To the Graduate Council:

I am herewith submitting a thesis written by Noel M. Burkhead entitled "The Life History of the Stoneroller Minnow, Campostoma a. anomalum (Rafinesque), in Five Streams in East Tennessee." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Zoology.

David A. Etnier

David A. Etnier, Major Professor

We have read this thesis
and recommend its acceptance:

J. Larry Wilson

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

THE LIFE HISTORY OF THE STONEROLLER MINNOW, *CAMPOSTOMA A. ANOMALUM* (RAFINESQUE), IN FIVE STREAMS IN EAST TENNESSEE

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

The life history of the stoneroller minnow, Campostoma a. anomalum (Rafinesque), was examined in five streams in East Tennessee. This study was part of a two report project initiated by the Tennessee Wildlife Resources Agency to assess the impact of commercial bait fishing on the sport fishery for this cyprinid fish. Food habits, age and growth, and reproduction were studied.

Campostoma is a detritivorous species feeding on the ubiquitous aufwuchs community that occurs on the hard substrates of the streams studied. The jaw structure and the intestine of Campostoma are specialized for feeding and assimilating detritus and algae. An estimated 70-90% of the gut contents were detritus, primarily organic ooze and fiberous plant material.

Male stonerollers live longer (four years versus three), and grow slightly faster than females. However, females generally outnumber males. The largest male collected was 173.8 mm SL and was four years old. The largest female collected was 130.0 mm SL and was three years old. No differences in length-weight relationships between sexes were detected within each study stream, but significant differences, sexes combined and within sexes were detected in the slopes of the length-weight regressions between streams. The latter is attributed to variation in males.

Campostoma spawned in the spring between April and June, and peak activity occurred in about mid-April. Aggregations of Campostoma congregated over concentrations of clean swept gravel to perform the spawning

ritual. Males dug shallow pits, maintained them, and defended them against intrusion by other males. Spawning was brief and occurred in these pits.

Development of gonads was highly correlated with the spawning season. Numbers of mature ova were significantly correlated with the size of females, thus age. *Campostoma* is generally more fecund than other cyprinids of similar to smaller sizes, but is considerably less fecund than larger cyprinids.

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I. INTRODUCTION

Origin and Scope of Study

The origin of this study reflects some of the unique cultural aspects of the mountain people in upper East Tennessee. It is not rare to fish for and consume certain native North American minnows, but the organized, avid interest in maintaining a viable sport-food fishery for the stoneroller minnow, *Campostoma anomalum*, within the five county study area, particularly Carter, Johnson, and Unicoi counties, is unique.

A conflict of interest developed between sport-food fishermen and commercial bait fishermen upon the completion of two major reservoirs, South Holston and Watauga, in the study area. These reservoirs, especially the latter, created a demand for hardy bait minnows, of which *Campostoma* is widely renowned (Dobie et al. 1956; Gunning and Lewis 1956). Bait fishermen developed efficient collection techniques and, on a successful night, purportedly captured several thousand *Campostoma* (techniques are discussed and figured by Beets 1979). *Campostoma* sport fishermen, particularly through the organized voice of the Carter County Rod and Gun Club, protested that the voluminous catches of the bait fishermen were decimating the sport fishery. Thus in 1975, the Tennessee Wildlife Resources Agency (T.W.R.A.) outlawed the sale of *Campostoma* in Carter, Johnson, Unicoi, Washington, and Sullivan counties. This stimulated the development of a healthy black market. In 1978 live *Campostoma* (colloquially known as "hornyheads") were selling for as much as $4.00/dozen.

In 1977 the T.W.R.A. made available funds for two students at The University of Tennessee, Knoxville, to study the population dynamics and life history of *Campostoma anomalum* in portions of a five county area in East Tennessee (Figure 1a). The population and life history studies were concurrently conducted and the former is reported on by Beets (1979). This report presents results of life history investigations.

Literature Survey

A review of pertinent literature is discussed where appropriate in each section (e.g. FOOD HABITS). A review of aspects of distribution and nominal forms, not discussed elsewhere, is provided in the following subsections.

