Interpreting Impacts of Introduced Trout Populations in Mountain Lakes

in the Era of Ecological Restoration

Queenie Z. Gray

A thesis

In the Department

of

Biology

Presented in Partial Fulfillment of the Requirements

For the Degree of Master of Science (Biology) at

Concordia University

Montréal, Québec, Canada

March 2013

CONCORDIA UNIVERSITY

School of Graduate Studies

This is to certify that the thesis prepared

By: Queenie Z. Gray

Entitled: Interpreting Impacts of Exotic Trout Populations on Mountain Lakes
            in the Era of Ecological Restoration

and submitted in partial fulfillment of the requirements for the degree of

Master of Science (Biology)

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Signed by the final examining Committee:

Salvadurai Dayanadan   Chair

David Walsh   Examiner

Robert Weladji   Examiner

Dylan Fraser   Supervisor

James Grant   Supervisor

Approved by   Patrick Gulick
            Chair of Department or Graduate Program Director

            Brian Lewis
            Dean of Faculty

            March 4, 2013
            Date

ABSTRACT

Stocking exotic trout species in high mountain lakes was a common practice in Rocky Mountain Lakes in the 20th century. Currently, restoration action to remove trout populations favours the conservation of native food webs. Meanwhile, little is known about the self-sustaining trout populations, particularly in our study area. We assessed impacts of stocking trout on naturally fishless foodwebs of mountain lakes. Results were applied to management goals in Waterton Lakes National Park. A comparison of mean abundances of zooplankton in fish and fishless lakes revealed differences in less than half the taxa encountered. Principle component analysis did not show an association between zooplankton community structure and fish presence. Paleolimnological analyses suggested an increase in relative abundance of large-bodied cladocerans, but statistical power was low. The results show the importance of identifying explicit restoration objectives because impacts may not be compelling. If restoration by trout eradication is pursued, demographic characteristics can aid in selecting which populations are more easily depleted by gillnetting. We used generalized linear models to examine four population characteristics associated with population decline: 1) catch per unit effort (CPUE), 2) proportion of females, 3) proportion of mature individuals and 4) length of mature individuals. There were significant differences between populations in CPUE and length at maturity, but not on the proportion of females or mature individuals. We thus incorporated the former characteristics into a basic assessment system and ranked the 11 salmonid populations by their susceptibility to eradication. We presented a simple yet meaningful step in facilitating management actions commonly constrained by a lack of biological knowledge.

ACKNOWLEDGEMENTS

CONTRIBUTIONS OF AUTHORS

The principal author of this study, Queenie Gray, performed the research, statistical analyses and writing for this project, with advice in regards to statistical tests and writing from Dylan Fraser, James Grant and Irene Gregory-Eaves. Cameron Goater provided the zooplankton data employed in chapter 1.

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GENERAL INTRODUCTION

Ecological restoration, aimed at repairing losses of native ecosystems due to anthropogenic disturbances, is an important component of current conservation efforts. Restoration differs from other conservation practices in that it requires the selection of a reference ecosystem as a target outcome. Yet, scientific attention directed towards at-risk species is not evenly distributed; listed aquatic invertebrates are ~1% as well studied as typical vertebrates (Strayer, 1996). This study explores the formation of restoration decisions in invertebrate-dominated aquatic ecosystems.

High mountain lakes in western North America were commonly fishless, with faunal assemblages consisting of various invertebrate phyla. However, thorough and intense stocking with trout species has potentially left few examples of intact original food webs (Donald 1987; Bahls 1992). Though stocking has ceased in most regions, many fish populations have persisted (Armstrong *et al.,* 2003). Hence, the restoration of mountain lakes to reverse past management practices has emerged as a current theme in aquatic conservation. Fish removal projects are or have been conducted in national parks in California, Montana, Wyoming and Alberta. Nevertheless, specific science-based goals that define the future state of the ecosystem are difficult to quantify in remote, aquatic ecosystems that lack an apex predator.

Waterton Lakes National Park (WLNP) (Alberta, Canada) provides an ideal landscape to determine ecosystem impacts of introduced trout. All 22 high mountain lakes were stocked in the 20th century, but fish populations remain in only 13 lakes, allowing comparisons of food webs with and without exotic trout. These trout populations have not been monitored since 1975 (Anderson & Donald 1976), and zooplankton data have not been analyzed since that time.

Comparisons of zooplankton communities have frequently been used to study the impacts of introduced trout, resulting in the prevailing dogma that these planktivorous fish shift zooplankton communities towards smaller-bodied taxa (Schindler & Parker, 2002; Eby *et al.,* 2006). Yet the direct application of such findings to restoration decisions requiring the removal of introduced trout populations has rarely been discussed in the literature.

If impact studies implicate restoration, the question of which populations to remove should be addressed by integrating physical lake characteristics, lake accessibility, management goals and fish population demographic characteristics. The latter can be hard to measure thereby limiting management action. Certain demographic characteristics, such as population size, age at maturity, and the proportion of reproducing individuals have been applied by conservation theory to predict a population's extinction risk. In the case of exotic populations, these characteristics can be applied to identify which populations may be more easily eradicated, if they vary across populations. Knowledge of demographic characteristics of introduced trout populations is hence important in selecting populations for eradication.

In the first chapter, I will assess the impact of introduced trout populations on zooplankton communities in WLNP, using spatial and temporal comparisons of fish and fishless conditions. The second chapter will address the next logical step in the restoration of invaded systems, *i.e.* selecting the most suitable exotic populations to eradicate. Together, the chapters are intended to provide necessary biological information to advance management of invaded systems, using WLNP as a model.

CHAPTER 1:

IMPACTS OF INTRODUCED TROUT ON ZOOPLANKTON COMMUNITIES

OF MOUNTAIN LAKES: RESTORATION OR LAISSEZ-FAIRE?

Queenie Z. Gray[1], Dylan J. Fraser[2], James Grant[3], Irene Gregory-Eaves[4], Cameron

Goater[5]

1 Concordia University, Montréal, QC Canada, qzgray@hotmail.com
2 Concordia University, Montréal, QC Canada, Dylan.Fraser@Concordia.ca
3 Concordia University, Montréal, QC Canada, James.Grant@Concordia.ca
4 McGill University, Montréal, QC Canada, irene.gregory-eaves@mcgill.ca

5 University of Lethbridge, Lethbridge, AB Canada, cam.goater@uleth.ca

ABSTRACT

Restoration of high mountain lakes following decades of stocking with exotic trout species is a current practice in conservation biology. Several studies had previously reported a shift towards smaller zooplankton species following trout introductions. We assessed the potential impacts of stocking in mountain lakes in Waterton Lakes National Park (WLNP), Canada, by a spatial comparison of zooplankton in 10 fish and 9 fishless lakes, and a temporal comparison of cladoceran subfossil remains in pre and post-stocking sediments in 6 lakes. No environmental variables, nor the taxonomic composition of zooplankton within lakes, were associated with fish versus fishless lakes. Although mean abundances of six out of 17 zooplankton taxa were statistically greater in lakes with fish, there was no difference in key taxonomic groups *Daphnia* and calanoid copepods. Lakes with fish also had greater overall mean zooplankton abundances and greater richness. Based on paleolimnological analyses, the introduction of fish explained only a modest, albeit significant (19%) amount of variation in zooplankton composition (inferred from cladoceran microfossils). However the dissimilarity of post-stocking to pre-stocking assemblages was not significantly different across fish and fishless lake classes. Results were applied to restoration goals identified by the Canadian government, with implications that: 1) the presence of a common exotic species does not imply that impacts are equal among affected systems, and 2) explicit restoration objectives should be specified, especially when results are not wholly supportive of restoration action.

INTRODUCTION

The overarching goal of ecosystem restoration for Parks Canada, the governmental

agency responsible for managing Canadian national parks, is to conserve ecological

integrity, a term applied to the condition of a natural and undisturbed system. This goal

can be assessed by quantifying: 1) changes in species richness, 2) the number and extent

of exotics, and, 3) changes in trophic structure, such as faunal size class distribution and

predation levels (Parks Canada and the Canadian Parks Council, 2008). Restoration

efforts were preceded by studies that outlined the trophic interactions within high

mountain lakes while giving evidence of impacts of trout generally supportive of theory

(Schindler & Parker, 2002; Eby *et al.,* 2006; Appendix 1). These studies posited that

planktivorous trout, which are visual foragers, reduce or eliminate large zooplankton

species through direct predation (Brooks & Dodson, 1965), resulting in a positive indirect

effect on small zooplankton and phytoplankton. This alternation of responses on

subsequent trophic levels follows classic trophic cascade theory (Carpenter *et al.,* 1985),

which has been extensively tested experimentally (Brett & Goldman, 1996). Yet the

application of trophic cascade theory to natural lake ecosystems has not been

demonstrated unequivocally (Drenner *et al.,* 2002). Furthermore, introduced trout species

vary in their degree of planktivory (Anderson *et al.,* 1980; Dawidowicz & Gliwicz, 1983;

Elser *et al.,* 1995) and this might dampen or amplify such cascades in mountain lakes.

