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EFFECTS OF INTRODUCED FISH ON MOUNTAIN LAKE ZOOPLANKTON COMMUNITIES

by

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ABSTRACT

Decades of fish introductions into mountain lakes have altered invertebrate communities. I assessed the current status of fish populations and their effects on crustacean zooplankton communities by sampling 37 lakes in the mountain parks, where stocking practices had been halted over 25 years ago. I discovered that introduced fish were more likely to persist in colder alpine lakes than in montane sites. However, their effects on total zooplankton biomass and species diversity increased with rising lake temperatures. Persistence of introduced fish in warmer lakes favored small-bodied zooplankton species, whereas larger-bodied communities in colder, larger alpine lakes were relatively unaffected. Greater resistance and resilience (i.e. recovery rate) of alpine zooplankton (e.g. *Hesperodiaptomus arcticus*) in deeper, fish-stocked lakes was likely attributable to a greater availability of refuge from predators and more abundant diapausing egg banks. Fish residence time and the species of stocked fish were key factors of taxonomic stability in perturbed zooplankton communities.

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CHAPTER ONE: GENERAL INTRODUCTION

INTRODUCTION

History of Stocking Mountain Lakes

Exotic fish introduction in mountain lakes was a common practice throughout North America (Bahls, 1992) and Europe (Gliwicz & Rowan, 1984), beginning in the Swiss Alps as early as the 16th century (Winder et al., 2001), and in North America in the mid 1800s (Knapp et al., 2001a). Fish introduction was originally intended to prevent the decline of angler catch rates, as angler pressure increased (Schindler & Parker, 2001). However, mountain lake stocking gained interest when anglers realized that these systems, many of which were naturally fishless, would provide excellent habitat and ample food resources for introduced fish species. In the North American mountain west, non-native species (e.g., Brook Trout, *Salvelinus fontinalis*) were often selected for fish introduction as anglers preferred them to the native species (e.g., Bull Trout, *Salvelinus confluentus*) that already inhabited those waters (Schindler, 2000). Aerial stocking, which began in the 1940s in North America (Bahls, 1992), allowed fish introduction to rapidly spread throughout relatively remote regions.

In the national parks of the Canadian Rocky Mountains, hundreds of naturally fishless lakes were stocked with non-native salmonids between the early 1900s and late 1980s (Donald, 1987). Many lakes did not support natural reproduction and thus these lakes eventually returned to a fishless state (McNaught et al., 1999). In lakes where fish were able to successfully reproduce, size-selective predation has substantially altered native biotic communities (Donald et al., 1994; Donald et al., 2001; Parker et al., 2001).

Impacts of fish introduction on native biota

Mountain lakes provide vital habitat for a variety of ecologically unique zooplankton species, many of which thrive only under fishless conditions. Naturally fishless alpine and subalpine lakes typically contain only two to three species of crustacean zooplankton (Anderson, 1971), while lower montane lakes are usually more diverse (Anderson, 1974). Naturally fishless mountain lakes are generally dominated by large-bodied predatory invertebrate species (*e.g. Hesperodiaptomus arcticus* in alpine systems) and larger, competitively superior grazers (e.g. *Daphnia middendorfianna* in alpine lakes) that limit the occurrence of smaller invertebrate species (Anderson, 1980; McNaught et al., 2000). Planktivorous salmonids introduced to fishless lakes significantly reduce the abundance of large-bodied zooplankton (Knapp et al., 2005) through intensive size-selective predation, resulting in an increase in the number and total biomass of small-bodied species (Schindler & Parker, 2002). In some cases, large-bodied zooplankton are completely eliminated from lakes where fish have been introduced (Parker et al., 2001), resulting in a loss of native biodiversity.

Change in management theory

The national parks of the Canadian Rocky Mountains were designated as World Heritage Sites in the 1980s, by the United Nations Educational, Scientific and Cultural Organization (Donald et al., 2001). With this designation came the development of new theories and ideas on how resources within the parks should be managed, including a focus on preserving indigenous biodiversity in all ecosystems (Schindler & Parker, 2002). Mountain lake stocking was reduced in the parks in the early 1970s (Donald, 1987), and the last lake was stocked in Banff National Park in 1988 (C. Pacas – unpubl. data). Following the change in management theory, biologists began focusing on the restoration of native biodiversity (Parker at al., 2001).

Restoration of Biodiversity

The recovery of mountain zooplankton populations from the effects of exotic sportfish introduction may take decades (Donald et al., 2001). Lakes that do not support natural reproduction of introduced salmonids show higher taxonomic resilience of the zooplankton community, with recovery generally beginning immediately after fish disappearance (Knapp et al., 2005). Where natural recruitment is successful, however, extended fish residence times can have significant negative effects on the ability of zooplankton communities to recover (Knapp & Sarnelle, 2008).

Beginning in 1997, Parker et al. (2001) assessed the feasibility of removing non-native fish from mountain lakes in Banff National Park using gill-net eradication techniques, to accelerate the recovery of native invertebrate populations. Since then, these techniques have been used to remove entire fish populations from other lakes in the Canadian Rockies (C. Pacas – personal communication), as well as in the United States (Sarnelle & Knapp, 2004). Successful removal of introduced fish populations has, in some cases, resulted in rapid recovery of extirpated zooplankton species (Schindler & Parker, 2002). However, not all organisms and systems respond in the same manner (Knapp et al., 2001b).

Studies have shown that the ability of mountain lake communities to fully recover from the effects of fish introduction is related to many factors including lake depth, fish stocking density, fish residence time, and lake elevation (Sarnelle & Knapp, 2004; Knapp & Sarnelle, 2008). Furthermore, differences in life history strategies between organisms can significantly influence whether certain species are able to re-colonize lakes following fish removal (Kramer et al., 2008). Zooplankton species that reproduce parthenogenically and produce longer-lived diapausing eggs (i.e., cladoceran spp.) are probably more resilient than species that reproduce sexually (i.e., copepod spp.; Sarnelle & Knapp, 2004). In some cases, zooplankton that cannot re-colonize lakes following fish removal may require re-introduction to facilitate recovery (McNaught et al., 1999).

Influence of climate and temperature in structuring aquatic communities

The structuring of aquatic communities in mountain lakes is largely dependent upon climatic factors including duration of the ice-free season, amount of precipitation, snowpack, and perhaps most importantly, lake temperature; all of which vary along an elevational gradient (Lamontagne et al., 1994; Hauer et al., 1997). As high-elevation alpine lakes typically experience shorter ice-free seasons and colder temperatures, the zooplankton species that exist in those systems are better adapted for dealing with harsh environmental conditions than lower montane species (Anderson, 1971). Most large-bodied alpine zooplankton exhibit relatively narrow thermal tolerances (Moore et al., 1996) and so may be especially sensitive to the increasing lake temperatures that are expected to occur with global warming (Hauer et al., 1997). If warming in cold alpine lakes suppresses the productivity of native large-bodied zooplankton (Strecker et al., 2004), the invasion potential of smaller, lower-elevation species would increase (Holzapfel & Vinebrooke, 2005). In turn, warming could decrease the susceptibility of zooplankton communities to fish predation as smaller species are less likely to be targeted as prey, relative to the larger species that currently inhabit those waters (Liss et al., 1998).

OBJECTIVES

The main objective of this study was to determine how long-term persistence of introduced sportfish affects mountain lake zooplankton communities in the Canadian Rockies. Also, given that the structure and taxonomic composition of zooplankton communities vary with lake temperature (Moore et al., 1996), my secondary objective was to determine whether the effects of fish predation on those communities are thermally dependent. Examining trends in biological communities over an elevational gradient is often used as an effective surrogate for studying the effects of climatic variation on aquatic communities (Karlsson et al. 2005). I hypothesized that, because alpine lakes are intrinsically more species-poor than warmer montane systems (Anderson, 1971), the effects of fish introduction in alpine lakes may be relatively more detrimental to their zooplankton communities, by significantly impoverishing the native species pool. I tested this by sampling the fish and zooplankton communities in 37 lakes over a wide range of elevation, in Banff, Jasper, Kootenay, and Yoho National Parks.

In alpine lakes especially, the extirpation of native invertebrate taxa may have long-lasting effects on food-web dynamics, as those systems are typically bound by relatively strong trophic linkages (Perez-Fuentetaja et al., 1996). When keystone invertebrate species (e.g., *H. arcticus*) are eliminated by introduced fish planktivory in alpine lakes, zooplankton communities may be completely restructured (McNaught et al., 1999). In larger alpine lakes, which provide a greater amount of off-shore and profundal habitat, large-bodied zooplankton may be better able to avoid fish predation, thereby resisting extirpation (Donald et al., 1994). To further investigate this phenomenon, I used data gathered from 18 alpine lakes in Banff and Yoho National Parks, to determine what environmental factors were associated with the ability of large-bodied zooplankton to resist extirpation by introduced salmonids. In lakes where fish introduction resulted in extirpation of native alpine zooplankton, I wanted to determine what factors (biotic and abiotic) were associated with the ability of zooplankton communities to return to their natural state following eradication or disappearance of the introduced salmonids. To address this question, I examined temporal changes in alpine lakes that were first stocked nearly 50 years ago, and have been fishless for over 20 years. As studies of the taxonomic resilience of zooplankton communities rarely encompass long-term data (Knapp et al., 2001b), this study provides an important perspective on the recovery over time of zooplankton populations.

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CHAPTER TWO: WARMER TEMPERATURES ENHANCE THE EFFECT OF EXOTIC FISH ON MOUNTAIN ZOOPLANKTON[1]

INTRODUCTION

The widespread introduction of exotic sportfish into naturally fishless mountain lakes has impoverished native fauna throughout North America and Europe (Gliwicz and Rowan, 1984; Schindler, 2000; Donald et al., 2001; Winder, Monaghan, & Spaak, 2001; Sarnelle and Knapp, 2004). For example, approximately 20 percent of lakes in the national mountain parks of Canada were stocked with non-native fish from the early 1900s to the late 1980s (Donald, 1987). The majority of these lakes were naturally fishless prior to stocking, and therefore, these novel predators suppressed native invertebrate communities (Parker, Wilhelm, & Schindler, 1996; Donald et al., 2001; Parker et al., 2001). Similarly, introduction of non-native fish into fishless lakes in the Sierra Nevada Mountains, California played a major role in the severe depletion of alpine lake fauna (Knapp & Sarnelle, 2008).

In the national mountain parks of Canada, stocking regimes were discontinued in the early 1980s and management strategies were re-focused, as part of the United Nations Educational, Scientific, and Cultural Organization's designation of these areas as a World Heritage Site (Donald, 1987; McNaught, Pavlik, & Schindler, 2000). New management practices recognized the importance of biological diversity, and emphasized the need for preserving native species in protected ecosystems. Since the termination of stocking in

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[1] *A version of this chapter has been submitted for publication, and is in review (Messner, J. S & Vinebrooke, R. D.)*

Canadian mountain park lakes, many fish populations have been effectively eradicated by gill nets (Parker et al., 1996; Parks Canada, unpubl. data) or have simply failed to naturally reproduce (Donald et al., 2001). Introduced fish have elsewhere continued to maintain healthy, naturally reproducing populations for the last 25 years since stocking was ceased (Parks Canada, unpubl. data).

Introduced invasive fish have been shown to play a major role in structuring aquatic food webs, especially those in alpine lakes (Paul et al., 1995; Donald et al., 2001; Knapp, Corn, & Schindler, 2001). Large-bodied organisms such as calanoid copepods (*e.g. Hesperodiaptomus arcticus*) are conspicuous in fishless alpine lakes wherein they often function as the stenothermic coldwater top predator (Anderson, 1971; Paul et al., 1995). In these systems, size-selective planktivory by visually feeding trout suppresses relatively large calanoid copepods and cladocerans (*e.g. Daphnia middendorfianna*) thereby releasing smaller zooplankton from competition and invertebrate predation pressure (Anderson, 1980; Paul et al., 1995; Parker et al., 1996, Donald et al., 2001). In contrast, smaller-bodied zooplankton are expected to be more common in warmer fishless montane lakes (Moore, Folt, & Stemberger, 1996), thereby reducing the probability of pronounced predatory effects by introduced sportfish that typically prefer larger zooplankton as prey (Zaret, 1980). The effects of introduced fish on the zooplankton community may therefore depend on climatic factors (Meerhoff et al., 2007) and variation in food web structure (Winder, Burgi, & Spaak, 2003) along an elevational gradient.

Climate warming may magnify the effects of invasive sportfish on native zooplankton in mountain lakes, as both tend to favor smaller organisms (Moore et al. 1996; Holzapfel & Vinebrooke, 2005; Schindler, 2000). For example, warming can stimulate feeding rates of zooplanktivorous fish (Gyllstrom et al., 2005), which can result in greater depletion of invertebrate top predators and competitively superior grazers (Gliwicz, Wursbaugh, & Szymanska, 2010). Further, warmer temperatures can impair larger zooplankton species native to alpine lakes, thereby potentially increasing their susceptibility to fish predation (Holzapfel & Vinebrooke, 2005). Alternatively, warming can metabolically favor smaller, less conspicuous zooplankton species (Moore et al., 1996), thereby reducing the impact of visually feeding fish (Brooks & Dodson, 1965).

The main goal of this study was to examine how the persistence of introduced invasive salmonids affects zooplankton communities in mountain lakes along an elevational gradient, which is often considered a reliable proxy for the ecological effects of climate change (Lamontagne, Donald, & Schindler, 1994; Vinebrooke & Leavitt, 1999b; Wilhelm & Schindler, 2000; Karlsson, Anders, & Janssen, 2005). The objectives of this study were to (*i*) determine the current status of introduced fish populations and zooplankton communities of 37 lakes, of which many had not been re-sampled in over 20 years, and (*ii*) quantify the relationship between introduced fish and zooplankton, in the context of other environmental variables that are also potential predictors of zooplankton production and species composition. I hypothesized that alpine zooplankton would be more adversely affected than their lower montane counterparts by the presence of invasive fish because relatively large-bodied and species-poor communities show less resistance to abiotic and biotic stressors (Vinebrooke et al., 2003).

METHODS

Surveyed lakes:

The 37 lakes are located in some of the National Parks of the Canadian Rocky Mountains. Specifically, 32 are in Banff (*n* = 25) and Jasper National Parks (*n* = 7), Alberta, and five are located in Yoho (*n* = 3) and Kootenay National Parks (*n* = 2), British Columbia. Lakes were chosen to encompass a range of physical features (maximum depth >5 m, water temperature, elevation, surface area <30 ha), in order to determine the influence of environmental gradients on zooplankton community parameters. Lakes were also selected based on their relative ease of accessibility, as well as the most recent accounts of their fish status and known stocking history (Charlie Pacas, Shelley Humphries, & Ward Hughson, Parks Canada, unpubl. data and personal communications). Each fish status/ stocking history category was meant to be represented by a number of lakes spread over the formerly mentioned physical gradients.

Study lakes ranged in elevation from 1120 m to 2392 m (mean 1870 m), surface area from 0.002 km^2 to 0.299 km^2 (mean 0.114 km^2), temperature from 4.2°C to 20.3°C (mean 11.0°C), and maximum depth from 2.5 m to 43.9 m (mean 13.3 m). Three study sites contained native fish prior to stocking, and the remaining lakes were all naturally fishless. The most recent stocking event occurred 22 years ago (mean 37 years; Parks Canada, unpubl. data). All lakes were visited at least once from 1 June to 14 August, 2010, or 1 August to 5 August, 2011.

