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ASSESSING THE EFFECTS OF *MYXOBOLUS CEREBRALIS* AND OTHER ENVIRONMENTAL FACTORS ON THE DYNAMICS, ABUNDANCE, AND DISTRIBUTION OF TROUT POPULATIONS IN THE LOGAN RIVER, UTAH

by

Ernesto A. de la Hoz Franco

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

2003

ABSTRACT

Assessing the Effects of *Myxobolus cerebralis* and Other Environmental Factors on the Dynamics, Abundance, and Distribution of Trout Populations in the Logan River, Utah

by

Ernesto A. de la Hoz, Master of Science

Utah State University, 2003

Major Professor: Dr. Phaedra Budy
Department: Aquatic, Watershed, and Earth Resources

The presence of nonnative trout and the recent introduction of *Myxobolus cerebralis* in the Logan River drainage pose a threat to the native Bonneville cutthroat trout population *(Oncorhynchus clarki Utah)*. The variability in the response of susceptible trout populations to *M. cerebralis,* causing agent of whirling disease, suggests that environmental factors may influence the effects of the parasite in infected environments. I investigated the relationship between temperature, discharge, substrate size, nutrient concentration (nitrogen and phosphorous), periphyton (chlorophyll *a*), and the relative abundance of *Tubifex tubifex* to the distribution, and prevalence of *M. cerebralis* in wild salmonid populations and sentinel fish in the mainstem of the Logan River and two of its tributaries. In addition, I investigated the potential influence of biotic (e.g., food availability, *M. cerebralis* prevalence) and abiotic factors (e.g., temperature) on the distribution, abundance, and condition of salmonid fishes.

Differences in mean temperature and discharge across sites explained most (> 70%) of the variability in prevalence of *M. cerebralis* observed along the Logan River. However, the prevalence of the parasite was not related to other factors that can influence its life cycle, such as productivity and substrate composition. The results also indicate that the fish fauna presents a longitudinal change reflected in a zonation pattern. Cutthroat trout dominates the headwaters and high-elevation reaches, while reaches at lower elevations of the mainstem and tributaries were dominated by brown trout. The transition between these species was consistent with changes in environmental characteristics. Cutthroat trout dominates the fish community in mainstem reaches with the lowest average minimum temperature and highest diel temperatures, and where small boulders and small cobbles are the predominant substrate.

This study provides insights of the abiotic and biotic factors that affect the distribution, abundance, and condition of salmonid populations along the Logan River. Identifying these factors is crucial to effectively manage this and other trout streams, where ensuring the conservation of native cutthroat trout populations is a priority. Further, I present baseline information of the potential linkages between environmental factors and *M. cerebralis* distribution and prevalence, which could be used to develop plans to minimize the potential negative effects of this parasite on wild salmonid populations.

(99 pages)

DEDICATION

Dedicated to my parents, Ernesto and Gloria de la Hoz, my wife and best friend, Rachael, and my daughter Daniela. Their encouragement, support, patience, and dedication not only have allowed me to achieve my goals, but also have made the realization of this work a pleasant experience.

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CHAPTER I

INTRODUCTION AND PROBLEM DEFINITION

Declines of native cutthroat trout populations have been evident throughout the intermountain west with only a few populations remaining. Factors that lead these declines include habitat degradation, hybridization, and competition with non-native species (Behnke 1992). The American Fisheries Society (AFS) designated the native Bonneville cutthroat trout *(Oncorhynchus clarki Utah)* as "threatened" throughout its range in 1979. This species was reclassified in 1989 as "endangered" and is currently considered a species of special concern in the state of Utah (Lentsch et al. 1997). According to the Utah Division of Natural Resources monitoring program, the Logan River provides habitat to one of the strongest and largest metapopulations of native Bonneville cutthroat trout remaining within their historic range (Thompson et al. 2000). However, the presence of brown trout (*Salmo trutta*) and other non-native species, as well as the recent introduction of *Myxobolus cerebralis* in this drainage pose threat to the conservation of this native trout population.

Myxobolus cerebralis, causative agent of whirling disease, has spread quickly since it first emerged in the United States during 1950s (Bartholomew and Reno 2002) and has been reported in at least 22 states (Bergersen and Anderson 1997). *Myxobolus cerebralis* was first detected in Germany in 1893, and since then it has been transferred worldwide most likely in shipments of infected frozen or live trout (Hoffman 1970). Experiments have shown that fish-eating birds may also transfer *M. cerebralis* via feces, but how far and for how long remains to be discovered (Taylor and Lot 1978). Other speculative modes of disease transmission include anglers (mud, boots, boats, or other equipment), water diversion, irrigation systems, and oligochaetes traded in pet stores (Bergersen and Anderson 1997)

In the United States, Snieszko and Hoffman first diagnosed *M. cerebralis* in 1958 in watersheds in western Nevada and eastern Pennsylvania (Hoffman et al. 1962). The detection of this parasite in the USA and Europe has often been associated with artificial rearing facilities. It was not until the 1990's that reports of *M. cerebralis* in natural populations increased with findings of clinical signs of the disease (black tail, whirling, and skeletal deformities) in Colorado (Nehring and Walker 1996) and Montana (Vincent 1996). Declines of recruitment in wild rainbow trout in various drainages of these states were attributed to the effects of *M. cerebralis* (Baldwin et al. 1998). Further, Nehring and Thompson (2001) showed evidence of *M. cerebralis* to be a decisive factor implicated in the loss of rainbow trout in several Colorado streams.

The response of susceptible trout populations to *M. cerebralis* has demonstrated substantial variability across and within different geographic areas. This parasite has been associated with severe declines of wild rainbow trout populations in Montana and Colorado (Nehring and Walker 1996; Vincent 1996), but population level responses have not been consistently observed in areas of other states where the parasite is also present (e.g., California; Modin 1998).

Further, Hiner and Moffitt (2001) demonstrated substantial variability in the effects of *M. cerebralis* within drainages and even within streams.

The inconsistency in responses of wild rainbow trout populations to *M. cerebralis* suggests that environmental factors may have an influence on the response of susceptible trout in infected environments (Schisler et al. 2000). Environmental factors and anthropogenic stressors can affect parasite-host interactions as they influence the physiological condition, reproduction, and survival of both groups (e.g., Lenihan et al. 1999). Infectious agents may cause a disease of the host when environmental conditions are favorable, when there are additional stresses, and sufficient interactions between these factors (Hedrick 1998; Lafferty and Kuris 1999). Further, fluctuations in prevalence and the degree of impact also depend on interactions between the host, the pathogen, and the environment (Reno 1998).

Myxobolus cerebralis was reported for the first time in Utah in a private fish hatchery during 1991 (Heckmann 1992). Subsequent examinations from various sites led to the discovery of new occurrences of *M. cerebralis* in Utah. Samples from the Little Bear River tested positive for the parasite (Wilson 1993), and in 1994 the parasite was detected in samples from Porcupine Reservoir, Cache County, Utah. The detection of the parasite at Porcupine Reservoir represented a significant increase in the prevalence of the disease in the population of kokanee salmon (*Oncorhynchus nerka*) since the beginning of a monitoring program that started in 1987 (C. Wilson, Utah Division of Wildlife Resources, personal communication). However, an assessment of the effects of

M. cerebralis on the stage-specific survival and growth of kokanee showed no conclusive evidence of population effects (Butts 2002). *Myxobolus cerebralis* was recently detected on the Logan River (Wilson 1999), but its potential effects on the native trout population and other salmonids in the Logan River remain unknown, as well as the physical, chemical, and biological factors that may be linked to its dispersal, infectivity, and prevalence.

Understanding the interactions between environmental factors, host, and pathogen is a critical component for assessing the potential effects of *M. cerebralis* and for developing management strategies to minimize the impact of the parasite in wild trout populations. However, identifying the environmental factors that influence *M. cerebralis* is complicated by the complexity of its life cycle, which involves two obligate hosts, fish and *Tubifex tubifex*, and two spore stages, myxospore and triactinomyxon (Hedrick 1998). The life cycles of *Myxobolus cerebralis*, its secondary host (*Tubifex tubifex)*, and fish, can be influenced by the characteristics of the environment. For example, water temperature affects the development of the infective spore stage (Et-Matbouli et al. 1999), its persistence (Markiw 1992), the growth of *T. tubifex* (Reynoldson 1987), and has been directly related to infectivity, lesion severity, and prevalence on wild and naturally exposed trout (Nehring and Thompson 2001; Hiner and Moffit 2002).

Advances in the knowledge of the biology and susceptibility of *T. tubifex* and different salmonid species as well as how the pathogen interacts with different species, is leading to the improvement of fisheries management and regulatory decisions (Bartholomew and Wilson 2002). However, environmental factors that might be related to the distribution of *M. cerebralis* and the susceptibility of its hosts are still poorly understood. Understanding the impact of the parasite on trout populations, given the importance of other environmental factors, requires the use of both laboratory and field experiments (Schisler et al. 2000).

The general objective of my research was two fold. First, to assess the distribution and prevalence of *M. cerebralis*, the potential relationships between environmental factors and the distribution and prevalence of the parasite, and its effects on salmonid populations; particularly on the native Bonneville cutthroat trout. And second, to assess the abundance, condition, and distribution of the salmonid populations along the Logan River and the interaction and influence of environmental factors associated with this distribution. To meet these objectives, I investigated the relationship between temperature, discharge, substrate size, nutrient concentration (nitrogen and phosphorous), periphyton (chlorophyll *a*), and the relative abundance of *T. tubifex* to the distribution, and prevalence of *M. cerebralis* in wild salmonid populations and sentinel fish in the mainstem of the Logan River and two of its tributaries. In addition, I explored the suitability of these factors in the development of a simple predictive model relating potential increases in prevalence of *M. cerebralis* to differences or changes in environmental factors. This assessment is discussed in detail in Chapter II. Secondly, detailed in Chapter III, I investigated the potential influence of biotic and abiotic factors on the distribution, abundance, and condition of salmonid fishes along the Logan River.

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CHAPTER II

LINKING ENVIRONMENTAL HETEROGENEITY TO THE DISTRIBUTION AND VARIABILITY IN PREVALENCE OF *MYXOBOLUS CEREBRALIS* ALONG THE LOGAN RIVER, UTAH[1]

Abstract. --Given the variable effects of *Myxobolus cerebralis* on trout populations in different streams across the intermountain west, it is important to try and understand the role of environmental variation in determining the distribution and prevalence of *M. cerebralis* in newly infected watersheds. I investigated the relationship between a selected group of environmental factors and the distribution and prevalence of *M. cerebralis* in both wild salmonid populations and sentinel fish in the Logan River. Results indicated that despite its recent widespread distribution, the prevalence of the parasite varied greatly across sites. The lowest prevalence among cutthroat trout (*Oncorhynchus clarki*) was found at the headwaters where the average summer temperature was below 9.5 °C, whereas high prevalence was associated with water temperatures above 12 °C. Further, prevalence in brown trout (*Salmo trutta*) and cutthroat trout increased with discharge reaching its highest levels at sites where the average base flow ranged between 0.7 and 1.1 m^3/s. Despite hypothesized mechanistic links to one or more stages or hosts on the *M. cerebralis* life cycle, we observed no relationship between *M. cerebralis* prevalence and substrate composition, nutrients (TN, TP), periphyton, and oligochaetes. However, multiple linear

[1] Coauthored by Ernesto A. de la Hoz Franco and Phaedra Budy

regression models that included average temperature and discharge explained most (>70%) of the variability in prevalence across sites. The diagnosis of the parasite also revealed inconsistencies among wild and sentinel fish, suggesting that fish movement may be one of the key vectors leading to the spread of the parasite along the drainage. These results indicate that changes in stream temperature or discharge, either natural or anthropogenic could reduce or increase the prevalence and ultimate effect of *M. cerebralis* on wild trout populations.

Introduction

The response of trout populations susceptible to *Myxobolus cerebralis* has varied widely across and within different geographic areas. *Myxobolus cerebralis* (Myxozoa: Myxosporea), the parasite that causes whirling disease, has been associated with declines of wild rainbow trout (*Oncorhynchus mykiss*) populations in Montana and Colorado (Nehring and Walker 1996; Vincent 1996), but population level responses have not been consistently observed in areas of other states where the parasite is also present (e.g., California; Modin 1998). Further, Hiner and Moffitt (2001) revealed evidence of the variability on the effects of *M. cerebralis* within drainages and even within streams. The reported inconsistency in responses of wild rainbow trout populations to *M. cerebralis,* suggests that environmental factors may influence the variability of the responses in infected environments (Schisler et al. 2000). Environmental factors and anthropogenic stressors can affect parasite-host interactions by influencing the physiological condition, reproduction, and survival of both groups (e.g., Lenihan et al. 1999).