Evidence of food web changes following trout introductions in natural lakes exists from

spatial and temporal comparisons, including paleolimnological approaches. First, studies

comparing zooplankton across fish and fishless lakes consistently report lower abundances of large, conspicuous taxa, such as calanoid copepods, when fish are present, and higher abundances of small, inconspicuous taxa, such as rotifers and small crustaceans (Bradford *et al.,* 1998; Knapp *& Sarnelle,* 2001; Donald *et al.,* 2001; Ellis *et al.,* 2002; Drouin & Sirois, 2009). Species assemblages were found to differ in composition in lakes with and without fish (Donald *et al.,* 2001; Drouin & Sirois, 2009). Second, temporal comparisons in alpine lakes corroborated spatial analyses: abundances of large crustacean species (*Hesperodiaptomus arcticus, Daphnia pulex*) decreased following trout introductions while smaller taxa such as rotifers increased (McNaught *et al.* 1999; Schindler & Parker, 2002). The species composition shifted as large species were sequentially replaced by increasingly smaller species. Recovery of altered zooplankton communities following trout introductions is known to take 10 to 20 years following the disappearance of trout populations in mountain lakes (Donald *et al.,* 2001; Knapp *& Sarnelle,* 2008). Finally, temporal comparisons through paleolimnological analyses of lake sediments before and after fish introductions, though less common, presented similar patterns. In oligotrophic lakes, smaller genera such as *Bosmina*, *Leydigii*, *Alona* and *Chydorus* were more abundant following establishment of fish populations (Brancelj *et al.,* 2000, Liu *et al.,* 2009).

Given the clear trends in existing publications, we hypothesized that trout affect the structure and composition of mountain lake ecosystems through size-specific predation of pelagic zooplankton taxa. Further predictions were: 1) abundances of large zooplankton taxa would decrease after fish introductions, 2) abundances of small zooplankton taxa

would increase, 3) taxonomic richness would decrease due to the elimination of large-bodied species, 4) body size would decrease through size-specific predation, and 5) an overall shift in community composition would occur.

This chapter tests these predictions in the high mountain lakes in Waterton Lakes National Park (WLNP), Alberta, Canada. Spatial comparisons of zooplankton characteristics across 10 trout-present and 9 trout-absent (hereafter referred to as "fish" or "fishless") lakes were supplemented by temporal analyses through a comparison of cladoceran crustacean microfossil abundances in pre- and post-stocking sediments. We then related our results to ecosystem integrity measures used to guide ecosystem restoration decisions. Thus, this study is an additional contribution to the literature on introduced predator impacts in aquatic ecosystems, but is distinguished by providing a direct link from theory to conservation practice, through multi-metric tests of changes in natural systems.

METHODS

Study Site and Design

WLNP (49.0458°N, 113.9153°W) protects 505 km^2 of the southern Canadian Rockies.

The weather is characteristic of mountain environments; the average snowfall is 481.5cm

per year and an average of 192 days per year have a minimum temperature above 0°C.

WLNP contains 22 high elevation lakes that range from 1524m to 2195m asl, of which

19 were contrasted in this study. Physical characteristics of the lakes are shown in Table

1.1. The lakes are representative of Rocky Mountain lakes in general, except WLNP

lakes are on average deeper (Figure 1.1). The period of trout stocking began in the 1920s

and ended in the 1980s, during which *Salvelinus fontinalis, Oncorhynchus clarki,* and

Oncorhynchus mykiss, were introduced. Currently, trout populations are self-sustaining in

12 lakes, 7 of which contain only *O. clarki,* 3 contain only *S. fontinalis,* 1 contains both

O. mykiss and *S. fontinalis,* and 1 contains only *O. mykiss.* The remaining 9 are devoid of

fish species. Study lakes were divided into two classes: fish and fish-less. Two fish lakes

(BE, AL) were excluded from further analyses because their depth or area was notably

greater than the rest of the lakes (Table 1.1) and their inclusion would render the classes

less comparable.

Data Collection

Due to the lack of historical ecosystem data, impacts of fish were assessed through two

means: (i) a spatial comparison of contemporary zooplankton composition across the two

lake classes, and (ii) a temporal comparison of cladoceran remains extracted from the tops and bottoms of sediment cores.

Lake physical characteristics and hydrochemistry – We first compared physical and chemical lake attributes between lake classes currently with and without fish to verify that classes were generally similar, so that meaningful comparisons of trout impacts could be drawn. Water chemistry measurements were taken in 2011 and 2012 using a YSI multi-meter. Lakes were visited twice each year during the ice-free season to measure temperature, specific conductivity (SC), Total Dissolved Solids (TDS), Dissolved Oxygen (DO) and pH of surface waters. At each visit in 2011, surface water samples were taken for nutrient analysis of total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC) and total dissolved solids (TDS). Morpho-edaphic index (MEI) was calculated as TDS divided by the maximum depth. Samples were kept cold until they could be refrigerated and sent to the Biogeochemical Analysis Service Laboratory at the University of Alberta (Edmonton, AB, Canada).

Contemporary Zooplankton – We compared zooplankton density, taxon richness and body lengths between fish and fishless lakes using the data from Barnes & Goater (2003, unpubl. data). Zooplankton were collected in the summer of 2003 by casting a standard zooplankton net (aperture size 165μm) into the lake and towing it horizontally towards shore. Up to four hauls were made in each lake, from north, south, east and west orientations. In the lab, 2mL subsamples were taken from each sample and the number of individuals of crustacean zooplankton and rotifera were counted and identified to the

finest resolution possible. Size information for copepod and cladoceran taxa, was collected by measuring the body length of a subset of the sample. Where possible, 50 individuals were counted for each lake, but smaller subsets were counted for less abundant taxa.

Historical Zooplankton – We compared relative abundances of cladoceran microfossils from two temporal periods using a paleolimnological approach. Surface sediment cores were successfully extracted from 12 study lakes in 2011 using a KB gravity corer with a tube diameter of 6.5cm. Cores were taken from the deepest basin of the lakes and extruded and sectioned in the field. The top 1cm of sediment represents the past *c.* 12 years, and was sectioned into four 25mm intervals, which was repeated every 5cm downcore. The bottom-most 1cm interval was used to represent the pre-stocking species assemblages. Chronology for one lake (LO) was obtained from ^{210}Pb isotope decay of freeze-dried sediments (Stewart*,* 2012, unpubl. data), measured with a Canberra Well-Detector Gamma-ray Spectrometer (Canberra, Meriden, CT, U.S.A.) and the constant rate of supply model (Appleby, 2001). In LO, sediments formed at a mean rate of 0.85mm per year, consistent with published sedimentation rates for high elevation lakes. The comparison of cladoceran microfossils was based on the assumption that the bottom sediments were formed previous to the initial introduction of trout. Sedimentation rates reported for Rocky Mountain lakes in several regions ranged from 0.5 to 2.5mm per year (Lamontagne & Schindler, 1994, Leavitt *et al.,* 1994, Knapp & Sarnelle, 2008, Wolfe *et al.*, 2001). We thus estimated that a sediment sample deeper than 10cm in a profundal

core was more than 100 years ago. Stocking commenced in the 1920s, so we extracted cores at least 10cm in depth.

Cladocera exoskeletons preserve in the sedimentary record and can be utilized in paleolimnological analyses (Korhola & Rautio, 2001). Microfossil remains were extracted from the top and bottom sediment samples following standard methods (Korhola & Rautio, 2001; Velghe *et al.,* 2012). First, 0.1 g of freeze-dried sediment was mixed with 50mL of 10% KOH and heated to 70°C for 30 minutes. Next, 5mL of HCL was added to neutralize the solution and the suspension was washed through a 38μm sieve then transferred to a 15mL centrifuge. Two 0.05mL drops of the slurry were then pipetted onto opposite ends of a slide and set using a safranin-glycerine jelly. We concentrated sediment samples by heating slides to reduce water content, and then added more slurry. Cladocera body parts (headshields, carapaces and post-abdomens) were identified using standard references (Frey 1959, 1960, 1962, 1980; Goulden & Frey, 1963; Chengalath & Hann, 1981; Sweetman & Smol, 2006; and Szeroczyn´ ska & Sarmaja-Korjonen, 2007). Slides were prepared and counted until a minimum of 40 individuals was obtained for each interval. Although generally larger count sizes are recommended (*i.e.* greater than 70 individuals), smaller counts of individuals are acceptable for low diversity samples (Kurek *et al*., 2010).

Statistical Analyses

Contemporary Zooplankton - Zooplankton characters selected for analyses were: density by taxonomic group, average taxonomic length, and taxonomic richness by lake. These

measures were averaged for fish and fishless lakes, then compared by Welch's Two-Sample T-Tests or Wilcoxon Rank Sum Tests, depending on whether or not normality of distributions was fulfilled. As a supplementary analysis, Principal Component Analyses (PCA) were used to show associations between lakes, fish or fishless lake class, zooplankton taxonomic composition, and environmental characteristics.

Historical Zooplankton - Counts from the tops and bottoms of sediment cores were converted to relative abundances then Hellinger-transformed to reduce the importance of large abundances (Legendre & Gallagher, 2001). Initially, a PCA was run on the transformed abundances. The results justified subsequent analyses using constrained methods to isolate the affect of fish. Significance was tested using a randomization procedure that permutes all possible values of the test statistic (pseudo-*F*) under rearranged labels for the observations.

