# COMPARISON OF ZOOPLANKTON COMMUNITES IN WILDFIRE DISTURBED AND REFERENCE LAKES IN THE SAHTÚ SETTLEMENT AREA

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By

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## **Abstract**

The Sahtú Settlement Area (SSA) in Canada's Northwest Territories is experiencing significant environmental changes. The mean annual temperature has increased >1.5°C in the past 50 years, and forest expansion and lighting ignitions are increasing the frequency and severity of wildfires. As fires increase in frequency, it is important to understand how aquatic ecosystems respond to changes in their water catchments. Changes in lake water quality associated with wildfires are likely to affect aquatic communities, including the zooplankton. Zooplankton play a vital role in freshwater food webs, as they transfer energy from primary producers to larger organisms such as macroinvertebrates and fish. Zooplankton were collected and water quality was measured in 20 lakes during 2018 and 2019 in the SSA: 9 lakes were affected by 2014 wildfires, and 11 had not been affected by fires since the 1970s. Zooplankton were identified down to the genus level, and communities were compared between burned and reference lakes to examine differences in richness, diversity, percent abundance of feeding groups, and relative abundance. There were no significant differences in any of these metrics between burned and reference lakes. Redundancy analysis revealed that the variation among zooplankton communities in the lakes sampled was best explained by calcium, temperature, macrophyte density, and total organic carbon, but again failed to identify differences caused by wildfires. Since no inherent differences were found between the northern zooplankton communities 4-5 years after fires, it suggests that they show a resiliency to wildfire disturbances similar to that found for southern communities. Further analysis of rotifer and fish assemblages within the lakes of the SSA is needed in order to gain a full understanding of the factors driving differences in zooplankton community composition among lakes.

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# 1.0 – Introduction

#### 1.1 – Background

The Sahtú Settlement Area (SSA) is located in the Northwest Territories, just south of Great Bear Lake in the taiga boreal ecoregion (Cott & Mochnacz, 2007). Five communities reside within the SSA; Norman Wells, Colville Lake, Déline, Fort Good Hope, and Tulita. Tulita, Norman Wells, and Fort Good Hope are located along the Mackenzie River, and use the river for transportation, drinking water, and fishing. The SSA is a discontinuous permafrost rich region, where 50-90% of the soil contains permafrost (Golder Associates, 2015; NWT Environmental Audit, 2005). Thousands of small waterbodies, ranging from lakes and ponds, to slow flowing sloughs are found across the landscape (Golder Associates, 2015). These small lakes are important habitat for a range of terrestrial and aquatic species valued by northern communities.

The mean annual temperature in the Sahtú Settlement Area (SSA) has increased by >1.5°C, the in the past 50 years (Woo et al., 2007). The increased temperature is allowing for flora density within the northern boreal forest to increase due to a northward shift in the boreal forest ecoregions (Veraverbeke et al., 2017). These new conditions coupled with the increase in lightning ignitions have led to a higher frequency of wildfires in the northern boreal ecosystems (Veraverbeke et al., 2017). One such fire burned through the SSA from July 10<sup>th</sup> to July 14<sup>th</sup>, 2014. This wildfire passed through watersheds, burning off >68% of the surrounding vegetation of the area's lakes. This drastic alteration of terrestrial vegetation in lake watersheds is a concern, as water quality and the composition of invertebrate communities can be influenced by interactions between lakes and their watersheds (Bisson et al., 2003). One group of invertebrates in lakes, the zooplankton, are particularly sensitive to changes in water quality. Although there

have been multiple studies regarding the impacts of wildfires on zooplankton communities in the southern boreal forest, there has yet to be research on the effects of wildfires on zooplankton community composition in northern boreal lakes (Jalal et al., 2005; Patoine et al., 2002). With growing concerns on the increasing frequency of wildfires in sub-arctic Canada, it is important to understand how ecological processes within lakes respond to wildfires.

#### 1.2 – Impacts of fires on Watersheds

Wildfires are a natural occurrence within the boreal forest. This has resulted in the aquatic biota that have lived in affected watersheds forming a natural resilience to wildfire disturbances (Bisson et al., 2003). The disturbances that do occur in northern boreal watersheds, however, have been shown to alter the stability of the environment, creating opportunities for organisms to thrive under new conditions, effectively increasing biological diversity (Bisson et al., 2003). While wildfires may have had a positive impact on the diversity of aquatic biota, there is still growing concern about the increased frequency of wildfires and the potential impacts on smaller water bodies (Walker et al., 2018). Due to the loss of vegetation in affected watersheds, there is a large impact on the sedimentation of these wildfire impacted lakes (Bisson et al., 2003). For example, a study of a 21,000 ha burn, near Lost Creek in Northern Alberta, showed that post burn, the amount of suspended solids within the water body increased 8-9 times above the reference measurements (Silins et al., 2009).

Sedimentation is of greater concern in areas of discontinuous permafrost, as vegetation regrowth is slower, allowing for more sediment loading to occur before the watershed's vegetation has made a recovery (Scrimgeour et al., 2001). It can take up to ten years before the insulating vegetation that protects the soil makes a full recovery post fire (Zhang et al., 2015). The active layer of soil increases within five years post fire, expanding the area of sediment that

can be eroded into the lake (Gibson et al., 2018). The increased sediment loading of lakes can also increase the amount of heavy metals that are loaded into the water body. One compound of concern is methylmercury (CH<sub>3</sub>Hg), which is readily bioavailable, and can bioaccumulate within aquatic food webs. (Garcia & Carignan, 2005; Kelly et al., 2006). Higher erosional rates can also increase nutrient loading to the surrounding water bodies, impacted food web dynamics and altering diversity for a variety of aquatic invertebrate communities (Lewis et al., 2014; Scrimgeour et al., 2001; Silins et al., 2014).

#### 1.3 – Impacts on Water Quality

Initial impacts on water quality post fire are quite severe. Fires in the catchments of subarctic lakes have been associated with increased total phosphorus (TP), and total nitrogen (TN)
(McEachern et al., 2000; Scrimgeour et al., 2001; Silins et al., 2014). Higher concentrations of
TN, and especially TP, can lead to a direct increase in primary production (phytoplankton
growth) within lakes, which increases turbidity. Turbidity can also be affected by increases in
erosion within the watershed due to loss of terrestrial vegetation (Tecle & Neary, 2015). Higher
rates of erosion and increased sediment loading can lead to increases in organic matter input to
lakes, causing decreased dissolved oxygen (DO) levels as aerobic bacteria break down organic
compounds (Lyon & O'Connor, 2008). The increase in organic matter input also can cause an
increase in dissolved organic carbon (DOC), total organic carbon (TOC), and colour in affected
lakes (Burd et al., 2018; McEachern et al., 2000; Scrimgeour et al., 2001). Since the SSA is
located in a taiga boreal ecoregion, it has high concentrations of lignin in peat soils (Gibson et
al., 2018) providing a large reservoir of organic material that can make its way to aquatic
ecosystems after a fire. Increases in dissolved organic carbon is also related to decreases in lake

alkalinity levels, making lakes more susceptible to acidification (McEachern et al., 2000). Finally, increased erosion and weathering can also increase ion transport to lakes, increasing conductivity levels (Silins et al., 2014; Silins et al., 2009; Scrimgeour et al., 2001; McEachern et al., 2000). Although these changes in water quality are significant in the short-term, studies suggest that lakes within boreal ecosystems are resilient to changes from wildfires. A study by McEachern et al. (2000) on lakes in northern Alberta, Canada showed that water quality recovered four years post fire, and Philibert et al. (2003) indicated through paleolimnological methods that the threat associated with forest fires in conifer dominated forests is low.

#### 1.4 – Zooplankton Ecology

Zooplankton are microscopic, heterotrophic aquatic organisms. The majority of zooplankton taxa are crustaceans, while a smaller subset are considered gelatinous animals (Thompson, 2012). Zooplankton play a vital role in the aquatic food-web, acting as both food for young-of-the-year (YoY) fish, and active grazers controlling the phytoplankton populations within lakes (Ovaskainen et al., 2019). Zooplankton have short generation times, allowing communities of zooplankton to adapt to changing environments quickly. Short generation times coupled with zooplankton being slow swimming organism with a variety of feeding habits, makes them the ideal bioindicators for examining the effects of stressors on lakes (Ovaskainen et al., 2019).