Understanding the interactions among environmental factors, hosts, and pathogen is critical for assessing the potential effects of *M. cerebralis* and developing management strategies to minimize the impact of the parasite in wild trout populations. However, identifying the environmental factors that influence *M. cerebralis* is complicated by the complexity of its life cycle, which involves two obligate hosts, fish and *Tubifex tubifex*, and two spore stages, myxospore and triactinomyxon (Wolf and Markiw 1984). Environmental factors such as water temperature, substrate composition, water velocity, and discharge may influence the life cycle of *M. cerebralis.*

Among these factors, temperature directly influences the parasite (spores and the infective triactinomyxon [TAM]), the tubificid secondary host, and fish. Experiments have shown that 12-15°C is the optimal temperature range for TAM production in infected *T. tubifex*; lower temperatures may retard the development and maturation of the spores while extending the period of spore production (El-Matbouli et al. 1999), and higher temperatures may decrease TAM persistence (Markiw 1992). In contrast, somewhat lower temperatures, between 10-13°C, have been associated with the optimal range for *T. tubifex* growth (Reynoldson 1987). Further, temperature has been directly related to infectivity, lesion severity, and prevalence of *M. cerebralis* on wild and naturally exposed rainbow trout (Nehring and Thompson 2001; Hiner and Moffit 2002).

In addition to temperature effects, the distribution of tubificid worms can be influenced by their preference for fine sediments (Sauter and Gude 1996; Arndt et al. 2002). Experiments have shown that *T. tubifex* prefer fine substrates where the associated microflora may offer concentrated bacterial food (Lazim and Learner 1987). Despite their preference for fine substrates, the abundance of heterotrophic aerobic bacteria may be a more important factor controlling substrate selection (McMurtry et al. 1983). In addition to a preference for fine substrate, high abundances of *T. tubifex* have been associated with increasing concentrations of nitrogen and phosphorous compounds (Lestochova 1994).

Water velocity may also determine, in part, the prevalence of *M. cerebralis* through its effects on sedimentation rates, TAM destruction, and dilution effects. Low water-velocity areas in streams, where silty organic material may be more abundant (e.g., backwaters, pools), have been related to higher abundances of tubificid worms (Lazim and Learner 1987). Kerans and Zale (2002) suggest that myxospores may not be very abundant in natural environments and point out the possibility of their passive dispersal to areas of low water velocity and fine sediments where tubificids may be more prolific. Conversely, high water velocity may reduce the rate of *M. cerebralis* infection by destroying TAMs, and high discharge may result in a reduction of their concentration (Kerans and Zale 2002; MacConnell and Vincent 2002).

The effects of *M. cerebralis* on salmonid populations along the Logan River are uncertain. The parasite poses a threat to salmonid populations, particularly to the endemic Bonneville cutthroat trout (*Oncorhynchus clarki Utah*) population, which may be one of the largest metapopulations with its historic range (Thompson et al. 2000). The recent detection of the parasite in this system (Wilson 1999), the higher resistance to infection of cutthroat trout and brown trout (*Salmo trutta*) in relation to rainbow trout, and heterogeneity in environmental characteristics in the Logan River, make this area an ideal study site to explore processes of invasion, persistence, and the role of environmental factors in determining the parasite's distribution and prevalence.

Numerous studies have focused on the biology of the *M. cerebralis* (Halliday 1976), *T. tubifex* (Hedrick and El-Matbouli 2002), and on the effects of the parasite on fish (MacConnell and Vincent 2002). Fewer studies have been designed to identify and enhance the understanding of the environmental factors that may be associated with the distribution, prevalence, and infectivity of the parasite (Hiner and Moffitt 2002). I investigated the relationship between environmental factors (i.e., water temperature, discharge, substrate size, nutrient concentration, primary productivity, and relative abundance of *T. tubifex*) to the distribution and prevalence of *M. cerebralis* in wild salmonid populations and sentinel fish in the mainstem of the Logan River and two of its tributaries. These factors were chosen *a priori* based on suggested relationships and hypothesized mechanistic links as discussed above. I also explored the use of these environmental factors to build a predictive model for potential increases in prevalence of *M. cerebralis*.

Methods

Eight sites within the Logan River drainage, in northern Utah, were selected to represent a wide range of environmental conditions. Sites included reaches at headwaters, tributaries, and lower stream sections developed for water management and influenced by artificial impoundments (Figure 2.1). Field surveys of fish populations and habitat characteristics were conducted at all sites during the summers of 2001 and 2002. Sentinel fish were exposed to natural stream conditions at six of these sites.

Fish sampling and M. cerebralis diagnosis

Salmonid populations were sampled at all sites using three-pass electrofishing depletion techniques during low-flow conditions in August of 2001 and 2002. When possible, 20 juveniles and subadults, and 10 adults from each species were sacrificed. Fish were examined in the field for external signs of whirling disease (i.e., black tail, whirling behavior, deformities). The head, including all gill arches and anterior spinal cord were removed, and frozen. Appropriate tissues were tested for the presence of *M. cerebralis* using the heat shock protein-70 WD polymerase chain reaction method (Hsp PCR; J. Wood, Pisces Molecular LLC, personal communication). Prevalence was quantified as the percentage of samples that tested positive as a function of the total number tested.

Sentinel fish exposures

Cutthroat trout alevins (< 5 weeks post-hatch) were obtained from a rearing facility free of *M. cerebralis*. Alevins were transported to a fish holding facility and maintained in pathogen-free water at 10°C until natural exposures were conducted. Natural field exposures were completed at three sites during summer of 2001, and at three additional sites during summer of 2002. In 2001, three sentinel cages holding 30 fish each (< 9 weeks post hatch) were deployed at each site. In 2002, I used the same number of cages per site with 14 fish (< 9 weeks post hatch) per cage. Fish were exposed 21 d at each site. After the exposure, survivors were returned to the laboratory and maintained in pathogen-free well water at 10°C. Fish from different sentinel cages were held in separate aquaria. Daily observations were made to detect clinical signs of whirling disease, and to remove dead fish. At 90 d post-exposure, fish were euthanized, and the heads, including all gill arches and anterior spinal cord were removed, and frozen. Fish heads were tested for the presence of *M. cerebralis* using the same Hsp-PCR method used in wild fish.

Environmental variables

Temperature. --Water temperature was recorded from July to September at all sites in 2 h intervals using temperature loggers. Daily, monthly, and summer minimum, maximum, average, and daily variations (diel = daily max – daily min) were calculated for each sampling site. Temperature was also recorded from October 2001 to June 2002 at five selected sites. In addition, thermographs were placed at the stream sites, along with sentinel cages during the field fish exposures.

Discharge. --Bi-weekly measurements were conducted during summer 2001 and 2002 at each sampling location. Discharge was estimated from cross-sectional measurements of water velocity at 10 to 20 equally spaced sites using an electromagnetic flow meter (Bain and Stevenson 1999). Measurements were also conducted bi-weekly during the field exposures at each site.

Substrate. --Substrate composition was determined for each site during low flow conditions in summer of 2001 and 2002. Substrate particles were collected randomly at riffle zones from four evenly spaced transects perpendicular to stream flow (Wolman 1954). A minimum of 100 particles was collected. The middle width (B-axis) of each particle was measured to determine average substrate size and percent fines (<10 mm in diameter). Substrate was classified according to the Wentworth Scale (Allan 1995).

Nutrient analyses. --Water samples were collected for nutrient analyses one day during late spring and one day during summer at each sampling site in 2001 and 2002. Bottles were pre-washed with 1N HCl and rinsed with stream water before the sample collection. Samples were kept on ice in the field and frozen until total nitrogen (TN) and total phosphorous (TP) analyses were conducted. Total nitrogen was determined by high-temperature catalytic oxidation (HTCO) with chemiluminescent nitrogen detection (Merriam et al. 1996). The ascorbic acid method was used for total phosphorous analysis (APHA et al. 1992).

Periphyton. --Chlorophyll *a,* extracted from periphyton, was used as an index of productivity (Wetzel and Likens 1991). In 2001, rocks were randomly collected in riffles at each site by walking three transects perpendicular to the stream flow. Ten rocks from each transect were collected, placed in plastic bags, and frozen. Methanol extraction of chlorophyll *a* was conducted at room temperature, in the dark for 24 h. From the extract, three 6-mL aliquots were analyzed fluorometrically (Welschmeyer 1994). The surface area of each rock was estimated by measuring three axes, length, width, and depth, and it was assumed that the area covered by periphyton was 60% of the estimated surface (Biggs and Close 1989). In summer 2002, three to five unpolished tiles (30 x 30 cm) were individually deployed across a riffle at each sampling site. Tiles where retrieved after 36 d, placed in plastic bags, stored in a cooler in the field, and frozen. Chlorophyll was extracted and measured following the same procedures used for periphyton on rocks. Chlorophyll concentrations were expressed in mg/m^2.

Oligochaetes and *Tubifex tubifex.* –Oligochaetes were collected during a 10- minute fixed-time collection at each site. Oligochaetes were collected during spring 2002 from habitats with soft, fine sediments using a 500 μm kick net. Samples were washed, sorted, and preserved in 70% methanol. Subsequently, oligochaetes were sorted and counted. All mature tubificids (bifid chaetae and hair with pectinate chaetae) were mounted on microscope slides and identified. If more than 100 tubificids were collected, 50 were randomly selected and mounted for identification.

Statistical Analyses and Modeling

The prevalence of *M. cerebralis* was evaluated only in wild cutthroat trout and brown trout. A two-way ANOVA was used to examine variability in the prevalence of *M. cerebralis*, and to evaluate differences in explanatory variables (e.g., average temperature, discharge) across all sites and between years. Scatterplots of the response versus each explanatory variable were examined for preliminary assessment of potential relationships and to evaluate the form of relationship if present (i.e., linear, non-linear). Scatterplots were also used to assess relationships among explanatory variables; apparent associations among these variables provided information about collinearity and were used to select a subset of variables for model selection. Multiple linear regression analysis was used to identity the environmental variables that best explained the variation in *M. cerebralis* prevalence in cutthroat trout and brown trout across sites. An analysis of residuals was included to assess assumptions of normality, homogeneity of variance, and linearity. Relationships between *M. cerebralis* prevalence among the sentinel fish and environmental factors were examined as described above for wild trout species. Prevalence data was transformed with an arcsine square-root function to meet assumptions of normality for statistical analyses.

Results

Myxobolus cerebralis diagnosis

Over 4200 fish representing five salmonid species (cutthroat trout, brown trout, brook trout *Salvelinus fontinalis*, rainbow trout, and mountain whitefish *Prosopium williamsoni*) where collected during 2001 and 2002. Clinical signs that could be attributed to whirling disease (e.g., black tail, cranial or spinal deformities) where observed on less than 1% of the total number of trout captured. However, *M. cerebralis* was detected with PCR assays at seven of eight sampling sites, demonstrating that the parasite was widespread in the basin. The overall prevalence of *M. cerebralis* across the basin in 2001 was 47% for cutthroat trout (n=91), 24% for brown trout (n=25), 0% for mountain whitefish (n=10), 75% for rainbow trout (n=4), and 0% for brook trout (n=4). In 2001, prevalence among cutthroat trout across sites ranged from 5% at the uppermost site (Franklin Basin) to 100% at a low elevation mainstem site (Third Dam). In 2002, prevalence in cutthroat trout ranged from 17 to 84%, again at the uppermost site (Franklin Basin) and a low elevation mainstem site (Third Dam), respectively (Figure 2.2). Differences in prevalence across sites were significant (df= 7, $P<0.01$), but differences between years were not (df=1, $P=0.1$). Similarly, the highest prevalence of the parasite in brown trout was observed at the lowermost site in 2001 and 2002 (Lower Logan; Figure 2.2). Prevalence in brown trout ranged from 0 to 60% in 2001, and 0 to 79% in 2002.

Sentinel fish exposures

Sentinel fish exposed to natural stream conditions did not develop clinical signs of whirling disease during the 90 d post-exposure period. The PCR analyses, however, indicated that some of the sentinel fish became infected with *M. cerebralis* during the 21 d exposure. Prevalence of *M. cerebralis* ranged from undetected at the uppermost site and the two tributaries to 56% at an upper-elevation mainstem site (Forestry Camp; Figure 2.3).

Environmental variables

Temperature. --Summer temperatures along the stream increased considerably from high to low elevation sites. Average summer daily temperatures (July-September) ranged from 9.2 to 15.9 °C in 2001, and from 8.8 to 15.7 °C in 2002 (Figure 2.4). Daily average temperatures were significantly different among sites (df= 7, P<0.01), but no differences where detected between years (df= 1, P=0.06). The lowest daily average temperature during the 21 d sentinel fish exposure was recorded at the uppermost site (Franklin Basin, 8.5 °C), while the highest was recorded at a low-elevation site (Third Dam, 12.4 °C; Figure 4). Average summer diel temperature in 2001 ranged from 1.8 °C at a tributary to 8.8 °C at a mainstem site; a similar pattern was observed in 2002 (Table 2.1). The daily maximum temperatures recorded from September to June at selected sites reached 8°C during fall, 4 °C during winter, and 10 °C during spring.

Discharge. --The highest summer discharge was recorded at a middle-mainstem site in 2001 (Twin Bridges, 1.73 m^3/s) and 2002 (Twin Bridges, 1.95 m^3/s). The lowest average discharge was observed in 2001 at one of the tributaries (Right Hand Fork, 0.19 m^3/s; Figure 2.5). In general, estimates of discharge were lower at high and low elevation sites and tributaries, while the highest estimates occurred at mainsteam sites. Significant differences in discharge among years were not detected across all sites (df=1, P=0.7).

Substrate. --Small boulders and large cobbles were predominant in headwaters and mainsteam sites. Coarse gravel was the most common substrate at the lowermost site (Lower Logan). Substrate at tributary sites (Temple Fork, Right Hand Fork) was predominantly small cobbles. The highest percentage of fine substrates ($\leq$10 mm) occurred in one of the tributaries (Temple Fork; 27%); lower percentages were estimated at low-elevation sites (Lower Logan, 3%; Third Dam, 3.5%; Table 2.1).

