Effects of Rainbow Trout on Brook Trout Population Size in Tributaries to Lake Superior in Cook County, Minnesota

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This study looked at the effects of Rainbow Trout stocking on the size of Brook Trout populations above migratory barriers. Linear mixed effects models were used to determine if there was a relationship between Brook Trout and Rainbow Trout catch rates. Age 1 or older Brook Trout populations were influenced by relative abundance of age 1 or older Rainbow Trout, according to the best supported model based on AIC scores. Population responses varied by stream, ranging along a gradient from high catch rates with a positive relationship to a negative relationship with low relative abundances. Streams with a positive relationship are likely more productive, with more prev and smaller territories, which allows for greater relative abundance. Streams with a weak relationship may have Brook Trout populations limited by the capacity for natural reproduction, a factor which would not influence Rainbow Trout. A clear negative relationship in some streams is likely due to density-dependent effects. This study did not perform an analysis comparing Brook Trout population sizes before and after the presence of Rainbow Trout. It is possible, but undetermined, that Brook Trout populations in this study would be larger if not for the introduction of Rainbow Trout. Management of Brook Trout and Rainbow Trout populations should be considered on a stream-by-stream basis due to the wide variation in population responses, and particular attention should be paid to the potential effects of Rainbow Trout introduction on streams with low abundances of Brook Trout.

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Introduction

Tributaries to Lake Superior were historically home to a single species of trout, the Brook Trout Salvelinus fontinalis, although there have been reports of migratory Lake Trout Salvelinus namaycush using them (Burnham-Curtis 2000). A distinct population of Brook Trout, known as "Coasters" would spend a substantial amount of their lives in Lake Superior, returning to tributaries to spawn. There is no longer a migratory population of Lake Trout, and there are relatively few Coasters, but there are large numbers of introduced species, including three species of Pacific salmon Oncorhynchus spp., Brown Trout Salmo trutta, and migratory Rainbow Trout Oncorhynchus mykiss. The historic environment Brook Trout evolved in has experienced significant change due to issues such as logging, destruction of headwater bogs, and invasive species.

Rivers along the North Shore of Lake Superior are steep and often contain natural migratory barriers in the form of waterfalls, limiting available spawning and rearing habitat. As the area was first developed in the 1800's, Brook Trout caught below the waterfalls were likely stocked above these barriers (Smith and Moyle 1944), possibly establishing new populations which were isolated from Lake Superior. The late 1800's saw heavy logging in the area, as well as the introduction of Rainbow Trout; simultaneously Coaster populations plummeted due to overharvest and habitat destruction. In the 1900's Sea Lamprey Petromyzon marinus and Rainbow Smelt Osmerus mordax were introduced, Lake Trout numbers crashed, and Pacific salmon were stocked to balance booming baitfish populations. Rainbow Trout populations began to decline in the 1970s and fisheries managers commenced stocking juvenile Rainbow Trout above the migratory barriers to increase populations of returning adults.

Rainbow Trout have been observed to displace Brook Trout in many streams where they have been introduced (Larson and Moore 1985). Stocking of Rainbow Trout above migratory barriers was largely discontinued in the early 1990's, in part due to concerns about the effects of Rainbow Trout on Brook Trout populations, although it continued as late as 2014 in two streams within the study area until it was discontinued due to low success and concerns about effects on Brook Trout populations (Persons 2017). This study will look at the effects of Rainbow Trout on Brook Trout population sizes above migratory barriers.

Methods

Site Selection

In order to study the effects of stocking Rainbow Trout above migratory barriers, nine rivers were selected (Figure 1). The selection criteria for these rivers were that the survey sites were located above a migratory barrier, five or more surveys had been performed at that site, at least three surveys with Brook Trout present, and there were interacting populations of Brook Trout and Rainbow Trout for some period of time. Study sites were selected above migratory barriers to avoid the presence of migratory populations of both Rainbow Trout and Brook Trout and the influence of their natural reproduction. Five or more surveys, with at least three capturing Brook Trout, were required to ensure a satisfactory number of observations on streams which had consistent, catchable populations of Brook Trout. Streams were also selected based on the presence of interacting populations of Brook Trout and Rainbow Trout because it would not benefit the study to observe streams in which the populations did not interact.

