Competition Between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for Positions in a Michigan Stream[1]

KURT D. FAUSCH AND RAY J. WHITE[2]

Department of Fisheries and Wildlife, Michigan State University,
East Lansing, MI 48824, USA

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Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo truttta*) was studied by measuring characteristics of daytime positions held by brook trout before and after removal of the brown trout from 1800 m of a stream. We used four criteria as indices of position quality: "water velocity difference" (the difference between velocity at the focal point and in the fastest current within 60 cm of the fish), water depth, distance to stream bed, and lighting. After brown trout removal, brook trout larger than 15 cm chose resting positions with more favorable water velocity characteristics and more often in shade. The position shift was greatest for the largest brook trout, those of 20–30 cm. Feeding positions of brook trout changed little upon brown trout removal according to our criteria. The shift in resting positions of brook trout after release from competition with brown trout indicates that brown trout excluded brook trout from preferred resting positions, a critical and scarce resource. The combined effects of such interspecific competition, differential susceptibility to angling, differential response to environmental factors, and predation of brown trout on juvenile brook trout may account for declines of brook trout populations while brown trout populations expand in many streams of the northeastern United States where the two species are sympatric.

Key words: brook trout, brown trout, competition, ecological release, microhabitat use, resting positions, feeding positions, stream, Michigan

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La compétition entre l'omble de fontaine (*Salvelinus fontinalis*) et la truite brune (*Salmo trutta*) a été étudiée par des mesures de caractéristiques des endroits occupés de jour par l'omble de fontaine avant et après l'enlèvement de la truite brune d'une portion de 1800 m d'un cours d'eau. Quatre critères ont été utilisés comme indices de qualité de position : "différence de vélocité de l'eau," (soit la différence entre la vélocité au point focal et au point de courant maximal en dedans de 60 cm du poisson), profondeur de l'eau, distance au lit du cours d'eau et éclairage. Après l'enlèvement des truites brunes, les ombles de fontaine de plus de 15 cm de long choisirent des endroits de repos avec caractéristiques de vélocité d'eau plus favorables et plus souvent à l'ombre. Le changement d'endroit a été le plus prononcé chez les grands ombles de fontaines, ceux de 20–30 cm. Les ombles de fontaine changèrent très peu d'endroit d'alimentation, selon nos critères, après l'enlèvement des truites brunes. Cette modification des endroits de repos de l'omble de fontaine après être libéré de la compétition de la truite brune indique cette dernière excluait les ombles de fontaine de leur endroit de repos préféré, une ressource critique et rare. Les effets combinés d'une compétition interspécifique de cette nature, d'une susceptibilité différentielle à la capture, d'une réponse différentielle à des facteurs ambiants et de la prédation de la truite brune sur les jeunes ombles de fontaine peuvent expliquer le déclin des populations de ces derniers, alors que celles de truites brunes

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[2] Present address (R. J. W.): Department of Biology, Montana State University, Bozeman, MT 59717, USA.

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prennent de l'expansion dans plusieurs cours d'eau du nord-est des États-Unis où les deux espèces sont sympatriques.

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POPULATIONS of brook trout (*Salvelinus fontinalis*) in streams of the northeastern United States have undergone marked changes since 1900. Anglers and fishery biologists generally concede that abundance, growth, and life span of brook trout have declined and the distribution of populations along stream courses has shifted. Concurrently, in many of the same streams brown trout (*Salmo trutta*) numbers have increased and their distribution has expanded. As brook trout populations appear to dwindle, there is concern that introduction and invasion of brown trout may be a major cause of their decline.

Brook and brown trout evolved separately. Brook trout were indigenous to eastern Canada and the northeastern United States (MacCrimmon and Campbell 1969) but in Michigan only to its upper peninsula (Smedley 1938; Westerman 1974). They were stocked in streams of Michigan's lower peninsula as populations of the now extinct Michigan grayling (*Thymallus tricolor*) declined. Brown trout were introduced from Europe to New York and Michigan beginning in 1883 (MacCrimmon and Marshall 1968). Growth of brook trout first introduced into Michigan's Au Sable River in 1885 declined markedly after brown trout were added in 1891 (Smedley 1938).

