

Using fine-scale GIS data to assess the relationship between intra-annual environmental niche variability and population density in a local stream fish assemblage

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Summary

1. Geographic information systems (GIS) have recently proved useful for estimating the environmental niche of species across broad geographic regions. However, the application of these niche-based GIS techniques has yet to be extensively applied to local systems. The assumptions of the methods are transferable across scales: species exist across a range of habitats, and these habitats represent a gradient of suitability that can be characterized using multivariate environmental data in association with known species occurrences.

2. Habitat availability and species' niche characteristics are often considered to be important predictors of population density. However, seasonal habitat variability and stochastic events have been hypothesized to limit interactions among species and confound the relationship between available habitat, species niche characteristics and community structure. This research examines the relationship between environmental niche breadth and niche position and population density among species of stream fishes in a seasonally variable environment using a novel application of fine-scale GIS data.

3. Niche breadth and niche position were estimated for 11 species in a local assemblage using five fine-scale (0.5 m) GIS-based environmental data sets collected during four different times of the year (July, October, January, April). We compared niche measures to variation in population density among species to determine whether environmental niche characteristics, in the context of available habitat, explain variation in numbers of individuals among species.

4. Variation in population density among species in the October sample was predicted by niche breadth measures ($R^2 = 0.752$), while variation in population density among species in the January sample was predicted by a model incorporating measures of both niche breadth and niche position ($R^2 = 0.953$). Measures of niche breadth and niche position were not correlated with variation in population density in the July and April samples.

5. Species presence and local abundance are often assumed to be predictable based on the availability of suitable habitat. However, little effort has been directed at understanding the influence of both niche breadth and niche position on local abundance. Our results suggest that the amount and distribution of available habitat can be a strong predictor of interspecific variation in population density, even in seasonally variable environments.

Key-words: abundance, aquatic, geographic information systems, niche breadth, niche position, seasonality

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Introduction

Identifying the factors responsible for variation in local population density among species is a fundamental goal in ecology (Brown 1984). Whittaker (1965, pg. 250) noted the common

pattern of a ‘...continuous progression of abundance among species from dominants through intermediates to rare species’. This relationship has been partially attributed to the differential response among species to available habitat, with highest population densities realized by species most suited to local conditions (Whittaker 1956, 1960, 1965; Brown 1984). If population density is associated with the extent of suitable habitat available for each species, then detailed quantification of the spatial variation in habitat at a particular locality, in conjunction with information on habitat occupied by a species, should provide insights into the relationship between species’ environmental niche characteristics, habitat availability, and variation in population density among species (Seagle & McCracken 1986).

The term ‘environmental niche’, based on the n -dimensional hypervolume described by Hutchinson (1957), has recently been used to refer to the integration of habitat and species distribution data to infer species’ abiotic requirements, often at landscape scales (Austin & Meyers 1996; Austin 2007). Although the quantification of the environmental niche generally avoids explicit reference to biotic interactions, this approach has proved useful for examining the relationship between available habitat, abundance and species distributions among taxa at broad spatial scales (Brandle & Brandl 2001; Heino 2005). In particular, this framework provides a foundation for the quantification of niche breadth and niche position of a species in relation to multivariate assessments of available habitat (Doledec, Chessel, & Gimaret-Carpentier 2000; Hirzel *et al.* 2002). Niche breadth represents the range of habitats occupied by a species, while niche position represents how far the mean of the habitat occupied by a species deviates from the mean of all available habitat (Hirzel *et al.* 2002). These measures provide information on habitat occupied by a species, as well as an equally important quantification and integration of measures of available habitat in a defined area.

While much research has been directed at the influence of environmental variability on population and community characteristics (e.g., Wiens 1977; Huston 1979; Chesson 1994; Chesson & Huntly 1997), limited attention has been directed at the relationship between intra-annual habitat variation and species’ niche characteristics and the subsequent influences on variation in population density. In communities at a stable equilibrium, a species with a relatively wide niche breadth could be predicted to have a high population density because of a greater range of suitable habitats at a site (Brown 1984; Gaston & Lawton 1990), while a species with a less marginal environmental niche (i.e., low niche position) could be predicted to have a high population density because of greater access to suitable habitat and the ability to tolerate shifts in available habitat (Dueser & Shugart 1979; Seagle & McCracken 1986). These predictions suggest that a similar amount and distribution of habitat is available throughout the year. Non-equilibrium theories suggest that seasonality as well as environmental perturbations and other stochastic events may inhibit competitive structuring of communities, because species are not able to access the same amounts of suitable habitat throughout the year (Chesson 1986; Chesson & Case 1986). Therefore, in variable environments, population size and com-

munity structure may not be predictable based on the relationship between niche characteristics and the amount and variety of available habitat (Chesson 1986, 2000; Chesson & Case 1986).

