

Habitat use by a Midwestern U.S.A. riverine fish assemblage: effects of season, water temperature and river discharge

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The hypothesis that temperate stream fishes alter habitat use in response to changing water temperature and stream discharge was evaluated over a 1 year period in the Neosho River, Kansas, U.S.A. at two spatial scales. Winter patterns differed from those of all other seasons, with shallower water used less frequently, and low-flow habitat more frequently, than at other times. Non-random habitat use was more frequent at the point scale (4.5 m²) than at the larger reach scale (20–40 m), although patterns at both scales were similar. Relative to available habitats, assemblages used shallower, swifter-flowing water as temperature increased, and shallower, slower-flowing water as river discharge increased. River discharge had a stronger effect on assemblage habitat use than water temperature. Proportion of juveniles in the assemblage did not have a significant effect. This study suggests that many riverine fishes shift habitats in response to changing environmental conditions, and supports, at the assemblage level, the paradigm of lotic fishes switching from shallower, high-velocity habitats in summer to deeper, low-velocity habitats in winter, and of using shallower, low-velocity habitats during periods of high discharge. Results also indicate that different species within temperate river fish assemblages show similar habitat use patterns at multiple scales in response to environmental gradients, but that non-random use of available habitats is more frequent at small scales.

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Key words: dynamic landscape model; river discharge; river fishes; water depth; water flow; water temperature.

INTRODUCTION

Recent conceptual models of temperate stream fish ecology, such as Schlosser's (1991, 1995) dynamic landscape model, emphasize habitat shifts in response to environmental variation. In this model, stream fishes move among different

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habitats in response to changing environmental gradients or life-history stages. In these temperate systems, strong environmental gradients are often generated by seasonal variation in water temperature and stream discharge. In many cases, stream fishes respond to this variation by altering use of available water flow velocities and depths.

Flow velocity has a strong influence on the energy expenditure required for a fish to maintain position in the water, and, for many fishes, on the supply of trophic resources. In summer, during periods of potentially high growth, occupied habitats are typically those that maximize food intake and growth (Hughes & Dill, 1990; Hill & Grossman, 1993; Grossman *et al.*, 2002), and are often characterized by high water flow velocities that supply drifting invertebrate food resources (Hill & Grossman, 1993; Nakano, 1995). During winter, cold water temperatures characterized by low growth potential (Keast, 1985; Zapata & Granado Lorenzo, 1993) predominate, making slower-flow velocity habitats most advantageous by allowing fishes to minimize energy expenditure (Cunjak, 1996). Likewise, as river discharge increases, fishes often seek refuge in slower-flowing waters (Harrell, 1978).

Water depth determines which habitats serve as refugia from biotic and abiotic threats. Shallow water provides protection from piscivorous fishes, and deeper water shelters fishes from avian and terrestrial predation (Power, 1987; Gorman, 1988). The importance of such refugia may vary with water temperature; as metabolism of exothermic predators slows in colder weather, the importance of refugia from predatory fishes may decrease. Abiotic factors also become important in winter; when air temperatures become extremely cold, shallow water is likely to be colder than deep water, and in temperate systems subject to freezing, scouring from ice break-up can increase the risk of occupying shallow water (Brown *et al.*, 2001). During periods of high stream discharge, however, fishes often inhabit shallow waters offering refuge from high-flow velocities (Ross & Baker, 1983; Matheney & Rabeni, 1995; Brown *et al.*, 2001), and, in some cases, access to increased levels of trophic resources (O'Connell, 2003).

The concepts above support a paradigm in which small-bodied fishes of temperate lotic systems are predicted to occupy shallower, higher-flow habitats in warm temperatures, and deeper, slower-flow habitats during cold temperatures. Increased stream discharge also should lead to fishes using shallower, slower-flow habitat. Thus, the influence of water temperature and stream discharge represents a potential paradigm of predictable habitat shifts in response to environmental variation, as predicted by Schlosser's (1991, 1995) model. Although this paradigm is intuitive, its support has been drawn largely from autecological work on salmonids (Heggenes *et al.*, 1993; Contour & Griffith, 1995; Young, 1999), or, less frequently, cyprinids (Matthews & Hill, 1980; Lucas & Batley, 1996; Clough & Beaumont, 1998). Few studies, however, have compared characteristics of occupied and unoccupied habitats throughout the year for speciose temperate lotic fish assemblages (Matthews & Hill, 1980; Bart, 1989). Such information is necessary before the paradigm above is applied at the assemblage level.

Ontogeny can also have a strong effect on habitat use by fishes in lotic systems. Adults often occupy deeper habitats, with higher flow velocities, than

juveniles (Schlosser, 1982; Gelwick, 1990). Thus, habitat use by riverine fish assemblages can be controlled both by extrinsic environmental factors and intrinsic characteristics of the assemblage itself.

The present study examined year-round use of available water depths and flow velocities at two spatial scales by fishes in the Neosho River, Kansas, U.S.A. This was done in two ways: (1) each species in each season was tested for patterns of non-random use of water depths and flow velocities; results for all species were then pooled by season to evaluate seasonal differences in frequency of these patterns. Because patterns of habitat use by lotic fishes can vary with spatial scale (Baxter & Hauer, 2000; Mattingly & Galat, 2002), the frequency of non-random habitat use at two different spatial scales was compared to evaluate the spatial extent of observed patterns and (2) for each collection, mean difference from average for water depths and flow velocities occupied by all fishes was calculated, then regressed against river discharge and water temperature. To evaluate the effect of ontogeny, this value was also regressed against the proportion of juveniles in the assemblage. The first approach assessed seasonal variation in use of available water depths and flow velocities by individual species, and the second the extent to which assemblage-wide patterns of water depth and flow velocity use were associated with water temperature, stream discharge and assemblage ontogenetic composition.

