

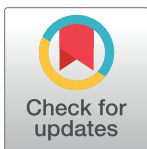
RESEARCH ARTICLE

Calanoid copepod zooplankton density is positively associated with water residence time across the continental United States

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OPEN ACCESS

Citation: Doubek JP, Carey CC, Lavender M, Winegardner AK, Beaulieu M, Kelly PT, et al. (2019) Calanoid copepod zooplankton density is positively associated with water residence time across the continental United States. *PLoS ONE* 14(1): e0209567. <https://doi.org/10.1371/journal.pone.0209567>

Editor: Hans G. Dam, University of Connecticut, UNITED STATES

Received: May 19, 2018

Accepted: December 9, 2018

Published: January 9, 2019

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Data Availability Statement: All data are available from the 2007 US Environmental Protection Agency's National Lakes Assessment and from the US Army Corps of Engineers' National Inventory of Dams: (1) <https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys> and (2) <http://nid.usace.army.mil/>. Those interested would be able to access the data in the same manner as the authors. The authors had no special access privileges.

Abstract

Inherent differences between naturally-formed lakes and human-made reservoirs may play an important role in shaping zooplankton community structure. For example, because many reservoirs are created by impounding and managing lotic systems for specific human purposes, zooplankton communities may be affected by factors that are unique to reservoirs, such as shorter water residence times and a reservoir's management regime, compared to natural lakes. However, the environmental factors that structure zooplankton communities in natural lakes vs. reservoirs may vary at the continental scale and remain largely unknown. We analyzed data from the 2007 U.S. Environmental Protection Agency's National Lakes Assessment and the U.S. Army Corps of Engineers' National Inventory of Dams to compare large-bodied crustacean zooplankton communities (defined here as individuals retained by 0.243 mm mesh size) in natural lakes and reservoirs across the continental U.S. using multiple linear regressions and regression tree analyses. We found that large-bodied crustacean zooplankton density was overall higher in natural lakes compared to reservoirs when the effect of latitude was controlled. The difference between waterbody types was driven by calanoid copepods, which were also more likely to be dominant in the >0.243 mm zooplankton community in natural lakes than in reservoirs. Regression tree analyses revealed that water residence time was not a major driver of calanoid copepod density in natural lakes but was one of the most important drivers of calanoid copepod density in reservoirs, which had on average 0.5-year shorter water residence times than natural lakes. Reservoirs managed for purposes that resulted in shorter residence times (e.g., hydroelectric power) had lower zooplankton densities than reservoirs managed for purposes that resulted in longer residence times (e.g., irrigation). Consequently, our results indicate that water residence time

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Funding: This work was supported by the National Science Foundation DEB-1601061, EF-1137353, EF-1137327, ICER-1517823, EF-1702506, Global Lake Ecological Observatory Network (GLEON), Virginia Tech Fralin Life Sciences Institute, and the Global Change Center.

Competing interests: The authors have declared that no competing interests exist.

may be an important characteristic driving differing large-bodied zooplankton dynamics between reservoirs and natural lakes.

Introduction

Zooplankton are a vital component of aquatic food webs and ecosystem functioning. Zooplankton provide a crucial link between primary producers and higher trophic levels [1–3], are important indicators of ecosystem change [4–7], and can play a key role in lake nutrient and carbon cycling [8–11]. Consequently, differences in zooplankton densities and community composition can have important implications for ecosystem-level processes in lakes, including trophic cascades and water quality [2, 12].

Waterbody origin, i.e., if a waterbody is naturally-formed or human-constructed (a reservoir), may play an important role in structuring zooplankton communities because of inherent differences between the two waterbody types [13–16]. For example, because many reservoirs are constructed by impounding lotic systems [17], they generally have faster flushing rates and shorter water residence times (WRT) than natural lakes [18]. These shorter WRT may result in different zooplankton communities in reservoirs relative to natural lakes. Consequently, reservoirs may have lower zooplankton densities and richness, on average, because zooplankton are continuously washed out of the water column [19–22]. Previous studies on WRT and zooplankton communities, however, have primarily been conducted at a single lake or regional scale. The generality of such relationships at the continental scale, to date, remains untested.

To the best of our knowledge, only two studies have directly examined how zooplankton communities vary between reservoirs and natural lakes [23, 24]. Both studies found that zooplankton community composition differed between the two waterbody types, with some cyclopoid and calanoid copepod taxa occurring more frequently in natural lakes compared to reservoirs [23, 24]. Lower zooplankton species richness in reservoirs and differences in zooplankton composition were attributed to the more eutrophic state, younger geologic age, and possibly greater disturbance of reservoirs compared to natural lakes. However, specific reservoir characteristics such as WRT were not considered in these analyses, and total zooplankton densities and taxa dominance were not directly analyzed. Moreover, the generality of the results may be limited due to the relatively small sample size of reservoirs (11 reservoirs vs. 68 natural lakes) [23], or the focus on waterbodies within only one geographical region (59 waterbodies in southern Brazil) [24].

Differences in reservoir management (here, defined as the primary purpose of a reservoir) may influence zooplankton communities because reservoir purpose may affect many environmental characteristics, such as WRT [22, 23]. For example, reservoirs used mainly for hydroelectric power generation may have shorter WRTs and thereby lower zooplankton densities than reservoirs managed for purposes that result in longer WRTs (e.g., water supply reservoirs) [22, 25]. In addition, reservoir purpose may disproportionately affect the density and richness of certain taxa in the zooplankton community. Because some copepods have long generation times (up to multiple months for an egg to develop into an adult) [1, 26–28], copepods may be more affected by reservoir purpose than cladocerans, which can have generation times of days [1, 26]. A WRT of 1–2 months may negatively affect calanoid copepods, because their generation times may extend up to eight months [1, 26, 28]. Conversely, a WRT of 1–2 months would likely have less of an effect on cladoceran populations, which would still have enough time to grow and reproduce. Thus, copepods may be flushed out of reservoirs with shorter

WRT systems compared to longer WRT systems before reaching reproductive adult stages. Because reservoir purpose may alter WRT, which in turn may affect zooplankton density and the dominance of different taxa, reservoir management regime may indirectly affect zooplankton community structure. To the best of our knowledge, such relationships have not yet been tested across reservoirs of multiple primary purposes and at the continental scale.

We analyzed data from the U.S. Environmental Protection Agency's (EPA) 2007 National Lakes Assessment (NLA) and the U.S. Army Corps of Engineers' National Inventory of Dams (NID) to test how environmental drivers of crustacean zooplankton density and genera richness (i.e., total crustacean, total copepods, cyclopoid copepods, calanoid copepods, cladocerans, and *Daphnia*) differed between the two waterbody types and across reservoirs of different purposes in the continental U.S. First, we compared zooplankton communities and environmental drivers known to be important factors shaping zooplankton density and composition (e.g., WRT, chlorophyll *a*) between natural lakes and reservoirs at the continental U.S. scale while controlling for the effect of latitude. We predicted that zooplankton density and genera richness would be overall lower in reservoirs than in natural lakes. Second, we focused specifically on reservoirs and analyzed the effects of reservoir primary purpose (e.g., hydropower, recreation) and environmental drivers on zooplankton density. We predicted that zooplankton densities would be lower in reservoirs used for purposes that generally result in shorter WRT (e.g., hydropower) than those used for purposes that result in longer WRT (e.g., recreation).

Methods

EPA NLA and sampling

The NLA sampled both natural lakes and reservoirs across the continental U.S. (Fig 1), providing a large-scale dataset to investigate relationships between the two waterbody types and zooplankton communities. The NLA 2007 data have been used to assess regional to continental

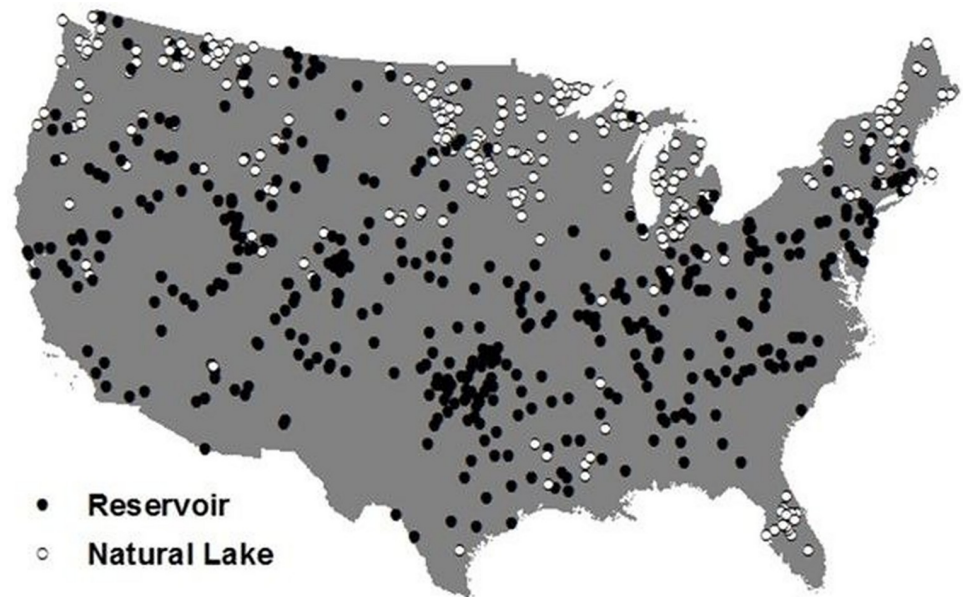


Fig 1. Locations of reservoirs (filled circles) and natural lakes (open circles) sampled in the 2007 National Lakes Assessment that were included in zooplankton analyses.

<https://doi.org/10.1371/journal.pone.0209567.g001>

patterns of land use, nutrient concentrations, and phytoplankton characteristics [29–34], but have not been used to examine differences in zooplankton density and richness between waterbody types in the U.S.

In 2007, the U.S. EPA sampled >1000 lakes and reservoirs across the U.S. during May to October. Some waterbodies in the NLA had replicate samples or were sampled more than once over the season. We only analyzed data collected on the first sample date to maintain consistency across waterbodies. The mean Julian day when a waterbody was sampled was 212, with a range from day 128 to day 291. No significant relationship existed between the Julian day of sampling and latitude ($P = 0.73$); therefore, there was likely a minimal effect of the time of year when natural lakes were sampled compared to when reservoirs were sampled. All sampled waterbodies were at least 0.04 km² and 1 m deep and were chosen using a random stratified design based on surface area, ecoregion, and state [35, 36]. Reservoir and natural lake designations were included in the NLA dataset and were based on maps, discussions with state and tribal resource managers, and on-site field crew observation. The natural lake category includes waterbodies with water level control devices on naturally-formed basins. Detailed sample collection methods, laboratory processing protocols, and all NLA data are publicly available online (http://water.epa.gov/type/lakes/lakessurvey_index.cfm); thus, we limited our description to the variables included in our analyses.

