THE EFFECTS OF ENVIRONMENTAL VARIABILITY AND RESOURCE AVAILABILITY ON THE NICHE STRUCTURE OF A DARTER COMMUNITY IN SALT CREEK, OSAGE COUNTY, OKLAHOMA

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PREFACE

The purpose of this study was to investigate how environmental variability, competition and resource availability interact to affect niche relationships and communtiy structure of a darter community in Salt Creek, Oklahoma.

I wish to thank Drs. O. Eugene Maughan, Stanley F. Fox and Sterling L. Burks for serving as members of my graduate committee. Grateful appreciation is extended to Dr. Rudolph J. Miller, my adviser, for his guidance and encouragement. I also wish to express appreciation to Ms. Iris McPherson who helped with the computer analyses and to Ray Jones who drew the figures in the text.

I am especially grateful to Stephen P. Vives, Linda J. Whitman, Sharon K. Bontrager and D. Allen Rutherford for their ideas, suggestions and friendship. Valuable field assistance was kindly contributed by Phyllis M. Lehtinen, E. David Wiseman and David L. McNeeley. A note of thanks is extended to Donetta Bantle for her typing. I also wish to express my gratitude to other graduate students and friends for their contribution to this thesis.

I acknowlege with special appreciation my parents, Mr. and Mrs. Harold A. Lehtinen, and my brother, Keith, whose encouragements have supported me throughout my education. I wish to thank Dr. Anthony A. Echelle, my master adviser and deeply respected friend, for making me aware of the mystery of nature and for his support and encouragement throughout my graduate education.

Last, and most important, I extend my deepest gratitude to my wife, Phyllis, whose never ending love and support are my inspiration.

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CHAPTER I

INTRODUCTION

In the past 20 years ecologists have become increasingly interested in the patterns of structure and organization in natural communities. Early researchers investigated the structure of communities by comparing species diversity and its associated components with the diversity of the environment the organisms inhabited (MacArthur, 1964; Cody, 1966; Karr, 1968; Pianka, 1967, 1969; Rosenzweig and Winakur, 1969). Generally, these studies demonstrated that bird, lizard and mammal community species diversity increased with increasing complexity of the vegetative habitat. More recently, ecologists have become concerned with understanding the effects of niche breadths, niche overlaps, species packing and guild structure on patterns of community organization (Cody, 1974; Cody and Diamond, 1975; Pianka, 1977; Pianka et al., 1979; Joern and Lawlor, 1980).

The patterns of community structure and organization revealed by investigating species diversity or niche dynamics are inherently based on ways various members of a community relate to and interact with each other (Pianka, 1973). Thus competition has been proposed to play a major role in the organization and structure of communities. With this underlying assumption in mind many biologists have made use of the competitive exclusion principle (whenever 2 or more species vie with one another for some feature of their environment that normally limits population growth, one will eventually replace the other) to explain niche shifts or niche separation between members of communities (Pianka, 1978; Cody and Diamond, 1974; Zaret and Rand, 1971).

Though some theoretical treatments of community structure assume competition, documentation of the role of competition in natural field communities has proven extremely difficult. There are several reasons for this. The first is that though it is possible to actually witness competitive interactions between organisms (as agonistic behavior), the overall impact of competition on community structure can only be documented over extended periods of time, usually longer than the observer can spend in the field. Second, interpreting observed community patterns within the existing framework of competition theory may be difficult because the theory oversimplifies nature by making four major assumptions. These oft-neglected assumptions are: 1) selection on the system of attributes considered is continuous and intense; 2) the system (populations, guilds, or communities) is at an equilibrium defined by resource limitations; 3) predation and environmental variability do not prevent population levels from reaching sizes where competition becomes intense; and 4) changes toward an optimal solution to competition do not lower but rather increase fitness

(Weins, 1977). These assumptions have led Weins (1977) to suggest it may be extremely difficult to document the role of competition in nature, especially if environments vary through time.

One way to document the role of competition in structuring natural field communities is provided by addition or removal experiments whereby the population density or niche use of a species is monitored in the presence and in the absence of its competitor, in an unchanged environment. Either density changes or niche shifts in response to the presence or absence of a competitor constitute direct evidence of interspecific competition under such conditions (Pianka, 1980). Unfortunately, when dealing with natural field communities such manipulations are difficult to accomplish and are open to question because they usually lack suitable controls (Colwell and Fuentes, 1975; Connell, 1975). An indirect way of documenting the role of competition on community structure of natural field populations was developed by Zaret and Rand (1971), who proposed to test the effect of competition on community structure by collecting data on shifts in species niche overlaps during different seasons in the tropics.

Information about species niche overlaps (e.g., habitat and diet) alone tells little about the nature of competition. However, if concurrent measurements of resource supply are obtained (a procedure rarely followed in community studies) seasonal variations in the resource base should bring about changes in the intensity of competition which should in turn be correlated with niche overlap measures. For example, if food supply and diet overlap are positively correlated, the situation could be interpreted as being competitively relaxed when both measures are high (Pianka, 1978). However, if food is in short supply, low dietary overlap could be interpreted as describing a more competitively intense situation. If correlations exist between resource availability and niche overlap and they tend to be predictable, competition may play a major role in the structure and organization of the community at hand.

Most studies on the community structure of natural populations have been conducted on the highly observable lizard and bird faunas, though several have dealt with the more cryptic small mammal communities (Pianka, 1978; Cody and Diamond, 1975; Brown, 1975). However, few quantitatively sound studies have been conducted on community structure in fishes. The studies that do exist focus on resource partitioning among selected faunal groups in streams, small lakes or ponds. Gibbons and Gee (1972), Gee and Northcote (1963), Mendelson (1975), Matthews (1982b) and Baker and Ross (1981) have demonstrated habitat partitioning in the temperate stream cyprinids _Rhinichthys_, _Ericymba_, _Hybognathus_ and _Notropis_. Resource partitioning has also been documented for stream dwelling darter communities (Smart, 1979; Wynes, 1979; O'Neil, 1980; Jones, 1981; Matthews et al., 1982a). Recently, lake studies on resource partitioning among cyprinids (Moyle, 1973) and centrarchids(George and Hadley, 1979; Cashner et al., 1979; Werner and Hall, 1976, 1977; Werner, 1977) have received considerable attention.

Studies on community structure related to seasonal environmental changes are rare. Rotenberry (1980) and Rotenberry and Weins (1979) studied seasonal changes in diet and habitat use within and between seasons for various shrub-steppe and/or grassland birds. Gorman and Karr (1978) noted seasonal changes in the correlations between fish species diversity and aquatic habitat diversity in North America and Panama. Werner and Hall (1979) documented habitat shifts in sunfishes (_Lepomis gibbosus_, _L._ _macrochirus_ and _L._ _cyanellus_) as resources declined in experimental ponds over the summer. Finally, Zaret and Rand (1971) demonstrated shifts primarily in food overlap between dry and wet seasons in a tropical streamfish community.

Of the seasonal studies cited above, only one investigated community structure over an entire 12 month season (Rotenberry, 1981). Werner and Hall (1979) looked at changes in habitat use between experimentally manipulated sunfishes during summer and early fall, whereas Zaret and Rand (1971) compared fish communities in April (wet season) and September (dry season). Two field studies, one controlled (Werner and Hall, 1979), and the other natural (Zaret and Rand, 1971), suggest that competition in the face of resource depletion (delineated more qualitatively than quantitatively) might be responsible for the observable shifts in the structure of the community under study.

As yet, no detailed seasonal study has quantitatively related community structure, based on the resource use of its members, to changes in either the availability of resources (i.e., food and habitat) or habitat structure in an environment that varies. The object of this study was to examine the role of environmental variability in shaping the community structure of a tightly knit taxonomic and ecological guild of streamfishes called darters, (_Etheostoma spectabile_, _Percina phoxocephala_, _Percina caprodes_, _Percina copelandi_) inhabiting Salt Creek, Osage County, Oklahoma. Using a methodology similar to that of Zaret and Rand (1971), the present study has been designed to answer the following questions:

1. Is the aquatic environment in Salt Creek variable? If so, can the variation be adequately measured?
2. Do seasonal environmental changes affect the complexity (diversity) of the aquatic habitat?
3. Does the supply of habitat and food resources vary seasonally? If so, do these parameters affect the organization and structure of the darter community in a predictable way?
4. Do shifts in the structure of the darter community fit in well with existing niche theory?
5. Does competition play an important role in structuring the niche dynamics of the community under study?

CHAPTER II

DARTER BIOLOGY

Darters are valuable investigative subjects because they can be observed and identified easily in the field and lab (Winn, 1958a; Lachner et al., 1950). They are habitat specific, usually focusing their life histories on shallow riffle and raceway environments which permits one or two persons to sample resources and demographic parameters fairly accurately. Most species are sexually dimorphic with males more colorful than females, though a few speices show only slight dimorphism during the breeding season.

Most darters are non-schooling, though _P_. _caprodes_ retains this presumably primitive condition (Winn, 1958a, 1958b, and Collette, 1974). Limited by their benthic existence, darters migrate little between and within riffle habitats during their adult life (Reed, 1968; Scalet, 1973; Marsh, 1980). Nevertheless, darter populations have been observed moving into fast water to spawn and into deep water under low temperatures (Winn, 1958a; Braasch and Smith, 1967; Page and Smith, 1971). Tied primarily to a two-dimensional, rheotaxic, relatively shallow-water existence, adult darters experience little piscine predation (Fahy, 1954; Braasch and Smith, 1967; Page and Smith, 1970, 1971;

Thomas, 1970; Scalet, 1974). Exceptions are noted by Scalet (1973), who found a single *E. spectabile* in the stomachs of specimens of *Micropterus salmoides* and *M. punctulatus* and McLane (1950) and Smith (1957) who indicated that *E. fusiforme* is represented in the diets of *Esox niger* and *M. salmoides*. Nevertheless, the possibility of predation by macroinvertebrates, other centrarchids, cottids and cyprinids has been alluded to by some authors (Fahy, 1954; Pflieger, 1966).

Vision is the primary sensory modality involved in feeding, with prey movements typically serving as the triggering stimulus (Roberts and Winn, 1962; Scalet, 1973; Schenck and Whiteside, 1976; Daugherty et al., 1976). Studies on the feeding chronology of darter populations report peak feeding activity in daylight (Mathur, 1973; Adamson and Wissing, 1977) with a few species (e.g., *P. phoxocephala* consuming prey under twilight conditions (Thomas, 1970). Darters feed almost exclusively on in-stream, aquatic insect larvae, whose greatest densities are found in riffles.

CHAPTER III

DESCRIPTION OF STUDY AREA

Salt Creek is located in the rolling hills region of the tall grass prairie in north-central Oklahoma. It is the largest stream in Osage County and drains a watershed of 547 km^2 along its 97 km length. The stream gradient is fairly steep, dropping about 1.6 m per km.

Terrestrial habitat bordering the stream proper includes a floodplain forest dominated by Hackberry, Ash and Elm, with cleared areas being used extensively as crop and pastureland. Stream habitats are composed of gravel to solid bedrock-bottomed riffles and raceways separated by long gravel pools. During dry times of the year, flow usually ceases, leaving only permanent pools in the lower three-fourths of the drainage.

The main study areas were located in the middle and lower thirds of the drainage proper. During the first field season (June, 1978 - August, 1979) collections were made at three sites (Figure 1; Sites A,C,E). The second field season collections (October, 1979 - August, 1980) were concentrated at two sites and on one occasion a third (Figure 1; Sites A,B,D). Each study area included a riffle with long shallow pools above and below. Substrates and

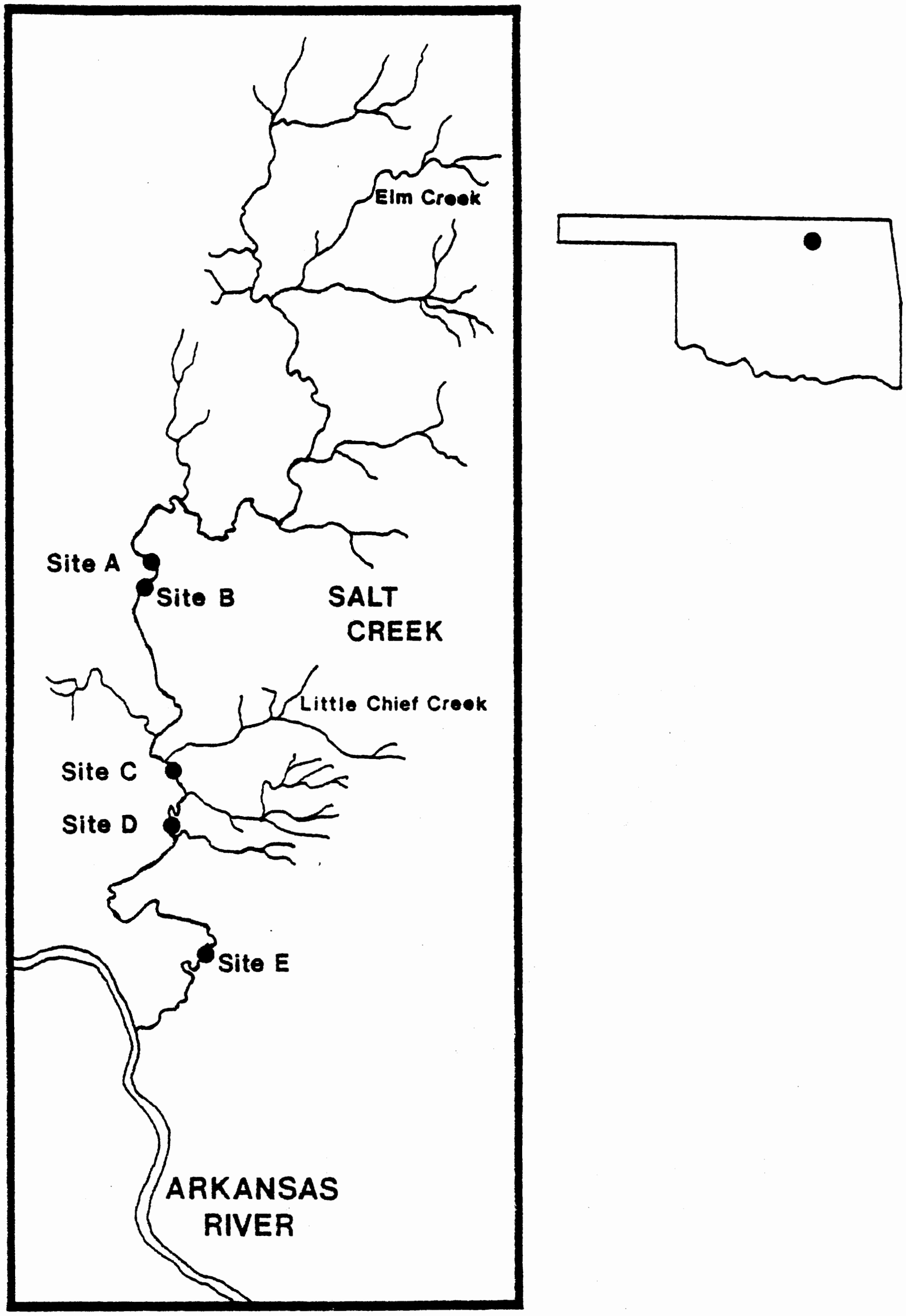

Figure 1. Location of sampling sites at Salt Creek, Osage County, Oklahoma

vegetative cover were similar for all sites.

The main sites (A and B), approximately 1.5 km in distance from each other, were located above Burbank, Oklahoma. Flow was ephemeral, normally ceasing from mid-summer to late fall.

The Salt Creek basin averages 86 cm of rain a year and has a mean yearly temperature of 14.4°C (National Oceanic and Atmospheric Administration reports for the Burbank and Ralston, Oklahoma stations), respectively. Water temperatures (°C) were recorded during each visit.

CHAPTER IV

METHODS AND MATERIALS

Seventeen fish collections were made at Salt Creek between June, 1978 and August, 1980, using either a 1.2 x 2.4 m straight or a 1.2 x 3 m, 5 mm, bar mesh bag seine. Darters were captured by vigorously kicking the substrate in front of the seine (1.5 - 2.0 m^2) and immediately sweeping the net through the disturbed area. To prevent decimation of the darter populations between June, 1978, and August, 1979, no more than 20 individuals of each species were preserved. Captured individuals exceeding the maximum were measured, sexed and returned to the water. During the second field season (October, 1979 - August, 1980) a more intensive collecting regime was initiated and all captured fish were preserved.

Drainage distributions for each darter species were established by making collections at 31 locations (May 23 - June 14, 1979) along Salt Creek and its major tributaries. Collecting efforts were standardized by pull and kick-seining a 100 m riffle-pool reach at each location for one hour. All darters collected were preserved and returned to the lab.

Habitat preferences for the darter species were determined (October, 1978 - August, 1979) at each site (A,C,E; Figure 1). Six categories were used to characterize the habitat. Habitat subsets included: (1) middle of pool above and below the riffle; (2) edge of pool above and below the riffle; (3) head of riffle; (4) edge of riffle; (5) middle of riffle; (6) and tail of riffle. Collections of darters in each habitat were standardized on a catch per unit basis.

During the second field season (October, 1979 - August, 1980) a different procedure was followed. Darters caught in single kick-seine hauls were preserved separately and a weighted fishing bobber with a number corresponding to a collection jar was placed at the approximate center of the haul area. Collecting proceeded upstream from the deepest seinable location (to 125 cm) in the pool below the riffle, through the riffle, up to the deepest seinable location in the pool above. Fifty to sixty kick-hauls were made throughout the study sites. Depth, substrate type and current speed data at each capture location were categorized following Table 1. Underwater observations show preference for similar microhabitats to those observed in this study (Lehtinen, pers. obs.), thus the kick-seine method appears to accurately reflect darter habitat preferences.

Individuals (>30 mm in length) collected to determine habitat use were also used to determine dietary preferences. Prey items were typically ingested whole and those present in the gut (i.e., first third before the pyloric sphincter) were identified, counted and measured to the nearest 0.5 mm in length under a dissecting microscope. Stomach fullness was estimated and numerical values assigned based on the degree of distension: (1) empty; (2) slightly full; (3) half full; (4) more than half full and (5) full.

Benthic insect populations were sampled (October, 1979 - August, 1980) using a modified Hess invertebrate sampler (Caryle and Strubb, 1978). Samples were taken at each site by vigorously turning 0.25 m^2 of the stream bottom for 90 seconds in each of the following habitats: mid-pool above riffle; mid-pool below riffle; pool edge above riffle; pool edge below riffle; head of riffle; middle of riffle; edge of riffle and tail of riffle. All materials collected were placed in 5% formalin and returned to the lab.