The two main groups of zooplankton I focus on for the current study, are the copepods (subclass Copepoda) and the cladocerans (suborder Cladocera). Within freshwater environments, the relative abundance of copepods and cladocerans is relatively equal (Richardson, 2008).

Copepods have streamlined bodies, powerful swimming appendages, and paired frontal antennae

that make them excellent swimmers (Richardson, 2008). Copepoda is divided into three functional feeding groups: Raptorial, stationary suspension, and current cruisers (Barnett et al., 2007). Raptorial copepods, like the order Cyclopoida, actively swim and have specialized grasping limbs for capturing prey items. Cyclopoids generally eat larger prey items and are the main omnivore-predators within zooplankton communities. Stationary suspension feeders, are less active, being more opportunistic as omnivores, while current cruisers actively swim creating small currents that cycle food particles for them to consume.

Cladocerans are predominantly herbivores and are considered the main grazers of zooplankton communities. Cladocerans are divided into four functional feeding groups:

Daphnia-type (D-type), Sida-type (S-type), Bosmina-type (B-type), and Chydorus-filtration (C-filtration) (Barnett., et al 2007). D-types filter from a stationary position, using their third, and fourth limbs to filter feed phytoplankton. S-types are similar to D-types; however, their feeding limbs are present on the first five pairs. B-types are characterized by their horizontal swimming, and less developed thoracic feeding appendages. C-filtration is a feeding method where a scraping action is used to scrape periphyton off of stationary submerged objects. Absence of grazing zooplankton, especially large cladocerans, is known to increase the concentration of chlorophyll-a within aquatic ecosystems, which in turn can result in algal blooms (Labaj et al., 2013).

Zooplankton communities have been impacted by wildfires in boreal forest regions, but just like the water chemistry and quality, have shown a natural resilience to fire disturbances. A study in the boreal region in Quebec, Canada showed an initial increase in zooplankton biomass post fire but given three years the zooplankton biomass returned to reference levels (Jalal et al., 2005). Another study in a southern boreal region measured zooplankton species richness and

diversity, which showed within one-year post-fire the zooplankton species richness and diversity had recovered (Patoine et al., 2002). Although past studies show that zooplankton communities may recover rapidly after wildfire impacts, these studies were conducted in southern boreal regions. Northern regions may be more susceptible to long term changes as vegetative regrowth takes longer, resulting in extended alteration of watersheds hydrological functions, and thus potentially affecting lake water quality for a longer period of time (Zhang et al., 2015).

#### 1.5 – *Objective*

The goal of this research is to identify if zooplankton communities in the northern boreal lakes show differences related to forest fires four to five years after the disturbance. Specifically, I have four objectives: (i) Count and identify zooplankton from eleven reference lakes and nine lakes that have experienced burns in their catchments; (ii) Examine if genus richness and diversity significantly differs between burned and reference lakes; (iii) Examine if the relative abundance of zooplankton genera differs between burned and reference lakes; and (iv) investigate if the relative abundance of zooplankton functional feeding groups differs between burned and reference lakes. This research will help bridge the gap in knowledge of how zooplankton communities respond to wildfire disturbances in northern boreal ecosystems.

## **2.0** – **Methods**

#### 2.1 – Study Area and Zooplankton Collection Method

Twenty lakes were sampled during the field seasons of 2018 and 2019 in the Sathú Settlement Area (SSA) northwest of Norman Wells, Northwest Territories Canada (65°31'15.376"N, 127°24'15.894"W). A wildfire burned through the SSA from June 10<sup>th</sup> to July

15<sup>th</sup>, 2014. Of the twenty lakes sampled, eleven were affected by the 2014 wildfires burning through the vegetation in the surrounding water basin, while nine were reference lakes that had not been affected by fires since at least the mid 1970s (CNFDB, 2018).

Study lakes were accessed by float plane, where water samples and invertebrate samples were collected from an inflatable dingy boat. Zooplankton samples were collected using a 64 µm mesh plankton tow net. Littoral zooplankton communities were collected by dropping the tow net to 1 m in depth, moving the boat approximately 5 m, then hand towing at an oblique 45° angle. This sampling method was repeated at three different stations per lake, giving a total of 60 zooplankton community samples. Once the samples were collected in the net, the zooplankton were transferred into 100 mL Nalgene containers and preserved in 95% ethanol for later analysis.

#### 2.2 – Water Quality and Lake Morphometry

Water quality was measured three times at each of the sampling areas where zooplankton samples were collected at approximately 1 m of depth. A YSI-Professional Plus meter (YSI), with an attached polarographic sensor probe, was used to measure DO at 0.5 m. The YSI was also equipped with a conductivity probe, which was used to measure conductivity at each location. Variables such as pH, and temperature were measured at each location using an Oakton 150 series pH probe. Each instrument was regularly calibrated and maintained for use, with instruction on how to do so coming from each instrument's respective manual.

To gain a full representative understanding of each lake's water quality, additional sampling was conducted in the middle of each lake. The water was collected at the centre of each lake using a 19 mm flexible polypropylene tube constructed into an integrated water sampler.

Each sample of water was taken by lowering the tube into the water to approximately 2 m and

then sealing the top of the tube to transfer the water to a 1 L Nalgene bottle. If the lake was shallower than 2 m, the depth of the sample would be adjusted to avoid disturbing the sediment bed. Water was collected to measure variables such as trace metal concentrations, dissolved organic carbon (DOC), total organic carbon (TOC), and total nitrogen (TN). Trace metals were measured in the Centre for Cold Regions and Water Science Analytical Laboratory at Wilfrid Laurier University using a Perkin Elmer Optima 8000 Inductively Couple Plasma-Optical Emission Spectroscopy. Concentrations of DOC, TOC, and TN were measured at the Centre for Cold Regions and Water Science using a Shimadzu TOC-LCPH Carbon and Nitrogen Analyzer. Chlorophyll a level was measured by collecting 250 mL of water at each sampling site, which was filtered through a 0.45 µm Millipore glass filter to collect algae. The algae communities were preserved in the laboratory by freezing the filter. The filter was then submerged in methanol to extract the chlorophyll a. After extraction, chlorophyll a was measured using a Turner Designs TD700 fluorometer. One litre water sample for each site were taken for further, on-site water chemistry analysis using the YSI in accordance to the Canadian Council of Ministers of the Environment (CCME) field manual.

Lake morphometry variables were measured using ArcGIS. Water catchment (WC) was outlined in ArcGIS, and variables such as wetland coverage (Ha), surface area (SA) of the water body (Ha), perimeter (km), elevation (m), drainage ratio (WC/SA), and slope (%) were found in ArcGIS for each catchment.

#### 2.3 – Analyses of Zooplankton Communities

Zooplankton samples were filtered out of ethanol preservative by pouring the samples through a 200  $\mu m$  mesh sieve. Using a squirt bottle filled with deionized (DI) water, the

zooplankton were washed out of a sieve into a 150 mL beaker. The beaker was filled to approximately 100 mL and placed on a magnetic stirrer. Using a small magnetic bar, the sample was stirred gently in order to keep the zooplankton specimens suspended, but also as to not damage the specimens. This was done to ensure that the sample was well mixed before extracting a sub-sample. Using a 5 mL Hensen-Stemple pipette, a proportion of the zooplankton sample was transported to a plankton counting wheel for tallying, and identification. Zooplankton were counted in at least three subsamples from each station, and a minimum of 100 individuals needed to be counted in each subsample to ensure accurate estimates of the relative abundance of zooplankton species in the sample as a whole. If there were not one-hundred organisms within an entire sample, then all organisms within that sample were counted. Once the zooplankton sub-sample was transferred to the plankton counting wheel, it was placed under a Leica dissecting scope to aid in identifying individuals for counting, and to look at key morphological features. If certain morphological features were unidentifiable using a dissecting scope, the specimen would be extracted using a glass pipette and placed onto a microscope slide for further examination under an Omax compound microscope. If even further examination is needed of a morphological feature, then a dissecting method using two needle probes isolates the morphological feature for further examination under the compound microscope. Once the counting of a 5 mL subsample was finished, the contents remaining in the plankton counting wheel were returned to the 100 mL solution, where more sub-sampling could take place if needed. Each of the zooplankton that were counted were identified down to the genus level through an online Image-Based Key to Zooplankton of North America (Haney et al. 2020), in combination with the Practical Guide to Identifying Freshwater Crustacean Zooplankton (Witty et al. 2004).