The two primary requirements of niche breadth and niche position calculations are data sets representing available habitat within a spatially defined region as well as data that characterize the habitat occupied by a species in that region. Geographic information systems (GIS) applications have recently proved useful for estimating environmental niche breadth and niche position for species across broad geographic regions because of the ability to accurately assess habitat occupied by a species in the context of available habitat across a defined area (Hirzel *et al.* 2002; Hirzel, Hausser, & Perrin 2006). However, the application of these broad-scale niche-based GIS techniques has yet to be applied to local systems, possibly because of the challenges associated with generating local-scale GIS habitat data. Nevertheless, the fundamental assumptions of the methods are transferable across scales: species are able to exist across a range of habitats, these habitats represent a gradient of suitability for a species, and these habitats can be characterized using multivariate environmental data in association with known species occurrences.

Habitat is generally an important contemporary predictor of species presence or absence for freshwater fishes, particularly in lotic systems (reviewed in Matthews 1998). However, because of the apparently stochastic nature of environmental fluctuations in flowing freshwater systems (Resh *et al.* 1998), debate has occurred regarding whether population density among species can be predicted based on the presence and extent of suitable habitat (Grossman, Moyle, & Whitaker 1982; Herbold 1984; Rahel, Lyons, & Cochran 1984; Yant, Karr, & Angermeier 1984). Aquatic lotic systems provide an opportunity to apply niche-based GIS techniques to the study of the influence of abiotic factors on local assemblage structure. Streams are relatively discrete habitats in the landscape that can be defined by upstream and downstream boundaries. The environmental variables that have been identified as important to the presence of species (e.g., flow rate, sediment size, depth) are easily quantified (Matthews 1998). Finally, because of the physical characteristic of streams (i.e., riffles, runs, pools), isolation of homogeneous microhabitats is relatively straightforward, thus allowing for reasonable assessment of species–habitat associations.

The purpose of this research is to examine the relationship between intra-annual GIS-based estimates of environmental niche characteristics (i.e., breadth and position), habitat variability and population density in freshwater stream fishes using sampling periods representing a range of seasonal variation. We also examine the consistency of the environmental niche variables across seasons in the context of the predictability of species abundance related to abiotic niche characteristics. By integrating species locality data and fine-scale GIS data, we test hypotheses that environmental niche breadth and environmental niche position are correlated with population density. An additional goal of this research is to determine whether the rapidly developing array of broad-scale niche-based GIS

applications can be applied in local assemblages to predict the relationship between environmental variables and species distributions.

Materials and methods

Research was conducted in Labarque Creek, a second-order tributary of the Meramec River in Jefferson County, Missouri, USA (38°42'54"N, 90°6'32"W). A 675-m section of Labarque Creek, contained within the property of the Tyson Research Center (TRC) (operated by Washington University in St. Louis), was used to investigate the relationship between environmental niche characteristics and population density of stream fishes. Labarque Creek contains *c.* 44 species of fishes; at least 25 of these species have been identified within the TRC property (J.H. Knouft, unpublished data). Habitat and fish data were collected during four time periods: 30 June–2 July 2007, 29–30 October 2007, 14–15 January 2008 and 26–27 April 2008. These dates represent periods of relatively high (January and April) and low (July and October) flows along with representation of a range of seasonal variation in temperature.

GIS CHARACTERIZATION OF HABITAT AND SPECIES LOCALITIES

Habitat data sets were generated within a GIS framework during each sampling period to characterize the abiotic variables potentially regulating fish assemblages in Labarque Creek. A Trimble GeoXH GPS unit (Trimble Navigation, Sunnyvale, CA, USA) was used to map the stream boundaries and generate georeferenced stream habitat data sets. The Trimble GeoXH provides sub-30 cm accuracy after differential correction of locality data during post-processing. Data for seven habitat variables including dissolved oxygen (ppm), benthic flow rate (m s^{-1}), midwater flow rate (m s^{-1}), surface flow rate (m s^{-1}), depth (cm), riparian vegetation < 3 m in height (% cover) (lower canopy cover) and sediment size were collected at georeferenced locations along Labarque Creek during each study period. During July 2007, dissolved oxygen and flow rates were measured at 127 locations, sediment size was measured at 185 locations, canopy cover was measured at 244 locations and depth was measured at 193 locations along the 675-m stream reach. The varying number of habitat data collection locations among variables during the initial sampling effort was required to ensure an accurate assessment of the different rates at which each habitat measure changed along the stream. All habitat variables were collected at 101 locations in October 2007, 97 locations in January 2008 and 83 locations in April 2008. The reduced number of habitat locations in October, January and April were determined to be sufficient to characterize habitat transitions based on the July sampling. The reduced number of sample sites also allowed us to complete habitat sampling in a single day and conduct fish sampling the next day.

