THE UNIVERSITY OF MANITOBA

SPECIES DIVERSITY AND WITHIN-STREAM DISTRIBUTION OF STREAM DWELLING FISHES FROM WESTERN MANITOBA

BY

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A THESIS

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"SPECIES DIVERSITY AND WITHIN-STREAM DISTRIBUTION OF STREAM DWELLING FISHES FROM WESTERN MANITOBA"

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ABSTRACT

Abundance of fishes was determined at stations located in several western Manitoba streams. By use of a multivariate classification procedure, groups of species were identified which were similar in their distribution among arbitrarily defined habitat types. The largest group of species was associated with areas of low current speed, but within high gradient sections of the streams. Species diversity (defined as the number of fish species present) was related to structural features of the environment. By an analysis of variance technique, it was concluded that stream gradient and current speed explained most of the variation in diversity. When a predator (Esox lucius) was present, diversity and abundance of the remaining species were both reduced.

ACKNOWLEDGEMENTS

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INTRODUCTION

This study attempts to examine the relationship between species diversity of stream fishes and certain structural features of their environment.

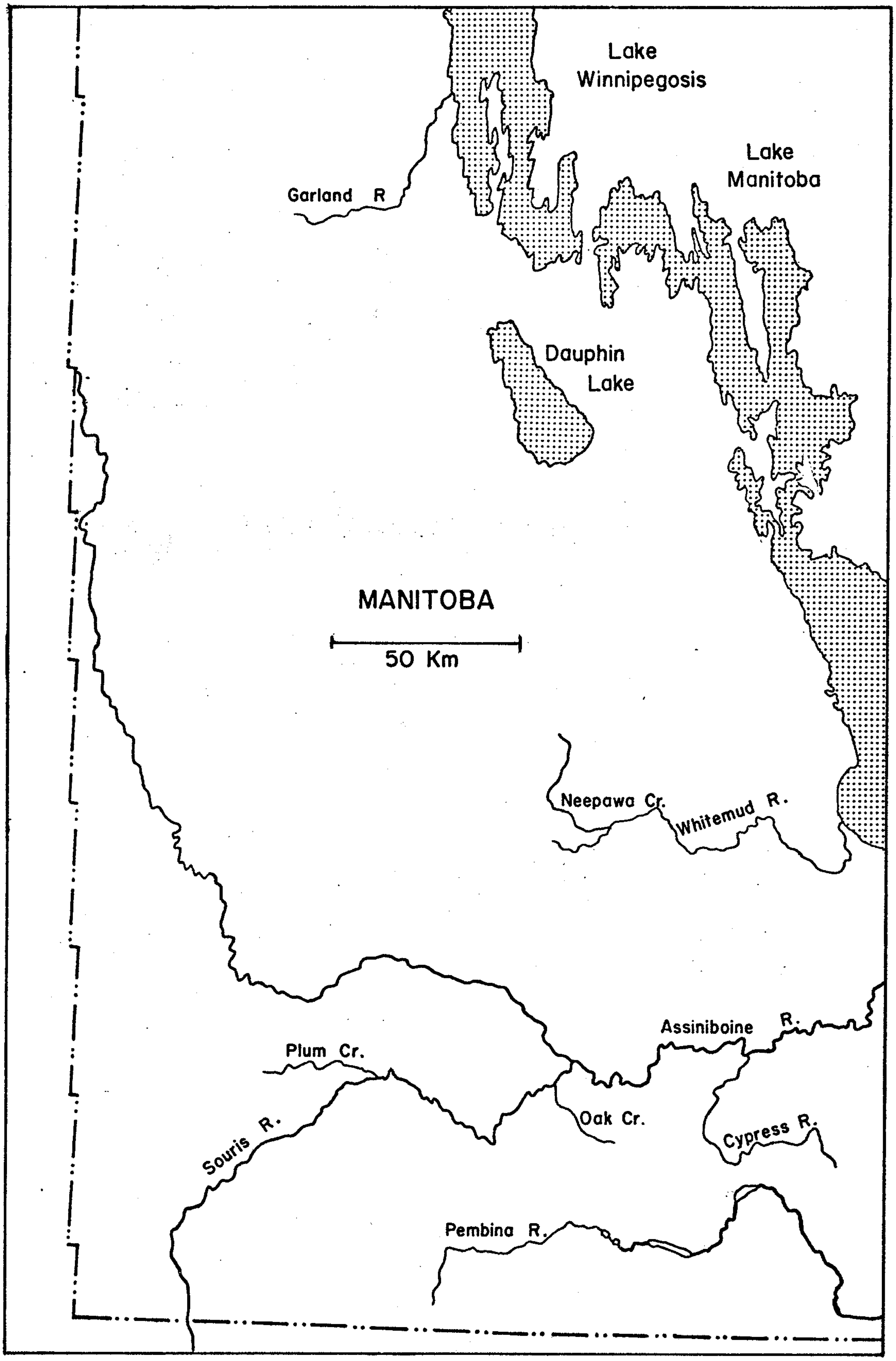
It is generally believed that the diversity of biological communities is related to environmental factors, but the nature of this relationship appears to vary considerably between different geographic areas or taxonomic groups. No model has been suggested which fits more than a small subset of the different community types. Even for a group as relatively homogeneous as temperate stream fishes, Hynes (1970) has suggested that the relationship between diversity and environmental factors depends a great deal on the identity of the component species. Therefore, in this study the discussion of species diversity was preceded by a description of the within-stream distributions of individual species. Also, some precision within any given stream was sacrificed in order to obtain an estimate of "among streams" variability, and hence an estimate of the consistency of the results.