Distribution, Habitat, and Abundance

The stoneroller minnow, *Campostoma anomalum*, is native to North America; it is one of the most widely distributed minnows in the contiguous United States, and is widespread in Tennessee (Trautman 1957; Figure 1b and c). Within the study area (Figure 1a), especially in Carter, Johnson, and Unicoi counties, *Campostoma* was the most abundant fish in both numbers and biomass (Beets 1979).

Campostoma anomalum is generally a lotic species associated with upland habitats, and occurs in small streams and large rivers (Jenkins et al. 1972). *Campostoma* is a ubiquitous species in riffles and runs over gravel and rubble, and is less common in pools except during the winter months. Miller (1964) found *Campostoma* to occur

Figure 1. Distribution of _Campostoma anomalum_ in A, the study area; B, Tennessee; C, North America. In A the large open circles are population and life history stations, the large closed circles are life history stations only, and the small closed circles are relative abundance survey sites.

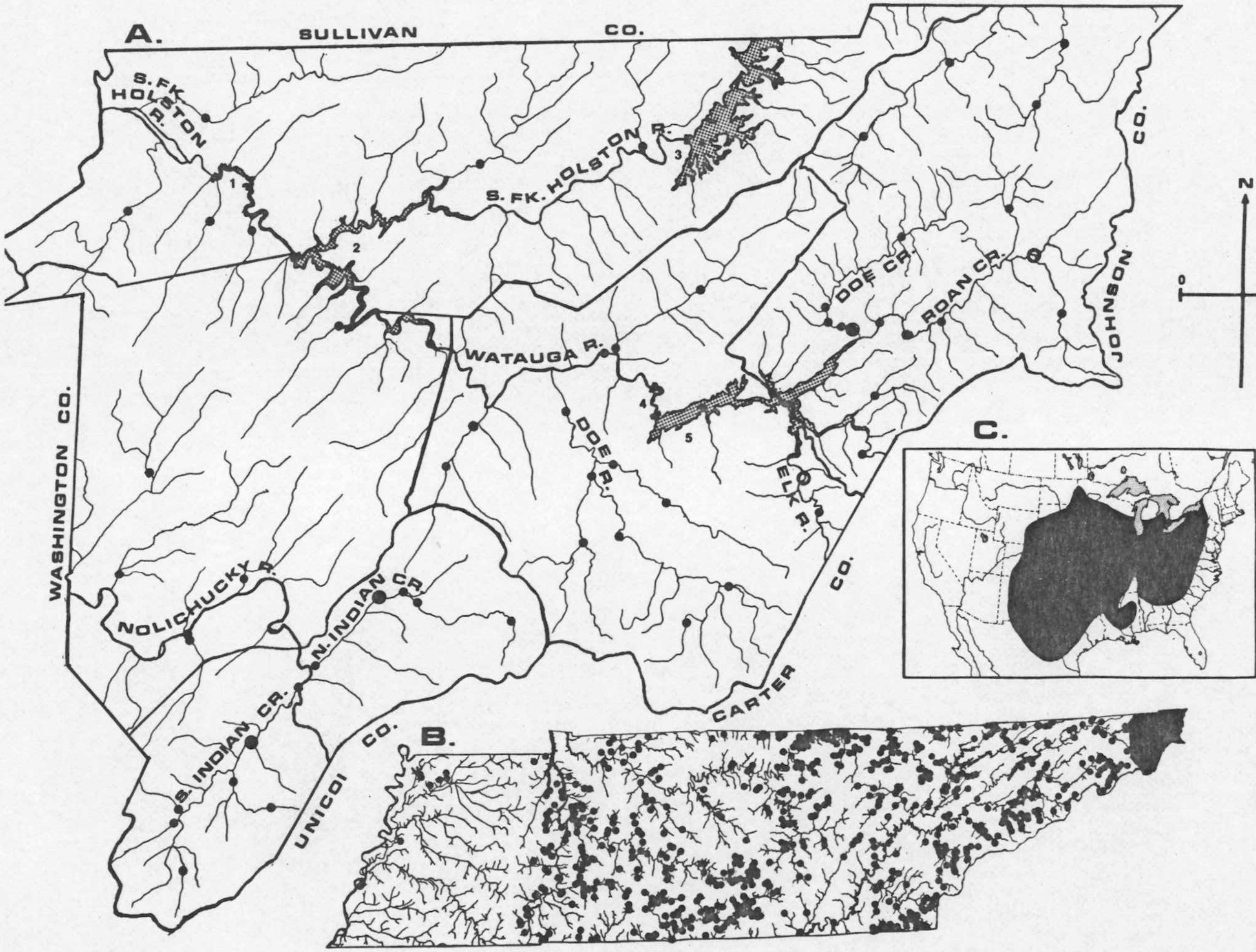
A.
SULLIVAN CO.
S. FK. HOLSTON R.
S. FK. HOLSTON R.
1
2
3
4
5
WATAUGA R.
DOE CR.
ROAN CR.
DOE R.
ELK R.
JOHNSON CO.
WASHINGTON CO.
NOLICHUCKY R.
N. INDIAN CR.
S. INDIAN CR.
UNICOI CO.
CARTER CO.
N
0
5
10 km
mi
B.
C.

