Conservation Biology Research Grant Program
Nongame Wildlife Program
Division of Ecological Services
Minnesota Department of Natural Resources

COMPARATIVE GROWTH, REPRODUCTION, HABITAT AND FOOD UTILIZATION OF DARTERS Of THE ST. CROIX RIVER DRAINAGE

FINAL REPORT

Submitted to:

Lee Ann Pfannmuller
Nongame Wildlife Program
Minnesota Department of Natural Resources
Box 7, 500 Lafayette Road
St. Paul, Minnesota 55146

Submitted by:

Jay T. Hatch, Ph.D.
Division of Science, Business, and Mathematics
General College
University of Minnesota
216 Pillsbury Dr. SE
Minneapolis, MN 55455

February 24, 1986

Introduction

One of the most abundant and ubiquitous groups of nongame fishes found in Minnesota is the darter group (Percidae: Etheostomatini). These lively and colorful fishes inhabit nearly all of our streams and rivers and many of our lakes (Eddy and Underhill, 1974). We know in general that darters play an important role in the trophic structure of stream ecosystems (Cummins 1980), and we know that some species are important indicators of general water quality (Gerking 1945; Smith 1971; Pflieger 1975; Burr 1980; Karr 1981). Yet, we know very little about the specific life histories of the darters of our state, and we know even less about how their resource utilization patterns change with changes in habitat and community structure.

To date, only three life history studies have been cared out on Minnesota darter populations. Erickson (1977) studied the banded darter *(Etheostoma zonale)* in the Cannon River; Coon (1982) studied several aspects of the comparative ecology of the rainbow (*E. coeruleum*), fantail (*E. flabellare*) and Johnny (*E. nigrum*) darters in the Root River; and Hatch (1982, 1986) studied the gilt darter (*Percina evides*) in the St. Croix River drainage. Information about food habits of logperch (*P. caprodes*) from Lake Vermilion and of Iowa (*E. exile*) and Johnny darters from Long Lake has been reported by Dobie (1959) and Moyle (1969), respectively.

In order to fill in some of the gaps in our knowledge of darter natural history, a series of studies funded by the Nongame Wildlife Program of the Minnesota Department of Natural Resources was begun in 1983 to elucidate the life histories of all fifteen Minnesota darter species. The approach has been to intensively study different but overlapping assemblages of darter species in geographically disjunct and physically diverse drainages.

What follows constitutes the final report of the first of these studies, which centered on the darters of the St. Croix River drainage upstream of the St. Croix Dalles. The specific objectives of the this study were: 1) to determine growth rates, length-weight relationships, fecundities, and fecundity relationships to length, weight, and age for populations of *Etheostoma nigrum, Percina caprodes P. maculata*, and *P. phoxocephala* from the Sunrise River, Chisago County, Minnesota; 2) to summarize microhabitat data and estimate the spawning period of the above species; and 3) to elucidate food utilization patterns of the above species and *P. evides* at riffles in the Sunrise and St. Croix rivers.

Habitat Terminology

To describe the general habitat of darters, 1 have used the following terminology throughout this report. Basically, the terms refer to a continuum of habitats distinguished primarily on the bases of flow characteristics, depths, and substrate types. **Riffles** are relatively shallow sections of stream exhibiting swift and turbulent current flowing over rocks of varying size. A prefix of boulder (greater than 6.5 cm in diameters or **cobble** (2.5 - 6.5 cm in diameter) indicates the predominant type of substrate in the riffle (or any other habitat). **Rubble riffles** are further distinguished by a non-homogeneous mixture of boulder and cobble substrates. **Raceways** are characterized by moderate depth and swift to moderate current that is not obviously turbulent. The reduction in turbulence is due primarily to their somewhat smaller and more homogeneous substrate. **Runs** are deep, usually straight sections of stream that may exhibit moderate to slow current depending upon their hydrologic origin. **Pools** are deep, very slow moving sections of stream that may have any type of substrate depending upon their age end hydrologic origin, although they most often have sand, silt or mud bottoms.

Materials end Methods

Growth Reproduction, end Habitat

Field Work--Most of the specimens of *Etheostoma nigrum, Percina caprodes, P. maculata* and *P. phoxocephala* analyzed in this study for rate of growth, length-weight relationships and fecundity were collected from the lower 440 m Sunrise River (Chisago County: T35N, R20W, S32). They were collected between April 1977 and July 1981 as part of a study of the life history of *Percina evides* (Hatch 1982x. A few additional specimens from 3 locations on the Snake River, 1 location on the Upper Tamarack River, and 2 locations on the St. Croix River also were analyzed (figure 1). Results that include these latter specimens are so designated.

In the Sunrise River, seasonal habitat utilization and movement were observed. Monthly sampling was conducted from April 1977 through October 1979 in each of 4 major habitats, except when ice cover or water level prevented it (figure 2, B-E; the rubble chute 'A' was treated as a portion of the rubble riffle 'B'). Each habitat was given approximately equal sampling effort relative to its size. Water depths and temperature were measured routinely, and substrate was characterized visually and by measuring diameters of stones collected haphazardly. On two occasions, benthic macroinvertebrates were sampled randomly in each habitat with a Waters stream bottom sampler (Waters and Knapp 1961). Periodically, subsurface current velocities were measured by repeatedly timing the movement of a neutrally buoyant plastic ball (5 cm diameter) over 5 to 25 m distances.

Laboratory Analyses - All specimens used had been fixed in 10% formalin and preserved in 40X isopropyl alcohol prior to analysis. None of the data reported herein has been adjusted to reflect shrinkage due to such preservation, but a figure of 3% shrinkage 1n total length can be used as a general correction factor if so desired. In the laboratory, darters were removed from alcohol and soaked in water for at least 24 hrs prior to analyses. Standard and total lengths were measured to the nearest 0.1 mm with a dial caliper. Total body weight was measured to the nearest 0.01 g on a Mettler H15 analytical balance after surface moisture had been removed by blotting. Adjusted body weight was determined to the nearest 0.0001 g in a similar manner after all viscera except gills and kidneys were removed. Gonads also were blotted dry and weighted to the nearest 0.0001 g. Sex was determined by examination of whole gonads or gonad squashes in the case of very young specimens (Hatch 1982). Specimens were aged by the scale method using key scales from the scale row just above the lateral line beneath the junction of the spinous and soft dorsal fins. Validity of the scale method for aging darters has been demonstrated by Lochner et al. (1950), Erickson (1977), and Hatch (1982).

The individual growth histories of specimens were determined by using the equation: $L_i = c + (S_i/s)(L-c)$, where L_i is the total length of the darter at the time of the ith annulus formation, c is the Y-intercept of the body-scale length regression equation for each sex of each species, S_i is the length of the middle anterior scale radius at the ith annulus (in mm at 150x), s is the length of the middle anterior scale radius at the time of capture, end L is the total length of the darter at the time of capture. For specimens collected from October through April, a period of insignificant growth, the length at capture was considered to be the length of the fish at the conclusion of its latest growing season. Mean lengths at age calculated from these data were denoted empirical growth estimates as opposed to back-calculated growth estimates. The two estimates were mathematically combined only when computing weighted mean growth and were always identified separately in the results reported. Differences in lengths of males and females at age were tested with Student's t-test. Relationships between length and weight, between total body weight and adjusted body weight, and between total length and standard length were determined by least squares regression and by the geometric mean functional regression outlined by Ricker (1973, 1975).

Fecundity was determined by making direct ova counts of females collected during the reproductive season (May through July, depending on species and year). Only yolked ova of > 0.9 mm in diameter were used in estimating fecundity. They were counted in both right and left ovaries, except in the case of *Percina caprodes,* where counts were made only on the left ovary. Relationships of fecundity to body length and adjusted body weight were determined by least-squares regression.

Food Utilization

Field Work--Specimens collected during the previous study were used to determine seasonal feeding activity and composition of diet of Sunrise River darter populations. Additional specimens of all species except *P. phoxocephala* were collected from several riffles in the St. Croix River (Figure 1) and from the mouth of the Sunrise River on August 8-12, 1983. Specimens were collected with Erickson nets (Erickson 1980), and riffles were qualitatively characterized as to current, substrate type and benthic macroinvertebrate assemblage.

Laboratory Analyses--The entire digestive tract of each specimen was removed and divided into stomach, proximal intestine and distal intestine (Hatch 1982). The latter two portions were analyzed qualitatively to see if stomach contents and intestinal contents were generally similar. Only organisms in the stomach were counted and identified to the lowest practical taxon. Food items from the 1983 specimens were enumerated according to 1-mm length groups. After counting, the entire stomach contents were placed in tared aluminum containers, dried to constant weight and weighed to the nearest 0.0001 g.

Feeding niche breadths were calculated for the 1983 specimens using Simpson's B (Levin 1968): $B = 1/ \Sigma(p_i)^2$ where, p_i = the proportion of the diet contributed by food item i. Estimates of feeding niche overlap for these specimens were calculated using Schooner's PSI (Schooner 1970): $PSI = 1 - 0.5\ (\Sigma|p_{i,j} - p_{k,j}|)$ where, $p_{i,j}$ = the proportion of food item j in the diet of species i and $p_{k,j}$ = the same for species k. In all cases, p was based on percent composition by number.

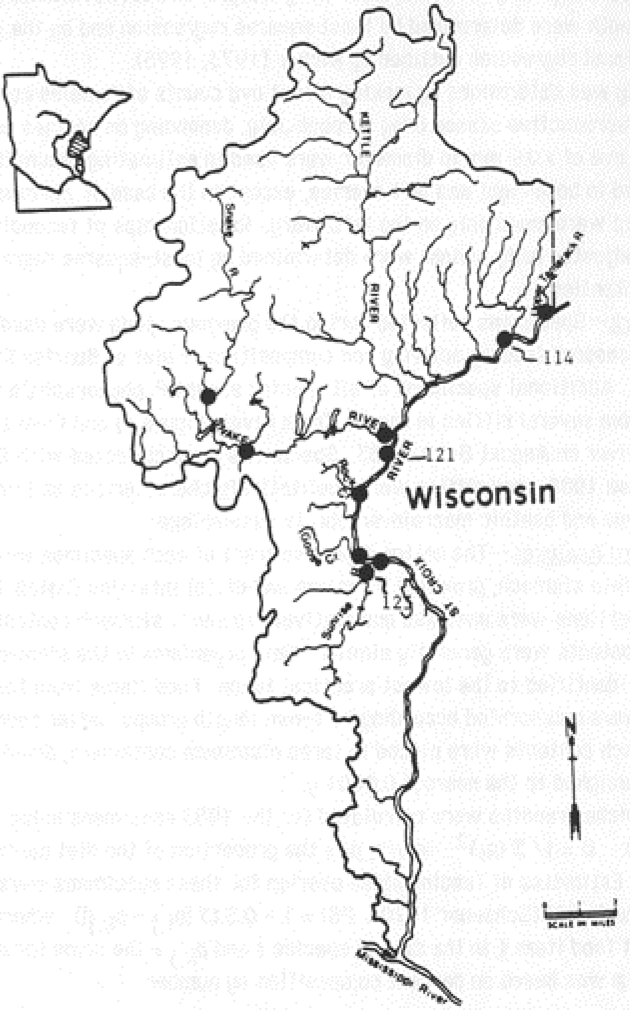

Figure 1. St. Croix River drainage showing collection sites of darters used in this study. (114, 121, and 125 denote locations sampled in August 1983.)

