Habitat partitioning in a patchy environment: considering the role of intraspecific competition

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Synopsis

Coexistence of many size groups of conspecifics in habitat patches may complicate resource partitioning and increase intraspecific interactions. The objectives of my study were to determine partitioning of habitat among age groups of rainbow trout, *Oncorhynchus mykiss*, coexisting in pool habitat of a headwater stream, and to determine the role of intraspecific competition for such resource partitioning. The trout population showed size and age specific patterns of habitat use, and trout selected locations based on depth and longitudinal position. This habitat use pattern decreased intraspecific overlap among the trout age groups for use of pool space. I used a removal experiment to determine if two-year old trout constrained habitat use by the smaller conspecifics. Although the experimental results imply that recent intraspecific competition was not present, the absence of competitive exclusion was not clearly demonstrated because of low experimental power. While this study identified habitat partitioning among the trout age groups, it remains unclear whether biotic interactions or size specific requirements were causing the habitat use patterns.

Introduction

Fish size groups typically segregate among riffle, run, and pool in large streams where these habitats exist. Larger fish are found in pools while smaller fish are found in shallower habitat such as run and riffle (Bohlin 1977, Schlosser 1982, Mahon & Port 1985, Moyle & Vondracek 1985, Greenberg 1991, Aadland 1993, Mullen & Burton 1995). The mechanism causing larger individuals to use different habitats than their smaller conspecifics may be related to interference competition (Jenkins 1969, Bohlin 1977, Van Horne 1982, Kincaid & Cameron 1985, Freeman & Stouder 1989) or predation (Schlosser 1988, Power et al. 1989, Harvey & Stewart 1991). Nevertheless, segregation by fish size and age among habitat types minimizes intraspecific niche overlap by increasing resource partitioning (Schlosser 1987).

In contrast, conditions suitable for fish growth and survival are limited in headwater streams. Whitewater and pool typically alternate, producing what can be considered a patchy distribution of optimal habitat in an otherwise suboptimal environment (Fretwell 1972, Wiens 1976, Fraser & Sise 1980). Fish may either coexist in pools or occupy unsuitable habitat and experience lower survival (Fretwell 1972, Fraser & Cerri 1982, Van Horne 1982) and growth rates (Ostfeld 1992). Consequently, many size groups of fish may concentrate in pools of headwater streams. Under such presumably constant environmental pressures, a population may evolve a space use pattern that minimizes the negative effects of many size or age groups of conspecifics coexisting and competing for space (Schoener 1977, Connell 1980).

The upper reaches of the North Fork San Gabriel River support a population of rainbow trout,

Oncorhynchus mykiss. Young-of-the-year, yearling, and two-year old trout are primarily confined to pools, which are separated from one another by high gradient reaches of swift, turbulent water. The study presented in this paper had two objectives. The first objective was to determine partitioning of habitat among the coexisting trout age groups. The second objective was to determine causal mechanisms underlying any observed habitat partitioning.

Study stream

The North Fork San Gabriel River is located in the Angeles National Forest, California (34°17′N, 117°50′30″W). The North Fork is a second order stream that originates at an elevation of about 1000 m, and flows 7 km through a narrow canyon to its confluence with the West Fork. This study was conducted in a 0.7 km reach of the North Fork located at an elevation of about 800 m and about 6 km upstream of its confluence with the West Fork. Instream habitat in the study reach was high gradient and shallow with turbulent stretches of water interspersed with pools. Boulder and cobble substrate were usually exposed in white water habitats, and were present along with gravel, sand, and smaller particles in most pools. White alder, *Alnus rhombifolia*, and arroyo willow, *Salix lasiolepis*, shaded the river in most areas I observed. Accumulations of small woody debris, less than 10 cm in diameter, were common along the stream banks. Discharge averaged 0.09 m³ sec⁻¹ during the study. Water clarity averaged 3.5 m. Mean water temperature was 14.9°C.

Methods

I combined measurement of microhabitat (depth and velocity) use and availability, and longitudinal position of trout in randomly selected pools (n = 13). Length of the pools ranged from 3.3 to 9.7 m. Mean pool width ranged from 2.9 to 7.6 m. All measurements were performed during the summer (July) when densities of young-of-the-year and older trout are expected to be at their highest, and competitive interactions and resource use overlap among trout age groups are probable.