Data Collection

Backpack electrofishing was performed at the survey sites between late July and early September at least five times between 1980 and 2017. Fish were sampled using a Smith Root model LR-24 backpack electrofisher. One backpack electrofisher was normally used, but when two were required to sample a stream, the second was the same model. Electrofishing settings such as volts, frequency, and duty cycle were recorded. Effort was recorded as time (seconds) of electrofishing at each station. Station length ranged from 76.2 to 182.9 m. All fish caught were identified and counted, and trout were identified as age 0 or age 1 or older. Catch per unit effort (CPUE) was calculated as number of fish caught per hour based on species and age group. Data Analysis

Linear mixed effects models were used to determine if there was a relationship between CPUE of age 1 or older Rainbow Trout and age 1 or older Brook Trout (Table 1). Linear mixed effects models were also used to determine what factor most influenced age 0 Brook Trout abundance (Table 2). Models tested used CPUE as a fixed effect and stream as a random effect. Akaike's information criterion (AIC) was used to determine the bestsupported model (Akaike 1987).



FIGURE 1. Cook County, MN, with study streams highlighted.

TABLE 1. Linear mixed effects models tested for age 1 or older Brook Trout CPUE. BCPUE1 represents age 1 or older Brook Trout CPUE. RCPUE1 and RCPUE0 represent age 1 or older and age 0 Rainbow Trout CPUE, respectively, and were fixed effects. Stream is the identity of the streams sampled and was a random effect.

Model	AIC score
BCPUE1~RCPUE1 Stream	1214.4
BCPUE1~1 Stream	1217.8
BCPUE1~RCPUE0 Stream	1220.6

TABLE 2. Linear mixed effects models tested for age 0 Brook Trout CPUE. BCPUE0 represents age 0 Brook Trout CPUE. RCPUE1 and RCPUE0 represent age 1 or older and age 0 Rainbow Trout CPUE, respectively, and were fixed effects. Stream is the identity of the streams sampled and was a random effect.

Model	AIC score
BCPUE0~BCPUE1 Stream	1196.1
BCPUE0~1 Stream	1207.0
BCPUE0~RCPUE0 Stream	1207.7
BCPUE0~RCPUE1 Stream	1210.6

Results

Age 1 or older

Based on AIC scores, the best supported model indicated age 1 or older Brook Trout CPUE was influenced by age 1 or older Rainbow Trout CPUE and that relationship varied by stream (Table 1;



FIGURE 2. Mixed effects linear models of age 1 or older Brook Trout catch per unit effort (CPUE; fish/hr) by stream as a function of age 1 or older Rainbow Trout CPUE.

Figure 2). The relationships existed along a gradient in which those streams with a positive relationship also had the highest relative abundances, and the streams with a negative relationship had the lowest relative abundances. Streams with weak relationships had relative abundances which were intermediate.

Age-0

The best supported model indicated CPUE of age 0 Brook Trout was most influenced by the CPUE of age 1 or older Brook Trout and this relationship varied by stream (Table 2, Figure 3). The relationships for age 0 and age 1 or older Brook Trout fell along a gradient similar to the observations of age 1 or older Brook Trout and Rainbow Trout. The same two streams exhibited a negative relationship when looking at each age group.

Discussion

Age 1 or older

Rainbow Trout appear to have varying effects on Brook Trout population size depending on the characteristics of individual stream. Streams which are more productive or have more suitable habitat are likely able to support higher populations of both Brook and Rainbow Trout. Streams with a positive relationship have the largest range of abundances, suggesting that in years when large amounts of production are possible both Brook Trout and Rainbow Trout populations both do well. A possible cause of the large populations and positive relationships could be an increased availability of food and subsequent reductions in territory size; Rainbow Trout have been observed to occupy smaller territories and exhibit aggressive behavior less often with increasing prey abundance (Slaney



FIGURE 3. Mixed effects linear models of age 0 Brook Trout catch per unit effort (CPUE; fish/hr) by stream as a function of age 1 or older Brook Trout CPUE.

and Northcote 1974). Territory size has been used as a predictor of maximum densities of salmonids in streams (Grant and Kramer 1990), and therefore an increase in prey availability and consequent reduction in territory size could explain the greater abundance of Brook and Rainbow Trout relative to other streams in this study.