THE STUDY AREA

A total of six streams in the escarpment region of western Manitoba were sampled during the summers of 1973 and 1974 (Fig. 1). These streams are small, generally less than four metres in width and one metre in depth. With one exception, it is possible to divide each stream into two sections based on gradient: a low gradient section in the upstream areas, and a higher gradient section closer to the stream mouth. The low gradient sections are meandering and silt-bottomed, often with considerable aquatic vegetation. These streams typically increase in gradient near their mouths as they enter the valley of a larger river. Plum Creek flows southeast into the Souris River at Souris, Manitoba. Oak Creek flows north into the Souris near Treesbank, Manitoba. The Cypress River flows north, entering the Assiniboine River east of Spruce Woods Park. The Pembina River flows east out of the Turtle Mountains. Neepawa Creek flows south-east out of the Riding Mountains and joins the Whitemud River, which flows into Lake Manitoba. The Garland River flows east out of the Duck Mountains into Lake Winnipegosis.

At first, only four of the streams were sampled, but the upper Pembina River was added in mid-summer of 1973 and the Cypress River was added during the summer of 1974 as a substitute for Plum Creek, which went dry the previous year.

Figure 1. Map of study area, showing locations of streams.


Lake
Winnipegosis
Lake
Manitoba
Garland R
Dauphin
Lake
MANITOBA
50 Km
Neepawa Cr.
Whitemud R.
Assiniboine R.
Plum Cr.
Oak Cr.
Cypress R.
Souris R.
Pembina R.

METHODS AND MATERIALS

SAMPLING

In 1973, twelve stations were chosen on each of the four original streams. These stations were allocated as follows: each stream was divided into two sections, based on gradient. Within each section, three shallow and three deep stations were chosen so that they consisted of one each of fine (silt or sand), medium (gravel) and coarse (rocky) substrates. Thus, each combination of two gradients x three substrates x two depths occurred once in each stream. Later, after some sampling had been done, it became clear that treating depth and substrate size as independent factors was somewhat unrealistic since, in running water, depth, substrate size and current speed are closely related. It was decided to combine the depth and substrate factors and to just call each station a riffle, channel or pool.

Each station was sampled in sequence to form one replicate. Four replicates were obtained, one in each of May, June, July and August. Replications are called "seasons" in the discussion of results, since their effect was one of seasonal changes. The nature of seasonal changes in species diversity was not known *a priori*, but all stations were sampled in the same order each time so as to keep the time between sampling periods nearly constant for each station. It was thought that this might reduce unexplainable variability.

In 1974, attention was confined to the high gradient sections of the streams, with only six stations (two channels, two riffles, two pools) in each stream. This change was made because stations in the low gradient areas were quite consistent in containing few species and it was decided that continued sampling effort in those areas would yield little new information.

MEASUREMENT OF DIVERSITY AND ASSOCIATED VARIABLES

In order to determine species diversity, each station was enclosed using barrier nets and seined repeatedly until three consecutive hauls yielded no fish. Fish taken from a station were identified and number of each species counted. In 1974, all fish taken were measured to the nearest millimeter fork length. Some additional measurements were taken to obtain more information about habitats occupied by individual species. Stream width was recorded at two points, two meters apart. Associated with each width measurement was a set of three depth measurements at 1/4, 1/2 and 3/4 of channel width. Water temperatures and time of day were recorded at each station. In 1973, a measure of surface velocity was obtained by timing a float over a fixed distance. In 1974, a current meter became available and current speed was obtained at the surface and next to the substrate at each point that a depth measurement was taken. In 1973, water chemistry characteristics were determined using a Hach kit, but since little variation was observed from station to station, this was abandoned the next year.

METHODS OF ANALYSIS

A study of the factors affecting species diversity is basically a study of the factors affecting niche overlap (Hutchinson 1959).

In Appendix 1, an argument is given for advantages of the species number, S, over more complex diversity indices, to the effect that other indices confound relative abundance and number of species. A certain loss of information is to be expected with any summary measure including S, however, and therefore it was decided to first consider the distribution of individual species in the hope that this would clarify the discussion of species diversity.

1. Distribution of species among habitats: In the overall sampling design, habitats were divided into three types: riffles, channels and pools. This rather coarse separation of habitats was necessary because each habitat was sampled in four streams, in two gradient sections and at four times during the first summer, and the product of these factors was near the maximum of stations it was possible to consider. When considering the "habitats" factor by itself, however, a finer division of habitat types was possible, and so the riffles, channels and pools defined in the sampling design were arbitrarily reclassified to form six habitat types with depths and current speeds as in Table 1. Not all habitats could be separated on depth and current speed alone. Deep areas were divided into three types (4, 5, 6) which were similar in depth and current speed, but which differed in shape, in substrate type and in proximity to riffles. Pools below riffles (type 4) generally had gravel substrates with no silt deposited. Type 5 pools were variable in substrate type: usually gravel with some silting evident. They were discrete units in the sense that they were bordered by shallower

Table 1. Defined Habitat Types

	Riffle (1)	Fast Channel (2)	Moderate Channel (3)	Pool Below Riffle (4)	Pool (5)	Deep Slow Channel (6)
Current speed (cm./sec.)	.75-2.0	.3-1.0	.15-.5	0-.15	0-.1	0-.1
Depth (cm.)	5-25	8-25	25-50	35-100	35-100	60-110
Substrate	Rock	Sand, gravel	Gravel	Gravel	Variable	Silt

areas, although they were not immediately adjacent to riffles. Deep slow channels (type 6) were sections of longer channels with slow flowthrough rate and silt and clay substrates. Since substrate type and proximity to upstream riffles determines to some extent the nature of the invertebrate bottom fauna (Hynes 1970) and drift (Waters 1972) respectively, it was expected that differences in fish species composition might exist among these three habitats.

