Food Resource Competition in Southern Appalachian Brook and Rainbow Trout

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Abstract: Food habits of sympatric and allopatric populations of adult brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) from 4 streams in the Great Smoky Mountains National Park were compared to determine if competition for food resources might explain the apparent exclusion of the former by the latter in Southern Appalachian streams. When diets of brook trout in sympatry with rainbow trout were compared with diets of brook trout in allopatry, there was little significant change in prey composition. Based on this information, exploitation competition for food resources does not seem to play a role in the invasion of rainbow trout into areas of Southern Appalachian streams occupied by brook trout.

Proc. Annu. Conf. Southeast Assoc. Fish and Wildl. Agencies 43:239–247

Over the last 70 years brook trout have undergone a dramatic range reduction in the southern Appalachians (Larson and Moore 1985). Although much of the initial loss can be attributed to declines in water quality associated with activities such as logging, declines have also been noted in areas where logging has not occurred or where streams have had enough time to recover from any negative impacts. In areas such as these, range loss by brook trout is directly correlated with expansion of the range of rainbow trout (*Oncorhynchus mykiss*, formerly *Salmo gairdneri*), which were introduced to complement or enhance the existing fishery. This correlation between loss of range by the native species and range expansion by the introduced

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species implies that competitive exclusion of brook trout by rainbow trout is occurring. The purpose of this study was to explore 1 aspect of this interaction, specifically if competition for food resources plays a role in range loss by brook trout. The diets of brook and rainbow trout were examined from areas where they occur together (in sympatry) and apart (in allopatry) to determine the degree of dietary overlap between the two species and also to detect any shifts in resource utilization resulting from the presence of the other.

The authors wish to acknowledge the assistance of S. Moore of the Resource Management Division and C. Parker of the Science Division at the Great Smoky Mountains National Park who provided logistic support for the sampling as well as advice and ideas over the course of the project. K. Fausch provided an insightful review of the original manuscript which greatly enhanced the final product.

Methods

Trout for this study were collected from 4 different streams in the Great Smoky Mountains National Park using a 700-volt AC backpack electroshocker. In an attempt to determine if the presence of 1 species affected food habits of the other, trout were collected in each stream from areas where brook trout occurred in allopatry, rainbow trout occurred in allopatry, and where brook trout and rainbow trout occurred in sympatry. Trout were obtained from Collins Creek in June 1984 and June 1986, while sampling in Cosby Creek and Indian Flats Prong occurred in August of the same years. Trout stomach contents were obtained from Sam's Creek during July, August, and September 1987. Two different methods of collecting stomach contents were employed. Trout obtained from Collins Creek, Cosby Creek, and Indian Flats Prong were preserved in 10% formalin and returned to the lab where the stomachs were removed and the contents examined. Stomach contents of trout captured from Sam's Creek were obtained with a gastric lavage method similar to that described by Light et al. (1983). Food items obtained from Sam's Creek specimens were placed in individual 60-ml Nalgene bottle containing 30 ml of Kahle's solution and returned to the lab for examination.

We used a 3-pass removal method (Bohlin 1982, Van Deventer and Platts 1983) to obtain population estimates in the sympatric areas of each stream. With the exception of Sam's Creek, population estimation was done at the same time as stomach collection. In Sam's Creek, the population estimation was done during July 1987. After each pass, lengths and weights were recorded for each species, then all trout were placed in holding nets outside the sampling area until sampling was completed. Although no block nets were placed at the upper and lower ends of the population estimation sections, natural obstructions such as waterfalls or cascades minimized movement of fish into and out of the sections during sampling. Population estimates were calculated by the MICROFISH 2.2 software package (Van Deventer and Platts 1985).

Stomach contents were examined in the laboratory using a dissecting microscope. Immature aquatic invertebrates were classified into 1 of 5 categories (Ephemeroptera, Plecoptera, Diptera, Trichoptera, and Other) using Merritt and Cummins (1978) and Brigham et al. (1982). All terrestrial invertebrates as well as adult aquatic invertebrates were classified as terrestrials. Two other categories were included, Vertebrata (which included fish and salamanders) and Decapoda (crayfish), for a total of 8 major prey categories. The total number of prey items in each category for a given stomach was then recorded.