We analyzed physical, chemical, and biological variables from the NLA dataset known to be important for zooplankton communities to examine potential differences of these variables between reservoirs and natural lakes and their relationships to zooplankton. The variables we included were maximum water column temperature [37–39], mean dissolved oxygen (DO) in the water column [40, 41], pH [42–44], chlorophyll *a* concentrations [45–47], and WRT [22, 48, 49]. Water temperature and DO depth profiles were collected with multi-parameter water quality sondes. Samples for water chemistry and chlorophyll *a* were collected with an integrated tube sampler from the photic zone up to 2 m depth from the surface and sent to a central lab for analysis [29, 32, 33]. WRT was quantified by $\delta^2\text{H}$ and $\delta^{18}\text{O}$ ratios from the integrated water sample (see [49] for detailed methods on WRT methods and calculations).

Other variables that may be important for zooplankton communities, such as dissolved organic carbon (DOC) and calcium, were not included because they were highly correlated with the aforementioned environmental variables (pH vs. calcium $r = 0.74$, DOC vs. chlorophyll *a* $r = 0.52$); other candidate environmental variables that had Pearson product-moment correlations of $r > 0.50$ with the focal environmental variables were excluded from analyses (see S1 Table for Pearson product-moment correlations between environmental variables). We used an r of 0.50 as a cut-off to obviate highly correlated variables confounding results in multivariate statistics (see below) [50–52].

Zooplankton

Zooplankton were collected with vertical net tows (Wildlife Supply Company, Yulee, FL, USA) during daytime on each lake. Natural lakes were sampled at the deepest location in the lake (up to 50 m deep). Reservoirs were sampled at a mid-point in the reservoir (up to 50 m deep). Nets were lowered to 0.5 m above the bottom for both reservoirs and natural lakes and pulled to the surface at a constant speed. A vertical net tow with a 0.243-mm mesh size was used to sample copepod (cyclopoid and calanoid) and cladoceran zooplankton. The plankton net had a 0.127-m diameter opening. All zooplankton were field-preserved with 95% ethanol and sent to a central lab for identification and counting. We acknowledge that the mesh size was larger than some smaller crustacean zooplankton taxa (e.g., *Bosmina* and *Chydorus*), and therefore, much of our focus is on large-bodied crustacean zooplankton which are retained in and

minimally affected by a 0.243-mm mesh [1, 26]. We do report results for some zooplankton groups that may be underestimated because of the mesh size, but our conclusions are based primarily on calanoid copepods and *Daphnia*.

Zooplankton were identified using a dissecting microscope. Most taxa were identified to the genus level. For some waterbodies, however, zooplankton were only identified to the order or subclass level (i.e., Cladocera, Calanoida, Cyclopoida, and Copepoda). Counts for cyclopoid and calanoid copepods consisted of copepodids and adults. Copepod nauplii were not considered as they were likely not quantitatively captured with the mesh size. To standardize taxonomic resolution across waterbodies, and because of our interest in analyzing taxa richness, we only included waterbodies that had zooplankton information to the genus level. Most waterbodies in the NLA were still included in our analyses ($N = 730$ waterbodies with zooplankton data).

The NLA reported zooplankton as the number of zooplankton taxa in each subsample, with a minimum of 200 and up to 400 maximum identified individuals. To compare zooplankton data across all waterbodies, we calculated zooplankton density in the water column (individuals L^{-1}) by scaling counts per subsample volume to the total volume sampled by the net tows in the water column [1]. Length measurements of zooplankton were not recorded; therefore, we could not calculate zooplankton biomass estimates to quantify potential effects of fish predation on zooplankton communities. More detailed information on zooplankton field and laboratory methods are publicly available online (https://www.epa.gov/sites/production/files/2013-11/documents/2009_12_31_lakes-lakessurvey_pdf_qualityassuranceplan.pdf).

The NLA only reported the presence (but not density) of large predatory zooplankton, such as *Leptodora*, and the insect larvae *Chaoborus*, and thus they were not included in our analyses. Other zooplankton sporadically noted in the dataset (e.g., zebra mussel veligers) were not included due to their rarity ($N < 20$ waterbodies). Fish data were not included in the NLA.

Statistical analyses

Analysis 1: Continental differences in large-bodied zooplankton density, taxa dominance, and genera richness between natural lakes and reservoirs. We first examined major differences in aggregated total density, taxa dominance, and genera richness for each zooplankton group between natural lakes and reservoirs across the continental U.S. The zooplankton groups included in these analyses were: total crustacean zooplankton (the sum of copepods + cladocerans), total copepods (cyclopoids + calanoids), cyclopoids, calanoids, and cladocerans. Total copepods also included harpacticoids, but due to their rarity in these samples ($n = 2$), they were not analyzed separately. In addition, we performed Analysis 1 for the cladoceran genus *Daphnia*, as an example of a larger-sized cladoceran taxa that should be minimally affected by the size of the zooplankton vertical tow nets [1]. The dominance of each taxon group in the crustacean zooplankton community was calculated by dividing the density of the group (total copepods, cyclopoids, calanoids, and cladocerans) by the total crustacean zooplankton density for each waterbody.

Many physical, chemical, and biological factors vary with latitude [53–55]. Consequently, we also accounted for latitude as a covariate in waterbody origin comparisons because of the large geographic disparity in the location of natural lakes (dominant in northern latitudes) vs. reservoirs (dominant in southern latitudes) in the U.S. The effects of waterbody type (natural lakes or reservoirs), latitude, and their interaction were analyzed on our response variables using multiple linear regression models with waterbody type as an indicator variable (coded as natural lakes as 0 and reservoirs as 1) [56]. The regression equation we used for each analysis

was:

$$Y = B_0 + B_1X_{\text{waterbody_type}} + B_2X_{\text{latitude}} + B_3X_{\text{waterbody_type} \times \text{latitude}} + \epsilon \quad (1)$$

where Y is the response variable of interest, B_0 is the intercept term, B_1 , B_2 , and B_3 are the respective model coefficient terms, and ϵ is the stochastic error term.

At the continental scale, we also tested the effects of waterbody type, latitude, and their interaction on maximum water column temperature, mean water column DO, pH, chlorophyll a , and WRT (environmental variables that are known to be important for zooplankton community structure) in multiple linear regressions, as in the above analyses for zooplankton. Because each zooplankton response variable and other environmental response variables were only used once in statistical analyses, and hence were in separate families of tests, correction of P -values was not necessary [56, 57].

Analysis 2: Regression tree analyses of the effects of environmental factors on large-bodied zooplankton densities. Analysis 1 tested for broad-scale differences in aggregated total density, taxa dominance, and genera richness between waterbody types across the U.S. For Analysis 2, we expanded on Analysis 1 by examining which environmental variables may contribute to differences in zooplankton densities between reservoirs and natural lakes. We performed regression tree analyses to compare the relative importance of the focal environmental factors on crustacean zooplankton, total copepod, calanoid, cladoceran, and *Daphnia* density between reservoirs and natural lakes. We did not include latitude in regression tree analyses because our goal was to assess the impacts of direct environmental variables (e.g., maximum water temperature, chlorophyll a , and WRT) on zooplankton communities and because latitude is highly correlated with many environmental variables in our analysis that have direct effects on zooplankton densities. However, we examined any latitudinal or regional clustering from the regression tree results by plotting the geographic location of crustacean zooplankton density groupings based upon the splits in the regression tree analysis.

Regression trees provide a robust statistical approach to handle potential non-linear relationships and nested effects among variables [58–60]. Pruned regression trees were chosen by minimizing cross-validation error [60, 61]. We performed regression trees for crustacean, total copepod, calanoid, cladoceran, and *Daphnia* density in all waterbodies together and then separately for natural lakes only and reservoirs only, focusing on the waterbodies that had all focal environmental variables available ($N = 688$ waterbodies). Regression tree analyses were performed using the R package “rpart” in R v3.2.4 [62].

Analysis 3: Relationships between reservoir primary purpose, environmental factors, and large-bodied zooplankton densities. Next, we examined how differences among reservoirs with varying primary purpose and environmental factors may affect crustacean zooplankton community structure. The NID (<http://nid.usace.army.mil/>) designates and defines the primary purpose of each reservoir in the U.S. as hydropower, recreation, water supply, irrigation, or flood control ($N > 20$ for each of these categories). We used the NID classifications to assess differences among primary purpose and maximum water column temperature, mean water column DO, pH, chlorophyll a concentrations, WRT, total crustacean, total copepod, cyclopoid, calanoid, cladoceran, and *Daphnia* density using one-way ANOVA with post-hoc Tukey pairwise comparisons. For the reservoir-only analyses, we included all the reservoirs in the NLA for which the NID also had available data on primary purpose ($N = 303$). In contrast to the reservoir vs. natural lakes comparison in Analysis 1, the use of ANOVA was appropriate for the reservoir-only analyses because reservoirs with different purposes were geographically distributed across diverse regions in the U.S., without a latitudinal bias as for all zooplankton response variables (S1 Fig contains the location of the five reservoir primary purpose types).

To meet assumptions of normality and equal variance, total crustacean zooplankton density, total copepod density, cyclopoid density, calanoid density, cladoceran density, *Daphnia* density, chlorophyll *a*, and WRT were ln-transformed for all statistical analyses. Variables expressed as proportions (total copepod, cyclopoid, calanoid, and cladoceran dominance) were logit-transformed prior to analyses [63]. If variables had zero values, the minimum observed value for each variable was added prior to transformation. The *P*-values for statistical tests were considered significant at $\alpha \leq 0.05$. All analyses were performed in R v3.2.4 [62].