Figure 1.

under stones and leaves in pools in winter, and Beets (pers. comm.) observed it lying on pool bottoms in a small stream in the Great Smoky Mountains National Park.

Nominal Forms

A synonomy and diagnosis of *Campostoma* appears in Jordan and Evermann (1896), and of *C. anomalum* in Burr (1976a). Currently three species of *Campostoma* are recognized: *C. anomalum* (Rafinesque), *C. oligolepis* Hubbs and Greene, and *C. ornatum* Girard; an undescribed form is known to occur in the Mobile basin. All forms are endemic to North America with *C. anomalum* occurring sympatrically with *C. oligolepis* in the central portion of its range (Burr and Smith 1976). *C. ornatum* is restricted to the southwestern United States and northern Mexico (Burr 1976b).

Two subspecies, *C. a. anomalum* (Rafinesque) and *C. a. pullum* (Agassiz), are currently recognized (Burr and Smith 1976). A third nominal subspecies, *C. a. michauxi* Fowler, occurs in the upland montane portions of the Tennessee, New (above Kanawha Falls), Santee, Roanoke, and James drainages (Ross and Carico 1963; Ross and Masnik 1971), but its status is uncertain at this time (Buth and Burr 1978). Until future studies clarify the subspecific status of *michauxi*, the form studied in this report is considered to be *C. a. anomalum*.

Location and Description of Study Area

Five counties, Carter, Johnson, Unicoi, Sullivan and Washington, were encompassed in the study area (Figure 1a and b). Five streams in the first three counties, Elk River, Roan Creek, Doe Creek, North

Indian Creek, and South Indian Creek, were intensively sampled, while some streams in the latter two counties were surveyed for the relative abundance of Campostoma (Figure 1). Elk River and Roan Creek were used for population and life history studies; the remaining three study streams were exclusively sampled for life history studies. The regularly sampled localities of the study streams are described in Table 1[1]. Species lists as well as species associates from all collections, including localities of the relative abundance surveys, are in Beets (1979).

An excellent description of land use, geography, and geology of the study area is found in Beets (1979); however, some aspects of these are reviewed. Carter, Johnson, and Unicoi counties occur almost entirely in the Blue Ridge physiographic province, while Sullivan and Washington counties are in the Ridge and Valley. Blue Ridge streams are typically higher gradient (more riffles than pools), and have on the average larger substrate sizes (more rubble and boulder) than those in the Ridge and Valley. Also the valleys are narrower with less flood plain than in the Ridge and Valley. Thus Carter, Johnson, and Unicoi counties are less agriculturally developed than Sullivan and Washington counties. Agricultural development, particularly soil erosion and subsequent siltation, probably affectts the distribution of Campostoma with in the study area more than any other factor. Although the study streams

[1] Table 1 and subsequent tables are found in Appendix.

had small to ocassionally moderate amounts of siltation, nearly all streams sampled in Sullivan and Washington counties had moderate to large amounts of siltation which covered substrates and plugged interstices between gravel particles. *Campostoma* was less abundant in streams in the latter two counties.

Two streams, North Indian Creek and South Indian Creek, were channelized at least twice during the study. *Campostoma* responded to channelization by declining sharply in abundance in the channelized sections, probably due to the destruction of the aufwuchs communities. *Campostoma* was common above and below these perturbed areas, and later re-established in the channelized sections when the aufwuchs recolonized. Beets (1979) found the macroinvertebrate fauna to be generally rich in species in the study streams, but also found that the effects of channelization on these faunas were evident in terms of low numbers and taxa.