During the second field season, habitats at each site (A,B,D) were characterized during visits beginning August 9, 1979, and ending August 10, 1980. Depth, current speed and substrate measurements were made at 2 m intervals along transverse transects spaced approximately 10 m apart throughout the study sites (Gorman and Karr, 1978).

Substrate type was categorized according to the major substrate present within a 30 cm radius of the transect point sample. Current speeds were measured with a Pygmy-Gurley current meter set at 0.6 of the vertical depth. Depths, substrate types and current speeds were recorded at approximately 80-120 locations.

The three habitat dimensions included 8 depths, 7 substrate types and 8 current categories (Table 1). Habitat diversity (Shannon and Weaver, 1948) was calculated for combinations of depths, substrates and currents (possible 448 categories). Not all categories of the above dimensions are found at any one site at any one time.

Data used to calculate habitat diversity were also used to estimate discharge at the study areas. Using the known depth and current speed for each 2 m distance along a linear transect, flow within that interval was estimated by multiplying the width times the depth, times the current speed. Estimation of the total amount of water passing across a transect was determined by adding up the discharges for each 2 m interval. The above procedure was repeated for 6 randomly selected transects, (three taken from each site) and an overall average flow determined.

All sites within each season were pooled, August, 1979, data however were not always used in the analysis of results from the second season. In general, the first field season produced 9 distinct, summary data points, while the second season usually produced 7 points, but sometimes only 6.

Table 1. Description of habitat categories used to calculate darter habitat overlap and breadth, and habitat diversity during the second field season.

	Category Number							
Dimension	1	2	3	4	5	6	7	8
Depth (cm)	0-2	2-4	4-8	8-16	16-32	32-64	64-128	128-
Current (cm/s)	0-2	2-4	4-8	8-16	16-32	32-64	64-128	128-
Substrate	Silt Sand	Sand Gravel	Gravel	Cobble	Rubble	Boulder	Bedrock	

CHAPTER V

DATA ANALYSIS

Habitat Complexity

Data on habitat structure at the Salt Creek study area were analyzed using the Shannon-Weiner Index formula for diversity (Margalef, 1968):

$$H' = \sum_{i=1}^{n} p_i \ln p_i \qquad (1)$$

where:

H' = the diversity of the aquatic habitat.

n = the number of aquatic habitat categories (maximum = 448).

p_i = the proportion of a category of the total sample belonging to the ith category.

Niche Overlap and Breadth

Measurements of niche overlap were made using the symmetrical similarity coefficient of Pianka (1973):

$$OV_{ij} = \frac{\sum_k p_{ik} * p_{jk}}{\sqrt{\sum_k p_{ik} * p_{jk}}} \qquad (2)$$

where:

OV_{ij} = Overlap between two species in a community; a number always ≤ 1.0.

p_i & p_j = Proportion of resource type k utilized by consumer i and j.

Niche breadth was computed using a measure developed by Levins (1968) and Pianka (1969):

$$B = (1/\sum_{K} p_i^{\,2})/n \qquad (3)$$

where:

B = The species breadth or diversity of use of a particular resource; can exceed 1.0.

p_i = The proportion of resource type k.

n = The number of resources available to the community as a whole.

In addition to the breadth measure above, during the second field season community diet breadth was also computed following:

$$W = \frac{U}{A} \qquad (4)$$

where:

W = The breadth of dietary resource use.

U = The diversity of food items found in stomachs of the entire darter community.

A = The diversity of aquatic insects in benthic samples.

Niche overlaps were calculated for all species' pairwise combinations with average community overlap equaling the pairwise mean. Mean community breadths were calculated by averaging individual species' breadths. Resource categories used to calculate habitat overlap and breadth changed from a maximum of 8 the first field season to a maximum of 448 the second field season

Multivariate Procedures

Food size similarity was determined by Factor Analysis using Varimax - Orthogonal rotation on the mean size of each prey taxon in each fishes gut (total N=25; 25 x 25 variance-covariance matrix). Eleven factors with eigenvalues greater than one accounted for 79% of the variance. Individual factor scores for each fish on each axis were then computed. Since the factors (i.e., axes) are orthogonal, each species food size position in a n- (11) dimensional hypervolume could be defined. The n-dimensional spacing between species pairs (Euclidean distances; Gatz, 1979) were calculated following:

$$D_{i,j} = \sqrt{\sum_{k=1}^{N} (x'_{i,k} - x'_{j,k})^2} \qquad (4)$$

where:

$D_{i,j}$ = The Euclidean distance between species i and species j.

$x'_{i,k}$ = The standardized mean for species i in factor k.

$x'_{j,k}$ = The standardized mean for species j in factor k.

N = The 11 dimensions.

The standardized means were computed as follows:

$$x'_{i,k} = (x_{i,k} - \bar{x}_k)/SD_k \tag{6}$$

where:

$x'_{i,k}$ = The standardized mean for species i in factor k.

$x'_{i,k}$ = The measured mean value for species i in factor k.

$\bar{x}_k$ = The mean value for all $x_{i,k}$ for factor k.

SD_k = The standard deviation for factor k.

Monthly Euclidean distances were calculated for all species pairwise combinations (6) with average community distance equaling the pairwise mean.

Within any analysis (i.e., darter diet and habitat) it was difficult to keep the sample size the same for all species. Valid samples for monthly analysis were possible for *E. spectabile* and *P. phoxocephala*, but sample size was highly variable for *P. caprodes* and *P. copelandi*. However, analyses were performed on all species because: (1) the relative number of captured individuals of each species probably reflected their numbers present in the community at that time, and (2) some species show low variability in habitat and dietary preference.

Pearson product-moment correlation coefficients were used to test the degree of relationship between sets of variables (abiotic and biotic). All analyses were executed using Fortran programs coupled with procedures from the Statistical Analysis System "1979 Edition" (Helwig et al., 1979).

CHAPTER VI

RESULTS

Environmental Data

Air Temperature and Precipitation

Climatic data for a major portion of the two field seasons (1979-1980) show similar seasonal patterns but differ slightly, with 1979 being warmer and dryer during the first half of the year and cooler and wetter the second half, while 1980 started out cooler and wetter and ended up warmer and dryer (Figure 2).

Habitat Diversity and Discharge

In October, 1979 and, August, 1980, when there was little or no flow in Salt Creek, habitat diversities were low. During months of moderate (April, 1980; August, 1979) and high flows (December, 1979; March, 1980; May, 1980), the diversity of the habitat increased. Stream discharge was positively correlated with habitat diversity (r= .91, p< .003; Figure 3).

Because discharge and habitat diversity are highly correlated, only one parameter, change in habitat diversity through time, will be used as the descriptor of

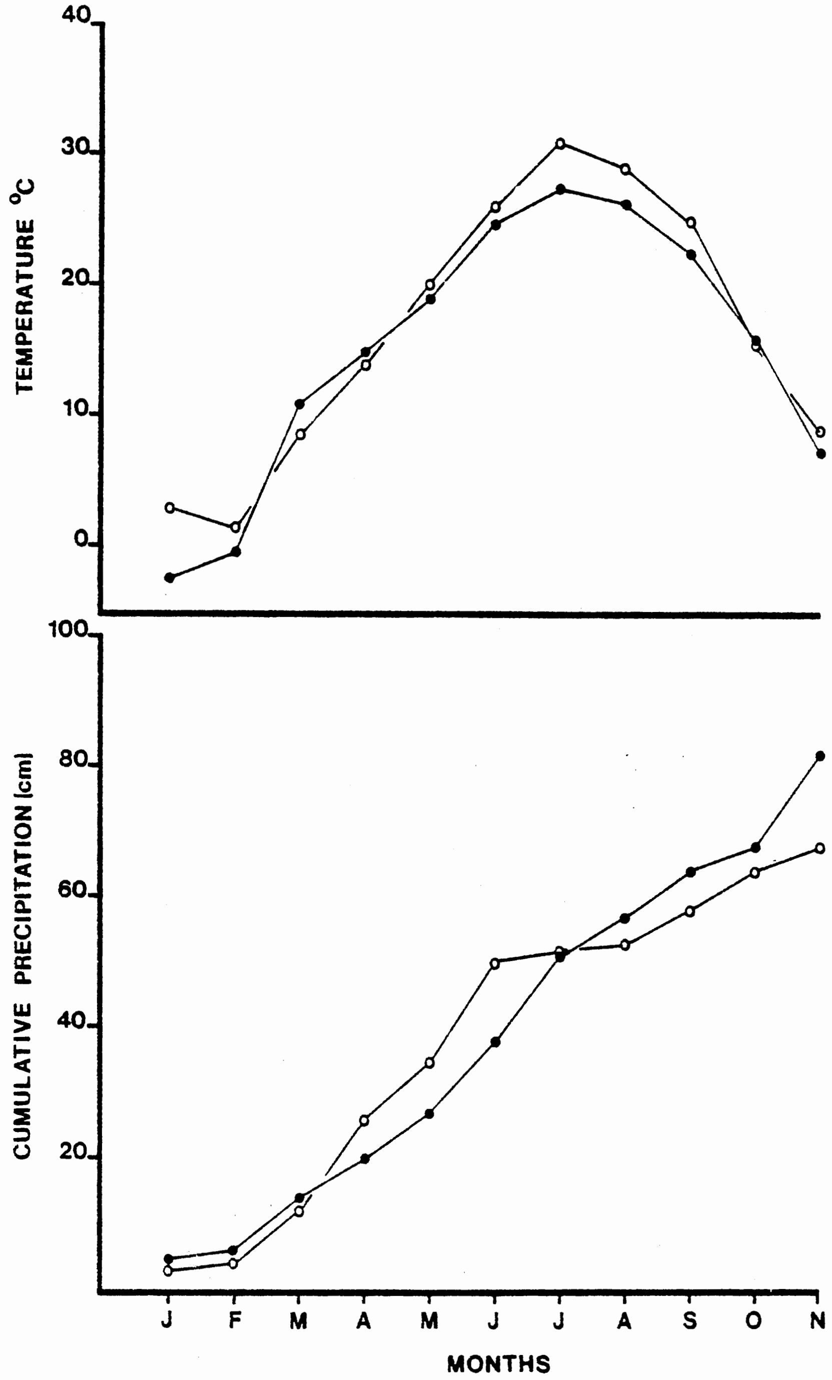

Figure 2. Average air temperature and cumulative precipitation in 1979 (●) and 1980 (O) at Burbank (top) and Ralston (bottom) , Oklahoma

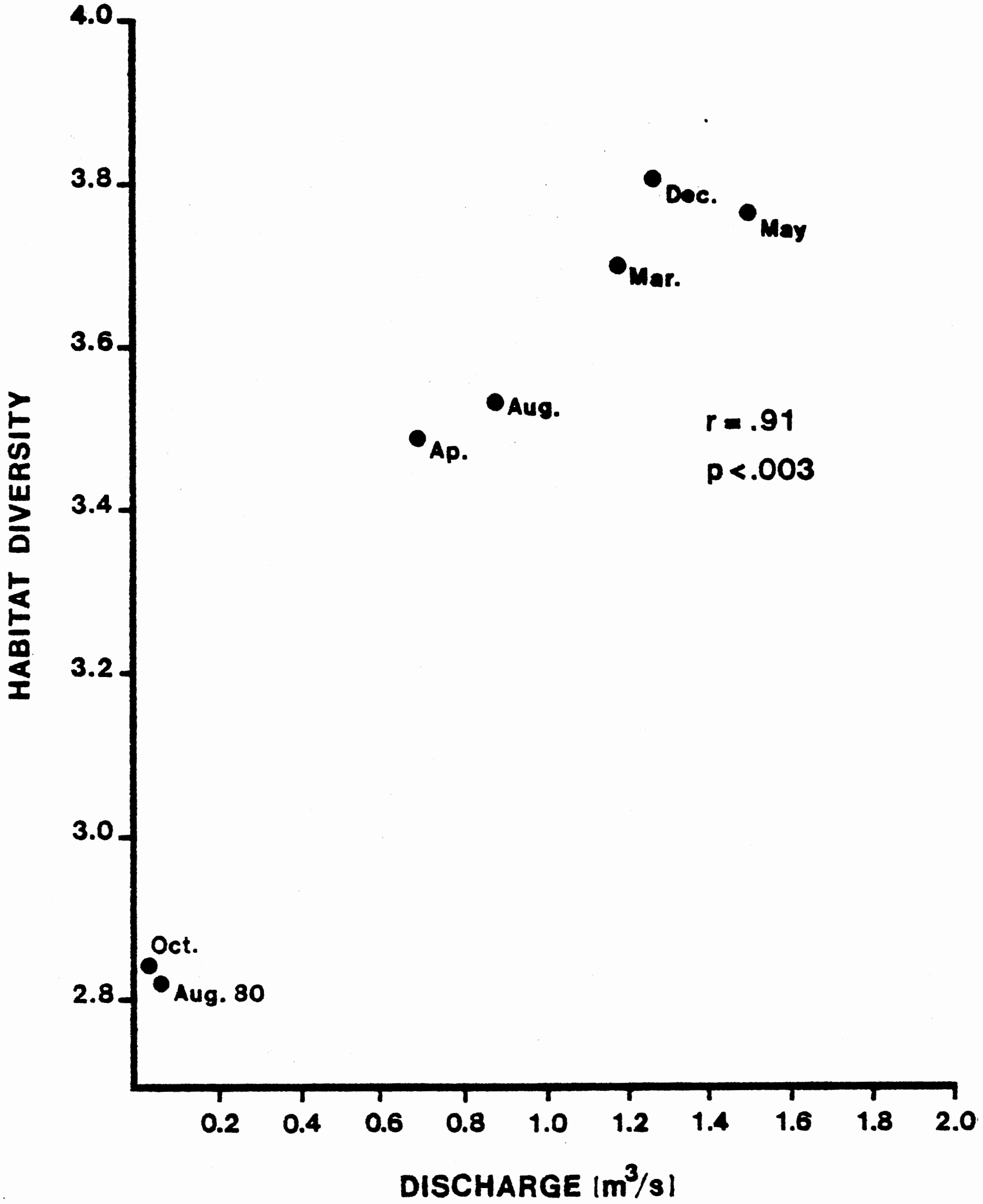

Figure 3. Discharge vs. habitat diversity in Salt Creek (August, 1979 - August, 1980)

environmental variability in the plotted relationships that follow.

Darter Community: Habitat Analysis

Macrodistributions

Etheostoma spectabile (Orangethroat Darter) were captured in the creek proper as well as in the upper and lower tributaries throughout. *Percina phoxocephala* (Slenderheaded Darter) were restricted to mainstream locations and overall were more abundant in the middle and lower thirds of the drainage. *Percina caprodes* (Logperch) inhabited mainstream habitats including the largest tributaries, Elm Creek and Little Chief Creek. *Percina copelandi* (Channel Darter) were distributed along the creek proper except for one tributary collection in Elm Creek (Figure 4a-d).

Seasonal Habitat Use

When habitat diversity and discharge were high the frequency of darters captured in riffle habitats exceeds the frequency captured in pools (Figure 5). During a fall drought (October, 1979) the majority of individuals of each darter species were captured in pools. Nonetheless, a few *E. spectabile*, *P. phoxocephala* and *P. caprodes* remained in the reduced riffles.

E. spectabile and *P. phoxocephala* were the only

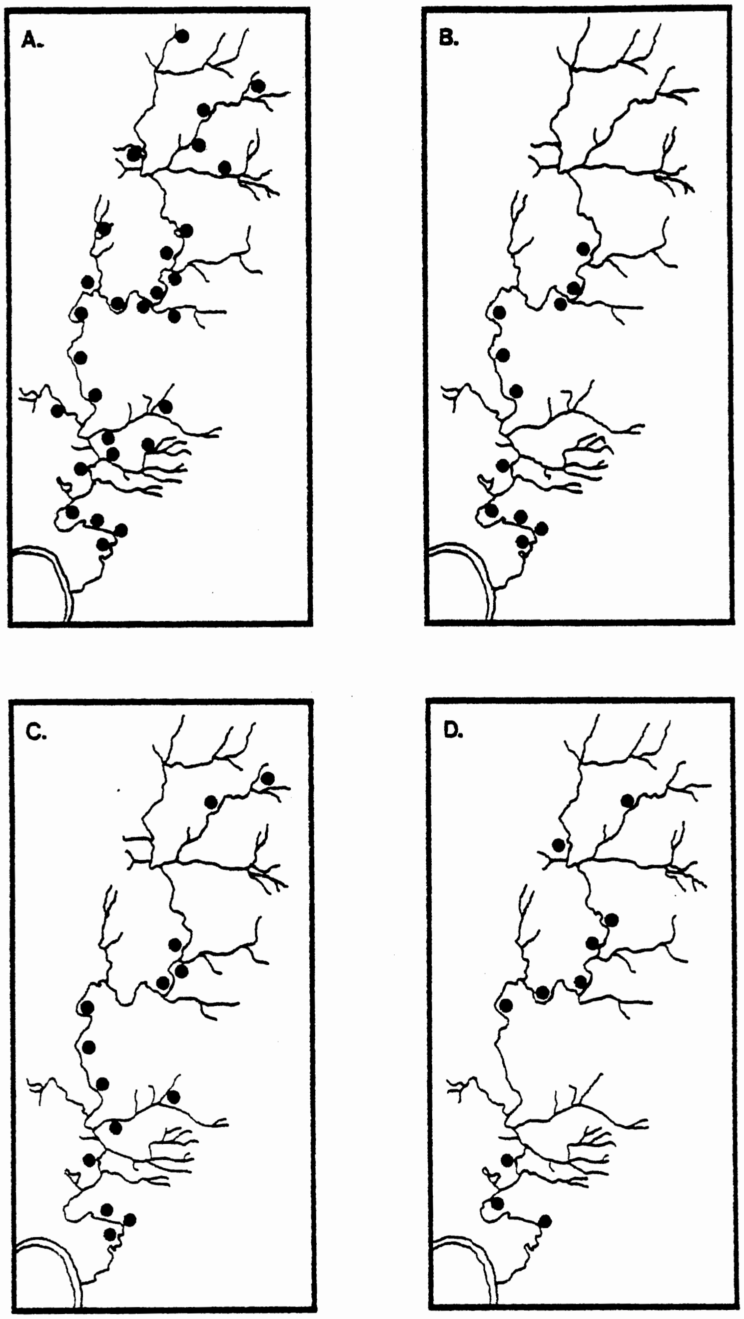

Figure 4. Distribution of darters in Salt Creek, Oklahoma : A) *Etheostoma spectabile*; B) *Percina phoxocephala*; C) *Percina caprodes*; D) *Percina copelandi*. *E. spectabile's* distribution represents 28 out of a possible 31 sampling locations

