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IS THE DECLINE OF BROOK TROUT IN THE SOUTHERN APPALACHIANS RESULTING FROM COMPETITIVE EXCLUSION AND/OR EXTINCTION DUE TO HABITAT FRAGMENTATION?

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ABSTRACT

The continuing loss of isolated headwater populations of brook trout (*Salvelinus fontinalis*) in the southern Appalachians cannot be attributed solely to competition from invading rainbow trout (*Oncorhynchus mykiss*). Brook trout in headwater habitats may even enjoy a competitive advantage over rainbows, yet they continue to experience local extinctions due to demographic stochasticity and natural catastrophes. Reintroduction of brook trout into headwater habitats currently occupied by rainbow trout may be a useful addition to current management policies designed to arrest the decline of brook trout.

INTRODUCTION

In recent years a number of studies have documented the continuing loss of native brook trout (*Salvelinus fontinalis*) populations in the southern Appalachians. The most detailed information on this decline consists of a series of reports on the brook trout of the Great Smoky Mountains National Park (King 1937, Lennon 1967, Jones 1978, Kelly et al. 1980, Larson and Moore 1985), but Bivens et al. (1985) demonstrated that this continuing loss has also occurred for eastern Tennessee populations in streams located outside the Park. These authors generally agreed that the initial major losses of brook trout populations in the early 1900s were due largely to habitat destruction associated with widespread logging and forest fires. Since that period, habitat degradation has ceased or even reversed in some watersheds, but the loss of brook trout populations has continued (Bivens et al. 1985).

There is also general agreement that the continuing decline of brook trout can be attributed largely to competitive replacement by the introduced rainbow trout (*Oncorhyncus mykiss*). Moore et al. (1983) provided experimental support for this hypothesis by removing rainbow trout from third–order streams containing sympatric populations of brook and rainbow trout. This manipulation resulted in an increase in brook trout density and biomass, but the increase did not completely compensate for the numbers and biomass of removed rainbows.

Current attempts to protect our declining brook trout populations emphasize exclusion or removal of competing rainbows (Bivens 1984; pers. comm. with Dean Elsen and Gordon Sloan, National Forest Service fisheries biologists). Since rainbow removal is very costly (Moore et al. 1983, Larson et al. 1986), these efforts have also included the construction of barrier dams to prevent the upstream movement of rainbows into headwater brook trout streams. This policy is based on the assumption that the competitive superiority of rainbow trout demonstrated by Moore et al. (1983) in areas of sympatric occurrence in third–order streams also exists in the second–order headwater refugia currently occupied by allopatric brook trout populations.

There are, however, two lines of evidence to suggest that brook trout may have a competitive advantage in headwater streams. First, a number of experimental studies have indicated that brook trout can establish dominance over similar–sized rainbows (Newman 1956, Wolfe 1978, Cunjak and Green 1984).

The second line of evidence for the brook trout's competitive success comes from an examination of the characteristics of the streams which still contain brook trout populations. Although all known brook trout populations have rainbow populations below them, Bivens et al. (1985) noted that only 33% of the remaining brook trout populations are known to be protected by barrier falls and 27% have no barriers to prevent entry of rainbows. No data were available for the remaining 40%. Larson and Moore (1985) also noted that in the Three Forks drainage in the Great Smoky Mountains National Park, rainbow trout have shown little invasion of the brook trout waters since 1935 even though these low–gradient streams are open to invasion. The failure of rainbows to replace brook trout in streams to which they have free access could be interpreted as evidence for a shift in competitive advantage in favor of the brook trout in small headwaters. Therefore, the continuing loss of isolated headwater populations of brook trout may be due to factors other than competitive replacement by rainbows.

Examination of data presented for 34 streams in northeastern Tennessee which had lost brook trout populations between the late 1960s (Tatum, unpubl. memo, Tennessee Wildlife Resources Agency) and the early 1980s (Bivens 1984) confirms the need for an alternative explanation. Of particular interest is the fact that 11 of these streams (32%) also lacked rainbow trout. This strongly suggests that factors other than rainbow competition contribute to loss of small headwater populations of brook trout. In the past, the presence of rainbows in what was formerly a headwater brook trout stream has been interpreted as evidence for competitive replacement. In view of the data just cited from Bivens (1984), it could also be interpreted as invasion by rainbows *after* a competitively successful brook trout population was eliminated or seriously reduced by other factors such as flood or drought.