Environmental monitoring:

On each sampling occasion, water temperature was measured at the deepest part of the lake (determined using a bathymetric map or handheld depth-finder) using a Flett MKII Thermometer. Water temperature was recorded at every meter from the lake surface to 1m above the lake bottom. Midsummer water temperature (taken between 15 July to 15 August) was calculated for each lake, as the mean water temperature from 2m below the surface to 10 m, or to the maximum depth in lakes <10 m deep (Donald et al., 2001). For part of the analysis, lakes were grouped into two temperature categories; cold (<11°C, mean 7.1°C) or warm (>11°C, mean 16.1°C). Cold water lakes were located in alpine and subalpine regions (1660 m – 2393 m, mean 2219 m), while warmer lakes were found in the montane and lower subalpine regions (1120 m – 1722 m, mean 1411 m).

I collected 500 to 1000 mL of lake water from 1m below the surface at each site, and lake water was passed through a 64 μm mesh-sized sieve to remove large invertebrates and debris for further chemical analysis. These samples were kept on ice, and transported to the Biogeochemical Analytical Facility at the University of Alberta, Edmonton (URL link:

http://www.biology.ualberta.ca/basl) to analyze total and dissolved phosphorus (TP, TDP) and nitrogen (TN, TDN) concentrations. Nutrient parameters were measured in the same way reported in Murphy, Thompson, & Vinebrooke (2010). Phytoplankton abundance was quantified by filtering 500 mL to 1000 mL of lake water through GF/F filters, to concentrate pigments for subsequent high-performance liquid chromatography (HPLC) analysis of total chlorophyll using the methods described by Vinebrooke & Leavitt (1999a).

Fish:

Lakes were first visited between 1 June to 22 July, 2010 to collect population data. A single sinking multi-mesh gill net (45 m long and 2 m deep) and two wire minnow traps were set overnight at most sites to assess fish presence, relative abundance (catch-per-unit-effort), and presence of recent natural reproduction (*i.e*. presence of age 1 - 2 fish). Gill nets consisted of six, 8 m panels of varying mesh sizes (13 mm, 19 mm, 25 mm, 32 mm, 38 mm, and 51 mm) and were always set perpendicular to shore, with the smallest-mesh end of the net anchored to shore. Minnow traps baited with white bread were anchored to shore as well, and placed in shallow (<1 m) bays or well-vegetated areas of the lakes, to assess presence/absence of young fish (Jackson & Harvey, 1997). Nets and traps were retrieved after 12 to 15 hours (mean 13 hours). Gill nets were not set in lakes that contained native fish populations (*e.g*. Westslope Cutthroat Trout, *Oncorhynchus clarkii lewisii* and Bull Trout, *Salvelinus confluentus*) (Parks Canada, unpubl. data), to avoid accidental injury or mortality to native fish. Presence of native fish in those lakes was confirmed based on angling. Fish captured in gill nets were weighed (g) and measured (fork length (mm)), and otoliths were taken from two to three representatives from each size class, for aging in the laboratory. Otoliths were cross-sectioned and burned, and annuli were read on the cross-section to determine the age of each fish (Christensen, 1964).

Zooplankton;

Lakes were visited between 15 July to 15 August, 2010, or 1 August to 5 August, 2011 to collect zooplankton. Zooplankton were collected from the entire water column (from 1m above the lake bottom, to the surface) by conducting 1-3 vertical tows in the deepest part of the lake, using a Wisconsin-style plankton net (63 µm-mesh, 20 cm diameter)(Donald et al., 2001). Zooplankton were preserved in 95% ethanol for enumeration back in the laboratory. Large crustacean zooplankton were examined and enumerated under a LEICA MZ 9.5 dissecting microscope (Leica Microsystems, Wetzlar, Germany) at 4x to 6x magnification, while small zooplankton were slide mounted under a compound microscope (40x to 100x) to key all organisms to species (Edmondson, 1959). Species biomass estimates from previous investigations in my study area (Anderson, 1980; Donald et al., 2001; Schindler & Parker, 2002) were used to calculate the total biomass for each sample. Species richness (total number of crustacean zooplankton species) was also calculated for each lake.

Data analysis:

Generalized linear model (GLM) regression analyses were performed to determine the significance of predictor variables of zooplankton species richness and total biomass. The species richness model was based on a quasi-poisson distribution, which adjusts the disperson parameter (variance) for count data that is either over- or underdispersed (Zeileis et al., 2008). The dispersion parameter for the final species richness model, using the quasipoisson distribution, was taken as 0.33 (much less than 1). Total biomass was distributed log-normally, and modeled as such. Both forward and backward selection of variables was used to determine the best model for explaining variation in species richness and log-total biomass. Predictor variables included measures of lake morphology (maximum lake depth, total surface area), water chemistry (TN, TP, and total chlorophyll), and connectivity with other communities (number of lakes within a 20-km radius), along with fish presence, stocking history, and water temperature. Elevation was not used as a predictor variable because of the high degree of correlation between elevation and lake temperature ($r^2 = 0.73$). On average, there was a 1.1°C decrease for every 100-m increase in elevation (*temperature(°C)* = -0.0098 *elevation (m)* + 29.64). Since I was interested in examining the effect of water temperature directly, and not elevation, I considered the effect of elevation to be inferred by the effect of water temperature in this study. Maximum depth and lake area for each lake were available through existing Parks Canada records (Parks Canada, unpubl. data; Mayhood & Anderson, 1976; Donald & Alger, 1984; Anderson & Donald, 1980). Number of lakes within 20 km was calculated by setting a 20-km buffer around the perimeter of each lake in ArcGIS 10 (Esri, Redlands, California), and counting the number of lakes within each buffer. Species richness and total biomass values for each study site included crustacean zooplankton only; however, biomass values for *Gammarus* and *Chaoborus* spp. were also used for ordination analysis, as these organisms can serve as significant food sources for trout in alpine lakes in my study region (Wilhelm, Parker, & Schindler, 1999).

GLM tests (*t*-tests and ANOVA) were conducted to determine whether there were significant differences ($\alpha = 0.05$) in crustacean zooplankton species richness and total biomass among various groups of lakes (*e.g.* fish-present lakes versus fishless lakes). Simple linear regression analysis was also performed to quantify trends in zooplankton richness and biomass along thermal gradients. All GLM tests (*t*-tests, ANOVA, and simple linear regressions) were conducted in R version 2.13.0 (R Development Core Team, 2011).

Ordinations were performed in CANOCO version 4.1 (ter Braak & Smilauer 2002). A 'species biomass by site' data matrix was constructed using all 37 of the sampled lakes, and the matrix was used to conduct canonical correspondence analysis (CCA). First, correspondence analysis was chosen because there is a wide range of variation in the community response data (determined by examining the length of the CCA axes; > 3 SD units) which attests to a unimodal ordination method being most appropriate for ordination of this taxonomic data set (ter Braak & Prentice, 1988). Second, CCA was chosen to identify significant environmental predictors of taxonomic variation in zooplankton communities across the surveyed lakes. Species biomass values were $\log_{10}(x+1)$-transformed to downweight the influence of the few most abundant taxa (*e.g.* immature *Daphnia* spp., copepod nauplii, and copepodids). Fish presence, stocking history, midsummer water temperature, lake area, max depth, total chlorophyll, total nitrogen, total phosporus, and number of lakes within 20 km were tested for their significance as environmental predictor variables. Forward selection of environmental variables using Monte Carlo permutation testing was conducted to determine the significance of each explanatory variable contained in the environmental data set. Nonsignificant environmental variables were not used in construction of the final ordination plots. Monte Carlo permutation testing was also used to identify the statistical significances of the first CCA axis and the entire ordination.

RESULTS

Fish status of surveyed lakes:

Lakes were grouped into the following four categories based on their stocking history and discovered fish status; SFP - stocked fish present (n = 12), SFA - stocked fish absent (n = 16), PRI – "pristine" not stocked, fish absent (n

= 6), and NFP - native fish present lakes ($n = 3$). Assessment of the current status of introduced fish revealed that only 12 of the 28 naturally fishless lakes, stocked at least once from 1966 to 1988, currently contained self-reproducing populations of Salmonids (Table 1.1). These 12 lakes had a mean mid-summer water temperature of 8.9°C and a mean maximum depth of 14.6 m. Naturally reproducing fish were not found in any montane lakes where mean water temperature > 14°C, with the exception of Johnson Lake, BNP (17.1°C). Almost all of the 30 stocked lakes in this study, with the exception of three that contained native fish (Moab Lake – JNP, Rainbow Trout; Arnica Lake – BNP, Cutthroat Trout; and Harrison Lake – BNP, Bull Trout), had been fishless prior to stocking. Of the 37 total lakes in this study, seven were never stocked with fish and are therefore relatively undisturbed by humans.

Environmental predictors of zooplankton species richness:

Fish presence, stocking history, and mid-summer lake temperature were identified as significant predictors of crustacean zooplankton species richness (GLM; quasi-Poisson, backward and forward selection of variables, Table 1.2). Mean zooplankton richness increased by 1.6 species for every 3°C warming of lake temperature (Figure 1.1a, *species richness* = 0.277 * *temperature(°C)* + 0.729, $r^2 = 0.52$, $p < 0.001$). The significant interaction between fish presence and lake temperature was explained by species richness being highest in warmer lakes that contained fish, regardless of their origin (Figure 1.1b). At colder lakes, in higher elevations, zooplankton richness did not differ significantly (GLM; $t = 0.49$, $p = 0.63$) between fishless and fish-present lakes.

The influence of fish on total zooplankton richness depended on their origin (Figure 1.1c; fish presence-stocking history interaction, $F = 5.41$, $p = 0.03$). The presence of native fish, although not statistically significant, doubled the total number of zooplankton species in unstocked lakes (GLM; $t = 1.83$, $p = 0.11$), whereas general fish presence did not affect zooplankton richness across all stocked lakes (GLM; $t = -0.59$, $p = 0.56$). However, zooplankton richness was enhanced in the presence of fish in the warmer stocked lakes (Figure 1.1d; fish presence-lake temperature, $F = 4.2$, $p = 0.05$). Further, native fish positively influenced zooplankton richness more so than did stocked fish, in both warm and cold lakes (Figure 2.1e; $F = 5.30$, $p = 0.04$).

Environmental predictors of total zooplankton biomass:

Fish presence, stocking history, and midsummer lake temperature were also identified as significant predictors of total crustacean zooplankton biomass (GLM; forward and backward selection, three-way interaction, $t = 1.90$, $p = 0.06$). Zooplankton biomass increased significantly with an increase in midsummer water temperature ($p < 0.001$) (Figure 1.2a). Fish amplified the positive influence of warmer lake temperature on total zooplankton biomass, although this was not statistically significant (Figure 1.2b; water temperature-fish presence, $F = 2.340$, $p = 0.14$). Fish presence, alone, did not significantly explain variation in total crustacean biomass (mean FP 12.8 ± 18.4 µg/L, and mean FA 36.7 $\pm$ 36.4 µg/L)(GLM; $t = -1.146$, $p = 0.26$). Although zooplankton biomass was higher in the presence of fish in both stocked and not-stocked lakes, this relationship was not significant (Figure 1.2c; $F = 0.2330$, $p = 0.63$). If only stocked lakes were considered however, warmer lakes showed significantly higher zooplankton biomass in the presence of fish (Figure 1.2d) (GLM; $t = 2.60$, $p = 0.02$). In colder lakes on the other hand, zooplankton biomass did not differ significantly between fishless and fish-inhabited sites (GLM; $t = -1.33$, $p = 0.20$). The influence of native or stocked fish on total crustacean zooplankton biomass was markedly different between warm and cold lakes (Figure 1.2e; lake temperature-stocking history interaction, $F = 4.675$, $p = 0.05$). While zooplankton biomass was significantly higher in the presence of native fish, as opposed to stocked fish, in colder high elevation lakes (GLM; $t = -2.221$, $p = 0.05$), stocked fish seemed to have a more positive influence than native fish on zooplankton biomass in warmer lakes (GLM; $t = 2.037$, $p = 0.13$).

Total zooplankton biomass in pristine fishless lakes (PRI) was mainly comprised of calanoid copepods (mean 77% total biomass) and cladocerans (mean 22% total biomass), while cyclopoids were rarely found (mean less than 1% total biomass). Stocked lakes, regardless of fish presence, were also largely dominated by calanoid copepods. In SFA lakes, calanoid copepods made up an average 54% of the total zooplankton biomass, while cyclopoids and cladocerans were typically less abundant (mean 9% and 24% of total biomass, respectively) (Figure 1.3). Similarly, calanoid copepods made up an average 78% of the total biomass in SFP lakes, while cyclopoid copepods and cladocerans accounted for an average of only 3% and 21% of the total zooplankton biomass, respectively. Lakes that contained native fish species (NFP lakes) were largely dominated by cyclopoid copepods, as they accounted for 74% of the total biomass, on average. Calanoid copepods only accounted for an average of less than 2% of the total zooplankton biomass in NFP lakes. Non-zooplankton organisms (*i.e. Gammarus* and *Chaoborus* spp.) rarely accounted for a significant proportion of the total biomass collected in any of my study sites with the exception of SFA lakes, in which they made up an average of 13% of the total biomass. The 35 invertebrate species collected during my survey are listed in Table 1.3.

Environmental predictors of zooplankton community composition:

Across all surveyed 37 lakes, species turnover was best explained by lake temperature and fish status (Figure 1.4). Forward selection of environmental predictors identified lake temperature as the most significant ($p < 0.002$) explanatory variable, which best defined CCA axis 1. Along the axis from left to right, smaller species detected in the warmer low-elevation lakes were replaced by large-bodied species found predominantly in the colder and deeper alpine lakes. Maximum lake depth was also a significant variable ($p < 0.002$) that captured variation along CCA axis 1. Species replacement along CCA axis 2 was best explained by the presence of fish ($p < 0.002$), and specifically of native fish (NFP; $p < 0.002$). Lake classifications based on fish status (pristine (PRI), stocked fish absent (SFA), and stocked fish present (SFP)) were also found to be significant in the ordination ($p = 0.03$, $p < 0.002$, and $p = 0.006$, respectively). In general, smaller zooplankton species that were most abundant in the presence of native fish (upper left ordination quadrant) were replaced by larger zooplankton that resided in lakes that had either been stocked or not.

In the colder high-elevation lakes, variation in zooplankton species composition was best explained by native fish presence ($p < 0.002$) along CCA axis 1 (Figure 1.5). Calanoid copepods and large cladocerans (*e.g. Daphnia middendorffiana)* dominated both fishless lakes and lakes with stocked fish, while lakes with native fish contained a large abundance of cylopoid copepods. In general, the only large-bodied crustacean zooplankton found in lakes with native fish were *Daphnia pulex*. Variation in species along CCA axis 2 was mainly explained by water temperature ($p < 0.002$). Increased water temperatures in cold fishless lakes favored smaller species such as *Bosmina longirostris* and *Daphnia catawba*, while increased temperatures in cold lakes with fish tended to favor *Orthocyclops modestus* and *Macrocyclops albidus*.

In the warmer low-elevation lakes, the number of lakes within 20 km best defined ($p < 0.002$) CCA axis 1 (Figure 1.6). Overall, a greater diversity of zooplankton species appearing in the left-hand quadrants of the ordination plot were associated positively with lakes that were in closer proximity to other lakes. Fish presence ($p = 0.10$) and presence of native fish ($p = 0.006$) best explained variation in zooplankton community composition along CCA axis 2. Lakes that contained fish, regardless of their origin, were discriminated from all other lakes along CCA axis 2, and were associated with higher abundances of *B. longirostris*, *Polyphemus pediculus*, *Daphnia rosea*, and *Ceriodaphnia pulchella*. Lakes that no longer contain fish (SFA and PRI) were generally indistinguishable from one another based on community composition.

