NICHE RELATIONSHIPS OF THE CYPRINID FISHES OF SPRING CREEK, A TRIBUTARY OF THE NEOSHO RIVER, OKLAHOMA

By

DAVID L. MCNEELY

Bachelor of Science
University of Texas at Arlington
Arlington, Texas
1967

Master of Science
North Texas State University
Denton, Texas
1972

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Oklahoma State University
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Thesis Approved:

Rudolph J. Miller
Thesis Adviser

William A. Drew

Don Holbert

Stanley Fox

O. Eugene Maughan

Norman N. Durham
Dean of the Graduate College

PREFACE

This study was financed in part by the Oklahoma Cooperative Fishery Unit of Oklahoma State University. The computer analysis was funded by the Zoology Department of Oklahoma State University.

I thank Dr. R.J. Miller, the chairman of my graduate committee, for his guidance and encouragement in all phases of the study, for giving me the opportunity for graduate study, and especially for his confidence in my ability to complete the project when others might have considered such confidence misplaced. I also am thankful for the help that Dr. Eugene Maughan provided in securing travel money and supplies for the project, for his technical advice, and for serving as a member of my graduate committee. I thank Dr. Donald Holbert for his patience with me when I was even more ignorant of multi-variate statistics than I am now, for helping me through my inabilities with its use, and for serving on my graduate committee. Dr. Stanley Fox, I thank for many valuable discussions of community ecology and for advice on the design of the study, for serving on my graduate committee and assisting in the field. I also thank Dr. William Drew, who gave me advice on the design of the project and served on my graduate committee.

I cannot offer enough gratitude to my wife, Bonnie McNeely, for unfailing encouragement, unflagging assistance, and wonderful loving companionship in the field and otherwise. She also typed all drafts of the manuscript and did much of the card punching for data storage and analysis.

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The following individuals also contributed valuable ideas and comments at various stages: A.P. Blair, Bill Matthews, George Luker, Hague Lindsey, Ron Harrell, Ron Boyer, Dan Overdeer, Henry Robison, John Walker, and Bob Tafanneli. I am grateful to the late Dr. Richard Wallace for his encouragement and provision of freedom to pursue the project when he was my supervisor in the Life Sciences Division at Tulsa Junior College, and to Clifford Wood for allowing me the freedom to travel to Stillwater from Grayson County College when needed.

I also thank the staff and programmers in the OSU Computer Center for much valuable assistance. I thank Dr. Steve Ross of Southern Mississippi University for suggesting the use of discriminant analysis, but if it's misused, I did so, not Steve.

I must thank the many residents of the Spring Creek region who gave me directions and helped me interpret maps, and directed me to landowners. And certainly, I must thank those many landowners who allowed access to the stream. I especially am grateful to the two unidentified men who worked for an hour under a broiling sun to extricate my vehicle from the loose gravel of a primitive ford and then would accept only one beer between them in payment.

Drs. Bill Shephard, Glenn Wiggins, and Branley Branson freely gave their technical assistance in identifying aquatic invertebrates, and I thank them.

Despite all the valuable assistance and encouragement I received from these and a multitude of uncited teachers, colleagues and friends, and the importance of their ideas to the development of my own, all errors of logic and concept, and all inadequacies of this document in fulfulling its stated purpose, are my own creation.

I also, and perhaps most importantly, must thank Spring Creek, itself, which is a magnificent work of nature in all ways. The crystal water, sparkling fish, deep wooded valleys, and the people of the Ozarks draw me back even though this project is completed. Despite some local abuses, it remains biologically healthy. May the People of the United States and Oklahoma be able to overcome their present preoccupations and prejudices and see the value in keeping it and other places always so. If all could see their own local versions of Spring Creek, whether field, stream, or pond, through the eyes of Camille, I believe they would. It is the duty of biologists, and especially teachers, to give them that opportunity.

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CHAPTER I

INTRODUCTION

In 1959 G.E. Hutchinson asked the simple question, "Why are there so many kinds of animals?" The question has been answered most often by resort to the competitive exclusion principle, as defined by Gause (1934) and redefined and extended by Hardin (1960). According to this explanation, communities are diverse because the members of an assemblage avoid competition, and thus extinction in the face of a more efficient relative, by specialization. Such specialization is thought to minimize overlap of niches along limiting dimensions. If resource limitations are removed, greater overlap is expected to occur. Community studies by Echelle *et al.* (1972) and Pianka (1974a) further suggest that diffuse competition from an entire community may be more damaging to the success of a species than the overlap offered by one ecologically similar species. Recent theoretical discussions of competitive exclusion have focused on formal logic and mathematical proof of that logic (summarized very well by Armstrong and McGehee, 1980), but the ultimate test of any theory is empirical.

Schoener (1974) reviewed resource segregation and found it common in animal groups from protozoans to birds and mammals. Many ecologists have long accepted lack of overlap as indicating that past competition has honed community structure until potential competitors have become separate ecologically (Whitaker, 1967, 1975; May and MacArthur, 1972; Colwell and Futuyma, 1971; Sale, 1974; Mathur, 1977). However, recent papers by Wiens (1977) and Rotenberry (1980) emphasize a failure of competition to shape non-equilibrium communities, and a lively debate currently exists as to the relative contributions of physical environment and competition to community structure.

Most of the works Schoener reviewed dealt with terrestrial vertebrates and arthropods. Though more than the four fish studies he included were available, the relative contributions of terrestrial and aquatic vertebrates to this important area of ecology were properly reflected. Since 1974 this gap has been partially filled.

Most of the new and earlier papers demonstrate that fishes do divide resources in a pattern predicted by competitive avoidance (Zaret and Rand, 1971; Gibbons and Gee, 1972; Tyler, 1972; Everest and Chapman, 1972; Mendelson, 1975; Mathur, 1977; Baker and Ross, 1981; and numerous others). Werner (1977) and Werner and Hall (1976, 1977) provided especially strong arguments that competition has produced the observed patterns.

However, notable exceptions exist also in reports by Harrell (1978) and Matthews and Hill (1980) which demonstrate that stream fish in unstable environments are far less distinct in their resource use patterns than competition theory predicts.

Pianka (1974b) and Huston (1979) have pointed out that many factors besides competitive exclusion interplay in structuring niche relations and species numbers and kinds in communities. Paine (1966) showed that predation removes competitive advantages and allows blurring of niche distinctions in intertidal communities. Glasser (1979) logically extended this principle to a variety of community types.

Sale (1977) argued that coral reef fish communities maintain high species diversity because physical factors prevent populations from reaching biotic balance and that competitive relations are not controlling in such systems. Wiens (1974, 1976) and Weins and Rotenberry (1979) and Rotenberry and Weins (1980a, 1980b) have argued for a similar phenomenon in grassland birds. Wiens (1977) has attempted to convince us that it is general.

No one has argued strongly that physical factors are more important to stream fish community structure than biotic relationships are, but neither have such factors been ignored. The red shiner, a widely distributed stream fish in the Central and Southwestern U.S., for example, is sharply limited in local distribution due to physico-chemical factors (Matthews and Hill, 1979). The current efforts of the Cooperative Instream Flow Service Group, United States Fish and Wildlife Service (Orth, 1980) show confidence in the importance of physical factors in fish distributions.

Fish species diversity in streams may be related to habitat complexity. This suggestion is supported by the relationship of species diversity to stream order (roughly, distance downstream) discussed by Shelford (1911), Harrell _et_ _al_. (1967), Sheldon (1968), and Gorman and Karr (1978). Most authors have assumed that increased diversity in downstream reaches is due to increased complexity of environment. Gorman and Karr (1978) demonstrated this in small streams in both Indiana and Panama. However, a recent study by Matthews and Styron (1981) supports a hypothesis suggested by Starrett (1951) that upstream areas are less physico-chemically stable than downstream areas, and are thus habitable only by species tolerant to environmental extremes.

Schoener (1974) stated that habitat partitioning is more important than trophic partitioning in terrestrial systems, but claimed that the opposite is probably true in aquatic systems. But, as Zaret (1976) pointed out, aquatic systems have contributed relatively little to theoretical ecology. In the six years since his statement that weakness has been somewhat remedied. The available studies, particularly Winn (1958), Zaret and Rand (1971), Everest and Chapman (1972), Mendelson (1975), Werner (1976, 1977), and Ross and Baker (1981) indicate that Schoener was wrong. Mendelson (1975) and Werner and Hall (1976) in fact stated that trophic segregation in their studies was due to spatial segregation. No study has effectively separated the roles of spatial and trophic partitioning in stream fishes, particularly minnows. Both Mendelson (1975) and Werner and Hall (1976) for example, confounded the two.

The preceding discussion points up major questions in stream fish ecology: 1) To what degree are habitat (or spatial) and trophic niche partitioning controlling factors in stream fish communities? 2) Is niche segregation a function of habitat diversity, of longitudinal zonation, or both? If so, is competition implicated as having produced the pattern of segregation observed? This study of Spring Creek cyprinids was undertaken to help answer these questions.

CHAPTER II

SPRING CREEK

Spring Creek, an Ozark Plateau stream in Northeastern Oklahoma (Fig. 1) is well suited to the present study. It meets the two major criteria of 1) habitat diversity independent of distance downstream (or stream order), as is shown by data contained in the results below, and 2) a minnow species association that is relatively constant and abundant.

Spring Creek arises in relatively flat terrain in Delaware County, Oklahoma, then flows through the Cookson Hills, a fairly rugged region, for most of its approximately 60 km length. Elevation at the source is approximately 355 m, dropping to 165 m at the confluence with the Neosho River in Ft. Gibson Reservoir in Mayes County. The stream is dammed 6.7 km above the confluence, forming the small Cedar Crest Reservoir. Upstream from this reservoir the channel is in nearly native condition with the exception of road crossings.

Spring Creek and its major tributaries are perennially fed from seepage and numerous small and moderately large springs. At times of low discharge as prevailed during the summer and fall of 1980, subsurface flow predominates along

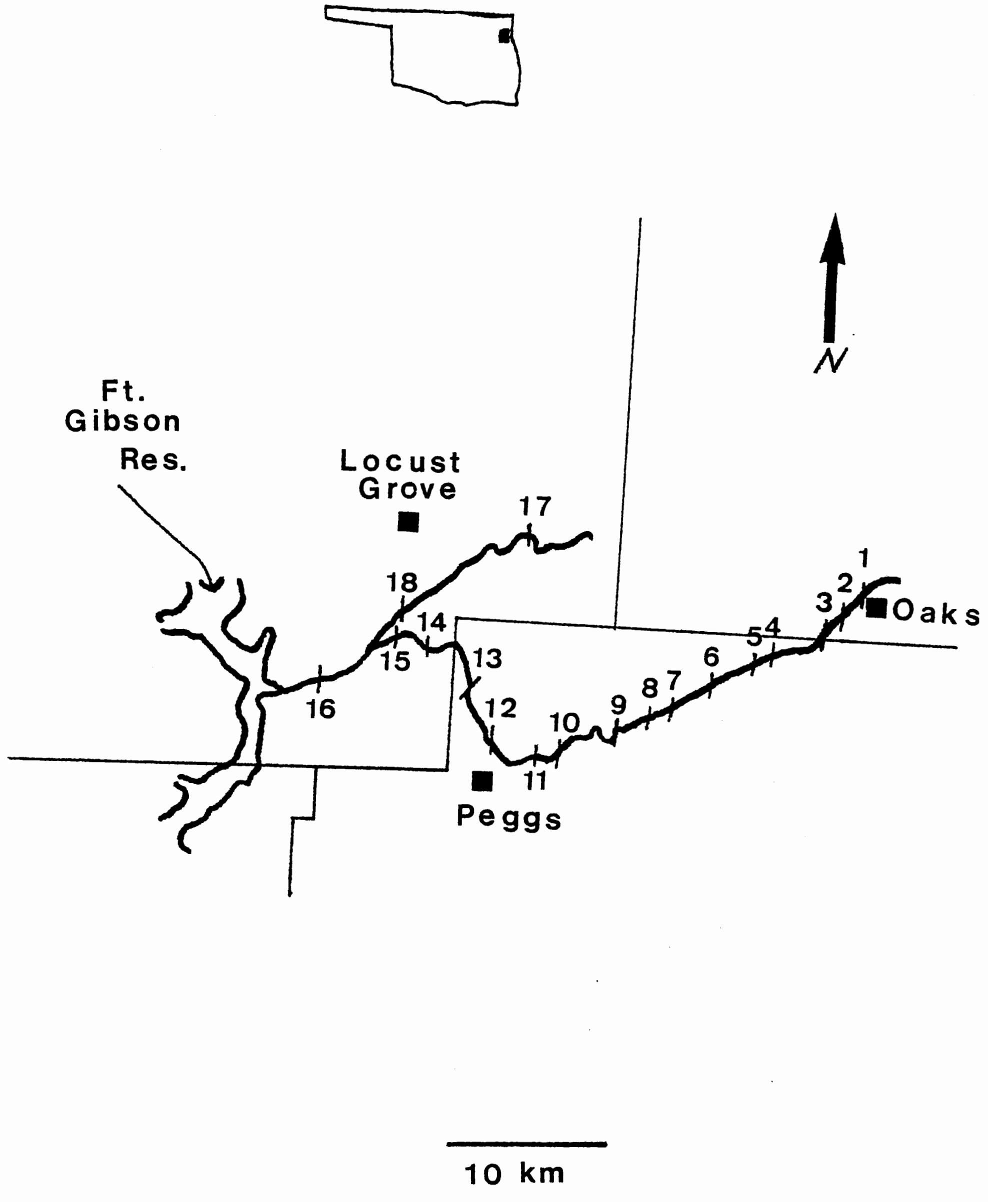

Figure 1. Spring Creek, showing its location and 18 study sites visited in 1979-1981.

much of the channel. Water quality in the stream is high, and water clarity is exceptional for streams in the region. Spring Creek and two tributaries, Bryant Hollow Branch and Snake Creek, have no known significant point sources of pollution (Oklahoma Water Resources Board, 1976).

Basin land is mostly in pasture, with some woodland and cropland. Spring Creek receives little use as a fishery, though it supports a healthy smallmouth bass population. It does receive heavy recreational use on weekends at several locations - mainly for swimming. Landowners are quite protective of the stream.

Minnow Association of Spring Creek

Spring Creek has a typical Ozarkian fish fauna, including such species as *Micropterus dolomieui* (smallmouth bass), *Noturus exilis* (slender madtom), *Etheostoma flabellare* (fantail darter), and *Cottus carolinae* (banded sculpin). All these species range widely through the Ozark Plateau (Pflieger, 1975). However, there are fewer minnow species than in nearby streams.

The minnow association comprises eight species: *Semotilus atromaculatus* (creek chub), *Nocomis asper* (red spot chub), *Phoxinus erythrogaster* (Southern red-bellied dace), *Dionda nubila* (Ozark minnow), *Notropis pilsbryi* (dusky-striped shiner), *Notropis rubellus* (rosy-faced shiner), *Campostoma anomalum* (stoneroller), and *Hybopsis amblops* (big-eye chub). *N. rubellus* was rare but occurred at half the sites studied in this project. Hybopsis amblops was extremely rare and occurred at only 3 of 18 sites. The other species were common and widespread.

Notropis boops, Notropis camurus and N. lutrensis have been collected from Spring Creek (Oklahoma State University Museum records) but apparently were always rare and have been absent from numerous collections made over the past 20 years by H. Lindsey, A.P. Blair, and R.J. Miller (personal communications).

Semotilus atromaculatus

The creek chub is the largest native minnow in Spring Creek. Miller and Robison (1973) and Pflieger (1975) report that this fish reaches 300 mm in length. In the Eastern U.S. and Canada adults and large juveniles prey on crayfish and noncyprinid fish (Barber and Minkley, 1971; Moshanka and Gee, 1973; Newsom and Gee, 1978), as does the congeneric fallfish (Reed, 1971). In Spring Creek large individuals are solitary and are almost always associated with cover in the form of overhanging banks, logs, branches, roots, and boulders. They resort to this cover much more quickly than do other minnows when disturbed. Smaller specimens seem to behave in a more typically cyprinid fashion. They swim in schools or mixed aggregations with other minnows and range widely over pools and raceways.

The large solitary individuals are rare. This rarity, coupled with their seeming inclusion in a centrarchidpredator guild, was the basis for my decision to exclude these very large creek chubs from this study. The smaller more common individuals are included.

The creek chub is readily distinguished from other Spring Creek minnows by snorklers. The body is robust, the head is as wide or wider than the body, the lower lip is white, and there is a brown or copper colored spot at the lower anterior corner of the dorsal fin. All these features are distinguishable underwater at a distance.

Nocomis asper

The red-spot chub is also a large minnow, reported by Pflieger (1975) to reach 250 mm in Missouri. None larger than 150 mm total length were collected in this study. Larger individuals are also predaceous on fish and crayfish through to a lesser degree than is the creek chub. They tend to resort to cover when disturbed like _Semotilus_, but this behavior is less evident than with _Semotilus_. Even the largest individuals observed in this study ranged with other minnows in pools and channels, and were definitely minnow-guild fish. Lachner and Jenkins (1971) split this species from the more easterly _N_. _biguttatus_. That species has a catholic diet of mainly benthic invertebrates and algae in New York (Lachner, 1950). Except for one population in south central Oklahoma, _N_. _asper_ is restricted to the Southwestern Ozarks (Pflieger, 1975; Miller and Robison, 1973).

Nocomis is readily distinguished from all minnows in Spring Creek except *Semotilus* by an overall robustness, and from *Semotilus* by a more olive (rather than brown) ground color, subterminal rather than terminal lips, and the absence of a dorsal fin spot. These traits are readily seen by snorklers.

Notropis pilsbryi

The most abundant fish in Spring Creek, and the Southwestern Ozarks generally, belongs to what Gilbert (1964) called the *zonatus* group of *Notropis* subgenus *Luxilus*. I follow Gilbert (1964), Rainboth and Whitt (1974), Buth (1979), and Buth and Mayden (1981) in treating it as *Notropis pilsbryi*, distinct from *N. zonatus* of the Northern and Eastern Ozarks, rather than as a subspecies of the latter form as held by Menzel and Cross (1977).

Little is known of its biology. Just as *N. asper* is presumed to be very much like *N. biguttatus* in ecology, so *N. pilsbryi* is presumed to be like *N. zonatus*. Matthews and Shephard (1978) reported this fish to eat a variety of benthic macro-invertebrates.

Dusky-striped shiners may be easily recognized underwater by their overall body conformation, sharply oblique snout and a pair of narrow black or coppery lateral bands. In breeding males a single dark lateral band obscures these.