MATERIALS AND METHODS

STUDY SYSTEM

The Neosho River, of the Arkansas River drainage, is fifth-order in the study reach. It flows south-east in Lyon County, KS, U.S.A., through mixed-grass prairie and cropland. Mature riparian vegetation, with associated canopy cover, occurs in some sections. Riffle-pool geomorphology occurs, and is especially pronounced during periods of low river discharge. The substratum is rocky, composed primarily of gravel <64 mm in diameter, with clay and silt, sand, boulder and some bedrock also present. Water is turbid all year-round, with mean turbidity of 37.7 nephelometric turbidity units (NTU) measured over the study period (D. Gillette & J. Tiemann, unpubl. data).

Eight sites were sampled along a 34 km stretch of the Neosho River from Americus to Emporia, KS; one site was eliminated prior to analyses (*a priori*) because lack of landowner permission made it impossible to adequately assess available habitat. This resulted in seven sites retained for analysis (Fig. 1); the excluded site was located between sites 1 and 2. Study sites were chosen that were both representative of available habitat in this river section, and that could be sampled well with the methodology used. At each site, five permanent transects were fixed perpendicular to shore, spaced equally every 5 to 10 m, depending on length of the reach to be sampled. Width of cross-stream transects varied from 14 to 35 m.

SAMPLING

Each site was sampled monthly from November 2000 to October 2001, between the 9th and 22nd of each month, during daylight hours. Sampling order was randomized each month. Due to ice cover, sites 4 and 5 could not be sampled from December to February. In addition, flow velocities were too low at site 5 in September, October and November, site 6 in August and December, and site 4 in November, to be sampled effectively. These collections were omitted from analyses, resulting in a total of 72 collections. Sampling at each site proceeded from downstream to upstream transects, and from near shore to far shore points along each transect. A maximum of five points were sampled along each

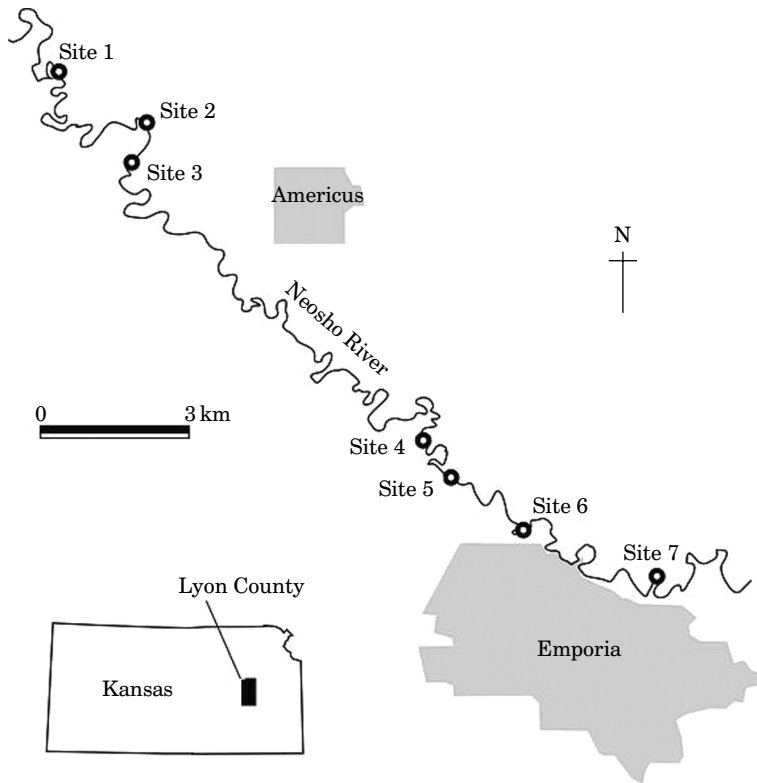


FIG. 1. Map of study reach of the Neosho River in Lyon County, KS, U.S.A., showing seven study sites.

transect, depending on river width and depth, and landowner permission. Points along each transect were spaced at least 0.5 m apart to minimize disturbing adjacent points. At each point, fishes were sampled by kick-seining, using a 3 mm mesh seine. While one person fixed a 1.5 m seine at a sampling point, another person disturbed the substratum, moving downstream from a starting point 3 m upstream. In this manner, fishes within a 4.5 m² area were carried downstream and 'chased' into the seine. This methodology has been shown to effectively capture fishes from shallow, lotic habitats (Matthews, 1990; Wildhaber *et al.*, 1999). Fishes were counted and identified as juvenile or adult, using a 30 mm total length (L_T) maximum juvenile length for minnows (*Camptostoma*, *Pimephales*, *Cyprinella* and *Notropis* spp.) and darters (*Etheostoma* and *Percina* spp.), and a 50 mm L_T maximum juvenile length for madtoms (*Noturus* spp.) and sunfishes (*Lepomis* spp.) (Gelwick, 1990).

Water depth and flow velocity at 60% depth were measured at each point. Water depth was measured with a metre-stick, reading depth from the downstream edge. Water flow velocity was measured with a Global Flow Probe (Global Water Company, Inc., Gold River, CA, U.S.A.). For each site in each month (collection), surface water temperature was measured using a laboratory thermometer, and river discharge from the United States Geological Survey (U.S.G.S.) gauging station in Americus, KS, U.S.A., was obtained *via* the U.S.G.S. web site (<http://www.waterdata.usgs.gov/ks/nwis/rt>).

