TROUT POPULATION RESPONSES TO WHIRLING DISEASE EPIZOOTICS IN MONTANA RIVERS

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ABSTRACT — Whirling disease has spread rapidly throughout the United States the past 20 years, but predicting its impacts to trout populations has been problematic. Using a database that contained mark-recapture information for 384,938 trout during the years 1980-2007, a before-after control-impact study design was used to analyze data from infected river sections and non-infected reference sections on six blue-ribbon Montana rivers (Missouri, Blackfoot, Bitterroot, Gallatin, Ruby rivers and Rock Creek) having severe whirling disease infections. A Bayesian mark-recapture model indicated that disease had a strong negative effect on abundance of small (200-300 mm total length) rainbow trout *Oncorhynchus mykiss*, with abundance declining an average of 50% (range 30-69%) of pre-disease levels. This marked decline was consistent across all study rivers. In contrast, a parallel decline in larger fish was not observed; instead, the numbers of rainbow trout >300 mm long either remained the same or increased after whirling disease, with the magnitude of the changes varying by river. Rainbow trout of all size classes showed no reduction in growth or condition after a whirling disease outbreak, suggesting that those fish that survive initial infection do not suffer survival or performance deficits even in highly infected systems. As anticipated, there were generally few changes in brown trout density following whirling disease. The exception was in Rock Creek, where decline in rainbow trout from 90% of total trout density to 20-30% after whirling disease was met by a similar magnitude increase in brown trout. Across all rivers, high infectivity levels coincided with low stream flows since 2000, indicating drought may have exacerbated whirling disease impacts on rainbow trout.

INTRODUCTION

Whirling disease, an infection of salmonids caused by the non-indigenous metazoan parasite *Myxobolus cerebralis* has rapidly expanded over the past 20 years (Bartholomew and Reno 2002). The parasite has now been detected in 22 states, and continues to spread, threatening wild salmonid populations (Bartholomew and Reno 2002; Arsan et al. 2007). Whirling disease has led to major declines in high value recreational trout fisheries throughout the western United States (Nehring and Walker 1966; Vincent 1996). In Colorado, an estimated 560 km of premier trout streams have experienced long-term declines in rainbow trout *Oncorhynchus mykiss* populations; in some locales, declines of 90% of rainbow trout density and biomass have persisted for over 10 years (Nehring and Thompson 2003). For example, in the Gunnison River, Colorado, 150-mm and larger rainbow trout during pre-whirling disease years of the 1980s averaged about 3,400 per km, but subsequent population estimates yielded 531 per km in 1998 and 86 in 2003 (Nehring 2006).

Whirling disease was first confirmed in Montana in 1994 following sharp declines in Madison River rainbow trout (Vincent 1996). This discovery precipitated a statewide program to monitor the spread of the parasite using caged sentinel fish (Baldwin et al. 1998). The disease is now found in most western Montana trout rivers at varying severity levels (Vincent 2003).

One of the perplexing problems with whirling disease has been the high variation reported in population responses to infection. Some infected trout populations have severely declined (Vincent 1996; Nehring 2006), whereas others reportedly showed no detectable effects (Modin 1998; Kaeser et al. 2006). In a review of whirling disease impacts in Colorado, such a wide range of responses led Nehring (2006) to conclude that "it is very difficult to predict with any degree of certainty where, when and under what circumstances the impact of *M. cerebralis* might be devastating and where it would be benign." Although the difficulty in forecasting population impacts from the disease is not unexpected given the dynamic and complex nature of the host-parasite-environment relationship (Kerans and Zale 2002), how the parasite affects salmonids at the population level is of key interest for assessing disease impacts; however, there have been few in-depth studies of trout population dynamics following epizootic outbreaks of whirling disease (Karr et al. 2005).

E. R.Vincent (Montana Fish, Wildlife, and Parks, pers. comm.) noted that rainbow trout population declines in some Montana rivers occurred when 50% or more of sentinel fish had disease severity scores of 3 or more on the MacConnell-Baldwin scale (0 = uninfected, 5 = severe infection). Fish with this level of infection exhibit clinical symptoms of disease including whirling behavior, blacktail, skeketal deformities, and poor survival and performance (Ryce et al. 2005; DuBey et al. 2007). However, the linkage between disease severity observed in sentinel fish and disease severity and population effects in wild fish is uncertain. If population-level effects could be tied to a disease-severity threshold measured from sentinel fish, trout population response could be more reliably predicted based on measured infectivity levels in the field, which would thereby result in improved risk-assessment (Bartholomew et al. 2005).