RESULTS

Lake Physio-chemistry

Mann-Whitney tests showed that fish lakes did not differ significantly from fishless lakes in terms of maximum depth and elevation (W=21.5, p=0.060; t(16.78)=0.90, p=0.38) but were larger in area (W(11.4)=16.5, p=0.02, Figure 1.2). Lake classes were found to be similar in all chemical characteristics by t-tests and Mann-Whitney tests (Figure 1.2). Similar distributions of fish and fishless lakes around environmental gradients were observed in the PCA ordination (Figure 1.3a). Thus, overall, further comparisons of biological data across fish and fishless lake classes were deemed suitable.

Contemporary Zooplankton

The overall mean density of zooplankton was higher in the fishless lake class (W(219.1)=10749, p=0.0013), although few differences were found among the 17 taxonomic groups encountered (Figure 1.4). Fish lakes had significantly higher mean densities of copepod nauplii larvae, and the rotifer *Kellicottia* (W(9.8)=12.5, p=0.0073 and W(9)=6.5, p=0.0016, respectively). As well, two cladoceran taxa were exclusively present in fish lakes: Harpaticoida and Macrothricidae (Figure 1.4). Fishless lakes were not found to contain any taxonomic group in higher abundance than fish lakes, although one species of rotifer, *Keratella hiemalis* was unique to this class. Zooplankton richness was higher in fish lakes (t(18)=-2.69, p=0.016), however Shannon diversity did not differ (t(16.2)=-1.69, p=0.11), meaning that the evenness of individuals across taxa was similar between the two classes. Body lengths of calanoid copepods were on average smaller in

fish lakes, while cyclopoid copepods and *Daphnia* were larger in fish lakes, although no statistical significance was detected.

PCA revealed that communities were dominated either by calanoida, cyclopoida or rotifera (Figure 1.3b). The first PC axis (PC1) explained 44% of the variance in the dataset and is negatively associated with cyclopoid copepods; PC2 explained 31% of the variance and distinguished calanoid copepod dominance from rotifer dominance. The remaining taxonomic groups had little weight in the overall composition. Considering the distribution of samples scores from fish and fishless lakes, no obvious community patterns were evident from the PCA.

Historical Zooplankton

Cladoceran microfossils were counted and identified for four lakes with fish (LO, AK, CL, CR) and two fish-less lakes (RU and RL). Sufficient counts could not be made for the remainder of the cores due to extremely low microfossil concentrations. A total of 22 littoral and pelagic cladoceran taxa, including species groups, were identified in the top and bottom sediments (Figure 1.5).

Overall, the subfossil assemblage analyses show that fish and fishless lakes differed in zooplankton composition prior to the introduction of fish (Figure 1.5), but that fish lakes experienced greater, albeit statistically non-significant changes (M= 0.720, SD=0.269) than the fishless lakes (M=0.457, SD=0.273; t(2.04)=1.11, p=0.38), based on Bray-Curtis distances (Figure 1.6). Changes in cladoceran assemblages due to fish were inferred from

the PCA on microfossil abundance data (Appendix 2). The first two PCs explained 40%

and 21% of the variation in the microfossil dataset, respectively. Species with high

loadings on the first component were *Alona rectangula* (0.76), *B. longispina* (-0.42), and

Bosmina spp (-0.30). The second component was associated with *Daphnia pulex* (0.48)

and *Chydorus cf sphaericus* (-0.32). Thus, both components represented gradients from

pelagic types (*Bosmina* and *Daphnia*) to littoral chydoridae species (*Chydorus* and

Alona).

PC1 divided currently fishless lakes from fish lakes while PC2 was associated with

temporal changes in the fish lakes. The two fishless lakes RL and RU were closely

associated and *A. rectangula* was the dominant taxon throughout all intervals. In contrast,

pelagic taxa were present but varied in relative abundances across the lakes with fish

present (Figure 1.7). Additionally, fishless lakes appeared to be less homogenous in their

distribution in ordinal space, but when mean Bray-Curtis distances were tested across

lake type, the larger distance observed in fish lakes was not significant (p=0.38, Figure

1.6).

The proximity of RL and RU top and bottom sediments suggested recovery of native

faunal assemblages after the disappearance of fish populations (Figure 1.7). Changes in

assemblages in fish lakes were evident on PC2. Two fish lakes, CR and LO shifted

upward on PC2, towards higher importance of *Daphnia* species and lesser importance of

Chydorus species. These two lakes showed little horizontal change along PC1, suggesting

that *Alona* and *Bosmina* species were not affected by trout. AK did show a small

horizontal shift towards *Bosmina* species, as well as a minor shift towards Daphnia

species. CL had a bottom assemblage characteristic of the currently fishless lakes (*Alona*-

dominated), but the top assemblage was more characteristic of lakes containing fish

(*Bosmina* and *Chydorus*-dominated).

Overall, no true change from the original composition was detected by paired sign tests

on site scores (Table 1.2), though statistical power was low due to a small sample size.

Three of the four fish lakes shifted upwards on PC2 from *Chydorus* species inhabiting the

littoral zone towards a pelagic species, *Daphnia*. All lakes shifted slightly along the PC1.

A power test on the PC1 scores showed that a sample size of 13 paired samples (top and

bottom sediments) would have been needed to obtain t-test results at a significance level

of 0.05.

The effect of fish presence was tested as a constrained variable in a RDA (Figure 1.7), in

which all bottom sediments, as well as top sediments of fishless lakes were assigned a

fishless designation. Fish presence was a significant factor in the variance in cladoceran

assemblages (p=0.03), explaining 19.4% of the total variance. Fish and fishless lakes

were divided along a gradient of *Bosmina*-dominance to *A. rectangula*-dominance. One

key exception to this trend is the surface sediment from Lone Lake (LO-T), which

appeared to be associated with Daphnia. However, our stratigraphic analysis (Figure 1.5)

clearly shows that although both Daphnia taxa are present in the bottom sediments, their

relative abundances are only a fraction of what they were in the modern sediments.

DISCUSSION

Our results do not show marked differences between current and target ecosystems that typically drive restoration. According to Parks Canada, the target ecosystem is one that maintains ecosystem integrity, which is assessed by species richness, the presence of exotics and changes in trophic structure (Parks Canada and the Canadian Parks Council, 2008). Overall, we have found that natural variability across mountain lakes in WLNP has probably maintained the ecological integrity on the landscape scale by varying the impacts of introduced trout.

The predictions regarding fish impacts on zooplankton were only moderately supported. The linked predictions that larger taxa of zooplankton would be more abundant in the fishless state and that smaller taxa would be more abundant in the fish state were partially confirmed, but not across all measures. Abundances of nauplii and one rotifer, both smaller taxa, followed predictions of the trophic cascade theory, but cladocerans such as Daphnia, copepods and other taxa did not. Richness was enhanced in the presence of fish, but body size was not. Overall composition of zooplankton communities was not different in the spatial analyses, but appeared to change over time.

An unexpected finding was the degree to which lakes vary, independent of the presence of introduced trout. Variation was evident in lake morphology and chemistry (Figure 1.3a and Table 1.1), contemporary zooplankton (Figure 1.3b), historical zooplankton (Figure 1.7) and benthic macroinvertebrates. Considering widely variable food web composition, the impact of trout is likely dependent on the specific structure of each lake (Winder *et*

al., 2003). Hence, different impacts on native taxa across multiple lakes are expected to be antagonistic and result in muted overall impacts. Variation within a small geographical region indicates that temporal analyses may be more appropriate to identify anthropogenic impacts than a spatial comparison (Velghe *et al.,* 2012).

In mountain lakes, trout are generalists that prey on benthic invertebrates such as chaoborids and *Gammarus*, as well as large zooplankton such as daphnia and copepods (Schindler *et al.,* 2002;Vander Zanden & Vadeboncoeur*,* 2002). We found evidence that trout diet in WLNP mountain lakes consists largely of adult and larval stages of terrestrial and aquatic insect species, through an analysis of stomach contents (Appendix 3). The analysis showed that trout fed intensively on a food type when it was available, but was not restricted to any one prey item. Carpenter *et al.* (1985) reported that, if other prey is unavailable, trout will exert stronger pressure on zooplankton, but otherwise, lake-dwelling trout are not known to be effective planktivores when compared to invertebrates such as *Gammarus*. Therefore, the higher abundances of smaller zooplankton we observed, may have been due to trout predation on native zooplanktivores, such as calanoid copepods. The resulting shift to smaller-bodied zooplankton taxa is a common finding in the literature (Bradford *et al.,* 1998; Knapp & Sarnelle*,* 2001; Donald *et al.* 2001; Ellis *et al.,* 2002).

However, in lakes not dominated by calanoid copepods, trout likely reduced a more effective, native planktivore through predation or competition for resources. In our study lakes as well as other lakes (Carpenter *et al.,* 1985), *Gammarus lacustris*, an amphipod,

was found to be an important structural component to mountain lake ecosystems.