#### 2.4 – Statistical Analyses

All statistical analysis and calculations were performed in the statistical software R-Studio. Richness in this study was defined as the number of zooplankton genera found per lake. Due to the differing total number of individuals counted for each lake, I used rarefaction (sample size = 198) to avoid bias in estimates of richness. Rarefaction is a process that considers the number of individuals counted in a sample and corrects for differences in sample size. Since some lake samples contained more identified organisms, then it is statistically more likely for a higher richness to be observed (Chao et al., 2014). Once the rarefied richness values are calculated, the means of the burned and reference lakes were tested using a two-sample t-test to determine if the mean values of richness differed significantly between the two groups. Shapiro-Wilks tests were implemented to ensure normality.

Diversity in this study was calculated using the Shannon-Weiner Diversity (SWD) index The SWD index is one of the most common indices used in ecology, where  $p_i$  represents the proportion of the entire population made up of genera i and G represents the number of genera encountered (Peet, 1974).

$$H' = -\sum_{i=1}^{G} p_i ln p_i$$

The values obtained from this index were also used in a two-sample t-test to determine if the mean diversity differed significantly between burned and reference lakes.

Percent abundance of feeding groups for individual lakes was calculated by dividing the number of organisms within a feeding group by the total organisms counted in a lake. Those percent feeding group values were then averaged over the entirety of either burned or reference lakes to have the percent feeding groups values for the two types of lakes. Averaging the values

also allowed standard deviation to be calculated, which was used to discern if there were any significant differences in the abundance of feeding groups between lake types.

For examining differences in the relative abundance of species between burned and reference lakes, a Principle Component Analysis (PCA) was implemented. A matrix of specimen abundances was used to conduct the PCA. Ordination diagrams produced by a PCA can provide visual representation of differences in the relative abundance of zooplankton found among lakes. If burned lakes group out close to an arrow for a certain genus, then this would suggest that the associated genus is more abundant in burn lakes. Rare species, which are defined as genera that appear in 20% or less of the lakes, were removed prior to this analysis, and the data were Hellinger transformed to reduce the influence of zeroes (Svenning & Skov, 2005). Cluster analysis was used along with the PCA to determine if natural groupings of certain genera existed as a means to explain any natural variation that was seen. This was done by using an elbow plot to determine the optimal number of groupings to cluster, then using a k-means cluster analysis and plotting the groupings onto the ordination diagram produced by the PCA (Liu & Tan, 2019). A Redundancy Analysis (RDA) was used to determine if differences in the relative abundance of genera among lakes was related to differences in water quality variables such as pH and dissolved oxygen. Using a stepwise regression procedure (ordistep in the Vegan package for R), the statistically significant explanatory variables remained in the RDA, while the statistically insignificant were removed.

# **3.0** – **Results**

#### 3.1 – Zooplankton Communities

During the counting and identification of zooplankton communities, 19 different genera were identified. The maximum number of zooplankton specimens identified from a single lake

was 760, while the minimum value was 48. The lake with the minimum value was omitted from the richness and diversity data. Three lakes did not meet the minimum 300 organism count, and all of the specimens within those lake stations were counted. This altered the use of rarefaction, where instead of rarefying to 300, the lakes were rarefied to 198 as a means to eliminate bias. The most abundant genus of zooplankton within the lakes was *Leptodiatomus*, an omnivorous suspension feeder, with 2968 identified, while the least abundant was *Diacyclops*, a raptorial carnivore, with only three identified. There were 7331 identified organisms among the 20 lakes with the vast majority being copepods, where 6215 organisms were identified compared to the 1116 consisting of cladocerans.

#### 3.2 – Univariate Metrics

Richness did not differ significantly between burned and reference lakes (two sample t-test, t-value = 1.5884, p-value = 0.1316; Fig. 1). Diversity also did not differ significantly between burned and reference lakes (two sample t-test, t-value = 1.4283, p-value = 0.1715; Fig. 2). Percent abundance of feeding groups did not differ significantly between burned and reference lakes, as the standard deviation of each feeding group overlapped (Fig. 3). In both burned and reference lakes the dominant group were the suspension feeders, while the second most abundant group were the raptorial predators (Fig. 3).

#### 3.3 – Multivariate Analysis

The PCA showed no distinct groupings of burned or reference lakes, with very little patterning of genera preferences (Fig. 4). The first axis explained 42.8% of variation, where lakes with higher scores had more small cladoceran genera such as *Bosmina*, *Chydorus*, *Alona*,

and Alonella, while lakes with more generalist copepod groups like Leptodiaptomus, Skistodiaptomus, and the immature calanoids tended to have lower scores (Fig. 4). The second axis explained 19.3% variation, where lakes with lower scores had more Daphnia, Heterocope. and Sida, while lakes with higher scores had more of the predatory copepod Microcyclops (Fig. 4).

The elbow plot used to determine the number of groups for cluster analysis revealed that the optimum number of clusters was between three to four (Fig 5). K-means cluster analysis showed four distinct natural groupings of lakes and their associated genera (Fig. 6). Group 1 lakes tended to have more littoral cladoceran groups like *Daphnia* and *Sida* (Fig. 6). Group 2 lakes had more abundant cyclopoid copepods, including *Microcyclops*, while group 3 lakes contained smaller sized cladoceran groups like *Bosmina*, *Chydorus*, *Alona*, and *Alonella* (Fig. 6). Group 4 lakes were dominated by diaptomid copepods, including *Skistodiaptomus*, *Leptodiaptomus*, and immature calanoids (Fig. 6).

Our redundancy analysis revealed that the four most important variables for explaining differences in relative abundance among lakes were: Alkalinity, TOC, temperature, and short-wave infrared 1 (SWIR<sub>1</sub>), which is associated with macrophyte density. Axis 1 explained 32.71% of the variation among lakes, and lakes with higher scores were more alkaline, while lakes with lower scores were warmer, and tended to have a higher density of macrophytes. Axis 2 only explained 8.45% of the variation, and lakes with lower scores tended to have higher levels of TOC. From the RDA and the interpretation of the PCA, genera like *Bosmina, Chydorus, Alona* and *Alonella* tended to be more abundant in lakes that were alkaline, with the latter three genera also preferring lakes with higher TOC. *Microcyclops* also preferred lakes with higher TOC, while *Daphnia* and *Sida* preferred less. The calanoids like *Leptodiaptomus, Skistodiaptomus,* 

*Heterocope* and the immature calanoids preferred to be in warmer lakes with higher density of macrophytes (Fig. 7).

## 4.0 – Discussion

#### *4.1* − *Richness and Diversity*

Both richness and diversity did not differ significantly between burned and reference lakes, which matches with results from previous studies conducted in the southern boreal ecoregion that showed zooplankton communities recover rapidly after a wildfire (Jalal et al., 2005; Patoine et al., 2002). Lake morphometry (lake size and depth), is the key variable in explaining differences in the richness and diversity of zooplankton communities among lakes (MacLeod et al., 2018). Smaller, shallower lakes tend to provide a lower diversity of habitats, and therefore provide fewer unique niches for zooplankton (MacLeod et al., 2018). Physical factors are not the only influence on zooplankton richness and diversity. Water quality variables such as pH and conductivity also play a vital role in zooplankton community composition (Soto & De Los Rios, 2006; Bleiwas & Stokes, 2011; Gray & Arnott, 2009; Small & Sutton, 1986). It is no surprise then that richness and diversity do not differ between burned and reference lakes in my study, as there are no significant differences in lake morphometry or water quality variables between these two groups.