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Those Brook Trout streams which had intermediate catch rates were not affected by Rainbow Trout numbers. Two of these streams with a weak relationship had the lowest observed catches; this may be due to the small size of these streams. The cause of the weak relationship between Brook Trout and Rainbow Trout abundances may be due to limited spawning habitat for Brook Trout, which rely entirely on natural reproduction in the study streams, a factor that would not influence the stocked Rainbow Trout. If the spawning habitat is the limiting factor for Brook Trout abundance in these streams, yet populations do not show densitydependent effects due to Rainbow Trout stocking, it is unlikely that inter-specific competition for space or food is occurring.

In streams with a negative relationship, it is clear that Rainbow Trout have density-dependent effects on the size of Brook Trout populations. It was observed by Rose (1986) that age 0 Brook Trout daily growth rates decreased dramatically following the emergence of Rainbow Trout; this decrease in growth rates may result in increased overwinter mortality and is a possible explanation for the negative relationship on these streams. In a model of competition between Rainbow Trout and Brook Trout in Appalachian streams Clark and Rose (1997) found that competitive advantage for food was unlikely to explain Rainbow Trout dominance and that, while possible, warmer temperatures and limited spawning habitat are unlikely explanations. The most likely cause of Rainbow Trout dominance was the lower fecundity and more frequent failure of year classes in Brook Trout (Clark and Rose 1997). Adult Brook Trout have exhibited densitydependent effects, particularly with warmer water (Utz and Hartman 2009). The two streams that exhibited negative relationships may be less thermally suited to trout species in general, and Brook Trout in particular, than the other streams studied.

Age 0

Catch of age 0 Brook Trout varied by stream but was driven by CPUE of age 1 or older Brook Trout rather than CPUE of age 0 or age 1 or older Rainbow Trout. This is a reasonable thing to expect, as Brook Trout in these streams are supported entirely by natural reproduction. If there are competitive effects due to the presence of Rainbow Trout they would likely appear in the CPUE of age 1 or older Brook Trout as a result of reduced overwinter survival (Rose 1986).

Most streams exhibited a positive relationship between catch rates of age 0 and age 1 or older Brook Trout. This is likely due to the greater reproductive success which can be expected with a larger reproducing population. Some streams exhibited little or no relationship between CPUE of age 0 and age 1 or older Brook Trout, and this may be due to limited spawning habitat in these streams.

A negative relationship existed between age 0 and age 1 or older Brook Trout in two streams. These are the same streams exhibiting a negative relationship between CPUE of age 1 or older Rainbow Trout and age 1 or older Brook Trout, which is an indication of density-dependent effects. This could be due to intra- and inter-specific competition for limited resources or predation.

Conclusion

Brook Trout have been observed to dominate Rainbow Trout in different habitats, flow rates, and across a range of temperatures (Cunjak and Green 1984, 1986 and Magoulick and Wilzbach 1998). In spite of these observations, Rainbow Trout have often displaced native Brook Trout, and interspecific competition is well documented (Larson and Moore 1985, Lohr and West 1992, Rose 1986). The Brook Trout populations in this study displayed responses to the introduction of Rainbow Trout ranging from a clear reduction in catch rates in streams with low abundance to a positive relationship between relative catch rates of Rainbow Trout and Brook Trout. The specific nature of interspecific competition is unclear, as observed by the overlap in models of exploitative and spatial competition by Ward et al. (2006), although the gradient of responses by different populations of Brook Trout is notable. The different responses exhibited in this study are likely due to the variations in prey and territory availability in the different streams, and the specific mechanism of competition likely also varies by stream. This study does not perform an analysis comparing Brook Trout population sizes before and after the presence of Rainbow Trout. It is possible, but undetermined, that Brook Trout populations in this study would be larger if not for the introduction of Rainbow Trout. Management of Brook Trout and Rainbow Trout populations should be considered on a stream-bystream basis due to the wide variation in population responses, and particular attention should be paid to the potential effects of Rainbow Trout introduction on streams with low abundances of Brook Trout due to the greater density-dependent effects observed by Grant and Imre (2005) and the clear negative relationships observed in this study.

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