Weidman *et al.* (2011) showed that trout reduce predation by *Gammarus* on benthic

invertebrates and integrate pelagic and benthic zones. Likewise, lower *Gammarus*

densities could also relieve predation on large herbivores such as Daphnia (Schindler &

Parker*,* 2002), which is consistent with the shift towards this species inferred from our

paleolimnological analyses. The alleviation of predation is also consistent with the

suggestion that trout increased the richness of small taxa (rotifera), possibly due to

increased phytoplankton availability when larger-bodied Daphnia are reduced by

Gammarus. A similar increase in richness has been reported by Donald et al (2001) in

other Canadian mountain parks.

Fish can also affect oligotrophic lakes by bottom-up processes, namely nutrient

enrichment, rather than top-down predation (Simon & Townsend, 2003). Yet, the effect is

debatable, as some research suggests that benthic invertebrates such as *Gammarus*, not

fish, increase nutrient levels, resulting in higher concentrations in lakes without fish

(Willhelm *et al.,* 1999; Weidman *et al.,* 2011). Whether the mechanism is top down,

bottom up, or both, fish can cause taxonomic size shifts in zooplankton communities by

replacing native planktivorous predators. However, the direction of the resulting shift is

dependent on food web structure, and variation therein has likely masked the resulting

changes on the landscape scale.

Alternatively, the weak support for impacts induced by trout stocking in WLNP could

simply be attributed to a lack of significant predation or competition on native food web

components. That is, the difference in predation pressure between natural, non-fish predators and introduced trout may be negligible. As previously discussed, trout have been shown to feed across many taxa as well as across trophic levels, resulting in a muted impact on any particular prey item. In addition, their utilization of renewable, allochthonous pathways minimizes impacts on aquatic, and certainly pelagic prey. This is consistent with Winder *et al.* (2003), who found that *Daphnia galeata* was not affected by trout due to the dominance of adult trout that feed mainly on benthic prey, not pelagic. We have found that mature trout in WLNP mountain lakes comprise the majority of individuals within populations, and that natural recruitment of juveniles is likely much lower than artificial recruitment during the period of stocking. Therefore, zooplankton species that were able to survive this period probably do not continue to experience intense levels of trout predation. Calanoid copepods may also have been able to survive the period of fish stocking by dormancy. Resting eggs are produced under suboptimal conditions such as high predation and cannibalism (Santer, 1998), when environmental conditions become favourable again they are able to re-colonize the lake. We also found that trout density (CPUE) varied up to five-fold across the fish lakes (Figure 2.1a), indicating that the intensity of predation by trout in the lower density lakes may have been insignificant.

The intensity of trout predation can also be dissipated by predator evasion. For example, morphological adaptations to predation stress were observed in *Daphnia*, such as variation in body shape, size and caudal spine length (Ranta *et al.,* 1993; Lampert, 1993). Behavioural predator evasion was seen in *Hesperodiaptomus* species that migrated along

vertical gradients to avoid diurnal periods of intense feeding by trout (Drenner &
Hambright, 2002). Predator evasion can be further facilitated through habitat complexity,
which offers refuge to prey species (Diehl, 1992; Warfe & Barmuta, 2004). Top-down
predation was accordingly found to be more important in shallow lakes than deep lakes
(Jeppesen *et al*., 1997). These mechanisms of predator evasion could explain reduced
predation levels in WLNP lakes.

A final explanation for the lack of impacts by trout is environmental control of food
webs. Oligotrophic systems can be limited by nutrient availability, rather than top-down
predation, blocking the potential trophic cascade by invaders (Simon & Townsend,
2003). As well, lakes in WLNP may have been buffered from the effects of trout by their
low water temperature and productivity. Recent work by Messner *et al.* (2013) revealed
that cold and clear Rocky Mountain lakes were relatively unaffected by *S. fontinalis*;
trout only stimulated increases in zooplankton richness and biomass in warmer lakes
(>10°C mean summer temperature). Furthermore, zooplankton species turnover and thus
community composition, was also primarily driven by DOC and warmer lake
temperatures.

Caveats and Study Limitations

We feel that two limitations of our research are notable to consider. First, the data used
for the comparative analyses represent "snap shots" of dynamic ecosystems. Zooplankton
abundances are known to fluctuate seasonally and annually, though we tried to
compensate by using sediments that represent an accumulation of multiple years. Second,

a low number of cores was used in the paleolimnological analysis, which limited the statistical power of the results. However, extremely low cladoceran remains may not be unique to this study (Drake & Naiman, 2002). We were unable to reach the recommended number of samples (*i.e.* three times the number of species represented in the data) to properly use eigenvalue tests to detect patterns in PCA's of assemblage structure data (Grossman *et al.,* 1991). We determined that twice as many lakes would need to be cored in order to obtain a sample size capable of yielding significant results.

Implications

Our results have notable implications for the restoration of mountain lake ecosystems. We saw opposing assessments of ecological integrity depending on the criteria measured, that is: 1) species richness was enhanced following fish introductions, 2) introduced trout were the only exotic species encountered, and 3) no changes in trophic structure were seen, although the composition of species was marginally changed. If reduced taxonomic richness or changes in trophic structure and function are the more important criteria, restoration by trout removal is not recommended. On the other hand, if ecosystem impairment is assessed by the mere presence of an exotic species or slight shifts in native composition, then restoration of stocked mountain lakes is in order. WLNP managers should weigh the conservation benefits of removing exotics from ecosystems that are otherwise functionally intact with the costs of intensive restoration efforts. This study demonstrates the importance of stating clear restoration goals based on in-depth knowledge of the specific ecosystem, prior to forming decisions to restore.

Figure 1.1: Boxplots of physical and chemical lake characteristics of Rocky Mountain

Lakes (R) and WLNP Lakes (W), showing median, 25% and 75% quantiles, maximums

and minimums; data from Anderson, 1975. Depth was significantly greater in WLNP

lakes (p=0.01).

Figure 1.2: Boxplots of physical and chemical lake characteristics for fish (Y) and

fishless (N) lakes, showing median, 25% and 75% quantiles, maximums and minimums.

Area was significantly greater in fish lakes (p=0.02).

Figure 1.3: Biplots of first two principle components extracted from a) physical and chemical lake characteristics, and b) zooplankton taxa, of 19 study lakes. Lake codes as per table1; circled text denotes lakes with fish.

Figure 1.4: Mean densities (± standard errors, SE) of zooplankton taxa in mountain lakes of WLNP (after log transformation of densities plus one). Black bars are fishless lakes, grey bars are lakes with fish. Numbers after each taxon name represent the number of fishless lakes and fish lakes represented, respectively. Dotted lines separate broader taxonomic groups; *p<0.05 and **p<0.005.

Figure 1.5: Stratigraph showing relative abundances of cladoceran microfossil remains in bottom (black bar) and top (white bar) sediments for six lakes for a) *Alona spp*, b) *Chydorus* – type species and c) the pelagic species *Bosmina* and *Daphnia*.

Figure 1.6: Bray-Curtis distances of cladoceran zooplankton communities extracted from top and bottom sediments of the four lakes with fish (light grey), the two lakes without fish (dark grey), and the means (± standard errors, SE) of the two lake types (black).

Figure 1.7: Biplot based on the redundancy analysis of the cladoceran microfossil dataset constrained by the presence of fish. Sites that currently contain fish are circled.

Table 1.1: Physical characteristics of study lakes in WLNP, data from Anderson 1975. Horizontal line separates lake classes.

Watershed acronyms are as follows: CL=Cameron Lake, CC=Cameron Creek, UWL=Upper Waterton Lake, BB=Blakiston Brook,

BC=Bauerman Creek WBC = West Boundary Creek. Sampling codes describe types of sampling undertaken at each lake: F=fish, HC

= hydrochemistry, C = Coring, Cl = cladocera count.