DATA ANALYSIS

Statistical analyses were performed using SPSS v.12 (SPSS, Inc.), SAS v.8 (SAS Institute, Inc.), and Resampling Stats v.5.0.2 (Resampling Stats, Inc.). Species occurring

in <10% of all collections were omitted from analyses because small sample sizes were unsuitable for statistical testing. Seasonal variation in available water depths and flow velocities was tested by one-way ANOVA, with collections as replicates and season as treatment. Seasons were defined monthly as follows: autumn (September to November), winter (December to February), spring (March to May) and summer (June to August). Independence of water depth and flow velocity was evaluated using Pearson's r .

Testing for non-random use of available water depths and flow velocities for each species in each season was conducted at two spatial scales. At the larger scale, mean depth and flow velocities of occupied stream reaches were compared to those of unoccupied stream reaches within each season, subsequently referred to as 'reach scale.' Each collection represented one stream reach, and mean reach depth and flow velocity were calculated by averaging all points sampled for a given collection. At the smaller scale, depth and flow velocities of individual occupied points were compared to those of unoccupied points within each collection, referred to as 'point scale.' If habitat use by a species is random with respect to water depth or flow velocity, then the expected value for the difference between occupied and unoccupied habitats would be zero. Different methods were used to test this hypothesis at each spatial scale.

At the reach scale, a randomization procedure (Manly, 1991) was used to test the null hypothesis that there was no difference in mean water depth and flow velocity between occupied and unoccupied reaches in a given season. For each species in each season, mean depth and flow velocity of occupied reaches was calculated, and the value for unoccupied reaches subtracted. To generate the probability of this value occurring under the null hypothesis (random habitat use), all available stream reaches for that season were pooled, and 10 000 samples randomly selected with N equal to the number of reaches that the species being tested occurred in. For each sample, the difference between the means of selected and unselected depth and flow velocities was calculated. The proportion of differences from these random samples \geq a positive observed difference, or \leq a negative observed difference, represented the probability of the observed difference occurring under the null hypothesis, random habitat use (Manly, 1991). For example, ghost shiner *Notropis buchanani* Meek occurred in eight of 17 available stream reaches in autumn 2000. To test for non-random use of water depth, mean water depth was calculated for the eight occupied reaches, and mean water depth of the nine unoccupied reaches subtracted, producing a difference between means of occupied and unoccupied depths for *N. buchanani* in the autumn of 0.53 cm. To generate the probability of this difference occurring under the null hypothesis (random habitat use), 10 000 random samples of eight water depths were generated from the 17 available reaches in autumn, and the difference between selected and unselected depths calculated for each. The proportion of random samples with differences ≥ 0.53 was 0.473 (4730 out of 10 000 samples). Thus H_0 : (random use of available depths) was retained for *N. buchanani* in autumn, with a P value of 0.473.

At the point scale, a one-sample t -test was used to test the same hypotheses. For each species in each collection, mean depth and flow velocity of unoccupied points was subtracted from that of occupied points. The resulting values were pooled by season, and the t -test used to generate the probability of the observed value occurring under H_0 : (random use of available habitat). A significant positive t indicated occupied > unoccupied, and a significant negative t indicated occupied < unoccupied.

The analyses above yielded a data set showing, for each species in each season, non-random patterns of habitat use at each scale, and the direction of such patterns (e.g. inhabited shallower or deeper water than expected at random). To test for differences in frequency of these patterns by season and spatial scale, further analyses were conducted on these results. Frequency was defined as the proportion of species showing a given habitat use pattern (e.g. the number of species using slower flow velocities), divided by the total number of species tested. For the seasonal analysis, this hypothesis was first tested for all non-random habitat use patterns combined [e.g. H_0 : (combined frequency of all types of non-random habitat use does not vary by season)], then separately for each of the four specific patterns: use of shallower habitats [e.g. H_0 : (frequency of shallower habitat use does not vary by season)], use of deeper habitats, use of faster-flowing

habitats and use of slower-flowing habitats. For the purpose of this analysis, all randomization and t -tests with $P [H_0: (\text{occupied} = \text{unoccupied})] < 0.05$ were considered significant. Although this rather liberal criterion increases probability of overall type I error, it does not affect results of testing for pattern frequency, as it was applied equally to all categories of comparison.

To test if frequency of non-random habitat use differed by season, the likelihood-ratio χ^2 test was used. Before proceeding, however, the appropriateness of combining results from point and reach scale analyses was first checked, using χ^2 to test whether or not both scales showed the same frequency of non-random habitat use patterns by season. If both scales showed the same pattern, the results were pooled to test for seasonal differences. The likelihood-ratio χ^2 tests the hypothesis that the frequency of an event (non-random habitat use) is independent of the level of a categorical variable (season), and is the most appropriate test of this hypothesis for small to moderate sample sizes such as those in this study (Agresti & Finlay, 1997). For significant χ^2 comparisons, adjusted residual analysis was used to determine the cells responsible for the observed difference; this methodology is equivalent to using *post hoc* multiple comparison procedures to determine where differences lie for a significant ANOVA (Agresti & Finlay, 1997). To test if frequency of non-random habitat use was independent of scale, a z -test was used (Agresti & Finlay, 1997). To compare spatial scale of non-random habitat use to that of variation in habitat parameters, mean coefficient of variation (CV) for points within each collection and collections within each season was calculated for water depth and flow velocity.