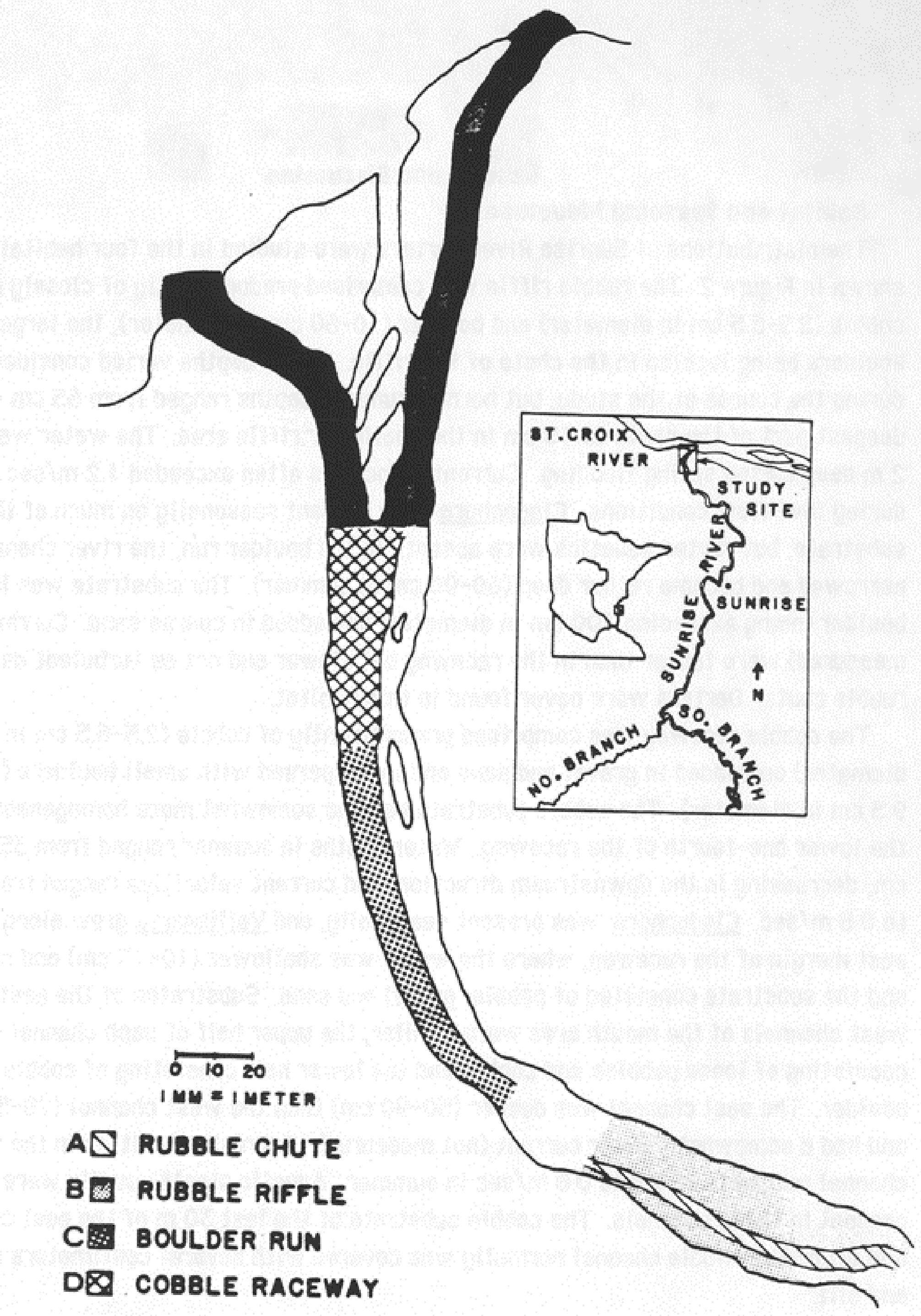

Figure 2. Location of the Sunrise River study site in Chisago, County, Minnesota, and a detail of the four major habitats studied. The "rubble chute" (A) is considered part of the "rubble riffle" (B). Areas without patterns were not sampled.

Results and Discussion

Habitat and Seasonal Movements

The distributions of Sunrise River darters were studied in the four habitats shown in Figure 2. The rubble riffle was comprised predominantly of closely packed cobble (2.5-6.5 cm in diameter) and boulder (10-60 cm in diameter), the larger boulders being located in the chute of the riffle. Water depths varied considerably during the course of the study, but normal summer depths ranged from 65 cm in the deepest part of the chute to 15 cm in the shallower riffle area. The water was over 2 m deep during spring flooding. Current velocities often exceeded 1.2 m/sec even during low-flow conditions. Cladophora was present seasonally on much of the substrate, but rooted aquatics were absent. In the boulder run, the river channel narrowed and became rather deep (60-90 cm in summer). The substrate was large boulder (many exceeding 100 cm in diameter) embedded in coarse sand. Currents (not measured) were faster than in the raceway but slower and not as turbulent as in the rubble chute. Darters were never found in this habitat.

The cobble raceway was comprised predominantly of cobble (2.5-6.5 cm in diameter) embedded in gravel and sand and interspersed with small boulders (up to 9.5 cm in diameter). The cobble substrate became somewhat more homogeneous in the lower one-fourth of the raceway. Water depths in summer ranged from 35 to 50 cm, decreasing in the downstream direction, and current velocities ranged from 0.5 to 0.8 m/sec. Cladophora was present seasonally, and Vallisneria grew along the east margin of the raceway, where the water was shallower (10-15 cm) and slower, and the substrate consisted of pebble, gravel and sand. Substrates of the east and west channels of the mouth area were similar, the upper half of each channel consisting of loose pebbles and cobble and the lower half consisting of cobble and boulder. The east channel was deeper (50-90 cm) than the west channel (28-50 cm) and had a somewhat slower current (not measured). Current velocities in the west channel ranged from 0.5 to 0.8 m/sec in summer. Aquatic plants usually were not present in these charnels. ,The cobble substrate of the last 30 m of the east channel and all of the middle channel normally was covered with several centimeters of sand and silt.

All five species of darters were found in the rubble riffle area during the spring (April and May), but each species utilized somewhat different microhabitat. *Percina evides* clearly preferred the rubble chute area, where depth usually exceeded 0.65 m and currently velocities were 1.2 m/sec or greater. *Percina phoxocephala* also was

found in the chute, but nearly always in the downstream portions, where the water was shallower and *P. evides* was somewhat less abundant. Still, these two species showed a high degree of microhabitat overlap and were collected together in the same net sample frequently in this habitat. *Percina caprodes* was sometimes found right at the edges of the rubble chute but was clearly more abundant along the western margins of the riffle. Here the current was considerably slower (0.1-0.3 m/sec) and the cobble and boulder were more widely spaced by sand and gravel. In the spring, *P. caprodes* was particularly abundant in a small back-eddy pool just below the chute. The pool was about 1 m deep at summer low-flow and its cobble was often completely covered with sand. *Etheostoma nigrum* generally was confined to the shallower, slower eastern portion of the riffle, where it occupied both cobble and sand substrates. Large males occasionally were taken early in the spring just east of the chute area among small boulders. *Percina caprodes* was not abundant in this area but was taken in the same net haul with *E. nigrum* on several occasions. At the rubble riffle, *P. maculata* was collected only from the eastern margins of the chute and in the slower eastern portion of the riffle, where it overlapped with *E. nigrum* and to a lesser extent with *P. caprodes.*

The abundance of all darter species at the rubble riffle declined during the summer, and virtually no darters occupied the chute in June and July. Small numbers of *P. nigrum, P. phoxocephala*, and *P caprodes* remained in the area, but *P. evides* and *P. maculata* were virtually absent. In late May and June, the latter two species became increasingly more abundant in the cobble raceway. *Percina evides* occupied nearly ail areas of the raceway and channels but was most abundant the swifter, deeper portions of these habitats. *Percina maculata* almost always was found in association with vegetation or detritus along the lower margins of the raceway and along the edges of the islands in the west channel. *Percina caprodes* also utilized the raceway but mostly the western half. Individuals were found often in the west channel but rarely the east channel. *Etheostoma nigrum* was abundant all along the eastern portion of the raceway; adult *P. phoxocephala* was found between the central portions of raceway and the western margins but was not abundant anywhere. Young-of-the-year of all species utilized the raceway area as a nursery through out the summer. While they showed greater microhabitat overlap than adults, they still showed preferences basically similar to those of the adults.

Collections in the raceway in late fall and early spring and in the chute area in the winter months indicated that *P. evides* and *P. phoxocephala* moved to swift, deep water in winter. *Percina maculata* also was present at the edges of the chute in the winter and early spring, which suggests it, too, may make a winter migration. Winter or hiemal migration has been reported for *P. phoxocephala* (Page and Smith 1971) and *P. sciera* (Page and Smith 1970) in Illinois, and it has been suggested for Virginia populations of *P. evides* (Denoncourt 1969). The decrease in abundance of all species in the rubble riffle area in late spring is probably a result of dispersal associated with spawning, which is common in many darter species (see 'Spawning Periods' below. It seems likely that the movements in this case were downstream, but marking studies were inconclusive. In other studies where direction of movement associated with breeding has been investigated, the movements were upstream (Winn 1958; Reed 1968; Scalet 1973).

Age Composition and Longevity

The age compositions of the darters used to determine growth are shown in Table 1. Scales of darters collected at one to two-week intervals in May and June indicated that most annuli were laid down in late May and early June. Thus, June was selected as the 'birthday month' for all specimens in this study. Except in the case of *P. evides* (Hatch 1982), the data in Table 1 should not be viewed as demographic statistics because of the biases in the sampling regime, which are particularly evident in the *P. phoxocephala* data. Nevertheless, it is clear that darters exhibit very high mortality during their first year of life, and very few individuals survive into their fourth summer. Although no *P. maculata* specimens older than 24 months were collected in this study (I have 4+-year old specimens from other Minnesota drainages), I believe ail four of the *Percina* species in the upper St. Croix have individuals that survive to 4 years. Most *Percina* species that have been studied live 3 or 4 years, although 5-year old *P. maculata* have been reported from Illinois (Thomas 1970) and 6-year old *P. rex* have been reported from Virginia (Jenkins *at el.* 1980). Lutterbie (1976) reported 4+-year old *P. evides* from the St. Croix, but I found no specimens in his samples older than 28 months (3 growing seasons).

I am uncertain about the longevity of *E. nigrum* in the St. Croix drainage. The oldest specimens collected in this study were 36 months old, and I know of no older specimens from the state at this time. Speare (1960) found no 4-year olds and only six 3-year olds out of 556 specimens from Michigan, and Karr (1963) found only one 4-year old out of 55 in his Iowa study.

Table 1. Age composition of St. Croix drainage darters analyzed for growth (sexes combined)

Species	Range of Age in Months					Percentage				
	01–12	13–24	25-36	37–48	49	01–12	13–24	25–36	37–48	49
E. nigrum	113	28	8	0	0	75.9	18.8	5.3	0.0	0.0
P. caprodes	170	41	13	1	0	75.6	18.2	5.8	0.4	0.0
P. evides	484	55	16	1	0	87.1	9.8	2.9	0.2	0.0
P. maculata	84	7	0	0	0	92.3	7.7	0.0	0.0	0.0
P. phoxocephala	25	29	18	6	1	31.6	36.7	22.8	7.6	1.3

Table 2. Least-squares regression equations of total length (TL) on scale radius length (SR) for St. Crook darters (standard length (SL) on scale margin length for *P. evides*).

Species	Sex	Regression Equation	r	N
E. nigrum	F	TL = 7.933 + 0.406 SR	0.932	50
	M	TL = 9.375 + 0.388 SR	0.960	41
P. caprodes	F	TL = 16.736 + 0.548 SR	0.983	38
	M	TL = 13.947 + 0.570 SR	0.980	60
P. maculata	F	TL = 14.312 + 0.488 SR	0.986	27
	M	TL = 8.821 + 0.528 SR	0.965	41
P. phoxocephala	F	TL = 12.706 + 0.501 SR	0.971	14
	M	TL = 14.637 + 0.467 SR	0.959	61
P. evides	F	SL = 5.450 + 0.490 SR	0.979	100
	M	SL = 4.540 + 0.509 SR	0.976	100

Growth

Relationships between scale radius length at 150x and total length as determined by least squares regression are given in Table 2. The intercepts of these equations were used as the 'c' value in computing the growth histories of individual fish. The equations for *P. evides* relate scale radius length at 150x to standard length rather than total length. Relationships between total length and standard length are given in Table 3.

