A Comparative Study of the Diets and Morphometrics
of Two Sympatric Larval Salamanders,
Gyrinophilus porphyriticus, the Spring Salamander (Green),
and *Pseudotriton ruber*, the Red Salamander (Latreille).

by

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ABSTRACT

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The aquatic larvae of *Gyrinophilus porphyriticus* and *Pseudotriton ruber* consumed a wide variety of prey over a study period of six months. A large proportion of the diets consisted of aquatic insect larvae, supplemented with non-insect and some terrestrial prey items. There appeared to be seasonal feeding preferences for each species, and the diets of each species were different from one another. Both species preferred certain prey items over others when their diets were compared to prey availability in the environment.

Predator-prey size relationships were examined for both species by comparing volumes of the largest and smallest prey items in the diet with the snout-vent lengths and head widths of salamanders. A relationship for *G. porphyriticus* was not evident, but, for *P. ruber*, a significant size relationship was found. This suggested that ontogenetic diet shifts occur in larvae of *P. ruber* but not in larvae of *G. porphyriticus* in this study.

Linear regressions were calculated for paired size measurements from each species. From these regressions, a significant difference in the slopes was detected when comparing standard length with head length for each species. However, a size ratio that distinguishes the two species could not be determined because the means of standard length/head length for each species, as well as for ratios from other size pairings, were insignificant.

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INTRODUCTION

Two of the largest and most colorful salamanders in Ohio, *Gyrinophilus porphyriticus* (Green), the spring salamander, and *Pseudotriton ruber* (Latreille), the red salamander, are members of the very successful lungless salamanders, Family Plethodontidae. Both are considered to be uncommon in Ohio (Pfingsten and Downs, 1989). Two subspecies of *Gyrinophilus* occur in Ohio, *G. porphyriticus porphyriticus*, the northern spring salamander, and *G. porphyriticus duryi*, the Kentucky spring salamander (Brandon, 1989). The subspecies involved in this study is *G. p. porphyriticus*.

Cool temperatures and heavily shaded, wooded areas are required by *Gyrinophilus* and *Pseudotriton* (Brandon, 1989; Pfingsten, 1989). Whitford and Hutchison (1965) explained that the lungless salamanders, e.g., *G. porphyriticus* and *P. ruber*, are confined to cool streams and springs where sufficient oxygen can diffuse across the skin. They both occur throughout the eastern United States where these conditions occur (Fig. 1, 2).

Sympatric populations of spring and red salamander larvae occupy a small, spring-fed stream with a well developed canopy in a tract of land known as the Arboretum in Trumbull Co., Ohio and owned by Youngstown State University. Neither species has been reported from the county previously and, in the case of *Gyrinophilus*, represents one of a very few records in the glaciated Allegheny Plateau in Ohio (Fig. 1, 2, Brandon, 1989; Pfingsten, 1989).

Studies of the feeding ecology of aquatic salamander larvae have been conducted. Among the genera examined were *Ambystoma* (Dodson and Dodson, 1971; Leff and Bachmann, 1986, 1988; McWilliams and Bachmann, 1989), *Notophthalmus* (Hamilton, 1940; Burton, 1977; Attar and Maly, 1980), *Triturus* (Avery, 1968; Ranta and Nuutinen, 1985; Kuzmin, 1991), *Eurycea* (Petranka, 1984), and *Dicamptodon* (Parker, 1992, 1994). These salamanders are all considered to be non-plethodontids with the exception of *Eurycea*.

The occurrence of two larval populations of uncommon Ohio salamanders in the same stream offered a unique opportunity to examine dietary habits of two potentially competing species of
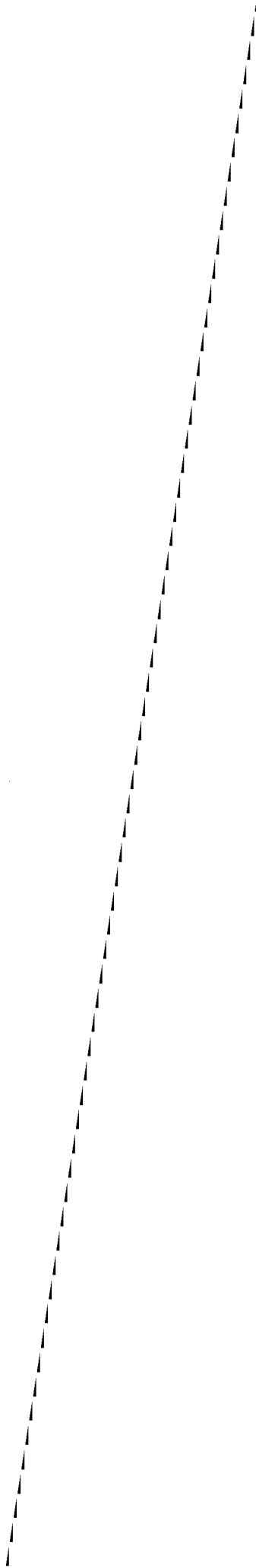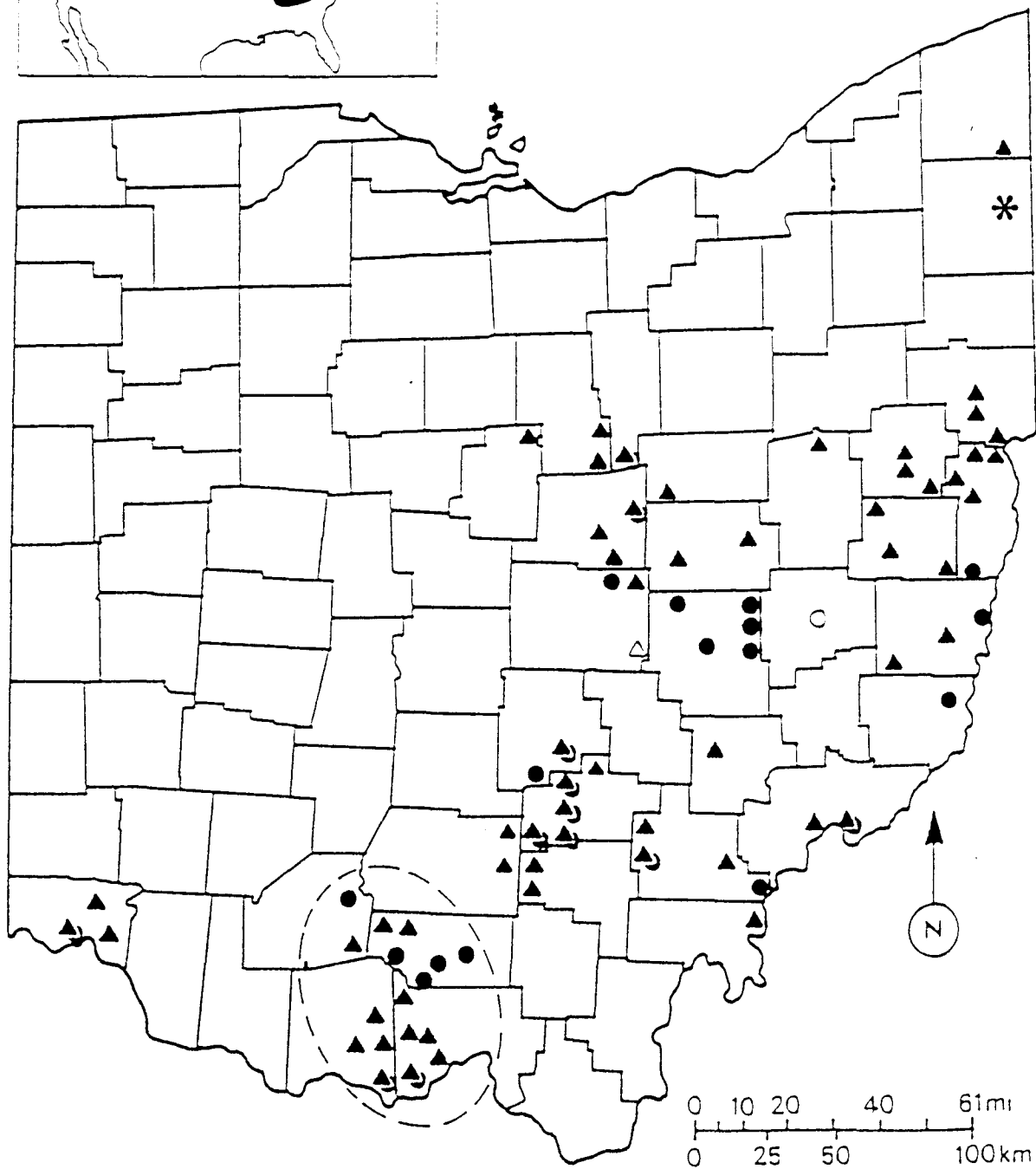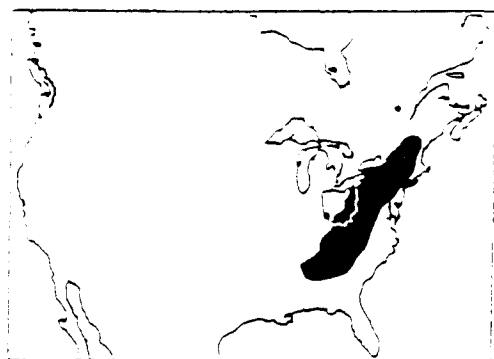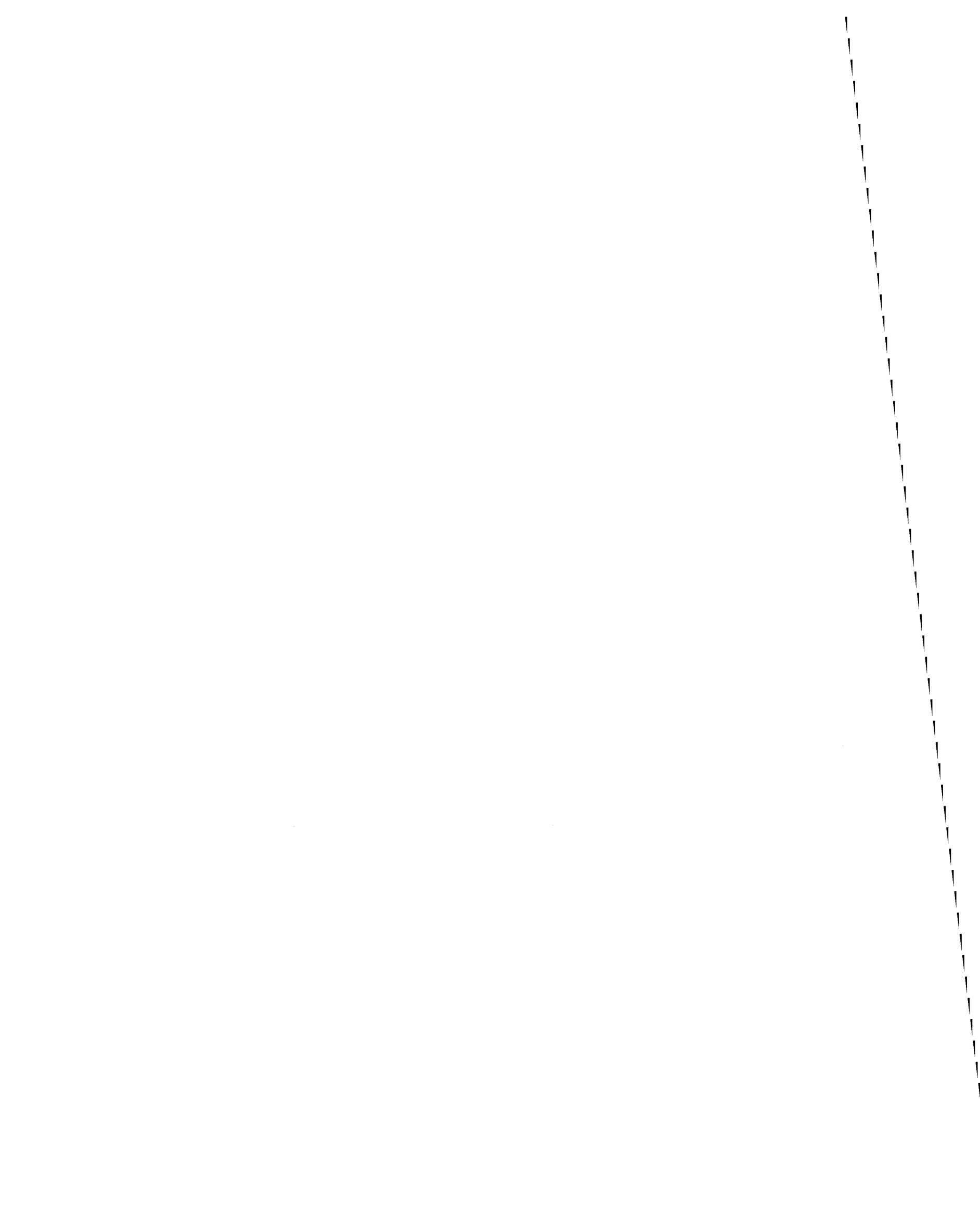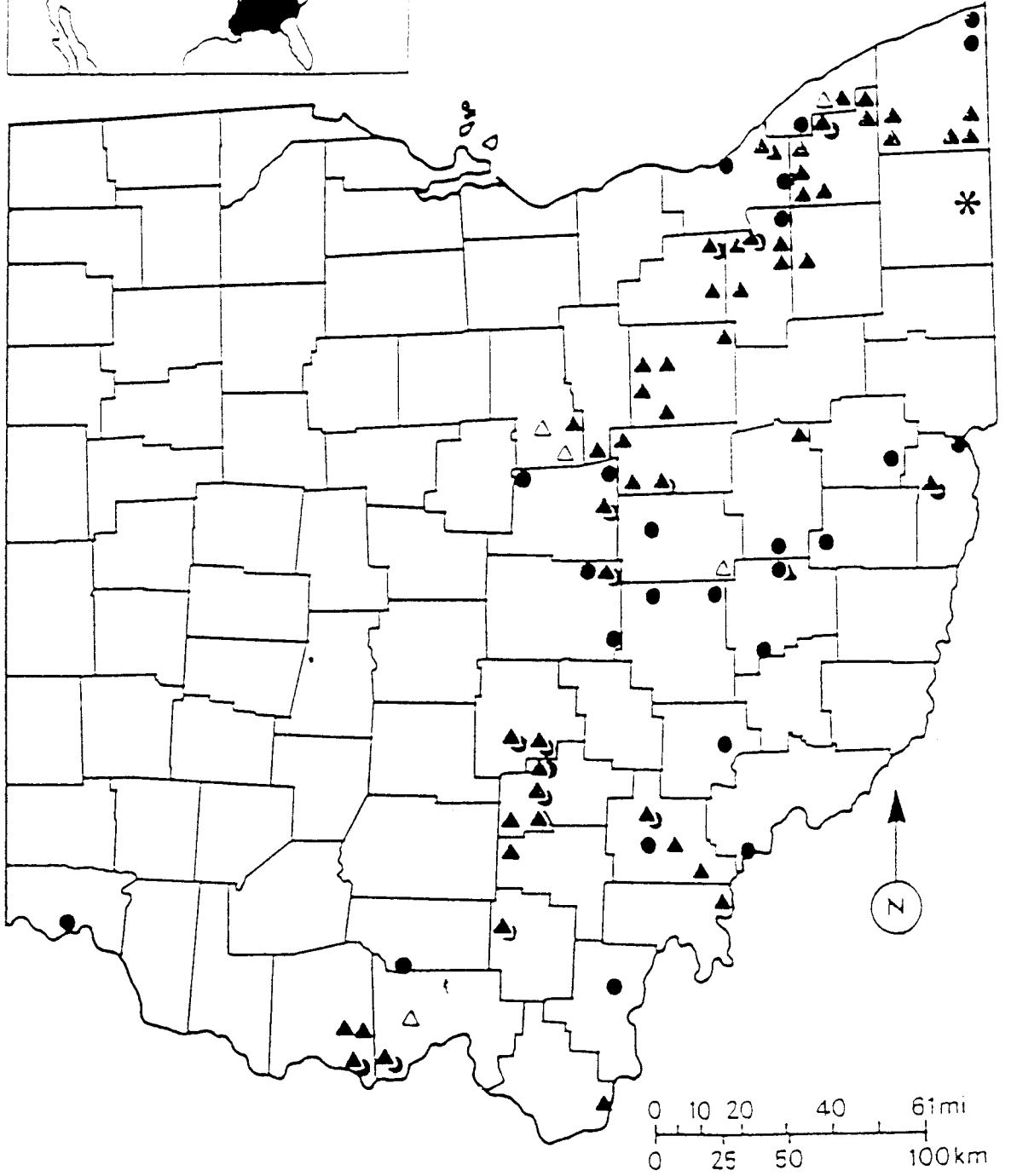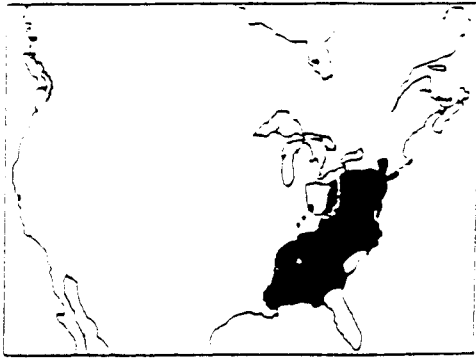
plethodontid salamanders.   Parker (1994) suggested that stream-dwelling salamander larvae feed primarily on benthic prey throughout the larval stage, and that pond-dwelling salamanders, for which most of the previous work has been conducted, ingest mainly zooplankton or alternate between planktivory and benthic feeding as they grow.   Therefore, stream-dwelling larvae probably exhibit different feeding habits and place stronger predatory pressures on benthic communities than pond-dwelling larvae.