For the assemblage-level analysis, linear regression was employed to relate use of available water depths and flow velocities to river discharge and water temperature. For each collection, the difference between occupied and unoccupied depths and flow velocities was calculated for all species, and these differences averaged to produce single values for water depth and flow velocity for each collection. These values are referred to as 'assemblage depth shift' and 'assemblage flow shift' and represent the extent to which species in a given collection collectively exhibited non-random use of available water depths and flow velocities. These values for all collections were then regressed against water temperature, \log_{10} of mean daily river discharge and proportion of juveniles in the assemblage. Simple linear regression was used to evaluate predictive ability of variables. Independent predictive ability of collinear variables was assessed using regression on residuals. Multiple linear regression with backwards elimination was used to compare predictive ability of all significant independent variables.

RESULTS

Fourteen species occurred in at least 10% of collections, and were retained for analyses (Table I). Water temperature and river discharge varied seasonally (Fig. 2), leading to seasonal differences in available flow velocities and water depths (Fig. 3); available flow velocities were higher in winter and spring, and available depths greater in spring and summer. Sampled points ranged in depth from 2 to 121 cm, and in flow velocities from 0 to 1.7 m s⁻¹. Water depth and flow velocity were not significantly correlated at the point ($r = 0.045$, $P = 0.103$) or reach ($r = 0.031$, $P = 0.799$) scale, allowing independent analysis of these two habitat measures.

Non-random habitat use was frequent; 32% (61 of 193) of all comparisons were significant at $\alpha = 0.05$, and 9% (18 of 193) at sequential Bonferroni-corrected α (Rice 1989; Table I). Non-random patterns of habitat use differed seasonally for three species. Neosho madtom *Noturus placidus* Taylor occupied deeper points with slower-flow velocities in winter, but shallower points with higher-flow velocities in summer. Channel darter *Percina copelandi* (Jordan)

TABLE I. Results of seasonal test for non-random use of available water depths and flow velocities at two spatial scales for 14 fishes collected in the Neosho River, Lyon County, KS, U.S.A., from November 2000 to October 2001. Probabilities of the observed habitat use pattern occurring under H_0 : (random habitat use) are shown. If significantly different from random, two-letter abbreviations describe occupied habitat relative to available habitat (Sh, shallower; De, deeper; Sl, slower flow; Fa, faster flow). Capital letters denote conditions under which testing for non-random habitat use could not be conducted (A, occurred in all collections; AO, occurred in all but one collection; N, none collected; AB, absent at all but one site; F, degree of freedom 1)

Season	Species	Depth		Flow Velocity	
		Reach	Point	Reach	Point
Autumn 2000	Central stoneroller <i>Campostoma anomalum</i> (Rafinesque)	0.039 Sh*	0.459	0.048 Fa*	0.359
	Red shiner <i>Cyprinella lutrensis</i> (Baird & Girard)	A	0.0014 Sh**	A	0.197
	Ghost shiner <i>Notropis buchanaui</i> Meek	0.473	0.318	0.204	0.900
	Sand shiner <i>Notropis stramineus</i> (Cope)	0.277	0.877	0.064	0.957
	Bluntnose minnow <i>Pimephales notatus</i> (Rafinesque)	0.339	0.608	0.189	0.030 Sl*
	Slim minnow <i>Pimephales tenellus</i> (Girard)	0.331	0.281	0.190	0.362
	Bullhead minnow <i>Pimephales vigilax</i> (Baird & Girard)	0.355	0.808	0.250	0.065
	Stoneroller <i>Noturus flavus</i> Rafinesque	0.135	0.021 Sh*	0.112	0.054
	Neosho madtom <i>Noturus placidus</i> Taylor	0.096	0.144	0.293	0.214
	Orangespotted sunfish <i>Lepomis humilis</i> (Girard)	0.091	0.230	0.005 Sl*	<0.0001 Sl**
	Orangethroat darter <i>Etheostoma spectabile</i> (Agassiz)	0.034 Sh*	0.085	0.033 Fa*	0.101
	Slenderhead darter <i>Percina phoxocephala</i> (Nelson)	0.007 De*	0.080	0.469	0.0004 Fa**
	Logperch <i>Percina caprodes</i> (Rafinesque)	0.101	0.317	0.278	0.0017 Sl**
	Channel darter <i>Percina copelandi</i> (Jordan)	0.137	0.391	0.052	F

Winter 2000–2001	<i>C. anomalum</i>	0-403	0-202	0-249	0-040 Fa*	
	<i>C. lutrensis</i>	0-299	0-328	0-162	0-0070 SI**	
	<i>N. buchacani</i>	AB	AB	AB	AB	
	<i>N. stramineus</i>	N	N	N	N	
	<i>P. notatus</i>	0-405	0-705	0-0042 SI**	0-021 SI*	
	<i>P. tenellus</i>	0-080	F	0-186	F	
	<i>P. vigilax</i>	0-424	0-167	0-0001 SI**	0-014 SI*	
	<i>N. flavus</i>	N	N	N	N	
	<i>N. placidus</i>	0-030 De*	0-013 De*	0-481	0-011 SI*	
	<i>L. humilis</i>	0-183	0-645	0-0021 SI**	0-0037 SI**	
	<i>E. spectabile</i>	0-442	0-300	0-074	0-835	
	<i>P. phoxocephala</i>	0-030 De*	0-310	0-250	0-450	
	<i>P. caprodes</i>	0-141	F	0-047 SI*	F	
	<i>P. copelandi</i>	N	N	N	N	
	<i>C. anomalum</i>	0-017 Sh*	0-396	0-071	0-109	
	Spring 2001	<i>C. lutrensis</i>	AO	0-031 Sh*	AO	0-0024 SI**
		<i>N. buchacani</i>	0-208	0-041 De*	0-219	0-037 SI*
<i>N. stramineus</i>		0-0039 Sh**	0-234	0-073	0-595	
<i>P. notatus</i>		0-022 De*	0-014 Sh*	0-354	0-0038 SI**	
<i>P. tenellus</i>		0-029 De*	0-258	0-331	0-074	
<i>P. vigilax</i>		0-490	0-956	0-428	0-026 SI*	
<i>N. flavus</i>		0-039 Sh*	F	0-115	F	
<i>N. placidus</i>		0-190	0-135	0-253	0-449	
<i>L. humilis</i>		0-015 De*	0-012 Sh*	0-331	0-0039 SI**	
<i>E. spectabile</i>		0-016 Sh*	0-0004 Sh**	0-167	0-396	
<i>P. phoxocephala</i>		0-094	0-243	0-290	0-0018 Fa**	
<i>P. caprodes</i>		0-446	0-757	0-113	0-438	
<i>P. copelandi</i>		0-010 De*	0-751	0-0016 SI**	0-146	