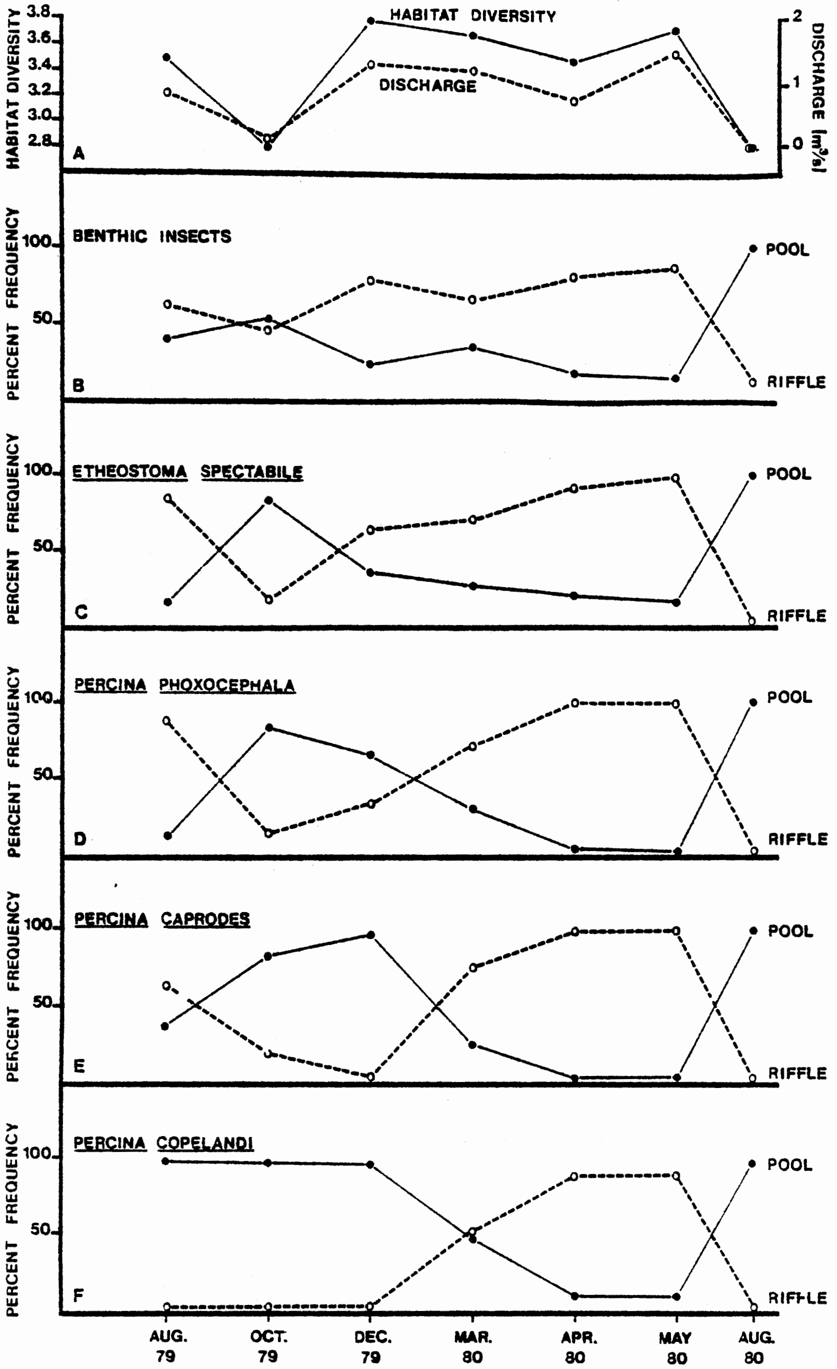

Figure 5. Habitat diversity, discharge and percent frequency of benthic insects, *E. spectabile*, *P. phoxocephala*, *P. caprodes* and *P. copelandi* in riffle and pool habitats (August, 1979 - August, 1980)

species captured in riffle habitats during high flows in December, 1979. No fish were found in riffles in February, 1979, when water temperatures were below 4°C. Movement out of available riffle habitats in winter may be a behavioral response to cold temperatures. Similar cold weather emigrations from riffles have been documented for _P_. _sciera_ (Page and Smith, 1970) and _P_. _phoxocephala_ (Page and Braasch, 1971) in Illinois. By early spring (March, 1980) darters were again captured in riffles (Figure 5c-f).

Seasonal Microhabitat Use

During months when flow was absent (October and November, 1978) the majority of _E_. _spectabile_ were captured in shallow pool habitats (< 50 cm) whereas the majority of captures for P. _phoxocephala_, _P_. _caprodes_ and _P_. _copelandi_ occurred in deep pool habitats (< 50 cm; Figure 6a and b). As stream discharge returned in the spring (March, 1979 - June, 1979), darters reappeared in riffles (Figures 6c, 7, 8a).

During low flows in July, 1979, darters emigrated from the reduced riffles (Figure 8b). _E_. _spectabile_ and _P_. _phoxocephala_ were the only darters caught in mid-riffle habitats; the head and edge of riffle habitats were abandoned by all species. _P_. _caprodes_ was most common in pools. _P_. _copelandi_ were taken only in pool habitats, occurring in deeper water more often than shallow.

Concurrent with heavy rainfall in August, 1979, flow

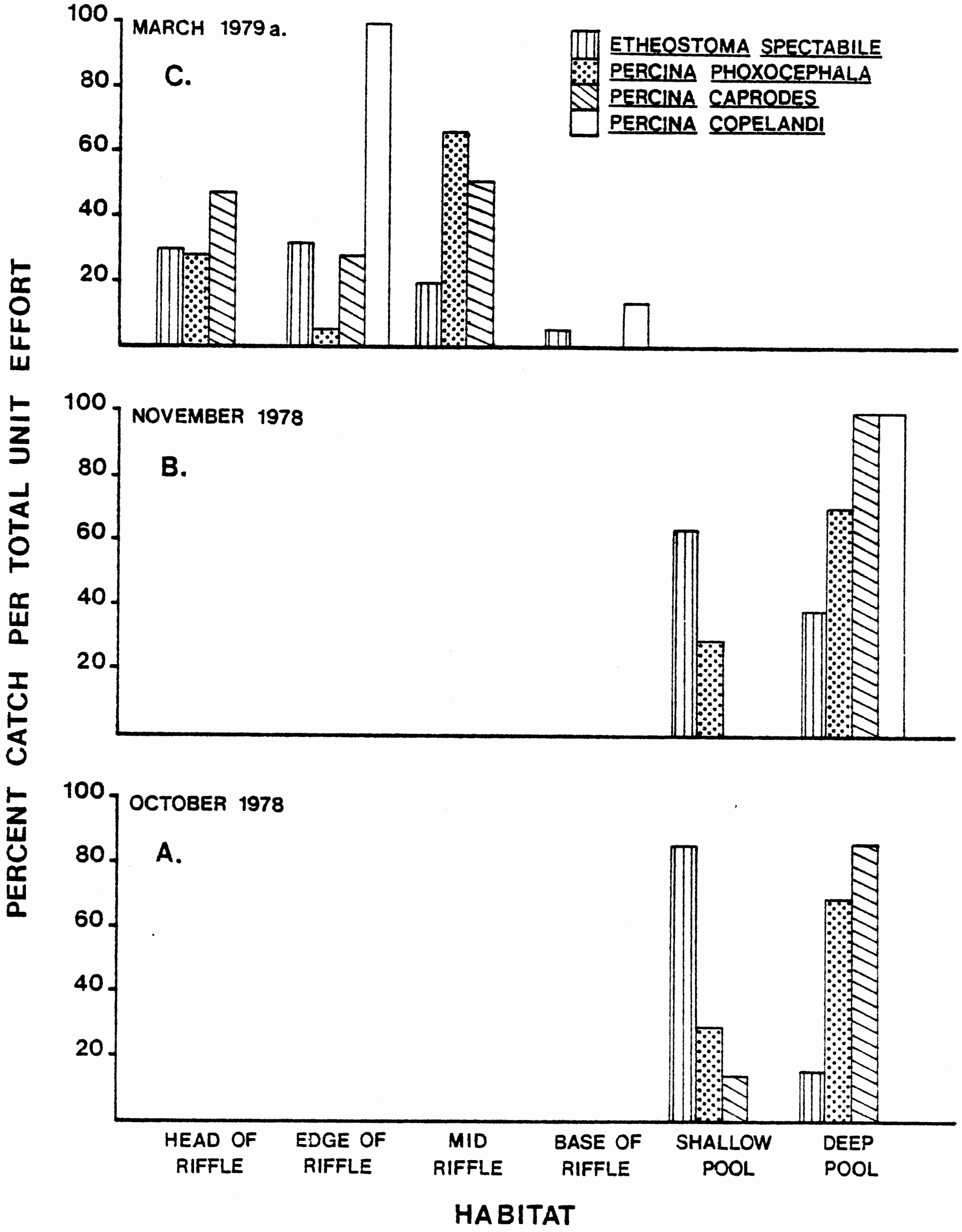

Figure 6. Microhabitat use of E. spectabile, P. phoxocephala, P. caprodes, and P. copelandi in Salt Creek (October, 1978 - March, 1979a). Percent frequency in microhabitats based on total catch per unit effort

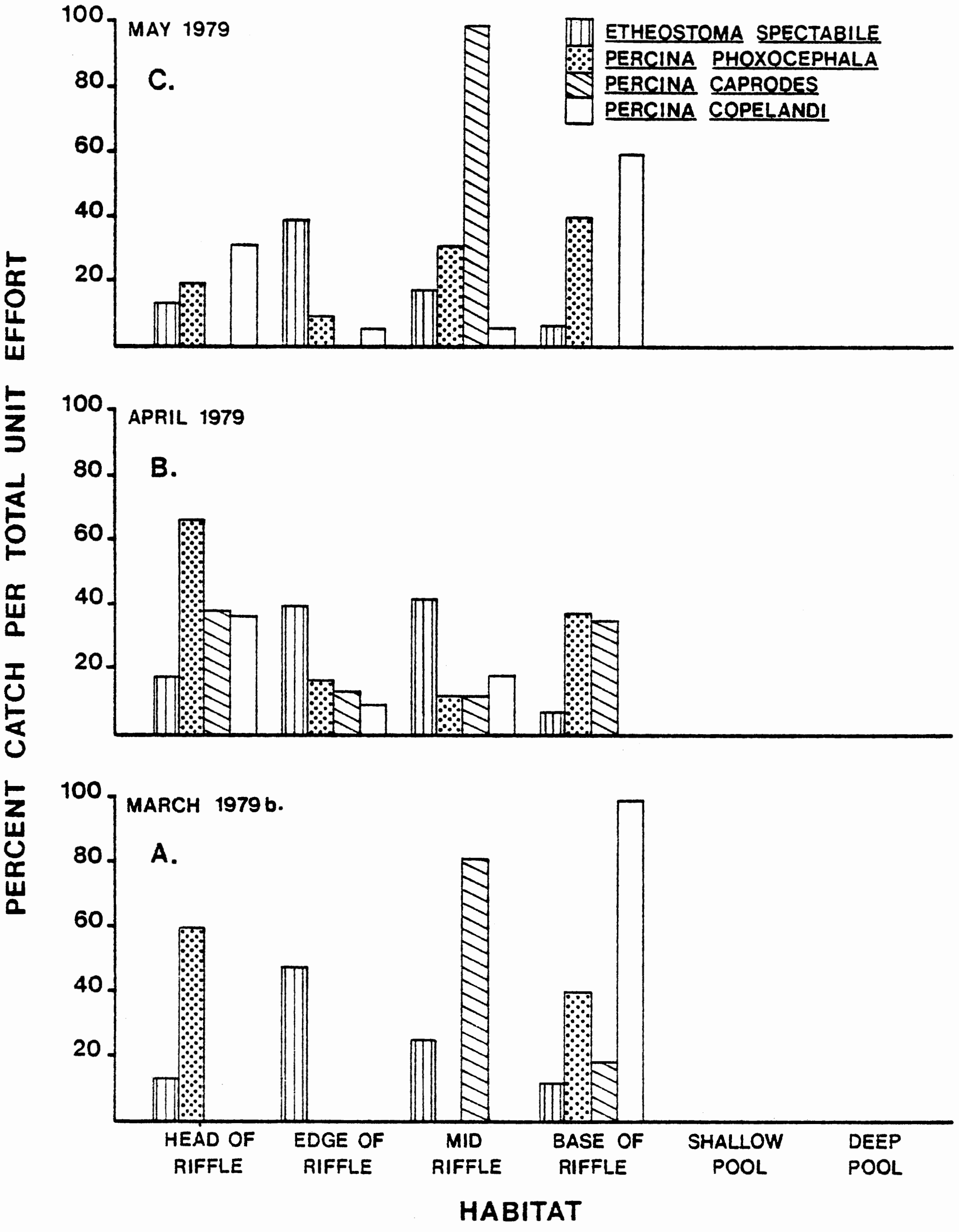

Figure 7. Microhabitat use of E. spectabile, P. phoxocephala, P. caprodes and P. copelandi in Salt Creek (March, 1979b - May, 1979). Percent frequency in microhabitats based on total catch per unit effort

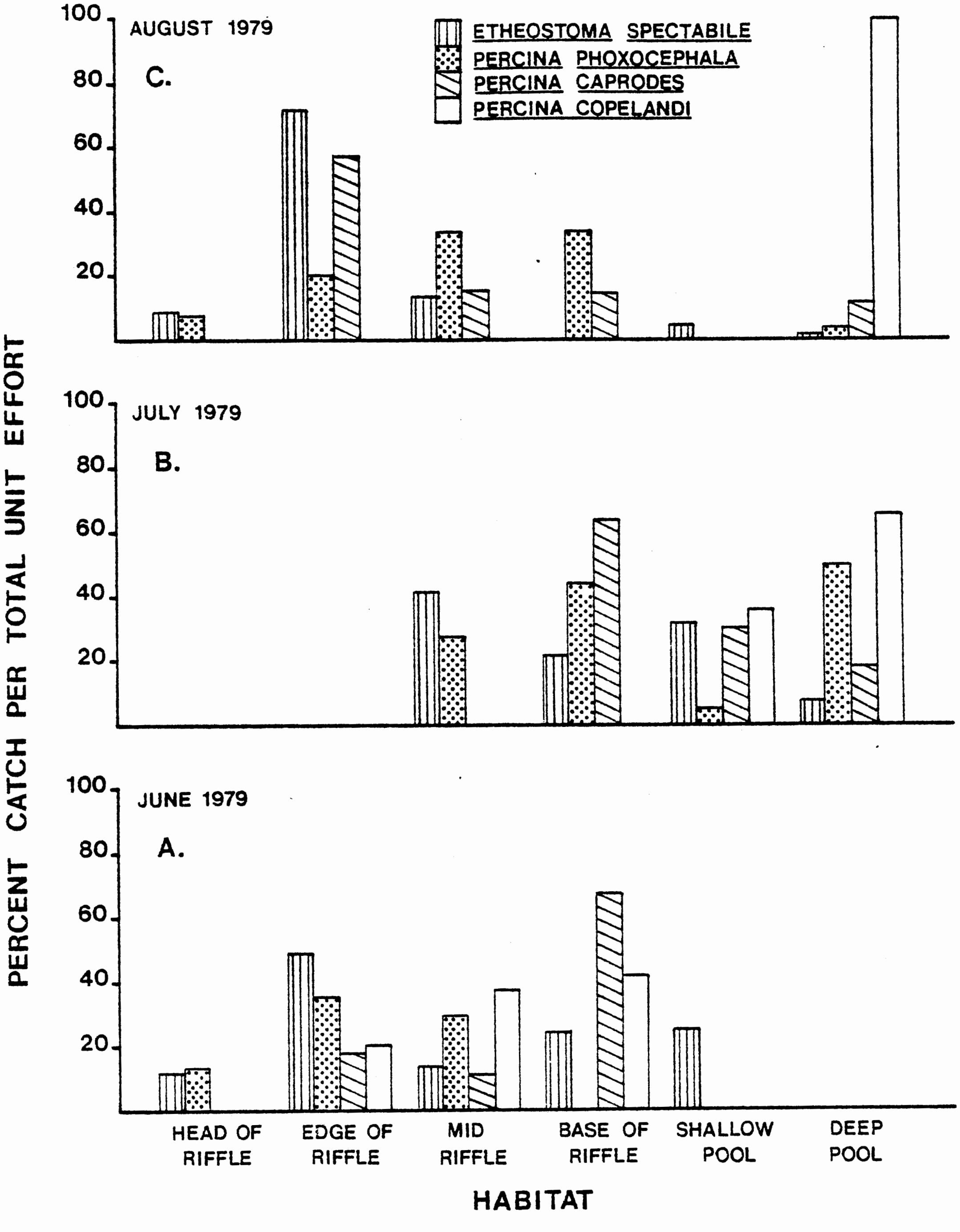

Figure 8. Microhabitat use of E. spectabile, P. phoxocephala, P. caprodes and P. copelandi in Salt Creek (June, - August, 1979). Percent frequency in microhabitats based on total catch per unit effort

returned to Salt Creek (Figure 8c). Three species reappeared in the riffles. *E. spectabile* and *P. caprodes* occupied primarily edge of riffle habitats, whereas *P. phoxocephala* were more frequent in mid- and base of riffle habitats. *P. copelandi* remained exclusively in deep pool habitats.

Habitat Overlap and Breadth:
10/78 - 8/79

When stream flow was absent (October, 1978; November, 1978; July, 1979) both community habitat breadths overlaps were high (Table 2). Habitat overlap was positively correlated with habitat breadth (r=.56, p<.05; Figure 9).

Habitat Overlap and Breadth:
10/79 - 8/80

Seasonally, community habitat overlap was high in October, 1979, low in December, 1979, and gradually increasing through August, 1980 (Table 2). Community habitat breadth exhibited a similar seasonal pattern. Darter community habitat overlap was positively correlated with habitat breadth (r=.83, p<.003; Figure 10).

Community habitat overlap was negatively correlated with habitat diversity (r=.72, p<.10; Figure 11). The same negative relationship existed between overlap and habitat diversity for each pair of darter species (Figure 12a-f).

Table 2. Summary table of various community habitat analyses for the darter community present in Salt Creek, Osage County, Oklahoma, (October, 1978 - August, 1980).