However, while both richness and diversity were not statistically different, there appeared to be small differences, with higher values in burned lakes. While this may be due to natural variation among lakes, it could also represent communities slowly recovering from exaggerated richness and diversity values caused by the wildfire disturbance (Jalal et al., 2005; Patoine et al., 2002). The increase in richness following a disturbance might be explained by the intermediate

disturbance hypothesis, where a disturbance to the ecosystem could allow more niches to form and prevent a small number of species from becoming dominant (Fox, 1979). In this case, the fires that occurred in the catchments of the lakes in the SSA likely caused a disturbance of water quality due to increases in nutrient loading, DOC, and humic acids exported from the watershed. Changes to water quality could then promote increases in richness and diversity of the zooplankton communities, as has been shown in other invertebrates (Bisson et al., 2003). For example, the increase of sedimentation, which carries nutrients, is prominent in watersheds post fire (Bisson et al., 2003; Silins et al., 2009). The increase of nutrients could promote the growth of macrophyte communities, or an increase in algal density, which in turn would increase the variety of niches within the environment for zooplankton taxa that are more reliant of vegetation, or more adapted to grazing on large algal masses (McGowan et al., 2005; Thompson et al., 2019). While this was not explicitly shown in my study, I speculate that it may have been one of the many initial changes to the zooplankton communities before vegetative regrowth occurred in catchments and the nutrient loading through sedimentation stopped. Patoine et al., (2002) noticed an increase in richness and diversity initially onset by wildfire disturbance, but just given one year that initial spike had abruptly returned to normal. A similar process may have occurred in the lakes of the SSA, just with a slower recovery time due to the higher latitude. Lake recovery post fire is connected to the watershed's vegetation recovery (Scrimgeour et al., 2001), and with vegetation regrowth largely limited at higher latitudinal positions, the recovery of richness and diversity may be slower (Zhang et al., 2015). With richness and diversity values being noticeably, but not significantly higher in burned lakes, the values calculated may be showing the tail end of the initial increase to richness and diversity.

#### 4.2 – Percent Abundance of Feeding Groups

There were no significant differences in the percent abundance of feeding groups between burned and reference lakes. The two largest feeding groups in my study, suspension feeders and raptorial predators, were both copepods. While usually the ratio of copepod to cladoceran abundances is about equal in freshwater systems (Richardson, 2008), that ratio tends to get skewed in favour of copepods for lakes at higher latitudes (Novichkova & Azovsky, 2017). This is mostly due to air temperature being a defining variable for the abundance of copepods and cladocerans. With a 1°C drop in mean annual air temperature, cladocerans groups can experience a 53% drop in abundance, whereas copepods only experience 17-24% drop (Novichkova & Azovsky, 2017). This sensitivity to temperature may also explain why I saw larger variability in the copepod:cladoceran ratio for reference lakes. Higher elevation lakes tend to have a lower abundance of cladocerans and are therefore more often dominated by copepods (Novichkova & Azovsky, 2017). In my study, there was more variability in elevation for reference lakes, with the difference between the maximum and minimum values being 277 m, while the difference for burned lakes was 180 m. With a wider range of elevations for reference lakes, we might expect there to be a wider range of copepod to cladoceran ratios. Thus, this may explain why I found higher variability with feeding groups such as suspension feeders, B-types, and C-filtration in reference lakes.

Although elevational differences might have explained some of the variability in the percent abundance of feeding groups in my study, it is important to note that the overall copepod feeding group percent population for burned lakes (81.99%) is higher than reference lakes (70.56%), despite burned and reference lakes having mean elevations of 170.67m and 256.55 m, respectively. This difference may be due to lower elevation lakes being able to support small

cladocerans, and therefore a niche for predatory zooplankton that eat cladocerans. Stewart et al. (2010) measured zooplankton production before and after the invasion of the predatory zooplankter *Cercopagis*. They found that zooplankton production dropped by half after *Cercopagis* had been introduced due to the predatory behaviour. Another example of this can be found in the invasive zooplankter *Bythotrephes longimanus*. With its presence in the Rocky Mountain lakes zooplankton abundance has decreased due to its predatory behaviour (Hasnain & Arnott, 2019). I hypothesize that the observed percent population of these cladocerans is smaller in lakes of lower elevation, despite those lakes being more suited to them, due to the presence of predators that are driving down their abundance. For example, in my study there was a larger population of predatory raptorial copepods within burned lakes (*Microcyclops*), which could limit the presence of their prey.

#### 4.3 – Relative Abundance and Cluster Analysis

The PCA showed no discernable groupings of zooplankton genera that corresponded with the burn status of the lakes (i.e. burned versus reference). However, there did seem to be different types of communities in different lakes. My k-means cluster analysis showed that there were four distinct natural groupings of zooplankton genera within the lakes sampled: Group 1 lakes were littoral cladoceran-dominated lakes, along with some immature calanoids; Group 2 lakes were cyclopoid dominated with a high relative abundance of *Microcyclops*; Group 3 lakes were dominated by smaller cladoceran genera; and Group 4 had large populations of diaptomids like *Skistodiaptomus*, and *Leptodiaptomus*. I speculate that these four community types may occur due to fish presence or absence within the lakes, where lakes with higher axis scores may have a larger fish presence than lakes with lower axis scores. Diaptomids are quite susceptible to

fish predation due to their size. With the presence of a visual hunter like juvenile fish, large calanoid copepods have been observed to either be fully eradicated or have their abundance extremely reduced (Schabetsberger et al., 2009). The possible lack of fish in group 4 lakes could allow diaptomids to thrive, as they are suspension feeding omnivores, the most generalist diet with regards to zooplankton, which could outcompete most other larger zooplankton that have a particular niche (Barnett et al., 2009). On the opposite end of the PCA, group 3 might have had the most intense fish predation, as the smallest cladoceran groups were most abundant. With fish presence the small benthic C-filtration cladocerans tend to survive over the pelagic D-type zooplankton (Gayosso-Morales et al., 2019). Group 3 also has a large abundance of *Bosmina*. Bosmina-dominated communities are associated with high fish predation, which again suggests intense fish presence within group 3 lakes (Norlin et al., 2006). For example, one of the lakes within group 3 is called "Jackfish Lake", which is named due to the presence of Jackfish, also commonly known as Northern Pike. Although Northern Pike are not planktivorous, they are known predators of lower trophic fish that do rely on zooplankton for sustenance (Anaya-Rojas et al., 2019; Reist, 1983)

Group 1 and 2 lakes may also have fish, but I suspect that predatory zooplankton may have a more important effect in these lakes. The large predatory copepod *Heterocope* was abundant in Group 1 lakes, and it is known to prey upon other large zooplankton genera like *Daphnia*, so having their relative abundances closely tied within the same group suggests the presence of *Daphnia* may be dictating the presence of *Heterocope* as well (Luecke & O'Brian, 1983). Group 2 lakes also had an abundance of an important zooplankton predator, the small and aptly named *Microcyclops*. *Microcyclops* may be small enough to avoid fish predation and seems to have ample food supply within group 2 lakes due the abundance of small cladocerans such as

Chydorus, and Alona (Gayosso-Morales et al., 2019; Gutiérrez-Aguirre & Cervantes-Martínez, 2016). Microcyclops also preys upon rotifers, so perhaps the presence of this genus indicates that there are abundant rotifer populations within these lakes (Sato & Hurlbert, 1991). Norlin et al. (2006) characterized distinct groupings of zooplankton in shallow western boreal wetlands. They observed groupings similar to this study, with small cladoceran communities dominated by Bosmina, copepod and rotifer dominated lakes, and lakes dominated by littoral grazers such as Daphnia. Norlin et al. (2006) also suggested that these differences were linked to fish communities. However, fish presence and rotifers were not measured in my study, so further observations are needed to move beyond the realm of speculation.

#### 4.4 – Redundancy Analysis

The RDA explained 41.16% of the variation in zooplankton communities among lakes. The four most important variables that explained variation in zooplankton communities among lakes were alkalinity, temperature, TOC, and SWIR<sub>1</sub> (macrophyte biomass). There were no distinct groupings of lakes according to burn status in the ordination diagram. However, the RDA indicated that *Daphnia* tended to be found in lakes with lower TOC, while more *Microcyclops, Chydorus* and *Alona* were found in lakes with higher TOC. TOC and humic substances are a known variable that increases in aquatic ecosystems post fire (Rosén et al., 2009). With an increase in carbon colouration from TOC and humic substances within boreal lakes, it limits the production of phytoplankton, thus limiting the populations of larger grazing zooplankton such as *Daphnia* (Anas et al., 2019; Hansson et al., 2019). Although TOC does not differ singificanlty between burned and reference lakes, with reference lakes actually having a

higher mean value of TOC, thus natural variability of conditions within lakes best explains this difference between the two groups.

