L'HABITAT À L'ÉCHELLE LOCALE : DISTRIBUTION MULTIPARAMÈTRE DES POISSONS D'EAU COURANTE.

M.B. BAIN

New York Cooperative Fish and Wildlife Research Unit,
Fernow Hall,
Cornell University,
Ithaca, NY 14853, USA.

RÉSUMÉ (traduit par les éditeurs)

Des analyses quantitatives de l'utilisation de l'habitat à l'échelle locale par les poissons ont été réalisées pendant plus d'une décennie dans de nombreux cours d'eau d'Amérique du Nord. Des descriptions mathématiques des paramètres physiques qui permettent de définir statistiquement différents microhabitats ont été réalisées pour les larves, juvéniles et adultes de plus de 100 espèces de poissons d'eau courante. Ces résultats ont été obtenus en utilisant une approche non conventionnelle d'analyse de l'utilisation du microhabitat basée sur de nouveaux protocoles d'étude, des mesures de l'habitat physique, des échantillonnages des poissons, des analyses de données et leur interprétation. Les microhabitats étaient considérés comme des unités d'échantillonnage plutôt que les localisations des poissons, afin de recueillir également des données sur les microhabitats non utilisés. Les variables physiques de l'habitat ont été mesurées à des échelles cohérentes et les jeux de données ont été configurés en matrices échantillons par variable (variable physique et présence ou abondance de poissons). Pour chaque espèce, l'hypothèse testée était que le microhabitat occupé était une sous unité des microhabitats disponibles. Seules les variables d'habitat différentes entre les groupes d'échantillons occupés et inoccupés ont été prises en compte dans la caractérisation de l'habitat au niveau de l'espèce.

La plupart des espèces et des stades de développement de poissons d'eau courante utilisent un microhabitat statistiquement défini, presque toujours caractérisé par quelques variables physiques. Il en est de même des larves qui sélectionnent des habitats à une toute petite échelle, là où la vitesse du courant est inférieure à leur vitesse critique de nage. La profondeur de l'eau est presque toujours la principale variable caractérisant l'habitat utilisé, mais d'autres variables sont importantes pour quelques groupes d'espèces. Cinq groupes d'utilisation de l'habitat sont distingués pour des petites rivières aux caractéristiques physiques différents en compensant la précision du choix spécifique de chaque espèce par la simplicité d'un arrangement multi-espèce de l'habitat. Les cinq groupes sont associés à différents types d'habitat et ces cinq microhabitats sont caractérisés par des valeurs numériques. Les cinq types d'habitat se recouvrent dans l'espace et une portion non négligeable de l'habitat de nombreux cours d'eau ne croise aucun des critères. Globalement, les poissons d'eau courante semblent utiliser l'habitat de manière très souple et les facteurs responsables des variations d'utilisation du microhabitat à l'échelle locale sont encore très mal connus.

Article available at http://www.kmae-journal.org or http://dx.doi.org/10.1051/kmae:1995019

HABITAT AT THE LOCAL SCALE : MULTIVARIATE PATTERNS FOR STREAM FISHES.

SUMMARY

Quantitative analyses of local-scale habitat use by fish has been conducted for more than a decade in numerous streams and rivers of North America. Mathematical descriptions of the physical attributes that define statistically distinct microhabitats have been developed for the mobile life stages (larval, juvenile, and adult) of more than 100 species of stream and river fish. These results were obtained using a non-traditional approach to analyzing microhabitat use that employed new study designs, physical habitat measurements, fish sampling, data analyses, and interpretation. Microhabitats were the units of sampling rather than fish locations so that data are obtained on occupied and unoccupied microhabitats. Physical habitat attributes were usually measured on a consistent scale, and the data sets were configured as a sample by attribute (physical habitat attributes and fish presence or abundance) matrix. For each species, the hypothesis was tested that the occupied microhabitats were a distinct subset of the available microhabitats. Only physical attributes that differ among occupied and unoccupied sample groups were included in the definition of species-level microhabitats.

Most species and life stages of stream and river fish used a statistically distinct microhabitat, and those microhabitats were almost always defined by a few physical attributes. This includes larvae that selectively used very small-scale habitats when current velocity was less than their maximum sustained swimming speed. Water depth was most often the primary attribute defining microhabitat use, but all other physical attributes were important to some group of species. Five habitat-use assemblages have been identified for physically diverse, small rivers by balancing species-specific precision with the simplicity of a multispecies-habitat pattern. The five assemblages were associated with distinct types of habitat, and these five microhabitats have been defined with numeric criteria. The five habitat types overlap in space, and a substantial portion of the aquatic habitat in most streams does not meet any criteria. Overall, stream fish appear very flexible in microhabitat use and there is little understanding of the factors responsible for variation in microhabitat use at the local scale.