Dissolved oxygen was measured at the middle of the water column with a YSI DO 200 dissolved oxygen/temperature meter (YSI Incorporated, Yellow Springs, OH, USA). Benthic flow rate was measured 2 cm above the substrate, midwater flow rate was measured in the middle of the water column, and surface flow rate was measured 2 cm below the surface. All flow rates were measured with a Marsh-McBirney Flo-mate flow meter (Hach Company, Loveland, CO, USA). Lower (riparian) canopy cover was estimated with a spherical densitometer. Substrate size was estimated as the mean maximum width of five randomly chosen pieces of substrate within 1 m^2 of the georeferenced habitat data collection point.

Fishes were collected with seine nets (1.2 m \times 2.4 m, 6.4 mm mesh) and a Smith-Root LR-20 backpack electrofisher (Smith-Root Inc., Vancouver, WA, USA) during each sampling period. Sampling of fishes began at the downstream edge of the stream reach to prevent disturbing subsequent sampling sites. Sample sites were selected so that the area within the site contained homogenous habitat (i.e., all riffle, run or pool habitat). Riffle and run habitat were sampled with seine nets, and pools were sampled with the electrofisher. Sampling sites were *c.* 12 m^2 in area and were isolated with net barriers and physical habitat. Although different sampling methods were used in different habitats, the relatively small size of the sample area (12 m^2), in combination with habitat-appropriate sampling methods, afforded the opportunity to intensively sample to near-depletion with each method. Thus, we assume the bias associated with different sampling methods is minimal. A sample area of 12 m^2 was used because of the convenience and flexibility of field-based estimation of each sample site (i.e., 1 m \times 12 m, 2 m \times 6 m, 3 m \times 4 m). The centre of the each sampling point was recorded with the Trimble GeoXH GPS unit. All individuals were identified to species at the time of capture and then returned to the stream. Individuals were measured [total length (TL), mm] at each sample site during July 2007 and October 2007; however, measurement of body size was discontinued during the January 2008 sampling period because of the concerns of mortality owing to cold air temperature.

Georeferenced habitat data sets for each sampling period were imported as shapefiles into ArcGIS, version 9.2 (ESRI, Redlands, CA, USA). Each shapefile contained the georeferenced habitat sampling localities with associated habitat data. Raster (continuous) data layers were then generated from the seven habitat shapefiles for each habitat variable at a 0.5 m resolution by applying an inverse distance weighting (IDW) interpolation methodology using the three closest habitat measures to estimate the habitat for each cell in the raster data set (Fig. 1). The GIS-based raster format allows visualization and manipulation of continuous data across a defined area. The choice of the IDW interpolation method using the three nearest habitat measures was based on the results of tests of interpolation accuracy using a range of sample sizes and multiple interpolation methods (see Results).

Depth and dissolved oxygen data sets were \log_{10} -transformed and the lower canopy data set was arcsine-square root-transformed for statistical analyses. Benthic, midwater and surface flow rates were highly correlated during each sampling period (e.g., $r > 0.9$). Therefore, the average of these three variables was calculated to generate a single average flow rate measure. Fish collection points for each species were also imported as shapefiles into ArcGIS 9.2. This process resulted in five continuous habitat layers (depth, mean flow rate, dissolved oxygen, canopy cover, sediment size) from which species-habitat occupancy can be estimated based on localities where individuals were collected.

Many of the environmental data sets co-vary; therefore, a principal components analysis (PCA) was conducted on the environmental data sets to produce uncorrelated GIS data sets [BIOMAPPER 3.2 (Hirzel, Hausser, & Perrin 2006)]. Data from all sample periods were included in a single PCA so that niche measures are comparable across seasons. Principal component score GIS data sets representing principal components with eigenvalues > 1.0 were retained for further analyses. Habitat use data were then compiled for each species in each sampling period by calculating the average of PC1 and PC2 scores within each 12 m^2 sample area and assigning these values to species collected at that site. This effort resulted in principal component scores characterizing habitat use for each species at