Table 3. Least-squares regression equations of total length (TL) on standard length (SLR and standard length on total length for. St. Croix River drainage darters

Species	Sex	Regression Equation	r	N
E. nigrum	F	TL = 0.482 + 1.179 SL	0.998	56
	M	TL = 0.034 + 1.195 SL	0.999	48
P. caprodes	F	TL = 2.505 + 1.124 SL	0.999	27
	M	TL = 0.307 + 1.158 SL	0.999	47
P. evides	F, M	TL = 0.125 + 1.163 SL	0.999	28
P. maculata	F	TL = 1.315 + 1.145 SL	0.966	29
	M	TL = 0.253 + 1.161 SL	0.988	46
P. phoxocephala	F	TL = 2.567 + 1.117 SL	0.999	18
	M	TL = 0.196 + 1.162 SL	0.999	61
E. nigrum	F	SL = -0.250 + 0.845 TL	0.998	56
	M	SL = 0.073 + 0.835 TL	0.999	48
P. caprodes	F	SL = -2.206 + 0.889 TL	0.999	27
	M	SL = -0.133 + 0.862 TL	0.999	47
P. evides	F,M	SL = -7.440 + 0.859 TL	0.999	29
P. maculata	F	SL = -0.725 + 0.866 TL	0.966	29
	M	SL = 3.077 + 0.856 TL	0.988	46
P. phoxocephala	F	SL = -2.201 + 0.894 TL	0.999	18
	M	SL = -0.038 + 0.859 TL	0.999	61

Tables 4 and 5 summarize the average growth increments for Sunrise River specimens of *P. caprodes, P. maculata, P. phoxocephala*, and *E. nigrum* analyzed in this study and for *P. evides* analyzed in a previous study (Hatch 1982). Year-classes 1973 through 1980 were combined to produce these tables in order to increase sample sizes of older fishes. All species exhibited high variation in yearly growth, even when only a single year-class was analyzed (Figures 3 and 4), so that during the second or third growing seasons there was marked overlap in the lengths of fishes of different ages. Growth during the first 4 months of life was very rapid for all species (Table 6). All species (sexes combined) attained 60-70% of their average total growth during the first growing season. Such rapid first year growth is to be expected in species whose life spans are but 3 or 4 years. *Percina caprodes* clearly was the fastest growing species, followed by *P. maculata* *Percina phoxocephala* and *P. evides* grew at about the same rate and reached similar maximum size. *Etheostoma nigrum* was the slowest growing of the darter and attained the smallest overall size.

Tendencies toward sexual differences in growth rates were exhibited by three species*: P. caprodes, P. evides* and *E. nigrum*. The differences were statistically significant (P 10.05) for *P. caprodes* and *P. evides* but not for *E. nigrum*. Males of *P. evides* were longer than females after only one year's growth (this also was established for the 1979 year-class, Hatch 1982). Disparity in length between, the sexes increased with age so that 3-year old females were about the same size as 2-year males. Male and female *P. caprodes* grew to approximately the same length in their first year, but afterwards males grew faster showing the same pattern in years 2 and 3 as *P. evides*. I believe that *E. nigrum* males also attain greater lengths than females during their second and third years, although the present data do not support this conclusion statistically. Such a pattern was noted by Speare (1960) for an *E. nigrum* population in Michigan, but it was not noted in two previous studies of *P. caprodes* in Illinois (Thomas 1970). No influence of sex on size was found in studies of Illinois populations of *P. maculata* (Thomas 1970) and *P. phoxocephala* (Thomas 1970; Page and Smith 1971).

Table 4. Weighted mean total lengths and growth increments of Sunrise River *P. maculata* and P. *phoxocephala* collected April 1977 through July 1980.

		Mean TL (2 SE) at Annulus			
No. Annuli	**No. Fish**	**I**	**II**	**III**	**IV**
***P. maculata* females**					
1	**2**	**57.5 (6.1)**			
(Empirical Method)		**57.7 (1.4)**	**74.2 (- -)**		
	[N]	**[37]**	**[1]**		
Weighted Mean		**57.7**	**74.2**		
Average Growth Increments		**57.7**	**16.5**		
***P. maculata* males**					
1	**6**	**56.6 (4.5)**			
(Empirical Method)		**60.0 (2.1)**	**73.0 (3.6)**		
	[N]	**[24]**	**[6]**		
Weighted Mean		**59.8**	**73.0**		
Average Growth Increments		**59.8**	**13.2**		
***P. phoxocephala* females**					
1	**5**	**51.6 (3.3)**			
2	**7**	**47.1 (4.9)**	**66.5 (3.6)**		
3	**4**	**43.0 (7.1)**	**62.0 (3.2)**	**72.2 (1.9)**	
(Empirical Method)		**53.8 (6.3)**	**70.8 (4.1)**	**73.2 (2.0)**	**77.6 (3.2)**
	[N]	**[2]**	**[2]**	**[7]**	**[4]**
Weighted Mean		**48.2**	**65.8**	**72.8**	**77.6**
Average Growth Increments		**48.2**	**17.6**	**7.0**	**4.8**
***P. phoxocephala* males**					
1	**35**	**48.5 (1.7)**			
2	**10**	**46.7 (3.6)**	**65.2 (3.0)**		
3	**3**	**47.2 (10.2)**	**64.9 (7.0)**	**74.9 (4.0)**	
(Empirical Method)		**51.0 (3.5)**	**68.0 (2.2)**	**72.5 (2.4)**	**78.9 (4.0)**
	[N]	**[12]**	**[13]**	**[8]**	**[3]**
Weighted Mean		**48.6**	**66.6**	**73.2**	**78.9**
Average Growth Increments		**48.6**	**18.0**	**6.6**	**5.7**

Table 5. Weighted mean total lengths and growth increments of Sunrise River *P. caprodes, P. evides*, and *E. nigrum* collected April 1977 through July 1980.

		Mean TL (2 SE) at Annulus			
No. Annuli	**No. Fish**	**I**	**II**	**III**	**IV**
		***P. caprodes* females**			
1	**14**	**69.6 (3.8)**			
2	**5**	**70.7 (1.7)**	**98.0 (6.6)**		
(Empirical Method)		**67.4 (3.2)**	**95.7 (3.8)**	**107.7 (6.0)**	
	[N]	**[16]**	**[14]**	**[5]**	
Weighted Mean		**68.8**	**96.3**	**107.7**	
Average Growth Increments		**68.8**	**27.5**	**11.4**	
		***P. caprodes* males**			
1	**28**	**73.5 (2.6)**			
2	**8**	**73.9 (7.0)**	**105.9 (5.2)**		
3	**1**	**73.7 (- -)**	**103.2 (- -)**	**123.2 (- -)**	
(Empirical Method)		**69.1 (2.6)**	**107.8 (2.6)**	**118.8 (4.4)**	**129.9 (- -)**
	[N]	**[18]**	**[16]**	**[8]**	**[1]**
Weighted Mean		**71.9**	**107.0**	**119.3**	**129.9**
Average Growth Increments		**71.9**	**35.1**	**12.3**	**10**
		***P. evides* females[1]**			
1	**42**	**44.7 (NA)**			
2	**18**	**43.7 (NA)**	**59.8 (NA)**		
3	**1**	**38.3 (- -)**	**54.3 (- -)**	**64.6 (- -)**	
(Empirical Method)		**45.0 (NA)**	**60.7 (NA)**	**67.5 (NA)**	**69.9 (- -)**
	[N]	**[284]**	**[32]**	**[10]**	**[1]**
Weighted Mean		**44.9**	**60.3**	**67.2**	**69.9**
Average Growth Increments		**44.9**	**15.4**	**6.9**	**2.7**
		***P. evides* males[1]**			
1	**43**	**47.2 (NA)**			
2	**15**	**51.4 (NA)**	**71.1 (NA)**		
(Empirical Method)		**48.0 (NA)**	**68.0 (NA)**	**80.4 (NA)**	
	[N]	**[311]**	**[31]**	**[13]**	
Weighted Mean		**48.0**	**69.0**	**80.4**	
Average Growth increments		**48.0**	**21.0**	**11.4**	
		***E. nigrum* females**			
1	**19**	**39.9 (2.5)**			
2	**2**	**36.1 (4.3)**	**54.2 (3.6)**		
(Empirical Method)		**43.6 (1.5)**	**51.5 (1.3)**	**58.4 (2.8)**	
	[N]	**[30]**	**[4]**	**[2]**	
Weighted Mean		**41.9**	**52.4**	**58.4**	
Average Growth Increments		**41.9**	**10.5**	**6.0**	
		***E. nigrum* males**			
1	**29**	**42.0 (1.4)**			
2	**6**	**42.6 (4.1)**	**59.4 (4.6)**		
(Empirical Method)		**43.9 (3.3)**	**56.8 (1.3)**	**64.0 (5.9)**	
	[N]	**[17]**	**[6]**	**[5]**	
Weighted Mean		**42.7**	**58.1**	**64.0**	
Average Growth Increments		**42.7**	**15.4**	**5.9**	

[1] Original calculations based on SL were converted to TL using the equation in Table 3.

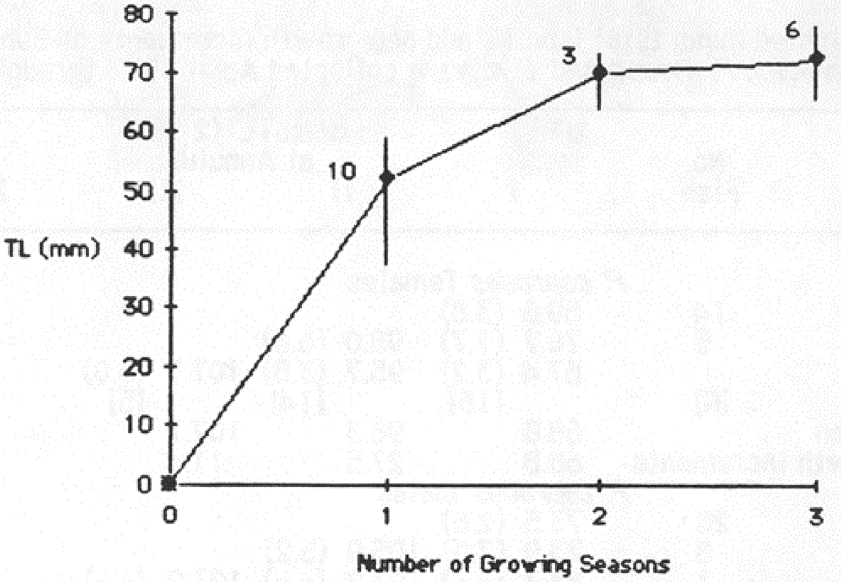

Figure 3. Empirical mean and range of growth of 1976 year-class *Percina phoxocephala* from the Sunrise River.