No attempt was made to estimate the distributions of species which were represented by fewer than twenty individuals over the two year period. The distribution of each species was then expressed as a set of six probabilities, of observing each species in each habitat type. The probability of observing species (i) in the (j)th habitat type was estimated as

$$p_{ij} = S_{ij} / N_{ij} \cdot T_i, \; i = 1, 2, \ldots, 13; \; j = 1, 2, \ldots, 6,$$

where S_{ij} = number of species (i) observed in all stations of type (j),

N_{ij} = number of stations of type (j) in streams in which species (i) was present,

$T_i = \sum_j S_{ij} / N_{ij}$.

In words, p_{ij} is the fraction of individuals belonging to species (i) which were found in habitat type (j); the number of habitats of each type available to species (i) was defined to be the number of stations of each type which occurred in the streams in which species (i) was present. P_{ij} is thus independent of both species (i)'s population size and identity of streams in which species (i) was present. This allows comparison of species on a basis of the proportion of each species observed in each habitat type without regard to abundance or streams occupied. These probabilities were determined from those stations for which length measurements were made.

The thirteen species were then successively combined to form groups which were similar in habitat selection, according to the following procedure, modified from Orloci (1967): the within-group dispersion of a group A, consisting of n species, was defined as

$$Q_A = \sum_j \sum_i (p_{ij} - \bar{p}_j)^2$$

where $\bar{p}_j$ is the average probability, for all species, of occurring in habitat (j). (This is just the total squared distance of the points in the group from their average, and is thus a measure of the group's heterogeneity.) At any step in the procedure, two groups A and B were joined to form a new group AB if

$Q_{AB} - (Q_A + Q_B) \leq Q_{CD} - (Q_C + Q_D)$, $\forall$ C, D ε U, where U is the set of all possible groups.

Thus, if two groups were fused at an early stage of the grouping procedure, the two groups were considered similar in habitat selection.

Only those stations at which all fish had been measured were considered; several authors have indicated (Gibbons and Gee 1972; Trautman 1957) that smaller fish of some species occupy a different spatial niche than older, larger individuals. Gibbons and Gee (1972), for example, demonstrated that fry of both Rhinichthys species occupied areas of lower current speed than adults. Therefore, a measure of size for each fish was necessary in order to account for the presence of fish of different ages. Length measurements were made in August, 1973 and throughout 1974. To account for the possible differences in spatial niche between small and large individuals within species, an attempt was made to separate each species into two size classes based on length frequency plots. Where possible, the size classes conformed to fry and older age classes, respectively. However, blackside darters were insufficiently abundant to make a decision on this basis, and were divided arbitrarily into small and large size classes. White suckers, sand shiners and fathead minnows were not separated. White suckers spawn in small streams, but the offspring move into larger bodies of water before age one (Scott and Crossman 1973). Sand shiners were encountered only in those streams flowing into the Souris River, and in the Pembina River. They were uncommon in these small streams, but were the most abundant species present in a few seine hauls made in the Souris River. Scott and Crossman (1973) describe this species as preferring lakes and large rivers. Since individuals found in the small streams were quite uniform in size, and no fry were observed, no attempt was made to separate this species into size classes. The size frequency distribution of fathead minnows appeared to be unimodal, with little variability so this species was likewise not divided into size classes. The criteria for separation of size classes are given in Table 2.

The original intent was to treat each size class as a separate "species" and then repeat the above analysis, but computer

Table 2. Criteria for Separation of Size Classes

Species	Smaller size class if <
Etheostoma nigrum	39
Percina maculata	44
Notropis dorsalis	32
Notropis stramineus	--
Notropis cornutus	32
Semotilus atromaculatus	50
Rhinichthys cataractae	40
Rhinichthys atratulus	30
Catostomus commersoni	--
Pimephales promelas	--
Semotilus margarita	41
Chrosomus neogaeus	40
Culaea inconstans	32

space limitations (APL/360) made a modification to this approach necessary. The analysis was repeated, using probabilities calculated for the larger of the two size classes only, for the ten species which were divided. The remaining three species were included as before.

2. Species Diversity: To examine the effects of environmental variables on species diversity, data collected in 1973 were analyzed as an analysis of variance, with factors as defined in the sampling design. As in the usual ANOVA layout, interactions between factors were included as part of the model, but it was decided to include only the two-way interactions since higher order interactions are often difficult to interpret and would add considerably to complexity of the model.

Since diversity of species was observed in the same set of stations at four times, the values of diversity observed in one station at successive times are not independent; for example, there is a possibility that, if a given station gave a high yield at one time, it might have been expected to give a high yield in the next time period. Therefore, observations on the same station at different times do not constitute true replications: the correct error term for testing stream, gradient and habitat effects is a mean square based on replications of these treatments in space (this will be called "replications of sites" in subsequent discussion). This type of design is called a "split plot" (Snedecor and Cochran 1967).