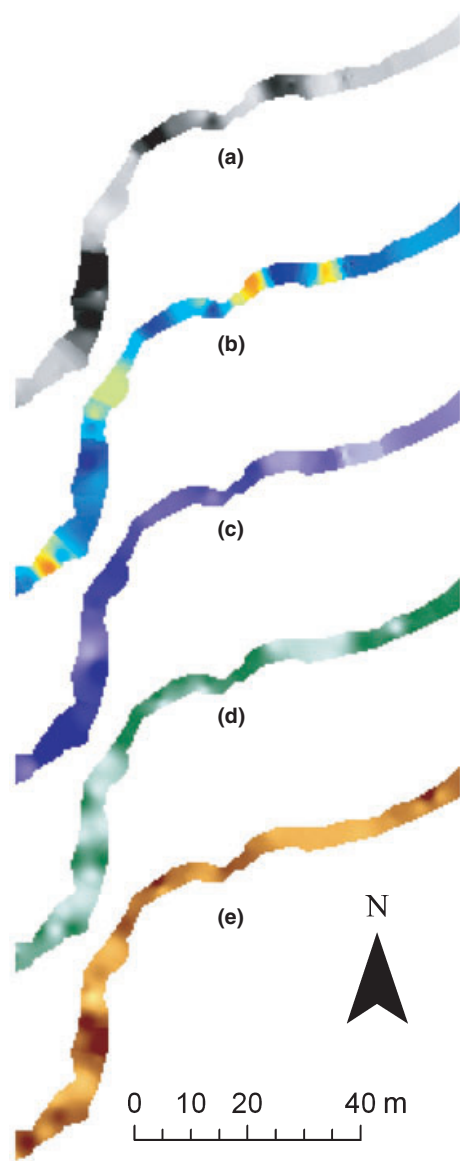


Fig. 1. Maps of July 2007 Labarque Creek geographic information systems habitat data sets. (a) Depth (0.00 cm–60.00 cm; grey–black), (b) mean flow rate (0.00–0.35 m s⁻¹; blue–red), (c) dissolved oxygen (7.50–8.50 ppm; light blue–dark blue), (d) riparian canopy cover (0.00–100.00%; light green–dark green), (e) mean sediment size (0.00–7.00 cm; yellow–brown). A central 100-m subsection of the total 675-m stream reach is presented for visualization purposes.

each locality the species was collected in Labarque Creek for each sampling period.

CHARACTERIZATION OF NICHE BREADTH AND NICHE POSITION

Individuals within a species generally occur in a non-random subset of environmental conditions, and this non-random distribution should reflect a relationship to the optimum range of conditions for the species (Hirzel *et al.* 2002). The degree of specialization (niche breadth) and marginality (niche position) of the habitat occupied by a species can be quantified by comparing the mean and variance of the habitat occupied by the species to the mean and variance of the total (global) range of habitats available across the area of interest. Niche

breadth is quantified as the standard deviation of the global habitat divided by the standard deviation of the species habitat and measures the relative range of habitat in which a population occurs (Hirzel *et al.* 2002). Species with low scores (high niche breadth) can be considered habitat generalists that occupy habitats with a relatively high variance compared to the global habitat variance, while species with high scores (low niche breadth) can be considered habitat specialists that occupy narrow ranges of habitat with a relatively low variance compared to the global habitat variance (Doledec, Chessel, & Gimaret-Carpentier 2000; Hirzel *et al.* 2002). We will refer to estimates of niche breadth as ‘niche specialization’ because this is conceptually more straightforward. With this terminology, species with high niche specialization scores have narrower niche breadths and species with low niche specialization scores have wider niche breadths.

Niche position measures the deviation of the species–habitat mean from the global habitat mean and is quantified as the absolute difference between the global habitat mean and the species–habitat mean, divided by 1.96 standard deviations to remove bias associated with variance in the global distribution (Hirzel *et al.* 2002), thus allowing for comparisons across sites or sampling periods. Species with high niche position scores occupy habitat with a mean that is relatively distant from the mean of the global habitat, while species with low niche position occupy a range of habitat with a mean that is similar to the mean of the global habitat. Niche position scores can range from *c.* 0 to 1, with a score of 0 indicating a species mean at the global mean, while a score of 1 indicates a species that occupies habitats relatively far from the global mean (Hirzel *et al.* 2002).

Niche specialization and niche position estimates were generated for each species during each sampling period using global mean and standard deviation values calculated from each GIS-based PC data set and the mean and standard deviation measures of species’ habitat use. Body size for each species was calculated as average TL [$\log_{10}(\text{mm})$] of all individuals collected during the July 2007 and October 2007 sampling periods. Population density (individuals/collection site) for each species was calculated as the total number of individuals collected divided by the total number of collection sites (total fish collection sites: July = 60, October = 56, January = 46, April = 56).

Multiple regression models (ordinary least squares) were used to test three hypotheses regarding the relationship between niche measures and population density: (i) niche specialization is negatively correlated with population density among species; (ii) niche position is negatively correlated with population density among species; and (iii) a model incorporating measures of niche specialization and niche position will predict variation in population density (SYSTAT, version 11.00.01; Systat Software Inc., Chicago, Illinois, USA). Population density was also regressed on body size for the July 2007 and October 2007 sampling periods to determine whether body size could confound the relationship between niche measures and population density.

Principal component scores from each seasonal data set were assembled from five meter intervals along the stream reach and compared with MANOVA to assess variation in habitat among seasons (i.e., available environmental niche space) (SYSTAT, version 11.00.01). To examine the relative consistency of species environmental niche measures across seasons, species were ranked by niche specialization and niche position scores from each sampling period. Kendall’s coefficient of concordance of ranks (W) was calculated for each PC variable niche measure to assess the consistency of habitat availability among seasons for species in Labarque Creek (SPSS, version 16.0). The test statistic (W) can range from 0 to 1, with 0 indicating no agreement among ranks across seasons and 1 indicating complete agreement among ranks across seasons.