Nutrient analyses. --Higher nitrogen concentrations were detected at high and low-elevation sites, as well as in the tributaries as compared to sites in middle sections of the mainstem. Differences between years were not significant (df=1, P=0.06; Table 2.1) but sites were significantly different (df= 7, P<0.01). Total nitrogen concentrations ranged from 0.07 to 0.21 mg N/L, corresponding to the upper (Franklin Basin) and lowermost (Lower Logan) sampling sites. No significant differences were detected in total phosphorous concentrations among sites (df= 7, P=0.09) or between years (df=1, P=0.4; Table 2.1).

Periphyton. --Extracts of chlorophyll *a* from rocks in 2001, and from artificial substrates in 2002 did not reveal a consistent pattern in primary productivity along the stream. Chlorophyll *a* concentration from rocks ranged between 12 and 183 mg/m^2, and between 74 and 96 mg/m^2 on tiles (Table 2.1). There were no significant differences between sites (df= 7, P=0.56) or years (df=1, P=0.64).

Oligochaetes and Tubifex tubifex. --In total, 1210 oligochaetes were collected at the eight sites. Four species of Tubificidae were identified (*Tubifex tubifex*, *Rhyacodrilus coccineus*, *Limnodrilus hoffmeisteri*, and *Telmatodrilus vejdovskyi*). Five other families were identified (Naididae, Enchytraeidae, Lumbriculidae, Lumbricidae, and Sparganophilidae), with *Eiseniella tetraedra* representing the only mature Lumbricidae. The largest numbers of oligochaetes were collected at an upper-elevation mainsteam site (Forestry Camp; Table 1); 854 out of 857 worms at this site were tubificids with hair and pectinate chaetae, and of the 50 mounted and identified, 49 were *T. tubifex*. Samples from headwaters and high-elevation mainsteam sites contained mostly tubificidae, while tributaries and low-elevation sites contained more lumbriculids or lumbricids. *Tubifex tubifex* was not found at a low-elevation mainsteam site (Third Dam) or at the lowermost site (Lower Logan).

Relationships among environmental factors and prevalence

The prevalence of *M. cerebralis* was similar for cutthroat trout and brown trout. Prevalence of *M. cerebralis* in cutthroat trout appeared to increase with water temperature (Figure 2.6). The highest prevalence of the parasite was detected in water temperatures around 12 °C. In addition, *M. cerebralis* prevalence showed a nonlinear relationship with discharge (Figure 2.6). The highest prevalence, at a low-elevation mainstem site (Third Dam), was associated with discharge estimates ranging between 0.6 and 1 m^3/s. A similar pattern was observed for prevalence in brown trout in relation to temperature and discharge.

In contrast to wild fish, the prevalence of the parasite among sentinel fish did not show a clear pattern that could be related to any of the environmental variables considered in this study. There was no apparent relationship between *M. cerebralis* prevalence in wild trout and periphyton (Chl *a*), nutrient concentration (TN, TP), substrate size, percent fines (<10 mm), or relative density of oligochaetes. Further, scatterplots did not reveal any apparent associations between oligochaete density and productivity (Chl *a*), nutrient concentration (TN, TP), or substrate composition (Figure 2.7).

Multiple linear regression models that included average water temperature and discharge were significant overall and explained a large portion of the variation in prevalence of *M. cerebralis*. For cutthroat trout, the model accounted for 74% of the variability in prevalence observed across sampling sites (df=11, Adjusted R^2=0.74, P $\leq$0.01; Table 2.2). A similar model explained 83% of the variability in prevalence among brown trout (df=7, Adjusted R^2=0.83, P=0.018; Table 2.3).

Discussion

Since *M. cerebralis* was first detected in the Logan River in 1998, its range has broadened along the mainstem and its tributaries. Suspected vectors of the parasite include, fish eating birds, anglers' equipment, and fish (Taylor and Lott 1978; Bergersen and Anderson 1997; Schisler and Bergersen 2002). The diagnosis of *M. cerebralis* in wild and sentinel fish revealed that at some sites the parasite was not detected among sentinel trout, while highest prevalences were observed among wild trout. These inconsistencies suggest that fish movement is one of the vectors leading to the spread of the parasite along the stream and its tributaries. Differences in prevalence among juvenile and adult trout also support this hypothesis. A study conducted in a tributary of the Logan River demonstrated that the behavior of cutthroat trout ranges from almost completely stationary to frequent and wide-ranging movements (Hilderbrand 1998), depending on time and season, and life history stage. Cutthroat trout on the mainstem may exhibit similar behavior, and infected fish could act as important vectors for the transport and spread of *M. cerebralis* spores to tributaries and headwaters.

Despite its widespread distribution, the prevalence of *M. cerebralis* along the Logan River varies greatly within the basin. This high variability in prevalence was not surprising; other studies have shown evidence of variability in prevalence and severity of infection across and within drainages (Baldwin et al. 1998; Hiner and Moffitt 2001). In this study, differences in average summer temperature and discharge along the river explained most of the variability (>70%) in prevalence observed across sites. Across sites where cutthroat trout were present, the lowest prevalence was observed in the headwaters, where the daily average water temperature was 9.2 °C, while the highest was observed at a low-elevation site, where the average temperature was the highest (>12 °C). Likewise, the low prevalence of brown trout in the tributaries and high prevalence at the lowermost site was consistent with the lowest (10-11 °C) and highest (16 °C) average summer temperatures across stream reaches where this species was distributed. Water temperatures that are close to the ideal for TAM production (12 °C; Markiw 1992) and persistence (15 °C; El-Matbouli et al. 1999), could explain the high prevalence of the parasite at lower sections of the river, in both cutthroat trout and brown trout. Similarly, lower temperatures may retard spore development (El-Matbouli et al. 1999) and lead to lower prevalences, as we observed in trout from headwaters and tributaries.

This study also demonstrated that differences in base flow discharge along the river may influence the variability in prevalence. The prevalence of the parasite in cutthroat trout increased with increasing discharge. Lower prevalence rates were observed at headwaters and one of the tributaries where discharge was low, while the highest prevalence was observed at a low-elevation mainsteam site where discharge was higher. These results were consistent with the pattern observed in prevalence among brown trout. Other authors have suggested that high flows could destroy or dilute TAMs, thus reducing infection in susceptible fish (Kerans and Zale 2002; MacConnell and Vincent 2002). Conversely, this study showed a nonlinear relationship between the range of flows observed in the Logan River and the prevalence of the parasite. Prevalence in cutthroat trout and brown trout increased with discharge reaching its highest levels at sites where average base flow ranged between 0.7 and 1.1 m^3/s; prevalence then decreased at the site where the highest discharge was estimated.

The asymptotic relationship between discharge and prevalence suggests that lower discharge at headwaters and tributaries may decrease the probability of spores contacting and infecting fish. On the other hand, higher discharge likely disturbs areas where spores may be concentrated, thus increasing the probability of infection to a maximum. Above this threshold, higher discharge could lead to lower infections, as the concentration of TAMs in the water column is reduced. Further, the presence of artificial impoundments at lower sections of the Logan River may favor higher spore concentrations, as spores may be passively transported to areas of low water velocity (Hiner and Moffit 2002; Kerans and Zale 2002; Nehring et al. 2003), thus leading to the higher prevalences observed at low-elevation reaches.

The lack of clinical signs (e.g., deformities, black tail) in wild and sentinel fish suggest that the abundance of TAMs along the Logan River is low. Similarly, we have observed no population level declines in the trout populations of the Logan River since 1999 (Budy et al. 2003). Spore concentration (dose) is directly related to the development of clinical signs of whirling disease and its severity (Markiw 1992). However, other factors such as fish age (Markiw 1991), size (Thompson et al. 1999), species (Hedrick et al. 1999; Sollid et al. 2002; Vincent 2002), and environmental factors at the time of the exposure may also influence the susceptibility of fish to the disease. Highly susceptible cutthroat trout fry could be exposed to low TAM concentrations during spring; low temperatures may also retard spore development and production, and flushing or diluting effects may also result from high discharge during this season. The effects of these environmental variables may also explain the response in brown trout fry that emerge during autumn. Results from this study are consistent with the hypothesis formulated by Hubert et al. (2002) for cutthroat trout in spring streams of the Salt River drainage; that is their life history patterns may reduce the susceptibility to *M. cerebralis* as fish migrate from the mainstem to smaller tributaries and headwaters to spawn, and fry use these lower water temperature streams as nursery habitat.

Other factors such as primary productivity, relative abundance of oligochaetes (*T. tubifex*), substrate composition, and nutrient concentrations (TN, TP), were not related to the prevalence of the parasite among trout in the Logan River. Despite the potential influence of these factors on the life cycle of *M.*

cerebralis, and thus on its distribution and prevalence, our results do not provide evidence of such relationships. Other authors have revealed that *T. tubifex* is not ubiquitous, and where present, densities can vary greatly from less than 100 to >1000 worms/m^2 (Särkkä 1987; Zendt and Bergersen 2000). The large differences in oligochaete abundance across the sites sampled in the Logan River therefore reflect the pattern observed in other intermountain west streams. The lack of correlation between oligochaete density and productivity (Chl *a*), nutrient concentration (TN, TP), or substrate composition, suggests that in the Logan River other biological factors (e.g., abundance of heterotrophic bacteria) may be more important than physical or chemical factors on their substrate selection (McMurtry et al. 1983).

The low variability in environmental factors (i.e., temperature, flow) between 2001 and 2002, and the fact that these factors were assessed mainly during base flow conditions potentially limit our results. Logistical limitations impeded the measurement of environmental factors year-round. In addition there are other variables, which we did not measure here (e.g., abundance of food source or predator of tubificids), that may determine, in part, the pattern of distribution and abundance of *M. cerebralis*. However, results from this study should serve as a solid starting point or reference for others investigating potential linkages between environmental factors (e.g., water quality, discharge, distribution and abundance of *T. tubifex*) and *M. cerebralis* distribution and prevalence. In addition, our results suggest that changes to stream temperature or discharge, either natural or anthropogenic, could alter the spread and impact of *M. cerebralis* in mountain streams.

Many authors have addressed the need to investigate pathogen-host-environment interactions in order to fully understand and assess the potential effects of a disease in fish populations (Hedrick 1998; Reno 1998). Similarly, understanding the role of fish stressors, and synergistic effects of stress or disease and the environment, is also key to evaluating and managing the health and status of fish populations (Budy et al. 2002). This study was conducted to provide baseline information for the distribution and prevalence of *M. cerebralis* along the Logan River, and to assess potential relationships between environmental factors and the parasite. Understanding the environmental variables that influence the distribution and prevalence of diseases and the mechanisms for its dispersal, are tools that fishery biologists and managers could use to limit the spread of parasites, and to develop plans to minimize potential negative effects on wild salmonid populations.

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TABLE 2.1. Number of wild cutthroat trout and brown trout infected. Temperature measurements, average substrate size, percent fines (<10 mm), nutrient concentrations (TN, TP), chlorophyll *a* concentration from rocks (2001) and artificial substrates (2002), total oligochaetes, and number of *T.tubifex* collected.

		Species				Temperature		Substrate		Nutrients		Periphyton	Oligochaeta	
		Cutthroat		Brown trout		summer average	diel average	average	fines	average TN	average TP	Chl *a*	Total [a]	*T. t* [b]
Site	year	number infected	n	number infected	n	(°C)	(°C)	(mm)	(%)	(mg/L)	(ug/L)	(mg/m²)		
Franklin Basin	2001	1	20	0	0	9.2	7.3	209	1	0.07	17.7	47		
Red Banks	2001	9	14	0	0	11.0	7.7	287	0	0.08	21.9	44		
Forestry Camp	2001	11	17	0	0	12.1	8.8	283	10	0.07	21.8	120		
Twin Bridges	2001	10	19	0	0	11.8	6.2	143	6	0.03	21.9	64		
Third Dam	2001	8	8	0	0	12.1	6.0	38	6	0.09	15.2	182		
Lower Logan	2001	0	0	6	10	16.0	2.5	137	1	0.21	22.5	95		
Temple Fork	2001	4	13	0	5	10.6	8.5	23	24	0.12	21.3	183		
R. H. Fork	2001	0	0	0	10	10.8	1.8	46	13	0.16	24.2	12		
Franklin Basin	2002	3	18	0	0	8.8	6.7	173	14	0.14	21.0	74	62	6
Red Banks	2002	15	20	0	0	10.6	7.3	252	14	0.07	19.2	80	12	7
Forestry Camp	2002	15	20	0	0	11.6	8.5	258	14	0.05	19.4	86	857	49 [c]
Twin Bridges	2002	15	19	7	20	11.7	5.5	236	4	0.06	15.5	78	16	4
Third Dam	2002	12	14	13	20	12.3	4.1	205	1	0.10	11.7	75	92	
Lower Logan	2002	0	0	15	19	15.7	3.2	40	5	0.27	28.6	91	6	
Temple Fork	2002	9	19	1	11	10.6	8.1	123	30	0.13	18.3	75	39	2
R. H. Fork	2002	0	0	0	10	10.7	1.7	105	11	0.22	21.7	96	126	11

[a] 10 m fixed-time collection.

