitive advantage over larger crustaceans that are more dependent on higher quality phytoplankton as a food resource and more susceptible to predation.

In this study, both *B.* (*B.*) cf. *longirostris* and *B.* (*L.*) cf. *hagmanni* showed high biomass under elevated nutrient and chlorophyll conditions, although *B.* (*B.*) cf. *longirostris* biomass was highly variable. Other taxa either showed a moderate negative relationship (*B.* (*E.*) *coregoni*) or no relationship (*B.* (*L.*) cf. *tubicen*, *B.* cf. *longispina* and *B. deitersi*) with nutrient concentrations. Because *B.* (*B.*) cf. *longirostris* biomass was by far the highest in comparison to other bosminid taxa, it is most useful to examine this taxon in the context of varying environmental conditions. The high variability of *B.* (*B.*) cf. *longirostris* observed in this study may be the result of the sample collection strategy, which was designed to capture a wide range of environmentally variable lakes and reservoirs in the U.S. The highest mean total Bosminidae biomass (primarily consisting of *B.* (*B.*) cf. *longirostris*) was realized in three of the four ecoregions (Temperate Plains, Southern Plains, and Western Xeric) with well described planktivorous fish communities. Gizzard shad (*Dorosoma cepedianum*), an omnivorous pump filter feeder, are widely distributed throughout lakes of the Temperate Plains and Southern Plains (Fuller & Neilson 2017a) and are known to depress the size of crustacean zooplankton communities through predation impacts (Havens & Beaver 2011; Beaver *et al*. 2014). Similarly, threadfin shad (*Dorosoma petenense*) has been widely stocked in reservoirs of the Western Xeric ecoregion (Fuller & Neilson 2017b) and are highly effective size-selective predators on large-bodied zooplankton crustaceans (Loomis *et al*. 2011; Beaver *et al*. 2014). Distributions of Bosminidae in lakes of the continental U.S. from this study are consistent with the notion that trophic level interactions can favor these small-bodied taxa in the plankton of eutrophic lakes.

Limitations and future research. Within this survey, only six discrete Bosminidae taxa were observed. However, previous studies have reported additional species of Bosminidae that occur within the U.S., for example *B.* (*Bosmina*) *freyi*, *B.* (*Liederobosmina*) *huaronensis*, *B.* (*Bosmina*) *liederi* and *B.* (*Lunobosmina*) *oriens* (Kotov *et al*. 2009). Several possibilities exist that could explain the absence of these taxa from our study, the first of which is that the observed specimens were not able to be identified due to lack of reliable taxonomic keys. For example, *B.* (*L.*) *oriens* was not identified due to lack of males. Furthermore, the rationale for identification of *B.* (*L.*) *oriens* in De Melo & Hebert (1994a) requires a fully mature female, which often was not the case. Similarly, available keys had either no mention of *B.* (*L.*) *huaronensis* (i.e. Dodson *et al*. 2010), a poor morphological justification (De Melo & Hebert 1994a), or was based on male specimens (Kotov *et al.* 2009). Both *B.* (*B.*) *liederi* and *B.* (*B.*) *freyi* can be confused with *B.* (*B.*) *longirostris* but were not recognized because the available key for discrimination of these three taxa (De Melo & Hebert 1994a) relied on inconsistent and unclear morphological features. Identification of these species would have been possible if male specimens had been present. It is also possible that certain species, especially rarer taxa, were missed due to random chance in site selection. This study was confined only to the pelagic region of lakes and reservoirs. Unobserved bosminid taxa may have been more abundant in littoral areas of lakes and reservoirs, or in other types of aquatic habitats such as wetlands, streams and rivers.

The taxonomic designations used in this study stem primarily from morphological and phylogenetic studies of female bosminids (De Melo & Hebert 1994a; Dodson *et al*. 2010; Taylor *et al*. 2002; Haney & Taylor 2003), since the vast majority of specimens found in this survey were female. However, Kotov *et al*. (2009) found that male morphological characteristics were in better agreement with concurrent phylogenetic analyses than were female morphological characteristics. Although male bosminids have been shown to be a more accurate and preferred method for species level identification, further research is needed to improve identification of female bosminids. Female identification is most relevant for individuals identifying bosminids in samples from the field, where encountering a male is less likely. Male bosminids tend to have shorter life spans, investing more metabolic energy into development of reproductive structures while females tend to have longer life spans, investing more metabolic energy into the development of predator avoidance characteristics (Kotov 1996). The nature of the sampling regime in this survey (i.e. taking only one sample from each lake on one day during the spring/summer) likely contributed to the overwhelming ratio of females to males observed.

Nomenclatural complications addressed in this study and others highlight the ongoing study of specific taxonomy within Bosminidae. Attempts to determine phylogenetic species designations on an individual basis was beyond the scope of work and would have been impractical for this already exhaustive study; however such information would be necessary to make more explicit and conclusive species determinations. The current report is meant to be a resource for bench-level taxonomists performing routine monitoring of lakes and reservoirs on a time- and fund-limited basis. For a more robust analysis of bosminid biogeography within the U.S., morphological characterization should be coupled with phylogenetic analyses in order to obtain a more thorough account of distributional differences between species.

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