Results

Analysis 1: Continental differences in large-bodied zooplankton density, taxa dominance, and genera richness between natural lakes and reservoirs

Natural lakes across the U.S. had higher total crustacean zooplankton density than reservoirs ($F_{3,726} = 5.26$; $P = 0.02$; Fig 2A) when also accounting for latitude. Natural lakes had an

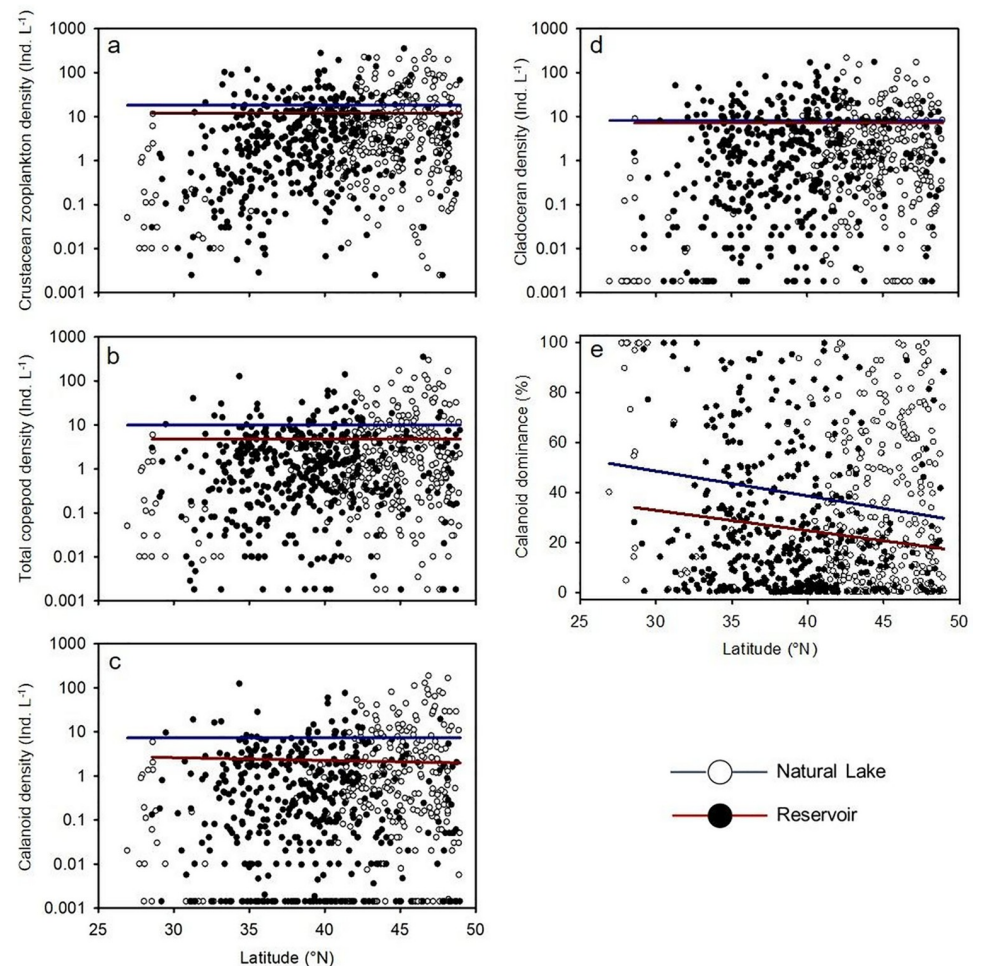


Fig 2. U.S.-scale comparisons of a) crustacean zooplankton (copepod + cladoceran), b) total copepod (cyclopoid + calanoid), c) calanoid, and d) cladoceran density, and e) calanoid dominance in the zooplankton community between natural lakes and reservoirs and across latitude. Note that the y-axis is in log scale for the zooplankton density panels.

<https://doi.org/10.1371/journal.pone.0209567.g002>

Table 1. Comparison of each zooplankton group and other environmental variables between natural lakes and reservoirs across the continental U.S., with each variable's untransformed mean values and standard errors (SE).

Variable	Natural Lakes Mean ± SE	Reservoirs Mean ± SE
Zooplankton response variables		
Total crustacean density*	18.1 ± 2.3 L ⁻¹	11.8 ± 1.5 L ⁻¹
Total copepod density*	9.9 ± 1.6 L ⁻¹	4.7 ± 1.0 L ⁻¹
Cyclopoid density	2.6 ± 0.7 L ⁻¹	2.4 ± 0.8 L ⁻¹
Calanoid density*	7.3 ± 1.2 L ⁻¹	2.3 ± 0.4 L ⁻¹
Cladoceran density	8.1 ± 1.3 L ⁻¹	7.1 ± 0.9 L ⁻¹
<i>Daphnia</i> density	3.4 ± 0.5 L ⁻¹	3.3 ± 0.5 L ⁻¹
Total copepod dominance*	54.0 ± 1.8%	49.0 ± 1.4%
Cyclopoid dominance*	19.2 ± 1.4%	23.5 ± 1.2%
Calanoid dominance*	35.1 ± 1.8%	25.8 ± 1.3%
Cladoceran dominance*	46.8 ± 1.7%	52.0 ± 1.4%
Total crustacean zooplankton genera richness	4.15 ± 0.09	4.08 ± 0.07
Total copepod genera richness	1.94 ± 0.04	1.86 ± 0.03
Cyclopoid genera richness	0.94 ± 0.02	0.96 ± 0.02
Calanoid genera richness*	1.01 ± 0.03	0.90 ± 0.02
Cladoceran genera richness	2.21 ± 0.07	2.22 ± 0.05
Other environmental variables		
Maximum water column temperature*	22.9 ± 0.2 °C	24.7 ± 0.2 °C
Mean water column dissolved oxygen*	6.4 ± 0.1 mg L ⁻¹	6.0 ± 0.1 mg L ⁻¹
pH	8.1 ± 0.05	8.0 ± 0.03
Chlorophyll <i>a</i>	38.6 ± 5.1 µg L ⁻¹	23.6 ± 2.3 µg L ⁻¹
Water residence time*	1.3 ± 0.1 years	0.8 ± 0.1 years

The response variables that were significantly different between natural lakes and reservoirs when also accounting for latitude in models are highlighted with an asterisk (*). All statistics for the natural lakes vs. reservoirs comparison are given in Table 2.

<https://doi.org/10.1371/journal.pone.0209567.t001>

untransformed mean density (± 1 SE) of 18 ± 2 individuals L⁻¹ compared to reservoirs which had 12 ± 1 individuals L⁻¹. The difference in crustacean zooplankton density was driven primarily by more than 3× higher densities of calanoid copepods in natural lakes versus reservoirs, which resulted in more than 2× higher densities of total copepods in natural lakes ($F_{3,726} \geq 8.36$; $P \leq 0.004$; Tables 1 and 2; Fig 2B and 2C; S2 Fig). In contrast to calanoids, cladoceran (Fig 2D), *Daphnia*, and cyclopoid copepod densities did not differ significantly between waterbody types ($P \geq 0.40$). No interaction existed between waterbody type and latitude for any zooplankton density response variable (all $P \geq 0.13$).

Copepods, predominantly calanoids, dominated the large-bodied crustacean zooplankton community in natural lakes (defined by the proportion of each taxon in the crustacean zooplankton community for each waterbody; $F_{3,726} \geq 4.62$; $P \leq 0.03$; Fig 2E), whereas cladocerans dominated in reservoirs ($F_{3,726} = 5.96$; $P = 0.01$). On average, total copepods composed ~5% more, and calanoids composed ~10% more, of the crustacean zooplankton community in natural lakes than in reservoirs (Tables 1 and 2; S2 Fig). The interaction of waterbody type and latitude was significant for the dominance of copepods in the zooplankton community ($P = 0.03$); the differences in copepod dominance between waterbody types became similar at higher latitudes between natural lakes and reservoirs.

Calanoids had higher genera richness in natural lakes than in reservoirs ($F_{3,726} = 2.49$; $P = 0.01$); however, no difference existed in crustacean zooplankton, copepod, cladoceran, or

Table 2. Multiple linear regression model statistics for the effects of waterbody type as an indicator variable (with natural lakes coded as 0 and reservoirs coded as 1), latitude, and the interaction of waterbody type and latitude on zooplankton and other environmental variables.

Response Variable	<i>n</i> _{lakes}	<i>n</i> _{reservoirs}	Intercept parameter ± SE	Waterbody Type		Latitude		Interaction	
				Value ± SE	<i>P</i>	Value ± SE	<i>P</i>	Value ± SE	<i>P</i>
Zooplankton									
ln(crustacean zooplankton density)	301	429	-6.57 ± 1.12	1.69 ± 1.48	0.02	0.18 ± 0.03	< 0.0001	-0.03 ± 0.04	0.37
ln(total copepod density)	301	429	-6.21 ± 1.16	1.57 ± 1.53	0.004	0.15 ± 0.03	< 0.0001	-0.03 ± 0.04	0.34
ln(cyclopoid density)	301	429	-9.32 ± 1.46	3.68 ± 1.92	0.47	0.17 ± 0.03	< 0.0001	-0.07 ± 0.05	0.13
ln(calanoïd density)	301	429	-7.21 ± 1.50	2.48 ± 1.98	< 0.0001	0.15 ± 0.03	< 0.0001	-0.07 ± 0.05	0.14
ln(cladoceran density)	301	429	-10.37 ± 1.36	2.87 ± 1.79	0.40	0.23 ± 0.03	< 0.0001	-0.05 ± 0.04	0.25
ln(<i>Daphnia</i> density)	301	429	-12.72 ± 1.55	1.90 ± 2.04	0.74	0.26 ± 0.04	< 0.0001	-0.02 ± 0.05	0.69
logit(total copepod dominance)	301	429	3.57 ± 0.50	-1.84 ± 0.66	0.03	-0.08 ± 0.01	< 0.0001	0.03 ± 0.02	0.03
logit(cyclopoid dominance)	301	429	-0.78 ± 0.57	0.70 ± 0.76	0.002	-0.01 ± 0.01	0.12	-0.01 ± 0.02	0.50
logit(calanoïd dominance)	301	429	1.74 ± 0.61	-1.01 ± 0.80	< 0.0001	-0.05 ± 0.01	< 0.0001	0.01 ± 0.02	0.60
logit(cladoceran dominance)	301	429	-1.76 ± 0.46	0.70 ± 0.61	0.02	0.04 ± 0.01	< 0.0001	-0.01 ± 0.01	0.52
Total crustacean zooplankton genera richness	301	429	-0.44 ± 0.73	4.23 ± 0.96	0.59	0.11 ± 0.02	< 0.0001	-0.10 ± 0.02	< 0.0001
Total copepod genera richness	301	429	0.66 ± 0.33	1.33 ± 0.43	0.10	0.03 ± 0.01	0.02	-0.03 ± 0.01	0.002
Cyclopoid genera richness	301	429	0.45 ± 0.21	0.54 ± 0.27	0.43	0.01 ± 0.005	0.13	-0.01 ± 0.01	0.07
Calanoïd genera richness	301	429	0.21 ± 0.24	0.79 ± 0.32	0.004	0.02 ± 0.01	0.05	-0.02 ± 0.01	0.007
Cladoceran genera richness	301	429	-1.01 ± 0.58	2.56 ± 0.76	0.86	0.07 ± 0.01	< 0.0001	-0.06 ± 0.02	0.002
Other environmental variables									
Maximum water column temperature	300	425	41.52 ± 1.86	3.04 ± 2.44	< 0.0001	-0.43 ± 0.04	< 0.0001	-0.09 ± 0.06	0.15
Mean water column dissolved oxygen	298	394	4.29 ± 1.07	-3.46 ± 1.42	0.01	0.05 ± 0.02	< 0.0001	0.08 ± 0.03	0.01
pH	301	429	7.61 ± 0.38	-0.72 ± 0.49	0.22	0.01 ± 0.01	0.0006	0.02 ± 0.01	0.13
ln(chlorophyll <i>a</i>)	300	426	6.02 ± 0.79	-1.19 ± 1.04	0.81	-0.09 ± 0.02	< 0.0001	0.02 ± 0.02	0.41
ln(water residence time)	301	429	-2.31 ± 0.61	0.69 ± 0.81	< 0.0001	0.05 ± 0.01	0.001	-0.03 ± 0.02	0.14

Predictor term parameters with their standard error (SE) are provided for each model component. Statistically significant results are highlighted in bold and *n* is the sample size of waterbodies in each analysis. ln() and logit() denote ln-transformations and logit-transformations of certain response variables, respectively.