[b] *Tubifex tubifex*.

[c] 50 out of 415 mature tubificidae collected at this site were identified.

Table 2.2. Summary of linear regression model for prevalence of *M. cerebralis* in cutthroat trout in the Logan River, Utah. Parameter estimates are also given.

Source of variation	df	Sum of Squares	Mean Square	*F*	*P*	Adjusted R^2
Model	3	1.1467	0.3822	11.28	0.0030	0.7371
Error	8	0.2710	0.0338			
Total	11	1.4178				

Variable	df	Parameter estimate	Standard error	*t*	*P*
Intercept	1	-- 1.7796	0.5880	-- 3.03	0.0164
Average temperature	1	0.1816	0.0646	2.81	0.0229
Average discharge	1	0.0405	0.0178	2.28	0.0524
(Average discharge)^2	1	-- 0.0004657	0.0002087	-- 2.23	0.0262

Table 2.3. Summary of linear regression model for prevalence of *M. cerebralis* in brown trout in the Logan River, Utah. Parameter estimates are also given.

Source of variation	df	Sum of Squares	Mean Square	*F*	*P*	Adjusted R^2
Model	3	1.3492	0.4497	12.12	0.0178	0.8265
Error	4	0.1485	0.0371			
Total	7	1.4977				

Variable	df	Parameter estimate	Standard error	*t*	*P*
Intercept	1	-- 1.1070	0.4540	-- 2.44	0.0713
Average temperature	1	0.0669	0.0522	1.28	0.2693
Average discharge	1	0.0546	0.0231	2.37	0.0767
(Average discharge)^2	1	-- 0.0005913	0.0002862	-- 2.07	0.1077

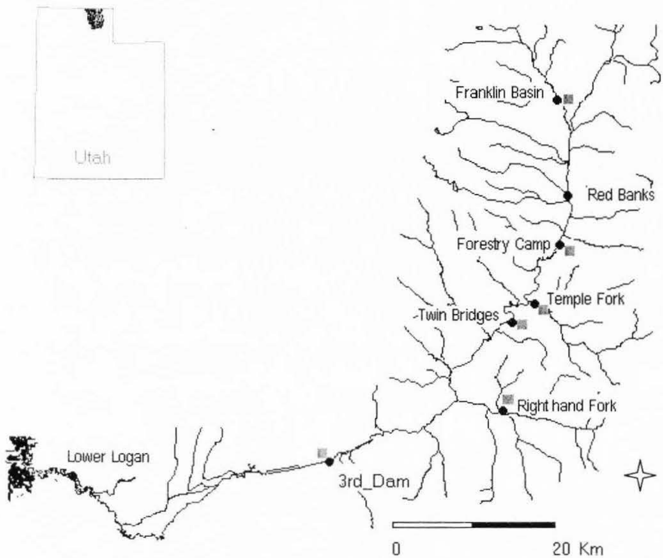

Figure 2.1. Map depicting the location of study sites within the Logan River basin, Utah. Circles represent sites where wild fish where collected and environmental factors measured. Squares indicate sites where sentinel fish where exposed.

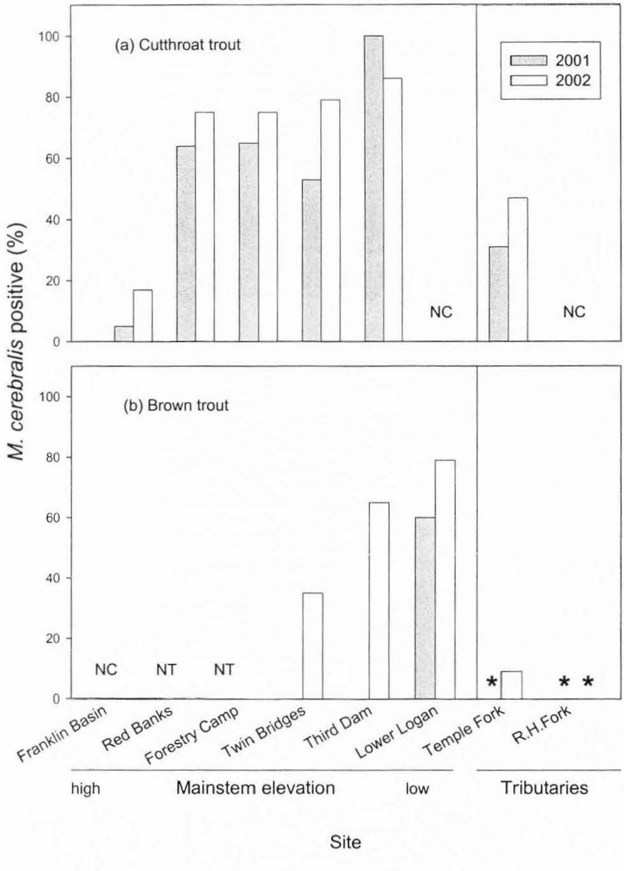

Figure 2.2. Prevalence of *Myxobolus cerebralis* (% testing positive) in wild cutthroat trout (a) and brown trout (b) at 6 sites along the Logan River and 2 tributaries in 2001 (gray bars) and 2002 (white bars). The asterisks show sites where the parasite was not detected. NC indicates that no fish were captured at a particular site. NT indicates that fish have not been tested.

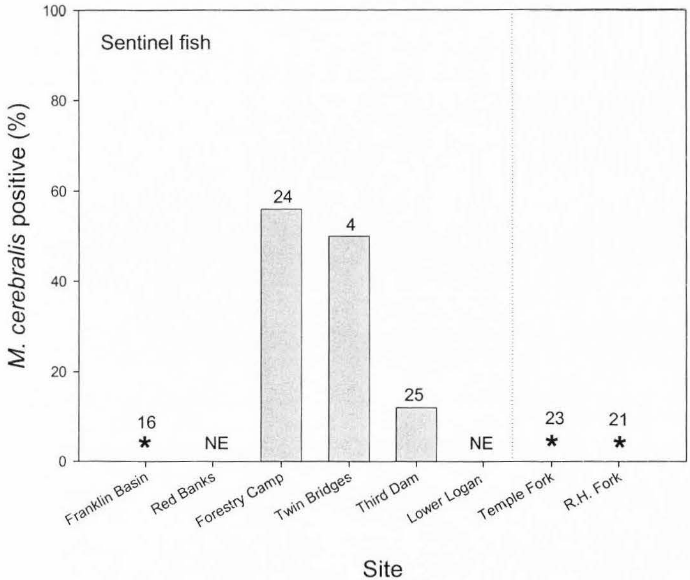

Figure 2.3. Prevalence of *M. cerebralis* in field-exposed sentinel fish at sample sites on the Logan River, Utah, 2001. Asterisks depict sites where the parasite was not detected in sentinel fish. NE indicates sites where no exposures where conducted. Sample sizes (n) are indicated. Sites to the right of the vertical dashed line are tributaries to the mainstem Logan River.

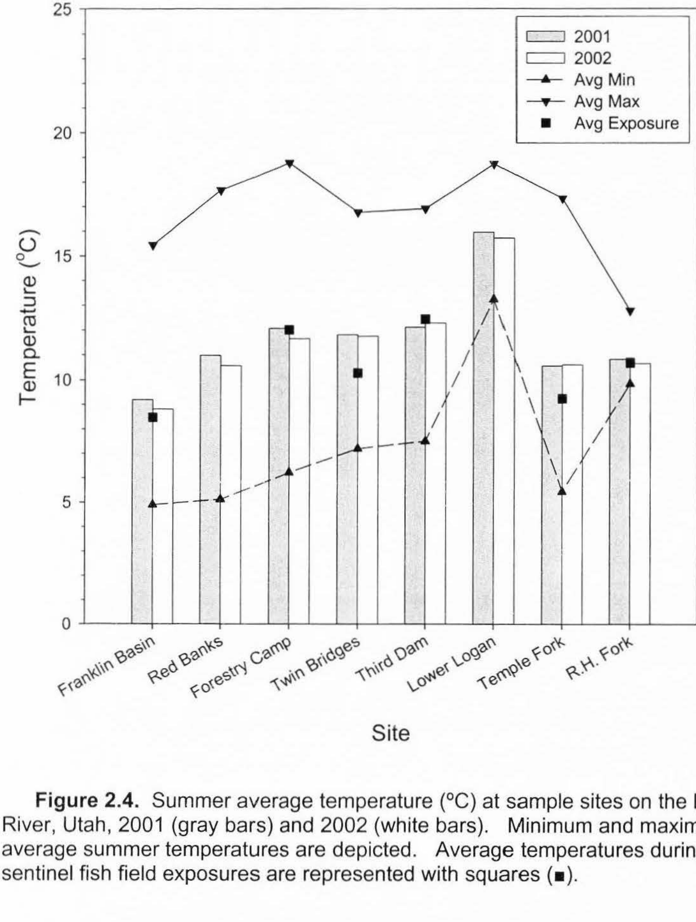

Figure 2.4. Summer average temperature (°C) at sample sites on the Logan River, Utah, 2001 (gray bars) and 2002 (white bars). Minimum and maximum average summer temperatures are depicted. Average temperatures during sentinel fish field exposures are represented with squares (■).

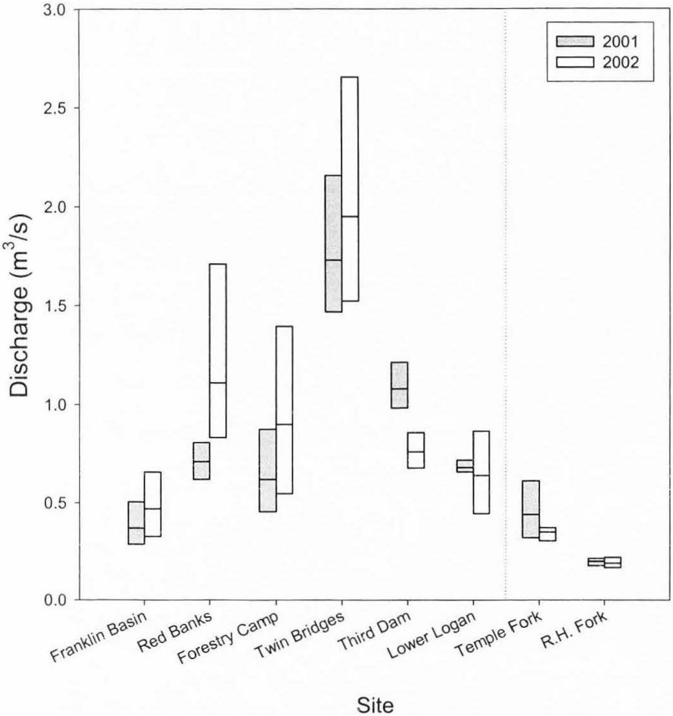

Figure 2.5. Discharge (m^3/s) at mainstem sites and tributaries on the Logan River, Utah, during summer 2001 (gray) and 2002 (white). Boxes depict minimum and maximum discharge. Horizontal lines in boxes indicate averages.

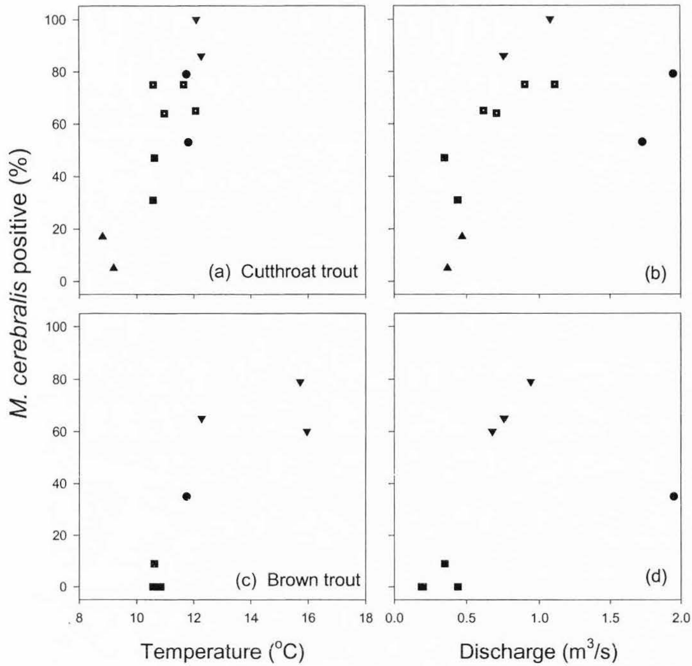

Figure 2.6. Prevalence (%) of *M. cerebralis* in wild cutthroat trout (a-b) and brown trout (c -d) as a function of average summer temperature and discharge in the Logan River, Utah, 2001 and 2002. Symbols depict sampling sites: Headwaters (▲), tributaries (■), high (◘), middle (•), and low-elevation (▼) reaches.