The majority of streams in the Blue Ridge in this study, especially the order 1 tributaries, are pristine in condition, and many harbor trout.

II. MATERIALS AND METHODS

Study Stations and Sampling Intervals

Five study stations were selected in January 1977 (Table 1, Figure 1a). Stations were selected based on general similarity of flow, gradient, substrate composition, and accessability. Due to frequent rains and two major floods in spring and summer 1977, the stations were intermittently sampled for this period. An additional six months were added to the project resulting in all stream stations being sampled at least once per month, except for December.

Sampling Techniques

Two sampling techniques were generally employed to collect *Campostoma*. The first technique used a backpack shocker and a seine (1.8 m X 3.7 m X 6.35 mm mesh, 6 ft X 12 ft X $\frac{1}{4}$ in); the latter was used as a portable blocknet. About 3 m of stream was shocked for each effort afterwhich the net was lifted, and the fish removed. Three backpack shockers were used: a gasoline operated 1 H.P. O and R "Tiny Tiger," a model BP-1C Coffelt battery unit, and finally, an Echo model SRM-302-ADX gasoline unit. Considerable mechanical problems were encountered with the Tiny Tiger units (two were always taken into the field, one being used for parts), and the Coffelt unit, which only worked once. The Echo unit worked satisfactorily, but was only used in the last few months of the study. Frequent shocker malfunction often forced seining for specimens, an inefficient technique due to extremely coarse substrates.

The second method, used during spring and summer in Elk River and Roan Creek involved the blocking off of a 75 - 100 m stream section with two blocknets, and application of an ichthyocide at the upstream net. The two nets each had dimensions of 15.2 m X 1.8 m X 12.7 mm stretch mesh (50 ft X 6 ft X $\frac{1}{2}$ in). The specimens from these collections were used for population studies (Beets 1979) and for life history analysis. Upon collection all specimens were preserved in 10% formalin in 3.8 l (1 gal) jars, and eventually stored in 45% isopropanol for analysis.

Specimen Analysis

Standard lengths (SL) were recorded to the nearest 0.1 mm using Helios dial calipers for each of the 4,161 specimens collected. Weights for all specimens were determined to the nearest 0.1 g using a top loading Sartorious balance. Sex was recorded for all specimens by gonadal inspection except for 224 age class 0 specimens (unsexed). Generally specimens smaller than 40 mm SL required microscopic examination of gonadal squash preparations to determine sex. Gonadal squashes were prepared by removing the gonads and lightly pressing them between two slides for viewing.

Each gonad was assigned a size category of small, small-moderate, moderate, moderate-large, and large. These categories were later numerically ranked where small = 1.0 and large = 5.0, and used in an index to correlate relative gonadal development with season. Categories were ranked in proportion to body size so small specimens of either sex could have high values. This was done because some small age class I specimens were sexually mature. A gonad means index was devised by plotting the monthly mean index value for each sex for the five study streams against an index scale.

Ova numbers were determined by direct enumeration. The right ovary was removed from females (greater than 60 mm SL) collected in April through June and broken apart. The ruptured ovary was placed in a 3.8 l jar, filled with water, and shaken to further free the ova from ovarian connective tissue. Usually some ova remained embedded in the connective tissue. Most of these were stripped free of the tissue by pulling the tissue through a pair of compressed forceps, and by picking them out. After nearly all ova were freed of tissue, they were returned to the 3.8 l jar, shaken, and poured into an enamel pan (about one l at a time), and counted. The enamel pan was subdivided into eight quadrants; counts were recorded using a hand counter.

Food habit studies consisted of qualitative analysis of intestinal contents. The entire intestine was removed from the specimens examined and cut into small sections. Each section was slit lengthwise and its contents washed into a petri dish with a fine stream of 45% isopropanol. Intestinal contents were examined under a variable magnification stereo dissecting scope and compound microscope. Slides for microscopic inspection were prepared in a standard manner using large (50 mm) cover slips. Organisms, when present, were identified to the lowest possible taxon.

Age, age class sizes, and growth increments were estimated from length frequency distributions. Age class terminology refers to the system where age class 0 are those specimens collected prior to 1

January of a given year, and were spawned in the preceeding spring or summer (Tesch 1971).