In this study, we used a before-after control-impact (BACI) study design to assess if trout populations in six different river drainages in Montana exhibit similar responses to severe whirling disease epizootics. These drainages have a unique combination of long-term fish population, whirling disease, and environmental data that allow a detailed analysis of population response to a whirling disease epizootic under varying biotic and abiotic factors. We also assessed possible compensatory growth and survival responses to whirling disease outbreaks by examining other metrics in addition to changes in abundance including recruitment, growth, condition, size structure, and trout species composition before and after the onset of whirling disease.

Methods

We estimated trout population change before and after whirling disease outbreaks on the Missouri, Gallatin, Ruby, Blackfoot, and Bitterroot rivers, and Rock Creek. We compared disease 'impacted' sections to un-impacted 'reference' river sections using a before-after (BA) control-impact (CI) design. 'Reference section' was a river reach that had no or low infection (0-2 disease severity ranking) relative to 'impacted' river sections where there has been a sustained infection risk of 50% or more of sentinel cage fish showing moderate to severe lesions (>3 disease severity ranking) indicative of severe infection. Reference sections were located from 16 to 55 km from impacted sections, a sufficient distance such that the sections can be reasonably considered independent of each other. Infection severities were based on sentinel fish cages deployed on each river since the mid-to-late 1990s (Vincent 2003).

Trout population data were obtained from Montana Fish, Wildlife, and Parks records. Trout population data have been collected in a consistent fashion on Montana rivers since the early 1980s using electrofishing mark-recapture techniques over the same, long sampling sections (1.5-9.0 km) at multiple sites within each drainage (Vincent 1982). The final database was comprised of 384,938 trout collected during the years of 1980 to 2007. Population estimates were generated for all length classes of rainbow trout and brown trout *Salmo trutta* using a Bayesian mark-recapture population estimator developed specifically for this study. Bayesian estimators offer advantages over traditional maximum likelihood estimators (Link and Barker 2010), particularly when the number of parameters is large, as it was for these data, when some of the parameters are related in a hierarchical manner, and when there is interest in estimating additional quantities that are derived from the estimated parameters. The year of first severe whirling disease (WD) infection for the 'infected' reach demarcated the 'before' versus 'after' population estimates. For each site, averaged population size before that time point was used to create a baseline 'before whirling disease' abundance estimate. To quantify population changes after whirling disease, all 'after whirling disease' abundance estimates were divided by their respective baselines, and the population change values were transformed using the $\log_2$ scale because on this scale a doubling of population will be conveniently indicated as a +1 and a halving by -1. Three models were fitted for each set of data: (Model 1) no whirling disease effect (no BA x CI interaction); (Model 2) whirling disease effect (BA x CI interaction term included); (Model 3) whirling disease effect by river (additional variable added to account for variation in response to the disease among individual rivers). Model outputs were generated for 2,400 runs using WinBUGS, a Bayesian software program for conducting Markov chain Monte Carlo analyses (Lunn et al. 2000). We used the 'deviance information criterion' or DIC, an information-theoretic based model selection procedure that can be used in a Bayesian setting (Spiegelhalter et al. (2002) to select among the three competing models. The BACI analyses were run for the four rivers with adequate BACI data: Blackfoot, Gallatin, Missouri, and Ruby rivers; all four rivers had both reference and severely infected sections and multiple years of post-whirling disease data. Two other study rivers, Rock Creek and the Bitterroot River, were treated separately; Rock Creek had before-after data but no reference section, and the Bitterroot River had only one year post-whirling disease data. In addition to the BACI analysis comparing population responses by individual length classes, we also compared total density, biomass, relative species composition, relative weight *Wr*, and growth rate.