<https://doi.org/10.1371/journal.pone.0209567.t002>

cyclopoid genera richness between waterbody types ($P \geq 0.10$; Table 1). A significant waterbody and latitude interaction was also present for calanoïd genera richness ($P = 0.007$): calanoïds had higher genera richness in natural lakes vs. reservoirs at higher latitudes ($>38^\circ\text{N}$) and higher genera richness in reservoirs vs. natural lakes at lower latitudes. Although differences in genera richness of calanoïds between natural lakes and reservoirs were relatively small, natural lakes were 2× more likely to have at least two calanoïd genera present compared to reservoirs (Tables 1 and 2; S2 Fig).

Reservoirs, on average, had about half the WRT compared to natural lakes ($F_{3,729} = 52.10$; $P < 0.0001$; 0.8 ± 0.1 years vs. 1.3 ± 0.1 years) and were 2°C warmer than natural lakes across the continental U.S, while controlling for latitude ($F_{3,724} = 44.52$; $P < 0.001$; $24.7 \pm 0.2^\circ\text{C}$ vs. $22.9 \pm 0.2^\circ\text{C}$, respectively; Tables 1 and 2). Although not significantly different, reservoirs had, on average, one-half of the chlorophyll *a* concentration of natural lakes ($P = 0.81$; $23.6 \pm 2.3 \mu\text{g/L}$ vs. $38.6 \pm 5.1 \mu\text{g/L}$). A significant waterbody type and latitude interaction existed for mean DO concentrations ($P = 0.03$); reservoirs had greater mean DO concentrations than natural lakes at higher latitudes ($>40^\circ\text{N}$) and lower mean DO concentrations than natural lakes at lower latitudes (Tables 1 and 2). pH values were similar between waterbody types across the U.S ($P = 0.22$).

Analysis 2: Regression tree analyses of the effects of environmental factors on large-bodied zooplankton densities

Maximum water column temperature and pH were the most important focal environmental variables affecting crustacean zooplankton density when both waterbody types were aggregated across the U.S. (Fig 3; S2 and S3 Tables provide all the regression tree statistics for all response variables for all waterbodies, reservoirs only, and natural lakes only). The highest

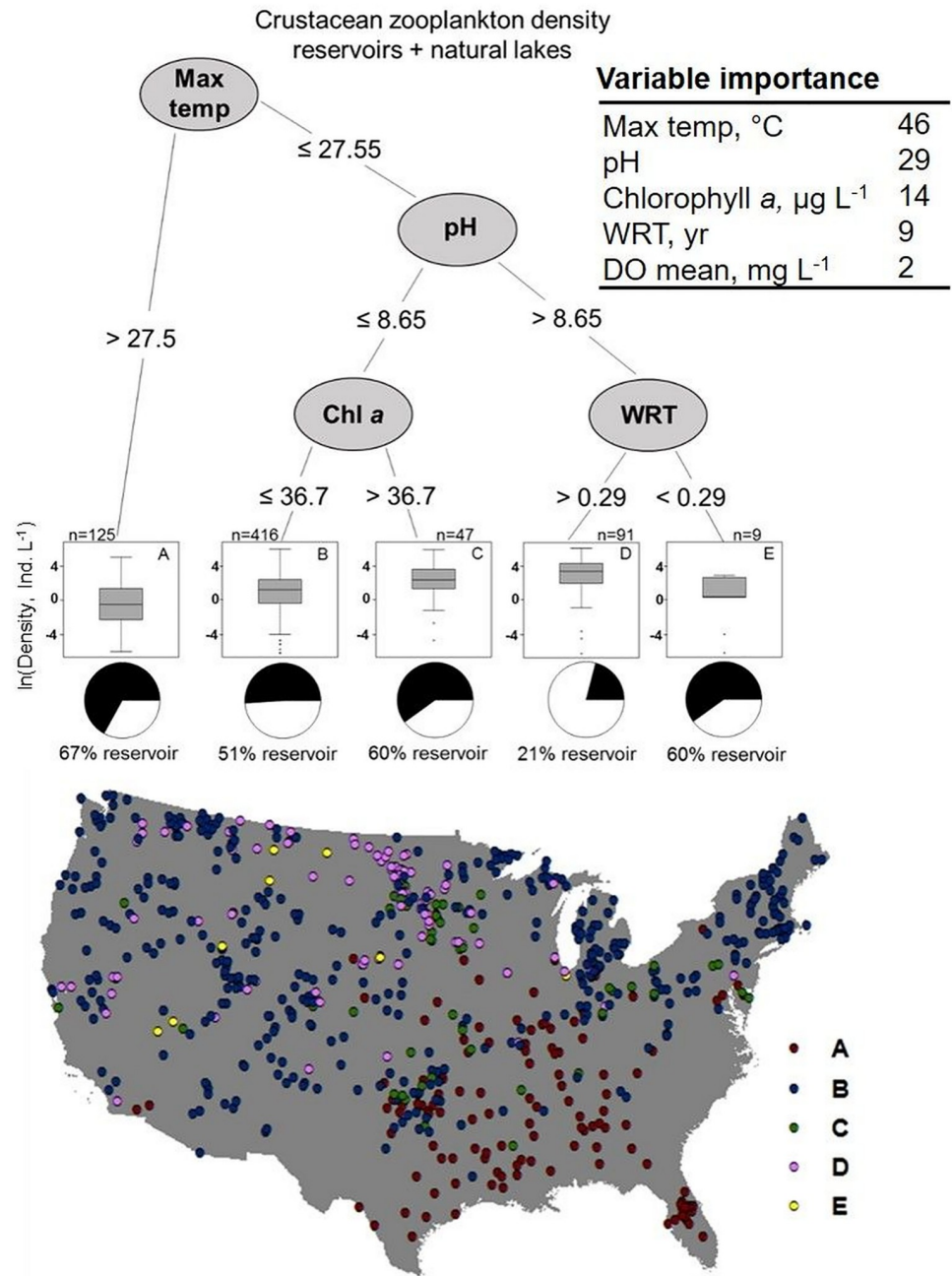


Fig 3. Regression tree analysis for crustacean zooplankton densities aggregated across all waterbodies in the U.S., with the locations of the waterbodies from the regression tree groupings shown with different colors on the map. In the pie charts, white refers to natural lakes and black refers to reservoirs.

<https://doi.org/10.1371/journal.pone.0209567.g003>

crustacean zooplankton densities were found in waterbodies that had less than 27.5 °C maximum water column temperature (the first split in the regression tree), greater than 8.65 pH, and longer WRT (> 0.29 years; Group D in Fig 3). Crustacean zooplankton in these waterbodies had a mean density of 48.7 ± 6.7 zooplankton L^{-1} , which was approximately 2× higher than the mean zooplankton density in waterbodies with lower pH, but higher chlorophyll *a* concentrations (29.2 ± 7.0 zooplankton L^{-1} , Group C in Fig 3). Waterbodies that had the longest WRT and highest crustacean zooplankton densities were predominantly natural lakes (79%) and were spread throughout many regions in the U.S (Group D in Fig 3). Of all waterbodies, those with shorter WRT, despite lower temperatures and higher pH concentrations, had the lowest mean density of crustacean zooplankton (6.0 ± 2.1 zooplankton L^{-1} , Group E). Mean water column DO concentration was the least important focal environmental variable in explaining crustacean zooplankton densities across all waterbodies.

Across all aggregated waterbodies, pH was the first split in the regression tree for calanoid density and thus the most important of the focal environmental variables, with WRT as the second most important variable (Fig 4). Mean calanoid density was highest in waterbodies with higher pH (> 8.7) and longer WRT (> 0.34 yrs; Group D, Fig 4). Regardless of pH, waterbodies with shorter WRT had approximately 9× lower calanoid densities than waterbodies with longer WRT (2.6 ± 0.9 vs. 18.7 ± 3.3 calanoids L^{-1} , respectively). Only 19% of the waterbodies with longer WRT and higher pH were reservoirs (Group C in Fig 4), whereas reservoirs

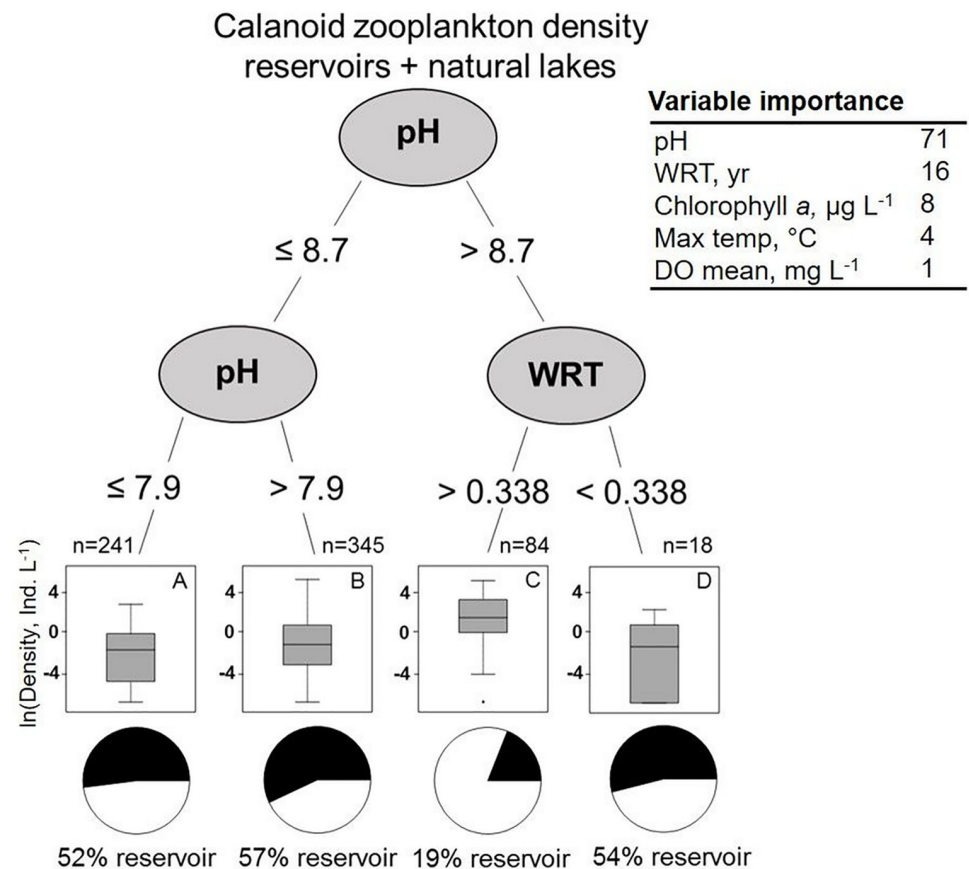


Fig 4. Regression tree analysis for calanoid zooplankton density aggregated across all waterbodies (reservoirs and natural lakes together) in the U.S. In the pie charts, white refers to natural lakes and black refers to reservoirs.