Measurement of microhabitat use and availability

I collected microhabitat use and availability data to test the null hypothesis of no difference in use of microhabitat among the trout age groups and availability. I measured trout use of microhabitat by performing snorkeling surveys. For each pool, I entered the stream then crawled upriver to the downstream boundary of the pool to minimize the chance of frightening trout. Trout location was marked on the pool channel bed using a set of sequentially numbered markers. Total trout length and vertical distance above the channel bed (focal height) were estimated to the nearest 1 mm. Estimates of trout length and focal height were frequently calibrated with a hand held ruler and comparison of substrate particles of known length. The dive survey proceeded from downstream to upstream for each pool; trout usually swam downstream past me after I marked their location, thereby decreasing the chance of making repeated observations on the same individual. Trout obviously frightened were not included in observations. A total of 150 microhabitat observations were made. I revisited each microhabitat marker after snorkeling and measured streamflow velocity (cm sec⁻¹) and water column depth (cm) with an electronic flow meter. Measurement of streamflow velocity was made at the trout focal height.

The distribution of depths and water velocities available to trout was estimated by measuring streamflow velocity and total depth at randomly selected channel cross-sections. At least two cross-sections were placed in each pool, but three cross-sections were used in relatively long pools. A minimum of 12 velocities and depths were measured along each cross-section at equally spaced intervals. Streamflow velocity was measured at 4 cm above the channel bottom, the modal focal height determined during preliminary surveys. A total of 629 depths and water velocities were measured.

Measurement of longitudinal position

I measured the longitudinal position held by trout to test the null hypothesis of no segregation among the trout age groups. Trout position was estimated by dividing each pool into three zones then noting the presence of trout in each of the zones. The pool zones were: a downstream zone that I termed the tail, a middle zone, and an upstream head zone. The head zone was usually the deepest part of the pool, and exhibited the highest proportion of surface turbulence and bubble screen (entrained air). Boulder and cobble were predominate along the margins at the head of pools. The tail was the shallowest area of the pool, and bubble screen and surface turbulence were minimal if present. Substrate

in the tail was mostly small gravel and sand particles. The physical characteristics of the middle zone were intermediate between those of the head and tail. The number of markers placed on the pool channel bed during microhabitat use measurements, and therefore the number of trout and their estimated lengths, were tallied for each of the zones. The positions held by trout were divided by pool length to express longitudinal position as a continuous variable. Hereafter I refer collectively to microhabitat and longitudinal position as habitat.

Removal experiment

I performed a removal experiment to test the null hypothesis that two-year old trout did not constrain use of microhabitat by their smaller younger conspecifics. My rationale was that the younger conspecifics would detect the absence of two-year old trout and occupy deeper water locations toward the pool head. A difference in microhabitat use by the younger trout after I removed the two-year old trout would indicate interference competition.

The removal experiment involved three equally replicated (n = 2) treatments: removal, electrofishing treated, and untreated. Experimental pools were randomly selected from the pools where habitat use and availability measurements were performed. Treatment type was assigned randomly. The removal treatment involved capturing and removing two-year old trout using a backpack electrofisher. A 0.5 cm stretch mesh blocknet was placed at the downstream boundary of each pool before electrofishing to prevent trout emigration. No blocknet was placed at the upstream pool boundary because the high gradient habitat probably prevented trout from migrating out of the pool in this direction. The area of each pool was electrofished beginning at the downstream boundary and then slowly moving upstream. I removed all two-year old trout from each pool (a total of six trout, length range 15 to 20 cm). I knew in advance to remove fish of this length because preliminary analyses based on scale readings indicated that trout 15 cm and longer exceeded one year of age. The treated treatment involved electrofishing but removing no trout. No electrofishing or trout removal was conducted for the untreated treatment. Two days were allowed to elapse before repeating microhabitat use and availability measurements at the experimental pools. The duration of this rest period was within the range used by other investigators (two hours Freeman & Stouder 1989, 24 hours Harvey 1991, five days

Fausch & White 1981). Although no enclosure was used during the removal experiment, I observed no two-year old trout in the pools during repeated surveys performed after removal. I expected no change in trout density among the experimental pools during the relatively short two-day rest period.