Notropis rubellus

This fish is uncommon in Spring Creek. Of all the cyprinids collected in the present study, only *Hybopsis amblops* was found at fewer sites or in lower numbers. Only 50 specimens could be obtained for food habits analysis despite special collecting efforts.

The life history, ecology and behavior of *N. rubellus* are much better known than those of any other species in the present study except *Campostoma anomalum*. They were described in detail in other parts of its widespread Eastern North American distribution (Miller and Robison, 1973; Pflieger, 1975 contain summaries of these accounts). Reportedly this rather small (maximum total length in this study about 60 mm), very slim, very silvery shiner prefers stronger currents than most *Notropis*, and is more frequently associated with surface water strata. The very bright silvery (or steely blue) color coupled with extreme slenderness and an oblique flattened mouth make this fish quite distinctive underwater.

Dionda nubila

The Ozark minnow is the second most abundant minnow in Spring Creek. Large numbers were present at all but three of the sites I studied. This fish is shiner-like in general aspect and may belong to the genus *Notropis* (Smith, 1979; Lee, 1980). It differs from other *Notropis* in the possession of a long coiled gut and in having hooked pharyngeal teeth. Its greatest abundance is in the Ozarks, though scattered populations exist in the Midwest (Pflieger, 1975; Smith, 1979). The genus seems to be confined to or reach its greatest abundance in uplifted limestone areas with strongly flowing streams of high water quality (Lee, 1980).

Dionda is easily distinguished underwater from other minnows in Spring Creek by the combination of overall straw color (except spring males), a pale lateral band (dark at times), and most diagnostically, a row of copper colored dots along the dorsum behind the dorsal fin.

Campostoma anomalum

The common stoneroller has the widest distribution of all the Spring Creek minnows, occurring throughout the Eastern half of North America in a wide variety of streams (Trautman, 1957). Summaries of the many published accounts of its biology are in Trautman (1957), Cross (1967), Miller (1962, 1964, 1967), Miller and Robison (1973), Pflieger (1975) and others. Most authors state that the fish is strictly herbivorous, and it has two anatomical adaptations that support this conclusion. The lower jaw is modified into a scraper that is very effective at removing algae from stones, and the gut is the longest of any North American minnow. However, Trautman (1957) suggested that some invertebrates are included in the diet. The present study supports his conclusion.

The stoneroller is almost as abundant in Spring Creek as the dusky-striped shiner and Ozark minnow, but is more sporadic in distribution, being absent or rare at several of the study sites.

Stonerollers are unmistakeable underwater. The small head, slightly hump-backed appearance, and dark coloration make them easily distinguishable from other fish in Spring Creek.

It is possible that the largescale stoneroller, *Campostoma oligolepis*, occurs in Spring Creek. Burr *et al*. (1979) reported its occurrence in the adjacent Illinois River. The fish is not nearly so common in that drainage as is *C. anomalum*, and if present in Spring Creek is not likely to be of major ecological significance. In lab studies of Spring Creek fish, spot-checking of scale counts and measurements revealed no *C. oligolepis*. The two fish are not distinguishable by snorklers.

Phoxinus erythrogaster

The Southern red-bellied dace is characteristic of small streams throughout eastern N. America (Trautman, 1957), but in the Ozarks occurs primarily in those heavily influenced by spring flow (Pflieger, 1975), like Spring Creek. In Spring Creek, though the fish is widely distributed and abundant, its largest populations are in spring runs and stretches of the main channel with abundant ground water seepage. In these locations, the stream resembles a spring (Blair, 1956).

Pflieger (1975) said that the long gut of *Phoxinus* suggests a diet of plant materials. Prior to the present study only anecdotal reports of the diet were available.

Phoxinus is readily distinguishable from other Spring Creek minnows by snorklers by the general body conformation, the dark olive or gray back and white underbelly, and black x-shaped marks on the back, together with a dark double lateral band. These fish exhibit much slower body movement, even in currents, than do the other minnows.

Hybopsis amblops

The big-eye chub is the rarest of Spring Creek cyprinids. Only eleven specimens from three locations were collected in the present study. According to Cross (1967) its characteristic habitat in Kansas has firm, non-flocculant substrates, and moderate currents. All the specimens collected in this study were from habitats with little or no flow, with either bedrock or gravel bottoms covered with a thin layer of silt and algae. Low numbers precluded the use of this fish in my study. However, two specimens were dissected and the gut contents examined. Both fish were full of a mixture of cladocerans, copepods, and ostracods. A diet of zooplankton could account for its rarity in Spring Creek. The stream has little habitat suitable for the development of zooplankton, and large populations of planktivorous young sunfish, which could theoretically result in intense competition (Zaret, 1980).

CHAPTER III

METHODS

The objectives of this study required physical habitat descriptions, benthic invertebrate inventories, calculation of fish species diversities, determination of relative abundance of each minnow species, proportionate food use, and proportionate habitat use by the minnow species at a series of sites from simple to complex throughout the watershed. The methods used for collecting these data are described in this chapter. The analytical treatment of the data is described in subsequent chapers.

I visited 18 sites on Spring Creek between October 1979 and May 1981. Site number 15 was visited 10 times from October 1979 through August 1980. Site number 12 was visited 10 times from July 1980 through May 1981. Each site was visited in July 1980, and 13 of them (not including sites 1,8,9,13 and 17) in August 1980 (Fig. 1), for a total of 47 site visits. I did not visit all sites in August due to a combination of time limitations and site inaccessibility.

Habitat

On each visit I collected data on six habitat variables in a manner like that used by Gorman and Karr (1978). At each site I (or an assistant) stepped off a 100 m stretch of the stream and marked 20 transects of the stream width at 5 m intervals within this stretch. At five points along each transect, spaced so as to evenly cover the stream width, the substrate, vegetation, structure, temperature, current speed, and depth were recorded. All are recognized as influencing fish distributions (Hynes, 1970; Moyle, 1973). This scheme is shown in Fig. 2. This yielded 100 values for each variable. The data were recorded according to the following scheme.

Substrate

At each point the substrate was judged as silt, sand, gravel, cobble, rubble, boulder, or bedrock, and a value of 0 - 6 was recorded. I considered silt to be particles fine enough to remain suspended in still water, sand to be up to pea sized particles (about 4 mm), gravel up to about 50 mm, cobbles to about 150 mm, rubble to about 300 mm. Larger stones were recorded as bedrock if they were so firmly integrated with the surrounding substrate as to present a flat stream-bed, boulders if they projected upward and formed a three dimensional stream-bed. In practice the assignments were subjective, but periodic checks of previously recorded points showed consistency.

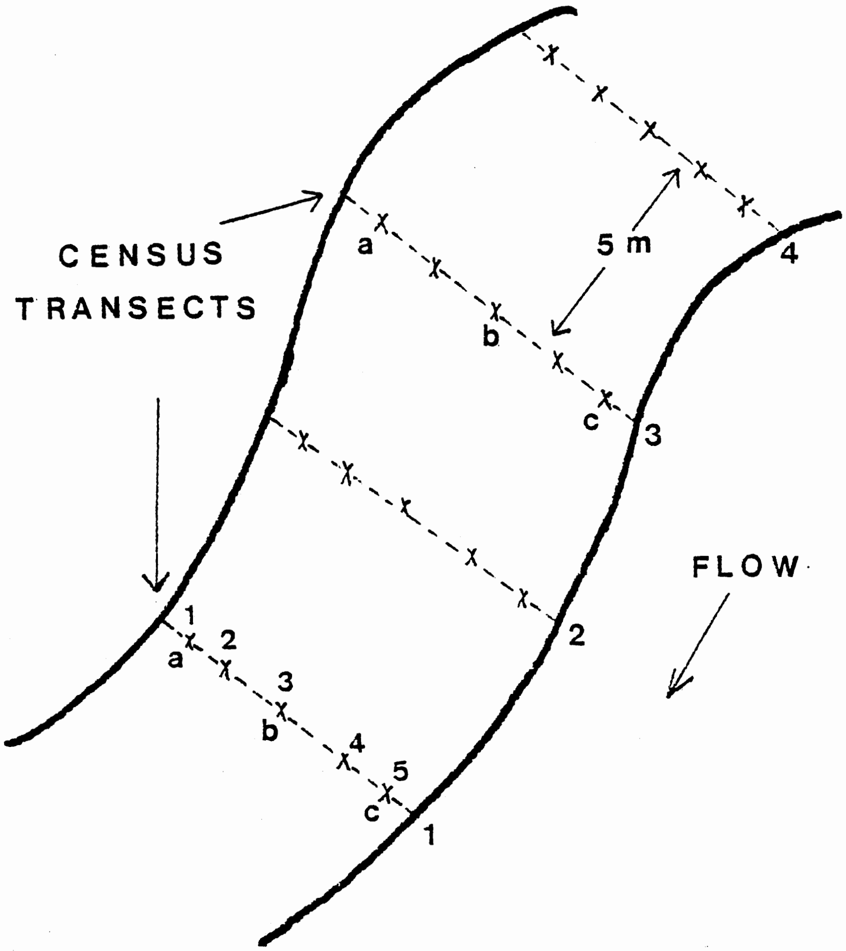

Figure 2. Transect scheme for habitat data and minnow census. Each census point (a,b,c) was described by using the four habitat points near it (for a and c) or the six points near it (for b). For example, on transect 1, point a, habitat points 1 and 2 of transects 1 and 2 were used. See text for further explanation.

Vegetation

I used a scale of zero (none present) to five (the water column filled with plants, including filamentous algae, mosses, vascular plants, and leafy terrestrial plant materials) to record the quantity of vegetation present. The scale used was logarithmic, with a value of four representing half as much vegetation as five, three half as much as four, and so forth.

Structure

I used a scale like that for vegetation to record the amount of structure, This included branches, logs, tree roots, cut banks, and similar materials.

Temperature

Temperature was measured to the nearest 0.5 °C with either a YSI 43TD Telethermometer or a glass alcohol thermometer.

Current

This variable was measured with a Gurley pigmy current meter in $\mathrm{cm} \times \mathrm{sec}^{-1}$ at 60% of the depth. This approach yields the average velocity (Hynes, 1979). These ratings were then scaled into five categories: slack (0-4 cm/sec), slow (5-20 cm/sec), moderate (21-40 cm/sec), fast (41-100 cm/sec) and torrential ($>$100 cm/sec).

Depth

I measured depth with a calibrated staff. In the winter, when chest waders were necessary, I estimated depths over 100 cm by visually examining stream bed contours. Depths were categorized as 1 (≤20 cm), 2 (21-40 cm), 3 (41-60 cm), 4 (61-80 cm), 5 (81-100 cm), or 6 (>100 cm).

Benthic Invertebrates

Benthic invertebrates were collected with a D-net 50 cm wide covered with polyester netting of approximately 50 threads per cm. I took approximately 50 "scoops" with this net, distributed throughout the 100 m stretch so as to include all visually recognized habitat types. The edge of the net was placed against the substrate, with the open end upstream, and the area extending about 50 cm upstream was disturbed by kicking and scuffing the substrate. In rapidly flowing water the natural flow resulted in the disturbed fine sediments, plants, and animals drifting into the net. In slowly flowing water the net was then swept several times through the area above the disturbed substrate. This technique also takes some planktonic forms, but these are extremely rare in flowing streams (Hynes, 1970). The materials were placed in one container with water. Then stones, sticks, and plants were hand picked from the sample and organisms were washed from them back into the sample. The resultant "screenings" were then preserved as one sample with approxiimately 5% formalin, returned to the laboratory and hand sorted to remove all animals visible to the naked eye. The animals were sorted into the lowest identifiable taxa and counted. Selected molluscs were sent to Dr. Branley Branson of Eastern Kentucky University, stoneflies and mayflies to Dr. Kenneth Stewart of North Texas State University, caddisflies to Dr. Glenn Wiggins of the Royal Ontario Museum, and beetles to Dr. William Shephard of North Texas State University for verification of identifications. Mr. Geoffory Russell of Ponca City, Oklahoma sorted and identified all the chironomid larvae. The institutions cited retained specimens in their museums. Based on these samples, I calculated the Shannon-Wiener index of diversity for each site on each date it was visited.

Fish Species Diversity

On each of the 13 visits in August 1980, after having collected all other data, I collected samples to estimate fish species diversity. I used a 20 ft. x 6 ft., 3/16 inch Ace mesh nylon seine (Nylon Net Company). The entire 100 m stretch was seined from upstream to downstream, with riffles being seined by blocking sections and driving fish downstream into the blocking seine. This technique was also used in dense vegetation. I collected fish until a one gallon jar was filled with fish, thus providing a sample of 300-800. Removal of this number of small fish from small stream segments probably does not alter populations significantly

(Brant and Schreck, 1975). Large specimens of *Lepomis*, *Ambloplites*, *Micropterus*, *Catostomus*, *Hypentelium*, and *Moxostoma* were identified, recorded in field notes, and either returned to the stream or preserved separately. There were usually no more than two or three of these in a sample. I fixed the fish in 10% formalin, returned them to the laboratory, washed them, preserved them in 70% isopropyl alcohol, identified them, counted each species, and calculated the Shannon-Wiener Diversity index for each sample. Presently, I retain in my personal collection all specimens not sacrificed for the food habits analysis described below.

Cyprinid Food Habits

I collected minnows by seining for food habits analysis on each visit to Spring Creek. In December 1980, January 1981, and February 1981, I also collected *Nocomis asper* by hook and line. All minnows were fixed immediately upon collection in 10% formalin. I dissected the fish and removed the digestive tracts in the laboratory. For *Notropis*, *Nocomis*, and *Semotilus* only the gut anterior to the first 180° turn was examined. For *Phoxinus* and *Dionda* approximately the anterior one-third of the gut was used. For *Campostoma* the anterior portion of the gut including the first complete turn about the swim bladder was examined.

I used Hynes' points method (Hynes, 1950) to analyze the gut contents. Each gut was assigned a fullness value up to 20 points for full, 10 points for half-full, and so forth. Each food category present was assigned a fraction of the total points based on its relative contribution to the bulk of the contents. I then calculated the proportionate importance for each food category for each specimen and for each species (by pooling all specimens) at each site. Animal materials were identified to the lowest recognizable taxon by reference to a collection of invertebrates made at the same site, usually genus for insects, order for other groups. Non-animal materials were identified as sand, detritus, non-filamentous algae, filamentous algae, or vascular plant parts.

Minnow Census

I used one set of data for both relative abundance of minnows at each site and habitat use within each site (Fig. 2,3). I marked ten transects of the stream within each 100 m stretch. At three points on each transect, near each shoreline and in midstream (Fig. 2), I used a face mask to visually estimate the numbers of each minnow species visible in three strata of water. I thus obtained estimates of abundance for each species at 90 discreet resource points within each 100 m stretch (Fig. 3). The transects used corresponded to the odd numbered transects of the physical habitat section. Using that transect and the physical habitat transect immediately upstream, I assigned a value for each physical variable to each observation point based upon the physical variable points corresponding to the observation

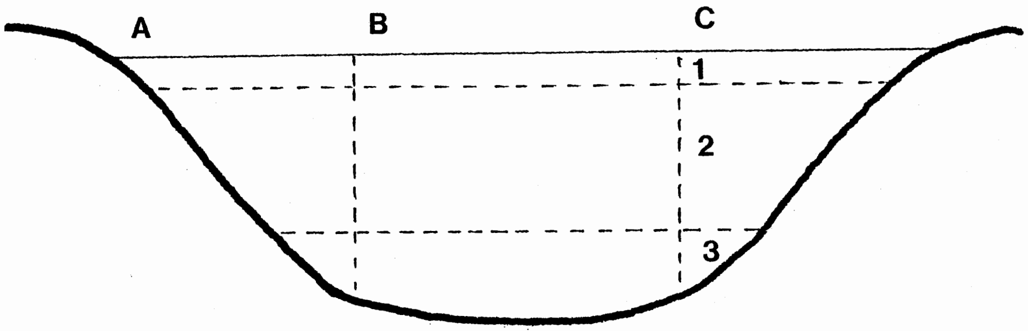

Figure 3. Cross section of an idealized transect used for the minnow census, showing the nine resource spaces used. The top and bottom strata were thin compared to the middle stratum because it was judged that only very near the surface and bottom were distinct habitats present. The behavior of the fish confirmed this. A single resource space extended upstream some 3-6 m depending on visibility.

point. For the edge points, four physical variable points were used, and for the midstream points, six were used.

In summary, at each of 30 points I estimated the number of each minnow species visible in the surface, midwater, and bottom strata of water from a fixed point looking immediately upstream. Each observation consisted of a number for each minnow species, a depth (the maximum of 4 or 6 measurements), a current speed (the mean of 4 or 6 measurements), a substrate size value (mode of 4 or 6 values), a vegetation value (mode), a cover value (mode), and a temperature (mean). Each observation also had two positional values - either a 1 or 2 for edge or midstream, and a 1,2 or 3 for surface, midwater, or bottom.

Minnow numbers were recorded once in mid-morning and once in early to mid-afternoon. Physical data were always collected between these two snorkling sessions. One snorkling session required about one hour. When I snorkled, minnows responded to my presence in the water by first moving away from me, but within 5 sec resumed their feeding and station-holding movements. The estimates were recorded in intervals of 1 for 10 or fewer, 5 for up to 50 individuals, and intervals of 25 for larger numbers. I was able to estimate up to 400 individuals (the largest number seen) by first estimating the number I could block out of my visual field by extending my hand at arms length and then multiplying that number times the number of hands required to block the entire school out of my field of vision. The procedure was repeated for each species. I used as an index of the relative abundance of each minnow species at each site the mean of the total numbers seen in morning and afternoon snorkling.

CHAPTER IV

PHYSICAL HABITAT

For each location and date for each habitat variable, habitat complexity, HC, was calculated by the Shannon-Wiener diversity formula (Gorman and Karr, 1978).

When p_i is the proportionate occurrence of a given habitat type for one variable, then

$$HC = -\sum p_i \ln p_i .$$

A composite HC was also calculated for each site and date as the mean of the six individual values (Table 1). The above procedure differs from that of Gorman and Karr in that my composite HC is a mean of HC values. I found their procedure impractical for this study due to the extremely large number of possible habitat types resulting in each separate point usually constituting a different habitat. Since the purpose was to characterize the complexity of a site, I judged mean value of complexities to be effective.