Alkalinity was also an important predictor variable in the RDA. Alkalinity is synomonous with pH buffering capacity, and changes in pH are known to severely affect cladoceran groups, with the exception of *Bosmina*, which has shown to be resilient to acidification (Bleiwas & Stokes, 2011; Gray & Arnott, 2009; Small & Sutton, 1986). The other dominant groups of cladocerans in my study such as *Chydorus*, *Alonella*, *Alona*, *Daphnia* and *Sida*, prefer more alkaline waters over acidic conditions, which is a pattern shown in my study, as well as many others (Jeziorski et al., 2014; Labaj et al., 2014). Alkaline conditions are still preferred for calanoids as well, as depletion of calcium within a system (alkalinity is often measured as Ca) also reduces calanoid abundance (Jeziorski et al. 2014). Despite this sensitivity to acidic conditions, a genus such as *Skistodiaptomus* still show positive growth in acidic conditions, and another diaptomid genus *Leptodiaptomus* can tolerate highly acidic conditions (Gray and Arnott, 2009), which may explain why I saw an abundance of diaptomids in less alkaline lakes in my study.

SWIR<sub>1</sub> remote sensing readings, used to measure macrophyte biomass, were also a significant predictor in my RDA. Macrophyte coverage can provide refuge for larger bodied zooplankton, so large calanoids like *Leptodiaptomus*, and *Skistodiaptomus* may be able to avoid fish predation by hiding in macrophytes. Du et al. (2015) showed a positive correlation between macrophyte coverage and calanoid abundance, so the higher populations of calanoids in SSA lakes with high macrophyte biomass may be caused by the same mechanism. Similar relationships can occur for large-bodied cladocerans, but not all cladocerans rely on macrophytes for refuge (McGowen et al., 2005).

Temperature was the final predictor in my RDA. Peak recruitment of *Leptodiaptomus* occurs between July and August, where warmer temperatures are preferred for that genus within the subarctic (Marion et al., 2016). This may explain why we see higher *Leptodiatomus* abundances in lakes with higher temperatures.

#### 4.5 – Conclusion

There were no discernable differences between the zooplankton communities of burned versus reference lakes in the SSA using both univariate, and multivariate metrics. Any initial differences in richness and diversity of zooplankton that might have existed after the fire appear to have subsided by the time we sampled these lakes four to five years post fire. The percent abundance of functional feeding groups also failed to show any differences between lakes, but latitudinal and elevation positioning were highlighted as potential explanations for the variability in functional feeding group composition among lakes. Four distinct groupings of zooplankton genera were found in the 20 study lakes. These four groups were defined as small cladoceran and Bosmina dominated lakes, pelagic filter feeding Daphnia dominated lakes, predatory cyclopoid Microcyclops dominated lakes, and diaptomid dominated lakes. Variation among and within these groupings could be best explained by physical characteristics such as lake morphometry, ecological characteristics such as predator prey interactions, or the measured characteristics of temperature, TOC, alkalinity, and SWIR<sub>1</sub> as demonstrated by our redundancy analysis (RDA). According to our RDA, cladocerans preferred more alkaline lakes, and *Daphnia* specifically preferred lakes of low TOC, which is most likely due to high TOC being linked with lack of periphyton production. While TOC is known to increase post fire, there were no significant differences in TOC among burned and reference lakes, and therefor the relative abundance of

*Daphnia* was attributed to natural variability among lakes. Diaptomids were abundant in more acidic conditions and displayed a preference for warmer temperatures in their peak recruitment periods. Further data on rotifer and fish assemblages is needed to fully explain the factors driving differences in zooplankton communities among lakes in the SSA.

# **List of Tables**

Table 1. Summary of raw counts for each lake sampled in the SSA. The values displayed are how many individuals of a genus were found within a single lake. Zooplankton genera are displayed on the left and which lake they were found in along with the status of that lake is displayed on top. Reference lakes have an "R" in the ID.

Tropocyclops	Epischura	Diacyclops	Heterocope	Leptodiaptomus	Skistodiaptomus	
0	0	0	8	476	31	RN 1
0	0	0	0	15	0	RS 1
0	0	0	0	12	0	RS 4
0	0	0	0	0	0	RS 5
0	0	0	0	0	0	RS 6
0	0	ĸ	22	201	21	RW 1
0	0	0	12	137	74	RN 4
0	0	0	23	195	09	RN 5
2	0	0	8	330	21	RE 1
0	0	0	0	350	0	RE 2
0	0	0	16	186	96	RE 3
0	Н	0	0	163	3	N1
0	0	0	7	363	30	N2
0	0	0	ı	107	7	N3
0	0	0	28	92	6	N4
П	65	0	14	П	0	W2
0	0	0	8	195	2	W3
10	124	0	25	34	2	E1
0	0	0	12	43	34	E2
0	0	0	26	84	4	E4

0 0	Cerromapinia	Sida	Bosmina	Chydorus	Alona	Alonella	Daphnia	Acanthocyclops	Ergasilus	Microcyclops
	)	0	0	0	0	0	0	0	0	13
	<b>\</b> 1	1	19			9	0	0	0	25
0 23		0	18	41	29	12	7	0	11	160
0	- (V	2	21	0	2	20	0	0	0	0
0		8	108	13	0	0	09	0	0	6
0		0	0	16	0	0	12	0	0	17
0		0	0	0	0	2	2	0	0	10
0		0	0	0	0	0	0	0	0	∞
0		0	0	0	0	1	4	0	0	∞
1 18		0	0	0	0	0	20	0	0	62
0		0	0	1	0	3	14	П	0	6
16 15		0	0	0	н	0	0	0	0	99
0		0	0	0	0	0	8	0	П	308
2		10	44	0	0	0	$\vdash$	0	8	569
0		14	5	0	0	0	41	0	0	23
0	15	71	11	0	0	0	0	0	0	20
8		2	Н	. 15	_	0	7		Н	33
6 22		2	9	2	0	2	0	0	Н	19
0	.,	2	0	0	0	0	93	0	0	15
0		12	0	0	0	0	123	11	2	14

Harpacticoida	Polyphemus	Immature Calanoids
0	0	179
0	T	0
25	37	2
0	0	0
0	0	0
0	0	35
0	0	109
0	0	79
0	0	51
0	0	36
0	0	54
0	0	54
0	0	48
0	0	20
0	0	142
0	0	116
0	0	59
0	0	52
0	0	230
0	0	25

Table 2. Error! Reference source not found. (Courtesy of Tom Pretty)

	Reference lakes (n= 11)			Burned lakes (n= 9)				
Variable	mean	sd	min	max	mean	sd	min	max
Alkalinity (mg/L CaCO <sub>3</sub> )	131.36	42.55	65.00	205.00	113.89	45.54	40.00	165.00
Ca (mg/L)	39.32	15.96	19.03	64.33	40.67	29.74	9.51	109.59
Chlorophyll-a (µg/L)	0.44	0.30	0.13	1.13	0.43	0.26	0.15	0.87
Colour (mg/L Pt)	40.45	34.46	0.00	95.00	60.00	32.60	25.00	120.00
Conductivity ( $\mu$ S/cm)	315.50	203.51	107.10	663.25	243.92	162.98	66.70	566.75
<b>DO</b> (mg/L)	9.95	1.48	7.50	12.03	9.21	1.01	7.14	10.54
DOC (mg/L)	12.49	6.27	5.08	28.17	10.85	1.92	8.64	15.04
Drainage Ratio (WC/SA)	55.37	135.17	2.50	460.91	54.25	93.44	1.73	297.55
Elevation (m. a.s.l.)	256.55	74.67	55.00	332.00	170.67	73.27	76.00	256.00
Fe (mg/L)	0.02	0.03	0.00	0.07	0.05	0.04	0.01	0.12
Macrophytes -SWIR $_1(\lambda)$	292.10	168.42	95.50	632.47	353.91	166.81	163.89	634.69
Macrophytes -SWIR <sub>2</sub> ( $\lambda$ )	116.00	211.01	22.00	744.00	241.50	300.91	65.00	784.00
<b>Maximum Depth</b> (m)	3.94	3.59	0.85	9.78	3.06	1.87	0.91	6.77
рН	8.10	0.67	6.46	8.75	7.88	0.59	6.51	8.32
Phenols (mg/L C <sub>6</sub> H <sub>5</sub> OH)	0.17	0.11	0.00	0.37	0.23	0.22	0.00	0.57
Slope (%)	10.98	6.50	2.88	22.75	11.33	6.13	3.10	24.68
Surface Area (ha)	55.96	68.45	6.76	228.97	47.48	33.93	10.37	101.03
Temperature (°C)	14.48	1.70	11.88	16.98	14.23	0.84	12.88	15.40
TN (mg/L)	0.53	0.29	0.02	1.11	0.39	0.10	0.28	0.60
TOC (mg/L)	15.25	9.92	7.69	35.63	10.70	2.12	8.60	15.61
burned Drainage Ratio	0.16	0.37	0.00	1.10	51.12	92.42	1.65	292.11
Total ha Burned	5.19	14.02	0.00	46.31	1350.33	1427.93	25.12	4202.71