Date	Habitat Overlap	Habitat Breadth	Habitat* Overlap	Habitat* Breadth
10-78	.62	.54	-	-
11-78	.76	.52	-	-
3a-79	.57	.35	-	-
3b-79	.33	.28	-	-
4-79	.68	.43	-	-
5-79	.54	.35	-	-
6-79	.54	.45	-	-
7-79	.51	.61	-	-
8-79	.39	.34	-	-
10-79	-	-	.75	.65
12-79	-	-	.04	.37
3-80	-	-	.12	.22
4-80	-	-	.32	.34
5-80	-	-	.37	.35
8-80	-	-	.36	.34

* Number of resource categories used to calculate niche overlap and breadth increased during the second field season (see text).

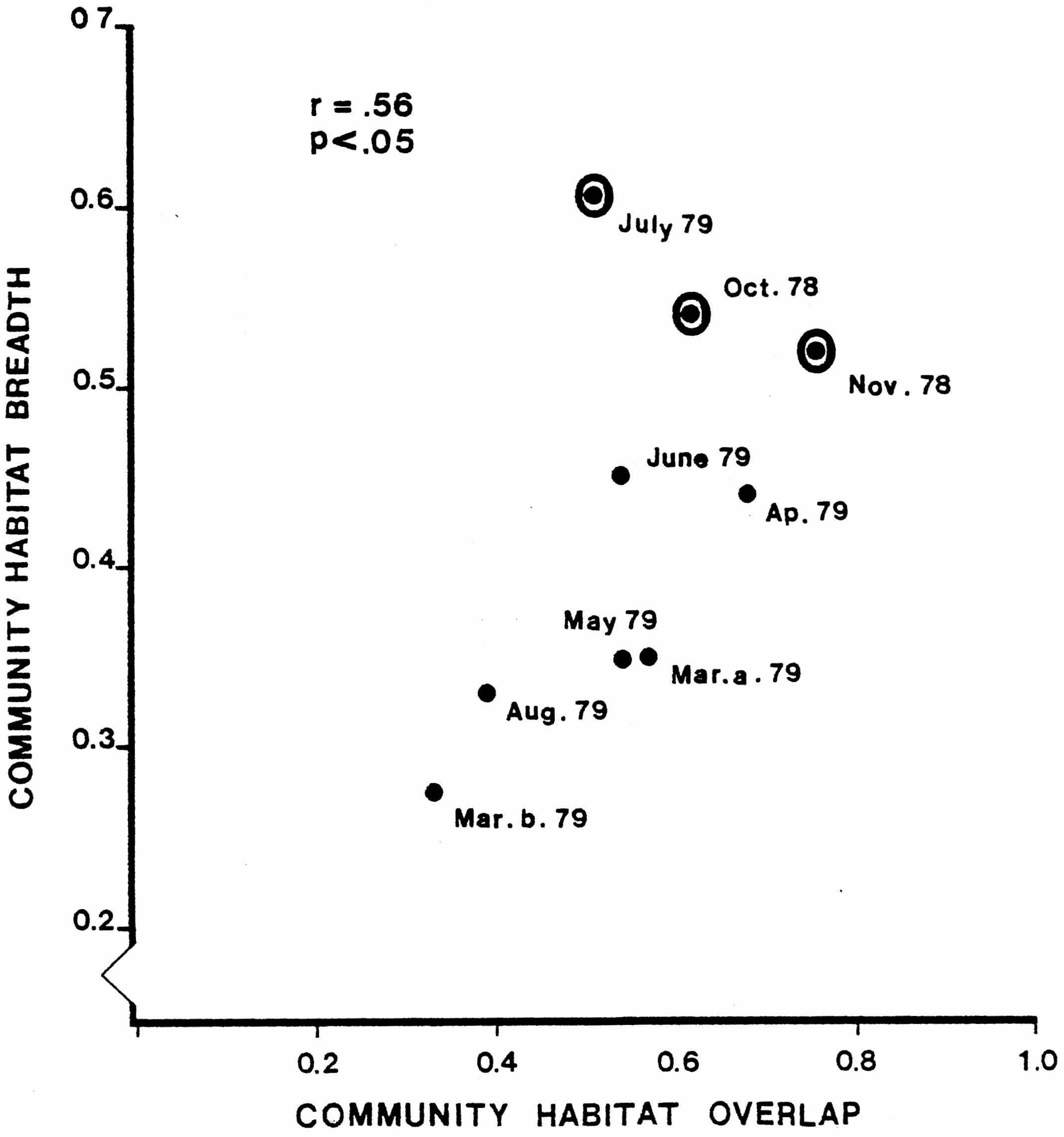

Figure 9. Community habitat overlap vs. breadth (October, 1978 - August, 1979). (◉) = sample dates when stream flow was absent

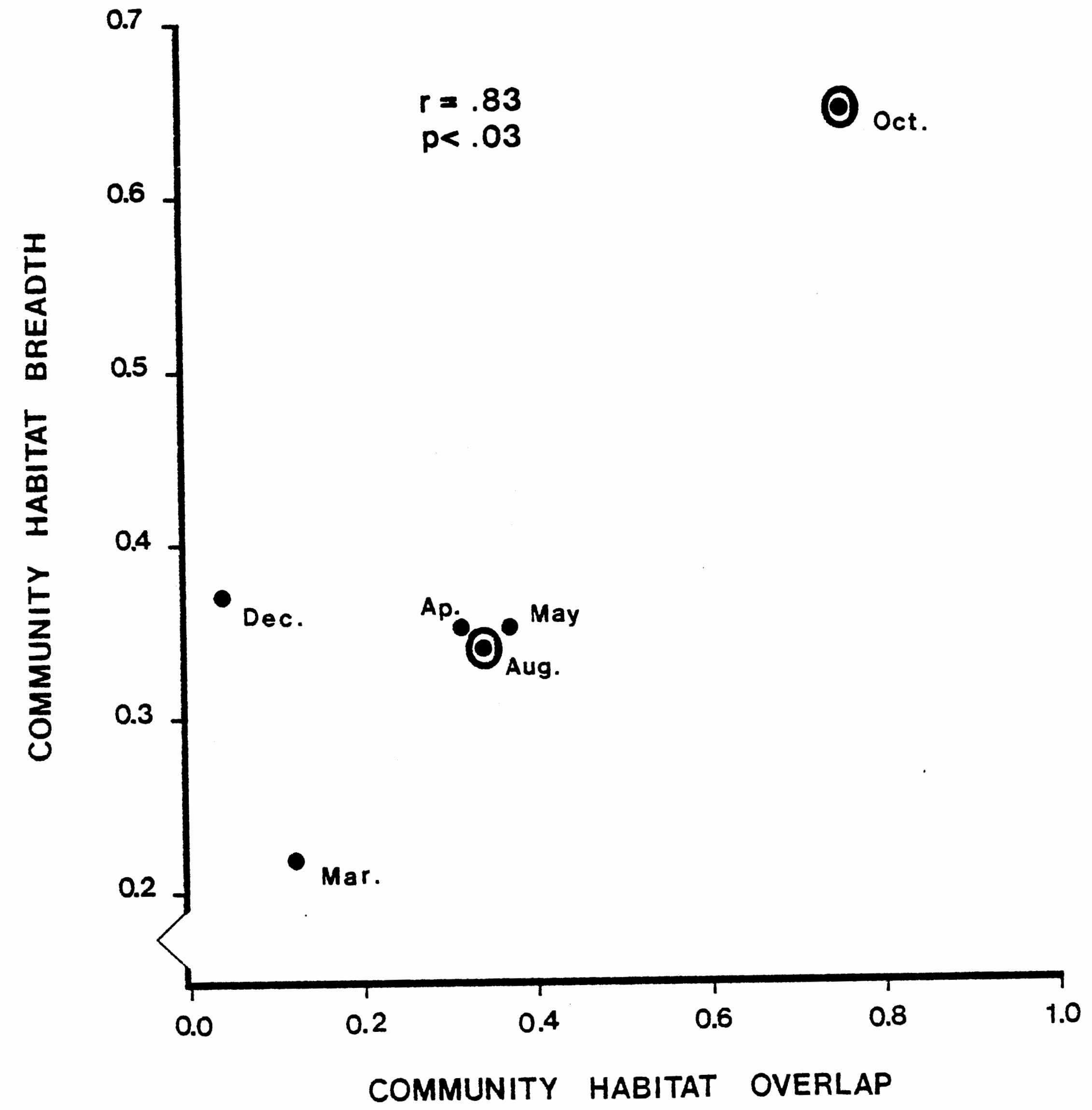

Figure 10. Community habitat overlap vs. breadth (October, 1979 - August, 1980). (◉) = sample dates when stream flow was low or absent

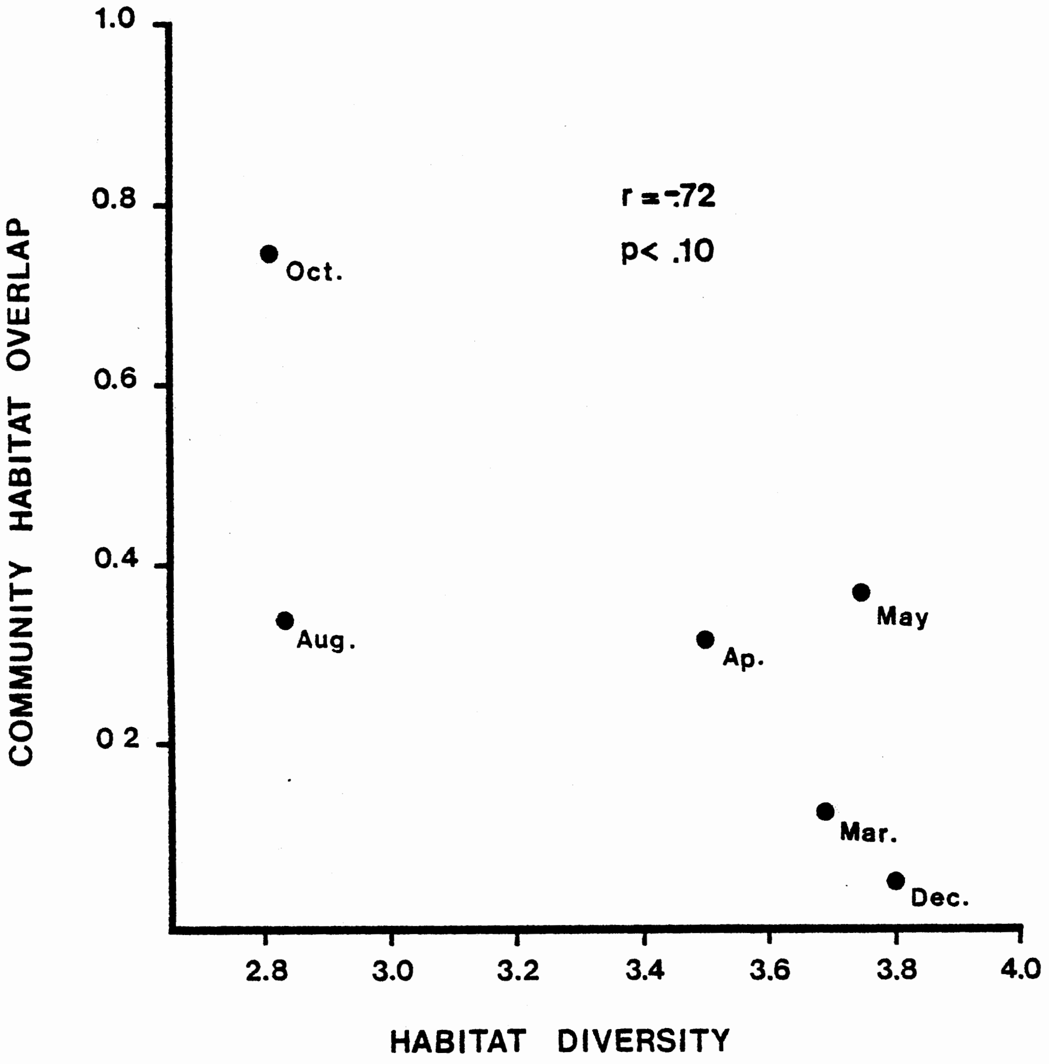

Figure 11. Community habitat overlap vs. habitat diversity (October, 1979 - August, 1980)

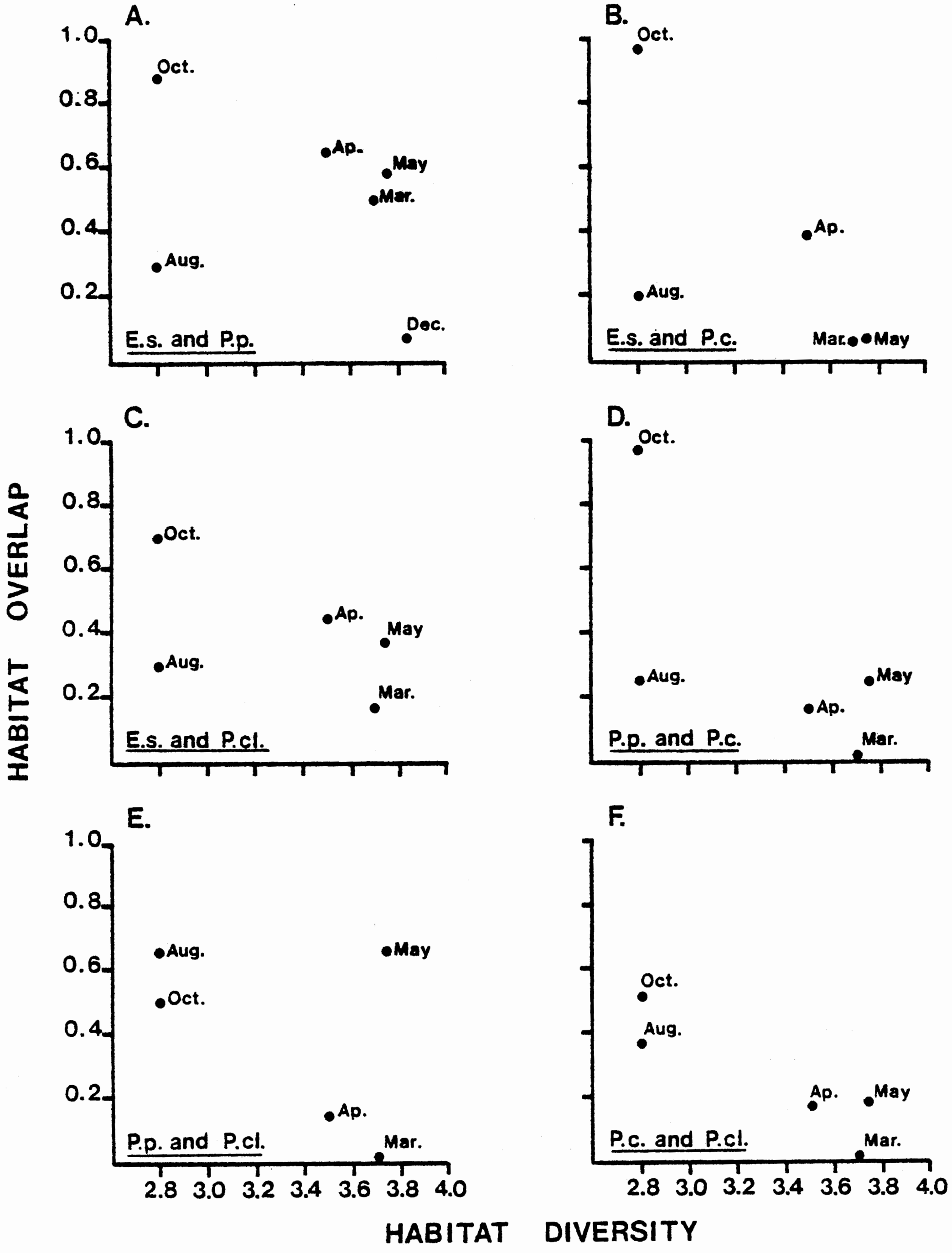

Figure 12. Species pairwise habitat overlaps vs. habitat diversity (October, 1979 - August, 1980). (E.s. = *E. spectabile*; P.p. = *P. phoxocephala*; P.c. = *P. caprodes*; P.cl. = *P. copelandi*)

Darter Community: Diet Analysis

Food Habits: Overall

The major food groups present in darter diets (Table 3) were: dipterans (38-81%), mostly chironomid and *Simulium* larvae; trichopterans (0.2-7%), primarily *Cheumatopsyche* larvae; ephemeropterans (1-10%), mostly *Stenonema* and *Isonychia* nymphs; fish eggs (1-18%) and zooplankton (5-53%).

The most frequent food of *E. spectabile* and *P. caprodes* was chironomid larvae, whereas *Simulium* larvae and zooplankton were most frequently ingested by *P. phoxocephala* and *P. copelandi*, respectively (Table 3). Overall diets were richer for *E. spectabile* and *P. caprodes* (prey taxa=29) than for *P. phoxocephala* (prey taxa=17) and *P. copelandi* (prey taxa=20).

Average stomach fullness was similar for *E. spectabile* ($\bar{x}$=3.3) and *P. phoxocephala* ($\bar{x}$=3.2) while *P. caprodes* ($\bar{x}$=3.0) and *P. copelandi* ($\bar{x}$=3.0) were slightly lower (Table 3). The mean number of prey items consumed per fish varied, however, with *E. spectabile* ($\bar{x}$=10.3) and *P. phoxocephala* ($\bar{x}$=12.8) showing markedly lower rates of ingestion than *P. caprodes* ($\bar{x}$=34.9) and *P. copelandi* ($\bar{x}$=30.8; Table 3).

Table 3. Overall food habits (June, 1978 - August, 1980) of the Salt Creek darter community. Values are percent frequencies of each taxa found in the species' diet.

	Species			
Prey Taxon	*Etheostoma spectabile*	*Percina phoxocephla*	*Percina caprodes*	*Percina copelandi*
Collembola			0.01	
Ephemeroptera				
Baetis *sp*.	0.33	1.45	0.95	0.42
Caenis *sp*.	0.31	0.22	0.78	0.10
Tricorythodes *sp*.	0.19	1.29	0.83	0.13
Choropterpes *sp*.	0.03	0.55	0.11	
Habrophlebia *sp*.	0.02		0.13	
Leptophlebia *sp*.			0.04	
Isonychia *sp*.	1.18	3.94	0.74	0.39
Stenonema *sp*.	0.84	2.37	2.20	0.23
Total Ephemeroptera	2.9	9.82	5.79	1.27
Odonata				
Agrionidae	0.07	0.58	0.17	0.21
Plecoptera				
Perlidae	0.09		0.06	0.06
Trichoptera				
Cheumatopsyche *sp*.	2.04	4.67	6.49	0.19
Hydroptilidae	0.03		0.11	
Psychomyiidae	0.09	0.03	0.15	0.03
Total Trichoptera	2.16	4.70	6.75	0.22
Coleoptera				
Elmidae adult			0.02	0.03
Elmidae larvae			0.36	
Total Coleoptera			0.38	0.03

Table 3. Continued.