Longitudinal Habitat Zonation

Pearson Product Moment Correlations of habitat variables with distance downstream from the most upstream site of known permanent flow (Table 2) as judged from the drought

Table 1. Physical habitat including mean value (MN) and habitat complexity (HC) for each variable recorded on 47 visits to Spring Creek. S = substrate, V = vegetation, ST = structure, DP = depth (cm), T = temperature (°C), C = current (cm x sec^{-1}), D = distance from Oaks (site 1) in km. For sites 17 and 18, D = distance from Snake Creek Spring in km.

Location	Date	S		V		ST		DP		T		C		Mean	D
		MN	HC	MN	HC	MN	HC	MN	HC	MN	HC	MN	HC	HC	
(1)	(07-80)	2.4	1.64	1.0	1.26	0.9	1.37	21.4	1.07	21.5	0.63	5.9	0.75	1.12	0
(2)	(07-80)	4.1	1.36	1.6	1.62	1.3	1.49	20.5	0.80	23.1	0.69	5.6	0.88	1.14	3.4
(3)	(07-80)	3.9	1.33	1.0	1.29	0.7	1.02	17.2	0.67	24.6	1.30	10.2	1.11	1.12	7.2
(4)	(07-80)	2.6	1.31	0.7	1.14	0.4	0.88	20.6	0.88	20.5	0.64	13.3	1.23	1.01	16.8
(5)	(07-80)	2.8	1.29	0.8	1.15	0.7	1.06	36.8	1.49	18.5	1.66	4.7	0.70	1.23	17.5
(6)	(07-80)	2.2	0.85	0.5	0.81	0.8	1.14	23.0	0.97	23.4	1.94	14.0	1.09	1.13	21.3
(7)	(07-80)	2.0	1.46	1.2	1.48	1.1	1.29	46.5	1.42	24.3	1.34	0.2	0.00	1.16	23.3
(8)	(07-80)	2.1	1.32	2.1	1.73	0.4	0.82	54.4	1.74	24.4	1.37	0.3	0.09	1.18	25.7
(9)	(07-80)	2.3	1.08	0.7	1.14	1.4	1.41	31.0	1.37	21.3	1.04	4.8	0.78	1.14	27.6
(10)	(07-80)	3.0	1.48	0.2	0.56	0.6	1.01	28.3	1.17	24.1	1.06	9.5	1.05	1.06	31.2
(11)	(07-80)	2.3	0.90	0.1	0.34	0.4	0.72	27.9	1.15	21.3	1.30	10.6	0.86	0.88	31.9
(12)	(07-80)	2.8	1.00	0.9	1.11	0.6	0.97	32.9	1.38	20.6	1.53	7.9	0.97	1.16	36.0
(13)	(07-80)	2.4	1.22	0.3	0.71	0.3	0.67	19.8	0.92	22.2	2.01	3.3	0.56	1.02	38.8
(14)	(07-80)	3.2	1.58	1.2	1.40	0.7	1.10	34.8	1.30	24.1	1.26	2.6	0.17	1.13	43.4
(15)	(07-80)	1.6	1.24	1.5	1.59	1.6	1.66	45.4	1.65			2.1	0.29	1.29	44.8
(16)	(07-80)	1.9	0.86	1.8	1.58	0.7	0.85	35.7	1.46	23.4	1.12	17.1	1.21	1.18	48.0
(17)	(07-80)	2.1	1.19	1.1	1.41	1.4	1.57	26.5	1.21	24.0	0.89	1.7	0.30	1.09	3.4
(18)	(07-80)	4.0	1.60	1.5	1.55	0.6	1.02	25.8	1.11	22.0	1.71	3.1	0.50	1.25	14.9
(2)	(08-80)	3.4	1.33	1.5	1.53	1.8	1.59	25.3	0.90	24.0	0.86	5.7	0.81	1.17	3.4
(3)	(08-80)	2.5	1.28	1.3	1.51	1.0	1.33	15.7	0.59	24.6	0.74	4.3	0.72	1.03	7.2
(4)	(08-80)	2.6	1.07	1.4	1.46	0.7	1.13	18.5	0.89	22.9	1.02	6.4	1.02	1.10	16.8
(5)	(08-80)	2.6	1.24	1.5	1.59	0.8	1.23	32.4	1.35	19.0	1.76	1.0	0.21	1.23	17.5

Table 1. (Continued).

Location	Date	S		V		ST		DP		T		C		Mean HC	D
		MN	HC	MN	HC	MN	HC	MN	HC	MN	HC	MN	HC		
(6)	(08-80)	1.9	0.96	1.0	1.31	1.0	1.28	22.8	1.04	23.8	1.31	6.6	0.80	1.12	21.3
(7)	(08-80)	1.9	1.40	0.9	1.23	0.8	1.24	22.0	0.99	24.4	1.77	1.0	0.26	1.15	23.3
(10)	(08-80)	3.0	1.37	0.4	0.77	0.9	1.29	28.9	1.14	23.9	1.04	3.3	0.59	1.03	31.2
(11)	(08-80)	2.5	0.95	0.1	0.19	0.3	0.64	22.2	0.95	23.5	1.15	1.5	0.24	0.68	31.9
(12)	(08-80)	2.2	1.09	1.4	1.52	0.8	1.13	31.8	1.36	23.1	1.64	4.4	0.68	1.24	36.0
(14)	(08-80)	3.3	1.49	1.2	1.47	0.9	1.30	32.8	1.23	22.5	1.12	0.7	0.20	1.13	43.4
(15)	(08-80)	1.7	1.36	1.7	1.60	1.8	1.68	50.4	1.69	24.0	0.99	0.0	0.00	1.22	44.8
(16)	(08-80)	2.1	1.34	1.5	1.50	0.5	0.83	22.6	0.93	23.8	1.69	6.5	0.91	1.20	48.0
(18)	(08-80)	3.6	1.74	1.0	1.73	2.0	1.32	25.6	1.08	21.6	1.47	2.4	0.41	1.29	14.9
(15)	(10-79)	1.6	0.96	0.7	1.05	1.0	1.27	52.6	1.73	17.3	1.01	8.2	0.81	1.14	44.8
(15)	(11-79)	1.7	1.02	1.5	1.55	1.4	1.54	62.8	1.74	16.7	0.11	40.1	1.57	1.26	44.8
(15)	(12-79)	1.6	0.86	0.4	0.70	1.3	1.47	59.3	1.77	12.1	0.33	18.5	1.33	1.08	44.8
(15)	(01-80)	1.7	0.91	0.4	0.80	1.1	1.34	57.8	1.76	10.0	0.00	18.2	1.32	1.02	44.8
(15)	(02-80)	1.8	0.87	0.6	1.05	1.0	1.26	62.1	1.70	9.0	0.00	33.5	1.31	1.03	44.8
(15)	(04-80)	1.8	0.89	1.5	1.47	1.8	1.67	63.1	1.74			18.4	1.27	1.41	44.8
(15)	(05-80)	1.6	0.86	0.9	0.98	1.2	1.30	60.4	1.77	15.1	0.39	13.6	1.18	1.08	44.8
(15)	(06-80)	1.6	1.10	1.3	1.46	1.5	1.57	58.0	1.76	21.5	0.99	8.0	0.97	1.31	44.8
(12)	(09-80)	2.2	0.99	1.8	1.67	1.2	1.49	34.4	1.45	21.7	1.28	2.8	0.58	1.24	36.0
(12)	(10-80)	2.2	0.90	2.1	1.67	1.5	1.58	35.4	1.46	19.6	1.13	1.2	0.29	1.17	36.0
(12)	(12-80)	1.9	0.93	1.7	1.50	1.3	1.60	49.8	1.62			6.3	0.87	1.30	36.0
(12)	(01-81)	2.3	0.79	1.9	1.64	1.3	1.50	45.0	1.60	10.0	0.50	3.2	0.58	1.10	36.0
(12)	(02-81)	2.2	0.94	2.4	1.60	1.4	1.56	47.0	1.64	12.1	0.30	6.0	0.90	1.15	36.0
(12)	(03-81)	2.2	0.97	2.4	1.63	1.7	1.68	45.2	1.58	11.8	0.74	12.1	1.12	1.28	36.0
(12)	(04-81)	2.3	0.98	2.3	1.67	1.7	1.67	41.6	1.54	14.0	0.00	9.4	1.07	1.15	36.0
(12)	(05-81)	2.2	0.94	2.1	1.61	1.6	1.60	47.6	1.64	14.8	0.62	13.9	1.17	1.26	36.0

Table 2. Pearson Product Moment Correlations of habitat variables with distance downstream from the most upstream site of known permanent flow.

Variable	July[a] Correlation with distance		August[b] Correlation with distance	
	Mean	HC	Mean	HC
Substrate	-.42	-.37	-.38	.01
Vegetation	-.03	-.09	-.02	-.16
Structure	-.03	-.34	-.31	-.29
Depth	.43	.51*	.53	.55*
Temperature	.03	.40	.13	.27
Current	-.18	-.08	-.28	-.32
Composite HC		.04		-.01

[a] 18 pairs, d.f. = 16
[b] 13 pairs, d.f. = 11
*significant at .05 level, Rohlf and Sokal (1969)

conditions of the summer of 1980 show Spring Creek to be remarkably lacking in longitudinal zonation, though it is not physically uniform (Table 1). There was no consistent longitudinal pattern in any physical variables but substrate, (a slight tendency for coarser substrates upstream) and depth (deeper downstream). However, even depth was not consistent, with some downstream sites quite shallow. Neither trend was found to be statistically significant.

HC shows greater evidence of longitudinal habitat zonation, but no consistent pattern is discernable. There is a tendency for depth and temperature to vary more at downstream than upstream sites (higher HC values, significantly so for depth) and for structure to vary more at upstream sites, but there are high values both upstream and downstream for all three of these. Composite HC shows no correlation with distance.

CHAPTER V

FISH SPECIES DIVERSITY AND HABITAT COMPLEXITY

No overall trend is evident in FSD, but the collections fall into two groups (Tables 3, 5; Fig. 4). FSD declined steadily from upstream sites 2 and 3 (FSD = 1.43 and 1.73) to sites 10 and 11 (FSD = 0.31 and 0.46) (Table 3). Further downstream all collections had high values (1.62 to 1.96). For the nine upstream to midstream collections FSD was significantly negatively correlated with distance from the source ($r = -.91^{**}$, probability of a larger $r < .01$). When all 13 collections were considered $r = .18$, and was not statistically significant (Fig. 4).

A plot of FSD against composite HC revealed the probable source of the above equivocal results (Fig. 5). Evidently high FSDs occur with high HCs. The low FSD values in midstream reaches simply correspond to low HCs. FSD is positively correlated with four of the six separate HC estimates, and with composite HC (Table 4).

In summary, FSD in August collections from Spring Creek and its tributary Snake Creek show a consistent pattern of high values at sites with high habitat complexity or more variable habitat, and low values at sites with low habitat

Table 3. Fish species diversities at 13 sites in August, 1981.

Site		Distance from source	FSD	Composite HC
Two Creeks	(2)	3.4km	1.43	1.17
Rocky Ford	(3)	7.2	1.73	1.03
Teresita Br.	(4)	16.8	.79	1.10
Teresita Cem.	(5)	17.5	1.18	1.23
Teresita Fd.	(6)	21.3	.64	1.12
Lick Spring	(7)	23.3	.76	1.15
Upper Baker	(10)	31.2	.31	1.03
Lower Baker	(11)	31.9	.46	.68
Timber	(12)	36.0	1.70	1.24
Barrett	(14)	43.4	1.62	1.14
Lefty's C.	(15)	44.8	1.96	1.22
Cedar Ck.	(16)	48.0	1.62	1.20
Goforth	(18)	14.9	1.41	1.29

Table 4. Correlations of FSD with HC for each variable and composite HC for the 13 collections of Table 3.

Variable	r (d.f. = 11)
Substrate	+.40
Vegetation	+.69**
Structure	+.39
Depth	+.27
Temperature	-.04
Current	-.11
Composite	+.57*

*Significant at the .05 level
**Significant at the .01 level

Table 5. Counts by species of fish collections used to estimate FSDs in Spring Creek.

Species	Site Number												
	2	3	4	5	6	7	10	11	12	14	15	16	18
Notropis pilsbryi	170	202	349	80	462	526	232	494	162	251	126	333	187
N. rubellus		6			4				9				
Dionda nubila	80	213	6	1		28		3	80	97	74	166	57
Hybopsis amblops										1	1	9	
Nocomis asper	28	26	16	1	9	21	6	10	21	31	50	89	2
Semotilus atromaculatus		33	20	34	37	17	1	1	2	17	59	24	1
Phoxinus erythrogaster		34	6	126	22				24		22		38
Campostoma anomalum	60	171		6	3	6	3	6	72	129	96	146	20
Catastomus commersoni	2	2											
Moxostoma erythrurum		1							1	1	1		
Hypentelium nigricans		2							1		2		
Noturus exilis			1						1			1	
Fundulus olivaceous	4												
Gambusia affinis	10	6		1		1	1			9	4	26	3
Micropterus salmoides	2	1				6	1	1		3		1	1
M. dolemieui	2	3	1	1	4	17	3	19	11	6	8	2	1
Ambloplites rupestris	2		3		1	1	1	1	5	7	1	2	1
Lepomis cyanellus							1	1			1		1
L. macrochirus										1	1		1
L. megalotis						2				3	1		
Percina caprodes												1	
Etheostoma blennioides										1			
E. spectabile	4	5	2			1		1		1		3	5
E. punctulatum			1						1			1	
E. crageni													1
E. flabellare	4	5	3		1			3	2			1	1
E. microperca										4			
Cottus carolinae	10	6		1		1	1			9	4	26	3
Total specimens	378	717	420	251	543	629	249	721	393	644	448	807	308

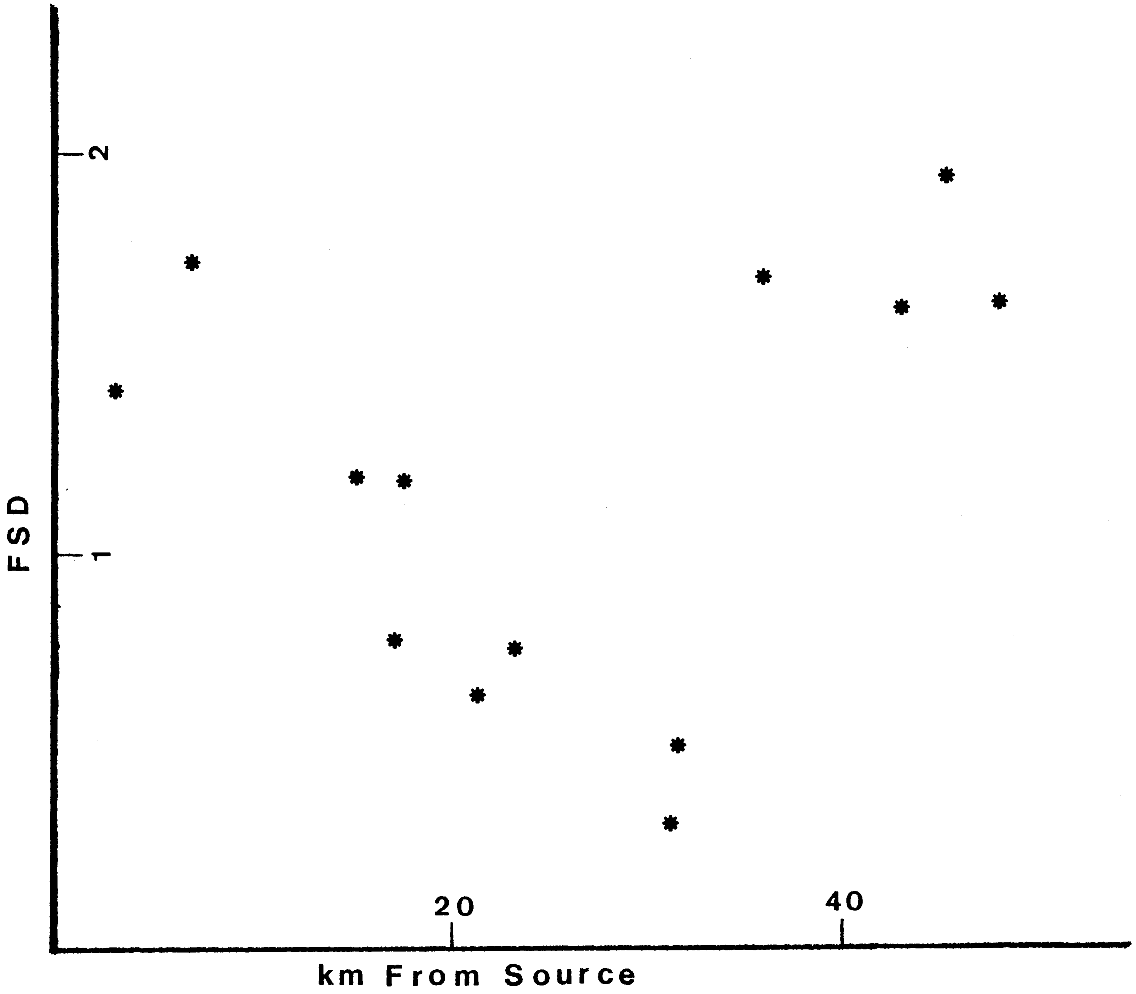

Figure 4. FSDs and distances downstream for 13 sites visited in August 1980.