# **List of Figures**

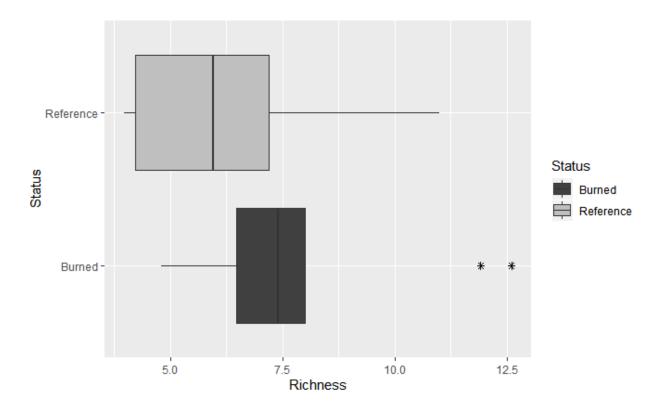


Figure 1: Comparison of rarefied richness values for zooplankton communities in the SSA.

Sample sizes are rarefied to n = 198. The darker gray box represents the burned lakes, while the lighter gray are the reference lakes. \* are outlier values.

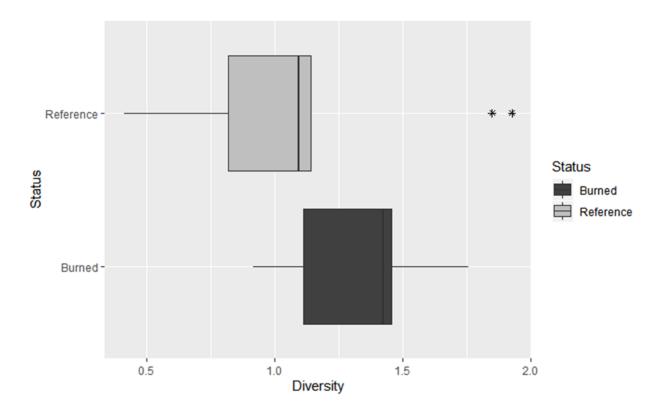


Figure 2: Comparison of Shannon Diversity values for zooplankton communities in the SSA.

Sample sizes are rarefied to n = 198. The darker gray box represents the burned lakes, while the lighter gray are the reference lakes. \* are outlier values.

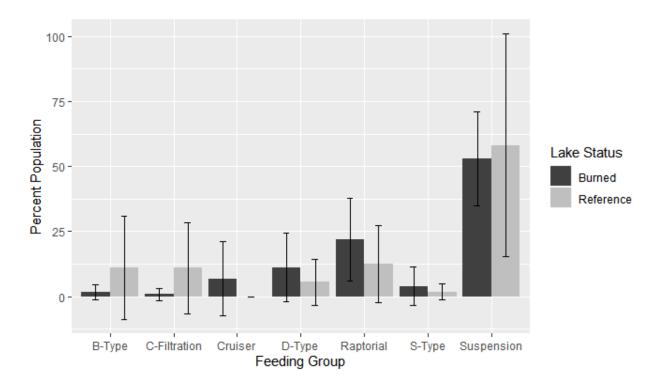


Figure 3: Bar chart comparing the percent feeding groups of zooplankton communities collected in the SSA. Burned lakes are represented by the darker gray bars, while the lighter gray bars represent the reference lakes. (Suspension = Skistodiaptomus, Leptodiaptomus, immature calanoids. S-Type = Sida, Polyphemus. Raptorial = Heterocope, Diacyclops, Tropocyclops, Microcyclops, Acanthocyclops, Ergasilus, Harpacticoida. D-Type = Daphnia, Ceriodaphnia, Diaphanosoma. Cruiser = Epischura. C-Filtration = Chydorus, Alonella, Alona. B-Type = Bosmina)

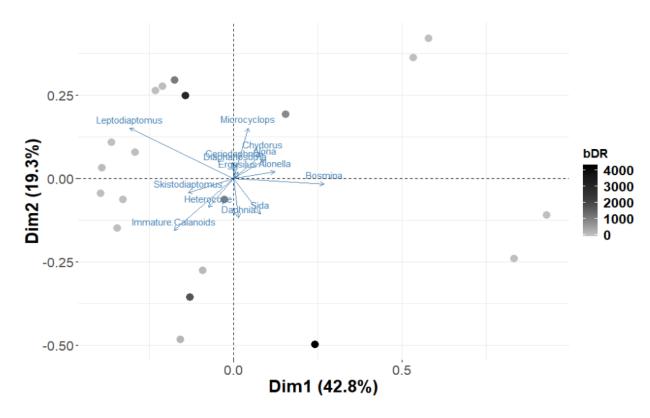


Figure 4: Principle component analysis (PCA) showing differences in the relative abundance of genera (Blue arrows) among lakes (points) within the SSA. Darker points represent lakes with a higher log burned drainage ratio (bDR = number hectares burned / lake surface area).

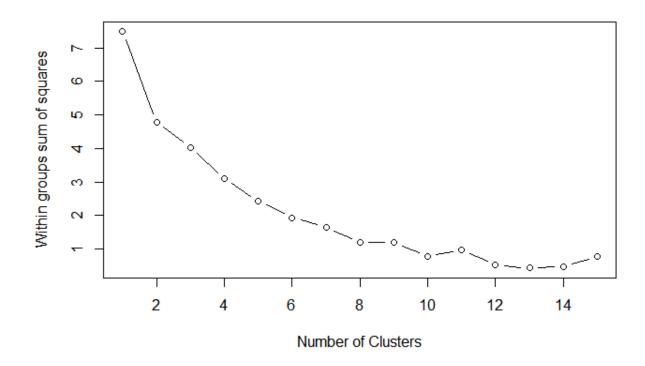


Figure 5: Elbow plot showing the number of clusters versus the within groups sum of squares.

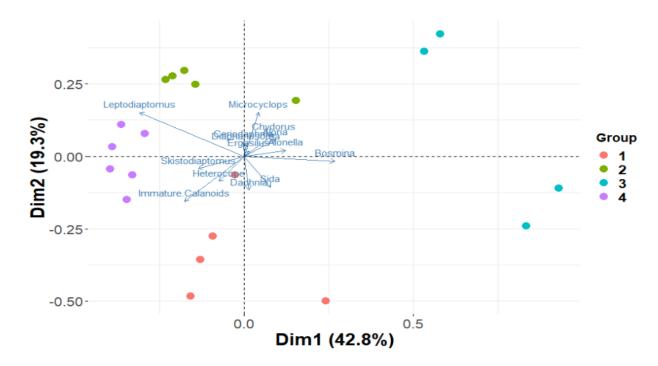


Figure 6: Principal component analysis of zooplankton genera with clusters identified according to k-means cluster analysis. Point colour indicates cluster and blue arrows represent zooplankton genera.

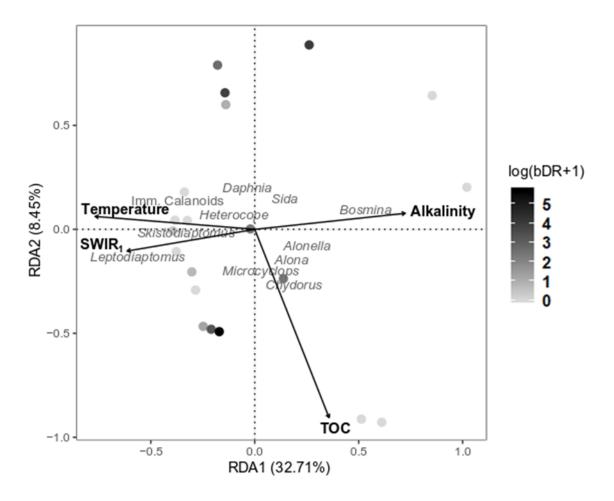


Figure 7: Redundancy analysis (RDA) of zooplankton relative abundance within the (SSA).