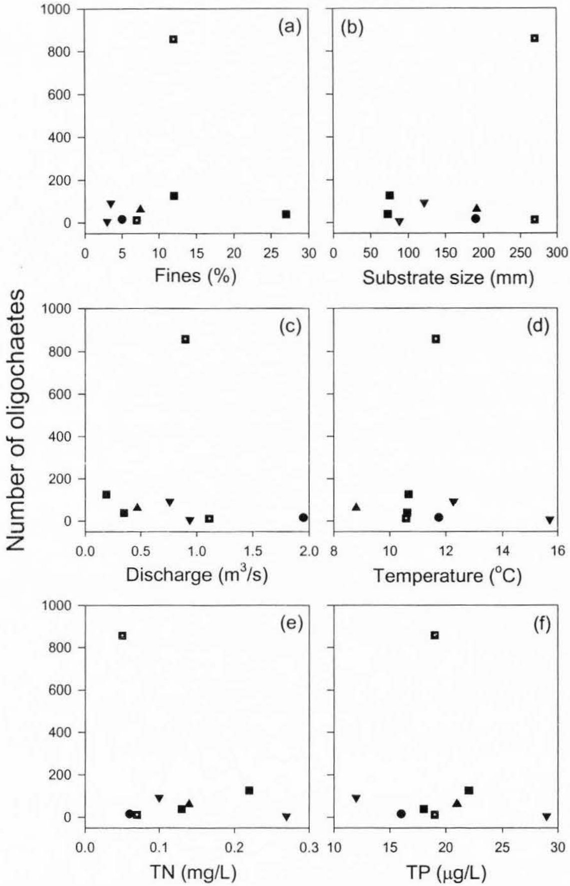

Figure 2.7. Total number of oligochaetes collected at sample sites in the Logan River, Utah, 2002, in relation to percent fines (a), average substrate size (b), average summer discharge (c), average summer temperature (d), total nitrogen (e), and total phosphorous (f). Symbols depict sampling sites: Headwaters (▲), tributaries (■), high (◘), middle (•), and low-elevation (▼) reaches.

CHAPTER III

EFFECTS OF BIOTIC AND ABIOTIC FACTORS ON THE DISTRIBUTION OF TROUT ALONG A LONGITUDINAL STREAM GRADIENT[1]

Abstract. --Given the widespread decline of cutthroat trout across their native range, it is important to identify the factors that determine their distribution in populations that have persisted and reside in relatively intact stream systems. I examined the potential influence of biotic (e.g., competitors, parasite prevalence) and abiotic (e.g., temperature, discharge) factors on the distribution, abundance, and condition of salmonid fishes along a longitudinal gradient in a mountain stream. Field surveys of fish populations and environmental factors were conducted during the summer of 2001 and 2002. I observed a longitudinal change in fish distribution with native cutthroat and introduced brown trout demonstrating a distinct pattern of allopatry. Cutthroat trout dominated headwaters and high elevation reaches, while reaches at lower elevations were dominated by brown trout (*Salmo trutta*). A transition zone between these populations was associated with changes in average and diel temperature, and substrate size. In addition, I observed considerable overlap in the diet of sympatric cutthroat and brown trout, suggesting that both biotic and abiotic factors influenced their distribution and abundance. Regression models provided additional evidence of these relationships; the best model for cutthroat trout abundance included abundance of brown trout and diel temperature (R^2= 0.86)

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[1] Coauthored by Ernesto A. de la Hoz Franco and Phaedra Budy

as explanatory variables. In contrast, the best model for explaining brown trout abundance and distribution included diel temperature and sediment size (R^2=0.97). These results suggest that brown trout may have a greater effect on the species distribution than cutthroat trout and indicate the potential for competitive interactions among the two species. Further, the diagnosis of *Myxobolus cerebralis*, the causative agent of whirling disease, revealed that the parasite is widespread along the river but has not impacted the population abundance as of yet. Results suggested that the range of environmental characteristics in the Logan River (e.g., temperature, discharge) may contribute to the variability of the parasites' prevalence, and could explain in part why clinical signs of whirling disease were rare. The results from my study can aid biologists in developing robust conservation and management strategies for cutthroat trout in western streams, based on the biotic and abiotic factors that determine their abundance and distribution.

Introduction

The spatial arrangement of biotic and abiotic habitat components may influence not only the distribution and abundance of individual fish species across many scales (Bozek and Rahel 1991; Grossman et al. 1995; Rahel and Nibbelink 1999) but also community-level properties such as species richness and production (Hawkes et al. 1986; Hughes and Gammon 1987; Rahel and Hubert 1991). Biotic factors that affect fish populations and communities include inter and intraspecific competition (e.g., Fausch and White 1981), predation (e.g., Gilliam and Fraser 2001) and food availability (e.g., Bowlby and Roff 1986). Temperature and discharge are among the abiotic factors that affect fish at this level of organization in stream ecosystems (e.g., Jackson et al. 2001). Further, the interaction of biotic and abiotic factors can also determine the distribution of species arranged along altitudinal gradients in streams, as demonstrated by Fausch et al. (1994), where the distribution and hierarchy among sympatric char species was driven by temperature, habitat type, and interspecific competition, depending on the spatial scale (e.g., regional, watershed, stream) of the observations. An allopatric pattern of species distribution is often observed in streams that provide a longitudinal gradient of habitat for salmonids, where the species that is present at high-elevation reaches overlaps very little with another species that occupies reaches at low elevations (Fausch 1989). Competition is a key factor influencing the distribution of species in such streams (Fausch 1988; Nakano 1995); however, significant changes in abiotic factors (e.g., temperature) along an altitudinal gradient may regulate these types of biotic interactions (De Sato and Rahel 1994; Taniguchi et al. 1998). Limitations in the distribution of salmonid populations as a result of thermal constraints have been firmly established (Keleher and Rahel 1996; Dickerson and Vinyard 1999; Schrank et al. 2003).

In addition to the influence of thermal constraints and interspecific interactions, other biotic factors such as parasites and disease also play an important role in fish population dynamics and community structure. Examples include, *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD), and *Myxobolus cerebralis*, the parasite that causes whirling disease. Juvenile chinook salmon (*Oncorhynchus tshawytscha*) infected with BKD may become more vulnerable to predation (Mesa et al. 1998), and similarly, *M. cerebralis* has been directly implicated in juvenile mortality and severe declines of salmonid year-classes in some streams (Nehring and Walker 1996; Vincent 1996).

The goal of this study was to examine the potential influence of biotic (e.g., competitors, *Myxobolus cerebralis* prevalence) and abiotic (e.g., temperature, discharge) factors on the distribution, abundance, and condition of salmonid fishes along a longitudinal gradient in a mountain stream. The Logan River, Utah provides habitat to one of the few populations of Bonneville cutthroat trout (BCT; *Oncorhynchus clarki Utah*) throughout its historical range, what may be one of the strongest and largest populations remaining (Thompson et al. 2000). However, declines in the population of the native cutthroat trout throughout the intermountain west are evident, with few populations remaining (Behnke 1992). Habitat degradation, hybridization, and competition with nonnative species led the American Fisheries Society (AFS) to designate BCT as "threatened" throughout its range in 1979. In 1989, this species was reclassified as "endangered" and is currently considered a species of special concern in the state of Utah (Lentsch et al. 1997). Within the Logan river drainage specifically, the presence of non-native trout (especially brown trout) and the recent discovery of *M. cerebralis* in this drainage are potential threats to the native cutthroat trout population.

Understanding the factors that influence the distribution, abundance, and condition of trout and salmon populations in these mountain streams is critical to effectively manage this system, and to ensure the long-term conservation of native cutthroat trout through out their range. The objectives of my study were to 1) evaluate the status and distribution of trout in the Logan River, 2) understand the role of abiotic and biotic factors in determining the abundance and distribution of these fishes, and 3) develop tools for predicting the abundance and distribution of cutthroat trout, to aid in the conservation and management of these endemic fish.

Methods

Study area

The headwaters of the Logan River are located in the southeastern corner of Idaho. The river enters the northeast corner of Utah at an elevation of 2590 m and runs through Logan Canyon for forty miles to reach the city of Logan, dropping to an elevation of approximately 1371 m. The gradient on the main stream varies from 6 to 32 m/km, and the higher gradients of the tributaries reach 75 m/km (Thoreson 1949). Climate is predominantly cold and snowy during the winter, followed by hot, dry summers, in which diel water temperatures can range 9 °C, and maximum temperatures range from 12 to 19 °C in tributaries and in low elevation reaches of the mainsteam, respectively (*see* Chapter II; Figure 2.4). Eight sites within the Logan River Drainage were surveyed, ranging from headwaters and tributaries to low elevation sections (*see* Chapter II; Figure 2.1).

Fish species found in the Logan River include Bonneville cutthroat trout, brown trout (*Salmo trutta*), stocked and wild rainbow trout (*Oncorhynchus mykiss)*, brook trout (*Salvelinus fontinalis*), mountain whitefish (*Prosopium williamsoni*), and sculpin (*Cottus bairdi*). Field surveys of fish populations and environmental characteristics were conducted at all sites during the summer of 2001 and 2002.

Fish population abundance and condition

Fish population abundance was estimated based on three-pass depletion electrofishing. Small-mesh seines were used to block the upper and lower end of 200 m reaches on mainsteam sites, and 100 m on headwaters and tributary sites. All fish species collected were counted, and their lengths and weights recorded. Fish densities were then estimated using the removal method of Zippin (1958). Fulton's (K) condition factor was used to assess the condition of the fish (Anderson and Newman 1996).

Parasite analyses

When possible, 20 juveniles and sub adults, and 10 adults from each species were kept for diet and *Myxobolus cerebralis* analyses; these fish were euthanized using a lethal dose of tricaine methanesulfonate (500 mg/L). The head, including all gill arches and anterior spinal cord was removed, and frozen. Fish were examined in the field for external signs of whirling disease (e.g., black tail, deformities). Fish heads were tested for the presence of *M. cerebralis* using the heat shock protein-70 WD polymerase chain reaction method (Hsp PCR; J. Wood, Pisces Molecular LLC, personal communication).

Invertebrate abundance, diet analyses, and prey selection

Data on invertebrate abundance and composition were provided by the National Aquatic Monitoring Center (M. Vinson, National Aquatic Monitoring Center - Utah State University, personal communication). Aquatic invertebrates were sampled at each site in years 1997-2000 with a kick net or surber sampler. Three to twelve samples collected during summer months of one to three years were averaged for each site. Diet analyses were conducted on fish samples from 2001. Stomach contents from the same fish samples used for parasite analyses were removed by dissection and fixed with 10% formalin. Contents were examined from each fish specimen, and the number of organisms belonging to each particular taxa (i.e., genus) was determined. Blot-dry wet weights were recorded to the nearest milligram. I estimated the percent composition by number and weight, as recommended by Bowen (1996). Chesson's alpha prey selectivity index (Chesson 1978) was used to compare the diets of cutthroat trout and brown trout to invertebrate abundance.

Environmental variables

Temperature. --Water temperature was recorded from July to September at all sites in 1 h intervals using temperature loggers. Minimum, maximum, and average daily, monthly, and summer water temperatures were estimated for each site, as well as diel variations during these same time periods (diel = daily max – daily min).

Discharge. --Bi-weekly measurements were conducted during summer 2001 and 2002 at each sampling location. Discharge was estimated from cross-sectional measurements of water velocity at 10 to 20 equally spaced sites. Velocity was measured at two thirds of the depth of the water column using an electromagnetic flow meter (Bain and Stevenson 1999).

Substrate. --Substrate particles were randomly collected at riffle zones from four evenly spaced transects perpendicular to the stream flow according to the Wolman pebble count method (Wolman 1954). At least 100 particles were blindly collected; the middle width (B-axis) of each particle was measured to determine average substrate size and percent fines (<10 mm in diameter). Substrate composition was evaluated according to the Wentworth Scale (Allan 1995).

Periphyton. --Chlorophyll *a*, extracted from periphyton was used as an index of productivity (Wetzel and Likens 1991). In 2001, rocks were randomly collected in riffles at each site by walking a transect perpendicular to the stream flow. Ten rocks were collected from each of three transects, placed in whirl-packs and maintained frozen until the extraction of chlorophyll *a* and fluorometric analyses were completed. Chlorophyll *a* was extracted in methanol in the dark for 24 h at room temperature. From the extract, three 6 ml aliquots were analyzed fluorometrically (Welschmeyer 1994) and the concentrations were expressed in mg/m^2. The surface area of each rock was estimated by measuring length, width, and depth, and it was assumed that the area covered by periphyton was 60% of the estimated surface (Biggs and Close 1989). In 2002, three to five unpolished tiles (30 x 30 cm) were arranged across a riffle at each sampling site. Tiles were retrieved after 6 weeks, placed in plastic bags, and frozen. Chlorophyll *a* was extracted and analyzed following the same procedures used for rocks.

Statistical analyses

I used ANOVA to examine differences in response variables (i.e., fish abundance), and to evaluate differences in explanatory variables (e.g., temperature, discharge, invertebrate abundance) among sites. I initially used scatterplots and Pearson correlations to examine the factors that potentially affect the distribution of cutthroat trout and brown trout, and to assess relationships among explanatory variables. Evident associations among variables provided information about collinearity and were used to select a subset of variables for model selection.

Best-subset regression was used to select variables to be used in linear regression analyses; I used the following model selection criteria: adjusted-R^2, R^2, mean square error (MSE), Mallows' Cp, and Akaike's information criterion (AIC). I used these models to identify the variables that best explained the variation in cutthroat trout and brown trout abundance across sites, and used prediction sum of squares (PRESS) residuals (Myers 1990), to evaluate the predictive performance of the regressions. Residuals were estimated by withholding the observations from 2002, and subtracting observed values from those predicted by the regression model based on the observations from 2001. Data were transformed with square root or logarithmic functions to meet assumptions of normality and homogeneity of variance.