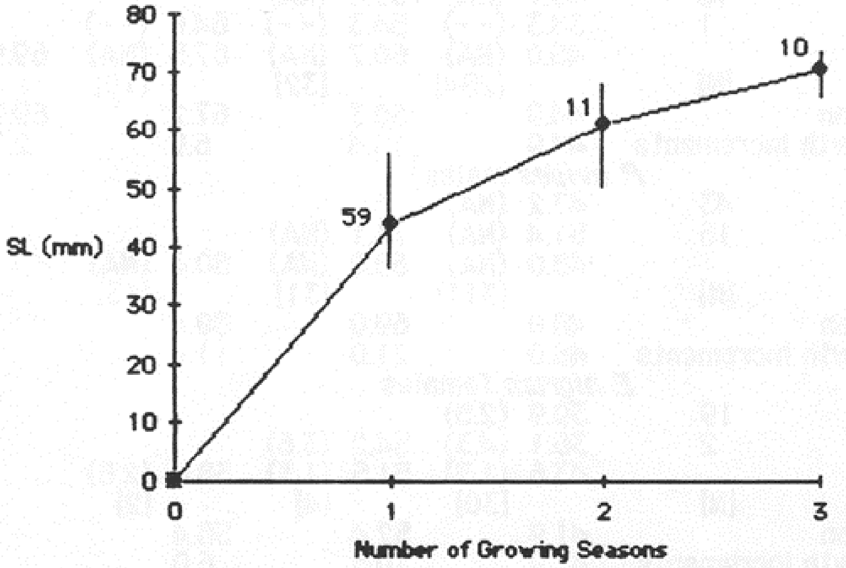

Figure 4. Empirical mean and range of growth for 1976 year-class male *Percina evides* from the Sunrise River.

Table 6. Average growth of 1977 year-class Sunrise River darters during their first four months of life (2 SE). Sexes combined except for *P. evides*.

		Months of Growth			
Species		**1**	**2**	**3**	**4**
E. nigrum		**28.1 (2.0)**	**34.6 (2.0)**	**40.9 (2.8)**	**- - - -**
	N	**17**	**13**	**15**	
P. caprodes		**45.1 (3.1)**	**50.0 (4.2)**	**- - - -**	**70.0 (4.3)**
	N	**2**	**6[a]**		**6**
***P. evides* (females)**		**31.3 (1.0)**	**38.6 (1.0)**	**41.8 (1.0)**	**41.4 (1.4)**
	N				
***P. evides* (males)**		**30.9 (1.6)**	**39.8 (1.0)**	**45.0 (1.0)**	**45.9 (1.4)**
	N				
P. maculata		**38.9 (1.9)**	**42.8 (4.5)**	**51.1 (1.6)**	**60.8 (2.1)**
	N	**6**	**6[b]**	**8[c]**	**15**
P. phoxocephala		**- - - -**	**- - - -**	**41.2 (- -)**	**50.6 (- -)**
	N			**1**	**1**

[a] 4 specimens from 1979 year-class

[b] 3 specimens from 1979 year-class

[c] 6 specimens from 1979 year-class

Length-Weight Relationship:

Two relationships between total length and body weight were determined for each darter species in this study (Table 7). Total lengths and adjusted body weights were not determined routinely during the previous study of *P. evides* and, therefore, only equations relating standard length to total body weight are available (Table 8). Correlations between total length and both body weight measures were very high (r > 0.93 in all cases). However, in the case of total body weight, the equations for P. evides show that the magnitude of the regression slopes is increased considerably by the contribution of gonad weights in fish that are ripe or near-ripe. Thus, if accurate weights need to be determined from lengths of darters it is probably to use a series of equations as in Table 8 or an equation that relates adjusted body weight to length.

Table 7. Least-squares regression equations of total body weight (TBW) and adjusted body weight (ABW) on total length (TL) for upper St. Croix drainage darters (r = regression coefficient; N = sample size).

Species	Sex	Regression Equation	r	N
		Total Body Weight on Total Length		
E. nigrum	F	log TBW = -5.639 + 3.286 log TL	0.991	55
	M	log TBW = -5.726 + 3.338 log TL	0.994	48
P. caprodes	F	log TBW = -5.973 + 3.434 log TL	0.989	26
	M	log TBW = -5.690 + 3.272 log TL	0.988	50
P. maculata	F	log TBW = -6.097 + 3.532 log TL	0.954	20
	M	log TBW = -5.973 + 3.468 log TL	0.993	34
P. phoxocephala	F	log TBW = -5.963 + 3.468 log TL	0.979	15
	M	log TBW = -6.457 + 3.723 log TL	0.988	50
		Adjusted Body Weight on Total Length		
E. nigrum	F	log ABW = -5.698 + 3.239 log TL	0.978	73
	M	log ABW = -6.107 + 3.506 log TL	0.989	66
P. caprodes	F	log ABW = -5.759 + 3.251 log TL	0.993	29
	M	log ABW = -5.898 + 3.328 log TL	0.989	54
P. maculata	F	log ABW = -5.831 + 3.314 log TL	0.933	23
	M	log ABW = -5.963 + 3.403 log TL	0.993	39
P. phoxocephala	F	log ABW = -5.977 + 3.407 log TL	0.976	17
	M	log ABW = -6.814 + 3.871 log TL	0.989	50

According to Ricker (1973, 1975), length-weight relationships are better best described by geometric mean functional regressions rather than least-square regressions. These equations are shown in Table 9. Although these equations may be statistically preferable, they have not been used traditionally to describe these relationships in darters. Thus, least-squares regressions would most likely be used to make comparisons among species.

Table 8. Least-squares regression equations of total body weight (TBW) on standard length (SL) for Sunrise River *Percina evides* in three reproductive conditions (r = regression coefficient; N = sample size).

Reproductive Condition	Regression Equation	r	N
	FEMALES		
Ripe	log TBW = -5.531 + 3.454 log SL	0.893	20
Maturing	log TBW = -5.200 + 3.236 log SL	0.959	40
Immature	log TBW = -5.272 + 3.275 log SL	0.998	60
	MALES		
Ripe	log TBW = -5.620 + 3.489 log SL	0.971	14
Maturing	log TBW = -5.432 + 3.372 log SL	0.983	37
Immature	log TBW = -5.252 + 3.255 log SL	0.998	60

Table 9. Geometric mean functional regression equations of total body weight (TBW) and adjusted body weight (ABW) on total length (TL) for upper St. Croix drainage darter (r = regression coefficient; N = sample size).

Species	Sex	Regression Equation	r	N
		Total Body Weight on Total Length		
E. nigrum	F	log TBW = -5.767 + 3.316 log TL	0.991	55
	M	log TBW = -5.816 + 3.358 log TL	0.994	48
P. caprodes	F	log TBW = -6.047 + 3.472 log TL	0.989	26
	M	log TBW = -5.908 + 3.381 log TL	0.988	50
P. maculata	F	log TBW = -6.617 + 3.702 log TL	0.954	20
	M	log TBW = -5.802 + 3.490 log TL	0.993	34
P. phoxocephala	F	log TBW = -5.841 + 3.542 log TL	0.979	15
	M	log TBW = -6.407 + 3.768 log TL	0.988	50
		Adjusted Body Weight on Total Length		
E. nigrum	F	log ABW = -5.874 + 3.312 log TL	0.978	73
	M	log ABW = -6.322 + 3.545 log TL	0.989	66
P. caprodes	F	log ABW = -5.855 + 3.274 log TL	0.993	29
	M	log ABW = -5.971 + 3.365 log TL	0.989	54
P. maculata	F	log ABW = -6.463 + 3.552 log TL	0.933	23
	M	log ABW = -6.037 + 3.427 log TL	0.993	39
P. phoxocephala	F	log ABW = -6.026 + 3.491 log TL	0.976	17
	M	log ABW = -6.670 + 3.914 log TL	0.989	50

Reproduction

Spawning Period-- The precise periods and durations of spawning of Sunrise River darters were difficult to determine because dispersal behavior and spring-early summer water conditions reduced sampling success and made direct observations difficult. Estimates were made, however, based on the periodic occurrence of ripe adults, seasonal changes to gonosomatic indices, and the appearance of larval and juvenile darters in the seasonal catch. These estimates, except in the case of *P. evides*, should be considered tentative.

The spawning durations of all species appeared to extend for at least 4 weeks and, therefore, there was considerable overlap among spawning periods. *Percina caprodes* showed signs of spawning readiness as early as middle April, and peak activity appeared to occur in early to middle May in most years. There was no indication of spawning in June by this species. *Percina maculata* reached spawning readiness in late April shortly after *P. caprodes* and its peak activity occurred about the middle of May. It is unlikely that *P. maculata* spawned much in June, but I have very little data from early in the month. *Etheostoma nigrum* also showed signs of spawning readiness by late April, with indications of sustained spawning throughout May and perhaps into early June. *Percina evides* began spawning usually in late May and continued throughout June and into early July. Peak spawning occurred in middle June. *Percina phoxocephala* also was mainly a June spawner, but it too spawned into July. Its peak activity was not determined.

In 1977, a year of warm spring temperatures and low water flow, all species showed evidence of beginning spawning about 1-2 weeks earlier than in 1978-1980. In 1978 and 1979, years of cool springs and high water conditions, at least 3 species extended there spawning seasons for 1-3 weeks. *Etheostoma nigrum* spawned into middle June (1979), *P. evides* spawned passed middle July (both years), and *P. phoxocephala* spawned into late July (1979). Climatic interruptions of spawning have been reported for numerous midwestern darter populations (Winn 1958; Speare 1965; Thomas 1970; Page and Smith 1971; Troutman 1981; Hatch 1986). It may be that in highly fluctuating stream environments selection has favored protracted spawning since most midwestern stream populations of darters appear to protracted spawners.

Spawning Habitat--In the Sunrise River, darters spawned primarily in the cobble raceway area and the lower portion of the rubble riffle. *Etheostoma nigrum* spawned on the undersides of loose cobble, small logs, bark, and clam shells along the east margin of the cobble raceway where current velocities were less than 0.1 m/sec. This species did not appear to utilize vegetation as a spawning substrate in the raceway, although *Vallisneria* was available. *Percina caprodes* utilized gravel and

pebble substrates along the margins of the cobble raceway and the downstream margins the rubble chute. Current velocities where they spawned were moderate (approximately 0.1-0.3 m/sec), and often, especially near the rubble chute, the flow produced eddies. *Percina evides* spawned in the central portion of the raceway where the current velocities were very high (0.5 to 0.8 m/sec). The substrate was predominantly cobble, 2.5-6.5 cm in diameter, embedded in gravel and sand and interspersed with small boulders. Water depths there varied from 30 to 90 cm. At the cobble raceway *Percina phoxocephala* appeared to use the area between the central portion and the margins. On several occasions ripe males were found in the rubble riffle in moderately swift current (velocity not measured). Ripe adult *P. maculata* were found in the *Vallesnaria* along the downstream margins of the cobble raceway in its lower 30 m and in the vegetation (mostly grasses) and detritus along the edges of the islands of the east and west channels (Figure 2, E). I was unable to verify that spawning took place on the surfaces of rooted vegetation, but I suspect that it did. Currents in these areas were slow to moderate (< 0.1 - 0.3 m/sec).

<u>Reproductive Cycles and Sexual Maturity</u>- In a previous study (Hatch 1982), I calculated gonadosomatic indices (GSI) for a cohort of male and female P. evides throughout their life cycle. The data showed a regularly repetitive reproductive cycle for both males and females. Following the spawning season, gilt darters entered a recovery period that extended into March of the following gear. Between middle March and June, the gonads developed very rapidly leading to spawning in June and July. During the spawning period, the GSIs of mature males and females were about 1 and 20, respectively. For both males and females, the GSIs were an order of magnitude lower during the recovery periods. The GSI data also showed that roughly 672 of the males reached sexual maturity in their first potential spawning season, while only a few percent of the females did. Minimum size (50 mm SL) was the determinant of maturity rather than age.

