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Zooplankton nearshore compared to offshore in historically fishless lakes of high elevation are influenced by the introduction of planktivorous fish and water residence time

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Abiotic and biotic factors, such as water movement and planktivorous fish, have separately been shown to influence spatial distribution of zooplankton in lakes. The present study examines the independent and combined roles of fish and water residence time (WRT), which influences water movement, in the distribution of zooplankton. Greater zooplankton biomass and body size were expected nearshore as greater offshore water movement causes drift and avoidance of flowing water, and because offshore planktivores consume zooplankton and release kairomones that zooplankton avoid. Effects of WRT and fish on biomass varied depending on major taxonomic group. Total zooplankton biomass was greater nearshore across WRTs in lakes with fish. Alternatively, in lakes without fish, zooplankton biomass was greater nearshore when WRT was shorter and offshore when WRT was longer. Body size was greater nearshore and not influenced by WRT or fish. Species richness was greater nearshore in lakes with short WRT and offshore in lakes with long WRT. Each lake showed moderately unique communities that exhibited reasonable species turnover between near and offshore areas. The present study suggests that fish and water movement do not act independently in their influence on zooplankton distribution.

KEYWORDS: Zooplankton; high elevation lakes; fish; water residence time

INTRODUCTION

A central issue in understanding spatial patterns of zooplankton is identifying factors that drive spatial variation and whether they operate independently or in concert. Small lakes (lakes less than 100 ha) provide a unique opportunity for studying factors that drive spatial distribution of zooplankton because, unlike large lakes, they have shorter distances between nearshore and offshore areas resulting in high connectivity. High connectivity in small lakes reduces the likelihood of variation between areas driven by random chance or confounding due to other factors that differ between nearshore and offshore areas (Hall *et al.*, 2003). Studies of spatial variation of zooplankton in small lakes indicate that abiotic factors, such as location relative to outlets or shore (Lacroix and Lescher-Moutoué, 1995; Wicklum, 1999; Detmer *et al.*, 2017a), and biotic factors, such as macrophytes (Pennak, 1966) or fish (Wicklum, 1999), can independently influence zooplankton distribution. The roles of interaction between abiotic and biotic factors in the spatial distribution of zooplankton are, however, poorly understood.

In addition to suppressing zooplankton biomass and altering composition of zooplankton (e.g. Carpenter *et al.*, 1987; Detmer *et al.*, 2017a; Collins *et al.*, 2018), fish also influence the spatial distribution of zooplankton in lacustrine ecosystems (e.g. Burks *et al.*, 2002; Tronstad *et al.*, 2011; Detmer *et al.*, 2019). Fish influence zooplankton spatial distribution by both consumption and release of kairomones (also known as infochemicals). Fish consumption in some and not other areas, can lead to areas of local depletion of zooplankton (Tronstad *et al.*, 2011; Bartrons *et al.*, 2015). Fish infochemicals cause avoidance by zooplankton of fish occupied areas, resulting in occupation by zooplankton of otherwise less desirable habitats (reviewed in Burks *et al.*, 2002; Lass and Spaak, 2003). Therefore, the presence of fish, through a combination of effects, can strongly influence zooplankton spatial variation.

Spatial organization of zooplankton by fish has been observed in many studies. Studies have shown both greater zooplankton biomass nearshore compared to offshore (e.g. Pennak, 1966; Pinel-Alloul *et al.*, 1999) and offshore compared to nearshore (e.g. Johannsson *et al.*, 1991; Gliwicz and Rykowska, 1992; Hall *et al.*, 2003; Estlander *et al.*, 2009), depending on the habitat most commonly used by dominant planktivores. Studies relating fish presence to the spatial distribution of zooplankton, however, have tended to focus on large lakes with diverse assemblages of fish where optimal foraging of fishes differs between nearshore and offshore areas (Lewis, 1979; Bartrons *et al.*, 2015). Small lakes may not exhibit patterns observed in larger lakes because fish can move more easily from nearshore to offshore areas. Studies of the effects of fish on the spatial distribution of zooplankton have also generally focused on the effects of a dominant planktivore in a broader community of fishes (Lewis, 1979; Bartrons *et al.*, 2015; Detmer *et al.*, *in press*). Only one study has evaluated the role of planktivore introductions in historically fishless lakes (Wicklum, 1999). In that study, differences in nearshore and offshore areas were only detected in some lakes and not others suggesting that although important, fish are not the only factor influencing the spatial distribution of zooplankton.