One of the assumptions necessary for F-tests to be valid is that variances within the treatment combinations are the same (homogeneity of residual variances). A plot of the residuals, or the difference between the predicted and the observed Y values, versus the predicted Y values, is given in Fig. 2, for Y = S, the number of species. Since the numbers of species were all small integers, a $Y = \sqrt{S + 1}$ transformation was applied to the data. This seemed to improve the distribution of the residuals slightly (Fig. 3) and also appeared to increase additivity somewhat, and so this transformation was retained in the subsequent analysis.

Because of changes in the original layout, and because some observations were missing due to other causes, such as stations going dry, the design lost its original orthogonality. This means, in effect, that the sum of squares attributable to treatments cannot be partitioned into sums of squares due to individual factors, because of covariances among the factors. As a result, the significance of each factor must be tested individually (Armitage 1971) by calculating a separate regression on all independent variables except those representing the factor in question, and then determining the reduction in the sum of squares due to treatments for this "reduced" model against the complete model. Details on the model used and methods of calculation are given in Appendix 2.

Figure 2. Plot of residuals versus expected Y-values, for Y = S.

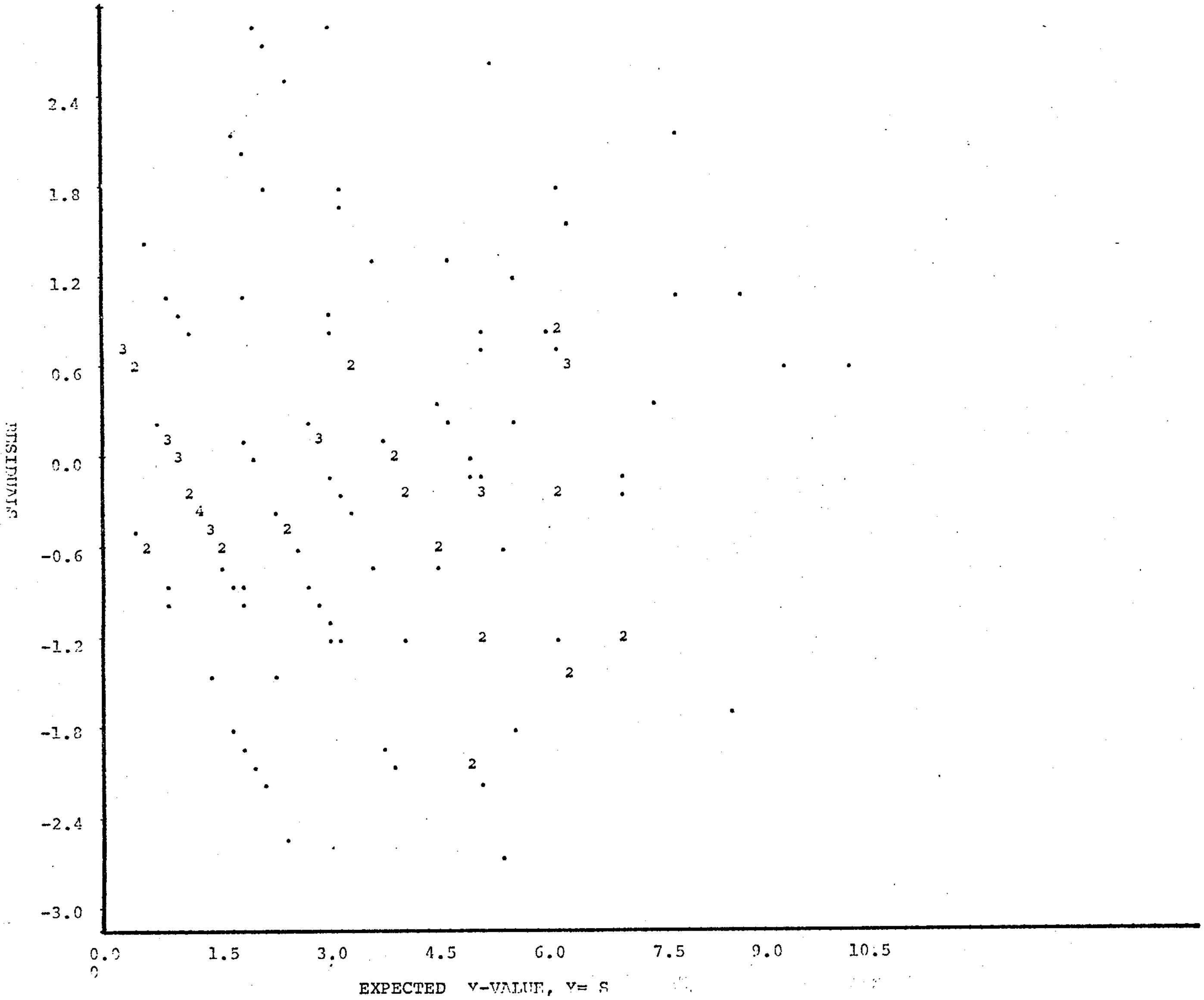
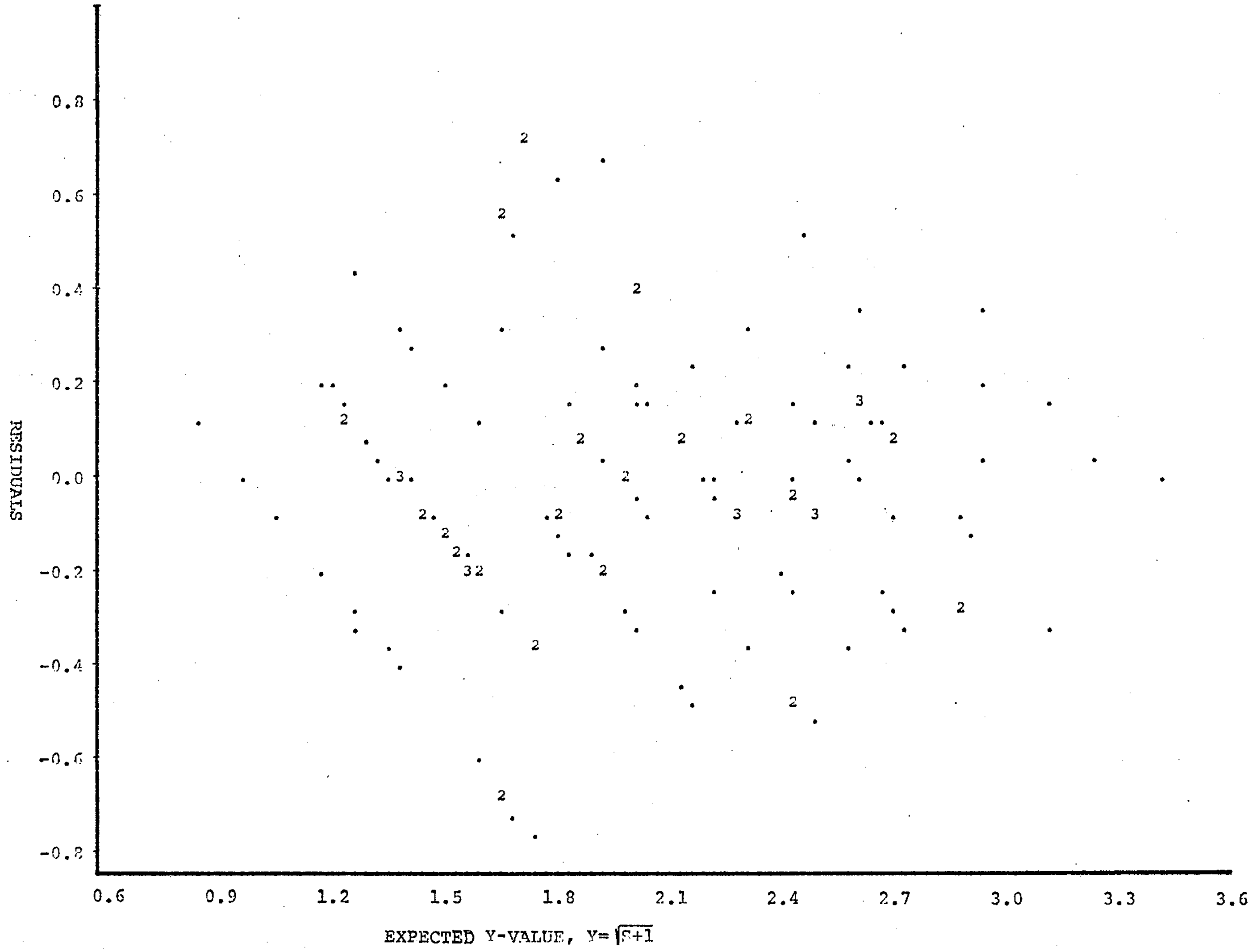