In northeastern United States streams where brown trout were introduced or have invaded, brook trout tend now to be more abundant in headwaters and brown trout more abundant downstream. There is often a long zone where populations of the two species overlap, but in many streams brown trout gradually encroach farther upstream each year. This distributional pattern may be due to (1) changes in physical characteristics along the stream course (Gard and Flittner 1974), (2) differential effects of angling, owing to greater catchability of brook trout (Cooper 1952), (3) predation by large brown trout on small brook trout (Alexander 1977), and (4) competition between the two species (Nyman 1970).

The purpose of this study was to examine interspecific competition of adult brook and brown trout for stream positions. Interspecific competition may be defined as the demand by two or more species for a resource in short supply, and requisites for its study are (1) identification of the resources involved and (2) a method to measure competition for these resources.

Previous research indicates that salmonids compete for stream positions that maximize their chances for survival and growth. Kalleberg (1958) proposed that the aggressive defense of territories by salmonids evolved as a mechanism for efficient use of the food supply. Stream salmonids maintain relatively fixed positions with respect to the stream bed, termed focal points, and make short forays from them to feed on invertebrates drifting nearby. Chapman (1966) suggested that competition for space has been substituted for competition for food among stream salmonids. He hypothesized that territory size is linked to food supply as a mechanism to regulate population density. Slaney and Northcote (1974) tested this relationship and found that both salmonid aggression and territory size increased as abundance of drifting prey was reduced. These investigations indicate that space is a critical resource for which stream salmonids compete.

However, because space is linked to food supply, a stream salmonid should compete not just for a certain amount of space but also for an advantageous position offering the best opportunity for securing food and, ultimately, for growth and survival. To achieve this, the fish should maintain positions in slowly flowing water to minimize energy expenditure, but near fast currents carrying more food per unit time to maximize energy intake. Salmonids in Pacific Northwest streams are reported to use positions with these water velocity characteristics (Chapman and Bjornn 1969; Everest and Chapman 1972; Griffith 1972).

"Water velocity difference" is the term Fausch (1978) used to denote the difference between water velocity at the focal point and velocity of the strongest current occurring within 60 cm of the focal point. We assume that positions with the greatest water velocity difference are most advantageous and we use magnitude of velocity difference as the principal criterion of trout position quality. Because we suspect choice of advantageous positions by trout involves not only water velocity and food supply, but also physical structure of the channel and lighting, we also examine other position characteristics.

Because brook and brown trout evolved in similar environments, it is not surprising that they appear to use similar resources. In theory, when similar species occur in sympatry, the competitively subordinate species shifts its use of resources to reduce niche overlap with the dominant (Morse 1974). Nilsson's (1967) review revealed that niche shifts are common among fishes, especially salmonids, and he called the reduction in niche breadth with addition of a species interactive segregation. Conversely, when the dominant species is removed, the subordinate should shift to use more of the preferred resources, a phenomenon termed ecological release.

The ecological release by brook trout to more advantageous positions after removal of the brown trout was our basis for judging whether brown trout dominated and excluded brook trout from preferred positions. Our objective was to compare brook trout position characteristics before and after brown trout removal, using water velocity difference and other measures.

Study Area and Stream Conditions

The study area of the East Branch of the Au Sable River has a low gradient (1 m/km) typical of streams in the glacial deposits of Michigan's northern lower peninsula. It consisted of 1800 m of stream measured upstream from the south edge of Sec. 14, T27N, R3W (44°43′41″N, 84°38′36″W). Here the stream was third order (Strahler system) and averaged 7.5 m wide and 60 cm deep. The channel bed was sand and gravel with only two pools deeper than 100 cm. The discharge is stable, with mean summer base flow of 1.07 m^3/s (37.7 cfs) at the U.S. Geological Survey gaging station 13 km below the study area, and a 10-to-90% duration discharge ratio of 1.53 (Hendrickson et al. 1973). During the study, discharge at the U.S.G.S. gage ranged from 0.85 to 0.99 m^3/s (30.0–35.0 cfs), about one standard deviation below the 1959–73 mean for July–August, indicating that the study occurred during summer base flow.