	Species			
Prey Taxon	*Etheostoma spectabile*	*Percina phoxocephla*	*Percina caprodes*	*Percina copelandi*
Diptera				
Chironomidae larvae	69.63	25.95	55.82	35.83
Simulium larvae	10.32	31.52	2.44	1.14
Simulium pupa	0.03	0.55	0.44	0.03
Dipteran adults	0.03	0.03		0.16
Dipteran pupa	1.03	2.98	5.94	0.94
Total Diptera	81.04	61.03	64.60	38.10
Zooplankton	9.23	4.86	12.80	53.22
Miscellaneous				
Ostracoda	2.02		0.02	0.06
Fish eggs	1.45	18.45	7.80	6.82
Gastropoda	0.10		0.38	
Plecypoda	0.19		0.47	
Arachnida	0.19		0.04	0.03
Trichopteran purse			0.30	
Terrestrial Oligochaete	0.02			
Aquatic Oligochaete	0.10			
Trematoda	0.02		0.04	
Crayfish	0.02			
Seeds	0.03			0.06
Unidentified	0.36	0.55	0.36	0.10
Total Miscellaneous	4.50	19.00	9.41	7.07
Number of items	5847	3252	4717	3078
Number of fish	568	255	135	100
Number of items/fish	10.3	12.8	34.9	30.8
Number of taxa	29.0	17.0	29.0	20.0
Mean stomach fullness	3.3	3.2	3.0	3.0

Darter Food Habits: Seasonal

The most frequent monthly food item found in the diet of *E. spectabile* was chironomid larvae (Table 4). Zooplankton, *Cheumatopsyche* larvae and *Stenonema* nymphs were also ingested regularly. Zooplankton and ostracod consumption was highest during months with low or no flow (September, 1978 - November, 1978; July, 1979; October, 1979; August, 1980). Fish eggs were consumed in both the spring and fall (September and November, 1978).

Chironomid larvae were the most frequent prey items found in the diet of *P phoxocephala* (Table 5). *Simulium* larvae were heavily consumed in the late spring and early summer. Other taxa consistently present in the diet were *Stenonema* nymphs and dipteran pupae. Heaviest zooplankton consumption occurred during low stream flow. Fish eggs were consumed from spring to early summer.

Chironomid larvae and dipteran pupae were consumed year round by P. caprodes (Table 6). Additionally, *Stenonema* nymphs, *Caenis* nymphs, *Cheomatopsyche* larvae and zooplankton were ingested often. Fish eggs were consumed during late spring and early summer.

Chironomid larvae and zooplankters were consistently found in the diet of *P. copelandi* (Table 7). Ephemeropteran nymphs and trichopteran larvae were ingested sparingly. Fish eggs were consumed during late spring and early summer.

Table 4. Dietary composition of _E. spectabile_, 1978-1980. Values are percent frequencies of each taxon in each collection.

	Collection Date								
Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Ephemeroptera									
Baetis sp.				0.64					0.57
Caenis sp.							0.26	1.29	0.57
Tricorythodes sp.	0.81		1.55	2.56					
Choropterpes sp.					0.60				
Habrophlebia sp.									
Isonychia sp.	12.10			0.64				20.65	3.45
Stenonema sp.	3.23		1.92	0.60			0.26	1.29	0.37
Odonata									
Agrionidae	0.81			0.64	0.60				
Plecoptera									
Perlidae									
Trichoptera									
Cheumatopsyche sp.	9.68	0.50	6.19	1.8				0.65	1.15
Hydroptilidae									
Psychomyiidae									1.72

Table 4. Continued.

	Collection Date							
Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Ephemeroptera								
Baetis *sp*.	0.62	0.72	1.47	0.47		0.31	0.86	
Caenis *sp*.		1.44	0.07			0.94	1.21	1.11
Tricorythodes *sp*.	0.62	0.72	0.74					
Choropterpes *sp*.	0.62							
Habrophlebia *sp*.			0.74					
Isonychia *sp*.	0.62	0.72				0.94	1.73	
Stenonema *sp*.	1.23	5.04	8.82	0.68	0.09	0.62	0.17	2.22
Odonata								
Agrionidae					0.09			
Pletoptera								
Perlidae						1.25	0.17	
Trichoptera								
Cheumatopsyche *sp*.	11.73	11.51	5.15	0.61	0.18	0.31	6.04	2.22
Hydroptilidae	0.62			0.07				
Psychomyiidae				0.14				

Table 4. Continued.

	Collection Date								
Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Diptera									
Chironomidae	70.16	15.84	5.15	23.72	47.90	89.31	33.94	67.10	85.63
Simulium larvae	1.61		14.95	7.69	46.71		50.52	3.87	
Simulium pupa									
Dipteran adults				0.64	0.60				
Dipteran pupa			1.03			2.29	0.26		
Zooplankton		57.92	64.43	34.62	1.20	2.29	4.40		4.60
Miscellaneous									
Ostracoda		20.30		21.15	0.60		0.52		1.15
Fish eggs	0.81	1.98		1.92		5.73	9.33		
Gastropoda			1.03	0.64					
Plecypoda			4.64						
Arachnida	0.81		0.52				0.52		0.57
Trichoptera purse									
Aquatic Oligochaete								2.58	
Trematoda								1.29	
Crayfish									
Seeds		0.99							
Unidentified		2.48	0.52	1.92	1.20	0.38		1.29	
Number of items	124	202	194	156	167	262	386	155	174
Number of fish	10	20	20	20	20	20	20	20	20

Table 4. Continued.

Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Diptera								
Chironomidae	49.38	69.06	26.47	95.33	92.66	17.81	84.28	
Simulium larvae					2.78	73.75	1.04	
Simulium pupa				0.54		0.62		
Dipteran adults								
Dipteran pupa			2.21		3.76	0.31	0.86	
Zooplankton	17.90	10.07	46.32	1.28	0.27	0.31	0.17	88.89
Miscellaneous								
Ostracoda	15.43		4.41	0.41				2.22
Fish eggs					0.18	2.81	2.59	
Gastropoda								
Plecypoda	0.62	0.72		0.20				
Arachnida	0.62		1.47					2.22
Trichoptera purse				0.07				
Aquatic Oligochaete				0.07			0.35	
Trematoda								
Crayfish							0.17	
Seeds								
Unidentified			2.21	0.07			0.35	1.11
Number of items	162	139	136	183	1117	320	579	90
Number of fish	20	20	26	60	194	38	31	9

Collection Date spans columns 7-79 through 8-80.

Table 5. Dietary composition of *P. phoxocephala*, 1978-1980. Values are percent frequencies of each taxon in each collection.

	Collection Date								
Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Ephemeroptera									
Baetis sp.									12.23
Caenis sp.						0.61	0.35		
Tricorythodes sp.	28.89	2.26	4.00	1.55					2.66
Choropterpes sp.		13.53							
Isonychia sp.	24.44						0.12	21.43	19.15
Stenonema sp.	2.22		4.00	2.07		1.21		2.26	1.06
Odonata									
Agrionidae	1.11	5.26	0.52	0.26	3.03	0.12	0.38		
Trichoptera									
Cheumatopsyche sp.	36.67	6.77		1.55	0.26		15.41	7.98	
Psychomyiidae									
Diptera									
Chirononomidae	2.22	51.88	36.00	9.84	64.48	58.18	5.14	9.40	4.26
Simulium larvae	3.33			17.26	28.68	3.03	28.04	42.86	51.06
Simulium pupa		0.75				0.61	0.12		0.53
Dipteran adults			0.52						
Diptran pupa		8.27			2.33	26.67.	0.47		0.53

Table 5. Continued.

Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
	Collection Date							
Ephemeroptera								
Baetis sp.	3.28					0.96	18.50	
Caenis sp.		4.65			0.21			
Tricorythodes sp.		6.98	3.23					
Choropterpes sp.								
Isonychia sp.		11.63		25.00		0.48	4.63	
Stenonema sp	18.03	16.28	45.16		0.42	2.40	1.85	86.36
Odonata								
Agrionidae	1.64		3.23					
Trichoptera								
Cheumatopsyche sp.	29.51	30.23			0.42		15.74	
Psychomyiidae		2.33						
Diptera								
Chironomidae	42.62	13.95	12.90	50.00	49.58	0.96	30.56	
Simulium larvae					43.64	92.79	21.30	
Simulium pupa					2.12	1.44	0.93	
Dipteran adults								
Dipteran pupa	3.28	6.98	6.45		3.39	0.96	1.85	4.58

Table 5. Continued.

Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
	Collection Date								
Zooplankton		5.26	44.00	65.28					
Miscellaneous									
Ostracoda									
Fish eggs						6.67	65.54	8.27	0.53
Unidentified	1.11	6.02	12.00	1.04			0.12		
Number of items	90	133	25	193	387	165	856	266	188
Number of fish	9	20	20	18	7	17	20	20	20

Table 5. Continued.

	Collection Date							
Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Zooplankton	1.64	2.33	29.03		0.21			9.09
Miscellaneous								
Ostracoda								
Fish eggs							4.63	
Unidentified		4.63		25.00				
Number of items	61	43	31	4	472	208	108	22
Number of fish	20	20	15	3	15	12	14	5

Table 6. Dietary composition of *P. caprodes*, 1978-1980. Values are precent frequencies of each taxon in each collection.

	Collection Date								
Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Collembola									
Ephemeroptera									
Baetis sp.									2.45
Caenis sp.					1.35			0.20	1.44
Tricorythodes sp.			0.20						0.87
Choropterpes sp.									0.29
Habrophlebia sp.									
Leptophlebia sp.									
Isonychia sp.								5.05	0.29
Stenonema sp.					0.39		0.66	3.64	1.73
Odonata									
Agrionidae				99.99			0.22		0.14
Plecoptera									
Perlidae									
Trichoptera									
Cheumatopsyche sp.			0.61					13.33	11.54
Hydroptilidae								0.20	
Psychomyiidae									
Coleoptera									
Elmidae adult									0.14
Elmidae larvae			0.20					0.20	0.43

Table 6. Continued.

	Collection Date							
Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Collembola			0.99			0.96		
Emphemeroptera								
Baetis sp.	4.23	1.25	3.96				3.95	0.18
Caenis sp.	0.70	1.25	0.99			2.88	0.56	1.10
Tricorythodes sp.	4.23	4.08	6.93					
Choropterpes sp	0.70							
Habrophlebia sp.		1.25	1.98					
Leptophlebia sp.		0.63						
Isonychia sp.		1.88					1.13	
Stenonema sp.	9.51	4.70	1.98		0.98		2.26	3.31
Odonata								
Agrionidae	0.70	0.31	1.98					
Plecoptera								
Perlidae							1.69	
Trichoptera								
Cheumatopsyche sp.	5.28	36.05	6.93		0.98		10.73	
Hydroptilidae	1.06					0.96		
Psychomyiidae		1.57	1.98					
Coleoptera								
Elmidae adult								
Elmidae larvae	2.11	0.31	2.97				1.13	

Table 6. Continued.

	Collection Date								
Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Diptera									
Chironomidae			17.00		86.71	89.40	59.96	34.55	60.75
Simulium larvae					0.19		12.69	5.66	0.58
Simulium pupa							0.66	1.62	
Dipteran pupa			0.40		10.60	10.50	3.50	3.43	0.72
Zooplankton			80.57		0.58				12.70
Miscellaneous									
Ostracoda									
Fish egs							21.88	31.92	2.16
Gastropoda							0.22	0.20	1.44
Plecypoda									1.59
Arachnida			0.20						
Trichoptera purse									0.58
Trematoda							0.22		0.14
Unidentified			0.81		0.19				
Number of items			494	1	519	427	457	495	693
Number of fish			11	2	6	14	8	13	20

Table 6. Continued.

	Collection Date							
Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Diptera	50.00	39.50	45.54		97.06	1.92	58.19	89.71
Chironomidae								
Simulium larvae					0.98	19.23	1.69	
Simulium pupa						4.81	1.69	
Dipteran pupa	2.46	4.70	3.96			1.92	6.78	1.84
Zooplankton	11.27	0.94	16.83			1.92		1.84
Miscellaneous								
Ostracoda	0.35							
Fish eggs						65.38	10.71	
Gastropoda	0.35	0.63	2.97					
Plecypoda	3.52	0.31						
Arachnida								0.18
Trichoptera purse	3.52							
Trematoda								
Unidentified		0.63						1.84
Number of items	284	319	101		102	104	177	544
Number of fish	16	15	5		4	4	5	12

Table 7. Dietary composition of *P. copelandi*, 1978-1980. Values are percent frequencies of each taxon in each collection.

	Collection Date								
Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Ephemerotpera									
Baetis sp.									0.82
Caenis sp.								11.11	
Tricorythodes sp.	1.12								
Isonychia sp.	2.24							33.33	0.14
Stenonema sp.	1.12								
Plecoptera									
Perlidae									
Trichoptera									
Cheumatopsyche sp.	0.84								0.14
Psychomyiidae									
Coleoptera									
Elmidae adult									0.14

Table 7. Continued.

	Collection Date							
Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Ephemeroptera								
Baetis sp.			1.01			1.23	0.32	0.28
Caenis sp.					33.33	1.23		
Tricorythodes sp.								
Isonychia sp.								
Stenonema sp.								
Plecoptera								
Perlidae							0.32	
Trichoptera								
Cheumatopsyche sp.							0.32	
Psychomyiidae						1.23		
Coleoptra								
Elmidae adult								

Table 7. Continued.

Prey Taxon	6-78	9-78	10-78	11-78	3a-79	3b-79	4-79	5-79	6-79
Diptera									
Chironomidae	84.87				70.59	89.4	11.94	44.44	18.13
Simulium larvae	0.28						8.96	11.11	0.14
Diptera adults									0.69
Diptera pupa	0.56				23.53	10.50	1.49		0.14
Zooplankton	0.56				5.88		36.57		72.12
Miscellaneous									
Ostracoda	0.56								
Fish eggs	7.00						41.04		7.28
Arachnida	0.28								
Seeds	0.56								
Number of items	357				17	19	134	9	728
Number of fish	7				1	1	10	4	8

Table 7. Continued.

	Collection Date							
Prey Taxon	7-79	8-79	10-79	12-79	3-80	4-80	5-80	8-80
Diptera								
Chironomidae	55.32		2.51		33.33	6.17		0.17
Simulium larvae						17.28		
Simulium pupa								
Dipteran adults								
Dipteran pupa			0.50		33.33			0.28
Zooplankton	44.68	99.99	95.98			2.47		98.30
Miscellaneous								
Ostracoda						70.37		
Fish eggs								
Arachnida								
Seeds								
Number of items	47	147	199		3	81	633	704
Number of fish	2	2	3		1	11	23	8

Dietary Overlap and Breadth

During the first field season community dietary overlaps were low in the fall (September, 1978; November, 1978), high in early spring (March, 1979) and decreased until summer (June, 1979; Table 8). On collecting dates when measures of discharge and habitat diversity were made (i.e., second field season), diet overlap was almost complete during high flows (December, 1979; May, 1980), moderate during lower flows (August, 1979; October, 1979; March, 1980; April, 1980), and low when flow ceased (August, 1980). Dietary overlap was positively correlated with habitat diversity for both community ($r=.74$, $p<.05$; Figure 13) and individual species pairs (Figure 14a-f).

Darter community diet breadth gradually increased from winter through summer in the first field season. The same pattern held true during the second field season (Table 8). Darter community dietary breadth measures were generally higher at low habitat diversities than at high habitat diversities (Figures 15 and 16).

