Taxonomic changes in mountain zooplankton communities over a 50-year period reveal a loss of calanoid copepods

by

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ABSTRACT

Historical species datasets are key to evaluating community responses to long-term environmental change. Yet, ecological studies related to assessing species diversity are often dominated by spatial scales, with less attention dedicated to temporal applications. The main goal of my research was to determine whether crustacean zooplankton communities in 64 lakes along a 1400-m elevation gradient across the Canadian Rocky Mountains have shifted between 1966 and 2017. A generalized estimating equation (GEE) analysis of two measures of community change revealed that cladocerans showed greater taxonomic turnover at lower elevations, while their species richness remained relatively static over time. In contrast, copepods showed a temporal decline in species richness and limited turnover along the elevation gradient. An evaluation of colonization and extinction rates, as related to the Island Biogeography Theory, provided further insight into these patterns. Cladocerans displayed offsetting colonization and extinction events, thereby maintaining relatively constant species diversity. In contrast, copepods did not show compensatory dynamics in that extinction rates exceeded colonization rates, rendering communities less species-rich over time. Further, an analysis of body size revealed the decline in copepod richness may be best explained by the loss of large-bodied calanoids through relatively higher extinction rates across the entire study region. My findings highlight how the survivorship of calanoid copepods may be compromised due to poor dispersal potential, mate limitation and lack of tolerance to increased environmental temperatures.

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Chapter 1 | Introduction

1.1 | The mechanisms of colonization and extinction

Temporal and spatial changes in community composition have garnered much research attention since MacArthur and Wilson's (1967) *The Theory of Island Biogeography*. This conceptual framework predicts patterns of species diversity on islands based on island size and relative isolation by quantifying rates of species colonization and local extinction. The Island Biogeography Theory (IBT) posits that islands close to the mainland support greater species richness, than islands that are further away, because it is easier for species to immigrate to these geographically "near" islands (MacArthur and Wilson 1967). Similarly, large islands have greater species richness, than small islands, as they typically offer a wider range of habitats and have more available resources to support more diverse communities. Accordingly, these small islands become species-saturated with a fewer number of species than large islands, and as the number of species habiting an island reaches carrying capacity, the probability of one of these species extirpating also increases, leading to quicker extinction rates (MacArthur and Wilson 1967). A graphical interpretation of these concepts suggests that a greater number of species will occur on large islands that are close to the mainland, and fewer species will occur on islands that are further away (MacArthur and Wilson 1963).

The relationship between colonization and extinction rates can be expressed as turnover, where the loss of a resident species is replaced by a new immigrating species. The IBT further suggests that small islands, close to the mainland will have greater turnover than large islands that are further away, because colonization rates are higher for near islands and extinction rates are higher for small islands (MacArthur and Wilson 1963). Through this dynamic process, species diversity tends toward a state of equilibrium, as colonization and extinction rates roughly equilibrate (MacArthur and Wilson 1963). Measuring patterns in turnover, as related to colonization and extinction rates, require intermediate time scales (many years), whereby, patterns of turnover in short timescales are largely dominated by seasonality effects , while turnover in long timescales are more often related to evolutionary factors (Korhonen et al. 2010).

The implicit steady-state equilibrium that exists within communities is key to the IBT. Traditionally, an ecosystem is considered stable when colonization and extinction rates are at equilibrium, leaving little variation in the number of species over time (Connell and Sousa 1983). However, this contention would exclude systems which may exhibit non-equilibrium dynamics in the short-term, such as seasonal variability in species indices (Nuvoloni et al. 2016). As such, a broader definition proposes the “loose equilibrium” (DeAngelis et al. 1985), which has gained support as it encompasses non-directional, temporal fluctuations in community change within some average condition (Matthews and Marsh-Matthews 2016). Similarly, communities may display shifting equilibrium patterns in the long term as related to changing environmental conditions, which may favour a species colonization or extinction rate (Jones and Gilbert 2017).

Despite some criticism towards IBT that this model oversimplifies ecological processes (Lomolino 2000), the offsetting dynamics of colonization and extinction remain useful in the exploration and understanding of natural systems (Haila 2002, Macdonald et al. 2018). The IBT continues to be advanced from a simplified, classic equilibrium model that predicts a community’s richness (Fox 2006) by integrating functional traits (Jacquet et al. 2017), trophic interactions (Gravel et al. 2011) and predicts patterns in spatial β-diversity, the ratio between regional and local diversities (Lu et al. 2019). Further modification to the theory has seen it expanded from islands to now include any isolated system within unsuitable habitat (Haila 2002). For example, lakes may be analogous to islands, as they are insular systems surrounded by terrestrial landscapes (Lassen 1975, Warren et al. 2015). Given such developments to the original IBT, the use of the concepts described by the model may continue to provide theoretical explanations for variation in species colonization and extinction dynamics.

1.2 | Zooplankton dispersal and colonization success

Community composition is influenced by regional and local factors, with the relative importance of these two processes depending on the spatial and temporal scales in question (Shurin 2000, Louette and De Meester 2005, Hanly and Mittelbach 2017). At a regional scale, dispersal limitation may be the primary mechanism driving community composition. Whereas on the local level, ecological interactions, such as ambient environmental conditions and competition between resident species, will largely structure communities. Whether regional or local processes are principally controlling community structure is largely contingent upon colonization and extinction rates (Cohen and Shurin 2003). If colonization rates exceed the number of species that can coexist, then local factors will constrain community membership. Alternatively, if extinction rates are high and dispersal opportunities are low, then regional factors shape the community.

Recently, an increasing number of experimental and observational studies of zooplankton dispersal patterns have been conducted to better understand community dynamics in freshwater systems. Zooplankton rely on passive dispersal by both abiotic and biotic vectors. Arguably, wind is believed to be the dominant mode of zooplankton dispersal, as colonization rates were observed comparable in artificial sites, which restricted animal access in some sites (Cáceres and Soluk 2002, Cohen and Shurin 2003). A similar study, which used windsocks to collect zooplankton species, highlighted the importance of wind direction and frequency in the dispersal of zooplankton (Vanschoenwinkel et al. 2008). Additional abiotic vectors include rivers and streams, whereby zooplankton may be carried in flowing water from one site to another (Havel and Shurin 2004). Biotic vectors, such as birds, also play a role in the transportation of zooplankton (Green and Figuerola 2005). Notably, zooplankton were found to survive the intestinal tract of waterfowl, where they may be excreted at new locations, providing colonization opportunities (Proctor and Malone 1965).

Regional processes that influence the dispersal ability of zooplankton have been studied, where high colonization rates were observed in closely connected sites (Cohen and Shurin 2003, Louette and De Meester 2005). The opposite trend has also been shown, where low colonization rates occurred within isolated systems (Jenkins and Underwood 1998, Vanschoenwinkel et al. 2011). This suggests that colonization success of zooplankton is related to the degree to which habitable sites are connected. Lakes along an elevation gradient may exhibit these regional processes as insular alpine lakes are less connected than montane lakes, potentially leading to dispersal limitations at high elevations (Warren et al. 2015). Further, when considering unassembled communities, which lack any zooplankton species, research has found that zooplankton have high colonization rates as the community develops (Hanly and Mittelbach 2017), particularly within short (< 3km) dispersal distances of neighbouring source pools (Louette and De Meester 2005). However, if communities are saturated, local ecological interactions will have a strong influence on community composition and may preclude further species membership (Shurin 2000).

These local ecological interactions may be expressed through species competition and habitat filtering, where the local environmental conditions select against certain intolerant species (Ricklefs 1987). Such may be the case within mountain zooplankton communities, where research found that increased environmental change has led to a decrease in thermally sensitive, large-bodied species, which are being compensated for by successful establishemnt of small-bodied species (Loewen and Vinebrooke 2016, Jones and Gilbert 2017). Caution is advised when making inferences regarding habitat filtering and species competition processes, as environmental conditions directly relate to species survival, while also indirectly contributing towards some species competitive advantage (Cadotte and Tucker 2017). Understanding how local and regional processes shape community composition through biogeographical mechanisms (i.e. colonization and extinction rates) is paramount in assessing future ecosystem functioning.

1.3 | Thesis outline

This thesis begins with a brief overview of the ecological theories and concepts that aid in the understanding of observed patterns in community diversity. McArthur and Wilson's Island Biogeography Theory was the first experimental analysis of how community compositions are maintained through the loss and gain of species over time. Here, the dynamic relationship between colonization and extinction can be measured as species turnover, where the extinction of a resident species is replaced by a new colonizing species. Should these two processes have equal rates, community equilibrium dynamics are achieved. Finally, the regional and local processes that structure zooplankton community composition were considered, as related to colonization and extinction.

Drawing on these theories and models, chapter two aims to highlight which zooplankton communities in the Canadian Rocky Mountains have exhibited the greatest temporal change in community composition. I analysed cladocerans and copepods to identify which communities along the elevation gradient are most vulnerable to continued environmental change. I achieved this through extensive sampling of 64 lakes along an elevation gradient from Jasper National

Park in the north, to Waterton Lakes National Park in the south. These contemporary surveys were compared to preceding surveys to evaluate zooplankton community change since 1966. Further, the last chapter provides insight to managers and policy makers by predicting how these aquatic ecosystems, along the elevation gradient, will be altered given continued shifts in zooplankton communities. This thesis concludes with an accounting of insights gleaned through the course of this research and offers recommendations for improved zooplankton taxonomic enumeration methods.

The research objectives of this thesis are as follows:

1. Evaluate taxonomic changes in crustacean zooplankton communities along an elevation gradient in 64 lakes of Canadian Rocky Mountains by assessing species turnover and total richness over a period of five decades,
2. Investigate underlying patterns in species colonization and local extinction rates,
3. Identify relationships between zooplankton species body size, and colonization and extinction rates, and
4. Consider the long-term impacts of changing community composition on mountain lake ecosystem dynamics and functionality.

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Chapter 2 | Temporal analysis of mountain zooplankton communities over a 50-year period along an elevation gradient

2.1 | Introduction

The species equilibrium model paradigm, of the late 1960s, was the first analytical approach to consider that ecosystems reach a steady state through the disappearance of resident species, which are then continuously replaced by new, immigrating species (MacArthur and Wilson 1967). The colonization and extinction curves of this heuristic model are foundational to ecology and have since been extended to consider new approaches to assessing species diversity, such as metacommunity and neutral theory (Ricklefs 1987, Leibold et al. 2004, Losos and Ricklefs 2010, Warren et al. 2015). However, these ecological concepts and related models are now dominated by spatial scales, with less attention being dedicated to temporal applications (Wolkovich et al. 2014, Warren et al. 2015). This is particularly important during the Anthropocene, where ecological responses to chronic disturbances, such as climate change, are complex and require long-term studies (Wolkovich et al. 2014, Donohue et al. 2016). Such temporally extensive datasets are important in generating baseline data from which turnover and changes in biodiversity may be measured and related to ecosystem stability (McCann et al. 1998, Magurran et al. 2010).

Temporal turnover considers the variation in species composition within a community over time. The ecological components of turnover include the colonization rate of new species and the local extinction rate of existent species (Anderson et al. 2011). Monitoring such temporal-dependent ecological processes along an environmental gradient, such as elevation, allows for a multifaceted approach to assessing patterns in community composition. Additionally, mountain landscapes offer a viable proxy for climate change, given that the physical environment changes rapidly across a relatively short vertical distance (Beniston 2006). The unique study of mountains facilitates the monitoring of changes within communities of thermally sensitive alpine species, and their use as relevant indicators of environmental change (Schneider and Mazer 2016, Praeg et al. 2019). Research on elevation-dependent warming indicates that ecosystems at higher elevations are subjected to greater warming rates and endure more frequent and intense weather events, than ecosystems at lower elevations (Rangwala and Miller 2012, Higuchi and Joncas 2015, Pepin et al. 2015). Specifically in Banff, meteorological data has revealed that the climate has become progressively warmer more variable in extreme weather events since the 1890s (Parker et al. 2008, Vinebrooke et al. 2010).