The macrophyte *Valisneria americana* was abundant along the silted stream margin in water less than 30 cm deep. Resident fishes included brook and brown trout, slimy and mottled sculpin (*Cottus cognatus* and *C. bairdi*), blacknose dace (*Rhinichthys atratulus*), and Johnny darter (*Etheostoma nigrum*). Brook, brown, and rainbow trout (*Salmo gairdneri*) had been stocked in various amounts and locations in the East Branch until 1964. Current deflectors and overhanging bank coverts made of logs had been installed about 1960 and, although deteriorating, still provided most of the instream cover for trout.

Methods

The senior author used a wet suit, mask, and snorkel to observe positions held by adult brook trout in sympatry with brown trout (July 21–23 and August 11, 1977). Then the brown trout were removed by electrofishing and, after 5 d to allow trout behavior and physiology to return to normal, the observations were repeated (August 20–23).

On each day of diving 2–3 h was spent underwater beginning at 8:30 EDT and a similar period beginning at 13:30. The diver progressed upstream, covering a previously undisturbed 100- to 300-m reach each half day. After removing the brown trout, 300 m at the study area's downstream end and 400 m at the upstream end were omitted from observation as a precaution against observing brook trout that might have been affected by brown trout immigrating from adjacent areas.

Changing underwater visibility complicated observation on most days. It was measured by recording the distance at which an object in the stream disappeared from view. Visibility usually decreased from 4 m or more at 8:30 EDT to 2.5 m or less by 16:30. The decrease was probably caused by light reflecting from colloidal-sized particles, and the diurnal cycle suggests a fine $CaCO_3$ precipitate due to increased photosynthesis of aquatic plants.

To measure positions of trout, the diver crawled slowly along the stream bed, investigating all artificial and natural cover large enough to conceal adults. Most trout remained undisturbed when approached within viewing distance from downstream. Upon sighting an adult trout, the diver remained motionless for 1–2 min. During this period he assessed whether the fish had been disturbed and noted the (1) species, (2) type of position (resting or feeding), (3) size-class of the fish, (4) location of the focal point, and (5) distance of the fish's head from the stream bed. Positions of visibly disturbed fish were disregarded. Fish holding positions beneath submerged cover that was 15 cm or closer to the stream bed were judged to be resting. All other fish positions were classed as feeding. These criteria coincided with observed resting and feeding behavior of East Branch trout.

Brook trout were recorded by three size-classes: 15–20 cm, 20–25 cm, and 25–30 cm. To determine the size of a fish, the stream bed features at its snout and tail were noted and the distance between them measured. With practice, lengths of trout were easily judged to the nearest centimetre without the stream bed measurement.

After underwater observation of a fish, the diver placed a marker in the stream bed and measured five position variables at the focal point: (1) water velocity, (2) maximum water velocity within 60 cm, (3) water depth, (4) distance to nearest cover, and (5) light class. Water velocities were measured with midget Bentzel speed tubes, built according to Everest (1967). Nearest cover was defined as the nearest submerged object that could fully conceal the fish from overhead view. Because resting trout were beneath cover, distance to nearest cover for these fish was zero.

Light at the focal point was visually judged according to three classes: direct light, indirect light, and shade. Direct light was where sunlight reached the stream bed. Indirect light included positions illuminated by sunlight reflected from the stream bed or diffused through riparian foliage. Positions in dark shadows beneath submerged cover were classed as shade. All observations were made at times of bright sunlight.

To remove the brown trout population, we electrofished the entire study area three times during 3 consecutive days. Brown trout abundance was estimated by the improved Leslie method (Ricker 1975) and brook trout abundance by the Schaefer modification of the Petersen mark–recapture method (Regier and Robson 1967). The marking and recapture of brook trout were done on the first and last electrofishing runs. Scales were sampled from a wide range of trout sizes for aging.