TABLE I. Continued

Season	Species	Depth		Flow Velocity	
		Reach	Point	Reach	Point
Summer 2001	<i>C. anomalum</i>	0.007 Sh*	0.0005 Sh**	0.472	0.087
	<i>C. lutrensis</i>	A	0.818	A	0.996
	<i>N. buchamani</i>	0.061	0.038 De*	0.015 Fa*	0.220
	<i>N. stramineus</i>	0.083	0.172	0.255	0.525
	<i>P. notatus</i>	0.331	0.108	0.091	0.031 Sl*
	<i>P. tenellus</i>	0.209	0.858	0.407	0.212
	<i>P. vigitax</i>	0.309	0.122	0.266	0.012 Sl*
	<i>N. flavus</i>	0.008 Sh*	0.112	0.259	0.038 Fa*
	<i>N. placidus</i>	0.025 Sh*	0.744	0.390	0.023 Fa*
	<i>L. humilis</i>	A	0.242	A	0.013 Sl*
	<i>E. spectabile</i>	0.499	0.0010 Sh**	0.480	0.086
	<i>P. phoxocephala</i>	0.441	0.167	0.013 Fa*	0.038 Fa*
	<i>P. caprodes</i>	0.330	0.013 Sh*	0.063	0.530
	<i>P. copelandi</i>	0.200	0.021 Sh*	0.411	0.867

* Test significant at $\alpha = 0.05$.** Test significant at sequential Bonferroni-corrected α (Rice, 1989) applied seasonally.

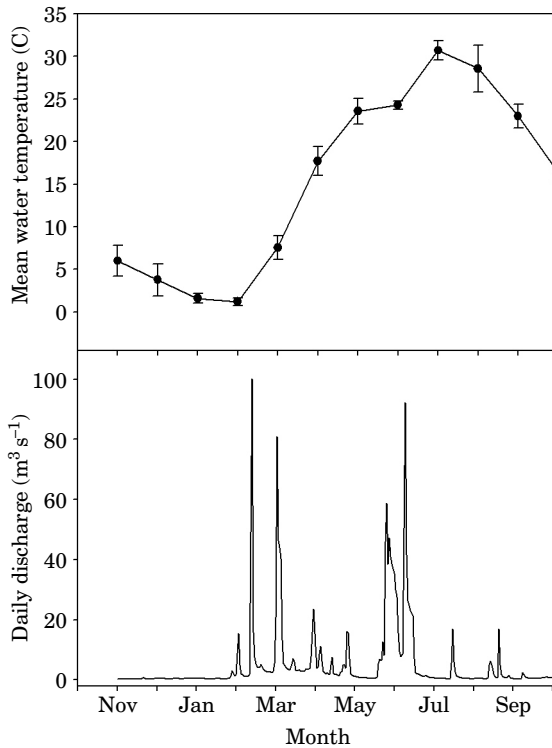


FIG. 2. (a) Mean \pm s.d. monthly surface water temperature from seven study sites and (b) daily river discharge measured at the United States Geological Survey gauging station on the Neosho River at Americus, KS, U.S.A., from November 2000 to October 2001.

used shallower points in summer, but used deeper reaches, or used depths randomly, in all other seasons. *Notropis buchmanii* used slower-flow points in spring, but higher-flow reaches in summer. In spring, two species showed scale-specific patterns of habitat use. Orangespotted sunfish *Lepomis humilis* (Girard) and bluntnose minnow *Pimephales notatus* (Rafinesque) occupied reaches deeper than available at random, but points shallower than available at random.

Reach and point scale analyses showed the same seasonal patterns of non-random habitat use frequency (χ^2 , $0.25 < P < 0.90$ for all, shallower, deeper, slower and faster). That is, patterns of habitat use (e.g. shallower habitat use) occurring frequently in a given season at one scale, also occurred frequently in the same season at the other scale. Consequently, results from the point and reach scale were combined for analysis of seasonal frequency patterns. Combined frequency of non-random habitat use did not vary by season (Table II), nor did that of deeper or faster-flowing habitat use. Frequency of shallower habitat and slower-flowing habitat use did vary, however (Table II). Both of these differences were driven by winter patterns; z -scores from adjusted residual analysis showed significant results for only two cells: proportion of species using shallower ($z = -1.88$, $P = 0.030$) and slower-flowing ($z = 2.43$, $P = 0.008$) habitat in winter (Table II). Thus, during winter, fishes used