The earliest responses to such dramatic environmental changes in aquatic systems are often realized in shifts of community composition, particularly in small and fast reproducing organisms, such as plankton (Schoener 1983, Schindler 1987). Zooplankton are ideal study organisms of these early environmental shifts, having demonstrated sensitivity to acute changes in limnological variables (Jansson et al. 2010, Fischer et al. 2011, Vadadi-Fülöp et al. 2012). As such, zooplankton communities exposed to environmental change may display increased rates of species turnover, as small-bodied species are being favoured over thermally intolerant and large-bodied species (Loewen and Vinebrooke 2016). Similar research has demonstrated that low latitude zooplankton communities illustrate greater temporal turnover than those at high latitudes (Shurin 2007). This change is driven by an increase in colonization events at lower latitudes, rendering these communities more species-rich over time (Jones and Gilbert 2017). However, the effect of elevation on zooplankton species' temporal turnover remains unknown.

In this research, I analyzed the crustacean zooplankton, of 64 lakes along a 1,400 m elevation gradient in the Canadian Rocky Mountains to determine how community compositions have changed from 1966 to 2017. Temporal turnover was hypothesized to be greater at high elevation lakes compared to low elevation lakes due to increasing environmental change in the alpine. Specifically, I predicted that colonization rates at high elevations would be lower, due to limited dispersal opportunities to these insular, alpine lakes. Similarly, I also predicted that extinction rates in the alpine would be higher as elevation-dependent warming will lead to uninhabitable environments for thermally sensitive species. This anticipated variability in colonization and extinction events will create asynchronous species replacement patterns, thereby altering species richness over time. Further, it was expected that there would be a temporal shift towards smaller, more generalist taxa, as they may withstand more varied environmental thresholds and maintain greater dispersal potential. This research considers the following:

1. Is there an effect of elevation on taxonomic changes in zooplankton communities over time?
2. How are colonization, or local extinction rates, contributing to taxonomic variance in these communities?
3. Have there been body-size shifts in zooplankton community compositions?

2.2 | Materials and Methods

2.2.1 | The study area

Study sites were systematically selected from an established database of various limnological surveys conducted in western North America (Loewen et al. 2019). Focusing on the Canadian Rocky Mountain National Parks data, the earliest surveys were conducted by the Canadian Wildlife Service in the 1960s to support fisheries management (Mayhood and Anderson 1976). Environment Canada continued limnological surveying in the late 1980s to mid-1990s to assess the condition of these previously stocked lakes. Further, the database includes contemporary environmental-zooplankton surveys, as research and monitoring of Canada’s mountain headwaters remains a priority (eg. Donald et al. 2001, Fischer et al. 2015).

As this research aimed to evaluate zooplankton temporal turnover, selected sites in 2017 required a minimum of two preceding surveys to capture how community compositions have changed over the past five decades (supplementary material, figure A1). Correlations of site physical characteristics, such as latitude, longitude, fish (presence/absence), depth and surface area, were made to assess for any confounding effects on the community composition measures (supplementary material, figure A2). Notably, it has been identified that the presence of fish drastically alters zooplankton community composition (Donald et al. 2001, Messner et al. 2013). Therefore, only “natural state” lakes, which have either remained fishless throughout historical stocking initiatives, or lakes that have always supported fish populations, were considered in this analysis (supplementary material, figure A3).

Sixty-four lakes were resampled during the ice-free season of 2017 within five Canadian Mountain National Parks. The study area spans nearly 550 km along the Continental Divide, from Jasper National Park in the north to Waterton Lakes National Park in the south (Figure 1). Limestone formations comprise much of the bedrock within the study area, with feldspathic quartz formations in the northern regions (Anderson 1974). The elevation extent of the sites lay between 1,020 m to 2,423 m asl*,* with lake surface area ranging from 0.1 ha to 172 ha and maximum depth between one meter and 70 m (supplementary material, Table A1). A complete list of the sampling sites and their physical attributes is illustrated in Table 1.

2.2.2 | Field sampling protocol and zooplankton enumeration

To ensure the validity of comparison between past and present surveys, sampling methods replicated those previously used by Environment Canada and Parks Canada during the original surveying efforts (Anderson 1971). Surveys were conducted in a south to north, low to high elevation pattern, to account for species maturation throughout the growing season. This remains consistent with historical data collection, where only surveys completed between June to August were considered in the analyses. The collection of samples was conducted using an inflatable boat paddled to the profundal zone of each site. A depth finder and bathymetry maps were used to locate the deepest point of the lake from where samples were then collected.

Zooplankton were collected using a 64-µm mesh-size conical Wisconsin net that was hauled vertically from one meter above the lake bottom up to the surface at a rate of 1 m/sec. If the lake was less than five meters deep, horizontal tows of known length were performed to collect zooplankton. Horizontal tows were done by placing the net in the boat, paddling to the deepest point of the lake, and having the surveyor onshore pull the net towards them at a rate of 1 m/sec, ensuring that the mouth of the bridal did not drag in the sediment. The sample collected from three vertical hauls and three horizontal tows were placed into a 250 mL Nalgene container. The net was carefully rinsed with lake water to dislodge any residual organisms that may have attached to the sides of the net and added to each sample, which were then immediately preserved in a 70% ethanol solution.

Zooplankton enumeration was completed at the University of Alberta's Vinebrooke Lab. Cladocerans and copepods were identified to genus level using a dissecting scope at 16 and 32-times magnification before being slide-mounted and placed under a compound microscope for species identification at 4 and10-times magnification. The enumeration process occurred as follows: the contents of each sample bottle were rinsed with distilled water through a 64-µm mesh-size sieve, then collected in a beaker and diluted with distilled water to 50 mL total volume. A 5 mL subsample was retrieved from the well-mixed contents of the beaker using a Cole-Parmer pipettor and placed in a Ward Zooplankton Counting Wheel to be viewed under the dissecting scope. Mature cladoceran and copepod individuals were identified to the species level when possible (Edmondson 1959) until >300 individuals were counted (Mack et al. 2012). If 300 individuals were attained before reaching the end of the counting wheel, identifications of the subsample would continue until the entire wheel had been examined. At some sites, where species diversity was low or where there were many immature individuals, the entire contents of the sample container were examined.

To harmonize species-level identifications with past surveys, taxonomic records were standardized to account for species hybridization, indistinguishable species, and changes in nomenclature. Therefore, the taxonomic resolution for some morphologically similar species was decreased to the genus level without compromising the quantitative community assessments (Jones and Gilbert 2017, Roden et al. 2018). In the case of *Daphnia* species, two groups were created, one group for large species (*D. middendorffiana, D. pulex* and *D. galeata*) and a second group for small species (*D. dentifera, D. schødleri, D. catawba* and *D. longiremis*). Similarly, rare species (< 0.01 probability of detection throughout the study duration) were removed from the analysis, as rare species inflate calculated turnover (Arnott et al. 1999). This conservative approach resulted in a consolidated list of 28 species-level identifications and five genus-level groups. The genus groupings will be referred to as species throughout this chapter, resulting in a final total of 33 species used in the analysis (Table 2).

2.2.3 | Statistical analysis

Zooplankton species surveys were initially separated into two taxa (cladocerans and copepods), which were then translated into incidence matrices of occurrence by site. A size variable was included in each of the taxa matrices such that, cladoceran species were divided into large, (body length >0.5 mm, n= 6) and small (<0.5 mm, n= 10) size categories. Similarly, copepods were separated into their order-levels; calanoids (n= 10) and cyclopoids (n= 8). For simplicity, calanoids will also be referred to as large-bodied and cyclopoids as small-bodied. Temporal changes in turnover were examined by comparing the results of sampling surveys within a site to their most recent, preceding survey, such that second earliest survey (T_2) was compared to the earliest survey (T_1), and T_3 to T_2 etc. Time was considered in the analysis as the intra-annual variability (< 365 days) and inter-annual variability (> 365 days) between surveys, to account for differences in survey dates. This was achieved by tailing the number of Julian days between each sequential survey first by only considering the month and day (intra-annual variability) and then considering the year, month and day (inter-annual variability).

Community change was evaluated using two measures: turnover and species richness. Using both measures is an essential consideration as high turnover may not reflect a change in richness if colonization and extinction events occur at equal rates. Conversely, a community showing minimal turnover may still demonstrate a change in richness if species replacement (i.e., an extinction event followed by a colonization event) is low, but the community is still gaining or losing species over time. Species turnover was calculated between each sequential survey within a site, using Jaccard's pairwise dissimilarities:

$$J_{diss} = 1- [A / (A + B + C)]$$

Where, A is the number of species that remained the same, B is the number of species that colonized, and C is the number of species that went extinct. Results ranged from zero to one, with these extremes indicating either no change or complete turnover in community composition respectively. Jaccard's Dissimilarity was chosen to measure the amount of variation in zooplankton communities as this index highlights the number of unique species from each survey as a proportion of the total species richness (Baselga 2012). Results of Jaccard's Dissimilarity ranged from zero (no change) to one (complete turnover).

The colonization and extinction components of turnover were partitioned to determine how the immigration of new species and the disappearance of resident species effects community composition, and if observed patterns differ for cladocerans and copepods. This was achieved by determining the proportion of species in the current survey that were not in the preceding survey (i.e., colonization event), as well as the proportion of species found in the preceding survey that were not in the current survey (i.e., extinction event). This method was applied to each pairwise step within a site and accounted for differences in richness among lakes.

The nonmetric multidimensional scaling (NMDS) ordination analysis was performed using CANOCO software, version 5 (ter Braak and Smilauer 2012). Here, community composition for each site from the 2017 surveys were ranked using Jaccard's dissimilarity distances in two-dimensional ordination space to identify patterns in diversity (supplementary material, Figure A5 and A6). This was achieved by taking the NMDS results of the primary axes for each site and plotting it against elevation to illustrate that sites which are closer together in geographical space (i.e. along the elevation gradient) have similar taxonomic communities (Jones and Gilbert 2017).

All other analyses were performed in R statistical software, version 3.5.3 (R Core Team 2017). Due to temporal autocorrelation within sites, the community composition measures were modelled using generalized estimating equations (GEE) from the 'geepack' package (Hojsgaard et al. 2006), which accounts for clustered categorical responses (Zuur et al. 2009). Each model was fit with an *exchangeable* correlation structure to the within lake observation IDs and was confirmed by an autocorrelation plot of the residuals (supplementary material, Figure A4). A binominal distribution was applied as the response variable for Jaccard's Dissimilarity and the proportion of events (either colonization or extinction), was constrained between 0-1. The species richness model used count data in the response variable and was, therefore, fit with a Poisson distribution. All explanatory variables were included in the model selection process and systematically removed using the *drop1()* command until only statistically significant covariates remained (Table 3 and 4). When plotting the models, the significant covariates were held at their means and 95% confidence intervals calculated. This was achieved by first transforming the GEE models to general linear models (GLM), which allows for the *predict()* function in R to calculate to confidence intervals, but has no bearing on the results (Scott-Hayward et al. 2013).

2.3 | Results

Elevation patterns of diversity showed that for the 2017 surveys, species richness of zooplankton significantly declined with increasing elevation (Figure 2a, $p < 0.0001$). The results of the primary axis of the nonmetric multidimensional scaling (NMDS), with a two-dimensional solution (supplemental figure A5), based on Jaccard's Dissimilarity, were plotted against elevation (stress = 0.22). This shows that lakes within similar elevations contained taxonomically similar zooplankton communities (Figure 2b, $p < 0.0001$). This means that low elevation sites had analogous communities to one another, while high elevation sites had comparable community compositions.