Statistical Anlaysis

Numbers of mature ova were compared to female lengths for each study stream by correlation. Length-weight relationships were determined for each study stream by lumping all observations and performing a least squares regression of log - log (base 10) transformed data. Correlations and regressions were performed at The University of Tennessee Computing Center utilizing a SAS program. From statistics generated by the SAS program, an analysis of covariance was performed comparing the regression slopes of the length-weight regressions between the five study streams, sexes combined and within each sex. Analysis of covariance followed methods outlined by Sokal and Rolf (1969 p.477-8). Differences in length-weight regressions between sexes within study streams were determined by calculating slope and y - intercept confidence intervals as in Walpole and Myers (1978 p.289-291).

Behavioral Observations

Spawning observations were made underwater, standing in the water, and from the stream bank. Underwater observations utilized snorkeling gear and a full wetsuit; the latter proved essential for extended observations. In order to obtain the smallest possible observation distance, it was necessary to limit appendicular movement as much as possible. This was accomplished by keeping arms retracted underneath body and legs together, generally imitating a log. Movement towards the subjects was achieved by creeping on fingers and toes. Using this method, the author was able to get within 0.3 m of spawning male Campostoma. The longest observation period was four hours (interrupted ca. every 45 min to record notes) and the shortest ca. 30 min. A 150 mm (6 in) rule was placed near subjects to aid in size estimation.

Feeding observations were made by snorkeling on numerous occasions at several localities in the Little River, Blount County, Tennessee. Observations were also made of specimens maintained in an aquarium.

Stream Parameters

Physical characteristics of the study streams were recorded on 14-15 April 1978 during a period of low-moderate flow (Table 2). Discharge was calculated using the method of Robins and Crawford (1954). Water temperatures were measured to the nearest 0.1 degree for most collections using a glass thermometer. Stream lengths and elevations were estimated using a K and E map measurer and U.S.G.S. 1:250,000 scale topographic maps. Gradients were calculated from these data. A summary of water quality data is in Beets (1979). Terminology describing habitat components (e.g. gravel, riffles) refers to definitions found in Hynes (1970), with a few changes. Rubble substrates are equivalent to cobble, and runs (not defined by Hynes) are ecotonal habitats occurring between pools and riffles. Runs are typically intermediate in depth between pools and riffles, exhibit greater water velocities than in pools, but do not have extensive portions of disturbed stream surface as in riffles.

Additional discussion of particular methods are found in the following sections.

III. FOOD HABITS

Trophic Classification

Campostoma feeds on the ubiquitous aufwuchs community that flourishes on the hard substrates of the study streams. This epilithic community occurred on all substrate sizes, except for sand and small gravel, and was most abundant in riffles and runs. Aufwuchs were uncommon in pools, presumably due to silt deposition.

Although filamentous algae represented the predominant ingested, identifiable taxa, *Campostoma* are here considered to be detritivores by virtue of an estimated 70-90% detritus content present in the alimentary tracts of all specimens examined. It is unknown, however, whether the majority of the nutrients utilized are derived from detritus or algae.

Recent investigations of the importance of ingested plant items (primarily algae) in fish diets have shown that there is some nutrient uptake derived from the plants. When fed a mixed diet of algae and oligochaetes or mealworms, *Lepomis macrochirus* had greater weight increases than when only fed either animal food items. However, when fed only algae, *L. machrochirus* lost weight (Kitchell and Windel 1970). Radioactively tagged ^{14}C *Spirogyra* sp. and *Anabaena flos-aquae* were assimilated by *Ictalurus nebulosus* within nine hours of ingestion. The ^{14}C from these tagged algae were primarily absorbed in the foregut, and overall assimilation rates of 23 and 67%, respectively were reported (Gunn et al. 1977). However, the herbivorous pupfish, *Cyprinodon nevadensis*, exhibited low energy uptake (kcal m^{-2} day^{-1}) from algae and detritus, but consumed about 30% of its body's energy content per day in comparison to ca. 3% for carnivorous fishes (Naiman 1976).