Results

Fish population abundance and condition

The fish community changed longitudinally from high elevation sites to low elevation sites (Figure 3.1). The distribution of cutthroat trout and brown trout was inversely related with the highest abundances of native cutthroat trout observed at high elevation reaches and none observed at lower elevations. Conversely, brown trout were observed in highest abundance at low elevation sites and in one of the tributaries, but were not present at high elevations sites. Further, little overlap was observed in the distribution, with both species present in relatively low abundance at only two sites on the mainstem (Figure 3.1). Abundance of both cutthroat and brown trout was high (as many as 2000 fish/km) and fluctuated little over the two years of this study.

Fulton's condition factor (K) for cutthroat trout and brown trout ranged from 0.9 to 1.1, respectively, indicating that these populations are composed of relatively healthy individuals for both species (Table 3.1). Condition was positively correlated with the elevation of mainstem sites for subadult cutthroat trout (R^2=0.45; df=8; P=0.049), but not for adults (R^2=0.33; df=7; P=0.13). Similarly, the condition of both subadult (R^2=0.64; df=6; P=0.03) and adult brown trout (R^2=0.71; df=5; P=0.03) increased as a function of mainsteam site elevation.

Parasite analyses

Clinical signs that could be attributed to *M. cerebralis* (e.g., black tail, spinal deformities) were observed on less that 1% of more than 4000 trout captured during the field surveys; however, PCR analyses indicated that the parasite was widespread along the drainage. The prevalence of the parasite among cutthroat trout and brown trout varied greatly across sites, from headwaters, to tributaries, to low elevation reaches (*see* Chapter II; Figure 2.2). Differences in prevalence were explained largely by variations in temperature and discharge along the river (*see* Chapter II; Table 2.2 –2.3).

Analyses of invertebrate abundance,
diet, and prey selection

The abundance of invertebrates ranged from 2794 organisms/m² at Forestry Camp to 7082 organisms/m² at Twin Bridges (Table 3.1). Ephemeroptera, Diptera, Trichoptera, and Chironomidae were the most abundant invertebrate groups. The composition of invertebrates did not differed significantly across sites (df=6; P=0.73; Figure 3.2). Fish consumed a variety of aquatic invertebrates (Figure 3.2), organic and inorganic matter, and terrestrial invertebrates (e.g., beetles, crickets, ants). A few cutthroat trout and brown trout diets contained fish (including sculpins). Cutthroat trout and brown trout appeared to have similar prey preferences at Forestry Camp, Third Dam, and

Temple Fork, (Figure 3.3); these species also appeared to select oligochaetes at Twin Bridges and Temple Fork.

Environmental variables

Temperature. --Summer water temperatures along the stream increased from high to low elevation reaches. Average summer daily water temperatures (July-September) ranged from 9.2 °C to 15.9 °C in 2001, and from 8.8 °C to 15.7 °C in 2002. These average daily water temperatures were significantly different among sites (df= 7; P<0.01). Average summer diel temperature in 2001 ranged from 1.8 °C, at one of the tributaries, to 8.8 °C at a mainstem site; a similar pattern was observed in 2002 (Table 3.1).

Discharge. --In general, lower estimates of discharge were observed at high and low-elevation sites and tributaries, while higher estimates were observed at middle-elevation mainsteam sites (Table 3.1). I measured the lowest discharge at one of the tributaries in 2001 (Right Hand Fork, 0.19 m^3/s). The highest summer flows were recorded at a middle elevation mainsteam site in 2001 (Twin Bridges, 1.73 m^3/s) and 2002 (Twin Bridges, 1.95 m^3/s).

Substrate. --Small boulders and large cobbles were predominant in headwaters and mainsteam sites. Coarse gravel is the most common substrate at the lower most site (Lower Logan), while small cobbles were most common at the tributaries (Temple Fork, Right Hand Fork). The highest percentage of fine substrates ($\trianglelefteq$0mm) was observed in one of the tributaries (Temple Fork, 27%). Lower percentages of fines were estimated at low elevation sites (Lower Logan, 3%; Third Dam, 3.5%; Table 3.1).

Periphyton. --A consistent pattern in primary productivity was not evident based on extracts of chlorophyll *a* from rocks in 2001 and from tiles in 2002. Chlorophyll concentrations from rocks ranged between 12 and 183 mg/m², and between 74 and 96 mg/m² on tiles (Table 3.1). No significant differences between sites (df= 7; P=0.56) or years (df=1; P=0.64) were detected.

Factors associated with fish distribution,
abundance, and condition

The abundance of cutthroat trout was positively associated with sediment size (R^2=0.88; P<0.0001) and diel water temperature (R^2=0.68; P=0.003), and negatively associated with brown trout abundance (R^2=0.69, P=0.0029; Figure 3.4). In contrast, brown trout abundance was inversely associated with sediment size (R^2=-0.78; P<0.01), diel water temperature (R^2= -0.57; P=0.02), and discharge (R^2=-0.56; P=0.02; Figure 3.4). Like abundance, cutthroat trout condition was positively associated with sediment size (R^2=0.68; P=0.012) and negatively associated with the abundance of brown trout (R^2= -0.84; P=0.0005; Figure 3.5). Conversely, the condition of brown trout appeared to be associated only with the average minimum water temperature (R^2=-0.64; P=0.03).

Based on this screening for factors associated with cutthroat trout abundance, I selected a two variable model that included the abundance of brown trout and diel water temperature for explaining the variation observed abundance of cutthroat trout across sites (Table 3.2). Sediment size was not included due to its auto-correlation with diel water temperature (R^2=0.62; P=0.01). This model accounted for over 80% of the variation in cutthroat abundance across sites (Table 3.3). For brown trout abundance, we also selected a two variable model that included diel water temperature and sediment size as explanatory variables (Table 3.4). The model explained more than 95% of the variation in abundance of brown trout across sites (Table 3.5). In both cases, models predicted observations well; PRESS residuals representing the difference between observed and predicted numbers of fish were small, averaging 2±6 cutthroat trout and 15±19 brown trout (Figure 3.6).

Discussion

The fish fauna of the Logan River are distributed longitudinally with a distinct allopatric pattern. Cutthroat trout dominated the mainstem headwaters and high-elevation reaches (altitudes above 1800 m), while brown trout dominated reaches at lower elevations of the mainsteam and tributaries. Similar patterns of biotic allopatry, zonation, and species addition along an altitudinal gradient have been documented in other studies (e.g., Fausch 1989). In Sagehen Creek, California, only brook trout were present at high-elevation reaches while three other trout species along with sculpins, suckers, and whitefish were observed at lower elevations (Gard and Flittner 1974). In a Rocky Mountain stream, Rahel and Hubert (1991) identified a fish community pattern that followed the temperature variation along the stream; a coldwater trout assemblage inhabited high-elevation reaches while a warm water assemblage of minnow-sucker (Cyprinidae -Catostomidae) dominated low-elevation reaches. And like in our study, Rahel and Hubert (1991) identified a major gradient of habitat change from high elevation to low elevation sites. Similar examples of biotic zonation and species addition have been documented by Fausch et al. (1994) for two charr species (*Salvelinus leucomaenis* and *S. malma*) in a Japanese island, and by Taniguchi et al. (1998) for brook trout (*Salvelinus fontinalis*), brown trout, and creek chub (*Semotilus atromaculatus*) in Rocky Mountain streams.

The transition between the cutthroat trout and brown trout zones was consistent with changes in environmental characteristics along the Logan River. Cutthroat trout dominated the fish community in mainsteam reaches with the lowest average minimum water temperatures, highest diel water temperatures, and where small boulders and large cobbles were the predominant substrate. In contrast, brown trout dominated reaches where the average minimum water temperature was at least one degree higher than at high-elevation reaches, diel temperature did not exceed 6.2 °C, and the primary substrate types were small cobble and coarse gravel. These results were consistent with other studies that have provided evidence of abiotic factors (e.g., water temperature, discharge, substrate) influencing the distribution and abundance of individual fish species (e.g., Lotrich 1973), as well as the community composition (Hughes and Gammon 1987). These transitions in community composition can be expected in mountainous regions where an increase in water temperature is consistent with a decrease in altitude (Rahel and Hubert 1991). However, even when the temperature does not vary dramatically within the stream, changes in fish community composition and production can also result from shifts geomorphologic features such as stream gradient (Guillory 1982).

Based on the physiological limits of cutthroat trout, it is unlikely that the replacement of cutthroat trout in some reaches and tributaries by brown trout can be attributed to abiotic factors alone (i.e., water temperature). The maximum daily average summer water temperature in the Logan River (8.8 –16 °C) is well below the upper thermal tolerance limit for Bonneville cutthroat trout. Laboratory experiments indicated that 24.2 °C is the estimated 7 d incipient lethal temperature for this species, and that mortality occurs at temperature over 25 °C (Johnstone and Rahel 2003). These experiments also show that fish survived 7 d exposures to a diel cycle of 16 to 26 °C despite a daily-6 h exposure to temperatures higher than 24.2 °C. In addition to these experimental results, field studies indicated that Bonneville cutthroat trout neither moved nor experienced mortality in spite of water temperatures as high as 27 °C in a Wyoming stream (Schrank et al. 2003). The results from all these studies combined suggest that trout survival may depend more on the large daily water temperature fluctuations (10 –13 °C) caused by low nighttime temperatures, as compared to the daily average or maximum temperature. Thus I suspect that higher temperatures (<16 °C) at low-elevation sections of the Logan River, relative to high and middle sections, are not a limiting factor for the distribution of the native cutthroat trout population in this system. Conversely, however, minimum temperatures (this study; Vincent and Miller 1969) and discharge Lobón-Cerviá (2003) may limit brown trout distribution.

Regression analyses provided additional evidence of the influence of both biotic and abiotic factors on trout and salmon distribution and abundance. The best overall model predicting cutthroat trout abundance included the abundance of brown trout as an important factor, as well as diel temperature. In contrast, the best overall model predicting brown trout density included diel temperature and sediment size. These results suggest that brown trout may have a greater effect than cutthroat trout on the longitudinal species distribution and on the abundance of the native cutthroat trout. While declines in cutthroat trout abundance have not been documented in the Logan River during the past decade, it is clear that the brown trout population may contribute to the observed distribution pattern and to any differences in river-wide cutthroat abundance relative to pre-brown trout establishment.

When cutthroat and brown trout do co-exist, we observed lower relative abundances of both species and also a considerable overlap in their diets. Ephemeroptera, Plecoptera, and Trichoptera were the most preferred prey for both trout species, results that are consistent with other studies that have also identified these invertebrates to be among the major components of trout and salmon diets (Glova and Sagar 1991; Kusabs and Swales 1991; Sagar and Glova 1995). The overlap in the diets of native cutthroat trout and brown trout, and the inverse correlation between the condition of cutthroat trout and the abundance of brown trout suggest the potential for competitive interactions among these species. The combination of results from this study demonstrated the potential for negative interactions, perhaps in the form of competition, between native cutthroat trout and introduced brown trout. In related experimental work on the same system, cutthroat trout appeared to be more affected by brown trout than the converse. When held in sympatry, cutthroat trout demonstrated lower growth and condition as compared to allopatric treatments. Conversely brown trout appeared to be largely unaffected by cuts and were more affected by intraspecific increases in density (Budy et al. 2003). Interspecific competition among salmonids has been documented in other studies and is suspected to lead to the altitudinal distribution patterns observed in many trout streams (Fausch and White 1981; Fausch 1988; Nakano 1995). Competitive interactions may also play a decisive function in the replacement of species. For example, Fausch (1989) and De Sato and Rahel (1994) provided evidence of the vulnerability of cutthroat trout to displacement by brook trout, a factor that is considered to be a major contributor in the displacement of native cutthroat trout from their native range (Gresswell 1988).

Finally, my analyses indicated that in addition to the potential interspecific interactions among trout species, the widespread distribution of *Myxobolus cerebralis* along the Logan River poses an additional threat to the native cutthroat trout population. This parasite has been implicated in severe trout population declines in other streams (Nehring and Walker 1996; Vincent 1996). Despite the distribution and high prevalence of *M. cerebralis*, there has been no evidence of population level effects in the Logan River as of yet (Thompson et al. 2000; Budy et al. 2002). However, given that the parasite became recently established in this drainage, the overlapping cohorts of all ages of trout (Budy et al. 2003), and that the susceptibility to the parasite is greater on juvenile fish, there could be a considerable time lag before a population level effect could be observed. Further, the range of environmental characteristics of the Logan River (e.g., temperature, discharge) also appear to contributed to the variability in *M. cerebralis* prevalence, and could explain in part why clinical signs of whirling disease were rare (*see* Chapter II).

Identifying the factors, whether biotic, abiotic, or a combination of both, that determine the distribution and abundance of trout species is crucial to effectively manage the Logan River and other trout streams, where ensuring the conservation of native cutthroat trout populations is a top priority. This study was conducted to provide insights to the factors that affect the distribution, abundance, and condition of salmonid populations. I identified abiotic and biotic factors that appear to determine, in part, the distribution of fish along the Logan River; identifying the mechanisms that drive this pattern warrant further consideration. Moreover, I provide base line information for the distribution and prevalence of *M. cerebralis*. The effects of this parasite on the salmonid populations in the Logan River, and particularly on the native cutthroat trout, may not be fully realized yet. Changes in environmental characteristics (e.g., an increase in temperature) or biotic variables (e.g., expansion of less vulnerable brown trout that act as disease vectors) could lead to higher probability of infection, the development of whirling disease, and detrimental effects at a population level. Finally, my regression models for predicting cutthroat and brown trout abundance and distribution may aide in developing sound management and conservation plans for trout and salmon populations in similar stream systems across the intermountain west.