Data analysis

A length-frequency distribution was prepared using the trout lengths (mm converted to cm for analysis) estimated during the snorkel survey. Length observations were separated into young-of-the-year, yearling, and two-year old groups, based on the age group peaks. Separation of age groups was validated with the analysis of scales using standard methods (Jerald 1983).

Test of significant (type I error rate = 0.05) differences among trout age groups in use of depth and velocity and in availability was determined using one-factor univariate analysis of variance (ANOVA). Tukey's a posteriori test was used to determine which level means were different from one another.

Simple linear regression was used to describe and model the relationship between trout length and use of microhabitat. I examined plots of residuals against estimated predicted values to assess the appropriateness of the regressions; outliers were identified based on studentized residuals (Montgomery & Peck 1992, Wilkinson et al. 1994). I used stepwise regression to assess the contribution of longitudinal position and depth at locations used for explaining variation in trout length. I used one-factor univariate ANOVA to test for differences in longitudinal position among the trout age groups.

The one-sample t-test was used to test the null hypothesis of no difference in mean microhabitat availability before and after removal of two-year old trout. I used one-factor univariate ANOVA to analyze the removal experiment data using as the response variable the difference in means of microhabitat use before and after removal.

Results

Size and age composition

Small (≤ 14 cm total length) trout numerically dominated the pools. Three trout age groups were observed and most individuals were young-of-the-year (41%) or

yearling (43%), with some two-year old trout (16%). The mean total lengths for each of the age groups were: young-of-the-year, 6.9 cm; yearling, 12.4 cm; and two-year old, 16.0 cm.

Use of habitat

The trout population showed age and size associated differences in use of habitat. Depths at locations used among the age groups and those available were different (Figure 1; ANOVA: $F_{3,44} = 26.46$, p < 0.0005). The multiple comparison test indicated young-of-the-year used shallower depths than did yearling and two-year old trout (Tukey's test: both comparisons p < 0.0005). Two-year old and yearling trout used locations with similar depths (p = 0.679). Yearling and two-year old trout used depths that were deeper (both comparisons p < 0.0005) than what would have been used if depth had been randomly selected. The depths used by young-of-the-year were similar to availability (p = 0.627). Water velocities at locations used by the age groups and those available were not different (Figure 2; ANOVA: $F_{3,44} = 0.169$, p = 0.917).

The regression showed depths at locations used were related to trout length (Figure 3; $F_{1,143} = 138.51$, p < 0.0005). The variation in water column depth explained by the model was about 49%, and use of depth increased about 2.9 cm for each 1.0 cm increase of trout length. In contrast, water velocities at the locations used were not related to trout length ($F_{1,148} = 0.397$, p = 0.530).

The ANOVA of longitudinal positions held by trout indicated the age groups distributed non-randomly within the pools (Figure 4; ANOVA: $F_{2,32} = 6.347$, p = 0.005). On average, young-of-the-year held position close to the pool tail, whereas two-year old trout held position close to the pool head. Yearlings held an average longitudinal position in the middle zone. The multiple comparison test indicated yearling trout held pool positions that were similar to young-of-the-year (p = 0.160) and two-year old trout (p = 0.367). Young-of-the-year held positions that differed from positions held by two-year old trout (p = 0.004). Stepwise regression indicated longitudinal position and depth at locations used explained a significant amount of variation in trout length (for the individual variables, depth use: F = 69.430, p < 0.0005; longitudinal position: F = 12.241, p = 0.001), and therefore longitudinal position was not a redundant variable.