There were three objectives in the present study: (1) detection of seasonal feeding patterns when comparing the diets of the two species; (2) determination whether the two species exhibited prey preference; and (3) investigation of a possible relationship between prey size and salamander size.

When the study was undertaken, it immediately became apparent that distinguishing between the two larvae was difficult. Two identification methods involving costal grooves were used to help identify the species.   In addition, a number of routine measurements, e.g., total length, snout-vent length, head length, were made to determine differences in the sizes of the two species.

MATERIALS AND METHODS

A. The Study Site

The study was conducted in a first-order, perennial spring-fed stream, which is an unnamed tributary that feeds into Yankee Run in Hartford TWP, Trumbull Co. (41° 16' N), Ohio. The stream exists in a natural forest which is a small section (about 20%) of the 118-acre Trumbull Arboretum of Youngstown State University, purchased in 1965 for use in scientific and geological investigations. The stream is covered by an extensive canopy of deciduous trees, most of which are Sugar Maple (*Acer saccharum*), and American Beech (*Fagus grandifolia*), with some Sour Gum (*Nyssa sylvatica*), Black Walnut (*Juglans nigra*), and Sassafras (*Sassafras albidum*). The remainder of the Arboretum was created by a special interest group in the 1940s to provide an area for studying trees. Many different species of trees were planted in the artificial section of the Arboretum when it was first created, but very few of these remain due to competition from Red Maples (*Acer rubrum*) and American Elms (*Ulmus americana*), which came in naturally throughout this section of the Arboretum. Some of the trees that still remain are various species of Pine (*Pinus*), various species of Oak (*Quercus*), White Spruce (*Picea glauca*), White Ash (*Fraxinus americana*), Tulip (*Liriodendron tulipifera*), Black Locust (*Robinia pseudo-acacia*), American Hazelnut (*Corylus americana*), and Gray Dogwood (*Cornus racemosa*).

The stream measures approximately 443 m from its underground source to a culvert with railroad tracks, and an unmeasured portion extends from this point to its junction with Yankee Run. The study was conducted in a portion of the stream that stretches from the source to about 254 m downstream (Fig. 3).

The depth of the stream usually varied from 2.5 cm to 10.5 cm at its deepest points, while the width varied between 30 and 60 cm. During the spring, the water level seemed to be the greatest due to spring runoff and seasonal rain. Following periods of rain, the stream increased to almost twice its normal level in width and depth. After about 45 minutes following precipitation, the stream receded

Trumbull
County

N

Hartford
Township

Yankee
Run

Study site

1 Km
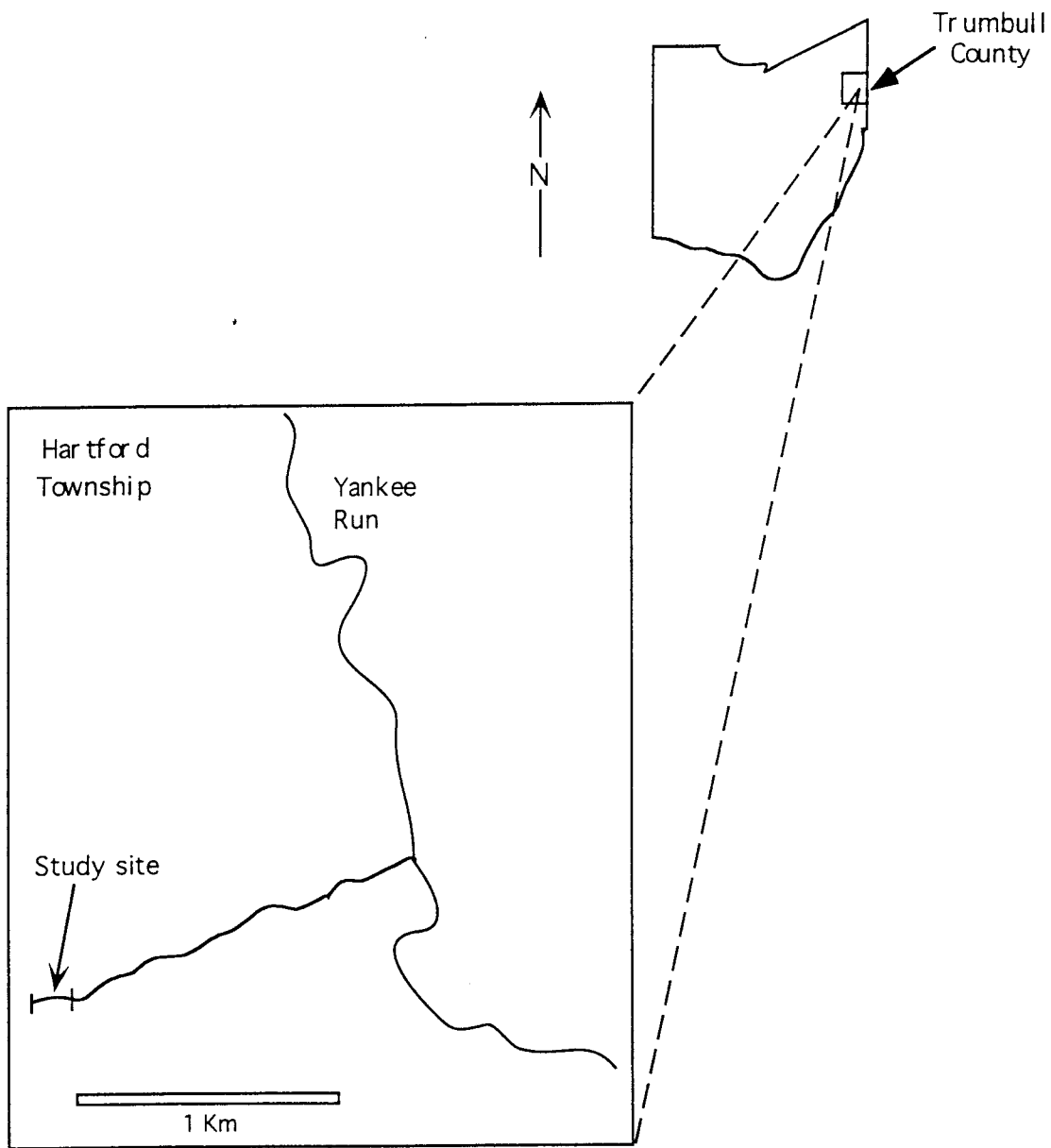
to its normal level. In 1995, a dry period during July and August caused the stream flow to decrease considerably, resulting in an even narrower and shallower stream.