Temporal turnover, as a measure of Jaccard's Dissimilarity, showed a significant, negative relationship with increasing elevation (Figure 3; $p = 0.0017$). Overall, the cladocerans showed significantly ($p < 0.001$) greater taxonomic change than did the copepods over time, particularly at lower montane sites. Inter-annual variability was also highly significant ($p < 0.001$), which reflected how a longer duration between sampling events would favour greater species turnover. The second measure of community change, species richness, decreased significantly over the past fifty years (Figure 4; $p = 0.0117$). The overall decline in species richness was related to the loss of copepods ($p = 0.0412$), but not cladocerans.

Elevation ($p < 0.001$) and maximum depth ($p < 0.001$; a proxy for lake size) were also significant in the richness model. Here, deep and/or low elevation sites had greater richness than did shallow and/or high elevation sites. Notably, fish presence/absence was not significant in either model (turnover model, fish $p = 0.3437$; richness model, fish $p = 0.1360$), showing that sites with or without fish populations have statistically similar rates of community change. Likewise, intra-annual variability was not significant ($p = 0.0972$), suggesting that for the sites in this study, there were no notable differences in community composition when sampled in June, July and/or August.

Due to the differing elevation patterns in taxonomic turnover among the cladocerans versus copepods, these two groups were separated into different models when assessing colonization and extinction rates. Beginning with cladocerans, the proportion of colonization and extinction events were significantly greater at low elevations (Figure 5a; $p < 0.0001$), but there was no significant difference between the two events ($p = 0.7989$). These results suggested that colonization by non-resident species offset the influence of resident species extinctions on total species richness. In contrast, copepods did not exhibit any change in colonization and extinction rates across the elevation gradient ($p = 0.3376$). However, copepod extinction rates exceeded their colonization rates (Figure 5b; $p = 0.0026$). Inter-annual variability was again significant for both models (cladoceran, $p < 0.0001$; copepod, $p < 0.0001$), as was the categorical body-size variable (cladoceran, $p = 0.0014$; copepod, $p < 0.0001$).

A closer examination of the body-size covariate for each taxon revealed that the average proportion of colonization and extinction events for large and small cladocerans were relatively equal. However, small-bodied cladocerans exhibit overall greater change than large-bodied cladocerans (Figure 6a; $p < 0.0001$). Similarly, for the copepod taxa, the small-bodied cyclopoids, showed a greater change in the average proportion of colonization and extinction events than the large-bodied calanoids (Figure 6b; $p < 0.0001$). Interestingly, it was here that the decline of copepods over time was attributable to the loss of large-bodied calanoids, whereby the average proportion of extinction events surpassed the average proportion of colonization events.

2.4 | Discussion

My findings highlight differences in the sensitivities to environmental change of mountain zooplankton communities, given the observed gradational dependency of colonization and extinction rates. The implicit assumption that alpine communities experience greater adverse environmental conditions than montane communities was not supported, as turnover was higher at low elevations. Here, cladocerans showed greater temporal turnover than did copepods, whereby the loss in species richness was compensated through increased colonization. In contrast, copepods did not show similar compensatory dynamics, resulting in a net decrease in species richness over the past five decades. This decline in copepod richness may be best explained by the loss of large-bodied calanoids through relatively higher extinction rates across the entire study region.

The observed negative turnover trend with elevation has been previously documented (Mori et al. 2013, Tello et al. 2015, Sabatini et al.2018), however the cause of this decline has been highly debated in the field of ecology (Kraft et al. 2012, Qian et al.2012, Tuomisto and Ruokolainen 2012, Ulrich et al. 2017). Despite criticism that measured turnover along environmental gradients is simply an artifact of varying species pools (Kraft et al. 2011), it has been further argued that turnover along latitude and elevation gradients is indeed driven by local and regional community structuring processes (Qian et al. 2013, Sabatini et al.2018). Further, pairwise multivariate distances, as used in this research, have proven to act independently of regional species pools, and therefore do not influence measured turnover (Bennett and Gilbert 2015). As such, interpreting variation in temporal turnover within-sites along an elevation may be achieved. The following considers regional and local processes which shape the observed changes in community composition as outlined by my key findings. First, regional factors, namely dispersal ability, determine the likelihood of a species relocating to a new site (Shurin 2000). Second, local processes, such as habitat filtering and species competition within the establish community (Cadotte and Tucker 2017), will determine if the newly immigrated species will colonize successfully. These ecological interactions may be explained through direct and indirect changes in environmental conditions which exclude some species while favouring others (Viana et al. 2016). Finally, a review of these processes specifically related to calanoid copepods is presented to help explain their decline in richness over the past fifty years.

As temporal turnover was greatest at low elevations, this indicates that regional and local processes infuencing community composition are stronger in montane regions. As such, regional factors are influenced by greater connectivity between low elevation lakes, which promotes the immigration of species between sites. Colonizing zooplankton rely on passive dispersal methods by both abiotic vectors, such as wind and rain (Cáceres and Soluk 2002, Cohen and Shurin 2003, Vanschoenwinkel et al. 2008) and biotic vectors, such as birds and mammals (Proctor and Malone 1965, Green and Figuerola 2005). Zooplankton species differ in their ability to disperse (Cáceres and Soluk 2002, Havel and Shurin 2004) particularly in remote, insular mountain lakes (Vanschoenwinkel et al. 2011). In these instances, small-bodied species have illustrated greater colonization rates than large-bodied species (Hanly and Mittelbach 2017, Jones and Gilbert 2017). This supports my finding where small-bodied cladocerans and cyclopoids showed greater average number of colonization events than their large-bodied counterparts. Further, zooplankton may disperse as adults, or as desiccation-resistant propagules, the later of which favours long-distance dispersal as cladoceran ephippia and copepod diapause eggs may travel further out of water than adult specimen (Allen 2007).

In addition to dispersal dynamics, local processes through ecological interaction also contribute to establishing community composition. In such instances, environmental change may preclude certain thermally intolerant species through habitat filtering, while also presenting indirect advantage to other species. The environmental conditions in the Canadian Rocky Mountains have witnessed a positive trend in annual mean temperatures over the past century, particularly in the winter months (Jiang et al. 2015, Kienzle 2017). Pronounced winter warming is of importance for lake ecosystems, where increases in air temperatures dramatically prolong the ice-free season (Karlsson et al. 2005, Parker et al. 2008), resulting in elevated water temperatures (Thompson et al. 2005). These environmental changes alter the thermal stratification and mixing regimes of lake ecosystems (De Stasio et al. 1996, Adrian et al. 2009), which has a direct effect on planktonic productivity and biomass (Winder et al. 2009, Fischer et al. 2011, Vadadi-Fülöp et al. 2012).

This perceived environmental change may result in habitat filtering where climatic warming selects against thermally intolerant species. Studies have shown that large-bodied species are declining as they experience greater metabolic cost while attempting to maintain homeostasis in the face of higher temperatures (Daufresne et al. 2009). As well, lake warming favours smaller phytoplankton species (Winder and Sommer 2012, Ruland et al. 2015), which may provide a competitive advantage to the filter-feeding cladocerans who consume smaller food particles, where as raptoral-feeding copepods generally target larger food items (Barnett et al. 2007). Further, the higher incidence of colonization events by cladocerans, compared to copepods, may be also be attributable to their reproductive processes. Cladocerans display facultative sexual reproduction, allowing for both sexual and asexual reproduction, such that they are not restricted by mate limitation upon immigrating to a new site, unlike copepods, which are obligately sexual (Allan 1976, Henriques-Silva et al. 2016). For these reasons, small-bodied cladocerans have a competitive advantage over large-bodied copepods. As such, this could explain the off-set colonization and extinction dynamics of the cladocera taxa observed in this study, whereas copepods extinction rates were not balanced by colonization rates.

The observed decline in copepod species richness is a systematic pattern which may only be revealed when multiple-decade time series data are considered (Gonzalez et al. 2016). The extirpation of large-bodied calanoids, across the elevation gradient over the past five decades, suggests that these copepods could be experiencing environmental change to the degree that is beyond their tolerance thresholds. Research has shown that calanoid populations, particularly juvenile nauplii, are highly influenced by temperature (Rhyne et al. 2009), and lakes that are susceptible to an annual mean temperature increase of 1.5 ºC may see a decline in the abundance of calanoid species (Winder et al. 2009). Similar research has also shown a decline in thermally intolerant, large-bodied species, however it was found that these species were compensated for by smaller species (Loewen and Vinebrooke 2016), thereby rendering communities more species-rich over time (Jones and Gilbert 2017). This work highlights the need for further studies on the directionality and rate of community change along various environmental gradients.

Research has found that the loss of a single species can destabilize a community (McCann 2000), particularly when it lacks species that are functionally redundant (Naeem and Li 1997). This follows the insurance hypothesis which posits that greater diversity increases the likelihood that a functionally similar species will compensate for the decreased contribution of another species (Yachi and Loreau 1999). However, this may pose significant challenges for alpine ecosystem process where zooplankton diversity is relatively low (Figure 2a). As such, should alpine calanoids, primarily *Hesperodiaptomus* species, be extirpated, a functionally redundant species may not exist to compensate for this loss. Studies have shown that the extirpation of *Hesperodiaptomus arcticus* from an alpine lake, caused a significant shift in ecosystem functioning, as overall zooplankton biomass declined, allowing phytoplankton to proliferate and thereby compromising the typically oligotrophic lake (Parker and Schindler 2006). Further, research suggests that montane species may not exhibit dispersal limitations (Loewen et al. 2019) and could therefore replace disappearing alpine species. However, as this research revealed, calanoid species are disappearing across the elevation gradient, indicating that lower elevation species may not be available to functionally compensate for a loss of species at higher elevations.

The natural recovery of calanoid copepods is quite low (Sarnelle and Knapp 2004), and with continued environmental change the future of these species is unknown. As such, the survivorship of calanoids remains a topic for further exploration, particularly in alpine lakes where their extirpation may have detrimental consequences for ecosystem functionality. This area of research would benefit from a species abundance analysis, where changes in zooplankton community biomass may be quantified. As demonstrated by my research, renewed interest in the changing zooplankton community structure, particularly for thermally sensitive species, is critical for mitigation and conservation initiatives in rapidly changing environments.

2.5 | Conclusion

This research analyzed a comprehensive zooplankton species dataset from the Canadian Rocky Mountains to illustrate the stochastic mechanisms influencing temporal community compositions. By evaluating cladocerans and copepods separately, I showed that cladocerans had higher temporal turnover at lower elevations. Here, offset dynamics in their colonization and extinction rates was maintained, allowing for species richness patterns to remain relatively constant over the past five decades. Conversely, I observed non-equilibrium dynamics for copepods, whereby a change in their distribution patterns illustrated that local extinction rates exceed colonization rates. This pattern proved particularly true for calanoid copepods, which are generally larger than cyclopoids, suggesting that calanoid species are at risk of extirpation across the elevation gradient. This evidence supports the need for a multifaceted approach to assessing changes in community composition and highlights the importance of species-specific analysis. Further, as this research is the first to quantify zooplankton community change across an elevation gradient in the Canadian Rocky Mountains over the past five decades, it significantly contributes to our understanding of spatiotemporal patterns of species distribution under increasing climatic variability.

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2.7 | Tables

Table 1: Sample sites in Jasper, Banff, Yoho, Kootenay and Waterton Lakes National Park. Lake data presented incudes geographic location (latitude and longitude), elevation (m asl), surface area (ha), max depth (m) and fish status, either present (1) or absent (0).