Darker points represent lakes with a higher log burned drainage ratio +1 (bDR). Zooplankton genera labels near the center were removed. Genera were moved slightly to avoid overlap.

Macrophytes = SWIR<sub>1</sub>, and total organic carbon = TOC.

# References

- Anas, M. U. M., Scott, K. A., & Wissel, B. (2019). Water chemistry, landscape, and spatial controls of δ13C and δ15N of zooplankton taxa in boreal lakes: One size does not fit all. Freshwater Biology, 64(11), 2006–2025. https://doi.org/10.1111/fwb.13389
- Anaya-Rojas, J. M., Best, R. J., Brunner, F. S., Eizaguirre, C., Leal, M. C., Melián, C. J., Seehausen, O., & Matthews, B. (2019). An experimental test of how parasites of predators can influence trophic cascades and ecosystem functioning. *Ecology*, *100*(8), *Article Number*: e02744. https://doi.org/10.1002/ecy.2744
- Barnett, A. J., Finlay, K., & Beisner, B. E. (2007). Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology*, *52*(5), 796–813. https://doi.org/10.1111/j.1365-2427.2007.01733.x
- Bisson, P. A., Rieman, B. E., Luce, C., Hessburg, P. F., Lee, D. C., Kershner, J. L., Reeves, G. H., & Gresswell, R. E. (2003). Fire and aquatic ecosystems of the western USA: Current knowledge and key questions. *Forest Ecology and Management*. 178(1-2), 213-229. https://doi.org/10.1016/S0378-1127(03)00063-X
- Bleiwas, A., & Stokes, P. (2011). Filtering rates of Diaptomus minutus, Bosmina spp.,

  Diaphanosoma sp., Holopedium gibberum (Crustacea), and Zooplankton Community

  Grazing Rates in Some Acidic and Circumneutral Ontario Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 495–504. https://doi.org/10.1139/f90-055
- Burd, K., Tank, S. E., Dion, N., Quinton, W. L., Spence, C., Tanentzap, A. J., & Olefeldt, D. (2018). Seasonal shifts in export of DOC and nutrients from burned and unburned peatland-rich catchments, Northwest Territories, Canada. *Hydrology and Earth System Sciences*. 22, 4455-4472. https://doi.org/10.5194/hess-22-4455-2018

- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*. 84(1), 45-67. https://doi.org/10.1890/13-0133.1
- Cott, P. A., & Mochnacz, N. J. (2007). Bull trout, salvelinus confluentus, and North American porcupine, erethizon dorsatum, interaction in the mackenzie mountains, Northwest Territories. *Canadian Field-Naturalist*. *121*(*4*), *437-438*. https://doi.org/10.22621/cfn.v121i4.523
- Du, X., García-Berthou, E., Wang, Q., Liu, J., Zhang, T., & Li, Z. (2015). Analyzing the importance of top-down and bottom-up controls in food webs of Chinese lakes through structural equation modeling. *Aquatic Ecology*. 49, 199-210. https://doi.org/10.1007/s10452-015-9518-3
- Fox, J. F. (1979). Intermediate-disturbance hypothesis. *Science*. 204(4399), 1344-1345. https://doi.org/10.1126/science.204.4399.1344
- Garcia, E., & Carignan, R. (2005). Mercury concentrations in fish from forest harvesting and fire-impacted Canadian Boreal lakes compared using stable isotopes of nitrogen.

  Environmental Toxicology and Chemistry. 24(3), 985-693. https://doi.org/10.1897/04-065R.1
- Gayosso-Morales, M. A., Nandini, S., Martínez-Jeronimo, F. F., & Sarma, S. S. S. (2019). Fish-mediated zooplankton community structure in shallow turbid waters: a mesocosm study.
  Wetlands Ecology and Management. 27, 651-661. https://doi.org/10.1007/s11273-019-09684-1-

- Gibson, C. M., Chasmer, L. E., Thompson, D. K., Quinton, W. L., Flannigan, M. D., & Olefeldt, D. (2018). Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature Communications*. *9*, *Article Number:* 3041. https://doi.org/10.1038/s41467-018-05457-1
- Gray, D. K., & Arnott, S. E. (2009). Recovery of acid damaged zooplankton communities: Measurement, extent, and limiting factors. *Environmental Reviews*. *17(NA)*, *81-99*. https://doi.org/10.1139/A09-006
- Gutiérrez-Aguirre, M. A., & Cervantes-Martínez, A. (2016). Taxonomic evaluation of eleven species of Microcyclops Claus, 1893 (Copepoda, Cyclopoida) and description of Microcyclops inarmatus sp. n. from America. *ZooKeys*. 603, 33-69. https://doi.org/10.3897/zookeys.603.7480
- Hansson, T. H., Grossart, H. P., del Giorgio, P. A., St-Gelais, N. F., & Beisner, B. E. (2019). Environmental drivers of mixotrophs in boreal lakes. *Limnology and Oceanography*. *64*(4), *1688-1705*. https://doi.org/10.1002/lno.11144
- Hasnain, S. S., & Arnott, S. E. (2019). Anti-predator behaviour of native prey (Daphnia) to an invasive predator (Bythotrephes longimanus) is influenced by predator density and water clarity. *Hydrobiologia*. 838, 139-151. https://doi.org/10.1007/s10750-019-03983-7
- Jalal, W., Pinel-Alloul, B., & Méthot, G. (2005). Mid-term study of the ecological impacts of forest fires and timber harvesting on zooplankton communities in lakes of the boreal ecozone. *Revue Des Sciences de l'Eau. 18, 221-248.*
- Jeziorski, A., Paterson, A. M., Watson, I., Cumming, B. F., & Smol, J. P. (2014). The influence of calcium decline and climate change on the cladocerans within low calcium, circumneutral lakes of the Experimental Lakes Area. *Hydrobiologia*. 722, 129-142. https://doi.org/10.1007/s10750-013-1691-6

- Kelly, E. N., Schindler, D. W., St. Louis, V. L., Donald, D. B., & Vladicka, K. E. (2006). Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proceedings of the National Academy of Sciences of the United States of America*. 103(51), 19380-19385. https://doi.org/10.1073/pnas.0609798104
- Labaj, A. L., Jeziorski, A., Kurek, J., & Smol, J. P. (2014). Long-term trends in cladoceran assemblages related to acidification and subsequent liming of Middle Lake (Sudbury, Canada). *Water, Air, and Soil Pollution.* 225, *Article Number:* 1868. https://doi.org/10.1007/s11270-014-1868-2
- Labaj, A. L., Joshua, K., Weeber, R. C., & Smol, J. P. (2013). Long-term changes in invertebrate size structure and composition in a boreal headwater lake with a known minnow introduction. *Journal of Limnology*. 72(2), 215-226. https://doi.org/10.4081/jlimnol.2013.e17
- Lewis, T. L., Lindberg, M. S., Schmutz, J. A., & Bertram, M. R. (2014). Multi-trophic resilience of boreal lake ecosystems to forest fires. *Ecology*. *95*(*5*), *1253-1263*. https://doi.org/10.1890/13-1170.1
- Liu, Z., & Tan, V. Y. F. (2019). The Informativeness of K-Means for Learning Mixture Models.