DISCUSSION

My results showed that the influence of sportfish presence on mountain zooplankton communities increased with rising lake temperature. Specifically, the presence of fish in warmer montane lakes, relative to those in colder high-elevation lakes, significantly enhanced total zooplankton biomass and species richness. Fish presence and warmer lake temperatures were also associated with more diverse zooplankton communities, consisting mainly of small cladocerans and cyclopoid copepod species. In contrast, colder fishless lakes typically contained zooplankton communities composed of fewer and larger species. Native and introduced fish appeared to exert different influences on zooplankton communities. Zooplankton communities in cold, higher-elevation lakes were more diverse and abundant in the presence of native fish while the opposite was true for warmer lakes. Although the effect of fish presence was stronger in montane systems, the likelihood of introduced salmonids to persist in stocked lakes was much greater in colder high-elevation lakes. Regardless of the fish status of a lake, total zooplankton biomass and species richness were positively related to lake temperature. Below, I discuss some potential ecological explanations and implications of these findings.

The positive influence of fish on zooplankton richness in only warmer lakes may be explained by the release of several smaller zooplankton species from competition and predation. Planktivorous fish can suppress competitively superior larger zooplankton (Amundsen et al., 2009) and predatory invertebrates, resulting in increased abundance and facilitated coexistence of several visually undetectable smaller zooplankton (Shurin, 2001; Shurin & Allen, 2001; Gliwicz et al., 2010). Further, a greater diversity of smaller zooplankton species are commonly found in warmer mountain lakes (Anderson, 1974; Starkweather, 1990; McNaught et al. 2000), enabling a stronger prey richness response to the effects of fish predation. In addition, fish feeding and growth rates increase with lake temperature (Allan & Castillo, 2007), thereby potentially increasing direct and indirect effects of zooplanktivory in warmer lakes.

A potential explanation for fish also contributing to the positive effect of lake temperature on total zooplankton biomass is that fish help grazers meet their increased metabolic needs by stimulating algal food production via increased nutrient cycling (Shurin, 2001; Eby et al., 2006). While moderate warming increases zooplankton feeding rates, it also raises both respiratory costs and demand for greater food availability (see review by Moore et al., 1996). Nutrient release by fish could provide the necessary resources for enhanced algal growth, which might otherwise be sequestered as inedible particulates into lake sediments. Further, fish can also function as a vector of allochtonous nutrients to plankton (Buchaca et al., 2011) by converting aeolian inputs (e.g., aerial insects) into bioavailable nutrients.

In colder alpine lakes, lower species turnover potential and pronounced top-down forcing by the dominant zooplankter, *H. arcticus*, may account for the lack of detectable zooplankton responses to fish presence. Due to the insular nature of colder high-elevation lakes, zooplankton species colonization can take decades (Donald et al. 2001) likely owing to pronounced topographical barriers (*i.e.* mountain ridges) impeding species dispersal. Holzapfel and Vinebrooke (2005) showed that many of the zooplankton species that would otherwise be affected by fish predation are not present in alpine lakes in part due to dispersal limitation. Further, the relatively low number of species found in alpine lakes may exhibit strong trophic linkages which help resist change in community composition (Perez-Fuentetaja et al., 1996). The keystone omnivore *H. arcticus* predominates in most naturally fishless alpine lakes in the Canadian Rockies (Parker et al., 2001), maintaining the composition of smaller consumers and primary producers via predation and grazing (Paul et al. 1995).

Substantial changes in zooplankton communit structure occurred in colder, high-elevation lakes where fish had eliminated the top predator, *H. arcticus*. As large-predaceous diaptomids compete for resources with, and prey upon, smaller zooplankton species (Liss et al., 1998), elimination of *H. arcticus* by fish introduction can result in complete re-structuring of the zooplankton community (Parker et al., 1996; McNaught et al., 1999). In the Canadian Rockies, smaller-bodied zooplankton that were previously un-reported in those systems emerged and subsequently increased in abundance as a result of *H. arcticus* elimination by introduced fish (Parker et al., 2001). The occurrence of coexistence between *H.*

arcticus and introduced fish may be fairly high in alpine lakes, as they are typically much deeper than lower montane systems. Donald et al. (1994) found that the likelihood of coexistence between *H. arcticus* and fish predators was much greater in deeper lakes (> 11m, maximum depth) in the Canadian Rockies. Further, multiple studies show that deeper lakes harbour larger deposits of diaspausing eggs (Knapp et al., 2005; Knapp & Sarnelle, 2008), which may allow native alpine zooplankton to slowly re-colonize lakes even in the presence of introduced fish. The mechanisms allowing coexistence are not fully understood, but are important for understanding the effects of fish introduction on a lake-by-lake basis.

My discovery that the influence of fish presence on zooplankton richness differed between native and introduced species counters the findings reported by Wilhelm et al. (1999) and Donald et al. (2001). Zooplankton communities in cold alpine lakes that contained native fish were more similar to those communities found in warmer montane lakes than they were to other alpine lakes than contained stocked fish. Two of the lakes that contained stocked fish however, Ptarmigan and Castilleja, both of which are relatively shallow systems that have contained brook trout for decades, also seemed to be highly impacted by fish presence. Decades of fish persistence can significantly increase the negative impacts of exotic fish introduction in mountain lakes (Knapp & Sarnelle, 2008). Zooplankton resting egg banks can be depleted with extended fish residence times, and the process can occur much faster in shallower systems as egg bank size is positively related to lake depth (Knapp et al., 2005). Elimination of large-bodied predatory zooplankton could allow the colonization of smaller species to become more successful. Further, the establishment of dominance by small predatory cyclopoid species (*e.g. Diacyclops bicuspidatus thomasi*) can be enough to prevent re-emergence of native alpine zooplankton species in some lakes (Parker et al., 2001). Certain large-bodied species however (*e.g. D. pulex*), may be more likely to coexist with native fish, as a high reproductive rate allows them to be a superior competitor and flourish in the absence of large-bodied predators (Dodson, 1984). The nearly complete dominance by small-bodied zooplankton in lakes where native fish are present, suggests that over longer time frames (*i.e.* centuries) stocked fish may completely eliminate native alpine zooplankton, allowing colonization by smaller montane species.

The significant positive relationship between lake temperature and total zooplankton richness was attributable to a high diversity of smaller species being more common in the warmer lakes. Warmer montane lakes are inherently more species rich than higher-elevation, ultra-oligotrophic alpine lakes (Anderson, 1971). In warmer systems, smaller zooplankton are better suited, metabolically, than larger species to summer warming events, greater nutrient availability, and avoidance of fish predation (Moore et al., 1996). Few small crustacean zooplankton species inhabit colder environments (Shurin et al., 2010) and rarely occur in alpine lakes unless native large-bodied zooplankton have been extirpated (i.e. Schindler & Parker, 2002). On the other hand, large predatory calanoid copepods are better suited than smaller cladocerans and cyclopoids for survival in harsh alpine environments (Anderson, 1980). Earlier studies have shown that, under warming conditions, zooplankton communities dominated by larger species can experience a size-selective shift toward smaller individuals (Strecker, Cobb, & Vinebrooke, 2004). Total commmunity biomass is further increased as warmer temperatures increase reproduction and feeding rates of the zooplankton community (Moore et al., 1996). Futher, species richness can be a function of dispersal capabilities of nearby communities, making lower-elevation montane systems more easily colonized than alpine systems that are limited by topography (Donald et al., 2001).

The increased likelihood of introduced sportfish persisting in colder high-elevation lakes than in lower montane sites can be attributed to better habitat quality and lower angling presssure. Earlier surveys show that some of the montane lakes I sampled likely lacked suitable spawning habitat to support reproduction by introduced fish (Anderson & Donald, 1980). In many of these montane lakes, the littoral substrate is primarily composed of silt and sand, with little to no outlet area available for spawning, which together are associated with unsuccessful fish colonization (Donald, 1987). Further, since lower montane lakes are typically more easily accessibile to anglers, angling pressure may play an important role in eliminating fish from these lakes more rapidly. Bailey & Hubert (2003) suggest that angler accessibility was the most important factor in determining the structure of the fish community in the Bighorn Mountains, Wyoming. Since higher elevation lakes are typically much more remote, they tend to see fewer anglers per year. Higher elevation lakes also tend to exhibit more favorable conditions for natural recruitment and survival of stocked salmonids (*i.e.* cold temperatures and high dissolved oxygen concentration). In 1992, it was estimated that nearly 95% of large (>2 ha), deep (>3 m), high-elevation lakes throughout western North America contained introduced salmonids (Bahls, 1992; Armstrong & Knapp, 2004).

These findings suggest that zooplankton communities in warmer montane rather than colder alpine lakes may be more resistant to rapid climate warming for several reasons. Firstly, diverse and abundant assemblages of more thermally tolerant, smaller zooplankton species (Moore et al. 1996) already exist within the warmer lakes. In contrast, the surveyed alpine lakes contained larger coldwater stenothermic zooplankton (*i.e. H. arcticus*, *D. middendorfianna*) having relatively narrow thermal tolerances (5-10°C) (Moore et al., 1996; Schindler, 1997). However, *H. arcticus* were found in many alpine lakes where midsummer water temperature fell below 10°C, suggesting their thermal tolerances may not be chronically exceeded for quite some time. Further, as studies have shown that slow exposure to toxicant metals can result in the development of tolerance in zooplankton (Muyssen, Janssen, & Bossuyt, 2002; Ponti, Piscia, & Bettinetti, 2010), the same might occur with gradual exposure to warming over several decades. Finally, increased thermal variability should suppress zooplanktivory by introduced fish as extreme summer heating events impair salmonid development and reproduction.

Future research should focus on understanding the ecological mechanisms that drive the inferred interactive effects of fish predation and warming on zooplankton communities in climatically sensitive lake ecosystems. An important question to answer would be whether size-selective fish predation increases the resistance of zooplankton communities to increasingly common extreme climate events by removing sensitive larger prey and favoring thermally tolerant smaller zooplankton. Also, other investigations need to be performed to identify the mechanisms that are responsible for determining whether or not large-bodied alpine zooplankton are able to coexist with fish, and what causes certain zooplankton species to be extirpated. It may also benefit resource managers to understand whether or not there is a long-term difference in the species-specific (*i.e. Oncorhynchus* spp. or *Salvelinus* spp.) effects of fish on alpine zooplankton communities. If prolonged persistence of stocked fish in alpine lakes, for multiple decades, has the same effect on the zooplankton community as the presence of native fish, alpine communites will be increasingly altered with longer fish residence times. More research is also needed to determine the role that diel migration and other avoidance strategies may play in allowing introduced fish and large-bodied zooplankton to coexist under future climate regimes.

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Table 1.1: Elevation, water temperature, morphometry, fish species, stocking history, and zooplankton species richness and total biomass for 37 lakes surveyed during the ice-free periods of 2010 and 2011 in Banff, Jasper, and Yoho National Parks, Canada.

				Morphometry		**Fish History**			**Zooplankton**	
No.	Lake	Elevation (m)	Mid-summer temp (°C)	Area (ha)	Maximum depth (m)	Fish species present	Last stocked	# of years stocked	Species richness	Total biomass (ug/L)
Never stocked - Fish absent										
1	J392	1120	15.5	0.2	8.0				4	102.51
2	K13	1295	18.4	2.5	6.0				5	34.19
3	Hamilton	2140	9.4	5.0	12.2				1	4.40
4	Eiffel	2271	9.5	7.4	13.5				2	16.43
5	Oesa	2285	6.3	16.2	39.0				1	7.72
6	Upper Devon	2331	5.0	28.7	24.0				2	2.23
Native fish present										
7	Moab *	1240	13.5	23.9	18.0	RBT, LKT, MW	1972	13	9	16.66
8	Harrison	2240	8.2	5.1	10.6	BLT			3	314.21
9	Arnica *	2314	9.0	5.2	15.5	WCT	1966	3	4	59.31
Stocked - Fish absent										
10	Marjorie	1143	18.2	7.3	8.0		1986	43	5	21.32
11	Kootenay Pond	1213	20.3	2.6	6.0		1972	unk.	5	111.81
12	Virl	1305	17.8	3.5	6.0		1986	14	5	68.69
13	Copper	1442	18.5	1.3	10.4		1985	27	5	8.77
14	Cutt	1455	17.5	15.5	7.5		1986	10	4	70.35
15	Golden	1485	14.3	13.4	10.3		1986	11	5	7.18
16	Kingfisher	1539	18.3	1.4	7.2		1988	40	4	22.30
17	Island	1570	18.2	14.8	6.4		1960	7	4	88.22
18	Lost	1722	18.1	4.3	5.5		1972	12	5	36.67
19	Schaeffer	2170	9.9	0.4	2.5		1966	unk.	2	66.89
20	Pipit	2210	6.3	8.0	20.4		1966	3	3	2.20
21	Merlin	2249	6.7	29.9	30.0		1964	1	5	3.33
22	Brachiopod	2271	10.3	0.9	3.0		1967	7	2	24.12
23	Bighorn	2301	7.1	1.5	9.2		1972	2	3	2.64
24	Middle Devon	2316	4.5	12.5	24.1		1966	3	3	0.63
25	Snowflake	2332	8.0	5.2	12.8		1966	3	3	15.55
Stocked - Fish present										
26	Johnson	1420	17.1	15.6	5.2	BKT	1986	45	7	406.00
27	Warden	1470	12.0	6.8	2.2	BKT	1988	29	6	142.76
28	Little Herbert	1570	12.6	0.4	8.2	BKT	1988	24	4	262.63
29	Mud	1600	11.7	5.9	7.2	BKT	1968	24	6	41.63
30	Cavell	1660	7.0	12.9	6.2	BKT	1966	2	3	16.65
31	Upper Consolation	1951	4.2	9.9	16.2	BKT, WCT	1981	33	2	23.91
32	Taylor	2057	10.1	26.4	43.9	YCT	1953	4	4	1.36
33	Castilleja	2148	7.2	3.5	5.0	BKT	1964	unk.	1	0.00
34	Hidden	2271	6.2	10.2	32.3	BKT	1966	6	2	2.79
35	Ptarmigan	2332	7.9	25.7	21.3	BKT	1967	13	4	0.32
36	Rockbound	2362	5.9	26.5	16.0	BKT	1972	11	3	6.36
37	Redoubt	2393	5.2	18.8	11.0	BKT	1971	11	1	0.36

* although Moab and Arnica show stocking histories, these lakes probably contained native fish prior to being stocked (Charlie Pacas – unpublished data), thus are categorized as such.

Table 1.2: Significance of parameters from multiple regression forward and backward selection of variables that describe variation in zooplankton species richness across the 37 lakes.

Variable	***t*-value**	***p*-value**
fish presence	0.129	0.898
midsummer water temp	4.387	<0.001
stocking history	3.320	<0.001
fish presence X temp	3.675	<0.001
fish presence X stocking history	-3.480	0.002
temp X stocking history	-2.815	0.009

Table 1.3: List of invertebrates collected in the 37 lakes. Species numbers and abbreviations provided as they appear in ordination figures.