RESIDUALS
2.4
1.8
1.2
0.6
0.0
-0.6
-1.2
-1.8
-2.4
-3.0
0.0
1.5
3.0
4.5
6.0
7.5
9.0
10.5
EXPECTED Y-VALUE, Y= S

Figure 3. Plot of residuals versus expected Y-values, for $Y = \sqrt{S+1}$.


0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
RESIDUALS
0.6
0.9
1.2
1.5
1.8
2.1
2.4
2.7
3.0
3.3
3.6
EXPECTED Y-VALUE, Y=√S+1

RESULTS

1. *Distribution of species among habitats*: Twenty-seven species were observed in the sampling area (Table 3). The estimated distribution of probabilities of observing each of the thirteen common species in each of the six habitat types (as defined in Table 1) is given in Table 4.

The results of the grouping procedure are given in Fig. 2. The horizontal axis is Q, and so is a measure of the heterogeneity of the groups formed. It appears from inspection of Fig. 2 that three groups of species were formed at a fairly low level of fusion, while subsequent combinations of these three were less similar. The three groups were (approximately in order of decreasing current speed preference)

1) *Rhinichthys cataractae* (longnose dace)
   R. atratulus (blacknose dace)
   Percina maculata (blackside darter)
2) *Notropis dorsalis* (bigmouth shiner)
   Etheostoma nigrum (johnny darter)
   Catostomus commersoni (white sucker)
   Semotilus margarita (pearl dace)
   N. stramineus (sand shiner)
   N. cornutus (common shiner)
3) *Pimephales promelas* (fathead minnow)
   S. atromaculatus (creek chub)