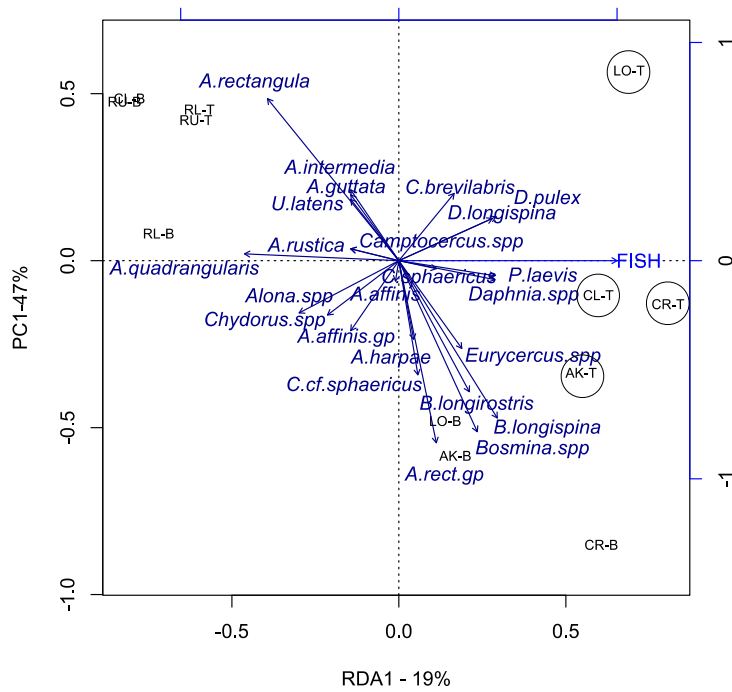| Lake	Code	Lattitude	Longitude	Elevation (m asl)	Mean Depth (m)	Max Depth (m)	Area (ha)	Watershed	Fish	Sampling
Crypt Pond	CP	49° 00' 85" N	113° 84' 70" W	1713	-	2	2.7	UWL	N	HC, C
Upper Carthew	CU	49° 02' 00" N	113° 59' 00" W	2195	5.9	13	4.35	CC	N	HC
Lineham South	LS	49° 05' 00" N	114° 04' 00" W	2165	8.2	17	5.78	CC	N	HC
Lost	LT	49° 09' 00" N	114° 09' 00" W	1875	3.9	12	1.57	BB	N	HC
Ruby	RB	49° 06' 00" N	114° 01' 00" W	2064	2.1	4.2	2.35	BB	N	HC, C
Lower Rowe	RL	49° 03' 00" N	114° 03' 00" W	1957	2.3	8	1.97	CC	N	HC, C
Middle Rowe	RM	49° 03' 00" N	114° 03' 00" W	2162	-	12	2.21	CC	N	HC
Upper Rowe	RU	49° 03' 00" N	114° 03' 00" W	2168	-	3	7.2	CC	N	HC, C
Summit	SU	49° 00' 00" N	114° 01' 00" W	1931	-	2	2.03	WBC	N	HC, C
Akamina	AK	49° 01' 00" N	114° 02' 00" W	1655	-	5	4.65	CL	Y	F, HC, C, Cl
Alderson*	AL	49° 02' 00" N	113° 59' 00" W	1811	21.5	60	10.19	CC	Y	F, HC
Bertha*	BE	49° 02' 00" N	113° 57' 00" W	1774	18.1	50.3	30.2	UWL	Y	F, HC
Lower Carthew	CL	49° 02' 00" N	113° 59' 00" W	2159	4.8	11	7.33	CC	Y	F, HC, C, Cl
Crandell	CR	49° 05' 00" N	113° 58' 00" W	1524	7.9	15.5	4.53	BB	Y	F, HC, C, Cl
Crypt	CT	49° 00' 00" N	113° 50' 00" W	1963	16.9	44	13.44	UWL	Y	F, HC
Goat	GO	49° 10' 00" N	114° 05' 00" W	1982	3.4	9.3	2.35	BC	Y	F, HC, C
Lineham Hourglass	LH	49° 05' 00" N	114° 04' 00" W	2111	10.4	23	12.64	CC	Y	F, HC
Lineham North	LN	49° 05' 00" N	114° 04' 00" W	2170	11.6	29	18.96	CC	Y	F, HC, C
Lone	LO	49° 05' 00" N	114° 07' 00" W	2027	5.4	13	2.53	BB	Y	F, HC, C, Cl
Lower Twin	TL	49° 08' 00" N	114° 09' 00" W	1927	3.6	8	2.72	BB	Y	F, HC, C
Upper Twin	TU	49° 08' 00" N	114° 09' 00" W	1963	5.1	13	6.44	BB	Y	F, HC, C

Table 1.2: Site scores for each lake on PC1 and PC2. The horizontal line separates fish lakes from fishless lakes. Only fish lakes were included in sign tests and no statistically significant results were obtained.

Lake	PC1 fish	PC1 no fish	ΔPC1	PC2 fish	PC2 no fish	ΔPC2
LO	-0.24920	-0.23720	-0.01200	1.19777	0.33283	0.86494
AK	-0.48430	-0.21500	-0.26930	-0.53287	-0.64127	0.10840
CR	-0.55000	-0.54640	-0.00360	0.30194	-0.03420	0.33614
CL	-0.38780	0.61860	-1.00640	-0.47708	0.03543	-0.51251
RL	0.51290	0.39500	0.11790	0.10677	-0.17576	0.28253
RU	0.52210	0.62140	-0.09930	-0.07226	-0.04129	-0.03097

CHAPTER 2:

DEMOGRAPHIC CHARACTERISTICS IDENTIFY SUSCEPTIBILITY OF

INTRODUCED TROUT POPULATIONS TO DEPLETION BY GILLNET FOR

MOUNTAIN LAKE RESTORATION

Queenie Gray[1], Dylan J. Fraser[2], James Grant[3]

1 Concordia University, Montréal, QC Canada, qzgray@hotmail.com
2 Concordia University, Montréal, QC Canada, Dylan.Fraser@Concordia.ca
3 Concordia University, Montréal, QC Canada, James.Grant@Concordia.ca

ABSTRACT

The introduction of fish to mountain lakes has created challenges for native invertebrate assemblages and resource managers who are faced with decisions on how to deal with disturbed aquatic ecosystems. While extensive research has illuminated the physical habitats and complex food webs of mountain lake ecosystems, little is known about the self-sustaining fish populations, particularly in our study area, Waterton Lakes National Park (WLNP), Canada. We used generalized linear mixed models to examine four population characteristics associated with the vulnerability of populations to depletion by gillnetting: 1) catch per unit effort (CPUE), 2) proportion of females, 3) proportion of mature individuals and 4) length of mature trout, as a proxy for age at maturity. There were significant differences between populations in CPUE and length of mature trout, but not in the proportion of females or mature individuals. We thus incorporated the former characteristics into a basic assessment system and ranked 11 salmonid populations by their susceptibility to eradication. The application of demographic characteristics to select introduced populations for eradication is a simple yet meaningful step in restoration commonly constrained by a lack of biological knowledge.

INTRODUCTION

The stocking of salmonid fishes into historically fishless mountain lakes of western North America was so widespread in the twentieth century that it created a landscape in which almost all lakes have been affected (Bahls, 1992). In waters where introduced fish populations have become self-sustaining, native, fishless ecosystems have been replaced with novel systems dominated by large planktivores. If ensuing impacts are severe, resource managers may decide to restore the native ecosystems by removing introduced salmonid populations. Here, we investigate variability in demographic characteristics across introduced salmonid populations in Waterton Lakes National Park (WLNP), AB, Canada, and apply our results to restoration decisions. The goal is to rank the lakes according to their suitability for restoration based on demographic characteristics that may render them more susceptible to depletion and ultimately extinction.

Gillnetting is a viable method of eradicating trout populations in mountain lakes, though success requires multiple years of netting, substantial resources and is constrained by lake morphology (Knapp & Matthews, 1998). Gillnets function by lethally entangling fish at the gills as they attempt to swim through the undetectable mesh. The successful removal of *S. fontinalis* from a small Sierra Nevada lake required 3679 net days over three years (Knapp & Matthews, 1998). Five additional lakes in Sierra Nevada were restored by gillnet from 1996 to 2003 (Vredenburg, 2004). The removal of the same species from Bighorn Lake in Banff required over 10,000 net nights over three years (Parker *et al.* 2001). Other trout-removal projects occurred in the Devon Lakes system in Banff

National Park and an additional six lakes in Sierra Nevada, (Pacas, 2010, pers. comm.; Knapp *et al.*, 2007); both spanned multiple years. Gillnets have also been used effectively to suppress trout population density in several mountain lakes under intense netting regimes (Gresswell, 2009; Rosenthal *et al.,* 2012). Despite the sheer effort required, gillnetting is typically preferred over the application of piscicides such as rotenone, which have lethal affects on invertebrates and can prolong time to recovery (Anderson, 1970). Gillnetting, in contrast, has little to no impact on non-target species.

Given the substantial effort required to reduce fish populations and the number of mountain lakes affected by trout introductions, a simple method of prioritizing lakes for management would facilitate restoration decisions. Indeed, ranking systems are widely used for invasive non-native plants for which numerous infestations of the same species exist, rendering management priorities, exacerbated by limited resources, difficult to assign (*e.g.* Pheloung *et al.,* 1999; Skurka Darin *et al.,* 2011). Knapp and Matthews reported that success of gillnetting in mountain lakes is dependent on lake depth, surface area, outlet width and area of stream spawning habitat (1998). Though the biota of mountain lakes remains relatively unstudied, physical morphometric characteristics are usually known. Hence, we are interested in quantifying trout biology characteristics that influence the susceptibility of populations to over-exploitation by gill net.

Conservation theory suggests that certain demographic characteristics increase a population's extinction risk, specifically population size, proportion of breeding females, age-at-maturity, and body size at maturity. These characteristics can be reversed to

identify exotic populations vulnerable to depletion. First, as the effect of demographic stochasticity is stronger on smaller populations (Lande, 1988), population size is also negatively associated with extinction risk. Second, the proportion of females in a population has a similar association, particularly in sexually-reproducing organisms where females limit reproduction rates, such as in some salmonids (Blanchfield & Ridgway, 1997). Third, age-at-maturity has been used to predict extinction risk across multiple taxa (Hutchings *et al.*, 2012), and is positively correlated with extinction risk in freshwater fishes (Anderson *et al.*, 2011). Marschall and Crowder (1996) found that average size and age-at-maturity affected brook trout population viability; populations reacted most negatively to factors that decreased the survival of large juveniles and small adults, and removing large mature individuals was not necessarily detrimental to the persistence of the population because brook trout can reproduce at a small size (1996). Finally, body size is also a factor in the efficiency of gillnets, since catchability generally increases with fish size (Jensen, 1995; Finstad *et al.* 2010; Borgstrøm *et al.,* 2012). Individuals that mature at a large body size are thus easier to remove than individuals that mature at a smaller body size.