No.	Species	Abbrev.
Cladocera		
1	*Alonella nana*	
2	*Alona* spp.	
3	*Bosmina longirostris*	*B lon*
4	*Ceriodaphnia lacustris*	
5	*Ceriodaphnia pulchella*	*C pul*
6	*Ceriodaphnia quadrangula*	
7	*Chydorus sphaericus*	
8	*Diaphanasoma brachyurum*	
9	*Daphnia catawba*	*D cat*
10	*Diaphanasoma leuchtenbergianum*	
11	*Daphnia middendorffiana*	*D mid*
12	*Daphnia rosea*	*D ros*
13	*Daphnia schodleri*	
14	*Daphnia pulex*	*D pul*
15	*Daphnia pulicaria*	
16	*Daphnia* spp.	
17	*Macrothrix montanus*	
18	*Polyphemus pediculus*	*P ped*
19	*Scapholeberis kingi*	
Calanoida		
20	*Acanthodiaptomus denticornis*	
21	calanoid copepodid	
22	calanoid nauplii	
23	*Hesperodiaptomus arcticus*	*D arc*
24	*Diaptomus leptopus*	
25	*Diaptomus tyrelli*	
Cyclopoida		
26	*Acanthocyclops vernalis*	
27	cyclopoid copepodid	
28	cyclopoid nauplii	
29	*Diacyclops bicuspidatus thomasi*	
30	*Eucyclops agilis*	
31	*Macrocyclops albidus*	*M alb*
32	*Microcyclops varicans rubellus*	
33	*Orthocyclops modestus*	*O mod*
Amphipoda		
34	*Gammarus lacustris*	*Gamm*
Diptera		
35	*Chaoborus* spp.	*Chao*

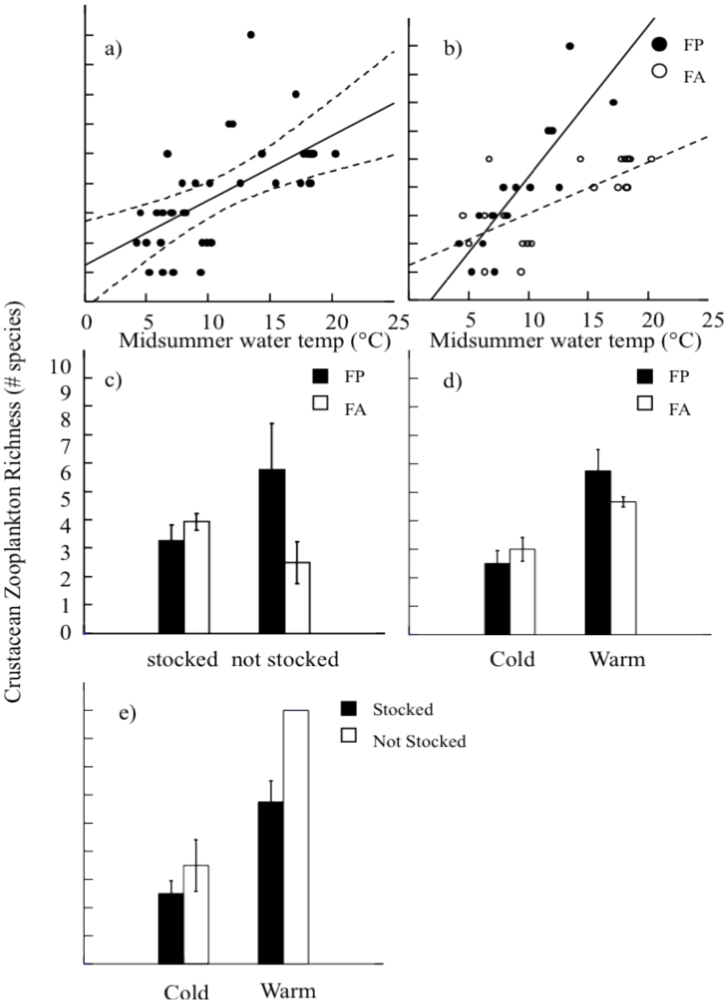

Figure 1.1: Environmental predictors of crustacean zooplankton species richness across 37 lakes in Canadian national mountain parks. a) Effect of midsummer water temperature. Solid line represents regression trendline and dashed lines represent 95% confidence interval for the slope of the regression line. b) Temperature-dependent influence of fish presence (FP) versus absence (FA). Solid line represents significant relationship between richness and mid-summer temperature for FP lakes (*n* = 15) and dashed line is for FA lakes (*n* = 22). c) Mean zooplankton richness (±SE) across previously stocked and non-stocked lakes in the presence (FP) and absence (FA) of fish. The four lake groups represented are stocked fish present (SFP, n = 12), stocked fish absent (SFA, *n* = 16), not stocked fish present (called: native fish present, NFP, *n* = 3), and not stocked fish absent (called: "pristine", PRI, *n* = 6). d) Mean zooplankton richness (±SE) across cold (<11°C, mean 7.1°C) and warm (>11°C, mean 16.1°C) stocked lakes in which fish had persisted (FP) or were absent (FA). e) Mean zooplankton richness (±SE) in the presence of fish (stocked = introduced fish, not stocked = native fish) in cold and warm lakes.

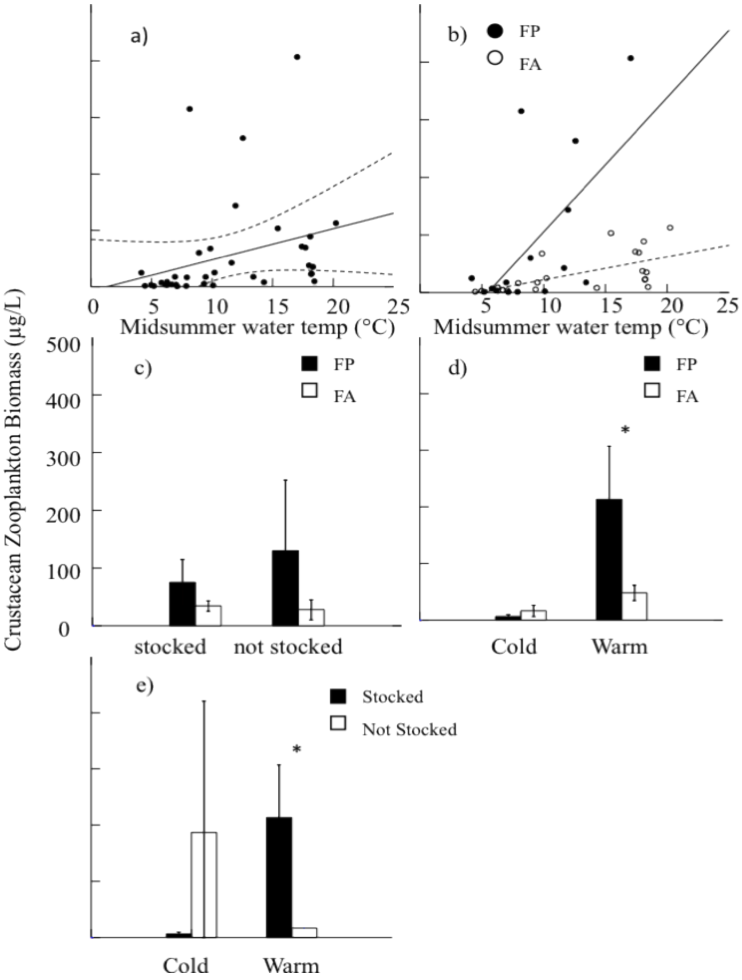

Figure 1.2: Environmental predictors of total crustacean zooplankton biomass across 37 lakes in Canadian national mountain parks. a) Effect of midsummer water temperature. Solid line represents regression trendline and dashed lines represent 95% confidence interval for the slope of the regression line. b) Temperature-dependent influence of fish presence (FP) versus absence (FA) on biomass in previously stocked lakes. Solid line represents significant relationship between richness and mid-summer temperature for FP lakes (*n* = 12) and dashed line is for FA lakes (*n* = 16). c) Mean total zooplankton biomass (±SE) across previously stocked and non-stocked lakes under cold (<11°C, mean 7.1°C) or warm warm (>11°C, mean 16.1°C) conditions. d) Mean crustacean biomass (±SE) across cold (<11°C, mean 7.1°C) and warm (>11°C, mean 16.1°C) stocked lakes in which fish had persisted (FP) or were absent (FA). Asterix denotes significant difference (*t*-test; $p < 0.05$). e) Mean zooplankton biomass (±SE) in the presence of fish (stocked = introduced fish, not stocked = native fish) in cold and warm lakes.

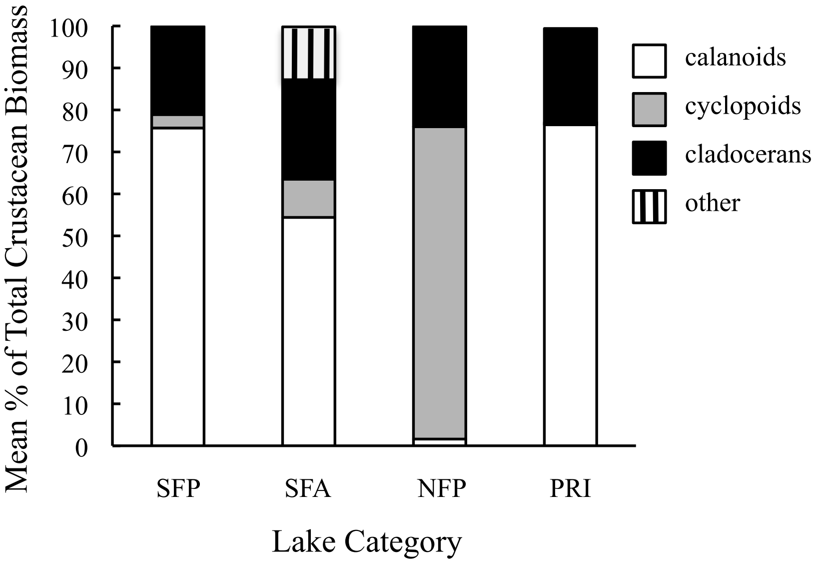

Figure 1.3: Mean percent of cladocerans (black), cyclopoid copepods (grey), calanoid copepods (white), and other invertebrates (Gammarus, Chironomids, and Chaoborus spp.)(dashed lines) that made up the total biomass found in stocked fish present (SFP, *n* = 12) lakes, stocked fish absent (SFA, *n* = 16) lakes, native fish present (NFP, *n* = 3) lakes, and "pristine" never stocked fish absent (PRI, *n* = 6) lakes.

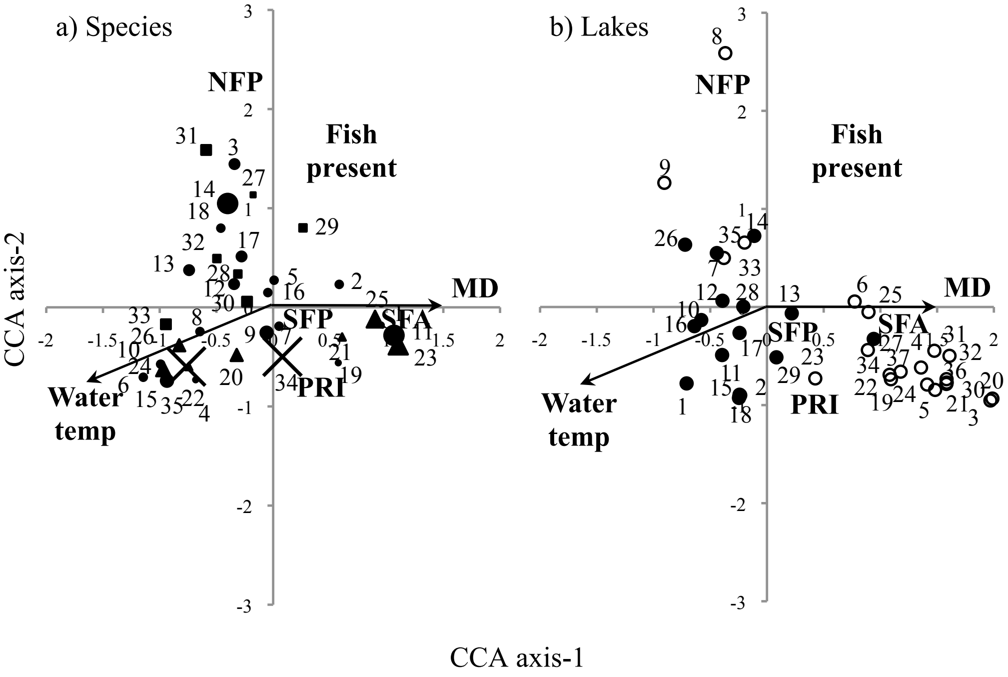

Figure 1.4: (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected during 2010 and 2011 from 37 lakes located in Banff, Jasper, and Yoho National Parks. Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares), cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 1.3. Bolded words represent centroids of lake categories (SFP, stocked fish present; SFA, stocked fish absent; PRI, "pristine"; NFP, native fish present). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of all lakes according to their zooplankton species community composition. Labels for lakes are found in Table 1.1. Open circles represent cold lakes (<11°C, mean 7.1°C, *n* = 21) and closed circles represent warm lakes (>11°C, mean 16.1°C, *n* = 16).

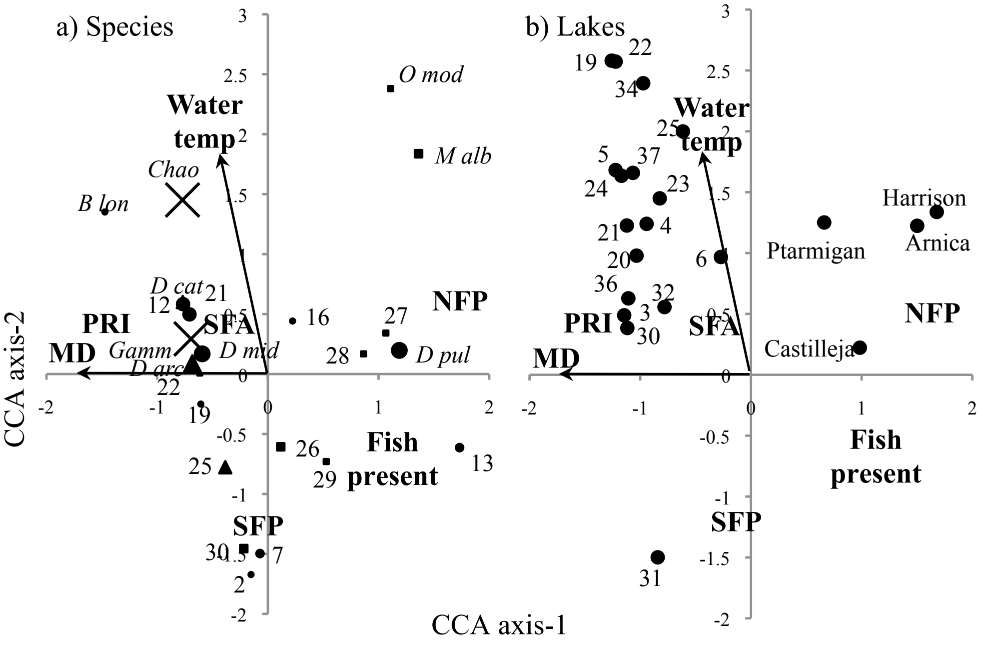

Figure 1.5: (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from the colder (<11°C, mean 7.1°C), high-elevation lakes (*n* = 21). Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares) , cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 1.3. Bolded words represent centroids of lake categories (SFP, stocked fish present; SFA, stocked fish absent; PRI, "pristine"; NFP, native fish present). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of fishless lakes according to their zooplankton species community composition. Labels for lakes are found in Table 1.1.