Two separate types of analyses were carried out on the stomach content data. Initially, the mean number of prey items in stomachs of brook and rainbow trout in allopatry and sympatry for a given stream were compared by prey category using Tukey's studentized range test to determine if there were any significant differences between the differing distributions for a given prey type. Because prey availability in streams tends to be seasonal, the Sam's Creek data from July, August, and September were analyzed by month. Because sampling was carried out during the same weeks each year in Cosby Creek, Collins Creek, and Indian Flats Prong, data from 1984 and 1986 were combined.

In the second phase of data analysis, we used the PROC DISCRIM procedure of PC SAS to develop discriminant functions based on prey occurrence patterns in the stomachs of allopatric brook and rainbow trout from each sample. Trout from the sympatric areas were then treated as unknowns and the discriminant function applied in an effort to classify them as either brook trout or rainbow trout. The rationale behind this analysis is that if changes in food habits of either species occurred due to the presence of the other species, the ability of the discriminant function to correctly classify sympatric fish as rainbow or brook trout would be diminished. All stomach data were analyzed using Version 6.02 of PC SAS.

Results

Prey type comparisons are presented in Table 1. There were no significant differences ($P > 0.05$) between sympatric and allopatric trout of a given species for any prey type or for the total number of prey items in any of the samples. Differences between sympatric brook and rainbow trout in each stream were also non-significant ($P > 0.05$). There were significant differences ($P < 0.05$) between allopatric brook trout and allopatric rainbow trout for at least 1 prey category in 4 of the 6 samples. Allopatric rainbow trout in Cosby Creek had significantly higher numbers of terrestrial prey items and a higher total number of prey items than allopatric brook trout. In Indian Flats Prong, the situation was reversed, as allopatric brook trout had significantly more terrestrials and higher total number of prey items per stomach than did allopatric rainbow trout. In Sam's Creek, allopatric rainbow trout had significantly greater numbers of trichopterans than did allopatric brook trout in both August and September.

The results of the classificatory discriminant analysis are presented in Table 2. The discriminant functions correctly classified a higher percentage of brook trout in Collins Creek, Cosby Creek, and the Sam's Creek samples from August and September. For Indian Flats Prong and the Sam's Creek sample from July the reverse was

Table 1. Mean number of prey per stomach for all prey types, species distributions, and streams. Collins Creek, Cosby Creek, and Indian Flats Prong 1984 and 1986 data have been combined. Monthly samples from Sam's Creek have been listed separately. Means for a given prey type from the same stream with the same letter are not significantly different (Turkey's HSD, $P > .05$). (TERR = terrestrial, EPHE = Ephemeroptera, PLEC = Plecoptera, DIPT = Diptera, TRIC = Trichoptera, DECA = Decapoda, VERT = Vertebrata, OTHE = other, ABKT = allopatric brook trout, SBKT = sympatric brook trout, SRBT = sympatric rainbow trout, ARBT = allopatric rainbow trout.)