RESULTS

Model analysis revealed a strong negative effect of whirling disease on abundance of small rainbow trout (model 2 favored as best model). For all rivers combined, the median proportional decline in small rainbow trout 200-300 mm long after whirling disease was greater than two-fold (0.55 or -1.15 on the $\log_2$ scale; Figure 1). For individual rivers, the decline was highest for the Gallatin (0.69) and Missouri rivers (0.59) and less so for the Blackfoot (0.46) and Ruby (0.30) rivers. In contrast, larger rainbow trout (300-450 mm) showed a significant positive increase (1-2 fold increase) after whirling disease, depending on river (model 3 favored). The strongest increase was shown in the Gallatin and Missouri rivers, and little to no response in the Ruby and Blackfoot rivers. For the largest rainbow trout size class (475-500 mm), all three models had nearly equal DIC values, indicating all three were equally plausible, suggesting the lack of a strong effect of whirling disease.

The before-after analysis of Rock Creek, which lacked a disease-free reference section, showed an even stronger negative whirling disease effect. For rainbow trout 200-300 mm long, there was nearly a four-fold (-1.99 on $\log_2$ scale) decline in abundance after whirling disease (Figure 2). As in other rivers, there was a significant increase in the largest rainbow trout (425-450 mm) after whirling disease, although this response was observed in only one of the two sampling sections. There was only one year of post-whirling disease population data for the main stem Bitterroot River. However, it is noteworthy that the abundance of small rainbow trout 200-300 mm in the whirling disease-positive Darby section was only 30 fish per km in the post-WD year of 2005, 90% below the long-term pre-whirling disease average density of 286 per km from 1989-2002. In contrast, the abundance of small rainbow trout in the reference section (Bell) was similar across all years.

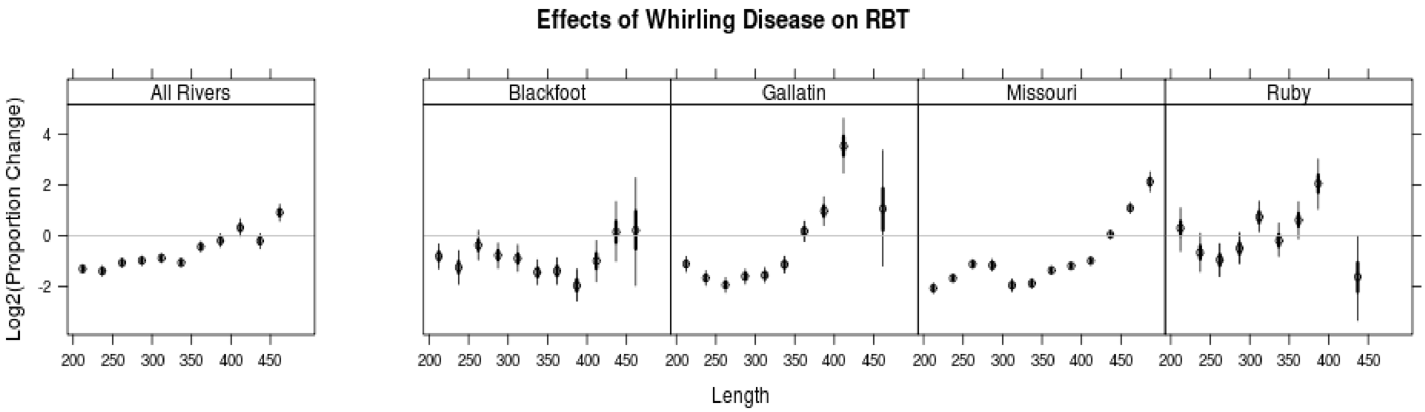

Figure 1. Proportional change in rainbow trout (RBT) density (by length class) after whirling disease outbreaks in four Montana rivers. Analyses based on data collected from 1980 to 2007. The "0" line indicates no difference between reference and whirling disease-infected sites. Values below the line indicate a decrease in density, and values above the line indicate an increase in density compared to the baseline 'pre-whirling disease' density.