Similar detailed analyses of the remaining Sunrise River darter species were not possible, but some tentative patterns did emerge from the fragmentary data available. Tentatively, it appears that the GSIs of mature female *P. caprodes* are about 20 during the spawning season and 2 or below shortly after spawning. By the end of fall, however, the GSIs are back up to around 10. Lutterbie (1976) found a reasonably similar pattern for this period in Wisconsin populations. Very tentatively, it seems that the GSIs remain at about 10 through the winter and then increase very rapidly to 20 in March and April. The occurrence of 5- and 6-month old females, some with GSIs of 2 and others with GSIs of 10, suggests that not all females reach maturity by the end of their first year. The

pattern is less clear for males. Mature male GSIs during the spawning period range from 0.8 to 4.8 and then fall to between 0.2 and 0.4 in the early recovery period. What happens during the recovery period cannot be determined at this time. One 18-month old male (November) had a GSI of 1.6, yet several 21-month old males (February)-were between 0.6 and 0.8. The fact that one 12-month old male had a GSI of 4.8 while several others had GSIs of 0.04 indicates that, like females, not all males reach maturity at the end of their first year. Failure of some males to reach maturity at the end of the first year may account for the disparity in GSIs seen in 18 to 21-month old fish. Other investigators have indicated that sexual maturity at the end of the first year is rare in this species (Will 1931; Winn 1958; Thomas 1970; Lutterbie 1976).

Contrary to the findings of Thomas (1970) and Lutterbie (1976), the data available for *P. maculata* from this study indicate that most males and females reach maturity at the end of the first year. Increase in GSIs of young-of -the-year is very rapid, reaching 2 to 7 in females and 1 to 2 In males by September of the first year. All 1 l-month old females analyzed exhibited GSIs between 9 and 22, while male GSIs ranged between 1.4 and 2.4 Following spawning, female GSIs dropped to between 1 and 4 and male GSIs dropped to between 0.3 and 0.5. If this pattern holds true for older fish, the recovery period of males, at least, Is rather short with a majority of seasonal gonadal development taking place in the post-spawning season rather than the pre-spawning season.

The reproductive cycle a for *P. phoxocephala* to is not at all clear. June and July are extremely important months for this species and very few GSIs are available from these two months. Thus, GSIs during peak spawning (June) are not known, although they are probably similar in magnitude to those of the other species. Two females from late May had GSIs of 11.1 (1977) and 21.6 (1978). GSIs for mature males during this period were around 0.5, but ASIA of 1.1 were recorded from two males collected 15 August 1977. It appears that the recovery period for males lasts through the winter perhaps into April when GSIs begin to increase from around 0.2 to 0.5 or so. Females going into the winter had GSIs of about 3 and these increased to about 6 by April, but what happened in February and March is not known. Female *P. phoxocephala* in Illinois (Page and Smith 1971) showed peak gonadal development in June with a gradual recovery period from July to February, after which time development accelerated almost exponentially. In this study, most 12-month old males and females had GSIs $\geq$ 0.1, and it is likely that these individuals would not have reached maturity during their first potential spawning season. Page and Smith indicated that Illinois males were mature at

one year, while females that reached at least 42 mm , SL were mature at one year. More data will be required before conclusions can be drown about Minnesota populations.

Female *E. nigrum* exhibited GSIs over 30 from late April through middle May. The indices fell precipitously to about 0.4 (some as low as 0.1) following spawning. By fall (October and November), GSIs had risen to between 0.9 and 3.1. This pattern is almost identical to that reported by Speare (1965) for a Michigan population. That population showed a rapid increase in gonadal development between December and March, and it is likely that the Sunrise River population would do the same. The GSIs of fully mature males again seemed to be in the range of about 1 to 2, but males remained reproductively active (milt flowing) down to about 0.5. By late June males were in the recovery period (GSI < 0.1), which appeared to last into August. Gonadal development resumed toward the end of the growing season, and several males were back to a GSI of 0.9 by late September. Mature males from April exhibited similar GSIs. Eleven-month old males (40 mm TL consistently had GSIs below 0.1, which is probably an indication that they would not have reached maturity in their first potential spawning season. Five 11-month females had GSIs between 1.5 and 3.5, while six others had GSIs above 20. This suggests that either some females do not mature in their first potential spewing season or they reach maturity very late in the season (perhaps at reduced fecundity).

The only pattern of age or size at maturity that has emerged from the studies carried out thus far is that maturity seems to vary from population to population even within a species. It seems reasonable that species with a 2-year life must become mature in the first tear and longer lived species might wait until late in the first potential spawning year or until the second year. All short-lived species that have been investigated show nearly 100X maturity in the first year (Lutterbie 1976; Schenck and Whiteside 1977; Starnes 1977; Burr and Page 1978, 1979). Some longer lived species show nearly 0X maturity in the first year (Winn 1958; Page 1978); while others show almost 100X (New 1966; Page and Smith 1970, 1971). Still others, like P. evides in this study, show intermediate percentages and differences between male and female maturity (New 1966; Page 1978). It is probably the case that the onset of maturity is a function both of genetics and local environmental circumstances.

<u>Fecundity</u> -- A summary of fecundity estimates for each species appears in Table 10. Each estimate, except for *P. caprodes* Is based on the mean of the direct total count of all yolked ova > 0.9 mm in diameter. Estimates for *P. caprodes* are based on 2 times the count in the left ovary. Fecundity, as measured by mature ova counts, was directly related to body length and adjusted body weight - in *E. nigrum, P. caprodes*, and *P. evides* (Table 11). In *P. maculata* fecundity was not related to either of these parameters

(Figure 5). There was also a tendency for fecundity to increase with age in *P. caprodes* and *P. evides*. There were too few 2- ,and 3-year specimens to examine this relationship in the other species.

Table 10. Summary of fecundity estimates from St. Croix drainage darters. Each estimate is the mean of direct counts of all yolked ova > 0.9 mm in diameter, except for *P. caprodes* where 2 times the count of the left ovary was used.

Species	No. Fish	Mean ± 2 SE	Range	Mean Diameter Ova (mm) ± 2 SE
E. nigrum	19	136 ± 27	67 – 254	1.15 ± 0.07
P. caprodes	10	1134 ± 436	322 – 2376	1.17 ± 0.09
P. evides	15	247 ± 42	132 – 397	1.25 ± 0.06
P. maculata	15	121 ± 31	41 – 262	1.34 ± 0.08
P. phoxocephala	1	22		1.28

In general, longer lived darters exhibit a strong positive correlation between fecundity and size, and fecundity and age, at least as measured by ova counts (citations above and Mather 1973; Erickson 1977; Pflieger 1978). The question of whether or not increased body size in darters actually enhances reproductive potential remains to be answered. Hubbs (1958) and Hubbs et al. (1968) have shown that in some species it is Individual egg size rather than egg number that changes with body size and geographical distribution.

Table 11. Relationships between fecundity (F) and body length (SL or TL) and adjusted body weight (ABW) based on least-squares regressions.

Species	Regression Equation	r	N
	Fecundity and Body Length		
E. nigrum	Log F = -5.179 + 4.374 log TL	0.833	19
P. caprodes	Log F = -3.686 + 3.386 log TL	0.846	10
P. evides	Log F = -4.542 + 3.975 log SL	0.919	15
	Fecundity and Body Weight		
E. nigrum	F = -38.82 + 397.19 ABW	0.843	19
P. caprodes	F = -214.66 + 267.57 ABW	0.893	10
P. evides	F = 37.87 + 110.54 ABW	0.892	15

Food Habits

Seasonal Feeding Activity - Seasonal trends in feeding activity were examined for the Sunrise River populations. The pattern for *P. evides* (determined in a previous study) is shown in Figure 6. Annual feeding activity essentially began in April, remained at high levels through August, declined sharply in September, and remained very low throughout the fall and winter: In the present study, I computed a different index of fullness based on the relationship of stomach content weight (dry) to adjusted body weight (wet). In order to cover the April to September period, I had to use specimens collected in different years. Still, Figures 7-9 suggest that *E. nigrum, P. caprodes* and *P. maculata* show general seasonal feeding activity patterns similar to that of *P. evides*. Figure 10 suggests a progressive decline for *P. phoxocephala*, but this may be a result of the small sample sizes and pooling of different biological years for July and August.

Low levels of feeding activity during the winter seem to result more from reduced foraging activity than from reduced food availability, since large numbers of food organisms were collected along with darters throughout the winter. The ultimate cause of the reduced foraging activity is not known, but low water temperatures (near 0 ° C or below in some cases) probably had a proximate effect by reducing metabolic rates in general and digestion rates in specific. Normally only head capsules and other heavily scleritized portions of exoskeletons were found in the distal intestine. However, the distal intestines of several winter-caught darters contained whole chironomid and simuliid larvae indicating that digestion was not taking place.

Seasonal Composition--While all five darter species ate the same basic food items (immature forms of Ephemeroptera, Diptera and Trichoptera), the compositions of their diets seasonally were substantially different (Figures 11-15). *Etheostoma nigrum* consumed primarily chironomid larvae (Deplete) throughout the feeding season, while *P. maculata* and *P. phoxocephala* concentrated primarily on baetid mayfly naiads (Ephemeroptere). *Percina caprodes* and *P. evides* consumed a greater diversity of food items throughout the feeding season, and they changed their diets more substantially through the season. In May, *P. caprodes* fed primarily on baetid mayfly naiads and chironomid larvae. Chironomid and hydropsychid (Trichoptera) larvae became increasingly more important as the season progressed. *Percina caprodes* also consistently consumed small numbers of young snails and freshwater

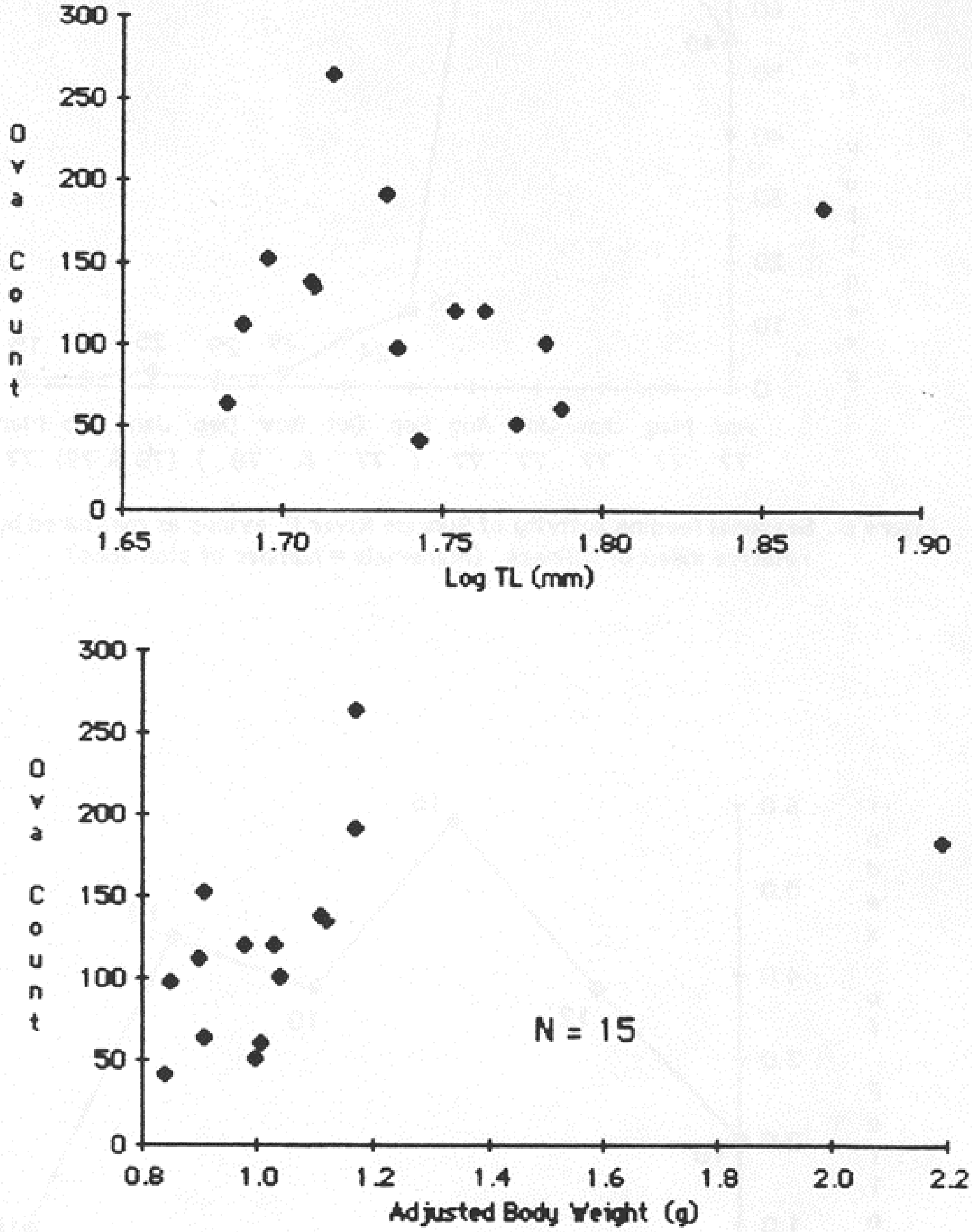

Figure 5. Scatter plots of ova counts versus log TL and adjusted body weight for *Percina maculata* from the Sunrise River.