Lake	**Latitude (north)**	**Longitude (west)**	**Elevation, m asl**	**Surface Area, ha**	**Max Depth, m**	**Fish Status**
Jasper National Park, Alberta						
Annette	52°90’	118°04’	1024	28.6	23	1
Beauvert	52°88’	118°06’	1030	32.3	25	1
Buck	52°55’	117°66’	1405	34	6	1
Cabin	52°87’	118°13’	1217	32.2	20.5	1
Caledonia	52°86’	118°16’	1161	13	11	1
Celestine	53°18’	118°04’	1260	39	14	1
Christine	52°88’	118°24’	1338	7	8	1
Dorothy	52°88’	118°22’	1336	25.1	14.6	1
Edith	52°91’	118°04’	1024	50	18	1
Honeymoon	52°55’	117°67’	1405	18.4	7	1
Horseshoe	52°69’	117°86’	1230	13	23	1
Iris	52°87’	118°22’	1302	5.1	13.2	1
Leach	52°69’	117°90’	1237	13.1	11	1
Mile 16 ½	52°70’	117°91’	1174	9	6	1
Mina	52°88’	118°12’	1214	8.3	13.2	1
Moab	52°66’	117°95’	1204	23.9	18	1
Osprey	52°55’	117°66’	1387	3.4	7.5	1
Patricia	52°90’	118°10’	1180	69	42	1
Pyramid	52°92’	118°09’	1186	127.4	19	1
Banff National Park, Alberta						
Annette	51°36	116°20	1966	5.3	11.7	0
Baker	51°49	116°04	2207	36.4	11.6	1
Boom	51°26	116°09	1893	99.6	13.2	1
Eiffel	51°32	116°24	2281	13.5	10.6	0
Hidden	51°48	116°10	2271	13.3	32.3	1
Louise	51°41	116°22	1731	84.5	70.1	1
Mud	51°44	116°17	1600	7.3	7.2	1
O’Brien	51°28	116°08	2118	4.6	20.7	1
Ptarmigan	51°48	116°07	2332	27.9	21.3	1
Redoubt	51°47	116°07	2393	19.1	11	1
Sentinel	51°33	116°22	2423	2.8	6.7	0
Smith	51°24	115°92	1560	3	9.7	1
Temple	51°36	116°18	2179	3.1	14	1
Vista	51°23	116°02	1567	6.6	6.5	1
Waterfowl (lower)	51°84	116°63	1670	48	4.7	1

Yoho National Park, British Columbia						
Celeste	51°51’	116°51’	1293	0.06	1.6	0
Duchesnay	51°52’	116°50’	1595	3.5	1	1
Emerald	51°44’	116°53’	1310	116	28	1
Hamilton	51°45’	116°57’	2160	5	12.2	0
Hungabee	51°34’	116°31’	2243	1.7	2.7	0
O’Hara	51°35’	116°33’	2014	34.4	38.1	1
Sherbrooke	51°45’	116°38’	1803	35	12	1
Sink	51°45’	116°30’	1622	5	2	1
Summit	51°45’	116°29’	1634	2	1.2	1
Wapta	51°43’	116°34’	1595	24.1	8.2	1
Kootenay National Park, British Columbia						
Cobb	50°66’	115°87’	1260	2.5	8	1
Dog	50°78’	115°92’	1184	15.1	4.7	1
Floe	51°05’	116°14’	2036	57.5	61	1
Olive	50°67’	115°93’	1631	2	3.5	1
Waterton Lakes National Park, Alberta						
Alderson	49°02’	113°97’	1811	10.19	60	1
Allison	49°12’	113°81’	1274	4.05	2.4	0
Bertha	49°02’	113°94’	1774	30.2	18.1	1
Buffalo Creek	49°12’	113°85’	1323	0.96	2	0
Cameron	49°00’	114°04’	1660	172.3	39	1
Crandell	49°08’	113°96’	1524	4.53	15.5	1
Indian Springs W46	49°12’	113°87’	1351	5.88	1.5	0
Indian Springs W48A	49°12’	113°87’	1351	3	2	0
Indian Springs W48B	49°12’	113°87’	1351	0.28	1	0
Linnet	49°06’	113°90’	1280	3.52	3.2	1
Lonesome	49°07’	113°89’	1280	12.67	2.6	0
Lost	49°14’	114°14’	1875	1.57	12	0
Maskinonge	49°10’	113°83’	1276	65	2	1
Rowe (lower)	49°05’	114°05’	1957	1.97	8	0
Rower (upper)	49°05’	114°05’	2168	7.2	3	0
Temporary Pond W60	49°06’	113°88’	1293	0.06	1.6	0

Table 2: Zooplankton species identified in historical and contemporary surveys. Species bolded within the same box were statistically analysed as a single genus-level group.

Taxon	Sub-group	Species
Cladoceran	Large	**_Daphnia middendorffiana_ Fischer, 1851** **_Daphnia pulex_ Leydig, 1860** **_Daphnia galeata_ Birge, 1918**
		Eurycercus lamellatus Müller, 1776
		Leptodora kindtii Focke, 1844
		Polyphemus pediculus Linnaeus, 1761
		Sida crystallina Müller, 1776
		Simocephalus vetulus Müller, 1776
	Small	_Acroperus harpae_ Baird, 1834
		Alona affinis Leydig, 1860 **_Alona costata_ Sars, 1862** **_Alona intermedia_ Sars, 1862** **_Alona quadrangularis_ Müller, 1776** **_Alona guttata_ Sars, 1862** **_Alona rectangular_ Sars, 1861**
		Alonella excisa Fischer, 1854[*] **_Alonella exiguaI_ Lilljeborg, 1853** **_Alonella nana_ Baird, 1850**
		Bosmina longirostris Müller, 1776
		Ceriodaphnia acanthina Ross, 1897 **_Ceriodaphnia affinis_ Lilljeborg, 1900** **_Ceriodaphnia lacustris_ Birge, 1893** **_Ceriodaphnia pulchella_ Sars, 1862** **_Ceriodaphnia quadrangular_ Müller, 1785** **_Ceriodaphnia reticulate_ Jurine, 1820**
		Chydorus sphaericus Müller, 1785
		Daphnia catawba Coker, 1926 **_Daphnia dentifera_ Forbes, 1893** **_Daphnia longiremis_ Sars, 1861** **_Daphnia schodleri_ Sars, 1862**
		Diaphanosoma birgei Korinek, 1981
		Graptoleberis testudinaria Fischer, 1848
		Scapholeberis kingi Sars, 1888
Copepod	Calanoid	_Acanthodiaptomus denticornis_ Wierzejski, 1887
		Aglaodiaptomus forbesi Light, 1938
		Aglaodiaptomus leptopus Forbes, 1882
		Arctodiaptomus arapahoensis Dodds, 1915
		Hesperodiaptomus arcticus Marsh, 1920
		Hesperodiaptomus novemdecimus Wilson, 1953
		Hesperodiaptomus shoshone Forbes, 1893
		Leptodiaptomus nudus Marsh, 1904
		Leptodiaptomus sicilis Forbes, 1882

		Leptodiaptomus tyrrelli Poppe, 1888
	Cyclopoid	*Acanthocyclops vernalis* Fischer, 1853
		Diacyclops thomasi Forbes, 1882
		Diacyclops navus Herrick, 1882
		Eucyclops agilis Koch, 1838
		Eucyclops speratus Lilljeborg, 1901
		Macrocyclops albidus Jurine, 1820
		Microcyclops varicans Sars, 1863
		Orthocyclops modestus Herrick, 1883

Table 3: Summary of generalized estimating equations (GEE) logistic regression predicting Jaccard's Dissimilarity with elevation and species richness over time.

Variable	**Standard Error**	**Wald χ**	***p***
Jaccard's Dissimilarity			
Intercept	0.2847	2.230	0.1343
Taxa	0.1475	21.254	< 0.0001
Elevation (m asl)	1.973×10^{-4}	9.841	0.0017
Inter-annual variability	1.352×10^{-5}	19.218	< 0.0001
Species Richness			
Intercept	6.010	8.96	0.0027
Julian date	2.44×10^{-6}	6.70	0.0096
Taxa	6.84×10^{-2}	4.12	0.0423
Elevation (m asl)	1.07×10^{-4}	58.61	< 0.0001
Depth (max, m)	4.07×10^{-3}	16.51	< 0.0001

Table 4: Summary of generalized estimating equations (GEE) logistic regression predicting colonization and extinction rate over elevation for cladoceran and copepod taxa. Event refers to either colonization or extinction.

Variable	**Standard Error**	**Wald χ**	***p***
Cladocerans			
Intercept	0.314	0.44	0.5097
Elevation (m asl)	2.14×10^{-4}	24.023	< 0.0001
Size	0.166	13.624	< 0.0001
Inter-annual variability	1.32×10^{-5}	10.178	0.0014
Copepods			
Intercept	0.226	140.91	< 0.0001
Size	0.195	16.41	< 0.0001
Event	0.093	9.09	0.0026
Inter-annual variability	1.58×10^{-5}	20.37	< 0.0001

2.8 | Figures

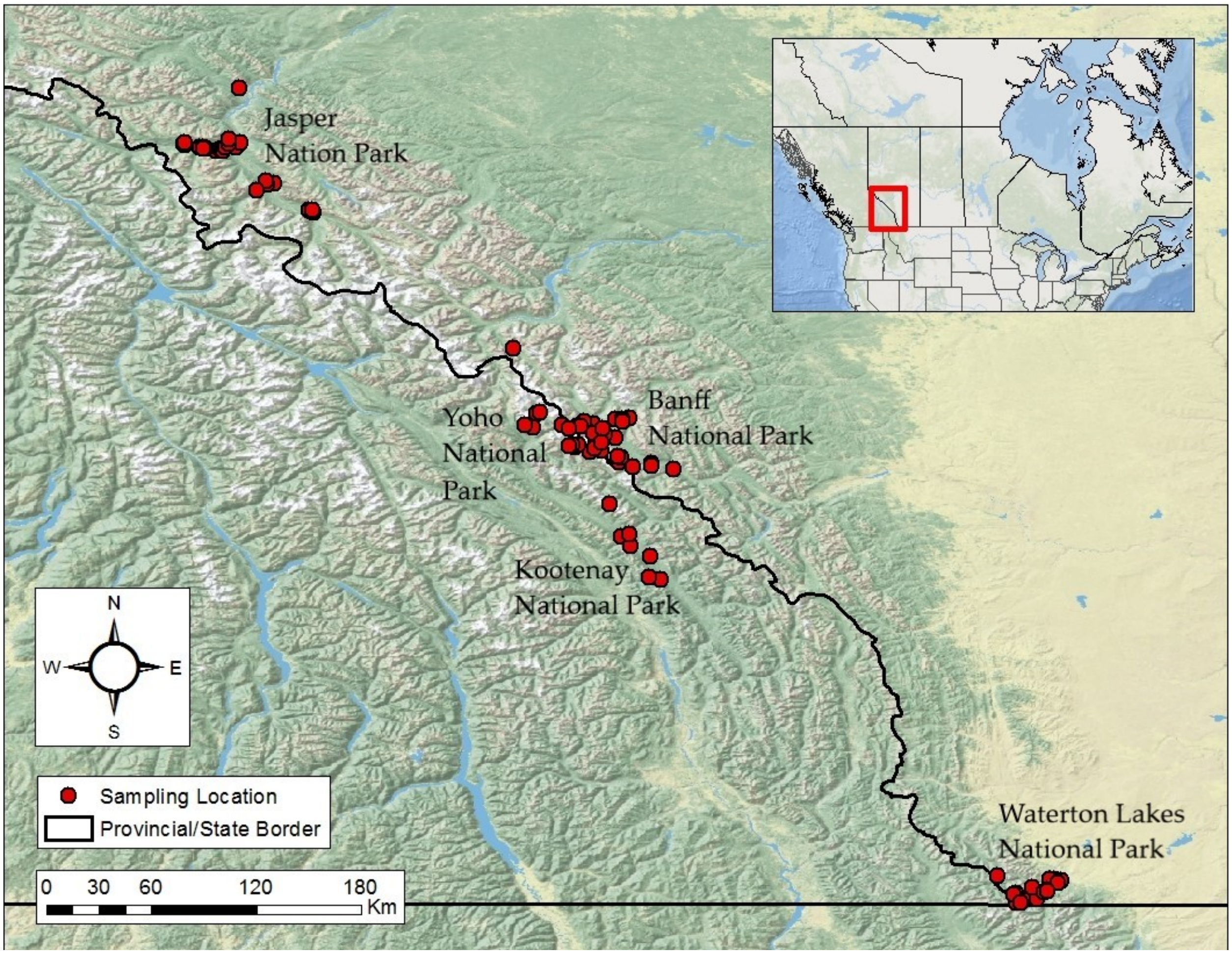

Figure 1: Map of sample site locations in British Columbia and Alberta, Canada. A total of 64 sites were surveyed in the National Mountain Parks. Nineteen sites were sampled in Jasper National Park, 15 in Banff National Park, 10 in Yoho National Park, 4 in Kootenay National Park and 16 in Waterton Lakes National Park.