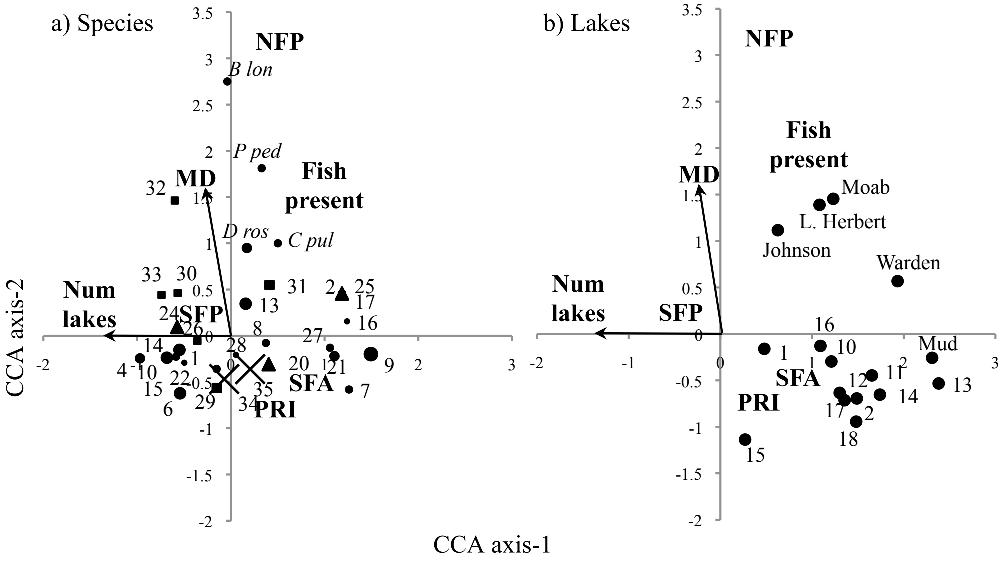

Figure 1.6: (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from warmer (>11°C, mean 16.1°C), low-elevation lakes (*n* = 16). Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares) , cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to abbreviations appear in Table 1.3. Bolded words represent centroids of lake categories (SFP, stocked fish present; SFA, stocked fish absent; PRI, "pristine"; NFP, native fish present). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of warm lakes according to their zooplankton species community composition. Labels for lakes are found in Table 1.1.

CHAPTER THREE: TAXONOMIC RESISTANCE AND RESILIENCE OF ZOOPLANKTON IN FISH-STOCKED ALPINE LAKES

INTRODUCTION

Alpine environments have been, and continue to be, strikingly altered by human perturbations, such as recreational tourism, acid deposition, dam construction, and introduction of exotic fish (Schindler, 2000; Chimner et al., 2010). Introduced exotic sportfish have extirpated native large-bodied invertebrates from alpine lakes in both Canada and the United States (Parker et al., 2001; Schindler & Parker, 2002; Knapp & Sarnelle 2008), thereby biologically impoverishing native zooplankton communities. High-elevation environments are also predicted to be highly sensitive to global warming (Hauer et al., 1997), possibly resulting in further re-structuring of alpine zooplankton communities (Strecker et al., 2004; Holzapfel et al., 2005). Scientific insights into the ecological resistance and resilience (i.e. recovery rate) of perturbed zooplankton communities are essential to their use as indicators of the stability of mountain lake ecosystems (Knapp et al., 2001).

The effects of introduced fish on alpine lake food webs differ regionally (i.e. Parker et al., 2001; Sarnelle and Knapp, 2004; Winder et al. 2003). Even though Winder et al. (2001) concluded that the occurrence of large-bodied zooplankton in Swiss alpine lakes was not related to fish presence, studies in North America have shown that size-selective predation by fish can result in significantly diminished populations of, and sometimes complete elimination of, large diaptomid copepods, alpine daphnids, and Gammarid amphipods (Parker et al., 1996; Liss et al., 1998; McNaught et al., 1999; Knapp & Sarnelle, 2008). Extirpation of the omnivorous calanoid copepod *Hesperodiaptomus arcticus* from lakes in the Canadian Rockies resulted in emergence of small cyclopoid copepods (*Diacyclops bicuspidatus thomasi* and *Acanthocyclops vernalis*) that had never been detected in those systems previous to fish introduction. The resulting zooplankton communities, containing a high diversity of small species, were more closely similar to those typically found in warmer eutrophic systems (Buchaca et al. 2011).

Variation in the resistance of alpine zooplankton to the effects of fish introduction also appears attributable to differences in lake morphometry. Donald et al. (1994) found that native large-bodied zooplankton were able to coexist with salmonids in lakes that were large enough (> 16 ha) and deep enough (> 16 m) to allow a sufficient amount of littoral and profundal refuge for zooplankton to escape complete elimination by fish. However, Winder et al. (2001) found that lake size did not influence the ability of large-bodied zooplankton to coexist with fish in the Swiss Alps. Whether other mechanisms also help large alpine zooplankton to resist the negative consequences of fish introduction is unknown.

Much of the recent management focus has been placed on removing introduced exotic sportfish from alpine lakes, and examining how zooplankton communities recover (Latta et al., 2010). In the Canadian Rockies, stocking was halted in the 1980s and management strategies re-focused to remove planktivorous introduced fish from several alpine lakes, in an attempt to restore native zooplankton biodiversity (Parker et al., 2001). Although most studies that examine ecological resilience are typically short-term (Knapp et al., 2005), maintenance of long-term datasets for many lakes in the Canadian Rockies (i.e. Anderson, 1971; Anderson, 1974; Schindler & Parker, 2002) provides a unique opportunity to observe changes that have occurred in the zooplankton community, in response to fish introduction and subsequent disappearance, throughout nearly half a century.

The mechanisms driving the ecological resilience of alpine zooplankton are complex (e.g. Parker et al., 1996; Donald et al., 2001; Knapp et al., 2005; Kramer et al., 2008). While cladocerans reproduce parthenogenically, and produce a resting egg stage that can reside in sediments for over 125 years (Caceres, 1998), copepods can have a much more difficult time re-colonizing lakes once introduced fish are no longer present (Knapp et al., 2001; Kramer et al., 2008). Factors such as lake depth, elevation, connectivity to other systems, fish stocking density, fish species stocked, and fish residence time may all contribute to whether extirpated zooplankton are able to fully recover from fish introduction following their disappearance (Donald et al., 2001; Knapp et al., 2001; Knapp et al., 2005; Knapp & Sarnelle, 2008; Kramer et al, 2008).

The main objectives of this study were two-fold. First, I wanted to identify the biotic and abiotic factors that are associated with high taxonomic resistance, by native zooplankton communities, to elimination by introduced fish in 18 alpine lakes. As naturally fishless alpine systems are dominated by large diaptomid copepods and large Daphnia species (Anderson, 1974) that are highly susceptible to extirpation by visually-feeding salmonids (Anderson, 1980), resistance is here defined primarily by the ability of these species to persist in the presence of introduced fish. The second objective was to examine the resilience (i.e. recovery rate) of native zooplankton communities after exotic fish have been extirpated. Taxonomic resilience of zooplankton communities was defined as the rate at which perturbed communities began to taxonomically resemble those communities found in naturally fishless lakes, following the extirpation of introduced fish. My examination of resilience was made possible by compilation and analysis of long-term limnological monitoring data sets in four select alpine lakes in Banff National Park.

METHODS

The Study Lakes:

The surveyed alpine lakes are located in Banff (n = 16) and Yoho (n = 2) National Parks (Table 2.1). Study sites range in elevation from 1951 to 2393 m asl (mean = 2250 m), having maximum depths ranging from 5 to 43.9 m (mean = 20 m) and total water surface areas from 1.5 to 29.9 ha (mean = 13.6 ha). All lakes are considered to have been fishless prior to the 20th century, except Harrison and Arnica (Parks Canada stocking records – unpubl. data; C. Pacas – personal communication; Ward, 1974). Four lakes (Upper Devon, Oesa, Hamilton, and Eiffel) have never been stocked with fish (Parks Canada stocking records – unpubl. data) and are therefore considered relatively “pristine” reference sites. The remaining 12 lakes were stocked with Rainbow Trout (*Oncorhynchus mykiss*), Cutthroat Trout (*Oncorhynchus clarkii*), or Brook Trout (*Salvelinus* *fontinalis*), either singly or in combination, for one or more years from 1922 to 1974 (Parks Canada stocking records – unpubl. data). Fish stocking was terminated in the parks in the late 1980s (Donald, 1987). While fish populations in most stocked lakes were left to respond naturally to the cessation of stocking (Upper Consolation, Ptarmigan, Castilleja, Hidden, Redoubt, Taylor, Rockbound, Merlin, Snowflake, and Pipit), fish were actively removed from Bighorn (1997) and Middle Devon (2001) by implementing intensive gill-net eradication regimes (Parker et al., 2001; C. Pacas – unpubl. data). In the absence of fish, researchers re-introduced *H. arcticus* into Snowflake (1992) and Bighorn (2001) Lakes (B. R. Parker, PhD thesis, University of Alberta; Schindler & Parker, 2002).

Environmental Sampling of Study Lakes:

I assessed lake morphological characteristics that are generally associated with the availability and quality of spawning habitat, by determining the number, quality (poor, fair, good, excellent), and size (width and depth) of lake inlets and outlets, as well as the dominant shoreline substrate (according to criteria outlined in Armstrong & Knapp, 2004). Researchers walked the shoreline perimeter of each lake to access all lake tributaries, and examine the shoreline substrate. The average width, depth, and dominant substrate was assessed for the portion of each tributary from the lake to 75 m, or to an impassible barrier. Suitable spawning tributaries were considered to be those which were primarily (40 - 100%) composed of gravel (0.5 - 4 cm), not cemented, and in water no less than 10 cm deep. Likewise, gravel-dominated shorelines were considered to be the most desirable quality for littoral reproduction. Mean lake depth, maximum lake depth, surface area, and lake volume were also considered to be important variables for our analysis. The values for those measures were obtained from previous reports in our study area (Mayhood and Anderson, 1976; Anderson and Donald, 1978; Parks Canada - unpubl. data).

Water chemistry was analyzed by collecting 500 mL of lake water from 1 m below the surface at each site. Lake water was passed through a 64 μm mesh-sized sieve to remove large invertebrates and debris, and samples were transported to the Biogeochemical Analytical Facility at the University of Alberta, Edmonton (URL link: http://www.biology.ualberta.ca/basl) for phosphorus (TP, TDP) and nitrogen (TN, TDN) analysis. Nutrient parameters were measured in the same way reported in Murphy et al. (2010). Total chlorophyll was quantified by filtering 1000 mL of lake water through GF/F filters, to concentrate pigments for high-performance liquid chromatography analysis using the exact methods described in Vinebrooke & Leavitt (1999).

Climate:

Midsummer water temperature (taken between 15 July to 15 August) was also measured for each lake in 2010/2011. A temperature profile was conducted by measuring water temperature at each meter from the lake surface to 1 m above the lake bottom, in the deepest part of each lake. Midsummer water temperature was then calculated, as the mean water temperature from 2 m below the surface to 10 m, or to the maximum depth in lakes < 10 m deep (Donald et al., 2001). We also calculated midsummer water temperature in Pipit, Snowflake, Bighorn, and Harrison lakes, during years when temperature profiles were conducted at those lakes (mid-1990s to 2005) (D. W. Schindler - unpubl. data). The average change in midsummer water temperature, per year, was then calculated to determine the overall trend over the past decade and a half. To further examine the thermal/ climatic effects, we used a climate-modeling program (ClimateBC) (Mbogga et al., 2009) specifically designed for generating data to be used for climate change studies in Western Canada. We entered latitudinal and longitudinal coordinates, as well as elevation for each lake, and the modeling program returned estimates for each year: approximate Julian date when frost-free period began, mean summer air temperature (June through August), annual precipitation as snow (August of previous year to May of current year), and mean spring air temperature (March through May) for each site.

Sampling of Fish Communities:

In the 1970s and 1980s, the majority of stocked lakes were visited to determine the success of stocking programs, and the health of fish populations in the mountain park lakes (Donald, 1987). At most lakes, fish were sampled using monofilament gill nets (25 - 30 m long by 1.8 m deep), consisting of five or six panels of 25 mm, 38 mm, 51 mm, 76 mm, 102 mm, and occasionally 127 mm mesh sizes (Donald, 1987). I visited 18 alpine lakes in 2010 and 2011 to determine the current status of their fish populations. The presence of fish was determined using one sinking, multi-mesh gill net (45 m long and 2 m deep) and two minnow traps set overnight for a period of 12 to 15 hours (mean = 13 hours). Gill nets consisted of six, 8 m panels of 13 mm, 19 mm, 25 mm, 32 mm, 38 mm, and 51 mm mesh sizes, and were always set perpendicular to shore, with the small-mesh end of the net anchored to shore. Minnow traps were anchored to shore as well, and placed in shallow (< 1 m) bays or well-vegetated areas of the lakes, to determine presence/absence of young fish (Jackson & Harvey, 1997). In 2010 and 2011, gill nets were not set in lakes that contained native fish populations (i.e. Westslope Cutthroat Trout, *Oncorhynchus clarkii lewisii* and Bull Trout, *Salvelinus confluentus*), to avoid accidental injury or mortality to native fish. Presence of native fish in these lakes was confirmed however, based on angling.

Relative abundance (catch-per-unit-effort; CPUE) of fish in each lake was determined by counting the number of fish caught per 100m of net, per net hour (Donald, 1987). Fish caught in gill nets were weighed (g), measured (fork length (mm)), and aged, using otoliths, for determination of population structure. Otoliths were taken from two to three individuals in each size class, and otoliths were split, burned, and examined under a dissecting microscope to count growth rings (Christensen, 1964). A length-frequency histogram was constructed and, in conjunction with otolith data, ages were assigned to all fish captured in the nets. These ages were used to calculate the average length and weight of particular age groups in each lake, for comparisons with historic catch data.

Sampling of Zooplankton Communities:

Crustacean zooplankton have been periodically sampled in many lakes in the national mountain parks of Canada as far back as the mid-1960s (Anderson, 1971; Anderson, 1974; Donald et al., 2001; Schindler & Parker, 2002). Zooplankton were collected from the deepest part of each lake by conducting vertical tows, at a rate of 0.5 $m\bullet s^{-1}$, using Wisconsin-style plankton nets (65 µm mesh, 25 cm diameter in the 1970's and 1980's; 63 µm mesh, 30 cm diameter in the 1990's; 63µm mesh, 20 cm diameter in 2010 and 2011). In previous years, plankton were enumerated according to the methods of Anderson (1974). In 2010 and 2011, zooplankton were preserved in 95% ethanol for enumeration back in the laboratory. Large crustacean zooplankton were examined and enumerated under a LEICA MZ 9.5 dissecting microscope at 4x to 6x magnification, while small zooplankton were slide mounted under a compound microscope (40x to 100x) to key all organisms to species (Edmondson, 1959). Species biomass estimates from raw data in those studies by Anderson (1971, 1974), Donald (2001), and Schindler & Parker (2002) were used to calculate the biomass (µg/L) for each species collected, as well as total biomass for each site.