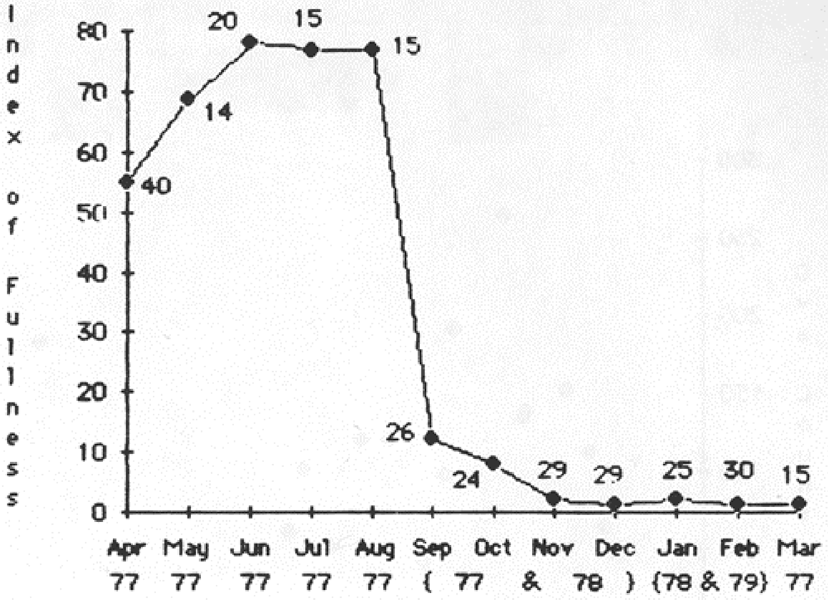

Figure 6. Seasonal feeding activity of Sunrise River P. evides as measured by relative index of fullness. (Numerials = number of stomachs)

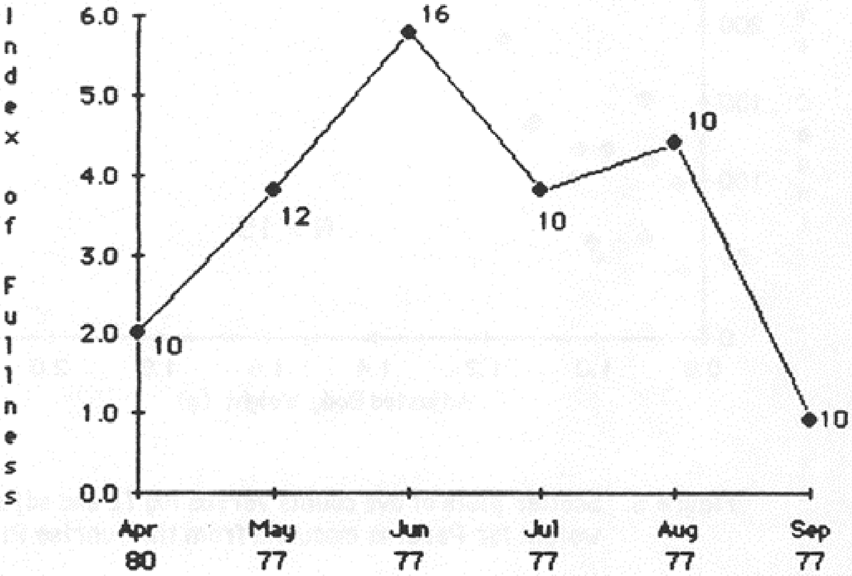

Figure 7. Seasonal feeding activity of Sunrise River E. nigrum as measured by index of fullness. (Numerials = number of stomachs)

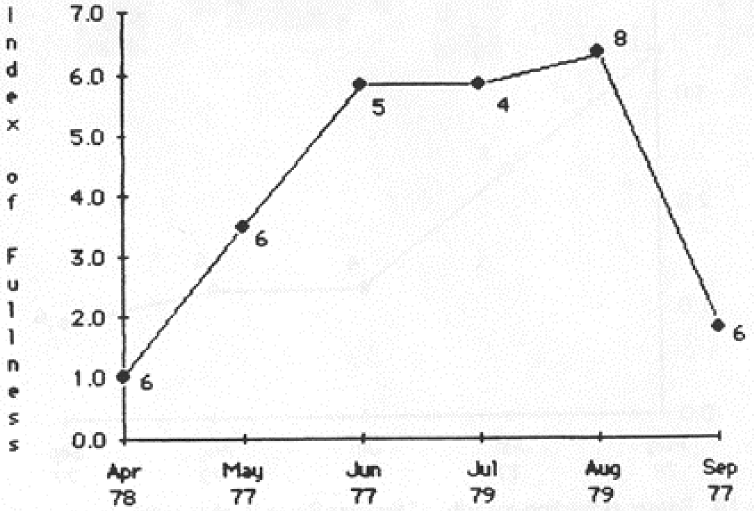

Figure 8. Seasonal feeding activity of Sunrise River P. caprodes as measured by index of fullness. (Numerials = number of stomachs)

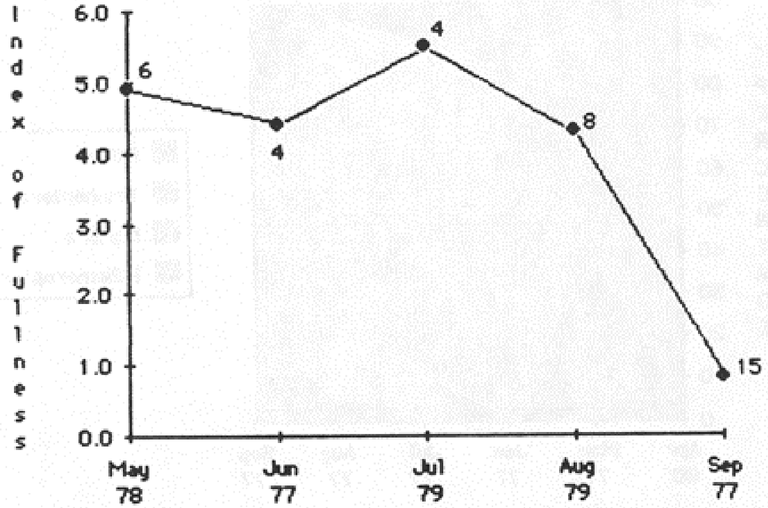

Figure 9. Seasonal feeding activity of Sunrise River P. maculata as measured by index of fullness. (Numerials = number of stomachs)

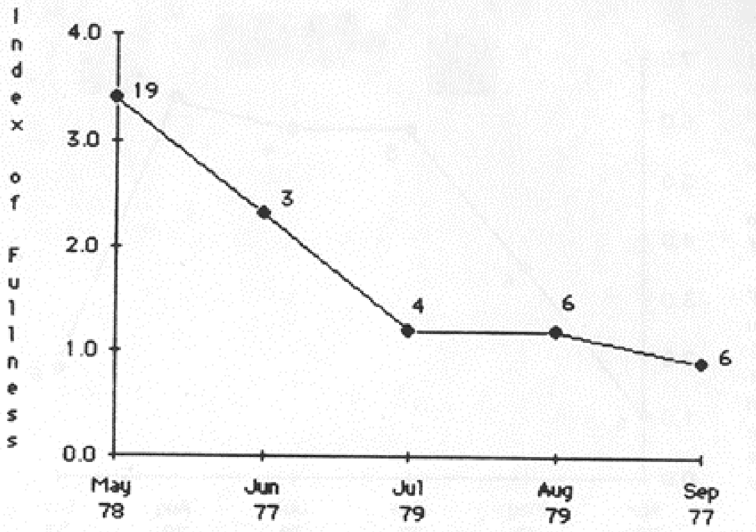

Figure 10. Seasonal feeding activity of Sunrise River P. phoxocephala as measured by index of fullness. (Numerials = number of stomachs)

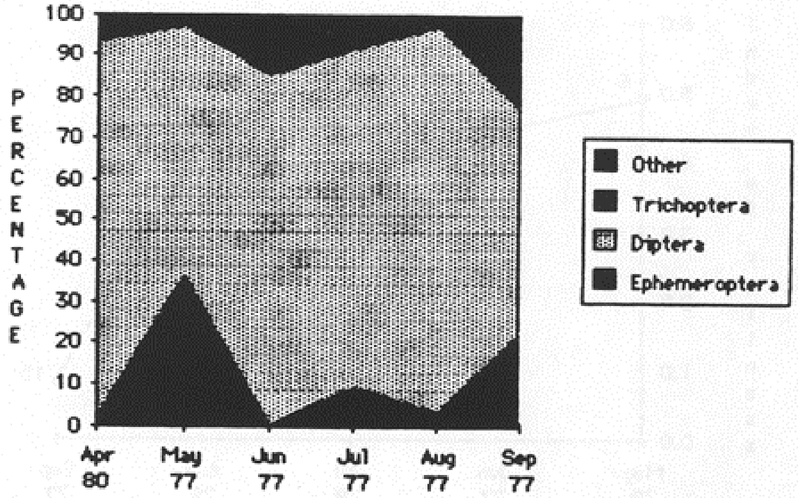

Figure 11. Seasonal composition of major food items in stomachs of Sunrise River E. nigrum.

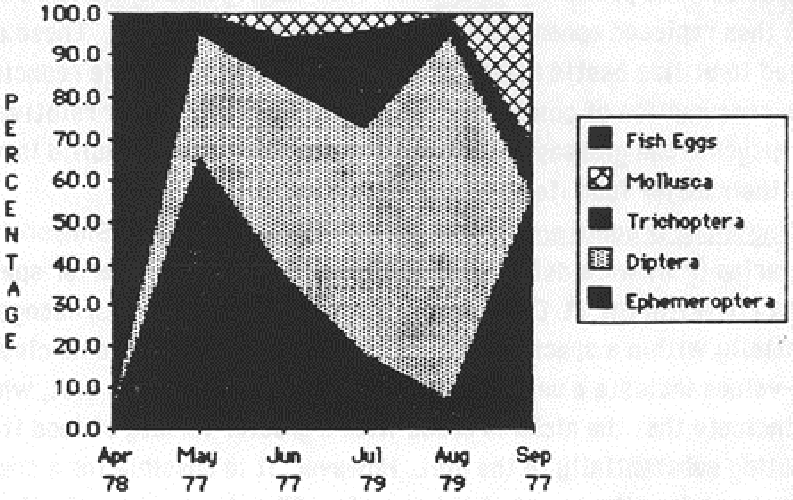

Figure 12. Seasonal composition of major food items in stomachs of Sunrise River P. caprodes.