Table 3. Checklist of Species

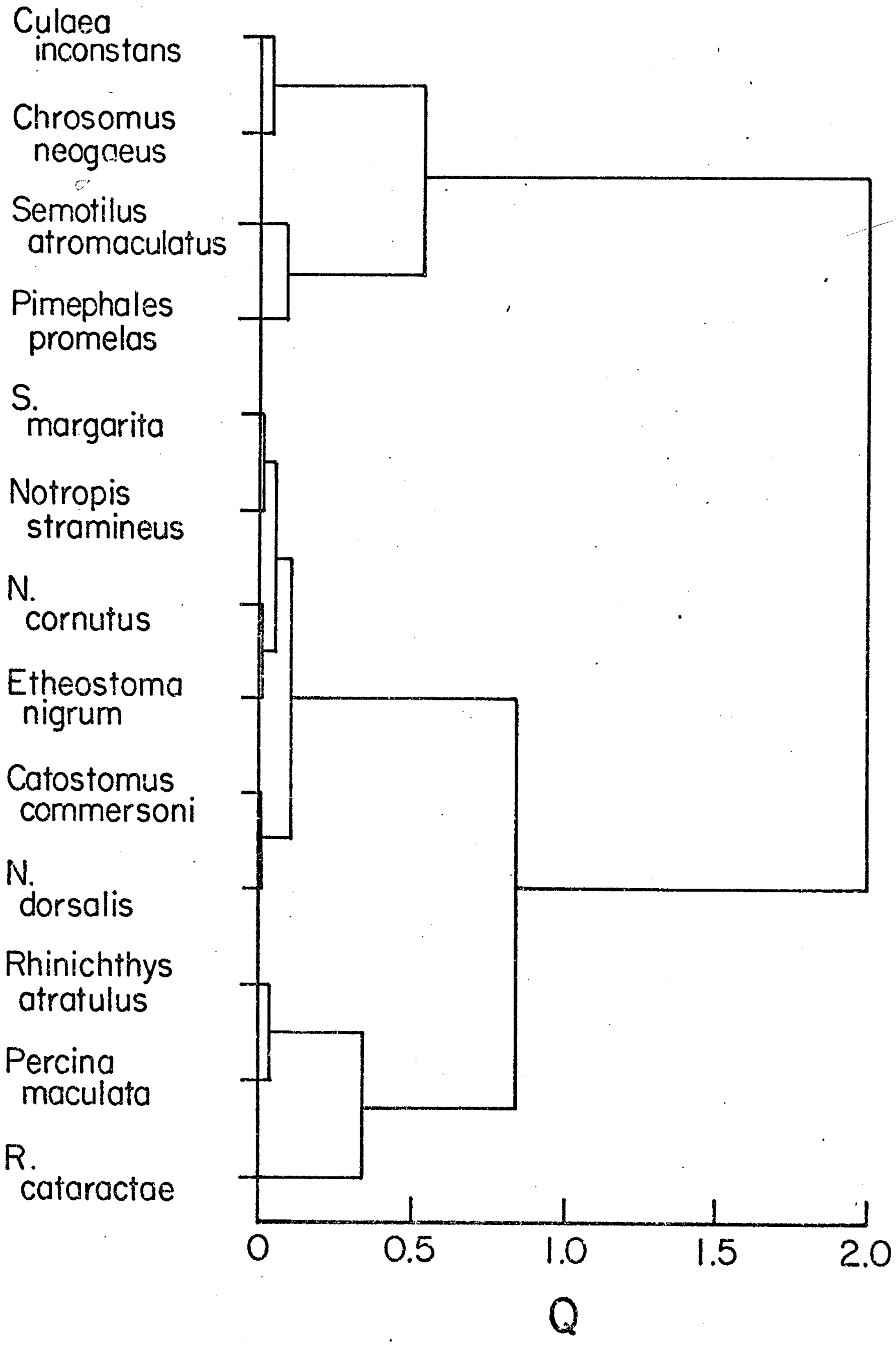
	Pembina	Cypress	Oak	Plum	Neepawa	Garland
*Salvelinus fontinalis**					x	
Chrosomus neogaeus					x	x
*Cyprinus carpio**	x	x				
*Hybognathus hankinsoni**	x					
Notropis cornutus	x	x	x			
N. dorsalis	x	x	x			
*N. heterodon**			x			
*N. heterolepis**			x			
*N. hudsonius**			x			
N. stramineus	x	x	x			
Pimephales promelas	x	x	x	x	x	x
Rhinichthys atratulus	x	x	x	x	x	x
R. cataractae		x	x	x		
Semotilus atromaculatus	x	x	x		x	
S. margarita			x		x	x
*Carpiodes cyprinus**		x				
Catostomus commersoni	x	x	x	x	x	x
*Percopsis omiscomaycus**	x		x			
*Esox lucius**	x		x			
*Lota lota**			x			
Culaea inconstans	x		x	x	x	x
*Etheostoma exile**				x		x
E. nigrum	x	x	x	x	x	x
*Perca flavescens**	x		x			
Percina maculata	x	x	x			
*Stizostedion vitreum**			x			
*Ambloplites rupestris**			x			

* An asterisk following a species' name indicates that the species was uncommon.

Table 4. Probabilities of Observing Each Species in Each Habitat Type (All Individuals)

Species	Habitat Type (1)	(2)	(3)	(4)	(5)	(6)
Rhinichthys cataractae	0.61	.06	.00	.30	.03	.00
Rhinichthys atratulus	.11	.06	.42	.05	.29	.07
Percina maculata	.11	.03	.32	.25	.16	.13
Notropis dorsalis	.03	.06	.00	.59	.15	.17
Etheostoma nigrum	.06	.05	.05	.49	.13	.22
Catostomus commersoni	.01	.03	.01	.59	.21	.15
Semotilus margarita	.00	.01	.23	.40	.24	.12
Notropis stramineus	.00	.03	.08	.46	.28	.15
Notropis cornutus	.00	.02	.15	.44	.14	.25
Pimephales promelas	.00	.00	.01	.03	.88	.08
Semotilus atromaculatus	.02	.03	.03	.11	.52	.29
Culaea inconstans	.03	.02	.02	.18	.28	.47
Chrosomus neogaeus	.00	.00	.02	.17	.13	.68

Figure 4. Dendrogram showing pattern of fusion of species into groups, for both size classes. Q is the within-group dispersion.