  \*IEEE Transactions on Information Theory. 65(11), 7460-7479.

  https://doi.org/10.1109/TIT.2019.2927560
- Luecke, C., & O'Brian, W. J. (1983). The effect of Heterocope predation on zooplankton communities in arctic ponds. *Limnology and Oceanography*, 28(2), 367–377.
- Lyon, J. P., & O'Connor, J. P. (2008). Smoke on the water: Can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology*. *33*(6), 794-806. https://doi.org/10.1111/j.1442-9993.2008.01851.x

- MacLeod, J., Keller, W., & Paterson, A. M. (2018). Crustacean zooplankton in lakes of the far north of Ontario, Canada. *Polar Biology*. 41(6), 1257-1267. https://doi.org/10.1007/s00300-018-2282-9
- Marion, A., Plourde, S., & Sirois, P. (2016). Mortality and recruitment in two copepod populations in a subarctic oligotrophic reservoir and the influence of environmental forcing. *Journal of Plankton Research*. 38(4), 915-930. https://doi.org/10.1093/plankt/fbw040
- McEachern, P., Prepas, E. E., Gibson, J. J., & Dinsmore, W. P. (2000). Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll a concentrations in boreal subarctic lakes of northern Alberta. *Canadian Journal of Fisheries and Aquatic Sciences*. 57(2), 73-81. https://doi.org/10.1139/f00-124
- McGowan, S., Leavitt, P. R., Hall, R. I., Anderson, N. J., Jeppesen, E., & Odgaard, B. V. (2005).
  Controls of algal abundance and community composition during ecosystem state change. *Ecology*, 86(8), 2200–2211. https://doi.org/10.1890/04-1029
- Norlin, J. I., Bayley, S. E., & Ross, L. C. M. (2006). Zooplankton composition and ecology in western boreal shallow-water wetlands. *Hydrobiologia*. 560, 197-215. https://doi.org/10.1007/s10750-005-1185-2
- Novichkova, A. A., & Azovsky, A. I. (2017). Factors affecting regional diversity and distribution of freshwater microcrustaceans (Cladocera, Copepoda) at high latitudes. *Polar Biology*. *40(1)*, *185-198*. https://doi.org/10.1007/s00300-016-1943-9
- Ovaskainen, O., Weigel, B., Potyutko, O., & Buyvolov, Y. (2019). Long-term shifts in water quality show scale-dependent bioindicator responses across Russia Insights from 40 year-long bioindicator monitoring program. *Ecological Indicators*, 98, 476–482. https://doi.org/10.1016/j.ecolind.2018.11.027

- Patoine, A., Pinel-Alloul, B., & Prepas, E. E. (2002). Effects of catchment perturbations by logging and wildfires on zooplankton species richness and composition in Boreal Shield lakes. *Freshwater Biology*. *47*(10), 1996-2014. https://doi.org/10.1046/j.1365-2427.2002.00947.x
- Peet, R. K. (1974). The Measurement of Species Diversity. *Annual Review of Ecology and Systematics*. 5, 285-307. https://doi.org/10.1146/annurev.es.05.110174.001441
- Philibert, A., Prairie, Y. T., & Carcaillet, C. (2003). 1200 Years of fire impact on biogeochemistry as inferred from high resolution diatom analysis in a kettle lake from the Picea mariana-moss domain (Quebec, Canada). 30(2), 167-181. Journal of Paleolimnology. https://doi.org/10.1023/A:1025526200880
- Reist, J. D. (1983). Behavioral variation in pelvic phenotypes of brook stickleback, Culaea inconstans, in response to predation by northern pike, Esox lucius. *Environmental Biology of Fishes*. 8, 255-267. https://doi.org/10.1007/BF00001091
- Richardson, A. J. (2008). In hot water: Zooplankton and climate change. *ICES Journal of Marine Science*. 65(3), 279-295. https://doi.org/10.1093/icesjms/fsn028
- Rosén, P., Cunningham, L., Vonk, J., & Karlsson, J. (2009). Effects of climate on organic carbon and the ratio of planktonic to benthic primary producers in a subarctic lake during the past 45 years. *Limnology and Oceanography*. *54*(*5*), *1723-1732*. https://doi.org/10.4319/lo.2009.54.5.1723
- Sato, D., & Hurlbert, S. H. (1991). Long-term experiments on calanoid-cyclopoid interactions. *Ecological Monographs*. 61(3), 245-265. https://doi.org/10.2307/2937108

- Schabetsberger, R., Luger, M. S., Drozdowski, G., & Jagsch, A. (2009). Only the small survive: Monitoring long-term changes in the zooplankton community of an Alpine lake after fish introduction. *Biological Invasions*. *11*(6), *1335-1345*. https://doi.org/10.1007/s10530-008-9341-z
- Scrimgeour, G. J., Tonn, W. M., Paszkowski, C. A., & Goater, C. (2001). Benthic macroinvertebrate biomass and wildfires: Evidence for enrichment of boreal subarctic lakes. *Freshwater Biology*. 46(3), 367-378. https://doi.org/10.1046/j.1365-2427.2001.00682.x
- Silins, U., Bladon, K. D., Kelly, E. N., Esch, E., Spence, J. R., Stone, M., Emelko, M. B., Boon, S., Wagner, M. J., Williams, C. H. S., & Tichkowsky, I. (2014). Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology*, 7(6), 1508-1523. https://doi.org/10.1002/eco.1474
- Silins, U., Stone, M., Emelko, M. B., & Bladon, K. D. (2009). Sediment production following severe wildfire and post-fire salvage logging in the Rocky Mountain headwaters of the Oldman River Basin, Alberta. *Catena*. 79(3), 189-197. https://doi.org/10.1016/j.catena.2009.04.001
- Small, M. J., & Sutton, M. C. (1986). A regional pH-alkalinity relationship. *Water Research*. 20(3), 335-343. https://doi.org/10.1016/0043-1354(86)90081-3
- Soto, D., & De Los Rios, P. (2006). Influence of trophic status and conductivity on zooplankton composition in lakes and ponds of Torres del Paine National Park (Chile). *Biologia*. 61(5), 541-546. https://doi.org/10.2478/s11756-006-0088-7

- Stewart, T. J., Johannsson, O. E., Holeck, K., Sprules, W. G., & O'Gorman, R. (2010). The Lake Ontario zooplankton community before (1987-1991) and after (2001-2005) invasion-induced ecosystem change. *Journal of Great Lakes Research*. *36*(4), *596-605*. https://doi.org/10.1016/j.jglr.2010.07.010
- Svenning, J. C., & Skov, F. (2005). The relative roles of environment and history as controls of tree species composition and richness in Europe. *Journal of Biogeography*. *32*(6), *1019-1033*. https://doi.org/10.1111/j.1365-2699.2005.01219.x
- Tecle, A., & Neary, D. (2015). Water Quality Impacts of Forest Fires. *Journal of Pollution Effects & Control. 3(3), Article Number: 1000140.* https://doi.org/10.4172/2375-4397.1000140
- Thompson, P. A. (2012). Plankton. A Guide to Their Ecology and Monitoring for Water Quality.

  \*Austral Ecology. 37(2), e7-e8. https://doi.org/10.1111/j.1442-9993.2012.02360.x
- Thompson, V. F., Marshall, D. L., Reale, J. K., & Dahm, C. N. (2019). The effects of a catastrophic forest fire on the biomass of submerged stream macrophytes. *Aquatic Botany*. 152, 36-42. https://doi.org/10.1016/j.aquabot.2018.09.001
- Veraverbeke, S., Rogers, B. M., Goulden, M. L., Jandt, R. R., Miller, C. E., Wiggins, E. B., & Randerson, J. T. (2017). Lightning as a major driver of recent large fire years in North American boreal forests. *Nature Climate Change*. *7*, *529-534*. https://doi.org/10.1038/nclimate3329

- Walker, X. J., Rogers, B. M., Baltzer, J. L., Cumming, S. G., Day, N. J., Goetz, S. J., Johnstone, J. F., Schuur, E. A. G., Turetsky, M. R., & Mack, M. C. (2018). Cross-scale controls on carbon emissions from boreal forest megafires. *Global Change Biology*. 24(9), 4251-4265. https://doi.org/10.1111/gcb.14287
- Woo, M. K., Modeste, P., Martz, L., Blondin, J., Kochtubajda, B., Tutcho, D., Gyakum, J.,
  Takazo, A., Spence, C., Tutcho, J., Di Cenzo, P., Kenny, G., Stone, J., Neyelle, I., Baptiste,
  G., Modeste, M., Kenny, B., & Modeste, W. (2007). Science meets traditional knowledge:
  Water and climate in the Sahtu (Great Bear Lake) Region, Northwest Territories, Canada.
  Arctic. 60(1), 1-113. https://doi.org/10.14430/arctic263
- Zhang, Y., Wolfe, S. A., Morse, P. D., Olthof, I., & Fraser, R. H. (2015). Spatiotemporal impacts of wildfire and climate warming on permafrost across a subarctic region, Canada. *Journal of Geophysical Research F: Earth Surface*. 120(11), 2338-2356. https://doi.org/10.1002/2015JF003679