Results

Quantification of the environmental niche suggests that the range of habitats identified for each species supports positive population growth rates (*sensu* Hutchinson 1957). Although we do not have population growth rate estimates, we assume that if a species is detected in the sample area throughout the year, the available habitat is able to support the persistence of the population. Consequently, although we collected 25 species during the study, only the 11 species that were present in all sampling periods are retained for our analyses (Table 1). The remaining 14 species were generally rare when they were sampled (i.e., collected at only one or two localities in a particular season). Relative population density estimates for the 11 study species were similar across sample periods (July vs. October: $R^2 = 0.519$, $F_{1,10} = 9.723$, $P = 0.012$; July vs. January: $R^2 = 0.567$, $F_{1,10} = 11.759$, $P = 0.008$; July vs. April: $R^2 = 0.338$, $F_{1,10} = 4.595$, $P = 0.061$), suggesting that coverage of habitats during each sampling period was consistent among seasons. In addition, $\log_{10}(\text{population density})$ was not correlated with $\log_{10}(\text{TL})$ among species during the July or October sampling periods (July: $R^2 = 0.211$, $F_{1,10} = 2.404$, $P = 0.156$; October: $R^2 = 0.067$, $F_{1,10} = 0.644$, $P = 0.443$).

Sampling dates were planned so that no precipitation occurred in the Labarque Creek watershed during data collection or the 5 days preceding the collection of habitat and fish data. Habitat and fish data collection was planned on consecutive dates with similar predicted weather. For example, the maximum air temperature on July 1 (26°C) was similar to the high air temperature on July 2 (28°C) when fishes were collected. While environmental data were not collected on the same day as the fish data, the majority of the variables (depth, sediment size, canopy cover, flow rate) were likely consistent

within each sampling period. Dissolved oxygen was likely not exactly the same between sample days; however, the minimal variation in maximum air temperature between days (e.g., July sample, 2°C) and the consistent physical factors that can influence dissolved oxygen (e.g., flow rate) presumably resulted in relatively similar dissolved oxygen profiles across the stream reach (e.g., higher dO₂ in riffles, lower dO₂ in pools).

Five GIS-based environmental data sets (0.5 m resolution) were generated with an IDW interpolation method using georeferenced habitat data collected from Labarque Creek for each sampling period (Fig. 1). We selected the IDW interpolation methodology, using the three closest habitat measures to estimate the habitat for each cell in the raster data set, based on the results of a broader assessment of interpolations generated using IDW and kriging approaches, with varying numbers of habitat measures used to generate interpolations. For example, in July 2007, depth measurements were collected at 193 locations along the 675-m stream reach. To assess the interpolation accuracy of the IDW and kriging approaches, we separated data from the 193 locations into 163 training points (used to generate the interpolated raster) and 30 testing points (used to test the accuracy of the interpolation). Interpolations were generated using both IDW and kriging techniques with the number of data points used to generate the interpolations varying from three to ten. For each of the 16 interpolated data sets (2 methods × 8 sample sizes), the field-measured depth at the 30 testing locations was compared to the interpolated values at the same location by generating a Pearson product-moment correlation coefficient statistic (R^2). The IDW interpolations produced higher R^2 values than the kriging interpolations at all sample sizes (Fig. 2). In addition, the use of three points with the IDW method resulted in the highest correlation

Table 1. Species collected, total number of localities sampled and number of localities sampled for each species during each sampling period

Species	July (N)	October (N)	January (N)	April (N)
Total localities sampled	60	56	46	56
<i>Campostoma anomalum</i> Rafinesque	31	28	22	23
<i>Ericymba buccata</i> Cope	8	7	5	3
<i>Etheostoma flabellare</i> Rafinesque	12	9	14	16
<i>E. spectabile</i> Agassiz	17	18	15	25
<i>Fundulus catenatus</i> Storer	6	7	3	7
<i>F. olivaceus</i> Storer	10	17	7	9
<i>Lepomis macrochirus</i> Rafinesque	8	13	3	7
<i>L. megalotis</i> Rafinesque	13	11	3	10
<i>Luxilus chrysocephalus</i> Rafinesque	15	22	7	12
<i>Lythrurus umbratilis</i> Girard	23	15	6	9
<i>Semotilus atromaculatus</i> Mitchell	14	12	8	7

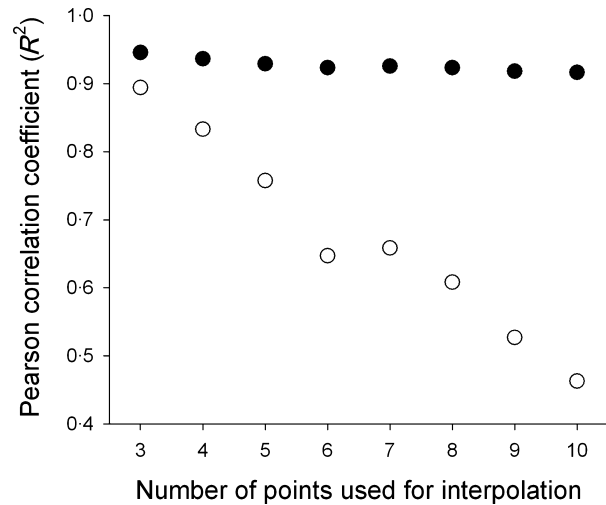


Fig. 2. Results of the assessment of the predictive abilities of inverse distance weighting (IDW) and kriging interpolation methods using various numbers of samples to generate habitat estimates. Black circles represent correlations between field-collected depth measures and interpolated depth estimates from IDW interpolations, and white points represent correlations between field-collected depth measures and interpolated depth estimates from kriging interpolations.