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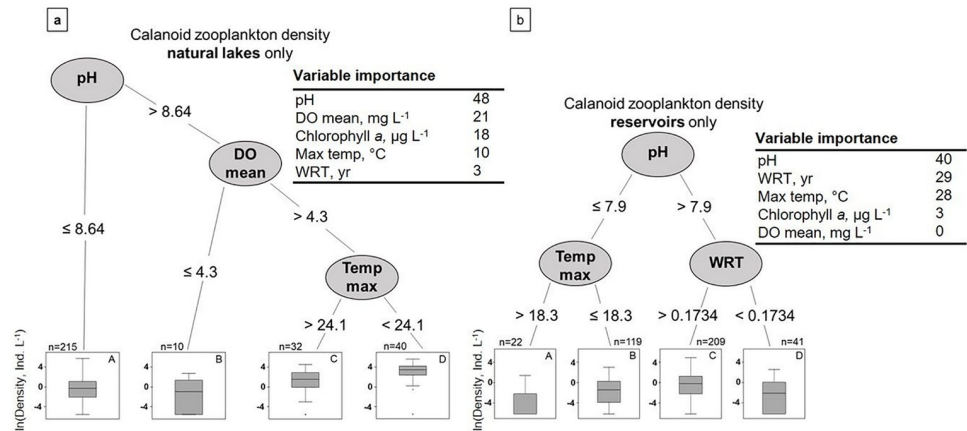


Fig 5. Regression tree analysis for calanoid zooplankton density conducted separately for a) natural lakes and b) reservoirs.

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composed 54% of the shorter WRT waterbodies in Group D. Waterbodies across the regression tree splits for calanoid densities were generally located across multiple regions in the U.S. (S3 Fig).

The separate regression trees for reservoirs and natural lakes highlight that different factors were responsible for driving calanoid density in the two waterbody types (Figs 4 and 5). Specifically, WRT was about 10× more important for calanoid copepods in reservoirs compared to natural lakes likely due to overall shorter WRT in reservoirs (Fig 5; S2 and S3 Tables). In natural lakes, pH, DO, and chlorophyll *a* concentrations were the most important environmental variables for calanoid density, whereas WRT was the least important variable. In comparison, in reservoirs, WRT was the second most important variable behind pH, contributing a similar amount of variance to calanoid copepod density as maximum waterbody temperature. In reservoirs, the highest calanoid densities were in waterbodies that had higher pH (> 7.9) and longer WRT (> 0.17 years; 3.8 ± 0.8 calanoids L⁻¹, Group C in Fig 5B). Despite having higher pH, calanoids in shorter WRT reservoirs had approximately 4× lower densities than calanoids in longer WRT reservoirs (1.1 ± 0.4 calanoids L⁻¹; Fig 5B, Groups C and D). WRT in natural lakes and reservoirs was not as important for cyclopoid or cladoceran density compared to calanoids (S2 and S3 Tables). Regression tree results for *Daphnia* density were similar to results for cladoceran density in all waterbodies, in just natural lakes, and in just reservoirs (S2 and S3 Tables); pH and maximum water column temperature were the most important environmental factors for *Daphnia* density.

Chemical and biological variables (DO, chlorophyll *a*, and pH) were overall more important for zooplankton groups in natural lakes, whereas physical variables were more important for zooplankton in reservoirs (maximum water temperature and WRT; Fig 5; S3 Table).

Analysis 3: Relationships between reservoir primary purpose, environmental factors, and large-bodied zooplankton densities

Total crustacean zooplankton, total copepod, calanoid, and cladoceran densities were significantly different across reservoirs used for different primary purposes ($F_{4,298} \geq 3.43$; $P \leq 0.009$; Fig 6). On average, total crustacean zooplankton densities were about 4× lower in hydroelectric reservoirs (mean 3.1 ± 1.1 zooplankton L⁻¹) than in reservoirs primarily used for irrigation (14.0 ± 3.0 zooplankton L⁻¹; $P < 0.0001$) or recreation (14.2 ± 4.8 zooplankton L⁻¹; $P = 0.001$), and half as low as in reservoirs primarily used for flood control and water supply (7.7 ± 1.6 and

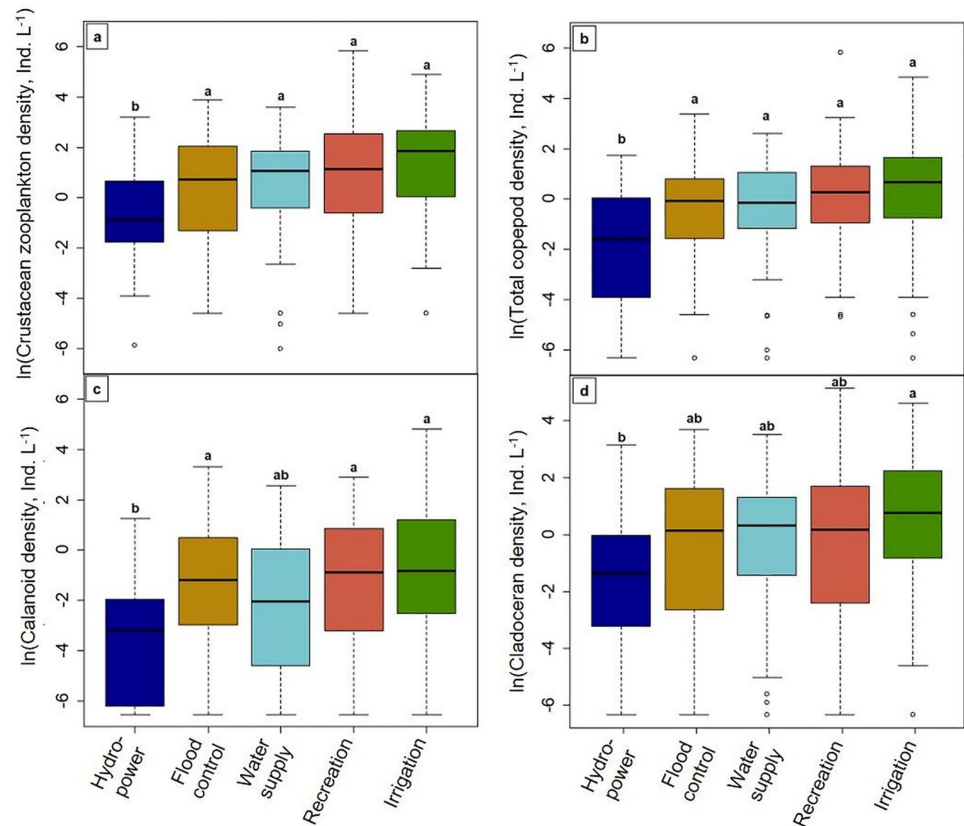


Fig 6. Relationships between reservoir primary purpose and a) total crustacean zooplankton, b) total copepods, c) calanoids, and d) cladocerans. Letters above each boxplot denote statistical differences of zooplankton among reservoir primary purpose.

<https://doi.org/10.1371/journal.pone.0209567.g006>

5.9 ± 1.0 zooplankton L^{-1} , respectively; $P \leq 0.03$; Fig 6A). Total copepod (Fig 6B) and calanoid densities (Fig 6C) were about an order of magnitude lower in hydroelectric reservoirs (0.8 ± 0.2 and 0.4 ± 0.1 individuals L^{-1} , respectively) than reservoirs primarily used for irrigation (5.7 ± 2.0 copepods L^{-1} and 4.0 ± 1.9 calanoids L^{-1}) and recreation (7.1 ± 4.2 copepods L^{-1} and 1.6 ± 0.3 calanoids L^{-1} ; all $P \leq 0.007$). Cladoceran density in hydroelectric reservoirs was only significantly lower than in reservoirs used for irrigation (Fig 6D), and *Daphnia* density was only significantly lower in reservoirs used for recreation than reservoirs used for irrigation ($F_{4,298} = 3.11$; $P = 0.02$).

WRT varied significantly across reservoirs with different primary purposes ($F_{4,298} = 5.32$, $P = 0.0004$; Table 3). WRT was approximately 2× shorter in reservoirs used for hydroelectric power, flood control, or recreation than reservoirs used primarily for irrigation (all $P \leq 0.008$). Water supply reservoirs had intermediate WRT (Table 3). Maximum water column temperature was significantly different across reservoirs with different purposes ($F_{4,295} = 15.35$; $P < 0.0001$; Table 3), with reservoirs used primarily for irrigation having lower temperatures than reservoirs used for recreation, flood control, or water supply (all $P \leq 0.01$). Chlorophyll *a* was also significantly lower in reservoirs primarily used for irrigation or hydroelectric power than reservoirs used for recreation ($F_{4,296} = 4.47$; $P = 0.002$). Reservoirs used for irrigation had a greater mean water column DO than reservoirs used primarily for recreation or flood control ($F_{4,269} = 3.73$; $P = 0.006$). No significant difference in pH across reservoir purposes was observed ($P = 0.24$).

Table 3. Mean values (± 1 SE) for the focal environmental variables across reservoirs of different primary purposes, ordered by their WRT.