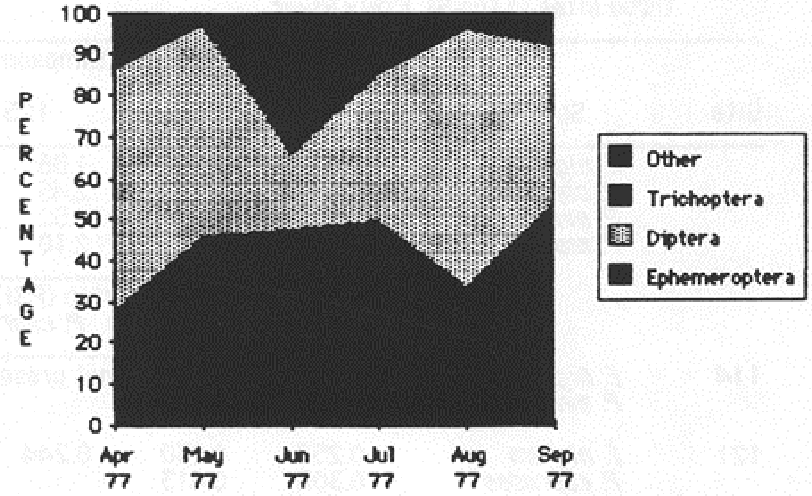

Figure 13. Seasonal composition of major food items in stomachs of Sunrise River P. evides.

limpets (*E. nigrum* was the only other species that occasionally consumed limpets). *Percina evides* fed primarily on ephemerellid mayfly naiads and chironomid larvae in April then replaced ephemerellid naiads with baetids in May. These darters continued to utilize baetid naiads heavily in June and July while reducing their relative consumption of chironomid larvae and increasing their relative consumption of hydropsychid and glossosomatid larvae. Chironomid and simuliid larvae then became their major food items in August.

<u>Feedings Niche Breadth and Overlap</u> - Feeding niche breadth (Simpson's B) and niche overlap (PSI) were determined for two assemblages of darter species at three different riffles in the St. Croix River (Table 12). Niche breadth changed substantially within a species from site to site, but there were no clear patterns. Low 'B'-values indicate a narrow feeding niche and monotonous diet, while high values indicate that the niche is broad with a greater variety of food items contributing substantially to the diet. However, it is possible for a species to eat a fair variety of food items and still have a low 'B'-value because the items are weighted by proportion. For instance, at each site *E. nigrum* consumed the

Table 12. Feeding niche breadth and overlap for *E. nigrum, P. caprodes, P. evides* and *P. maculata* collected August 1983 from three sites in the St. Croix River.

		Feeding Niche Breadth (Simpson's B)		
		Site Number		
Site	Species	114	121	125
	E. nigrum	1.47	2.36	1.86
	P. caprodes	Not present	3.14	2.45
	P. evides	2.60	2.21	4.52
	P. maculata	1.23	4.23	2.10
		Feeding Niche Overlap (PSI)		
		P. maculata	*P. evides*	*P. caprodes*
114	*E. nigrum*	0.082	0.127	Not present
	P. evides	0.651		
121	*E. nigrum*	0.257	0.230	0.244
	P. caprodes	0.308	0.413	
	P. evides	0.378		
125	*E. nigrum*	0.095	0.314	0.752
	P. caprodes	0.436	0.488	
	P. evides	0.612		

greatest number of kinds of food items (Figures 16-18), yet these darters consistently had a low niche breadth because just three of these items comprised over 84% of their diets in each case. The high values for P. maculata at site 121 and f' evides at site 125 resulted from having consumed food items in only 7 and 6 families, respectively, but in fairly even proportions. The very low value for P. maculata at site 114 resulted from the consumption of 90% simuliid larvae. Figures 16-18 indicate that diet composition of a given species was different at different sites, in some cases substantially different. They also indicate that diet compositions among species at a given site differed quite substantially. There were only three comparisons of food niche overlap that exceeded a PSI of 0.5 (Table 12). Typically, *E. nigrum* showed the least amount of overlap with the other species (except with P. caprodes at site 125), while *P. evides* and *P. maculata* showed the greatest overlap.

Most darters from stream environments primarily consume dipteran, mayfly and caddisfly immatures, although darters that inhabit slower water incorporate more microcrustaceans into their diets than do darters living in swift currents (Khuene and Barbour 1983; Page 1983). The general opinion about darters at this time is that they are opportunistic feeders that in sympatry show a high degree of overlap in feeding niches. Based on the data from this study and my previous study, I agree that darters are indeed opportunistic and their apparent selectivity for or against some food items maybe mechanistic, as in the case of young centrachids (O'Brien 1979).

I also agree that as a group darters show substantial overlap in feeding niches. Some investigators have interpreted this overlap as an indication that interspecific competition for food is not important in structuring community assemblages (Toth 1978; Coon 1982; Schlosser and Toth 1983). Other investigators, however, maintain that competition for food and/or microhabitat (which are of ten. hard to distinguish) may play a substantial role especially in habitats that many be suboptimal for several species in sympatry (Paine et al. 1981; Matthews et al. 1982; Wynes and Wissing 1982.)

The present study indicates that substantial differences in diets of assemblages of St. Croix River darters do exist and these differences become more striking as food items are identified to lower and lower taxonomic levels. Diet overlap based on PSI is not as high as it appears from a cursory examination of percentage

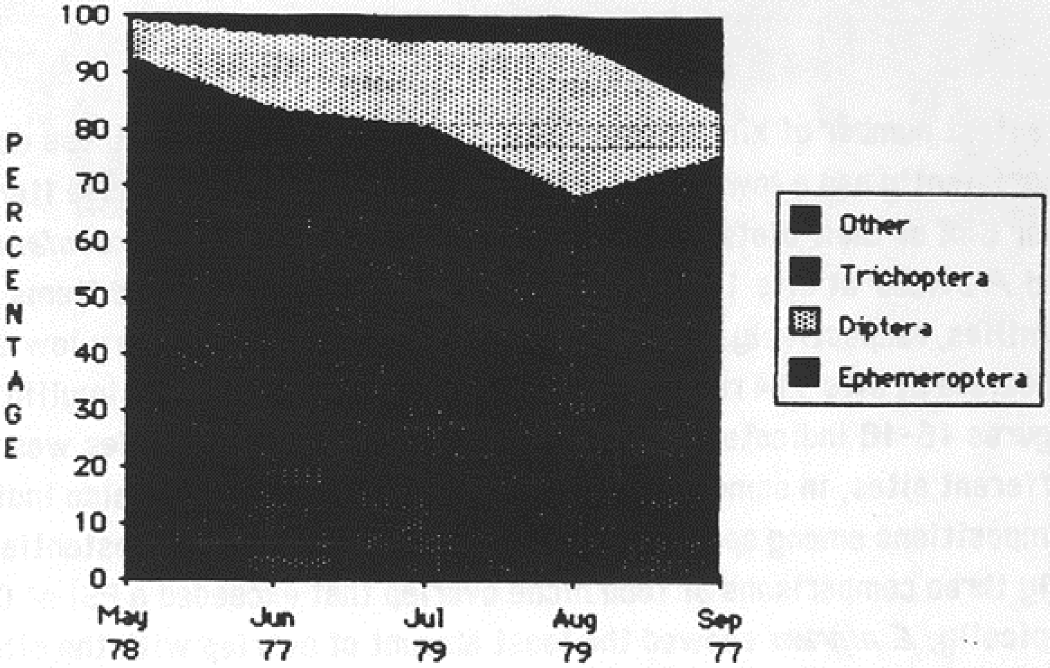

Figure 14. Seasonal composition of major food items in stomachs of Sunrise River P. maculata.

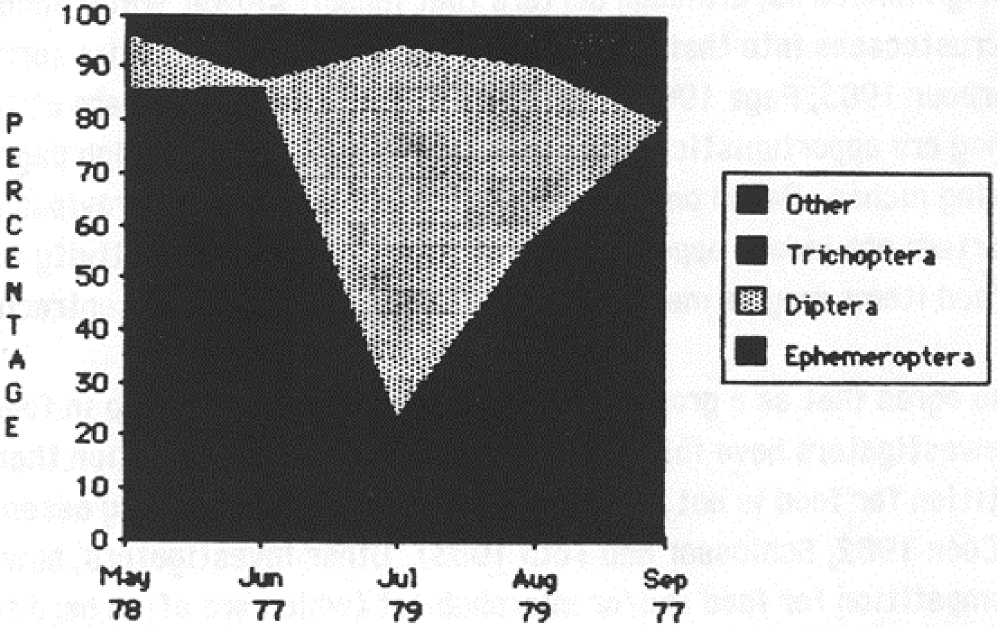

Figure 15. Seasonal composition of major food items in stomachs of Sunrise River P. phoxocephala.

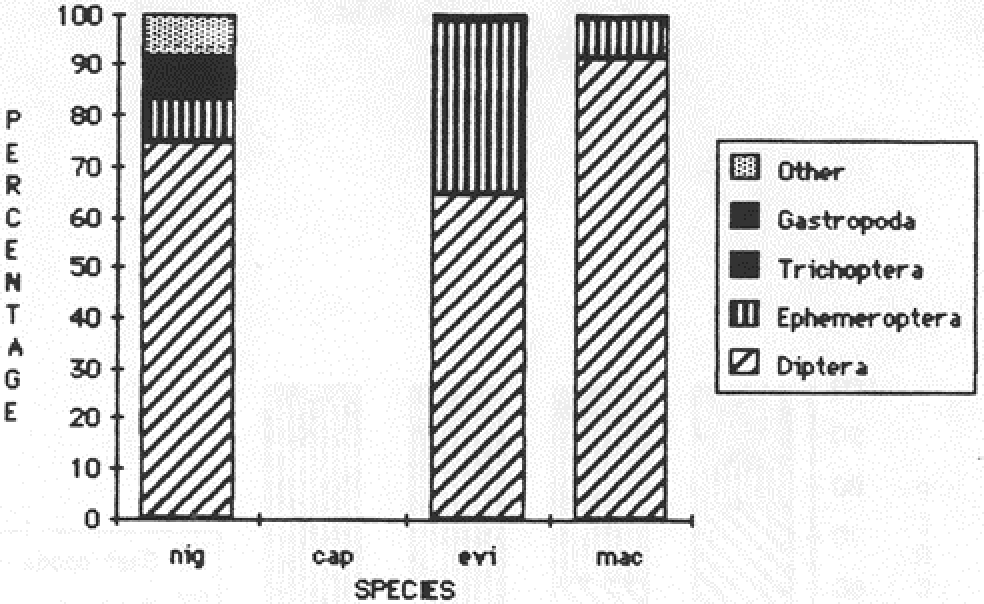

Figure 16. Composition of diet of St. Croix River darters captured at station 114 on August 8, 1983.