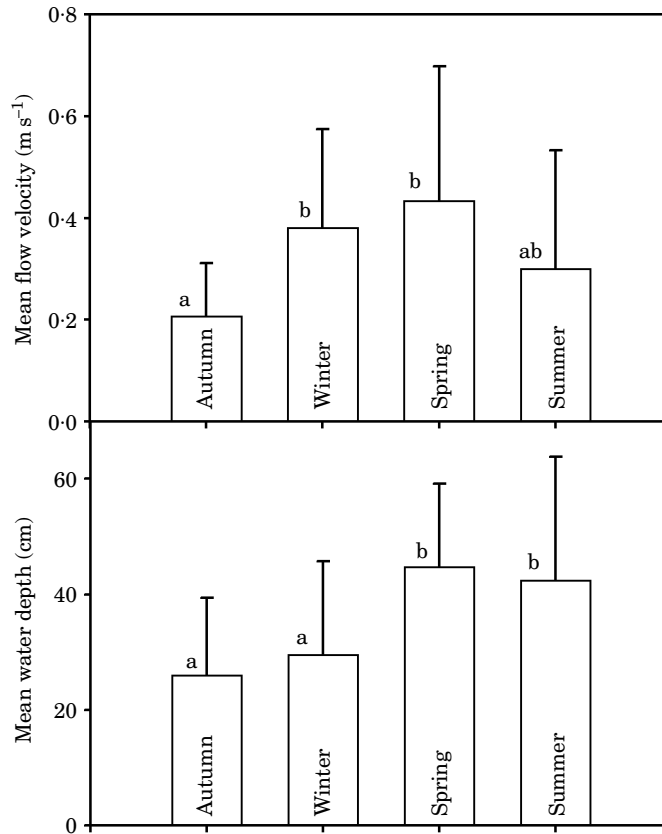


FIG. 3. Mean \pm s.d. (a) flow velocity and (b) water depth by season for 72 collections from the Neosho River, Lyon Co., KS, U.S.A., from November 2000 to October 2001. ANOVA results were (a) $F_{3,69} = 3.828$, $P = 0.014$ and (b) $F_{3,69} = 5.325$, $P = 0.002$. Lowercase letters indicate results of *post-hoc* least-significant difference tests.

shallower habitat significantly less frequently, and slower-flowing habitat significantly more frequently, than in other seasons.

Non-random habitat use was significantly more frequent at the point scale (36.1%) than the reach scale (27.1%, $z = 6.30$, $P < 0.001$). Mean CV for reaches in each season (mean \pm s.d. water depth = 47.90 ± 9.26 cm and flow velocity = 61.49 ± 13.07 m s⁻¹) was similar to that for points within each reach (mean \pm s.d. water depth = 42.54 ± 11.01 , flow velocity = 85.32 ± 35.94), indicating that similar levels of variation in available water depths and flow velocities existed at both scales.

Assemblage-level analysis revealed a significant relationship between assemblage depth and flow shifts, and mean daily river discharge and water temperature (Fig. 4). As river discharge increased, assemblages used shallower, slower-flowing habitat than that available. As water temperature increased, assemblages used shallower and swifter-flowing habitat than that available. For both assemblage depth shift and flow shift, however, mean daily river discharge had the strongest effect, with standardized regression coefficients greater than those of water

TABLE II. Proportions of fish species collected in the Neosho River, Lyon County, KS, U.S.A., from November 2000 to October 2001 showing non-random habitat use patterns by season, with results of χ^2 test for seasonal differences in frequency of each pattern

Habitat use pattern	Season				Likelihood-ratio χ^2 results
	Autumn	Winter	Spring	Summer	
Combined	0.231	0.361	0.385	0.308	$\chi^2 = 3.29$, d.f. = 3, $P = 0.349$
Shallower	0.148	0.000**	0.308	0.269	$\chi^2 = 10.92$, d.f. = 3, $P = 0.012^*$
Deeper	0.037	0.167	0.192	0.038	$\chi^2 = 5.67$, d.f. = 3, $P = 0.129$
Slower	0.154	0.500**	0.231	0.115	$\chi^2 = 9.38$, d.f. = 3, $P = 0.025^*$
Faster	0.115	0.056	0.038	0.192	$\chi^2 = 3.90$, d.f. = 3, $P = 0.272$

* Comparisons significant at $\alpha = 0.05$.

** Cells differing significantly from expected values as determined by z-test from adjusted residual analysis.

temperature for both multiple regressions (Table III). This difference was strongest for the depth shift regression, where water temperature did not have a significant effect when included in the multiple regression model with river discharge. Water temperature and mean daily river discharge were not collinear ($r = 0.114$, $P = 0.342$). The proportion of juveniles in the assemblage had a significant effect