Food Size Similarity

Food size similarity based on calculated Euclidean distance measures represents the mean distance between the food size niche centroids of the darter community. As the distance between the species becomes smaller or larger the similarity of food size use becomes greater or lesser,

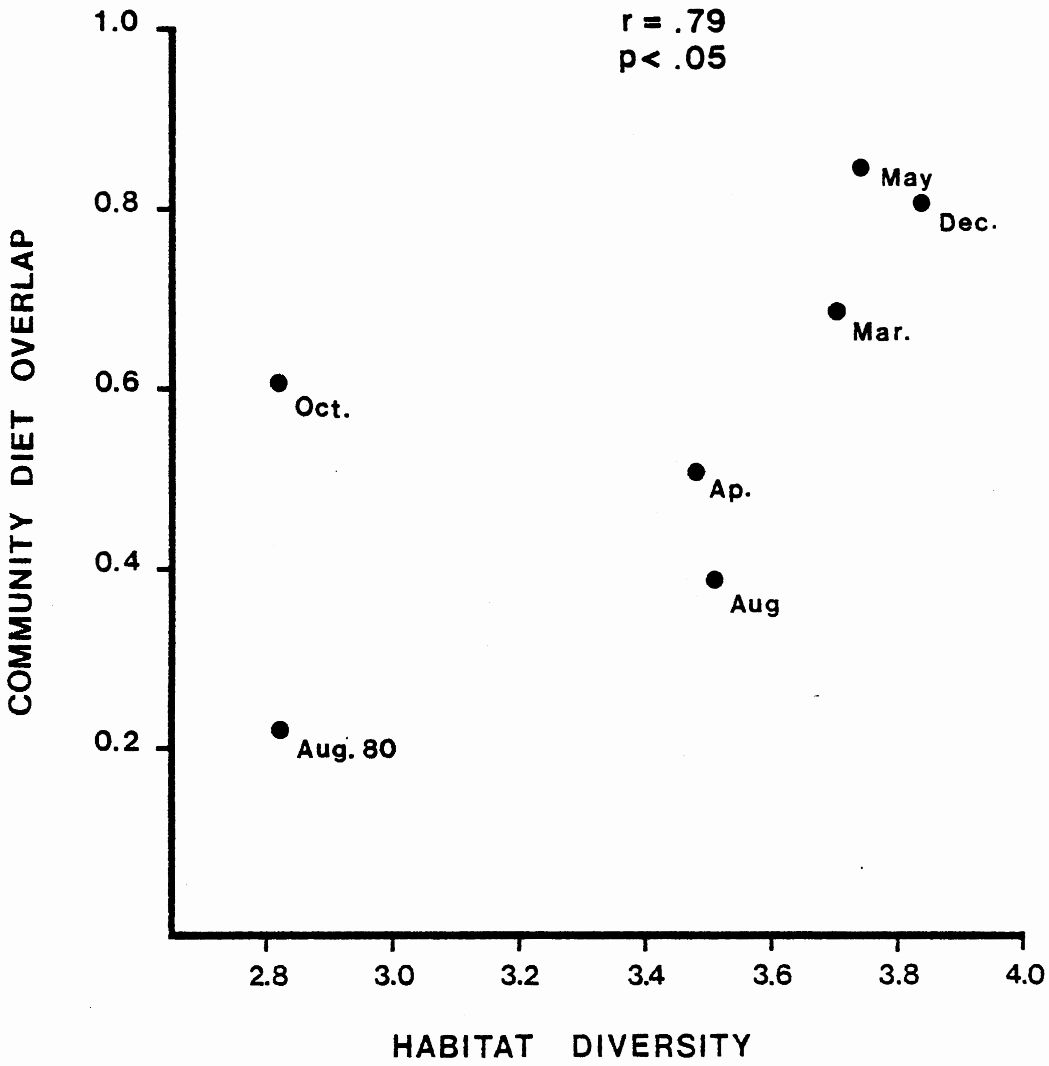

Figure 13. Community dietary overlap vs. habitat diversity (August, 1979 - August, 1980)

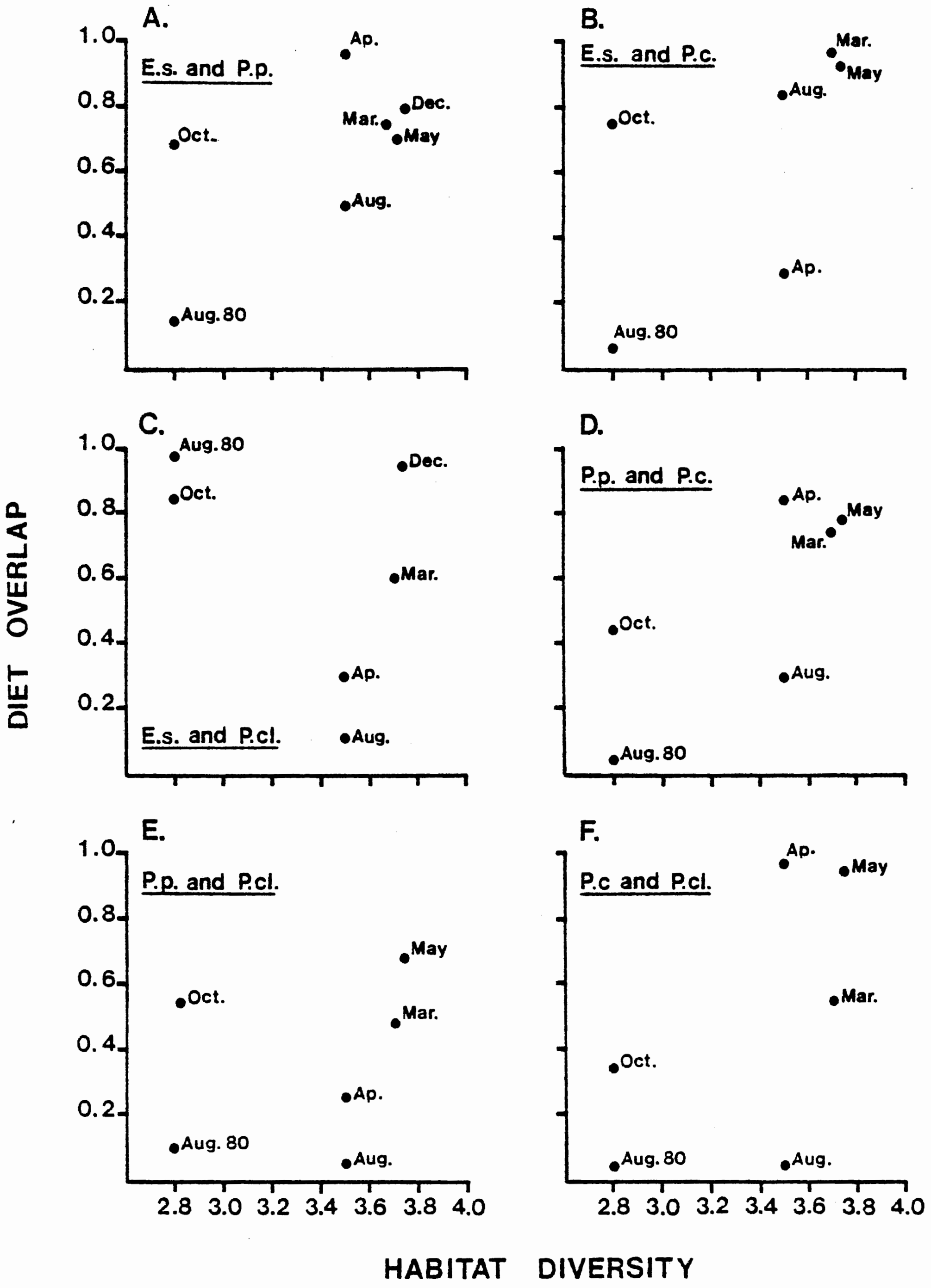

Figure 14. Species pairwise dietary overlaps vs. habitat diversity (August, 1979 - August, 1980). (E.s. = E. spectabile; P.p. = P. phoxocephala; P.c. = P. caprodes; P.cl. = P. copelandi)

Table 8. Summary table of various community dietary analyses for the darter community present in Salt Creek, Osage County, Oklahoma, (June, 1978 - August, 1980).

Date	Diet Overlap	Diet Breadth (B)	Diet Breadth (W)	Euclidian Distance	Average stomach fullness
6-78	.42	2.14	*	7.08	4.40
9-78	.33	3.11	*	6.89	3.05
10-78	.87	2.93	*	6.00	2.60
11-78	.28	3.38	*	10.82	2.40
3a-79	.85	2.22	*	13.87	4.50
3b-79	.93	2.63	*	4.81	3.20
4-79	.55	3.24	*	5.27	3.30
5-79	.59	3.28	*	6.99	3.00
6-79	.32	3.19	*	10.43	3.05
7-79	.82	3.83	*	9.62	2.95
8-79	.39	2.99	*	10.86	3.05
10-79	.60	4.17	.74	9.83	2.88
12-79	.82	1.79	.17	17.40	3.20
3-80	.69	2.09	.33	11.69	3.05
4-80	.52	2.44	.48	8.36	3.10
5-80	.85	4.07	.65	14.66	3.10
8-80	.23	2.48	.78	6.20	2.75

(B) - Community breadth calculated using formula: $B = (i/p_i^2)/n$; for diets n is constant; community index is average of species' breadths. (W) - community breadth calculated using formula: $W = U/A$; communtiy index treats all species as one. * - data not available.

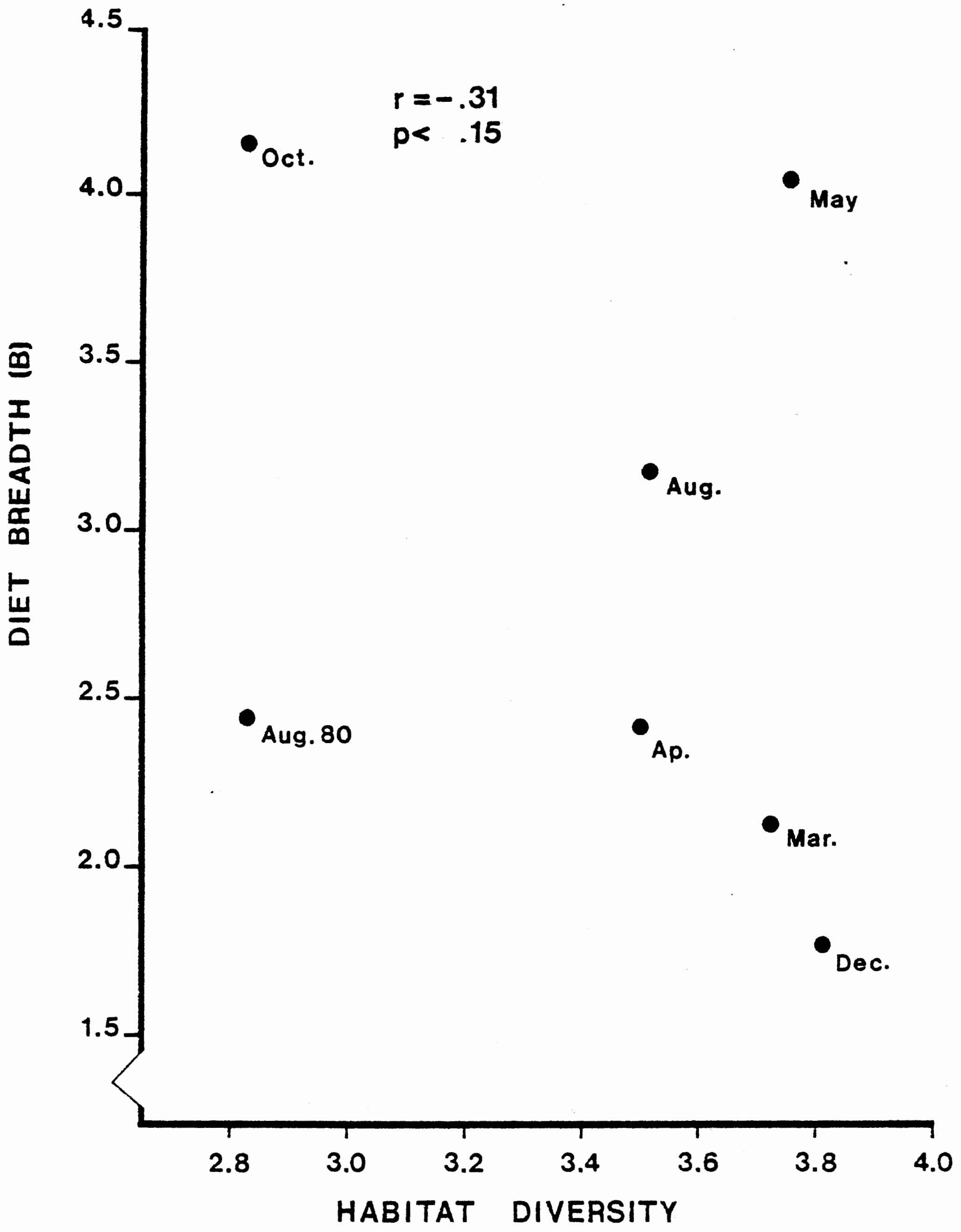

Figure 15. Community diet breadth (B) vs. habitat diversity (August, 1979 - August, 1980). Community breadth is average of species breadths

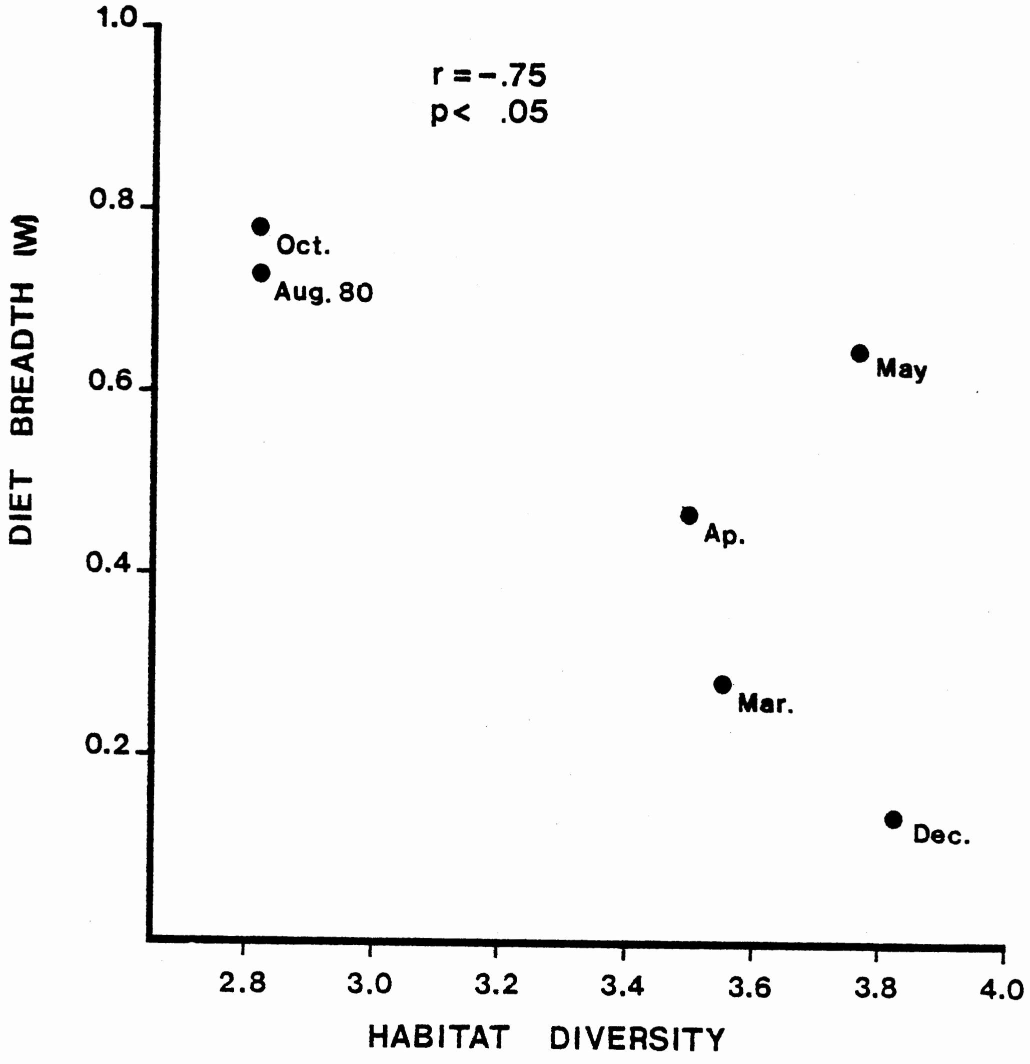

Figure 16. Community diet breadth (W) vs. habitat diversity (October, 1979 - August, 1980). Community breadth treats all species as one

respectively. Euclidean distances were generally higher in the winter and early spring, tapering off through the late spring and summer. Exceptions were found during periods of high flow in May, 1979, and no flow in July, 1979 (Table 8). Habitat diversity was positively correlated with Euclidean distance ($r=.79$, $p<.03$; Figure 17). Similar relationships between habitat diversity and Euclidean distance of species pairs are illustrated in Figure 18 (a-f).

Monthly Stomach Fullness

In months when flow was absent (September, 1978; October, 1978; November, 1978; July, 1979; October, 1979; August, 1980) average stomach fullness was lower ($\bar{x}=2.77$) than during times when flow was present ($\bar{x}=3.35$; Table 8). The relationship between mean community stomach fullness and habitat diversity was highly significant ($r=.94$; $p<.002$; Figure 19).

Benthic Community: Habitat Analysis

Habitat Use

When habitat diversity and discharge were high, the frequency of benthic invertebrates inhabiting riffles was greater than the frequency inhabiting pools (Figure 5b). As discharge declined, members of the benthic community disappeared from the riffles (October, 1979; August, 1980). Within riffles the benthic insect community favored

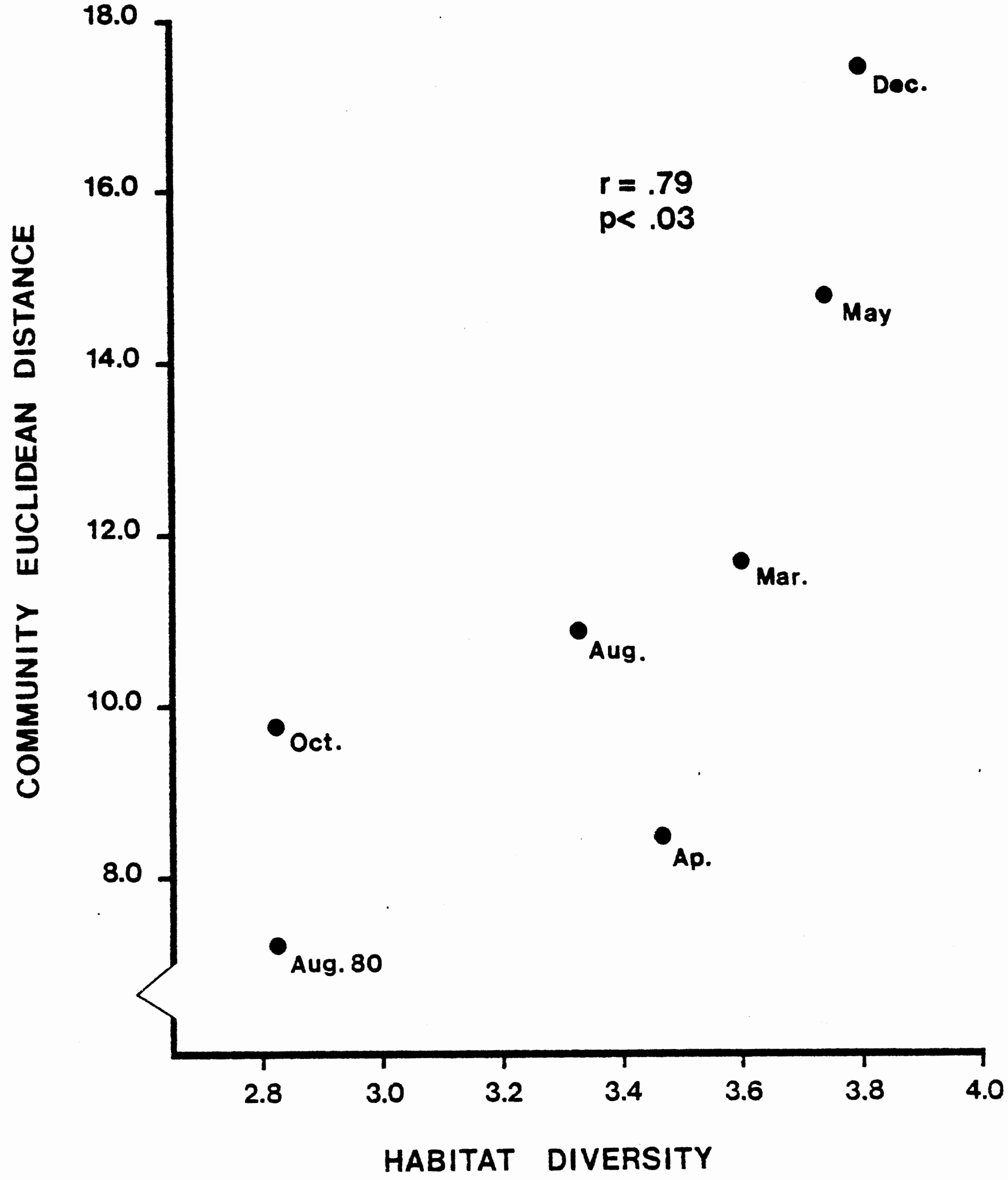

Figure 17. Community food size dissimilarity (Euclidean distance) vs. habitat diversity (August, 1979 - August, 1980). Higher distance values denote less community food size similarity. Lower values denote greater commuity food size similarity