A variety of fishes, marine and freshwater, have exhibited cellulase activity when assayed (Prejs and Blaszczk 1977; Stickney 1976). The former authors determined that cellulase activity was exogenous in origin (microbial flora) and had the highest correlation with the presence of detritus in the gut. Stickney's study suggested that cellulase activity was independent of the food type ingested. However, Stickney's method of correlating ingested food items with cellulase activity was not by gut examination, but rather by comparing food habits reported in the literature to the assay results of the species surveyed. Thus, his results are believed to be questionable. Gunnison and Alexander (1975) found some algal species to be more susceptible to microbial decomposition than others. *Ulothrix frimbrata* was one of the susceptible forms assayed, and *Ulothrix* sp. was the only alga identified from *Campostoma* guts in this study (Table 3).

Campostoma probably derives nutrition from both detritus and algae, and as suggested by the forgoing literature review, it is probably able to assimilate algal carbon by the action of exogenous microbial flora occuring in detritus.

Alimentary Morphology and Diet

Campostoma lack a true stomach or diverticula, and may have the most elongate, coiled gut of any North American cyprinid. Kraatz (1924) found the gut to be up to 7.94 times its body length (interpreted as total length). In general, minnows with elongate, coiled guts that deviate from the simple "S" shaped configuration have been associated with herbivory: *Acrocheilus alutaceus*, Moodie and Lindsey 1972; *Dionda nubila*, Pflieger 1975; *Hybognathus hankinsoni*, McPhail and Lindsey 1970; *H. nuchalis*, Carlander 1969; *Notemigonus crysoleucas*, Carlander 1969 and Snelson 1975; *Phoxinus cumberlandensis*, Starnes and Starnes 1978, *P. erythrogaster*, Philips 1969. The old world tostol, *Hypophthalmichthys molitrix*, is a phytoplanktivorous cyprinid exhibiting extreme gut elongation, up to 15 times its body length (Nikolskii 1954).

When the gut of *Campostoma* is uncoiled as in Figure 2, the juxtaposition of intestinal sections with opposite directions of alimentary flow is evident. This morphology suggests the interesting possibility of a counter-current mechanisms which would allow additional nutrient catabolism by transportation of partially digested nutrients from posterior to anterior intestinal sections.

Feeding Behavior

Campostoma possess a cartilaginous pad on the lower jaw which is used to scrape the aufwuchs off stream substrates. Scraping is accomplished by obliquely directed glancing movements. A similar method of grazing is found in *Achrocheilus alutaceus*, which also possesses a cartilaginous pad on the lower jaw (Moodie and Lindsay 1972).

Campostoma was most often observed feeding in schools which were generally uniform in specimen size. When maintained in an aquarium, *Campostoma* fed on algae growing on the substrate and aquarium walls as well as on prepared fish food. Fish food was most often taken in midwater. A single incidence of scale eating was observed in an aquarium. An age class I specimen, ca. 70 mm SL, was observed "shadowing" several