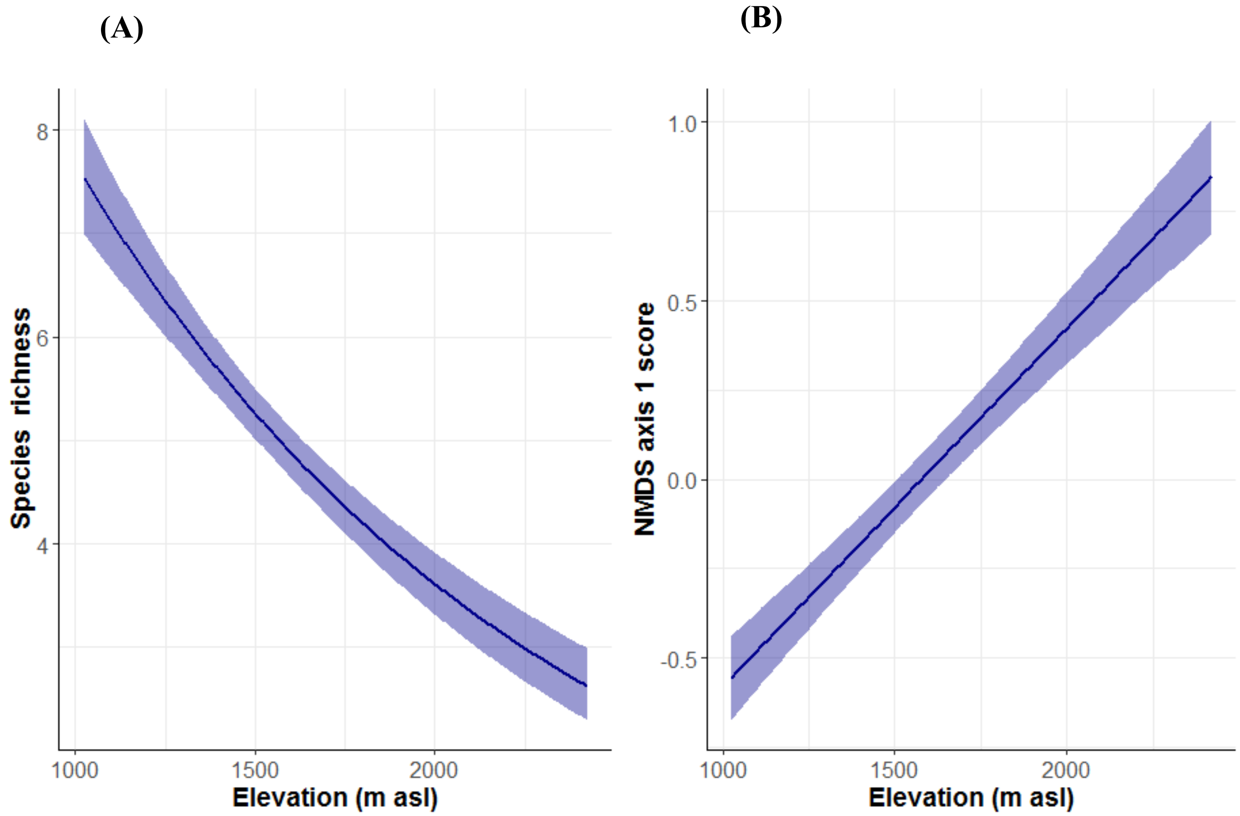

Figure 2: Elevational patterns of diversity. (A) Generalized estimating equations (GEE) plot illustrating zooplankton species richness (cladocerans and copepods combined) decreases with elevation ($p < 0.001$). (B) Nonmetric multidimensional scaling (NMDS) with a Hellinger transformation and a 2D solution representing the y-axis, plotted against elevation indicating that community assemblages within similar elevations are compositionally analogous (stress = 0.22, $p < 0.001$).

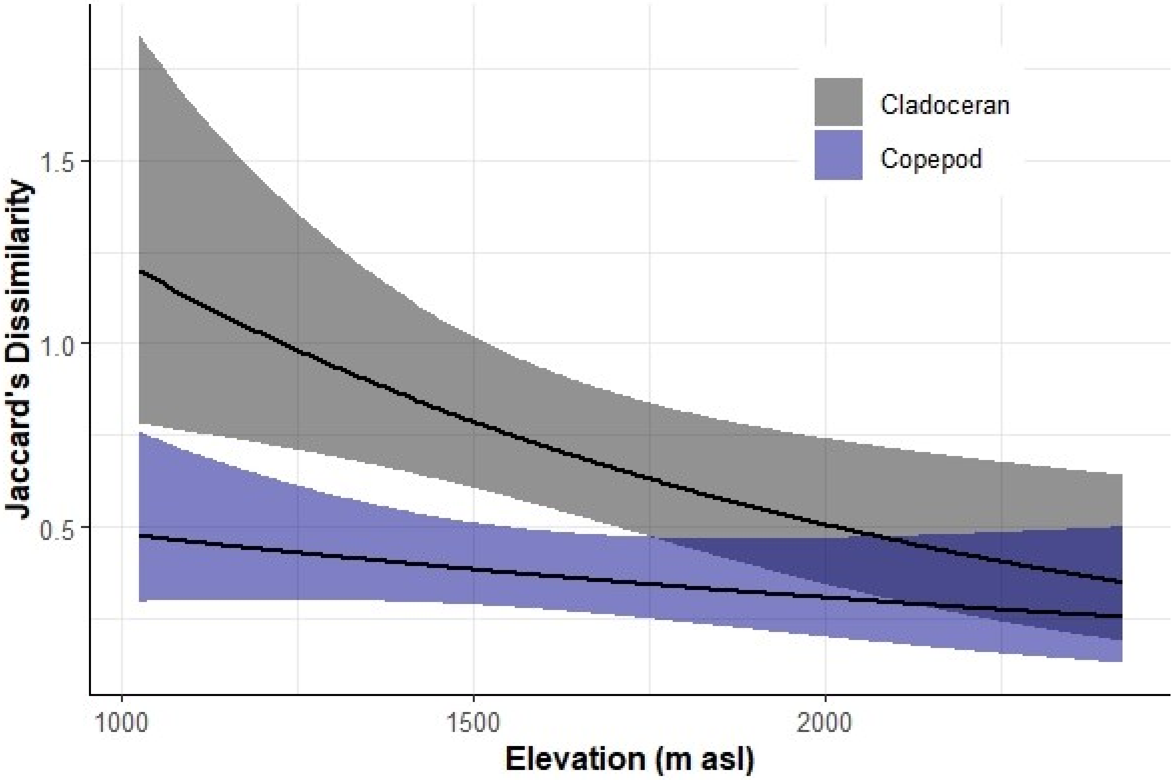

Figure 3: Temporal turnover of zooplankton taxa with elevation. Jaccard's Dissimilarity significantly decreases with elevation ($p = 0.0017$) and there is significant difference between taxa ($p < 0.001$).

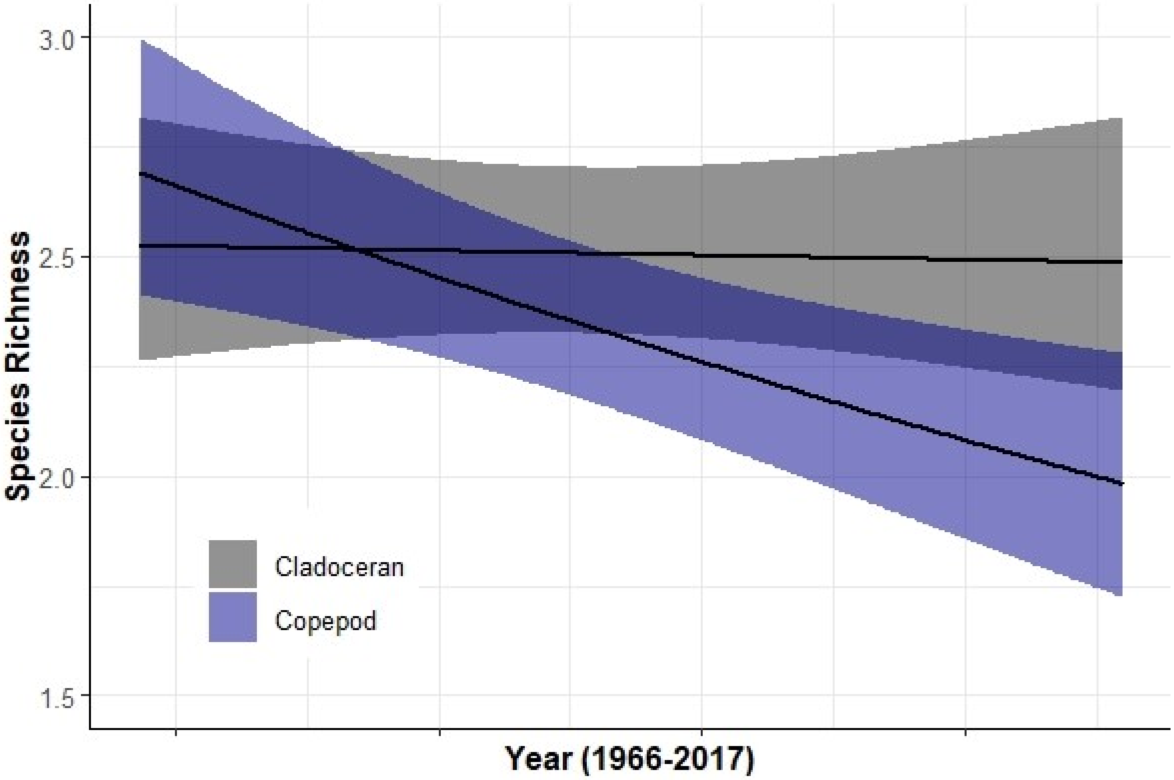

Figure 4: Species richness over time. There has been a significant decrease in richness over the past five decades ($p = 0.0096$). Copepods illustrate a greater loss in richness than cladocerans ($p = 0.0423$).