Culaea inconstans
Chrosomus neogaeus
Semotilus atromaculatus
Pimephales promelas
S. margarita
Notropis stramineus
N. cornutus
Etheostoma nigrum
Catostomus commersoni
N. dorsalis
Rhinichthys atratulus
Percina maculata
R. cataractae
0
0.5
1.0
1.5
2.0
Q

Culaea inconstans (brook stickleback)

Chrosomus neogaeus (finescale dace)

The distribution of probabilities for the larger size class alone is given in Table 5. The results of this analysis are given in Fig. 5. The groups formed were the same as in the previous case, except that the pearl dace changed its group membership from group 2 to group 3.

2. Species Diversity: The results of the analysis are given in Table 6. The four treatment effects, with their two-way interactions, accounted for nearly 80 percent of the variability in Y (not including "replications of sites", which is basically an error term).

DISCUSSION

1. Distribution of species among habitat types: By inspection of Fig. 5, it appears that three groups of species can be defined on the basis of observed distribution over habitats of the larger size class.

Group 1: Longnose dace, blacknose dace, blackside darter. The latter two species were most commonly found in moderate channels (type 3) and to a lesser extent in riffles and pools. Larger blackside darters seemed to be associated more with large rock substrates than with any particular current speed, at least in areas with current speed less than about 0.5 m/sec. This apparent affinity has been noted previously for *Percina shumardi*, the river darter (Trautman 1957), but Karr (1963) and Scott and Crossman (1973) have said that the blackside darter usually is found in deep pools.

Adult longnose dace were found almost entirely in riffles. Their high probability of occurrence in this habitat type separated them somewhat from the other two species in this group. This difference corresponds to the description given by Gibbons and Gee (1972) of separation between longnose and blacknose dace.

Group 2: Bigmouth shiner, johnny darter, white sucker, sand shiner, common shiner. The species in this group all had a high probability of occurrence in pools, and in particular in those pools located below riffles. Allocation among other habitats was somewhat variable: johnny darters were frequently found in riffles, but less

Table 5. Probabilities of Observing Each Species in Each Habitat Type (Larger Size Class)

Species	Habitat Type (1)	(2)	(3)	(4)	(5)	(6)
Rhinichthys cataractae	0.80	.00	.00	.18	.02	.00
Percina maculata	.26	.00	.35	.13	.26	.00
Rhinichthys atratulus	.18	.04	.35	.08	.25	.10
Etheostoma nigrum	.15	.08	.09	.36	.17	.15
Notropis dorsalis	.01	.11	.00	.59	.21	.08
Catostomus commersoni	.01	.03	.01	.59	.21	.15
Notropis stramineus	.00	.03	.08	.46	.28	.15
Notropis cornutus	.01	.03	.04	.46	.18	.28
Pimephales promelas	.00	.00	.01	.03	.88	.08
Semotilus margarita	.01	.00	.14	.23	.38	.24
Culaea inconstans	.08	.06	.04	.09	.44	.29
Semotilus atromaculatus	.03	.03	.04	.12	.36	.42
Chrosomus neogaeus	.00	.00	.00	.19	.10	.71

Figure 5. Dendrogram showing pattern of fusion of species into groups, for the larger size class. Q is the within-group dispersion.