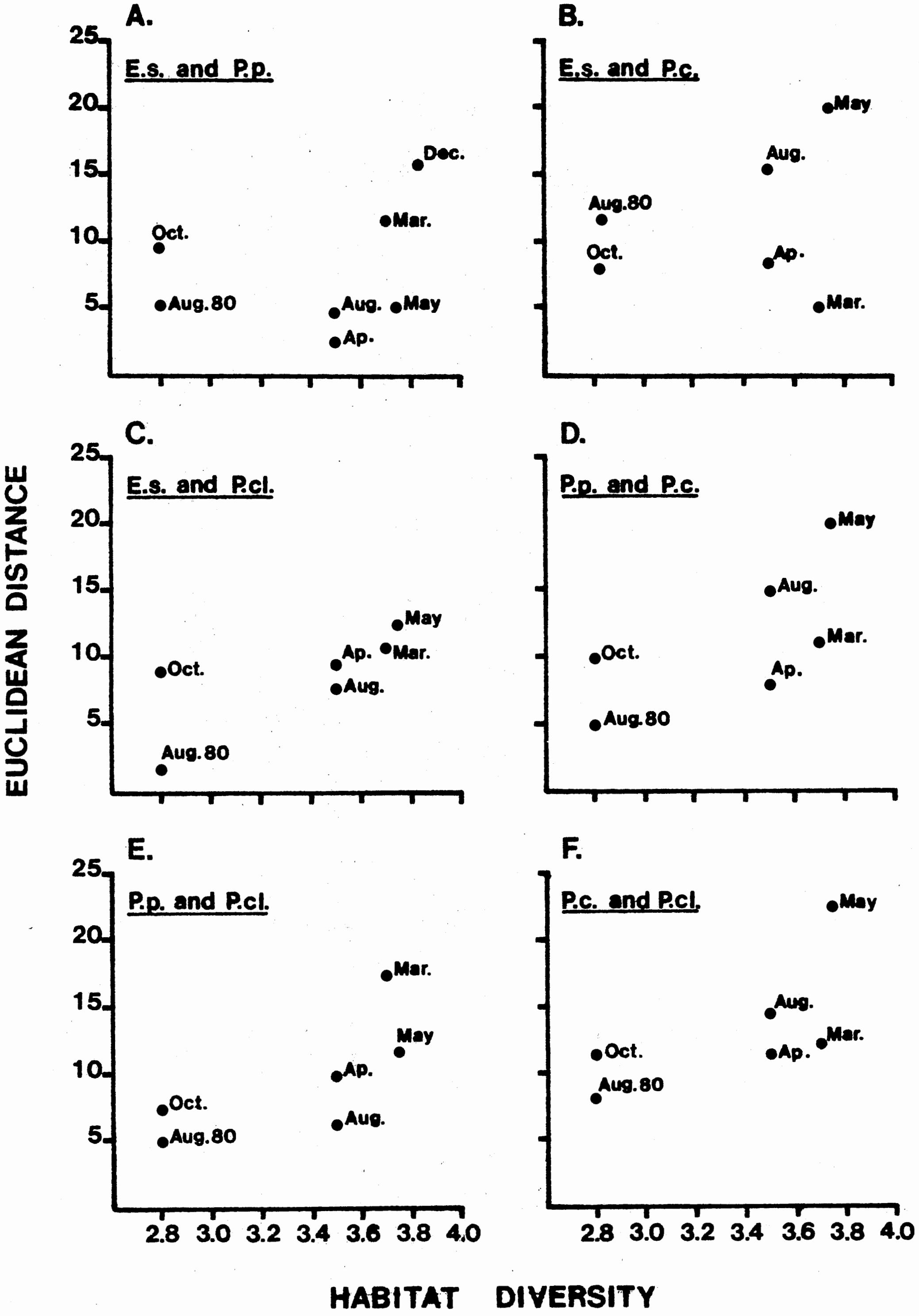

Figure 18. Species pairwise food size dissimilarities vs. habitat diversity (August, 1979 - August, 1980). E.s. = E. spectabile; P.p. = P. phoxocephala; P.c. = P. caprodes; P.cl. = P. copelandi)

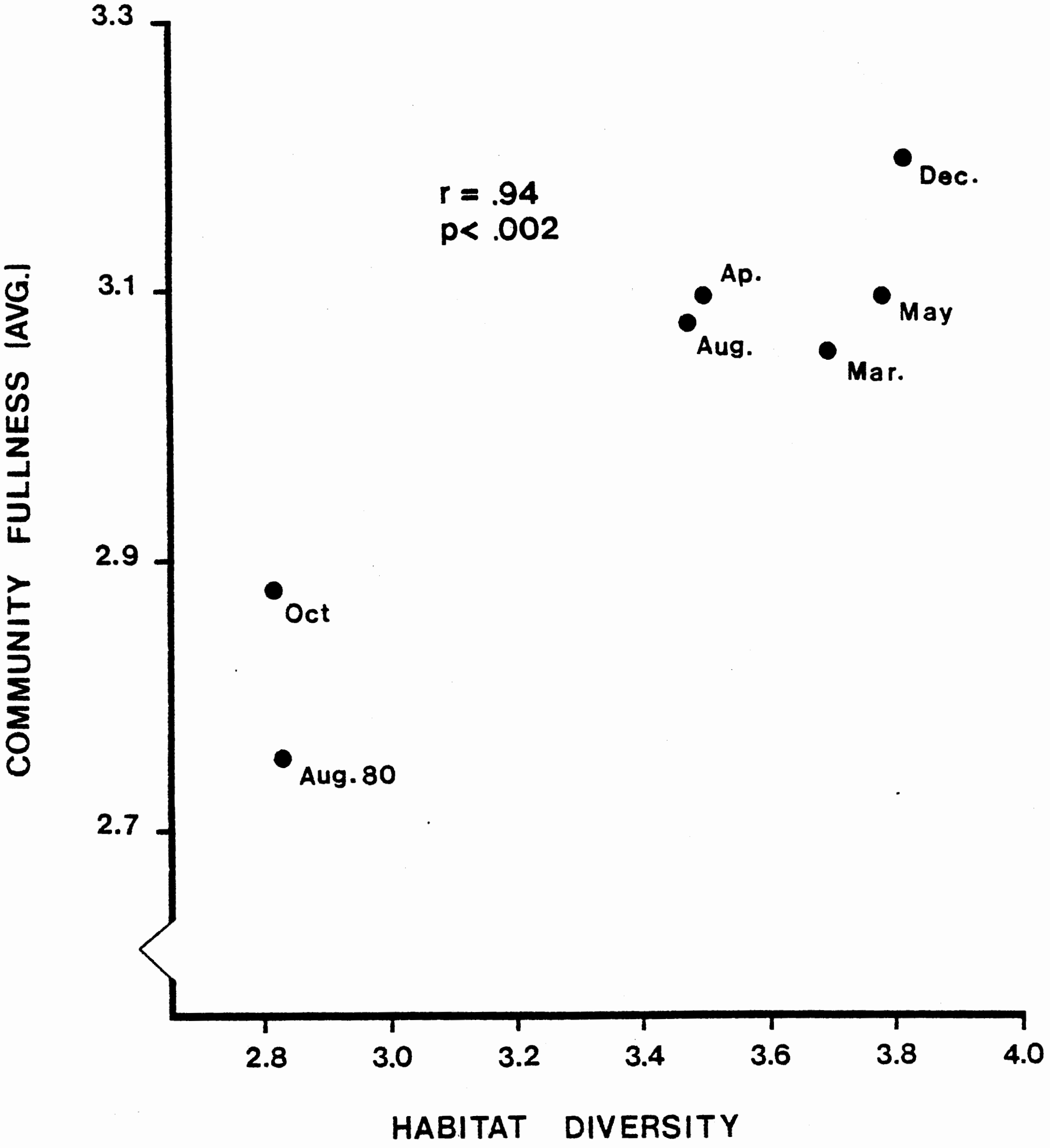

Figure 19. Average community stomach fullness vs. habitat diversity (August, 1979 - August, 1980)

mid-riffle and edge of riffle habitats over head and tail of riffle habitats (Figure 20).

If benthic insect density in each microhabitat was analyzed on a monthly basis, the number of benthic insects in three out of four pool habitats above and below the riffle were negatively correlated with habitat diversity (Table 9). Conversely, in three out of four riffle habitats, benthic insect densities were positively correlated with habitat diversity. As flow increased aquatic insects shifted from pool habitats into riffle habitats.

Benthic insect densities increased from December, 1979, through May, 1980, with minimum densities occurring in August, 1980, and October, 1979 (Table 10). The relationship between benthic insect density and habitat diversity was positive ($r=.84$; $p<.05$; Figure 21).

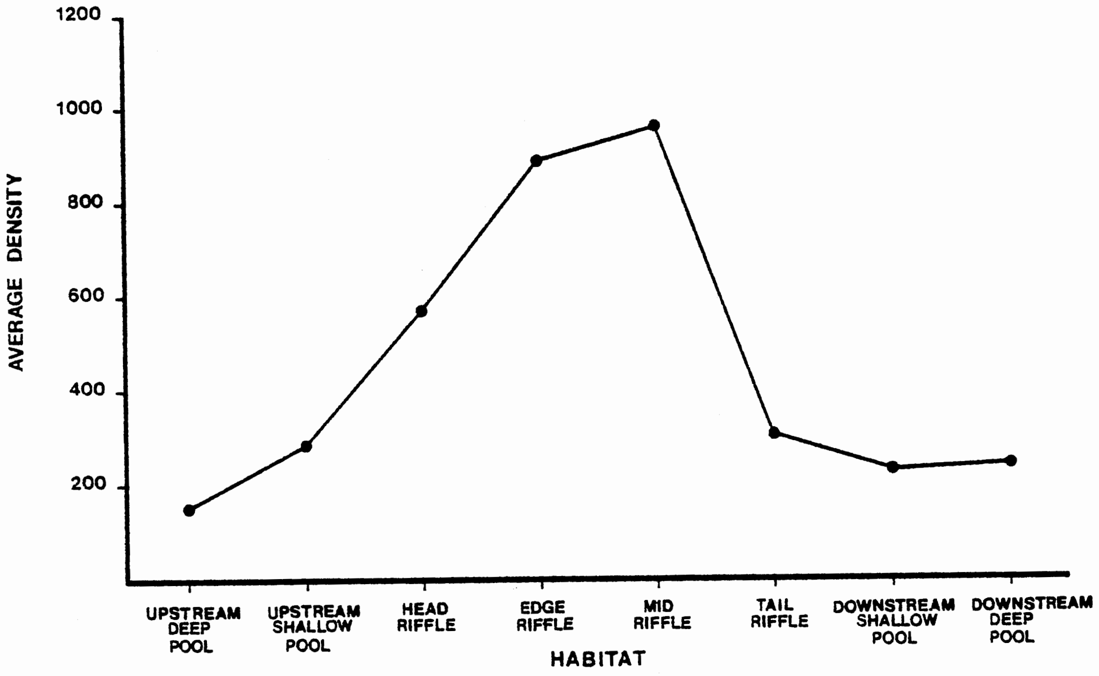

Figure 20. Average density of benthic insects in different habitats present at the Salt Creek study area (October, 1979 - August, 1980).

Table 9. Correlations between benthic insect density in each microhabitat and habitat diversity (Ocotber, 1979 - August, 1980).

Microhabitat	Correlation Coefficient (r)
upstream shallow pool	-.22
downstream shallow pool	-.21
upstream deep pool	-.41
downstream deep pool	+.21
head of riffle	+.45
edge of riffle	+.44
mid of riffle	+.47
tail of riffle	-.05

Table 10. Average density of benthic insects in Salt Creek, Osage County, Oklahoma, (October, 1979 - August, 1980).

Date	N	Density/0.25 m^2
10-79	7	140
12-79	12	120*
3-80	16	430
4-80	8	330
5-80	16	560
8-80	7	240

* December, 1979, underestimated due to sampling inefficiency.

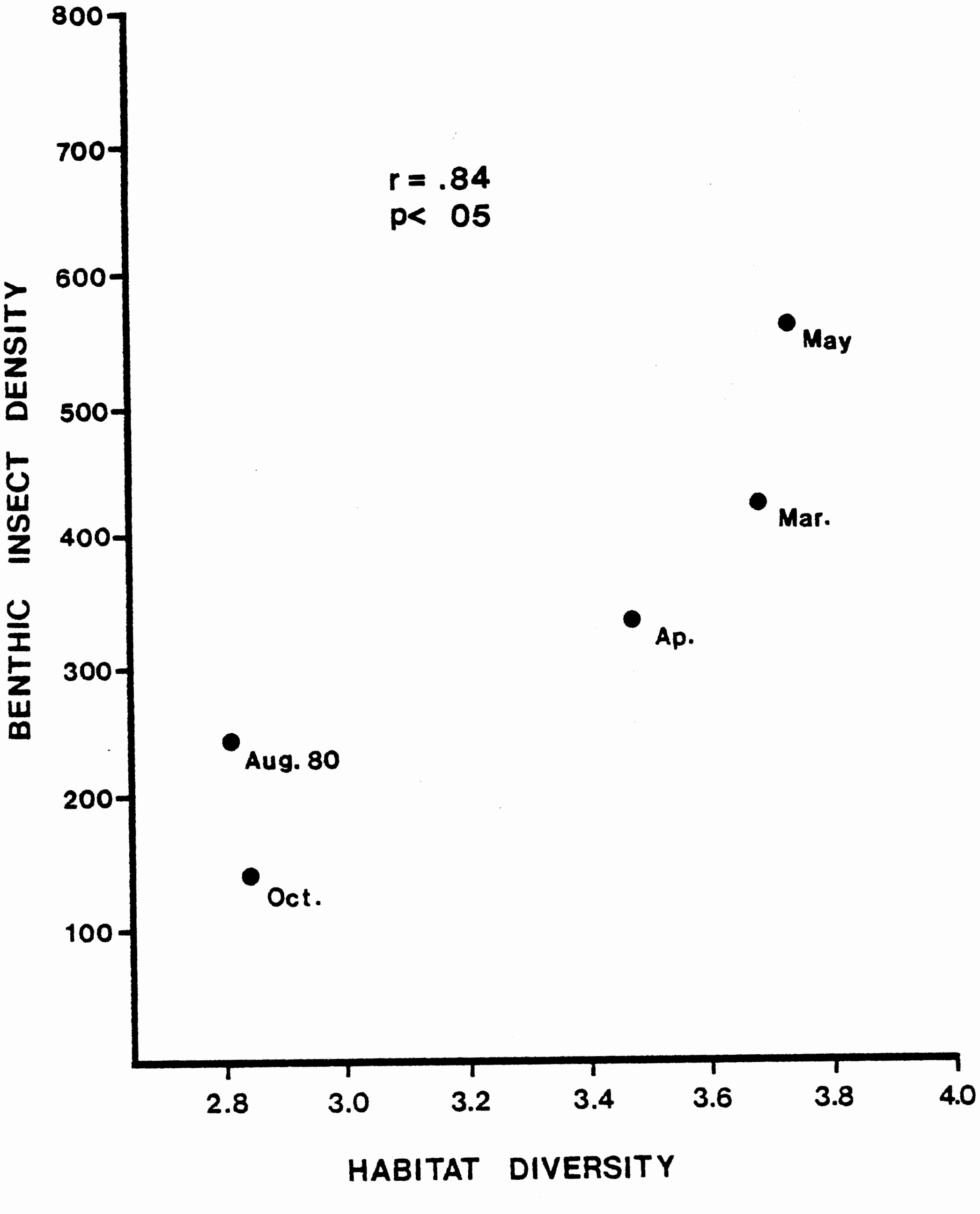

Figure 21. Average benthic insect density vs. habitat diversity (October, 1979 - August, 1980). December, 1979, not included in the analysis due to sampling inefficiency

CHAPTER VII

DISCUSSION

Though most all stream environments vary seasonally (Hynes, 1970), small streams experience environmental variations of a greater magnitude over shorter periods of time than larger streams and rivers. Data from Horowitz (1978) supports the above statement by demonstrating that daily flow rates were more variable in small headwater stream sections than in downstream sections in North American river systems. Horowitz (1978) further noted that runoff-fed headwater streams had more highly variable flow patterns than spring-fed or karst headwater streams. Salt Creek is a headwater, runoff-fed stream, with the potential to oscillate from a flowing environment to a low or non-flowing environment within a single season (e.g., June - August, 1979). Salt Creek thus provides a unique opportunity to: (1) document the niche relationships of darter species in a seasonally variable stream and; (2) shed light on how environmental variability, competition and resource availabilty affect niche relationships and community structure. In the following discussion, I first establish a reliable measure of seasonal aquatic environmental variation. I then discuss the relationship between environmental variability and habitat and food resource supply. Next, I relate community habitat and dietary niche structure to environmental variability and resource supply. Finally, I discuss the general relationships between environmental variability, competition, resource availability and community structure of the darters in Salt Creek.

Measurement of Stream Variability

In Salt Creek qualitative characterizations of seasonal stream conditions are adequate only when describing environmental extremes (i.e., droughts or floods). However, because intermediate environmental conditions are difficult to describe, a better descriptor of variation in aquatic stream environments is provided by measures of changes in discharge or aquatic habitat diversity through time.