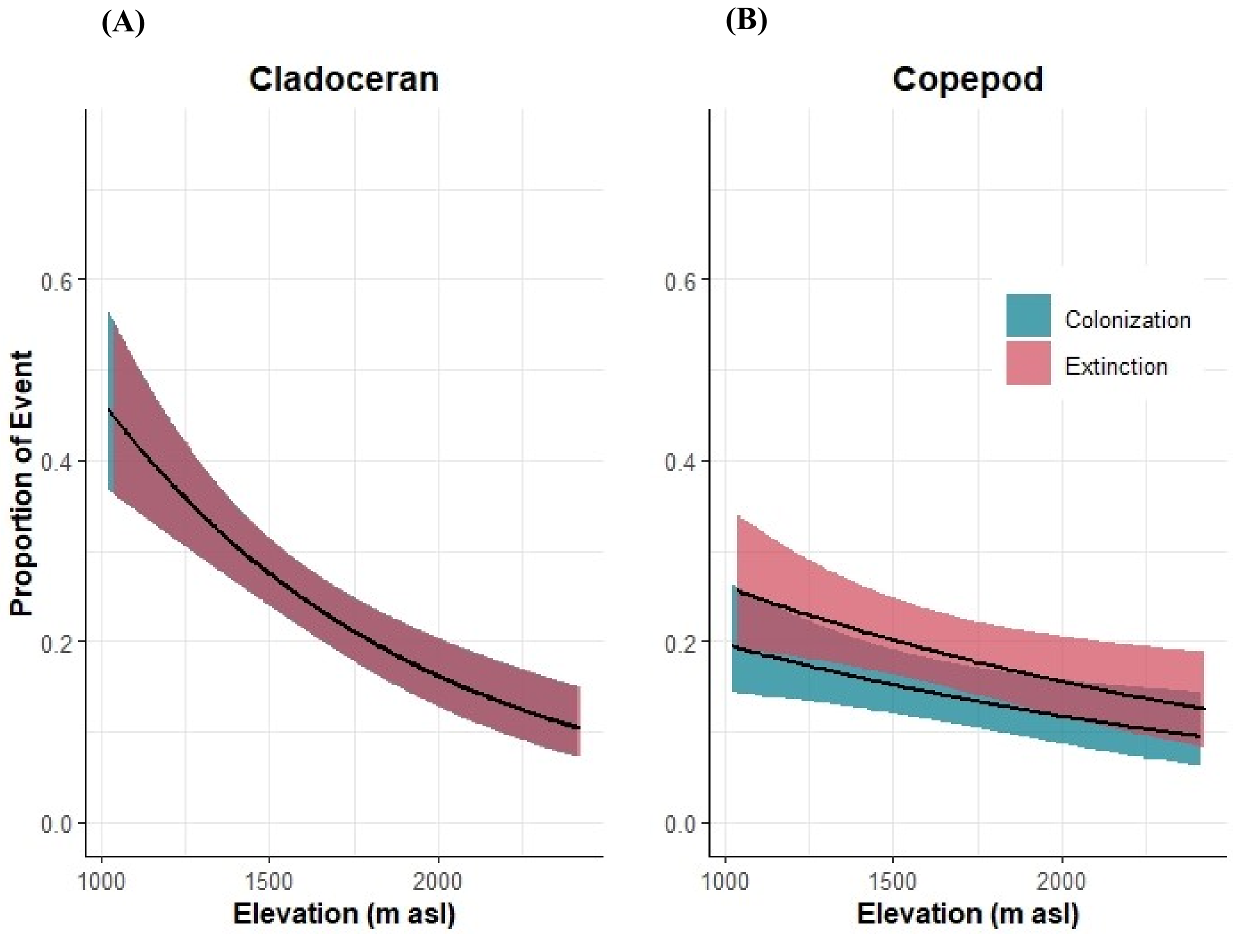

Figure 5: Colonization and extinction rates for each taxon over elevation. (A) Cladocerans illustrate a significant decline in the proportion of colonization and extinction events with elevations, however there is no difference between the events ($p < 0.001$). (B) The rate of colonization and extinction events did not significantly change with elevation for copepods, but extinction rates exceed colonization rates ($p = 0.0026$).

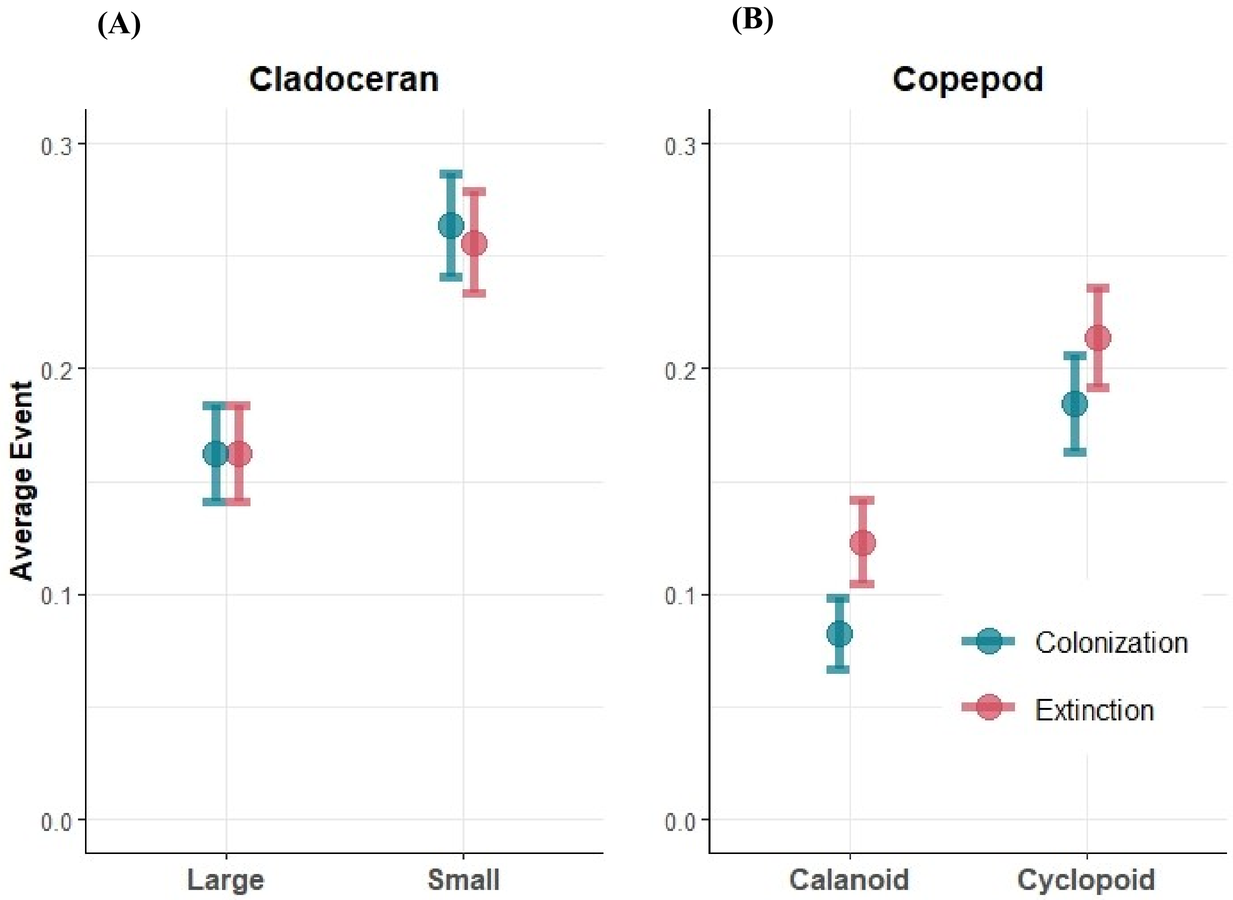

Figure 6: Average proportion of colonization and extinction events for each taxon. (A) Cladocerans illustrate a significant difference between their size variable ($p < 0.001$), but no difference between colonization and extinction events (p=0.7989). (B) Copepods illustrate a significant difference between their size variable ($p < 0.001$) and illustrate a significant difference between colonization and extinction events ($p = 0.0026$).

Chapter 3 | Recommendations and Improvements

3.1 | The unpredictable future of the calanoid copepod

The alarming loss of biodiversity is of a global scale, as species are rapidly disappearing from ecosystems around the world in what has been coined the 6th mass extinction (Ceballos et al. 2015). This biodiversity loss has primarily been attributed to large scale anthropogenic disturbances, witnessed through unsustainable logging and fisheries practices, mass agricultural development and urban sprawl. In Canada alone, the World Wildlife Fund's Living Planet Index has reported a decline in 451 species between 1970 and 2014, where, of the 222 monitored fish species in this study, 51% have seen a loss in abundance since 1970 (WWF-Canada 2017). Often, National Parks are considered home to pristine landscapes, where their UNESCO World Heritage Site designation renders them protected from large-scale anthropogenic impacts (Schindler 2000). However, as this research illustrates, despite the protected status of Canada's Mountain National Parks, the aquatic ecosystems in these areas are continuing to be exposed to indirect, anthropogenic disturbances, mainly due to chronic environmental change.

Air temperatures in Alberta have shown a general increase in the last century, particularly in the Canadian Rockies (Rangwala and Miller 2012, Borsdorf et al. 2015). This overall increase in temperature has been attributed to a rise in daily minimum temperatures rather than daily maximum temperatures (Diaz and Bradley 1997). As such, winter temperatures are not as cold as they historically have been, while summer temperatures have remained more stable (Jiang et al. 2015, Kienzle 2017). Aquatic ecosystems at an elevation range between 1500 m to 2000 m are considered even more sensitive to climate change as the ice-off season is particularly variable (Nevalainen et al. 2014). Research revealed that a one degree mean increase in air temperature can prolong the ice-free season by 30 days and that if air temperature continues to rise, lakes in mid-altitudes could face a 12°C increase in water temperature by the year 2100 (Thompson et al. 2005).

These prolonged ice-free seasons, and increased water temperatures are shifting lake processes by altering thermal stratification and mixing depth regimes (Schindler 2009, Winder et al. 2009, Fischer et al. 2011). Research demonstrates that with increased temperatures the water density gradient changes, making the thermal stratification more intense and longer lasting (De Stasio et al. 1996, Adrian et al. 2009). Although undeveloped thermal stratification conditions have been found in high elevation lakes (Karlsson et al. 2005), including lakes in Banff National Park (McNaught et al. 1999), with continued climate variability, these limnological regimes are expected to change as thermoclines develop (Parker et al. 2008, Nevalainen et al. 2014).

Further, these observed environmental changes in mountain lakes lead to an increase in productivity (Karlsson et al. 2005), which, in turn, encourages zooplankton growth until a maximum water temperature threshold is reached and further warming induces physiological stress on species, leading to declines in abundance (Fischer et al. 2011, Nevalainen et al. 2014). Such may be the case for calanoid copepods as observed in this study, whereby their abundances have fallen to a point past detection level, thus resulting in their localized extinction. Indeed, as supported by other research, warmer water temperatures, and an increased stratification period, resulted in a decline in calanoid abundance (Winder et al. 2009). Such an effect was observed in an experimental warming study that demonstrated contrasting effects on copepod survivorship, thus causing a shift in typical alpine zooplankton populations towards small cladocerans (Holzapfel and Vinebrooke 2005). This was further supported by observations that the demise of large-bodied zooplankton led to an increased abundance of smaller-bodied zooplankton, such as rotifers (Strecker et al. 2004). This is likely caused by large-bodied calanoids feeding on rotifers and copepod nauplii, thereby supressing their biomass (Paul et al. 1995). As such, the extirpation of calanoid species may release these small-bodied zooplankton from predation, allowing rotifers, cyclopoids and some cladocerans to dominate zooplankton populations (McNaught et al. 1999).

I anticipate that the continued demise of copepods will drastically alter aquatic ecosystems along the elevation gradient. Should thermally sensitive zooplankton be eliminated from the ecosystem, overall zooplankton biomass may be limited, despite the increased abundance of thermally tolerant zooplankton, as these small, generalist species may not fill the ecological functioning of their large-bodied counterparts (Parker and Schindler 2006). Further, cascading trophic interactions may be disrupted by warming temperatures and prolonged ice-free seasons as the reproductive cycle of a calanoid species no longer synchronizes with the seasonal dynamics of lakes (Winder et al. 2009). In such circumstances, phytoplankton may proliferate as large-bodied zooplankton are no longer available to maintain predation of suspended organic particles, thereby decreasing transparency of typically clear, mountain lakes (Parker and Schindler 2006). As demonstrated in this study, the interactions between environmental change and zooplankton community composition are complex and require future research to monitor and understand the ecological effects of losing an integral group of species.