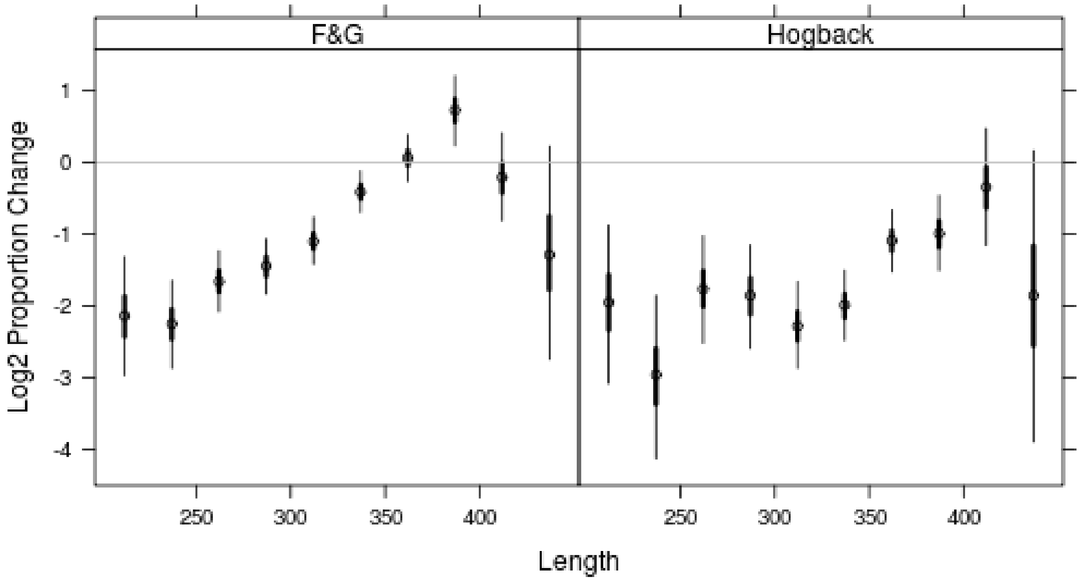

Figure 2. Proportional change in rainbow trout density by length class in two river sections of Rock Creek, Montana, after whirling disease (F&G=Fish and Game section). Analyses based on data collected from 1981 to 2006.

As expected, whirling disease had little effect on brown trout abundance of any size class (model 1 most favored; Figure 3). Rock Creek was an exception, with significant positive increases in abundance of some size classes after whirling disease. The strongest response was shown for brown trout 325-400 mm long, where abundance increased about 2-to-4-fold after WD.

Rainbow trout were the predominant trout in all study rivers, ranging in proportion from 60-90% pre-whirling disease. Most rivers showed little change in the overall proportion of rainbow trout and brown trout pre- and post-whirling disease, with the exception of Rock Creek, which showed a major shift from rainbow trout to brown trout over the study period, from >90% rainbow trout to about 20-30% of total density from 2000-2006.

Whirling disease did not appear to adversely affect trout condition. Trout in the Missouri River were the only group that showed a significant decline in *Wr* after whirling disease. However, this decline was observed in rainbow trout in both the disease-positive (Craig) and disease-negative (Cascade) sections so that the increase could not be clearly attributed as a response to whirling disease. Whirling disease appeared to result in increased

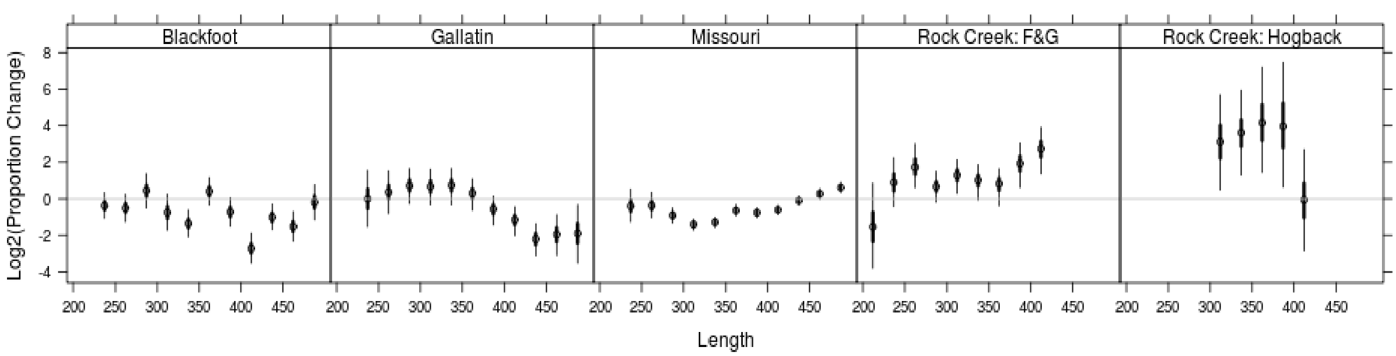

Figure 3. Proportional change in brown trout density in four Montana rivers after whirling disease. Analyses based on data collected from 1980 to 2007.