INTRODUCTION

Ichthyologists and fish biologists have been describing local-scale habitat use of fish from nearly the beginning of these professions. Most descriptive accounts of the microhabitats used by freshwater fish are qualitative (for example, quiet backwaters with cover, swift riffles with boulders and cobble) and based on field observations and sampling experience. Nevertheless, these qualitative descriptions of microhabitat use remain the only available information for most species of freshwater fish.

Beginning in about the mid-1970s, many fishery biologists became involved in assessing impacts of human developments on waterways (for example; navigation structures, hydroelectric dams, water supply diversions), and this task often required quantitative assessments of habitat needed to maintain and protect fish. The most common approach to microhabitat quantification has been fairly simple: measure physical habitat attributes (mostly water depth, current velocity, bottom substrate) at the location where individuals of a species are encountered. These data are then summarized as microhabitat criteria where the range of inhabited conditions defines the suitable microhabitat for a species, and the attributes of the most often used habitats define optimal microhabitat. Microhabitat use is sometimes combined with measures of habitat availability to develop criteria based on microhabitat selection.

The accumulation of species habitat criteria from many settings led to the recognition that fish species rarely use just one set of microhabitat conditions. Attempts to explain variable microhabitat use have identified a major shortcoming of the standard approach to quantifying microhabitat: a lack of statistical evidence that a species is responding to measured habitat attributes. Statistical analysis of microhabitat use has almost always been impossible because data have not been collected in non-used or unoccupied microhabitats. Therefore, further advancement in our understanding of habitat use at the local scale will require adopting a different approach to habitat research and assessment.

How could fish biologists advance beyond the simple numerical descriptions of microhabitat use to conduct rigorous tests and analyses of fish responses to physical habitat attributes? In this paper, I develop a non-traditional approach to statistically identifying microhabitat use by employing new study designs, physical habitat measurements, fish sampling, data analyses, and interpretations. Although the approach described here is not new, it has not been widely adopted for fish habitat studies. Results from research on streams and rivers are synthesized and reviewed to illustrate how new information can be obtained, and to show how that information advances our understanding.

METHODS

The approach developed to analyze microhabitat use by stream fish is based on five principles. First, sample habitat rather than fish locations so that data are obtained on occupied and unoccupied microhabitats. Habitat sampling should be designed using a statistically-based (include a random element), site selection protocol that avoids or minimizes investigator decisions in the field (BAIN and FINN, 1991). Second, whenever possible, measure physical habitat attributes on a consistent measurement scale (for example, as continuous variates) so that the data can be analyzed in a comprehensive manner with hypothesis-testing multivariate statistics. Third, treat fish species as habitat attributes so that the data set is configured as a sample by attribute (physical habitat attributes and fish presence or abundance) matrix. Fourth, test the hypothesis that each species uses a distinct subset of the available habitat. That is, test for statistical differences in microhabitat attributes among occupied and unoccupied sample groups. If differences are found, then identify which microhabitat attributes explain differences among occupied and unoccupied sample groups. Fifth, report data for only the influential microhabitat attributes useful in statistically defining a species microhabitat. Field methods used for this approach are reviewed below for streams and small rivers that are largely wadeable (> 1.0-m water depths are fairly uncommon) and large rivers that pose significant sampling problems.

Some of the methods and results reported here are from studies conducted to determine the effects of flow regulation caused by hydroelectric dams. These were comparative, unregulated and regulated river studies of fish community composition and species-level microhabitat use. Study area descriptions and results of these studies have been reported by BAIN *et al.*, 1988 ; KINSOLVING and BAIN, 1993 ; SCHEIDEGGER and BAIN, 1995. Here, I use the data from the unregulated rivers (West River in the northeastern United State [Vermont] and the Cahaba River in the southeastern United States [Alabama]) that were included in the comparative studies. In addition, some results presented here are from a 1989-1990 study of seven, large but wadeable streams in the Tallapoosa River basin in the southeastern United States (Alabama). The objective of this study was to identify robust patterns of fish-habitat relations in streams that had similar mean annual discharge (3.6 to 8.2 m^3/s) but varied greatly in natural flow variation and channel morphology. Data from the six most heavily sampled streams are used in this paper: Terrapin Creek, Hillabee Creek, Oakmulgee Creek, Uphapee Creek, Little River North (northern part of basin), and Little River South (southern portion of the basin).

Sampling Design

The ideal of fully random sampling of microhabitats in flowing waters has been impractical because of high habitat heterogeneity and time constraints limiting the number of samples. Therefore, a systematic sampling design has been used that incorporated some random element in site selection. Also, an *a priori* site selection protocol was adopted to eliminate site selection in the field. In all cases, the size of microhabitat included in each sample was chosen in advance, and fixed for the study. In stream and small river studies, major macrohabitat types (riffles, runs, pools, etc.) were identified in the field, and two transects were randomly chosen perpendicular to flow in each type of macrohabitat. The number of transects per site (6) were chosen to allow the site to be completely sampled in one field day. Sampling sites can be positioned along the transect in a systematic or random manner. In large rivers, random sites were selected within long reaches, and samples were deployed at each site according to a strict protocol. For example, rivers were divided into 2-km reaches. Sampling sites within each reach were located by traveling at a low speed in a boat for a randomly chosen number of seconds.

Physical Habitat Measurements

Microhabitats were sampled as rectangular units of set size oriented parallel to the current. The dimensions of sampled microhabitats varied among studies depending on fish sampling gear (described below), fish density (avoid large numbers of empty samples), and study objectives. In most studies, physical habitat attributes were measured at the four corners of each microhabitat following collection of all fish. Physical habitat measurements were usually made so that all attributes were recorded on a continuous scale. Current velocity was measured at the mean point (0.6 depth from the surface) of the water column with a current meter. Water depth was recorded with a ruled wading rod that supported the current meter, or by dropping a weighted measuring tape into the water.

Substrate, cover, and other physical habitat attributes (for example, vegetation) posed problems because they have been typically recorded as categorical or percentage data. To circumvent this, substrate and cover measurement were made by taking many categorical observations for each microhabitat and computing a mean to use as data for that attribute. The field methods to do this have been described in BAIN *et al.* (1985a) for substrate and KINSOLVING and BAIN (1990) for cover. Substrate is measured by recording the dominant substrate at multiple locations within each sampled microhabitat using the codes of BAIN *et al.* (1985b) : 1 = smooth clay or bedrock, 2 = silt and soft clay (fine, clouds water), 3 = sand (≤ 2 mm diameter), 4 = gravel (> 2-16), 5 = pebble (> 16-64), 6 = cobble (> 65-256), 7 = boulder (> 256). Similarly, cover has been recorded as the number of objects breaking vertical (water surface to substrate) planes distributed around or through a sampled microhabitat. For example, counts have been done for three 0.5-m planes on 6 evenly spaced cross-sections traversing a microhabitat to obtain 18 cover observations. The mean of these 18 observations was used as a cover density value for one sampled microhabitat.

For studies in large rivers, physical habitat measurements were taken on either side of a boat at evenly spaced intervals through a sampled microhabitat. Current velocity was measured at the surface by timing the float of a wood chip over a 1-m distance. Water depth was recorded from a ruled fiberglass pole. The dominant substrate type is estimated by striking and scraping the substrate with the ruled fiberglass pole, and using an abbreviated set of ordered substrate categories. An index of cover was recorded as the number of times the boat anchor hit a solid object when dragged along the river bottom through a sampled microhabitat.

Fish Sampling

Adult and juvenile fish of all species were collected in each microhabitat using prepositioned area electrofishing for studies in wadable streams (most habitats less than 1.5-m water depth) and the shoreline waters of large rivers. A device for this type of sampling was introduced by BAIN *et al.* (1985b) and has since been modified only in construction details, power supply specifications, and rectangular dimensions. The sampler is a rectangular electrode (parallel wires) that is preset at a microhabitat and activated remotely after time (for example, 0.5 h) was allowed for fish to return after disturbance. The dimensions of the sampler have been selected to balance sampling effectiveness (electric field constrains sampler width to no more than about 2 m), logistics (transporting several samplers in the field), and the fish capture rate (moderate numbers of fish without many empty samples). Prepositioned area electrofishers have ranged from 1 x 2 m in mid-sized streams to 1.5 x 12 m for the shoreline waters of large rivers. The dimensions selected in a study have determined the size of microhabitat units for the study.

Snorkeling was used to sample fish in microhabitats in a few stream habitats that were deeper than about 1 meter. However, fish habitat studies in large rivers required a different fish sampling approach. Two macrohabitats have been defined in rivers with large areas of deep (>1 m) water: shoreline waters sampled with prepositioned area electrofishers, and channel habitats sampled with standardized boat electrofishing. Channel microhabitats were 100-m long and 4-m wide (distance effectively sampled by an electrofishing boat). At a pre-selected river location, three pairs of buoys were anchored 50-m apart to mark a rectangular area for sampling, and these areas were positioned parallel to the current. One microhabitat was located off either bank (1 m or greater depth) and in midstream, but offset from one another so that they were at least 100-m apart. The electrofishing boat had forward booms powered by a 5,000 watt alternating current generator and a Smith-Root Inc., type VI-A, variable-voltage pulsator set to DC output. To collect fish, the electrofishing boat was navigated downstream and then upstream through the marked microhabitat. Usually, the sampled waters were 2 to 4 m deep.

All captured fish were weighed, measured, and released at the capture location unless a species identification could not be made in the field. Some large fish species clearly use different microhabitats at different sizes. For these, small and large size classes were defined after reviewing plots of habitat attributes versus fish length. Most size class divisions are made at 100 mm total length. Full analysis of microhabitat use was conducted for species and size classes that were recorded in 5 %, or at least 5, of the microhabitat samples in any one data set.

Larval fish habitat

Larval fish are widely distributed in stream and river habitat because very small fish are not able to control their movements except in the slowest currents. Therefore, analyses of larval fish should delete habitats where the distribution of larvae is largely determined by passive drift. Nursery habitats may be critical for larval fish survival, and SCHEIDEGGER and BAIN (1995) assumed these were habitats where larvae can control their positions and microhabitat use. In river studies, nursery habitats were defined as those areas where larval fish could selectively use microhabitats because current velocity was less than their maximum sustained swimming speed. Sustained swimming speed for most fish, including larvae, has been estimated as 3 to 7 body lengths per second (WEBB, 1975). Using this relation, SCHEIDEGGER and BAIN (1995) estimated the maximum current velocity of 8.4 cm/s (i.e., 7 body lengths x 12-mm long larvae) as the upper velocity limit defining potential nursery habitat for fish families likely to be encountered in the study rivers. Offshore and nearshore habitats with current velocities greater than 8.4 cm/s were assumed to be dominated by fish larvae being passively transported in river currents.

A 1-m^2, 500-µm mesh seine was used to collect larval fish in potential nursery habitat. Seine samples were collected along five fixed transects in each study site. Transects were positioned perpendicular to the flow and to included the range of habitats at a site. One seine sample consisted of three contiguous seine hauls (2-m long, total distance seined = 6 m) taken perpendicular to a transect (parallel to flow). Two seine samples were taken on each shore end of a transect presumably covering the range of potential nursery habitat. The first sample on each transect end was centered on a point 1-m from the shore. The second sample was located as far as 5.0 m from shore but just prior to the point where the current speed exceeded 8.4 cm/s or the water depth exceeded 1.3 m. For each sample, the following microhabitat attributes were recorded : depth (nearest 0.1 m), current velocity (cm/s), density of cover, density of vegetation, and the dominant substrate. The relative density of cover and vegetation was visually estimated on a scale of 1 (absent) to 5 (dense amounts). Cover included any woody debris, while vegetation included only green, herbaceous matter.

Larval fish were preserved immediately after capture in 10 % formalin, and later transferred to 5 % buffered formalin. Larvae were measured (nearest 0.1 mm total length) with a dissecting scope, and identified to the lowest possible taxonomic level. Data were analyzed at the family level to reduce the possibility of inaccurate conclusions from misidentifications, and to accommodate poor representation of some species. Taxon specific microhabitat use was based on data collected one field day prior to the first appearance of a taxon to the first field day after the disappearance of that taxon. Taxa recorded in ten or more samples were analyzed for microhabitat use.

Data Analysis

Statistical analyses were conducted separately for each data set (streams or macrohabitats). Fish species or size classes that used a distinct subset of microhabitat conditions were identified using multivariate analysis of variance (MANOVA, also called Hotteling's multivariate T-test since there were two groups of samples) and univariate analysis of variance (ANOVA or equivalent to a t-test). These procedures tested the hypothesis that there was no difference in habitat between two groups of samples: those with a particular species (present) and those without a particular species (absent). MANOVA tested this hypothesis with all physical habitat attributes combined, and it allows for interactions among attributes that may be important in defining the microhabitat for a species. ANOVA tested the hypothesis with data on a single habitat attribute, and these univariate tests indicate which attributes are individually important in defining a species microhabitat. A species or size class was determined to use a distinct microhabitat within the available habitat when significant differences are found between present and absent sample groups. ANOVA results were then used to identify which habitat attributes were individually useful in defining a species microhabitat. Larval fish microhabitat analyses could not be done with the benefit of multivariate hypothesis testing because some habitat attributes were recorded on a categorical scale. Microhabitat comparisons between sample groups with a taxon present and absent were made with ANOVA (t-tests) for continuous habitat variables and chi-square tests for categorical habitat variables.

Tests among present and absent sample groups have a potentially important flaw: the presence of a species in a sample indicates a suitable microhabitat, but its absence does not necessarily imply unsuitable habitat. It seems reasonable to expect that not every suitable microhabitat will be occupied at the time of sampling. Consequently, a species that uses a specific microhabitat will be found in a less variable set of conditions than that of the available habitat. MANOVA and ANOVA assume equality of variance for each sample group. Fortunately, the tests are conservative (error is biased against identifying a significant microhabitat) when one group has both a larger sample size (absent samples) and the larger variance. As a check, one principal component plot (habitat space) of samples in both groups should show the species was concentrated in a distinct portion of the available habitat.

For species using distinct microhabitats, the mean position in habitat space was plotted using principal component analysis to illustrate community-level relations. Principal component analysis generates uncorrelated, multivariate habitat combinations (principal components) in order of decreasing importance (% or overall variance explained). Eigenvectors from these analyses were used to interpret the orientation of components. Principal components analysis has also been used to pool species into groups using similar microhabitats. Finally, this analysis technique was used to identified key stream microhabitats and the characteristics species occupying the key microhabitats.

RESULTS

A total of 1,578 microhabitat samples recorded 13,527 fish of 79 species in 10 wadable mid-size stream sites in the Tallapoosa River basin in 1989 and 1990. The West River was another largely wadable stream that was sampled (864 microhabitats) in 1982 and 1983 (BAIN *et al.*, 1988) producing data on 3,039 fish of 23 species. For brevity, select results are presented for two species representing extremes of microhabitat use, and results are summarized for two streams with diverse and well sampled fish faunas. Family-level patterns are summarized for seven of the most sampled streams, and key habitats are identified from the analysis of species-habitat patterns in the 10 Tallapoosa River study streams.

The sunfish (Centrarchidae) *Lepomis macrochirus* was commonly recorded in microhabitat samples in four study streams (Table I). This species used statistically distinct microhabitats in these streams but the attributes of those microhabitats varied. *Lepomis macrochirus* microhabitat was defined by a variable list of attributes and the order of importance of those attributes differed among multivariate habitat models. Also, the mean value of the attributes that defined the microhabitat of *Lepomis macrochirus* varied strongly among study streams. Mean water velocity of microhabitats used by *Lepomis macrochirus* varied the most (0.7 to 3.8 cm/s) followed by mean water depth (23 to 76 cm). *Lepomis macrochirus* was an example of many species that used distinct microhabitats in individual study streams, but the attributes and mean physical conditions of the microhabitats varied among study streams.

In contrast to *Lepomis macrochirus,* the darter (Percidae) *Etheostoma jordani* was among the most consistent species in microhabitat use (Table I). Water depth, current speed, and substrate were always important attributes of *Etheostoma jordani* microhabitat with shallow water, fast currents, and coarse substrates characterizing the microhabitat. Despite this consistency among streams, the three important attributes varied in their order of importance, and there was variation in the mean values of the important microhabitat attributes. Mean current speed appeared to vary the most among microhabitats used by *Etheostoma jordani* in the different streams.

Tableau I : Conditions moyennes de l'habitat physique utilisé par deux espèces dans deux rivières différentes en 1989. Les valeurs moyennes et les déviations standard (entre parenthèses) sont données pour les paramètres dont l'importance a permis de définir les microhabitats. Les descripteurs qualitatifs du microhabitat sont donnés pour les paramètres présentant une différence entre échantillons occupés et inoccupés pour chaque ruisseau.

Table I : Mean physical habitat conditions of microhabitats used by two species in different streams during 1989. Mean values and standard deviations (in parentheses) are reported for microhabitat attributes that were important in defining microhabitats. Qualitative microhabitat descriptors are shown for attributes found to differ between occupied and unoccupied samples in each stream.

Species and study stream	Cover (index)	Mean (standard deviations) of occupied samples: Water depth (cm)	Current velocity (cm/s)	Sub-strate (index)	Descriptors of attributes in multivariate habitat model ranked by order of influence
Lepomis macrochirus (Centrarchidae)					
Little River, North			0.7 (1.9)		Slow
Hillabee Creek		76 (25.8)	0.7 (1.8)	3.0 (0.9)	Slow, deep, fine substrate
Terrapin Creek	25 (24.7)	23 (6.9)	0.8 (2.5)	3.5 (0.8)	Cover, fine, slow, shallow
Little River, South	26 (13.6)	31 (9.0)	3.8 (2.8)		Cover, shallow, slow
Etheostoma jordani (Percidae)					
Little River, North		28 (11.7)	50.3 (32.1)	4.8 (0.3)	Shallow, coarse, fast
Hillabee Creek		36 (13.4)	69.2 (30.5)	4.4 (0.6)	Fast, coarse, shallow
Uphapee Creek		22 (8.6)	56.6 (25.9)	3.8 (0.7)	Shallow, fast, coarse

High variation in the attributes of distinct microhabitats remains apparent at the family level (Table II). Although there is some consistency among important attributes (for example, water depth) and qualitative descriptors (for example, shallow) for species within families, there appears to be substantial variation in the frequency that attributes are found important among streams. Results by study stream were pooled to produce a summary by family (Table III). Most (85 %) of the species tested were found to occupy a statistically distinct microhabitat. Water depth was most often found to be a key attribute of stream fish microhabitats, and the vast majority of populations sensitive to depth were concentrated in shallow water. Current velocity was the second most commonly identified attribute defining microhabitats, but populations of stream fish were mixed in their orientation to either above (fast current) or below (slow current) average velocities. Substrate was commonly incorporated in species microhabitat definitions, and most substrate-orienting species were concentrated in microhabitats with coarse gravel, cobble and boulder material. Cover was least often found to be important, and when it was, all populations were concentrated in microhabitats with cover.

Tableau II : Résumé des tests statistiques des différences de microhabitat entre échantillons avec ou sans espèce (groupées par familles) de deux des ruisseaux étudiés. Les descripteurs des paramètres permettant de définir des microhabitats distincts ont été regroupés par famille (familles dominantes). Une espèce est considérée comme utilisant un microhabitat si une MANOVA permet de mettre en évidence une différence statistiquement significative entre les habitats où elle est présente et ceux dont elle est absente.

Table II : Summary of statistical tests of microhabitat differences between samples with and without a species (grouped by family) from two select study streams. Descriptors of those attributes found to define distinct microhabitats were tallied by family (dominant families). Species were identified as using a microhabitat if there were statistically significant differences in habitat between present and absent samples using MANOVA.

Stream and family	Number of species tested	Species using a micro-habitat	Water depth		Mean current velocity		Cover		Substrate	
			Deep	Shallow	Fast	Slow	Present	None	Fine	Coarse
Oakmulgee Creek										
Cyprinidae	10	7		6		3	1			2
Centrarchidae	1	1				1	1			
Catostomidae	2				1					1
Percidae	3	3		3	1		1			1
Hillabee Creek										
Cyprinidae	9	7	1	4		3	1		1	2
Centrarchidae	4	3	1			3			1	1
Catostomidae	5	4				3	1		1	
Percidae	5	5		5	1					2

Tableau III : Résumé des résultats des tests statistiques des différences de microhabitat entre des échantillons avec et sans poissons pour toutes les populations régulièrement étudiées (espèces par ruisseau). Les descripteurs des paramètres permettant de définir des microhabitats distincts ont été regroupés par famille (familles dominantes).

Table III : Summary of statistical test results of microhabitat differences between samples with and without fish for all commonly recorded study populations (species by study stream). Descriptors of those attributes found to define distinct microhabitats were tallied by family.

Family	Number of populations tested	Populations using a microhabitat	Water depth		Mean current velocity		Cover		Substrate	
			Deep	Shallow	Fast	Slow	Present	None	Fine	Coarse
Cyprinidae	43	36	2	26	6	9	4		3	7
Centrarchidae	16	14	1	6		11	4		3	2
Catostomidae	13	9	3	2	2	6	1		2	1
Percidae	20	19		14	7	3	2		1	8
Fundulidae	3	3		3		2	1			
Ictaluridae	4	4		1	3					3
Cottidae	2	2		1	1					1
Anguillidae	1									
	102	87	6	53	19	31	12	0	9	22

Classes of microhabitat were identified (Table IV) by assessing similarities in the mean location of species in habitat space (principal components analysis) and similarities in the important attributes of microhabitats. The five classes of microhabitat do not include all possible stream habitats, and they were most often defined on the basis of water depth and current speed. Coarse substrate and cover were important for several species so classes of habitat were defined with these qualities. The fish taxa commonly using these microhabitat varied greatly and can be roughly described at the family level.

A total of 271 shoreline microhabitat samples recorded 18,391 fish of 31 species in the Cahaba River from 1988 to 1990, and 188 channel microhabitat samples recorded 545 fish of 29 species during the same years. A total of 487 microhabitat samples were taken in potential nursery habitat of larval fish in the Cahaba River during 1988 and 1989. The samples recorded 13,666 larvae representing 12 families of which 6 were commonly captured.

Most (69 %) species were found to use a distinct microhabitat in shoreline waters of the Cahaba River (Table V). Current velocity and cover were attributes that most often determined microhabitats, and the species were about evenly divided in their orientation to current speeds and the presence or absence of cover. Substrate was the next most commonly important microhabitat attribute followed by water depth. There were clear differences in the attributes and descriptors of microhabitats among years for most families. The discharge of the Cahaba River was unusually low during most of 1988 because dry weather in central Alabama produced stream flows less than 25 % of long-term averages. However, streamflows in most of Alabama and the Cahaba River were well above normal during much of the 1989-1990 period due to high regional rainfall.

Tableau IV : Définition des microhabitats-clés dans les ruisseaux et les rivières avec les taxons dominants.

Table IV : Definition of key-microhabitats in streams and rivers with the dominant fish taxa.

Definition of habitat classes	General characteristics of associated fish fauna
Shallow water (≤ 35 cm) Fast water (≥ 55 cm/s)	Some species of Ictaluridae, Percidae, Cottidae, and high numbers of *Campostoma spp.* (Cyprinidae)
Slow water (≤ 20 cm/s) Cover present	Many species of Centrarchidae and Catostomidae and some Cyprinidae and Fundulidae
Deep water (≥ 35 cm) Fast water (> 45 cm/s)	Some species of Catostomidae
Shallow water (< 35 cm) Slow water (< 35 cm/s)	Largely species of Cyprinidae
Shallow water (< 35 cm) Coarse substrate (gravel or larger)	Many species of Percidae and Cyprinidae

Most (87 %) species were found to use a distinct microhabitat in channel waters of the Cahaba River (Table V). Cover was clearly the dominant attribute influencing microhabitat use, and all species orienting to cover were concentrated in microhabitats with cover. Shallow water and slow currents were sometimes important in microhabitat descriptions, and deep waters and coarse substrate was important for two families.

In potential nursery waters of the Cahaba River, catostomid larvae were using shallow microhabitats with vegetation (Table VI). Percids and centrarchids were concentrated in structurally complex microhabitats (typically abundant woody cover). Within these high cover microhabitats, percids were associated with the deeper waters, and centrarchids weakly associated with slow currents and still waters. Cyprinids were concentrated in shallow microhabitats that had slow current and vegetation. The single species of Fundulidae, *Fundulus olivaceus*, and the only Poeciliidae, *Gambusia affinis*, were more commonly collected in shallow microhabitats.

DISCUSSION

Hypothesis-based, statistical analysis of species-habitat relations revealed new information about habitat use at the local scale. While most species use a distinct microhabitat, not all do, and simple quantification of microhabitat use with all physical attributes will likely include unimportant information. Of the majority of species using distinct microhabitats, some were very consistent in the habitat attributes that defined their microhabitat in different streams. Nevertheless, even among these species there is substantial variation in the numerical values for the microhabitats that were used. For example, *Etheostoma jordani* may consistently be found in shallow waters with fast currents and cobble substrates, but the actual depths, current speeds, and substrate mixes used in different streams can be very different. Therefore, microhabitat use appears flexible even among the most narrowly adapted species so single sets of habitat criteria will not

Tableau V : Résumé des résultats des tests statistiques des différences de microhabitat entre échantillons avec et sans poissons, par espèces et par classes de taille regroupées par famille et par macrohabitat. Les descripteurs des paramètres permettant de définir des microhabitats distincts ont été regroupés par famille.

Table V : Summary of statistical test results of microhabitat differences between samples with and without fish by species and size classes grouped by family and macrohabitat. Descriptors of those attributes found to define distinct microhabitats were tallied by family.

Stream and family	Number of species tested	Species using a micro-habitat	Water depth		Mean current velocity		Cover		Substrate	
			Deep	Shallow	Fast	Slow	High	Little	Fine	Coarse
Shoreline habitat, 1988										
Cyprinidae	12	10		2	5			4		4
Centrarchidae	4	4	1		1	1	2		1	2
Catostomidae	2									
Percidae	1									
Fundulidae	1	1				1	1			
Poecillidae	1									
Shoreline habitat, 1989-1990										
Cyprinidae	10	8		4	1	4		2	1	2
Centrarchidae	3	2	1			1	2		1	
Catostomidae	2									
Percidae	2	2			1		1			
Poecillidae	1									
Channel habitat, 1989-1990										
Cyprinidae	1	1					1			
Centrarchidae	3	3		2		3	3			
Catostomidae	4	4		1			2			2
Clupeidae	2	2		1		1	1			
Sciaenidae	1	1	1				1			
Ictaluridae	1	1				1	1			
Lepisosteidae	2	1					1			
Anguillidae	1									

Tableau VI : Résumé des résultats des tests statistiques des différences de microhabitat entre échantillons avec ou sans larves de poissons regroupées par familles dans les zones de croissance de la rivière Cahaba, Alabama (USA). Les descripteurs des paramètres permettant de définir des microhabitats distincts sont indiqués.

Table VI : Summary of statistical test results of microhabitat differences between samples with and without families of larval fish in nursery waters of the Cahaba River, Alabama (USA). Descriptors of those attributes found to define distinct microhabitats are indicated.

Family	Water depth		Mean current velocity		Cover		Substrate		Vegetation	
	Deep	Shallow	Fast	Slow	High	Little	Fine	Coarse	Present	None
Cyprinidae		✓		✓					✓	
Centrarchidae				✓	✓					
Catostomidae		✓							✓	
Percidae	✓				✓				✓	
Fundulidae		✓								
Poecillidae		✓								

likely succeed in accurately describing species microhabitats. In contrast with species like *Etheostoma jordani*, many other species used distinct microhabitats in different streams but the key attributes and actual physical conditions varied substantially. These species are very flexible in microhabitat use and they respond differently to microhabitat in different stream environments. Explaining microhabitat use in these species will probably remain a challenge for a long time.

At the family level, trends in microhabitat attributes and descriptors support general trends identified in fish faunal books. For example, most darters (Percidae) are widely regarded as riffle oriented fish. In mid-sized streams, percids were most often found to be depth and current sensitive with a heavy concentration in shallow water and fast currents. Water depth appears to be the microhabitat attribute that most often defines fish distributions in streams. After water depth, current velocity is frequently important in defining species microhabitats. Although much less important, substrate and cover are key habitat attributes for many species. The common assumption that microhabitats should be defined using depth, velocity, substrate, and cover does not appear supported for single species.

Analyses of habitat-use patterns across mid-sized streams in the Tallapoosa River basin identified five habitat-use assemblages which appeared distinct in microhabitat use. Some species were strongly oriented to cover, and others were restricted to microhabitats that were shallow. Both groups of species were found in microhabitats that had cover in shallow water even though our statistical analyses indicated they were using these microhabitats for different reasons. From this example, it is clear why the five classes of microhabitat could not be defined in a non-overlapping manner. The five classes of microhabitat were defined to encompass conditions that were important to five groups of species that used microhabitat in different ways.

The five microhabitat classes are generalized because they were developed from streams differing greatly in morphology, hydrology, species composition, and species-level use of habitat. Consequently, this simplified model of fish-microhabitat relations does not precisely fit most species distributions in any single stream. Nevertheless, the process of defining key classes of habitat forced the recognition of new properties in the relations between fish and habitat at the local scale. First, not all or even a majority of stream habitat is important to fish because the five classes do not include all habitats in any stream. Second, dividing stream habitat into exclusive categories does not appear possible because different species may co-occur by responding to different habitat attributes. Without identifying what attributes were responsible for statistically distinct patterns in microhabitat use, it would not have been possible to recognize these findings.

Like the wadeable streams, most species of fish inhabiting large rivers used a statistically distinct microhabitat in either shoreline or channel habitats. Water depth was not often a key attribute defining microhabitats although the study design largely factored out water depth by separating shallow, shoreline waters from deep (>1 m) channel habitats. Like wadeable streams, microhabitat use was highly variable with respect to key attributes and actual conditions inhabited. Clear variation in microhabitat use was apparent among shoreline fishes between periods of very low and high river discharge. Consequently, river volume appears likely to influence the way species respond to habitat and the actual physical conditions used. Microhabitats in the deep, channel habitats were very often defined by the presence of cover or sub-surface structure. However, some species were found to be concentrated in open water microhabitats where some other attributes were most influential. Study methods were capable of defining microhabitats for species in large rivers, and the flexibility of microhabitat use was again found to be a common property.

All larval fish families commonly recorded in nursery waters of the Cahaba River appeared to use a distinct microhabitat. The descriptive statistics on occupied small-scale samples, univariate tests of habitat associations, and multivariate pattern display provide detailed data on habitat use. The regular occurrence of statistically significant microhabitats within the sampled range of conditions supported the definition of nursery habitat based on an estimated maximum current speed. Although there were undoubtedly some larvae passively drifting in sampled microhabitats, the frequency that larvae were statistically associated with physical habitat attributes indicated active orientation. The recurring importance of shallow, edge microhabitats, and the presence of vegetation or woody debris may have been a consequence of vision as the dominant initial sense in early larval development. The availability of gradually sloping shoreline waters with debris and vegetation may be important for providing nursery habitat in rivers without extensive backwaters and off-channel habitats. The detailed findings reported by SCHEIDEGGER and BAIN (1995) are the first quantitative and statistically-based analysis of larval fish microhabitat use in rivers, but this study did not fully employ the study approach found effective for comprehensively analysing habitat use in juvenile and adult fish. Better designed studies of larval fish microhabitats are needed to advance our knowledge of this ecologically distinct life stage.

In all stream settings, fish appear highly flexible in microhabitat use. Fish ecologists should advance beyond simply describing habitats associated with fish species. Habitat use should be regarded as a behavior that is just as flexible as food selection by fish. Undoubtedly, the environmental setting of fish heavily influences the microhabitat use. Other influences such as species interactions, food availability, and predation threat probably effect the way fish respond to habitat and select distinct microhabitats. The next step in fish habitat research will be to explain the wide variation in habitat use now recognized at the local scale.

REFERENCES

BAIN M.B., FINN J.T., 1991. Analysis of microhabitat use by fish: investigator effect and investigator bias. *Rivers, 2,* 57-65.

BAIN M.B., FINN J.T., BOOKE H.E., 1985a. Quantifying stream substrate for habitat analysis studies. *N. Ame. J. Fish. Manage., 5,* 499-500.

BAIN M.B., FINN J.T., BOOKE H.E., 1985b. A quantitative method for sampling riverine microhabitats by electrofishing. *N. Ame. J. Fish. Manage., 5,* 489-493.

BAIN M.B., FINN J.T., BOOKE H.E., 1988. Streamflow regulation and fish community structure. *Ecology, 69,* 382-392.

KINSOLVING A.D., BAIN M.B., 1990. A new approach to measuring cover in fish habitat studies. *J. Freshw. Ecology, 5,* 373-378.

KINSOLVING A.D., BAIN M.B., 1993. Fish assemblage recovery along a riverine disturbance gradient. *Ecological Applications, 3,* 531-544.

SCHEIDEGGER K.J., BAIN M.B., 1995. Larval fish distribution and microhabitat use in free-flowing and regulated rivers. *Copeia,* 125-135.

WEBB P.W., 1975. Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Board Canada, 190,* 1-158.