3.2 | Insight on zooplankton sampling and enumeration

The two limiting factors of this research were the seasonal variability in zooplankton community composition and the species-level taxonomic enumeration. Beginning with the former, the issue of detectability when estimating species diversity can be quite challenging due to complex temporal and spatial variability of community assemblages (Yoccoz et al. 2001). This challenge is compounded when single-season zooplankton surveys are used to infer intraand inter-annual ecological patterns (Rusak et al. 2002). This “snapshot” approach to zooplankton sampling has been employed in other mountainous regions where survey sites are remote and embedded in rugged landscapes (Skála 2015, Kammerlander et al. 2016). Here, expendable financial resources and available time are often the limiting factors when developing sampling methods. Arguably, due to the limited number of ice-free days in the Rockies and the comparably lower zooplankton diversity of these sites, perhaps single-season surveys are sufficient in representing the species pool. This is provided sampling is focused late in the growing season, to allow zooplankton communities time to mature (Brönmark and Hansson 1998).

However, single-season surveying may come at the expense of valuable, long-term data. Research found that single sampling events of zooplankton capture for less than fifty percent of the species pool (Arnott et al. 1998), and it has been suggested that monthly, or even biweekly surveys are required to effectively estimate population densities (Rusak and Montz 2009). Although some research has followed this recommended best practice (Winder and Schindler 2004, Fischer et al. 2015), often a minimal sampling frequency of four times per growing season is realized (Hessen et al. 2006, Shurin 2007) and in some cases, single-season surveys are accepted (Stemberger et al. 2001, Pinel-Alloul et al. 2013). Currently, the effectiveness of single-season sampling methods of zooplankton communities remains formally untested in the Rocky Mountains and therefore presents a limit in our knowledge of community dynamics. I suggest that more robust sampling practices be adopted in the Rockies until standardized methods are developed, especially as mean annual temperatures continue to increase, thereby prolonging the growing season and adding to the intricacy of ecological processes.

Furthermore, when contemporary surveys are to be compared to historical samples, intra-annual variability may be controlled to a degree by replicating the survey dates. I suggest that if a site was previously sampled in mid-August, efforts should be made to resample during mid-August. Although some consideration was given to this issue when planning the logistics for this research, arguably, this could have been made a greater priority. Instead, sampling began mid-June in the southern regions of Waterton Lakes National Parks and continued north, sampling lakes at low elevations. By mid-July, sampling resumed in Waterton Lakes National Park to survey higher elevation lakes and proceed northward again. The idea was that this would allow communities in these higher alpine elevations time to mature. In hindsight, had greater consideration been made to replicate previous survey sample dates, some problems with seasonality may have been alleviated during the data analysis process.

The second limiting application of this research concerns species-level taxonomic enumeration. At the forefront of this problem is the widely accepted *Daphnia pulex* complex, whereby numerous species hybridize resulting in highly morphologically similar species (Vergilino et al. 2011). Physical attributes of the survey site, such as pond vs. lake, or alpine vs. montane, are not reliable indicators of differences in *Daphnia* species. Similarly, although I used species lists from historical surveys as a tool to guide contemporary identifications, these records should not be given too much weight, as the *Daphnia pulex* complex has existed for decades (Dodson 1981). As such, I caution those conducting species-level enumerations, particularly to the novice zooplankton taxonomist. An accepted solution to this problem is to simply group morphologically similar species together (Jones and Gilbert 2017), as I did with this research. Here, not only were *Daphnia* species categorized into small and large groups, but other species were also grouped into their genus-levels, such as *Ceriodaphnia*, *Alona* and *Alonella*. Should this approach be adopted early in the enumeration process, it will undoubtingly save the taxonomist many hours of laborious work when attempting to identify morphologically indistinguishable species. Similarly, I found that attempting to identify juvenile species is ineffective and advise that only adult specimens be considered. In the case where species-level identifications are required, or where a sample is dominated by immature organisms, using DNA sequencing may be an option. Although DNA sequencing is in its relative infancy, this technology is quickly advancing and offers promising results in the field of biodiversity monitoring, particularly in the face of rapid environmental change (Lindeque et al. 2013, Chain et al. 2016).

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Appendix

Table A1: Mean, median and range values for lake physical characteristics

Variable	***Min***	***Max***	***Mean***	***Median***
Elevation	1024	2423	1584.9	1464.5
Surface area	0.06	172.3	24.3	11.43
Max depth	1	70.1	14.2	11

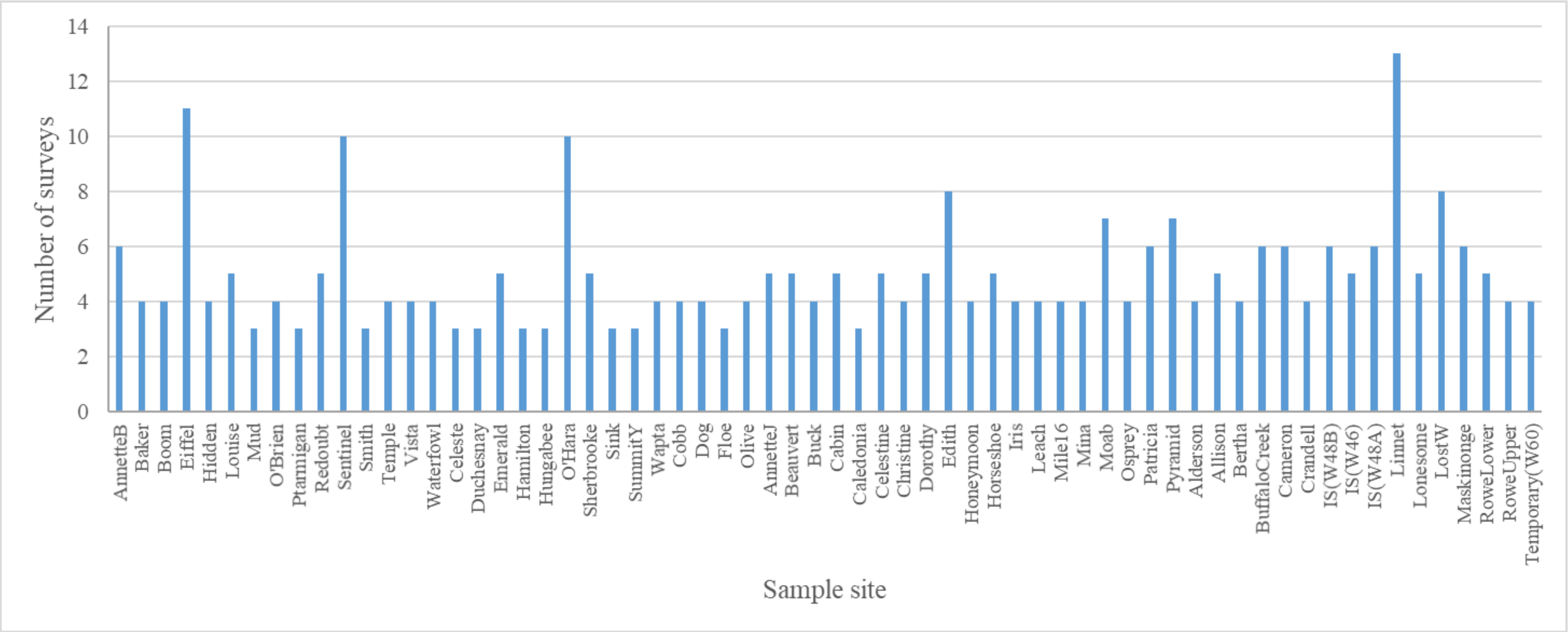

Figure A1: Site sampling frequency. The number of times each site was surveyd between 1966 and 2017

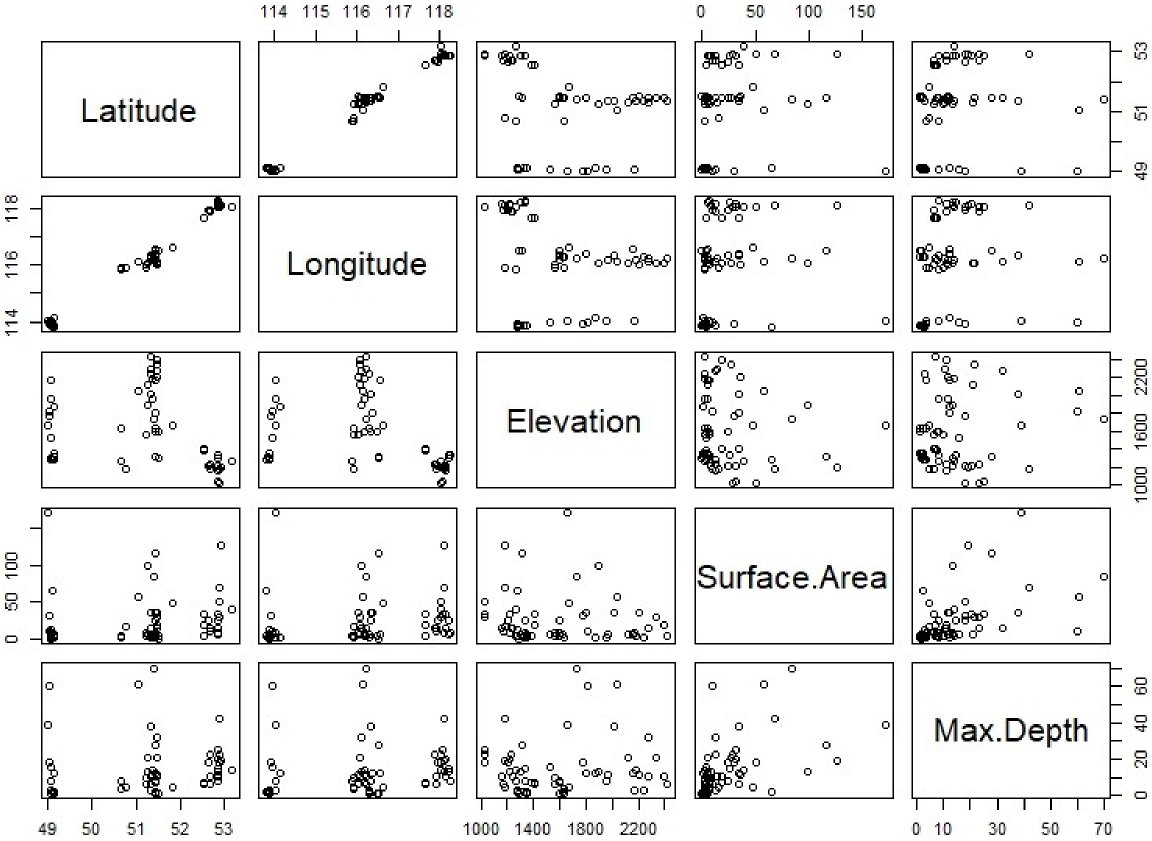

Figure A2: Pairplot of explanatory variables. These include latitude, longitude, elevation (m asl), surface area (ha) and maximum depth (m). Correlation is evident between surface area and max depth, but as these variables were not significant in the model, no consideration was made.