We therefore examined variation in population density (in lieu of population estimates), the proportion of females and mature individuals in the population, and the length of mature individuals, as a proxy for age-at-maturity, across 11 previously stocked lakes in WLNP. We assumed that trout populations that are characterized by low density, few females, few mature individuals, and a large body size at maturation, would be more amenable to eradication by gillnet.

MATERIALS AND METHODS

Study Site

WNLP is home to 22 high elevation lakes that were stocked with salmonid species at different frequencies and intensities from the 1920s to the 1980s. Presently, 11 lakes retain trout populations that have become self-reproducing. Refer to Materials and Methods in Chapter 1 for further information on the study site (Table 1.1).

Data Collection

Trout populations - Trout populations in twelve mountain lakes were sampled, but two lakes were confirmed fishless. All lakes were sampled twice in the ice-free season, between July and September, 2011, except for Crypt lake (CT), which was sampled in July and August, 2012. Spring sampling occurred between June and July, summer sampling occurred in July and August. Multiple visits were made to quantify seasonal variation.

Between one and five monofilament gillnets were set in each lake depending on lake size (manufactured by Lundgrens Fiskredskapsfabrik AB, Stockholm, Sweden). The overnight bottom sets optimized periods of high trout activity and we aimed for a consistent net duration of 14 hours. Nets were 30m long, with five 6m panels of different mesh gauge (18.5mm, 25.0mm, 38.0mm, 43.0mm and 55.0mm), arranged sequentially. The nets were set perpendicular to the shoreline, with one end secured to a fixed feature on shore and the deep end anchored to the substrate. The orientation of the smallest mesh

was alternated equally between lake-end and shore-end to reduce bias towards fish size. Nets were spaced evenly around the perimeter of the lake and all shoreline types were covered as best as possible. Locations were marked using GPS.

In the morning, nets were collected from an inflatable raft. Fish were measured to the nearest millimetre, weighed to the nearest gram, identified to species, and assessed for sex and maturity. Sex and maturity were determined by dissecting each fish and observing gonads. Each fish was assigned a unique number; the corresponding mesh size and net was recorded. A subsample of the catch representing the range of sizes caught was sampled for stomach contents and age determination.

Statistical Analyses

We used generalized linear models (GLMs) to assess variation in the four demographic characteristics (density, length of mature individuals, proportion of females and proportion of mature individuals) across populations. The characteristics were calculated for each net, so each lake was represented by multiple datapoints. Catch per unit effort (CPUE) was used as a proxy for density and calculated as a ratio of number of individuals caught to duration of net set. Fork length of mature trout, a proxy for age-at-maturity, was the mean fork length of only the mature fish in the catch. Proportions were calculated as the number of female individuals and mature individuals divided by the total catch per net. CPUE and length data were normally distributed hence were modeled with a Gaussian distribution. Data for the proportion metrics were not normally distributed, so a binomial distribution was applied, weighted with the number of fish

caught. Explanatory variables other than population included in the model were fish species, sampling period, and their interaction. The Akaike Information Criterion (AIC; Akaike, 1973) was used to select among the ten models for each demographic characteristic; the lowest AIC value represents the most parsimonious model and models within 2 ΔAIC were ordered by the number of variables (Burnham & Anderson, 2002). All statistical analyses were performed in R Statistical Software (R Development Core Team, 2012).

Ranking Lakes for Trout Eradication

We used the above analysis of demographic characteristics to indicate suitable factors on which to rank populations for removal. Lakes were ranked from one to eleven for each characteristic applied, where one represents the condition of the population that is most amenable to eradication. Scores for each characteristic were summed for each lake, yielding a final ranking of lakes by their suitability for restoration.

RESULTS

Fifty nets were set in 12 lakes in 2011, plus an additional eight nets in the remaining lake (CT) in 2012. A total of 1369 trout were caught in ten of the lakes sampled. Two lakes yielded no fish. Three species were represented: *Oncorhynchus clarki* (Cutthroat trout), *Salvelinus fontinalis* (Brook trout), and *O. mykiss* (Rainbow trout). All lakes contained exclusively either *O. clarkii* or *S. fontinalis*, except Little Akamina Lake, in which a small number of *O. mykiss* were caught. No further analysis was done on this species. A combined total of 706 *S. fontinalis* were caught in CR, TU, TL and AK, while 649 *O.*

clarki were caught in LN, LH, CL, AL, GO, LO and CT (lake acronyms defined in Table 1.1). Gillnetting confirmed an absence of fish in LS and CU.

Demographic Characteristics of Trout Populations

We found that population was the most important variable explaining the variation in two demographic characteristics: CPUE and fork length of mature fish. For the GLMs based on CPUE data, the best-fit model included population and season and explained 83% of the variability in the dataset (Table 2.1; r^2=0.83, F(11,46), p<0.001). Removing the season variable revealed that the variation across populations was far more important than that across seasons (r^2=0.77, F(10,47)=15.43, p<0.005). CPUE was consistently higher in the spring than in the summer (Figure 2.1a). When averaged over season, CPUE ranged from 0.63 (LH) to 1.71 (CL), except in two lakes where CPUE was much higher (TU=2.49, TL=2.59; Figure 2.1a). Correlation analysis showed that CPUE was not affected by variable set durations (r(52)=0.060, t=0.45, *p*=0.7).

The model that best explained fork length of mature trout included only population as an explanatory variable (Table 2.1; $r^{2=}$0.81, F(10,47), p<0.001). Average values were distributed evenly across a range of 195.2mm (TU) to 292.2 (LN), but mature trout were far larger in CT (327.4mm; Figure 2.1b).

Variation across population was not evident in the remaining two demographic characteristics: the proportion of females and the proportion of mature trout (Table 2.1 and Figures 2.1c and d). GLMs revealed that the best model for both characteristics was

the null model, indicating that variation was also not evident across season or species (Table 2.1).

Ranking Lakes for Trout Eradication

Our ranking system identified two lakes, Lineham Hourglass (LH) and North Lineham (LN), as the most suitable for trout eradication by gillnet (Table 2.2). The evaluation employed CPUE and length of mature individuals at equal weights, as our GLMs suggested that population had a similarly strong influence on both. We excluded the proportion of females and mature individuals from the assessment because we found no evidence of significant variation across populations (Table 2.1). AL, LO, CT, CR and AK were the next highest-ranked lakes, followed by CL and GO. TU and TL were by far, the least appropriate lake for restoration by trout removal (Table 2.2).

DISCUSSION

Demographic Characteristics of Trout Populations

Our results indicated that variation in two demographic characteristics (CPUE and fork length of mature individuals) of WLNP trout populations was explained by population-level differences. These characteristics are therefore pertinent to the selection of introduced populations for removal in the event of lake restoration.

The finding that CPUE and fork length at maturity varied across populations was not unexpected given the substantial variation in lake morphometry (Table 1.1), chemistry (Figure 1.3b), and food web composition (zooplankton communities, Figure 1.3a)

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(Chapter 1). Stocking histories and fishing use also differed from lake to lake and are further sources of variation. Similar ranges in density ($<$0.1-6.8 fish hr^{-1} per 30.5m net) and mean lengths (11-56cm) were reported for *S. fontinalis* in 183 Rocky Mountain lakes in Wyoming, USA (Chamberlain & Hubert, 1996). Lacustrine populations in the eastern, native range also demonstrated impressive variation in CPUE and mean length (Lachance & Magnon, 1990; Quinn *et al.,* 1994; Magnan *et al.*, 2005).

The reported variation in these stocked populations was generally attributed to lake morphometrics (size and elevation of lake) and the density of other fishes (Chamberlain & Hubert, 1996), while fishing intensity, the density of competitors and community complexity explained variation in density in the native range (Lachance & Magnon, 1990; Quinn *et al.,* 1994; Magnan *et al.*, 2005). Growth rate of Alberta populations was related to amphipod abundance, productivity, water temperature and negatively related to elevation (Donald *et al.* 1980). Variation in the eastern distribution was explained by competitor biomass, community complexity, salmonid diversity and fishing intensity (Lachance & Magnon, 1990; Quinn *et al.,* 1994; Magnan *et al.*, 2005).

O. clarki populations display similar variation in CPUE and body length, but perhaps for different reasons. In the Bighorn Mountains of Wyoming, mean total length ranged from 220-425mm and density from 0.4-2.4 fish net^{-1} hour^{-1}, across 19 lakes (Bailey & Hubert, 2003). Unlike *S. fontinalis, O. clarki* mean length was not associated with environmental factors but with density and lake accessibility (Bailey & Hubert, 2003). Meanwhile, accessibility was the only factor associated with CPUE. In the absence of further studies

on lake populations, spatial variability in size at maturity was observed *O. clarki* in

Montana streams (110mm to 180mm, Downs *et al.,* 1997). Overall, the demographic

characteristics of density and length, of both *S. fontinalis* (in novel and native habitats)

and *O. clarki,* are spatially variable due to physical and chemical lake attributes, food

web composition, fishing intensity and the density of other fishes.