Throughout the stream there are small rocks, sticks, some moss-covered logs, and leaf packs which provide cover. Near the origin, large moss-covered rocks are found embedded in the substrate. In the spring, a patch of skunk cabbage grows along a small section of the study site near its center. In late fall, the entire stream is covered with fallen leaves, almost blocking the current.

Along the entire length of the stream, the nature of the sediments is variable. Some areas seem to have a sandy and fine gravelly substrate, while other areas consist mainly of silty mud. There is also a great deal of coarse to fine organic matter.

Temperatures in the stream varied during the study period from 9° to 19° C. In May, the temperature was 9.5^{o} C. In the summer months, June - August, the temperature was warmer, averaging 18° C. In September and October, the stream decreased in temperature and averaged 11.5^{o} C. The origin of the stream was considerably cooler than the rest of the stream (11° C in July; 13.5^{o} C in August), and the temperature progressively increased downstream.

B. Sampling Procedures

Mixed populations of two species of salamander larvae, *Gyrinophilus porphyriticus* and *Pseudotriton ruber*, were sampled twice each month during the period May through October, 1995, allowing a month to pass between the sampling dates. One day each was devoted to the upstream (about 97.5 m) and downstream (about 156.5 m) portions. Salamanders were captured with small dipnets after carefully lifting logs, sticks, rocks, and leaves.

The salamanders were then anesthetized individually in a 0.03% solution of MS-222 (methane tricaine sulfonate) buffered to a pH of 7.0 with sodium bicarbonate (Parker, 1994; Fellers et al., 1994). The knockout times of the animals varied, ranging from five to sixteen minutes. The animals at first would wiggle around and

then progressively decrease their body movements. When fully anesthetized, the salamanders had their appendages extended outward and their bodies almost perfectly straightened.

Stomach contents of the salamanders were obtained using a method similar to the one developed by Legler and Sullivan (1979). All larvae that were gut-flushed measured over 22.96 mm snout-vent length (SVL), which was the length of the smallest salamander used for this procedure. Salamanders under this size were not used in the procedure because their very narrow body width was too small for the flushing apparatus. The salamanders that were flushed had bodies large enough to have the apparatus inserted into their digestive canal.

Polyethylene tubing small enough to fit into the mouth and esophagus of the salamanders, but large enough for food to be regurgitated, was used (0.88 mm ID and 1.27 mm OD attached to a 20G stub adapter). A stub adapter was fitted to a 10 ml syringe that automatically filled with water after pumping. Filtered stream water was used to fill the syringe. To open the mouth of the salamanders, a microspatula was inserted to limit the handling time and to prevent possible damage to the skin and gills of the animals. While the mouth was held open, the tubing was carefully inserted into the mouth, esophagus, and stomach of the animals until resistance was encountered from the pyloric section of the stomach. Water was pumped into the salamander until a bolus of food was regurgitated or no food particles were seen leaving the mouth. Food samples were washed onto a square of 52 μm mesh nylon material (Parker, 1994). This size was chosen to ensure that particles leaving the animal would not pass through the pores of the material. The cloth containing the fresh gut sample was folded, placed in air-tight polyethylene bottles, and returned to the laboratory in a cooler. Samples were stored in a freezer until they could be analyzed in the laboratory.

Identification of living larvae of *G. porphyriticus* and *P. ruber* in the field is difficult since they are very similar morphologically. Among characteristics that have been listed as useful to distinguish between them are: (1) the number of intercostal spaces between

adpressed limbs, and (2) the number of costal grooves. The number of intercostal spaces are counted by pressing the hindlimb parallel to the body axis with the toes pointing anteriad, and by placing the forelimb parallel to the body axis with the fingers pointing posteriad (Fig. 4a). If the organism had 5.5 or fewer intercostal spaces, then the salamander was identified as *P. ruber*. If the animal had more than 5.5 intercostal spaces, the salamander was identified as *G. porphyriticus* (Downs, 1989). The number of costal grooves, which are vertical grooves between the hind- and forelimbs and indicate the position of the ribs, were also counted (Fig. 4b). The costal groove count for the two species are 15-17 for *P. ruber* and 17-19 for *G. porphyriticus* (Brandon, 1966, 1989; Pfingsten, 1989). A consistent correlation was found between these two characteristics, and they were used throughout the investigation.

Once the salamanders were identified, a series of measurements were made with calipers scaled to the nearest 0.01 mm. These included the total length (TL), from the tip of the snout to the tip of the tail, snout-vent length (SVL), from the tip of the snout to the anterior edge of the cloacal aperture, standard length (STL), from the tip of the snout to the posterior edge of the cloacal aperture, head length (HL), from the tip of the snout to the edge of the gular fold, and head width (HW), the widest part of the head region (Fig. 4c). After the measurements were taken, the animals were placed in a small plastic bowl and weighed on an electronic balance to the nearest 0.01 g.

Frequently, the larvae would begin to recover from the anesthetic during the weighing process. All were placed in a net, submerged in the stream for further recovery, and were released as close to the capture site as possible.

During each of the field dates (May through October), a benthic invertebrate sample, correlating with the section of the stream studied on that particular day, was collected. Methods for collecting samples were similar to those used by Parker (1994). The sample was collected from microhabitats similar to those in which salamanders had been found. All samples were collected by marking an area with a wire coat hanger bent into a 25 X 25 cm template.

t   h

a

b

c

head

snout-vent

standard
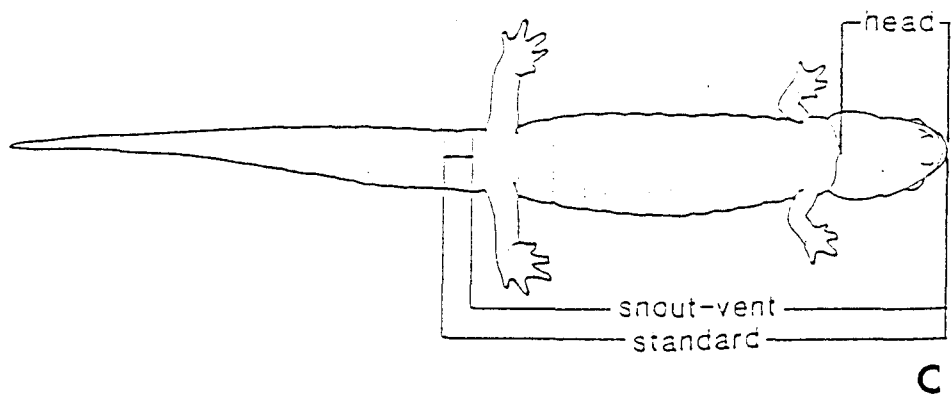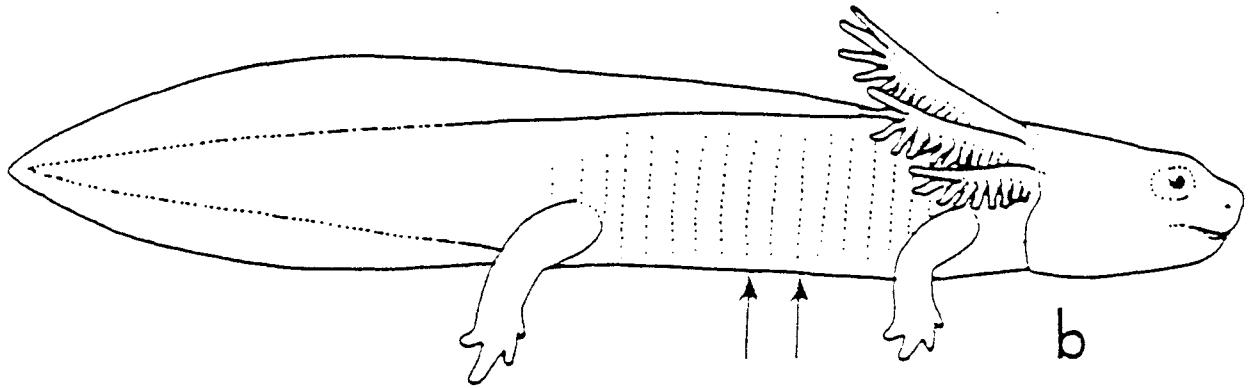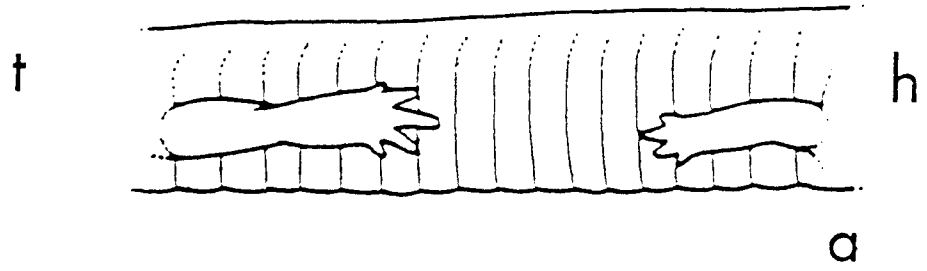
The template was placed in the sample area immediately upstream of a D-frame net (0.32 mm mesh). Benthic organisms were captured by stirring the substrate by hand, allowing the loosened debris to flow into the net. Contents of the net were then preserved with 80% ethanol in sample jars and kept in the laboratory until the samples could be analyzed.

C.   Laboratory Procedures

Frozen gut samples brought back to the laboratory were unfolded, and the material was placed in a small bowl. Three main references, McCafferty (1983), Merritt and Cummins (1984), and Pennak (1989) were used to identify the prey to the lowest possible taxonomic level (order or family) using a dissecting microscope. The microscope was fitted with a calibrated ocular micrometer to measure the length (excluding antennae and cerci), average width, and average thickness. These measurements were used to estimate volumes of all intact prey with the assumption that each approximated a rectangular or cylindrical solid, depending upon their shape (Maiorana, 1978; Parker, 1994; Petranka, 1984). Volumes of partially digested prey and head capsules were estimated by measuring the length, width, and thickness of head capsules.

While the nylon mesh material was in the small bowl, deionized water was poured into it, and all prey and prey parts were scraped from the material with a microspatula. Stomach contents were carefully funneled onto filter paper and transferred to petri dishes that had been dessicated for 24 hours in a dessicator and preweighed on an electronic balance. The prey and prey parts were dried to constant weight (65° C for 48 hours) and total stomach content mass was measured, weighing them to the nearest 0.01 mg on an electronic balance (Parker, 1994).

Benthic stream samples taken were examined in individual subsamples of about 25 ml or more. The subsamples were poured into a deep pan, and the macroinvertebrates were hand-sorted from the sediments. The remaining sediment was examined in a small bowl under a dissecting microscope to sort smaller invertebrates or

those missed in the initial sorting. All hand-sorted organisms were placed into a separate marked container denoting the section of the stream from which they came. They were identified under the dissecting microscope to the lowest possible taxonomic level (order or family) and counted.

D. Data Analysis

To determine whether any differences existed in seasonal feeding patterns among the larvae, the volumes and relative abundances of prey in the gut samples were compared. In addition, Spearman's coefficient of rank correlation was calculated for both species to detect any correlation between prey availability and diet composition, which would suggest that a particular prey preference exists for either species (Parker, 1994; Conover, 1982). To conduct Spearman's rank correlation, the relative abundances of the major prey taxa from the stream and the stomach contents of both species were summed over the study period. The summed relative abundances were then ranked for each species and compared to the ranked relative abundances from the stream. Spearman's coefficient of rank correlation was calculated for each species using MYSTAT (Hale, 1992).

Additionally, Vanderploeg and Scavia's (1979) relativized electivity index (E*) was calculated to determine consistent over- or underrepresentation of certain dietary prey items in proportion to their availability in the environment (Parker, 1994). E* is calculated as

$$E^* = [W_i - (1/n)]/[W_i + (1/n)]$$

$$\text{with } W_i = r_i/p_i/\Sigma \ r_i p_i \qquad\qquad (1)$$

where r_i is the relative abundance of prey type i in the diet, p_i is the relative abundance of prey type i in the environment, and n_i is the sum of the prey types used in the electivity index. Other indices exist, but this one is considered to be the best, especially when there

is variation in the number of prey types among sampling periods (Lechowicz, 1982; Parker, 1994).

In order to detect any relationship between prey size and salamander size, a regression of volumes of the largest and smallest prey items ingested with salamander size (SVL) was calculated for both species (Parker, 1994). If a significant relationship exists, this regression may show that salamanders choose larger prey items as they grow.

A regression of volumes of the largest and smallest ingested prey items with salamander head widths (HW) was made. A significant relationship would indicate that head width could influence the size of prey selected. This is known as gape-limitation, and it is the mechanism that most often influences salamanders of different size classes to consume certain sizes of prey (Zaret, 1980; Parker, 1994).

Further, to determine any relationship between the various size measurements of each species, linear regressions were calculated. The measurements which were regressed included the following: TL vs STL, TL vs SVL, SVL vs STL, HL vs HW, and STL vs HL. After the regressions were conducted, the slopes of the regression lines for all size comparisons were tested using t-tests to detect differences in the two species (Zar, 1996). If any significant differences in the regression lines exist between the measurements, a size ratio may be calculated that would distinguish the two species, providing a method of identification of the salamanders in addition to the number of intercostal spaces and costal grooves. Statistical procedures were conducted using MYSTAT (Hale, 1992).

RESULTS

The composition of the diets of *Gyrinophilus porphyriticus* and *Pseudotriton ruber* was determined, and the relative abundances and volumes of the major prey taxa are presented in Tables 1 and 4. From these two tables, it is evident that considerable variation in abundances and volumes of prey existed over the study period. The two comprehensive lists presented in Tables 2 and 5 illustrate the specific macroinvertebrate families ingested by the two species of salamanders and the frequencies of their appearance in the diets. It is obvious that aquatic insects were an important source of food for both species, and that non-insect prey were an additional source of food. The stream contained a large variety of aquatic insects as well as non-insect invertebrates. The densities of common benthic macroinvertebrates from the stream were calculated, and these values were compared to the stomach contents of both species to indicate the types of prey that were ingested and avoided (Table 3).

Numerically, dipterans were the most important source of food for *Gyrinophilus*, comprising 30 - 67% of the total prey consumed during the study (Table 1). The total number of dipterans ingested by *Gyrinophilus* was 44, representing the highest total among all insect orders. A large proportion of salamanders ingested dipteran prey (Table 2), however, these prey items only consisted of 0.14 - 17% of the total stomach volume in *Gyrinophilus* (Table 1). Dipterans were the most common and diverse aquatic insects in the stream available to *Gyrinophilus* (Table 3). Of the dipterans in the stream (Table 3), *Gyrinophilus* ingested mainly midges (Chironomidae). Other abundant families of dipterans, e.g., crane flies (Tipulidae), horse and deer flies (Tabanidae), and biting midges (Ceratopogonidae), were eaten less often (Table 2). The next most frequently ingested prey items (Tables 1 and 2) were copepods, fingernail clams (Pelecypoda), and stoneflies (Plecoptera). Stoneflies were found in the stream in spring and early summer but were not reported in late summer and early fall (Table 3). Copepods and fingernail clams were abundant in the stream throughout the

Table 1. Proportions of Major Prey Groups in Stomach Contents of Larval *Gyrinophilus porphyriticus* on 12 Dates from May, 1995 to October, 1995. %N is the proportion of total identifiable prey and %V is the proportion of total prey volume. Numbers in parentheses indicate the number of salamanders that actually had prey.

Taxon	May %N	May %V	June %N	June %V	July %N	July %V
Ephemeroptera	8.82	34.82	5.88	13.38	7.69	0.02
Plecoptera	13.73	8.57	----	----	----	----
Trichoptera	2.94	6.54	----	----	15.38	3.69
Diptera	30.39	16.44	29.41	2.88	38.46	11.02
Coleoptera	0.98	2.39	11.76	3.87	15.38	5.89
Lepidoptera	----	----	----	----	----	----
Odonata	0.98	1.42	----	----	----	----
Pelecypoda	5.88	6.00	11.76	2.61	7.69	2.63
Copepoda	32.35	0.35	11.76	0.02	----	----
Ostracoda	2.94	0.06	17.65	<0.01	----	----
Terrestrial prey	0.98	23.11	11.76	88.35	15.38	76.75
Total: prey/volume	102	249.606	17	333.611	13	298.670
No. of salamanders	11 (11)		8 (7)		6 (6)	
Mass: gut contents (*)	3.912 (0.356)		3.004 (0.429)		2.521 (0.420)	

Taxon	August %N	August %V	September %N	September %V	October %N	October %V
Ephemeroptera	----	----	----	----	----	----
Plecoptera	----	----	----	----	----	----
Trichoptera	----	----	----	----	----	----
Diptera	66.67	5.45	----	----	25.00	0.14
Coleoptera	33.33	94.55	----	----	----	----
Lepidoptera	----	----	----	----	25.00	80.89
Odonata	----	----	----	----	----	----
Pelecypoda	----	----	----	----	25.00	7.85
Copepoda	----	----	----	----	----	----
Ostracoda	----	----	----	----	----	----
Terrestrial prey	----	----	----	----	25.00	11.12
Total: prey/volume	3	8.297	0	0.00	4	108.409
No. of salamanders	4 (1)		1 (0)		2 (2)	
Mass: gut contents (*)	0.240 (0.240)		0 (0)		1.770 (0.885)	

(*) average relative gut content mass per salamander in parentheses

Table 2. Prey Items at the Family Level Ingested by *Gyrinophilus porphyriticus* during the Study Period (May through October, 1995). %F represents the proportion of stomachs containing prey (N = 32 salamanders) and %N represents the proportion of total prey.

Taxon	%F	%N	Number of stomachs with prey	Number of prey	Number of dates prey found in stomachs
Ephemeroptera					
Siphlonuridae	0.0 - 15.63	0.0 - 5.04	5	7	1
Baetidae	0.0 - 3.13	0.0 - 0.72	1	1	1
Others	0.0 - 6.25	0.0 - 2.16	2	3	2
Plecoptera					
Nemouridae	0.0 - 15.63	0.0 - 7.91	5	11	1
Taeniopterygidae	0.0 - 3.13	0.0 - 1.44	1	2	1
Others	0.0 - 3.13	0.0 - 0.72	1	1	1
Trichoptera					
Lepidostomatidae	0.0 - 3.13	0.0 - 0.72	1	1	1
Polycentropodidae	0.0 - 3.13	0.0 - 0.72	1	1	1
Others	0.0 - 9.38	0.0 - 2.16	3	3	2
Diptera					
Chironomidae	0.0 - 46.88	0.0 - 27.34	15	38	8
Tipulidae	0.0 - 3.13	0.0 - 1.44	1	2	1
Simulidae	0.0 - 3.13	0.0 - 0.72	1	1	1
Ceratopogonidae	0.0 - 9.38	0.0 - 2.16	3	3	3
Coleoptera					
Hydrophilidae	0.0 - 18.75	0.0 - 4.32	6	6	6
Lepidoptera					
Pyralidae	0.0 - 3.13	0.0 - 0.72	1	1	1
Odonata					
Unknown	0.0 - 3.13	0.0 - 0.72	1	1	1
Pelecypoda					
Sphaeriidae	0.0 - 25.00	0.0 - 7.19	8	10	5
Copepoda	0.0 - 18.75	0.0 - 25.18	6	35	3
Ostracoda	0.0 - 9.38	0.0 - 4.32	3	6	2
Terrestrial prey					
Oligochaeta	0.0 - 15.63	0.0 - 3.60	5	5	3
Trichoptera: adult	0.0 - 3.13	0.0 - 0.72	1	1	1
Total prey				139	

Table 3. Densities (no./m^2) of Common Benthic Macroinvertebrates in the Section of the Unnamed Stream during the Study Period (May through October, 1995) at the Trumbull Arboretum.

Taxon	May	June	July	Aug	Sept	Oct
Ephemeroptera						
Baetidae	48	----	----	----	----	----
Siphlonuridae	80	----	----	----	----	----
Plecoptera						
Nemouridae	64	16	----	----	----	----
Other	----	48	32	----	----	----
Trichoptera						
Lepidostomatidae	624	176	224	----	48	----
Odontoceridae	80	----	----	32	32	128
Psychomyidae	32	----	----	----	----	----
Polycentropodidae	32	----	16	----	16	----
Hydropsychidae	----	----	----	64	----	----
Diptera						
Chironomidae	608	544	1968	4704	1216	752
Tipulidae	128	128	432	1456	2144	1584
Ceratopogonidae	144	16	112	176	304	384
Psychodidae	32	----	----	----	----	----
Ptychopteridae	16	----	----	32	64	128
Ephydridae	16	48	----	16	----	----
Syrphidae	32	----	----	----	----	----
Tabanidae	----	64	32	240	592	336
Dixidae	----	16	----	----	----	16
Simulidae	----	16	----	----	----	----
Coleoptera						
Hydrophilidae	----	----	----	16	----	----
Odonata						
Cordulegastridae	----	16	----	32	----	----
Gomphidae	----	----	----	48	32	16
Non-insects						
Pelecypoda	----	480	880	944	1392	560
Copepoda	1088	1456	1920	1840	1264	1392
Ostracoda	848	720	1120	816	512	1600
Oligochaeta	----	32	240	112	112	314

sampling period (Table 3). However, copepods were found in stomach samples of *Gyrinophilus* in May and June, whereas fingernail clams were present in food samples throughout the sampling period (Tables 1 and 2). Several families of caddisflies (Trichoptera) were abundant in the stream (Table 3), but few occurred in the stomach contents of *Gyrinophilus* (Table 2). Usually, only the head capsules of caddisflies were present in food samples, and two were identified to family (Table 2). Even though ostracods were abundant in the stream, they made up a small (0.0 - 4.32%) proportion of the diet of *Gyrinophilus* (Table 3).

Larger prey types comprised a greater proportion of stomach content volume. For example, mayflies (Ephemeroptera), 9% of the prey ingested in May, comprised 35% of the stomach content volume. Earthworms (Oligochaeta), comprised 23 - 89% of the stomach content volume on any date but were not very abundant in the diet (Table 1). Copepods, 33% of the prey ingested in May, comprised only 0.35% of the total stomach content volume (Table 1). The September sample consisted of one salamander with an empty stomach. Two salamanders were collected in October each containing two prey items.

The diet of *Pseudotriton* was different from *Gyrinophilus*. The most frequently ingested prey items were copepods, comprising 18 - 69% of the prey in the stomach, but their contribution to total stomach content volume was very small, 0.08 - 2% (Table 4). In the stream throughout the study period, copepods were the most common non-insect prey item. Unlike *Gyrinophilus*, copepods were found in the stomach samples of *Pseudotriton* throughout the investigation. Fingernail clams were the next most abundant non-insect prey in the *Pseudotriton* diet with 15 clams found in the food samples, which were found over the study period as in *Gyrinophilus* (Table 5). In the stream, fingernail clams were found to be abundant as well (Table 3). The most abundant aquatic insects in the diet were dipterans with 17 prey items ingested during the study period (Table 5). Of these, most were midges. The stream had a wide variety of Diptera available for ingestion (Table 3), but dipterans, other than midges, were found infrequently in stomach samples of

Table 4. Proportions of Major Prey Groups in Stomach Contents of Larval *Pseudotriton ruber* on 12 Dates from May, 1995 to October, 1995. %N is the proportion of total identifiable prey and %V is the proportion of total prey volume. Numbers in parentheses indicate the number of salamanders that actually had prey.

Taxon	May %N	May %V	June %N	June %V	July %N	July %V
Ephemeroptera	----	----	----	----	----	----
Plecoptera	----	----	----	----	----	----
Trichoptera	----	----	----	----	5.56	2.52
Diptera	----	----	27.27	8.56	33.33	5.30
Coleoptera	----	----	18.18	37.40	22.22	4.96
Lepidoptera	----	----	----	----	----	----
Odonata	----	----	----	----	----	----
Pelecypoda	----	----	36.36	53.96	11.11	1.17
Copepoda	----	----	18.18	0.08	----	----
Ostracoda	----	----	----	----	----	----
Terrestrial prey	----	----	----	----	27.78	86.05
Total: prey/volume	0	0.00	11	41.573	18	362.679
No. of salamanders	0 (0)		13 (5)		15 (11)	
Mass: gut contents (*)	0 (0)		1.792 (0.358)		6.800 (0.618)	

Taxon	August %N	August %V	September %N	September %V	October %N	October %V
Ephemeroptera	----	----	100.00	100.00	----	----
Plecoptera	----	----	----	----	----	----
Trichoptera	3.17	3.64	----	----	20.00	30.79
Diptera	12.70	4.67	----	----	----	----
Coleoptera	1.59	3.39	----	----	----	----
Lepidoptera	----	----	----	----	----	----
Odonata	----	----	----	----	----	----
Pelecypoda	11.11	9.92	----	----	40.00	68.05
Copepoda	68.25	1.48	----	----	40.00	1.16
Ostracoda	----	----	----	----	----	----
Terrestrial prey	3.18	76.90	----	----	----	----
Total: prey/volume	63	61.000	1	7.784	5	5.239
No. of salamanders	8 (6)		1 (1)		2 (2)	
Mass: gut contents (*)	1.390 (0.232)		0.023 (0.023)		0.205 (0.103)	

(*) average relative gut content mass per salamander in parentheses

Table 5. Prey Items at the Family Level Ingested by *Pseudotriton ruber* during the Study Period (May through October, 1995). %F represents the proportion of stomachs containing prey (N = 39 salamanders) and %N represents the proportion of total prey.

Taxon	%F	%N	Number of stomachs with prey	Number of prey	Number of dates prey found in stomachs
Ephemeroptera					
Siphlonuridae	0.0 - 2.56	0.0 - 1.02	1	1	1
Plecoptera	0.0	0.0	0	0	0
Trichoptera					
Polycentropodidae	0.0 - 2.56	0.0 - 1.02	1	1	1
Others	0.0 - 7.69	0.0 - 3.06	3	3	2
Diptera					
Chironomidae	0.0 - 25.64	0.0 - 14.29	10	14	4
Tipulidae	0.0 - 5.13	0.0 - 2.04	2	2	2
Empididae	0.0 - 2.56	0.0 - 1.02	1	1	1
Coleoptera					
Hydrophilidae	0.0 - 12.82	0.0 - 5.10	5	5	4
Dytiscidae	0.0 - 2.56	0.0 - 1.02	1	1	1
Others	0.0 - 2.56	0.0 - 1.02	1	1	1
Lepidoptera	0.0	0.0	0	0	0
Odonata	0.0	0.0	0	0	0
Pelecypoda					
Sphaeriidae	0.0 - 17.95	0.0 - 15.31	7	15	4
Copepoda	0.0 - 15.38	0.0 - 47.96	6	47	3
Ostracoda	0.0	0.0	0	0	0
Terrestrial prey					
Oligochaeta	0.0 - 10.26	0.0 - 5.10	4	5	2
Ant	0.0 - 2.56	0.0 - 1.02	1	1	1
Salamander parts	0.0 - 2.56	0.0 - 1.02	1	<u>1</u>	1
Total prey				98	

Pseudotriton (Table 5). Several families of caddisflies (Trichoptera) were abundant in the stream (Table 3), but they were infrequent in the food samples from *Pseudotriton* (Table 5). Even though many ostracods were present in the stream (Table 3), they were not found in the stomach contents of *Pseudotriton* (Table 5). In September, one salamander was found, and it had one prey item in its stomach. Cannibalism occurred in August when a forelimb, hindlimb, and torso of a larval salamander of unknown genus was found in a stomach sample from a metamorphosing *P. ruber* that had a total length of 71.68 mm (Tables 4 and 5). The larger prey items composed most of the stomach content volume as in *Gyrinophilus*.

Terrestrial earthworms that may have been washed into the stream, fingernail clams, copepods, and ostracods represented a source of food other than aquatic insects for both species. Other terrestrial prey included an ant ingested by *Pseudotriton*, which was the same organism that cannibalized a larval salamander, and an adult trichopteran eaten by *Gyrinophilus* (Tables 2 and 5).

Relative mass of the stomach contents (mg dry mass of stomach contents/g salamander live mass X 100) of both species was calculated for each month (Parker, 1994). The average relative gut content mass per salamander was also calculated for each species. The average gut content mass per salamander varied for each species from month to month. For *Gyrinophilus*, the average relative gut content mass per salamander was higher than *Pseudotriton* in May and June (Tables 1 and 4). In July, *Pseudotriton* had its highest average relative gut content mass of the study period (Table 4). This measure for *Pseudotriton* substantially decreased in August and remained at low levels through the end of the study (Table 4). The average gut content mass for *Gyrinophilus* appeared to be higher than *Pseudotriton* throughout the study (Tables 1 and 4). For example, in July, the average relative gut content mass of six spring salamanders (0.420) was slightly less than the average relative gut content mass of eleven red salamanders (0.618). Additionally, in August, one *Gyrinophilus* was found, but it had a relative gut content mass (0.240) that was slightly greater than the average relative gut content mass of six *Pseudotriton* larvae (0.232).

Spearman's coefficient of rank correlation was calculated to determine whether *G. porphyriticus* and *P. ruber* exhibited prey preferences. A significant positive correlation indicates that salamanders consume encountered prey in direct proportion to their relative abundances in the environment; on the other hand, if a significant correlation does not occur, this would suggest that certain prey types are preferred by salamanders, while other types are avoided, not available, or capable of escaping (Elliott, 1970; Allan, 1981; Parker, 1994). The null hypothesis, that there was no correlation between the relative abundances of prey in the stream and prey in the stomach contents of either salamander species, was not rejected (*Gyrinophilus*: $r_s = 0.264$; *Pseudotriton*: $r_s = 0.409$; $0.20 < P < 0.50$; $N = 11$). The results suggested that both *G. porphyriticus* and *P. ruber* prefer some prey over others since their coefficients (r_s) were less than the critical value $[(r_s)_{.05,(2),11} = 0.618]$.

Electivity index values may detect the types of prey ingested by both species that were either over- or underrepresented in proportion to their availability in the environment (Tables 6 and 7). Index values range from -1.0 to +1.0, with values near zero (i.e., -0.05 to +0.05) having neutral selection (Parker, 1994). Since prey that is rare in either the diet or in the benthos causes E* to be vulnerable to errors in sampling (Lechowicz, 1982; Parker, 1994), only taxa that had a relative abundance of at least 1% in the benthos and the stomach contents were included in the analysis. Generally, taxa with relative abundances greater than 1% were present in all twelve stream samples, while taxa having lower abundances were rarely present in the samples (Parker, 1994). Consistently high negative electivity values indicate that prey items are underrepresented in the diet, whereas high positive values indicate overrepresentation. In *Gyrinophilus*, the prey taxa that had consistently high negative electivity values included Chironomidae, Sphaeriidae, Copepoda, and Ostracoda. For May, stoneflies (Nemouridae) and mayflies (Siphlonuridae) each had a positive index value close to neutrality (Table 6). The prey taxa from the stomachs of *Pseudotriton* that had consistently high negative electivity values were Chironomidae, Tipulidae, Sphaeriidae, and Copepoda (Table 7).

Table 6. Electivities (Vanderploeg and Scavia's E*) for Prey Items Consumed by *Gyrinophilus porphyriticus* during the Study Period (May through October, 1995).
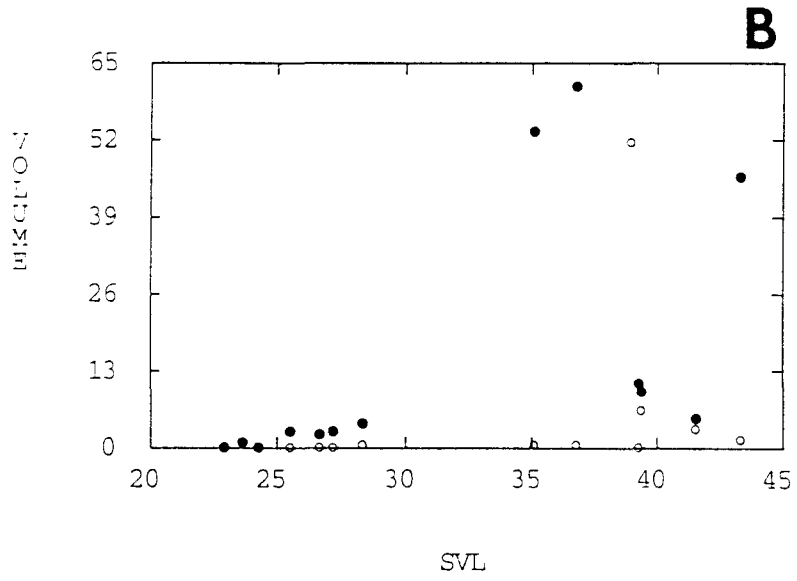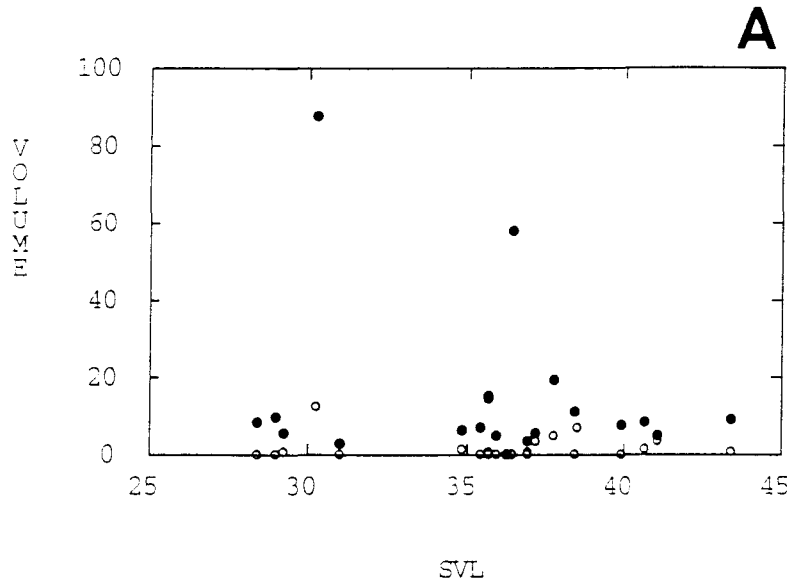
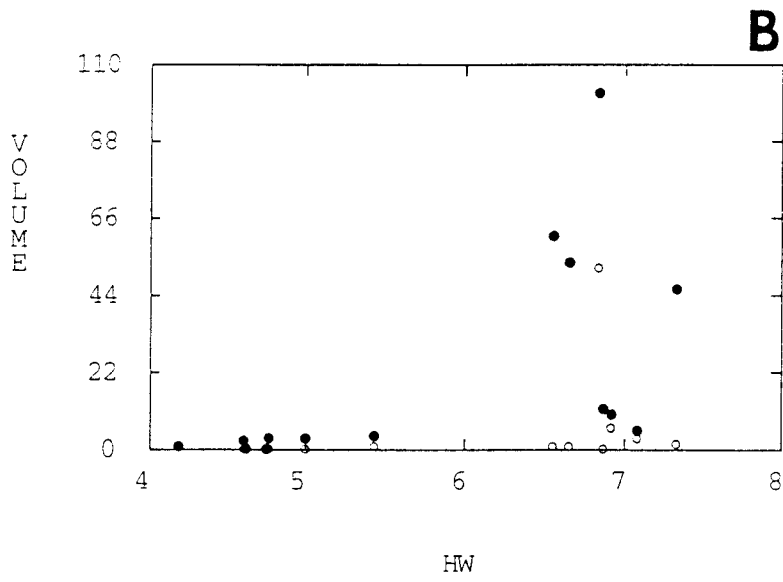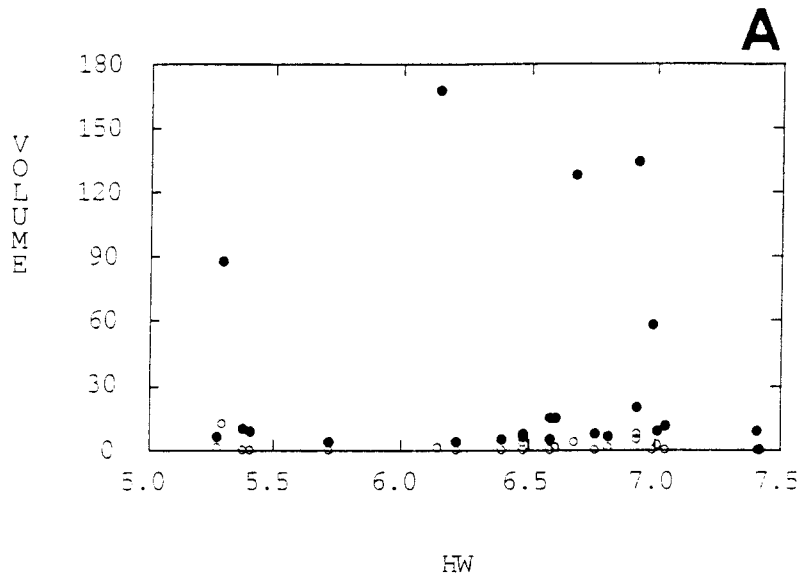| Taxon	May	June	July	August	October
Siphlonuridae	0.08	---	---	---	---
Nemouridae	0.29	---	---	---	---
Chironomidae	-0.99	-0.99	-0.99	-0.99	-0.99
Tipulidae	---	---	-0.81	---	---
Ceratopogonidae	-0.92	---	---	-0.22	---
Sphaeriidae	---	-0.98	-0.98	---	-0.97
Copepoda	-0.99	-0.99	---	---	---
Ostracoda	-0.99	-0.98	---	---	---
Oligochaeta	---	---	-0.49	---	---

(---) = prey less than 1.0% of diet or benthos (Parker, 1994)

Table 7. Electivities (Vanderploeg and Scavia's E*) for Prey Items Consumed by *Pseudotriton ruber* during the Study Period (May through October, 1995).

Taxon	May	June	July	August	October
Chironomidae	---	-0.99	-0.99	-0.99	---
Tipulidae	---	---	-0.87	-0.98	---
Sphaeriidae	---	-0.98	-0.99	-0.99	-0.98
Copepoda	---	-0.99	---	-0.98	-0.99
Oligochaeta	---	---	-0.49	---	---

(---) = prey less than 1.0% of diet or benthos (Parker, 1994)

A

V
O
L
U
M
E

100

80

60

40

20

0

25   30   35   40   45

SVL

B

V
O
L
U
M
E

65

52

39

26

13

0

20   25   30   35   40   45

SVL
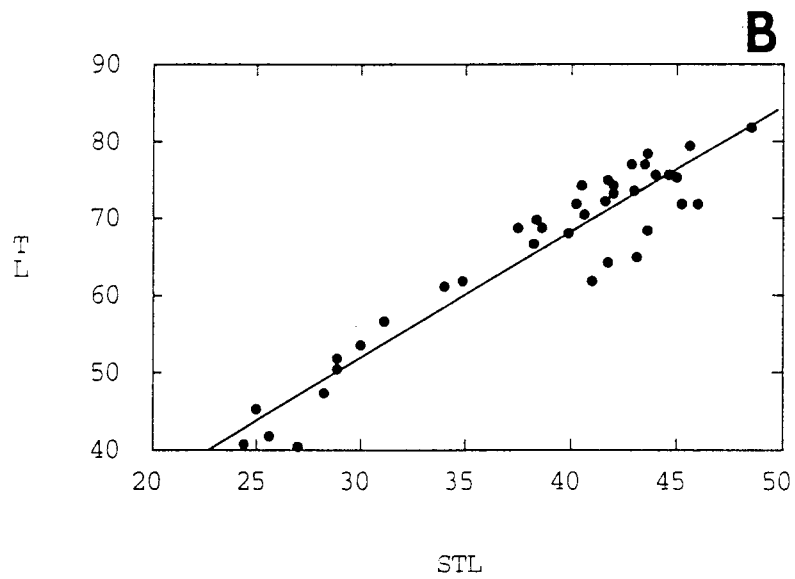
A

B

Gyrinophilus and for *Pseudotriton* (Fig. 7), but, when comparing their two slopes, there was no significant difference (t = 1.331; 0.10 < P < 0.20; alpha = 0.05). When a regression of TL with SVL was calculated, a significant relationship was found between the measurements for *Gyrinophilus* and for *Pseudotriton* (Fig. 8). However, there was no significant difference in the two slopes (t = 1.623; 0.10 < P < 0.20; alpha = 0.05). When a regression of SVL with STL was calculated, a significant relationship was found between the measurements for *Gyrinophilus* and for *Pseudotriton* (Fig. 9), but there was no significant difference in the two slopes (t = 0.6182; P > 0.50; alpha = 0.05). When a regression of HL with HW was calculated, a significant relationship was found between the measurements for *Gyrinophilus* and for *Pseudotriton* (Fig. 10). However, there was no significant difference in the two slopes (t = 0.3609; P > 0.50; alpha = 0.05). When a regression of STL with HL was calculated, a significant relationship was found between the measurements for *Gyrinophilus* and for *Pseudotriton* (Fig. 11). The slopes of these regressions were significantly different (t = 7.887; P < 0.001; alpha = 0.05).
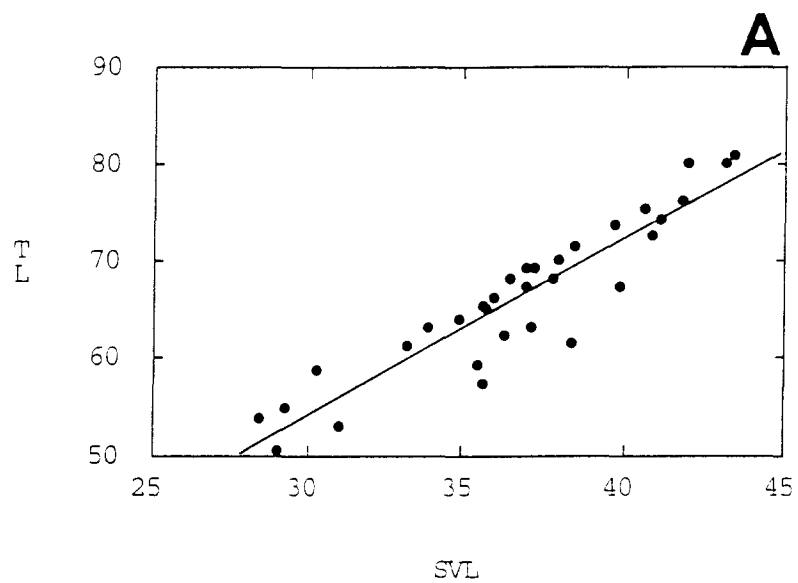
Size ratios for each of the paired measurements were calculated, and the means of these ratios from each species were compared using independent t-tests (alpha = 0.05). No significant differences between the two species for any of the size ratios could be detected (Table 8).
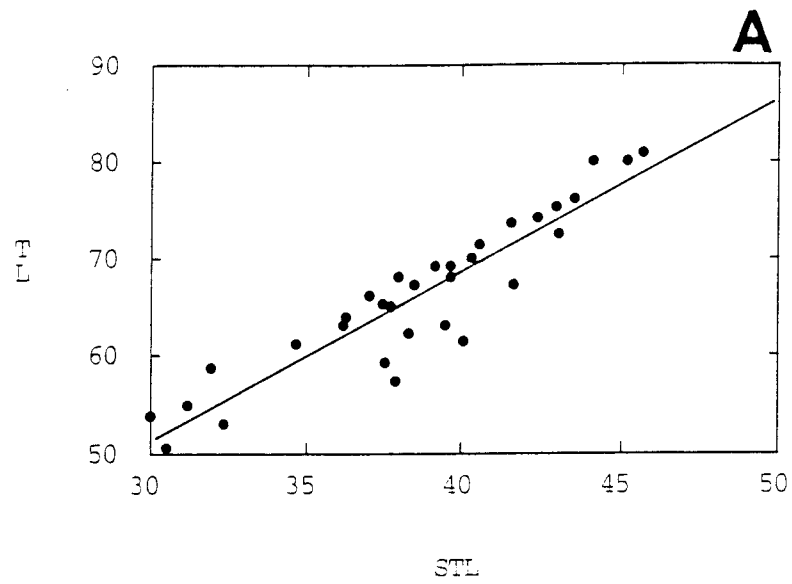
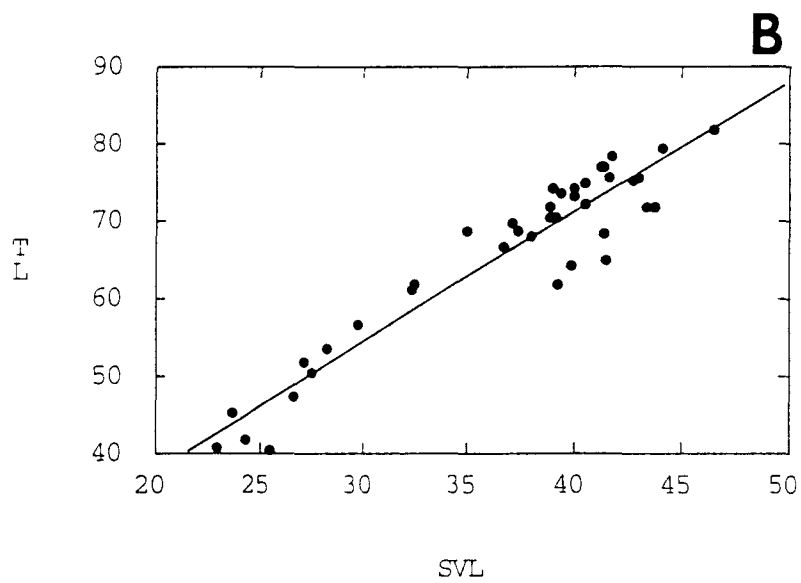TL=-1.564+1.761*STL

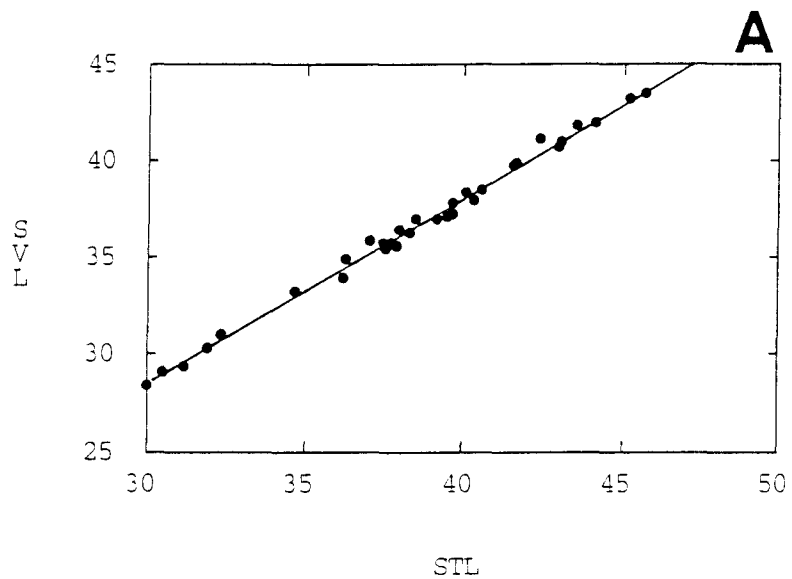TL=3.051+1.628*STL

A

TL=-0.716+1.828*SVL
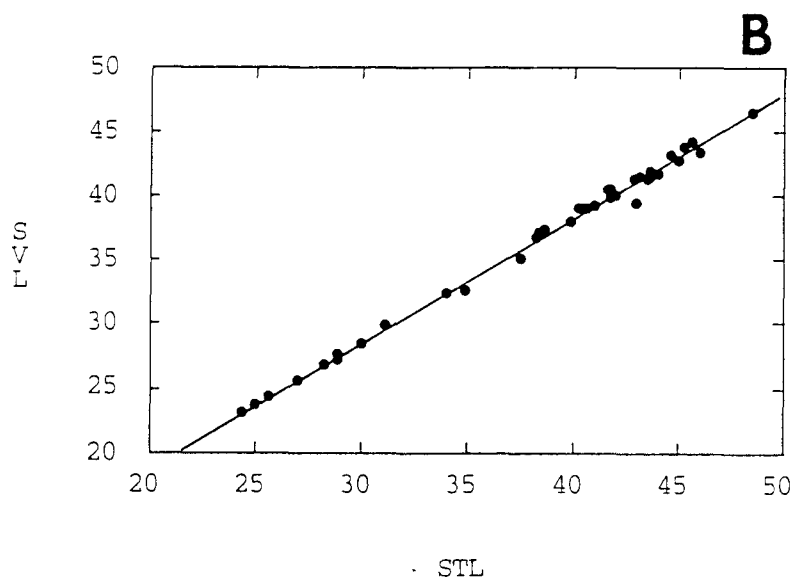

B

TL=4.509+1.667*SVL

A

SVL=-0.410+0.962*STL

B

SVL=-0.793+0.975*STL

A

HL=-0.035+1.179*HW

B

HL=0.575+1.117*HW
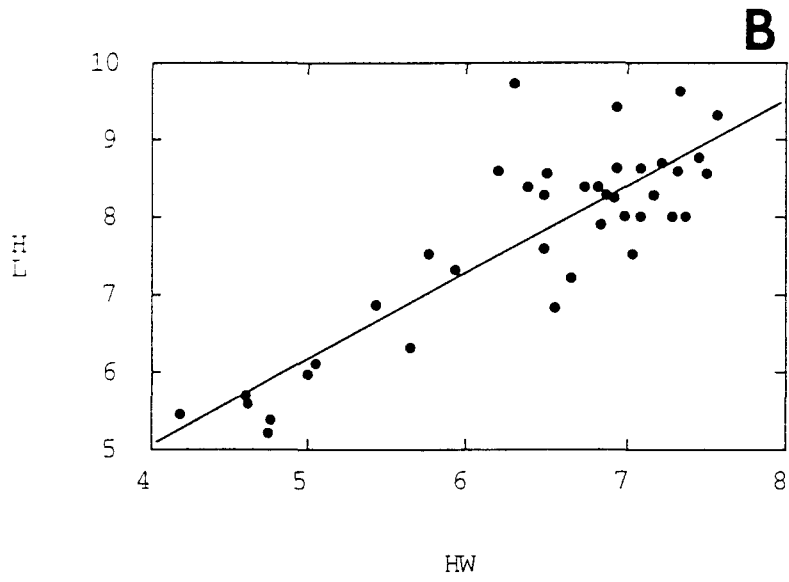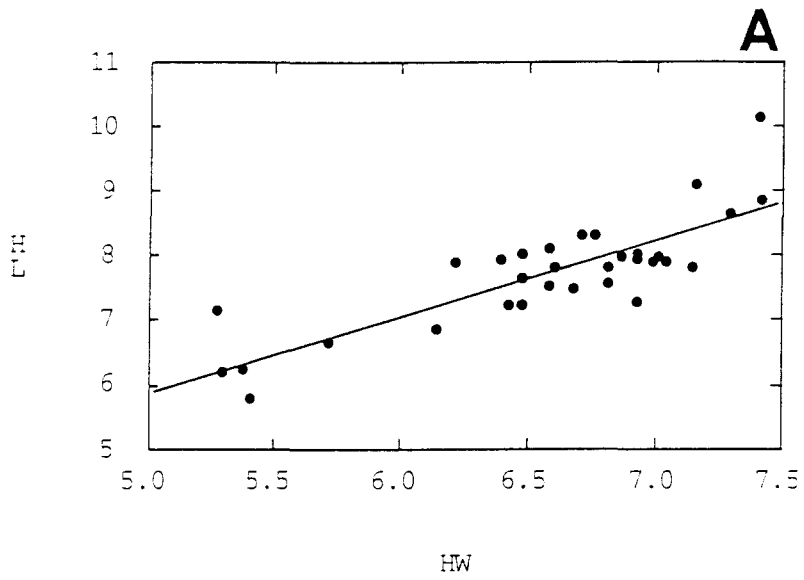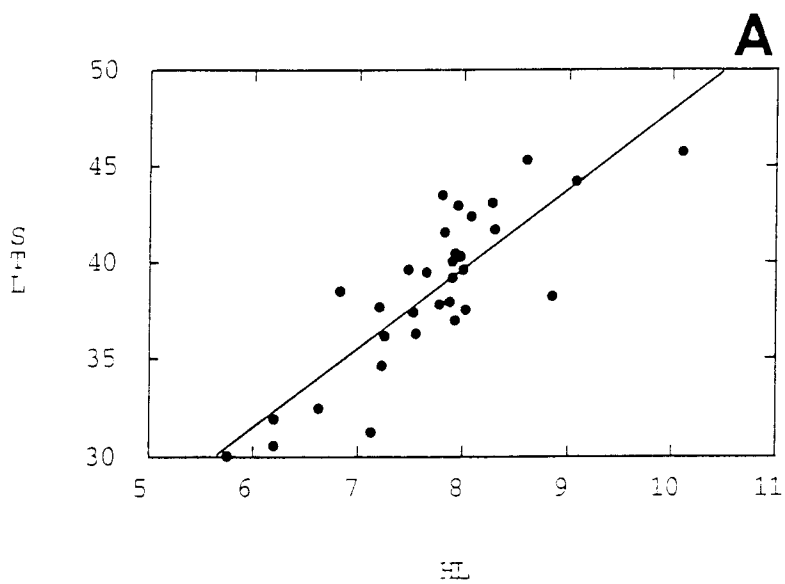
STL=6.906+4.104*HL
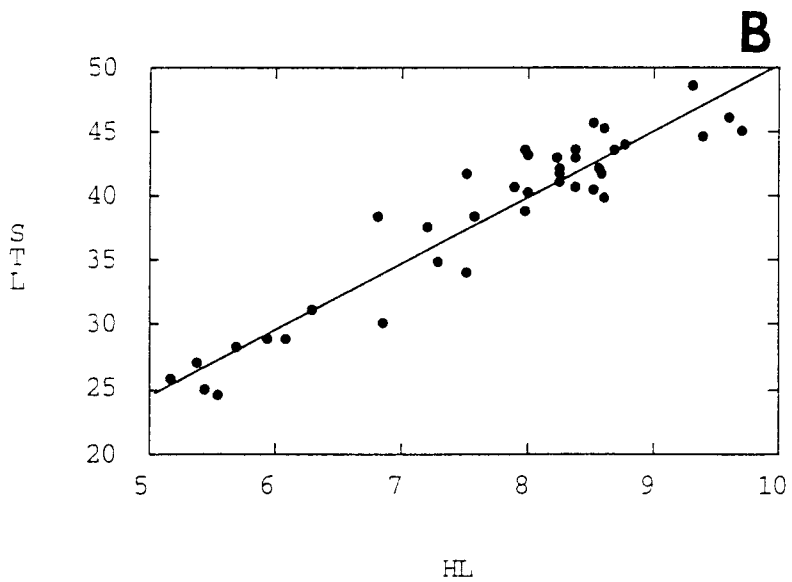
STL=-1.156+5.134*HL

Table 8. Results of the Independent t-tests for the Paired Measurements of *Gyrinophilus porphyriticus* (N = 32) and *Pseudotriton ruber* (N = 39).

Ratios	*Gyrinophilus porphyriticus*		*Pseudotriton ruber*		Independent t-tests	
	Mean	SD	Mean	SD	t-value	P
TL vs STL	1.720	0.081	1.709	0.096	0.513	0.610
TL vs SVL	1.808	0.085	1.793	0.102	0.683	0.497
SVL vs STL	0.951	0.009	0.953	0.012	-0.841	0.403
HL vs HW	1.174	0.073	1.208	0.099	-1.626	0.108
STL vs HL	5.009	0.304	4.978	0.292	0.434	0.667

DISCUSSION

Seasonal preferences for both *Gyrinophilus porphyriticus* and *Pseudotriton ruber* appear to exist. When examining the stomach contents of *Gyrinophilus*, stoneflies were not consumed in any other month except for May, copepods were consumed in May and June, and fingernail clams appeared in the food samples throughout the study period. These results might suggest a seasonal pattern for certain prey. Stoneflies and ostracods were not found in the stomach samples of *P. ruber*, and only one mayfly was reported in September. Additionally, copepods were ingested in the spring, summer, and fall, unlike *G. porphyriticus*, indicating a seasonal preference for certain prey items in *P. ruber*.

A large component of the diet of *G. porphyriticus* and *P. ruber* consisted of aquatic benthic insects. Another important source of food for both species were aquatic non-insects such as fingernail clams, copepods, and ostracods and terrestrial earthworms that may have fallen into the stream. Parker (1994) explained that aquatic insects and non-insects were found in the stomachs of *Dicamptodon tenebrosus*, suggesting that the non-insect component represented an important alternative source of food. The fact that *Gyrinophilus* and *Pseudotriton* ingested both types of food items illustrates that there are alternative prey items available for them to eat.

There are other species of plethodontid salamanders that coexist with *G. porphyriticus* in a sympatric environment (Bruce, 1980). Some examples are *Eurycea bislineata*, and *Desmognathus fuscus* (Brandon, 1989), and both species were found in the stream at the study site. Early studies have reported that adult *G. porphyriticus* feed on terrestrial and aquatic invertebrates and on other salamanders such as *D. fuscus* and *E. bislineata* (Surface, 1913; Hamilton, 1932; Bishop, 1941; Burton, 1976; Brandon, 1989). According to Brandon (1989), *Gyrinophilus* are less abundant than the other sympatric plethodontid salamanders because of their larger body size, higher trophic level (cannibalism), and demanding habitat requirements. Additionally, even though little is known about their distribution underground, *G. porphyriticus* often construct deep

tunnels within the stream bed in the gravel and rock (Bruce, 1980; Brandon, 1989). These factors may explain why the two species studied coexist, and why the larvae of *G. porphyriticus* are difficult to find.

Most salamander larvae are generalist feeders, which means they eat a wide variety and size range of invertebrate prey (Petranka, 1984; Parker, 1994). *G. porphyriticus* is considered to be a generalist predator, and Bruce (1980) and Brandon (1989) reported that larvae and adults of *G. porphyriticus* are generalized feeders. Little is known about the feeding habits of *P. ruber*, but, considering the results of this study and the fact that *P. ruber* is a plethodontid salamander, one can speculate that this species may also be a generalist predator. However, Spearman's coefficient of rank correlation between the relative abundances of prey in the diet and the relative abundances of prey in the environment suggested that these two species of salamanders preferentially feed on certain prey items. In the stream, there is a large variety of dipterans, such as chironomids, tipulids, tabanids, and ptychopterids, but chironomids were the most common dipterans in the stomach samples of both species through the study period (0.0 - 27.34% for *Gyrinophilus*; 0.0 - 14.29% for *Pseudotriton*). This may indicate that midges are preferred by *Gyrinophilus* and *Pseudotriton*, which Spearman's correlation predicts. These results agree with Parker's study (1994), which found that stream-dwelling *D. tenebrosus* prefer certain prey items over others. Preferential feeding by stream-dwelling salamanders may exert different predation pressures on benthic communities by favoring some prey items over others.

Electivity index values showed that the more common prey types found in the stomach samples of both *G. porphyriticus* and *P. ruber* were consistently underrepresented in the diet according to their availability in the environment. The prey taxa included in the analysis had a relative abundance in the benthos much larger than that of the stomach contents of both species. This illustrates that *G. porphyriticus* and *P. ruber* did not consume prey in similar proportions to their relative abundances in the stream, and demonstrates that certain prey types were preferred. Parker (1994)

concluded that prey types not consumed were either avoided, encountered less often, or possessed the ability to escape ingestion.

Previous food studies have determined ontogenetic diet shifts in larval salamanders (Petranka, 1984; Parker, 1994). Petranka showed that as *E. bislineata* larvae grew, they progressively incorporated larger prey items into their diets but still ate smaller prey items as well. Parker's study illustrated that only larger *D. tenebrosus* larvae eat rare, large prey, but they still ingested smaller dietary items. *G. porphyriticus* did not show any significant predator-prey size relationships. Smaller spring salamanders were found to ingest the same large prey items, such as fingernail clams and parts of earthworms, that were ingested by larger salamanders. The larger salamanders, in addition, continued to incorporate small prey, such as copepods and midges, into their diet. This could indicate that ontogenetic dietary shifts are not pronounced in the larval stages of *Gyrinophilus*, however, the larval classes for this species are difficult to determine.

Bishop (1941) estimated the larval period of *Gyrinophilus* to be about three years. In his study, he listed measurements of total length to be 26-28 mm for young-of-the-year, 64 mm at the end of the first year, 90 mm at the end of the second year, and 124 mm at the end of the third larval year. A more recent study, however, illustrated larval development in this species to last four years (Bruce, 1980). In the present study, *Gyrinophilus* young-of-the-year could not be identified since they are very similar to young-of-the-year of *P. ruber* and *E. bislineata*, and no transforming larvae were found. Most of the larvae collected and sampled were in their first or second year. According to Bishop's (1941) definition of size classes for total length, the size ranges for *Gyrinophilus* in the present study were 50.55-63.25 mm (TL) for first year larvae and 64.06-80.90 mm (TL) for second year larvae. Based on the food samples from the two larval periods, there was no relationship between prey size and salamander size (SVL). Bruce (1972a) indicated that a pronounced dietary shift does not occur until after metamorphosis when transformed individuals begin to heavily

incorporate larger prey items in their diet such as adult salamanders of other species.

Pseudotriton ruber has also been found to have an extended larval period. Bishop (1941) and Bruce (1972b) found that the larval stage in the red salamander lasts approximately two to three years. Pfingsten (1989) listed the considerably overlapping size ranges for snout-vent length to be 13-25 mm for first year larvae, 20-40 mm for second year larvae, and 40-54 mm for third year larvae. In the present study, *Pseudotriton* young-of-the-year could not be identified because of their similarities to other plethodontid salamanders, but there were three salamanders found (40.51 mm SVL, 43.05 mm SVL, and 43.36 mm SVL) that were in the act of transformation. Most of the larvae collected and sampled were in their second or third year. According to Pfingsten's (1989) definition of size classes for snout-vent length, the sizes ranges for *Pseudotriton* in the present study were 22.96-39.85 mm (SVL) for second year larvae and 40.01-46.51 mm (SVL) for third year larvae. The data indicated that *P. ruber* ingested prey according to their size (SVL) because smaller larvae did not have prey with large volumes in their stomachs and only larger salamanders ingested larger prey items. A relationship between prey size and salamander size was found in this study, suggesting that an ontogenetic dietary shift does occur between the larval stages.

Another indicator of predator-prey size relationships may be the comparison of volumes of the largest and smallest prey items with the head widths of salamanders. This could show that salamanders may be limited to certain prey sizes because of a physical constraint in jaw width, in which case, they would be considered to be gape-limited. Most often, the size of prey ingested by predators is controlled by the mechanism known as gape-limitation (Zaret, 1980; Parker, 1994). Petranka (1984) suggested that gape-limitation was responsible for ontogenetic diet shifts in small larvae of *E. bislineata*. Hudson (1955) reported the total lengths of first year larvae for this species to range from 14.2-25.3 mm and gave a mean of 42 mm total length for second year larvae. Petranka also noted that the larval period for *Eurycea* in that study

lasted for about one year, and they usually transformed at a total length of 52 mm (1984). These salamanders are relatively smaller than *Gyrinophilus* and *Pseudotriton*. Parker (1994), on the other hand, showed that gape-limitation does not occur in the larvae of *D. tenebrosus*. These salamanders are larger in size than both *Gyrinophilus* and *Pseudotriton*. Gape-limitation probably does not occur in *Dicamptodon* because the younger salamanders are able to ingest the larger prey types without being constrained by jaw width. Parker (1994) reported the total lengths of *D. tenebrosus* to be 45-50 mm for young-of-the-year, 80-120 mm for second year larvae, and 105-153 mm for third year larvae. The results in the present study indicated that small larvae of *G. porphyriticus* were not gape-limited, but that small larvae of *P. ruber* could be constrained by jaw width. Some of the small larvae of *G. porphyriticus* ingested larger prey items, while small larvae of *P. ruber* ingested only the smaller prey items.

Studying the gut contents of young-of-the-year would probably involve preservation and dissection of the larvae because of their small size. Since both species are considered to be uncommon in Ohio, the present study focused on gut-flushing living larvae to obtain food samples and releasing the specimens after they recovered from the anesthetic.

Size comparisons between the measurements from both species were conducted to determine a size ratio that would distinguish the larvae of *G. porphyriticus* from *P. ruber*. Obtaining such a ratio was desirable because both species have very similar pigmentation and are difficult to identify in the field. Both larval plethodontids display a reddish, pinkish, or salmon-colored ground color with black flecks or dots marked on the dorsal surface (Brandon, 1989; Pfingsten, 1989). Additionally, only two methods can be used in the field to clearly identify the two species, and they involve counting the number of intercostal spaces between adpressed limbs and counting the number of costal grooves. Sometimes, however, these two methods are difficult to use because, while observing young-of-the-year larvae and when collecting on cloudy days, a count of the number of costal grooves becomes obscure. A size ratio, which could

classify the two species, may be more beneficial and reliable. However, the only significant difference in the slopes from the size comparisons was the regression of standard length with head length. Additionally, when comparing the ratios of the paired measurements for each species, a significant difference could not be found. The measurements of these two species were very similar, and the only way to tell them apart was to count the number of intercostal spaces and costal grooves.

The populations of each species at this study site appeared to be small. One reason for the small number of salamanders may be the extremely small stream. There is not much area available for large salamander populations to coexist. In addition to *Gyrinophilus* and *Pseudotriton*, *Eurycea* and *Desmognathus* also inhabit the study site. Another reason for finding small numbers of *Gyrinophilus* may be that they often burrow deep in underground tunnels within the stream bed (Bruce, 1980; Brandon, 1989). This habit may make finding these salamanders difficult. A third reason for finding few numbers of salamanders may be that, in 1995, a hot, dry period during July and August caused the stream to decrease in depth and flow. These two species prefer cool stream temperatures, and they might have burrowed into the stream bed to avoid the heat and low water levels. Throughout the study period, there was evidence of raccoon footprints lining the edges of the shallow stream. Additionally, in May of 1994, a half-eaten adult *G. porphyriticus* was found near the study site and preserved. This evidence might indicate that raccoons are preying upon salamanders, providing another reason for the small number of salamanders in the population.

LITERATURE CITED

Allan, J. D. 1981. Determinants of diet of Brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquati. Sci. 38:184-192.

Attar, E. N., and E. J. Maly. 1980. A laboratory study of preferential predation by the newt *Notophthalmus v. viridescens*. Can. J. Zool. 58:1712-1717.

Avery, R. A. 1968. Food and feeding relations of three species of *Triturus* (Amphibia: Urodela) during the aquatic phases. Oikos 19:408-412.

Bishop, S. C. 1941. The salamanders of New York. State Mus. Bull. 324:1-365.

Brandon, R. A. 1966. Systematics of the salamander genus *Gyrinophilus*. Illinois Biol. Monogr. 35:1-86.

_____. 1989. *Gyrinophilus porphyriticus* (Green), spring salamander. Pp. 213-222. *In*: R. A. Pfingsten and F. L. Downs (eds.), Salamanders of Ohio. Ohio Biol. Surv. Bull., n.s., 7(2).

Bruce, R. C. 1972a. Variation in the life cycle of the salamander *Gyrinophilus porphyriticus*. Herpetologica 28:230-245.

_____. 1972b. The larval life of the red salamander, *Pseudotriton ruber*. J. Herpetol. 6:43-51.

_____. 1980. A model of the larval period of the spring salamander, *Gyrinophilus porphyriticus*, based on size-frequency distributions. Herpetologica 36(1):78-86.

Burton, T. M. 1976. An analysis of the feeding ecology of the salamanders (Amphibia, Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. J. Herpetol. 10(3):187-204.

—————. 1977. Population estimates, feeding habits and nutrient and energy relationships of *Notophthalmus v. viridescens*, in Mirror Lake, New Hampshire. Copeia 1977:139-143.

Conover, W. J. 1982. Practical Nonparametric Statistics. John Wiley and Sons, New York, New York.

Dodson, S. I., and V. E. Dodson. 1971. The diet of *Ambystoma tigrinum* larvae from western Colorado. Copeia 1971:614-624.

Downs, F. L. 1989. Key to the larval salamanders of Ohio. Pp. 60-64. *In*: R. A. Pfingsten and F. L. Downs (eds.), Salamanders of Ohio. Ohio Biol. Surv. Bull., n.s., 7(2).

Elliot, J. M. 1970. Diel changes in invertebrate drift and the food of trout *Salmo trutta*. J. Fish Biol. 2:161-165.

Fellers, G. M., C. A. Drost, and W. R. Heyer. 1994. Handling live amphibians. Pp. 275-276. *In*: W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.

Hale, R. L. 1992. MYSTAT: Statistical Applications, Macintosh Edition. Course Technology, Inc., Cambridge, Massachusetts.

Hamilton, W. J., Jr. 1932. The food and feeding habits of some eastern salamanders. Copeia 1932(2):83-86.

————————. 1940. The feeding habits of larval newts with reference to availability and predilection of food items. Ecology 21:351-356.

Hudson, R. G. 1955. Observations on the larva of the salamander *Eurycea bislineata bislineata*. Herpetologica 11(3):202-204.

Kuzmin, S. L. 1991. Food resource allocation in larval newt guilds (genus *Triturus*). Amphibia-Reptilia 12:293-304.

Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22-30.

Leff, L. G., and M. D. Bachmann. 1986. Ontogenetic changes in predatory behavior of larval tiger salamanders (*Ambystoma tigrinum*). Can. J. Zool. 64:1337-1344.

————————, and ————————. 1988. Basis of selective predation by the aquatic larvae of the salamander, *Ambystoma tigrinum*. Freshw. Biol. 19:87-94.

Legler, J. M., and L. J. Sullivan. 1979. The application of stomach-flushing to lizards and anurans. Herpetologica 35:107-110.

Maiorana, V. C. 1978. Behavior of an unobservable species: diet selection by a salamander. Copeia 1978:664-672.

McCafferty, W. P. 1983. Aquatic Entomology: The Fishermen's and Ecologists' Illustrated Guide to Insects and Their Relatives. Jones and Bartlett Publishers, Inc., Boston, Massachusetts.

McWilliams, S. R., and M. Bachmann. 1989. Predatory behavior of larval small-mouthed salamanders (*Ambystoma texanum*). Herpetologica 45:459-466.

Merritt, R. W., and K. W. Cummins (eds.). 1984. An Introduction to the Aquatic Insects of North America. Second Edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Parker, M. S. 1992. Feeding ecology of larvae of the Pacific giant salamander (*Dicamptodon tenebrosus*) and their role as top predator in a headwater stream benthic community. Unpubl. Ph.D. diss., Univ. of California, Davis.

————. 1994. Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). Copeia 1994:705-718.

Pennak, R. W. 1989. Fresh-Water Invertebrates of the United States: Protozoa to Mollusca. Third Edition. John Wiley & Sons, Inc., New York, New York.

Petranka, J. W. 1984. Ontogeny of the diet and feeding behavior of *Eurycea bislineata* larvae. J. Herpetol. 18:48-55.

Pfingsten, R. A. 1989. *Pseudotriton ruber* (Latreille), red salamander. Pp. 269-275. *In*: R. A. Pfingsten and F. L. Downs (eds.), Salamanders of Ohio. Ohio Biol. Surv. Bull., n.s., 7(2).

————, and F. L. Downs (eds.). 1989. Salamanders of Ohio. Ohio Biol. Surv. Bull., n.s., 7(2).

Ranta, E., and V. Nuutinen. 1985. Foraging by the smooth newt (*Triturus vulgaris*) on zooplankton: functional responses and diet choice. J. Anim. Ecol. 54:275-294.

Surface, H. A. 1913. First report on the economic features of the amphibians of Pennsylvania. Pennsylvania Dept. Agri. Zool. Bull. 3:68-152.

Vanderploeg, H. A., and D. Scavia. 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecol. Model. 7:135-149.

Whitford, W. G., and V. H. Hutchison. 1965. Gas exchange in salamanders. Physiol. Zool. 38(3):228-242.

Zar, J. H. 1996. Biostatistical Analysis. Third Edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.

Zaret, T. M. 1980. Predation and Freshwater Communities. Yale Univ. Press, New Haven, Connecticut.