Statistical Analyses:

Ordinations were performed using CANOCO version 4.1 (ter Braak and Smilauer 2002) to quantify differences in pelagic invertebrate communities among lakes and across sampling years. A ‘species biomass (µg/L) by site’ data matrix was constructed for all organisms (crustacean zooplankton, *Chaoborus* spp., and *Gammarus lacustris*).

I used taxonomic zooplankton data for each lake, during midsummer (July 15 to August 15), for each year that we had on record (i.e. 1966 to 2011 for long-term dataset) to assess temporal changes in community structure. Canonical correspondence analysis (CCA) was used in order to explain the significance of measured environmental variables in influencing changes in zooplankton community composition (ter Braak and Smilauer 2002) between lakes and over time within lakes. First, correspondence analysis (CA) was performed to determine the amount of taxonomic variation contained within the entire data set. If represented by > 3 SD units along the first CA axis (which is true), this indicated that use of a unimodal ordination model (i.e. CA, CCA) was most appropriate (ter Braak & Prentice, 1988). CCA was chosen in order to identify significant environmental predictors (i.e. explanatory variables) of changes in zooplankton community composition across space and time (ter Braak & Prentice, 1988; ter Braak & Smilauer, 2002). Species biomass values (non-grouped) were $\log_{10}(x+1)$ transformed to downweight the influence of abundant taxa. Overall fish presence, native fish presence, stocking history, midsummer water temperature, lake area, max depth, nutrient concentrations (TP, TN), date when frost-free period begins, mean summer air temperature, mean spring air temperature, and number of lakes within 20 km were tested for their significance as environmental predictor variables. The number of lakes within 20 km of each study site was calculated by setting a 20 km buffer around the perimeter of each lake in ArcGIS 10, and counting the number of lakes within each buffer. Forward selection with Monte Carlo permutation testing was used to identify significant environmental variables, which were then included in the final CCA. Monte Carlo permutation testing was also used to determine the statistical significance of primary axes and overall CCA ordinations.

To quantify resistance and resilience of zooplankton communities to fish introduction, Euclidean distance (SD units) was measured between lakes of interest in two-dimensional ordination space. Resistance to fish introduction was determined by examining the separation between lakes still containing exotic fish and non-stocked fishless lakes, assuming both lake types had, prior to fish introductions, contained highly similar zooplankton assemblages – an assumption supported by earlier by findings by Anderson (1974). Taxonomic resilience or recovery rate was determined by ordination of stocked lakes that had been sampled over a period of years prior to and after the removal of introduced fish. Distance travelled in ordination space by a lake following the removal of exotic fish divided by the span of sampling years was used to quantify resilience.

RESULTS

Fish communities:

The status of introduced and native fish varied among the surveyed lakes (Table 2.2). Gill-netting in 2010 determined that naturally reproducing populations of salmonids currently persist in Taylor (Yellowstone Cutthroat Trout), Rockbound (Brook Trout), Redoubt (Brook Trout), Ptarmigan (Brook Trout), Hidden (Brook Trout), Castilleja (Brook Trout), and Upper Consolation (Brook Trout and Yellowstone Cutthroat Trout) Lakes. Relative abundance (catch-per-unit-effort; CPUE) of fish in 2010 was as follows: Taylor (3.31 fish/hr – up from 0.78 fish/hr in 1974), Hidden (3.31 fish/hr – down from 7.91 fish/hr in 1973), Ptarmigan (4.44 fish/hr – slightly down from 4.7 fish/hr in 1973), Redoubt (1.54 fish/hr – down from 9.55 fish/hr in 1973), Upper Consolation (0.23 fish/hr – down from 1.15 fish/hr in 1974), Rockbound (2.12 fish/hr – no previous data), and Castilleja (2.31 fish/hr – no previous data). Stocked fish were not detected in Snowflake, Merlin, Pipit, Bighorn, and Middle Devon Lakes. However, Bighorn and Middle Devon no longer contained detectable exotic salmonids as a result of successful eradication of these invasive species via intensive gill-netting efforts that took place a decade ago. Gill netting removed a total of 261 Brook Trout from Bighorn Lake between 1997 and 2000 (Parker et al., 2001), and 1547 Brook Trout from Middle Devon between 2001 and 2006 (Charlie Pacas, personal communication).

Comparison of fish size in certain lakes was possible using well-catalogued historic catch data. In Taylor Lake, the average length of age 4 fish increased 48 mm (up from 210 mm), and average weight increased 64 g (up from 90.2 g), since 1974. In Hidden, Ptarmigan, and Redoubt Lakes, the average length of age 3 fish increased 24 mm (up from 167 mm), 67 mm (up from 171 mm), and 34 mm (up from 232 mm), respectively, while average weight increased 6 g (up from 52.8 g), 68 g (up from 55 g), and 36 g (up from 156.5 g) respectively, since 1973. Historic measurement data did not exist for Rockbound, Castilleja, or Upper Consolation Lakes.

Factors associated with fish persistence

Fish persistence in our study lakes could only be related to the presence/ absence of suitable spawning habitat (Figure 2.1; Tables 2.1 and 2.2). All lakes that contained native fish and all stocked lakes except Bighorn, Snowflake, Pipit, and Merlin, had tributaries (at least one inlet and/or outlet) that were considered sufficient for natural reproduction by salmonids (Table 2.2). Merlin, Pipit, Snowflake, and Ptarmigan Lakes did not contain sufficient shoreline substrate for natural reproduction, as the littoral zone around Merlin was mostly bedrock surface, and sand was predominant in the latter three. Gravel was the primary littoral substrate of all other stocked lakes. The outlets of both Harrison and Arnica lakes were considered large enough for natural reproduction of salmonids, and both lakes contained native fish populations. Shoreline substrate in Arnica was predominately gravel, while a large proportion of the littoral zone in Harrison was sand-dominated.

Temporal changes in climate:

Mean annual estimates of climatic conditions using the ClimateBC modeling program revealed gradual warming of annual air temperatures over the past two decades. Mean spring air temperature has likely warmed an average 0.2°C annually since the mid-1990's in the upper Cascade River drainage (vicinity of Harrison, Bighorn, Pipit, and Snowflake Lakes). Further, annual snowfall in that region was predicted to be decreasing by approximately nine mm annually since the mid 1990s. As a result, temperature profiles taken nearly every year since 1996 show an increasing trend in midsummer water temperature for all four lakes (Harrison: mean = 0.07 °C per year, Pipit: mean = 0.13°C per year, Snowflake: mean = 0.10°C per year, and Bighorn: mean = 0.17°C per year).

Influences of fish and climate on zooplankton communities:

Presence of native fish explained 56% of variation in zooplankton community composition based on CCA of all lakes across all years (Figure 2.2). Along with native fish presence, the presence or absence of introduced fish ($p < 0.002$) (30% of residual variation) and maximum depth (15% of residual variation) ($p < 0.002$) were the most significant explanatory variables defining CCA axis 1. Zooplankton communities in lakes containing native salmonids (Harrison and Arnica Lakes) were markedly different from those species found in fishless alpine lakes, as they were characterized by a high diversity of relatively smaller species, such as *D.b. thomasi*, *A. vernalis*, and *Macrocyclops albidus*. Further, species found in deeper lakes were more similar to those found in fishless lakes, rather than in lakes where fish were present. Cylopoid copepods (*A.*

vernalis, *Orthocyclops modestus*, *M. albidus* and *D.b. thomasi*) and certain daphnids (*Daphnia schodleri* and *Daphnia pulex*) were most abundant in shallower lakes and lakes where salmonids were present. In contrast, communities in both deeper and fishless lakes were comprised mainly of large calanoid copepods (*Diaptomus tyrelli* and *H. arcticus*), *Gammarus lacustris*, *Chaoborus* spp., and the large cladoceran species *Daphnia middendorffiana*. While other cladocerans (*Bosmina longirostris*, *Daphnia rosea*, *Daphnia catawba*, and *Chydorus sphaericus*) and some cyclopoid copepods (*Eucyclops agilis*) were also present in these lakes, they represent only a minor component of community total biomass.

Taxonomic variation among zooplankton along CCA axis 2 was best explained by mean midsummer lake temperature, accounting significantly ($p < 0.002$) for 20% of taxonomic variation (Figure 2.2). Lakes that are expressed temporally in the diagram (i.e. Pipit, Harrison, Snowflake, and Bighorn) show a general warming trend over the last 50 years. Temporal changes in taxonomic composition along CCA axis 2, from the bottom of the diagram to the top, favors zooplankton species like *B. longirostris* and *Scapholoberis kingi* in fishless lakes (left side of diagram), and *O. modestus* and *M. albidus* in lakes with fish (right side of diagram).

Influence of fish presence on large-bodied zooplankton:

The large-bodied Diaptomid copepod, *H. arcticus*, was present in 100% of “pristine” fishless lakes/years, and 82% of lakes/years where fish were stocked but no longer present (Table 2.3). The only cases where *H. arcticus* did not occur in fishless systems (remaining 18%), were lakes/years where it had previously been eliminated by fish introduction (i.e. Bighorn and Snowflake Lakes). When *H. arcticus* was present, total cyclopoid copepod biomass was significantly lower than when *H. arcticus* was absent (t = -2.743, df = 136, p = 0.006). *H. arcticus* was absent from 53 of 66 lakes/years (80%) when fish were present (native and introduced), and the large-bodied organisms *Gammarus lacustris* and *Chaoborus* spp. were absent from 100% of lakes/years that contained fish (Table 2.3). Taylor, Redoubt, Rockbound, and Ptarmigan were the only lakes that contained *H. arcticus* in the presence of fish, all of which are larger (surface area >11ha) than lakes where *H. arcticus* and fish did not coexist (Table 2.1). In the ordination diagram (Figure 2.2), Euclidean distance from the “fishless” centroid to each of these lakes, except Ptarmigan, was much shorter (Taylor = 0.54 SD units, Redoubt = 0.65 SD units, Rockbound = 0.30 SD units, Ptarmigan = 1.00 SD units) than for lakes where *H. arcticus* was absent (Castilleja = 1.59 SD units, Upper Consolation = 2.05 SD units, Hidden = 0.85 SD units, Arnica = 3.09 SD units, Harrison = 3.08 SD units). In Taylor, Redoubt, Rockbound, and Ptarmigan Lakes, the mean densities of *H. arcticus* in the presence of fish was 0.976/L, 0.362/L, 0.530/L, and 0.001/L, respectively, compared to 0.431 organisms/L in “pristine” fishless lakes. All large-bodied zooplankton, in general, were completely absent in Bighorn, Snowflake, and Pipit during years when fish were present (*e.g.* 1970s), and from Arnica and Castilleja Lakes, both of which presently contain fish (native and introduced, respectively). Harrison, Upper

Consolation, and Hidden Lakes each contained one species of large bodied zooplankton (*Daphnia pulex*, *D. tyrelli*, and *D. tyrelli*, respectively).

Temporal changes in zooplankton communities

If the lakes of the Cascade Valley are viewed separately from the other lakes ordinated in Figure 2.2, then comparisons can be made more easily regarding the relative sensitivities of their zooplankton communities to fish and climate change in the long-term (Figures 2.3 – 2.6). For instance, maximum variation in taxonomic composition along CCA axis 1 was much lower in non-stocked, native fish-containing Harrison (Figure 3; 0.82 SD units) than in previously stocked Pipit, Snowflake, and Bighorn Lakes (Figures 2.4 – 2.6; 1.23 SD units, 2.84 SD units, 2.83 SD units, respectively). Fish introduction resulted in elimination of large zooplankton (*e.g. H. arcticus* and *D. middendorfianna*) from all three lakes at the end of the 1960's, and subsequent emergence of smaller cyclopoid copepod species (*i.e. A. vernalis* and *D.b. thomasi*). Shifts in taxonomic composition due to establishment of introduced fish populations, in all three lakes, is noted by the Euclidean distance between years, within sites, across CCA axis-1 between 1966 and the mid 1970s (i.e. 1966 - 1972; Pipit = 1.22 SD units, Snowflake = 1.18 SD units, Bighorn = 1.25 SD units).

When fish became absent in Pipit (Figure 2.4) and Snowflake (Figure 2.5) by the mid 1980s, the zooplankton community in Pipit was twice as resilient as the community in Snowflake Lake (between 1977 and 1991; 0.08 SD units per year and 0.04 SD units per year, respectively), owing to the immediate re-emergence of extirpated large-bodied zooplankton in Pipit (*H. arcticus* and *D. middendorffiana*). In Snowflake and Bighorn Lakes (Figures 2.5 and 2.6), movement along CCA axis-1 was not associated with the disappearance of fish (mid-1980s and 1997, respectively). Rather, the return to a fishless state in Snowflake and Bighorn coincided with reintroduction of *H. arcticus* in 1992 and 2001, respectively. Although all three lakes are now fishless, the zooplankton community in Pipit Lake has remained extremely stable since 1991 to present, while a great deal of variability still occurs in Snowflake and Bighorn throughout the years.

Climate-related taxonomic variability of zooplankton communities along CCA axis 2 differed among the four lakes (Figures 2.3 – 2.6). In non-stocked, native fish-containing Harrison Lake, rising annual mid-summer surface temperatures and earlier frost-free seasons accounted for most of the species turnover from 1966 to 2006 (Figure 2.3). Similarly, most of the taxonomic variation in the zooplankton of Pipit Lake is also best captured by the climate-defined CCA axis 2 (Figure 2.4). Taxonomic variation along CCA axis 2 is also evident for zooplankton in Snowflake (Figure 2.5) and Bighorn (Figure 2.6), but more overshadowed by species turnover attributable to changes in the abundance of stocked fish and *H. arcticus*. Maximum Euclidean distance traveled in ordination space along CCA axis 2 was relatively similar for all four lakes (Harrison = 5.03 SD units, Pipit = 3.34 SD units, Snowflake = 4.31 SD units, Bighorn = 5.66 SD units).

DISCUSSION

Stocked fish persisted more in the surveyed alpine lakes that contained adequate spawning gravels in tributaries or along shorelines. If introduced or native fish were detected in a lake, then large-bodied alpine zooplankton (*e.g. H. arcticus* and *D. middendorfianna*) were usually absent. Fish presence was also a key determinant of zooplankton species turnover in the lakes. Taxonomic resistance and resilience of zooplankton to fish were related positively to lake size. A large amount of temporal variation in taxonomic composition of the zooplankton across the alpine lakes was also explained by rising annual midsummer surface water temperatures, especially in the case of non-stocked Harrison Lake and the deepest of the stocked lakes (Pipit). Unexplained taxonomic variation in zooplankton communities was likely attributable to biomanipulations such as fish introduction and eradication, and invertebrate re-introduction. Potential explanations for these key findings are discussed below.

Environmental factors affecting fish persistence

My results showed that the ability of stocked fish to persist in alpine lakes was related to spawning habitat. Evidence suggests that approximately 25% of alpine lakes in North America would support natural recruitment of introduced salmonids if stocked (Bahls 1992). Both, Donald et al. (1994) and Armstrong and Knapp (2004) also found that stocked fish persistence could be predicted based on the availability of spawning habitat. Although all mountain salmonid species generally require clean gravels for building redds (Magee et al., 1996), not all species require the same exact conditions. *Onchorhynchus* spp. (i.e. Rainbow and Cutthroat Trout) typically only spawn in areas with flowing water, as their eggs require high oxygen and low sediment load (Bjornn & Reiser, 1991). On the other hand, Brook Trout are often observed spawning in littoral zones and at groundwater upwellings (Raleigh, 1982) if lake tributaries do not offer sufficient spawning habitat. This greater flexibility in spawning conditions may allow Brook Trout to be more effective at maintaining self-supporting populations in mountain lakes, resulting in a higher probability of extended residence.