growth of larger rainbow trout and brown trout. Mean length at age-4+ rainbow trout in the disease-positive Craig section was 499 mm after whirling disease, an increase of 31 mm from pre-whirling disease years ($P = 0.03$). Mean length of age-3 rainbow trout was also substantially higher after whirling disease (+22 mm; $P = 0.07$). In contrast, there were no differences in length at age for any age class among rainbow trout from the Cascade reference section. Age estimates were not available for any other river, limiting comparisons of survival and growth among specific age groups.

Discussion

Overall, we found that whirling disease outbreaks led, on average, to a 50% decline (range 30 to 69%) in rainbow trout in the 200-300 mm size class. The decline is likely due to poor survival of age-0 cohorts, because rainbow trout < 9 weeks of age and <40 mm in length are the most highly vulnerable life stage to whirling disease (Ryce et al. 2005). Contrary to our expectations, the marked decline in smaller rainbow trout after whirling disease outbreak did not lead to major declines in larger fish, as observed in Colorado rivers (Nehring and Thompson 2003). Instead, the numbers of rainbow trout >300 mm long either remained the same or increased after whirling disease, with the effects varying by river. Though the lack of decline could be partially attributed to a lag effect wherein low age-0 recruitment has not yet had time to negatively affect subsequent numbers of larger fish, rivers with 5 or more years since the inception of high infectivity (Blackfoot, Gallatin, and Missouri rivers, Rock Creek) showed a similar pattern of stable or increasing numbers of larger trout. The rapidity of the response in abundance, particularly among very large rainbows >400 mm long, coupled with increased growth shown by large Missouri River rainbow trout following whirling disease, suggests a compensatory response in survival and growth. Small and large fluvial rainbow trout share a similar (insectivorous) diet and display strong inter-cohort competition; marked reductions in the density of small trout, as observed in our study, has been shown to increase growth and survival of large trout (Nordwall et al. 2001). In the Missouri River, adult declines have been anticipated for many years once older rainbow trout died out, but the adult population remains robust and the average size of large trout continues to increase, suggesting that survival and growth of large, old rainbow trout in river systems may be much more flexible than previously thought. More detailed examination of age, growth, and survival of these older fish would be a fruitful area for further research.

Why the recruitment declines in rainbow trout we observed were not as severe as those in previous reports of trout response to whirling disease epizootics is uncertain. Declines of juvenile trout recruitment by 90% or more were reported for multiple Colorado rivers (Nehring and Thompson 2003; Nehring 2006) and for the Madison River in the first 8 years following whirling disease outbreak (Vincent pers. comm.) compared to the 50% decline observed in our study. High infectivity of young trout by the parasite requires high spatial overlap between infective spore release and fry emergence within a relatively narrow time window (Downing et al. 2002; MacConnell and Vincent 2002). We suspect that the lack of severe recruitment decline of juvenile rainbow trout was due to the continued presence of uninfected spawning areas even in highly infected rivers (Granath et al. 2007; Pierce et al. 2009). Recruitment from these sites likely serves to maintain rainbow trout populations in these systems, although the relation between recruitment sources and infection risk has not been investigated in detail (but see Pierce et al. 2009).

As expected, whirling disease did not appreciably influence brown trout abundance. Brown trout populations remain largely unchanged in multiple Colorado rivers experiencing major declines in rainbow trout after whirling disease outbreaks (Nehring 2006). In our study, reductions in rainbow trout biomass or density after whirling disease were generally compensated to a similar degree by an increase in biomass and density of brown trout. Though the two species generally occupy different fluvial habitats as adults, the two species may still compete for preferred habitats (Gatz et al. 1987). The major shift in dominance from rainbow trout to brown trout observed in Rock Creek has not been reported in any other rivers following a whirling outbreak. Berg (2004) hypothesized that a combination of high infection risk, low flows, and warmer temperatures over the past 10 years has likely promoted this shift to brown trout dominance in that system.