Table 2. PC1 and PC2 loadings from principal components analysis of Labarque Creek habitat data

Environmental variable	PC1	PC2
Average flow rate	-0.674	0.234
Canopy cover	-0.807	-0.309
Depth	0.127	-0.800
Dissolved oxygen	-0.734	-0.313
Sediment size	-0.291	0.753

between field-measured depth and the interpolated value ($R^2 = 0.945$).

Two principal components had eigenvalues > 1.0 . The first and second principal components (PC) explained 64.0% of the overall variance in the habitat data (PC1 = 34.9%, PC2 = 29.1%). PC1 scores are negatively correlated with flow rate, dissolved oxygen and canopy cover, while PC2 scores are negatively correlated with depth and positively correlated with sediment size (Table 2).

A visual examination of the GIS-based environmental niche estimates for each species during each season indicates the expected relationships between species and habitat occupancy (Fig. 3). For example, *Etheostoma flabellare* (Fantail Darter), which was found almost exclusively in shallow riffles with relatively high flow rates and large sediment, is represented in the upper left region of each graph, while *Lepomis* species (sunfish), which are generally found in deeper pools with low flow and smaller sediment, are represented in the lower right region of each graph (Fig. 3). Low flow rates in July and October resulted in the homogenization of the habitat described by PC1. For example, 79.2% of the stream area in July had flow

rates $< 0.1 \text{ m s}^{-1}$, whereas only 5.3% of the stream area in April had flow rates $< 0.1 \text{ m s}^{-1}$. As flow rates increased in January and April, habitat partitioning among species along the PC1 axis became apparent.

A total of 12 multiple regression analyses were conducted to examine the relationship between niche characteristics and population density (4 seasons \times 3 models). Consequently, a sequential Bonferroni correction (α') was applied to reduce the likelihood of a Type-I error ($\alpha = 0.050$, 12 tests). None of the models for the July 2007 or April 2008 samples predicted variation in population density among species. However, the niche specialization model (PC1 specialization + PC2 specialization) explained a significant amount of variation in population density in the October sample ($R^2 = 0.752$), while the full niche model (PC1 specialization + PC2 specialization + PC1 position + PC2 position) explained a significant amount of variation in population density in the January sample ($R^2 = 0.953$) (Table 3). As predicted, both PC1 and PC2 measures of niche specialization were negatively correlated with population density in the October sample (i.e., more specialized species tended to have lower population densities (Table 4). In the January sample, the predicted relationships were only realized for measures of PC1 position and PC2 specialization (Table 4).

The results of the comparisons of habitat data from each sample period indicates differences in available habitat among seasons (MANOVA: Wilks' Lambda = 0.203, $F_{6,870} = 176.900$, $P < 0.001$) (Fig. 4). The assessment of the consistency of the niche measures among seasons indicated that PC1 niche specialization ranks ($W = 0.011$, $\chi^2 = 0.368$, d.f. = 3, $P = 0.947$), PC2 niche specialization ranks ($W = 0.009$, $\chi^2 = 0.312$, d.f. = 3, $P = 0.958$), PC1 niche position ranks