This brief review of our current understanding of the status of southern Appalachian brook trout populations suggests the following hypotheses relevant to the future status of these populations, both of which were tested in this study. First, at least some of the continuing loss of headwater brook trout populations may be due to demographic stochasticity and natural catastrophes (MacArthur and Wilson 1967, Shaffer 1981) independent of the presence or absence of rainbow trout. Second, persistence of brook trout populations in second–order headwater streams open to rainbow invasion suggests a competitive advantage favoring the brook trout in these habitats.

METHODS

The first hypothesis was tested with a computer simulation model developed by a class in theoretical ecology at East Tennessee State University taught by Dan Johnson (Biological Sciences) and Larry Neal (Computer and Information Sciences). In this model we used an 11–year data set on population structure, mortality, and fecundity of a brook trout population in Lawrence Creek, Wisconsin (Hunt 1974) to provide the basic data for demographic variation. These yearly data sets were randomly sampled (boot–strapped, Diaconis and Efron 1983) to generate population predictions for a series of years. Population sizes were held to an upper limit based on my unpublished estimates of carrying capacities in headwater streams. Variables included stream length (proportional to population size), frequency of year class failure, and number of years the model followed the population.

The second hypothesis was tested in a field study initiated in the fall of 1983 in Briar Creek, Washington County, Tennessee. This is a typical second–order headwater stream (Nagel and Deaton 1989) which contained a population of naturally–reproducing rainbow trout. Brook trout from local populations were introduced into a 1.4–km section of stream (referred to below as the introduction zone) and rainbows were thinned annually from the start of the study until the spring of 1986 to ensure the establishment of a reproducing brook trout population. Rainbows were not removed from a 0.7–km downstream section terminating at a 10–m barrier falls, and a 0.7–km upstream section of suitable habitat (referred to below as invasion zones) to test the ability of the brook trout to invade these areas and resist encroachment of rainbows into the introduction zone.

Population density and size structure were monitored with annual electrofishing samples taken during periods of low water in late summer or early fall of each year. Total length (TL) of each captured fish was measured to the nearest mm and young-of-the-year (YOY) were given a unique fin clip to identify the year class in subsequent years. Fish were then returned to the stream at the point of capture. Initial efforts to estimate true population density by the Petersen mark–and–recapture method (Ricker 1975) and the Seber and LeCren (1967) two–step removal method were abandoned when it became evident that this relatively small population was experiencing significant mortality due to the trauma of capture. Estimates for probability-of-capture on 10 different occasions averaged 42% and 60% for the Petersen and the Seber and LeCren methods, respectively. These estimates were significantly different at the 0.001 level by the Seber and LeCren (1967) T4 test. The most likely cause of this discrepancy would be mortality of fish captured and marked on the first electrofishing pass. A less likely explanation assumes that fish not captured on the first pass had a consistently higher probability of capture when sampled a week later. Since the fall of 1986 all sampling has been restricted to a single pass with the electrofishing unit to yield an index of relative abundance. Unpublished data from the initial population estimates indicate that the sampling efficiency of this method is approximately 60%.

RESULTS

Hypothesis I

The simulation indicated that these small, isolated populations have a high probability of extinction due to demographic stochasticity and natural catastrophes alone. Typical sets of 1000 simulations for 30–year periods with 20% per year probability of year class failure due to natural catastrophes indicate that 2.5–km streams have a 56% probability of local extinction; for 0.5–km streams, that probability increases to 92% (Phillips et al. 1987).

Hypothesis II

Brook trout introduced into the 1.4–km introduction zone of the study area quickly spread into the 0.7–km invasion zones above and below the introduction zone. By the spring of 1986, reproducing populations of brook trout had become established in all three areas. Table 1 summarizes total one–pass catches of both species in the lower and upper invasion zones for the fall of 1990.

Table 1. Relative fall abundance of young-of-the-year (TL < 100 mm) and adult (TL > 100 mm) trout in the invasion zones of Briar Creek in 1990.