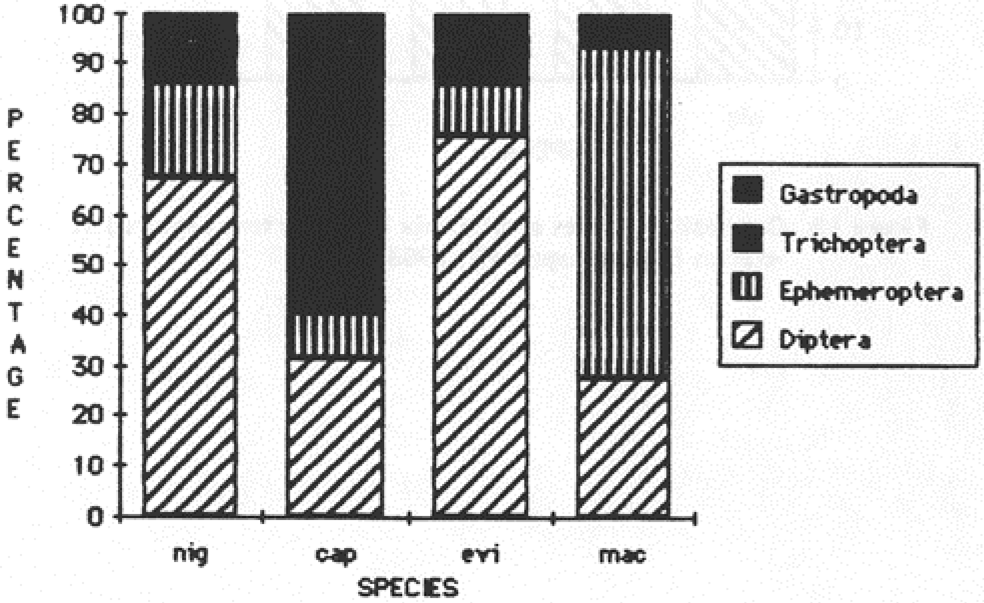

Figure 17. Composition of diet of St. Croix River darters captured at station 121 on August 10. 1983.

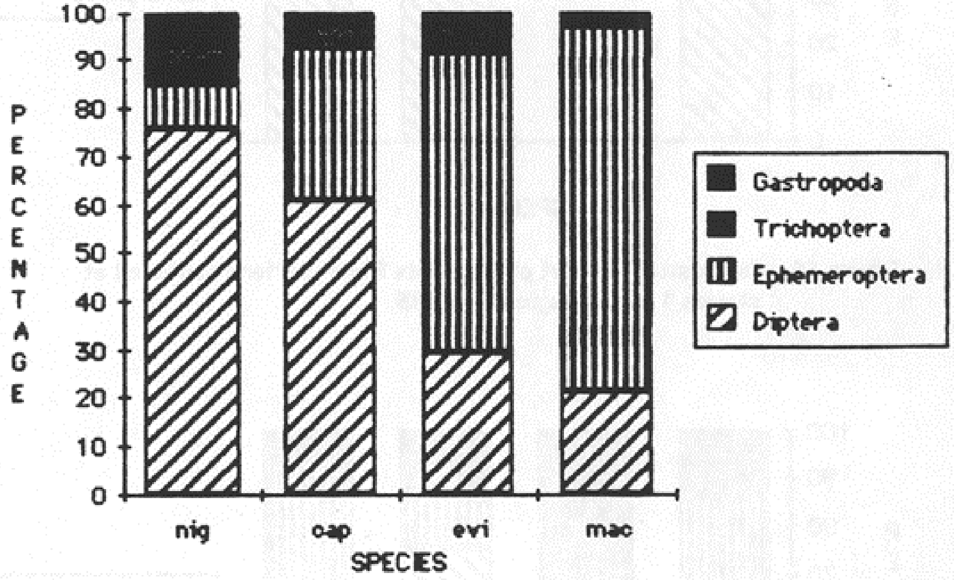

Figure 18. Composition of diet of St. Croix River darters captured at station 125 on August 12, 1983.

compositions. This may be due to differences in food availability in different microhabitats, or it may be a reflection of subtle but real differences in food partitioning due to competitive encounters, or both. Clearly, more detailed analyses of dietary changes with changes in habitat complexity will be necessary to draw conclusions about how important feeding competition is in controlling community structure of darters.

Literature Cited

Burr, B. M. 1980. A distributional checklist of the fishes of Kentucky. Brimleyana. 3:53-84.

________, and L. M. Page. 1978. The life history of the cypress darter, *Etheostoma proeliare*, in Max Creek, Illinois. Ill. Nat. Hist. Surv. Biol. Notes 106:1-15.

________, and L. M. Page. 1979. The life history of the least darter, *Etheostoma microperca,* in the Iroquois River, Illinois. Ill. Nat. Hist. Surv. Biol. Notes 112:1-15.

Coon, T. G. 1982. Coexistence in a guild of benthic stream fishes: The effects of disturbance. Ph.D. Thesis, Univ. Cal if., Davis. 191 pp.

Cummins, K.W. 1980. The natural stream ecosystem. pp. 7-24, in: J.V. Ward and J. A. Standford, editors. The ecology of regulated streams. Plenum Pub]. Corp.

Denoncourt, R. F. 1969. A systematic study of the gilt darter *Percina evides* (Jordan and Copeland) (Pisces, Percidae). Ph.D. Thesis, Cornell Univ., Ithaca.

Dobie, J. 1959. Note on food of northern log perch. Trans. Amer. Fish. Soc. 88:213.

Eddy, S. and J. C. Underhill. 1974. Northern fishes with special reference to the upper Mississippi Valley. 3rd ed., revised. Univ. Minn. Press, Minneapolis, MN. 414 pp.

Erickson, J. E. 1977. The life history of the banded darter, *Etheostoma zonale zonale* (Cope), in the Cannon River, Minnesota. Ph. D. Thesis, Univ. of Minnesota, Minneapolis.

___________, 1980 Winter sampling of benthic stream fishes in Minnesota with a one-man net. J. Minn. Acad. Sci. 4:2-3.

Gerking, S. D. 1945. The distribution of the fishes of Indiana. Invest. Indiana Lakes and Streams 3:1-137.

Hatch, J. T. 1982. Life history of the gilt darter, *Percina evides* (Jordan and Copeland), in the Sunrise River, Minnesota. Ph. D. Thesis, Univ. of Minnesota, Minneapolis. 152 pp.

___________, 1986. Distribution, habitat and status of the gilt darter (*Percina evides*) in Minnesota. J. Minn. Acad. Sci. [in press).

Hubbs C. 1958. Geographic variations in egg complement of *Percina caprodes* and *Etheostoma spectabile* Copei a 1958: f2-105. M. M. Stevenson, and A. E. Peden. 1968. Fecundity and egg size in two central' exas darter populations. Southwest. Nat. 13:301-324.

Karr, J. R. 1963. Age, growth and food habits of Johnny, slenderhead and blackside darters of Boone County, Iowa. Proc. Iowa Acad. Sci. 70:228-237.

____________, 1981. Assessment of biotic integrity using fish communities. Fisheries 6:21-27.

Kuehne, R. A. and R. W. Barbour. 1983. The American darters. The Univ. Press of Kentucky, Lexington. 177 pp.

Lachner, E. A., E. F. Westlake and P. S. Handwerk. 1950. Studies on the biolog of some percid fishes from western Pennsylvania. Amer. Mid. Nat. 43: 92- 11.

Levin, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton.

Lutterbie, G. W. 1976. The darters (Pisces: Percidae: Etheostomatinae) of Wisconsin. M.S. Thesis, Univ. Wise-Stevens Pt. 307 pp.

Mathur, D. 1973. Some aspects of the life history of the blackbanded darter, *Percina nigrofaciata* (Agassiz), in Halawakee Creek, Alabama. Amer. Mid. Nat. 43:92-111.

Matthews, W. J., J. R. Bek and E. Surat. 1982. Comparative ecology of the darters *Etheostoma podostemone, E. flabellare* and *Percina roanoka* in the Upper Roanoke River drainage, Virginia. Copeia 1982:805-8 1 4.

Moyle, P. B. 1969. Ecology of the fishes of a Minnesota lake with special reference to the cyprinidae. Ph.D. Thesis, Univ. of Minnesota, Minneapolis. 169 pp.

New, J. 6. 1966. Reproductive behavior of the shield darter, *Percina peltata peltata* in New York. Copeia 1966:20-28.

0'Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Amer. Scientist 672-581.

Page, L. M. 1978. Redescription, distribution, variation and life history notes on *Percina macrocephala* (Percidae). Copeia 1978:655-664.

__________, 1983. Handbook of darters. 111. Nat. Hist. Surv., Champaign. 271 pp.

__________, and Smith, P. W. 1970. The life history of the dusky darter, *Percina sciera* in the Embarras River, Illinois. Ill. Nat. Hist. Surv. Biol. Notes No. 69:1-15.

__________, 1971. The life history of the slenderhead darter, *Percina phoxocephala* in the Embarras River, Illinois. Ill. Nat. Hist. Surv. Biol. Notes No. 74:1-14.

Paine, M. D., J. J. Dodson, and G. Power. 1982. Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. Can. J. Zool. 60:1635-1641.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Dept. Conservation. 343 pp.

___________, 1978. Distribution, status, and life history of the Niangua darter, *Etheostoma nianguae.* Missouri Dept. Conservation Aquat. Ser. No. 16:1-24.

Reed, R. J. 1968. Mark and recapture studies of eight species of darters (Pisces: Percidae) in three streams of northwestern Pennsylvania. Copeia 1968:172-175.

Ricker W. E. 1973. Linear regression in fishery research. J. Fish. Res. Bd. Canada 36:409-434. i

___________, 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Bd. Canada, Bull. 191.

Scalet, C. G. 1973. Stream movements and population density of the orangebelly darter, *Etheostoma radiosum cyanorum* (Osteichthyes: Percidae). Southwest. Nat. 17:381-387. i

Schlosser, I. and L. A. Toth. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. Oikos 42:229-238.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology 51:8-418.

Schenck, J. R. and B. G. Whiteside. 1977. Reproduction, fecundity, sexual dimorphism and sex ratio of *Etheostoma fonticola* Osteichthyes: Percidae). Amer. Mid. Nat. 98:365-375.

Smith, P. W. 1971. Illinois streams: A classification based on their fishes and an analysis of factors responsible for disappearance of native species. Ill. Nat. Hist. Surv. Bibl. Notes No. 76.

Speare, E. P. 1960. Growth of the central Johnny darter, *Etheostoma nigrum nigrum* (Rafinesque) in Augusta Creek, Michigan. Copeia 1960:241-243.

_____________, 1965. Fecundity and egg survival of the central Johnny darter (*Etheostoma nigrum nigrum*) in southern Michigan. Copeia 1965(3):308-314.

Starnes.- W. C. 1977. The ecology and life history of the endangered snail darter, *Percina (imostoma) tanasi* Etnier. Ph.D. Thesis, Univ. Tenn. Knoxville, TWRA Tech. Rep. No. 77-52.

Thomas, D. L. 1970. An ecological stud of four darters of the genus *Percina* (Percidae) in the Kaskaskia River, Illinois. Ill. Nat. Hist. Surv. Biol. Notes No. 70:1-18.

Toth, L. A. 1978. Resource partitioning between two species of darters, *Etheostoma coerulum* and *Etheostoma flabellare.* M.S. Thesis. North. Ill. Univ., Dekalb.