To the Graduate Council:

I am submitting herewith a dissertation written by Wayne C. Starnes entitled "The Ecology and Life History of the Endangered Snail Darter, *Percina (Imostoma) tanasi* Etnier." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

David A. Etnier, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

THE ECOLOGY AND LIFE HISTORY OF THE ENDANGERED SNAIL DARTER, *PERCINA* (*IMOSTOMA*) *TANASI* ETNIER

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Wayne C. Starnes

March 1977

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ABSTRACT

A 2-year study of the ecology and life history of the snail darter, *Percina tanasi*, was conducted from 1974 to 1976. The snail darter was found to be a strictly benthic species principally associated with a large river gravel shoal habitat where it feeds and reproduces. Its present range is restricted to the lower Little Tennessee River and a small adjacent portion of the Tennessee River. It is speculated that *P. tanasi* once occupied a much wider range in the upper Tennessee River drainage which has since been curtailed by impoundments. This species was found to be a short-lived darter which, along with other members of the subgenus *Imostoma*, spawns in mid-winter. Larval drift is a significant event in the life of the snail darter, and early development is very slow. Adults are migratory, especially during the breeding season. The principal diet constituents are gastropods; there is some utilization of insects. A high degree of selectivity is exercised in procuring the gastropod diet, and there are seasonal trends in both diet composition and consumption levels. *P. tanasi* occupies a remote position in the Little Tennessee food web. Predation is thought to be high on the eggs and larval stages of *P. tanasi* but low on adults. Parasitism is very low. The present ecological situation of the snail darter is thought to be considerably altered from that of preimpoundment days. It is threatened with extinction if the remainder of its habitat is inundated by the Tellico Dam.

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INTRODUCTION

In August, 1973, an unknown species of darter of the genus *Percina* was discovered in the lower Little Tennessee River at Coytee Springs in Loudon County, Tennessee. It was discovered by David A. Etnier and Robert A. Stiles of The University of Tennessee and Samford University, respectively. It was subsequently described as a new species by Etnier (1975) after further collections revealed the occurrence of a viable and apparently restricted population.

The new *Percina* proved to be a member of the subgenus *Imostoma*, which includes four rather closely related saddle-backed species and a fifth more distantly related member, *P. shumardi*. The four saddle-backed members are *P. ouachitae* (Jordan and Gilbert), a widespread form in the central United States; *P. (Imostoma)* sp., a form currently being described from the upper Coosa system (Williams and Etnier, in press); *P. uranidea* (Jordan and Gilbert), now restricted to the White and Saline systems of Arkansas and Missouri; and its closest relative, *P. tanasi*, the new form from the Little Tennessee (Etnier, 1975). The now restricted range of *P. tanasi*, the snail darter, is the apparent result of impoundments which have inundated the remainder of its speculated natural habitat. A large river form, the snail darter was probably once abundant in the main channel of the Tennessee River and perhaps the lower reaches of some larger tributaries prior to impoundment. The natural range may have extended from the lower Clinch, French Broad, and Holston rivers downstream in the Tennessee drainage to perhaps the bend of the river area in northern Alabama. Thousands of collections have not revealed

its continued presence elsewhere besides the lower Little Tennessee River and proximate portions of the Tennessee.

The discovery and restricted nature of the snail darter have placed it at the center of great controversy. The Tennessee Valley Authority's Tellico Dam Project, begun several years before the discovery of the snail darter, would inundate or considerably alter the darter's entire known range upon completion. *Percina tanasi* was placed on the Federal Endangered Species List in fall of 1975. At present, the fate of the snail darter and the Tellico Project lie in the hands of Congress.

Due to the unique situation and uncertain future of the snail darter, it was decided to embark upon a study of its life history and ecology. To be gained from such a study would be valuable information, otherwise possibly lost forever, on a unique large river species. In addition, possible insight into many of the reasons which had contributed to its demise elsewhere as well as that of other fluvial species might be gained. With these objectives in mind, the life history research was initiated in the summer of 1974 and continued through the summer of 1976 with support from a research assistantship sponsored by the Tennessee Valley Authority (TVA).

From the outset there were a number of difficulties associated with the study. The Little Tennessee presents a rather difficult study situation due to daily high flows and some extended periods of high discharge from Chilhowee Dam upstream of the snail darter's habitat. Fishes were not abundant in the lower Little Tennessee and collection of snail darters and associated species required a considerable amount of manpower. The endangered status of *P. tanasi* placed limitations on

the amount of data which could be gathered. In spite of these adversities, it was possible, through help from associates at The University of Tennessee and TVA biologists, to assimilate a considerable amount of data which is analyzed and discussed herein along with speculations pertaining to the snail darter's ecology and life history.

This study constitutes only the second life history investigation on a member of the subgenus *Imostoma*. Thomas (1970) discussed many aspects of the life history of *P. shumardi* in an ecological comparison with three other darters of the genus *Percina*. Unfortunately, the inclusiveness of the study demanded that he treat each species with brevity, and some aspects were omitted or were not ascertained. In addition to *P. shumardi*, more or less complete life history information has been published on only 4 of the 30 named members of the genus *Percina*: *P. caprodes* and *P. maculata* (Thomas, 1970), *P. phoxocephala* (Page and Smith, 1971), and *P. sciera* (Page and Smith, 1970). Howell (1971) completed an excellent but as yet unpublished study of *P. aurantiaca* at The University of Tennessee. In addition to these more complete studies, several publications treat one or more aspects of the life histories of various species of *Percina*. Turner (1921) and Mullan et al. (1968) considered only feeding habits of *P. caprodes*. Reproduction was the main thrust of studies on *P. caprodes* (Hubbs, 1961; Reighard, 1913; Winn, 1958), *P. copelandi* (Winn, 1953), *P. maculata* (Petravicz, 1938), *P. notagramma* and *P. peltata* (New, 1966; Loos and Woolcott, 1969), and *P. nigrofasciata* (Mathur, 1973). This summarizes most papers which treat life histories or ecologies of the genus in any depth. It is clear that there is considerable yet to be learned about

this important group of fishes which are so indicative of certain kinds of environmental quality.

This study is offered as a contribution to the limited knowledge we now have of the ecological requirements of large river species. In particular, it attempts to help fill the void which has thus far existed concerning a poorly known subgenus of percid fishes--in spite of the notoriety of one of its members, the snail darter.

CHAPTER I

METHODS

Snail darter studies were conducted primarily at the natural habitat in the lower Little Tennessee River. A study site of particular note is the type locality at Coytee Spring which serves as perhaps the population center for *P. tanasi* and is easily accessible. Here data were gathered concerning all aspects of the snail darter's life history. Surveys related to distribution and habitat definition were conducted throughout the lower 30 km of the river as well as in the Tennessee River proper. In excess of 80 trips were made to the Little Tennessee and other rivers during the 2-year period from June, 1974, to June, 1976. Some additional insight was gained from observation of specimens retained in aquaria.

Techniques used in gathering data and/or snail darter specimens were underwater observation and photography, seining, and sodium cyanide applications. Underwater observations were most often accomplished by snorkeling and occasionally by scuba diving. The temperature regime of the Little Tennessee demanded the use of a wetsuit throughout the year. Underwater photographs were taken with a standard Kodak XL-10 Super 8 mm movie camera encased in an Ikelite housing. The use of high-speed Ektachrome film (Kodak 464) made available daylight adequate for this purpose.

Fish to be captured were usually seined. The relatively low density of fishes in the lower Little Tennessee along with strong currents and the general demeanor of the snail darter and its associates

made fishes difficult to collect compared with most other rivers. A seining crew of five or more persons was virtually a necessity for effective collecting. Seines 4 m in length having 5 mm mesh were commonly used, and the most effective technique was kicking downstream into a seine which had been set against the current in shoal areas. Additional specimens were collected by using sodium cyanide as an immobilizing agent. Applications of this chemical were generally placed 30 m above a 6 m or 16 m block net. This method was efficient only during periods of warmer water temperatures. Other specimens were captured by the use of a hand net while diving. All specimens to be retained alive were transported in styrofoam containers, and all specimens to be preserved were placed in 10 percent formalin.

Habitat

Surveys of habitat and general behavior were conducted by underwater observation. Various details of the habitat and behavior were recorded on movie film for later study. The entire lower river was surveyed with respect to potential habitat and the occurrence of snail darters by diving, seining, and cyanide techniques. Much of this survey was accomplished on a series of canoe trips down the Little Tennessee which included the area from Toqua Creek at river km 35.2 to the mouth as delineated by TVA map 65-MS-453 obtained from the Maps and Services Branch. Thermographic, discharge, and water quality data were obtained indirectly from the Hydrologic Data Branch or Data Service Branch of TVA through their biologists. A study of current velocities was also conducted using a USGS Gurley-type pigmy current meter, and thermographic

data were supplemented by a pocket thermometer.

Population Studies

Population characteristics presented perhaps one of the most challenging problems in the study. The aforementioned difficulties in obtaining substantial numbers of snail darters limited conventional studies on population dynamics to a great extent. However, reasonably effective studies were conducted in gravel shoal areas.

In addition to relative seining results, attempts to quantify local density were accomplished in two ways. During the warmer months (August to October, 1975), a series of sodium cyanide applications were employed covering various habitats in the Tolliver Island-Coytee Spring area. A 16 m small mesh block net was anchored 5 m from either end, and the ends were quietly as possible brought parallel to the current forming three sides of a box. A 5-m seine placed across the upstream opening completed the enclosure. Thus, 25 m^2 were completely closed to fish movement into and out of the area, and all specimens collected against the block net after cyanide application should have represented the per-area density. Sodium cyanide was placed in the water approximately 30 m above the enclosure to insure effectiveness. Specimens were quickly revived after removal from the net by placing them in styrofoam containers filled with fresh water and were retained therein until completion of the survey.

A second method of density estimation was employed by TVA biologists. Some of their findings are incorporated into this study. Swimming transects over various habitat types were conducted by divers below Davis Island, at Morganton Ferry, in the Coytee-Tolliver Island

area, and below Davis Ferry. Transects approximately 5 m in width and 16 m long were covered by four observers. A bar was pushed ahead of the swimmers to dislodge snail darters from their hiding places. However, these observations were conducted a few weeks after the cyanide census and following removal of over 400 specimens by TVA for transplantation. Therefore, they could in no way be directly correlated with the results of the cyanide census, and it was not possible to estimate the efficiency of the transect method in light of the possible absolute densities determined by the cyanide method. An example of raw transect data with a measure of variability appears in Table 1 and seasonal results appear in Table 2.

Some mark and release studies were initiated by both the author and TVA biologists in attempts to achieve population estimates and study movements, but these proved to be of marginal success due to the infeasibility of capturing and releasing large numbers of snail darters in a short time. Pelvic fins were clipped as marks of identification.

Sex and age composition and mortality rates of the population were determined from data taken largely from 273 snail darters collected by TVA biologists in February, 1976, for transplantation to the Hiwassee River. Sex composition was easily determined due to the marked dimorphism of the anal fin. Length-frequency analysis was employed to determine age composition. Specimens captured throughout the 2-year study period were also utilized to supplement this data in certain analyses.

Table 1. Example of TVA *Percina tanasi* Population Study Transect Observation Data (Observations/80 m^2) with a Measure of Variability (SD)

Run No.	Transect Area 1	2	3	4	5	Overall
1	2	3	0	0	2	
2	2	4	0	0	0	
3	2	2	1	1	3	
4	0	0	-	3	3	
5	0	1	-	1	1	
$\bar{X}$	1.20	2.00	.33	1.00	1.80	1.34
SD	1.09	1.58	.57	1.22	1.30	1.26

Table 2. Mean Seasonal Observation Frequencies in TVA *Percina tanasi* Population Transect Studies

Habitat Area	River km	Summer	Winter	Spring
Below Davis Ferry	6	.65	--	1.56
Coytee Spring-Tolliver Island	11	.70	1.06	.63
Morganton Ferry	20	.15	.03	.42
Davis Island	25	.07	.13	.16

Age and Growth

Age and growth studies were facilitated by scale analysis, length-frequency data, and length-weight relationships. All body measurements were based on standard length determined by use of vernier calipers. Scale analysis was accomplished by selecting five scales in succession from the scale row immediately below the lateral line at a point beneath the dorsal fin origin. Scales were removed from the right side of 72 snail darters ranging from 38 mm to 67 mm standard length and mounted between glass slides secured at the ends with mounting cement (Fisher Permount) and tape to prevent slippage. Scales were read by projection at 80X magnification on an Eberbach 2700 scale projector. Scale slides to be photographed were mounted on a Unitron Series N inverted microscope with 35 mm camera attachment. The relationship between scale growth and body growth was determined by linear regression analysis, and application of logarithms to the back-calculated growth curve gave the best illustration of growth rate. Length-frequency data used in the age study were adapted from measurements taken from the TVA transplant material as stated previously. Where necessary, total length measurements employed by TVA biologists were converted to standard length to facilitate comparisons in this study. This was accomplished by multiplication of total length by 0.87, a conversion factor determined from measurement of standard and total lengths of a series of adult snail darters of various lengths.

Data for length-weight studies were collected from 30 snail darters preserved over the course of the study. Eviscerated individuals were weighed to the nearest 0.01 mg on an Ainsworth Type 10N balance after

thorough blotting; the abdominal contents were removed to prevent miscalculations due to varying stomach contents or gonad weights. Regression analysis was again employed in studying length-weight relationships.

Reproduction and Early Development

Studies on reproductive aspects of snail darter life history also proved difficult, although some facets such as spawning season determination were quite easily achieved by examination of a few specimens. Spawning behavior and details of the spawning habitat were studied in the Little Tennessee River by means of underwater observations. These activities were recorded on movie film for later analyses as well as being recorded in field notes. Seining surveys aided in determining the distribution of individuals within the spawning habitat at various times during the season. Details of breeding coloration were taken from photographs of freshly preserved individuals and from notes taken in the field.

Gonadal development and fecundity were determined by dissection data taken from the 72 snail darter specimens preserved during the study. Fecundity was estimated by placing both ovaries from an individual into a gridded counting cell. The ova were scattered over the cell in a single layer and mixed so as to be as heterogenous as possible with respect to size. Four samples were taken by removing and counting all ova from four random grid squares. Ova were segregated and counted as to maturity. Ova 1.5 mm in diameter and dark yellow in color were considered mature. The mean values for each class were multiplied by the total number of grid squares to achieve the estimates.

Early development was studied by means of artificial fertilization. Approximately 90 eggs were stripped from a ripe female snail darter and fertilized in a shallow dish with milt stripped from a nuptial male. All ova were deposited in a small amount of water before fertilization approximately 20 seconds later. Complete fertilization was achieved despite the interlude by bathing the eggs in the concentrated milt solution for about 30 seconds, then placing them in a pint jar of water. They immediately became adhesive to the sides of the jar and were thus transported in a cooler to the laboratory. At the laboratory, they were transferred to two small aquaria containing about 3 cm of clean river water. An airstone was placed at one end of each container for aeration and both were maintained in an incubator at 12.5° C. Eggs and larvae were periodically removed by means of a baster, placed in a watch glass, and examined alive beneath a dissecting scope. Some specimens were periodically removed for preservation in 5 percent formalin. In this way, ova and larvae were maintained and studied for 24 days before the last larva succumbed. Developmental stages and structures were studied with referral to Bolin (1930), Lippson and Moran (1974), and Oppenheimer (1937). *Artemia* and *Daphnia* cultures were initiated to feed the larval snail darters had they survived.

Food and Feeding

Data on dietary habits were gathered both by direct underwater feeding observations and analysis of dissected specimens. Feeding observations were conducted on snail darters as well as associated species to gain insights into possible feeding interrelationships.

A total of 244 fishes from the Little Tennessee River was dissected for this study, including 67 snail darters and 177 specimens of associated species. Excision data for 10 snail darters and 77 associates were obtained from TVA biologists and incorporated into the results summarized in Appendix A. Specimens for dissection were collected periodically throughout the 2-year study and represented all seasons of the year. These specimens were preserved immediately upon capture to minimize loss of gut contents. Prey items were identified with assistance from Burke (1953), Hitchcock (1974), Johannsen (1969), Pennak (1953), Ross (1944), and Ward and Whipple (1959). Gastropod identifications were verified by D. J. Bereza and S. L. H. Fuller of the Philadelphia Academy of Natural Sciences. Hydropsychid caddisfly larvae were verified by G. A. Schuster, The University of Tennessee. All prey items excised were segregated with respect to occurrence in the stomach or intestine to aid in analyzing temporal feeding patterns. Biomass determinations of individual prey items were made by weighing large series of undigested items (blotted) to the nearest 0.01 mg and selecting the mean. Gastropods were weighted with the shell removed.

Several attempts were made to obtain quantitative data on Little Tennessee benthos for use in food availability studies. Surber samplers were experimented with initially, but it became obvious upon examination of sample contents that gastropods, important snail darter prey items, were not being adequately sampled; they were not easily swept into the sampler due to their excessive weight. Another method involved simply handpicking all snails from a given area (0.1 m^2), but this, too, proved not feasible, especially during periods of high flow. Ultimately, TVA

biologists employed a suction dome sampler which attained better results. Seasonal data from this sampler were incorporated into the availability-selectivity analysis included herein which was based principally on methods set forth by Ivlev (1961).

Aquaria

Two types of aquaria were employed during the course of this study, both of which proved successful in maintaining snail darters but neither of which was successful in achieving the principal goal--observations on reproduction. However, some valuable data on feeding and other behavior were obtained.

The first type of aquarium was a 3700 l vinyl backyard wading pool. Natural substrate from the Little Tennessee River was placed on the bottom and a plastic 37 l garbage container weighted with rocks was placed in the center. A submersible pump, the intake covered by screening, was placed in the pool to provide circulation. Thus, a circular raceway complete with recycling current was provided. Kept out of direct sunlight, this arrangement proved quite satisfactory for maintaining snail darters, but they were difficult to observe from above.

A second container was simply a 370 +l aquarium about 2 m in length. Again substrate was provided and a submersible pump placed at one end. The intake hose for the pump was situated at the opposite end of the tank creating a flow cycle. Light was provided by an overhead fluorescent strip light activated by a timer to control photoperiod. Maintained in a basement atmosphere, the water temperature remained nearly constant at 15° C.

Based on personal experience, snail darters were one of the darter species slowest to acclimate to confinement, seriously limiting chances of observing spawning behavior. Once acclimated, however, they became able competitors in the aquarium, quickly outcompeting species such as *P. burtoni*, which fed more delicately.

CHAPTER II

GENERAL CHARACTERISTICS AND BEHAVIOR

Specific characteristics or behavior related to feeding and reproduction are discussed later in appropriate chapters. Aside from these, general characteristics of snail darters may be broadly categorized.

Like most darters, *P. tanasi* demonstrated a principally benthic mode of life. Accordingly, snail darters possess many of the adaptations evolved thus far by bottom-dwelling inhabitants of lotic environments. Pectoral and pelvic fins are located ventrally to facilitate gaining purchase on the substrate and the pectoral fins in particular serve as hydrodynamic adaptations to enable the darter to maintain its position in strong current (Hynes, 1970).

Adult and subadult snail darters were observed to maintain a rheotaxic orientation at all times in areas of strong current. Though the body may have been sometimes oblique or even perpendicular to the current, the head was usually oriented upstream regardless of the activity. They were reluctant to abandon this orientation and usually did so only in the face of overt downstream pursuit. Individuals observed in deeper areas with slower current were considerably less oriented to the direction of flow. When contending with very strong current, snail darters occasionally braced themselves between stones with outstretched pectoral fins or reposed transversely on the upstream face of a stone.

As further adaptation to its habitat, the snail darter has evolved an effective pattern of protective coloration. Like three other

members of its subgenus, *P. tanasi* has a strongly developed set of dorsal saddles (Figure 1) which serve as disruptive coloration camouflaging it against the gravel-sand substrate. Remaining sedentary for long periods of time, snail darters were virtaully invisible against this background. In addition to members of *Imostoma*, similar color patterns have independently evolved in several gravel-associated species such as *Hypentelium nigricans*, several *Cottus* species, and a dozen or so darters of the genus *Etheostoma*, as well as *Ammocrypta asprella*. The coloration advantages possessed by these species are clearly evident in the highly contrasting color realm of the gravel areas, but they further possess the ability to blanch out their strong dorsolateral markings in conformance with more uniformly colored substrate, such as sand, and thus remain nearly invisible. In addition to this colorific behavior, snail darters confined to aquaria often buried themselves beneath the sand substrate with only the eyes remaining visible. This was very likely a demonstration of natural behavior. As an avoidance measure against predation, or simply a respite from the current for energy conservation, this behavior afforded obvious advantages.

There was little dimorphism in color pattern between male and female snail darters. However, intensity varied greatly especially during spawning activities. As with other members of *Imostoma*, there was marked dimorphism in the length of the anal fin, the male's being much longer.

Unlike the more advanced percids of the genus *Etheostoma*, *Percina* generally do not exhibit territoriality, though some may exercise a degree of moving territory maintenance or individual space

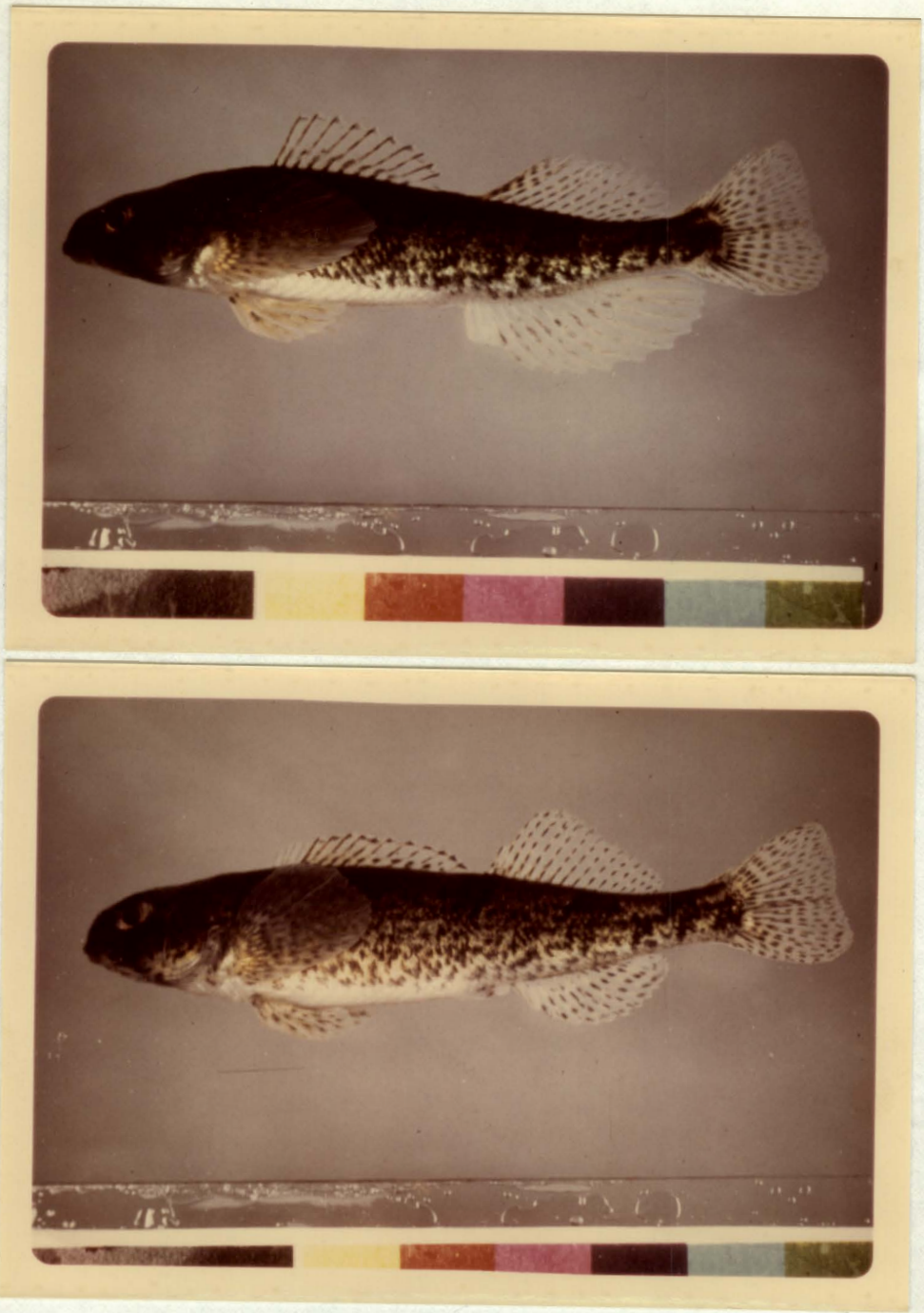


Figure 1. Adult male (top) and female *Percina tanasi* (1.2 x life size). (Color prints are provided in five original copies of this dissertation.)

(Winn, 1958). Accordingly, *P. tanasi* seemed to move randomly about the habitat with no established territories. Low population densities did not permit observations on moving territory maintenance. Aquarium-held specimens were, to the contrary, quite gregarious and were timid in the face of aggression from even smaller darters of the genus *Etheostoma*. Within a period of a few months, a given gravel shoal area may have served as a home range for a particular snail darter individual, but migration patterns indicated that this would not have been true on a long-term basis. Thus, the concepts of territoriality and/or home range generally were not applicable to *P. tanasi*.

Concerning behavioral interactions with other species, it was stated above that snail darters were nonterritorial and unaggressive towards other species while in confinement. On the rare occasions when interspecific encounters were observed in the field, little interaction occurred. Once or twice snail darters followed the other individual briefly, but generally they resumed original activity within a short time. Again, low population densities simply did not permit adequate observations of this nature in the natural habitat.

CHAPTER III

HABITAT

The known macrohabitat of the snail darter is the lower Little Tennessee River system and a small portion of the main Tennessee River. Though the Little Tennessee system is 214 km in length, the known range of the snail darter was found to be the lower 28 km or so of the river and also may extend downstream in the Tennessee River 16 km or more to the vicinity of Loudon, Tennessee, from time to time.

The Little Tennessee is essentially a mountain river throughout much of its length. However, the lower 48 km flows through a wide valley, and the stream is much more pastoral in nature, flowing through farm land and patchy forests. One principal tributary, Tellico River, enters the Little Tennessee just above the upper extremity of the snail darter's habitat, and a number of lesser tributaries enter the 28-km stretch of river below this point (Figure 2). Tributaries apparently do not constitute any portion of the snail darter's habitat. In 1957 the lower Little Tennessee was impounded 53 km above the mouth by Chilhowee Dam near Tallassee, and the entire critical portion of *P. tanasi*'s habitat now falls under the influence of its tailwaters.

Within its macrohabitat, *P. tanasi* prefers the extensive gravel shoal areas. Population densities were highest in the shoal areas where snail darters reproduce and feed extensively. Such shoals exist today in the Davis Ferry area from 6.4 to 9.6 km above the mouth of the Little Tennessee (Figure 2 and Figure 3). Additional shoals occur in the

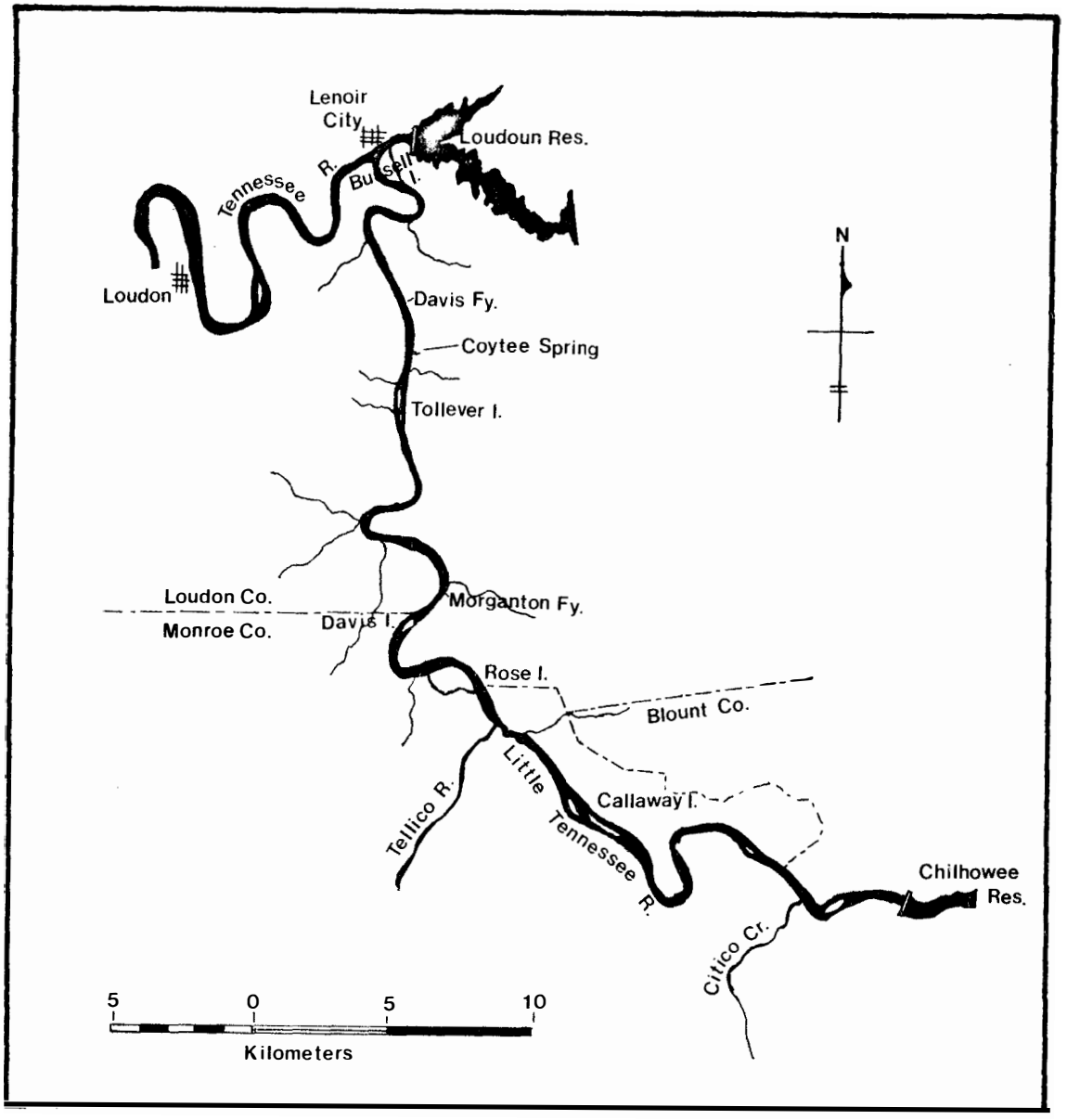


Figure 2. Map of lower Little Tennessee River, Tennessee.

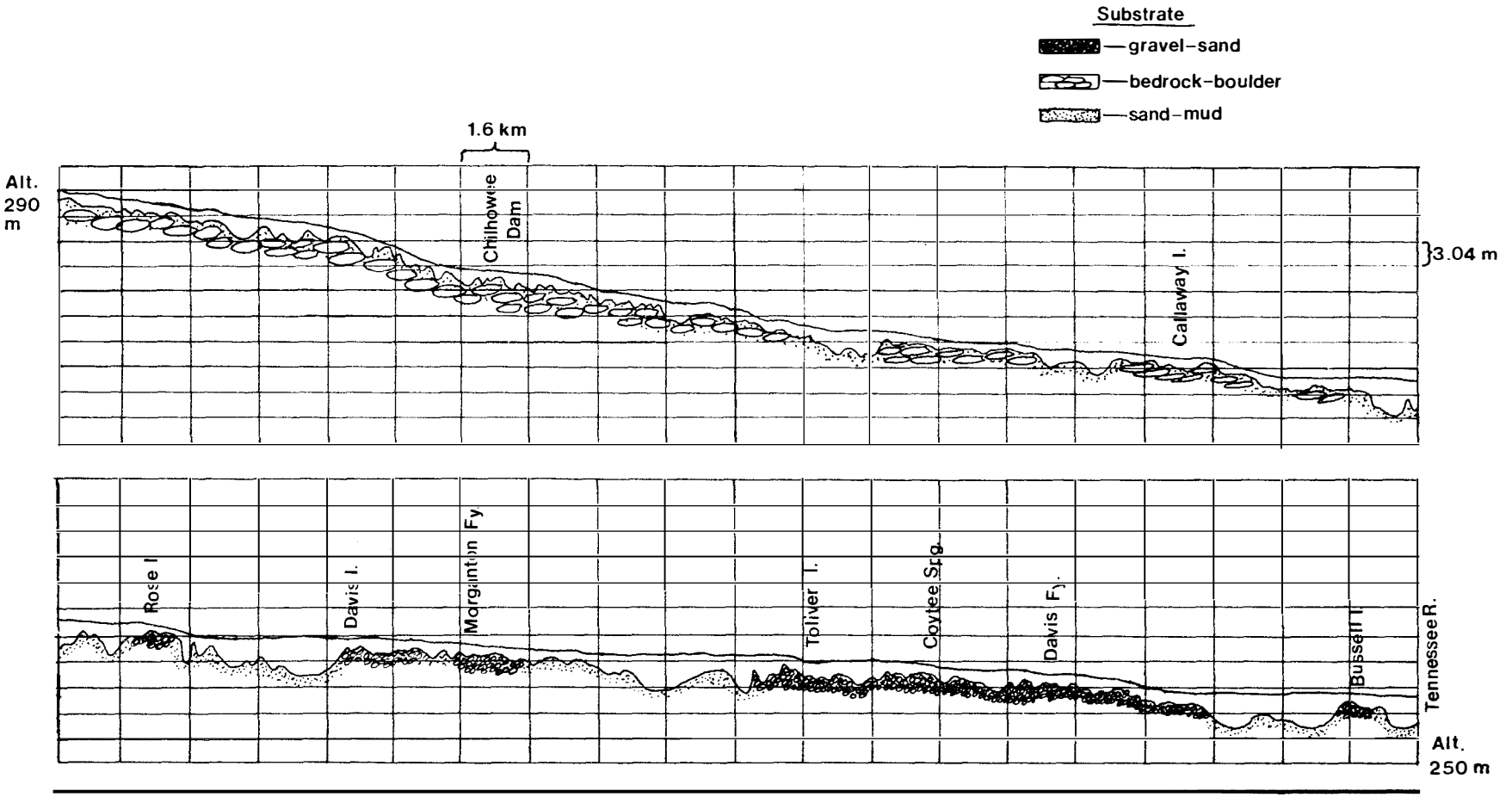


Figure 3. Profile of lower Little Tennessee River showing bottom configuration, predominant substrate types, and principal landmarks (adapted in part from Kingmann, 1900).

Tolliver Island-Coytee Spring area 11.2 to 15.6 km upstream of the mouth; Morganton Ferry, river km 19.6 to 22.4; and Davis Island at river km 25. Marginal habitat exists at Rose Island (river km 27), but observations and cyanide sampling failed to demonstrate the presence of snail darters there. Kingman (1900) indicated that a similar shoal existed near the mouth (Figure 3) on the west side of Bussell Island before alterations resulting from dam construction occurred.

In terms of habitation, deep water areas at first glance appeared to constitute a relatively unimportant and little utilized portion of the macrohabitat. However, as will be discussed under reproduction, these areas may serve as critical refugia for the early development of larval snail darters and were inhabited to some extent by transient adults. Such deep water basins (Figure 3) occur between Bussells Island and Davis Ferry (river km 1.6 to 4.8), below Morganton Ferry (about river km 17.6), and below Davis Island shoals (river km 25 to 28).

Dimensions

The lower portion of the Little Tennessee has an average width in excess of 100 m. It may approach 200 m in areas interspersed with islands.

Depth in the Little Tennessee is highly variable with respect to both the nature of the bed and flow regime. Aside from the relatively small volume of input by tributaries, the flow of the lower river is regulated solely by Chilhowee Dam. In a normal year, flows vary from lows of 135 m^3/sec to near 1,440 m^3/sec during the winter (adapted from TVA data). In times of heavy flooding, discharges may exceed the normal

maximum with a record discharge of over 2,160 m^3/sec recorded in 1973. Normally, discharge was low overnight and high flows resumed during the day at peak generation hours. A 4- to 8-hour lag occurred before discharge increases were realized in the lower river. Thus, flows and depths typically increased every afternoon and were low during the morning.

At low flow, depths in the gravel shoal habitat areas ranged from a few centimeters to 3 m or so. Areas where *P. tanasi* most frequently was encountered ranged from 0.3 to 0.7 m in depth. At normal high flow (540-630 m^3/sec), depths increased by approximately 0.5 m (Table 3). Deeper areas of the river below the shoal areas ranged from 5 to 6 m at low flow. Though steamers negotiated the Little Tennessee as far upstream as Citico Creek in the 1800s, minimum channel depths in shoal areas approached 0.6 m (Kingman, 1900). Further examination of Figure 3 indicated that, at low flow, depths were not substantially altered from preimpoundment days, as the present depth profile remaines essentially the same.

Current Regime

Current ranged from moderate to very strong in shoal areas most frequented by snail darters. It varied directly with discharge from Chilhowee Dam and, thus, usually fluctuated widely on a daily basis. Current velocities at high and low discharge recorded from a transect study spanning the gravel shoal habitat at Coytee Spring are compared in Table 3. Flow rates ranged from 0.38 m/sec at low discharge to 0.98 m/sec at high flow. On the average, flow increased by about

Table 3. Comparison of Depths and Current Velocities Recorded from Transects at Coytee Spring, Little Tennessee River at High (540 cms) and Low (135 cms) Flows (Transformed from TVA Data)

Sta. No.	Depth (m)			Current Velocity (m/sec)		
	High	Low	Diff.	High	Low	Diff.
1	1.32	.75	.57	.98	.34	.64
2	1.32	.81	.51	.48	.38	.10
3	1.11	.75	.36	.85	.45	.40
4	1.11	.69	.42	.93	.45	.48
5	1.29	.66	.63	.76	.44	.32
6	1.20	.66	.53	.80	.54	.26
7	1.20	.69	.50	.91	.46	.45
		Mean Diff.	.50		Mean Diff.	.37

0.40 m/sec at high discharge except in areas which had been physically more restricted at low flow. In deeper portions of the river, current was extremely sluggish and backwaters in these areas had virtually no flow.

Current ranged from a moderate 0.25 m/sec to nearly 0.7 m/sec at low flow in the particular areas most frequented by snail darters. However, flow over the shoal area was somewhat turbulent and current near the substrate was extremely erratic and difficult to measure. It was estimated that the average current velocity was 75 percent less near the substrate interface than in the water column above. Therefore, snail darters were actually contending with velocities of a few centimeters per second most of the time. However, blasts of high velocity current were observed to come in contact with the substrate quite often, and snail darters, though enduring these intrusions most of the time, were occasionally swept downstream after sudden dislodgement.

It appears that current velocity was on the average lower in pre-impoundment days. Kingman (1900) reported current velocities not exceeding 0.63 m/sec in the Coytee Spring area. This closely approximates measurements taken in this study at low discharge, but, if Kingman was accurate, velocities at high discharge may now have increased the average flow rate by approximately 30 percent as a result of the tailwater influence.

Temperature Regime

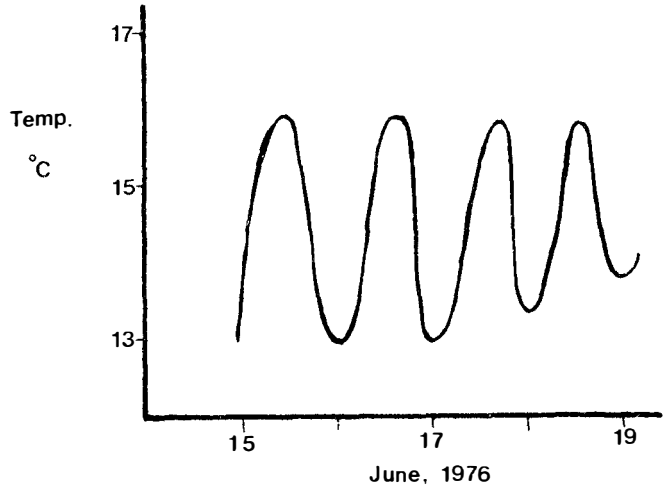
Temperatures varied widely on a daily basis in the lower Little Tennessee River but were confined to a narrow overall range annually.

Temperatures varied indirectly with flow, dropping considerably when cold waters were discharged from Chilhowee Reservoir and other impoundments above and warming somewhat as flow diminished. Figure 4 dramatically illustrates the daily rhythmic cycling of temperature fluctuations. Cycles are most pronounced in the summer with daily fluctuations of 3° C not uncommon. In winter, fluctuations are typically less than 1° C to 2° C but may occasionally change drastically with flow conditions.

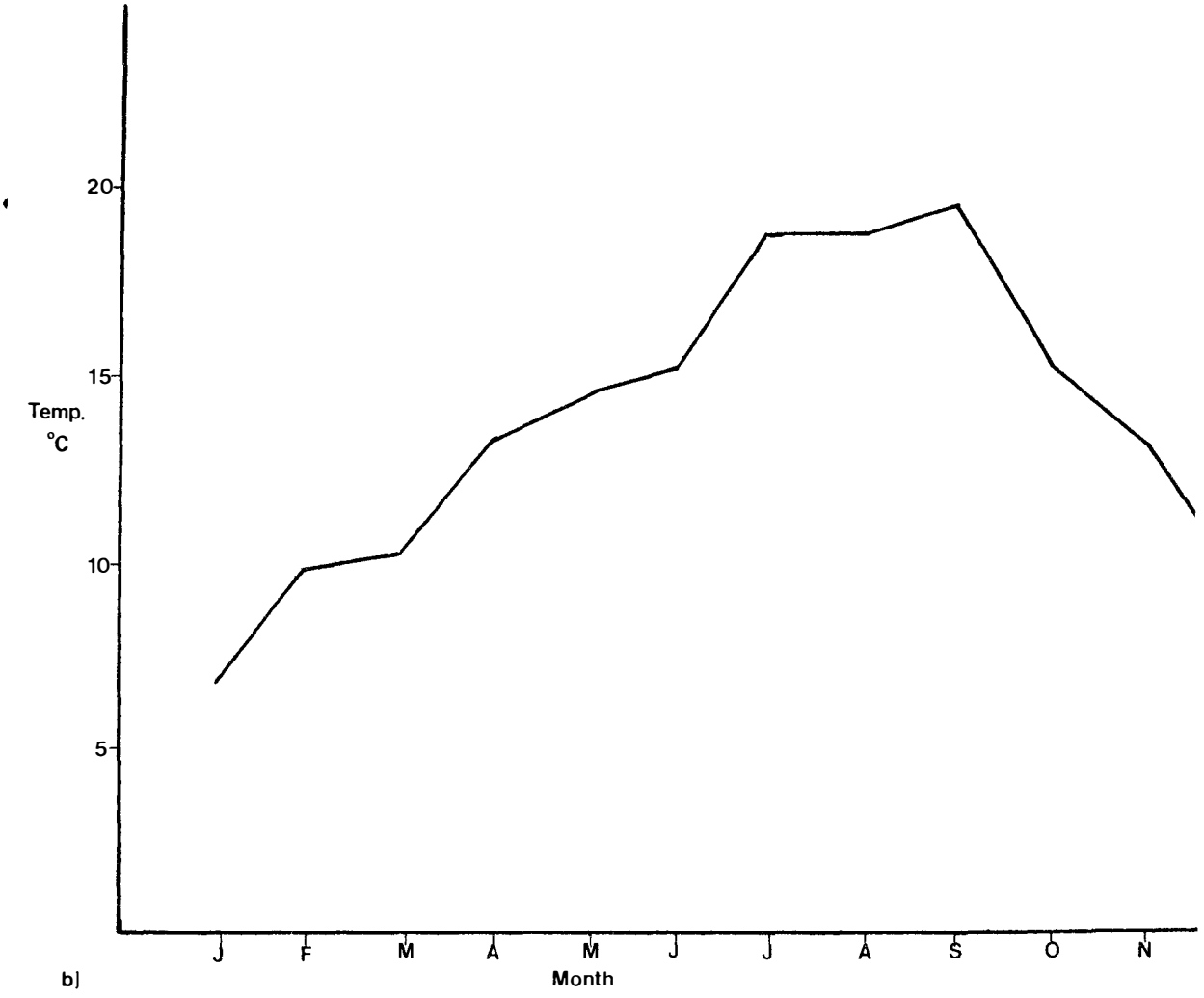
Winter temperatures ranged from 5° to 12° C in 1976, and upstream reservoirs probably buffered temperatures against decreasing below these levels. Summer temperatures averaged near 18° C, and highest recorded temperatures were in early fall (20° C). Monthly average temperatures are graphically represented in Figure 4, part b.

Therefore, while temperature extremes have been curtailed, impoundment of the lower Little Tennessee almost certainly has lowered the average annual water temperature. Pfitzer (1954) documented the virtual absence of trout at a point 12.8 km below Calderwood Dam now inundated by Chilhowee Reservoir. Warmwater species predominated indicating that temperatures prior to impoundment of Chilhowee must have averaged considerably higher in the lower river at that time. Populations of warmwater fish species were observed to be sparse in the lower river in this study.

Comparison of Chilhowee tailrace temperatures with thermographic data from the Coytee Spring area indicates that there is minimal warming of water at high flow between these points. Thus, the upper limit of snail darter habitat is thought to be determined by other factors.



a)



b)

Figure 4. Temperature regime of lower Little Tennessee River showing: (a) example of daily vacillations, (b) monthly average temperature, 1975.

Water Quality

Water quality in the lower Little Tennessee River could generally be considered excellent. Heavy forestation in the mountainous headwaters must reduce silt-laden runoff substantially, and upstream reservoirs serve as settling basins for suspended solids. The system is virtually free of industrial pollution.

Turbidity was virtually nonexistent as measured at the Chilhowee tailrace, for instance never exceeding 10 JTU in 1974 (TVA data). However, local input from Tellico River and lesser tributaries added considerably to turbidity in the lower river, and it occasionally became quite turbid for short periods following heavy rainfall.

The Little Tennessee may presently be an overall less turbid stream than in preimpoundment days. Kingman (1900) described the tremendous timber removal operations in effect in the late 1800s, and these, coupled with primitive farming practices, probably increased siltation and turbidity considerably. In recent months, however, turbidity and siltation have increased noticeably in the lower river probably as a result of bank clearing prior to impoundment.

Other parameters further describe the water quality of the Little Tennessee. The river was well oxygenated, with D.O. ranging from 5.5 to 10.7 mg/l in 1974 at the Chilhowee tailrace (TVA data). Water is generally soft (total hardness $CACO_3$, 7-23 mg/l) and mildly acidic (pH 6.0 to 6.7).

Substrate

The substrate of the Little Tennessee River is characterized by bedrock-boulder, boulder-cobble, sand-gravel, sand, and silty sand. The

shoal habitat most utilized by the snail darter is generally composed of dark micaceous sand, swept reasonably free of silt, and contains scattered gravel 3 to 10 cm in diameter which covers 25 to 50 percent of the area. Stones are not often contiguous and are usually well impacted. The gravel is usually light brown in color contrasting with the dark sand. Another conspicuous substrate component which has become increasingly dominant in recent years is the Asiatic clam, *Corbicula mannilensis*, which often occurs in densities exceeding 500/m^2. An expanse of such shoal is illustrated in Figure 5.

Peripheral shoal habitats utilized to a much lesser degree by *P. tanasi* are generally composed of either gravel blackened by manganese or more coarse cobble substrates covered with *Podostemum* and filamentous algae. Both habitats apparently are largely avoided by snail darters. The deepest portions of shoal areas often have bedrock substrates. Several aquatic plant genera are generally common along the margins of shoal areas in quiet water, including *Ceratophyllum*, *Potamogeton*, and *Vallisneria*, but these are not closely associated with snail darter habitat.

Deeper portions of the Little Tennessee generally have sand or silty sand substrates as well as considerable bedrock exposure. Localized detritus deposits often accumulate to considerable depths in these slack water areas. Such substrates may characterize the habitat of larval and early juvenile stages of *P. tanasi*.

As stated earlier, the particular gravel-sand shoal habitat preferred by the snail darter extends only to about Rose Island at river km 28. Kingman (1900) described all substrate upstream of this point as



Figure 5. Expanse of gravel shoal habitat at Coytee Spring, Little Tennessee River (low flow).

"rocky or rock ledge," and this was quite evident in examination of the present tailwater. The upstream curtailment of preferred substrate may be the chief limiting factor in snail darter distribution.

Associated Fish Species

Closest associates of *P. tanasi* were those fish species which frequent the gravel shoal habitat. Two additional species of *Percina* frequent the shoals, *P. caprodes* and *P. evides* and were perhaps *tanasi*'s closest associates, although *P. shumardi* also occurred occasionally. Two sculpins, *Cottus bairdi* and *C. carolinae* inhabited the shoals, but *C. bairdi* occurred mostly upstream of the snail darter's habitat. *Hybopsis aestivalis*, *Nocomis micropogon*, and *Phenacobius uranops* were cyprinid species sometimes encountered as was the catostomid *Hypentelium nigricans*. In peripheral habitats, *Etheostoma blenniodes* and *E. rufilineatum* occurred in rocky areas, and *E. simotenum* inhabited the quieter margins of the river along with a few cyprinid species. Potential predatory species were *Salmo trutta*, *Morone chrysops*, *Stizostedion canadense*, *S. vitreum*, and possibly species of *Micropterus*.

A complete list of fish species known to occur in the Little Tennessee system, some of which may occasionally associate with *P. tanasi*, has recently been compiled by Winfield (1976). Various relationships or potential relationships between the snail darter and associated species will be discussed later under appropriate headings.

CHAPTER IV

POPULATION CHARACTERISTICS

Distribution

As discussed previously, the present overall habitat of the snail darter extends roughly from the confluence of the Tennessee and Little Tennessee rivers upstream in the Little Tennessee to the area of Davis Island 24 km above the mouth. Possible marginal habitat exists on the north side of Rose Island 28 km above the mouth and may represent the upstream extent of the range, but this was not demonstrated by seining or cyanide applications. Snail darters were found to be distributed throughout this habitat from Davis Island downstream in the Little Tennessee to the Tennessee, and a few specimens were recorded from the Tennessee River (Watts Bar Reservoir) as far downstream as Loudon, 16 km below the confluence of the two rivers. The downstream drift phenomenon evident in young snail darters was probably responsible for the occurrence of the Watts Bar specimens, and populations there were most likely marginal and dependent on Little Tennessee populations for recruitment. Abundance varied greatly within the macrohabitat just described, dependent upon microhabitat and season.

Density-Dispersion

The density and dispersion parameters were inseparable in an analysis of snail darter populations, being highly interdependent. Density varied greatly with respect to microhabitat and season. Maximum density is apparently reached on the gravel shoals in the Coytee Spring-

Tolliver Island area, and greatest seasonal density probably occurs during the spawning season, February to April. Water temperatures prevented cyanide sampling during the spawning season, but in excess of 400 snail darters were seined for transplantation by TVA biologists with comparative ease during this period in 1976. *P. tanasi* was observable more concentrated on the shallower shoal areas at this time than in late summer, 1975, when they averaged 6.6 ind/100 m^2 in the approximate same areas as determined by cyanide census. Density may have approached an overall 10 ind/100 m^2 at this time with localized spawning aggregations creating patches of much higher density. TVA transect observations (Table 2, page 10) indicated that snail darters were 1.68 times more abundant in the Coytee Spring area during the winter spawning season than in the following spring. This may have been attributable in part to the removal of 100 to 200 individuals for transplantation in the intervening period, but the magnitude of the decrease suggested natural movements were responsible for a substantial portion. It is speculated that densities at Coytee-Tolliver returned to normal levels (6 to 7 ind/100 m^2) in spring as many individuals left the spawning shoals to return to deeper shoal areas. Densities in the shallow areas of Coytee-Tolliver were lowest in summer but nearly approximated spring levels (Table 2, page 10).

Gravel shoal areas having possibly overall less dense populations exist below Davis Ferry 7 km to 8 km above the mouth of the Little Tennessee. However, TVA transect data indicated that density was considerably higher in this deeper shoal area in spring than at Coytee Springs. This shoal area was too deep for observations during winter.

Density decreased dramatically in upstream habitat areas (Table 2, page 10). Shoals at Morganton Ferry (river km 22) and Davis Island (river km 24) yielded no specimens to cyanide applications in September, 1975. However, TVA transect observations indicated that low density population (possibly 1 ind/100 m^2 or less) existed at Davis Island the following winter, while deeper shoals at Morganton averaged even less. However, in spring density increased at Morganton, possibly indicating some downstream migration from Davis Island. Summer levels at both shoals were low possibly averaging less than 1.0 ind/100 m^2.

No data were available for snail darter population densities in deeper areas of the Little Tennessee River, although it was observably much lower than in shoal areas. At this writing a tremendous concentration of snail darters exists in the deep water below the Tellico Dam site at 9 m to 10 m depths. This, however, is regarded as an artificial assemblage of individuals created by the obstruction of upstream migration.

With regard to dispersion, the distribution or relative densities of *P. tanasi* within the gravel shoal areas was clumped, being highly correlated to the distribution of the preferred substrate type. In areas of sand-gravel substrate, density averaged 8 ind/100^2 during the cyanide census. However, deeper areas having more coarse substrate averaged only about 4 ind/100 m^2, while cobble or bedrock portions yielded almost no snail darters in sampling. Within the preferred habitat areas, snail darters appeared to be rather randomly dispersed throughout most of the year. In winter, however, spawning activities played an important role in dispersion with males first aggregating at

relatively high densities in the shallower, swifter areas. Based on seining observations, density may approach 40 ind/100 m^2 in these highly localized spawning aggregations, as occasionally up to three individuals were taken in a single 4-m seine haul. Spawning females apparently distributed in somewhat slower and slightly deeper portions of the shoals as discussed under spawning behavior.

Despite the apparent low density of fishes in the Little Tennessee River, figures reported for *P. tanasi* compared favorably with those in the literature for other *Percina* in less altered habitats. Page and Smith (1970, 1971) reported extrapolated population densities of about 4 ind/100 m^2 and 2.5 ind/100 m^2 for *P. sciera* and *P. phoxocephala*, respectively. Regarding *Imostoma*, however, population densities of *P. ouachitae* have been observed to be exceedingly high on numerous occasions in unaltered habitat situations, and the same was true of *P. shumardi*. It is felt that the innate tendencies of *Imostoma* populations might be towards high densities where habitat permits, and it seems equally probable that the expansive habitat in the Little Tennessee, and probably the upper Tennessee River, once supported much higher population densities of *P. tanasi* than in their present altered state.

Migration

Movements of individual snail darters have been previously discussed under general behavior. On a collective basis, there were strong indications of migratory trends in snail darter populations, especially in young-of-the-year. There is evidence that larval drift may be a

highly significant event in the life history of the snail darter. This theory was substantiated by the apparent absence of larval or very young snail darters in the gravel shoal spawning areas in the months following reproduction. It appears that *P. tanasi* larvae may drift for considerable distances. After closure of the channel on the east side of Bussell Island near the mouth of the Little Tennessee by the Tellico Project in 1976, large concentrations of young-of-the-year snail darters occurred in the deep, current-swept channel below the dam. Further, first year darters were essentially absent from the shoal areas upstream of the dam after its closure. Apparently, larvae were drifting downstream into the deeper, calmer waters of the lower Little Tennessee and, to some extent, the Tennessee River for early development. Their subsequent upstream migration was being obstructed by the dam. In previous years, when natural migration could occur, young snail darters began appearing in the shoal areas in June at the age of 3 to 4 months and, by August, were relatively abundant. Thus, upstream migration of several kilometers may occur as a natural event following early development of *P. tanasi*.

While Age Class 0 fishes were evidently migrating, it appeared that Age Class I snail darters remained in residence at or near the principal population centers on the gravel shoals. Several second year *P. tanasi* were still present in TVA collections subsequent to closure of the dam.

Lake (1936), Winn (1953, 1958), and Page and Smith (1970, 1971) discussed migratory movements associated with spawning in darters. Of these, the longest noted was about 2 km in *P. copelandi* (Winn, 1953).

Density changes associated with spawning season in *P. tanasi* have already been discussed and were highly indicative of some reproductive migration. Comparative densities between populations on shallow and deep shoals on a seasonal basis may give some insight to migration. Based on transect observations (Table 2, page 10) and seining data, the deeper shoal areas below Davis Ferry and at Morganton Ferry were considerably less populated in winter than in spring while the reverse was true on shallower shoals above these sites (Coytee Spring and Davis Island), indicating that migration may have occurred in response to reproduction. Migration to a lesser degree probably occurred in snail darters already inhabiting the marginal areas of the shoals as they moved to the swift, shallow portions to join spawning aggregations.

Winn (1958) in a study of 14 species of darters noted some evidence that males migrated shortly before females. There was strong evidence that this was also true of snail darters as substantiated by examination of sex composition in samples totaling 273 individuals collected during the spawning season for transportation (Figure 6, part a). Though females comprised only 3 percent of snail darters seined from shallow shoals early in the spawning season, they quickly increased in numbers as the season progressed comprising 43 percent on February 10 and 62 percent on February 17. There was also some indication that larger individuals (Age Class II) may have moved to the spawning shoals relatively early as they attained highest percentages of catch early in the sampling period (Figure 6, part b). This may have been because they were already in residence on or near the Coytee Spring shoal and did not have to migrate as far as younger individuals.

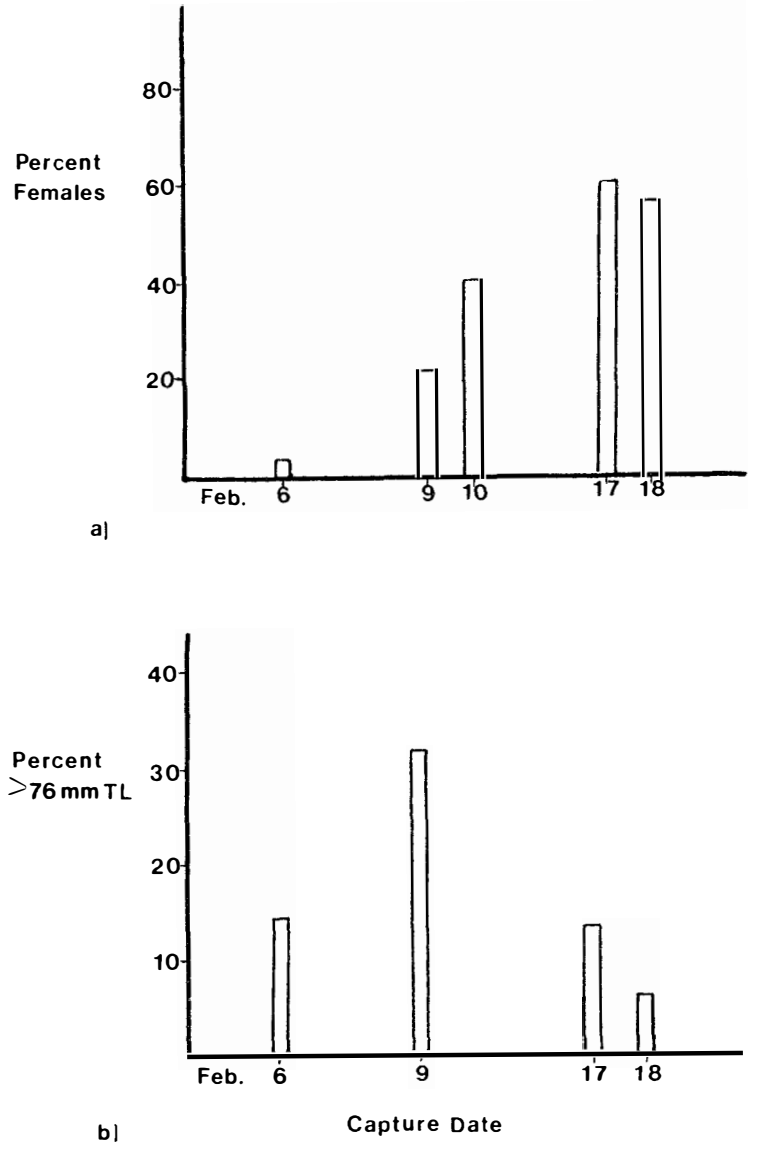


Figure 6. Catch composition of 273 *Percina tanasi* on successive capture dates with respect to (a) sex and (b) size (age).

The reciprocal seasonal movement patterns between shallow and deeper water exhibited by *P. tanasi* were noted in the studies of Page and Smith (1970, 1971) on *P. sciera* and *P. phoxocephala*, respectively, and Howell (1971) found similar movements in *P. aurantiaca*.

Sex Composition

Page and Smith (1970) assumed a sex ratio of 1:1 for *P. sciera* based on collections of 291 specimens from a 2-year period. Lake (1936) concluded without a doubt that female *Etheostoma flabellare* outnumbered males 2 to 1 based on three large collections from a single locality. However, Page and Smith (1971) stated that 1.5:1 was probably not the true sex ratio for *P. phoxocephala*, though this ratio was indicated by a sample of 238 collected over a 3-year period; he felt the sample insufficient and inconclusive. A knowledge of the biology of the species involved is essential to accurate interpretation of data.

The single largest collection of snail darters available for analysis, 273 collected February, 1976, has a sex ratio of 1.81 males to 1 female (Figure 7). The sex ratio of this collection, conducted mainly by seining on shallow shoals early in the spawning season, was probably highly influenced by the distribution of sexes at a time when females characteristically lie in somewhat deeper portions of the shoals and probably was no true indication of the population's sex composition.

The sex ratio of snail darters captured throughout the 2-year study period (Appendix A, Table 7) considered collectively was 1.1:1



Figure 7. Age composition (based on total length) and sex composition of 273 *Percina tanasi* collected February, 1976 (females in black).

and probably better represents the true sex ratio than data influenced by reproductive activities. Page (1974) concluded that the high ratio of female to male *Etheostoma squamiceps* may have been the result of selection against high numbers of males since only a few participated in reproduction. The same appears true in other members of the subgenus *Catonotus* and may be true in other advanced nest-building darters of the genus *Etheostoma*. There would be no such apparent advantage, however, in having fewer males in a population of relatively random spawners, such as *P. tanasi*, and a near 1:1 sex ratio seems a most valid assumption.

Age Composition

Darter populations which have been discussed in other papers typically were skewed towards younger individuals. *Percina* studies indicated that young-of-the-year darters comprised 49 percent to 85 percent of populations sampled (Page and Smith, 1970, 1971; Thomas, 1970). All studies were conducted in relatively unaltered rivers, and, in the face of natural mortality, such distributions of age classes indicated healthy reproducing populations. Based on length-frequency data (Figure 7), Age Class I snail darters comprised 83 percent of 273 individuals collected in February, 1976 (all snail darters less than 77 mm total length were considered as Age Class I since that length represented the trough minimum of the bimodal distribution, Figure 8). The remaining 19 percent comprised Age Class II. There was, however, likelihood of error in this estimation as doubtless (based on scale analysis) some Age Class II individuals failed to exceed 76 mm total length and, thus, were included in Age Class I. This may have been

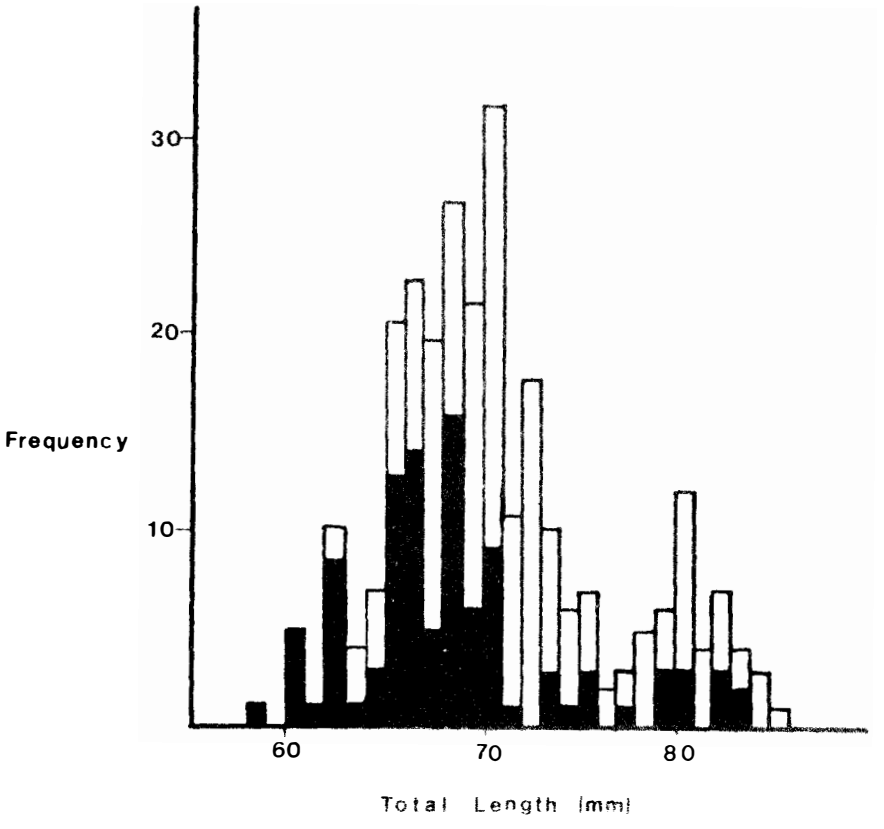


Figure 8. Length-frequency distribution of 273 *Pereina tanasi* captured February, 1976 (females in black).

especially true of females considering their slower growth rate (Chapter V). Analysis of age composition on various capture dates as discussed under migration (Figure 6, part b, page 40) indicated that Age Class II individuals were probably adequately sampled with regard to varying densities through the sample period. Therefore, with length-frequency interpretation being the sole source of error, it appears that Age Class II may have comprised a slightly higher percentage of the population than indicated by this analysis but probably less than 25 percent.

Mortality

Based on analysis of Figure 7, it is clear that mortality was quite high for snail darters during the second year of life. There was an overall 80 percent decrease in numbers of individuals between year classes I and II. However, since Age Class II may have comprised up to 25 percent of the population as just discussed, it is probable that the actual survival rate was between 20 and 25 percent. This compared closely to that of *Percina* studied in less altered habitats (20 percent in *P. sciera*, Page and Smith, 1970).

The mortality rate of *P. tanasi* less than 1 year of age could not be estimated due to the lack of quanitative data for juveniles or overall population fertility. Studies of large samples of *P. sciera* (Page and Smith, 1970) revealed a probable mortality rate of 83 percent in young-of-the-year, and it is conceivable that the vagaries of extensive larval drift and prolonged early development might have dictated an even higher figure for *P. tanasi*.

The sex composition of Age Class I and II (Figure 7) may indicate relatively higher mortality in female snail darters as they comprised 37 percent and 26 percent of these classes, respectively. However, it is again stressed that these low percentages may be an artifact of collection technique and time. As shown in Figure 6, part a, page 40, females were increasingly abundant in samples as the collecting progressed into the spawning season, and a more balanced sex ratio may have been attained if sampling data were available for subsequent collections. It is conceivable, however, that gravid, less mobile females may be more vulnerable to whatever predation pressure is present, though the protective coloration and secretive habits of snail darters probably nearly offset this threat. Aside from this, complications associated with reproduction, such as being "eggbound," may have caused some higher mortality in females.

CHAPTER V

AGE AND GROWTH

Aging

Difficulties in scale analysis of *P. tanasi* were alluded to in Chapter I, page 5. Carlander (1974) discussed problems which arose in interpreting scales which had nebulous, nonexistent, or false annuli. Failure to form annuli generally resulted from a total lack of growth due to crowding (Bucholz and Carlander, 1963) or other circumstances which brought about starvation. Temperature uniformity had similar effects in the tropics (Fagade, 1974), making age determination difficult or impossible in these climates. A substantial number of snail darter scales had little indication of annulus formation either being indiscreet, nebulous, or nonexistent (Figure 9). Overcrowding or starvation certainly did not appear to be the case in the Little Tennessee, but temperature uniformity on an annual basis may well have been applicable. Though fluctuating widely on a daily basis, temperatures ranged over but about 15 degrees annually (5° C to 20° C) constituting perhaps an analogous situation to the tropics though at the other extreme. Seasonal diet analysis indicated that food intake and perhaps growth were not closely linked to water temperatures, further clouding the question.

Apparent false annuli were evident in some snail darters, especially those collected in August, 1973 (Figure 10). Linfield (1974) attributed false annuli or checks to periodic sudden increases in growth

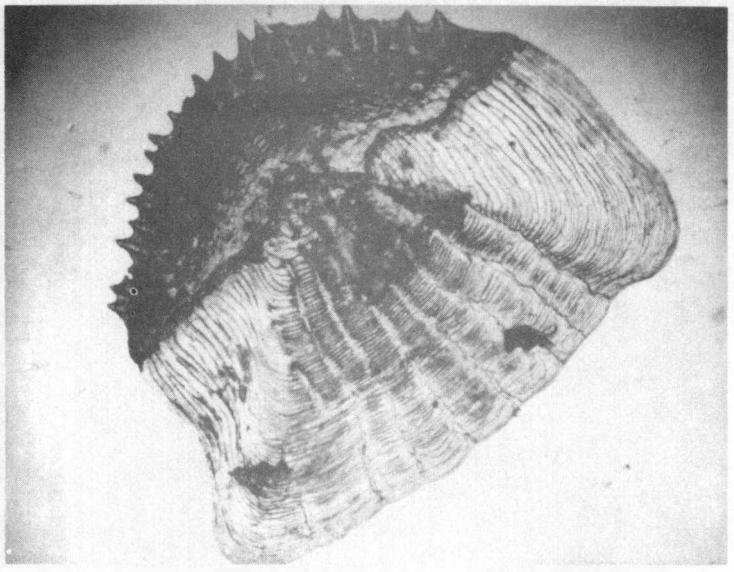


Figure 9. Scale removed from 64 mm SL female *Percina tanasi* captured February 6, 1976, showing little or no annulus formation (50 x mag).

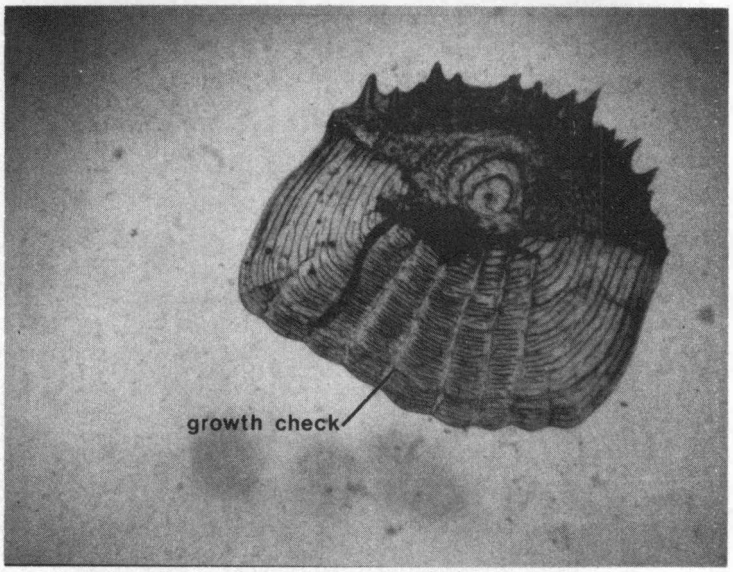


Figure 10. Scale removed from 44 mm SL juvenile *Percina tanasi* captured August 16, 1973, showing growth check (62.5 x mag).

rate. Carlander (1974) suggested that changes in food habits as well as spawning can cause false annulus formation. Possible reasons for such checks in snail darters will be discussed later.

After much study of scale formations, collections from different seasons, and length-frequency relationships, it was possible to finally discern the probable annulus pattern and life cycle of *P. tanasi*. After initially being misled by probable false annuli, it became apparent after sufficient material was procured that the majority of snail darter scales examined (Appendix A, Table 7) had formed an annulus at an average of 37.4 mm (at 80X magnification) from the focus on the anterior field, and a second at 52.0 mm in sufficiently large specimens (Figure 11). This situation was clearly evident in at least one and occasionally all scales removed from each of the 53 largest specimens. The remaining 19 specimens were subadults, having no annulus, or a false annulus (1973) at 29-33 mm from the focus. Inspection of scales from specimens collected in various months of the year correlated with annulus deposition indicated that deposition probably occurred in the late summer or early fall. Several specimens indicated an August annulus deposition. This is unusual and perhaps unprecedented in fish age and growth studies. The classical concept of annulus deposition has been one corresponding with increased growth in spring following water temperature increases or spawning activities. However, Karpinska-Walus (1961) found substantial checks in fall due to sudden growth surges in *Rutilus rutilus*, though a typical annulus had also been deposited in spring. An analogous situation may have existed in the snail darter with the spring deposition lacking. It is probable that first annulus deposition occurs in the

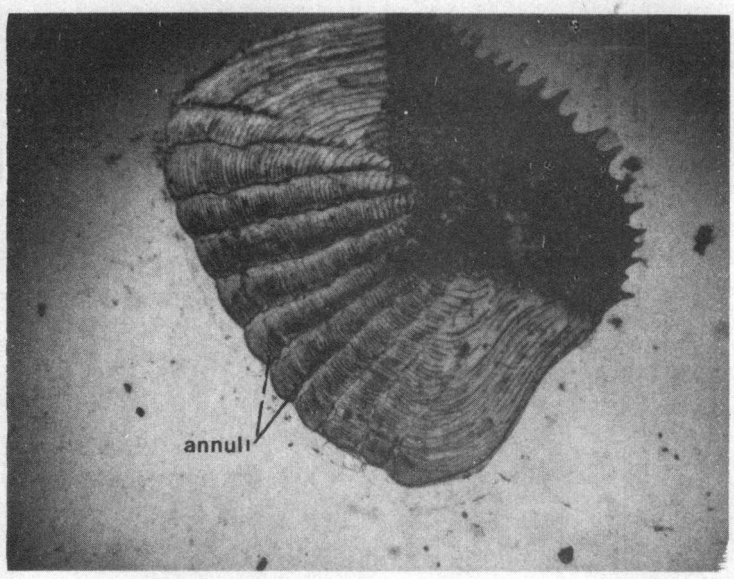


Figure 11. Scale removed from 61 mm SL male *Percina tanasi* captured November 6, 1973, showing good annulus formulation (50 x mag).

first fall of life at the age of 5 to 7 months, and it follows that deposition of the second annulus would occur at the age of 17 to 19 months the next fall. Snail darters apparently succumb following their second spawning season at the age of 24-plus months. No snail darters could be substantiated with certainty to be over 2 years old based on scale analysis; length-frequency data fully corroborated this finding, having only a bimodal distribution (Figure 8, page 44). A short life span may characterize the subgenus, *Imostoma*, as Thomas (1970) reported only a 2-year life span for *P. shumardi* compared to 4 years in other *Percina* species studied.

With the pattern of annulus deposition apparent, it was then possible to analyze reasons for growth checks or false annuli. The most conspicuous checks were those found in the August, 1973, specimens mentioned earlier. A logical explanation for their occurrence might have been temporary growth reduction due to some environmental perturbation. Examination of 1973 precipitation records (TVA, 1973a) revealed that abnormally high rainfall occurred in the Little Tennessee watershed in late May to early June (11.4 cm). For this or other reasons, all dams on the Little Tennessee system were gated, resulting in record high discharges (TVA, 1973b). Chilhowee Dam had a record high discharge over a 5-day period averaging over 2,100 m^3/sec and unusually high flows occurred throughout most of June. This corresponded almost directly with the check found on scales from the August specimens and checks found on older specimens collected in 1974. It seems plausible that cessation or reduction of feeding may occur during times of extreme flooding due possibly to displacement, high turbidity, or unusual temperature changes.

A second reason for the occurrence of the false annuli might have been the change in diet from insects to one predominately of snails, causing either a growth check or spurt, but this would seemingly have been present in every year class. The highly coincidental occurrence of the 1973 growth check and period of flooding makes it the most plausible explanation.

Growth

Regression analysis of the standard length-scale radius relationship for adult and subadult snail darters combined yielded a regression line described by L = .91R + 10.1 (L = standard length; R = anterior scale radius in mm at 80X) (Figure 12). Based on this relationship, back calculation of standard lengths at annulus deposition resulted in an average SL of 45.6 mm (SD = 2.45) at annulus I and 57.3 mm (SD = 2.64) at annulus II (Appendix A, Table 7). However, examination of empirical data revealed that observed standard lengths exceeded back calculated lengths throughout the size range (Figure 13). Further, no annuli appeared on snail darters less than 48 mm SL.

This discrepancy in back calculation has been a common occurrence in age and growth studies and is termed "Rosa Lee's phenomenon" (Royce, 1972). It has usually been explained by allometric growth of hard parts, in deference to the basic assumption of the regression analysis, which assumes isometric growth of scales with body length. Accordingly, the standard length-scale radius relationship for adult snail darters considered alone yielded a quite different regression line (L = .72R + 20.1) (Figure 11) from that of all ages combined, and it was apparent that

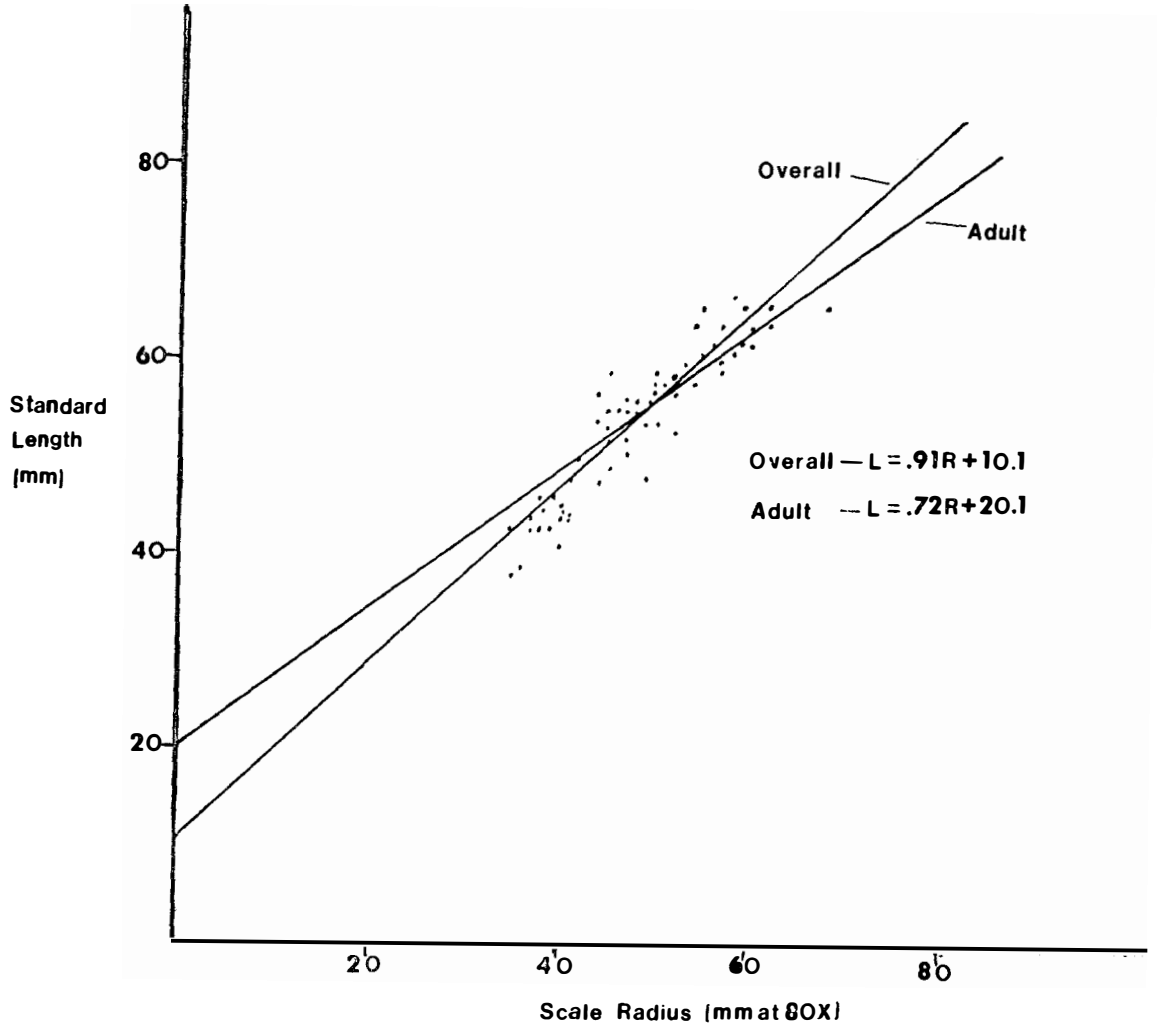


Figure 12. Linear regression lines for standard length-scale radius relationship for adults (> 48 mm SL) and overall subadults and adults combined of *Percina tanasi*.

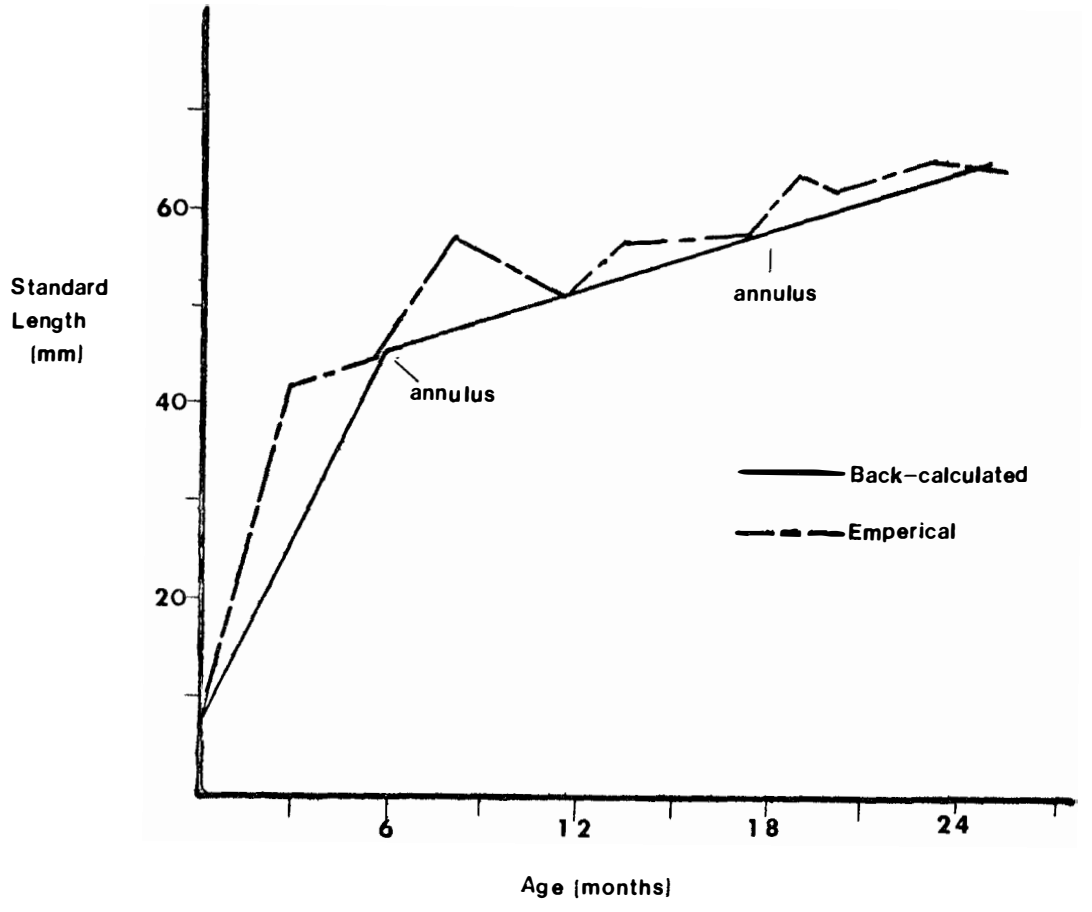


Figure 13. Back-calculated growth and empirical growth (based on mean standard length of monthly age class samples) for *Percina tanasi*.

scale growth increased in older fishes with respect to body growth, thus, being allometric. Back calculations using the adult regression line gave values of 47.0 mm and 57.5 mm, respectively, for standard length at annulus I and II, and it was clear from examination of empirical data that the adult line more closely approximated the true body length-scale radius relationship for purposes of back calculation than the conventional overall regression line for both subadult and adult snail darters employed in constructing Table 7 in Appendix A.

Based on the calculated standard length of snail darters at fall annulus deposition, it was possible to construct a picture of growth and growth rate throughout the darter's life (Figures 13 and 14). *P. tanasi* apparently grows rapidly during the first spring and summer of life, attaining a standard length of 45 to 50 mm by early fall. Age Class 0 specimens obtained during summer months typically ranged from 38 mm SL (June) to 46 mm SL (August). Though impossible to discern from empirical data, a possible sudden increase in growth may have occurred in early fall corresponding to the diet increases to increase in growth causing annulus deposition may be noted in Chapter VII. A more plausible explanation for deposition, however, may be a sudden decrease in growth with the onset of gonadal development in the late summer. Annuli were generally more discreet on scales from female specimens, possibly reflecting a more drastic reduction in growth related to relatively greater demands of ovarian production. A relatively wide distance between circuli just preceding annulus deposition in many specimens may have indicated that the fall feeding level increases preceded the reproductive metabolic demands in some instances.

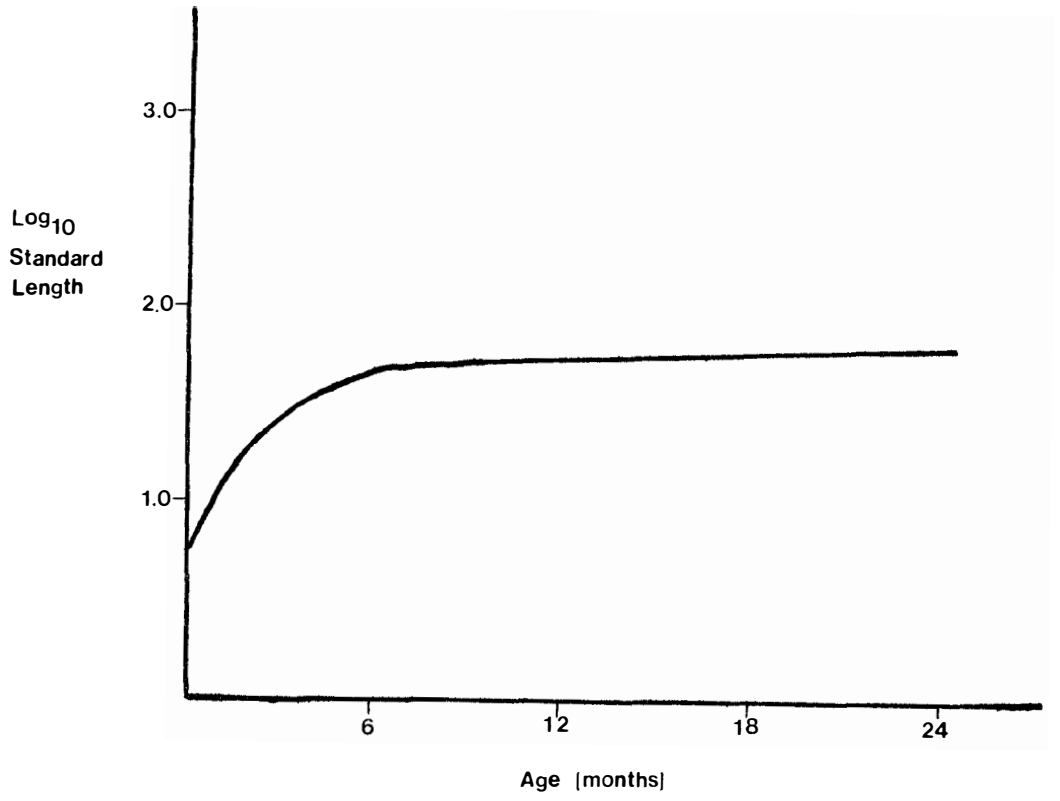


Figure 14. Growth rate of *Percina tanasi* based on Log_{10} of back-calculated standard lengths in growth curve (Figure 13).

Length-frequency data indicated that snail darters generally attained a standard length of about 52 mm to 66 mm at Age I (February to April) (adapted from total length data in Figure 8, page 44). The growth rate was decidely less the 2nd year of life (Figures 13 and 14) with a standard length of 60 to 70 mm at second annulus deposition in the fall and a maximum 67 to 74 mm at Age II the second winter-spring. Wide ranges in lengths appeared to be due to sexual differences in growth rate as well as age differences as will be discussed later.

The standard length/total length proportion in the snail darter is about 0.87; therefore, the maximum total length is probably in excess of 85 mm. The largest known specimen is 85 mm TL.

The apparent differences in growth rate of adult and subadult snail darters have already been discussed. It is also apparent that there were substantial differences in growth rates between sexes. Separate back-calculated growth curves (Figure 15) for each sex indicated that female growth was less than that of males during the first year, averaging 2 mm shorter at annulus deposition, and was equal to or very slightly exceeded male growth the second year. Length-frequency data substantiated this finding with females having a modal SL of 59 mm compared to 61 mm for 1-year-old males. Age Class II individuals exhibited a mode of 70 mm SL for both sexes. Thomas (1970) graphed a very similar relationship for *P. shumardi*.

As discussed with regard to annulus deposition, differences in growth rate may be due to the greater metabolic demands of ovarian development in females, especially during the first year when body growth demands are also high. In the second year growth demands are less and may

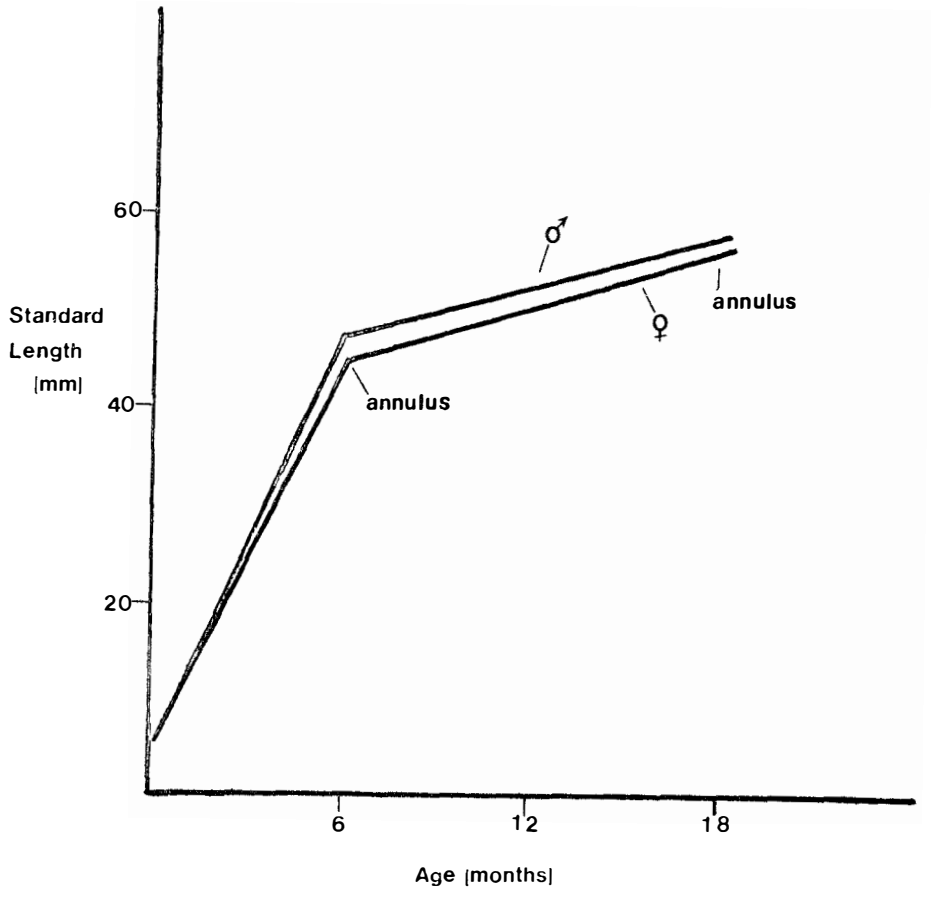


Figure 15. Back-calculated growth for male and female *Percina tanasi* based on scale radius-standard length relationship (L = .91R + 10.1).

be more easily met over and above requirements for reproductive development. This may account for the higher growth rate relative to males during the second year.

The length-weight relationship of *P. tanasi* demonstrated further the differences in growth rate between adult and subadult darters and between sexes. The regression lines for the length-weight relationship of each sex are shown in Figure 16. Weight increase rates diverged at approximately 50 mm SL (Figure 17), corresponding closely to sexual maturity and the onset of gonadal production.

Juvenile growth rate in terms of weight gain was necessarily extrapolated (Figure 17) and apparently is complementary to growth of body length. Thus, instead of decreasing with age, the rate of growth with regard to weight increased over time until an average weight of 2.15 g was attained at sexual maturity (about 50 mm SL). There, male and female growth rates diverged, but both continued to gain weight at a high and nearly uniform rate (Males, W = 1.90L-7.35; Females, W = 1.61L-5.81) over the remaining 17 to 20 months of life, with an ultimate average difference in weight of about 0.35 g at Age II.

Length and/or weight ranges and discrepancies within apparent year classes may have been due in a large part to differences in age caused by the long spawning season or delays in spawning which gave some year classes or fractions of year classes a later start in life. This phenomenon will be discussed under reproduction.

Based on the analyses herein, if an investigator chose to accept the length-weight relationship as representative of growth, then the growth rate of snail darters persisted at a high rate throughout its

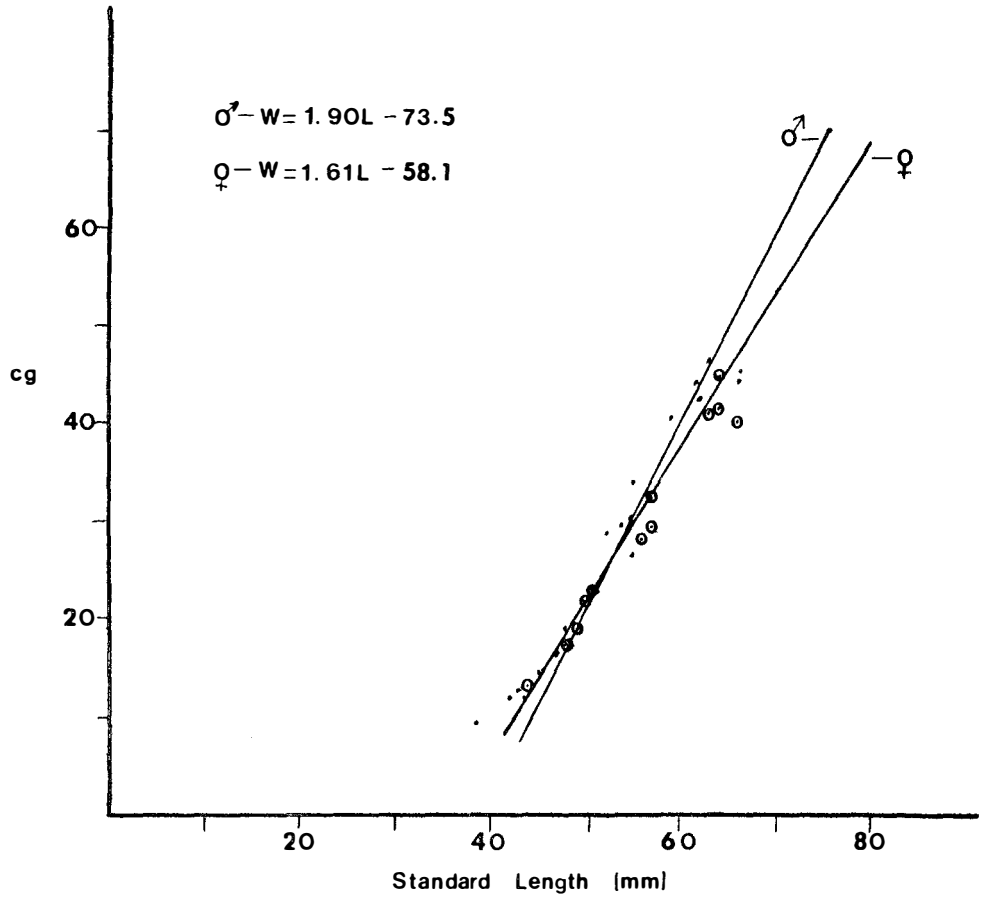


Figure 16. Length-weight regression lines for 19 male and 12 female (circles) *Percina tanasi*.

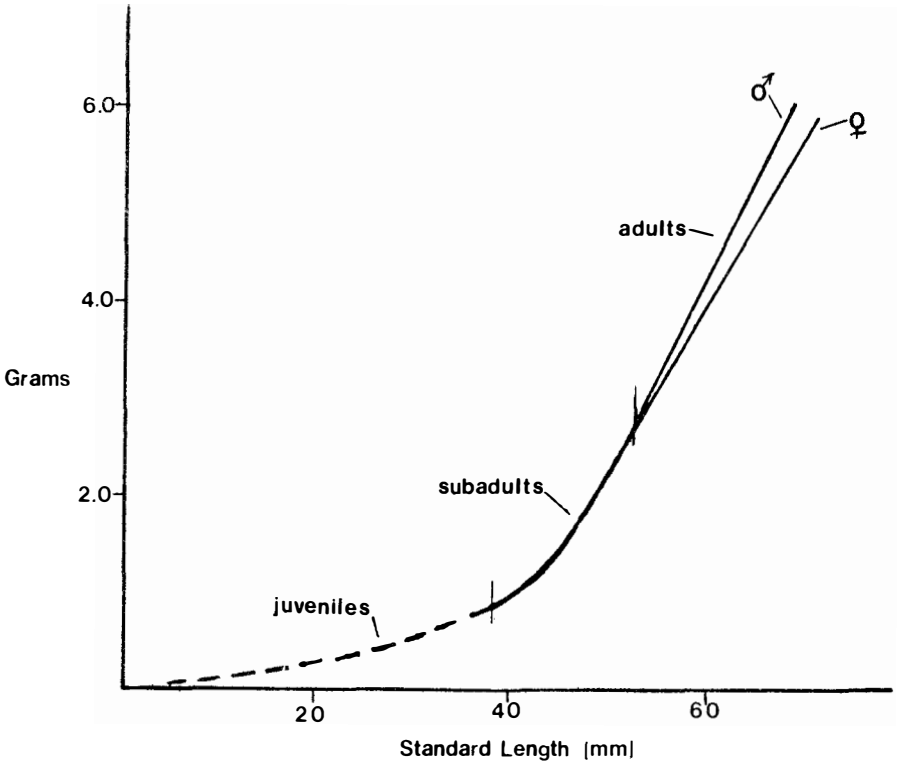


Figure 17. Extrapolated growth curves for male and female *Percina tanasi* based on length-weight relationships (Figure 16) and empirical subadult data.

relatively short life. Regrettably, other studies involving *Percina* have not investigated length-weight relationships, so it was not known if a high growth rate persisted in darters having greater longevity. If, on the other hand, one chose standard length as the index of growth, then *P. tanasi* exhibited growth curves similar to other species of *Percina*, growing much slower in later months of life (Page and Smith, 1970, 1971; Thomas, 1970).

CHAPTER VI

REPRODUCTION

Spawning Season

Apparent spawning aggregations of snail darters appeared on the gravel shoals of the lower Little Tennessee very early in the year (February) and continued through mid-spring. Migratory activities apparently attributable to spawning have been previously discussed. Large numbers of nuptial males with freely flowing milt congregated on shallowest portions of the shoals by early February and were followed by ever increasing numbers of gravid females as the month progressed (Figure 6, part a, page 40). By mid-February most females were flowing freely with little pressure applied to the abdomen and there was strong circumstantial evidence of heavy spawning activity. Some female specimens appeared already spent as early as late February, and most specimens captured in April were well spent. However, actual spawning behavior was observed on April 17, 1976, and specimens still flowing were collected April 23, 1975, documenting the continuation of some spawning activity. Based on these observations, *P. tanasi* spawns from mid-winter to mid-spring with heaviest activity in February and possibly into March, and it is doubtful that spawning continues much beyond the end of April.

The winter spawning season of *P. tanasi* precedes that of any other species of *Percina* recorded in the literature or those personally observed. However, *P. shumardi* in spawning condition were collected concurrently with spawning snail darters by TVA biologists in February.

P. (Imostoma) sp. collected in November from the Conasauga River (upper Coosa River system) were in a similar state of nuptial condition as snail darters collected that same month, the males already flowing milt. Moreover, *P. ouachitae* collected February 7, 1969, from Pearl River, Mississippi, were in high nuptial condition, and they were speculated to spawn in mid-February by Collette (1965). All four species are members of *Imostoma*, and it appears that this subgenus may be unique and consistent in exhibiting winter spawning behavior. *P. nigrofasciata* (Mathur, 1973) and *P. sciera* (Page and Smith, 1970), both members of *Hadropterus*, spawned May to July. *P. maculata* (Thomas, 1970; Petravicz, 1938) and *P. peltate* (New, 1966), subgenus *Alvordius*, spawned April to June, *P. phoxocephala* (Page and Smith, 1971; Thomas, 1970), subgenus *Swainia*, spawned in June; and *P. (Percina) caprodes* (Reighard, 1913; Thomas, 1970) spawned in early summer. *P. (Cottogaster) copelandi* reproduced in early to mid-summer (Winn, 1953); and *P. aurantiaca*, subgenus *Hypohomus*, spawned in mid-summer also (Howell, 1971). *Percina* sp. and *P. cymatotaenia*, subgenus *Odontophilus*, were examined and found to have strongly developed caudal keels in late May. Collette (1965) described tuberculation on males of *P. (Ericosma) evides* captured in April, and they were observed to attain nuptial condition in the Little Tennessee in late spring. Thus, all recognized subgenera of *Percina* were covered in at least some depth with one or two representative species, and it appears that none approach the early spawning dates of *Imostoma*.

The stimulus (or stimuli) which triggers the onset of the spawning season in *P. tanasi* is difficult to determine. Winn (1958) discussed the obvious effects of temperature on spawning in several species of darters,

indicating the apparent importance of warming water temperatures in triggering spawning behavior. The Little Tennessee River, however, does not warm appreciably until April, 2 months after initiation of the spawning season. Therefore, temperatures could hardly play a role in the timing of reproduction. This leads to the conclusion that other factors such as photoperiod are responsible. However, Hubbs and Strawn (1957) offered convincing evidence that photoperiod did not play a part in reproduction in another darter, *Etheostoma lepidum*, and this further clouds the question. With these factors excluded, it seems most plausible that reproductive periods are simply determined by an annual hormonal cycle governing sexual maturation, and that, since females ripen after the males, spawning behavior is triggered by threshold hormone levels after ova have matured sufficiently for deposition. If general environmental conditions are favorable, they join the males in the spawning microhabitat at this time.

It seems likely that snail darters have the capacity to postpone spawning for considerable lengths of time if conditions are not right for spawning. The capture of unusually small specimens in December, 1974 (38 mm TL, TVA) may indicate that spawning was delayed several months by the almost continued flooding during the previous winter and early spring. Other length disparities in age classes may also have been due in a large part to various spawning delays.

Spawning Habitat

As previously mentioned under population characteristics, the apparent general spawning habitats of *P. tanasi* are the gravel shoals of

the lower Little Tennessee River. The greatest expanse of this habitat is located at Tolliver Island-Coytee Spring about 11 km above the mouth. Additional habitat is located 13 km upstream at Davis Island. Somewhat deeper shoal areas occur at Morganton Ferry and below Davis Ferry.

With respect to the spawning microhabitat of *P. tanasi*, the locations of spawning aggregations and an observation strongly suggested that spawning was nearly limited to the swiftest portion of the shoals, which generally were relatively shallow and situated mid-stream or considerably offshore. Current in such areas was measured at near .66 m/sec at low flow, though turbulent flow observably permitted much slower velocities at the substrate interface. Substrate at an observed spawning site and in areas of most dense spawning aggregations was generally composed of large, smooth gravel, 4 cm to 10 cm in diameter, scattered over a basal layer of silt-free sand. Stones were usually somewhat impacted in the sand, very stable, and rarely contiguous to one another. It was possible that the spawning microhabitat of *P. tanasi* was also utilized by associated species. However, there was no competition for spawning sites, as other species would have spawned much later. Howell (1971) discussed the growing evidence that all members of *Percina* spawn upon clean sand or sand-gravel substrate. Certainly *P. tanasi* and probably the entire subgenus *Imostoma* as well could be added to this list.

Water temperatures during the spawning season ranged from lows of 5° C in February to highs of 16° C in April (Figure 5, page 32) with daily fluctuations of 2 to 3 degrees. Average temperature over the season was probably near 11° C and ranged from 9° C to 12° C during the period of heaviest spawning activity in late February. Photoperiod

ranged from 10 hours 45 minutes to 11 hours 52 minutes (sunrise to sunset).

As observed in the discussion on migration, seining results seemed to indicate that males arrived at the spawning microhabitat first, early in the season. Most females seined at this time typically were lying in somewhat deeper portions of the shoals, a meter or more in depth, and possibly many more remained in the even deeper portions of the river. As the season progressed, females apparently migrated in increasing numbers to join the males in the spawning microhabitat.

It was not possible to conclude that spawning was restricted solely to the swifter and more shallow shoal areas of the Little Tennessee, but aggregations and migration patterns strongly suggest that the majority of such activity occurred in these areas. Therefore, the deeper shoals at Morganton Ferry and below Davis Island may serve as marginal spawning habitats, while no reproduction at all probably occurs in the deeper portions of the river. Population density was quite low at the upstream shoal area near Davis Island, and indications are that the shoal complex at Tolliver Island-Coytee Spring probably serves as the center of reproduction for the entire snail darter population.

Gonadal Development and Fecundity--Females

Growth analysis and dissection data indicated that snail darters became sexually mature in the first year of life. Those surviving the second year spawned a second time.

In preparation for the early winter spawning season, the onset of gonadal development was accordingly early, becoming evident in early fall. In females some degree of maturation was evident as early as

September, with some specimens showing an increase in gonad size over the normal 1 to 1.5 mm diameter of flacid ovaries. By late October, gonad diameter averaged 3.2 mm, increased to 5 mm in December, and attained as much as 7 mm diameter in February. The number of mature ova (Figure 18) increased greatly as the spawning season approached and offered a good timetable of ovarian activity. At the onset of development, perhaps 1,000 ova became discreet, though all remained immature through late October. However, rapid maturation of ova ensued, and specimens examined in mid-December contained an average of over 600 mature eggs. This number marked the maximum of mature ova excised from any specimens (though a January sample might have yielded a few more were it available), and this figure probably approximates the average fecundity of the snail darter. By mid-February, average mature ova had dropped to 427, indicating some may have already been expelled in spawning endeavors. By late April only about 100 mature eggs remained in females. Fecundity estimates of all females examined from each sample were comparable regardless of body length; therefore, large differences in fecundity between sample periods should have been attributable to reasons other than body size.

Of the initial 1,000 or so discreet oocytes observed in fall, apparently 400 to 500 did not mature prior to the spawning season (Figure 18). It appeared that some may have matured as the season progressed, but, at the end of the season (April), 250 to 300 immature ova remained and apparently would have undergone reabsorption. Discreet ova were not discernible in June specimens. Speare (1965) reported similar results in an analysis of fecundity of *Etheostoma nigrum*, stating

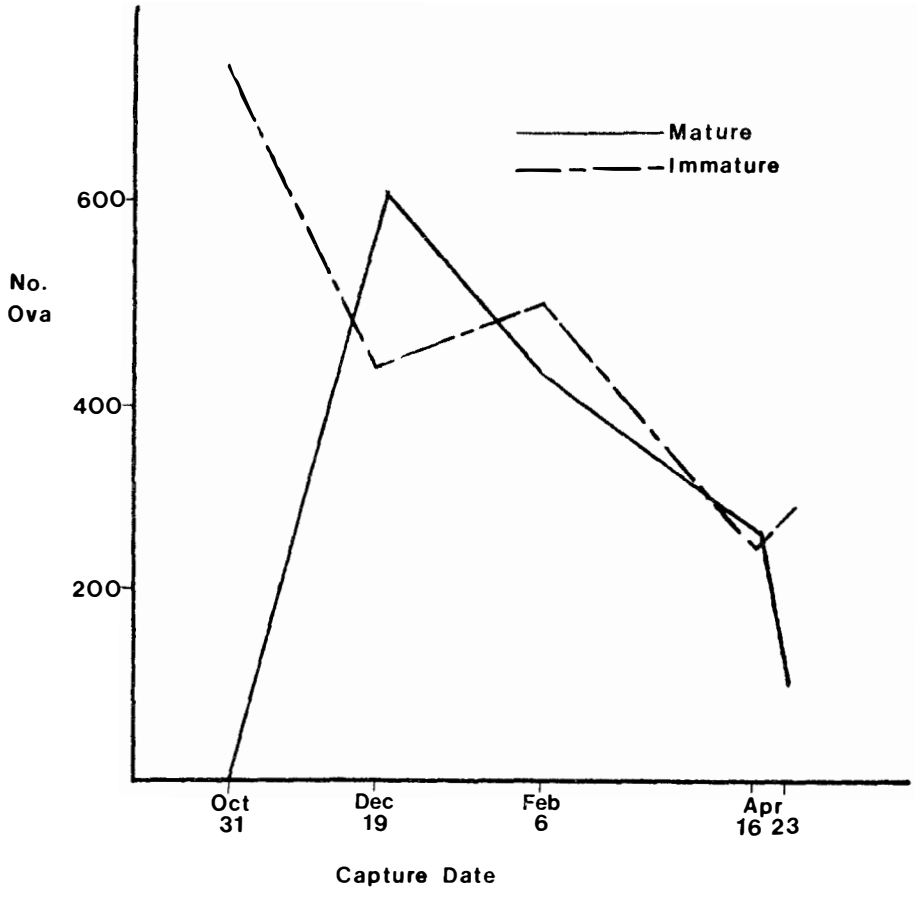


Figure 18. Average number of mature and immature ova excised from female *Percina tanasi* captured Fall, 1975, to Spring, 1976.

that only eggs containing a yolk and oil droplet were deposited in spawning, while some 64 percent were reabsorbed. But, he also concluded that no immature eggs were deposited along with ripe ova during spawning based on their absence from nests and, in addition, the maturation process took too long for eggs to ripen after initiation of the spawning season. Perhaps larger samples of *P. tanasi* females would have yielded similar results with average initial immature oocytes and residuals at the end of the season being more nearly equal.

The fecundity figure of about 600 mature ova in *P. tanasi* exceeded that of other *Percina* reported with the exception of *P. caprodes*, *P. maculata*, and *P. copelandi* (Winn, 1958)--*P. caprodes* was reported to deposit nearly 2,000 eggs. It greatly exceeded that reported by Mathur (1973) for *P. nigrofasciata* (38-250) and by Page and Smith (1970) for *P. sciera* (200). Page and Smith (1971) reported averages of 83-220 for *P. phoxocephala*, though one specimen contained 720, and Howell (1971) reported up to 518 in *P. aurantiaca*. Unfortunately, Thomas (1970) did not report fecundity in his study of *imostoma* member *P. shumardi*.

As stated previously, all female snail darters dissected during months of reproductive development or activity had comparable complements of mature ova regardless of body size. Bagenal (1966) examined the body length-fecundity relationship in detail for fishes representing several families, and Mathur (1973) elucidated the relationship for a member of the genus *Percina*, *P. nigrofasciata*, finding a highly positive correlation. Unfortunately, the small samples of female *P. tanasi* available for gonadal inspection would not permit an in-depth examination of this nature. Uniform fecundity within small samples of females of various

sizes (up to 16 mm difference in SL) may have indicated that a positive body length-fecundity relationship was not so pronounced in a short-lived species such as the snail darter.

Gonadal Development--Males

As with females, male snail darters exhibited noticeable signs of gonadal development by early fall of the 1st year of life. Testis diameter increased from a flaccid minimum of 1 mm or so to 3 mm in some September specimens. By December, testis diameter had increased to as much as 5 mm. Winn (1958) stated that males ripened 1 or 2 weeks before females in all 14 darter species studied by him. Male snail darters, however, were flowing by mid-November, a full 2-1/2 months prior to spawning, and the same phenomenon was observed in a second *Imostoma*, *Percina* sp., from the upper Coosa system. All males examined from late April samples appeared to be almost completely spent. Again, the reproductive cycle of the subgenus *Imostoma* appears to be temporally quite unique among *Percina*.

Tuberculation and Coloration

Etnier (1975) described the nuptial tuberculation of male snail darters in detail. Specimens he examined which were collected in April samples possessed uniserial tubercles on the anal rays, ventral surfaces of the median four pelvic fin rays, lower caudal rays, and on the branchiostegals. He questioned the possibility of tubercles on the pelvic and/or anal spines, but examination of highly nuptial specimens collected in February matched his description of April specimens. In addition to fin ray and branchiostegal tuberculation, tubercles were

present on the cheeks, breast, and venter. These tubercles were evident on specimens collected as early as October, and they had become highly prominent on February specimens. In addition, the modified row of mid-ventral scales became more prominent with moderately developed teeth evident by February. These teeth were relatively weak compared to many other species of *Percina*, however (Collette, 1965).

Since *P. tanasi* does not possess striking chromatic breeding coloration, differences in coloration during the spawning season are somewhat subtle. It was stated in Chapter III that there is no real sexual dimorphism in the color pattern of *P. tanasi*. However, there are varying degrees of intensity from time to time. There was a general brightening of coloration of males encountered during the spawning season, and color patterns were noticeably intensified during courtship on a momentary basis as will be discussed later. Generally the sides and venter of the body became more irridescent with pale blue-green than normal, and the dorsum, which varied from brown to olive, was bright olivaceous. Gold was brighter than usual ventrolaterally and conspicuously flecked the cheeks. Irridescent turquoise blue was evident in the branchiostegal region and prepectoral area. Fin rays were washed in orange-yellow with this pigment most prominent at the bases of the pectoral, pelvic, and caudal fins. Perhaps most striking was the eye which had a glaring effect produced by an intense yellow ring about the pupil and yellowish iris. Dorsal saddle patterns were often strikingly blackened on the males.

Female snail darters tended to subdue color patterns during the breeding season. Dorsal saddles were most often blanched out, making

them most difficult to discern against a sandy substrate. Irridescent blue-green or gold colors along the sides and venter were noticeably subdued compared to those of the males; however, orange-yellow in the fin rays was of nearly equal intensity to that of the males.

Spawning Behavior

All *Percina* species thus far discussed in the literature are multiple and probably promiscuous spawners. No real territory is established with the possible exception of *P. copelandi* (Winn, 1958) and *P. peltata* (New, 1966), and parental care is not exercised. They probably should not be termed random spawners, however, in the sense that percid members *Perca* and *Stizostedion* are so termed, since some degree of site selection is apparently exercised. Their behavior is intermediate between those random spawning genera and that of *Etheostoma*, which is more complicated and ritualized. Winn further stated the generally accepted notion that complexity of behavior is directly correlated with evolutionary advancement and, thus, *Percina* are somewhat primitive percids.

New (1966) and Winn (1958) have pointed out the gregarious nature of *Percina* when spawning. Winn added that continued contacts between members of the spawning school might serve as stimuli to males to sustain spawning condition. The aggregations of *P. tanasi* on spawning shoals may indicate a similar behavior pattern. Within such aggregations, a degree of moving territory maintenance was observed in *P. (Cottogaster) copelandi* (Winn, 1958) and *P. (Alvordius) peltata* (New, 1966), and dominance patterns were observed among male *P.*

(Hypohomus) aurantiaca by Howell (1971). On the rare occasions when two males of *P. tanasi* were observed simultaneously, no such aggressive behavior was observed. However, the generally low population density of snail darters permitted only two such observations during spawning season, and they are, therefore, inconclusive. Snail darters held together in aquaria exhibited no territorial tendencies whatsoever and were, in fact, quite gregarious regardless of sex.

Under natural field conditions, however, the intensified color patterns of males may indicate that some moving territoriality and/or dominance pattern was being exercised. This might have been especially true in preimpoundment days when the Little Tennessee habitat may have permitted higher population densities. Observable tendencies indicate that *P. tanasi* exhibited very similar collective reproductive behavior to other *Percina* thus far discussed in the literature.

On the individual level, the long reproductive period and gradually decreasing fecundity of snail darters indicated that they are multiple promiscuous spawners. Some evidently entered into spawning encounters much more frequently than others, as a considerable number were nearly spent by mid-season (March). Probably only a small number of eggs are deposited in each spawning endeavor. As stated in the discussion of migration, males migrate into the spawning shoals first to be joined later by females for occasional spawning encounters. Such an encounter was observed and filmed on April 16, 1976, on the shoal area at Coytee Spring, and the following discussion relates how it was conducted.

When first encountered, the snail darter pair was situated in a sandy area interlying several small stones such as those described in the discussion of spawning microhabitat. Current throughout most of the water column in this same area was earlier measured at 0.66 m/sec under similar flow conditions. The water was slightly dingy and reportedly had been at low flow for 2 days. Water temperature was 16° C, and time was 1430 hours on a clear, hot day.

Throughout the encounter, the color patterns of the male were striking, the saddles being very salient, the head markings harlequin-like, and the eyes with the iris intense yellow. The female, on the other hand, was blanched out to the point that she was virtually invisible against the sand and was, in fact, not noticed for a full 15 to 20 seconds though she was situated right before the male. She was visibly quite gravid.

When first noticed, the female was motionless in front of the male, facing directly upstream. The male's head was to her right, and he was oblique to the current. After perhaps 30 seconds, he moved upstream beside but slightly downstream of the female at a distance of about 5 cm. At this point, the male raised slightly off the substrate and vigorous tail-wagging was observed. After 15 to 20 seconds, he dropped downstream a couple centimeters and nearer to her peduncle. He then nudged her peduncle four to five times in rapid succession with his head. This sequence was repeated twice with the male again moving upstream beside her between nudging encounters. It was not clear whether the tail-wagging at this point was an attention-getting motion or just for maintenance against the current, but its repetition at

precise points seems to indicate the former. Following this sequence, the male again dropped behind the female and situated himself oblique to the current, this time with the head on the left. Fifteen seconds later he quickly returned to the female's right side and placed his left pectoral fin over her peduncle. Momentarily, he began stroking her peduncle, doing so four or five times. He then placed himself across her body in the peduncle region and stroked with the right pectoral fin twice. The sequence was then partially repeated with the male retreating behind the female again momentarily, then returning to the stroking position, this time stroking her peduncle 10 to 12 times with the left pectoral fin.

Throughout the above encounter, the female had remained motionless. Following this routine, however, she finally moved upstream 6 to 8 cm. The male quickly settled beside her to the right, then turned and nudged her head two or three times. Subsequently, he dropped downstream and placed his body diagonally across her peduncle once again and stroked with the left pectoral fin. At this juncture, the pair moved upstream in unison. However, it seemed the female was attempting to move from beneath the male and, after losing his mount, the male followed the female in erratic dashes until she again settled to the substrate perhaps a meter upstream where he rejoined her. He then resumed the pectoral stroking position, again stroking her first with the left pectoral fin 7 or 8 times, then the right. The female then moved ahead slowly while vigorously wagging the caudal region, and her anal fin appeared to be sweeping the sandy substrate. The male followed immediately and was seen to repeat the vigorous wagging maneuver

over the same area. Following this, a few more nudging and stroking sessions occurred before the pair suddenly darted away and were lost from sight.

The account just related could probably have been construed as heavy courtship behavior and an unsuccessful attempt at spawning by the male. The female appeared to be apprehensive at the presence of the observer and may not have been responding to the male's advances in a normal manner. The only possible maneuver which could have represented spawning was the vigorous wagging of the peduncle and burying of the anal fin into the sand by the female which was immediately followed by a similar maneuver by the male. In light of the tuberculation, caducous scales, and anal fin morphology of the males, however, it is most likely that *P. tanasi* spawns in a manner more closely approximating that described for other species of *Percina* rather than by the procedure just noted.

Perhaps the most explicit descriptions of spawning in *Percina* were those of New (1966) and Howell (1971). New described in detail the spawning act of *P. peltata*, beginning the description with an account of female solicitation stimuli. No such motions were observed in *P. tanasi*, but the courtship encounter was already in progress when the observation began, so this was inconclusive. After mounting, the male *peltata* rubbed the female's nape region with his isthmus. Since male *peltata* possessed no breeding tubercles (Collette, 1965), New concluded that the caducous belly scales alone served as tactile stimulatory organs and abrasive surfaces to aid the male in maintaining his purchase on the female. As stated by Page (1976) caducous scales

are not highly developed in *Imostoma*, and they play a relatively minor role in these functions. Therefore, spawning procedure in *Imostoma* might be expected to approximate more closely that of other tuberculate species. Unfortunately, accounts for highly tuberculate species were nonexistent. Reighard (1913) and Winn (1958) gave brief accounts of behavior in *P. caprodes*, which is only slightly tuberculate. The observed *caprodes* simply mounted the female's back with the peduncle off to one side and down on the substrate. Presumably tactile stimulation to the female's back was achieved by use of the tubercles during quivering which ensued. The ventral tubercles on the head and pelvic fins of *P. tanasi* probably serve comparable functions. Tubercles on the male's long anal fin and caudal fin may serve as additional stimulatory organs applied to the female's peduncle, or their chief function may be more concerned with securing a purchase by clasping opposite sides of the female caudal region. At no time during the encounter of *P. tanasi* was synchronous quivering observed, and it was for this reason that it was believed that actual egg deposition was not achieved.

Snail darters retained in aquaria failed to spawn. Though some following behavior was observed in males, females appeared disinterested or perhaps were not sufficiently acclimated to the captive surroundings.

It seems plausible that the elaboration of tubercles in *Imostoma* may be a result of selection for mechanisms favoring achievement of more adequate stimulation and clasping ability while contending with strong current. A survey of subgenera lacking tubercles taken from Collette (1965) compared with various published life histories and personal observations on members of the groups revealed that species having an

absence or a reduction of tubercles typically spawn in more gentle riffles or runs than highly tuberculate species. *Imostoma* and *Ericosma* are the most elaborately tubercled groups, and both contend with strong current situations when spawning.

Early Development

As stated in Methods, snail darter eggs were artifically fertilized in the field at 6° C, brought to the laboratory, and incubated at 12.5° C after acclimation. Initially, 80 to 90 ova were fertilized at 1230 hours on February 9, 1976, and incubation of ova was begun at 1530 hours. The following chronological account describes the early development of the eggs and larvae.

Age 3 hours (Figure 19, part a). Oil droplet was completely coalesced in ova and situated in vegetal hemisphere. Blastodisc had formed about the animal pole. Perivitelline space was very wide and, therefore, yolk was not contiguous with chorion as illustrated for similar stages of some other perciform fishes (Bolin, 1930), having already been lysed free by the cortical alveoli.

Age 51 hours. Some cleavage was evident in blastodisc area. Number of cells was difficult to determine.

Age 96 hours. Embryonic axis was now apparent. Body shield and cephalic region were evident. Gastrulization appeared 40 percent complete.

Age 130 hours (Figure 19, part b). Development was advancing rapidly. Gastrulization was complete excepting blastopore. Optic vesicles were visible in cephalic region and Kupffers vesicle was formed posteriorly.

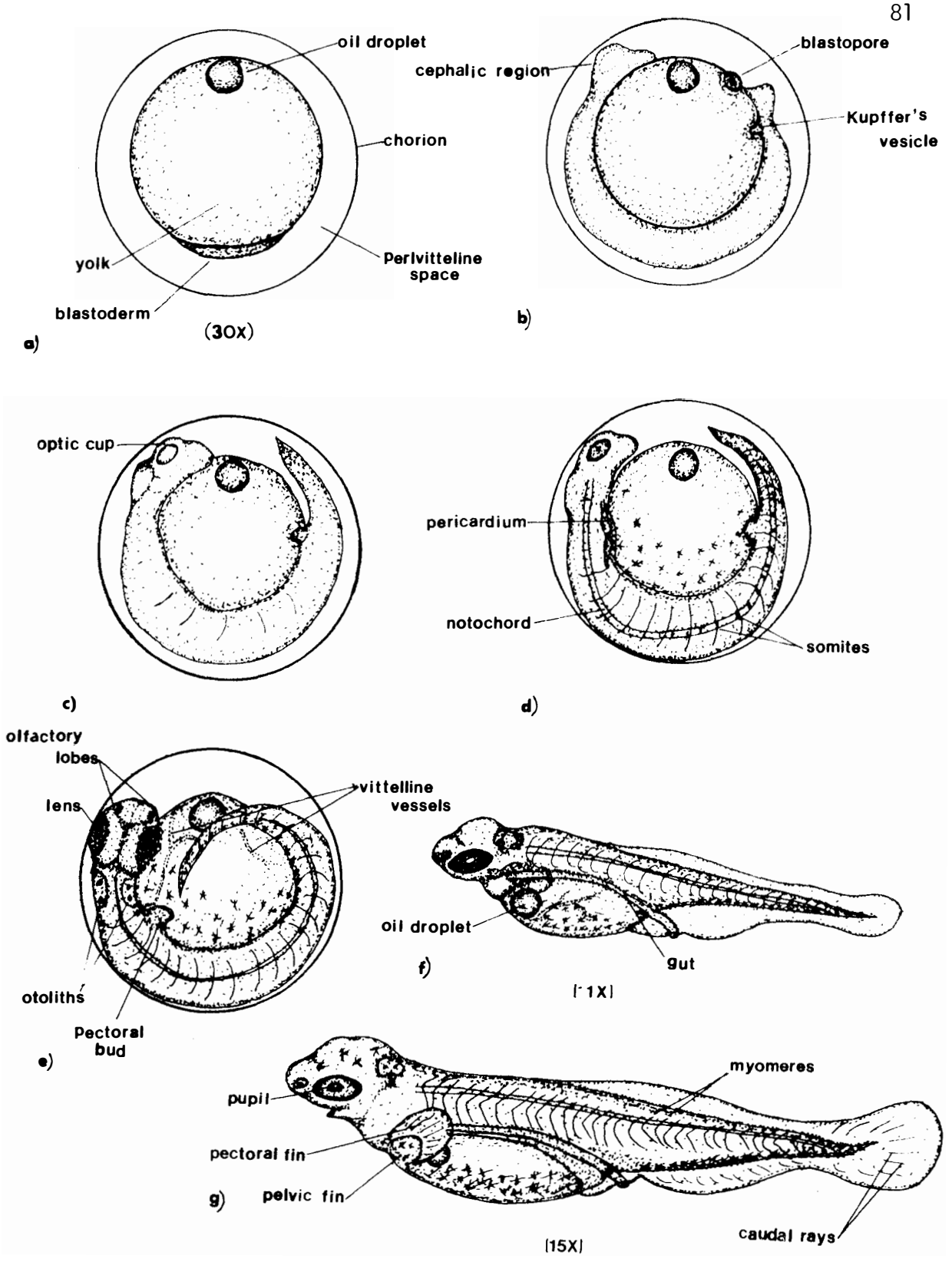


Figure 19. Egg and larval stages of *Percina tanasi* at: (a) 3 hours, (b) 130 hours, (c) 180 hours, (d) 203 hours, (e) 276 hours, (f) 257 hours, and (g) 596 hours.

Age 150 hours. Blastopore was definitely closed. Somites were developing, at least four pair being evident.

Age 170 hours. Embryo was now occasionally rotating within the chorion.

Age 180 hours (Figure 19, part c). Caudal region was now free from yolk sac. Head remained attached near oil droplet. Brain regions were differentiating.

Age 196 hours. Somites developed along entire body region. Some pigment was evident in intersomitic areas along notochord on posterior 1/3 of body.

Age 203 hours (Figure 19, part d). Embryos were moving freely. Head was free from yolk sac. Pericardium was formed and heart beat had begun. Ventral region of tail and yolk sac now had scattered melanophores, and optic cups were outlined with pigment.

Age 228 hours. Eyes completely pigmented. Violent rotations within egg occurred often.

Age 252 hours. Blood flow was now evident in dorsal aorta to tail region and also across vitelline membrane. Ootiliths and olfactory lobes were well formed. Myomeres were clearly defined.

Age 264 hours. Pectoral buds were now apparent.

Age 276 hours (Figure 19, part e). Pectoral fins had continued to develop. Also clusters of differentiating cells at juncture of venter and yolk sac may have represented pelvic development. Lens of eye was distinct within optic cup. Primitive gut tube was clearly present.

Age 290 hours. Blood had reddened being especially evident in heart area. Heart rate was 120/minute.

Age 345 hours. Tail had lengthened considerably. Body was wrapped within egg about 1.5 times.

Age 357 hours (Figure 19, part f). Four or five eggs had hatched. Larvae were 6 mm total length. Primitive mouth was formed. Heart appeared as three bulbous inflations presumably differentiating into chambers. Heart rate remained at 120/minute. Oil droplet was situated forward in the yolk sac. Melanophores were confined ventrally on tail and to lower half of yolk sac. No pigment occurred in anal region between yolk sac and tail. Embryos in process of hatching were observed to roll and thrash vigorously popping first the tail free, then the head.

Age 359 hours. All eggs had hatched.

Age 405 hours. Yolk sac larvae were occasionally very active, swimming about periodically between respites on bottom of container. Pigment patterns and heart rate were unchanged. Caudal fin was developing, but no rays were apparent. Pectoral rays were faintly discernible, and pelvic fins had appeared beneath pectorals. Total length was now 7 mm.

Age 433 hours. Pigment intensity had decreased in optic cup and pupil was apparently formed. Mouth was open, but digestive system appeared nonfunctional as connection to gut tube was incomplete. Considerable yolk remained and oil droplet had decreased little. Pigmentation still was unchanged.

Age 478 hours. Larvae were swimming continuously. Mouth appeared to be approaching functional status.

Age 500 hours. Pigment had scattered about head and was intensifying in anal area. Some caudal rays were now discernible.

Age 524 hours. Larvae appeared to be strongly phototaxic, lying quiescent in dark and becoming very active in light. They were immediately drawn to any area of light bottom in the container. They were not responsive to food. Oil droplet was still large.

Age 572 hours. About 20 to 24 rays were now apparent in caudal region from anus around caudal fin. Seven pectoral rays had developed. No pelvic rays were evident. Myomeres totaled 37.

Age 596 hours (Figure 19, part g). Anal fin differentiated from caudal. Pigment was still concentrated along ventral portion of peduncle and about gut tube. Pigment was heavy on yolk sac. About three melanophores had appeared on either pelvic fin. Pigment well scattered in head region. Some yolk remained and gut was apparently still not functioning. Food was refused. Total length attained was 7.5 mm.

Following this observation, the last remaining larvae had succumbed. There had been steady mortality of larvae since hatching. They did not seem able to tolerate heavy turbulence as many died when an air hose accidently submerged to the bottom of a container and churned the water for a few hours. Egg mortality was relatively low with less than 20 percent dying before hatching.

It is clear from these observations that the early development is a prolonged process. From initial fertilization on February 9, a full

15 days elapsed before hatching on February 24. This rate of development occurred at 6° C above that of the natural habitat, and it is speculated that hatching and other stages of the development process would have taken days longer in the spawning habitat. The only other *Percina* species for which early development was recorded, *P. sciera*, required but 90 hours to hatch (Page and Smith, 1970). However, these specimens were developing at 23° C, emphasizing the important effect of water temperature on development time. The snail darter's development time compared favorably with that of *E. blenniodes* which required 18 days to hatch at 13.5° C (Fahy, 1954). Fifteen days probably represented the minimum hatching time required for *P. tanasi* in the Little Tennessee River as water temperatures averaged only about 12° C to 13° C during April, the warmest month of the spawning season.

Speare (1965) correlated the hatching success of darter eggs with water temperature. Success of *Etheostoma nigrum* eggs laid in May was 14 percent higher than those deposited in the colder month of April. It is conceivable that such a relationship exists for *P. tanasi*. However, Hubbs (1961) discussed the narrow temperature tolerance range for *Percina* eggs (*P. caprodes* and *P. sciera*), and it may be more important to a species adapted to winter reproduction that temperatures did not warm considerably over the spawning season. As noted, hatching success was high in the laboratory, about 80 percent, and might have been even higher under ideal natural conditions, barring predation.

Most critical to the survival of young snail darters may have been the prolonged larval period which may be the result of low water temperatures. It would appear that *P. tanasi* would be most vulnerable

to predation or general vagaries of their environment at this time.

Larval Drift

As mentioned under migration, there was substantial evidence that larval snail darters drifted for great distances downstream after hatching. The plight of large concentrations of young-of-the-year snail darters trapped below Tellico Dam after its closure, coupled with their virtual absence in the river above, dramatically emphasized this fact. Intensive collecting with plankton gear in the peripheral slow water habitat adjacent to shoal areas failed to produce any larval snail darters. This seemed to indicate that larvae were carried considerably downstream after hatching to deep areas of the river where they might contend with minimal current. Deep basins in the river below Davis Island, Morganton Ferry, and Davis Ferry (Figure 2, page 22) may have served as refugia for larval development, or the majority may have been transported completely downstream beyond the confines of the Little Tennessee as had apparently happened in 1976. It is conceivable that increased rates of flow since impoundment of Chilhowee Dam have enhanced and magnified this phenomenon. In this manner recruitment for marginal populations in the Tennessee River must also have been facilitated.

As determined in the laboratory, the active prolarval stages (yolk sac) were highly phototaxic and swam at the surface under lighted conditions. This may have been some indication of their behavior in the natural environment. The prolarval and postlarval stages of snail darters may have behaved essentially as semi-planktonic animals in the quiescent portions of the river, feeding chiefly on micro-invertebrate

plankton, possibly near the surface. The inactivity of larvae placed in darkness in the laboratory suggested that they may demonstrate strong diurnal tendencies in their early stages, possibly to the point of daily migration.

Fahy (1954) estimated a period of about 15 to 20 days necessary for *Etheostoma blenniodes* larvae to transform to the juvenile stages. At similar temperatures, this period seemed applicable to *P. tanasi* in light of the equality of hatching times of these two species. After undergoing transformation to the juvenile stage, it is presumed that the young snail darters would assume a benthic mode of life. This would occur a month or more after hatching. As juveniles become able to contend with current, most individuals must then migrate upstream. They begin to appear in the shoal areas upstream in June at the age of 3 to 4 months and a standard length of 40 mm or less, and they become more abundant as the summer progresses thus completing an early and highly critical stage of life.

CHAPTER VII

FEEDING AND DIET IMPLICATIONS

Alimentary Analysis

Following is a general recapitulation and discussion of diet constituents excised from the alimentary tracts of snail darters and associated species. Tables 8 and 9, Appendix A, is a complete presentation of summarized seasonal food data in terms of numbers of organisms consumed, and Table 4 lists a seasonal comparison of relative biomass intake of the more common food organisms.

The constituents of overwhelming importance in the diet of *P. tanasi* were several species of small gastropods 5 mm or less in diameter. In the 67 specimens examined, by far the most common gastropod prey item was *anculosa subglobosa* which comprised 46 percent of organisms consumed in the overall annual diet. Second in importance were snails of the genus *Physa* which comprised 11 percent of organisms consumed. In combination, these two prey species provided 59.7 percent of the biomass in the annual diet. Other gastropods taken in far less numbers were snails *Lithasia verrucosa*, *Pleurocera canaliculata*, *Menetus* sp., and the limpet, *Ferrissia* sp.; another molluscan consumed was the fingernail clam, *Sphaerium* sp. Mollusks totaled 58.5 percent of the total number of organisms consumed. One terrestrial gastropod, *Retinella* sp., was excised from a Tennessee River specimen of *P. tanasi*. Though exceedingly abundant, the Asiatic clam, *Corbicula mannilensis*, was not utilized as food by snail darters or associated species.

Table 4. Daily Biomass (mg) and Percentages of Biomass Consumed by Seasonal Samples of *Percina tanasi* for Five Predominant Prey Items

	Mean Wt. Per Organism	Winter	Spring	Summer	Fall	Overall Annual
No. stomachs		11	15	24	17	67
Anculosa-Physa	3.3	326.7 (95)	141.9 (14)	643.5 (71)	858.0 (82)	1970.1 (59)
Brachycentrus	13.1		406.1 (40)		78.6 (07)	484.7 (15)
Hydropsyche	14.9		29.8 (03)	44.7 (05)	74.5 (07)	149.0 (04)
Glossosoma	1.7		10.2 (01)	64.6 (07)	5.1 (01)	79.9 (02)
Simulium	.4			106.4 (12)		106.4 (03)
Other		14.4 (05)	419.6 (42)	41.4 (05)	24.9 (03)	500.3 (15)
Total Biomass Consumed By Sample		341.1	1008.5	900.6	1046.5	3296.7
Mean Daily Intake/Individual		31.0	67.2	37.5	61.5	49.2

A second major group, the tricohptera, were next in importance in the annual diet. They provided 10.4 percent of prey items consumed and 21.6 percent of the biomass. Most notable among the Trichoptera was *Brachycentrus etowahensis* which was exceedingly abundant in the river and in the diets of associated species. It comprised 14.7 percent of annual biomass consumed by *P. tanasi*. Further contributions were made by *Hydropsyche morosa* and *H. venularis* (4.5 percent) and *Glossosoma nigrior* (2.4 percent). Tiny *Lepidostoma* sp. appeared in one sample.

Other insect orders played a minor role in the diets of dissected snail darters. Of most importance among them were dipterans of which a single genus, *Simulium*, was important. It occurred in large numbers (50 percent of organisms consumed in the summer diet) but constituted only 12 percent of the summer biomass consumed and just 3.2 percent on an annual basis. Other dipterans of sporadic occurrence in the diet were chironomids, blephariceridS, and the tipulid *Antocha saxicola*. Plecopterans were nonexistent in the diet of snail darters and ephemeropterans comprised less than 1 percent of the annual diet and, therefore, contributed little to injested biomass.

A final, and possibly surprising, component of the snail darter's diet was fish eggs. A substantial number (11 percent) appeared in the spring and early summer diet. Those consumed earlier in the spring were almost certainly representative of cannibalistic intake of snail darter eggs, as they were percid eggs, and *P. tanasi* was the only species spawning at that time with the exception of a few *P. shumardi*. Several eggs had well developed embryos indicating that they had been deposited for several days prior to consumption.

There appeared to be no difference in the snail darter's diet with respect to age in adult or subadult classes. Darters of different length classes (age) contained essentially the same prey items, and ration size (biomass) did not vary in any certain way in this respect. The smallest *P. tanasi* dissected (38 mm SL) contained food items similar to older individuals in the sample. However, there was some possibility that gastropods were not utilized by *tanasi* until they reached considerable size. Four specimens ranging from 40 to 45 mm SL sampled in mid-June had no snails in the digestive tract, but they contained several small trichopterans (*Glossosoma*). Eleven specimens ranging from 55 to 70 mm SL collected 10 days earlier were laden with gastropods. This might have appeared conclusive initially, but a 55 mm specimen collected along with the subadults also contained no snails. Therefore, availability or selectivity may have been a factor. A 46-mm-SL specimen collected in early August contained 14 *Anculosa*, so there was some possibility that gastropods entered the diet sometime during the first summer of life. The gape of 40 mm SL specimens appeared large enough to accommodate snails 5 mm or less in diameter.

Information concerning the diet of larval or juvenile snail darters remains speculative, as none were collected despite many efforts to do so by the author and TVA biologists. Nor were the very young of associated darter species captured for comparative purposes. Many young of *Cottus carolinae* were encountered, but their extremely large gape would have permitted ingestion of large prey items, and their diet, in all probability, would differ considerably from that of juvenile snail darters.

The only *Percina* for which the diet of very young individuals is recorded is *P. maculata* (Thomas, 1970). There was a preponderance of microcrustaceans in the diet (copepods and cladocerans) with a transition to small insects already apparent by the time the darter had attained 18 to 24 mm TL. Benthic samples taken from the Little Tennessee River during and after the spawning season revealed an abundance of microcrustaceans (copepods, ostracods) as well as tardigrades and small oligoghaetes in slow-water areas. Circumstantially, larval snail darters probably fed on a diet composed of these items during the first month or so of development in their deep-water refugia until small insects such as chironomids could be consumed.

Seasonal Diet Trends--Composition

Results of alimentary analyses revealed a number of seasonal trends in the diet of the snail darter and its associates. These are evident in Table 3, page 26, and Tables 8 and 9, Appendix A.

Considering first *P. tanasi* with respect to composition, the year-around staple prey item, gastropods, represented a very high percentage (71 to 95 percent) of the seasonal diet throughout the year except in spring when the diet was most varied. In specimens examined, a relatively low percentage of biomass intake (14 percent) was represented in the spring diet by gastropods. At this time the trichopteran *Brachycentrus etowahensis* was exceedingly abundent in stomachs of Little Tennessee darters including *P. tanasi* accounting for 23 percent of the number of organisms consumed and 40 percent of the biomass ingested (Table 4). Slightly larger percentages of other Trichoptera species

were also utilized at this time as well as ephemeropterans (*Stenonema*, *Ephemerella*), dipterans (blepharocerids, chironomids), and the fore-mentioned fish eggs. The diversity of the spring diet was exemplified by the fact that prey items aside from the five most commonly encountered species in the overall annual diet accounted for 42 percent of the biomass consumed. The possibilities of diet fluctuations being governed by relative availability of prey items will be discussed later.

In early summer, there was a significant return to gastropods as a diet staple (40 percent of ingested organisms, 71 percent of biomass). However, the trichopteran *Glossosoma nigrior* was prominent for a time in the early summer diet and was reflected as an overall summer increase for this prey item in Table 9, Appendix A. However, its small size limited its contribution to biomass (7 percent). Very prominent in the summer diet were simuliid dipteran larvae (50 percent by number) which were apparently locally abundant at times in the spring and summer. Again, however, their relatively small size reduced their biomass contribution to just 12 percent.

Least diverse of all were the fall and winter diets. An overwhelming percentage of the diet was gastropods, 81 and 91 percent, respectively. Little else in the way of prey items was reflected in the winter diet, and small but significant contributions were made to the fall diet by the trichopterans *Brachycentrus* and *Hydropsyche* (7 percent each).

Seasonal trends in the diet composition of associated species were somewhat less evident due to the lack of a salient diet standard in which changes could readily be detected. Most notable in the diets

of *P. evides*, *P. caprodes*, and *C. carolinae* was the heavy consumption of trichopterans in the winter and spring. As with *P. tanasi*, chief among these was *Brachycentrus* with considerable numbers of *Hydropsyche* also present, especially in the logperch, *P. caprodes*. Also, as in *P. tanasi*, *Glossosoma* was a conspicuous element of the early summer diet. Fall usage of trichopterans was generally also low in associates though considerably higher than in *P. tanasi*. Conspicuous in the winter diet of *C. carolinae* were the plecopterans *Pteronarcys* and *Isogenus* which, though low in numbers, accounted for a considerable percentage of the biomass consumed. They were insignificant in samples from other seasons.

In terms of numbers consumed, chironomids comprised what might be construed as the most staple item in the diets of snail darter associates. While comprising relatively high percentages of *C. carolinae*'s diet throughout the year (32 to 64 percent), much more drastic fluctuations were recorded from samples of the associated darter species. From heavy consumption in winter-spring (92 and 69 percent), *P. evides*' intake of chironomids dropped to 6 and 17 percent in the summer and fall, respectively. *P. caprodes*, while also decreasing chironomid intake drastically in the summer (1 percent), retained high utilization of chironomids in fall (76 percent). *Simulium* appeared as a high percentage of the summer diet of *P. evides* concomitant with its increase in *P. tanasi*'s diet. Other dipterans (*Antocha*, blephacerids) which occasionally occurred in the winter or spring diets of associated species were insignificant or nonexistent in the summer-fall months.

Trends noted in the diets of *P. sciera* (Page and Smith, 1970) and *P. phoxocephala* (Page and Smith, 1971) from Illinois were dissimilar to

those of snail darter associates in the Little Tennessee River. Utilization of trichopterans was found highest in the summer diet in Illinois species in contrast to lower summer occurrence in snail darter associates. However, a somewhat similar trend was noted in the dipterans as utilization of chironomids and simuliids dropped in mid to late summer. One *P. tanasi* associate, *P. caprodes*, was studied in Illinois by Thomas (1970), but he unfortunately did not discuss seasonal trends in the diet. Mullan et al. (1968) tabulated year-around consumption of ephemeropterans and dipterans in *caprodes*, but these were sampled from a reservoir situation.

Seasonal Diet Trends--Consumption Levels

Considering now the seasonal trends in overall consumption levels, the mean daily biomass intake per individual snail darter fluctuated greatly on a seasonal basis. A high of 62.2 mg/ind was recorded from spring samples with a sharp decrease to 37.5 mg/ind in summer (Table 4, page 89). In fall, there was a marked increase to 61.5 mg/ind and a sharp decline in winter to 31 mg/ind.

Similar trends have been noted in *P. sciera* and *P. phoxocephala* (Page and Smith, 1970 and 1971). They stated that feeding became heavy as spawning season approached and decreased sharply upon its arrival. In contrast, Fahy (1954), reporting a study of *Etheostoma blenniodes*, attributed consumption trends solely to water temperatures. His conclusion was based on the apparent peak in feeding activity in mid-summer when streams were warmest. *P. tanasi*'s consumption levels, in the face of thermographic data (Figure 20), supported the findings of other *Percina*

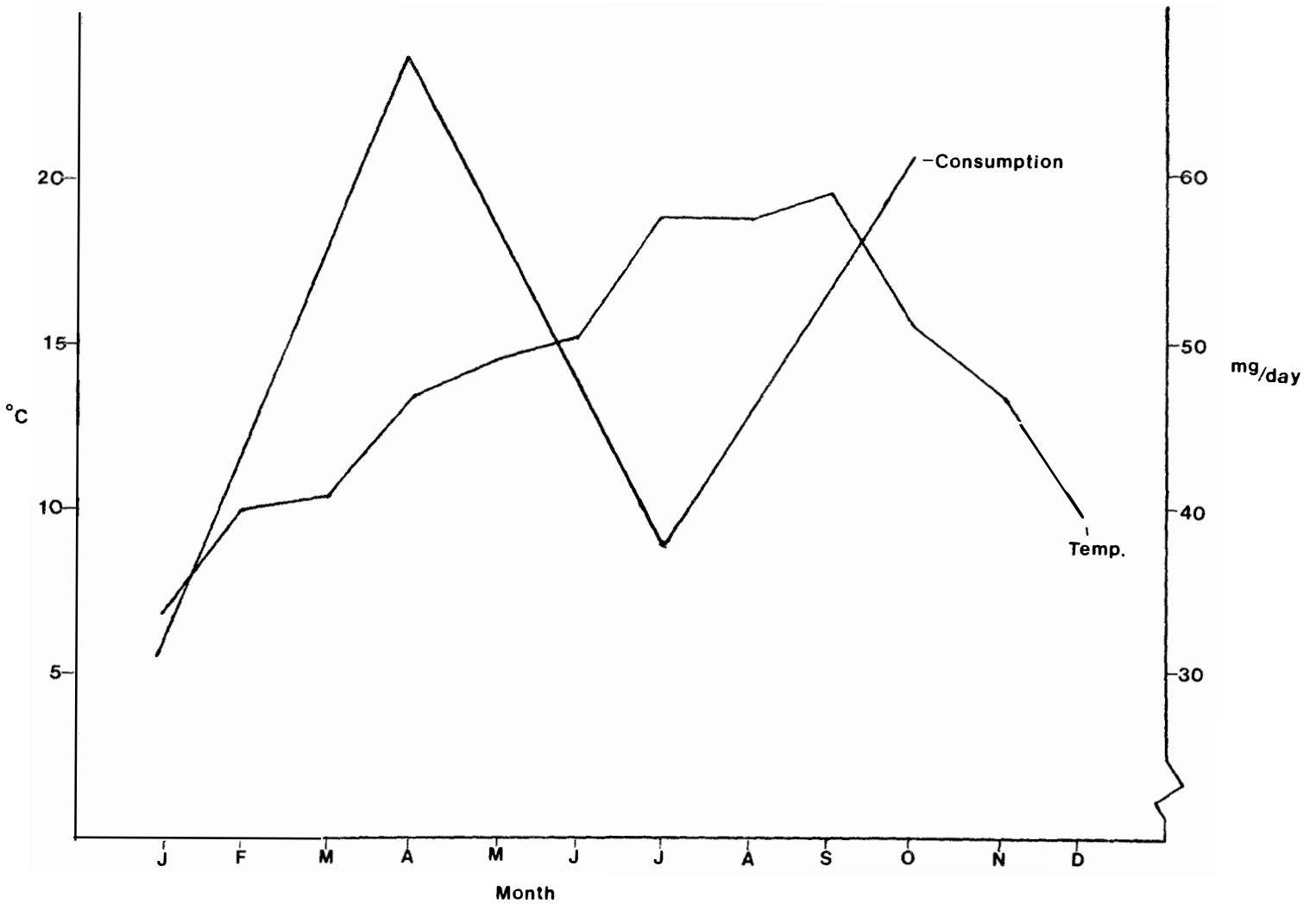


Figure 20. Monthly average water temperatures of the Lower Little Tennessee River and season food consumption levels of *Percina tanasi*.

studies with consumption dropping in mid-summer despite rising temperatures. There may have been some correlation of consumption and water temperature, as intake did increase with temperature in spring and, indirectly, increased as temperatures decreased in the fall. It seemed most likely, however, that consumption levels were governed by a combination of factors involving both temperature dependent metabolic requirements and requirements linked with reproductive development. As was discussed under reproduction, gonadal development began in early fall with rapid development occurring as the winter spawning season approached. It seems most plausible that the fall diet increase was a reflection of needs linked to this growth. Further, increases in fall diet levels were not noted in other published studies of *Percina* nor were there notable increases in those of snail darter associates. All species concerned spawned much later than *P. tanasi* and had heavy diet increases in the spring months before spawning, further associating consumption with reproductive requirements.

Functional Morphology and Digestion

Weatherly (1972) discussed the digestive systems of various fishes possessing different dietary regimes. Carnivorous fishes generally possess well defined stomachs and a short thick-walled intestine. This type of alimentary system typifies all the darters including the snail darter. Organisms consumed by the snail darter are ingested whole and undergo initial digestion in the stomach. Gastropods, the principal diet element, are ingested whole and undergo a partial dissolution of the shell in the stomach. Upon reaching the pyloric area, these

shells are usually well cratered, and digestion of the animal inside apparently is well underway. Shells excised from the rear portion of snail darter guts apparently had undergone further craterization, and the snail itself was 40 to 60 percent digested. This relatively low digestive efficiency is apparently offset by the high volume of intake.

The relatively "harder" diet of the snail darter might suggest the presence of more powerful digestive enzymes relative to other darters, but indications were this may not be true. Prey organisms other than gastropods apparently did not undergo greater digestion than those consumed by associated species, and the few gastropods found in the stomachs of associates were in comparable states of digestion to those consumed by *P. tanasi*.

Adaptations suited to the ingestion of overall larger or non-compressible prey items might be expected in a darter which routinely consumes snails. Comparison of gape sizes between the snail darter and its darter associates lent substance to this theory. A contrived index of gape size (jaw length plus mouth width expressed in thousandths of standard length) was employed in this comparison, and the average gape index value of *P. tanasi* (194) was 16 percent greater than *P. evides* (167) and 67 percent greater than *P. caprodes* (116). Further, cursory examination of several other *Percina* species representing other subgenera indicated that snail darters and other members of *Imostoma* may have the largest relative gape size of any members of their genus.

Feeding Classification

Percina tanasi could be broadly classified as an obligate bottom feeder and a sight feeder. It spends all of its time on or near the

substrate and, therefore, must obtain food there. Such benthic behavior typifies the more advanced members of the genus *Percina* including *Imostoma* as outlined by Page and Smith (1970) and Winn (1958).

More specifically, *P. tanasi* might be classified as a selective forager. Within a given collection of snail darters, diet was quite similar in composition, regardless of the fact that individuals were collected from various parts of the habitat. This indicated that a degree of selectivity was in effect in the face of differences in local abundance of prey items. There are indications that this selectivity changed only on a seasonal basis as will be discussed later.

In contrast, associated species appeared to be much more opportunistic and could best be classified as opportunistic foragers based on observations that principal diet constituents varied considerably between individuals of the same species within a given collection probably reflecting local abundance of prey. Based on these observations, the more selective *P. tanasi* might necessarily have to range farther than its associates to obtain a meal; the extent and duration of the feeding foray being, of course, dictated by relative abundance of preferred food items.

Feeding Habitat

Alimentary analysis indicated that *P. tanasi* fed chiefly on organisms which were associated with the community of clean current-swept gravel substrates. Most prey species were those which characteristically were attached to stones in the gravel shoal areas such as snails and caddisflies.

The particular feeding microhabitat of the snail darter was further defined by the microdistribution of commonly consumed prey items. A fairly detailed knowledge of distribution of occasional prey items, caddisfly larvae of the genus *Hydropsyche*, was available due to observations of G. A. Schuster (pers comm). Two species encountered in the diet of *P. tanasi*, *H. morosa* and *H. venularis*, are commonly associated with smaller substrate constituents such as gravel. Notably absent from the diet was a common Little Tennessee hydropsychid, *H. sparna*, which was commonly associated with larger rocks. This may indicate a lack of feeding activity in areas of more course substrate or rubble. There is some possibility, however, that were *P. tanasi* feeding in areas of larger substrate, *H. sparna* might not have been accessible.

Other key prey items of the snail darter's diet were the gastropods. *Pleurocera canaliculata*, commonly associated with areas of slower current and varied substrate, was seldom encountered in snail darters. On the other hand, *Anculosa subglobosa* and *Physa* sp., both common in current-swept gravel areas predominated in gut samples.

A considerable amount of evidence, including alimentary analyses and feeding observations, indicates that *P. tanasi* feeds predominantly on or near the gravel shoal habitat it frequents the most.

Feeding Procedure

The manner in which *P. tanasi* obtains food was unique and differs considerably from that of any of its associates in the Little Tennessee River.

A typical feeding foray was that observed on October 13, 1974, and carefully recorded in field notes. An adult female snail darter was

encountered while snorkeling at about 0.6 m depth over the gravel shoal at Coytee Spring. Current was strong (approximately 0.5 m/sec), time was 1230 hours, and water temperature was 18° C.

After first regarding her observer for perhaps a minute, the snail darter appeared to resume her interrupted feeding foray. Maintaining a more or less rheotaxic orientation throughout, she fed in a systematic manner, traversing about 1 to 2 meters from side to side and progressing upstream in zig-zag fashion. The manner of progress was very halted, with long pauses and very short dashes. The pectoral, pelvic, and anal fins were apparently used as bracing or anchoring devices while the darter inspected the surface of stones for food items. The downstream faces of stones were carefully surveyed for organisms which were in abundance there. While resting behind a stone, the snail darter would carefully inspect individual organisms by slight turning of the head and rolling the eyes. If selected, the item was deftly snapped up by a quick sidewise motion of the head and slight forward movement. Caddisflies, if taken, were almost always extracted from their cases rather than ingested whole as evidenced by the scarcity of case remains in stomachs. Once the survey of a particular stone was completed, the snail darter resumed upstream or oblique movement in a halting manner until another stone was encountered for inspection. In this manner, the snail darter progressed about 4 m upstream in 20 minutes. At the end of this time, she released herself to be carried downstream, halting at times and facing obliquely downstream with caudal fin into the current until she was near the starting point of the initial foray. She then resumed feeding upstream again in a similar manner. Whether this maneuver

was an anomaly caused by the presence of the observer or was common to the behavioral repertoire is not understood. In other instances, snail darters were observed to feed in a continual upstream progression throughout the observation. Though *P. tanasi* is not particularly associated with vegetation, occasional strands of algae or *Podostemum* were encountered in habitat areas, and snail darters were observed to inspect this vegetation and pluck organisms from it on a few occasions.

Aquarium observations generally corroborated feeding behavior seen in the natural habitat during the first weeks after acclimation. The manner of feeding was quite similar to that employed in taking natural prey items as snail darters sought frozen brine shrimp (*Artemia*) which were placed in the tank. However, they quickly abandoned their benthic behavior after a few weeks, hastening to take food at the surface. Ultimately they fed quite recklessly and would even wrest food from the human hand.

Darter associates of *P. tanasi* were observed to feed in quite different manners. *P. caprodes* fed in a striking manner, often flipping and overturning stones with its nose in order to gain access to organisms beneath. After overturning a stone, *P. caprodes* inspected the under-surface and plucked desired food items before approaching another stone. They were observed to also feed on organisms attached to the substrate surface in a manner more similar to that of *P. tanasi*. Similar feeding behavior has been observed in other logperchs, including *P. burtoni* and *P. caprodes carbonaria* by the author and *P. rex* by R. E. Jenkins (pers comm). The other associated darter, *P. evides*, was observed to follow *P. caprodes* on occasion and clean those items missed by the logperch in

their feeding endeavors beneath stones. Usually, however, *P. evides* fed alone in a manner somewhat similar to the snail darter but covering the substrate much more rapidly and swimming a little above the substrate much of the time.

The third principal snail darter associate, *Cottus carolinae*, appeared primarily to employ ambush or stalking tactics in procuring its food items. Though never observed actually taking food, *C. carolinae* was often seen lying motionless beneath stones. In this manner, sculpins must surprise and quickly engulf the large prey items which often appear in the diet. Unlike darters, sculpins ingested caddisfly cases whole as evidenced by the preponderance of debris in the gut. The diet was highly varied, reflecting opportunistic feeding on whatever unwary prey items they could obtain.

Feeding in these varied fashions, the principal associates of the snail darter are quite divorced from *P. tanasi*'s feeding niche, and individual feeding behavior is an important definitive aspect of that niche.

Temporal Aspects of Feeding

It was noted in Chapter I that care was taken to excise stomach contents and segregate them from those of the hindgut. It was found in early dissection that snail darters retained alive for 24 hours or so generally defecated the entire contents of the alimentary tract. With this rate of voidance known, it was assumed that any contents of the hindgut were consumed within the 24 hours just prior to capture, and those of the stomach in the last few hours before capture. This was

further substantiated by the large percentage of fresh undigested organisms in stomachs. The ratio of food organisms in the stomach compared to the hindgut ranged from 71 percent to 97 percent on a seasonal basis. As all collections were obtained between the mid-day hours of 1000 and 1400, it was evident that feeding had taken place in the daylight hours, and hindgut contents appeared to be remains from the previous afternoon's feeding. Thus, feeding probably occurred periodically throughout the daylight hours classifying the snail darter as a diurnal feeder. A number of mid-day feeding observations seemed to preclude any possibilities of strictly crepuscular or morning-afternoon feeding patterns.

Diurnal feeding was evident in studies made on other members of *Percina* by Thomas (1970). Many snail darters observed during daytime hours were not feeding, even though they were given a wide berth to lessen the chances of fright and disturbance of natural activity. Therefore, it was assumed that feeding was a periodic phenomenon interspersed by periods of inactivity.

As noted in Chapter V, scale studies of *P. tanasi* indicated that there may have been cessation or reduction of feeding during times of excessive flooding. This could have been due to difficulties in locating food because of extreme turbidity. Other causes may have been displacement of snail darters from the feeding habitat or unusual temperature changes.

Selectivity versus Availability

Upon initial examination of dietary data, dominance of certain food items in the diets of *P. tanasi* and its associates indicate that

either high degrees of selectivity are being employed or availability is a strong governing factor in determining their respective diets.

Page and Smith (1970, 1971) concluded that relative availability of prey species governed the diets of *P. sciera* and *P. phoxocephala*, respectively. Thomas (1970), however, offered evidence that some selective feeding did occur since certain organisms seemed to be avoided by *P. maculata* and *P. phoxocephala* (elmid beetles, plecopterans). But, this seemed to be a misinterpretation of results, however, since these prey items live chiefly beneath stones and are hence essentially unavailable to these darters. The third species considered by Thomas, *P. caprodes*, feeds beneath stones and, as might be expected, elmids and plecopterans were present in the diet tabulations. Fahy (1954) considered the diet composition of *Etheostoma blenniodes* also to be a function of availability.

In order to ascertain the possibilities of selectivity being exercised in *P. tanasi* or its associates, it was necessary to analyze the respective diet compositions in light of availability. Ivlev (1961) discussed selectivity at great length and expressed a formula whereby indices of electivity (selectivity) could be realized by the ratio of the proportion of a given food item in the diet (ration) to the proportion available in the environment. The relationship was expressed as follows:

$$E = \frac{(r_i - p_i)}{(r_i + p_i}$$

where E represents electivity, r_i relative amount of a given food item in the diet, and p_i the proportion available. Ivlev published a nomogram to facilitate computations, and the results of this analysis applied to the 10 most common prey items of the snail darter and associated darter species appears in Table 5, based on 6 months of availability data. Electivity values range from -1 to +1, and the higher the E value, the higher the degree of selectivity exercised.

This analysis is, however, complicated by the relative accessibilities of certain prey items even though they were seemingly available based on benthic sampling data. The behavior of prey items as well as feeding behavior and capabilities of the predator determine this. Many prey items in Table 5 were most common beneath stones and, thus, most accessible to *P. caprodes* and *C. carolinae*. The best comparison, therefore, was between *P. tanasi* and *P. evides*, neither of which fed beneath stones. Considering first *P. tanasi*, it is evident from inspection of Table 5 that relatively high electivity values occurred in each of the sample periods for the gastropods *Anculosa* and for *Physa* during two periods. Some selection for *Glossosoma* was indicated in the spring diet, but values for all other prey items were low or negative implicating inaccessibility or actual avoidance of available organisms. However, chironomids were clearly available as indicated by the diet of *P. evides*, although they were almost entirely avoided by *P. tanasi*. *P. evides*, on the other hand, tabulated relatively low values of electivity for chironomids and showed high selectivity, only for simuliids in early summer. Other items had mostly negative values which were

Table 5. Electivity Values (E) (Expressed in Hundredths) for 10 Predominant Prey Items Based on Monogram (Ivlev, 1961) Considering Proportion of Item Available (Pi) and Ration (ri) in the Diets of *Percina tanasi* (*Pt*) and Three Associates, *P. evides* (*Pe*), *P. carbonaria* (*Pc*), and *Cottus carolinae* (*Cc*)

	Early Winter								Early Spring								Early Summer							
		Pt		*Pe*		*Pc*		*Cc*		*Pt*		*Pe*		*Pc*		*Cc*		*Pt*		*Pe*		*Pc*		*Cc*	
Prey Item	Pi	ri	E	ri	E	ri	E	ri	E	Pi	ri	E	ri	E	ri	E	ri	E	Pi	ri	E	ri	E	ri	E	ri	E
Amoeloma	13	89	75					03	60	09	32	55							15	22	19						
Phoxinus	02	06	50							01	0								01	15	81						
Percina copelandi	39			03	-86	02	-89	06	-72	47	23	-35	06	-78	06	-78	02	-92								07	71
Hybognathus	03			01	-60	04	16	26	76	01	02	10	01	0	04	34	11	76	01	01				32	89	11	72
Etheostoma	02					03	08	01	-34	01	05	45			01				07	07	-05	04	-34	34	65	03	-40
Luxilus cerasinus	02							03	08	06	04	-25					06	0	11			02	-68	01	-84		
Ephemerella	01							05	60	03	02	-26	05	10	03	0	14	54	03	01	-60	02	-26	01	-60	06	58
Stenonema	04	01	-60	01	-64	-01	-64	03	-20	01	02	10	01	0	01	0	05	60	01							03	32
Simulium	01			01	02	01				01	0		01	0	14	80			01			85	96	06	60	04	40
Chironomids	32			92	46	78	42	41	13	35	04	-60	69	32	62	28	52	19	59	01	-97	06	-81	01	-93	64	05

probably attributable to inaccessibility, thus, suggesting that *P. evides*' diet was governed largely by availability. *P. caprodes* and *C. carolinae*, with the full range of food items available to them, showed little selectivity, although *P. caprodes* possibly exhibited some preference for simuliids in the spring diet and possibly *Hydropsyche* and *Glossosoma* in the early summer. Largely, however, E values indicated that the diets of these two snail darter associates were also governed by availability. Oddly, the most abundant prey item in the river in winter and spring was *Brachycentrus*, and its use was not nearly proportional to its abundance indicating avoidance by all species studied. It may be possible that the bristled case serves as an effective deterrent to predation.

Considering both the electivity study and the overall annual diet, it was apparent that *P. tanasi* exercised exceptionally high selectivity throughout the year relative to its associates, specializing primarily on gastropods. The diets of associated species were governed to a much higher degree by availability of prey items which classified them largely as opportunistic. Although Thomas (1970) found no gastropods in the diet of *P. shumardi* from Illinois, they have been excised from specimens from the Buffalo River, Tennessee, as well as from *P. ouachitae*. All members of the subgenus *Imostoma* may have a predilection for specialization on a gastropod diet where these items are available.

Selection of prey size may also be a characteristic snail darter trait. Mouth size probably restricts the maximum diameter of gastropods consumed by *P. tanasi* to little more than 5 mm, and a full size range from 1 to 5 mm occurred in the diet. Figure 21 showed a positive relationship between sizes of prey consumed (shell diameter) and standard

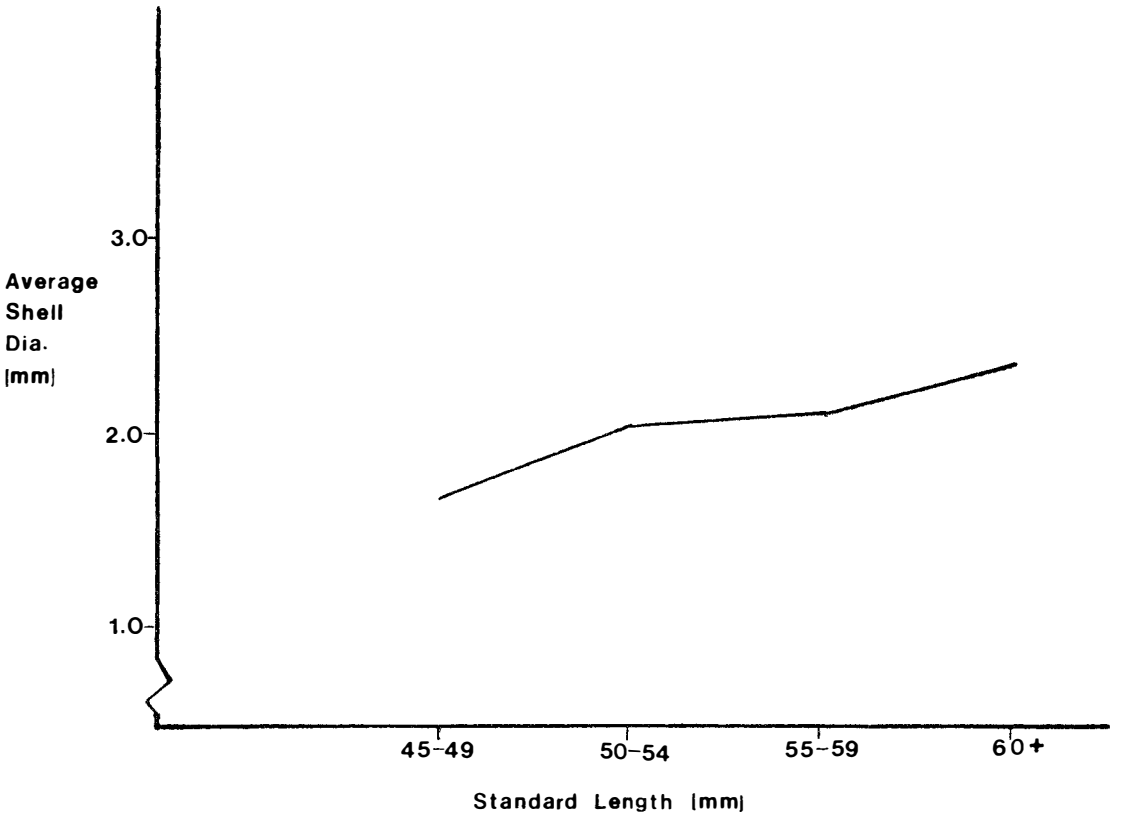


Figure 21. Average prey size (gastropod shell diameters) of different size classes of *Percina tanasi*.

length. On inspection of raw data, however, it is evident this relationship was caused by a high occurrence of 4 to 5 mm shells in the diet of larger individuals but not by the absence of smaller prey in these same individuals. Since an abundance of smaller prey was also present in larger snail darters, it seems clear that morphological restrictions rather than selectivity must be governing the size of prey items consumed by the various length classes of snail darters. Elongate prey items, such as insects, were consumed in random fashion with respect to size by all length classes examined, and prey items up to 10 mm in length were not uncommon in the diet. Therefore, prey size selectivity may be minimal or nonexistent.

Potential for Competition

Weatherly (1972) proposed a seemingly sound and applicable definition of competition: "The state existing between animals securing supplies of the same resource from one region of an environment, resulting in an interaction that produces some actually or incipiently deleterious effect on one or each of the animals involved." Care has been exercised throughout this work to refer to cohabitants of the snail darter as "associated species" rather than competitors. Thus, implication of the existence of a state of competition for food or other resources in the Little Tennessee was refrained from until the potential could be analyzed. Having at hand availability data on prey organism density and biomass from a 6-month period (Table 6) and over consumption figures for *P. tanasi* (Table 4, page 89), a crude analysis of competition potential is facilitated.

Table 6. Average Available Biomass per m^2 for 10 Principal Darter Prey Items From Gravel Shoal Habitat, Little Tennessee River

No. of Samples		15			11			15		
	Mean Wt. Per	Early Winter			Early Spring			Early Summer		
Prey Item	Organism (mg)	No.	S.D.	mg	No.	S.D.	mg	No.	S.D.	mg
Anculosa	3.3	15.4	17.2	50.8	14.2	16.4	46.8	20.6	30.8	61.9
Physa	3.3	3.7	4.8	9.9	.3	.6	.9	1.0	3.5	3.3
Brachycentrus	13.1	44.8	41.9	586.8	66.6	73.1	872.4	1.6	3.0	20.9
Hydropsyche	14.9	3.7	7.3	55.1	1.3	1.9	19.3	1.1	1.9	16.4
Glossosoma	1.7	2.0	2.7	3.4	1.6	1.0	2.7	10.3	12.2	17.5
Lepidostoma	.5	2.0	3.8	1.0	9.3	11.6	4.6	16.0	16.6	8.0
Ephemerella	13.9	.9	1.7	13.0	4.8	4.1	67.2	4.3	5.9	60.2
Stenonema	14.0	5.4	11.3	75.6	.4	1.2	6.3	2.1	3.0	29.4
Simulium	.4	---	---	---	---	---	---	1.7	3.9	.7
Chironomid	.4	37.1	52.0	14.8	55.2	55.2	22.0	83.3	123.3	33.3
Totals				810.4			1042.2			257.6
Average Overall Biomass/m^2										703.3

Before discussion of factors which complicated analysis of competition is offered, a grossly simple analysis can be made to provide a basis of discussion. Based on population estimates, density of snail darters was 6.6 ind/100 m^2 in the optimal habitat. Though no detailed study was conducted on density of associated species, it was inferable from collection efforts and field observations that the three principal ones occurred in roughly equal numbers to *P. tanasi* on an annual basis, though snail darters were periodically more dense. Thus, an average population estimate of about 25 to 26 ind/100 m^2 was ascertained for the four species combined. With the exception of fall, average daily biomass intake appeared to be roughly similar for all species involved except larger sculpins. These, however, most often occurred in areas of more coarse substrate which were peripheral to the microhabitat being analyzed.

Putting aside momentarily differences in accessibility, the average prey biomass available (predominant prey items) was 703.3 mg/m^2 based on winter-spring benthic data (Table 6) from the gravel shoal microhabitat. *P. tanasi*'s average daily intake was 49.2 mg based on annual diet data (Table 4, page 89), and a conservative estimate was that associates too required approximately 50 mg/day. Therefore, about 1,250 mg/day were required to maintain the 25 or so individuals in a 100 m^2 area on a given day. They could have been sustained at full ration for 56.2 days by the food supply available within that area (70,330 mg) assuming no replenishment. Based on this simple model, it was clear that competitive exclusion or diet reduction of all species involved would have occurred within 3 months if other factors were not involved.

Fish density was observably low in the Little Tennessee relative to most other rivers, but prey density seemed comparable to other streams. How then could there have been competition between the snail darter and associates when the competition potential was obviously much greater in other rivers supporting much larger fish populations?

The answer must be in factors which influence the true availability of food items to the snail darter and its associates. These, while complicating the model, were apparently responsible for allowing coexistence. First of all, production of various prey items would have been highly differential. Many prey organisms would have undergone almost continual replenishment on a short-term basis, while others by and large have only annual replacement cycles. Based on benthic data and life history information, prey items falling into the first group would have been gastropods and many dipterans, while trichopterans and ephemeropterans were basically annuals. Periodic benthic sampling indicated a reasonably constant influx of young snails and chironomids. These resources appeared to be replenished rather constantly as evidenced by consistency in benthic samples; therefore, about 12 percent of the biomass was being replaced on a short-term basis. Although this would have contributed a substantial amount to the carrying capacity of the habitat, it could hardly have accounted for the apparent over abundance of food items which existed there.

In addition to partial replenishment, supplemental food sources for one or more species involved must have played a role in creating the apparent surplus carrying capacity of the Little Tennessee gravel shoal habitat. Whereas the density of snail darters and probably

P. evides was greatest in the gravel shoal habitat; the other two associates, *C. carolinae* and *P. caprodes*, were observed to frequent a variety of other habitats. Thus, foraging widely for their food, pressure from these two species on the gravel shoal food supply would have been considerably lessened.

Another potential source of supplemental food was incoming drift from peripheral habitats upstream. Hynes (1970) cited several studies in which tremendous numbers of invertebrate organisms were found to drift through a given habitat in a short time. Whether this would have contributed significantly to the benthos in swifter shoal areas is questionable, and it may even have a negative effect, reducing the fauna in swifter areas.

Added to the above factors, the specialization, differences in accessibility, and partitioning of food that occurs between the snail darter and its associates must further lessen the potential of competition at present population densities. The snail darter's specialization on gastropods and the apparent avoidance of this prey item by other species creates a dietary regime little encroached on by associates. Therefore, based on this analysis and the evidence of food surpluses, it seems a valid conclusion that food competition is not a limiting factor to the present-day population of *P. tanasi* or its companion species.

To put competition into the proper perspective, it would be necessary to know conditions which existed prior to impoundment of the Little Tennessee River. If existing limitations acting on fish density are a function of physical factors of the tailwater regime as they seem,

then it is reasonable to assume that fish density was considerably greater in preimpoundment days. Food competition may then have been one of the several natural limiting factors to the snail darter population.

Food Web

The food web of the lower Little Tennessee River gravel shoal areas might have been considered a rather simple one in light of the relatively low species diversity. Considering only the snail darter and its three principal associates, along with the most commonly consumed prey items, a food web scheme as depicted in Figure 22 became evident. *P. tanasi* and its companion species would have constituted a high percentage of predators within the gravel-sand portions of the habitat under consideration.

The snail darter could be considered strictly a first level carnivore. All its prey items, gastropod or insect, were algal feeders or detritivores. The same was largely true of its darter associates, *P. caprodes* and *P. evides*, though *P. caprodes* did prey upon predaceous stoneflies to some extent, making it a second level carnivore to a small degree. *Cottus carolinae* consumed considerably more plecopterans and an occasional fish allocating them to multiple first, second, and third level positions in the web.

Relative width of connectives between the snail darter and its food sources in Figure 22 based on overall annual consumption figures and the distinctive food niche of the snail darter becomes vividly clear upon examination of these sources in light of the total food complex of

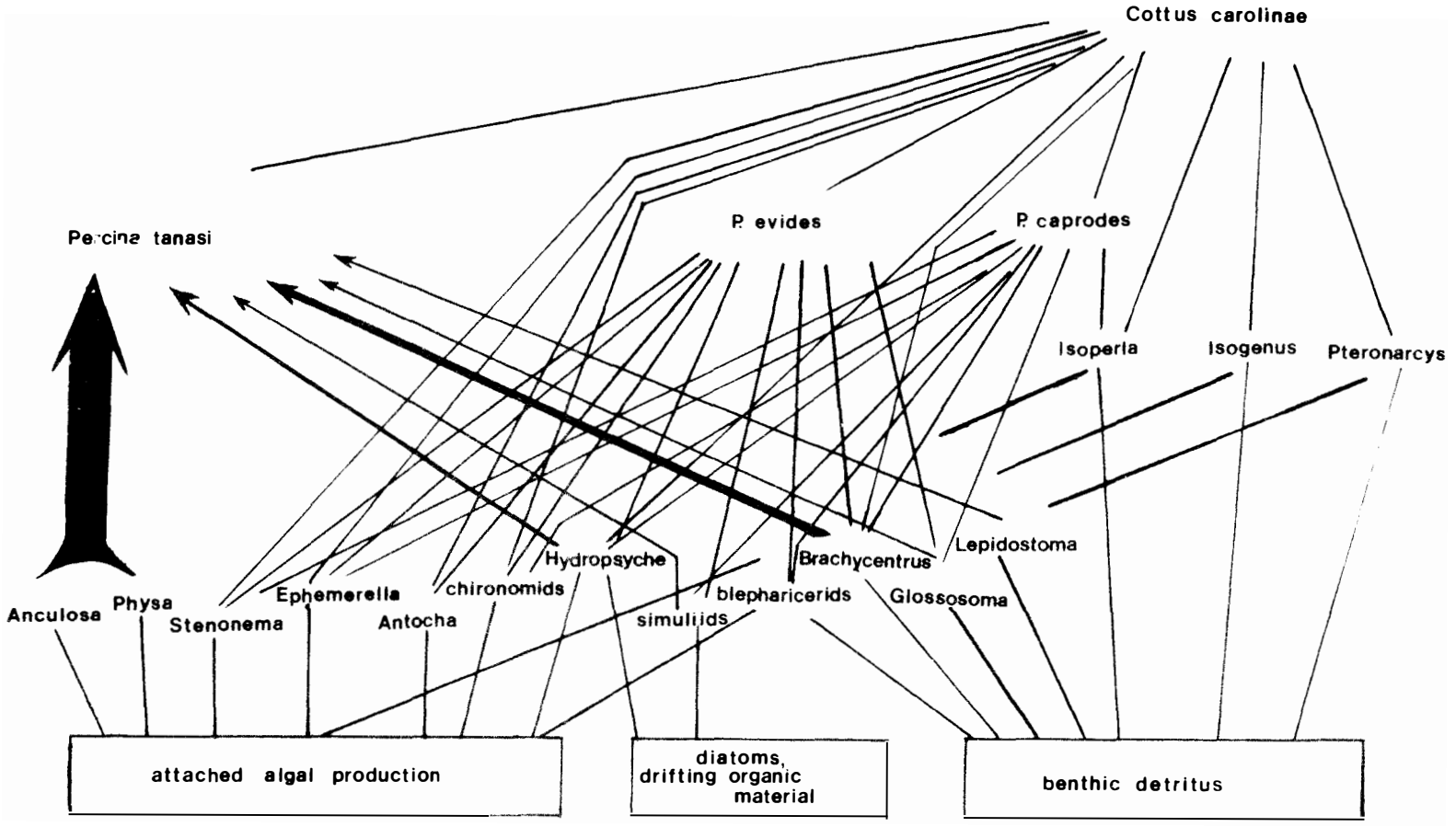


Figure 22. Food web of Little Tennessee River gravel shoal habitat considering *Percina tanasi* and its three principal associated fish species. Widths of connectives to *P. tanasi* reflect relative contributions of prey items to its diet. Food sources of invertebrates are based largely on Pennak (1953).

its habitat. Although positioned on the first carnivore level along with several of its associates, *P. tanasi*'s specialization on gastropods places it in a relatively remote position within the web. The relative position of other *Imostoma* in their respective habitats is probably quite similar where availability of preferred food items permits.

CHAPTER VIII

PREDATION AND PARASITISM

Predation on adult snail darters may well be an insignificant contribution to mortality under existing conditions. As stated in Chapter III, large potential predatory species known to occur in the Little Tennessee River are *Salmo trutta*, *S. gairdneri*, *Morone chrysops*, *Stizostedion canadense*, and *S. vitreum*, as well as possibly *Micropterus* species. Pfitzer (1954) described the tremendous influx of warm water fish species which occurred in the lower Little Tennessee prior to the creation of Chilhowee tailwater. *Morone* and *Stizostedion* were quite abundant and may have been formidable predators within the snail darter's habitat before alteration of the temperature regime. Presently, except for seasonal migrations, white bass (*Morone*) and sauger (*Stizostedion*) are far from abundant in portions of the river containing the majority of the snail darter habitat, and walleye (*S. vitreum*) are quite rare in the system.

The brown trout (*Salmo trutta*) has been known to consume sculpins (Dineen, 1951; Tebo, 1963) and presumably would take a snail darter if the opportunity presented itself. However, trout occur primarily upstream of snail darter habitat and, thus, are probably of little consequence.

Camouflaging dorsal patterns, benthic habits, and burrowing behavior of snail darters probably render them nearly inaccessible to most potential large predators which might forage in the shallower shoal

areas. Perhaps the most effective predators on adult snail darters may be sculpins. Sculpins are known predators on other small fish species (Bailey, 1952; Daiber, 1956) and may, by virtue of a large mouth, engulf prey almost as large as themselves. Further, the remains of an adult snail darter were excised from the stomach of a large specimen of *Cottus carolinae*. The ambush tactics of sculpins would render the passive defenses of the snail darter ineffective, and encounters between these two species may occasionally result in the demise of a snail darter.

It would seem that predation on adult snail darters would be relatively insignificant based on the above discussion. Yet, the mechanisms whereby the relatively high mortality between 1st and 2nd year classes was achieved has to be questioned. Perhaps periodically in their adult life snail darters are more susceptible to predation. This may occur during migrations through deeper water habitats where large predators are more prevalent, and the snail darter's passive defenses are less effective.

Predation doubtless is extremely high on the younger stages of the snail darter. Probable snail darter eggs were removed from the stomachs of adult snail darters, so they are in a sense cannibalistic. Fish eggs are consumed by all associates of the snail darter, and undoubtedly large numbers of *P. tanasi* eggs are consumed during the prolonged prehatching period. Even more prolonged is the early development phase of the larvae, which evidently drift great distances. Drifting larvae would be highly vulnerable to any small fish species, and the speculated semi-planktonic larval habits would further increase this vulnerability. Certainly a large percentage of snail darters must be

lost before undergoing transformation and returning to the relative safety of the substrate, and more are doubtless lost to predation before migrating to the shoal area.

Snail darters were relatively free of detectable macroparasites. A few leeches (*Piscicolaria reducta*) were removed from fins but were present on less than 3 percent of the specimens examined. Nematode parasites were common to abundant in alimentary tracts of all associated species but surprisingly were never present in snail darter stomachs. Further, examination of gills on several specimens failed to reveal any parasitism. All species examined from the Little Tennessee River appeared to be free of the metacercaria of trematode strigeoid parasites often encountered on fishes from other rivers.

It is difficult to speculate whether the apparent low rate of parasitism enjoyed by *P. tanasi* is a long standing natural situation. It seems quite conceivable that the cold tailwater regime of the lower Little Tennessee may not be highly conducive to parasitism, thereby reducing infestations below levels of many other streams.

CHAPTER IX

SUMMARY

A 2-year study of the ecology and life history of the snail darter has revealed many interesting facts concerning aspects of its lifestyle and interrelationships with its environment and three principal cohabitants. Some of the findings were anticipated while others were surprising and perhaps, at first, enigmatic.

The snail darter was found to be primarily a species of the benthos as are most other darters, although at some early stages in their life, they evidently might have been considerably less associated with the substrate. As with other fish species associated with strong current, they maintain an essentially rheotaxic orientation which, along with morphological adaptations, facilitates existence in their tumultuous environment.

As with other members of the genus *Percina*, *P. tanasi* exercises little or no territoriality, though a possibility exists that some moving territory maintenance occurs. Low population densities generally did not permit observations involving more than one individual, thus, making such assumptions difficult. Individuals appeared to forage in rather random manner throughout the shoal habitat though feeding was systematic on a localized basis.

As with many other fishes adapted to life in gravel riffle areas, *P. tanasi* has evolved a pattern of protective coloration. A disruptive pattern of dorsal saddles coupled with its habit of remaining motionless in the face of approach make snail darters virtually invisible against the substrate. Added to this is the ability to alter color

patterns according to various backgrounds, and burrowing behavior which assures the snail darter a high degree of passive defense against predation. Burrowing behavior may also be an energy conservation measure.

Investigations within the lower Little Tennessee and adjacent Tennessee rivers, coupled with numerous collection records from throughout the Tennessee drainage, indicated that the entire extant range of the snail darter was situated within the area of investigation. The upper extremity of *P. tanasi*'s range in the Little Tennessee may be the shoal area at Davis Island 24 km above the mouth, although some marginal habitat exists at Rose Island 3 km further upstream. It appears that the presence or absence of sand-gravel substrate may define the upper distribution limit.

A marginal, probably nonreproducing population in the Tennessee River about 16 km below the mouth of the Little Tennessee may represent the lower range extremity. Within this macrohabitat *P. tanasi* is usually most closely associated with the gravel shoal environment. It appears that most of the adult life of the snail darter may be spent in these areas which range from 0.3 m to nearly 2 m in depth and have current velocities ranging from 0.25 to nearly 1 m/sec. Substrate in these areas is typically micaceous sand with about 50 percent coverage of coarse gravel swept relatively clean of silt. Four principal areas of the river contained most of this habitat, including the rather deep shoal area below Davis Ferry, and shallower shoals at Coytee Spring-Tolliver Island, Morganton Ferry, and Davis Island. Deeper intervening portions of the river probably play important roles as refugia for

early development and probably harbor a low percentage of the adult population at times. The same may be true of the adjacent Tennessee River below the mouth of the Little Tennessee.

Age and growth analyses indicate that the snail darter lives but a little over 2 years reaching sexual maturing during the 1st year of life. A standard length of about 55 mm to 60 mm is commonly attained in the 1st year and 2-year-olds may reach 75 mm SL. If body length is chosen as a measure of growth, then snail darters exhibit a rather typical growth curve. Growth is rapid during the 1st year with about 85 percent of adult standard length attained. However, if one chooses to employ the length-weight relationship as an index of growth, the rate of increase is almost at unity throughout the 2-year lifespan. The growth of males exceeds that of females during the 1st year, averaging 3 percent greater standard length. However, during the 2nd year, females attain comparable lengths. This growth pattern may be attributable to greater metabolic demands on the females related to reproductive development.

The dispersion of snail darters within their range is highly localized with respect to density. Maximum density apparently is attained at the Coytee Spring-Tolliver Island area averaging 6 to 7 ind/100 m^2 and evidently even higher densities are reached during the reproductive period. Due to localized aggregations at this time, real density would be considerably in excess of this in small areas. Below Davis Ferry comparable densities probably exist during the late spring and summer on the deeper shoals there, but many of the individuals may migrate upstream during the spawning season. Progressing upstream,

population densities decrease drastically above Tolliver Island. The Morganton Ferry and Davis Island populations are much less dense, averaging 1 to 4 ind/100 m^2. Downstream, densities were probably quite high in summer due to a preponderance of young-of-the-year which drifted down as larvae.

There are strong indications of migration in snail darter populations. Reciprocating densities at shallow and deeper shoal areas suggest movements to shallow areas in response to reproduction. Further, there is an apparent mass upstream migration of young-of-the-year from deeper refugia downstream following early development. This occurs during the early summer months with individuals returning to the shoals at the age of 3 to 4 months and about 35 to 40 mm SL. Some may remain downstream for a time, persisting in the Tennessee River.

The age composition of this short-lived species is rather simple. It appears that mortality is rather high during the 2nd year of life (about 80 percent), and, thus, Age Class II individuals comprise but 20 to 25 percent of the population. Though available data indicated a sex ratio dominated by males, it is felt that this is an artifact of collection time and technique, and that the true ratio approaches 1:1.

Perhaps one of the most surprising discoveries of the study was the early spawning season. Although expected to spawn in spring as most other darters do, snail darters were observed to attain high nuptial condition during the fall. However, this development was understood when it became evident that spawning was occurring in mid-winter. No threshold condition could be detected which may have been responsible for triggering spawning behavior. Water temperature was definitely

ruled out. Photoperiod may be responsible, but this has been ruled out in experiments on other darters. A cycle based primarily on hormonal activities and triggered by threshold levels may be involved. Spawning season extends from early February to late April.

It became increasingly obvious as the study progressed that the spawning habitat was the gravel shoal areas of the Little Tennessee River. Relatively heavy concentrations of snail darters began appearing in the shoal areas during winter, and aggregations and spawning observations indicated that the shallower current-swept portions of the shoals were serving as the spawning microhabitat. Males precede the females to the spawning microhabitat, and the females become more abundant as the season progresses.

Fecundity is rather high in *P. tanasi*. Gonadal development begins in early fall in preparation for the winter spawning season, and by December or so an average 600 ova have matured. Data from small samples indicate that fecundity is not highly size-related in *P. tanasi*, although this has to remain somewhat inconclusive. In males, gonadal development is correspondingly early, and many individuals are flowing freely by late November.

As studies of other *Percina* have indicated, there is evidence to indicate that *P. tanasi* is a multiple promiscuous spawner reproducing over a period of several weeks. Courtship behavior observed and patterns of tuberculation suggest that snail darters spawn in approximately the same manner as other members of the genus, although probably in swifter water than most. Heavy tuberculation may be an adaptation to facilitate spawning in areas of strong current.

Lab studies on early development of the snail darter reveal a slow development process. At low winter water temperatures (6° C), hatching may take 18 to 20 days. It required 15 days for eggs to hatch at 12.5° C. At 30 days larvae were still subsisting on the yolk, and they probably would have existed as postlarvae for several weeks after this period under natural conditions before undergoing transition to juvenile stages. During this prolonged period, a substantial amount of larval drift apparently occurs, the young darters being transported to deeper areas considerably downstream of the shoal areas in the Little Tennessee and even into the Tennessee River. Survivors return upstream as juveniles.

Possibly most unique of all the aspects of *P. tanasi*'s ecology are the dietary relationships. As the name suggests, the snail darter specializes heavily on gastropods. Although varying seasonally, gastropods comprise nearly 60 percent of the annual diet in terms of biomass. Trichopterans provide the second most important food source constituting about 22 percent of the consumed biomass. This diet differs tremendously from associate species whose diet emphasis is on dipterans. In terms of overall consumption levels, the snail darter's intake increases markedly in fall (62.2 mg/day) in the months prior to spawning. There is low consumption during the winter breeding season (31 mg/day) and a substantial increase in spring following spawning to 67.2 mg/day. Summer levels are a lower 37.5 mg/day. Consumption levels seem to co-relate best with reproductive activities, being high just prior to and following the spawning season. They do not seem to correlate highly with water temperature.

Morphologically, snail darters are apparently well adapted to taking relatively large and incompressible prey. Gastropods in excess of 6 mm diameter are sometimes consumed. Relative gape size proves to be largest in *P. tanasi* in a survey of its associate darter species and several other species of *Percina*.

P. tanasi is broadly classified as an obligate bottom feeder and a first level carnivore. Its diet reflects the feeding habitat which apparently is largely confined to gravel-sand portions of shoals. The feeding manner of the snail darter is quite unlike any of its associates. Feeding activity is diurnal. With respect to availability, a high degree of selection is apparently exercised by snail darters most of the year with specialization on gastropods. Its associates appear more opportunistic. Food competition does not seem to be a reality in the Little Tennessee River at existing population levels. It would appear not to be a limiting factor on *P. tanasi* in its present environmental situation. The dietary regime of the snail darter is apparently little encroached upon by other species, and it seemingly occupies a remote position in the Little Tennessee food web.

The chief predator upon adult snail darters is probably *Cottus carolinae*. Other potential predators are *Salmo truttae*, *Stizostedion canadense*, *S. vitreum*, and *Morone chrysops*, although their contribution to predation is probably minimal most of the time. Larval snail darters and eggs are probably preyed upon heavily by darters of all kinds, including *P. tanasi*, as well as other species of small fish. Snail darters are virtually free of noticeable parasitism.

Conclusions

The summarized findings of this study, although not discussed in great depth, describe the ecological niche of the snail darter. Further, general niche definitions for this species may be applied in varying degrees to other members of the subgenus *Imostoma* as suggested by fragmented data and a single published life history.

The chief characteristics which probably divorce the niche of *Imostoma* and the snail darter from other *Percina* are aspects of diet and reproduction. Members of the subgenus spawn very early in the year, so they are temporally removed from competition for spawning sites. Within *Percina*, they spawn in perhaps swifter water than most other members, further limiting competition. Larvae are also spared food competition from later spawners. Further, the adults specialize in a diet of gastropods where availability permits, insuring for themselves a food source little contested by other darter species.

On the negative side, early spawning at cold water temperatures prolongs the early development phases of life. This sustained period of vulnerability surely must take its toll in mortality of the young. Perhaps the relatively high fecundity of snail darters, and probably *Imostoma*, may be an evolutionary response to counteract this situation. The larval drift phenomenon so dramatically implicated in this study is probably common to other *Imostoma* and many other fluvial species as well.

So evolved and specialized, the snail darter, as well as other fluvial species, is quite vulnerable to alterations of any one of the several microhabitats it requires throughout its life. The overall

effect of such perturbations may be either a reduction in population or complete extinction. The dependence on the flowing gravel shoal habitat for reproduction, and to some degree feeding, makes this species highly vulnerable to impoundments as evidenced by its restricted range. Denied access from such habitats, the snail darter has surely been extirpated from most of its more extensive former domain.

Although the Little Tennessee represents the last ecosystem containing all qualities upon which *P. tanasi* is dependent, there is evidence that considerable perturbation may have occurred there due to upstream impoundments. Although the water quality is exceptional, fish population density is quite low. Food appears not to be the limiting factor, thus, implicating reproductive success. The depressed temperature regime and extended development period probably adversely effects many species. However, in the case of an adapted winter spawner, such as the snail darter, the increased average current velocity may be a primary factor. Larval drift may be considerably enhanced to the point that most are swept entirely out of the river into areas of more intense predation and possibly limited food supply.

As an added result to decreased fish population levels, the tailwater regime of the Little Tennessee makes it impossible to ascertain what the ecological status of the snail darter and its associates were in preimpoundment days. It is difficult to place in perspective the various ecological relationships which may have existed when there was greater opportunity for interspecific and intraspecific interaction. Thus, a great deal must be left to speculation concerning the ecology and life history of the snail darter under natural conditions, and only

the details of what surely must be a substantially altered, but at least extant, lifestyle have been reported herein. *Percina tanasi* seems faced with almost certain extinction if the remainder of its habitat is inundated by the Tellico Dam project.

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APPENDIX

Table 7. Sex, Standard Lengths, Scale Lengths, and Back-Calculated Standard Lengths of 71 *Percina tanasi* at First (I) and Second (II) Annulus Deposition and Scale Edge (R)

Sex	SL	Scale Length I	Scale Length II	Scale Length R	Collection Date	Back-Calc. SL I	Back-Calc. SL II
J*	38			35	20 June 75		
J	39			36	16 Aug 73		
J	41			40	16 Aug 73		
J	43			37	20 June 75		
J	43			37	20 June 75		
J	43			39	16 Aug 73		
J	43			38	16 Aug 73		
J	43			35	16 Aug 73		
J	44			40	20 June 75		
J	44			37	16 Aug 73		
J	44			37	16 Aug 73		
J	44			41	16 Aug 73		
J	45			38	16 Aug 73		
J	45			40	2 Aug 75		
J	45			40	6 Sept 75		
J	46			39	6 Sept 75		
J	46			38	16 Aug 73		
F	48	38		44	6 Feb 76	44.6	
M	48			41	16 Aug 73		
?	48	44		49	2 Aug 75	50.1	
F	49	38		45	6 Sept 75	44.6	
M	50	35		42	6 Sept 75	41.9	
F	51	34		47	6 Feb 76	41.0	
M	52	38		45	16 Apr 76	44.6	
F	52	44		47	16 Aug 73	50.1	
M	53	39		52	31 Oct 75	45.5	
M	53	40		45	16 Aug 73	46.5	
M	54	31		44	6 Feb 76	38.3	
F	54	36		49	22 Apr 75	42.8	
F	54	36		49	16 Aug 73	42.8	
F	54	38		47	16 Aug 73	44.6	
M	54	38		50	16 Apr 76	44.6	
M	54	37		50	16 Apr 76	43.7	
F	55	35		46	20 June 75	41.9	
F	55	41		45	14 Nov 74	47.4	
M	55	39		46	16 Apr 76	45.5	
M	55	35		48	19 Dec 75	41.9	
F	55	37		47	19 Dec 75	43.9	
M	56	37		49	19 Dec 75	43.7	
F	56	39		47	19 Dec 75	45.5	
F	56	38		48	16 Apr 76	44.6	
F	57	38		50	16 Apr 76	44.6	

Table 7, continued

Sex	SL	Scale Length I	Scale Length II	Scale Length R	Collection Date	Back-Calc. SL I	Back-Calc. SL II
F	57	39		52	19 Dec 75	45.5	
F	57	34		64	16 Aug 73	41.0	
F	58	39		50	16 Aug 73	45.5	
M	58	42		52	22 Apr 75	48.3	
M	58	42		51	22 Apr 75	48.3	
F	58	41		54	16 Apr 76	47.4	
M	58	38		51	22 Apr 75	44.6	
M	59	39		57	31 Oct 75	45.5	
M	59	37		45	4 Nov 74	43.7	
M	59	40		50	16 Aug 73	46.5	
M	59	40		52	16 Apr 76	46.5	
F	60	36	55	57	4 Nov 74	42.8	60.1
M	60	30	49	53	4 Nov 74	37.4	54.6
M	61	40	52	55	6 Nov 73	46.5	57.4
M	61	38	55	58	4 Nov 74	44.6	60.1
M	62	39	54	60	31 Oct 75	45.5	59.2
F	62	39	53	57	6 Sept 75	45.5	58.3
M	62	38	51	56	6 Sept 75	46.5	56.5
M	62	41	49	57	19 Dec 75	47.4	54.6
M	62	37	55	59	22 Apr 75	43.7	60.1
F	64	39	55	62	22 Apr 75	45.5	60.1
F	64	41	44	54	6 Nov 73	47.4	54.6
F	64	37	49	60	31 Oct 75	43.7	54.6
F	64	36	47	57	6 Feb 76	42.8	52.8
F	66	39	54	68	31 Oct 75	45.5	59.2
M	66	37	51	55	4 Nov 74	43.7	56.5
F	66	40	49	59	6 Feb 76	46.5	54.6
M	66	41	57	62	31 Oct 75	47.4	61.9
F	67	40	52	58	22 Apr 75	46.5	57.4
	$\bar{X}$	37.4	52.0		$\bar{X}$	45.6	57.3
					S.D.	2.45	2.64
					Males Only	46.3	57.8
					Females Only	44.7	56.8

*Juvenile

Totals: 27 Males
26 Females
18 Juveniles

Table 8. Summarized Food Data of *P. tanasi* and Associated Species for Winter and Spring Stated as Total Number of Organisms Consumed and Percentage of Total Diet (Parentheses) to Nearest Whole Number

	Winter					Spring				
	P. tanasi	*P. evides*	*P. caprodes*	*C. carolinae*	Other*	*P. tanasi*	*P. evides*	*P. caprodes*	*C. carolinae*	Other*
N-------	11	24	11	31	7	15	17	19	15	0
Mollusea										
Sphaerium										
Anculosa	92(01)	2(01)		4(03)		43(32)				
Lithasia	2(01)									
Pleurocera	1(01)									
Physa	7(06)									
Ferrissia						15(11)				
Menetus										
Trichoptera										
Brachycentrus		11(03)	5(02)	8(06)	1(01)	31(23)	9(06)	23(06)	2(02)	
Hydropsyche		5(01)	12(04)	38(26)	1(01)	2(02)	2(01)	20(04)	14(11)	
Cheumatopsyche								2(01)	1(01)	
Macronemum										
Glossosoma			8(03)	2(01)		6(03)		1(01)		
Lepidostoma				4(03)	3(02)	5(04)			7(06)	
Ephemeroptera										
Ephemerella				7(05)		2(02)	8(05)	13(03)	18(14)	
Stenonema	1(01)	1(01)	2(01)	5(03)		2(02)	2(01)	7(01)	7(06)	
Plecoptera										
Pteronarcys				6(04)						
Isoperla				1(01)			1(01)	6(01)		
Isogenus			2(01)	5(03)						

Table 8, continued

	Winter					Spring				
	P. tanasi	*P. evides*	*P. caprodes*	*C. carolinae*	Other*	*P. tanasi*	*P. evides*	*P. caprodes*	*C. carolinae*	Other*
N	11	24	11	31	7	15	17	19	15	0
Diptera										
Chironomids		372(92)	216(78)	60(41)	118(96)	5(04)	109(69)	283(62)	65(52)	
Simulium		4(01)	1(01)				2(01)	63(14)		
Antocha	1(01)	7(02)	23(08)	5(03)			2(01)	10(02)	4(03)	
Blepharocerids		1(01)	9(03)			9(07)	21(13)	11(02)	7(06)	
Other										
Fish Eggs						11(08)	1(01)	15(03)		
Retinella (terrestrial gastropod)						1(01)				
Hymenoptera						1(01)				
Total Prey Items	103	403	278	145	123	133	157	454	125	

*Peripheral associates--*Hybopsis aestivalis*, *Nocomis micropogon*, *Phenacobius uranops*, *Hypentelium nigricans*, *Etheostoma rufilineatum*.

Table 9. Summarized Food Data of *P. tanasi* and Associated Species for Summer and Fall Stated as Total Number of Organisms Consumed and Percentage of Total Diet (Parentheses) to Nearest Whole Number

	Summer					Fall				
	P. tanasi	*P. evides*	*P. caprodes*	*C. carolinae*	Other*	*P. tanasi*	*P. evides*	*P. caprodes*	*C. carolinae*	Other*
N	24	6	4	10	4	17	8	10	14	7
Mollusca										
Sphaerium	5(01)									
Anculosa	115(22)					230(81)				
Lithasia										
Pleurocera	2(01)					3(01)				
Physa	80(15)					30(11)				
Ferrissia						1(01)				
Menetus	3(01)									
Trichoptera										
Brachycentrus				5(07)		6(02)		5(01)	13(52)	5(06)
Hydropsyche										
Chewmatopsyche	3(01)		22(32)	8(11)		5(02)		17(05)	3(12)	1(01)
Macronemum			2(03)		1(03)					
Glossosoma	38(07)	4(04)	23(34)	2(03)	3(17)	3(01)		18(05)		8(10)
Lepidostoma								10(03)		32(40)
Ephemaroptera										
Ephemarella	2(01)	2(02)	1(01)	4(06)		2(01)	34(81)	2(01)	1(04)	1(01)
Stenonema				2(03)		1(01)		26(07)		
Plecoptera										
Pteronarcys										
Isoperla										
Isogenus										

Table 9, continued

	Summer					Fall				
	P. tanasi	*P. evides*	*P. caprodes*	*C. carolinae*	Other*	*P. tanasi*	*P. evides*	*P. caprodes*	*C. carolinae*	Other*
N	24	6	4	10	4	17	8	10	14	7
Diptera										
Chironomids	3(01)	6(05)	1(01)	45(64)	6(33)	1(01)	7(17)	268(76)	8(32)	31(39)
Simulium	266(50)	93(85)	4(06)	3(04)	5(28)		1(02)			
Antocha	3(01)			1(01)	3(17)	1(01)		7(02)		2(03)
Blepharocerids										
Other										
Fish Eggs	9(02)	4(04)	15(22)							
Retinella										
Hymonoptera										
Total Prey Items	529	109	68	70	18	283	42	353	25	80

*Peripheral associates--*Hybopsis aestivalis*, *Nocomis micropogon*, *Phenacobius uranops*, *Hypentelium nigricans*, *Etheostoma rufilineatum*.

VITA

Wayne C. Starnes was born October 13, 1945, in San Bernadino, California, and resided there until 1950. After living in and attending schools in Natchez, Mississippi, and Dickson, Tennessee, he subsequently moved to Knoxville, Tennessee, in 1954. After graduation from Farragut High School of Knox County in 1964, he entered The University of Tennessee graduating with a Bachelor of Science degree in 1969. After serving as a lieutenant in the U. S. Army in Baltimore, Maryland, and Vietnam, he returned to The University of Tennessee and completed a Masters Degree with a major in Zoology in 1973. He subsequently entered the U. T. Graduate Program in Ecology in 1974 and received the Doctor of Philosophy degree in March, 1977. He is a member of the American Society of Ichthyologists and Herpetologists, the Association of Southeastern Biologists, the Southeastern Fishes Council, and the Tennessee Academy of Science. He is married to the former Lynn D. Betson of Maryville, Tennessee, currently a biologist with the Tennessee Valley Authority.