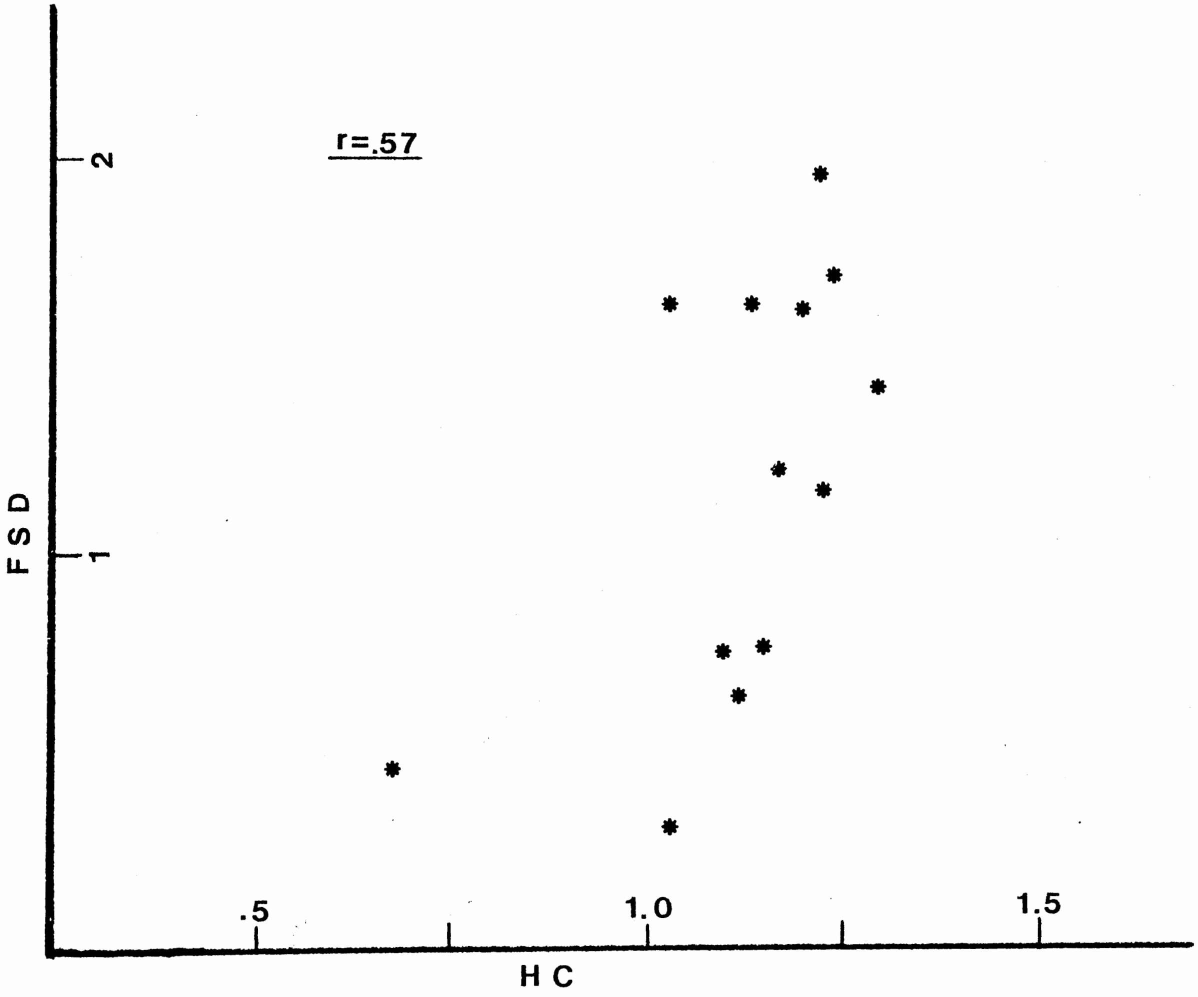

Figure 5. FSD and composite HC at 13 sites in August 1980.

complexity. This pattern is related to longitudinal position, with midstream reaches having lower habitat complexity and lower species diversity than either upstream or downstream reaches. The pattern of high FSD in complex habitats is consistent with the pattern found by Gorman and Karr (1978).

It is evident that vegetational complexity is the most important contributor to the HC - FSD relationship, and that neither temperature complexity nor current complexity make a significant contribution. This may be due to the fact that several of the sites which were most complex otherwise had little or no spring flow and thus at the low discharge levels of August were uniform with respect to currents, having little or no current at that time. Having little ground water flow, these sites also had uniform temperatures, as the greatest cause of temperature variation at a site was the difference between ground water temperature and surface water temperature.

Examination of topographical maps (USGS, 1972) showed the upstream sites with high FSDs had relatively low gradients (about 2.4 - 2.6 m x km^{-1}) and the downstream sites with high FSDs did also (about 1.7 - 2.1 m x km^{-1}). The middle sites with low FSDs had much higher gradients (about 3.0 - 4.3 m x km^{-1}). Gradient then might account for the low HC and thus the low FSDs.

CHAPTER VI

BENTHIC INVERTEBRATES

Benthic invertebrate collections were made primarily to provide a reference collection for identification of invertebrate remains in fish digestive tracts. However, in addition, invertebrate species diversity (ISD) was computed by the Shannon-Wiener formula for each collection as were HC values (Table 6). ISD was not correlated with composite HC (r = .24, not significant at the .05 level). As species identification was not made for most forms, no listing of forms collected is reported here.

Table 6. Invertebrate Species Diversities in 47 collections taken concurrently with habitat examination and minnow food habits collections.

Location		Month-Year	ISD	Composite HC
Oaks	(1)	Jul. 1980	1.67	1.11
Two Cks.	(2)	Jul. 1980	1.41	1.13
Rocky Fd.	(3)	Jul. 1980	2.05	1.12
Teresita Br.	(4)	Jul. 1980	1.25	1.01
Teresita Cem.	(5)	Jul. 1980	1.97	1.23
Teresita Fd.	(6)	Jul. 1980	2.17	1.13
Lick Spring	(7)	Jul. 1980	1.46	1.16
Cole's	(8)	Jul. 1980	2.19	1.18
Perona's	(9)	Jul. 1980	.89	1.14
Upper Baker	(10)	Jul. 1980	2.02	1.06
Lower Baker	(11)	Jul. 1980	1.94	.88
Timber	(12)	Jul. 1980	1.88	1.16
Zehr's	(13)	Jul. 1980	1.91	.92
Barrett's	(14)	Jul. 1980	2.01	1.28
Left's C.	(15)	Jul. 1980	1.56	1.28
Cedar Cr.	(16)	Jul. 1980	2.68	1.18
Upper Snake	(17)	Jul. 1980	1.26	1.09
Goforth's	(18)	Jul. 1980	2.19	1.25
Two Cks.	(2)	Aug. 1980	2.26	1.17
Rocky Fd.	(3)	Aug. 1980	2.03	1.03
Teresita Br.	(4)	Aug. 1980	2.19	1.10
Teresita Cem.	(5)	Aug. 1980	1.91	1.23
Teresita Fd.	(6)	Aug. 1980	1.12	1.12
Lick Spring	(7)	Aug. 1980	1.53	1.15
Upper Baker	(10)	Aug. 1980	1.41	1.03
Lower Baker	(11)	Aug. 1980	1.09	.68
Timber	(12)	Aug. 1980	2.26	1.24
Barrett's	(14)	Aug. 1980	1.59	1.14
Lefty's C.	(15)	Aug. 1980	1.26	1.22
Cedar Cr.	(16)	Aug. 1980	1.07	1.20
Goforth's	(18)	Aug. 1980	1.82	1.29
Timber	(12)	Sep. 1980	2.00	1.24
Timber	(12)	Oct. 1980	1.92	1.17
Timber	(12)	Dec. 1980	1.94	1.30
Timber	(12)	Jan. 1981	1.93	1.11
Timber	(12)	Feb. 1981	1.89	1.15
Timber	(12)	Mar. 1981	1.72	1.28
Timber	(12)	Apr. 1981	1.88	1.15
Timber	(12)	May 1981	1.68	1.26
Lefty's C.	(15)	Oct. 1979	2.22	1.14
Lefty's C.	(15)	Nov. 1979	2.17	1.26
Lefty's C.	(15)	Dec. 1979	2.11	1.08

Table 6. (Continued).

Location		Month-Year	ISD	Composite HC
Lefty's C.	(15)	Jan. 1980	2.19	1.02
Lefty's C.	(15)	Feb. 1980	2.26	1.03
Lefty's C.	(15)	Apr. 1980	2.26	1.41
Lefty's C.	(15)	May 1980	2.56	1.08
Lefty's C.	(15)	Jun. 1980	2.42	1.31

CHAPTER VII

CYPRINID FOOD HABITS

The gut contents of a total of 267 Campostoma anomalum, 348 Dionda nubila, 357 Nocomis asper, 481 Notropis pilsbryi, 50 Notropis rubellus, 183 Phoxinus erythrogaster, and 90 Semotilus atromaculatus with food were examined. Ninety per cent of the fish examined had food in the gut (Table 7).

C. anomalum, D. nubila, and P. erythrogaster may be classed as herbivores, using 97%, 94%, and 81% respectively non-animal foods. Nocomis asper, S. atromaculatus, and N. rubellus are carnivores, taking 5%, 0%, and 10% non-animal foods. Notropis pilsbryi is an omnivore, taking 42% non-animal foods and 58% animal foods.

C. anomalum guts contained mostly non-filamentous algae, mainly diatoms (38%), sand (28%), and unidentified plant detritus (21%). Lesser amounts of filamentous algae and aquatic vascular plants, mostly leaves, were in the guts. Although this species is widely believed to be strictly herbivorous (Miller and Robison, 1973; Pflieger, 1975) animal materials, though never abundant, were regularly found in the guts. These included forms (chironomid larvae, trichoptera larvae, protozoa) likely to be taken incidentally while scraping algae, but also included adult winged midges

Table 7. Foods utilized by cyprinids collected from Spring Creek, October 1979-May 1981. Mean Imp. = Mean importance.

Species (N)					
Campostoma anomalum (267)			*Dionda nubila* (348)		
Foods	Mean Imp.	± S.D.	Foods	Mean Imp.	± S.D.
Sand	.283	.435	Sand	.229	.395
Detritus	.214	.390	Detritus	.376	.435
Non-filamentous algae	.384	.451	Non-filamentous algae	.186	.337
Filamentous algae	.065	.210	Filamentous algae	.077	.192
Aquatic vascular plants	.026	.120	Aquatic vascular plants	.057	.191
Protozoa (*Diflugia* tests)	.002	.016	Oligochaeta	.004	.040
Trichoptera *Cheumatopsyche*	.004	.062	Gastropoda *Goniobasis*	.008	.084
Diptera Chironomidae larvae	.020	.104	Amphipoda *Hyallela*	.009	.072
Diptera Chironomidae adults	.001	.006	Plecoptera	.003	.038
			Ephemoptera L. *Stenacron*	.003	.055
			Ephemoptera L. *Stenonema*	.003	.054
			Ephemoptera L. *Baetis*	.009	.071
			Ephemoptera L. *Choroterpes*	.002	.032
			Ephemoptera L. Caenidae	.005	.060
			Trichoptera *Marilia*	.003	.031
			Trichoptera *Helicopsyche*	.0003	.0053
			Trichoptera *Oxyithera*	.0002	.0027
			Diptera L. Chironomidae	.011	.052
			Other Diptera L.	.001	.013
			Coleoptera L. *Psephenus*	.007	.049
			Terrestrial Ephemeroptera	.001	.011
			Terrestrial Coleoptera	.002	.027
			Terrestrial Formicidae	.001	.016
			Terrestrial Chironomidae	.002	.029
			Other Diptera - Terrestrial	.0003	.0054
			Araneae	.001	.013
			Pisces	.001	.011

Table 7. (Continued).

Species (N)

Nocomis asper (357)

Foods	Mean Imp.	± S.D.	Foods	Mean Imp.	± S.D.
Sand	.003	.029	Diptera L. Chironomidae	.033	.142
Detritus	.015	.108	Diptera L. *Tabanus*	.005	.044
Non-filamentous algae	.004	.035	Other fly larvae	.001	.026
Filamentous algae	.018	.099	Coleoptera L. Elmidae	.001	.008
Aquatic vascular plants	.008	.062	Coleoptera Elmidae adults	.003	.030
Oligochaeta	.003	.031	Coleoptera L. *Psephenus*	.041	.146
Gastropoda *Goniobasis*	.425	.405	Terr. Ephemeroptera A.	.001	.021
Other snails	.009	.076	Terrestrial Orthoptera	.009	.075
Pelecypoda	.002	.025	Terrestrial Plecoptera A.	.002	.022
Amphipoda *Hyallela*	.004	.041	Terrestrial Odonata adult	.006	.071
Isopoda *Asellus*	.001	.012	Terrestrial Trichoptera A.	.001	.026
Decapoda *Orconectes*	.112	.252	Terrestrial Coleoptera	.003	.025
Plecoptera	.012	.099	Terrestrial Formicidae	.002	.019
Ephemeroptera *Stenacron*	.005	.061	Terr. Other Hymenoptera	.001	.013
Ephemeroptera *Stenonema*	.003	.053	Diptera chironomidae adult	.002	.018
Ephemeroptera *Baetis*	.008	.077	Other Diptera adult	.005	.058
Ephemeroptera *Ephemerella*	.002	.039	Pisces (Eggs)	.012	.093
Ephemeroptera Caenidae	.004.	.041	Pisces	.014	.110
Anisoptera *Lanthus*	.021	.111			
Anisoptera *Boyeria*	.005	.061			
Zygoptera	.002	.030			
Megaloptera	.005	.070			
Trichoptera *Marilia*	.123	.257			
Trichoptera *Helicopsyche*	.057	.173			
Trichoptera *Cheumatopsyche*	.003	.035			
Trichoptera *Triaenodes*	.005	.054			
Trichoptera *Oxyithera*	.001	.026			

Table 7. (Continued).

	Species (N)	
	Notropis pilsbryi (481)	
Foods	Mean Imp.	± S.D.
Sand	.006	.065
Detritus	.067	.205
Non-filamentous algae	.052	.169
Filamentous algae	.138	.281
Aquatic vascular plants	.149	.288
Porifera *Spongilla*	.001	.023
Oligochaeta	.007	.068
Gastropoda *Goniobasis*	.057	.199
Amphipoda *Hyallela*	.022	.102
Decapoda *Orconectes*	.006	.050
Collembola	.0001	.0023
Plecoptera	.025	.113
Ephemeroptera *Ephemera*	.003	.042
Ephemeroptera *Stenacron*	.012	.080
Ephemeroptera *Stenonema*	.016	.099
Ephemeroptera *Baetis*	.016	.085
Ephemeroptera *Isonychia*	.002	.031
Ephemeroptera *Ephemerella*	.008	.077
Ephemeroptera *Choroterpes*	.003	.049
Ephemeroptera Caenidae	.007	.062
Ephemeroptera *Pseudocleone*	.001	.014
Anisoptera *Lanthus*	.006	.060
Anisoptera *Boyeria*	.001	.011
Zygoptera	.001	.057
Trichoptera *Marilia*	.044	.175
Trichoptera *Helicopsyche*	.001	.023
Trichoptera *Cheumatopsyche*	.004	.036
Trichoptera *Oxyithera*	.0002	.0036
Trichoptera *Chimara*	.0004	.0091
Diptera Chironomidae L.	.011	.059
Diptera *Tabanus* L.	.004	.058
Other Diptera L.	.001	.012
Coleoptera Elmidae L.	.003	.031
Coleoptera Elmidae A.	.017	.091
Coleoptera *Psephenus* L.	.115	.241
Other Coleoptera	.002	.032
Terrestrial Ephemeroptera	.011	.088
Terrestrial Orthoptera	.007	.061
Terrestrial Plecoptera	.004	.058
Terrestrial Odonata	.007	.069
Terrestrial Hemiptera	.002	.034
Terrestrial Trichoptera	.013	.091
Terrestrial Coleoptera	.035	.139
Terrestrial Formicidae	.031	.134
Terr. Other Hymenoptera	.011	.086
Terrestrial Chironomidae	.021	.086
Terr. Other Diptera	.035	.141
Terrestrial Araneae	.006	.060
Pisces (Eggs)	.002	.046
Pisces	.002	.036

Table 7. (Continued).

Species (N)					
Phoxinus erythrogaster (182)			Notropis rubellus (50)		
Foods	Mean Imp.	± S.D.	Foods	Mean Imp.	± S.D.
Sand	.196	.379	Non-filamentous algae	.020	.099
Detritus	.207	.362	Filamentous algae	.049	.172
Non-filamentous algae	.256	.375	Aquatic vascular plants	.027	.107
Filamentous algae	.083	.199	Amphipoda *Hyallela*	.040	.127
Aquatic vascular plants	.059	.176	Plecoptera	.009	.063
Oligochaeta	.001	.018	Ephemeroptera *Baetis*	.041	.164
Amphipoda *Hyallela*	.039	.168	Ephemeroptera Caenidae	.035	.160
Isopoda *Asellus*	.001	.015	Anisoptera *Lanthus*	.010	.071
Plecoptera	.009	.059	Zygoptera	.013	.094
Ephemeroptera *Stenacron*	.001	.018	Megaloptera	.005	.035
Ephemeroptera *Stenonema*	.001	.018	Trichoptera *Marilia*	.010	.071
Ephemeroptera *Baetis*	.028	.147	Trichoptera *Cheumatopsyche*	.004	.020
Ephemeroptera Caenidae	.024	.123	Diptera *Tabanus* L.	.005	.071
Zygoptera	.005	.047	Other Diptera L.	.003	.021
Trichoptera *Helicopsyche*	.008	.072	Coleoptera Elmidae L.	.010	.071
Trichoptera *Cheumatopsyche*	.005	.074	Coleoptera Elmidae A.	.068	.185
Trichoptera *Oxyithera*	.001	.015	Coleoptera *Psephenus* L.	.037	.117
Diptera Chironomidae L.	.018	.095	Terr. Ephemeroptera	.042	.164
Other fly larvae	.001	.005	Terrestrial Odonata	.020	.141
Coleoptera *Psephenus* L.	.001	.018	Terr. Trichoptera	.061	.187
Terr. Ephemeroptera	.005	.074	Terr. Coleoptera	.071	.179
Terr. Trichoptera	.011	.104	Terr. Formicidae	.241	.333
Terr. Coleoptera	.019	.095	Terr. Other Hymenoptera	.016	.080
Terr. Formicidae	.005	.052	Terr. Chironomidae A.	.054	.123
Terr. Chironomidae A.	.021	.122	Terr. Other Diptera A.	.078	.199
			Terr. Araneae	.025	.104

Table 7. (Continued).

		Species (N) *Semotilus atromaculatus* (90)			
Foods	Mean Imp. ±	S.D.	Foods	Mean Imp. ±	S.D.
Gastropoda *Goniobasis*	.167	.331	Terr. Coleoptera	.147	.277
Other snails	.011	.105	Terr. Formicidae	.091	.257
Amphipoda *Hyallela*	.009	.052	Terr. Other Hymenoptera	.038	.167
Isopoda *Asellus*	.002	.016	Terr. Chironomidae A.	.004	.026
Decapoda *Orconectes*	.039	.161	Terr. Other fly adult	.142	.296
Collembola	.002	.018	Terr. Araneae	.017	.090
Plecoptera	.019	.113	Pisces	.014	.099
Ephemeroptera *Ephemera*	.011	.105			
Ephemeroptera *Baetis*	.003	.027			
Ephemeroptera *Ephemerella*	.016	.107			
Ephemeroptera *Choroterpes*	.011	.105			
Anisoptera *Lanthus*	.014	.108			
Anisoptera *Boyeria*	.011	.105			
Zygoptera	.017	.091			
Trichoptera *Marilia*	.001	.011			
Trichoptera *Helicopsyche*	.003	.026			
Diptera Chironomidae L.	.006	.041			
Diptera *Tabanus* L.	.014	.095			
Coleoptera Elmidae L.	.006	.053			
Coleoptera Elmidae A.	.027	.129			
Coleoptera *Psephenus* L.	.022	.097			
Other beetles	.025	.119			
Terrestrial Orthoptera	.025	.138			
Terrestrial Plecoptera	.006	.053			
Terrestrial Odonata	.011	.105			
Terrestrial Hemiptera	.031	.158			
Terrestrial Trichoptera	.042	.196			

which must have been taken from the water surface. Examination of the distal intestine revealed that these animals were apparently digested. The only reference that I have found to carnivory by Campostoma is Trautman (1957) who stated that the stoneroller ate small plants and invertebrates.