Abiotic features of lakes and reservoirs have also been shown to influence the distribution of zooplankton. Some zooplankton taxa have lower abundance around lake inlets (Pinel-Alloul *et al.*, 1999; Bartrons *et al.*, 2015) and near lake outlets (Wicklum, 1999; Walks and Cyr, 2004). Reductions around inlets are likely caused by dilution of incoming water. Dilution driven depletion of zooplankton around inlets is likely caused by drift of zooplankton in water with unidirectional movement away from the inlet. In addition to lower biomass around inlets of lakes, drift by zooplankton from lakes has been observed in streams and rivers of various sizes and velocities (e.g. Sandlund, 1982; Walks and Cyr, 2004; Detmer *et al.*, 2017b). Around outlets, however, active avoidance by zooplankton has also been suggested as a mechanism causing lower zooplankton biomass (Wicklum, 1999; Walks and Cyr, 2004; Detmer *et al.*, 2017a). Fluid mechanics would suggest that in addition to velocity being greater around inlets and outlets, offshore water velocity is greater than nearshore water velocity (Vogel, 1994). It is likely, therefore, that drift and avoidance by zooplankton would also be greater offshore. The relative difference between near and offshore velocities, drift and movement of zooplankton would also be expected to be greater in lakes with shorter WRTs because the relationship between flow velocity and distance from a surface (such as the lake bottom or shoreline) is non-linear (Vogel, 1994). Further still, because suggestions that lower biomass around outlets is primarily driven by avoidance of large zooplankton (Wicklum, 1999; Detmer 2017a), in lakes with low WRT, body size of nearshore zooplankton would be expected to be greater than those observed offshore.

The objective of this study was to characterize the independent and interacting influences of fish and WRT on the distribution of zooplankton nearshore to offshore. Differences between areas were predicted to differ depending on both the presence of fish and WRT because planktivores selectively consume large bodied zooplankton (e.g. Carlisle and Hawkins, 1998; Knapp *et al.*, 2005; Detmer *et al.*, 2017a), which have been suggested to have greater capacity to avoid areas of greater water movement such as outlets (Wicklum, 1999; Walks and Cyr, 2004; Detmer *et al.*, 2017b). Also, for the same reasons, differences were explored in zooplankton community structure between nearshore and offshore areas in lakes with and without fish along a gradient of WRTs. Lakes at high elevation in the Rocky Mountains of Colorado, USA, offer a unique opportunity for testing the independent and combined roles of fish and WRT on the nearshore to offshore distribution of zooplankton because lakes of varying WRT are numerous and only some of which contain fish.

METHODS

To examine drivers of spatial variation in zooplankton biomass and community composition in lakes, we sampled zooplankton from eight lakes with fish and seven lakes without fish of varying WRT during a single time period from mid August to mid September, when zooplankton biomass is near the seasonal peak (Detmer *et al.*, 2017b). The fish of interest here are trout (*Oncorhynchus clarkii* and *Salvelinus fontinalis*), which are predominantly invertivorous in high elevation lakes (Finlay and Vredenberg, 2007) and strongly suppress zooplankton communities (e.g. Carlisle and Hawkins, 1998; Knapp *et al.*, 2005); no other fish were present (Table I). The study lakes are located in the headwaters of the North St. Vrain Creek of Rocky Mountain National Park, Colorado. Lakes in this study vary in elevation, watershed area, lake area, maximum depth, phytoplankton chlorophyll *a* concentration, Secchi depth, and WRT (Table I).

Records provided by the U.S. Fish and Wildlife Service indicate that among lakes containing fish, all have contained naturally reproducing fish for 30–70 years and therefore reflect communities containing fish (Knapp *et al.*, 2005). These records also indicate that of the seven fishless lakes, two were never stocked and five were stocked and these stocked now fishless lakes became fishless because of inadequate spawning habitat. The stocked and now fishless lakes have been intermittently surveyed by the U.S. Fish and Wildlife Service and the data indicate that the stocked and now fishless lakes have not contained fish for at least 30 years and therefore likely show no residual effects of having been stocked (Knapp *et al.*, 2005).

Bathymetric maps were created for each lake (Supplementary material, Fig. S1) using a global positioning system (GPS) unit and a portable sonar device at 45–200 points, depending on the lake size (Detmer, 2014). Bathymetry was used for volumetric calculations, which were subsequently used for estimates of WRT. Geographic information models and calculations were completed with ArcGIS version 10.2.2. On each sampling date at each lake at the deepest location in that lake (known here after as the offshore site), Secchi depth was recorded. Water residence time was calculated as the lake volume divided by lake discharge. Outlet discharge was measured for estimating WRT. Discharge was measured from the integration of velocity and depth across the lake outlet. Outlet width was measured and divided into 6 or 10 equal subsections. At the midpoint of each subsection, stream depth was measured and velocity recorded at 60% of the depth (Gordon *et al.*, 2004). Discharge, Q (m^3 s^{-1}) was calculated as follows: $Q = \Sigma\, w_n \times D_n \times v_n$ where w is the width of the subsection (m), D is the depth of the subsection (m), and v is the mean velocity of the water within that subsection (m s^{-1}).

As a proxy for phytoplankton biomass, a sample for chlorophyll *a* was collected at each offshore site. For chlorophyll *a* samples, two liters of water were collected from just below the surface. After collection, samples were kept cool and dark during transportation to the lab and filtered within 24 hours (frequently within 8 hours) through a glass fiber filter (effective pore size 0.7 µm) after which, they were stored in the dark at −20°C. Chlorophyll *a* was extracted with ethanol; extraction was accomplished through a brief hot extraction period followed by a 1 day cold extraction period at −20°C. Chlorophyll *a* concentration was then determined by spectrophotometry with corrections for phaeophytin (Marker *et al.*, 1980; Nusch, 1980; Sartory and Grobbelaar, 1984).

Zooplankton were collected by vertical tows of a conical zooplankton net (20 cm diameter, 53 µm mesh) from ~0.25 m above the bottom to the surface at a rate of about 0.5 m s^{-1}. Samples were collected at one offshore and at one nearshore site in each lake. Offshore sites were located at the deepest location in each lake. Nearshore sites were located at a location approximately the same distance between the inlet and the outlet as the offshore site. Nearshore sites were located 1–4 m from shore and at a depth of 20.4% (±1.0%) the depth of offshore sites among all lakes. The distance between the nearshore and offshore locations also did not differ between lakes with and without fish (Student's *t*-test, $t_{13} = 0.60$, $P = 0.56$) and among all lakes the mean distance between nearshore and offshore sites was 59.0 (±6.2) m.

Macrophytes have been shown to interact with fish in their influence on the spatial distribution of zooplankton because they influence susceptibility to predation and behavior of zooplankton (e.g. Burks *et al.*, 2001; Iglesias *et al.*, 2017). Zooplankton tend to avoid macrophytes and fish in the presence of each independently, but in the presence of both, zooplankton tend to prefer macrophytes to

Table I: Description of physical characteristics and fish condition of study lakes.

Lake	Latitude	Longitude	Fish	WRT	Secchi, m	Chl-*a*, μg L^{-1}	Max. depth, m	Watershed Area, ha	Area, ha	Elevation, m
Bluebird	40.19263	−105.65218	NF	35.5	7.50	0.70	9.3	317	5.0	3371
Eagle	40.11142	−105.65150	NF	26.8	8.00	1.47	16.2	359	5.2	3296
Falcon	40.22866	−105.65660	NF	34.1	5.50	3.97	7.7	72	1.1	3371
Finch	40.18334	−105.59421	NF	36.9	B	1.97	2.6	27	2.6	3021
LL1	40.22996	−105.63948	NF	1.0	B	1.30	2.8	325	1.8	3373
LL2	40.23671	−105.64125	NF	1.0	7.50	1.00	12.8	230	1.5	3469
Twin Lake 1	40.20884	−105.60809	NF	51.2	B	2.50	2.6	13	1.3	2991
Box	40.21348	−105.64746	BT	45.2	3.40	4.54	9.3	28	1.6	3266
Lower Hutch	40.17023	−105.62985	CT	1.2	5.80	0.90	7.6	396	1.7	3304
Middle Hutch	40.16936	−105.63760	CT	0.9	B	1.00	4.3	359	1.3	3326
Ouzel	40.19987	−105.62937	BT&CT	0.8	B	0.67	2.7	1028	2.0	3052
Pear	40.17707	−105.62273	CT	62.9	5.00	1.20	16.8	182	6.0	3225
Sandbeach	40.21680	−105.60171	CT	50.8	5.00	1.60	7.9	67	4.8	3135
Thunder	40.22188	−105.64497	CT	15.8	3.50	8.43	12.9	321	5.9	3225
Upper Hutch	40.17418	−105.64760	CT	4.5	5.20	0.70	5.2	272	2.8	3412

The letter "B" in Secchi depth represents a Secchi depth that exceeded the bottom and WRT is water residence time in days^{-1}. NF, no fish; BT, brook trout; CT, cutthroat trout.

fish (e.g. Lauridsen and Lodge, 1996; Burks *et al.*, 2001; Burks *et al.*, 2002). To ensure that proximity to shore was the driving factor and not macrophytes, the coverage of macrophytes was evaluated and samples not taken near them. Macrophyte patches were mapped as polygons by hand held GPS unit. Macrophyte polygon areas were divided by total lake area to determine percent coverage of emergent macrophytes. Macrophytes were rare or absent (<2% of the lake area) in all of the lakes except for two, Twin Lake 1 and Finch Lake, where they were observed along shorelines and covered 14% and 6% of the total surface area of the lake. Nearshore sites in all lakes were located at least 50 m away from aggregations of macrophytes to.

Zooplankton were identified to genus or species according to Stemberger (1979), Pennak (1989) and Thorp and Covich (1991), and were enumerated in a 1 mL Sedgewick Rafter cell or 20 mL modified Bogorov cell depending on the abundance in the sample. The quantity of sample processed was adjusted depending on abundance in individuals m^{-3}; between 20% and 50% of each sample was processed for all samples (16 samples), except when total density visually appeared to be below 5000 individuals m^{-3} (11 samples) when the entire sample was processed or when total density visually appeared to be above 100 000 individuals m^{-3} when 5% of the sample was processed (3 samples). Zooplankton abundances (individuals m^{-3}) were corrected for tow depth and were assumed to reflect a filtration efficiency of approximately 50% (Walters and Vincent, 1973; Lewis, 1979). Length was measured for all individuals of rare taxa (fewer than 100 individuals in an aliquot) and for 100 individuals of all other taxa. Length to mass regressions were used to calculate dry mass (μg individual^{-1}) for crustaceans, rotifers and *Chaoborus trivitattus* (Dumont and Balvay, 1979; EPA Great Lakes National Program Office, 2003), which was used to calculate biomass for each taxon.

Statistical analyses

Nearshore and offshore differences within lakes were evaluated for zooplankton biomass, body size and taxonomic richness. Because the focus of this study was to compare nearshore and offshore differences within lakes, for each of these metrics the ratio of nearshore to offshore for each metric was evaluated. Analyses were completed for all zooplankton collectively (total) as well as three major taxonomic groups of zooplankton, cladocera, copepods, and rotifers. For this nearshore to offshore ratio, a value of greater than one indicates greater biomass, body size, or species richness nearshore. A value of near one indicates that the two areas were approximately equivalent and, consequently, a value of less than one indicates that the offshore site was greater. An ANCOVA was used with this ratio to evaluate the effects of WRT and fish. This procedure was completed for biomass and body size for all zooplankton collectively (total) as well as the three major taxonomic groups of zooplankton, cladocera, copepods, and rotifers. The same procedure was followed for relating taxonomic richness to nearshore or offshore distribution, WRT and fish. If a taxon is observed only in one habitat (nearshore or offshore) in a small lake, it is unlikely that they are absent from the other habitat. Such a scenario would cause the nearshore to offshore ratio to be undefined. Therefore, conservatively, if no organisms were detected in one habitat for a major taxonomic group when they were present in the other habitat in the lake, then instead of adding one as is commonly done when a $\log_{10}$ transformation is completed on a group of values that includes zeros, one half of the minimum biomass for that group was used for biomass analyses and equal body size was assumed near and offshore for body size analyses. In analyses, ratio data for biomass and body size were normalized using a square root transformation. The taxonomic richness ratio analysis, however, did not require transformation. All statistical analyses were run in software R 3.2.4 (R Core Team, 2016, Vienna, Austria) and for all statistical tests, alpha was 0.05.

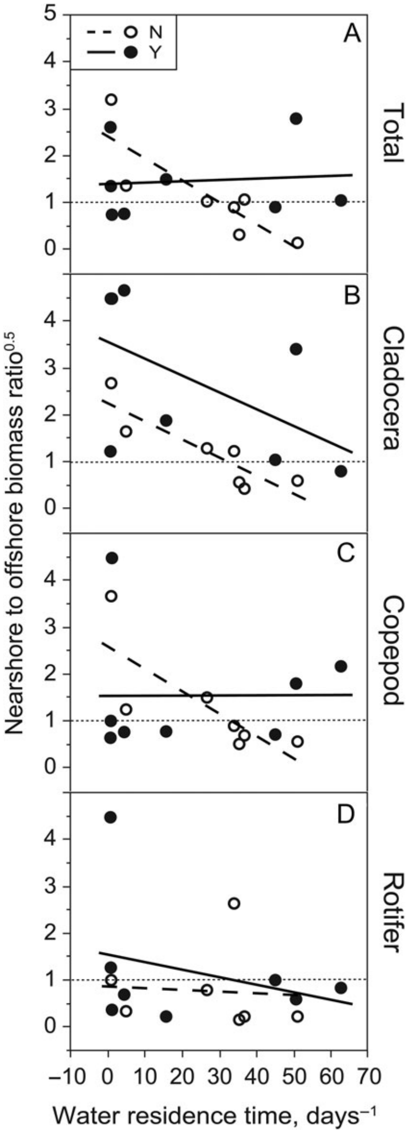

Fig. 1. The ratio of nearshore to offshore biomass related to WRT for the total biomass of zooplankton (**A**) as well as of major taxonomic groups including cladocera (**B**), copepods (**C**) and rotifers (**D**). The dotted line indicates equivalent taxonomic richness nearshore and offshore, therefore data that are above the dotted line show lakes where biomass was greater nearshore and data that are below the dotted line indicate lakes where biomass was greater offshore.

Communities were visually compared with an NMDS and mean beta diversity between nearshore and offshore pairs was contrasted between lakes with and without fish. To visualize changes in community structure by nearshore and offshore areas, the presence of fish, and WRT, densities of zooplankton were used to calculate a similarity matrix for nonmetric multidimensional scaling (NMDS; Minchin, 1987) with Bray–Curtis distance matrix (Bray and Curtis, 1957). Beta diversity (turnover of diversity over space) was quantified with Whittaker's index of beta diversity. Species turnover between near and offshore sites was calculated for each lake using Sorensen's index of beta diversity. An ANCOVA was used to evaluate the response of beta diversity within lakes among lakes with and without fish using WRT as a covariate. The analyses, the NMDS and beta diversity values were calculated using the software R 3.2.4 (R Core Team, 2016, Vienna, Austria) and the R *vegan* package (Oksanen *et al.* 2013). For the beta diversity analysis the alpha was 0.05.

RESULTS

Consistent with other studies, zooplankton biomass and body size differed between lakes with and without fish. Mean nearshore and offshore zooplankton biomass were strongly reduced in lakes containing fish, similar to observations of the effects of fish on zooplankton (e.g. Jeppesen *et al.*, 2000; Parker and Schindler, 2006; Detmer *et al.*, 2017a); $\log_{10}$ biomass in μg dry mass m^{-3} in lakes containing fish (3.01 ± 0.38) was lower than in lakes without fish (4.43 ± 0.40; Student's *t*-test $t_{13} = -2.56$, $P = 0.02$). Also similar to what has been observed in the literature, mean zooplankton body size in lakes containing fish was much smaller than in lakes without fish (e.g. Carlisle and Hawkins, 1998; Wicklum, 1999; Knapp *et al.*, 2005; Detmer *et al.*, 2017b); log10 body size in μg dry mass in lakes containing fish (−0.20 ± 0.18) was lower than in lakes without fish (0.48 ± 0.19; Student's *t*-test $t_{13} = -2.65$, $P = 0.02$).

Biomass

The relationship between the ratio of near to offshore total zooplankton biomass and WRT differed depending on if fish were present or absent in a lake (Fig. 1A; Fish × WRT, $F_{1,11} = 5.97$, $P = 0.03$). In lakes without fish the relationship between near and offshore zooplankton biomass was negative, with greater biomass of zooplankton nearshore in lakes with low WRT and greater biomass offshore in lakes with high WRT. In contrast, in lakes containing fish, there tended to be greater biomass nearshore independent of WRT.

All three of the major taxonomic groups (cladocera, copepods and rotifers) exhibited unique relationships among zooplankton occupied area, fish and WRT. Although the patterns were all unique, the combination of WRT and fish did not interact to influence cladocera (Fish × WRT, $F_{1,11} = 0.01$, $P = 0.93$), copepods (Fish × WRT, $F_{1,11} = 2.36$, $P = 0.15$) or rotifers (Fish × WRT, $F_{1,11} = 0.14$, $P = 0.71$). Cladocera biomass was much greater nearshore in lakes with short WRT (Fig. 1B) and approached equal near to offshore biomass in lakes with long WRT (WRT, $F_{1,12} = 7.32$, $P = 0.02$). Biomass for cladocera was also greater nearshore in lakes containing fish than in lakes without fish (Fish, $F_{1,12} = 5.32$, $P = 0.03$). Water residence time did not influence the ratio of near to offshore biomass for copepods (WRT, $F_{1,12} = 1.28$, $P = 0.37$). The presence of fish also did not influence the ratio of near to offshore biomass for copepods (Fish, $F_{1,12} = 0.08$, $P = 0.78$). The biomass of copepods was nearly equal near and offshore in most lakes, except Lion Lake 1 (without fish) and Lower Hutcheson Lake (containing fish) that both exhibited >10× the copepod biomass nearshore as offshore. The ratio of nearshore to offshore rotifer biomass was slightly over 20 times greater nearshore than offshore in Ouzel Lake (Fig. 1D). Ouzel Lake was anomalous, however, as the majority of lakes had much greater offshore biomass of rotifers and the median ratio of nearshore to offshore rotifer biomass including Ouzel Lake was only 0.62, suggesting that, in most lakes, rotifers tend to occur offshore. Near and offshore rotifer biomass, excluding Ouzel Lake, was not influenced by WRT (WRT, $F_{1,11} = 0.00$, $P = 0.98$) or the presence of fish (Fish, $F_{1,11} = 0.02$, $P = 0.89$).

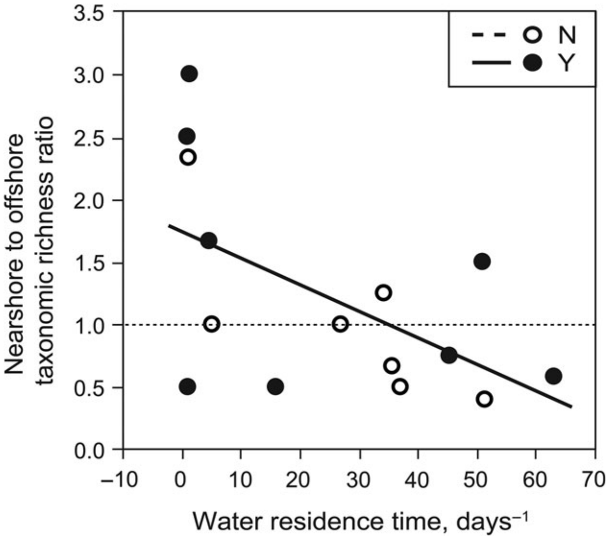

Fig. 2. The ratio of nearshore to offshore taxonomic richness as related to WRT. The regression line for all lakes is indicated by the solid black line. The dotted line indicates equivalent taxonomic richness nearshore and offshore, therefore data that are above the dotted line show lakes where taxonomic richness was greater nearshore and data that are below the dotted line indicate lakes where taxonomic richness was greater offshore.

Body size

The nearshore to offshore ratio of mean body size for the total zooplankton community was not influenced by WRT and fish together (Supplementary material, Fig. S2A; Fish × WRT, $F_{1,11} = 1.60$, $P = 0.23$) or independently (Fish, $F_{1,12} = 0.36$, $P = 0.56$; WRT, $F_{1,12} = 2.91$, $P = 0.12$). Collectively, among all lakes, the ratio of mean body size nearshore versus offshore was 1.61 (±0.26) indicating that, independent of WRT and the presence of fish, in high elevation lakes larger zooplankton are more common nearshore than offshore.

Cladocera, copepods and rotifers also showed no size discrepancy between near and offshore areas as a function of interaction between WRT and fish (Supplementary material, Figure S2B–D; all groups, Fish × WRT $P > 0.05$). Independently, WRT and fish also did not influence near to offshore size differences (WRT, all groups, $P > 0.05$; Fish, all groups, $P > 0.05$). Similar to the pattern observed among all zooplankton collectively, for the three major taxonomic groups, the mean body size also tended to be greater nearshore than offshore (cladocera, 1.45 ± 0.37; copepod, 1.20 ± 0.25; rotifer, 1.15 ± 0.16).

Zooplankton taxonomic richness nearshore and offshore

Fish and WRT did not interact to influence taxonomic richness nearshore to offshore (Fig. 2; Fish × WRT, $F_{1,11} = 0.16$, $P = 0.61$). Taxonomic richness was greater, however, nearshore in lakes with short WRT and greater offshore in lakes with longer hydraulic residence time (WRT, $F_{1,12} = 5.00$, $P = 0.05$). Taxonomic richness nearshore to offshore was not influenced by the presence of fish (Fish, $F_{1,12} = 0.04$, $P = 0.55$).

Zooplankton community structure nearshore and offshore

The NMDS indicated that the presence of fish and the WRT are drivers of community structure in lakes at high elevation. In lakes containing fish, community structure was highly variable in nearshore and offshore and differences were not consistent (i.e. tending from one set of taxa to another; Fig. 3). In lakes without fish, directionality and distance of communities between sites was generally more consistent with two exceptions. The two exceptions were Lion Lake 1, which had much greater community differences offshore to nearshore, and Falcon Lake, which had a community pattern shift that was nearly reverse that of other fishless lakes (Fig. 3).

Species turnover between nearshore and offshore sites evaluated with Sorensen's index was not influenced by an interaction between fish and WRT (Fish × WRT, $F_{1,11} = 0.32$, $P = 0.58$; Supplementary material, Figure S3). Fish and WRT also did not independently influence turnover between nearshore and offshore sites (Fish, $F_{1,12} = 1.16$, $P = 0.30$; WRT, $F_{1,12} = 0.72$, $P = 0.41$). The mean turnover between near and offshore sites among all lakes was moderate (0.59 ± 0.06), but ranged from 0 (complete turnover between nearshore and offshore) and 1 (identical assemblages between near and offshore).

DISCUSSION

Understanding factors that influence the spatial distribution of zooplankton in lakes and reservoirs is essential for understanding ecosystem structure and can provide insight regarding mechanisms influencing zooplankton populations. The present study shows that the spatial distribution of zooplankton in small, high elevation lakes can also be complex and governed by multiple and sometimes interacting factors, like observations of complex spatial patterns shown in large lakes and reservoirs (e.g. Lewis, 1979; Jones *et al.* 1995; Bartrons *et al.*, 2015). Comparable to what has been observed in many lakes (e.g. Pennak, 1966; Johannsson *et al.*, 1991; Warner *et al.*, 2006) and reservoirs (e.g. Clarke and Bennett, 2003; Castilho-Noll *et al.*, 2010) containing planktivorous fish, zooplankton biomass in lakes containing fish tended to be greater nearshore than offshore, particularly for cladocera, which exhibit strong behavioral responses to fish because of high predation by fish (Carlisle and Hawkins, 1998; Burks *et al.*, 2001). The exception was rotifers, which are not suppressed by trout (Carlisle and Hawkins, 1998; Knapp *et al.*, 2005; Detmer *et al.*, 2017a) and have greater biomass offshore independent of fish and WRT. Unique to this study is the observation that fish and WRT are interactive in their influences on zooplankton distribution. Body size tended to be greater nearshore, but contrary to predictions, nearshore size relative to offshore size was not influenced by either fish or WRT, which may be due, in part, to differences in nearshore and offshore community composition or because both factors cause greater nearshore body size. Zooplankton species richness tended to be greater nearshore in lakes with short WRT, like what has been observed in the literature and tended to be greater offshore in lakes with longer WRT. Species richness was not, however, influenced by the presence of fish. Turnover was moderate between nearshore and offshore areas and community structure, although influenced by both the presence of fish and WRT, was only modestly influenced by proximity to shore. Inconsistent differences between nearshore and offshore were likely influenced by the highly unique nature of zooplankton community in each lake.

It has been suggested that reduced abundance of zooplankton near lake outlets is driven by active avoidance by zooplankton of outlets or drift caused by directional velocity (e.g. Wicklum, 1999; Walks and Cyr, 2004; Demi *et al.*, 2012; Detmer, 2017a). The present study shows that zooplankton also tend to associate with nearshore and offshore areas differently depending on WRT. Based on velocity gradients designating that velocity increases with greater distance from ground and water interfaces (Vogel, 1994), this supports the concept that water velocity directly influences the distribution of organisms. Although a response was elicited, the present study was not able to decipher whether the predominant effect of velocity on the distribution of zooplankton is passive drift, a behavioral response, or both drift and behavior. Spatial responses of zooplankton suggest that although velocities are not likely great in lakes and reservoirs, comparable to flowing water bodies such as streams or rivers, variation in hydrodynamic forces is an important attribute in defining the spatial distribution of zooplankton.

Spatial distribution of zooplankton in lakes without fish provides insight into mechanisms influencing zooplankton absent of the effects of predation and complexities associated with a landscape of fear caused by fish infochemicals. Fishless lakes in the present study showed that spatial distribution of zooplankton was influenced by WRT for cladocera and copepod, but not for rotifers that generally had higher biomass offshore independent of WRT. Different pattern in rotifers relative to cladocera and copepods suggests that differences in body size of the different taxonomic groups may contribute to susceptibility to hydrodynamic forces; larger zooplankton, including cladocera and copepods, have a greater Reynolds number and are therefore less susceptible to export from drift and more likely to have the capacity to actively avoid risky habitat and seek alternative habitat. Greater offshore biomass of smaller rotifers therefore may indicate greater predation nearshore from predatory macroinvertebrates. For cladocera and copepods, risk to nearshore predation from macroinvertebrates

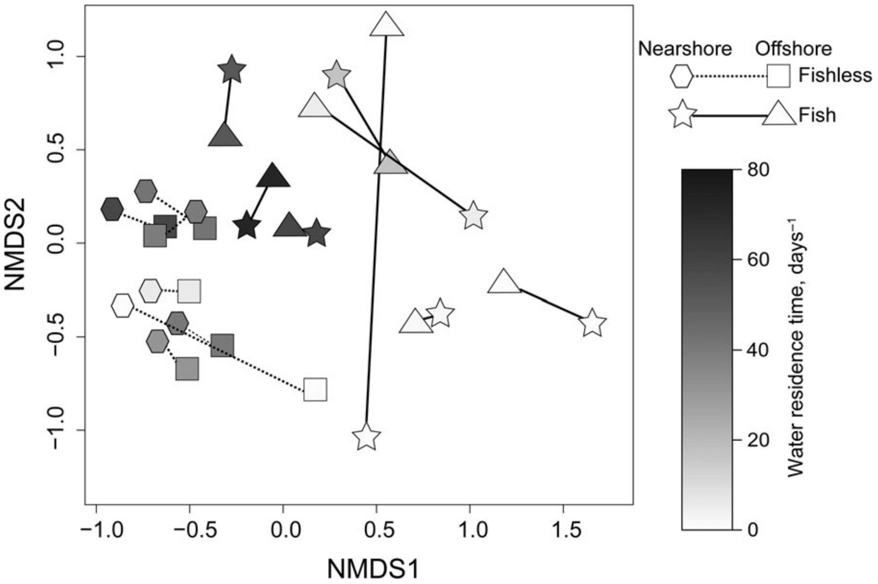

Fig. 3. Nonmetric multidimensional scaling (NMDS) ordination plot of zooplankton communities near and offshore in lakes with and without fish of varying water residence times. Nearshore and offshore locations in the same lakes are connected by lines.

may also be a driving force, but only in lakes with higher water residence times where there is lower risk of being exported. Experimental evidence suggests that zooplankton respond to macroinvertebrate predator infochemicals, similarly to their avoidance of fish infochemicals (Lass and Spaak, 2003; Boeing *et al.*, 2005). Another possible factor influencing the spatial distribution of zooplankton is resource distribution because phytoplankton are likely just as susceptible to drift and export in lakes with short WRT and some zooplankton in oligotrophic lakes have been shown to consume periphyton to supplement their diet of suspended resources (Siehoff *et al.*, 2009; Cazzanelli *et al.*, 2012). It is therefore likely in fishless lakes that zooplankton spatial distribution is driven through a combination of risks of predation and export as well as resource use.