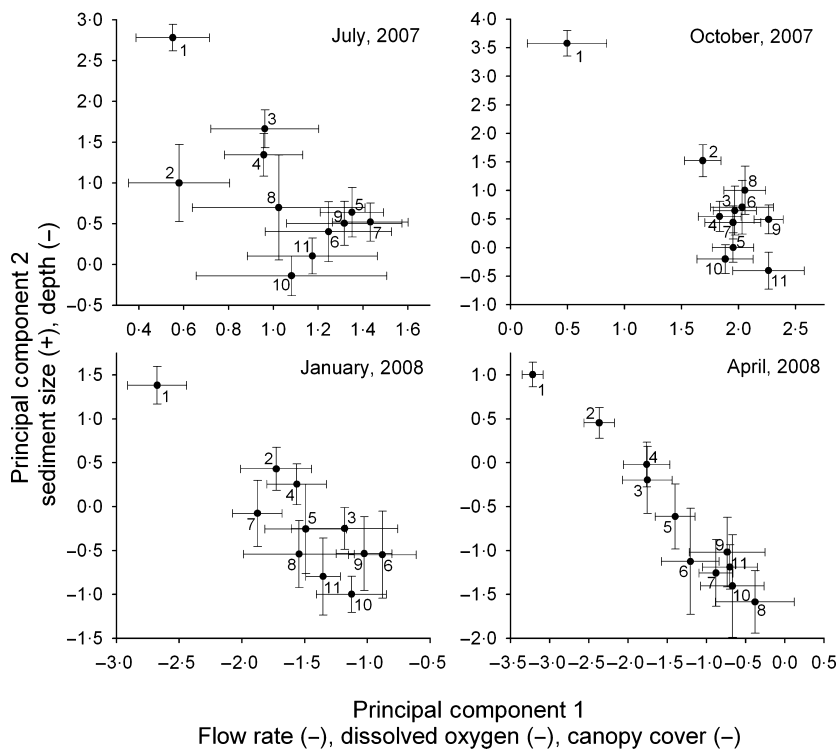


Fig. 3. Mean principal component 1 (PC1) and principal component 2 (PC2) scores for species in Labarque Creek during each sampling period. Error bars indicate standard error. Percidae – (1) *Etheostoma flabellare*, (2) *Etheostoma spectabile*; Cyprinidae – (3) *Semotilus atromaculatus*, (4) *Campostoma anomalum*, (5) *Luxilus chrysocephalus*, (6) *Ericymba buccata*, (7) *Lythrurus umbratilis*; Fundulidae – (8) *Fundulus catenatus*, (9) *Fundulus olivaceus*; Centrarchidae – (10) *Lepomis macrochirus*, (11) *Lepomis megalotis*.

Table 3. Results of multiple regression analyses of relationships between variation in niche characteristics and population density

	R^2	d.f.	F	P
<i>July</i>				
Niche specialization model	0.025	2,10	0.103	0.903
Niche position model	0.005	2,10	0.021	0.979
Full niche model	0.072	4,10	0.117	0.972
<i>October</i>				
Niche specialization model	0.752	2,10	12.116	0.004**
Niche position model	0.376	2,10	2.415	0.151
Full niche model	0.754	4,10	4.603	0.048
<i>January</i>				
Niche specialization model	0.410	2,10	2.778	0.121
Niche position model	0.699	2,10	9.308	0.008
Full niche model	0.953	4,10	30.265	< 0.001**
<i>April</i>				
Niche specialization model	0.243	2,10	1.282	0.329
Niche position model	0.268	2,10	1.463	0.287
Full niche model	0.275	4,10	0.568	0.696

Niche specialization model: PC1 specialization + PC2 specialization; Niche position model: PC1 position + PC2 position; full niche model: PC1 specialization + PC2 specialization + PC1 position + PC2 position. *** indicates rejection of null hypothesis using sequential Bonferroni correction (α') for 12 tests ($\alpha = 0.05$).

Table 4. Standardized coefficients (β) for variables included in models predicting significant amounts of variation in population density among species. (a) October niche specialization model; (b) January full niche model

Variable	β	t	P
<i>(a)</i>			
Constant	1.275	3.967	0.005
PC1 specialization	-0.716	-3.876	0.006
PC2 specialization	-0.749	-4.057	0.005
<i>(b)</i>			
Constant	0.000	-4.372	0.007
PC1 specialization	0.403	2.873	0.035
PC2 specialization	-0.593	-4.325	0.008
PC1 position	-0.907	-5.673	0.002
PC2 position	1.644	6.978	< 0.001

($W = 0.013$, $\chi^2 = 1.019$, d.f. = 3, $P = 0.797$) and PC2 niche position ranks ($W = 0.028$, $\chi^2 = 0.916$, d.f. = 3, $P = 0.822$) were not consistent among species across seasons. In combination, these results suggest that habitat varies among seasons and the amount of suitable habitat varies accordingly among species.

Discussion

The influences of habitat availability and habitat variability on population density and assemblage structure in stream fishes have been the topic of several studies (Grossman, Moyle, & Whitaker 1982; Grossman *et al.* 1998; Jackson, Peres-Neto, & Olden 2001; Taylor & Warren 2001). Much of this work suggests that the stochastic and seasonally variable nature of habi-

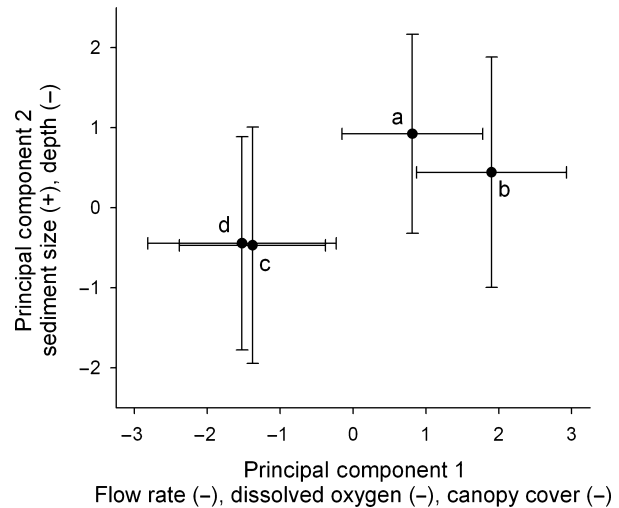


Fig. 4. Mean principal component 1 (PC1) and principal component 2 (PC2) scores of habitat data collected during different sampling periods in Labarque Creek [(a) July 2007; (b) October 2007; (c) January 2008; (d) April 2008]. Error bars indicate standard deviation.