Dionda ate mostly plant detritus (38%), sand (23%), and non-filamentous algae (mostly diatoms, 19%). Smaller quantities of filamentous algae and vascular plant parts including leaves, stems, and flower buds were also eaten. Additionally, very small quantities of a wide variety of predominately benthic animals were found in the guts. These included many that were likely to be taken incidentally to plant consumption (the larval trichopteran Cheumatopsyche and chironomids) but also included the larvae of Helicopsyche, which is a sand-case building form, and terrestrial invertebrates. The long coiled gut is an adaptation to herbivory.

Phoxinus used the same foods as the preceeding two species, but in different proportions. These included 26% non-filamentous algae (mostly diatoms), 21% plant detritus, and 20% sand. Smaller quantities of filamentous algae and vascular plant parts (buds and leaves) were also consumed. It took a wider range of animals than either Dionda or Campostoma, and amphipods, mayfly naiads, and aerial and terrestrial arthropods contributed significantly to the gut contents. The animal foods taken, as with Dionda, included forms from a variety of habitats, including riffles and swifter locations where Phoxinus was seldom seen in the stream. This observation suggests that deduction of habitat use from foods, as was done by both Mendelson (1975) and Werner and Hall (1976) is a questionable procedure unless it can be demonstrated independently that the proportion of the food consumed is a function of time spent in the habitat where the food occurs. Animals may resort to certain habitats specifically to obtain a particular food, but spend little time there for other purposes, such as nesting, displaying, or avoiding predators.

Notropis pilsbryi may be classified as omnivorous on the basis of this study, in contrast with the predominately carnivorous habit of Arkansas populations reported on by Matthews and Shephard (1978). The most important food items to it were vascular plant parts (flowers, leaves, and stems, 15%), filamentous algae (14%), and larvae of the water penny beetle Psephenus (12%). Unidentified plant detritus, non-filamentous algae (mainly diatoms), snails (mostly the very abundant Goniobasis), larval trichopterans, and assorted terrestrial forms also contributed significantly to the diet. Beetles, ants, flies, and the winged adults of aquatic forms were the most abundant organisms in the last category. The dusky-striped shiner also ate sponges, amphipods, stonefly larvae and adults, mayfly larvae and adults, midges, sand, fish, and fish eggs. Any food items available appear to be taken.

The predominance of plants and the water penny in the diet illustrates, when contrasted with Matthews' and Shephard's study (1978), the breadth of the species' fundamental niche. Plants were of minor importance to the Arkansas populations they studied, and aquatic beetles of all sorts occurred in such small quantities as to be given only passing mention in their report. I have no idea how common *Psephenus* is in Piney Creek, their study area, but it is one of the most abundant benthic forms in Spring Creek.

Notropis rubellus was, in contrast to *N. pilsbryi*, carnivorous, using 90% animal foods. Most individuals I examined contained only animal remains. Also in contrast to the other minnows, the rosy-faced shiner consumed mainly aerial and terrestrial animals (61% of the gut contents). The most important items were ants (24%) and adult flies (13%), mostly tabanids, muscids, and similar forms. Other important foods were mayfly naiads, terrestrial beetles, and adult trichopterans. The terrestrial diet of *N. rubellus* is in keeping with its apparent habitat preference.

Nocomis asper was almost totally carnivorous, consuming 95% animal materials in contrast to its close relative *N. biguttatus* (Lachner, 1950). Of all the minnows studied, the red-spot chub exhibited the greatest degree of diet specialization. The diet was 43% snails, almost all of them the extremely common *Goniobasis*. Other important foods were larval trichopterans (19%), mostly the sand case building *Marilia* and *Helicopsyche* (both very abundant at most locations studied) and crayfish (11%). Significant quantities of aquatic fly larvae (mostly midges) and aquatic beetle larvae (mostly *Psephenus*) were also consumed. Despite the dominance of a few foods in their diet, *Nocomis* ate a wider variety of foods than any fish studied except *Notropis pilsbryi*. Benthic items predominated to a greater degree than for any other fish, and aerial and terrestrial forms were of minor occurrence.

Semotilus atromaculatus was strictly carnivorous in this study. Like that of *Notropis rubellus*, its diet was dominated by materials of aerial and terrestrial origin (56%). These included 16% adult flies, mostly muscids, tabanids, and other large-bodied dark colored forms, 15% terrestrial beetles, 9% ants, and lesser quantities of grasshoppers, hemipterans, adult trichopterans, bees and wasps, and spiders. The most important benthic item was the snail *Goniobasis* (17%). The creek chub also consumed 4% crayfish. This analysis includes only juveniles and small adults. However, non-quantitative observations of the behavior of large creek chubs with respect to terrestrial drift seem to confirm the conclusions.

CHAPTER VIII

DISCRIMINANT ANALYSIS OF FOOD HABITS

To ascertain the distinctiveness of the food niches of these minnows, and to relate it to physical habitat and biotic relationships, I performed stepwise discriminant analysis, using the BMDP program P7M (Jennrich and Sampson, 1979) through the SAS interface program BMDP (SAS Institute, 1979) on the Oklahoma State University IBM 370 computer.

The aim of discriminant analysis is to distinguish between two or more independently defined groups of individuals. Group membership and individual attributes are known. The analysis then describes group membership in terms of linear functions (called <u>discriminant</u> <u>functions</u> or <u>canonical</u> <u>variables</u>) of the individual attributes. The original group definitions have a theoretical or empirical relationship to the particular research situation. A next step is to statistically test the utility of the discrimination for the original group divisions. Finally, if a successful discrimination was obtained, it may be used to classify individuals whose group membership is unknown or uncertain. The theory and mechanics of the technique are described in Klecka (1975) and in greater detail in standard multivariate statistical texts.

In this study group membership (taxonomic species) was known for the 1776 individuals whose food habits were described in Chapter VII. Importance values for each of the 56 food types served as independent variables (attributes) for each individual. The objective was to determine the usefulness of food habits data as an ecological discriminating tool for the seven species, and if a useful discrimination was found to infer ecological distinctiveness.

Baker and Ross (1981) and Green (1971,1974) used disciminant analysis similarly, but with habitat rather than food habits data. They discussed the use of discriminant analysis in ecological studies and pointed out that meeting the method's assumptions of randomness and independence of variables is extremely unlikely in field studies, but that interpretation of the results of such an analysis still offers much reward. Klecka (1975) claimed, in stating the theoretical assumptions of a multivariate normal distribution of discriminating variables and equal variance - covariance matrices within groups, that stepwise discriminant analysis is sufficiently robust that the assumptions need not be rigorously adhered to. Consequently, while recognizing the unlikelihood of meeting the assumptions with these data, I performed the analysis and examined the results.

A different discrimination will result if only a subset of the available variables is entered than if the entire set is, and it may be possible to find the one best of all possible discriminations. Stepwise discriminant analysis attempts to do this by sequentially entering variables, in order of discriminating power. In the method used here, since the addition of one variable can alter the relationship of previously entered variables, it is possible to replace them. This is called forward stepping. Twenty-seven steps were completed, and the results of step 27 are summarized in Table 8. There were 27 variables found to be useful (to add significant discriminating power to the functions) and 29 non-useful.

The analysis was highly significant as shown by the Wilks' Lambda value of 0.08 (probability of a larger value of F $<.001$). However, with 162 and 10249 D.F. the usefulness of this criterion for significance is questionable, and Green (1971,1974) held that ecological meaningfulness of the discrimination is more useful than the significance level. Klecka (1975) pointed out that statistically significant discriminations may not produce useful divisions of collections into groups, and the success of the analysis in discriminating among the original set of individuals is a better criterion of utility than is significance level.

With Green and Klecka's ideas in mind, the classification results (Table 9) of the food habits discrimination may be profitably examined. A majority (55.6%) of all fish were correctly classified by the discriminant analysis indicating that food habits may be an important distinction among these species. The most distinctive group, with 83% correctly classified, was *Nocomis asper*, and the earlier description of food habits revealed this species to be the most special-

Table 8. Discriminant analysis of minnow species by foods: Step number 27.

Variables Used*	Variables Not Used
Non-filamentous algae	Freshwater sponges
Sand	Oligochaetes
Plant detritus	Snails (not *Goniobasis*)
Filamentous algae	Pelycepods
Vascular plants	Isopods
Goniobasis(snail)	Collembola
Bees and wasps	Plecoptora(naiads)
Crayfish	*Ephemera*(mayfly naiads)
Helicopsyche(caddisfly naiad)	*Stenacron*(mayfly naiads)
Psephenus(water penny larva)	*Isonychia*(mayfly naiads)
Ants	*Ephemerella*(mayfly naiads)
Amphipods	*Choroterpes*(mayfly naiads)
Spiders	*Pseudocleone*(mayfly naiads)
Marilia	*Lanthus*(Dragonfly naiads)
Baetis(mayfly naiad)	*Boyeria*(Dragonfly naiads)
Adult flies(other than midges)	Damselfly naiads
Caenidae(mayfly naiads)	*Megaloptera*
Elmidae(adults,aquatic beetles)	Other fly larvae(non-midge)
Hemiptera(not aquatic)	*Triaenodes*(caddisfly naiads)
Aquatic beetles(not Elmid)	*Oxyithera*(caddisfly naiads)
Chironomidae larvae(midges)	*Chimara*(caddisfly naiads)
Adult mayflies	*Tabanus*(horsefly larvae)
Adult caddisflies	Elmid larvae
Diflugia(protozoan)	Grasshoppers
Cheumatopsyche(caddisfly naiad)	Adult Plecoptera
Stenonema(mayfly naiad)	Adult Odonata
Adult midges	Terrestrial beetles
	Fish eggs
	Fish

WILKS' LAMBDA	0.08	D.F.	27	6	1769
APPROXIMATE F	33.7**	D.F.	126	10,250	

Table 8. (Continued).

F-MATRIX[a] D.F. 27 1743

	CA[b]	DN	NA	NP	NR	PE
DN	5.06					
NA	125.39	126.18				
NP	66.38	58.04	66.72			
NR	34.22	30.81	29.42	12.84		
PE	5.33	3.43	78.42	29.86	22.57	
SA	59.60	55.54	29.36	22.05	9.70	41.58

*Listed in order of contribution to discrimination.

**Significant at .001 level.

[a] All values are significant at the .001 level.

[b] CA = *Campostoma anomalum*, DN = *Dionda nubila*, NA = *Nocomis asper*, NP = *Notropis pilsbryi*, NR = *Notropis rubellus* PE = *Phoxinus erythrogaster*, SA = *Semotilus atromaculatus*.

Table 9. Discriminant analysis of minnows by foods: Classification matrix. Species symbols as in Table 8.

Species	Per cent Correct	Number of Cases Classified Into Species						
		CA	DN	NA	NP	NR	PE	SA
CA	67.4	180	59	2	12	0	14	0
DN	42.2	127	147	3	31	1	37	2
NA	82.9	0	5	296	25	2	9	20
NP	51.8	14	31	52	249	47	30	58
NR	50.0	0	0	1	9	25	4	11
PE	20.2	70	45	3	17	9	37	2
SA	58.9	0	0	20	3	14	0	53
Total	55.6	391	287	377	346	98	131	146

ized of the minnows studied. Misclassified Nocomis were most frequently classified as Notropis pilsbryi (7%) and Semotilus atromaculatus (6%).

Campostoma anomalum, with 67.4% correctly classified, was also distinctive. This was at first confusing, but re-examination of the individual gut contents revealed that many individual Campostoma contained almost exclusively plant materials. Despite the heavy reliance of Dionda and Phoxinus on plants, many individuals contained other materials. Thus it makes sense that a "Campostoma" pattern was easier to identify than "Dionda" or "Phoxinus" patterns. Misclassified Campostoma were most frequently classified as Dionda (22%), Phoxinus (5%), and Notropis pilsbryi (4%).

Semotilus atromaculatus individuals were classified correctly in 58.9% of the cases. They were most commonly misclassified as Nocomis asper (22%) and Notropis rubellus (16%). These results are due to the benthic food items shared with Nocomis and the aerial and terrestrial items shared with N. rubellus.

Notropis pilsbryi individuals were correctly classified in 51.8% of the cases. Considering the catholic nature of their diet and the sharing of many food items with other species, this is a surprisingly high level of accuracy. Misclassifications were assigned most frequently to Semotilus atromaculatus (12%), Nocomis asper (11%), and Notropis rubellus (10%). Unlike more specialized forms, some Notropis pilsbryi were assigned to each other species. This was true of *Dionda* and *Phoxinus* also, but in those two forms most individuals were misclassified.

Dionda individuals were misclassified in a majority of cases, only 42.2% being assigned to the correct group. However, the largest single assignment of *Dionda* to any species was to *Dionda*. The majority of the misclassified cases, 37% of all *Dionda*, were assigned to *Campostoma*, in agreement with the high degree of shared plant and detrital foods. *Phoxinus* received 11% of the total classifications of *Dionda*. Some *Dionda* individuals were also assigned to each of the six other species, an indication of the breadth of this form's niche, like that of *Notropis pilsbryi*.

Only 20.2% of all *Phoxinus erythrogaster* specimens were classified correctly. Most were classified as *Campostoma anomalum* (38%), *Dionda nubila* (23%), or *Notropis pilsbryi* (9%). As with *Dionda* and *N. pilsbryi*, despite an apparent specialization on plant materials, some individuals were classified into each of the six other species, indicating a wide and variable niche.

A discriminant analysis constructs a set of synthetic variables that are composites of the original variables contributing to discrimination. These are called canonical variables (or discriminant functions). Step 27 of this analysis derived six such canonical variables, each of which contributed to separation of the seven species.

Table 10 shows the eigenvalues, relative contributions, to discrimination, and canonical correlations of the six variables with species. A large eigenvalue indicates a large contribution to total dispersion among groups, as does a large canonical correlation. The first two cannonical variables account for 89% of the diet dispersion and the third variable for an additional 6%. The remaining three account for only 5%. The canonical correlations confirm the conclusion that the first two variables are most useful in separating the species' diets, the third of moderate value, and the remaining three of less utility.

Table 10. Canonical variables derived from discriminant analysis of seven cyprinid species, their eigenvalues and cumulative and relative per cent contribution to total dispersion, and canonical correlations with species (group variables).

Canonical Variable	Eigenvalue	Cumulative %	Relative %	Canonical Correlation
I	3.17	70	70	.87
II	0.88	89	19	.69
III	0.27	95	6	.46
IV	0.12	98	3	.33
V	0.06	99	1	.24
VI	0.03	100	1	.17

The relative contributions of a given original variable to a particular canonical variable can be determined by

Table 11. Coefficients of original dietary variables for canonical variables, I-VI.

Original Variables	Canonical Variables I	 II	 III	 IV	 V	 VI
Aquatic						
Sand	4.59	1.26	-0.31	-0.89	0.07	0.24
Detritus	4.28	1.03	0.14	-0.59	-2.04	0.60
Non-filamentous algae	4.59	1.18	-0.28	-0.95	1.77	-0.09
Filamentous algae	2.49	-0.34	1.97	-0.46	0.09	-0.07
Vascular plants	2.23	-0.83	2.69	0.04	-0.08	-0.01
Protozoa	16.33	6.00	-11.66	1.23	47.64	34.67
Goniobasis (snail)	-0.89	2.44	-0.04	-0.86	-0.17	0.12
Amphipods	2.56	-0.61	1.11	-2.68	-0.77	-5.62
Crayfish	-1.28	3.06	-0.41	-1.21	-0.20	-0.00
Stenonema (mayfly)	1.54	-0.72	3.20	0.13	0.11	0.76
Baetis (mayfly)	2.15	-0.28	1.12	-3.47	-1.21	-3.52
Caenidae (mayfly)	2.22	-0.59	0.39	-5.10	-1.03	-5.70
Marilia (caddisfly)	-0.55	1.94	1.37	-1.21	0.23	0.92
Helicopsyche (caddisfly)	-1.12	3.99	-0.06	-2.60	-0.23	-1.30
Cheumatopsyche	3.08	0.84	0.98	-1.29	3.07	-3.25
Chironomidae larvae	0.65	2.44	0.35	-1.04	1.11	-0.83
Elmidae (adults)	0.44	-3.19	-0.65	-4.53	0.35	3.89
Psephenus larvae	0.84	-1.04	3.20	0.27	0.88	1.55
Other Coleoptera	-0.50	-2.68	-7.11	8.71	-0.41	-4.58
Aerial and Terrestrial						
Ephemeroptera	1.58	-1.92	1.23	-4.75	0.25	1.12
Hemiptera	-0.42	-2.28	-6.12	6.59	-0.53	-3.53
Trichoptera	1.12	-1.96	-1.38	-2.04	0.05	-1.35
Formicidae	0.58	-2.63	-2.47	1.41	-0.10	-1.40
Bees and wasps	0.52	-3.14	-2.19	-5.59	-0.47	3.46
Chironomidae	0.46	-2.54	-1.73	1.49	0.14	-0.17
Other Diptera	1.61	-2.23	1.47	-4.89	0.18	-2.78
Araneae	0.03	-2.48	-2.49	1.24	0.06	0.28

examining the coefficients of the original variables for canonical variables (Table 11). A large absolute value for a given coefficient reflects a large contribution to the canoniical variable. The sign of the coefficient indicates whether the original variable makes a positive or negative contribution.

It was not possible to identify one or two original variables as being of majority importance in any of the canonical variables except for the marginally useful fifth and sixth canonical variables. Rather, each one seemed to be a composite of several food items, usually related taxonomically and or by habitat.

Variable I is composed mainly of sediments, detritus, vegetable materials, and animal items associated with them, and can be called a vegetation-detritus continuum. Variable II has large positive values for several large benthic animal items not usually associated with sediments and vegetation, and large negative values for several aerial-terrestrial items and can be called a large-benthos continuum. It also includes some vegetation. Variable III also has large negative values for aerial-terrestrial items, and large positive values for smaller benthic animal items. Thus it can be called a small-benthos continuum. It too includes vegetation, of coarser nature than in Variable II.