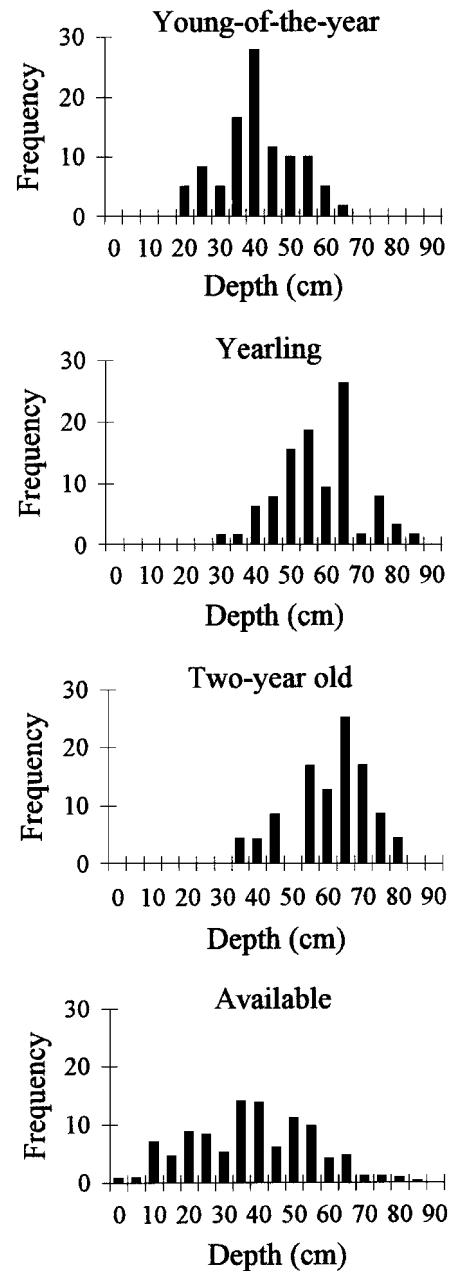*Figure 1.* Depths at locations used by young-of-the-year (n = 61), yearling (n = 65), and two-year old trout (n = 24), and available microhabitat (n = 629). Values are percent frequency of occurrence.

Effect of two-year old trout removal

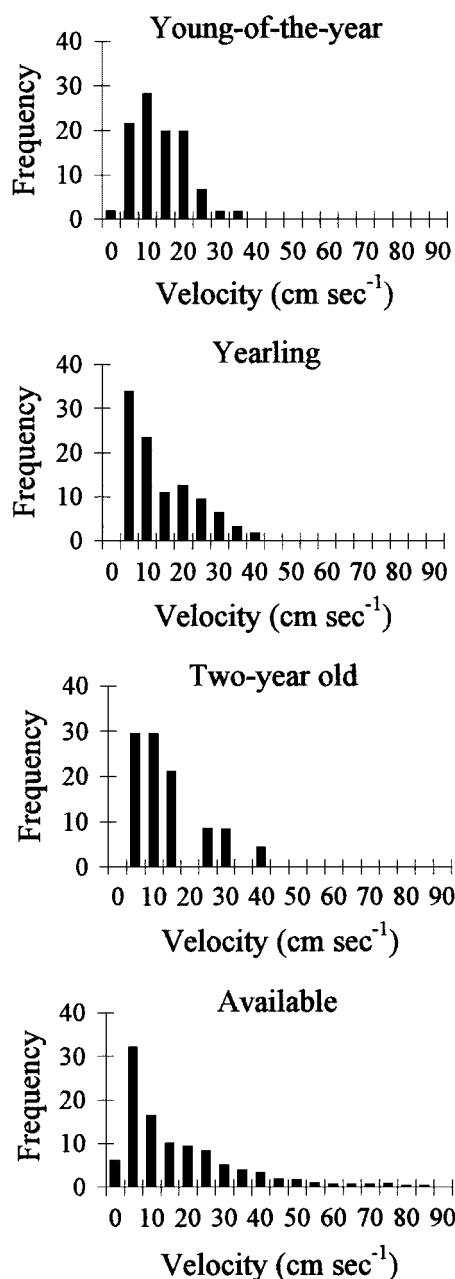Availability of velocity and depth was similar (Table 1; velocity: t = −0.118, p = 0.911; depth: t = 0.907,

Figure 2. Water velocities at locations used by young-of-the-year (n = 61), yearling (n = 65), and two-year old trout (n = 24), and available microhabitat (n = 629). Values are percent frequency of occurrence.

p = 0.406) before and after I removed two-year old trout. Therefore, a shift in microhabitat use by young-of-the-year or yearling trout was not the result of changes in availability.
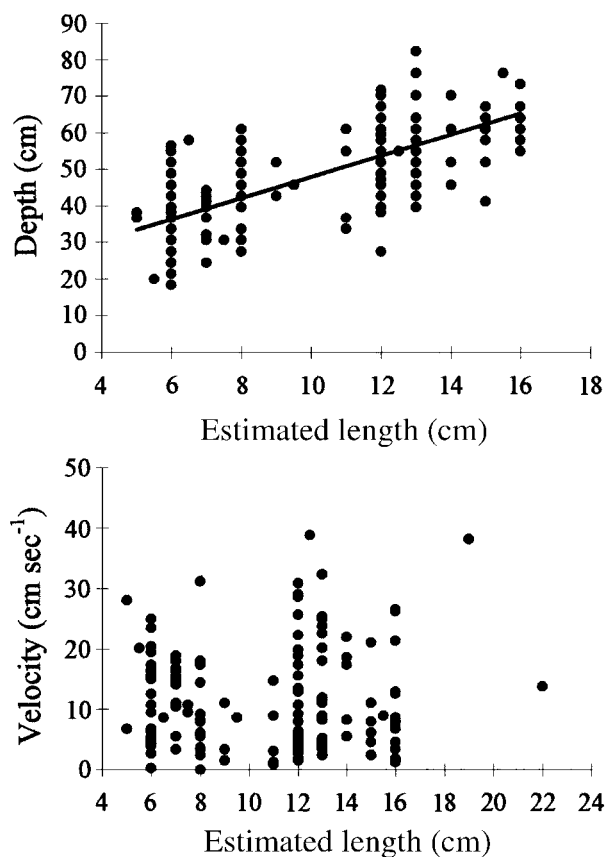

Figure 3. Regression of water column depth (n = 145, r^2 = 0.492, Y = 18.769 + 2.898X) and water velocity (n = 150) use measurements against estimated length of trout. Five outliers removed from the regression of depth.

Removing two-year old trout from pools had no effect on use of microhabitat by the smaller conspecifics (Table 2). Although young-of-the-year and yearling trout used locations characterized by slower water velocities after two-year old trout removal, the velocities used by trout among the experimental treatments were similar (young-of-the-year ANOVA: $F_{2,3}$ = 2.479, p = 0.231; yearling ANOVA: $F_{2,3}$ = 1.479, p = 0.357). Young-of-the-year and yearling trout used shallower depth locations, a direction not predicted, after two-year old trout were removed. The use of depth by trout among the experimental treatments, however, was similar for young-of-the-year (ANOVA: $F_{2,3}$ = 1.795, p = 0.307) and yearling trout (ANOVA: $F_{2,3}$ = 0.414, p = 0.694).
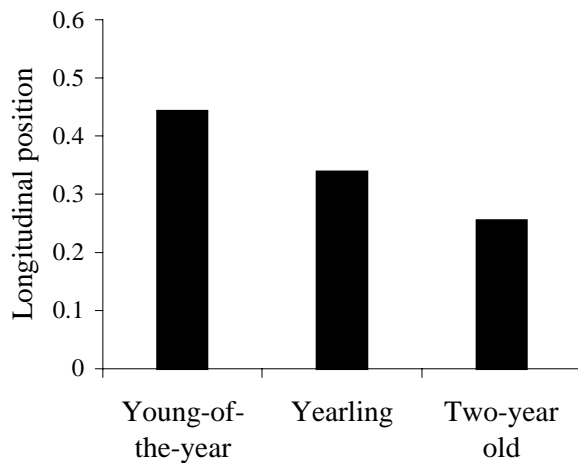
Figure 4. Average longitudinal position held by the three age groups of trout (n = 150). A relatively small value indicates position held near the pool head, whereas a large value indicates position near the pool tail.

Table 1. Differences in availability of velocity (cm sec^{-1}) and depth (cm) microhabitat before and after two-year old trout removal. The mean difference was always calculated as before means–after means for each pool; negative values indicate an increase in availability of that particular microhabitat variable after two-year old trout were removed.

Pool type	Velocity mean diff.	Depth mean diff.
Removal	−5.16	1.03
Removal	−0.12	1.83
Treated	2.47	1.23
Treated	−1.19	2.66
Untreated	1.67	−4.64
Untreated	1.52	4.98

Discussion

Results showed the trout population used habitats that decreased intraspecific overlap in use of pool space among the age groups. This may be a life history style for individuals of a population living in headwater streams where suitable living space is spatially patchy. An ontogenetic habitat shift such as the depth use pattern I determined seems common in stream fishes (Schlosser 1982, Baltz & Moyle 1984, Schlosser 1987, Baltz et al. 1991) and may reflect either biotic interactions or size specific habitat requirements.

Table 2. Effect of removing two-year old trout on use of velocity (cm sec^{-1}) and depth (cm) microhabitat by young-of-the-year and yearling trout. Values are differences in means of microhabitat use, and were always calculated as before means–after means for each experimental treatment (n = 2); negative values indicate an increase in use of that particular microhabitat variable after two-year old trout removal. The n values are the pooled number of trout used to compute a particular mean difference.

Treatment	Young-of-the-year			Yearling		
	velocity	depth	n	velocity	depth	n
Removal	2.97	7.16	9	13.39	4.70	7
Removal	4.17	1.29	12	6.51	4.49	17
Treated	0.91	−2.13	7	0.86	7.24	7
Treated	−2.95	11.07	17	5.70	−4.54	13
Untreated	2.11	−0.18	17	−7.27	−7.90	23
Untreated	7.54	−19.05	6	6.16	4.42	9

The results of the removal experiment imply that recent competitive exclusion was not responsible for microhabitat use by yearling and young-of-the-year conspecifics. This finding contradicts the notion (Bohlin 1977, Van Horne 1982, Kincaid & Cameron 1985) and evidence from manipulative experiments (Jenkins 1969, Freeman & Stouder 1989) that larger individuals displace their smaller conspecifics in the competition for space or food. In my study, young-of-the-year showed little overlap in habitat use with yearling and two-year old trout, suggesting that intraspecific competition was minimized by ontogenetic habitat shifts. I expected competitive release by yearling trout, however, because they showed considerable overlap in habitat use with two-year old trout. Low statistical power associated with the experimental study design may have prevented detecting a shift by the yearling trout. A posteriori power analysis (Zar 1996) indicated the one-factor ANOVA of the yearling depth use data had about 50% power (50% chance of committing type II error) to detect a minimum change of 10 cm. The removal experiment results should be therefore interpreted with caution.

The distribution and magnitude of surface water velocities in the pools and potential size related differences in foraging ability may presently dominate habitat selection in the trout population. My underwater observations indicated young-of-the-year, yearling, and two-year old trout held positions in slow water next to faster water, and selected food items from the faster water overhead of their position. This

behavior of stream-dwelling trout is thought to maximize food intake while at the same time minimize the cost of obtaining food (Jenkins 1969, Fausch 1984). Size associated differences in foraging ability may cause small fish to exploit food from different but adjacent environments as compared to large individuals (Mittelbach 1981); young-of-the-year may have occupied the pool tail because they can forage most efficiently in the slower surface water that characterized pool tails. Increased visual acuity (Mittelbach 1981) and swimming ability relative to smaller conspecifics, may have allowed the larger trout to be the only age group that can detect and capture prey in the faster, turbulent water that characterized the surface of pool heads. Results of analyses performed on water velocities at locations used and those available suggest subsurface water velocities were not responsible in segregating the trout age groups. Furthermore, the distribution of velocities available to trout (measured at 4 cm above the channel bed) were similar at the pool head and tail (two-sample t-test: $t = -0.031$, $df = 6$, $p = 0.977$). Thus, size related differences in abilities of trout to forage in the surface water may partially explain the size and age specific segregation. The role of predation in structuring the habitat partitioning is also of interest.

The size specific segregation observed in the trout population may be a response to a historical, selective predation risk. The use of depth by trout in my study was similar to the bigger fish in deeper water pattern of habitat use reportedly caused by a size specific risk of predation (Power 1987). Young-of-the-year trout may have used the shallowest depths and depths similar to availability because small fish are selected against in deep water by large predatory fish (Power 1987, Schlosser 1988). Two-year old trout used the deepest depths and depths that were deeper than what would have been used if depth had been randomly selected. This suggests an overall value of depth to the larger trout for avoiding wading and diving predators, which select large prey in shallow water (Power et al. 1989, Harvey & Stewart 1991). A size specific predation risk may partially explain the size dependent depth distribution observed in the trout population.

Overall, the study results showed that size and age specific patterns of habitat use by young-of-the-year, yearling, and two-year old trout are mechanisms by which the trout population partition space in pools. Although the removal experiment implies recent intraspecific competition from two-year old trout was not present, the absence of competitive exclusion was not clearly demonstrated because of low experimental power. The limited statistical power is therefore a concern for reaching conclusions. While this study identified habitat partitioning among the trout age groups, it remains unclear whether biotic interactions or size specific requirements were causing the habitat use patterns.

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