Elimination of large-bodied zooplankton

I found that the native large-bodied diaptomid copepod, *H. arcticus,* was typically absent where fish were present. This was likely a result of size-selective predation by planktivorous salmonids, which has been shown elsewhere to result in severely lowered abundance and often complete elimination of those taxa (Liss et al., 1998; McNaught et al., 1999; Knapp & Sarnelle, 2008). *H. arcticus* are keystone top predators in fishless lakes of the Canadian Rocky Mountains, and their presence or absence in mountain lakes can determine the entire structure of lower trophic groups (Anderson, 1980). *H. arcticus* was absent from Pipit, Snowflake, and Bighorn Lakes during years when adult fish were present, from all lakes that contained native fish, and from all small lakes (< 11 ha) that contained introduced salmonids. *H. arcticus* was always present in the absence of fish, except where they had previously been eliminated by introduced fish that had since disappeared (i.e. Bighorn and Snowflake Lakes).

Taxonomic resistance of zooplankton

I found that *H. arcticus* was able to coexist with introduced salmonids in larger lakes (> 11 ha). The ability of large-bodied zooplankton to resist extirpation in larger lakes most likely occurs because of the greater amount of prey refuge that is available, where there is a greater amount of profundal and offshore pelagic habitat (Donald et al., 1994). In Ptarmigan and Castilleja Lakes, the zooplankton communities seemed to be impacted more heavily than in any other lakes that contained stocked fish, which is likely attributable to relatively shallow water columns (approximately 80% of Ptarmigan Lake is < 12 m deep) (Mayhood & Anderson, 1976). Donald et al. (1994) also found that coexistence between *H. arcticus* and fish was more likely to occur in larger (> 16 ha) and deeper (> 16 m) lakes. Adaptive migration strategies may be one possible mechanism allowing large-bodied zooplankton to resist extirpation by fish in deeper lakes. Both diel vertical migration and depth selection have been observed as behavioral strategies that enable large zooplankton to avoid fish in the epilimnion when predation pressure is strong (Flik & Vijverberg, 2003). The costs associated with occupying colder temperatures in relatively food-poor deeper layers however, are not fully understood (Winder et al., 2003).

Taxonomic resilience of zooplankton

The quick recovery rate of the zooplankton community in Pipit Lake, relative to those in the other stocked lakes following the removal of fish, was likely a result of greater lake depth, shorter fish residence time, and introduction of Rainbow rather than Brook Trout. Greater lake depth is associated with increased resilience of zooplankton species in alpine lakes due to the positive relationship between lake depth and the size of diaspausing egg banks (Knapp & Sarnelle, 2008). Zooplankton communities in deeper lakes are therefore better suited for "waiting out" periods of intense fish predation, resulting in a higher probability of recovery. Further, long-term persistence of introduced fish may influence the ability of extirpated zooplankton to recover from perturbation, decreasing resiliency. Both, Donald et al. (2001) and Knapp & Sarnelle (2008), have concluded that longer fish residence times significantly affect the response of zooplankton communities to fish disappearance. When fish persist for longer periods, such as in Bighorn Lake, diapausing egg banks can become fully exhausted (Parker et al., 1996), resulting in a decreased probability of re-colonization of extirpated taxa. Lastly, it is possible that not all salmonid species have the same affect on alpine zooplankton communities. Spring-spawning species such as Rainbow Trout may have less of a negative impact on large-bodied zooplankton than fall-spawning species (i.e. Brook Trout), due to the timing of spawning events in conjunction with the most critical period of zooplankton production, which also takes place during the spring (Anderson, 1980).

Climate-related taxonomic variation in zooplankton communities

I also detected shifts in crustacean zooplankton community composition in four alpine lakes related to environmental warming, using long-term limnological data sets. In conjunction, temperature profiles conducted over the course of the study showed that those lakes (Pipit, Bighorn, Harrison, and Snowflake) have experienced an average annual 0.12°C increase in water temperature since the mid-1990s, probably as a result of factors such as decreased snowpack and warmer air temperatures, during one of the warmest decades ever recorded in the Northern Hemisphere (Houle et al., 2010). Increased water temperature in alpine environments can create optimal thermal regimes for smaller, lower elevation taxa (Holzapfel & Vinebrooke, 2005), resulting in the observed taxonomic shifts toward a greater diversity of smaller individuals (Moore et al., 1996; Strecker et al., 2004). The relatively narrow thermal tolerance of large zooplankton that are acclimated to alpine lakes makes them more sensitive to extreme warming events (Moore et al., 1996). If substantial increase in water temperature over the next century exceeds thermal optima of large alpine species, resulting in mortality, smaller montane species may subsequently invade the open niche.

Effects of previous management practices on zooplankton communities

The response to fish introduction in all three lakes in the long-term dataset was similar. Stocking in the late 1960's resulted in a shift toward smaller-bodied zooplankton species (*D.b. thomasi* in Bighorn and Snowflake, and *A. vernalis* in Pipit). As Pipit and Snowflake lakes did not support natural reproduction fish disappeared by the mid-1980s (Schindler & Parker, 2002). While the zooplankton community in Pipit Lake exhibited the highest degree of taxonomic resilience after fish disappearance, Snowflake remained dominated by *D. b. thomasi* well into the mid-1990s. *H. arcticus* failed to return in the lake by the early-90s, suggesting that re-colonization was not likely to occur (McNaught et al., 1999). Likewise, zooplankton community composition in Bighorn Lake remained in an altered state into the late-1990s, due to the persistence of introduced salmonids (Parker et al., 2001). Although gill-netting in 1997 resulted in an immediate increase in zooplankton biomass in Bighorn, *H. arcticus*, had still not returned to the lake as of 2000 (B. R. Parker, PhD thesis, University of Alberta). Re-introduction of *H. arcticus* adults into Snowflake and Bighorn in 1992 and 2001, respectively, resulted in restoration of those communities to their pre-stocking states. However, natural resilience was absent in both systems.

As the prospect of stocking native fish species in mountain lakes throughout western North America, as a way to preserve pure genetic strains and prevent decline of native stocks, is becoming more common (Bahls 1992, Wilhelm et al. 1999, Divens et al. 2000), many factors should first be considered. While this practice would surely help to eliminate extinction of threatened fish species (i.e. *Oncorhynchus clarkii lewisii* and *Salvelinus confluentus*), the effects on native invertebrate communities could be dramatic. If stocking is desired, resource managers should take all of the above considerations into account when determining appropriate strategies for fish introduction in naturally fishless alpine systems.

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Table 2.1. Fish status (stocked-fish absent, stocked-fish present, not stocked-fish absent = “pristine”, and native fish present), lake morphometry, and midsummer lake temperature for 18 alpine lakes surveyed in Banff and Yoho National Parks in 2010 and 2011.

	Lake	Elevation (m)	Max Depth (m)	Mean Depth (m)	Area (ha)	Lake Volume (x 10^4 m^3)	Temp (°C)
Stocked Fish Absent	M Devon	2316	24.1	*	12.5	*	4.5
	Bighorn	2301	9.2	3.1	1.5	6.65	7.1
	Pipit	2210	20.4	12.6	8.0	133.70	6.3
	Snowflake	2332	12.8	6.1	5.2	43.60	8.0
	Merlin	2249	30.0	*	29.9	*	6.7
Stocked Fish Present	U Consolation	1951	16.2	5.9	9.9	63.50	4.2
	Rockbound	2362	16.0	*	26.5	*	5.9
	Taylor	2057	43.9	14.7	26.4	396.40	10.1
	Redoubt	2393	11.0	4.5	18.8	85.40	5.2
	Hidden	2271	32.3	14.6	10.2	194.70	6.2
	Castilleja	2148	5.0	*	3.5	*	7.2
	Ptarmigan	2332	21.3	7.0	25.7	195.00	7.9
Pristine	U Devon	2331	24.0	*	28.7	*	5.0
	Oesa	2285	39.0	*	16.2	*	6.3
	Hamilton	2140	12.2	*	5.0	*	9.4
	Eiffel	2271	13.5	6.0	7.4	81.00	9.5
Native	Harrison	2240	10.6	5.4	5.1	45.80	8.2
	Arnica	2314	15.5	*	5.2	*	9.0

* Data not available through existing Parks Canada records

Table 2.2. Spawning suitability of lake tributaries (primarily gravels = 0.5 - 4 cm in diameter) along with their average width and depth, as well as classification of shoreline littoral substrates for lakes that have, at one time, contained fish.

	Lake	# Suitable Tributaries	Average Width (m)	Average Depth (cm)	Primary Littoral	Secondary Littoral
Stocked Fish Absent	M Devon *	3	1.7	20	gravel	sand
	Bighorn *	0	n/a	n/a	gravel	cobble
	Pipit	1	1.5	8	sand	silt
	Snowflake	0	n/a	n/a	sand	silt
	Merlin	5	5.2	8	bedrock	cobble
Stocked Fish Present	U Consolation	1	1.0	10	cobble	gravel
	Rockbound	2	2.1	23	gravel	silt
	Taylor	1	7.0	30	gravel	sand
	Redoubt	1	0.3	30	gravel	sand
	Hidden	5	4.8	21	gravel	sand
	Castilleja	1	3.0	30	gravel	sand
	Ptarmigan	2	0.2	17	sand	gravel
Native	Harrison	2	1.4	20	sand	gravel
	Arnica	1	2.0	50	gravel	cobble

*Natural reproduction did occur in these lakes. Fish are absent due to gill-net removal.

Table 2.3. Percent of lakes and years that contained listed invertebrate taxa collected in the alpine lakes, by fish status classification (not stocked-fish absent = PRI, native fish present = NAT, stocked-fish absent = SFA, stocked-fish present = SFP). Species numbers provided as they appear in ordination figures.

No.	Species	PRI (n = 10)	NFP (n = 19)	SFA (n = 61)	SFP (n = 47)
Cladocera					
1	*Alona* spp.	0	0	2	9
2	*Bosmina longirostris*	10	0	0	2
3	*Chydorus sphaericus*	0	16	10	17
4	*Daphnia catawba*	0	0	0	4
5	*Daphnia middendorffiana*	70	0	89	6
6	*Daphnia rosea*	0	0	0	4
7	*Daphnia schodleri*	0	5	2	
8	*Daphnia pulex*	0	95	11	13
9	*Daphnia* spp.	20	11	10	9
10	*Scapholoberis kingi*	10	0	0	0
Calanoida					
11	calanoid copepodid	100	5	77	32
12	calanoid nauplii	90	0	62	43
13	*Hesperodiaptomus arcticus*	100	0	82	28
14	*Diaptomus tyrelli*	40	5	33	47
Cyclopoida					
15	*Acanthocyclops vernalis*	10	16	8	32
16	cyclopoid copepodid	40	79	62	30
17	cyclopoid nauplii	40	79	67	36
18	*Diacyclops bicuspidatus thomasi*	10	89	20	28
19	*Eucyclops agilis*	0	0	0	2
20	*Macrocyclops albidus*	0	26	0	2
21	*Orthocyclops modestus*	0	5	0	4
Amphipoda					
22	*Gammarus lacustris*	40	0	52	0
Diptera					
23	*Chaoborus* spp.	0	0	2	0

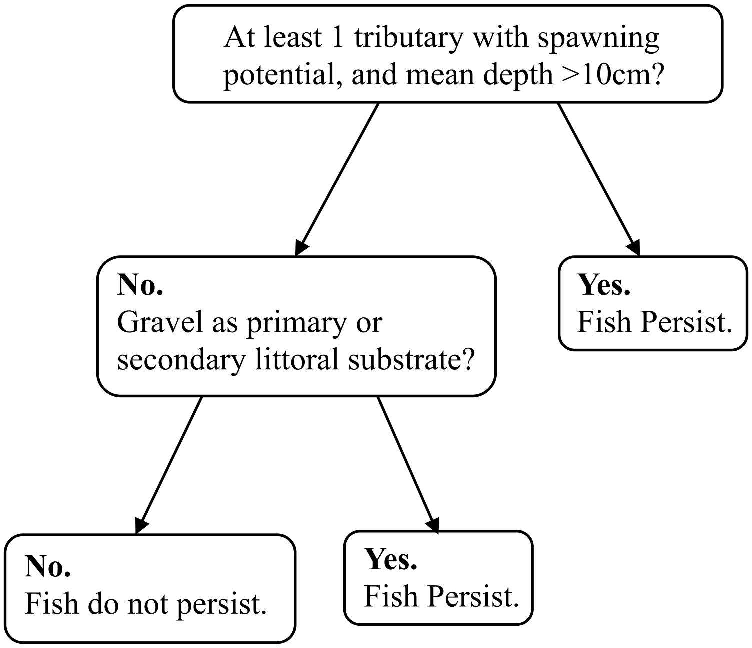

Figure 2.1. Schematic of criteria to determine whether stocked fish would establish naturally reproducing populations in alpine lakes in Banff and Yoho National Parks, based on our survey results.

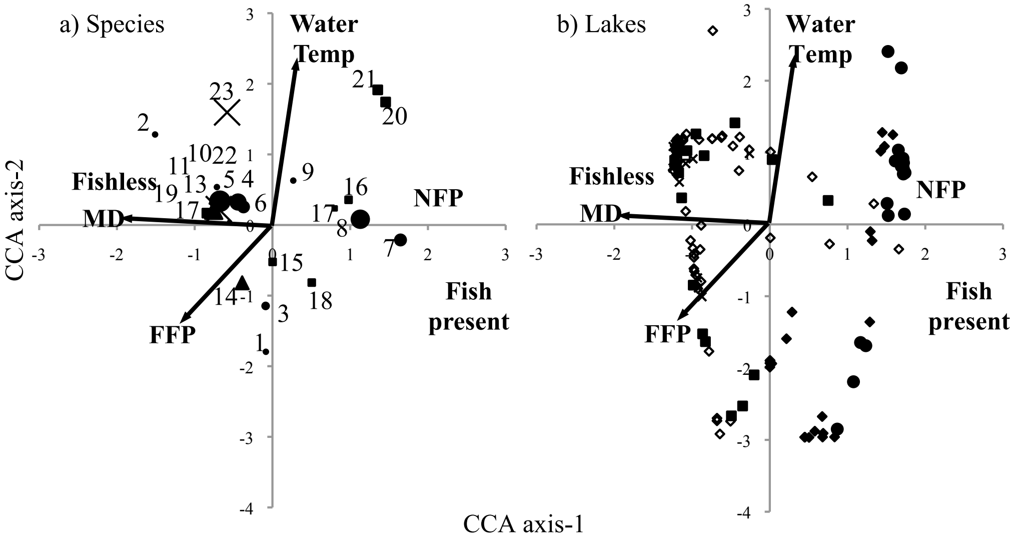

Figure 2.2. (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from alpine lakes in Banff and Yoho National Parks in 2010 and 2011. Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares), cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 2.3. Bolded words represent centroids of environmental variables (NFP = native fish present, FFP = start of frost free period, MD = maximum lake depth). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of all years for all 18 alpine lakes according to their zooplankton species community composition. Circles represent NFP lakes, X's represent not stocked-fish absent lakes, squares represent stocked-fish present lakes, and diamonds represent lakes from the long-term dataset (open diamonds = years when fish were absent, filled diamonds = years when fish were present).