The very large coefficients for protozoa in all but one of the canonical variables are confusing as protozoa (Diflugia) were identified in the diets of only a very few individual fish. However, only in the last two, marginally useful, variables do they contribute a majority of the variability.

Discrimination by this technique is based on the relative distance of an individual's position along the discriminating axes (canonical variables) from the various groups' mean positions (or centroids). Table 12 provides the groups' mean scores on each of the canonical variables, and Table 8 reports (as part of the summary for step 27) the F-matrix for testing the null hypothesis that the pairwise Mahalonobis' Distances between the group means is zero, or that the paired groups in the matrix are centered on the same point in multidimensional space. Since the test assumes random samples and equal variances, interpretation must be done with caution. However, as discussed above, the robustness of the technique allows considerable leeway in these assumptions.

Table 12. Average score of each minnow species on canonical variables, I-VI.

Species	Canonical Variable					
	I	II	III	IV	V	VI
<u>Campostoma anomalum</u>	2.12	0.49	-0.30	0.04	0.42	0.14
<u>Dionda nubila</u>	1.77	0.28	-0.03	0.08	-0.40	0.09
<u>Nocomis asper</u>	-2.52	1.29	-0.02	-0.10	-0.01	0.01
<u>Notropis pilsbryi</u>	-0.63	-0.93	0.60	0.14	0.07	0.02
<u>Notropis rubellus</u>	-1.15	-2.36	-0.85	-1.67	-0.08	0.27
<u>Phoxinus erythrogaster</u>	1.47	0.04	-0.01	-0.28	0.03	-0.47
<u>Semotilus atromatulatus</u>	-2.10	-1.46	-1.67	0.73	-0.05	-0.11

All the F values in the matrix are highly significant (probabilities of larger values of F are less than .001 for all pairs). This may be interpreted to mean that the diet niches of these species are separate. It does not treat niche overlap or width, as it tests only correspondence of centroids (mean position). Two species may have diet niches of different size, yet emphasize the same food items.

The conclusion from the F matrix that all seven species are significantly separated is reflected in Table 12. Variable I shows Campostoma anomalum to be the most herbivorous and Nocomis asper and Semotilus atromaculatous to be the least herbivorous. Variable II shows Nocomis asper to have the greatest dependence on large benthos with fine vegetation, and Notropis rubellus to have the least dependence on such materials. Variable III shows that Notropis pilsbryi has the greatest dependence on small benthos with coarse vegetation, while Semotilus atromaculatus and N. rubellus are the least dependent on these materials. These conclusions agree with those in the food habits discussion (Chapter VII).

An examination of the classifications of the original specimens (calibration set) can tell more about the usefulness of the discrimination. Each specimen was evaluated on the first two canonical variables and a cartesian plot of the case scores was produced (Fig. 6).

The mean positions of the groups are well separated, in agreement with Table 8 and Table 12. However, the plot shows

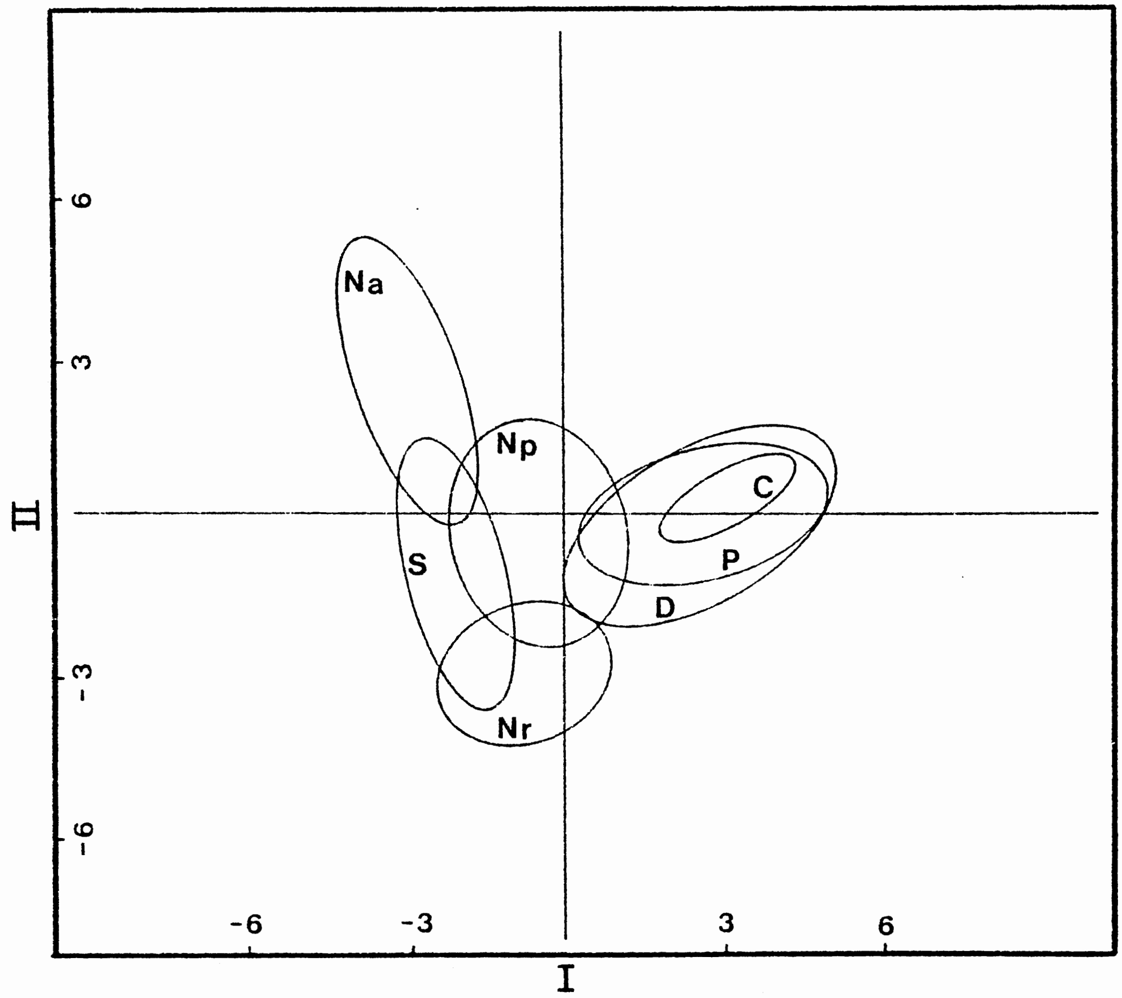

Figure 6. Ellipses enclosing 75% of cases of each cyprinid species plotted on canonical variables I and II. (Np = *Notropis pilsbryi*, Nr = *Notropis rubellus*, Na = *Nocomis asper*, S = *Semotilus atromaculatus*, D = *Dionda nubila*, P = *Phoxinus erythrogaster*, C = *Campostoma anomalum*). Enclosure of 90% of cases would show much broader overlap, particularly for *N. pilsbryi* with *Nocomis asper* and *N. rubellus*, and for *Dionda* with all other species.

that the two main canonical variables separate the seven species into two groups. The carnivores (Nocomis asper, Semotilus atromaculatus, and Notropis rubellus) are well separated. The herbivores (Campostoma anomalum, Dionda nubila, and Phoxinus erythrogaster) are very poorly separated from one another, and their diet niches might be described from this plot as nested, with the Campostoma niche within the Phoxinus niche, and both within the Dionda niche. This agrees with the food habits discussion (Chapter VII). Notropis pilsbryi, an omnivore, occupies a central position, with the largest niche of any species in the assemblage. It is reasonably well separated from the others.

CHAPTER IX

CYPRINID DISTRIBUTIONS WITH RESPECT TO HABITAT VARIABLES

The mean number of fish seen in 10 snorkling transects was used as an index to each species' abundance at the 18 sites studied (Table 13).

Notropis pilsbryi is the most abundant and most generally distributed minnow in the stream. Only 3 of 47 visits yielded fewer than 100 in ten transects. Its congener, N. rubellus is the rarest and most sporadically distributed of those studied.

Dionda nubila is a very common and widespread fish in Spring Creek, but its distribution is less consistent than that of N. pilsbryi. Several sites had few or none, and at Lefty's Camp, the second most downstream site (visited 10 times in 11 months) the fish varied widely in abundance, being abundant in most months but rare in late winter and late summer.

Nocomis asper is also an abundant and widespread minnow in Spring Creek. It was observed on all 47 visits, and was rare at only two upstream and one downstream locations, though it was not nearly so abundant at most sites as was N. pilsbryi. At Oaks (upstream) in July few fish of any

Table 13. Number of each species of cyprinid seen in 10 snorkling transects on each of 47 visits to Spring and Snake Creeks. Numbers are means of two observations except as noted.

Location	Mo/Yr	km from source	NP	NR	CA	NA	DN	SA	PE
Barretts	07-80	43.4	467	1	104	81	210	1	1
Barretts	08-80	43.4	597	5	171	70	201	22	0
[a]Cedar Cr.	07-80	48.0	227	0	205	183	151	0	0
Cedar Cr.	08-80	48.0	180	0	307	177	273	3	0
Cole's	07-80	25.7	570	4	101	79	49	7	6
Goforth's	07-80	14.9	393	0	268	41	124	24	77
Goforth's	08-80	14.9	227	0	58	25	160	20	155
[a]Lower Baker	07-80	31.9	450	0	145	95	0	0	0
Lower Baker	08-80	31.9	234	0	1	25	11	2	0
Lefty's C.	01-80	44.8	428	0	225	10	294	0	0
Lefty's C.	10-79	44.8	578	0	476	64	436	0	0
Lefty's C.	11-79	44.8	529	0	494	74	281	0	0
Lefty's C.	12-79	44.8	399	0	135	45	93	0	0
Lefty's C.	02-80	44.8	183	0	58	1	3	0	0
Lefty's C.	04-80	44.8	333	0	66	42	253	2	1
Lefty's C.	05-80	44.8	346	0	92	35	444	2	3
[a]Lefty's C.	06-80	44.8	253	0	139	42	175	1	2
Lefty's C.	07-80	44.8	328	0	71	64	168	12	13
Lefty's C.	08-80	44.8	55	0	13	26	14	29	0
Lick Spr.	07-80	23.3	262	1	90	36	10	5	13
Lick Spr.	08-80	23.3	338	0	11	36	20	4	4
Oaks	07-80	0.0	121	0	0	6	19	5	0
Perona's	07-80	27.6	247	1	26	52	11	1	2
Rocky Fd.	07-80	7.2	78	0	441	92	281	20	39
Rocky Fd.	08-80	7.2	63	8	334	57	298	17	83
Teresita Br.	07-80	16.8	107	1	0	20	14	0	21
Teresita Br.	08-80	16.8	127	0	1	16	2	13	2
Teresita C.	07-80	17.5	235	0	0	78	0	23	138
Teresita C.	08-80	17.5	148	0	13	2	0	2	126
Teresita Fd.	07-80	21.3	251	0	15	42	16	2	5
Teresita Fd.	08-80	21.3	275	13	22	35	1	31	37
Timber	01-81	36.0	251	3	13	22	45	3	25
Timber	10-80	36.0	329	12	116	55	170	4	65
Timber	12-80	36.0	275	2	25	29	53	4	29
Timber	02-80	36.0	261	0	253	45	67	4	30
Timber	03-80	36.0	345	1	69	51	46	1	38
Timber	04-80	36.0	255	0	39	39	41	2	23
Timber	05-80	36.0	537	0	46	33	67	5	37
Timber	07-80	36.0	347	15	104	63	158	1	41
Timber	08-80	36.0	512	36	405	110	300	5	112
Timber	09-80	36.0	268	5	108	42	146	3	32
Two Creeks	07-80	3.4	195	0	105	68	111	16	19
Two Creeks	08-80	3.4	312	1	201	68	112	13	0

Table 13. (Continued).

Location	Mo/Yr	km from source	NP	NR	CA	NA	DN	SA	PE
Upper Baker	07-80	31.2	195	11	7	36	0	0	4
Upper Baker	08-80	31.2	211	2	14	17	0	1	0
Upper Snake	07-80	3.4	109	0	242	46	0	54	41
Zehr's	07-80	38.8	458	0	212	106	144	12	10

[a]One observation only.

NP = _Notropis pilsbryi_, NR = _N. rubellus_, CA = _Campostoma anomalum_, NA = _Nocomis asper_, DN = _Dionda nubila_, SA = _Semotilus atromaculatus_, PE = _Phoxinus erythrogaster_.

species except _N. pilsbryi_ were present. At Teresita Cemetary (upstream) in August only two _N. asper_ were seen where 78 were seen in July. Physical conditions had changed little. At Lefty's Camp (downstream) in February only one _N. asper_ was seen though the species was common there in other months. This was true of other species also.

Campostoma anomalum was more abundant than any minnow in Spring Creek except _Notropis pilsbryi_, and more widespread than any except _N. pilsbryi_ and _Nocomis asper_. Like _Dionda nubila_, it was extremely abundant at some locations, with more than 300 seen in ten transects, but absent or rare at others. From Lefty's Camp and Timber data, visited 10 times each, this species seems to have more variation in local abundance with season than other species. This could conceivably relate to the food habits of the animal, since large numbers might be capable of reducing algal standing crop locally for short time periods.

Semotilus atromaculatus was not abundant at any site studied. The largest number seen was 54 at Upper Snake in July. However, it was generally distributed, being absent from only four sites. It exhibited seasonal variation at Lefty's Camp (common in summer, rare in other seasons), but no such pattern was seen at Timber.

The distribution of *Phoxinus erythrogaster* was similar to that of *Semotilus atromaculatus*, but *Phoxinus* was a far more abundant fish. Generally, where one was in greatest abundance, the other was also. An exception to this generalization was seen at Timber where *Phoxinus* was always common, but *Semotilus* was rare.

The distributions described above are difficult to relate to any obvious habitat variability (Table 14). When the entire year is considered *N. pilsbryi* is seen to be more abundant downstream at sites with greater depth and greater depth variability (Table 14), in agreement with Matthews and Shephard (1978). The trend is also present in the summer 1980 data. In addition, in summer, when stream temperature was relatively stable over the two month period of the observations, it was more abundant at sites with greater temperature variability.

Notropis rubellus abundance was not significantly correlated with any factor either throughout the year or in summer. It did show a slight tendency in summer to be more abundant where the bottom was less variable and in downstream locations.

Table 14. Correlations between cyprinid counts and physical habitat mean (MN) and HC values.

Correlations for 47 visits October 1979 - May 1981

	NP	NR	CA	NA	DN	SA	PE
Distance	.471*	.060	.126	.249	.328*	-.498*	-.357*
Bottom MN	-.146	-.008	-.008	.034	-.064	.291*	.329*
Bottom HC	-.170	-.073	-.049	-.017	-.077	.346*	.222
Vegtat MN	.035	.044	.088	.130	.029	.073	.184
Vegtat HC	-.054	.086	.146	.105	.110	.257	.347*
Struct MN	-.086	-.127	-.025	-.308*	.036	.161	.112
Struct HC	-.077	-.072	-.034	-.420*	-.002	.144	.035
Depth MN	.404*	-.133	.107	-.157	.227	-.330*	-.219
Depth HC	.424*	-.036	.007	-.130	.131	-.308*	-.113
Temp MN	-.201	.186	.028	.318*	-.074	.360*	.017
Temp HC	.042	.225	-.040	.352*	-.092	.195	.340*
Current MN	.142	-.159	.260	.019	.185	-.356*	-.276
Current HC	.004	-.082	.217	.083	.226	-.372*	-.227

Correlations for 31 visits July - August 1980**

	NP	NR	CA	NA	DN	SA	PE
Distance	.428*	.196	-.001	.494*	.182	-.367	-.296
Bottom MN	.050	-.131	.212	-.104	.322	.105	.249
Bottom HC	-.010	-.203	-.001	-.265	.165	.152	.180
Vegtat MN	.030	.035	.298	.246	.322	.255	.132
Vegtat HC	-.052	.055	.281	.114	.364	.357*	.327
Struct MN	-.311	-.093	-.062	-.288	-.035	.451*	.179
Struct HC	-.334	-.020	-.111	-.432	-.121	.486	.098
Depth MN	.327	.075	-.190	.074	-.199	-.034	-.025
Depth HC	.338	.150	-.265	.071	-.279	-.032	.064
Temp MN	-.007	.069	.317	.155	.238	.127	-.499*
Temp HC	.426*	.111	.118	.256	.127	-.134	.318
Current MN	-.221	.017	.081	.357*	.052	-.328	-.190
Current HC	-.297	.118	.143	.288	.133	-.253	-.096

*Significant at the .05 level (probability of a larger value of r less than .05).

**Included in the first section also.

The positive correlation with temperature year round is simply the result of more being seen in summer.

Dionda nubila was more abundant at downstream locations. This correlation was not statistically significant in summer. In summer there was an additional tendency for *Dionda* to be more abundant where there was greater variation in vegetation pattern, and some tendency (not statistically significant) for increased abundance with more vegetation and coarser substrates.

Nocomis asper abundance was negatively correlated with mean structure values and structural HC. This reflects fewer *Nocomis* seen where branches, roots, and similar items were most abundant and clumped. Such locations harbor small-mouth and large-mouth bass, and perhaps predator avoidance causes this observed distribution. If this explanation is correct, other minnows should have similar distributions then, but they do not. In summer this fish was more abundant downstream and where currents were stronger as well. Though the longitudinal position tendency persisted throughout the year (but below statistically significant levels), current was not important at other seasons.

Campostoma anomalum abundance did not correlate significantly with any variable. There was a tendency (not statistically significant) in summer for it to be more abundant at warmer locations, and those with more vegetation as well as more vegetational variation, and less abundant where depth was variable. On a year round basis, *C. anomolum* was slightly more abundant where currents were stronger and more variable.

Semotilus year round was rarer downstream at deeper locations, where depth was variable, and currents were strong and variable, and was more abundant where substrates were coarse and variable, as shown by significant correlations. There was a non-significant tendency for it to be more abundant where vegetation varied and structure was high and variable. In summer, distance (rarer upstream), vegetational variability, structure, and structural variability correlations were significant, and the remaining correlations still show the same tendencies as year round.

Phoxinus, on a year round basis, was more abundant upstream, where substrates were coarse, and vegetational variability was high. In summer, though, the most striking thing about its distribution is the correlation of -0.5 with temperature. It was far more abundant at cold (spring fed) locations than anywhere else.