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Table 3.1. Summary of trout condition (Fulton's K), invertebrate abundance, and environmental variables for 8 sites along the Logan River, Utah. *See* Figure 3.1 for site locations. Data for trout condition and environmental factors was collected during summer in 2001 and 2002.

SITE	Year	Elevation (m)	Condition (K)[a]		Invertebrates[b] (#/m²)	Temperature[c] (°C)				Discharge[d] (m³/sec)			Chl *a*[e] (mg/L)			Substrate[f]	
			cutthroat	brown		diel	min	max	avg	min	max	avg	min	max	avg	avg (mm)	fines (%)
Franklin Basin		2052	1.07		5676	7.3	4.9	15.4	9.2	0.26	0.55	0.37	14	81	47	209	1
Red Banks		1949	0.98			7.7	5.1	17.7	11.0	0.59	0.84	0.71	10	93	44	287	0
Forestry Camp		1889	1.05		2794	8.8	6.2	18.8	12.1	0.40	0.96	0.62	51	244	120	283	10
Twin Bridges	2001	1686	1.08	1.15	7082	6.2	7.2	16.8	11.8	1.38	2.30	1.73	18	116	64	143	6
Third Dam		1521	0.90	1.07	4806	6.0	7.5	16.9	12.1	0.95	1.26	1.08	52	447	182	38	6
Lower Logan		1370		0.92	3750	2.5	13.2	18.7	16.0	0.65	0.73	0.68	21	196	95	137	1
Temple Fork		1785	1.05	0.96	4752	8.5	5.4	17.3	10.6	0.28	0.67	0.44	60	437	183	23	24
R. H. Fork		1698		0.93	6494	1.8	9.8	12.8	10.8	0.17	0.22	0.20	0	64	12	46	13
Franklin Basin		2052	0.95			6.7	4.8	14.2	8.8	0.28	0.72	0.47	69	82	74	173	14
Red Banks		1949	1.02			7.3	5.6	17.1	10.6	0.74	1.91	1.11	67	106	80	252	14
Forestry Camp		1889	1.01	1.05		8.5	6.0	18.6	11.6	0.43	1.56	0.90	62	147	86	258	14
Twin Bridges	2002	1686	1.01	1.08		5.5	7.2	16.1	11.7	1.38	2.89	1.95	60	90	78	236	4
Third Dam		1521	0.93	0.96		4.1	8.8	16.1	12.3	0.65	0.89	0.76	60	95	75	205	1
Lower Logan		1370		0.92		3.2	12.4	19.0	15.7	0.64	1.55	0.94	76	103	91	40	5
Temple Fork		1785	0.90	1.13		8.1	5.5	17.0	10.6	0.29	0.38	0.35	61	114	75	123	30
R. H. Fork		1698		1.08		1.7	9.6	12.1	10.7	0.16	0.23	0.19	58	132	96	105	11

[a] Fulton's (K) condition factor.
[b] Estimates of invertebrate abundance provided by the National Aquatic Monitoring Center (M. Vinson, National Aquatic Monitoring Center- Utah State University, personal communication).Based on samples collected in 1997-2000.
[c] Estimated average diel, minimum, maximum, and summer (July-September) temperatures.
[d] Minimum, maximum, and average discharge during summer (July-September) base-flow conditions.
[e] Chlorophyll *a* extracted from rocks (2001) and artificial substrates (2002); used as an index of productivity.
[f] Average substrate size and estimated percentage of fine sediments (<10mm).

Table 3.2. Best-subset regressions for variables associated with the abundance of cutthroat trout. Natural log transformation is indicated by (ln). Square-root transformation is shown as (sqrt). The asterisks (**) indicate the model selected for multiple linear regression analyses.

Variables in model	R^2	Adjusted R^2	C(p)	AIC	MSE	Variables in Model
1	0.7472	0.7051	3.4449	36.4968	77.4611	ln_sediment [a]
1	0.7402	0.6969	3.6520	36.7163	79.6161	sqrt_btpop [b]
1	0.5522	0.4776	9.1879	41.0709	137.2142	ln_dieltemp [c]
2**	0.8597	0.8036	2.1323	33.7872	51.5942	sqrt_btpop ln_dieltemp
2	0.8183	0.7456	3.3525	35.8570	66.8285	ln_dieltemp ln_sediment
2	0.7803	0.6925	4.4693	37.3731	80.7725	sqrt_btpop ln_sediment
3	0.8642	0.7623	4.0000	35.5269	62.4275	sqrt_btpop ln_dieltemp ln_sediment

[a] Natural log of the average sediment size.
[b] Square-root of the estimated abundance (fish/km) of brown trout.
[c] Natural log of the average summer (July- September) diel water temperature.

Table 3.3. Summary of linear regression model for cutthroat trout abundance in the Logan River, Utah. Parameter estimates are also given.

Source of variation	df	Sum of Squares	Mean Square	*F*	*P*	Adjusted R^2
Model	2	1580.6468	790.3234	15.32	0.0074	0.8036
Error	5	257.9711	51.5942			
Corrected Total	7	1838.6179				

Variable	df	Parameter estimate	Standard error	*t*	*P*
Intercept	1	10.9287	11.6162	0.94	0.3900
sqrt_btpop [a]	1	-0.6017	0.1818	-3.31	0.0212
ln_dieltemp [b]	1	11.0172	5.3386	2.06	0.0940

[a] Square-root of the estimated abundance (fish/km) of brown trout.
[b] Natural log of the average summer (July- September) diel water temperature.

Table 3.4. Best-subset regressions for variables associated with the abundance of brown trout. Natural log transformation is indicated by (ln). Square-root transformation is shown as (sqrt). The asterisks (**) indicate the model selected for multiple linear regression analyses.

Variables in model	R^2	Adjusted R^2	C(p)	AIC	MSE	Variables in Model
1	0.8797	0.8596	23.2992	31.7810	42.9618	ln_sediment [a]
1	0.7402	0.6969	54.9453	37.9390	92.7643	sqrt_ctpop [b]
1	0.2711	0.1497	161.3616	46.1912	260.2355	ln_dieltemp [c]
1	0.0516	-0.1065	211.1757	48.2978	338.6298	ln_discharge [d]
2**	0.9710	0.9594	4.5859	22.4056	12.4373	ln_dieltemp ln_sediment
2	0.9572	0.9401	7.7080	25.5098	18.3334	sqrt_ctpop ln_sediment
2	0.8801	0.8321	25.2066	33.7539	51.3793	ln_discharge ln_sediment
3	0.9800	0.9649	4.5453	21.4389	10.7296	ln_dieltemp ln_discharge ln_sediment
3	0.9733	0.9533	6.0596	23.7393	14.3044	sqrt_ctpop ln_dieltemp ln_sediment

[a] Natural log of the average sediment size.
[b] Square-root of the estimated abundance (fish/km) of cutthroat trout.
[c] Natural log of the average summer (July- September) diel water temperature.
[d] Natural log of the average discharge during summer base flow conditions (July-September).

Table 3.5. Linear regression model with brown trout abundance as dependent variable, and sediment size and diel temperature as predictor variables.

Source of variation	df	Sum of Squares	Mean Square	*F*	*P*	Adjusted R^2
Model	2	2080.0695	1040.0347	83.62	0.0001	0.9594
Error	5	62.1867	12.4373			
Corrected Total	7	2142.2562				

Variable	df	Parameter estimate	Standard error	*t*	*P*
Intercept	1	107.3256	6.8642	15.64	<0.0001
ln_sediment[a]	1	-15.4742	1.4094	-10.98	0.0001
ln_dieltemp[b]	1	-9.1474	2.3067	-3.97	0.0107

[a] Natural log of the average sediment size.
[b] Natural log of the average summer (July- September) diel water temperature.

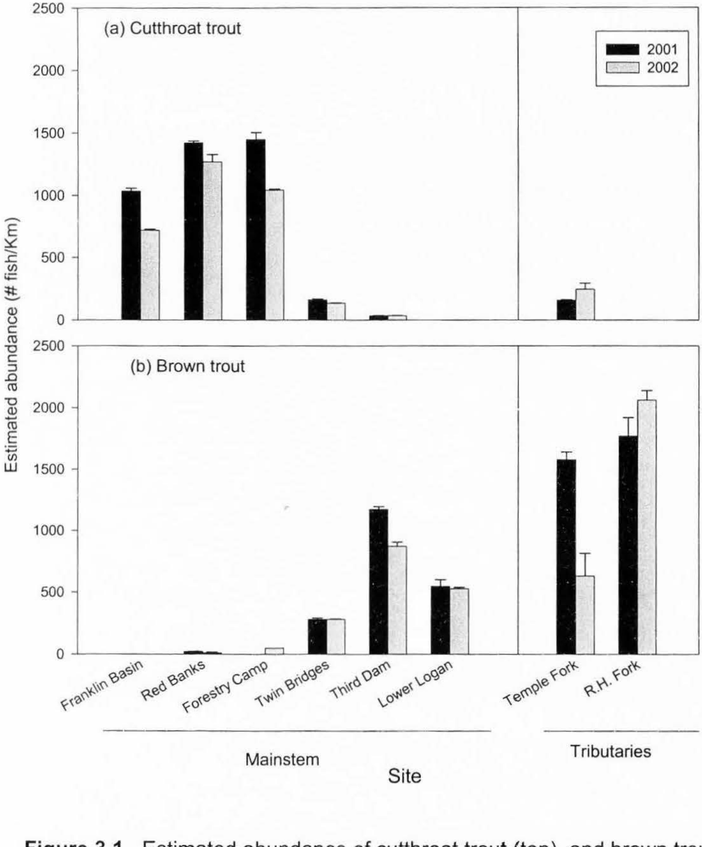

Figure 3.1. Estimated abundance of cutthroat trout (top), and brown trout (bottom) at mainstem and tributary sites in the Logan River, Utah. Mainsteam sites are organized left to right from high to low-elevation. Error bars represent ± 1 SE.

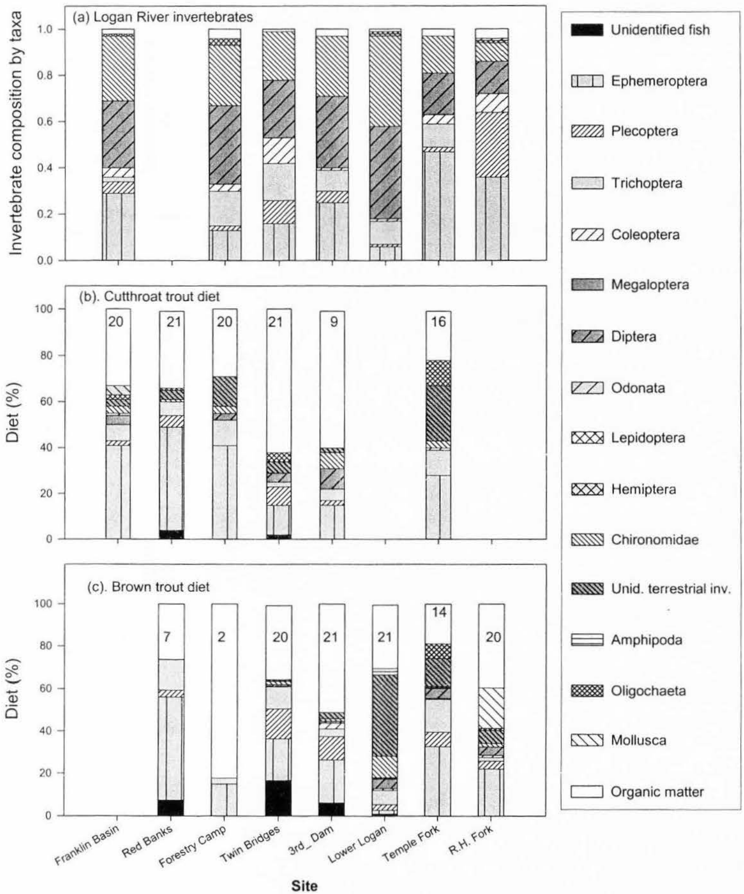

Figure 3.2. Invertebrate composition by taxa in the Logan River (a), and diet composition by wet weight in cutthroat trout (b) and brown trout (c). Sample size (n) is given on bars.