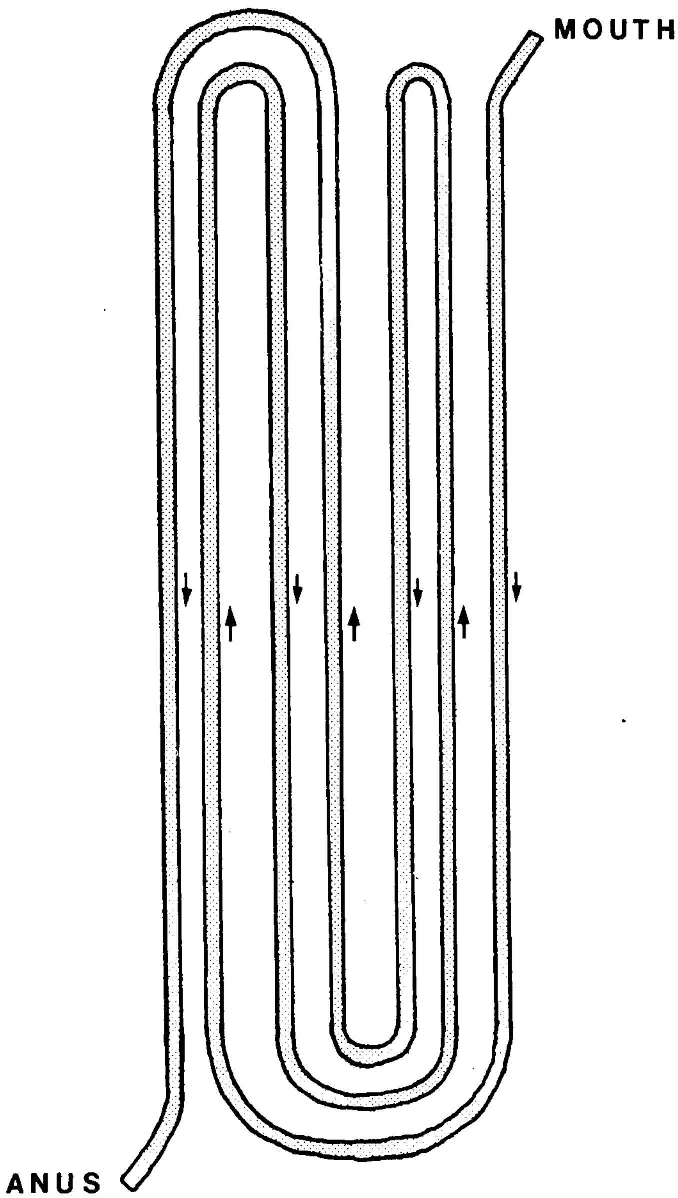

Figure 2. Configuration of an uncoiled gut of Campostoma anomalum. Arrows indicate direction of alimentary flow.

species of *Notropis* by frequently assuming a position above and behind them. At irregular intervals the *Campostoma* darted at these *Notropis* and glanced off their backs, apparently eating scales. No external parasites were present on these *Notropis*, and floating scales were observed after glancing attacks. Scales were found in the intestine of one specimen from Roan Creek (Table 3).

Gut Contents

The qualitative results of gut analysis appear in Table 3. In decreasing order of estimated abundance, intestinal contents are as follows: detritus, algae, diatoms, sand, chironomid larvae, several cycloid scales, fish eggs, and a single specimen of *Brachyptera* sp. (Plecoptera). Detritus was composed of amorphous organic ooze, fibrous plant material, and a few insect exuvia. A detailed study of *Campostoma* food habits by Kraatz (1923) showed very similar results. In young of year specimens he found high incidences of rotifers, copepods, and cladocerans. Similar intestional contents were also reported by Schmulbach (1957).

The gut contents of *Campostoma* were highly macerated. Filamentous algae was typically represented by short trichomes, and single broken cells were common. The chloroplasts of undamaged *Ulothrix* cells were usually present while diatom plastids were usually absent. The lack of cell wall erosion and the presence of many intact chloroplasts in the cells of trichomes suggest that degradation efficiency may be low. Rabe et al. (1973) thought that the intact nature of ingested algae in *Cyprinodon rubrofluviatilis* and *Fundulus zebrinus* suggested that the algae was not digested, whereas the absence of diatom plastids indicates solution of the diatom protoplasm.

The occurrence of sand in the gut may not be entirely incidental; it certainly functions to additionally macerate intestinal contents (Gunn et al. 1977).

During spring and to a lesser degree in winter, fishermen within the study area successfully angle for Campostoma using worms. The eating of worms by Campostoma and the feeding on fish food in aquaria indicate that it will feed opportunistically.

IV. AGE AND GROWTH

Longevity and Maximum Sizes

Previous studies of age and growth of Campostoma anomalum have utilized both scale analysis and length frequency distributions to determine age (Lewis and Elder 1953; Gunning and Lewis 1956; Schmulbach 1957; Lennon and Parker 1960). Gunning and Lewis (1956) and Schmulbach (1957) compared the two methods and found close approximation between them, especially in age classes 0, I, and II. The length frequency method was selected for use in this study primarily due to difficulty in detecting the first or third annulus in specimens in the vicinity of 100 mm SL, specimens which should have been age class III based on these previous studies.

Seasonal samples of sufficient size for length frequency analysis were only obtained from the population stations on Elk River and Roan Creek. The results of these analyses are protrayed in Figures 3 - 6 [2] for Elk River and in Figures 7 - 10 for Roan Creek. Age class size ranges for these streams are in Table 4. Due to persistent equipment malfunctions, large samples were irregularly obtained from Doe Creek, North Indian Creek, and South Indian Creek, thus disallowing a complete picture of population age structure. Length frequency distributions for these streams were plotted by combining all samples for each stream. However, these data were not figured or discussed as the lumping of all samples for each month for each stream obscured modal differences of age classes by increasing modal overlap. This was particularly true of a

[2] Figure 3 and subsequent figures appear in Appendix.

species with a protracted spawning period. Although the following discussion pertains specifically to results from Elk River and Roan Creek, it was assumed that comparable results would be obtained from the other streams since all streams were of similar size, occurred within the Blue Ridge, and were geographically proximate.