DIST	*N*	TERR	EPHE	PLEC	DIPT	TRIC	DECA	VERT	OTHE	TOTAL
					Collins Creek					
ABKT	15	5.00	0.53	0.20	0.73	0.60	0.33	0.00	0.00	7.34
		A	A	A	A	A	A	A	A	A
SBKT	15	2.73	0.47	0.13	0.40	0.53	0.27	0.00	0.07	4.60
		A	A	A	A	A	A	A	A	A
SRBT	6	3.17	1.50	0.00	0.33	0.33	0.17	0.00	0.17	5.67
		A	A	A	A	A	A	A	A	A
ARBT	15	2.87	1.07	0.27	0.20	1.93	0.20	0.00	0.00	6.53
		A	A	A	A	A	A	A	A	A
					Cosby Creek					
ABKT	24	1.79	0.25	0.21	0.25	0.33	0.21	0.04	0.00	3.08
		A	A	A	A	A	A	A	A	A
SBKT	28	3.18	0.57	0.04	0.39	0.75	0.32	0.18	0.00	5.43
		AB	AB	A	AB	A	A	A	A	AB
SRBT	26	3.38	1.35	0.08	1.38	1.19	0.31	0.04	0.08	7.81
		AB	B	A	B	A	A	A	A	AB
ARBT	15	5.27	0.80	0.40	0.67	1.07	0.20	0.00	0.07	8.47
		B	AB	A	AB	A	A	A	A	B
					Indian Flats Prong					
ABKT	20	4.95	0.45	0.10	0.35	1.50	0.15	0.00	0.05	7.55
		A	A	A	A	A	A	A	A	A
SBKT	27	3.00	0.15	0.11	0.30	1.07	0.44	0.00	0.07	5.15
		AB	A	A	A	A	A	A	A	AB
SRBT	29	2.45	0.31	0.34	0.34	1.24	0.14	0.00	0.00	4.83
		B	A	A	A	A	A	A	A	B
ARBT	27	1.48	0.33	0.22	0.37	1.85	0.11	0.00	0.00	4.37
		B	A	A	A	A	A	A	A	B
					Sam's Creek—July					
ABKT	34	7.35	0.68	0.15	0.94	0.50	0.18	0.06	0.15	10.00
		A	A	A	A	A	A	A	A	A
SBKT	14	5.37	0.71	0.00	0.29	0.21	0.21	0.00	0.00	6.79
		A	A	A	A	A	A	A	A	A
SRBT	15	7.60	1.07	0.33	0.47	0.60	0.00	0.00	0.20	10.27
		A	A	A	A	A	A	A	A	A
ARBT	27	4.26	1.26	0.29	0.22	0.67	0.04	0.00	0.04	6.78
		A	A	A	A	A	A	A	A	A

(*Continued*)

Table 1. (*Continued*)

DIST	*N*	TERR	EPHE	PLEC	DIPT	TRIC	DECA	VERT	OTHE	TOTAL
				Sam's Creek—August						
ABKT	25	4.84	0.20	0.00	1.28	0.12	0.16	0.00	0.04	6.64
		A	A	A	A	A	A	A	A	A
SBKT	10	3.90	0.40	0.00	0.00	0.10	0.00	0.00	0.00	4.40
		A	A	A	A	AB	A	A	A	A
SRBT	10	9.30	0.60	0.40	0.60	0.30	0.00	0.10	0.00	11.30
		A	A	B	A	AB	A	A	A	A
ARBT	29	5.28	0.66	0.10	0.14	0.59	0.00	0.07	0.03	6.86
		A	A	A	A	A	A	A	A	A
				Sam's Creek—September						
ABKT	29	5.69	0.13	0.07	0.38	0.21	0.03	0.10	0.00	6.62
		A	A	A	A	A	A	A	A	A
SBKT	10	9.40	0.30	0.00	0.10	0.10	0.10	0.00	0.00	10.00
		A	A	A	A	AB	A	A	A	A
SRBT	12	7.50	1.58	0.42	0.58	0.58	0.25	0.00	0.08	11.00
		A	A	A	A	AB	A	A	A	A
ARBT	28	4.75	0.68	0.07	0.32	1.07	0.04	0.04	0.00	6.96
		A	A	A	A	B	A	A	A	A

Table 2. Number of sympatric brook and rainbow trout correctly and incorrectly classified by classificatory discriminant analysis. Collins Creek, Cosby Creek and Indian Flats Prong 1984 and 1986 samples have been combined. Monthly samples are presented separately for Sam's Creek.

	Percent correctly classified		Percent incorrectly classified	
Stream	Brook Trout	Rainbow Trout	Brook Trout	Rainbow Trout
Collins Creek	67	33	33	67
Cosby Creek	79	46	21	54
Indian Flats Prong	30	76	70	24
Sam's Creek				
July	35	80	65	20
August	80	60	20	40
September	60	50	40	50

true, with a higher percentage of rainbow trout being correctly classified. The discriminant functions correctly identified 50% or more of both species in only 2 of the samples, those from Sam's Creek in August and September.

Population estimates and densities for the sympatric areas are presented in Table 3. In 1984, rainbow trout represented 43%, 62% and 90% of the trout populations in the sympatric areas of Collins Creek, Cosby Creek, and Indian Flats Prong, respectively. Rainbow trout densities in the same streams were 444, 305, and 598 trout/ha, while corresponding brook trout densities were 574, 183, and 65 trout/ha. In 1986, Collins Creek, Cosby Creek and Indian Flats Prong rainbow trout percentages were 41%, 67%, and 81% respectively. Densities were 255, 224, and 1,279 trout/ha while corresponding brook trout densities were 364, 112, and 310 trout/ha. In Sam's Creek during July 1987, rainbow trout comprised 27% of the total salmonid population in the sympatric area. Here, rainbow trout density was 163 trout/ha while brook trout density was 603 trout/ha.

Discussion

Competitive interactions can be grouped into 2 broad categories, interference-type competition and exploitation-type competition (Miller 1967). In the former, 1 species directly prevents the other species from gaining access to needed resources, usually by aggressive interactions or agonistic behavior. In the latter, 1 species depletes the supply of a limited resource, using it up so that it is no longer available to the other species. In both cases, the result is decreased fitness of the inferior competitor and ultimately, elimination from the system.

For exploitation competition to occur, there must be a high degree of overlap in the resource utilization patterns of the 2 species, and resources in common must be in short supply. The results obtained from the comparisons of mean number of

Table 3. Population and density estimates (*N*/ha) for brook and rainbow trout in the sympatric zones of the 4 study streams. Estimates for 1984 and 1986 are presented for Collins Creek, Cosby Creek, and Indian Flats Prong. The Sam's Creek estimates are for July 1987. Numbers in parentheses are 95% confidence intervals. The lower confidence interval has been set equal to the total catch in all cases.

		Brook Trout		Rainbow Trout	
Stream	Year	Population Estimate	Density (*N*/ha)	Population Estimate	Density (*N*/ha)
Cosby	1984	12 (12–12)	183	20 (20–22)	305
	1986	8 (7–14)	112	16 (12–30)	224
Collins	1984	31 (27–41)	574	24 (24–26)	444
	1986	20 (20–21)	364	14 (10–30)	255
Indian Flats	1984	4 (4–5)	65	37 (27–60)	598
	1986	16 (16–17)	310	66 (66–68)	1279
Sam's	1987	29 (29–31)	603	8 (8–8)	163

prey items in the stomachs of allopatric brook and rainbow trout indicate that there is indeed a high degree of overlap in the diets of the 2 species during the summer months, with both species relying primarily on terrestrial input for the bulk of their diet. Tebo and Hassler (1963) and Lohr (1985) observed similar overlap in Southern Appalachian streams.

Determining if food resources are in short supply is more difficult. Cada et al. (1987) found that low summer growth rates and declines in condition factor for salmonids in 5 third- and fourth-order Southern Appalachian streams were strongly correlated with the low level of invertebrates found in the stream drift. Although the streams in our study were either second-order or relatively small third-order, it seems reasonable to assume that their resource base was similar to those in the study by Cada et al. (1987).

Given significant overlap when 2 species are apart and assuming that resources are limiting, shifts in resource utilization by 1 species in the presence of the other have often been taken as strong evidence that competition is occurring (Diamond 1978, Fausch and White 1981). The results of the univariate multiple comparisons do not indicate any change in diet by brook trout when they are sympatric with rainbow trout. The results of the discriminant analysis are not as clear cut. In the July sample from Sam's Creek and the sample from Indian Flats Prong, the ability of the discriminant function to correctly identify brook trout was poor in comparison to the other four samples. One possible explanation for this is that the density of rainbow trout in the sympatric zone could influence the relationship between the 2 species, i.e. at higher rainbow trout densities, the effect of the introduced salmonid would increase in magnitude. This, however, seems unlikely, because while Indian Flats Prong had the highest proportion of rainbow trout, Sam's Creek had the lowest. In addition, the discriminant functions from Sam's Creek for August and September correctly identified a high percentage of sympatric brook trout. A second possible explanation would be that differences in the types of resources available over the course of the summer might influence the interaction. Again, this seems unlikely because samples from Indian Flats Prong, Cosby Creek, and Sam's Creek taken during August showed no consistent pattern. The discriminant functions for the latter 2 samples correctly identified 79% and 80% of the sympatric brook trout, respectively, while only 30% received correct classification from Indian Flats Prong. A third possible explanation relates to the nature of the statistical technique itself. The ability of a discriminant function to correctly identify unknowns depends in large part on the degree of separation between the samples which were used to develop the function initially. Differences between the diets of allopatric brook and rainbow trout were minimal, as evidenced by the univariate comparisons, and therefore the adequacy of the functions developed from these populations may be questioned. Given this information, exploitation competition for food resources does not seem to be an important factor in the interaction between the 2 species.