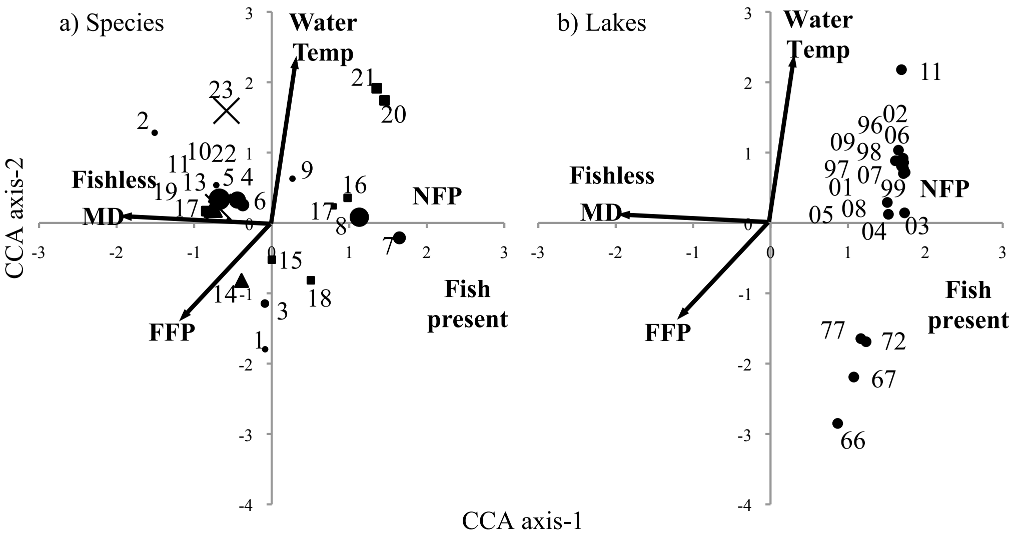

Figure 2.3. (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from Harrison Lake, Banff National Park, from 1966 to 2011(i.e. 72 = 1972). Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares), cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 2.3. Bolded words represent centroids of environmental variables (NFP = native fish present, FFP = start of frost free period, MD = maximum lake depth). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of all years that were sampled between 1966 and 2011 in Harrison Lake according to their zooplankton species community composition.

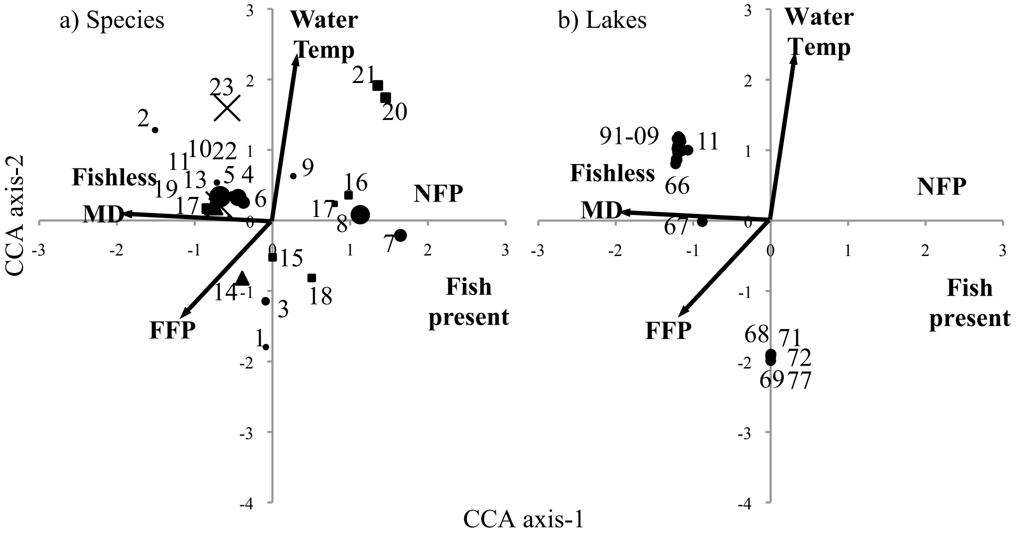

Figure 2.4. (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from Pipit Lake, Banff National Park, from 1966 to 2011(i.e. 72 = 1972). Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares), cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 2.3. Bolded words represent centroids of environmental variables (NFP = native fish present, FFP = start of frost free period, MD = maximum lake depth). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of all years that were sampled between 1966 and 2011 in Pipit Lake according to their zooplankton species community composition.

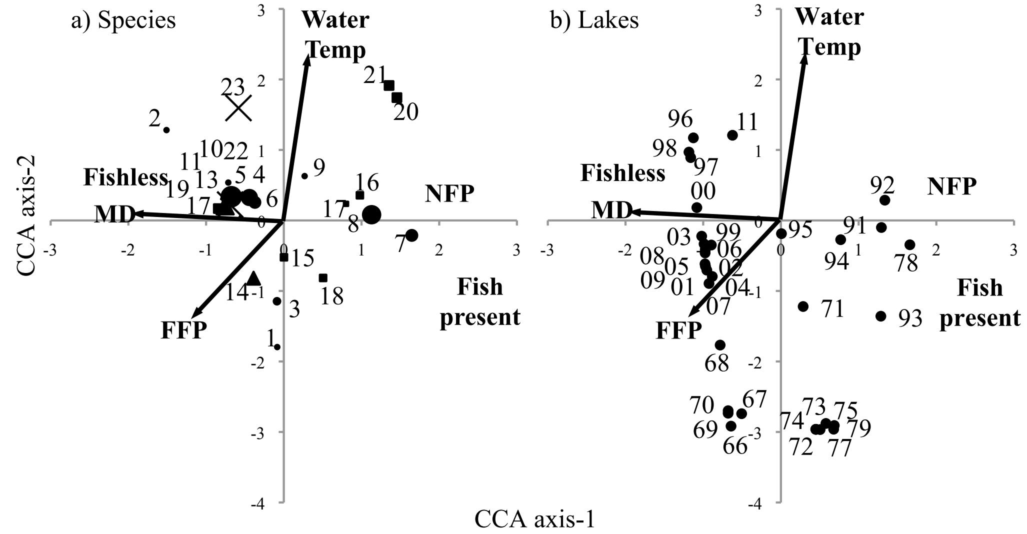

Figure 2.5. (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from Snowflake Lake, Banff National Park, from 1966 to 2011(i.e. 72 = 1972). Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares), cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 2.3. Bolded words represent centroids of environmental variables (NFP = native fish present, FFP = start of frost free period, MD = maximum lake depth). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of all years that were sampled between 1966 and 2011 in Snowflake Lake according to their zooplankton species community composition.

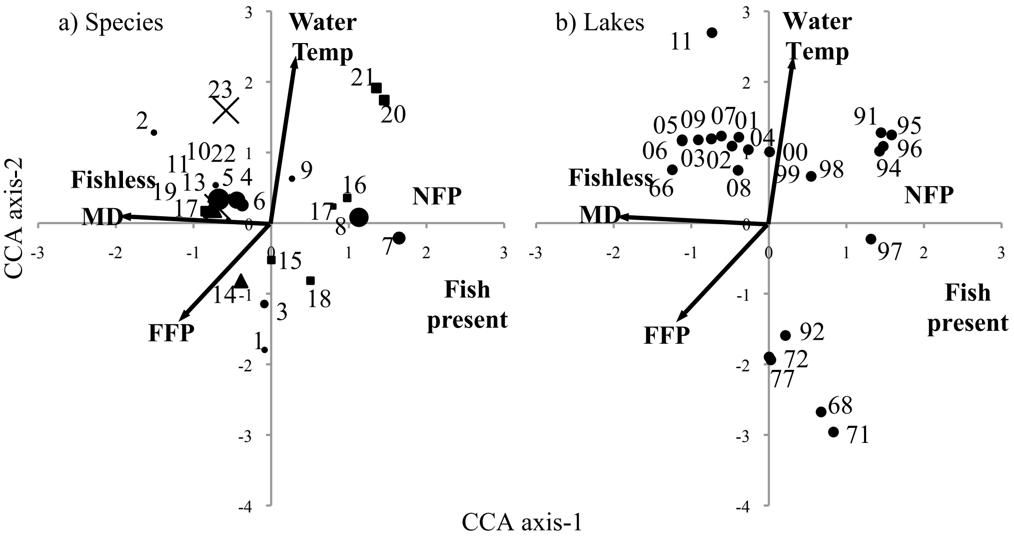

Figure 2.6. (a) Canonical correspondence analysis of mid-summer crustacean zooplankton species data collected from Bighorn Lake, Banff National Park, from 1966 to 2011(i.e. 72 = 1972). Symbols indicate calanoid copepods (triangles, cyclopoid copepods (squares), cladocerans (circles), and others (X). Size of each symbol represents relative body size of each species. List of species corresponding to labels appear in Table 2.3. Bolded words represent centroids of environmental variables (NFP = native fish present, FFP = start of frost free period, MD = maximum lake depth). Arrows indicate direction of environmental gradients shown in bold text. Arrows have been extended three times to emphasize gradients. (b) Ordination of all years that were sampled between 1966 and 2011 in Bighorn Lake according to their zooplankton species community composition.

CHAPTER FOUR: GENERAL DISCUSSION

CONCLUDING REMARKS

Long-term persistence of introduced fish can negatively impact mountain lake zooplankton communities (Donald et al., 2001). Although colder alpine lakes typically contain fewer zooplankton species than warmer montane systems (McNaught et al., 2000), my findings suggest that the effects of fish predation are more pronounced in warmer lakes. The presence of fish in those systems resulted in increased biomass and greater richness of smaller zooplankton. This may be partly due to the fact that warmer temperatures in lower elevation lakes promote increased feeding and growth rates of both the zooplankton (Moore et al., 1996) and fish (Gyllstrom et al., 2005) communities, thereby increasing predation rates by fish and subsequently increasing the response by the zooplankton community to predation. Cold oligotrophic alpine systems, on the other hand, exhibit strong trophic links that may help resist the influence of fish introduction (Perez-Fuentetaja et al., 1996). Those strong trophic links in fishless alpine lakes are usually maintained by the occurrence of keystone top-invertebrate predators (i.e. *Hesperodiaptomus arcticus*) (McNaught et al., 1999).

Elimination of *H. articus* can result in dramatic re-structuring of the zooplankton community in alpine lakes (Schindler & Parker, 2002). Lakes that are larger and deeper, however, may offer protection for large-bodied zooplankton, increasing their ability to resist elimination (Anderson, 1980; Donald et al., 1994). Likewise, greater lake depth also increases the ability of species to recover from elimination, following the reversion of lakes to a fishless state (Knapp & Sarnelle, 2008).

Future climatic changes in alpine ecosystems may influence the effects of introduced fish presence in alpine lakes. As midsummer lake temperature increases, conditions may begin to favor smaller zooplankton species that currently inhabit low elevation lakes (Holzapfel & Vinebrooke, 2005). Given the fact that cold, high elevation lakes in the Canadian Rockies currently show a relatively higher likelihood of introduced fish persistence, in relation to low elevation lakes (Messner & Vinebrooke, in review), increasing water temperatures may further enhance the effects of fish predation in alpine systems by increasing fish feeding and growth rates in those systems (Allan & Castillo, 2007). Increasing water temperatures in low elevation montane lakes on the other hand may have the opposite effect, as thermal optima for cold-water salmonids could be exceeded, resulting in decreased fitness of fish populations, and a subsequent reduction in size-selective planktivory.

Current lake management

The current management paradigm in the National Parks of the Canadian Rockies is focused on restoring the ecological integrity of aquatic systems (Parks Canada, 2010). One facet of this objective is the removal of invasive species. As visitation continues to increase in Banff National Park (Parks Canada, 2008), isolated alpine lakes where anthropogenic influence is relatively low offer unique opportunities for studies of techniques to remove invasive fish species. Using gill nets, Parks Canada aquatics staff and previous University of Alberta researchers (Parker et al., 2001) have successfully removed non-native fish from two alpine lake systems (the lakes and their connected tributaries) in Banff National Park, beginning in the late 1990s (C. Pacas – unpubl. data). More recently, efforts began in August 2011 to continue non-native fish eradication in two more alpine systems in the parks (S. Humphries – personal communication; C. Pacas – personal communication). The removal of non-native fish from those areas will hopefully allow native fish and invertebrate species to recover from the impacts of fish introduction (Parker & Schindler, 2000). Although alpine lakes, in particular, serve as excellent sites for this type of research (B. R. Parker, Ph.D. thesis, University of Alberta), there might also be value in performing similar studies in lower montane systems where the community response might be more intense, due to an intrinsically higher number of species in those systems (Anderson, 1974). Careful monitoring of chemical (i.e., nutrient concentrations), physical (i.e., turbidity), and biotic (i.e., algae and zooplankton) properties before, during, and after fish removal are necessary, and should continue, in order to fully determine the ecological consequences and benefits of the ecosystem restoration projects.

Re-introduction of extirpated invertebrates

Although most studies show that recovery of extirpated zooplankton is mainly facilitated by the hatching of diapausing egg banks (Parker et al., 1996; Sarnelle & Knapp, 2004), other mechanisms of re-colonization may also be important. Dispersal from nearby water bodies is another possible method of re-colonization. However, as it may be limited by topography, this mechanism could take decades in mountain regions (Donald et al., 2001). Re-introduction of extirpated zooplankton species has been conducted in both Canada (Parker & Schindler, 2006) and the US (Kramer et al., 2008) to artificially restore zooplankton communities when natural recovery was not immediate. Although this method has proven successful on multiple occasions, it prevents further study of natural recovery. Because natural re-colonization may take decades (Donald et al., 2001), annual monitoring following non-native fish removal, and maintenance of long-term datasets, are necessary for studying invertebrate taxonomic resilience/recovery.

Protection of native fish species

Historic introduction of non-native fish has also had a profound effect on native fish populations (Schindler, 2000). There are two native species of salmonids that currently inhabit aquatic systems in Banff National Park (Westslope Cutthroat Trout, *Oncorhychus clarkii* and Bull Trout, *Salvelinus confluentus*). Westslope Cutthroat Trout are currently listed as “Threatened” under the Federal Species At Risk Act (SARA) implemented in 2004, and native Bull Trout have been displaced by introduced Brook Trout, *Salvelinus fontinalis*, in many watersheds (Schindler, 2000). To prevent the loss of native fish species, management plans in the Parks (S. Humphries – personal communication; Parks Canada, 2010), and other regions in North America (Divens et al., 2000), focus on increasing their presence and abundance in natal systems. One way that aquatics managers have considered accomplishing this objective is by establishing "source populations" in headwater lakes (Wilhelm et al., 1999, S. Humphries – personal communication), some of which are naturally fishless. Although previous research has shown that native fish species may not have as detrimental an impact on native invertebrate communities as introduced fish species (Anderson, 1980; Wilhelm, 1999), this hypothesis has not been fully tested.

Further work is need to improve our understanding of the full range of ecological consequences and benefits of establishing native fish populations in mountain lakes where the native biota have never been subjected to fish presence. In cases where managers want to re-stock lakes that have historically held natural fish populations, but are unsure which lakes fit that criterion, sediment-core analysis may be useful in order to determine whether certain lakes have ever held fish (Lamontagne & Schindler, 1994). Finally, as the impacts of fish predation on native zooplankton communities likely depends on lake physical and morphological characteristics (Anderson, 1980; Donald et al., 1994), such factors should be taken into account when establishing source populations of native fish species, in order to prevent the loss of native invertebrate biodiversity.

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