	Total length	
Species	< 100 mm	> 100 mm
Lower invasion zone		
Brook trout	36	27
Rainbow trout	14	13
Upper invasion zone		
Brook trout	82	18
Rainbow trout	33	19

Results of the inventories for 1987–1990 in the introduction zone are summarized in Figure 1. This time period represents the four years following the cessation of rainbow removal in 1986. The low numbers of YOY (TL < 100 mm) rainbow trout in 1987 and brook trout in 1988 reflect year–class failures due to floods prior to the emergence of sac fry from the gravel. Rainbows experienced a similar failure in 1984 (Nagel and Deaton 1989). These failures resulted in the relatively few individuals of the corresponding species which were > 100 mm in the following year (rainbows in 1988 and brook trout in 1989). The fact that three year–class failures have been observed in Briar Creek since 1983 suggests that failure rates due to natural catastrophes used in the simulation model by Phillips et al. (1987) are realistic.

The overall pattern of year-to-year variation in abundance seen in Figure 1 supports the prediction of the simulation model by Phillips et al. (1987) that demographic stochasticity and natural catastrophes may be important factors in determining the size and persistence of headwater trout populations. However, Figure 1 also indicates that relatively low numbers of adult fish (TL > 100 mm) are capable of producing strong year–classes of YOY fish the following year. This is particularly striking in the case of the small 1989 adult brook trout population which produced the most abundant YOY year–class in the sequence in 1990. Platts and Nelson (1988) have noted similar fluctuations in population statistics for several species of trout in a number of western streams.

Finally, although brook trout have not established clear–cut dominance over the rainbows in Briar Creek during the period depicted in Figure 1, they seem to be successfully co–existing with the rainbows.

DISCUSSION

The attempt to arrest the continuing decline of brook trout in the southern Applachians by construction of barrier dams and removal of rainbow trout is based on the assumption that competition from rainbows is the primary cause of the decline. These methods do not address the problem of continued extinctions of these isolated populations due to stochastic events unrelated to rainbow competition (MacArthur and Wilson 1967, Shaffer 1981). Thomas (1990), in a

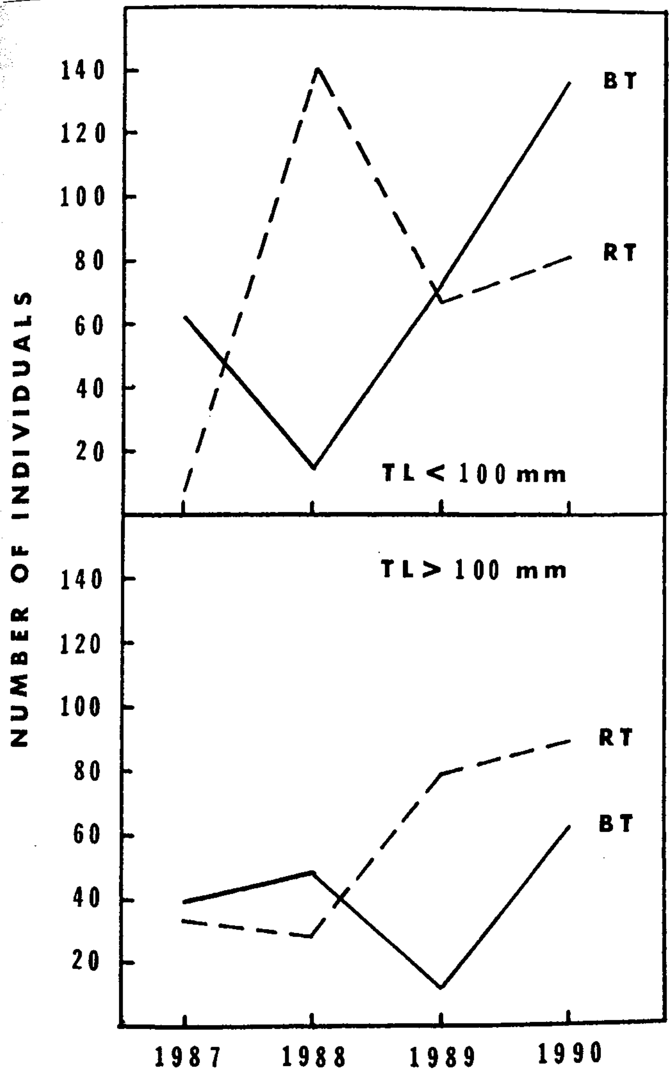

Figure 1. Relative fall abundance of young-of-the year (TL < 100 mm) and adult (TL > 100 mm) trout in the introduction zone of Briar Creek for the period 1987–1990. RT = rainbow trout, BT = brook trout.