Primary purpose	N	WRT (years)	Maximum water temperature ($^{\circ}$ C)	Mean DO (mg L^{-1})	pH	Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)
Recreation	83	0.50 \pm 0.05 (b)	26.1 \pm 0.4 (a)	5.6 \pm 0.3 (b)	7.9 \pm 0.09 (a)	37.8 \pm 8.0 (a)
Flood control	67	0.55 \pm 0.07 (b)	25.8 \pm 0.3 (ab)	5.5 \pm 0.2 (b)	8.0 \pm 0.06 (a)	20.1 \pm 3.4 (ab)
Hydropower	31	0.64 \pm 0.13 (b)	23.5 \pm 1.0 (bc)	6.2 \pm 0.4 (ab)	7.9 \pm 0.09 (a)	10.8 \pm 2.5 (b)
Water supply	58	0.70 \pm 0.10 (ab)	24.7 \pm 0.7 (ab)	5.9 \pm 0.3 (ab)	7.9 \pm 0.08 (a)	15.8 \pm 2.7 (ab)
Irrigation	64	1.2 \pm 0.17 (a)	21.5 \pm 0.4 (c)	6.8 \pm 0.3 (a)	8.1 \pm 0.07 (a)	20.1 \pm 6.2 (b)

Letters denote statistical differences across different reservoir purposes based on one-way ANOVA with post-hoc Tukey pairwise comparisons. *N* refers to the sample size of each reservoir purpose.

<https://doi.org/10.1371/journal.pone.0209567.t003>

Discussion

While many studies have quantified how many physical, chemical, and biological factors affect zooplankton community structure, results from our study highlight the role of waterbody type in driving large-bodied crustacean zooplankton (retained in mesh size > 0.243 mm) communities across the continental U.S. Overall, we found natural lakes to have significantly greater density and dominance by copepods, especially calanoid copepods. Calanoids were also more likely to have multiple genera present in natural lakes compared to reservoirs.

Calanoid copepods were responsible for most crustacean zooplankton density differences between waterbody types when also accounting for latitude. Shorter WRT in reservoirs compared to natural lakes may be a major factor explaining waterbody type differences in calanoid communities [20, 22, 48]. According to the regression tree analysis, we observed the highest calanoid and crustacean zooplankton densities in waterbodies that had longer WRT and higher pH, of which most (~80%) were natural lakes (Figs 3 and 4). In contrast, calanoid and total crustacean zooplankton densities were about 3 and 9 \times lower, respectively, in waterbodies that also had high pH, but shorter WRT. Many calanoid taxa may be particularly influenced by shorter WRT because individuals within these groups take longer to reach reproductive maturity, and exhibit fewer seasonal peaks in the density of egg-bearing females than cyclopoid copepods and cladocerans during a summer season [1, 26, 27].

The significance of WRT and calanoid copepod density is highlighted by the WRT values in the regression tree analyses (0.17 to 0.34 years) that result in decreased calanoid copepod density. Calanoid copepod taxa exhibit a large range in the duration of time for individuals to reach reproductive maturity. For example, smaller calanoids such as *Diaptomus* and *Epischura* can reach reproductive maturity within a few months, whereas larger calanoids such as *Limnocalanus* and *Senecella* can take 6–8 months [28, 64, 65]. Therefore, the exact threshold value of WRT (0.17 years in reservoirs, or ~2 months) may be a signal of the overall calanoid community composition in the U.S. Conversely, shorter WRT does not appear to have much effect on faster-growing Cladocera, such as *Daphnia*, which can grow and reach reproductive maturity within days [26]. Shorter WRT can also affect many other waterbody environmental conditions, such as chlorophyll *a* concentrations, which may indirectly affect zooplankton (in addition to the direct effect of physically flushing zooplankton out of a waterbody). However, previous studies have found that WRT has little effect on overall primary productivity because chlorophyll *a* is able to increase quickly after disturbance [48, 66]. Therefore, the direct and indirect effects of WRT are likely to negatively influence calanoid copepods more than cladocerans because cladocerans are overall more herbivorous than calanoids.

Other factors, such as chlorophyll *a*, likely play a role in zooplankton community differences among waterbody types [45, 67]. Calanoids often dominate zooplankton communities

in more oligotrophic systems [68–70]; however, reservoirs were more oligotrophic than natural lakes in the 2007 NLA dataset (Table 1), indicating that other environmental factors, such as shorter WRT, may be more important in driving the calanoid community than chlorophyll *a* concentrations in reservoirs.

Crustacean zooplankton density across all waterbodies was most strongly affected by maximum waterbody temperature, with decreased densities when maximum waterbody temperatures exceeded 27.5°C, likely because temperatures reaching 25–30°C are detrimental to crustacean zooplankton growth and survival in temperate waterbodies [71, 72]. Many high maximum temperature waterbodies were in warmer regions in the U.S., such as the Southeast and Central Plains, and two-thirds of these waterbodies were reservoirs (Fig 3). Other studies have observed decreased zooplankton densities in waterbodies in warmer regions in the U.S., predominantly of cladocerans [38, 73]. Cladocerans, exemplified by *Daphnia*, were most affected by maximum water column temperature compared to other zooplankton taxa (S2 Table; S4 Fig), indicating a possible lower thermal tolerance for cladocerans compared to copepods in temperate waterbodies [74]. Hence, higher water temperatures may be another reason for lower overall crustacean zooplankton densities in reservoirs, which is likely a result of the latitudinal distribution of natural lakes and reservoirs across the U.S. (Fig 1). In addition, pH was often an important variable for zooplankton density across analyses. Crustacean zooplankton densities were lower in waterbodies with pH less than ~7.8–8.7; as pH decreases, zooplankton growth and survival is constrained by increased stress to lower pH values, which overall lowers the density of zooplankton [75–77].

Maximum water column temperature or waterbody depth differences between reservoirs and natural lakes may have contributed to the lower number of calanoid genera generally present in reservoirs compared to natural lakes. Waterbody maximum depth is positively related to species richness because deeper waterbodies have more niches [78–80]; however, maximum waterbody depth was similar between natural lakes and reservoirs in the NLA (10.5 ± 13.0 m (1 S.D.) and 9.7 ± 9.9 m, respectively). Waterbody age differences between reservoirs and natural lakes may have also played a role in the richness differences. Younger, more geographically isolated reservoirs may have experienced lower rates of zooplankton dispersal, and thus fewer sexual-reproducing calanoid genera present than older natural lakes [27]. However, previous studies have found no significant relationship between reservoir age and zooplankton richness [23, 81], and we were not able to quantify the effect of age versus other environmental factors on calanoid genera richness with the 2007 NLA data.

The relative importance of environmental factors on zooplankton densities differed between natural lakes and reservoirs. In general, the focal physical variables (maximum water column temperature and WRT) were more important for zooplankton densities in reservoirs compared to natural lakes, whereas the focal chemical and biological factors were overall more important for zooplankton in natural lakes. Reservoirs are generally more common in warmer regions in the U.S. (Fig 1) [14, 82], and those constructed by damming lotic ecosystems are more greatly affected by WRT than natural lakes [20, 22, 48]; therefore, the greater relative importance of physical variables for zooplankton in reservoirs is not surprising. In contrast, because natural lakes generally have lower discharge rates and longer WRT [18], physical variables in natural lakes may be less important in structuring zooplankton communities compared to reservoirs. Subsequently, chemical and biological factors may be more important overall for zooplankton communities in natural lakes at single snapshots in time.

Reservoir WRT was significantly different across reservoirs of different primary purposes. Recreation, hydroelectric, and flood control reservoirs had half the WRT, on average, of reservoirs used for irrigation, which likely is related to differences in reservoir management operations. For example, hydroelectric reservoirs may have shorter WRT to meet electrical power

demands [83, 84], and flood control reservoirs may have shorter WRT because of the need to quickly store and release water levels in response to weather [85, 86]. Reservoirs used primarily for irrigation or water supply may be more likely, on average, to have longer WRT, because of the importance to maintain water levels for drinking water and irrigation.

Our results suggest that zooplankton densities differed between reservoirs of different primary purposes as a result of differences in WRT: hydroelectric reservoirs (with shorter WRT) had the lowest zooplankton densities and irrigation reservoirs (with longer WRT) had the greatest zooplankton densities. Total copepod and calanoid zooplankton densities were especially lower in hydroelectric reservoirs versus most other reservoir purposes (Fig 6), with densities typically <1 individual L^{-1} . High discharge reservoir purposes, such as hydroelectric reservoirs, may flush many of these taxa from the system before they become adults. Other factors certainly also play a role in these density differences across reservoirs of different purposes, as many other environmental factors varied across reservoir purposes. For example, chlorophyll *a* was lower in hydroelectric reservoirs versus some other reservoir types, which can result in lower zooplankton densities [2, 38, 66]. However, chlorophyll *a* was also lower in reservoirs used for irrigation, which had the greatest crustacean zooplankton densities. Overall, our results suggested that reservoir purpose likely affects multiple environmental factors, which in turn can indirectly alter zooplankton densities and community structure.

The EPA's NLA had excellent spatial coverage of waterbodies. However, one limitation of our work is that most lakes and reservoirs were sampled only once and thus each zooplankton sample represents a single "snapshot" of the system. Consequently, other important factors such as plankton succession [70, 87, 88], top-down control by fish [89, 90], and interactions among multiple variables, were not considered in our analyses. The fish community present in a waterbody can have a large impact on zooplankton dynamics [91–93], which likely played a role in the waterbody type differences in zooplankton densities found in this study. We also did not consider effects of elevation differences between waterbody types on crustacean zooplankton communities, which could impact our results [94]; however, the elevational difference between natural lakes and reservoirs was relatively similar in waterbodies in this study (natural lakes: 580 ± 650 m (1 S.D.); reservoirs: 740 ± 777 m). Lastly, we acknowledge that the vertical tow mesh size (0.243 mm) used in the waterbodies in the 2007 NLA may be large enough to miss smaller crustacean zooplankton taxa, especially in warmer regions of the U.S. Also, shorter WRT systems may contain smaller-bodied zooplankton that are removed from the system more quickly and are subsequently not able to reach as large of body sizes as in longer WRT systems [48, 66]. Therefore, we emphasize that our results are limited to crustacean zooplankton taxa retained by the 243-mm mesh. However, because calanoid taxa are generally much larger than many cladoceran taxa [1, 64], and juvenile and adult calanoids are larger (e.g., >0.5 – 1 mm in length) than the mesh size used in sampling, the overall result that calanoid density was greater in natural lakes than in reservoirs is supported. Furthermore, by including the larger-bodied cladoceran *Daphnia* in analyses, we were still able to compare calanoid copepods with one cladoceran taxa that was likely minimally affected by the sampling methods.

This study constitutes one of the most comprehensive spatial datasets for the analysis of zooplankton, spanning more than 700 waterbodies in the U.S. Altogether, our findings indicated differences in zooplankton community structure between natural lakes and reservoirs. Our results also indicated that the relative importance of environmental drivers on zooplankton communities varied between reservoirs and natural lakes. Such zooplankton community and density differences may in turn alter freshwater food webs and water quality [4, 5–7]. As the construction of reservoirs for many different human purposes increases in many regions

of the world [83, 95], so does the need to better understand the resulting consequences of reservoir characteristics on plankton community dynamics, food webs, and water quality.