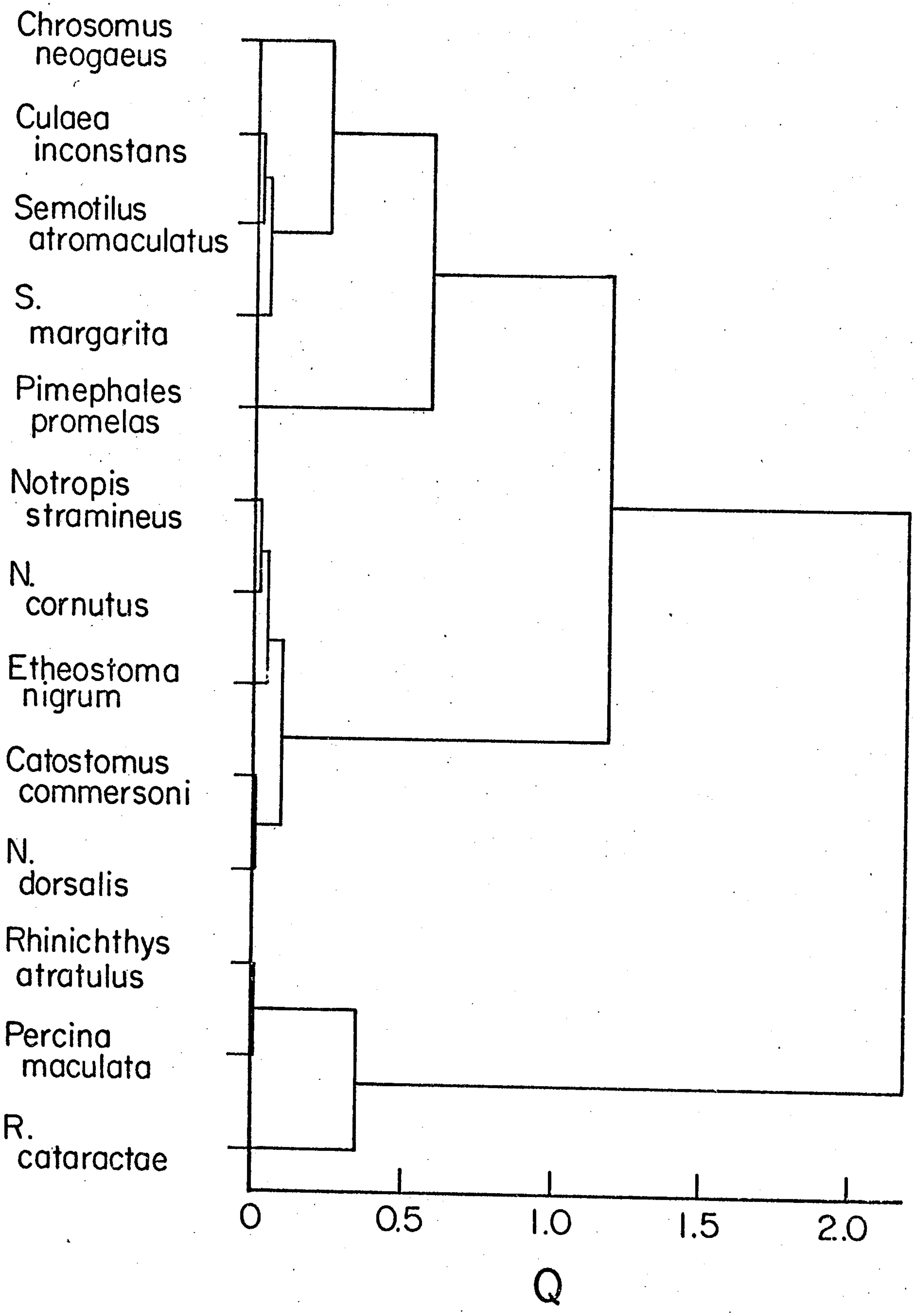

Chrosomus neogaeus
Culaea inconstans
Semotilus atromaculatus
S. margarita
Pimephales promelas
Notropis stramineus
N. cornutus
Etheostoma nigrum
Catostomus commersoni
N. dorsalis
Rhinichthys atratulus
Percina maculata
R. cataractae
0
0.5
1.0
1.5
2.0
Q

Table 6. Analysis of Variance of $Y = \sqrt{S+1}$, S = Number of Species.

Source	d.f.	S.S.	M.S.(M.S.*)	F
Due to all factors	51	40.7204	--	--
Gradient (after fitting)	1		0.078(0.195)	0.40
Remaining factors				
Streams ('')	3		0.067(.192)	0.40
Habitats ('')	2		0.090(.192)	0.47
Gradients x streams ('')	3		0.294(.257)	1.15
Gradients x habitats ('')	2		0.399(.145)	2.74
Streams x habitats ('')	6		0.136(.160)	0.85
Season ('')	3		0.016	0.17
Gradients x season ('')	3		0.122	1.34
Streams x season ('')	9		0.144	1.58
Habitats x season ('')	6		0.110	1.24
Error	73	6.6408	0.091	
Total	124	47.3612	$100R^2$=86%	

M.S.* is the "replications of sites" error term, for factors not involving season.

often in type 2 or 3 habitats. The remaining species in the group were uniformly low in their occurrence in the first three habitat types, with the exception of the bigmouth shiner, which showed the highest probability, of any of the thirteen species, of occurrence in shallow, gravel channels with moderate to high current speed. Small groups of bigmouth shiners were often observed in this type of habitat, maintaining position near the substrate; occasionally one individual would rise up to take a drifting insect or piece of algae, and then return to its former position. Hubbs (1941) gave a similar description of habitat preference of this species. The remaining three species in this group were found mainly in areas with little current. Sand shiners, common shiners and white suckers were encountered in habitat types 4, 5 and 6 combined with probabilities of 0.89, 0.92 and 0.95, respectively.

Group 3: Pearl dace, fathead minnow, brook stickleback, creek chub, finescale dace. This group of species was separated from the previous two by its greater weight on type 5 and 6 habitats. This group was also more variable than the other two, due to the high probability for fathead minnows in type 5 habitats and the high probability of observing finescale dace in type 6 habitats. The affinity of fathead minnows for type 5 pools was largely due to the aggregated nature of the distribution of this species among stations: a single station in Neepawa Creek contained 471 fathead minnows, and the inclusion of this value in calculating the p_{ij} greatly diminished the relative contribution (to the calculated probabilities) of a large number of other stations in which this species was less abundant. Finescale dace were at no time very abundant, but were quite consistent in occurring in deep, slow channels. Also, in the streams in which members of this species were present, they were mainly confined to the low gradient sections. Creek chub and sticklebacks were similar in their allocation to habitats, the latter species showing a somewhat higher weight on type 5 pools. Sticklebacks, however, were found in greatest abundance in low gradient sections, while creek chub were found in similar habitats but within the high gradient sections. Pearl dace were somewhat more variable in habitat selection than the other species in this group, occurring with fairly high probability in habitats 3 and 4 (moderate channels and below riffles, respectively) as well as types 5 and 6. Scott and Crossman (1973) said that pearl dace, finescale dace, brook sticklebacks and fathead minnows are often found in the same streams; it appears that this association may also occur at a level of habitats within streams as well as at a level of streams.

By inspection of the p_{ij} in Tables 4 and 5, it can be seen that removal of the smaller size class changed the apparent habitat preference of some species more than others. The greatest change was observed for those species occurring in higher current speeds as adults, which is an intuitively reasonable result, since smaller individuals probably have a similar lack of ability to resist strong current, irrespective of species. Longnose dace, blacknose dace and blackside darters seemed to change habitat preference by about