recent review of the minimum viable population question, suggested that a breeding population size of 5500 individuals is needed for long-term persistence of a population in the face of the kinds of stochastic events modeled in the simulation reported by Phillips et al. (1987). He pointed out that this is a difficult goal to achieve for most vertebrates, and in fact probably exceeds, by an order of magnitude, the size of most of our remaining brook trout populations. Thomas suggested a network of smaller populations (which currently exists) supported by artificial recolonizations and transfers, if necessary (which are not currently a part of our management plan). Current management policies tend to regard a headwater stream occupied solely by rainbow trout unsuitable for brook trout reintroduction without total removal of the rainbows (Bivens 1984). The preliminary results reported here for the recolonization of Briar Creek suggest that reintroduction without total removal of rainbows might be a useful and cost-effective addition to our current strategy.

As a final point, it should be noted that even though the preliminary results from the Briar Creek study suggest that brook trout can compete effectively with rainbows in the headwaters, the rainbow is still a serious competitor species, even in these habitats. All of our remaining brook trout populations exist in streams with flourishing rainbow populations below them. Stochastic reductions of brook trout, combined with pressures produced by competition from invading rainbows, may result in an extinction of the remaining brook trout which might not have occurred in the absence of either factor. Therefore, construction of barrier dams to prevent immigration of downstream rainbows should be continued as time and money permits.

Literature Cited

Bivens, R. D. 1984. History and distribution of brook trout in the Appalachian region of Tennessee. M.S. Thesis, Univ. of Tenn., Knoxville.

Bivens, R. D., R. J. Strange, and D. C. Peterson. 1985. Current distribution of the native brook trout in the Appalachian region of Tennessee. J. Tenn. Acad. Sci. 60:101–105.

Cunjak, R. A., and J. M. Green. 1984. Species dominance by brook trout and rainbow trout in a simulated stream environment. Trans. Am. Fish. Soc. 113:737–743.

Diaconis, P., and B. Efron. 1983. Computer-intensive methods in statistics. Sci. Am. 248:116–130.

Hunt, R. L. 1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wis. Dep. Nat. Resourc. Tech. Bull. No. 82.

Jones, R. D. 1978. Regional distribution trends of the trout resource. Pp. 1–10 *in*: Harshbarger, T. J. (ed.), Southeastern trout resource: ecology and management symposium proceedings. USDA, For. Serv., SE For. Exp. Stn., Asheville, NC.

Kelly, G. A., J. S. Griffith, and R. D. Jones. 1980. Changes in distribution of trout in Great Smoky Mountains National Park, 1900–1977. U.S. Fish Wildl. Serv. Tech. Pap. 102, Washington, DC.

King, W. 1937. Notes on the distribution of native speckled and rainbow trout in the streams at Great Smoky Mountains National Park. J. Tenn. Acad. Sci. 12:351–361.

Larson, L. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachians. Trans. Am. Fish. Soc. 114:195–203.

Larson, L. L., S. E. Moore, and D. C. Lee. 1986. Angling and electrofishing for removing nonnative rainbow trout from a stream in a national park. N. Am. J. Fish. Manage. 6:580–585.

Lennon, R. E. 1967. Brook trout of Great Smoky Mountains National Park. U.S. Fish Wildl. Serv. Tech. Pap. 15, Washington, DC.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.

Moore, S. E., B. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. N. Am. J. Fish. Manage. 3:72–80.

Nagel, J. W., and J. E. Deaton. 1989. Growth and longevity of rainbow trout in two headwater streams in northeastern Tennessee. J. Tenn. Acad. Sci. 64:9–12.

Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 19:64–81.

Phillips, R. A., L. Neal, D. M. Johnson, J. W. Nagel, T. F. Laughlin, and R. T. Lane. 1987. Simulating local extinction of trout populations. Pp. 24–27 *in*: Hawkins, R., and K. Klukis (eds.), Tools for the simulation profession. Society for Computer Simulation, San Diego, CA.

Platts, W. S., and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluation. N. Am. J. Fish. Manage. 8:333–345.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Seber, G. A. F. and E. D. LeCren. 1967. Estimating population parameters from catches large relative to the population. J. Anim. Ecol. 36:631–643.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience 31:131–134.

Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population sizes? Cons. Biol. 4:324–327.

Wolfe, J. R., Jr. 1978. Agonistic behavior expressed by brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) in an artificial stream environment. M.S. thesis, VA Polytech. Inst. and State Univ., Blacksburg.