Variation in habitat diversity through time in Salt Creek was directly proportional to increases in stream discharge (Figure 3). Explanations for this relationship are two-fold. First, as discharge increases above 0.0 m^3/s, current speed is added as a new tier of complexity to the aquatic habitat. Second, and not mutually exclusive from the first explanation, high discharge favors increases in habitat complexity because new habitats become incorporated into the site proper. Adding new habitat area with increased discharge, a long known hydrological relationship, can be visualized in Figure 22. As discharge increases in the lower half of the figure, flow that was once restricted

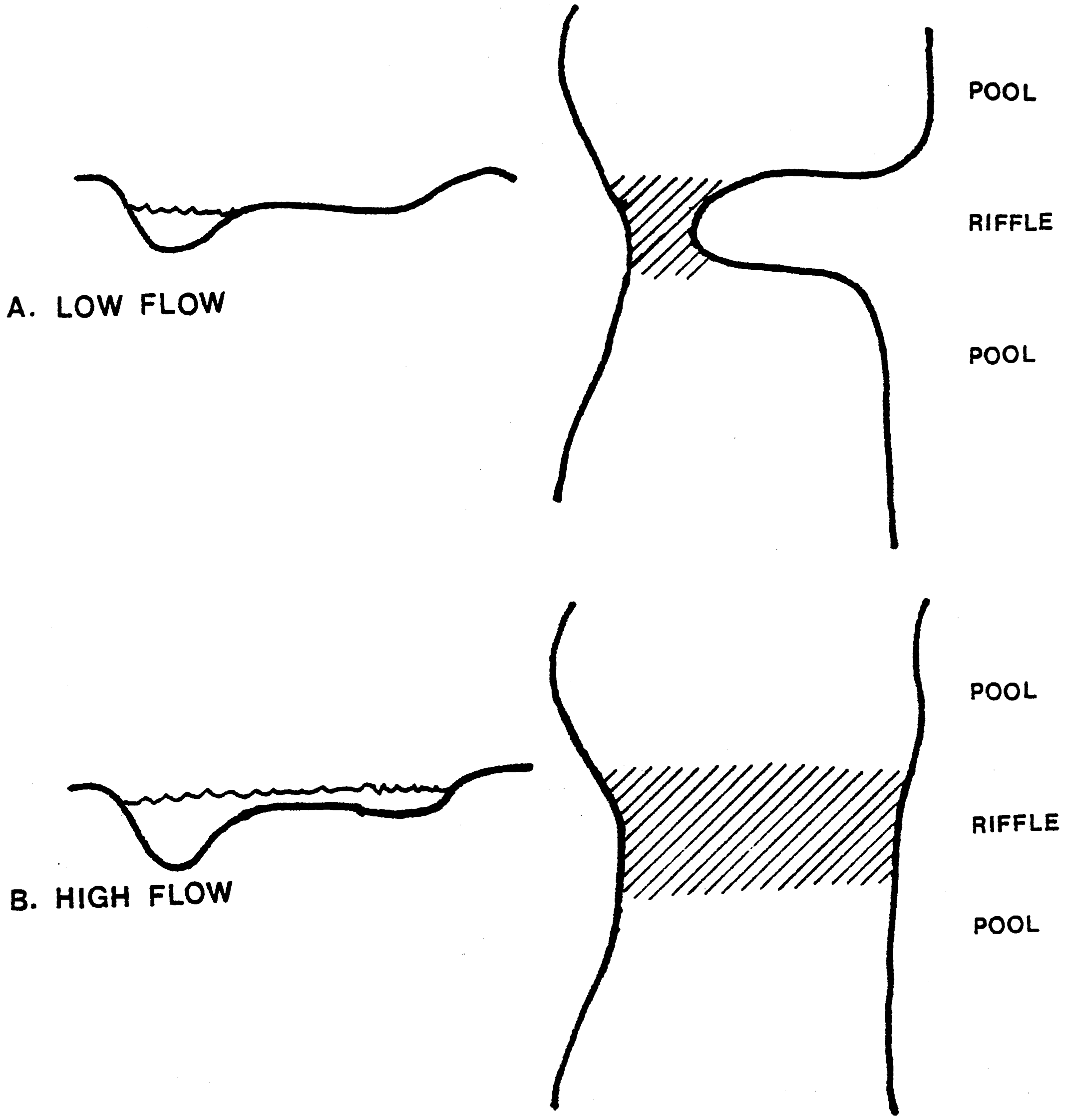

Figure 22. Stream profile (left) and area covered by water (right) for a hypothetical stream site under low (A) and high (B) flow. On right cross-hatching represents area of riffle covered by water clear areas represent pools

to a shallow depression spreads rapidly across the dry riffle until confined by the streambanks. The expansion of aquatic habitat at a riffle-pool site as flow increases adds new depths, substrates and current speeds to the study site, increasing its complexity.

Environmental Variability and Resource Supply

Several lines of evidence suggest that habitat and food supplies were more limited to darters during low diversity (low-flow) conditions. In Salt Creek, riffle area and habitat complexity decline with discharge (Figures 3 and 22), leaving the darter community with a habitat "niche volume" of lesser size than during high diversity (high-flow) conditions.

Limitation of food availability is reflected in the relationship between benthic insect density and habitat diversity (Figure 21). In Salt Creek, benthic sample data indicated insect densities up to 2-4 times greater (Table 10) under conditions of high habitat diversity than low.

If food is in short supply, one would expect that food consumption would be less during low flows. Available evidence supports this hypothesis. Community stomach fullness, in addition to being positively correlated with habitat diversity (Figure 19), demonstrated a significant positive relationship ($r=.93$; $p<.002$) with benthic insect density.

Environmental Variability and Darter
Community Niche Structure

Habitat Structure

Interpreting niche overlap indices requires information on the availability of the resource in question (Pianka, 1978). If the resource is abundant, high overlap implies a relaxed competitive state between species because there is plenty of the resource available to all. However, if the resource declines in availability and becomes limited in supply, competition theory predicts that the species should segregate along the immediate or another complementary niche dimension to reduce competitive intensity (Schoener, 1974; Pianka, 1972; Pianka, 1978).

Habitat avialability at Salt Creek was positively correlated with stream flow (Figure 3). With the exception of the October, 1979 collection, however, the darter community segregated (overlaps are low, less than .37) along the habitat niche dimension (Figure 11). Segregation when habitat resources are in short supply (August, 1980) is easy to explain using traditional competition theory but habitat segregation during habitat abundance (high flow-high diversity) is more difficult to explain. As habitat diversity (i.e., "habitat volume") becomes greater the darter species may be "pushed" by existing competitive interactions to seek refugia (Matthews, 1982b) or "pulled" by the increased habitat diversity into optimal habitats.

High habitat similarity in October, 1979, (Figure 11) appeared to be the result of darters attempting to remain closely asociated with riffles. As flow receeded darters emigrated (probably reluctantly as exemplified by *E. spectabile*, *P. phoxocephala* and *P. caprodes*' persistence in mid and base of riffle habitats during low flow in July, 1979; Figure 8b) out of shallow riffle habitats into the pools (Figure 23b). As a result, habitat overlaps between species pairs (excepting the overlap between *P. phoxocephala* and *P. copelandi*) were at their maximum (Figure 12). When riffles dried up and only pool habitats existed (Figure 23c; August, 1980) it appeared that the darter community, given enough time, segregated the existing habitat (Figure 11; August, 1980). When flow returned (Figure 23a) the increased diversity and availability of habitat permited habitat segregation to occur (Figure 11; March, April, May, December).

During both field seasons community habitat overlap and breadth were positively correlated (Figures 9 and 10). This relationship runs counter to niche packing theory which predicts an increase in habitat overlap should lead to a narrowing of community habitat breadth (tight-packing) and decreases in habitat overlap should lead to a broadening of habitat breadth (loose-packing; Pianka, 1974, 1978).

The relationship between habitat overlap and breadth might result from differences in habitat availability during high flows and low flows (previous discussion). It is

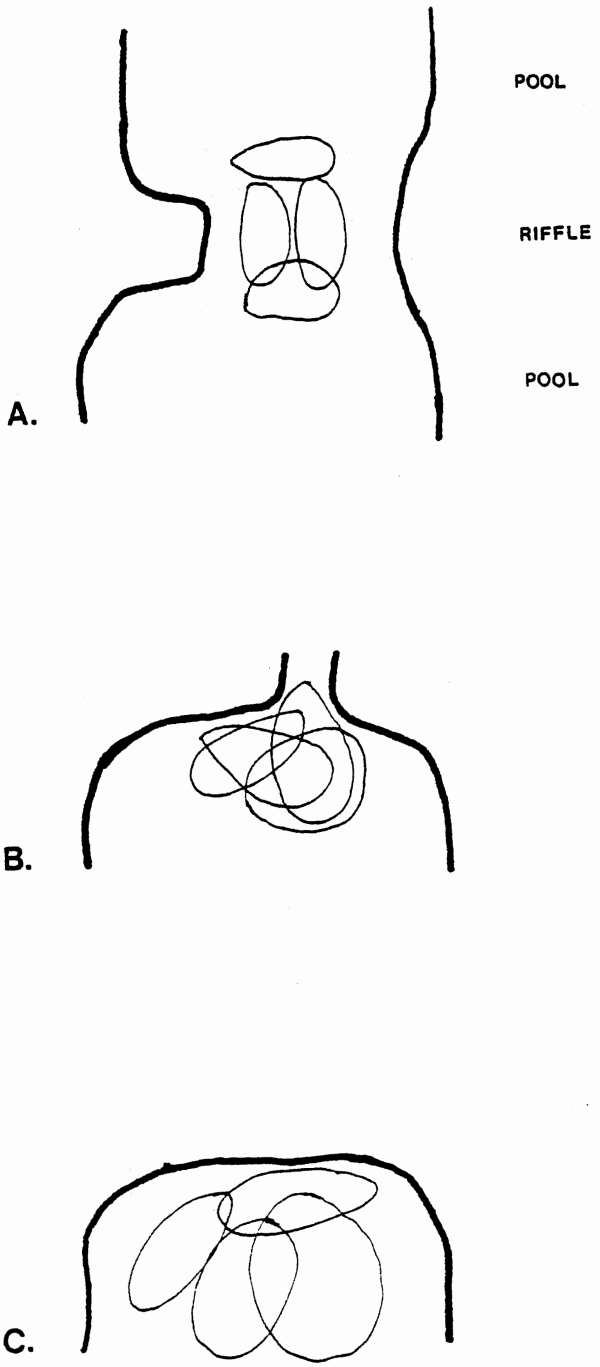

Figure 23. Hypothetical habit use by the darter community under different flow regimes. A = normal to high flow; B = reduced flow; C = no flow

probable that when flow (habitat diversity) is high there is a greater amount of prime habitat available to each of the darter species. Individuals of each species could focus on their optimal habitats and a decline in habitat overlap and habitat breadth could be expected. At low flows habitat diversity decreased, as does the amount of prime habitat. This should result in an increase in the amount of interactions between species. Increased similarity of habitat use could force the species to become generalized (spread out) over the remaining suboptimal habitats, increasing the breadth and overlap of the community's habitat use.

Diet Structure

Decreased community dietary segregation under high-diversity and high-food availability conditions and increases in dietary segregation under low-diversity and low- food availability (Figure 13) support Pianka's (1972) prediction that as food becomes less abundant, community dietary overlap should decrease. The occurrence of low community dietary overlaps when food is potentially limiting is consistent with the theory that predicts niche shifts in food use as a result of competitive interactions between species.

In many northern fish communities (Seaburg and Moyle, 1964; George and Hadley, 1979; Werner and Hall, 1979; Matthews et al., 1982b), community dietary overlap was greatest in spring followed by decreased values in the summer and fall. In Salt Creek, community diet overlaps appeared influenced more by irregular changes in the diversity of the aquatic habitat and concomitant changes in prey availability than by regular seasonality. For example, darters collected at higher habitat diversities in March and May, 1980, were exposed to greater prey availabilities and had higher dietary overlaps than those collected in April and August, 1980, when the diversity of the habitat declined.

As diversity of the aquatic habitat increased the food use of the darter community tended to become more specialized (lower breadths; Figures 15 and 16). Such a diet breadth shift seems to support optimal foraging theory (Werner and Hall, 1974; Zaret, 1980; Pianka, 1980) which predicts that dietary breadths should decrease as prey availability increases because expectancy of prey encounter is high and mean search time is low. Evidence of high prey densities (i.e., availability) when the diversity of the aquatic habitat was high has been documented earlier (Figures 19 and 21). Evidence for prey movements being greater in streams under high diversity (high-flow) situations has been documented by Minckley (1964), Williams (1977), Gray and Fisher (1981), and this study (Table 9).

Food Size Similarity

Based on measures of Euclidean distance, similarity of food size use between darter species was lower under conditions of high habitat diversity than under low habitat diversity (Figure 17). High dissimilarity of food size use at high diversities may result from different sized individuals of the benthic prey having high probabilities of occurrence in specific habitats. That benthic insects partition habitat on the basis of current speed has been documented by Linduska (1942) for mayfly species and by Allen (1951) for size classes of the trichopteran genus <u>Helicopsyche</u>. Hynes (1970) noted that the above differences are complex, variable in time and difficult to quantify accurately.

If benthic insect habitat segregation and habitat segregation are both strongly cued by the same habitat variable (current speed), then food size use differences between darters living under conditions of high habitat diversity may be explained by darters either passively foraging on food sizes available in their preferred habitat or selecting habitats in which they are efficient foragers. Data from Mendelson (1975) supports the first alternative by demonstrating that coexisting <u>Notropis</u> species segregate habitat first and then forage on what is available. The second alternative is supported by Werner and Hall (1976, 1979) who showed that sunfishes in experimental ponds segregate on the basis of microhabitats within which they seem to be the most efficient foragers. Determining which alternative best fits the darter community in Salt Creek is difficult, though the second is intuitively more appealing.

When habitat diversity was low (i.e., conditions more pool-like) the darter community's food size use appeared similar (Figure 17). One possible explanation for such a pattern is that habitat segregation cues for the benthic prey may have diminshed. As a result, different sized benthic prey would become more evenly distributed throughout the aquatic habitat causing community food size use to converge.

High similarity of food size use under low flow conditions could also result from specialized life history adaptations of benthic prey populations. For example, Ladle and Bass (1982) reported that intermittent streams favor taxa with strategies of rapid growth and pupation so that individuals can leave the flowing system as adults before flow ceases. Additionally Hynes (1970) and Gray and Fisher (1981) noted that many prey taxa evade stressful conditions during low flows by burrowing beneath the substrate. Removal of specific prey types or sizes from the system by pupation or burrowing during low diversity conditions would reduce the prey population size variance, forcing a greater similarity of food size use to occur.

Competition and Darter Community Structure

Competition occurs whenever two or more organisms or populations interfere with or inhibit each other (Pianka, 1980). Typically, the organisms are using resources that are in short supply. Because of the possibility of competitive exclusion, it is advantageous for either party involved in a competitive interaction to avoid the other whenever possible; competition therefore promotes the use of different resources and generates ecological diversity. The mechanism(s) used by members of a community to partition resources among themselves in order to reduce interspecific competition will invariably shape the structure of the community.

There are divisions among ecologists as to the probable importance of competition in structuring field communities. Some, like Pianka (1974, 1980), assume that increased densities in a finite environment or a reduction in resource availability under stable densities will eventually lead to some competition. Therefore, competition may be more intense at one point in time than another (i.e., competition continuum). Other ecologists (Weins, 1977; Rotenberry, 1980) suggest that competition is a rare or nonexistent phenomenom and therefore has little impact on natural communities. Evidence from the present study seem to support the first assumption - that competition changes in intensity from one time to the next depending upon resource supply.

In Salt Creek seasonal changes in niche structure of the darter community were correlated with seasonal changes in habitat and food supply. When both resources were in short supply, segregation within the darter community along habitat and dietary dimensions occurred (Figures 11 and 13).

Other studies have documented seasonal changes in niche relationships within bird communities (Gibb, 1954; Smith et al., 1979; Lister, 1980), tropical and temperate fish communities (Zaret and Rand, 1971; Baker-Dittus, 1978; Werner and Hall, 1979), tropical bats (Heithaus et al., 1975) and rain forest anoles (Lister, 1981). In all cases, overlap in food or both food and space decreased when food supplies were low. Such patterns led Lister (1981) to conclude that within communities habitat overlap appears to be inversely related to competition for food.

Patterns of dietary and spatial overlap exhibited by the Salt Creek darter species are consistent with overlap patterns in the studies cited above. Unlike Lister (1981), however, it is difficult to determine whether competition for food or competition for habitat better explains dietary and spatial niche segregation at low flows. Foraging theory suggests that when food supplies become limited (as in Salt Creek at low habitat diversities) species should cease foraging in areas where more efficient predators reduce prey intake. Spatial and food overlap, then, could be reduced by exploitative competition for food. Alternatively, when habitat (e.g., possibly cover from predation) becomes limited at low flows, interference competition for refugia could also be used to explain patterns of reduced spatial and dietary similarity. Though interference competition for cover in the presence of a natural predator (_M_. _punctulatus_) has been witnessed in a laboratory stream tank

(Lehtinen, pers. obs.), further field observations are needed to determine whether interspecific aggression for cover is the mechanism underlying habitat and dietary segregation at low flows.

Evidence supporting the possible importance of competitive mechanisms during high flows can be found by contrasting *E. spectabile's* habitat niche breadth in December, 1979, and May, 1980 (Table 11). *E. spectabile* in the absence of competitors (i.e., December, 1979) exhibited a wider habitat breadth (B=.62) than when all competitors were present (B=.31, May, 1981). Niche shifts by *E. spectabile* in response to the removal and subsequent addition of community members constitutes direct evidence for competition (Pianka, 1980). Though it might be argued that niche shifts resulted because of changes in habitat complexity, this was not the case. Measures of habitat diversity were essentially the same (December, 1979 = 3.81; May, 1980 = 3.76) during both collecting visits. Greenberg (pers. comm.) observed similar habitat shifts by *E. simoterum* in the absence of *E. rufilineatum* in the spring-fed Little River of eastern Tennessee.

Results of the present study strongly suggest interspecific competition as an important process affecting the community structure of darters inhabiting variable environments. Fishes with life histories closely tied to flowing habitats (esp. riffles) appear to have a strong potential to competitively interact as stream flow declines and habitat

Table 11. Habitat niche breadths (B) of *E. spectabile* *P. phoxocephala*, *P. caprodes*, and *P. copelandi* in Salt Creek, Osage County, Oklahoma.

Date	Species			
	E. spectabile	*P. phoxocephla*	*P. caprodes*	*P. copelandi*
12-79	.62	.13	-	-
5-80	.31	.35	.25	.50

and food resources become limiting. However, determining the exact mechanism(s) of competition, or the long-term importance of competition in influencing species coexistence, resource allocation, and, thus, community structure in variable environments will require a data base of longer term and greater resolution than the present study.

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VITA

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Doctor of Philosophy

Thesis: THE EFFECTS OF ENVIRONMENTAL VARIABILITY AND RESOURCE AVAILABILITY ON THE NICHE STRUCTURE OF A DARTER COMMUNITY IN SALT CREEK, OSAGE COUNTY, OKLAHOMA

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