Although evidence supporting exploitation competition is lacking, the possibility that interference competition is occurring can not be eliminated. The nature of such an interaction should be related to the factors that control population densities of stream salmonids. Chapman (1965) postulated that food and space work in consort to regulate population density in stream salmonids. The spatial component involves selection of optimal holding positions that serve 2 primary functions. First, optimal holding positions should be in low velocity current to minimize energy expended in swimming. Second, because lotic salmonids are primarily drift feeders, these positions should be adjacent to high velocity areas in order to maximize the number of available prey items passing by. Displacement of brook trout by rainbow trout from optimal holding positions through aggressive interaction would have predictable consequences from an energetic standpoint. If brook trout were forced to move into areas of higher current velocity, there should be little or no reduction in food intake. However, the energy expended by brook trout maintaining position would be increased, reducing energy available for growth and reproduction, and by extension, reducing fitness. Conversely, if brook trout were forced into areas of lower current velocity, energy expended in position maintenance would be decreased, but so would the availability of prey items, with resultant declines in energy available for growth and reproduction. Evidence supporting such a scenario can be found for other combinations of salmonids, as well as for brook and rainbow trout in other geographic areas. Fausch and White (1986) were able to demonstrate growth rate declines in subyearling brown and brook trout in the presence of subyearling coho salmon in stream aquaria. There was strong evidence that these declines were due to displacement of subordinate individuals to suboptimal holding positions. Rose (1987) noted growth declines by young-of-year brook trout after the emergence of rainbow trout in the rivers of Quebec.

Given the information presented above, exploitation competition does not seem to be the mechanism driving the exclusion of brook trout by rainbow trout in Southern Appalachian streams. Future work on this interaction should probably focus on interference competition. Examination of growth rate or condition factor of brook trout in the presence of rainbow trout could be combined with observational data on position choice. Declines in growth or condition could then be related to relegation of the native species to suboptimal habitat.

Literature Cited

Brigham, A. R., W. U. Brigham and A. Gnilka, eds. 1982. Aquatic insects and oligochaetes of North and South Carolina. Midwest Aquat. Enterprises, Mahomet, Ill. 837 pp.

Bohlin, T. 1982. The validity of the removal method for small populations: consequences for electrofishing practice. Rep. Inst. Freshwater Res. Drottingholm 60:19–24.

Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in Southern Appalachian soft-water streams. Trans. Am. Fish. Soc. 116:692–702.

Chapman, D. W. 1965. Food and space as regulators of salmonid populations in streams. Am. Nat. 100:345–357.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. Am. Sci. 66:322–331.

Fausch, K. D. 1986. Competition of juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Trans. Am. Fish. Soc. 115:363–381.

——— and R. J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Can. J. Fish. Aquat. Sci. 38:1220–1227.

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

Light, R. W., P. H. Adler and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. North Am. J. Fish. Manag. 3:81–85.

Lohr, S. C. 1985. Comparison of microhabitat selection and diet of brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) in a Great Smoky Mountains National Park stream. M. S. Thesis, West. Carolina Univ., Cullowhee, N.C. 84 pp.

Merritt, R. W., and K. W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall-Hunt Publishing Company, Dubuque, Iowa. 722 pp.

Miller, R. S. 1967. Pattern and process in competition. Advanced Ecol. Res. 4:1–74.

Rose, G. A. 1987. Growth decline in subyearling brook trout (*Salvelinus fontinalis*) after emergence of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 187–193.

Tebo, L. B. and W. W. Hassler. 1963. Food of brook, brown, and rainbow trout from streams in western North Carolina. J. Elisha Mitchell Sci. Soc. 79:44–53.

Van Deventer, J. G. 1985. A computer software system for entering, managing, and analyzing fish capture data from streams. U.S. Dep. Agric., For. Serv. Res. Note INT–352. 12pp.

——— and W. S. Platts. 1983. Sampling and estimating fish populations from streams. Trans. N. Am. Wildl. Nat. Resour. Conf. 48:349–354.