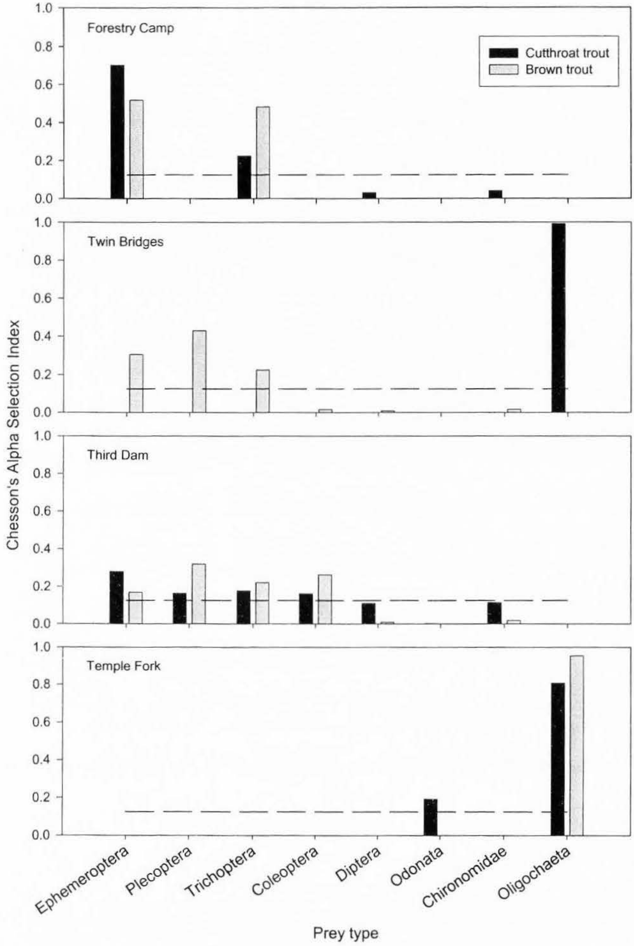

Figure 3.3. Chesson's alpha selection index for cutthroat trout and brown trout at four sites on the mainstem and one tributary (Temple Fork) of the Logan River, Utah. Dashed lines indicate the level at which there is a preference for a particular food item.

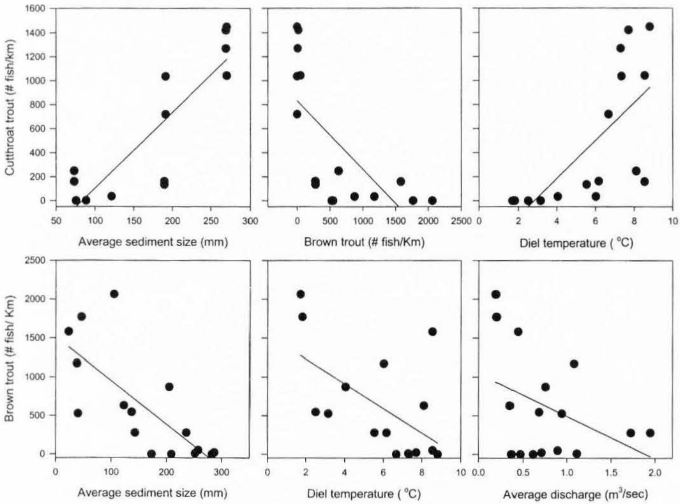

Figure 3.4. Scatterplots of cutthroat trout (top) and brown trout abundance (bottom) in relation to different environmental variables. Statistical results for Pearson correlations (lines) are provided in the text.

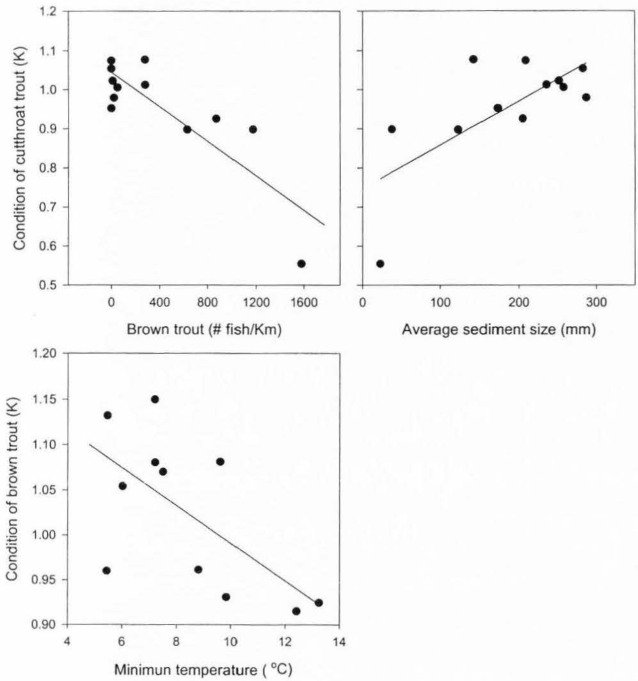

Figure 3.5. Scatterplots of Fulton's (K) condition factor for cutthroat trout (top) and brown trout (bottom).

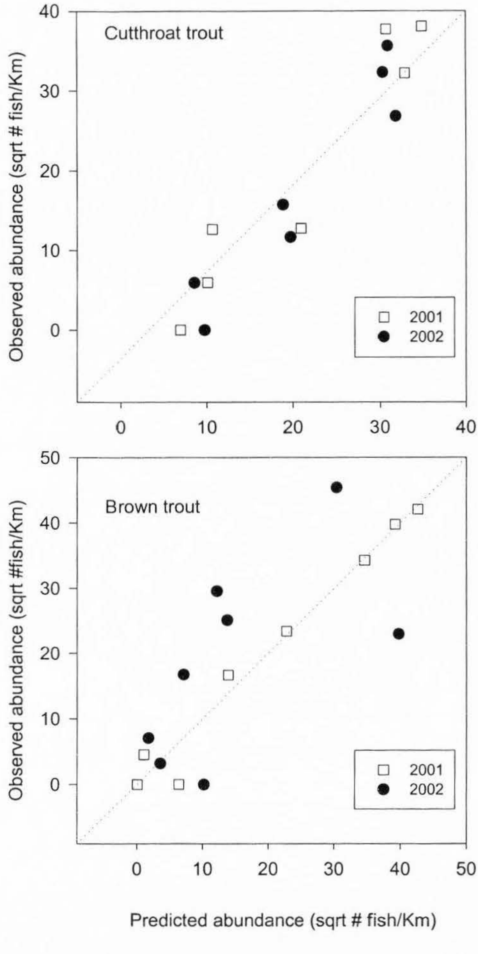

Figure 3.6. Predicted versus observed fish abundances based on PRESS residuals for cutthroat trout (top), and brown trout (bottom).

CHAPTER IV

SUMMARY

Understanding the current and potential effects of *Myxobolus cerebralis,* the parasite that causes whirling disease, in the Logan River is important to effectively manage this system, as well as other streams where native cutthroat populations are threatened. While other authors have suggested that environmental factors could lead to the variability in the response of susceptible trout populations to *M. cerebralis*, few studies have been designed to identify and enhance the understanding of such factors. In the first phase of my thesis, I investigated the potential relationship between the prevalence of *M. cerebralis* and suit of environmental variables hypothesized to be influential in determining its distribution and effects of in wild salmonid populations. To do this, I assessed potential relationships between temperature, discharge, substrate size, nutrient concentration, primary productivity, the relative abundance of *Tubifex tubifex*, and the distribution and prevalence of *M. cerebralis* in wild and sentinel fish. In addition, I evaluated the importance of these factors in the development of a predictive model relating potential increases in prevalence of the parasite to differences or variations in environmental factors.

The diagnosis of *M. cerebralis* in wild and sentinel fish revealed that the parasite is widespread along the mainstem and at least one of the tributaries of the Logan River. However, inconsistencies in the prevalence of wild and sentinel fish suggested that fish movement may be an important vector leading to the spread of the parasite in the Logan River drainage. In addition, much of the variability in prevalence across sites could be explained by differences in temperature and discharge. Temperatures above or below the ideal range for the life cycle of *M. cerebralis* at headwaters, tributaries, and low-elevation reaches of the Logan River, were associated with lower prevalence of the parasite detected at these sites. While other authors have suggested high water discharge may reduce the rate *M. cerebralis* infection by destroying the parasite's spores or diluting their concentration, my results indicated an asymptotic relationship between discharge and prevalence. This relationship indicated that low base flow discharge at headwaters and tributaries may decrease the probability of spores contacting and infecting susceptible fish. In contrast, higher base flow discharge likely disturbs areas where spores may be concentrated, therefore increasing the probability of infection up to a maximum. Above this maximum discharge level, the concentration of spores in the water column may be reduced and could lead to lower infection rates. In addition, multiple linear regression models that included both temperature and discharge were significant overall and explained a large proportion of the variability in the prevalence of *M. cerebralis*.

The second phase of my thesis research was intended to gain insight into the factors that influence the distribution, abundance, and condition of trout populations in the Logan River. My results indicated that the fish fauna are distributed longitudinally with an allopatric distribution of the two dominant species. Cutthroat trout dominated the headwaters and high-elevation reaches, while reaches at lower elevations of the mainstem and tributaries were dominated by brown trout. The transition zone between the two dominant populations was consistent with changes in environmental characteristics along the river. Cutthroat trout dominated the fish community in mainstem reaches with the lowest average minimum temperatures, highest diel temperatures, and where the substrate consists predominantly of small boulders and large cobbles. These results were consistent with other studies that have provided evidence of abiotic factors influencing the distribution and abundance of individual fish species.

Further, my analyses indicated a considerable overlap in the diets of sympatric cutthroat trout and brown trout. Linear regression models suggested that both biotic and abiotic factors influenced the trout distribution and abundance. For cutthroat trout, the best model for predicting abundance included brown trout abundance and diel temperature, whereas for brown trout, the best model for predicting abundance included diel temperature and sediment size. These analyses suggested that brown trout may have a greater effect on the species distribution and abundance of cutthroat trout, than the opposite, suggesting the potential for competitive interactions among these native and introduced species.

My study not only provides baseline information of the distribution and prevalence of a parasite that poses a threat to salmonid populations in the Logan River, but also provides insights of pathogen-host-environment interactions needed to fully understand and asses the potential effects of *M. cerebralis* in other trout populations. In addition, I identified abiotic and biotic factors that may determine, in part, the distribution of fish along the Logan River. My research contributes to the understanding of the factors that influence the distribution and abundance of trout species; the understanding of these factors is crucial to effectively manage this system and to ensure the conservation of native trout populations.

APPENDIX

Historical data on trout population abundance in the Logan River, Utah

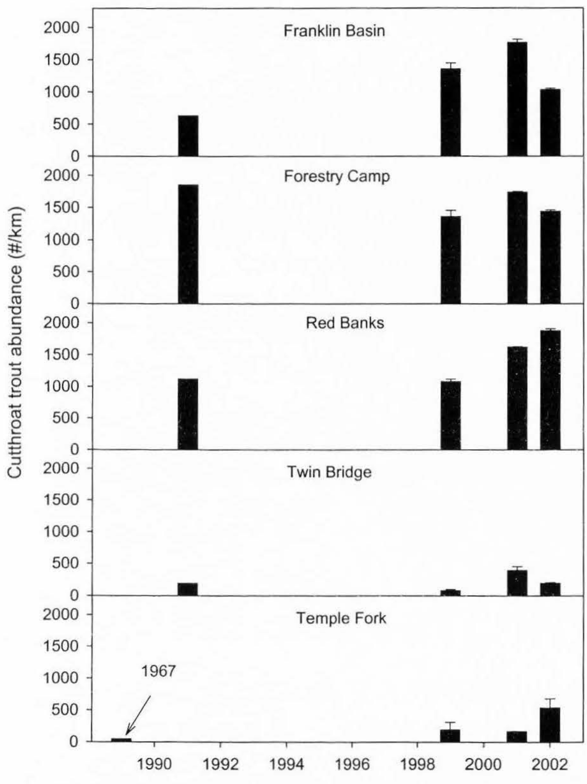

Figure A.1. Population estimates for cutthroat trout for four sites on the mainstem of the Logan River and one tributary (Temple fork). Error bars represent 95% confidence intervals. Based on Wullschleger (1991), and Thompson (1999).

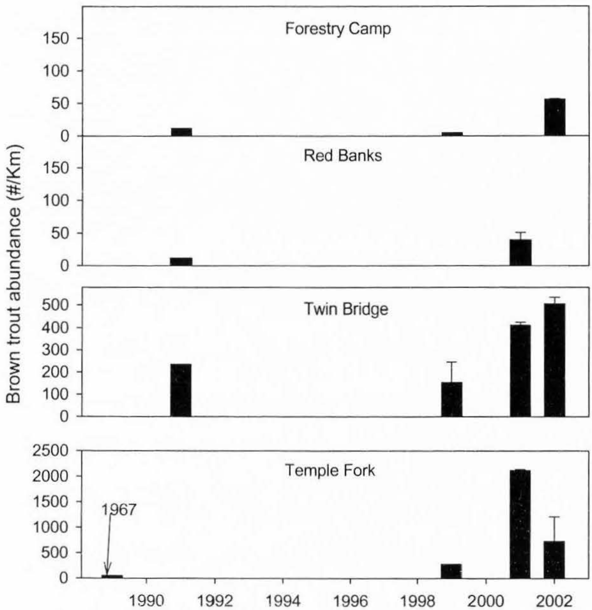

Figure A.2. Population estimates for brown trout for three sites on the mainstem of the Logan River and one tributary (Temple fork). Error bars represent 95% confidence intervals. Based on Wullschleger (1991), and Thompson (1999).

References

Thompson, P., S. Tolentino, K. Sorenson, and B. Nielson. 2000. Bonneville cutthroat trout (Oncorhynchus clarki Utah) survey and monitoring activities in the Logan River (Sections 05-07) Drainage, 1999. Utah Division of Wildlife Resources, Publication 00-3, Salt Lake City, Utah.

Wullschleger, J. 1991. Logan River fish population surveys: preliminary evaluation of special regulations. Utah Division of Wildlife Resources, Ogden, Utah.