Though population explained most of the variation in WLNP trout density, season also

had an effect. Densities were consistently lower in the summer, which could be due to

decreased activity in the littoral zone during the later sampling period. During the period

of summer stratification, *O. clarki* reportedly avoid near-surface waters but are nearer to

the surface when lakes are mixed (spring and fall) (Nowak and Quinn, 2002; Baldwin *et

al*., 2002). A similar trend in WNLP's dimictic lakes could be expected to reduce the

efficiency of shoreline gillnet sets in the summer. Densities could also have been reduced

by efficient gillnetting in the spring sampling period, leaving reduced numbers of trout

vulnerable to gillnets in the summer.

The proportion of females or of mature individuals did not vary across populations.

Rather, our results suggested a high amount of variability within each lake, particularly

for the proportion of females (Figure 2.1c). Though the mean values for both species

were comparable to reports by Downs *et al.* (1997) and Meyer *et al.* (2003), they do not

describe the variation within each lake. Despite literature support for these factors

weighing heavily on extinction risk due to female-limited reproductive strategies

(Blanchfield & Ridgway, 1997), we did not find the proportion of females or of mature

individuals to be useful in predicting population decline. These factors were thus omitted from our ranking of populations for depletion.

Management Implications

For aforementioned reasons, only trout density and fork length of mature trout were used in a ranking system to distinguish populations with higher susceptibility to population depletion by gillnet. Similar assessment tools have been principally developed for invasive land plants, where ecological gains can be optimized by prioritizing populations for management action (*e.g.* Pheloung *et al.,* 1999; Skurka Darin *et al.,* 2011). The management of freshwater fishes has also recently benefited from modifications of such tools to aquatic invaders. For example, Copp *et al*. (2009) developed the Fish Invasiveness Scoring Kit (FISK) to distinguish potentially invasive and non-invasive species, which was used as a pre-assessment for the more instructive modular assessment tool by Britton *et al.* (2011). The latter incorporates species prioritization, population-level risk to receiving waters, management action impacts and costs of management actions, to assess introduced fish populations for management priority. Such systems are effective because they can be molded to fit the values of a particular region while retaining the structure needed to maintain transparent decision-making in governmental organizations. Even within the umbrella of national mandates, regions may value resources differently (*e.g.* angling value) and managers can assign higher weight to the criteria that have greater importance in their particular jurisdiction. A downfall to the majority of ranking systems is that they are impact-based, which is impractical in situations where impacts are equal across the landscape, such as WLNP. Fine-tuning

existing assessment tools to hone in on demographic differences that affect management action success will improve their practicality in these landscapes.

We were able to identify demographic characteristics that varied across introduced trout populations in WLNP, and to apply them to indicate populations that are most susceptible to eradication. Our cursory ranking system specifically identified Lineham Hourglass Lake (LH) and North Lineham Lake (LN) as top candidates for trout depletion, based on demographic characteristics that had not previously been measured in WLNP. These lakes have a similar combination high density and low size of mature trout. They also represent similar points on environmental gradients including elevation, lake depth, lake area (Figure 1.1, Table 1.1), and accessibility. Though these lakes may contain the best populations to deplete base on biological characteristics, they are remote and difficult to access by foot and helicopter. The safest route to access LH and LN is via an 8km trail over a ridge, followed by a few kilometres of steep off-trail terrain. Unsurprisingly, these lakes receive low visitor use and fishing pressure, but are highly valued as representations of undisturbed ecosystems. Thus, further manipulation of the Lineham Lakes basin may be opposed by conservationists and backcountry users. Nevertheless, the results suggest that human and physical considerations could supersede biological factors when selecting lakes for restoration. The responsibility of resource managers to uphold regional values when making management decisions is facilitated by ranking systems such as that presented in this study, and by the provision of hard-to-measure biological data.

Ironically, this study concurrently instructs trout eradication and conservation. That is, we have found support of intraspecific diversity in exotic populations, which can be considered as biodiversity (Fraser & Bernatchez, 2001), particularly in western North American freshwater habitats depauperate of native fish fauna (Keeley *et al.* 2005). If restoration is not pursued, the population characteristics investigated in this study are still valuable for the management and continued monitoring of high mountain lakes.

Table 2.1. Results of two factor generalized linear models (GLMs) to assess the importance of population, season, species and the interaction of season and species on the variability of four demographic characteristics (CPUE, fork length of mature individuals, proportion of females and proportion of immature individuals).

Variable	Rank	Population	Season	Species	Interaction	AIC
CPUE	1	x	x			43.25
	2	x	x	x		43.25
	3	x	x	x	x	44.87
	4	x		x		58.59
	5	x				58.59
	6		x	x		109.17
	7		x	x	x	110.81
	8			x		110.89
	9		x			121.82
	10					122.95
Fork Length at Maturity	1	x				533.19
	2	x		x		533.19
	3	x	x			535.13
	4	x	x	x		535.13
	5	x	x	x	x	536.45
	6			x		590.21
	7		x	x		592.02
	8		x	x	x	593.6
	9					608.27
	10		x			610.18
Proportion Female	1					77.04
	2		x			77.56
	3			x		77.99
	4		x	x		78.55
	5		x	x	x	80.71
	6	x		x		88.41
	7	x				88.41
	8	x	x			89.24
	9	x	x	x		89.24
	10	x	x	x	x	91.4
Proportion Mature	1					19.17
	2			x		21.19
	3		x			21.22
	4		x	x		23.23
	5		x	x	x	25.37
	6	x		x		39.83
	7	x				39.83
	8	x	x			41.93
	9	x	x	x		41.93
	10	x	x	x	x	44.14

Table 2.2. Ranking of 11 previously stocked WLNP lakes by susceptibility, based on demographic characteristics CPUE and fork length of mature trout (FLM). Lake codes as per Table 1.1.

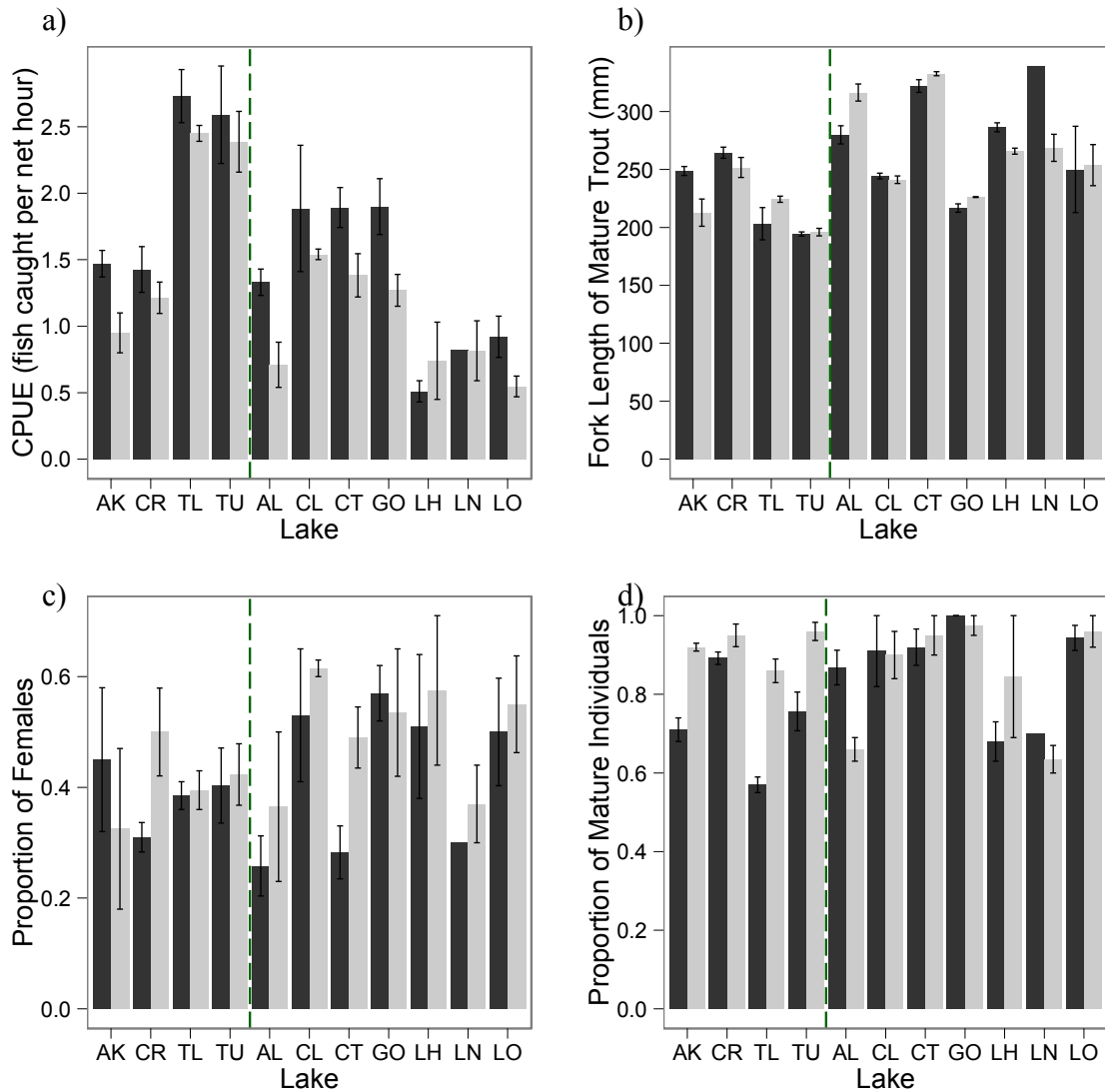| Code	CPUE	FLM	Total	Rank
AK	5	8	13	6
AL	4	3	7	2
CL	9	7	16	7
CR	6	5	11	5
CT	8	1	9	4
GO	7	9	16	7
LH	**1**	**4**	**5**	**1**
LN	**3**	**2**	**5**	**1**
LO	2	6	8	3
TL	11	10	21	8
TU	10	11	21	8

Figure 2.1. Mean values (± standard error, SE) of four demographic characteristics for eleven trout populations in WLNP. Lake codes as per Table 1.1. Dark grey bars represent spring data, light grey bars represent summer data. Dashed line divides *S. fontinalis* (left) from *O. clarki* (right). Only one net was cast in the spring in LN, so standard error could not be calculated.