Supporting information

S1 Table. Pearson product-moment correlations of focal environmental variables included in the analyses. “NS” refers to relationships that are not significant and “.” refers to empty cells. The focal environmental variables included in our analyses were: Temp max = maximum waterbody temperature ($^{\circ}\text{C}$), DO mean = mean water column dissolved oxygen concentration (mg L^{-1}), Chlorophyll *a* = chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), and WRT = water residence time (years). Also included are other environmental variables not included in our analyses because of correlations with $r > 0.50$ with the focal environmental variables: Max depth = maximum waterbody depth (m), Calcium = calcium concentration (mg L^{-1}), and DOC = dissolved organic carbon concentration (mg L^{-1}).
(DOCX)

S2 Table. Regression tree statistics for crustacean, total copepod, calanoid, and cladoceran density for all waterbodies, for just natural lakes, and for just reservoirs in the continental U.S. Reported for each regression analysis is each individual leaf group, *N* for each leaf, each leaf's response variable mean \pm SE, and the description for node splits for each leaf group. The percentage of the waterbodies that consist of reservoirs are provided for each leaf split, for analyses across both natural lakes and reservoirs.
(DOCX)

S3 Table. The variable importance of the focal environmental variables provided for all regression analyses. All refers to aggregated analyses with both natural lakes and reservoirs. Temp max = maximum waterbody temperature ($^{\circ}\text{C}$), DO mean = mean water column dissolved oxygen concentration (mg L^{-1}), Chlorophyll *a* = chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), and WRT = water residence time (years).
(DOCX)

S1 Fig. Location of reservoirs with different primary purposes across the U.S. Primary purpose was obtained for all reservoirs with available data from the U.S. Army Corps of Engineers' National Inventory of Dams database. $N > 20$ for each of these categories.
(TIF)

S2 Fig. Comparisons of a) crustacean zooplankton (copepod + cladoceran), b) total copepod (cyclopoid + calanoid), c) calanoid, and d) cladoceran, and e) crustacean zooplankton genera richness between natural lakes and reservoirs across the U.S.
(TIF)

S3 Fig. Locations of the regression analysis splits for calanoid zooplankton density across both natural lakes and reservoirs ($N = 688$). A refers to waterbodies that have $\text{pH} \leq 7.9$; B refers to waterbodies with $\text{pH} > 7.9$ but ≤ 8.7 ; C refers to waterbodies with $\text{pH} > 8.7$ and water residence times > 0.338 years; D refers to waterbodies with $\text{pH} > 8.7$ and water residence times < 0.338 years.
(TIF)

S4 Fig. Locations of the regression analysis splits for cladoceran zooplankton density across both natural lakes and reservoirs ($N = 688$). A refers to waterbodies that have maximum temperatures > 27.5 $^{\circ}\text{C}$; B refers to waterbodies with maximum temperature < 27.5 $^{\circ}\text{C}$ and $\text{pH} < 8.38$; C refers to waterbodies with maximum temperature < 27.5 $^{\circ}\text{C}$, $\text{pH} > 8.38$, and

water residence times > 0.177 years; D refers to waterbodies with maximum temperature < 27.5 °C, pH > 8.38, and water residence times < 0.177 years. (TIF)

Acknowledgments

We thank the University of Vermont for hosting a research workshop for this work. We thank Zach Gajewski for help in analyzing the NID, and the EPA for making their NLA dataset available to the public. The views expressed in this article are those of the authors and do not necessarily represent the views or policies of the U.S. Environmental Protection Agency.

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References

1. Downing JA, Rigler FH. Manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific Publications, Oxford, UK; 1984.
2. Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, et al. Regulation of lake primary productivity by food web structure. *Ecology*. 1987; 68: 1863–1876. <https://doi.org/10.2307/1939878> PMID: 29357166
3. Pace ML, Cole JJ, Carpenter SR, Kitchell JF, Hodgson JR, Van de Bogert MC, et al. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature*. 2004; 427: 240–243. <https://doi.org/10.1038/nature02227> PMID: 14724637
4. Søndergaard M, Jeppesen E, Jensen JP, Amsinck SL. Water Framework Directive: ecological classification of Danish lakes. *J Appl Ecol*. 2005; 42: 616–629.
5. Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T. Response of fish and plankton to nutrient loading reduction in 8 shallow Danish lakes with special emphasis on seasonal dynamics. *Freshwater Biol*. 2005; 50: 1616–1627.
6. Jeppesen E, Kronvang B, Meerhoff M, Søndergaard M, Hansen KM, Andersen HE, et al. Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. *J Environ Qual*. 2009; 38: 1030–1041.
7. Jeppesen E, Noges P, Davidson TA, Haberman J, Noges T, Blank K, et al. Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). *Hydrobiologia*. 2011; 676: 279–297.
8. Jones RI, Grey J, Sleep D, Arvola L. Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos*. 1999; 86: 97–104.
9. Bastviken D, Ejlertsson J, Sundh I, Tranvik L. Methane as a source of carbon and energy for lake pelagic food webs. *Ecology*. 2003; 84: 969–981.
10. Cole JJ, Carpenter SR, Kitchell J, Pace ML, Solomon CT, Weidel B. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proc Natl Acad Sci USA*. 2011; 108: 1975–1980. <https://doi.org/10.1073/pnas.1012807108> PMID: 21245299
11. Kelly PT, Solomon CT, Weidel BC, Jones SE. Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. *Ecology*. 2014; 95: 1236–1242. PMID: 25000755
12. Vanni MJ, Findlay DL. Trophic cascades and phytoplankton community structure. *Ecology*. 1990; 71: 921–937.

13. Jones JR, Bachmann RW. Trophic status of Iowa lakes in relation to origin and glacial geology. *Hydrobiologia*. 1978; 57: 267–273.
14. Thornton KW. Perspectives on Reservoir Limnology. In: Thornton KW, Kimmel BL, Payne FE, editors. *Reservoir limnology: ecological perspectives*. New York (NY): John Wiley and Sons Inc.; 1990. pp. 1–14.
15. Whittier TR, Larsen DP, Peterson SA, Kincaid TM. A comparison of impoundments and natural drainage lakes in the Northeast USA. *Hydrobiologia*. 2002; 470: 157–171.
16. Bernot RJ, Dodds WK, Quist MC, Guy CS. Spatial and temporal variability of zooplankton in a great plains reservoir. *Hydrobiologia*. 2004; 525: 101–112.
17. Thornton, KW, Kennedy RH, Carroll JH, Walker WW, Gunkel RC, Ashby S. Reservoir sedimentation and water quality—an heuristic model. In *Proceedings of the Symposium on Surface Water Impoundments*, American Society of Civil Engineers, Minneapolis; 1981. pp. 654–661.
18. Wetzel RG. Reservoir ecosystems: conclusions and speculations. In: Thornton KW, Kimmel BL, Payne FE, editors. *Reservoir limnology: ecological perspectives*. New York (NY): John Wiley and Sons Inc.; 1990. pp. 227–238.
19. Campbell CE, Knoechel R, Copeman D. Evaluation of factors related to increased zooplankton biomass and altered species composition following impoundment of a Newfoundland reservoir. *Can J Fish Aquat Sci*. 1998; 55: 230–238.
20. Lehman JT, Platte RA, Ferris JA. Role of hydrology in development of a vernal clear water phase in an urban impoundment. *Freshwater Biol*. 2007; 52: 1773–1781.
21. Beaver JR, Jensen DE, Casamatta DA, Tausz CE, Scotese KC, Buccier KM, et al. Response of phytoplankton and zooplankton communities in six reservoirs of the middle Missouri River (USA) to drought conditions and a major flood event. *Hydrobiologia*. 2013; 705: 173–189.
22. Silva LHS, Huszar VLM, Marinho MM, Rangel LM, Brasil J, Domingues CD, et al. Drivers of phytoplankton, bacterioplankton, and zooplankton carbon biomass in tropical hydroelectric reservoirs. *Limnologia*. 2014; 48: 1–10.
23. Merrix-Jones FA, Thackeray SJ, Ormerod SJ. A global analysis of zooplankton in natural and artificial fresh waters. *J Limnol*. 2013; 72: 140–153.
24. Simões NR, Nunes AH, Dias JD, Lansac-Tôha FA, Velho LM, Bonecker CC. Impact of reservoirs on zooplankton diversity and implications for the conservation of natural aquatic environments. *Hydrobiologia*. 2015; 758: 3–17.
25. Andradóttir HÓ, Rueda FJ, Armengol J, Marcé R. Characterization of residence time variability in a managed monomictic reservoir. *Water Resour Res*. 2012; 48: <https://doi.org/10.1029/2012WR012069>
26. Allan JD. Life history patterns in zooplankton. *Am Nat*. 1976; 110: 165–180.
27. Kramer AM, Sarnelle O, Knapp RA. Allee effect limits colonization success of sexually reproducing zooplankton. *Ecology*. 2008; 89: 2760–2769. PMID: [18959313](https://pubmed.ncbi.nlm.nih.gov/18959313/)
28. Doubek JP, Lehman JT. Historical biomass of *Limnocalanus* in Lake Michigan. *J Great Lakes Res*. 2011; 37: 159–164.
29. Beaulieu M, Pick F, Gregory-Eaves I. Nutrients and water temperature are significant predictors of cyanobacterial biomass in a 1147 lakes data set. *Limnol Oceanogr*. 2013; 58: 1736–1746.
30. Beaver JR, Manis EE, Loftin KA, Graham JL, Pollard AI, Mitchell RM. Land use patterns, ecoregion, and microcystin relationships in U.S. lakes and reservoirs: a preliminary evaluation. *Harmful Algae*. 2014; 36: 57–62.
31. Rigosi A, Carey CC, Ibelings BW, Brookes JD. The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic status and varies among taxa. *Limnol Oceanogr*. 2014; 59: 99–114.
32. Yuan LL, Pollard AI. Classifying lakes to improve precision of nutrient-chlorophyll relationships. *Freshw Sci*. 2014; 33: 1184–1194.
33. Yuan LL, Pollard AI, Pather S, Oliver JL, D'Anglada L. Managing microcystin: identifying national-scale thresholds for total nitrogen and chlorophyll *a*. *Freshwater Biol*. 2014; 59: 1970–1981.
34. Doubek JP, Carey CC, Cardinale BJ. Anthropogenic land use is associated with N-fixing cyanobacterial dominance in lakes across the continental United States. *Aquat Sci*. 2015; 77: 681–694.
35. U.S. EPA. National lakes assessment: a collaborative survey of the nation's lakes. United States Environmental Protection Agency. US Environmental Protection Agency, Office of Water and Office of Research and Development, Washington, DC. EPA 841-R-09-001; 2009.
36. Peck DV, Olsen AR, Weber MH, Paulsen SG. Survey design and extent estimates for the National Lakes Assessment. *Freshw Sci*. 2013; 32: 1231–1245.