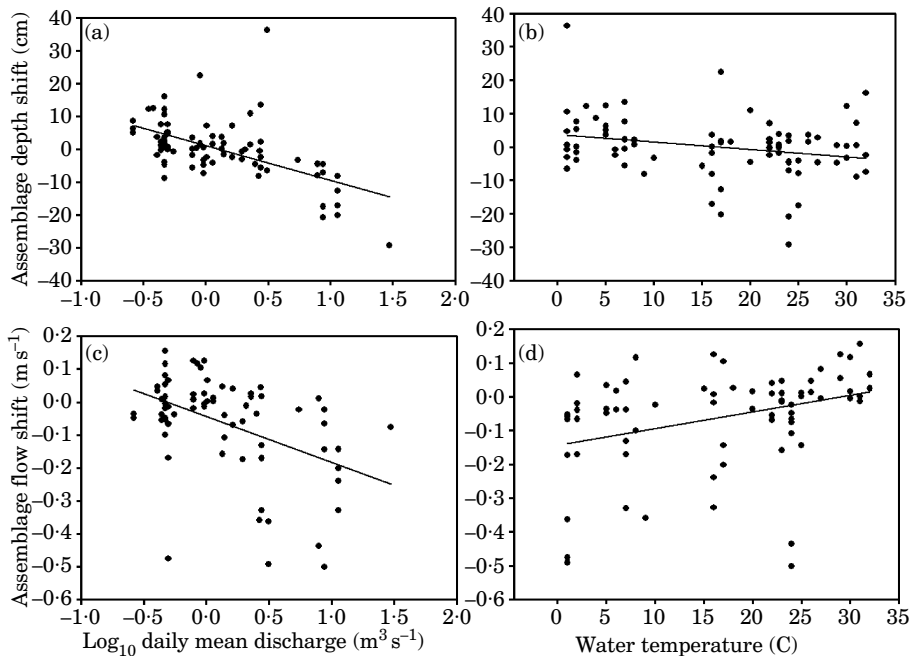


FIG. 4. Linear regression plots of (a) assemblage depth shift and river discharge, (b) assemblage depth shift and water temperature, (c) assemblage flow shift and river discharge and (d) assemblage flow shift and water temperature for 72 collections from the Neosho River, Lyon Co., KS, from November 2000 to October 2001. The curves were fitted by: (a) $y = 1.08 - 10.52x$ ($P < 0.001$), (b) $y = 3.74 - 0.23x$ ($P = 0.027$), (c) $y = -0.04 - 0.14x$ ($P < 0.001$) and (d) $y = -0.14 + 0.005x$ ($P = 0.004$).

TABLE III. Standardized regression coefficients for multiple linear regressions of fish assemblage depth and flow velocity shifts against water temperature and river discharge for 72 collections from seven sites in the Neosho River, Lyon County, KS, U.S.A., from November 2000 to October 2001

Variable				
Dependent	Independent	Coefficient	<i>t</i>	<i>P</i>
Depth shift	Water temperature	-0.179	-1.883	0.064
	River discharge	-0.529	-5.569	<0.001
Flow shift	Water temperature	0.391	4.016	<0.001
	River discharge	-0.497	-5.105	<0.001

on depth shift ($y = -4.88 + 16.01x$, $r^2 = 0.14$, $F_{1,71}$, $P = 0.001$), but not on flow shift ($F_{1,71}$, $P = 0.47$). The proportion of juveniles in the assemblage, however, was negatively correlated with daily river discharge ($r = -0.49$, $P < 0.001$). After removing the river discharge effect by taking residuals of the discharge-depth shift regression, juvenile composition no longer had a significant effect on depth shift ($F_{1,71}$, $P = 0.27$). After removing the effect of juvenile composition, however, the effect of river discharge on depth shift was still strong ($F_{1,71}$, $P < 0.001$). Thus, proportion of juveniles in the assemblage did not have an independent effect on either depth or flow shift.

DISCUSSION

Results of this study suggest that temperate riverine fishes use available water depths and flow velocities differently as environmental conditions change. This pattern fits conceptual models, such as Schlosser's (1991, 1995) dynamic landscape model, that regard movement among habitats as a central feature of lotic fish ecology. As previous authors have noted (Fausch *et al.*, 2002), application of this model in a conservation context necessitates recognition that species need multiple habitat types among which to move in response to changing environmental gradients. Certain habitats may be used rarely at one time, but more frequently at another. For example, winter habitat use patterns in this study differed markedly from those of other seasons, with increased use of slower-flow habitat, and decreased use of shallower water habitat.

The high frequency of non-random habitat use observed at two spatial scales in this study is similar to findings of previous authors at the microhabitat scale (Grossman & Freeman, 1987; Grossman & Ratajczak, 1998). Collectively, such results indicate that habitat selection is a characteristic of many lotic fish assemblages. Despite the large body of work demonstrating habitat selection by individual species (Fraser & Cerri, 1982; Holbrook & Schmitt, 1988; Schlosser, 1988; Fraser & Gilliam, 1992; Petty & Grossman, 1996; Utne *et al.*, 1997; Thompson *et al.*, 2001), studies documenting year-round patterns in entire fish assemblages are uncommon.

At both spatial scales, results of the present study support the hypothesis that fishes use slower, deeper water during cold temperatures, and swifter-flowing,

shallower water during warm temperatures (Bjornn, 1971; Matthews & Hill, 1979; Cunjak, 1996; David & Closs, 2003). This conclusion is based on seasonal frequencies of individual species patterns, as well as regression of assemblage depth and flow shifts against water temperature. The hypothesis above is based on the assumption that high-flow velocities are better foraging habitats (Garner *et al.*, 1998), but are more energetically expensive to occupy (Facey & Grossman, 1990); stream fishes often select habitats that maximize net energetic gain (Fausch & White, 1986).

Although this model has been applied primarily to drift-feeding invertivorous fishes, it can logically be extended to species with different trophic ecologies. Most fishes in this study feed on invertebrates, with the exception of the herbivorous central stoneroller *Camptostoma anomalum* (Rafinesque) (Pflieger, 1997). Of these, darters, madtoms and some minnows are benthic pickers (Matthews, 1998), gleaning invertebrates from the benthos. Many of the organisms these fishes consume require flowing water with high levels of dissolved oxygen, and silt-free, rocky substrata on which to graze and find shelter (Merritt & Cummins, 1995). Consequently, flow may be a requirement of good foraging habitat for benthic pickers as well as for drift feeders. Shallower, swifter-flowing areas may also provide the best feeding habitats for grazers, as siltation can hinder algivory by fishes (Power, 1984; Gelwick *et al.*, 1997), and light can limit benthic autotroph production in some lotic systems (Murphy & Hall, 1982; Keithan & Lowe, 1985; Lowe *et al.*, 1986). In turbid rivers such as the Neosho, deep water may limit light penetration for photosynthesis, potentially restricting *C. anomalum* foraging to shallow areas. Indeed, reaches occupied by *C. anomalum* were shallower than unoccupied reaches in all seasons except winter (Table I). Thus, shallower, swifter-flowing water may provide the best foraging habitat for most fishes in this study, predicting increased occupancy of such habitat during times of high energy expenditure in warmer months. In cold weather, conversely, shallower, higher velocity habitats become less advantageous as metabolism slows, reducing the amount of trophic resources required and making it more difficult to maintain position in swift river currents (Graham *et al.*, 1996).

Predation threat may also drive use of shallower water during warm months. Piscivorous fishes' high energetic requirements and associated feeding rates in summer could necessitate occupation of shallow water spatial refugia by small bodied fishes. In cold weather, predators' metabolisms slow, causing them to feed less (Little *et al.*, 1998), and potentially decreasing predation risk in deeper water.

In addition to temperature-driven seasonal variation, fish assemblage habitat use changed in response to river discharge. This effect was stronger than that of water temperature, as indicated by comparison of standardized regression coefficients. These results are consistent with findings of previous authors (Harrell, 1978; Ross & Baker, 1983; Matheney & Rabeni, 1995; Brown *et al.*, 2001), showing that fishes of lotic systems respond to rising water levels by increasing use of shallower, slower-flowing habitat. Presumably, such behaviour decreases downstream displacement (Harvey, 1987; Gido *et al.*, 1997; Brown *et al.*, 2001), and may increase access to trophic resources along channel margins (O'Connell, 2003). This strong effect of discharge on habitat use highlights the potential impact of altered flow regimes on riverine fishes, suggesting that maintenance of

natural flow regimes is an important part of conserving riverine fish faunas (Poff *et al.*, 1997).

Proportion of juveniles in the assemblage did not have an independent effect on assemblage-wide use of available depths and flow velocities. This result differs from previous work (Schlosser, 1982; Gelwick, 1990) showing ontogenetic habitat use differences between conspecifics. Although ontogeny had no effect in the present study, differences in habitat use between juveniles and adults may exist, but be overshadowed by assemblage-wide responses to changing discharge levels.

Habitat-use patterns of individual species in this study generally did not differ by season or scale. Three species (*N. placidus*, *P. copelandi* and *N. buchmanii*), however, showed non-random habitat use in one direction in one season, and in the opposite direction in another season. Two other species (*P. notatus* and *L. humilis*) showed non-random patterns of habitat use in one direction at one spatial scale, and in the opposite direction at the other scale. These four species illustrate the need for multi-scale, multi-season data to adequately describe habitat use patterns of certain taxa.

In this study, non-random habitat use was more frequent at the smaller point scale than at the larger reach scale. Because different statistical approaches were used at each scale, this difference could potentially be a statistical artefact. Randomization tests, however, generally have power equal to that of appropriate parametric statistics (Manly, 1991). Coefficients of variation for available depths and flow velocities were similar at both scales, indicating equivalent levels of habitat variation. Thus, low frequency of non-random habitat use at the reach scale was not due to a lack of habitat variation.

In many aquatic systems, comparison of similar patterns at multiple scales is inappropriate, because causal mechanisms can differ (Fisher, 1992). The present study, however, suggests that similar mechanisms operated at both point and reach scales. χ^2 analysis showed no difference in distribution of significant patterns by season; thus, frequency of use of each habitat type (shallower, deeper, slower- and faster-flowing) was distributed similarly among seasons at both scales. This indicates that the same pattern of habitat use occurred at both scales, but was stronger at the smaller point scale, leading to a higher frequency of significant differences.

In comparing occupied to unoccupied habitats, patterns can potentially be driven by changes in habitat availability, rather than by habitat selection. If a species tracks a constant water depth throughout the year, occupied depths could be less than unoccupied depths during high river discharge, and greater than unoccupied depths during low discharge. In the present study, however, this is probably not the case. The main seasonal pattern was increased frequency of slower-flow, deeper habitat use in winter. Winter flow velocities were fairly high (Fig. 3), so increased use of slower flows could potentially be a consequence of habitat availability. Available flow velocities were even greater in spring, when slower-flow habitat was used less than half as frequently. If fishes were indeed occupying the same velocity regardless of available habitat, frequency of slower-flow habitat use should be greater in spring than in winter. Instead, results suggest that fishes were selecting habitat differently in the two seasons. Likewise, available water depths in autumn and winter were similar. No species, however, used shallower habitat in winter, whereas several species did in

autumn. Thus, seasonal patterns in this study were due to changes in fish habitat selection, rather than changes in habitat availability.

Habitat shifts related to changing water temperature and river discharge, such as those documented in the present study, are an important component of seasonal habitat use patterns by temperate fish assemblages, and should be explicitly incorporated into conceptual models and conservation plans for fishes of these systems. From a conservation perspective, it is important to note that these patterns may be applicable on an assemblage-wide, and not just a species-specific level. This suggests that assemblage-wide conservation and management plans may be applicable to the Neosho River and similar systems, a view important in light of recent calls for conservation plans encompassing whole communities, rather than focusing on individual species (Rohlf, 1991; Sergio *et al.*, 2003).

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