tat availability in streams (Resh *et al.* 1998) limits the ability to predict variation in population abundance among species (e.g. Grossman, Moyle, & Whitaker 1982). Our results, while quantifying the expected hydrologically mediated seasonal variation in habitat (Grossman, Moyle, & Whitaker 1982), are in contrast with previous findings regarding the influence of abiotic factors on the predictability of population density in variable environments. In particular, the extent and distribution of available habitat is a strong predictor of variation in population density among species, but only during colder periods within a seasonally variable environment, with the understanding that our results are based on a single location.

Ross (1986) reviewed and commented on the likely importance of the relationship between habitat availability, species niche breadth and local assemblage structure in fishes, but suggested that assessing multivariate environmental niche characteristics is difficult because of the challenges associated with analysing multiple variables. The GIS approach applied in this study offers the ability to characterize multivariate niche breadth and niche position. Our methods have identified the expected habitat use for each species; however, the amount of various types of habitat differed among seasons. Moreover, the differences in ranks of species niche characteristics among seasons suggest that the differences in seasonal habitat availability, primarily because of the direct and indirect effects of flow variation, result in a situation where the extent and position of environmental niche space availability for each species is inconsistent among seasons. Nevertheless, the significant relationships between population density and niche characteristics in October and January suggest associations between species requirements, the distribution of available habitat and community structure, even though the system exhibits significant abiotic variability throughout the year.

Previous research indicates that bioenergetic demands of stream fishes may peak during the fall and winter because of

the lower temperatures (Rincón & Lobón-Cerviá 1993; Cunjak & Power 1987). A review by Hurst (2007) noted that significant mortality owing to reduced energy stores is not uncommon during this time of the year. Although stream fish continue feeding during this period, body condition (i.e., energy stores) tends to decrease because of the costs of maintaining metabolic rates during colder times of the year (Cunjak & Power 1987). The demand to limit energy expenditure while optimizing foraging should place a premium on occupying optimal habitat based on species requirements. While theoretical research has suggested that stochastic events and environmental variability will reduce abundance (and the intensity of interspecific interactions) among species throughout the year, our results suggest that selection during environmentally harsh times of the year may be a primary regulator of community structure, even in stochastic and seasonally variable environments.

In addition to habitat variability, biotic interactions such as predation as well as individual movements may be important influences on assemblage structure (Matthews 1982; Power, Matthews, & Stewart 1985; Grossman *et al.* 1998; Jackson, Peres-Neto, & Olden 2001; Mitchell & Knouft 2009). This study does not address the influence of predation, and all results reflect assemblage characteristics that account for ongoing predation and behavioural responses to predators. Although none of the species in this study exhibit dramatic migrations throughout the year, we do not assume that the system is closed. Intra-annual movements of stream fishes vary among species (Minns 1995; Smithson & Johnston 1999; Skalski & Gilliam 2000), but are generally sufficient to allow immigration and emigration of individuals to and from the Labarque Creek study area, which can be important to fish assemblage structure (Taylor & Warren 2001). Moreover, we recognize that movements outside of the study area may represent other uncharacterized aspects of the environmental niche. The focus of this research at Labarque Creek addresses abiotic variability, but certainly other aspects regulating fish assemblage structure are important, likely interrelated, and require further detailed examination to elucidate the contributions of each factor.

A common assumption is that species presence and local abundance are predictable based on the amount and availability of suitable habitat in a particular area (Whittaker 1956, 1960, 1965; Brown 1984). In this context, the use of the term 'environmental niche' has recently increased and often refers to the integration of spatially referenced habitat data sets and species locality data to identify the abiotic requirements facilitating species persistence (Austin & Meyers 1996; Austin 2007). Recent research has demonstrated significant relationships between regional estimates of niche breadth and niche position and species distributions as well as local abundance in a variety of taxa, including stream insects and lentic fishes (Heino 2005; Lappalainen & Soininen 2006). These studies, using environmental data across the species' range, have been based on predictions concerning habitat use of species in local communities; specifically, that which species are adapted to a particular type of habitat and the presence and distribution of this habitat will dictate local abundance (Whittaker 1956,

1960, 1965; Brown 1984). Interestingly, little effort has been directed at understanding the influence of local estimates of both niche breadth and niche position on local abundance (but see Seagle & McCracken 1986). Our application of this spatial approach has provided a detailed assessment of the extent of intra-annual variation in habitat and the subsequent effect of this variation on the environmental niche occupied by stream fish species. Results suggest that the amount and position of available habitat can be a strong predictor of interspecific variation in population density, even in seasonally variable environments.

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