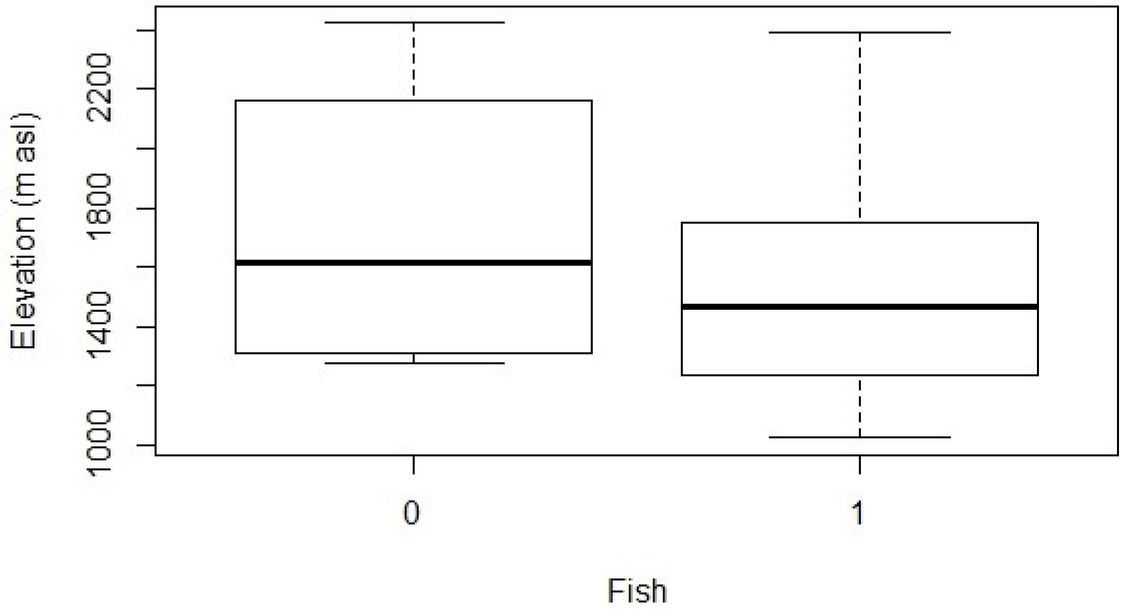

Figure A3: Boxplot of elevation on the binary variable fish (presences or absences)

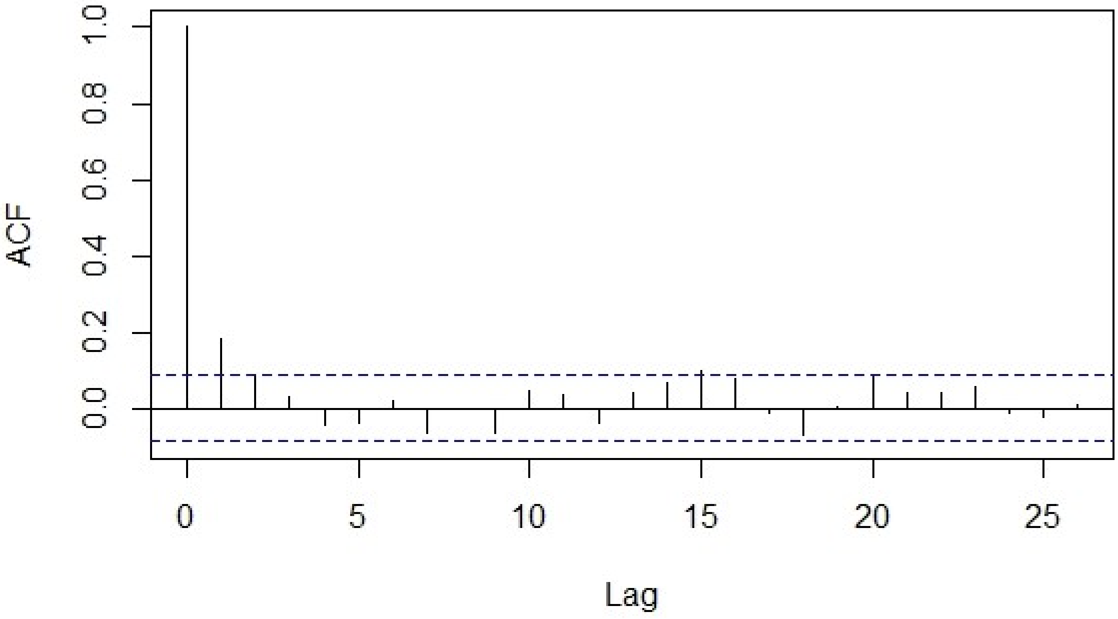

Figure A4: Auto-correlation plot of the residuals. The structure applied is the exchangeable auto-correlation, used for uneven time lags.

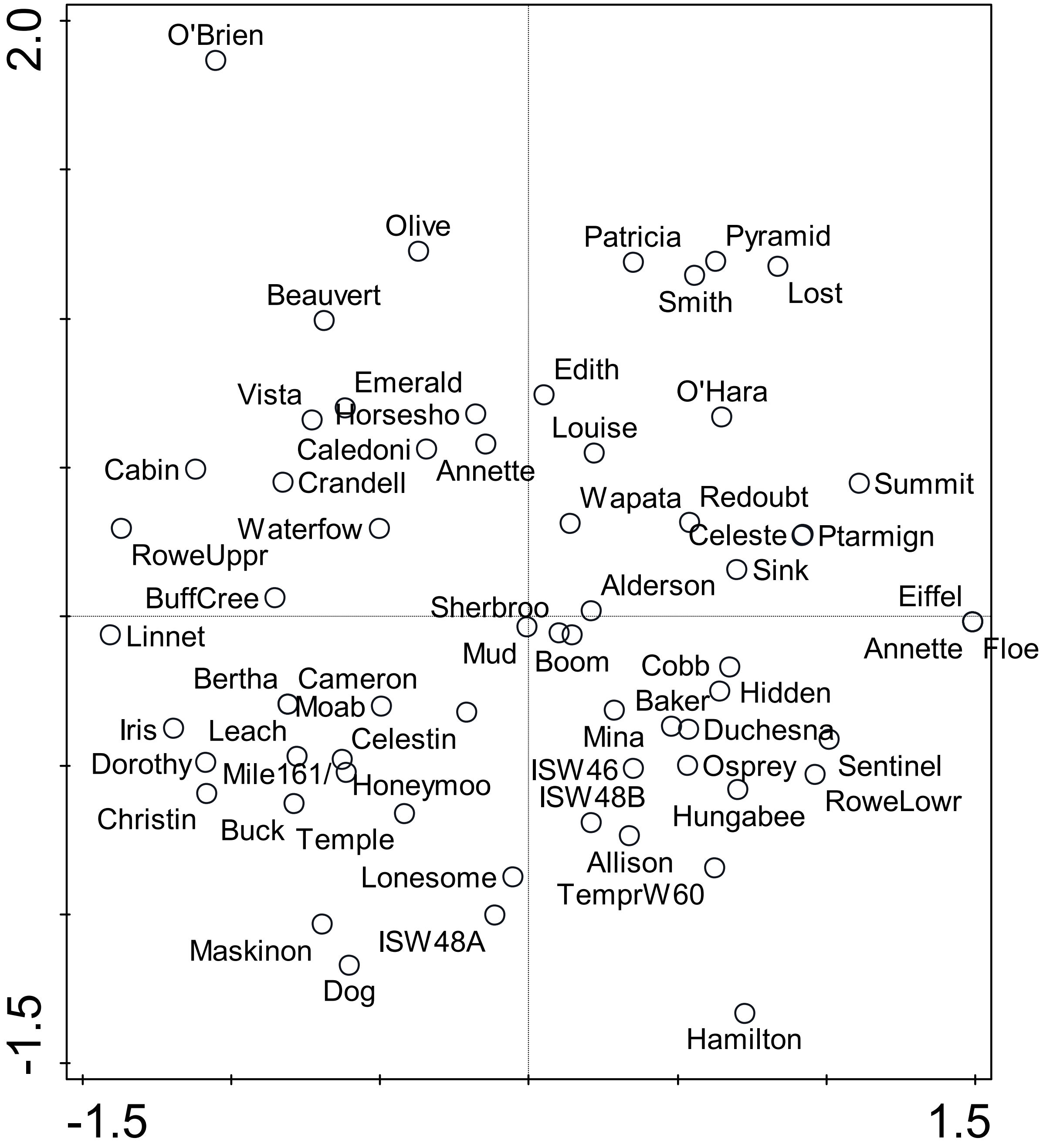

Figure A5: Nonmetric multidimensional scaling (NMDS) ordination based on Jaccard's Dissimilarity index examining community composition of each site. The first axis explains 58% of the variation while the second axes is 100% of the cumulative variation, stress= 0.22.

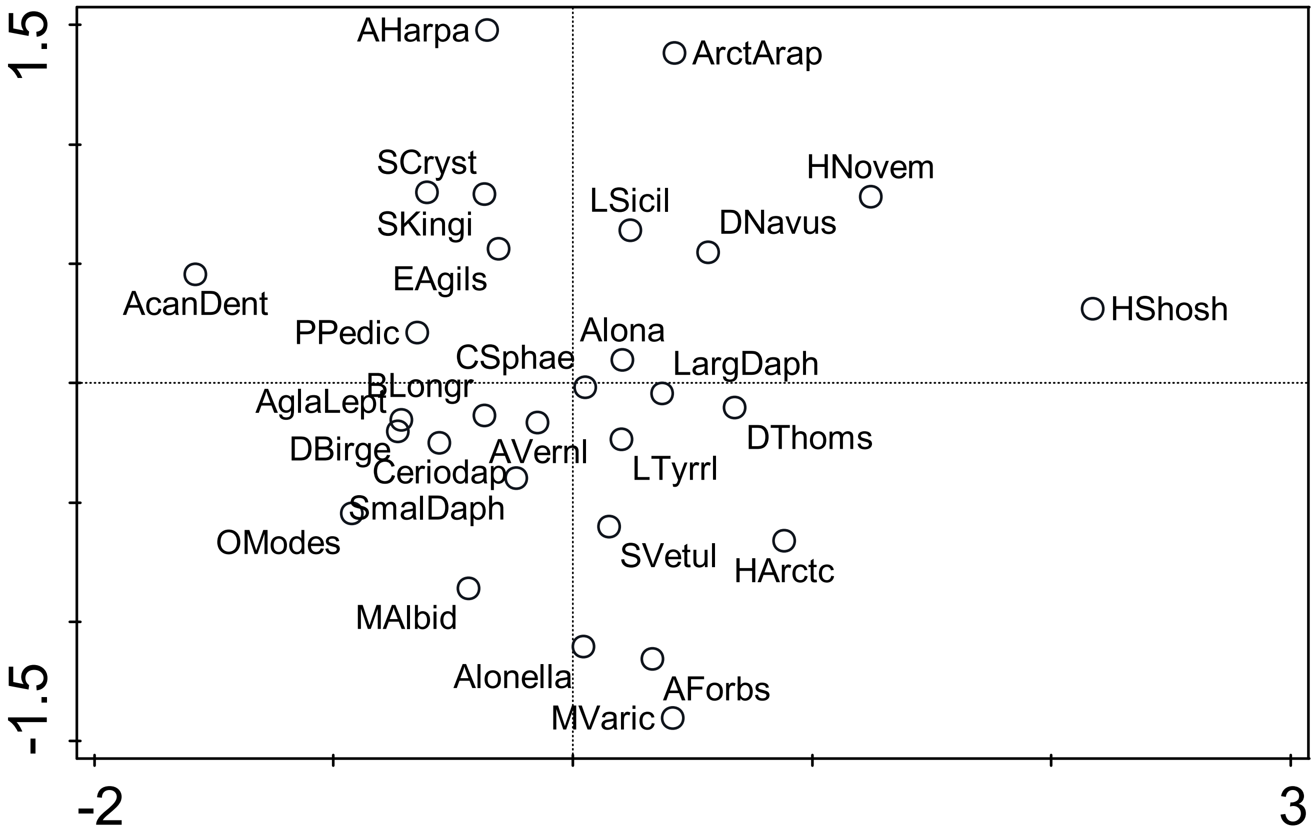

Figure A6: Nonmetric multidimensional scaling (NMDS) ordination based on species composition at each site in 2017. The first axis explains 51% of the variation while the second axes is 100% of the cumulative variation, stress = 0.15.