



Consistent and transient drivers of freshwater zooplankton communities

James S. Sinclair | Shelley E. Arnott | William A. Nelson | Kaitlyn B. Brougham

Department of Biology, Queen's University,
Kingston, ON, Canada

Correspondence

James S. Sinclair, Department of Biology,
Queen's University, 116 Barrie St, Kingston,
ON, Canada, K7L 3N6.
Email: sinclair.130@osu.edu

Funding information

Natural Sciences and Engineering Research
Council of Canada, Grant/Award Number:
388641, 388738 and 489908

Handling Editor: Jani Heino

Abstract

Aim: Inferences of the predominant processes that structure communities are commonly based on single 'snapshots' in time, which may miss temporally transient but important mechanisms. In this study, we compared key environmental and spatial drivers of zooplankton composition across multiple years to quantify shifts in their relative importance through time, and to identify any drivers of temporal change.

Location: Southern Ontario, Canada.

Taxon: Zooplankton.

Methods: Zooplankton were collected from 29 lakes in southern Ontario, Canada over four years (2013–2016). Variation partitioning was used to quantify the relative importance of independent and covarying components of local environmental conditions, regional east-west and north-south compositional trends, and inter-lake geographic distance in each year. Measured environmental metrics included aspects of lake morphology and chemistry, and spatial relationships were quantified using lake latitude/longitude coordinates and Moran's Eigenvector Maps (MEMs). Redundancy analyses (RDAs) were also used to compare the influence of individual environmental and spatial variables across years.

Results: Most local-scale and regional-scale community processes were consistently important across all surveyed years, but some were less consistent. Specifically, geomorphology was always an important driver of local environmental and regional spatial community patterns. This occurred because local community composition was strongly affected by whether a lake was shallower versus deeper, and due to spatial clusters of shallow and deep lakes that produced negative spatial autocorrelation in community composition. Conversely, the individual influences of lake chemistry and spatial east-west compositional trends were important in some years and not in others, potentially due to inter-annual shifts in the predominant environmental variables and extreme weather events.

Main conclusions: A single-year community snapshot can provide insight into consistent or slowly changing community structuring processes, such as those driven by geomorphology, but may not completely capture temporally transient mechanisms. Furthermore, snapshots collected during anomalous seasons or years may misrepresent which mechanisms are predominantly determining community composition.

Future efforts to understand local and regional community drivers would therefore benefit from considering which processes are likely temporally 'consistent' versus 'transient', and studies with more variable components would benefit from considering or controlling for temporal shifts in their importance.

KEYWORDS

abiotic niche, environmental change, environmental heterogeneity, local and regional, metacommunity, spatial autocorrelation, temporal scale, temporal variability

1 | INTRODUCTION

A principal goal of ecology and biogeography is to uncover the mechanisms that govern the composition and abundance of species, such as local environmental conditions and regional landscape patterns, inter-specific and intra-specific interactions, dispersal among communities, and speciation (Hanski, 1999; Leibold et al., 2004; Thompson et al., 2020; Vellend, 2016). Identifying the mechanisms that drive community structure, and the circumstances under which their individual and relative importance may shift, is crucial both for improving our theoretical understanding of how communities are formed (Cottenie et al., 2003; Ricklefs, 1987), and for informing practical efforts to better manage, conserve, or restore species and functional diversity (Simberloff, 2004; Temperton et al., 2004).

A common approach to determining the drivers of community composition is to sample a set of communities, divide potential structuring mechanisms into different categories, such as local (e.g., abiotic conditions in each community) versus regional (e.g., broad-scale environmental trends or physical habitat connectivity) processes, then quantify the relative influences of each category on species or trait composition (Brown et al., 2017; Cottenie, 2005; Heino et al., 2015; Hérault & Honnay, 2005; Lindström & Langenheder, 2012). This approach has shown that some communities are predominantly shaped by a single driver, such as when composition is primarily determined by environmental or spatial processes (e.g., Göthe et al., 2013; Urban, 2004; Van der Gucht et al., 2007; Verleyen et al., 2009). Conversely, other communities are shaped by multiple abiotic, biotic, or spatial mechanisms (e.g., Capers et al., 2010; Hoeinghaus et al., 2007; Moritz et al., 2013; Schweiger et al., 2005; Werner et al., 2007).

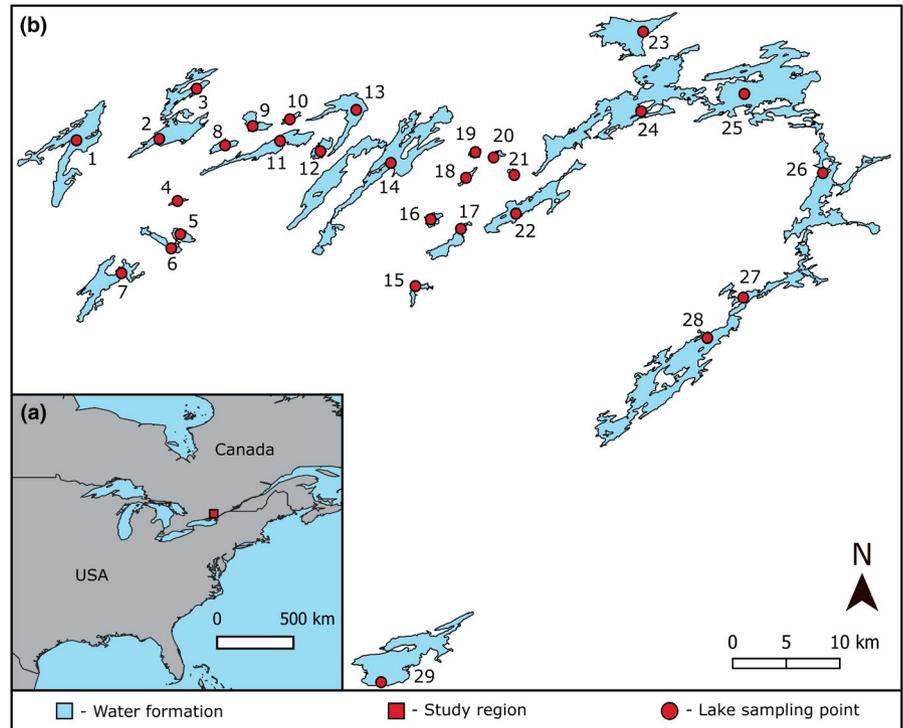
However, a frequent limitation of these studies is that community data are only collected from a single time period (Erős et al., 2012; Heino et al., 2015), either because examining temporal variation is not an objective or due to the complications involved in sampling multiple communities across seasons or years. This constraint restricts inference about the drivers of community structure to a single community 'snapshot', which could miss temporal variability in the relative importance of different structuring mechanisms. For example, the importance of environmental influences on species composition across communities is dependent upon the strength of the environmental gradient (e.g., Jackson et al., 2001; Moritz et al., 2013), which could change over time (Göthe et al., 2013).

Climatic inter-annual variability is also projected to increase as climate change progresses (Knapp et al., 2008), as is the frequency and severity of extreme weather events (Ummenhofer & Meehl, 2017), thus potentially creating more intense temporal swings in regional-scale environmental structuring processes. Similarly, the importance of dispersal among communities (usually quantified using proxies of spatial distance or connectivity) could also temporally vary. Species can become more or less dispersive as the quantity of available resources or density of conspecifics changes (Clobert et al., 2012). Physical connectivity between habitats can also shift over time due to changes in natural (e.g., dry versus wet periods; Cañedo-Argüelles et al., 2020; Fernandes et al., 2014; Sarremejane et al., 2017) or anthropogenic connections (e.g., canal construction; Wilson et al., 2009). As such, our understanding of the forces that shape community composition may not be robust given their potential dependence on when community snapshots are collected, how many snapshots are collected (Vagle & McCain, 2020), and whether the dominant processes wax and wane as abiotic and biotic conditions change. Improving our understanding of the processes that shape ecological communities, and practical management efforts that are informed by this understanding, thus requires further examination of how the individual and relative importance of community structuring mechanisms can change over time.

In this study, we addressed this question of temporal variance in community drivers using zooplankton collected from 29 lakes in southern Ontario, Canada over four years (2013–2016; Figure 1). These lakes are all within the Frontenac Arch region, which provides a variety of local and regional gradients. There is an order of magnitude of difference in lake areas (9–900km²) and maximum depths (5–70 m), and connectivity varies widely from isolated lakes without direct waterway connections to lakes that flow directly from one to the next. Zooplankton also provide a good study system for assessing temporal variability in community structuring processes. Zooplankton can readily disperse via wind, water, and animal vectors (Havel & Shurin, 2004), thus potentially connecting even isolated ecosystems that other animals, such as fish, cannot reach without human intervention. Many zooplankton species also exhibit relatively short generation times, with some species transitioning from birth to reproduction within days, allowing for rapid community response to inter-annual changes.

Our study had two objectives: (1) quantify the separate roles of local environmental and regional spatial processes on lake zooplankton

FIGURE 1 Zooplankton samples were collected from lakes in (a) the Great Lakes region of southern Ontario, Canada. A total of (b) 29 lakes were sampled, with red circles indicating the deepest point of each lake and thus where zooplankton tows were collected. Further details on the latitude/longitude coordinates and characteristics of individual lakes are provided in Appendix S1, Table S1.1



in each survey year; and (2) compare the influence of individual environmental and spatial variables across years to identify the drivers of any temporal changes. While we had no a priori expectation that any one specific local or regional characteristic of our study system might be changing across years, there are multiple potential sources of inter-annual variation that could affect zooplankton, such as lake chemistry responding to local environmental changes (Soranno et al., 1999), reduced lake ice due to a changing climate (Wang et al., 2012), and shifts in lake connectivity (e.g., due to drought events; Lake, 2003). In addition, changes in anthropogenic inputs to lakes can exhibit inter-annual variation in severity due changes in land use, temperature and precipitation (Brias et al., 2018; de Hoyos & Comín, 1999; Schindler et al., 1996). Thus, we expected that changing local and regional environmental factors and possibly spatial connections in our study region could translate to temporal shifts in the relative importance of different community structuring processes.

2 | MATERIALS AND METHODS

2.1 | Zooplankton and lake environment surveys

Zooplankton and water chemistry samples, and lake temperature and dissolved oxygen profiles, were collected from the deepest point of all lakes between mid-July to mid-August in 2013, 2014, 2015, and 2016 (see Appendix S1, Table S1.1 in Supporting Information for full lake details). Zooplankton were captured with vertical net hauls (80 μ m mesh) from 2m above the lake bottom up to the surface and preserved in 70% ethanol. Vertically integrated water chemistry samples were collected using a tube sampler (2.54 inner diameter)

that collected water from the top 5m of the water column. Water samples were filtered through an 80 μ m mesh, stored in sealed and ice-cooled sample bottles in the field, then stored at 3°C upon arrival at the lab. Cooled water samples were shipped generally within 48 hr of collection, which is within their perishable limit (www.desc.ca/water_chemistry), to the Dorset Environmental Science Center in Dorset, Ontario, Canada. These samples were processed following Ontario Ministry of the Environment protocols for alkalinity (E3042; mg/L of CaCO₃), calcium (E3249; mg/L), chloride (E3147; mg/L), conductivity (E3024; μ S cm⁻¹), dissolved organic carbon (DOC; E3422; mg/L), pH (E3042; analyzed as mol/L of hydrogen ions), total Kjeldahl nitrogen (TKN; E3424; mg/L) and total phosphorus (TP; E3036; μ g/L). Temperature and oxygen measurements were also collected from each lake at 1m intervals using a YSI 550A instrument (YSI Incorporated, Yellow Springs, OH). These measurements were used to estimate average bottom oxygen (mg/L), which is the amount of dissolved oxygen averaged across all depth intervals below the thermocline (calculated using the 'rLakeAnalyzer' package, v1.11.4.1 in R 3.6.1; Winslow et al., 2019, R Core Team, 2020). Bottom oxygen for lakes without a thermocline was calculated as the average dissolved oxygen across all depth intervals.

2.2 | Zooplankton identification

Cladoceran and copepod zooplankton were identified to species, with two exceptions owing to difficulties in morphological identification: (i) *Daphnia pulex* and *D. pulicaria* were grouped as *D. pulex/pulicaria*; and (ii) *Bosmina freyi* and *B. liederi* were grouped as *B. freyi/liederi*. All zooplankton identification was performed using Leica

MZ12 and MZ16 dissecting scopes, and a Leica DM E compound microscope (Leica Microsystems, Wetzlar, Germany). Zooplankton species densities (excluding juveniles) were determined following a standardized protocol from Girard et al. (2007). A known volume was repeatedly subsampled and all species in all counted subsamples were enumerated in their entirety. Subsampling concluded when at least 250 individual zooplankton had been identified, with no more than 50 individuals per species contributing to this total. All species counts were then converted into total density (individuals L⁻³) based on the total subsampled volume.

2.3 | Spatial community relationships

Potential spatial relationships among lakes were captured using two datasets: (i) lake latitude and longitude coordinates, used to capture broad east-west or north-south trends in zooplankton community composition (hereafter referred to as spatial 'trend' relationships); and (ii) Moran's eigenvector maps (MEMs; Dray et al., 2006) calculated from neighbourhood connectivity and spatial weighting matrices (detailed in Appendix S2). The MEM method is a spectral decomposition of the spatial relationships among sampling locations based on a connectivity scheme weighted by a distance function. Predictor variables produced using the MEM method represent spatial community relationships among habitats and can be used to model positive and negative community spatial autocorrelation. In our analyses, these variables were used to capture spatial relationships among our sampled zooplankton communities that were related to the geographic distances between different lakes (hereafter referred to as the spatial 'distance' relationships), which could be driven by inter-lake dispersal or spatially-structured environmental variation (Dray et al., 2012).

To calculate MEMs associated with the 2013–2016 zooplankton communities, we first removed the influence of any broad spatial trends by taking the residuals of a linear model of the community matrix from each year related to lake coordinates (a 'de-trended' community dataset; Legendre & Legendre, 2012). The de-trended community data for each year was then analysed using Mantel correlograms which depict compositional spatial correlations as a function of geographic distance between pairs of communities (Oden & Sokal, 1986), providing a visual guide to the type of spatial autocorrelation in our sampled zooplankton communities. This visualization step is important to better ensure that the candidate connectivity and weighting matrices used to calculate the MEM variables (Appendix S2) are those that likely capture real spatial relationships, and for improving MEM optimization by controlling the number of models being tested (Bauman et al., 2018). The de-trended zooplankton community composition matrices served as the ecological response variables for the Mantel correlograms, while lake latitude and longitude coordinates served as the geographic distance predictor matrix. In all four survey years, zooplankton communities exhibited significant ($p < 0.05$) negative spatial autocorrelation between lakes that were around 4–7km apart (see Appendix S2, Figure S2.1).

This spatial pattern indicated that the zooplankton communities of lakes an intermediate distance from one another were more dissimilar than expected. There was generally no significant positive or negative autocorrelation between very near or distant lakes, except for lakes in 2014 which exhibited significant negative autocorrelation at the smallest distance class of about 0.8km.

2.4 | Statistical analyses

Zooplankton densities were converted into a response matrix of community composition, with lakes in each survey year as rows and each species as columns. Any species that occurred in only a single lake per year (specifically *Daphnia ambigua* and *D. longiremis*) were excluded. The resulting zooplankton composition matrix was also Hellinger transformed (Legendre & Gallagher, 2001) prior to all analyses. All measured water chemistry variables were combined with measurements of maximum lake depth (m) and total lake area (km²) to create an 'environment' predictor matrix. Alkalinity, calcium and conductivity were always highly correlated ($r > 0.9$ for all years) with high variance inflation factors (VIFs > 10). We therefore used Principal Components Analysis (PCA) to condense these three variables into a single 'conductivity' PCA axis, which represented ~ 98% of their combined variability on PCA axis 1 in each year. The next highest correlations and VIFs were for TP and TKN ($r > 0.7$, VIFs > 9). These two variables were therefore condensed into a single 'nutrient' PCA axis, which represented more than 85% of their combined variability on PCA axis 1 in each year. All resulting lake morphology, water chemistry and PCA axes variables were then centred to their respective means and divided by their standard deviations prior to analyses.

We used variation partitioning (Legendre & Legendre, 2012) for each year to determine what amount of variability in zooplankton community composition was explained by the individual and co-varying components of local lake environment (i.e., centred lake depth, area and yearly water chemistry), broad-scale spatial trends (i.e., lake latitude and longitude), and spatial distances among lakes (i.e., yearly MEMs). Shared covariation between environment and spatial trends were interpreted as east-west or north-south trends in zooplankton community composition that also correlated to measured environmental variables. Shared covariation between environment and spatial distance were interpreted as underlying environmental relationships potentially driving the negative spatial autocorrelation detected in surveyed zooplankton communities. Significance ($p < 0.05$) of individual components in variation partitioning were assessed using global permutation tests (GPTs; Legendre & Legendre, 2012) of partial Redundancy Analyses (RDAs) that modelled the zooplankton community matrix in response to the matrix of the individual component of interest, conditioned on the other two predictor matrices. For example, a partial RDA model for determining the significance of the individual environment component in our variation partitioning analyses was structured as: Community composition ~ Environment, conditioned on

the effects of lake latitude/longitude coordinates and MEM variables. Additional RDAs of community composition in response to environmental or spatial variables were also used to aid in the post-hoc interpretation of the effects of individual environment, spatial trend and spatial distance variables within each year. All Mantel correlograms, variation partitioning and multivariate analyses were conducted in R 3.6.1 (R Core Team, 2020) using the 'vegan' package (v2.5–6; Oksanen et al., 2018). MEMs were created and selected using the 'adespatial' package (v0.3–7; Dray et al., 2019).

3 | RESULTS

3.1 | Variation partitioning

Local environment and spatial distance were both consistent and relatively equal independent structuring mechanisms of surveyed lake zooplankton communities in 2013, 2014, and 2015 (Figure 2). These components respectively explained between 11%–14% and 14%–19% of community variability (evidenced by significant GPTs of these individual components in these three years; Appendix S3: Table S3.2). However, in 2016, spatial distance independently explained ~ 10% of community variability, while local environment had no apparent relationship to zooplankton community composition, accounting for almost no explained community variability (Figure 2). This result was further evidenced by a non-significant GPT of the 2016 environment RDA ($n = 29$, 9 conditioning variables, $F_{8,28} = 0.97$, $p = 0.55$). The independent component of spatial directional trends in zooplankton composition were also inconsistent across years, capturing 12% and 9% of community variability in 2013 and 2015 respectively, but only 2% and 1% in 2014 and 2016 (evidenced by respective significant and non-significant GPTs in these years). The covarying component of environment and spatial trend, and environment and spatial distance, were both relatively consistent in importance across years, respectively accounting for between ~ 16%–24% and ~ 10%–20% of community variability in each year (Figure 2).

3.2 | Independent effects of environment on zooplankton

To isolate which environmental variables and zooplankton species were associated with the independent environment component, we used RDAs that related zooplankton composition to environmental variables separately for each survey year conditioned on the effects of spatial trend and distance. Lake maximum depth, chloride concentrations, DOC, nutrients and pH exhibited the most consistent relationships across 2013, 2014 and 2015, with evidence only for a possible influence of depth in 2016 (based on permutation tests in each year; Table 1). The most consistent zooplankton-environment relationship across years was *Diacyclops thomasi* which was generally associated with larger, deeper lakes that also tended

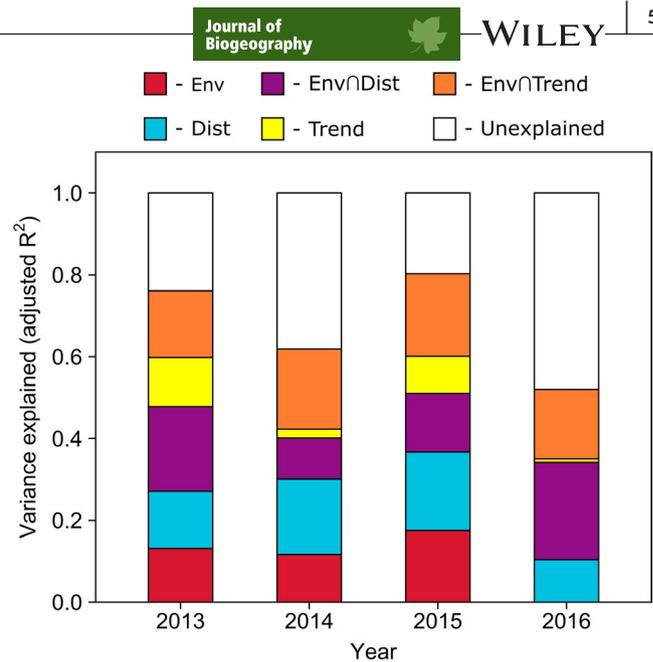


FIGURE 2 Variation partitioning of zooplankton community relationships to local lake environment, spatial trend and spatial distance in each survey year (2013–2016). The independent spatial distance component ('Dist'), and the covarying environment-distance ('Env ∩ Dist') and environment-trend ('Env ∩ Trend') components, are important across all years, while the independent environment ('Env') and spatial trend ('Trend') components are only important in some years. Note that spatial trend and distance have no covarying component because the zooplankton community data is de-trended prior to calculations of spatial distance relationships

to have higher values of bottom oxygen (Appendix S3, Figure S3.2 and S3.3). Other species-environment relationships were more variable across years, but *Daphnia pulex/pulicaria*, *Skistodiatomus oregonensis* or *Tropocyclops extensus* tended to dominate in shallower lakes.

3.3 | Independent and covarying effects of spatial trend on zooplankton

We investigated the independent relationship between spatial trend and the zooplankton communities using RDAs that related zooplankton composition to lake coordinates for each survey year, conditioned on the effects of environment and spatial distance. Only lake longitude (i.e., east-west trend) was consistently related to zooplankton composition in 2013 and 2015 (Figure 3; Appendix S4: Table S4.4), with no significant trend relationships in 2014 or 2016. In 2013 and 2015, there was an east-west shift in zooplankton composition from primarily small cladocerans (*B. freyi/liederi* and *Ceriodaphnia lacustris*) in eastern lakes to mixed communities of large cladocerans (e.g., *Daphnia dubia* and *D. mendotae*) and copepods (e.g., *Skistodiatomus oregonensis* and *Diacyclops thomasi*) in western lakes.

To disentangle the shared covariation between environment and spatial trend on zooplankton composition, we used RDAs to model community composition in each year in response to lake coordinates,

conditioned on the effect of spatial distance, then related the scores for any significant RDA axes to all environmental variables using linear regression (following methods in Legendre & Legendre, 2012). The covarying environment-trend component was consistently related to lake depth in all survey years (Appendix S4: Table S4.5), likely due to the tendency for lake depth to increase from east to west in our survey region. This directional, environmental gradient

TABLE 1 Results of permutation tests of individual environmental predictor variables from Redundancy Analyses (RDAs) in each survey year of the independent environment effect. RDAs used the zooplankton community in each survey year as the response variable, with all environmental variables as the predictors, conditioned on the effects of lake latitude/longitude coordinates and the Moran's Eigenvector Map variables

Survey year	Environmental predictor	F	p
2013	Bottom oxygen	2.03	0.042**
	Chloride	1.90	0.064*
	Conductivity (PCA 1)	1.32	0.23
	DOC	1.89	0.068*
	Nutrients (PCA 1)	2.32	0.025**
	pH	0.87	0.54
	Area	1.15	0.33
	Depth	4.23	<0.001**
2014	Bottom oxygen	1.33	0.22
	Chloride	2.00	0.046**
	Conductivity (PCA 1)	1.47	0.17
	DOC	1.03	0.42
	Nutrients (PCA 1)	1.47	0.16
	pH	1.98	0.045**
	Area	0.81	0.61
	Depth	2.32	0.022**
2015	Bottom oxygen	0.88	0.55
	Chloride	1.81	0.079*
	Conductivity (PCA 1)	0.94	0.49
	DOC	3.33	0.0022**
	Nutrients (PCA 1)	1.87	0.070*
	pH	3.58	0.0014**
	Area	1.39	0.20
	Depth	2.85	0.0060**
2016	Bottom oxygen	1.54	0.15
	Chloride	0.94	0.50
	Conductivity (PCA 1)	0.62	0.79
	DOC	0.98	0.45
	Nutrients (PCA 1)	0.37	0.96
	pH	0.54	0.85
	Area	0.85	0.56
	Depth	1.79	0.072*

* $p < 0.1$.

** $p < 0.05$.

had a strong influence on zooplankton composition because it determined whether communities were dominated by species characteristic of shallower (e.g., *Skistodiptomus oregonensis* and *Tropocyclops extensus*) versus deeper (e.g., *Limnocalanus macrurus* and *Diacyclops thomasi*) lakes.

3.4 | Independent and covarying effects of spatial distance on zooplankton

We investigated the independent relationship between spatial distance and the zooplankton communities using RDAs that related zooplankton composition to MEM variables for each survey year, conditioned on the effects of environment and spatial trend. We then extracted the scores from the first two RDA axes in each year, plotted these scores onto a map of our surveyed lakes, and assessed whether the MEM variables were capturing broad-scale, medium-scale or fine-scale spatial community patterns (Legendre & Legendre, 2012). The majority of MEM variables consistently captured fine-scale relationships between zooplankton composition and lake distance across years (Appendix S5: Figure S5.6). These patterns indicated that there were spatial clusters of similar zooplankton communities that tended to occur adjacent to very dissimilar clusters. Additionally, clusters further apart were more similar to one another than adjacent clusters, resulting in an alternating pattern of similar versus dissimilar groups of lake communities.

To disentangle the shared covariation between environment and spatial distance, we used RDAs to model community composition in each year in response to MEM variables, conditioned on the effect of spatial distance, then related the scores for only significant RDA axes to all environmental variables using linear regression. The MEM variables, which modelled negative spatial autocorrelation at intermediate distances, were most consistently related to bottom oxygen based on significant linear relationships in each year (Appendix S5: Table S5.6). Spatial clusters of lakes with lower bottom oxygen, which were primarily shallower lakes with a thermocline, tended to occur next to or an intermediate distance from clusters of lakes with higher bottom oxygen, which were either shallower lakes with no thermocline or deeper lakes.

4 | DISCUSSION

Our environmental and spatial datasets consistently explained between ~ 50%–80% of total community variability, which was high compared to other similar studies (~ 20%–40% is common; e.g., Cottenie et al., 2003; Fernandes et al., 2014; Strecker et al., 2011). This high explanatory power was due to three consistent components across all survey years: (i) the covarying environment-trend component; (ii) the covarying environment-distance component; and (iii) the independent spatial distance component. Each explained between 10%–20% of zooplankton community variability within years and combined always explained about 50% of total

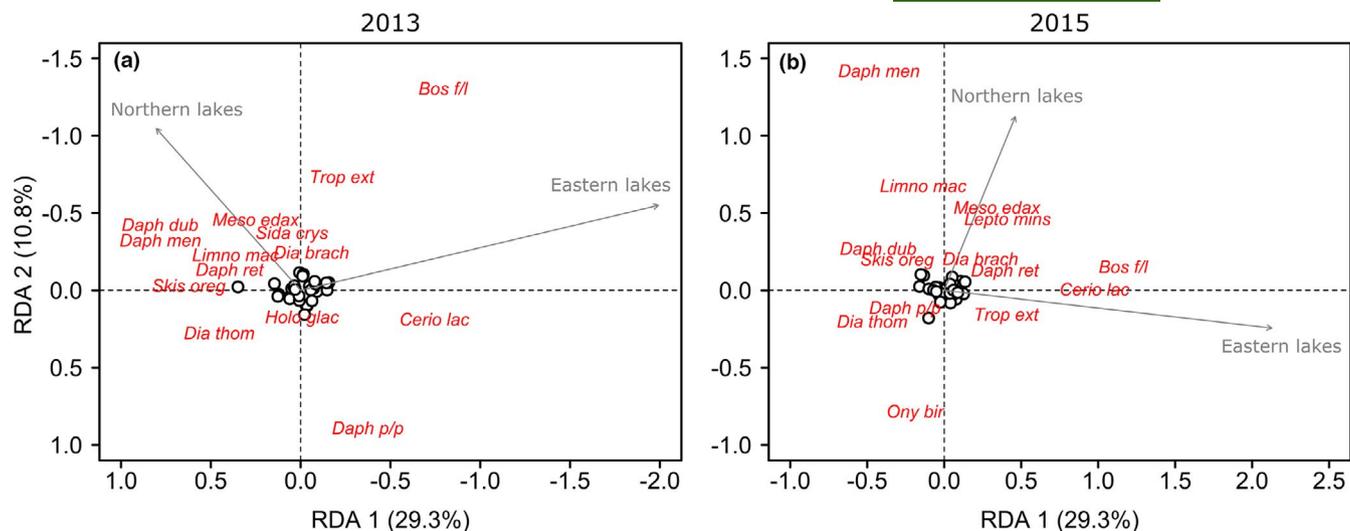


FIGURE 3 Redundancy analysis (RDA) of zooplankton community composition (white points) in (a) 2013 and (b) 2015 related to the independent influences of lake latitude and longitude (grey arrows). Longitude shows the strongest association with RDA axis 1 in both years. Lakes further east tend to be shallower and dominated by small cladocerans, such as *Ceriodaphnia lacustris*. Lakes further west tend to be deeper and dominated by a mixture of large cladocerans (e.g., *Daphnia mendotae*) and copepods (e.g., *Skistodiaptomus oregonensis*). Full names associated with the species abbreviations can be found in Appendix S3, Table S3.3. Note the change in the signs of the x- and y-axes across panels

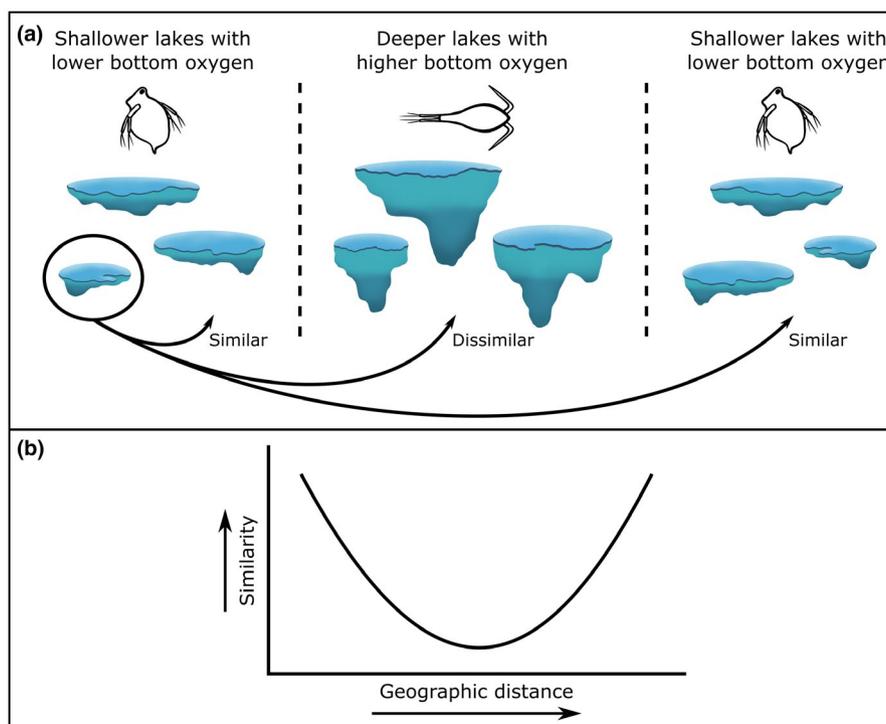


FIGURE 4 Negative spatial autocorrelation among surveyed zooplankton communities was related to lake bottom oxygen and depth. Spatial clusters of (a) shallow lakes with lower bottom oxygen tended to occur adjacent to clusters of deeper lakes with higher bottom oxygen in an alternating pattern. The zooplankton communities within each cluster therefore tended to be somewhat similar to one another, such as *Daphniidae* which were common across shallow lakes or *Diacyclops thomasi* in deeper lakes. Conversely, communities between adjacent clusters tended to be more dissimilar than expected based on their geographic distance due to large differences in their environments, while distant clusters were more similar due to their more similar environments. This alternating oxygen and depth pattern was also likely partly or wholly responsible for the spatial relationships detected in the Mantel correlograms (Appendix S2, Figure S2.1), and modelled by the MEMs, of (b) negative spatial autocorrelation among lakes an intermediate distance apart

community variation. Regarding the covarying environmental-spatial components, both the spatial trend and distance relationships were consistently related to lake depth and/or bottom oxygen, which likely occurred due to the underlying geology of our region. Lake depth tended to decline from west to east, with bottom oxygen tending to be higher in the western deeper lakes compared to the shallower eastern lakes that were deep enough to form a thermocline. Similarly, the covarying environment-distance component was consistently related to fine-scale negative spatial autocorrelation in which spatial clusters of shallow lakes with lower bottom oxygen occurred adjacent to clusters of mostly deeper lakes with higher bottom oxygen in an alternating pattern (visually summarized in Figure 4). These spatial patterns in how the lakes of our study region were initially formed thus affected compositional patterns by determining whether communities tended to be dominated by species characteristic of deeper, higher oxygen (e.g., *Diatom thomasi*) versus shallower, lower oxygen (e.g., *Daphniidae* and *Tropocyclops extensus*) waterbodies. Geomorphological heterogeneity is a key determinant of many environmental and spatial factors that can influence community composition in aquatic and terrestrial systems, including elevation (Altermatt et al., 2013; Lindholm et al., 2020) and soil drainage (Nichols et al., 1998), and our results indicate a similar influence of lake bathymetry. Notably, the consistent environmental relationship with geomorphology across all survey years suggests that even single-year snapshots can provide an accurate picture of how these types of slowly changing processes are acting to drive community structure.

The consistent explanatory power of inter-lake spatial distance across all years was also related to fine-scale negative spatial autocorrelation. This pattern was caused by spatial clusters of similar lake communities that were located adjacent to clusters of communities that were similar within their respective lake cluster, but very dissimilar to adjacent clusters. Community similarity also did not decrease linearly with distance, as would be expected if “near things are more related than distant things” (Tobler, 1970), because more distant community clusters were more similar than community clusters adjacent to one another. It is unlikely that this alternating similar-dissimilar spatial clustering pattern was due to the MEMs just modelling noise in our data (an issue discussed further in Gilbert & Bennett, 2010) because it matches the negative spatial autocorrelation at intermediate lake distances initially detected in our Mantel correlogram analyses, which we specifically designed the MEMs to model. It also parallels the type of negative spatial autocorrelation with depth and bottom oxygen that we detected in correlations between the MEM variables and the environmental predictors. Thus, it is likely that part or all of the independent spatial distance component was due to zooplankton responding to other, unmeasured abiotic or biotic variables related to this same alternating pattern of lake oxygen and morphology, such as similarities in dispersal or other environmental characteristics among proximate clusters of shallower versus deeper lakes.

In contrast with the consistent influences of the above community processes across all years, the independent environment

and regional spatial trend components were less consistent, ranging from both explaining a maximum of 25% down to a minimum of 1% of community variability depending upon the sampling year. This variability in explanatory power was especially evident for the independent environment component which consistently explained between 12%–17% of community variability from 2013 through 2015, but then explained almost no community variability in 2016. There were several possible explanations for this sudden lack of environmental relationships. One explanation is that lake chemistry was less heterogeneous in 2016, subsequently reducing compositional differences among lakes related to differences in their local environments. This was, however, unlikely as there were no evident changes in lake chemistry values nor variability across the study years (Appendix S3: Figure S3.4). Alternatively, the independent environment component that explained substantial community variability from 2013–2015 may have been captured by the MEM variables in 2016. A known complication with the MEM method is that it can model any spatially structured species relationships, including those driven by the environment (Gilbert & Bennett, 2010). We tested for this issue by correlating the environmental predictors to the MEM variables in each year and found no changes through time, but these tests only address linear relationships. MEMs can also model non-linear spatially structured species-environment relationships, which would therefore appear in the independent spatial component (Gilbert & Bennett, 2010). However, this explanation is also unlikely because there was no substantial increase in the amount of variance explained by the independent spatial component in 2016, which would provide evidence that the local environmental relationships from other years were ‘loading’ into the spatial portion. Additionally, it is implausible that all the linear species-environment relationships detected in 2013, 2014 and 2015 suddenly became non-linear relationships in 2016.

A more plausible explanation for the lack of independent environmental relationships in 2016 was the appearance of a new, unmeasured environmental gradient. Unmeasured ecological factors are a common problem when assessing the mechanisms that may be driving community composition because it is difficult to measure all aspects of an organism's environment. Results that appear to show a lack of environmental structuring may thus instead reflect a lack of data (Brown et al., 2017). Fortunately, a strength of temporal community analysis is in helping to identify where these data gaps are potentially occurring by comparing relevant variables through time. Our measured environmental variables explained a consistent portion of community variability from 2013 to 2015, indicating that in these years our metrics were capturing important environmental factors, suggesting that 2016 may have been an anomalous year in which a wider variety of data types were needed. Indeed, the spring and summer of that year were some of the driest periods on record for southern Ontario, which affected seasonal precipitation patterns (Figure 5). Zooplankton composition in our surveyed lakes may therefore have been responding to changes in lake water levels, total received runoff, or other water chemistry parameters related to precipitation that we did not have the data to quantify. Such temporal

swings in the importance of measured environmental variables may be rare if they are driven by extreme weather events, but extreme events are also becoming more frequent and severe with progressing climate change (Ummerhofer & Meehl, 2017). Communities may therefore increasingly experience large inter-annual or seasonal shifts in predominant environmental processes. This increasing variability highlights a need to consider which environmental mechanisms may become more relevant during anomalous periods, and a need to increase monitoring efforts to ensure that data types related to extreme events are being collected.

Temporal shifts in the variability explained by the independent spatial trend component were primarily driven by five, canal-connected shallower lakes (<20m maximum depth) clustered on the eastern side of our survey region, which contrasted with the mixture of naturally connected deep (>20m) and shallow lakes on the western side. The communities of the eastern, shallow lakes were primarily characterized by *Ceriodaphnia lacustris*, *Bosmina freyi/lieberi* and *Tropocyclops extensus*, all of which are smaller cladoceran and copepod species that may either succeed better in more littoral waterbodies (e.g., *Ceriodaphnia*; Lauridsen et al., 1999) or that can better survive predators that target larger-bodied zooplankton. The western lakes were characterized by larger-bodied cladocerans (*Daphnia dubia* and *D. mendotae*) and copepods (*Skistodiaptomus oregonensis*), and copepods that were always associated with the deeper lakes of our region (*Diacyclops thomasi* and *Limnocalanus macrurus*). All of these species are known to use diel vertical migration to avoid predation (Dodson, 1988; Wells, 1960), which may therefore be more effective in deeper lakes.

Importantly, there were some zooplankton that were consistently associated with eastern (smaller cladocerans and copepods) versus western (*Diacyclops thomasi* and *Limnocalanus macrurus*) lakes in all survey years, while other species varied among years, which drove inter-annual variability in the spatial trend component. *Daphnia*

mendotae and *Skistodiaptomus oregonensis* serve as good examples of this yearly variability. In 2013 and 2015, both species were generally not found in the more easterly shallow lakes (Figure 3), but they were found in these lakes in 2014 and 2016 (Appendix S4: Figure S4.5), resulting in little to no east-west trend in composition in the latter years. There are multiple possible explanations for these inter-year trend differences. Some unmeasured abiotic or biotic factor that was driving the east versus west community separation could be changing among years. If, for example, predation determined which species persisted in shallow eastern versus deeper western lakes, then inter-annual shifts in predator abundances or fishing pressure could have altered predation and allowed previously excluded species to establish. Alternatively, species occurrences in the eastern lakes in some years and not others could have resulted from how the sampling schedule overlapped with lake phenology. The timings of maximum zooplankton abundance vary seasonally, inter-annually, among species, and among lakes (e.g., Kratz et al., 1987), and happening to sample a particular species on a high abundance day in one year and a low abundance day in another could produce artificial community patterns (Arnott et al., 1999). This sampling effect is unlikely to be an issue for species with consistent environmental relationships across years, such as those always associated with a given lake depth, but it could be producing the inconsistent east-west compositional patterns across years for which we have no clear environmental explanation. Ultimately, both of these proposed mechanisms potentially driving temporal variation in the influence of the spatial trend are just possibilities and further research is required to determine the exact mechanism at work.

5 | CONCLUSIONS

Our surveyed lake zooplankton communities were structured by a complex mixture of local factors, such as lake chemistry, and regional-scale processes, such as geomorphological patterns of lake depth. The relative importance of most of these factors were generally consistent across years, particularly if they strongly related to community structuring mechanisms that exhibited little to no inter-annual variation (e.g., lake morphology), while the relative importance of other factors changed in certain years potentially because they were driven by more transient environmental mechanisms, such as extreme weather events. These inferences of consistent versus transient community structuring mechanisms suggests that studies which aim to uncover broad-level processes driving composition via community snapshots may accurately capture local or regional processes that are consistent or that change slowly over time. However, such studies may miss temporal variability in transient or rapidly changing local and regional processes. Furthermore, community snapshots collected in anomalous years may even fail to capture crucial mechanisms that are generally present at other time points. For example, if we only collected a community snapshot during the drought in 2016 then we may have concluded that there was little influence of our measured environmental variables, which would

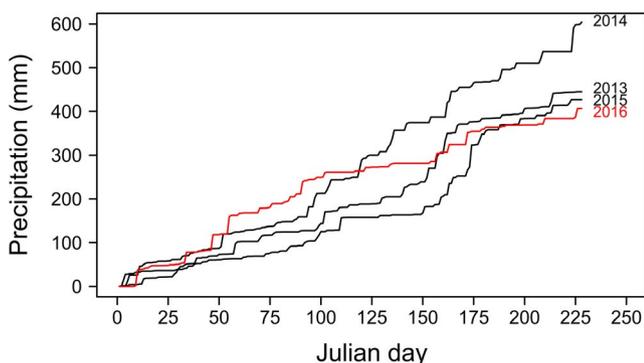


FIGURE 5 Cumulative precipitation in the study region from January 1 to August 16 (the final sampling day) from 2013 to 2016, with 2016 highlighted in red. Precipitation in 2016 was slightly above the other years until late-April to early-May, after which there was comparatively less precipitation, with very little rain falling from May to mid-June and from July to mid-August. Precipitation data were extracted from historical records for the Kingston, ON airport which were compiled by Environment Canada

misrepresent the generally important environmental relationships we found in all other years.

Efforts to disentangle the relative importance of local and regional community mechanisms could therefore benefit from further considering which processes are likely temporally 'consistent' versus 'transient'. In our study, lake depth was the most temporally consistent structuring mechanism because it does not change over time but also varied widely among our sampled lakes. Geomorphology is potentially not as important in other regions, such as those with low heterogeneity in elevation or bathymetry, but it provides a good example of a factor whose influence would be consistently captured in a variety of ecosystems regardless of which years are sampled. Some aspects of all ecosystems, aquatic or terrestrial, are likely to vary little over time or change slowly (e.g., elevation or soil profile), while others could be more changeable, such as weather, nutrients or anthropogenic impacts, and studies aiming to include the more transient components would benefit from considering and possibly sampling their temporal variation. Determining how species composition is affected by temporally consistent versus transient factors, and comparing conclusions across ecosystems, would be a valuable contribution to ongoing efforts to better understand the mechanisms driving community structure.

ACKNOWLEDGEMENTS

We thank Ayo Adurogbangba, Amelia Corrigan, Katrina Furlanetto, Ariel Gittens, Amelia Cox, Phil Anderson, Marcus Threndyle, Megan Borland, Lauren Witterick, Emily Drinkwater, and the Queen's University Biology Station for logistical support. Access to multiple field sites was also authorized by Frontenac Provincial Park. Funding was provided by an Alexander and Cora Munn Summer Research Award to Kaitlyn Brougham, along with Natural Sciences and Engineering Research Council (NSERC) Discovery grants to SEA and WAN, and an NSERC Canada Graduate Scholarship to JSS. Queen's University is situated on traditional Anishinaabe and Haudenosaunee Territory. Many of the lakes used in this study are situated on unceded Algonquin Anishinaabe territory which is a part of the Algonquin Land Claim by the Algonquins of Ontario currently under negotiation with the federal government of Canada. We recognize the precolonial history of this land and the peoples who lived here and continue to live here. The cultures and spiritualities of Indigenous peoples are connected to the land and the land is an integral part of their ways of knowing and living. We appreciate the opportunity to study and learn from these lakes.

DATA AVAILABILITY STATEMENT

Data is publicly available from the Dryad digital repository at <https://doi.org/10.5061/dryad.kh189323z>.

ORCID

James S. Sinclair  <https://orcid.org/0000-0003-0787-7342>

REFERENCES

Altermatt, F., Seymour, M., & Martinez, N. (2013). River network properties shape α -diversity and community similarity patterns of

- aquatic insect communities across major drainage basins. *Journal of Biogeography*, 40(12), 2249–2260. <https://doi.org/10.1111/jbi.12178>
- Arnott, S. E., Yan, N. D., Magnuson, J. J., & Frost, T. M. (1999). Interannual variability and species turnover of crustacean zooplankton in Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(1), 162–172. <https://doi.org/10.1139/f98-152>
- Bauman, D., Drouet, T., Fortin, M.-J., & Dray, S. (2018). Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. *Ecology*, 99(10), 2159–2166. <https://doi.org/10.1002/ecy.2469>
- Brias, A., Mathias, J.-D., & Deffuant, G. (2018). Inter-annual rainfall variability may foster lake regime shifts: An example from Lake Bourget in France. *Ecological Modelling*, 389, 11–18. <https://doi.org/10.1016/j.ecolmodel.2018.10.004>
- Brown, B. L., Sokol, E. R., Skelton, J., & Tornwall, B. (2017). Making sense of metacommunities: Dispelling the mythology of a metacommunity typology. *Oecologia*, 183(3), 643–652. <https://doi.org/10.1007/s00442-016-3792-1>
- Cañedo-Argüelles, M., Gutiérrez-Cánovas, C., Acosta, R., Castro-López, D., Cid, N., Fortuño, P., Munné, A., Múrria, C., Pimentão, A. R., Sarremejane, R., Soria, M., Tarrats, P., Verkaik, I., Prat, N., & Bonada, N. (2020). As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. *Journal of Biogeography*, 47(9), 1861–1874. <https://doi.org/10.1111/jbi.13913>
- Capers, R. S., Selsky, R., & Bugbee, G. J. (2010). The relative importance of local conditions and regional processes in structuring aquatic plant communities. *Freshwater Biology*, 55(5), 952–966. <https://doi.org/10.1111/j.1365-2427.2009.02328.x>
- Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (2012). *Dispersal ecology and evolution*. Oxford University Press.
- Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, 8(11), 1175–1182. <https://doi.org/10.1111/j.1461-0248.2005.00820.x>
- Cottenie, K., Michels, E., Nuytten, N., & De Meester, L. (2003). Zooplankton metacommunity structure: Regional vs. local processes in highly interconnected ponds. *Ecology*, 84(4), 991–1000.
- de Hoyos, C., & Comín, F. A. (1999). The importance of inter-annual variability for management. In D. M. Harper, B. Brierley, A. J. D. Ferguson, & G. Phillips (Eds.), *The ecological bases for lake and reservoir management* (pp. 281–291). Springer.
- Dodson, S. (1988). The ecological role of chemical stimuli for the zooplankton: Predator-avoidance behavior in *Daphnia*. *Limnology and Oceanography*, 33(6), 1431–1439. https://doi.org/10.4319/lo.1988.33.6_part_2.1431
- Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Wagner, H. H. (2019). *adespatial*: Multivariate multiscale spatial analysis. R package version 0.3-7. <https://CRAN.R-project.org/package=adespatial>
- Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, 196(3), 483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>
- Dray, S., Péliissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F. G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82(3), 257–275. <https://doi.org/10.1890/11-1183.1>
- Erős, T., Sály, P., Takács, P., Specziár, A., & Bíró, P. (2012). Temporal variability in the spatial and environmental determinants of functional metacommunity organization – stream fish in a human-modified landscape. *Freshwater Biology*, 57(9), 1914–1928. <https://doi.org/10.1111/j.1365-2427.2012.02842.x>
- Fernandes, I. M., Henriques-Silva, R., Penha, J., Zuanon, J., & Peres-Neto, P. R. (2014). Spatiotemporal dynamics in a seasonal metacommunity

- structure is predictable: The case of floodplain-fish communities. *Ecography*, 37(5), 464–475.
- Gilbert, B., & Bennett, J. R. (2010). Partitioning variation in ecological communities: Do the numbers add up? *Journal of Applied Ecology*, 47(5), 1071–1082. <https://doi.org/10.1111/j.1365-2664.2010.01861.x>
- Girard, R., Clark, B. J., Yan, N. D., Reid, R. A., David, S. M., Ingram, R. G., & Findeis, J. G. (2007). *History of chemical, physical and biological methods, sample locations and lake morphometry for the Dorset Environmental Science Centre (1973–2006)*. Ontario Ministry of the Environment Data Report.
- Göthe, E., Angeler, D. G., Gottschalk, S., Löfgren, S., & Sandin, L. (2013). The influence of environmental, biotic and spatial factors on diatom metacommunity structure in Swedish headwater streams. *PLoS One*, 8(8), e72237. <https://doi.org/10.1371/journal.pone.0072237>
- Göthe, E., Angeler, D. G., & Sandin, L. (2013). Metacommunity structure in a small boreal stream network. *Journal of Animal Ecology*, 82(2), 449–458. <https://doi.org/10.1111/1365-2656.12004>
- Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press.
- Havel, J. E., & Shurin, J. B. (2004). Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnology and Oceanography*, 49, 1229–1238. https://doi.org/10.4319/lo.2004.49.4_part_2.1229
- Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology*, 60(5), 845–869. <https://doi.org/10.1111/fwb.12533>
- Héroult, B., & Honnay, O. (2005). The relative importance of local, regional and historical factors determining the distribution of plants in fragmented riverine forests: An emergent group approach. *Journal of Biogeography*, 32(12), 2069–2081. <https://doi.org/10.1111/j.1365-2699.2005.01351.x>
- Hoeinghaus, D. J., Winemiller, K. O., & Birnbaum, J. S. (2007). Local and regional determinants of stream fish assemblage structure: Inferences based on taxonomic vs. functional groups. *Journal of Biogeography*, 34(2), 324–338. <https://doi.org/10.1111/j.1365-2699.2006.01587.x>
- Jackson, D. A., Peres-Neto, P. R., & Olden, J. D. (2001). What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(1), 157–170.
- Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Luo, Y., Reichstein, M., Smith, M. D., Smith, S. D., Bell, J. E., Fay, P. A., Heisler, J. L., Leavitt, S. W., Sherry, R., Smith, B., & Weng, E. (2008). Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, 58(9), 811–821. <https://doi.org/10.1641/B580908>
- Kratz, T. K., Frost, T. M., & Magnuson, J. J. (1987). Inferences from spatial and temporal variability in ecosystems: Long-term zooplankton data from lakes. *The American Naturalist*, 129(6), 830–846. <https://doi.org/10.1086/284678>
- Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology*, 48, 1161–1172. <https://doi.org/10.1046/j.1365-2427.2003.01086.x>
- Lauridsen, T. L., Jeppesen, E., Mitchell, S. F., Lodge, D. M., & Burks, R. L. (1999). Diel variation in horizontal distribution of *Daphnia* and *Ceriodaphnia* in oligotrophic and mesotrophic lakes with contrasting fish densities. *Hydrobiologia*, 408, 241–250.
- Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271–280. <https://doi.org/10.1007/s004420100716>
- Legendre, P., & Legendre, L. F. J. (2012). *Numerical Ecology*. Elsevier Science.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7(7), 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Lindholm, M., Alahuhta, J., Heino, J., & Toivonen, H. (2020). No biotic homogenisation across decades but consistent effects of landscape position and pH on macrophyte communities in boreal lakes. *Ecography*, 43(2), 294–305. <https://doi.org/10.1111/ecog.04757>
- Lindström, E. S., & Langenheder, S. (2012). Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, 4(1), 1–9. <https://doi.org/10.1111/j.1758-2229.2011.00257.x>
- Moritz, C., Meynard, C. N., Devictor, V., Guizien, K., Labruno, C., Guarini, J.-M., & Mouquet, N. (2013). Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. *Oikos*, 122(10), 1401–1410. <https://doi.org/10.1111/j.1600-0706.2013.00377.x>
- Nichols, W. F., Killingbeck, K. T., & August, P. V. (1998). The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. *Conservation Biology*, 12(2), 371–379. <https://doi.org/10.1046/j.1523-1739.1998.96237.x>
- Oden, N. L., & Sokal, R. R. (1986). Directional autocorrelation: An extension of spatial correlograms to two dimensions. *Systematic Zoology*, 35(4), 608–617. <https://doi.org/10.2307/2413120>
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., & Wagner, H. (2018). *vegan: Community ecology package*. R package version (p. 2.5–6.). <https://CRAN.R-project.org/package=vegan>
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ricklefs, R. E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, 235(4785), 167–171.
- Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T., & Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography*, 44(12), 2752–2763. <https://doi.org/10.1111/jbi.13077>
- Schindler, D. W., Bayley, S. E., Parker, B. R., Beaty, K. G., Cruikshank, D. R., Fee, E. J., Schindler, E. U., & Stainton, M. P. (1996). The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. *Limnology and Oceanography*, 41(5), 1004–1017. <https://doi.org/10.4319/lo.1996.41.5.1004>
- Schweiger, O., Maelfait, J. P., Van wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., & Bugter, R. (2005). Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology*, 42(6), 1129–1139. <https://doi.org/10.1111/j.1365-2664.2005.01085.x>
- Simberloff, D. (2004). Community ecology: Is it time to move on? (An American Society of Naturalists Presidential Address). *The American Naturalist*, 163, 787–799. <https://doi.org/10.1086/420777>
- Soranno, P. A., Webster, K. E., Riera, J. L., Kratz, T. K., Baron, J. S., Bukaveckas, P. A., Kling, G. W., & Leavitt, P. R. (1999). Spatial variation among lakes within landscapes: Ecological organization along lake chains. *Ecosystems*, 2(5), 395–410. <https://doi.org/10.1007/s100219900089>
- Strecker, A. L., Casselman, J. M., Fortin, M.-J., Jackson, D. A., Ridgway, M. S., Abrams, P. A., & Shuter, B. J. (2011). A multi-scale comparison of trait linkages to environmental and spatial variables in fish communities across a large freshwater lake. *Oecologia*, 166(3), 819–831. <https://doi.org/10.1007/s00442-011-1924-1>
- Temperton, V. M., Hobbs, R. J., Nuttle, T., & Halle, S. (2004). *Assembly rules and restoration ecology: Bridging the gap between theory and practice*. Island Press.
- Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptačnik, R., Vanschoenwinkel, B., Viana, D. S., & Chase, J. M. (2020). A process-based metacommunity framework linking local and regional

- scale community ecology. *Ecology Letters*, 23(9), 1314–1329. <https://doi.org/10.1111/ele.13568>
- Tobler, W. R. (1970). A computer movie simulating urban growth in the Detroit region. *Economic Geography*, 46, 234–240. <https://doi.org/10.2307/143141>
- Ummerhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1723), 20160135.
- Urban, M. C. (2004). Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, 85(11), 2971–2978. <https://doi.org/10.1890/03-0631>
- Vagle, G. L., & McCain, C. M. (2020). Natural population variability may be masking the more-individuals hypothesis. *Ecology*, 101(5), e03035. <https://doi.org/10.1002/ecy.3035>
- Van der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N., Cousin, S., Declerck, S., Jeppesen, E., Conde-Porcuna, J.-M., Schwenk, K., Zwart, G., Degans, H., Vyverman, W., & De Meester, L. (2007). The power of species sorting: Local factors drive bacterial community composition over a wide range of spatial scales. *Proceedings of the National Academy of Sciences*, 104(51), 20404–20409. <https://doi.org/10.1073/pnas.0707200104>
- Vellend, M. (2016). *The theory of ecological communities*. Princeton University Press.
- Verleyen, E., Vyverman, W., Sterken, M., Hodgson, D. A., De Wever, A., Juggins, S., Van de Vijver, B., Jones, V. J., Vanormelingen, P., Roberts, D., Flower, R., Kilroy, C., Souffreau, C., & Sabbe, K. (2009). The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos*, 118(8), 1239–1249. <https://doi.org/10.1111/j.1600-0706.2009.17575.x>
- Wang, J., Bai, X., Hu, H., Clites, A., Colton, M., & Lofgren, B. (2012). Temporal and spatial variability of Great Lakes ice cover, 1973–2010. *Journal of Climate*, 25(4), 1318–1329. <https://doi.org/10.1175/2011JCLI4066.1>
- Wells, L. (1960). Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. *US Fish and Wildlife Service Fishery Bulletin*, 60, 343–369.
- Werner, E. E., Yurewicz, K. L., Skelly, D. K., & Relyea, R. A. (2007). Turnover in an amphibian metacommunity: The role of local and regional factors. *Oikos*, 116(10), 1713–1725. <https://doi.org/10.1111/j.0030-1299.2007.16039.x>
- Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: Dispersal pathways affect invasion success. *Trends in Ecology and Evolution*, 24(3), 136–144. <https://doi.org/10.1016/j.tree.2008.10.007>
- Winslow, L., Read, J., Woolway, R., Brentrup, J., Leach, T., Zwart, J., Albers, S., & Collinge, D. (2019). *rLakeAnalyzer: Lake physics tools. R package version (p. 1.11.4.1.)*. <https://CRAN.R-project.org/package=rLakeAnalyzer>

BIOSKETCH

The work presented here resulted from a collaboration between the Arnott (arnottlab.weebly.com) and Nelson (nelsonw6.wixsite.com/mysite) labs at Queen's University. The focus of this collaboration was to develop a better spatial and temporal understanding of the local and regional drivers of community composition using zooplankton from lakes in the surrounding region as a study system.

Author contributions: JSS assisted with data collection, conducted the analyses, and wrote the majority of the manuscript. SEA funded and supervised the study, assisted with data collection, and wrote portions of the manuscript. WAN funded and supervised the study, assisted with data collection, and edited the manuscript. KBB assisted with data collection, processed zooplankton samples and edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sinclair JS, Arnott SE, Nelson WA, Brougham KB. Consistent and transient drivers of freshwater zooplankton communities. *J Biogeogr.* 2020;00:1–12. <https://doi.org/10.1111/jbi.14039>