Canonical Correlation

Since the above data were difficult to interpret, a canonical correlation of the abundance data was performed using the SAS program CANCORR (SAS Institute, 1979). Numbers seen in ten transects for each species were treated as dependent variables and distance from the source, mean value for each habitat variable , and HC for each habitat variable were treated as independent variables.

Canonical correlation derives two sets of canonical variables, one set being linear functions of the independent variables and one set linear functions of the dependent variables. Since the original independent and dependent variables are so designated because of theoretical reason to believe the independent ones influence the dependent ones, the correlations of the two sets of canonical variables can then be used to explain the dependent variables' variation.

Two pairs of significantly correlated canonical variables were derived (Table 15). Thus it can be concluded that the cyprinid counts are related to the set of habitat variables. The two habitat canonical variables comprise just a few of all the variables entered. W1 has a large negative correlation with distance, and it explains 75% of the variability in V1. Thus upstream areas may be expected to have relatively large numbers of cyprinids that correlate positively with V1 (_Phoxinus_, Table 15). Downstream areas conversely should have relatively large numbers of cyprinids that correlate negatively with V1 (_Nocomis_ and _Dionda_, Table 15). These conclusions are generally true, though less so for _Dionda_ than for _Phoxinus_ and _Nocomis_ and exceptions are frequent (Table 13).

W2 has a large positive correlation with temperature HC and a large negative correlation with structure HC, and explains 68% of the variability in V2. Thus sites with a wider temperature mix and less variability in amount of structure may be expected to have relatively large numbers of those

Table 15. Canonical correlation analysis of cyprinid counts with habitat variables for 47 visits at 18 sites on Spring Creek, 1979-1981.

Canonical correlations and their significances for variable pairs 1-7

Canonical variable pair	Canonical correlation	Approx. Std. error	Canonical R-squared	F statistic	DF		Prob>F
W1 - V1	0.864	0.038	0.746	1.778	91	158.1	0.0008
W2 - V2	0.823	0.049	0.678	1.462	72	141.8	0.0283
W3 - V3	0.713	0.074	0.509	1.134	55	123.9	0.2800
W4 - V4	0.646	0.088	0.417	0.946	40	104.2	0.5663
W5 - V5	0.542	0.107	0.293	0.741	27	82.4	0.8085
W6 - V6	0.394	0.128	0.155	0.559	16	58.0	0.9010
W7 - V7	0.333	0.135	0.111	0.535	7	30.0	0.8009

Correlations between the habitat variables and their canonical variables

	W1	W2
Distance	- .513	0.197
Bottom MN	0.321	0.168
Bottom HC	0.263	0.037
Vegtat MN	0.126	0.225
Vegtat HC	0.234	0.193
Struct MN	0.260	- .340
Struct HC	0.230	- .517
Depth MN	- .074	- .217
Depth HC	0.016	- .058
Temp MN	- .191	0.225
Temp HC	0.159	0.635
Currnt MN	- .246	- .176
Currnt HC	- .342	- .089

Correlations between the cyprinid variables and their canonical variables

	V1	V2
NP	- .093	0.256
NR	- .150	0.241
CA	- .291	0.090
NA	- .494	0.756
DN	- .421	0.081
SA	0.368	- .134
PE	0.721	0.389

species that correlate positively with V2 (Nocomis, Table 15). This is generally true, but exceptions are also common. The sites best described by V2 are generally located in downstream areas (Table 1, Chapter IV) so this conclusion is supportive of that drawn from the V1 - W1 relationship. According to this analysis habitat variability seems to have little relationship to variations in abundance of other species.

Species Relationships

Correlations among cyprinid counts for summer 1980 and the entire year (Table 16) show that Nocomis, Dionda and Campostoma were abundant together, and that there was a tendency for Notropis pilsbryi to be included in this grouping. There was also an association among Notropis rubellus, Phoxinus, and Semotilus, though N. rubellus was only weakly included. From the canonical and simple correlations these two groupings are roughly downstream, variable habitat groups and upstream, simpler habitat groups. Since the results are not clear cut, these are tentative conclusions, but Campostoma, Nocomis and Dionda clearly form a species cluster of strong association.

Summary

Examination of the pattern of individual cyprinid species' distributions with respect to longitudinal position and habitat variation is inconclusive. Canonical correlation pro-

Table 16. Correlations among cyprinid counts on 47 visits to Spring Creek, October 1979 - May 1981.

		All Dates						
		NP	NR	CA	NA	DN	SA	PE
Summer 1980	NP		.197	.321*	.238	.371*	-.261	-.131
	NR	.327		.181	.166	.191	-.003	.333*
	CA	.153	.319		.520**	.733**	.090	.035
	NA	.309	.136	.621**		.381**	.020	.050
	DN	.206	.368*	.819**	.599**		-.128	-.025
	SA	-.188	-.076	.234	-.133	.004		.320*
	PE	-.081	.281	.170	-.114	.220	.278	

*Significant at the .05 level
**Significant at the .01 level

vides some explanation for this. Habitat variation does influence the distributions of *Phoxinus*, *Dionda* and *Nocomis* but for other species no specific variables are identifiable as most important to distribution. Also, local variability of a variable (HC) frequently is more important than the mean value for that variable (Table 15). Further, the influence of habitat variables on abundance seems to be exerted on the cyprinid association rather than on a single species at a time. This conclusion is not to imply that these animals form a unified set in a super-organismic fashion or that a single species cannot have population fluctuations. Rather, any influences of habitat on one may be transferred throughout the association by positive and negative biotic interactions. These effects would of course include non-cyprinid species, a factor this study cannot address.

The above idea is reinforced by the finding that individual species correlate more strongly with each other than with either separate habitat variables, or with habitat canonical variables.

CHAPTER X

MICROHABITAT USE

Microhabitat use by 52,246 cyprinids was assessed by the snorkling procedure detailed in Chapter III. For purposes of microhabitat analysis, temperature was converted to a value of 0 (more than 1° C cooler than the mean for a site), 1 (within 1° C of the site mean), or 2 (more than 1° C warmer than the site mean). This excluded seasonal variation in temperature from affecting the analysis.

Since the cyprinids were not originally recorded as individuals, but as members of groups or aggregations, they are not truly individuals in a statistical sense. The score of a given fish on a particular variable is in fact derived from the score of a group of fish of which it is a member. This must be considered in the statistical analysis which follows, where they are treated as individuals. Also, the error in recording cyprinid numbers is unknown, although it is believed to be consistent.

The means for each cyprinid species on each of eight microhabitat variables are reported in Table 17. From these data emerges a picture of seven species each of which uses microhabitat in a widely variable and inconsistent pattern.

Table 17. Means (MN) ± S.D. (SD) for seven cyprinid species on eight microhabitat variables. Data from snorkling at 18 sites over 19 months in Spring Creek.

Variable	Species														All Species	
	CA		DN		NA		NP		NR		PE		SA			
	MN ±	SD	MN ±	SD	MN ±	SD	MN ±	SD	MN ±	SD	MN ±	SD	MN ±	SD	MN ±	SD
[a]HP (1-2)	1.5	.5	1.4	.5	1.6	.5	1.4	.5	1.4	.5	1.2	.4	1.2	.4	1.5	.5
VP (1-3)	2.9	.3	2.4	.5	2.7	.5	2.3	.5	2.0	.6	2.2	.4	2.4	.5	2.4	.5
S (0-6)	3.0	1.7	2.9	1.7	2.8	1.5	2.6	1.4	2.5	1.2	3.1	1.5	2.7	1.7	2.8	1.5
V (0-5)	1.5	1.4	1.7	1.4	1.6	1.5	1.5	1.4	1.7	1.6	2.0	1.6	2.1	1.6	1.6	1.4
St (0-5)	1.1	1.3	1.2	1.3	1.2	1.3	1.2	1.3	1.4	1.5	1.5	1.4	1.7	1.5	1.2	1.3
D (cm)	53.7	29.5	54.8	28.0	51.7	27.3	63.7	30.1	53.3	26.2	39.5	18.1	39.0	22.1	57.5	28.7
C	5.9	8.1	5.5	8.2	5.8	10.2	6.0	9.7	9.9	12.6	4.6	6.4	3.0	5.2	5.8	9.1
T (0,1,2)	1.0	.2	1.1	.3	1.0	.3	1.0	.3	.9	.2	1.1	.4	.9	.4	1.0	.3
Number* seen	9767		9801		4306		25040		282		2316		734		52,246	

*These values are based on the number recorded while snorkling.

[a]HP = horizontal position, VP = vertical position, S = substrate, V = vegetation, St = structure, D = depth, C = current (cm x sec^{-1}), T = temperature.

A group of 10 fish at a substrate value of 3 is equivalent to 10 separate individuals each at a value of 3.

However, a few generalizations may be drawn.

Notropis pilsbryi and *Campostoma* can be called midstream fishes and *Phoxinus* and *Semotilus* are edge species. *Campostoma* and *Nocomis* are benthic, while *Notropis rubellus* is a near surface form.

Phoxinus is found over coarser substrates than the other species, and *Notropis rubellus* over finer substrates. *Semotilus* and *Phoxinus* have higher values for vegetation than others, and *Notropis pilsbryi* and *Campostoma* have lower values. *Semotilus* occurs with higher structural values than others, and *Campostoma* with lower. *Notropis pilsbryi* prefers deeper water than the other species, while *Phoxinus* and *Semotilus* prefer shallower water. *Notropis rubellus* occurs in stronger currents than any other minnow in the study, and *Semotilus* in the slowest currents. *Semotilus* and *Notropis rubellus* show some tendency to be associated with cooler, and *Phoxinus* and *Dionda* with warmer, water than the other species within a site.

To some degree the microhabitat relationships cited above reflect distributional patterns described in Chapter Nine, and in fact might partially explain those patterns. *Semotilus* is apparently an edge fish and upstream habitats with narrower streams should have a higher proportion of total habitat as edge. As all species had very wide variation in microhabitat use as indicated by the large standard deviations, I used a multi-variate technique to attempt better resolution of the relationships.

Discriminant Analysis of Microhabitat Use

The multivariate technique used was stepwise discriminant analysis. The analysis was performed with BMDP program P7M (Jennrich and Sampson, 1979) through the SAS interface program BMDP (SAS Institute, 1979) as for the food habits analysis. The groups to be discriminated by the analysis were the seven species, and the variables used were the microhabitat variables described above. Each cypinid of the 52,246 recorded was assigned a value for each of the 8 variables based on the value recorded for the habitat space it occupied, usually as a member of a school or aggregate.

The analysis completed eight steps and all eight variables were included in step eight. The order of their contribution to discrimination, based on F to remove values was vertical position, depth, horizontal position, vegetation, structure, temperature, substrate, and current. The eighth step is summarized in Table 18. Overall the analysis was statistically significant (Wilks' Lambda = 0.71, approximate F = 388.2 with 48 and 257,007 d.f., probability of a larger F is less than 0.001). However, as stated earlier, this is not always a good criterion of a useful discrimination.

The centroids of the seven species differ significantly from each other (Table 18). This may be interpreted to mean that the niche centers are well separated. It says nothing about the overall discrimination, or the degree of niche confusion.

Table 18. Discriminant analysis of minnow species by microhabitat use: Step number eight.

Wilks' Lambda	0.71	D.F.	8	6	52,239
Approximate F	388.2**	D.F.	48	257,007	

	^{a}F-Matrix		D.F.	8	52,232	
	CA	DN	NA	NP	NR	PE
DN	582.81					
NA	77.28	169.45				
NP	1503.67	342.63	498.11			
NR	117.20	39.95	72.63	26.86		
PE	701.42	196.88	350.63	423.37	37.48	
SA	221.74	93.04	113.37	158.46	36.47	38.07

** Significant at .001 level

[a] All values are significant at .001 level.

Variables used (listed in order of contribution to discrimination): vertical position, depth, horizontal position, vegetation, structure, temperature, substrate, current.

Table 19. Discriminant analysis of minnows by microhabitat use: Classification matrix.

Species	PerCent Correct	Number of Cases Classified into Species						
		CA	DN	NA	NP	NR	PE	SA
CA	59.6	5823	30	2198	467	435	343	471
DN	0.4	2558	35	1287	2144	1378	1567	832
NA	17.9	1910	37	771	323	400	330	535
NP	36.7	4884	503	1814	9181	4127	2401	2130
NR	30.9	42	2	21	63	87	54	13
PE	39.0	200	1	142	325	232	903	513
SA	39.2	98	10	82	48	50	158	288
Total	32.7	15515	618	6315	12551	6709	5756	4782

The classification matrix is presented in Table 19. Only 32.7% of all cyprinids were correctly classified. No species except *Campostoma* was correctly classified more than half the time, and only 0.4% of all *Dionda* were correctly classified. Though statistically the fish were correctly classified more often than expected by chance, the analysis was not able to distinguish them effectively on the basis of the microhabitat variables.

The distribution of the classifications can still be instructive. Most misclassified *Campostoma* were assigned to *Nocomis*, the other benthic species. These two are very different in terms of food habits. Misclassified *Dionda* were assigned to all other species, though most frequently to *Campostoma* and *Notropis pilsbryi*. *Dionda* seems to have a very broad microhabitat niche in Spring Creek. *Nocomis* individuals, second only to *Dionda* in misclassification frequency, were assigned mostly to *Campostoma* but also frequently to all other species except *Dionda*. *Notropis pilsbryi* were assigned most frequently to their own group, *Campostoma*, and to their congener *N. rubellus*, but also frequently to other species. *Notropis rubellus* misclassifications were assigned mostly to *N. pilsbryi*, *Phoxinus*, and *Campostoma*. *Phoxinus* individuals were usually assigned to *Semotilus* or *N. pilsbryi*, but frequently also were assigned to all species except *Dionda*. *Semotilus* not correctly classified were generally classified as *Phoxinus* or *Campostoma*, but some were assigned to each group.

The most striking thing about this analysis is the lack of ability to correctly classify the fish from microhabitat data. In a general kind of way, each species is shown to be distinct from others, as shown by the F-matrix in Table 18. Even _Dionda_ is identified as having a microhabitat use centroid which differs significantly from that of each other species. But the breadth of overlap along discriminating variables is so broad that most species' total niche space can only be described as very much like that of each other species. This is most striking in the case of _Dionda nubila_, which evidently uses microhabitat in such a general way that individuals or groups are apt to be found in any space habitable by cyprinids in Spring Creek. Interestingly enough, this form is highly specialized in food niche, though it is poorly discriminated there also (Chapter VIII).

It is still a worthwhile exercise to examine details of the analysis. Six canonical variables were derived by step eight (Table 20). Of these, the first 2 account for 96 per cent of total group dispersion, and exhibit moderate canonical correlations with species (0.46 and 0.30). The remaining canonical variables contribute little to total dispersion and do not correlate well with species.

The coefficients for canonical variables I and II are presented in Table 21. Variable I consists almost entirely of vertical position, and variable II is mostly horizontal position and temperature. Thus, in terms of discriminating among these species, positional information seems

Table 20. Canonical variables derived from discriminant analysis of seven cyprinid species by microhabitat use, their eigenvalues and cumulative and relative per cent contribution to total dispersion and canonical correlations with species (group variables).

Canonical variable	Eigen value	Cumulative Per Cent	Relative Per Cent	Canonical Correlation
I	0.27	70.	70.	.46
II	0.10	96.	26.	.30
III	0.01	99	3.	.10
IV	0.00	99.5	0.5	.05
V	0.00	99.8	0.3	.03
VI	0.00	1.0	0.2	.03

Table 21. Coefficients for original microhabitat variables on the first two canonical variables.

Variables	I	II
Horizontal	-0.10	1.05
Vertical	2.06	0.37
Substrate	0.01	-0.08
Vegetation	0.05	-0.28
Structure	-0.04	-0.21
Depth	-0.00	0.02
Current	-0.01	0.00
Temperature	0.13	-0.67

more useful than physical descriptions of the habitat. Even temperature in the present example might be viewed as a positional variable since the temperature gradients within sites generally were uniform and resulted from ground water flow into one side of the stream, and sometimes from insolation over a shallow edge. Overall, however, these species have poorly defined habitat niches in comparison with the cyprinids studied by Baker and Ross (1981) and Mendelson (1975). To the extent that habitat separates these fish they are similar to Southeastern and Midwestern stream cyprinids in being distinguished by stream position, and unlike lake cyprinids (Moyle, 1973) which are distinguished by physical microhabitat variables.

A plot of the mean scores of each species on Canonical Variables I and II is presented in Figure 7 to illustrate average niche relationships of the animals. Plots of individual scores or total multi-dimensional space occupied as for food habits are not presented due to the extremely large number of points involved.