High infectivity and recruitment declines in juvenile rainbow trout in our study occurred concurrently with significant drought during 2000-2007. Summer flows during this period were 25% or more below the long-term average flow in at least 6 of the last 7 years. Many possible measures of flow were considered as possible covariates in the BACI model, and some of them improved the model fit, suggesting an interaction of whirling disease and flow, with lower flows and high whirling disease both negatively affecting young rainbow trout in the years since 2000.

The association between flow and rainbow trout population response to whirling disease lends support to the hypothesis that lower flows contribute to higher infectivity of salmonid hosts by *M. cerebralis* (MacConnell and Vincent 2002; Hallett and Bartholomew 2008). The reduced velocities at lower flows are thought to promote retention and accumulation of infective stages, settlement of salmonid carcasses, and the deposition of fine sediments that create habitat and a food source for the tubificid worm host (Kerans and Zale 2002; Hallett and Bartholomew 2008).

Conclusions and Management Considerations

Outbreaks of whirling disease epizootics in our Montana study rivers led to an average 50% decline in juvenile rainbow trout. Although the degree of recruitment decline in relation to infection grade level was not evaluated in this study, the results suggest that marked recruitment declines will occur in wild rainbow trout populations when sentinel cage infection levels exceed 50% or more with grade $\geq$3.

The marked decline in small rainbow trout after whirling disease outbreaks did not always lead to reduction in abundance of medium to large rainbow trout. Why severe recruitment declines in larger trout were not observed is uncertain. It is hypothesized that the continued presence of uninfected spawning and early rearing areas within otherwise highly infected rivers, may be the primary mechanism that buffers recruitment, although increased resistance to whirling disease (Miller and Vincent 2009) is another possible explanation.

Increased growth and survival of adult rainbow trout in the face of a whirling disease epizootic may be the result of a compensatory response to marked reductions in density of small rainbow trout. Continued long term monitoring of survival and growth of various size and age classes is needed to determine the stability of this pattern or if maintenance of adult recruitment is only a transitory response.

The lack of decline in growth or condition of rainbow trout after a whirling disease outbreak suggests that young fish that do survive the infection window of high susceptibility do not suffer later survival or performance deficits even in highly infected systems. Recruitment from whirling disease-free spawning and early rearing areas appears crucial for preventing collapse of rainbow trout populations. Protection and enhancement of a diversity of spawning areas and spawning and rearing life histories appears to allow resilience in the face of high infectivity (Pierce et al. 2009). More research is needed to test the proposal that habitat improvement of key infected spawning areas can reduce infectivity and result in population rebound (Thompson and Nehring 2004).

Continued monitoring of whirling disease severity in Montana rivers is needed to further build on the long term database used in this study, as our data suggest that population-level effects have not fully stabilized. Moreover, we found the extent of disease monitoring was limited in many rivers, making it difficult to adequately measure disease severity changes over time.

Given that some cutthroat trout subspecies (DuBey et al. 2007) and mountain whitefish *Prosopium williamsoni* (MacConnell et al. 2000) show even more susceptibility to whirling disease than rainbow trout, population declines of a similar or greater magnitude would also be expected to occur in native cutthroat trout *Oncorhynchus clarkii* and mountain whitefish populations if this infectivity threshold is exceeded.

Drought-driven lower flows may increase whirling disease infectivity. Anticipated declines in summer low flows from climate change will likely lead to further declines of whirling disease-susceptible trout species such as rainbow trout and cutthroat trout and replacement by more resistant species such as brown trout. Research is needed to test ideas to reduce increases in anticipated whirling disease severity in the face of climate change via flow manipulation (Hallett and Bartholomew 2008) and riparian vegetation and channel restoration measures that control temperature increases, maintain stream recharge, and reduce tubificid worm fine sediment habitat (Pierce et al. 2009).

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