GENERAL CONCLUSIONS

The management of mountain lakes with introduced trout populations is not clear-cut in the current era of ecological restoration. The impacts of trout are not easily understood because of the variability of mountain lake food webs, which can diminish their net effects on the landscape scale. Using spatial comparisons to identify differences between impacted and reference conditions may not be as informative as using temporal comparisons that detect changes in a particular system. However, long-term data of remote aquatic ecosystems is rare and paleolimnological techniques are not always applicable in mountain lakes. Cladoceran micro-fossil remains can be used effectively, but not consistently. To add further ambiguity, measures of community change may be contradictory; the presence of introduced species may implicate restoration while species richness or changes in trophic structure may implicate the maintenance of the current condition.

Further study on the role that introduced trout play in the novel ecosystem will further assist managers to decide their fate. Though trout may reduce densities of certain taxonomic groups of zooplankton, they can be a link in a food web connecting species that have higher conservation value, such as bears, birds of prey, piscivorous ducks, and otters. They may also be vectors of pathogens such as parasitic acanthocephalons. Exploration of reliable paleolimnological techniques for mountain lakes could also provide answers to questions regarding precise community shifts within a specific lake.

When managers decide that substantial change has occurred that requires restoration action, deciding where to direct limited resources becomes the next logical step, especially when restoration means extinguishing a population. Though many factors come into play relating to physical, environmental and human variables, the limiting factor is often the lack of biological information. Identifying demographic characteristics that are variable across the landscape allows managers to select and rank populations according to their suitability for depletion based on those characteristics. Future work to modify decision-making tools for the particular management of mountain lakes will enable managers to integrate science with other factors.

In conclusion, the systems we studied have endured a complete shift in ecosystem conservation paradigm. Though the period of stocking mountain lakes has undoubtedly left an impact, the formation of new concepts in conservation biology allows ecologists to appreciate the formation of novel ecosystems. Even though present conservation principles generally advocate restoration action, we suggest a laissez-faire approach over the removal of innocuous introduced trout populations.

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Appendix 1: Alpine lake food webs, reproduced with permission from Schindler &
Parker (2002) for a) fishless lake and b) lake with planktivorous fish.
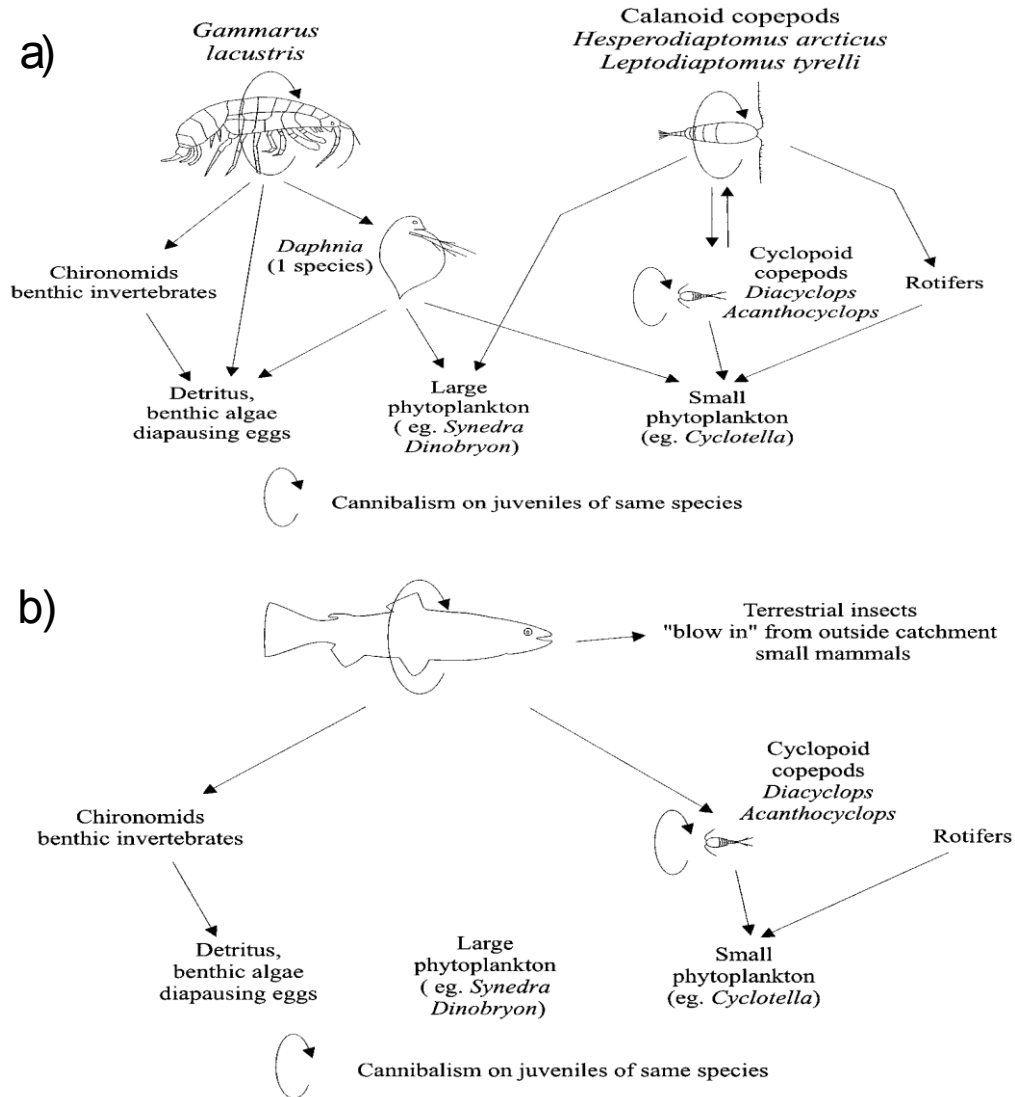
Appendix 2: Biplot of the first two principle components extracted from cladoceran microfossil data of top (T) and bottom (B) sediments from six lakes. Lake codes as per Table1.1; circled text denotes lakes with fish.
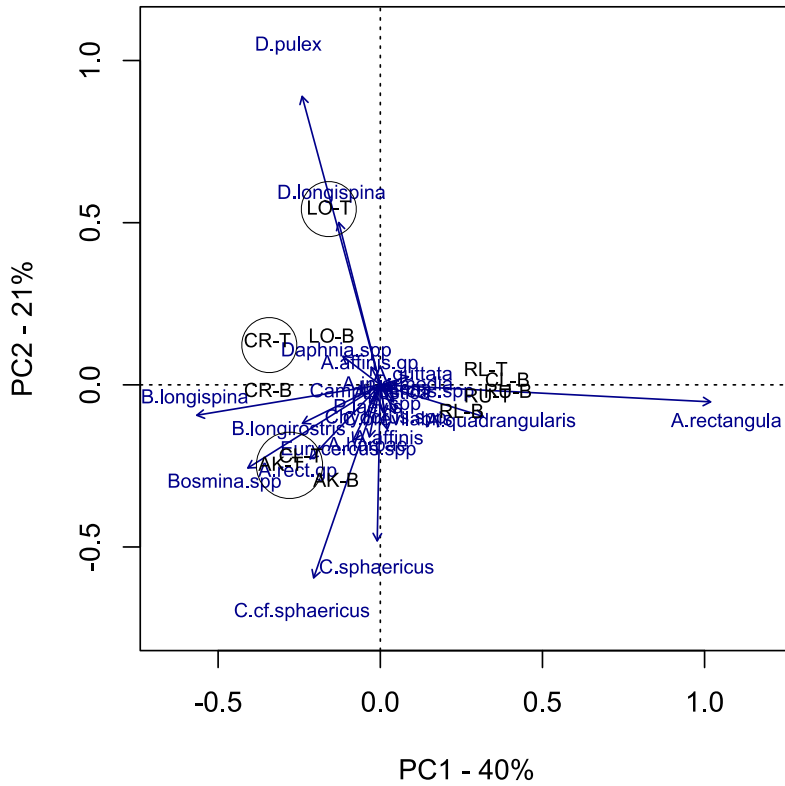
Appendix 3: Percentage of trout stomachs sampled in 2011 containing each taxonomic group of prey item. Adapted from Berman, 2012.