Because the majority of resting trout used positions beneath three types of submerged objects, deeply undercut banks in the two large pools, natural logs, and man-made log cover devices, the availability of each type was estimated. As indices of cover, we measured the length of logs and undercut banks beneath which a gauge 15 cm high and 9 cm wide would fit, the same criteria used by Wesche (1976) in his cover rating procedure.

We tested for interspecific competition by measuring change in brook trout position characteristics after brown trout were removed. Because we did not identify individual fish, we compared means of brook trout position variables measured in sympatry versus those in allopatry. Because the six variables at any one position (focal point water velocity, maximum water velocity within 60 cm, water depth, distance to stream bed, distance to cover, and light) were not statistically independent, we compared them simultaneously by multivariate analysis. Three position variables were sensitive indicators of changes in brook trout positions and were used in further tests. These were water velocity difference, water depth, and distance to stream bed.

The main comparisons were multivariate pooled T^2-tests (analogous to univariate t-tests) of brook trout positions in sympatry versus those in allopatry. Four separate tests were made for feeding and resting trout of 15–20 cm and 20–30 cm, only one fish of the latter group being in the 25- to 30-cm class. Heterogeneous variance prevented using a multivariate analysis of variance. When there was a significant difference between position variables in sympatry and allopatry, multivariate confidence intervals of the differences between means of the three variables were constructed to see which contributed most to null hypothesis rejection. All multivariate procedures are described in Kramer (1972).

Frequencies of brook trout positions in the three light classes were compared with expected frequencies using a contingency table. Sympatry was compared with allopatry in separate tests for resting and feeding brook trout of 15–30 cm.

Results and Discussion

Population Estimates

Numbers of brook and brown trout were grossly unequal in all size-classes except 20–25 cm (Fig. 1). Brook trout of 15–20 cm were much more numerous than brown trout of that size group. Only one brook trout over 25 cm was collected but there were 51 brown trout of 25–60 cm. In population estimates for four 400-m sections of the lower 1600 m of the study area, all but the downstream section held four to six 20- to 25-cm brook and brown trout.

Leslie estimates for brown trout were difficult to calculate because fewer fish were caught on the second electrofishing run than on the third. Therefore, in addition to the formal Leslie regression estimate, a maximum estimate was made using only the first and third runs. The two estimates indicated that 95–99% of brown trout over 15 cm had been removed by electrofishing, so the total number of brown trout captured was used as the population estimate.

Only one age-III brook trout was captured. The age distribution of brown trout was less truncated, with many surviving to age III and some to age V. Mean lengths of brook trout at ages 0 through III were 8.9, 15.9, 20.6, and 30.7 cm. Mean lengths of age 0 through V+ brown trout were 8.0, 18.0, 27.1, 34.9, 43.5, and 48.0 cm, respectively.

Brook Trout Position Shift

Brook trout held more favorable resting positions after brown trout were removed while feeding positions were relatively unchanged. Resting brook trout of both size-classes, 15–20 cm and 20–30 cm, chose positions with lower mean focal point velocity but greater water velocity difference after brown trout were removed. Water depth and distance to stream bed decreased from sympatry to allopatry for positions of 15- to 20-cm brook trout but increased slightly for the 20- to 30-cm class (Table 1).

Positions held by 15- to 20-cm resting brook trout differed in sympatry and allopatry ($P < 0.10$) but the multivariate confidence intervals (MCI) indicate that most of the difference was due to water depth and some to distance to stream bed (Table 2). Brook trout of 20–30 cm chose resting positions in sympatry that differed significantly from those in allopatry ($P < 0.025$). The MCI show that the difference was mainly due to increase in water velocity difference (Table 2). Resting brook trout of 15–30 cm chose positions with less light more frequently after brown trout were removed ($P < 0.10$). Resting brook trout were found in shade most often and in direct sunlight least often (Fig. 2).

Feeding brook trout chose positions with greater velocity difference and water depth after brown trout removal but these differences were not significant for either the 15- to 20-cm or the 20- to 30-cm size-class ($P >> 0.10$ for both sizes, Table 2). Brook trout of both size-classes fed closer to cover in allopatry but this difference was significant only for 15- to 20-cm fish ($P < 0.01$). Moreover, this position characteristic may be meaningless as trout rarely swam to the nearest cover when intentionally disturbed. Feeding brook trout (15–30 cm) also chose positions with less light more frequently after brown trout removal but the difference was not significant ($P > 0.30$). Brook trout were seen feeding most often in indirectly lit positions, less often in direct sunlight, and never in the shade (Fig. 2).

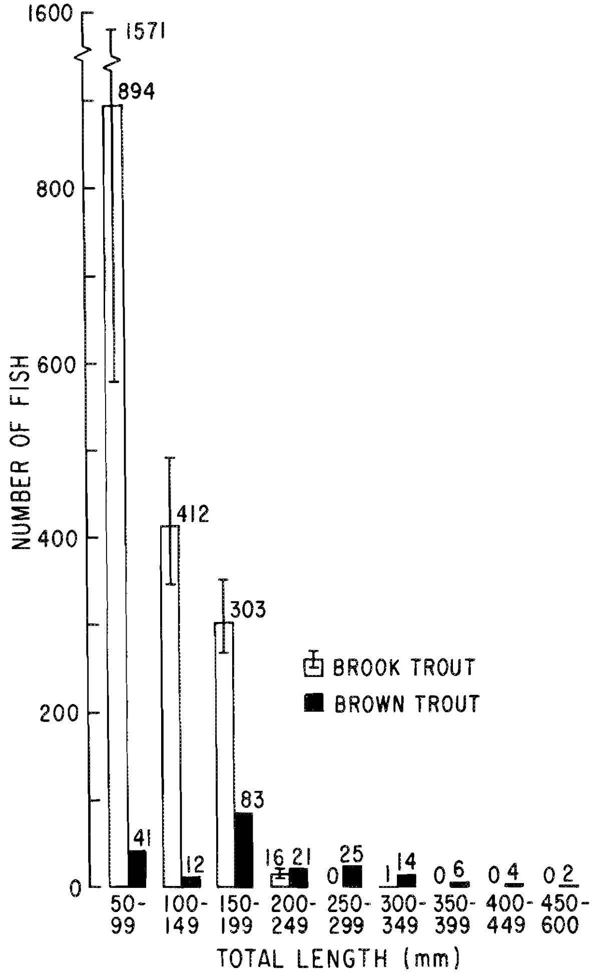

FIG. 1. Length frequency distributions of brook and brown trout in the lower 1600 m of the study area. For brook trout, 95% confidence intervals are indicated. Confidence intervals are not shown for brown trout, as the actual numbers captured were used (see text).

Evidence for Competition

According to our primary criterion of trout position quality, water velocity difference, adult brook trout occupied more advantageous resting places in the stream after brown trout were removed. In addition, brook trout spent less energy in

TABLE. 1. Characteristics of brook trout positions. Means ± SE are shown for each variable.

			Water velocity (cm/s)				Distance (cm)	
Position type	Population type	Sample size (n)	Focal point	Maximum within 60 cm	Difference	Water depth (cm)	To stream bed	To cover
			15- to 20-cm brook trout					
Resting	Sympatry	16	20.4±1.8	36.4±2.3	16.0±1.6	64.7±4.1	3.0±0.5	0.0[a]
	Allopatry	27	12.7±1.8	30.3±2.4	17.6±1.8	51.7±3.2	2.0±0.3	0.0[a]
Feeding	Sympatry	24[b]	26.8±1.6	43.4±2.2	16.6±2.5	66.6±3.7	6.5±0.7	187.3±12.1
	Allopatry	19	24.7±1.5	45.6±1.8	20.9±2.5	72.7±2.3	5.5±0.8	127.9±14.1
			20- to 30-cm brook trout					
Resting	Sympatry	5	19.5±3.0	36.0±3.4	16.5±2.1	61.6±5.6	2.4±0.9	0.0[a]
	Allopatry[c]	3	13.2±3.7	49.8±5.1	36.6±1.8	62.3±3.3	3.0±0.0	0.0[a]
Feeding	Sympatry	5	21.3±3.6	39.0±2.2	17.7±2.2	67.6±4.6	6.8±1.3	172.0±21.3
	Allopatry	5	18.3±2.7	48.8±8.8	30.5±8.8	74.2±5.0	7.0±1.4	134.0±32.2

[a] Resting fish were beneath cover.

[b] One outlier excluded according to the method of Grubbs and Beck described in Gill (1978).

[c] Includes one 25- to 30-cm brook trout.

TABLE. 2. Significance levels of multivariate tests and individual variables.

		Significance (P) of individual variables		
Comparison	Significance of main tests (P)	Water velocity difference	Water depth	Distance to stream bed
	15- to 20-cm brook trout			
Sympatry vs. allopatry				
Resting fish	<0.10	>>0.10	<0.20[a]	<0.30[a]
Feeding fish	>>0.10			
	20- to 30-cm brook trout			
Sympatry vs. allopatry				
Resting fish	<0.025	= 0.025	>>0.10	>>0.10
Feeding fish	>>0.10			

[a] Because table T^2 values were not available beyond $P = 0.10$, these are conservative estimates of the significance of these variables.

allopatric resting positions because focal point velocities were lower, and occupied more shaded positions after brown trout were removed. This type of ecological release or niche shift resulting from addition or removal of a closely related species is regarded as the strongest and most direct evidence to show interspecific competition for a resource (Diamond 1978; Sale 1979). In contrast, feeding positions of brook trout were similar before and after brown trout removal, indicating little competition for this resource during the study.

Competition can occur only when resources are in short supply. Evidence that resting positions were scarce but that feeding positions were plentiful lies in the hydrology and morphometry of the study area and in our measurements of instream cover.

Because flow in the East Branch is very stable, the trout population should be regulated mainly by the supply of space and food, and not by harsh environmental factors such as floods (Elwood and Waters 1969) and winter ice (Maciolek and Needham 1952). Predation, as well as intra- and interspecific competition for space should adjust the trout population to balance the resource supply (Chapman 1966).

The East Branch channel was wide, shallow, and devoid of trout cover in much of the study area, and there were only two pools with deeply undercut banks. Our cover measurements confirm that trout cover was scarce. In the lower 1600 m of the study area, only 224 m of cover was available to trout, of which 187 m (83%) was formed by man-made cover devices, 28 m (13%) was natural logs, and 9 m (4%) was deeply undercut banks. The mean density of cover was 140 m per stream kilometre. In comparison, a 2400-m study area of the nearby Pigeon River had a mean density of 432 m per stream kilometre of these three cover types (Enk 1977).

Moreover, the East Branch was one standard deviation below base flow during the study, which further limited the amount of resting cover that was submerged. This evidence supports our view that resting positions were in short supply for East Branch trout during the study. Increase in trout populations when permanent bank cover is added to streams also demonstrates that resting positions are a critical resource for stream salmonids in the long term (reviewed by White 1975).

In contrast, feeding positions were abundant in the study area. Trout choose feeding positions beneath principal lines of invertebrate drift but usually with some protection from swift currents (Jenkins 1969). However, channels of rather low

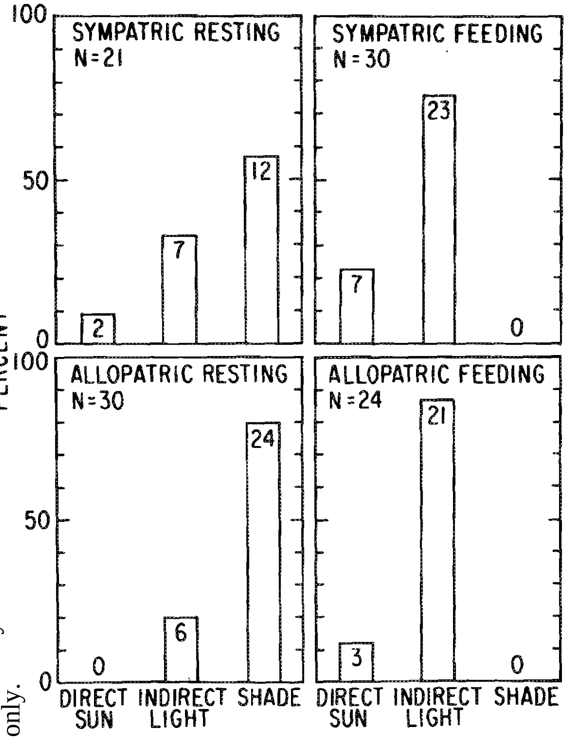

FIG. 2. Use of positions with different lighting by 15- to 30-cm brook trout in sympatry and allopatry. Numbers of observations are shown in bars.

gradient, uniform cross section, and smooth bed, such as the study area, have few refuges from ambient water velocity and lack strong principal currents. Instead, the fairly uniform distribution of water velocities and of invertebrate drift in such channels provides many feeding positions of about equal quality, and little competition for them should be expected. Bassett (1978) studied cover preference of brown trout in artificial channels and proposed that uniform velocity and drift pattern minimized intraspecific competition for feeding positions.

Trout were observed to occupy resting positions during the day unless sufficient invertebrate drift stimulated them to feed. During the study, most drift consisted of *Tricorythodes* mayflies emerging during the morning in late July and early August, and a general emergence of midges (Diptera) and small mayflies (Ephemeroptera) during late afternoon. Brook trout of 20–30 cm moved to daytime feeding positions only when invertebrate drift was far more abundant than that which stimulated 15- to 20-cm brook trout to feed. We assume that large trout fed mainly during late evening when larger stream insects emerged.

Brook trout of both size-classes preferred to feed from indirectly lit positions, using them more frequently after brown trout removal (Fig. 2). Brook trout of 20–30 cm usually held feeding positions in shade beneath instream cover more than 15 cm from the stream bed whereas 15- to 20-cm brook trout often fed in shadows from objects above the water, such as overhanging vegetation. Underwater observations offered an explanation for the use of shade. We speculate that in areas of direct sunlight, the light reflected from suspended particles hampers visibility of trout whereas drift is seen better from shaded positions. Brown trout were seen less often than brook trout, as they were less numerous and chose more concealed resting positions during the day. The seven brown trout observed held positions similar to those used by brook trout of equal sizes.

Our data indicate that resting brook trout held positions closer to swift currents, that is with greater water velocity difference, after brown trout were removed (Table 1). We speculate that trout prefer such resting positions because they allow fish to view organisms drifting nearby and to move to feeding positions quickly in response to increased drift. This visual sampling may be important for efficient foraging.

EFFECT OF BODY SIZE

Although adult brook trout displayed ecological release as predicted, interpretation is hampered because populations of each species were dissimilar in body size distribution (Fig. 1). However, we base most of our conclusions on 20- to 25-cm brook and brown trout, which were nearly equal in number.

Among both juvenile (Newman 1956) and adult salmonids (Jenkins 1969; Bassett 1978) dominance in intraspecific competition is bestowed on individuals of greatest size. Therefore, large brown trout (>30 cm) should have excluded smaller trout of both species from preferred resting positions. Given this, our results might be explained by the alternative hypothesis that the two species are of about equal competitive ability, and that after brown trout were removed, brook trout merely shifted to resting positions previously occupied by the larger brown trout. Had this been the case, however, the smaller brook and brown trout of equal size should have occupied "good" and "poor" resting positions in proportion to their numbers. If we assume that trout resting positions visible to the diver were poorer for survival and growth of trout than concealed positions, then some evidence to refute the "equal competitor" hypothesis is provided by the high ratio of brook to brown trout occupying these poorer (more visible) resting positions.

In the 15- to 20-cm size-class, the ratio of brook to brown trout was 3.65:1 (303:83) in the population but was 8:1 (16:2) in the visible resting positions. The proportion of brook trout observed in these relatively poorer resting positions was greater than the expected proportion found in the population, but not significantly greater ($P = 0.14$) according to a nonparametric test of binomial proportion (Hollander and Wolfe 1973). However, for 20- to 25-cm trout, the ratio of brook to brown trout observed in visible resting positions was 2.5:1 (5:2), significantly greater ($P = 0.07$) than the expected ratio of 0.76:1 (16:21) in the population. Therefore, even though populations were unequal, these results support the view that brown trout were able to exclude equal-sized brook trout from preferred resting positions.

In summary, our data indicate that brook and brown trout competed for preferred resting positions, a critical and scarce resource, and that brown trout were the dominant competitor because brook trout expanded their use of resources to include more advantageous resting positions when released from interspecific competition.

FORCES SHAPING SYMPATRIC POPULATIONS

Dominance of brown trout should be important in changing the relative distribution and abundance of sympatric brook and brown trout populations. However, environmental factors, fishing mortality, and predation may also favor one species in certain situations and thereby effect changes that are difficult to separate from those caused by interspecific competition.

The frequently observed pattern of brook trout in headwaters and brown trout in downstream reaches has commonly been correlated with gradients of water temperature, altitude, stream slope, and stream size (Vincent and Miller 1969; Lane and Skrzynski 1972; Gard and Flittner 1974). However, distribution of the two species cannot be attributed to any one factor because all are related.

Brook trout are more easily caught by fishing than brown trout (Cooper 1952). In a sympatric population exposed to fishing, Marshall and MacCrimmon (1970) found that no brook trout survived to age III but brown trout commonly lived to age V and one fish to age XIII. Similarly, in the East Branch where fishing pressure was moderate, few brook trout lived to age III but brown trout as old as age V were found. In unfished allopatric populations, the oldest brook trout found were age V or VI (Doan 1948; Cooper 1967; O'Connor and Power 1976). Jensen (1971) compared life tables of fished and unfished brook trout populations. In fished populations he found that the balance of birth and death rates was reestablished by drastic changes in age-specific fecundity with selection for early maturity. Male brook trout may be sexually mature as early as age 0 in these populations and females as early as age I. Exploited brown trout populations studied by McFadden and Cooper (1964) showed no such effects.

Predators also kill more brook than brown trout. Alexander (1977) found that adult brown trout ate 4728 and 2219 age-0 brook trout per stream kilometre in two sections of the North Branch of the Au Sable River, Michigan, while eating only 135 young brown trout per kilometre in each section. American mergansers (*Mergus merganser*), belted kingfishers (*Megaceryle alcyon*), great blue herons (*Ardea herodias*), mink (*Mustela vison*), and otter (*Lutra canadensis*) also preyed more heavily on brook trout of all ages than on brown trout (Alexander 1976).

Due to the interaction of competition, predation, fishing mortality, and environmental factors, the mechanisms causing change in sympatric populations remain unclear. However, it is evident that predation and fishing can selectively reduce brook trout populations while brown trout, being more resistant to both forces, typically maintain or increase abundance. Moreover, fishing causes concomitant alterations of brook trout growth and reproduction which reduce the ability of populations to maintain sport fisheries.

We speculate that, as brown trout populations gradually increase, they spread through stream systems to points where they encounter shallowness, undesirably cold or warm temperatures, or other unfavorable conditions. At these limits of distribution, brown trout may be unable to compete successfully with brook trout for space, cover, or food. But in areas where physical conditions are suitable for both species, our results indicate that brown trout can exclude brook trout from preferred resting positions. Gaining these positions should allow brown trout growth and survival to increase at the expense of the brook trout.

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