Only males reached age class IV, the fifth growing season, while the oldest females were age class III in both Elk River and Roan Creek (Table 4). Age class IV males were only collected in April from both streams while age class III females were detected in all samples for both streams except for June 1978 in Elk River, and September and February 1978 in Roan Creek (Table 4). The largest age class IV male collected was 173.8 mm SL from Roan Creek, and the largest age class III female was 130.0 mm SL from Doe Creek. Schmulbach (1957) also only detected age class IV specimens in April (sexes combined). The only study of Campostoma which detected a fifth age class (sixth growing season) was Lennon and Parker (1960) who, by the scale analysis method, reported age class V in both sexes. Size ranges of age class V specimens reported by them, sexes here combined, were 6.8 to 8.9 in total length (TL), ca. 145-189 mm SL (TL = 1.19 SL from Carlander 1969). The largest specimen recorded by them, although not analyzed in their data, was 11.3 in TL, ca. 241 mm SL.

The author has observed, by snorkeling, noticably larger specimens of Campostoma in the Little River in the Great Smoky Mountains National Park, one of Lennon and Parker's (1960) study streams. It is possible that Campostoma, within the study area of this report, could also occasionally reach age class V, although this is not evident from the length frequency distributions. Local fishermen reported that "years ago"

Campostoma "often" grew to 13 in (TL). The veracity of such statements is questionable, but if such lengths are reduced by 25-30%, the result is specimens in the 190-200 mm SL range, significantly larger than specimens collected in this study. Although many factors contribute to maximum size and age, it is possible that the heavy fishing pressure, both legal and illegal, on this species within the study area could contribute to the reduction or elimination of a fifth age class.

Demography

If an entire population of a relatively fast growing fish inhabiting temperate latitudes was sampled and the length frequency distributicn plotted, one would expect to observe successively decreasing modal amplitudes as age and size increased. Although "entire populations" obviously were not sampled, samples large enough to demonstrate this phenomenon were secured from Elk River (Figures 3 and 6) and from Roan Creek (Figures 7 and 9). The percent composition of each age class for both sexes from the sampled populations of Elk River and Roan Creek are in Table 4. As can be seen, the percent representation of each age class, for both sexes, decreased as age and size increased. The few exceptions were attributed to sampling artifacts rather than actual demographic composition. Beets (1979), in the complimentary population study of this report, calculated mortality (Z) and found it to increase generally with age and size.

The percent composition of age class IV specimens (males) from this study (Table 4) are similar to results of other studies reporting age class IV as the maximum age (Gunning and Lewis 1956, age class IV =

0.64%; Schmulbach 1957, age class IV = ca. 2.0%). The age class V specimens reported by Lennon and Parker (1960) ranged from 2.5 to 5.8%, whereas their age IV ranged from 11.5 to 33.3% of the population analyzed.

Sex ratios varied, and were generally skewed towards females (Tables 5 and 6). Schmulbach (1957) also detected lower numbers of Campostoma males to females, varying from 1:2.96 to 1:7.62. Unequal sex ratios have been reported for other cyprinids. Lachner (1952) found sex ratios skewed towards females in Nocomis biguttatus and N. leptocephalus, as did Cowell and Barnett (1974) for Notropis maculatus. Unequal sex ratios numerically favoring males were reported by Tarter (1969) for Rhinichthys atratulus, and for Semotilus margarita by Fava and Tsai (1974). Carlander (1969) omitted discussion of sex ratios because he felt that unequal ratios often resulted from a sampling bias towards one sex. This certainly would be true in adults, especially in Campostoma during the reproductive season where sexual segregation occurs. However, a sampling bias favoring one sex is difficult to envision in age class 0 and I specimens of Campostoma. The occurrence (on the average) of unequal sex ratios is interesting and appears to be more complex than differential survival of one sex. