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Habitat shifts in rainbow trout: competitive influences of brown trout

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Summary. We compared habitat use by rainbow trout sympatric (three streams) and allopatric (two streams) with brown trout to determine whether competition occurred between these two species in the southern Appalachian Mountains. We measured water depth, water velocity, substrate, distance to overhead vegetation, sunlight, and surface turbulence both where we collected trout and for the streams in general. This enabled us to separate the effects of habitat availability from possible competitive effects. The results provided strong evidence for asymmetrical interspecific competition. Habitat use varied significantly between allopatric and sympatric rainbow trout in 68% of the comparisons made. Portions of some differences reflected differences in habitats available in the several streams. However, for all habitat variables measured except sunlight, rainbow trout used their preferred habitats less in sympatry with brown trout than in allopatry if brown trout also preferred the same habitats. Multivariate analysis indicated that water velocity and its correlates (substrate particle size and surface turbulence) were the most critical habitat variables in the interaction between the species, cover in the form of shade and close overhead vegetation was second most important, and water depth was least important.

Key words: Habitat use – Interactive segregation – Niche shift – Stream – Trout

Our research was a comparative field study or natural snapshot experiment (sensu Diamond 1986) of interspecific competition between rainbow trout (*Salmo gairdneri*) and brown trout (*Salmo trutta*) in streams of the southern Appalachian Mountains. The autecologies of these species are well known, but not their synecology. The species have similar food habits (Maciolek and Needham 1952; Jenkins 1969a, b; Elliott 1973; Kaeding and Kaya 1978) and habitat preferences (Hartman 1963; Butler and Hawthorne 1968; Baldes and Vincent 1969; Jenkins 1969a; Lewis 1969; Le Cren 1973; Devore and White 1978; Horton and Cochnauer 1978; Binns and Eiserman 1979; Gosse and Helm 1981; Helm et al. 1981; Bachman 1982; Shirvell and Dungey 1983; Baltz and Moyle 1984; Fausch 1984). Hence, interspecific competition might be expected if either food or habitat were in short supply. Research by Shirvell and Dungey (1983) and Lewis (1969) led them to suggest that the microhabitats occupied by brown trout and rainbow trout, respectively, may reflect competitive effects with a congener, but neither study permits definitive statements to be made about competition between these two species in nature. Vincent (1987) reported that stocking hatchery rainbow trout in previously unstocked stream reaches in Montana led to decreased numbers and biomass of brown trout >25 cm long but not of smaller fish, whereas cessation of stocking led to increased numbers and biomass of both wild rainbow trout and wild brown trout.

Reduced population size, growth, or production of a species in the presence of another indicates competition by definition. In lieu of information of this sort, two other major lines of evidence are often used to show the existence of interspecific competition: (1) coexistence of two species with a high overlap in resource use; and (2) a reduction of the realized niche (Hutchinson 1957) or actual niche (Colwell and Futuyma 1971) of one species when in the presence of another (also termed an ecological shift by MacArthur and Wilson (1967), a niche shift by various authors (e.g., Werner and Hall 1976), and interactive segregation by Nilsson (1967)). Resource overlap alone does not necessarily mean that two species are competing (e.g. Wiens 1977; Sale 1979; Tinkle 1982; Wise 1981), but resource overlap together with niche shifts in sympatry are considered to be sufficient evidence of competition by some (e.g., Colwell and Futuyma 1971; Diamond 1978) but not all (e.g., Thomson 1980; MacNally 1983). We agree with Colwell and Futuyma (1971) and Diamond (1978) and, hence, compared habitat availability and use between streams inhabitated by both rainbow and brown trout (sympatric streams) and streams inhabited by rainbow trout alone (allopatric streams).

We emphasized habitat use because of the known importance of habitat on population size for trout. Habitat improvements in trout streams usually result in increased numbers of trout (e.g., Boussu 1954; Saunders and Smith 1962; Hunt 1976) and removal of good habitat results in decreased numbers of trout (e.g., Boussu 1954; Elser 1968; Elwood and Waters 1969; Mortensen 1977; Chapman and Knudsen 1980). Although exceptions to these results exist (e.g., Hartzler 1983), the results are frequent enough that competition for microhabitats was a realistic expectation for the streams used in this study. Population limitation by some factor other than habitat seemed much less likely.

The literature provides both general and specific expectations for our study. Brown trout are both more aggressive

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than other salmonid species and larger on the average than other stream dwelling touts (Kalleberg 1958; Nilsson 1963; Vincent and Miller 1969; Nyman 1970; Gard and Seegrist 1972; Fausch and White 1981; Waters 1983). Hence, brown trout should dominate any potentially competitive situation with a confamilial species (Newman 1956). Findings by Fausch and White (1981) who reported that brown trout excluded brook trout from their preferred resting areas, and by Shirveil and Dungey (1983) who found that brown trout occupied the same microhabitats whether or not rainbow trout were present, both support this inference. Based on this presumed competitive dominance of brown trout over rainbow trout and competition theory in general, we expected that rainbow trout sympatric with brown trout should show niche shifts away from habitats preferred by brown trout. Based on the data in Bovee (1978) and Butler and Hawthorne (1968), the specific niche shifts we expected were that rainbow trout should move to deeper, faster water with more surface turbulence and into more open areas with less close overhead vegetation and shade.

Our use of a comparative study or natural snapshot experiment (given that we ourselves did not make the species introductions) offered some advantages and some disadvantages relative to manipulative field experiments in the study of niche shifts. Manipulative field experiments offer the advantage that the investigator can ensure that the presence or absence of the suspected competitor is the only variable; strong evidence for competition results (Connell 1983; Schoener 1983). In contrast, any features that vary among study areas used in a comparative study besides the presence or absence of the suspected competitor (e.g., availability of resources, level of predation or parasitism, etc.), must form the basis of alternative hypotheses to be rejected before a hypothesis of competition can be considered corroborated (e.g., Schmitt and Coyer 1983). Furthermore, field manipulation can sometimes provide evidence for a niche shift not seen in a comparative study (e.g., Salzburg 1984). Potential advantages of a comparative study, however, are that information is gained about possible variations in resource use with differences in resource availability or predation pressure, and that the time required to obtain results can be substantially less than the years required by some but not all manipulative field studies (cf Vincent 1987, Werner and Hall 1976). Diamond (1983, 1986) and Schoener and Spiller (1987) offer further comments on the relative merits of these different experimental approaches.

Materials and methods

Study streams

We studied 150–400 m sections of one third-order and four fourth-order streams in the mountains of eastern Tennessee and western North Carolina. The streams are described in detail in Loar (1985). Rainbow trout were allopatric from brown trout in two streams, Abrams Creek (AC) and Mill Creek (MC) in Cades Cove, Great Smoky Mountains National Park, Tennessee. We captured only two adult brown trout at AC and two Age 0 brown trout at MC over a two-year sampling period (Loar 1985). Rainbow trout were sympatric with brown trout in the other three streams, Bradley Creek (BC = combined BC1 and BC2 in Loar 1985) in Henderson County, North Carlina, Lost Cove Creek (LCC) in Avery County, North Carolina, and the Nantahala River (NR = NR3 in Loar 1985). Only BC and LCC supported populations of Age 0 brown trout, but adult brown trout occurred in all three sympatric streams (BC, LCC, NR). Populations of other species of salmonids were lacking in all streams: only a single brook trout (*Salvelinus fontinalis*) was caputred at LCC in a two-year sampling period.

Sampling methods

We collected all data on habitat use and habitat availability in late summer and early fall, 1983 (23 August–9 November). Stream flows were low (average = 31% mean annual discharge) and hence habitat limitation likely. Chi-square tests showed no significant differences in habitat use over time, so we combined all data for subsequent analyses.

We collected trout with a Smith-Root Model XV electroshocker that produced pulsed DC output. One person operated the shocker and a second person used a dip net to catch stunned trout. Both individuals worked slowly upstream and normally sampled a single fish at a time. We marked the position at which we first saw each trout with a numbered float attached by cord to a 84-g weight. We marked the point of first sighting rather than the point of collection to minimize the effects of galvanotaxis (= movement of fish toward the anode). We recorded the total length (TL) and species of each trout, and then released it downstream from the point of collection. Scale analyses in Loar (1985) indicated that trout ≤ 11 cm TL were Age 0 and trout > 11 cm TL were Age ≥ 1. We did not use block nets because we did not want to trap any trout that managed to swim away from the electric field.

Electrofishing has been criticized as a means of collecting trout for microhabitat use data (e.g., Gosse and Helm 1981). We considered the primary difficulties associated with electrofishing – frightening fish and galvanotaxis – led to conservative errors in our study of niche shifts. Our procedures probably frightened a number of trout into refuge sites from the feeding sites they might be expected to occupy most of the day (Bachman 1982). Because these types of sites differ physically for at least those fish Age ≥ 1 (Helm et al. 1981), our data likely described characteristics of both feeding and refuge sites. Additionally, some galvanotaxis likely occurred before we noticed the fish, so the positions we characterized were unlikely the exact locations the trout occupied originally. Both difficulties undoubtably increased heterogeneity within species and age groups. High heterogeneity would have increased the difficulty of finding significant differences in habitat use between allopatric and sympatric rainbow trout and led to Type II statistical errors. We recognized that a distorting effect was possible for between-species or between-age comparisons if the different species or age groups differed greatly in responses or response thresholds to electrofishing. But these possibilities would have had no effect on our comparisons within a species or age group.

We note that any other technique besides electrofishing that we might have chosen to identify trout positions would have suffered from similar difficulties. For example, visual observation of fish underwater can also produce fright responses, and visual observations from land can be biased by missing trout in such locations as in deep water, under high surface turbulence, or under overhanging cover. As

Orth et al. (1981) and Bain et al. (1982) indicated, each technique for describing microhabitat use by fish can yield a unique result. We reemphasize our use of the same methods in both allopatric and sympatric streams; whatever types of sites we characterized, they were the same in all streams so our conclusions relative to competitive effects were sound.

We quantified habitat use by measuring six variables (depth, velocity, substrate, overhead vegetation, sunlight, and surface turbulence) at the position of each float. We measured water depth and velocity as continuous variables using a wading rod and a Price pygmy flow meter. We measured velocity both at 0.6 depth (i.e., mean water column velocity) and at 2 cm above the bottom (i.e., a depth that may more accurately reflect the location of the fish (Kalleberg 1958; Baldes and Vincent 1969; Chapman and Bjornn 1969; Jenkins 1969a; LeCren 1973; Gosse and Helm 1981; Bachman 1982; Shirvell and Dungey 1983)). We classified substrate visually into the single dominant category in the modified Wentworth particle size scale (Bovee and Cochnauer 1977). We included small boulders with small and large cobble in the rubble category. We measured distance from the surface of the stream to any vegetation directly overhead with a meter stick for heights up to 3 m and estimated greater heights. We categorized sunlight as full, partial, or shade (following Fausch and White [1981]) and categorized surface turbulence as moderate to high, low, or absent. One of us (AJG) collected all habitat measurements, so individual differences in classification of categorical data or in estimating distances were eliminated.

We estimated habitat availability using both grid and transect sampling. At three streams (AC, MC, and NR), we recorded depth, substrate, overhead vegetation, sunlight, and surface turbulence for a 1-m grid over the entire portion of each stream from which we collected trout and measured velocity at 0.6 depth at 1 m intervals along transects spaced 5 m apart along the same portion of each stream. We collected trout from longer portions of the other two streams (BC and LCC) and measured all six habitat variables at 1 m intervals along transects spaced 5 m apart in these streams. Sample sizes for habitat availability estimates ranged from 157 to 514.

Experimental design

Natural snapshot experiments seldom permit perfect site matching and preclude the regulation of independent variables. Hence, we had to perform a series of analyses to interpret our results relative to possible competitive interactions.

We first analyzed whether or not habitat availability differed among streams. If the sites had matched perfectly, we could have ignored availability in all subsequent analyses; because the sites differed, we had to consider availability in interpreting all our results. We did not test site matching relative to water quality or levels of predation and parasitism. Instead, we assumed that none of these features was important in the present study. Water quality was virtually identical in all streams except one (AC, Loar 1985), and we never observed any effects of parasitism. Most predatory effects varied little among streams. We assumed that potential natural mammalian and avian predators were similar at all streams and did not consider them to be a major source of mortality. Fishing pressure was extremely low in all streams. The major predatory difference among streams was the presence or absence of the only piscivorous fish in the streams, large brown trout. Thus the major possible predatory influences on habitat use by rainbow trout were entwined with competitive effects of sympatry with brown trout.

We next analyzed whether or not habitat use varied with habitat availability among either allopatric or sympatric populations. When no such differences occurred, we pooled the data on habitat use in all streams inhabited by the same species of trout. When such differences existed, we continued to consider habitat availability in further analyses and did not pool the data.

We next analyzed whether or not habitat use by rainbow trout varied between areas of sympatry and allopatry. We interpreted our results of these analyses according to the results of both of the preceding analyses. For example, if differences in habitat use between allopatric and sympatric streams paralleled differences in habitat availability between the two sets of streams, we made the parsimonious interpretation that the differences in habitat use were due to availability differences and not to interaction with a congener. In contrast, if availability and use varied in opposite directions, and if the sympatric rainbow trout were less like brown trout in their habitat use than were allopatric rainbow trout, then we concluded that a niche shift had occurred and inferred interspecific competition existed. A final complicating factor was the possibility of species-specific preferences that could be accentuated by differences in availability between the sympatric and allopatric streams. We therefore examined our results for this possibility, also.

Data analysis

We treated Age 0 and Age ≥ 1 trout of each species separately in all analyses. This eliminated 98% of the correlations of habitat use with length of fish.

We used nonparametric analysis of the data. None of the series of power transformations recommended by Sokal and Rohlf (1981) for positively skewed variables consistently removed both the skewness and kurtosis from the distributions of the variables. For comparisons among streams in habitat availability and comparisons at a single stream between habitat use and habitat availability, we used contingency tables and X^2 tests. For comparisons between streams of habitat use of continuous variables within a species and age group, we used Kruskal-Wallis analysis of variance of ranks followed by Dunn's multiple comparisons test for location, setting the experimentwise error level at $\alpha=0.15$ (Hollander and Wolfe 1973), and Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1981) for distribution. We made analogous comparisons for categorial variables using contingency tables and X^2 tests. For comparisons of habitat use between allopatric and sympatric populations of rainbow trout for continuous variables, we used both normal approximations to the Wilcoxon-Mann-Whitney test with corrections for continuity (Zar 1974) and Kolmogorov-Smirnov two-sample tests. For the analogous analyses of categorical variables, we used contingency tables. We used $\alpha=0.05$ throughout except for the Dunn's tests where the equivalent was used.

To detect pairwise associations of habitat variables available in the streams and habitat used by trout, we used contingency tables and X^2 tests. Comparisons of these anal-

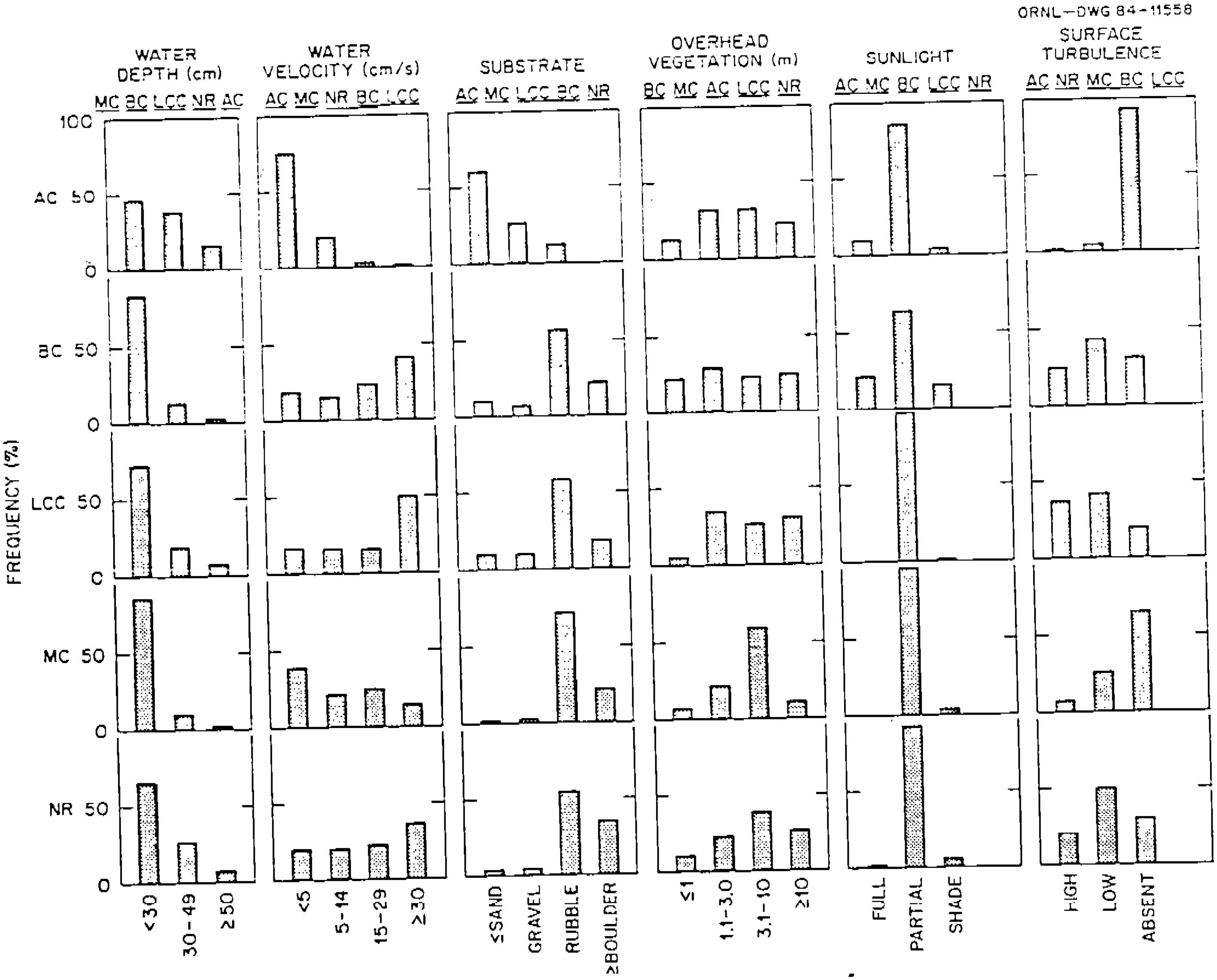

Fig. 1. Habitat availability in each of the streams. Lines beneath letter codes for streams connect streams not significantly different (X^2 tests, $P > 0.05$) from each other in availability

yses indicated which overall associations of variables in the streams were also shown by the trout and whether or not trout showed additional associations between variables in habitat use that were not shown in the streams.

We used principal components analysis on the correlation matrix for all habitat variables and varimax rotation to illustrate similarities and differences in habitat use by the various populations of trout. Following Feeley and Hill (1983), we used mean values for each species and age group at each stream. This analysis also gave information about which variables tended to be associated with each other and the relative importance of the several habitat variables in the separation of the species.

Results

Habitat availability

Habitat availability varied significantly among the streams for all six variables measured (Fig. 1). Each stream had a unique distribution of depths and overhead vegetation. Distributions of velocities, substrates, sunlight, and surface turbulence differed significantly among most but not all streams.

Habitat use relative to availability

Both species of trout showed habitat preferences, i.e., nonrandom use relative to availability. Preferences were statistically significant for 70% of the comparisons made (Tables 1 and 2). Habitat use varied only rarely with availability for either species in the sympatric streams, whereas habitat use varied with availability for rainbow trout in the allopatric streams.

The preferences shown by brown trout Age ≥ 1 were for deep, slowly moving water without surface turbulence over a sand substrate where the overhead vegetation was very close and thus provided shade (Table 1). The only significant differences in preferences among streams for brown trout Age ≥ 1 were the occupancy of more positions with

Table 1. Habitat use by brown trout compared with habitat available in the several streams. Results of X^2 tests are significant if entries other than all 0 or * appear; entries of + indicate moderate (cell $X^2 > 1$) and + + strong (cell $X^2 > 5$) concentration on a given category, entries of 0 indicate use in approximate proportion to availability, and entries of − indicate moderate and − − strong avoidance. Entries of * indicate that expected values < 5 precluded X^2 analysis. n = sample size

Habitat variable	Age ≥ 1			Age 0	
	BC ($n=34$)	LCC ($n=54$)	NR ($n=27$)	BC ($n=28$)	LCC ($n=10$)
Depth (cm)					
< 30	− −	− −	−	−	0
30–49	+ +	+ +	+ +	+	0
≥ 50	− −	+	0	0	0
Velocity (cm·s⁻¹)					
< 5	0	+ +	+ +	+	0
5–14	+ +	0	0	0	+
15–29	0	0	0	0	+
≥ 30	−	− −	−	−	−
Substrate					
≤ Sand	+ +	+ +	+ +	+	0
Gravel	0	+	0	0	0
Rubble	0	−	−	0	0
≥ Boulder	−	− −	0	−	0
Overhead vegetation (m)					
≤ 1.0	+ +	0	+ +	+ +	0
1.1–3.0	0	+ +	0	0	0
3.1–10	−	0	0	0	0
> 10	−	− −	− −	−	0
Sunlight					
Full	−	*	*	− −	*
Partial	−	*	*	0	*
Shade	+ +	*	*	+ +	*
Surface turbulence					
Moderate-high	0	− −	0	−	*
Low	0	0	0	0	*
Absent	0	+ +	0	+	*

overhead vegetation > 1 m above the stream at LCC than at either BC (Kolmogorov-Smirnov two-sample test, $D = 0.356$, $P \sim 0.01$) or NR ($D = 0.389$, $P < 0.01$) and the less frequent occurrence of trout in the shade at LCC than at BC ($X^2 = 5.594$, df = 1, $P < 0.025$). These differences paralleled major differences in habitat availability at the streams (Fig. 1): LCC had less vegetation ≤ 1 m above the surface of the water and more at the 1.1- to 3.0-m level than either of the other two sympatric streams; LCC also had the least shade while BC had the most. Age 0 brown trout showed preferences similar to their older conspecifics wherever samples sizes were sufficiently large to permit statistical analysis. We identified no significant differences in the habitat used by Age 0 brown trout between the two streams in which they were found.

Habitat availability had no effect on habitat use by rainbow trout in these same streams. We found no significant differences in habitat use for either age group. Sympatric rainbow trout Age ≥ 1 showed preferences similar to those of brown trout Age ≥ 1 for depth, substrate, overhead vegetation, and sunlight but different preferences for velocity (faster water) and surface turbulence (moderate to high). Age 0 rainbow trout only showed preferences for intermediate depths and for moderate to high surface turbulence; no other deviations from random use occurred consistently. Because habitat use varied so little with habitat availability for either species of trout in sympatry, we pooled data within species and age groups for further analysis of habitat use by these populations.

The situation in allopatric streams was markedly different. Numerous significant differences existed between the habitats used by rainbow trout in these two streams. Rainbow trout Age ≥ 1 used deeper water (Dunn's test, $P < 0.05$) over finer substrate ($X^2 = 29.351$, df = 2, $P < 0.001$) under closer overhead vegetation (Dunn's test, $P < 0.005$) more in the shade ($X^2 = 8.151$, df = 2, $P < 0.005$) and less in turbulent water ($X^2 = 18.293$, df = 2, $P < 0.001$) at AC than at MC. Only the velocity of water occupied by the trout did not differ between the two streams (Dunn's test, $P > 0.5$) despite the great differences in availability at the two streams (Fig. 1). All other between-stream differences in habitat use paralleled the between-stream differences in availabilites except for the use of shade (which did not differ in availability between the streams). Availability had much less influence on habitat use by Age 0 allopatric rainbow trout. The only significant difference ($X^2 = 15.068$, df 2, $P < 0.001$) was that Age 0 trout were above fine substrates more often at AC where these substrates were more available (Fig. 1) than at MC.

Habitat use relative to the presence of a potential competitor

Because habitat use varied with availability in the allopatric streams, we had to interpret all possible niche shifts carefully. We present these interpretations for each habitat variable seriatim.

Depth. Significant differences in use occurred between allopatric and sympatric rainbow trout of both age groups. The differences for fish Age ≥ 1 (Fig. 2) are consistent with the differences in availabilities (Fig. 1); there is no reason to invoke competition. This is not true for Age 0 fish. Contrary to the difference in habitat availability (we pooled the availability data for the allopatric streams because use did not vary with availability in these two populations), Age 0 rainbow trout occupied deep water more frequently in sympatric than in allopatric streams ($z = 3.904$, $P < 0.001$) and thereby also occupied deep water more frequently than the Age 0 brown trout with which they occurred ($z = 1.982$, $P = 0.05$). We interpreted these results to mean Age 0 brown trout displaced Age 0 rainbow trout from shallow water in the sympatric streams. Allopatric Age 0 rainbow trout occupied water of the same depths as Age 0 brown trout ($z = 1.397$, $P > 0.10$).

Velocity. Sympatric and allopatric rainbow trout differed in the velocity of water they occupied whether we measured velocity mid-water (MVEL) or at the bottom (BVEL), hence the precise location of trout in the water column matters little in our analysis of habitat shifts. Sympatric rainbow trout Age ≥ 1 occupied faster water than both their allopatric conspecifics Age ≥ 1 (MVEL: $z = 5.034$, $P < 0.001$; BVEL: $z = 4.953$, $P < 0.001$) and sympatric brown

Table 2. Habitat use by rainbow trout compared with habitat available. See Table 1 for key to symbols

	Age I¯					Age 0				
	AC ($n=45$)	BC ($n=41$)	LCC ($n=38$)	MC ($n=73$)	NR ($n-28$)	AC ($n=37$)	BC ($n=34$)	LCC ($n-20$)	MC ($n=44$)	NR ($n=40$)
Depth (cm)										
<30	− −	− −	− −	− −	− −	+ +	0	−	0	−
30–49	0	+ −	+ −	+ +	+	−	0	+	0	+ −
≥50	+ −	+ +	0	+ +	+	−	0	0	0	0
Velocity (cm/s)										
<5	−	−	+ +	0	0	− −	0	0	0	0
5–14	+ −	+ −	0	− +	0	0	0	0	0	0
15–29	+ +	+	+	−	0	+ +	0	+ +	0	0
≥30	0	− −	− −	0	0	+ +	0	−	0	0
Substrate										
≤Sand	+ +	+ +	+	+ +	0	0	0	0	0	+ +
Gravel	−	0	0	0	0	0	0	0	0	0
Rubble	− −	0	0	− −	0	0	0	0	0	0
≥Boulder	0	−	−	−	0	0	0	0	0	−
Overhead vegetation (m)										
≤1.0	+ +	0	−	+ +	+	0	0	0	+ +	0
1.1–3.0	− −	0	+	0	+ +	0	0	0	0	+ +
3.1–10	−	0	+	− −	−	0	0	0	− −	0
>10	− −	0	− −	0	−	0	0	0	+	− −
Sunlight										
Full	− −	− −	*	− −	*	−	0	*	*	*
Partial	− −	0	*	0	*	0	0	*	*	*
Shade	+ +	+ +	*	+ +	*	0	0	*	*	*
Surface turbulence										
Moderate to high	0	+ +	0	0	+ +	+ +	+ +	0	+ +	+ +
Low	0	0	0	0	0	+ +	0	0	0	−
Absent	0	−	0	0	−	− −	−	0	−	−

trout Age ≥1 (VEL: $z=2.036$, $P<0.05$; BVEL: $z=2.347$, $P<0.02$). Similarly, sympatric Age 0 rainbow trout occupied significantly faster water than either allopatric Age 0 rainbow trout or sympatric Age 0 brown trout (all z's >3.0, all P's <0.005). Because availability lacked an influence on the velocity of water occupied within either allopatric or sympatric streams, we rejected availability as the factor accounting for the allopatric-sympatric differences. Instead, we interpreted the significant differences just noted as indicating that, in both age groups, brown trout displaced sympatric rainbow trout to areas of faster water than they would have occupied otherwise.

Substrate. Habitat use varied between sympatric and allopatric rainbow trout of both age groups. For Age ≥1 fish, we attributed the differences to the combined effects of differences in habitat availability and competition, whereas for Age 0 fish, availability alone explained the differences. Consistent with the differences in availabilities, allopatric rainbow trout Age ≥1 occurred significantly more often over fine substrates than their sympatric counterparts (AC vs. sympatric: $X^2=57.083$, df$=2$, $P<0.001$; MC vs. sympatric: $X^2=7.700$, df$=2$, $P<0.025$). In spite of the availability differences, however, allopatric rainbow trout Age ≥1 at MC did not differ from the brown trout in substrate use ($X^2=1.359$, df$=2$, $P>0.5$), whereas the sympatric rainbow trout Age ≥1 did; they occupied water over coarser substrates than the brown trout Age ≥1 with which they coexisted ($X^2=8.252$, df$=2$, $P<0.025$). We interpreted this latter difference in habitat use, despite the same habitat availability, as a niche shift of rainbow trout. For Age 0 rainbow trout, the only significant difference was their more frequent occurrence over fine substrates in AC than in any other stream (all X^2's >11, all P's <0.005). Because AC had the highest availability of fine substrates of any stream (Fig. 1), we attributed all differences in use among Age 0 fish to differences in availability.

Overhead vegetation. Rainbow trout Age ≥1 occupied more positions with close overhead vegetation in allopatry than in sympatry, although the differences were not always significant (AC vs. sympatric rainbow trout: $z=6.701$, $P<0.001$, MC vs. sympatric rainbow trout: $z=0.921$, $P>0.25$). The direction of the differences ran counter to the differences in availability (Fig. 1), hence better fit an explanation based on competition than one based on availability. We interpreted the significant difference to mean that brown trout Age ≥1 competitively displaced sympatric rainbow trout Age ≥1 from areas with close overhead vegetation (Fig. 2). Age 0 rainbow trout showed no significant differences in their positions relative to overhead vegetation in allopatry and sympatry ($z=0.816$, $P>0.25$), and Age 0

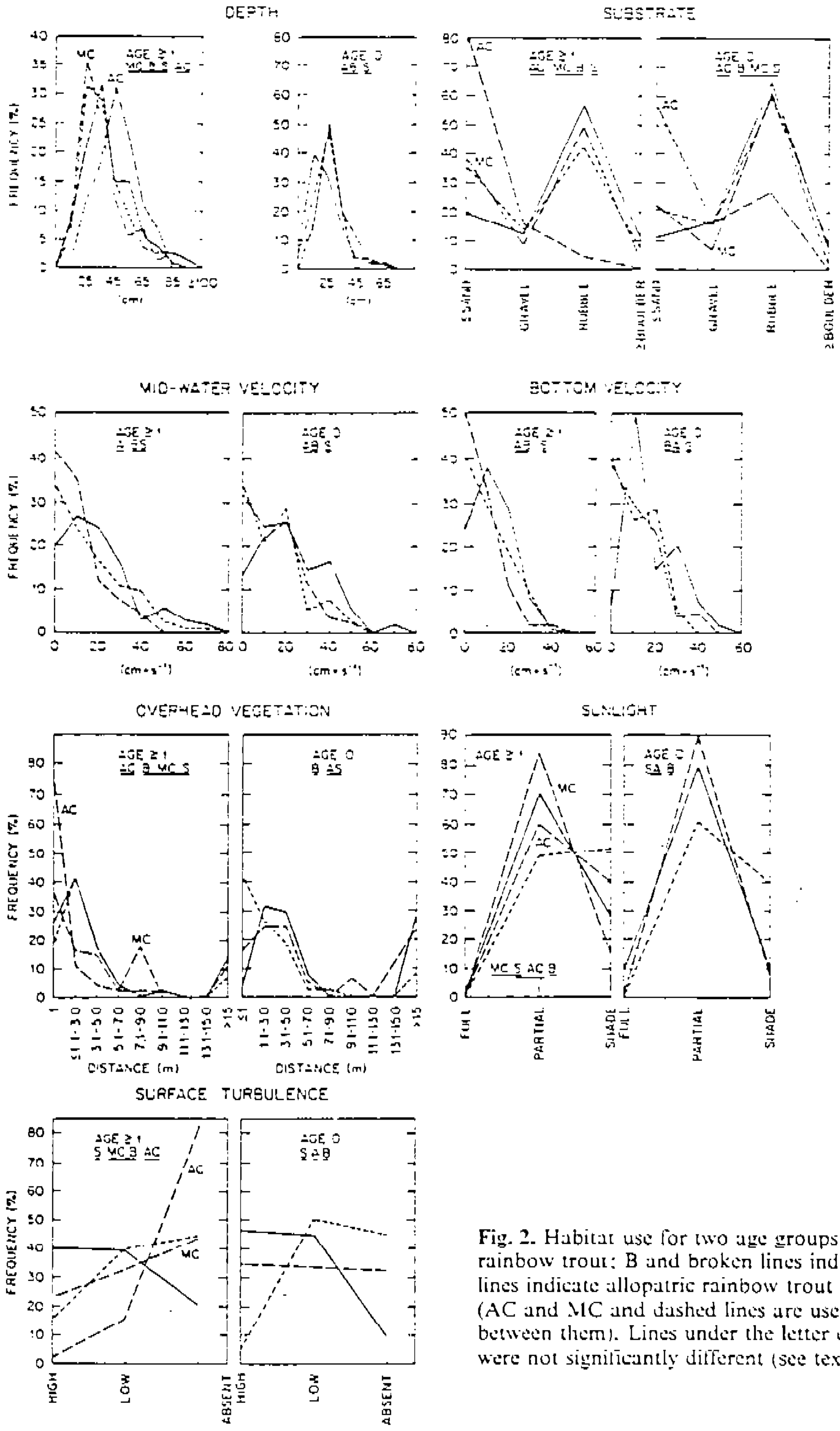

Fig. 2. Habitat use for two age groups of trout. S and solid lines indicate sympatric rainbow trout; B and broken lines indicate sympatric brown trout; and A and dashed lines indicate allopatric rainbow trout if habitat use does not differ between streams (AC and MC and dashed lines are used to denote these single streams if use different between them). Lines under the letter codes for populations connect populations that were not significantly different (see text for tests used) in habitat use

brown trout occupied more positions under close overhead vegetation than either group of rainbow trout (z's>3.4, P's<0.001). We interpreted the results for Age 0 trout to indicate species-specific habitat preferences unrelated to either availability or competition.

Sunlight. Allopatric and sympatric rainbow trout did not differ in habitat use relative to amount of sunlight (Fig. 2). We attributed all differences found to species-specific preferences. Significantly more brown trout in each age-group occupied areas of shade than did like-aged rainbow trout in either allopatric or sympatric streams (X^2's$=5.213$–18.897, df$=1$, P's<0.025–0.001).

Surface turbulence. Innate species preferences, habitat availability, and competition all seemed to affect habitat use of this variable. Innate species preferences occurred in that brown trout of both age groups more often occupied water

Table 3. Bivariate associations of available habitat. Entries indicate streams where the pair of variables showed significant nonrandom associations as identified by contingency tables and X^2 tests

Habitat variable	Velocity at 0.6 depth	Sub-strate	Over-head vege-tation	Sun-light	Surface turbu-lence
Depth	NR		NR		
Velocity at 0.6 depth		AC BC LCC NR	AC BC MC NR	BC NR	AC BC LCC MC NR
Substrate			BC	BC	AC BC LCC NR
Overhead vegetation				AC BC NR	BC MC NR
Sunlight					BC

Table 4. Bivariate associations of habitat used by brown trout Age ≥ 1. Entries indicate streams at which associations were significant as defined in Table 3. Associations not also seen in habitat availability are marked by an asterisk

Habitat variable	Velocity at 0.6 depth	Sub-strate	Over-head vege-tation	Sun-light	Surface turbu-lence
Depth	BC* NR	BC*			BC*
Velocity at 0.6 depth		BC	BC	BC NR	BC LCC NR
Substrate				BC	BC LCC
Overhead vegetation				BC LCC*	
Sunlight					BC

Table 5. Bivariate associations of habitat used by rainbow trout Age ≥ 1. Entries indicate streams at which associations were significant as defined in Table 3. Bold face type indicates sympatric streams; asterisks as in Table 4

Habitat variable	Velocity at 0.6 depth	Sub-strate	Over-head vege-tation	Sun-light	Surface turbu-lence
Depth	MC*				MC*
Velocity at 0.6 depth		AC **BC** MC*	AC MC	MC*	AC **LCC** MC
Substrate			MC*	MC*	**BC** MC*
Overhead vegetation				**BC** **LCC***	
Sunlight					**BC** MC*

lacking surface turbulence than either allopatric or sympatric rainbow trout of the same age (Fig. 2). Habitat availability effects existed in that rainbow trout Age ≥ 1 occupied more water with a turbulent surface at one allopatric stream (MC) than the other (AC): the significant difference ($X^2 = 18.368$, df = 2, $P < 0.001$) paralleled the difference in availability. A further availability effect was the even greater difference in the occupancy of water with a turbulent surface between sympatric rainbow trout Age ≥ 1 and conspecifics of the same age at AC, the allopatric stream with the lesser availability of turbulent water ($X^2 = 52.123$, df = 2, $P \ll 0.001$). Competitive displacement of rainbow trout Age ≥ 1 by like-aged brown trout occurred as shown by the lesser use of turbulent water in one allopatric stream (MC) than in the sympatric streams ($X^2 = 12.312$, df = 2, $P < 0.001$) despite the similarity in availabilities among all these streams (Fig. 1). Allopatric and sympatric Age 0 rainbow trout also differed in use of this habitat variable ($X^2 = 9.554$, df = 2, $P < 0.01$), but a separation of causes similar to that just given for fish Age ≥ 1 was less clear for these fish. Allopatric Age 0 rainbow trout more often occupied water lacking surface turbulence than their sympatric Age 0 conspecifics which corresponded to the difference in availabilities (Fig. 1). However, an even greater difference in availabilities between the two allopatric streams did not result in significant differences in habitat use between the two allopatric populations of Age 0 rainbow trout. Thus, we felt it inappropriate to attribute the entire allopatric-sympatric difference to differences in availabilities but rather considered a portion of the difference represented competitive effects.

In summary then, rainbow trout Age ≥ 1 occupied more areas with moderate to high velocity, coarser substrates, further from overhead vegetation, and offering less shade when in sympatry than in allopatry (Fig. 2). Age 0 rainbow trout also occurred in more areas of moderate velocity and moderate to high surface turbulence in sympatry than in allopatry. Additionally, Age 0 fish shifted to more areas of intermediate to deep water. Species-specific preferences occurred for areas occupied relative to sunlight (both age groups) and to overhead vegetation (Age 0 only).

Association of habitat variables

Only six of the 15 possible pairwise associations between variables for habitat availability were significant at three or more streams (Table 3). These associations were among slow velocities, fine substrates, close overhead vegetation, and low surface tubulence.

Large numbers of between-variable associations in habitat use occurred for trout in both age groups (Tables 4–7). The existence of such associations, especially associations that did not exist in habitat availability, indicated that trout selected particular combinations of habitat variables. For example, brown trout Age ≥ 1 in one stream (BC) avoided shallow water with a sand substrate, but used shallow water

Table 6. Bivariate associations of habitat used by brown trout Age 0. Entries indicate streams at which associations were significant as defined in Table 3. Associations not also seen in habitat availability are marked by an asterisk. Note: sample size was too small at LCC to permit analysis

Habitat variable	Velocity at 0.6 depth	Sub-strate	Over-head vege-tation	Sun-light	Surface turbu-lence
Depth	BC*				
Velocity at 0.6 depth		BC			BC
Substrate				BC	BC
Overhead vegetation					
Sunlight					

Table 7. Bivariate associations of habitat used by rainbow trout Age 0. Entries indicate streams at which associations were significant as defined in Table 3. Bold face type indicates sympatric streams; asterisks as in Table 4. Notes: samples size was too small at LCC to permit statistical analysis; NR was allopatric stream for Age 0 rainbow trout

Habitat variable	Velocity at 0.6 depth	Sub-strate	Over-head vege-tation	Sun-light	Surface turbu-lence
Depth	AC* NR*	AC*	AC*		AC*
Velocity at 0.6 depth		AC	**BC** MC NR	**BC** MC* NR	AC MC NR
Substrate					AC **BC**
Overhead vegetation				**BC** NR	**BC** MC
Sunlight					**BC**

with a rubble substrate and deep water with a sand substrate (Table 4). These associations of habitat variables were not present in the availabilities of depth and substrate in the stream as a whole (Table 3), so selection relative to the combination of depth and substrate was shown. As a further example, three other populations (Age 0 rainbow trout at AC, Age ≥1 rainbow trout at MC, and Age ≥1 brown trout at BC) occupied water with moderate to high surface turbulence where the water was shallow, but not where it was deep.

For fish Age ≥1, significant associations between variables for habitat use (Tables 4 and 5) occurred significantly more frequently in populations of brown trout and allopatric rainbow trout than in populations of sympatric rainbow trout ($X^2 = 5.807$, df = 1, $P < 0.025$). This difference included associations seen in both availability and use, and associations unique to habitat use. Specifically, brown trout Age ≥1 showed between-variable associations in habitat use for 59% of the associations in habitat availability that existed in the sympatric streams (cf., Tables 3 and 4) and allopatric rainbow trout Age ≥1 showed 62% of the analogous associations in the allopatric streams (cf., Tables 3 and 5). In contrast, sympatric rainbow trout Age ≥1 showed fewer than half as many (23%) of the corresponding associations (Table 5). For between-variable associations seen only in habitat use and not seen in habitat availability, the difference was even greater. Age ≥1 allopatric rainbow trout and brown trout showed 92% (12 out of 13) of such associations. Overall, sympatric rainbow trout Age ≥1 showed only 17% of the significant between-variable associations in habitat use for fish in that age group.

Table 8. Factor loadings and variance explained by principal component analysis followed by orthogonal rotation (varimax criterion). Variables with loadings >0.55 were considered to have contributed "significantly" to principal components (PC) and were marked by an asterisk

Habitat variable	PC I (61% variance)	PC II (22% variance)	PC III (9% variance)
Water depth	−0.04	0.39	0.89*
Velocity at 0.6 depth	0.96*	−0.12	0.13
Bottom velocity	0.85*	−0.41	−0.01
Substrate	0.86*	0.14	−0.39
Overhead vegetation	0.53	−0.75*	−0.16
Sunlight	−0.05	0.88*	0.34
Surface turbulence	−0.86*	0.42	0.09

The situation for Age 0 fish was somewhat different. Here, the hypothesis of equal proportions of between-variable associations in habitat use occurring in sympatric rainbow trout populations as in brown trout and allopatric rainbow trout populations was not rejected ($X^2 = 0.002$, df = 1, $P > 0.9$). However, all seven associations unique to habitat use (Tables 6 and 7) occurred among the populations of allopatric rainbow trout and brown trout.

Principal component analysis

Principal component analysis identified water velocity and its correlates (substrate and surface turbulence) as the most important habitat variables separating the several populations (Table 8). Two variables related to cover were of secondary importance, and water depth was of quite minor importance (Table 8). Populations of the same species, age, and distribution (allopatric or sympatric) tended to be grouped in multivariate space with only minimal dispersion (Fig. 3). We attributed this dispersion to differences in habitat availabilities in the streams (e.g., greater occurrence of Age 0 rainbow trout in the shade in one sympatric stream [NR] than in the other two [BC, LCC], or greater occupancy of areas of slow velocity, fine substrate, and water lacking surface turbulence by rainbow trout in one allopatric stream [AC] than the other [MC]). The relative positions of the species and age groups were as expected based on the univariate analysis of habitat use. Positions of the allopatric rainbow trout populations were similar to those of brown trout, although Age 0 allopatric rainbow trout occupied fewer areas of close overhead vegetation and shade than did the brown trout in the sympatric streams.

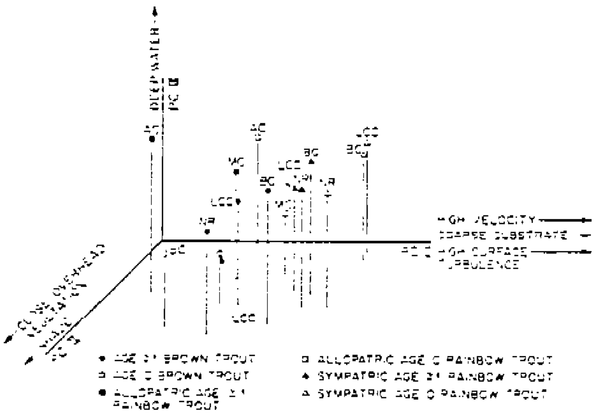

Fig. 3. Principal component analysis of habitat use by trout on three orthogonal axes. See Table 8 for detailed information about the axes. Individual populations are identified by stream (lettered abbreviation) as well as by age, species, and distribution

Discussion

Caveat

The patterns of habitat use we described in this paper should not be used as descriptions of microhabitat preferences for either species. Fright response and galvanotaxis undoubtably occurred, although these phenomena clearly did not render the study worthless. If these phenomena had been severe, then the locations we considered to be trout positions would not have differed from a series of random points in the streams, and we would never have found the nonrandom use relative to availability that we did for nearly all habitat variables and groups of trout. Still, our data likely reflected some mixture of feeding and refuge sites and perhaps some locations intermediate between these two. Jenkins (1969a) reported that refuge sites were different between brown tout and rainbow trout but that feeding sites were not. Because we found differences in habitat use between these species, refuge sites may have predominated in our measurements of habitat use. This interpretation is supported by the facts that refuge sites for trout Age ≥1 are in slower, deeper water and in closer association with cover than feeding sites (Kalleberg 1958; Helm et al. 1981) and that slow water close to cover was preferred by most of the Age ≥1 trout that we studied. An alternative interpretation, that the differences we found between species represented only differences in fright and electroshocking responses, is untenable because the differences existed only for sympatric trout; allopatric rainbow trout and brown trout showed the same habitat preferences. Still, we advocate the use of our data only for the purposes for which they were originally gathered.

Habitat use

All of the habitat variables that we measured were important to the trout. The majority of populations of each species used each variable nonrandomly relative to availability (Tables 1 and 2). We had not necessarily expected this based on the literature. For example, reports in the literature indicate depth is either unimportant because trout occupy water of different depths in proportion to availability, or at least less important than velocity in habitat choice (Jenkins 1969a, Lewis 1969, Gosse and Helm 1981, Shirvell and Dungey 1983). Similarly, substrate is generally considered unimportant to nonspawning trouts (Fausch and White 1981, Gosse and Helm 1981, Shirvell and Dungey 1983). In contrast to these two variables, numerous reports indicate that cover is generally important to trout (e.g., Needham and Jones 1959, MacCrimmon and Kwain 1966, Butler and Hawthorne 1968, Elser 1968, Allen 1969, Baldes and Vincent 1969, Chapman and Bjornn 1969, Elwood and Waters 1969, Kwain and MacCrimmon 1969, Lewis 1969, Devore and White 1978, Wiley and Dufek 1980, Gosse and Helm 1981, Wesche et al. 1987) although some suggest that cover matters to only portions of the population (Mortensen 1977, Bachman 1982, Bisson et al. 1981) or in particular situations (Kalleberg 1958; Jenkins 1969a, Gibson and Power 1975, Helm et al. 1981, Hartzler 1983). Given these latter restrictions, we had not necessarily expected near universal nonrandom use of cover, i.e., overhead vegetation, shade, and surface turbulence.

The differences we found in the relative importance of the habitat variables corresponded to published reports. Velocity is generally recognized as the most critical variable in microhabitat selection by lotic trout (e.g., Jenkins 1969a, Bachman 1984, Fausch 1984, de Graaf and Bain 1986) and, according to Lewis (1969), cover is the second key variable affecting distribution of trout. In our study, velocity and two associated variables [substrate and surface turbulence] formed PC I, and two measures of cover [distance to overhead vegetation and shade] formed PC II (Table 8, Fig. 3). In contrast, depth of water accounted for only 9% of the variance in the principal component analysis (PC III, Table 8) and was important only in separating Age 0 and Age ≥1 brown trout. The importance of velocity was further shown in that availabilities had no influence on what velocity of water was occupied by any species or age group of trout. Shirvell and Dungey (1983) similarly reported that availability had no influence on what velocities of water were occupied by brown trout.

Our finding of bivariate (Tables 4–7), if not multivariate (Table 8), selection of habitat variables was contrary to what Gosse and Helm (1981) reported, but in accord with Gibson and Power (1975). The latter workers found that small brook trout and also juvenile Atlantic salmon when alone, seek shade in shallow water, but not in deep water. When both species occurred together, Gibson and Power (1975) found that the trout displaced the salmon from the shade. Our results parallel those of Gibson and Power (1975) on both points. First, we found bivariate selection of habitat variables including trout having selected areas of surface turbulence and shallow water in several populations. We interpreted this joint selection to mean that when water depths alone were insufficient to provide cover, trout sought other forms of cover such as surface turbulence. Second, we found that the presence of a second species had an influence on whether or not bivariate selection of habitat variables occurred.

Specifically, our results indicated that brown trout and allopatric rainbow trout selected habitat variables in a bivariate manner (Tables 4–7) whereas sympatric rainbow trout much more often selected one critical variable (e.g., velocity) without regard to other aspects of the habitat. This result was especially clear for trout Age ≥1. Brown trout and allopatric rainbow trout averaged three times the number of between-variable associations per population as did sympatric rainbow trout. However, for both age groups of sympatric rainbow trout, 92% (11 of 12) of the between-variable associations were for pairs of variables that also were associated strongly in habitat availability. Hence, even these few associations that did exist could have been artifacts of selection for just one of the variables rather than bivariate selection. Competitive displacement of sympatric rainbow trout to water of high velocity would also have produced shifts to coarse substrate, distant overhead vegetation, and high surface turbulence merely because of the associations in the environment.

Interspecific competition

The two species we studied had allopatric recent evolutionary histories (rainbow trout in western North America and brown trout in Europe) until their widespread introductions into the same streams over the last century. Although the competitive exclusion principle would indicate that there must be some differences in resource use between the species for them to coexist following the introductions, this same principle provides no guidance as to whether coexistence is achieved through interactive or selective segregation (i.e., niche shifts or different genetic preferences). If the recent evolution of both species was in similar environments, then the genetic preferences of the species might also be similar. Niche shifts would be necessary to permit coexistence. Over evolutionary time, however, the co-occurring species should evolve complementary preferences (i.e., evolve selective segregation) and niche shifts no longer exist. The rate of such evolution would vary with the intensities of selective pressures.

Literature on salmonids offers limited support for these ideas. For salmonids sharing an extensive evolutionary history, two species pairs show selective habitat segregation (Everest and Chapman 1972, Schutz and Northcote 1972), but three other pairs of species show interactive habitat segregation (Hartman 1965, Gibson and Power 1975, Bisson et al. 1981). For salmonids more recently introduced to the same waters, two species pairs show interactive habitat segregation (Nilsson 1963, 1967; Fausch and White 1981) while a third pair shows both selective habitat segregatin (Griffith 1972) and interactive food segregation (Griffith 1974). Thus, although selective segregation is relatively less frequent in the latter situation, it apparently evolves quite slowly. Both theory and the slow rate of evolution shown by the confamilial comparisons indicate the likelihood of niche shifts for the species pair we studied. Niche shifts would indicate ongoing competition and should be accompanied by reduced growth and production; selective segregation would not.

Our results showed niche shifts were common for sympatric rainbow trout whereas selective segregation between the species was not (Fig. 2). Shifts occurred for habitat use relative to depth (Age 0 only), velocity (both age groups), substrate (Age ≥ 1 only), overhead vegetation (Age ≥ 1 only), and surface turbulence (both age groups). The niche shifts were away from the preferences of brown trout based on the literature (Butler and Hawthorne 1968, Bovee 1978) and our own measures of habitat preference of brown trout. Selective segregation between the species occurred only for areas occupied relative to sunlight (both age groups) and overhead vegetation (Age 0 only). We have no basis for speculating whether the latter species-specific preferences evolved recently or during an allopatric period in the history of the two species.

The results presented here indicated that interspecific competition existed between sympatric rainbow and brown trout in the streams and time period of our study. We do not known if niche shifts would be seen at different seasons when habitat availabilities would differ. In late summer and fall, overlap in habitat use was high (Fig. 2) and preferences relative to what was available (Tables 1 and 2) were similar for the two species. Niche shifts by rainbow trout away from the preferences of brown trout were common. Thus strong evidence for interspecific competition of the two types derived from niche theory – resource overlap and niche shift in sympatry – existed.

Evidence of the third type required by MacNally (1983), reduced population density or growth in at least one of the species undergoing interspecific competition, is found in Loar (1985). Biomass of Age 0 rainbow trout averages only 23% as high in sympatric as allopatric streams and production only 21% as high. Comparisons for rainbow trout Age ≥ 1 show biomass and production average 48% and 42% as high, respectively, in sympatric as allopatric streams. We interpreted the reduced biomass and production in the sympatric streams to be evidence for ongoing interspecific competition. Food availability, water quality, and interactions with nonsalmonids unlikely differ greatly among the streams (Loar 1985), and hence were inviable as alternative explanations.

We can only speculate about the precise mechanism of competition between brown trout and rainbow trout. A reasonable working hypothesis, based on the results presented here, was that interference competition occurred in which behaviorally dominant brown trout induced habitat shifts by rainbow trout. Brown trout would have forced rainbow trout into areas having some combination of the following deficiencies: higher water velocity, greater distance from cover, and lower food availability. The overall result would have been an increased net expenditure of energy per unit time. Even if food availability were not involved and feeding rates by rainbow trout were the same in allopatry and sympatry, the other two factors alone would reduce rainbow trout production in sympatry due to the higher metabolic costs associated with maintaining position (see Fausch 1984) and seeking refuge when disturbed.

The experimental work necessary to support this scenerio would include at least two types of observations. First, direct observations of interspecific interactions between fishes of both species and of various sizes are needed. They have not been made. Brown trout are competitively dominant over brook trout (Nyman 1970, Shetter and Alexander 1970, Fausch and White 1981) and brook trout are behaviorally dominant over rainbow trout of equal size (Newman 1956), so interference competition due to behavioral dominance of brown trout is a reasonable prediction. Second, metabolic measurements on rainbow trout of the sort obtained by Li and Brocksen (1977) in their study of intraspecific competition would be desirable to see if the hypothesized subordinance of rainbow trout to brown trout would decrease growth. The mechanism we propose here is analogous to that demonstrated by Werner and Hall (1979) for the asymmetrical competition between bluegill sunfish and green sunfish.

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