37. Gillooly JF, Dodson SI. Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocerans. *Limnol Oceanogr.* 2000; 45: 22–30.
38. Havens KE, Beaver JR. Composition, size, and biomass of zooplankton in large productive Florida lakes. *Hydrobiologia.* 2011; 668: 49–60.
39. Beaver JR, Tausz CE, Renicker TR, Holdren GC, Hosler DM, Manis EE, et al. The late summer crustacean zooplankton in western U.S.A. reservoirs reflects ecoregion, temperature and latitude. *Freshwater Biol.* 2014; 59: 1173–1186.
40. Vanderploeg HA, Ludsin SA, Cavaletto JF, Hook TO, Pothoven SA, Brandt SB, et al. Hypoxic zones as habitat for zooplankton in Lake Erie: refuges from predation or exclusion zones? *J Exp Mar Biol Ecol.* 2009; 381: S108–S120.
41. Vanderploeg HA, Ludsin SA, Ruberg SA, Hook TO, Pothoven SA, Brandt SB, et al. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *J Exp Mar Biol Ecol.* 2009; 381: S92–S107.
42. Confer JL, Kaaret T, Likens GE. Zooplankton diversity and biomass in recently acidified lakes. *Can J Fish Aquat Sci.* 1983; 40: 36–42.
43. Waervagen SB, Rukke NA, Hessen DO. Calcium content of crustacean zooplankton and its potential role in species distribution. *Freshwater Biol.* 2002; 47: 1866–1878.
44. Jeziorski A, Tanentzap AJ, Yan ND, Paterson AM, Palmer ME, Korosi JB, et al. The jellification of north temperate lakes. *Proc Roy Soc B.* 2015; 282: 20142449.
45. Dodson SI, Arnott SE, Cottingham KL. The relationship in lake communities between primary productivity and species richness. *Ecology.* 2000; 81: 2662–2679.
46. Chase JM, Ryberg WA. Connectivity, scale dependence, and the productivity-diversity relationship. *Ecol Lett.* 2004; 7: 676–683.
47. Hoffmann MD, Dodson SI. Land use, primary productivity and lake areas as descriptors of zooplankton diversity. *Ecology.* 2005; 86: 255–261.
48. Obertegger U, Flaim G, Braioni MG, Sommaruga R, Corradini F, Borsato A. Water residence time as a driving force of zooplankton structure and succession. *Aquat Sci.* 2007; 69: 575–583.
49. Brooks JR, Gibson JJ, Birks SJ, Weber MH, Rodecap KD, Stoddard JL. Stable isotope estimates of evaporation: inflow and water residence time for lakes across the United States as a tool for national lake water quality assessments. *Limnol Oceanogr.* 2014; 59: 2150–2165.
50. Johnson RK, Wiederholm T. Classification and ordination of profundal macroinvertebrate communities in nutrient poor, oligo-mesohumic lakes in relation to environmental data. *Freshwater Biol.* 1989; 21: 375–386.
51. Larsen J, Birks HJB, Raddum GG, Fjellheim A. Quantitative relationships of invertebrates to pH in Norwegian river systems. *Hydrobiologia.* 1996; 328: 57–74.
52. Griffith MB, Kaufmann PR, Herlihy AT, Hill BH. Analysis of macroinvertebrate assemblages in relation to environmental gradients in rocky mountain streams. *Ecol Appl.* 2001; 11: 489–505.
53. Abell JM, Ozkundakci D, Hamilton DP, Jones JR. Latitudinal variation in nutrient stoichiometry and chlorophyll-nutrient relationships in lakes: a global study. *Fund Appl Limnol.* 2012; 181: 1–14.
54. Winslow LA, Read JS, Hanson PC, Stanley EH. Lake shoreline in the contiguous United States: quantity, distribution, and sensitivity to observation resolution. *Freshwater Biol.* 2014; 59: 213–223.
55. Doubek JP, Carey CC. Catchment, morphometric, and water quality characteristics differ between reservoirs and naturally formed lakes on a latitudinal gradient in the conterminous United States. *Inland Waters.* 2017; 7: 171–180.
56. Kutner M, Nachtsheim C, Neter J, Li W. *Applied linear statistical models.* 5th ed. New York (NY): McGraw-Hill; 2005.
57. Quinn GP, Keough MJ. *Experimental design and data analysis for biologists.* Cambridge University Press, Cambridge, UK; 2002.
58. De'ath G, Fabricius KE. Classification and regression trees: a powerful yet simple technique for the analysis of complex ecological data. *Ecology.* 2000; 81: 3178–3192.
59. De'ath G. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology.* 2002; 83: 1105–1117.
60. McCune B, Grace JB. *Analysis of ecological communities.* MjM Software, Gleneden Beach, Oregon, USA; 2002.
61. O'Reilly CM, Sharma S, Gray DK, Hampton SE, Read JS, Rowley RJ, et al. Rapid and highly variable warming of lake surface waters around the globe. *Geophys Res Lett.* 2015; 42: 10773–10781.

62. R Development Core Team. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; 2016.
63. Warton DI, Hui FKC. The arcsine is asinine: the analysis of proportions in ecology. *Ecology*. 2011; 92: 3–10. PMID: [21560670](https://pubmed.ncbi.nlm.nih.gov/21560670/)
64. Balcer MD, Korda NL, Dodson SI. Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species. The University of Wisconsin Press, Madison, WI; 1984.
65. Cole GA. Some calanoid copepods from Arizona with notes on congeneric occurrences of *Diatomus* species. *Limnol. Oceanogr.* 1961; 6: 432–442.
66. Bum BK, Pick FR. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. *Limnol. Oceanogr.* 1996; 41: 1572–1577.
67. Hall SR, Pauliukonis NK, Mills EL, Rudstam LG, Schneider CP, Lary SJ, et al. A comparison of total phosphorus, chlorophyll *a*, and zooplankton in embayment, nearshore, and offshore habitats of Lake Ontario. *J Great Lakes Res.* 2003; 29: 54–69.
68. Richman S, Dodson SI. The effect of food quality on feeding and respiration by *Daphnia* and *Diatomus*. *Limnol Oceanogr.* 1983; 28: 948–956.
69. Pinto-Coelho R, Pinel-Alloul B, Méthot G, Havens KE. Crustacean zooplankton in lakes and reservoirs of temperate and tropical regions: variation with trophic status. *Can J Fish Aquat Sci.* 2005; 62: 348–361.
70. Straile D. Zooplankton biomass dynamics in oligotrophic versus eutrophic conditions: a test of the PEG model. *Freshwater Biol.* 2015; 60: 174–183.
71. Moore MV, Folt CL, Stemberger SR. Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. *Arch. Hydrobiol.* 1996; 135: 289–319.
72. Williamson CE, Grad G, De Lange HJ, Gilroy S, Karapelou DM. Temperature-dependent ultraviolet responses in zooplankton: implications of climate change. *Limnol. Oceanogr.* 2002; 47: 1844–1848.
73. Blancher EC II. Zooplankton-trophic state relationships in some north and central Florida Lakes. *Hydrobiologia.* 1984; 109: 251–263.
74. Helland IP, Freyhof J, Kasprzak P, Mehner T. Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake. *Oecologia* 2007; 151: 322–330.
75. Havens KE, Yan ND, Keller W. Lake acidification: effects on crustacean zooplankton populations. *Environ. Sci. Technol.* 1993; 27: 1621–1624.
76. Sprules WG. Midsummer crustacean zooplankton communities in acid-stressed lakes. *J. Fish. Res. Board Can.* 1975; 32: 389–395.
77. Yan ND, Girard R, Boudreau S. An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. *Ecol. Lett.* 2002; 5: 481–485.
78. Dodson SI. Predicting crustacean zooplankton species richness. *Limnol Oceanogr.* 1992; 37: 848–856.
79. O'Brien WJ, Barfield M, Bettez ND, Gettel GM, Hershey AE, McDonald ME, et al. Physical, chemical, and biotic effects on arctic zooplankton communities and diversity. *Limnol Oceanogr.* 2004; 49: 1250–1261.
80. Amsinck SL, Strzelczak A, Bjerring R, Landkildehus F, Lauridsen T, Christoffersen K, et al. Lake depth rather than fish planktivory determines cladoceran community structure in Faroese lakes—evidence from contemporary data and sediments. *Freshwater Biol.* 2006; 51: 2124–2142.
81. Dodson SI, Everhart WR, Jandl AK, Krauskopf SJ. Effects of watershed land use and lake age on zooplankton species richness. *Hydrobiologia.* 2007; 579: 393–399.
82. Canfield DE Jr, Bachmann RW. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. *Can J Fish Aquat Sci.* 1981; 38: 414–423.
83. Rosenberg DM, McCully P, Pringle CM. Global-scale environmental effects of hydrological alterations: introduction. *BioScience.* 2000; 50: 746–751.
84. Ray MR, Sarma AK. Minimizing diurnal variation of downstream flow in hydroelectric projects to reduce environmental impact. *J Hydro-Environ Res.* 2011; 5: 177–185.
85. Chou FNF, Wu CW. Stage-wise optimizing operating rules for flood control in a multi-purpose reservoir. *J Hydrol.* 2015; 521: 245–260.
86. Zhang W, Liu P, Chen XZ, Wang L, Ai XS, Feng MY, et al. Optimal operation of multi-reservoir systems considering time-lags of flood routing. *Water Resour Manag.* 2016; 30: 523–540.
87. Lampert W, Fleckner W, Rai H, Taylor BE. Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. *Limnol Oceanogr.* 1986; 31: 478–490.
88. Sommer U, Gliwicz M, Lampert W, Duncan A. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch Hydrobiol.* 1986; 106: 433–471.

89. Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*. 1997; 342: 151–164.
90. Vanni MJ, Layne CD. Nutrient cycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. *Ecology*. 1997; 78: 21–40.
91. Andersson G, Berggren H, Cronberg G, Gelin C. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia*. 1978; 59: 9–15.
92. Vanni MJ. Fish predation and zooplankton demography indirect effects. *Ecology*. 1986; 67: 337–354.
93. Romare P, Bergman E, Hansson L-A. The impact of larval and juvenile fish on zooplankton and algal dynamics. *Limnol Oceanogr*. 1999; 44: 1655–1666.
94. Karlsson J, Jonsson A, Jansson M. Productivity of high-latitude lakes: climate effect inferred from altitude gradient. *Glob. Chang. Biol*. 2005; 11: 710–715.
95. Downing JA, Prairie YT, Cole JJ, Duarte CM, Tranvik LJ, Striegl RG, et al. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol Oceanogr*. 2006; 51: 2388–2397.