Campostoma is shown to be benthic, as is *Nocomis*, while *Notropis rubellus* is a near surface species. *Phoxinus* and *Semotilus* occur at the stream edge while the other species are found nearer the middle. These results confirm the conclusions from the examination of individual variables. It cannot be emphasized strongly enough that for all species except *Campostoma anomalum* the adherence to these generalizations is so slight that any one of the cyprinids might

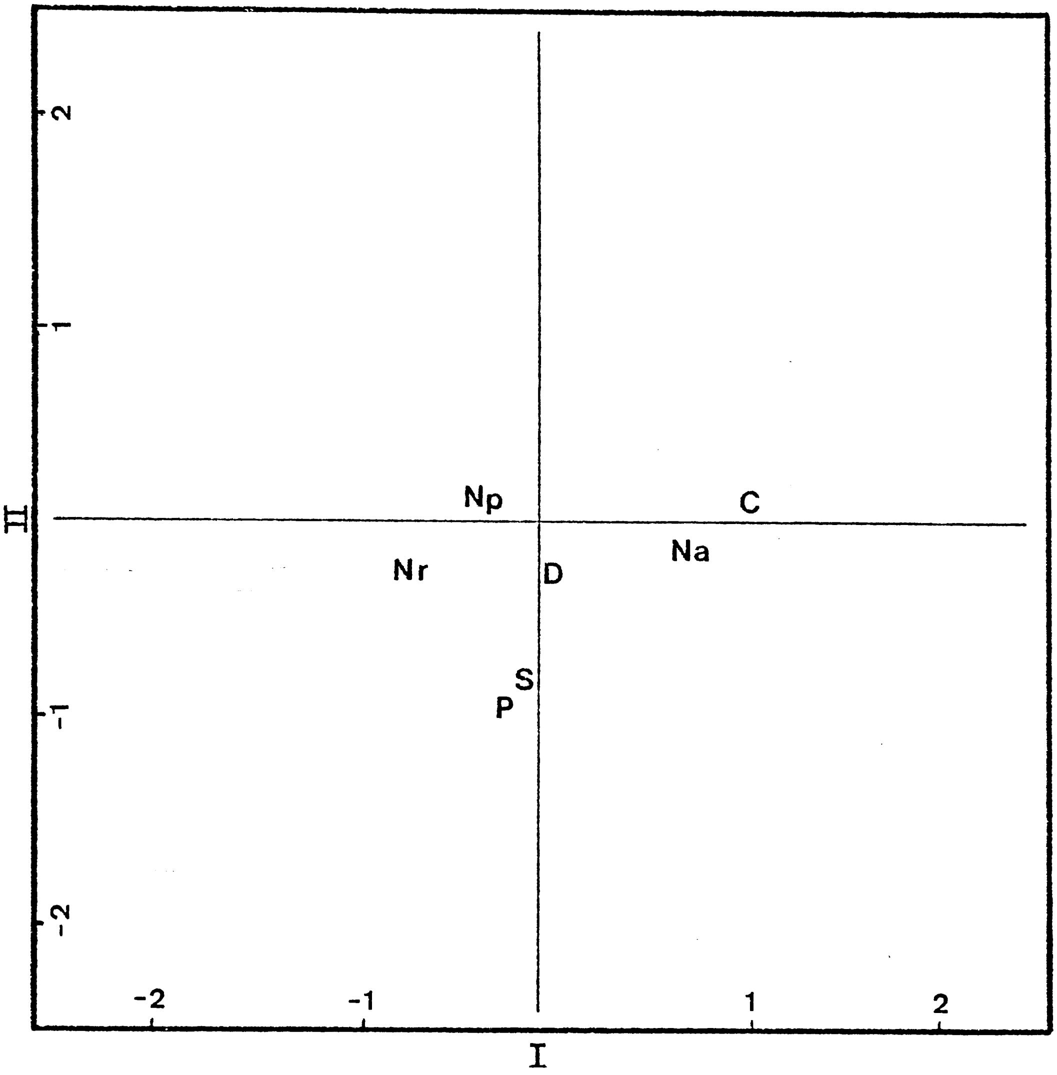

Figure 7. Mean positions of seven cyprinid species on canonical variables I and II from microhabitat discriminant analysis. Species symbols as in Fig. 6.

be found almost anywhere in the stream, in any sort of microhabitat.

CHAPTER XI

DISCUSSION AND EXTENSION

Microhabitat and Food Niches: A Comparison

It seems evident that the cyprinids of Spring Creek can be ecologically described in a way that illustrates individuality. Recognition of this distinctiveness requires consideration of both food and space resources. Discriminant analysis of food habits and microhabitat, and canonical correlation of macrohabitat demonstrate that food niches are more distinct than habitat niches.

Each species examined exhibits a tendency to be more frequent in some habitat types than in others. However, this tendency allows effective separation only for *Campostoma anomalum* which is strongly benthic. The other species are present in all habitat types.

Differences in food habits effectively allow identification of groups of carnivorous and omnivorous cyprinids, but herbivorous species are poorly discriminated. Of these herbivores, *Campostoma* is a habitat specialist.

The remaining herbivores, *Dionda* and *Phoxinus*, are similar in microhabitat use. However, *Phoxinus* is more limited in distribution than is *Dionda*, and the two species are not generally associated (if such a statement can be made in this fauna - they do occur at common sites). *Dionda* shows some tendency to be a downstream, complex habitat species, and *Phoxinus* to be an upstream, simple habitat form.

Schoener's prediction (1974) that aquatic vertebrates should be more dependent on food niche specialization than on habitat specialization is partially borne out by this study. However, recent findings of habitat segregation by cyprinids, particularly the importance of vertical position (Mendelson, 1975; Ross and Baker, 1981) are also supported, though less strongly.

Enough evidence now exists to say that cyprinid niches vary considerably from place to place, including mainly trophic specialization (Spring Creek), mainly habitat specialization (Mendelson, 1975, small Wisconsin stream) and lack of specialization due to habitat instability (Harrell, 1978, Devil's River, Texas; Matthews and Hill, 1980, S. Canadian R., Oklahoma). This is not surprising, but is in contrast to the mainly habitat specialization exhibited by darters (Jones, 1981; Lehtinen, in preparation).

Niche Plasticity and Habitat Stability: Speculation

Spring Creek habitats seem to be too homogeneous to support a typically diverse Ozarkian cyprinid fauna and the established fauna may prevent penetration by additional species because of full utilization of resources. Habitat homogeneity, coupled with trophic separation, support this hypothesis. But other explanations are available since the stream is spatially but not temporally homogeneous.

In 1980 extremely dry conditions during summer and fall led to drying of many Spring Creek habitats. Much of the discharge was in fact subsurface. This low flow reached severe limits beginning in mid-July and ending when fall rains occurred in October. As is common to upland streams (Starrett, 1951; Matthews and Styron, 1981), this drying effect was most severe in the headwaters. Headwater springs ceased to flow early in the summer and the headwaters had longer stretches of dry channel than did downstream areas. Because the stream is spring fed both in headwaters and lower reaches the habitat is similar in the two regions, but under drouth conditions headwater habitats are less permanent than downstream ones.

Misclassification of an individual by discriminant analysis indicates that that individual uses resources similarly to another species. It is located in the niche space of that other species. This is a working definition of niche overlap. A corollary to this definition is that any environmental factors which reduce niche overlap should also reduce misclassification frequency.

Zaret and Rand (1971) showed that in tropical stream fish, overlap is inversely related to competitive intensity. Numerous authors, including Sale (1974), Werner and Hall (1977), and Lister (1981) have supported this hypothesis and in fact treated low overlap as evidence of present or past competitive control of niche and community structure. As an extension of this hypothesis, I believe that misclassification frequency may also be used as an index to competition; more misclassification implies less competition.

Many variables have been claimed to alter competitive relationships and thus influence niche interactions. These include population density, habitat stability, and habitat complexity. I used my inverse measure of competitive intensity (% misclassification) against these three variables by correlating % misclassification by location with cyprinid numbers (from snorkling), HC, and distance downstream (which I equate with stability) (Table 22). The correlations are equivocal. In no species or the species collectively is percent misclassification significantly correlated with either cyprinid numbers or HC for either food or microhabitat. However, all species together do show a significant inverse correlation (r = -.39, d.f. = 45) of food habits percent misclassification with distance downstream. This relationship is due largely to the data for <u>Dionda</u> <u>nubila</u> (r = -.37, d.f. = 39). In addition there is a significant correlation

Table 22. Correlations of per cent misclassification by discriminant analysis with HC, distance downstream, and cyprinid counts.

Species	No. Dates	Food Habits			No. Dates	Microhabitat		
		HC	Distance	Cyprinid counts		HC	Distance	Cyprinid counts
Campostoma	(39)	.078	-.069	-.120	(44)	-.020	.010	-.263
Dionda[a]	(41)	.039	-.372*	.147	(42)	-	-	-
Nocomis	(45)	-.041	.145	-.006	(47)	.084	-.111	-.022
N. pilsbryi	(47)	-.141	.050	-.007	(47)	-.102	-.351*	-.064
N. rubellus	(14)	.258	-.077	-.313	(20)	-.177	.286	.055
Phoxinus	(30)	-.058	-.186	.024	(33)	-.174	.078	-.041
Semotilus	(21)	-.189	-.067	.105	(39)	-.146	.087	.242
All cyprinids	(47)	-.208	-.393**	.010	(47)	-.040	-.174	-.127

[a] 99.6% of all *Dionda* were misclassified on the basis of microhabitat.

in the data on microhabitat for N. pilsbryi (r = -.35, d.f. = 45), though there is no significant relationship of microhabitat percent misclassification to distance for all species combined.

Habitat instability might explain the observed differences in percent misclassification. MacArthur (1972) predicted increases in species diversity and related that prediction to an expected increase in niche overlap in stable environments. He later said that the prediction did not fit the real world, and that in fact niche overlap and stability are unrelated except at the extremes of the stability-instability spectrum (May and MacArthur, 1972). Despite this more recent result, and the demonstration by Pianka (1975) that it applies to desert lizards, others have continued to follow the earlier prediction, and have cited their own results as confirmation of it (Inger and Colwell, 1977; Lister, 1981). Lister (1981) suggested an increase in predation rates in stable environments as an explanation, and Paine (1966) had earlier shown that predation can increase species diversity. Regardless of the inconclusiveness of this series of studies and reports, no where is there any evidence that competition theory would predict increased misclassification (niche overlap) in unstable environments as I have found.

In contrast, others have claimed that instability may increase niche overlap by encouraging opportunism at the expense of specialization (Sale, 1977; Wiens, 1974, 1977; Rotenberry, 1980). According to their interpretations, in non-equilibrium systems specialization may be maladaptive regardless of the presence or absence of potential competitors because of environmental uncertainty. In this hypothesis competition is obviated as a controlling mechanism.

Two Spring Creek cyprinid species (Dionda nubila and Notropis pilsbryi) then seem to exhibit what is potentially an interesting relationship to habitat stability. Where habitat is more stable (downstream) they are faithful to their own niches, but where it is less so (upstream) they overlap more into the niche space of others. This result appears to be at odds with some aspects of niche theory (MacArthur, 1972; May and MacArthur, 1972; Lister, 1981), particularly the predictions of competitionists that environmental stability should either increase niche overlap or not affect it.

The cause of this relationship may be found in the relationship of habitat stability to opportunism claimed by noncompetitionists, particularly Wiens, in the above cited contributions. These authors contend that unstable systems, or temporally variable ones, are not in ecological equilibrium, and that such systems may be more common than those in equilibrium. In my opinion however, both types of systems surely exist, and it seems that many locations should contain traces of both. Spring Creek may be of this latter type, with competition predominating downstream, but not upstream.

Roughgarden (1972, 1974a, 1974b) has explained how generalism may be due to either a single broadly adapted phenotype, or to a population of individual specialists. The former type of generalists should have low genetic diversity, the latter high genetic diversity. Gillespie (1974) argued that genetic polymorphism should increase in environments that are either spatially or temporally heterogeneous and cited Avise and Selander (1972) who found that cave fish (characidae; Astyanax) have less genetic diversity than their surface relatives. Caves are extremely constant and simple environments. Bryant (1974a, 1974b) found that in a large series of studies climatic instability correlated with degree of genetic polymorphism in both vertebrates and invertebrates.

Both Dionda and N. pilsbryi are generalist species, Dionda for habitat and N. pilsbryi for foods. Upstream each tends to generalize additionally on a second dimension. If niche generalization, especially under habitat instability, does result from underlying genetic diversity, as is suggested above, then a generalist on one dimension may be preadapted to generalize on an additional dimension. If not, then one should not expect a microhabitat generalist to have any preadaptation to trophic generalism or vice versa.

A continuation of this study to substantiate and clarify the role of environmental instability in cyprinid niche interrelationships is appropriate. Such a study should focus on generalist species, should be expanded to other drainages, and should be long term so as to ascertain the generality of any stability-niche relationship. In addition the study should examine the movement of fish and degree of mixing of upstream and downstream groups. Presently the vagility of stream cyprinids is uncertain, though it is believed to be high (Pflieger, 1975). If vagility is high, then it is unlikely that headwaters populations could maintain a genetic diversity greatly different from that of downstream populations. Finally, genetic diversity should be measured. A greater frequency of enzyme polymorphism might be expected in the headwaters if vagility is not too high and if environmental instability does prevent niche specialization and favor generalization in the way I've hypothesized.

I feel compelled to restate the speculative nature of this section. I have no data on the genetics of these fish. This study was short term, about two years, and studies over a several year period might not substantiate the results. Wiens, in a personal communication to the Zoology Department of Oklahoma State University (1979) advocated at least ten years of data, and preferrably more before accepting the results of studies like this one. Though I used large numbers of fish for the food habits analysis, at some sites the samples for some species were small, though that was not the case for either <u>Dionda</u> or <u>N</u>. <u>pilsbryi</u>.

CHAPTER XII

SUMMARY AND CONCLUSIONS

Stream fish ecology has traditionally focused on autecological rather than synecological studies. This has left (unanswered) the question of complexity of community organization of stream fishes, and of the role of this group of vertebrates in competition and niche theory. This study has specifically attempted to answer two questions which could contribute to this important general area of ecology. First, to what degree are habitat and trophic niche partitioning related to stream fish community organization? Second, is niche segregation in such communities related to habitat diversity, longitudinal zonation, or both and if so, is competition inferred as a cause of such a pattern?

The cyprinid fauna of Spring Creek was selected for this study for several reasons. The stream has a variety of habitats, but variation is not due to longitudinal zonation. The fauna is small, only eight species. All common species are widely distributed in the stream.

Spring Creek fish species diversity follows the pattern described by Gorman and Karr (1978) for small streams of increasing diversity with increasing habitat complexity, but not that generally true of many streams of increasing diversity with downstream position. This is probably due to habitat complexity being no greater downstream, generally, than upstream. The least complex habitats in Spring Creek are in the middle reaches, and that is where the least diverse communities are located. The habitat complexity pattern may result from the gradient distribution of the stream.

Six common cyprinid species in Spring Creek are divisible, from examination of the gut contents of 1776 individuals and discriminant analysis of the importances of individual food types, into two feeding groups. Campostoma anomalum, Dionda nubila, and Phoxinus erythrogaster are herbivorous and detritivorous. Notropis rubellus, Semotilus atromaculatus, and Nocomis asper are carnivorous. A seventh species, Notropis pilsbryi, is an omnivore. The herbivores are not readily distinguishable from one another trophically, though finer distinction of food types might make that possible. The carnivores and the omnivore are quite distinctive. Nocomis asper specializes on large benthic items. Semotilus atromaculatus and Notropis rubellus specialize on aerial and terrestrial items, though both use moderate quantities of benthic foods. They are sufficiently distinct trophically for discriminant analysis to correctly identify most individuals from their foods. Notropis pilsbryi is also readily distinguishable, despite its catholic diet, from the other cyprinids.

Analysis of distributions of these seven species in Spring Creek revealed a pattern of habitat generality of the fauna. This observation does not mean that there is no habitat specialization, but rather that suitable habitat is widespread and general in distribution and that habitat influences these minnows in a complex way. There is some evidence from these data that *Campostoma*, *Dionda*, and *Nocomis*, and to a lesser extent *Notropis pilsbryi* are downstream complex habitat forms and that *Semotilus*, *Phoxinus* and to a lesser extent *Notropis rubellus* are upstream simple habitat forms. Lack of a consistent relationship of habitat to longitudinal position obscures the pattern, and what is seen is two clusters of broadly overlapping species.

Each species except *Dionda nubila* is shown to have, on the basis of discriminant analysis, some microhabitat specialization. Only *Campostoma anomalum* is sufficiently specialized to be consistently distinctive from other species, however. Rather, for each of the other forms there is a general concentration in one microhabitat type. For *Campostoma*, and to a lesser degree for other species, microhabitat specialization is more positional than due to typical physical variables. This is consistent with earlier studies of stream cyprinids.

When trophic and habitat-microhabitat niche patterns are considered together there emerges a pattern of mainly trophic specialization, especially by carnivores, reinforced and supplemented by a weaker pattern of habitat specialization, especially by herbivores. The four carnivorous-omnivorous species are trophically well separated. The three herbivores are poorly separated, but *Campostoma* has microhabitat specialization, and *Phoxinus* and *Dionda* show some tendency to be separated by location.

Spring Creek habitats are temporally unstable due to periodic drouths. This is most striking in upstream reaches. On the basis of per cent misclassification by discriminant analysis, cyprinids in general, and the habitat generalist *Dionda nubila* and food generalist *Notropis pilsbryi* in particular, exhibit less niche fidelity in upstream reaches. Though this is a tentative conclusion, and more complete data are needed, suggestions as to why this may exist are appropriate.

If upstream regions are unstable, i.e. unpredictable, then the best niche strategy may be to remain opportunistic. This could allow the appropriation of whatever niche space presents itself. This strategy could result in greater variability from individual to individual than would strong specialization. It could work only where competition is low. Periodic perturbations can reduce competition by reducing competitor numbers. Upstream populations of less specialized species, or less specialized populations of widespread species could both work in this way. The latter appears to be the case in Spring Creek. This could be either a functional or an evolutionary response to instability in the same sense as Thomson (1980) defined functional and evolutionary responses to competition. That is, it may be accomplished either opportunistically or by the formation of ecotypes. This follows Roughgarden's (1972, 1974a, 1974b) descriptions of generalism. Additional information, including both genetic and distributional data as well as data on frequency and rate of movement of populations could clarify this phenomenon.

This study supports conclusions that stream cyprinids are ecologically distinct, mainly by foods, but also by habitat, expecially positional microhabitat. This pattern is blurred in Spring Creek by habitat instability similar to the niche inconstancy demonstrated by the earlier cited studies of grassland birds by Wiens and Rotenberry. Competition has probably contributed to the pattern, especially downstream, where the habitat is more stable but HC is comparable to that upstream.

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VITA

David L. McNeely

Candidate for the Degree

Doctor of Philosophy

Thesis: NICHE RELATIONSHIPS OF THE CYPRINID FISHES OF SPRING CREEK, A TRIBUTARY OF THE NEOSHO RIVER, OKLAHOMA

Major Field: Zoology

Biographical:

Personal Data: Born 2 February 1945, Fort Worth, Texas. Parents John and Minnie McNeely. Married Bonnie Nell Michaels, 11 August 1967. Daughter Frances Camille born 10 April 1974.

Education: Graduated J.F. Kimball High School, Dallas, Texas 1963. Bachelor of Science in Biology, University of Texas at Arlington, 1967. Master of Science in Aquatic Biology, North Texas State University, 1972. Graduate study in Zoology, University of Oklahoma and Oklahoma Biological Station 1974-75. Completed requirements for the Doctor of Philosophy in Zoology with a specialization in fish ecology, Oklahoma State University, July, 1982

Professional Experience: Public high school biology teacher, Dallas, Texas 1967-70, and Big Spring, Texas 1972-74. Graduate Teaching Assistant and Environmental Protection Agency Graduate Trainee, North Texas State University 1970-72. Graduate Teaching Assistant, University of Oklahoma 1974-75. Graduate Teaching Assistant, Oklahoma State University 1975-76. Biology Instructor, Tulsa Junior College 1976-81. Biology Instructor, Grayson County College, Denison, Texas 1981 to present.

Professional Affiliations: Ecological Society of America, AAAS, American Institute of Biological Science, American Society of Ichthyologists and Herpetologists, Southwest Association of Naturalists, National Association of Biology Teachers.

Honors: NSF Summer Fellow, 1971; Phi Sigma; Sarkey's Foundation Scholarship Summer 1974, Summer 1975, Oklahoma Biological Station.