The present study indicates that the influences of fish and WRT cannot be evaluated independently of spatial distribution of zooplankton in small lakes. In small high elevation lakes in the present study, zooplankton tended to occupy nearshore areas independent of the presence of fish when WRT was short. At longer WRTs, however, there was divergence between lakes with and without fish; zooplankton tended to occupy areas nearshore when there were fish present and offshore areas when fish were not present. In large lakes and reservoirs, pelagic planktivores have been described as a primary driver of greater abundance of zooplankton in nearshore areas (Lacroix and Lescher-Moutoue, 1995). The divergence between lakes with and without fish at longer residence times suggests that in lakes with long WRT and fish, fish cause zooplankton to remain nearshore, likely because of consumption by fish of zooplankton in high elevation lakes (Carlisle and Hawkins, 1998; Knapp *et al.*, 2005; Detmer *et al.*, 2017b) and avoidance of planktivorous fish (Lauridsen *et al.*, 1999; Burks *et al.*, 2001; Lass and Spaak, 2003). Results in the present study are contrasted with the only other study of high elevation lakes where zooplankton abundance nearshore was not different than offshore, but WRT was not accounted for (Wicklum, 1999).

Differences in zooplankton distribution between lakes with and without fish were, in part, driven by variation in response of the different major taxonomic groups. Cladocera biomass was greater nearshore in lakes containing fish, like what has been observed in the literature (Lacroix and Lescher-Moutoue, 1995). Also, uniquely, greater nearshore biomass of cladocera was observed in lakes with shorter WRT than lakes with longer WRT. Differences in spatial distribution of zooplankton among lakes with differing WRT and the presence or absence of fish indicates a complex set of interactions among predation or perceived risk to predation, drift, resource availability and risk to entrainment or export from the lake. The present study also, therefore, suggests that the use of WRT as a covariate is important in evaluating the spatial distribution of zooplankton and may explain the null the results of work by Wicklum (1999).

Patterns in individual species present in a lake that result from abiotic and biotic factors contribute to the spatial arrangement of zooplankton communities. Despite the numerous studies indicating nearshore zooplankton species richness can equal or exceed offshore species richness and indicate that zooplankton community composition can differ between the nearshore and offshore areas (Pennak, 1966; Walseng *et al.*, 2006), many studies characterizing zooplankton taxonomic richness and community composition in lakes and reservoirs focus only on samples collected from offshore areas. Greater taxonomic richness nearshore in lakes with short WRT and offshore in lakes with longer WRT suggests that some taxa may be able to inhabit offshore areas only when WRT is long. This may be in addition to the suggestion that greater diversity can occur nearshore in some lakes because of the greater richness in microhabitats found there, created by course woody habitat, detrital material, sand, or rocks (Bini *et al.*, 1997). Specific patterns regarding nearshore and offshore communities are difficult to pinpoint, however, as species turnover between nearshore and offshore locations are moderate, but highly variable and not influenced by either WRT or fish. Further, the NMDS suggested that specific patterns in community structure between near and offshore areas within lakes may be obscured by the varied zooplankton composition among all lakes and the strong influences of fish and WRT on community structure. Observed high individuality of community composition in high elevation lakes is likely the result of highly variable habitat diversity and the addition of fish.

CONCLUSION

The present study shows that WRT and fish both influence the spatial distribution of zooplankton in lakes at high elevation and their influences are not independent. Although WRT is generally long and water velocity is not likely to vary greatly in large, natural lakes, reservoirs even of large size can have moderate or short WRTs (Hayes *et al.*, 2017). Data from the present study suggest that short water residence time in reservoirs may cause enhanced nearshore zooplankton biomass and species richness. As would be predicted from observations in the current study, zooplankton biomass has tended to be greater nearshore in reservoirs with prominent planktivores (e.g. Betsill and van den Avyle, 1994; Gazonato Neto *et al.*, 2014; Lodi *et al.*, 2014). No study of reservoirs, however, has evaluated the role of WRT as a mechanism controlling the relative biomass or species richness nearshore relative to offshore. Further, because offshore areas in rivers differ greatly from nearshore areas in velocity and fish community composition, observations from the current study also indicate that latitudinal nearshore to offshore variation is likely to play a substantial role in large rivers. This concept is supported peripherally by Wahl *et al.* (2008) where zooplankton abundance in the Illinois River main channel was lower than in side channel areas and connected backwater lake sites. In summary, further study of spatial variation of zooplankton in relation to WRT and different predator varieties is necessary because differences in abundance and communities among areas could to important differences in food web structure of lakes, reservoirs, and rivers.

SUPPLEMENTARY DATA

Supplementary data are available online at the *Journal of Plankton Research* online.

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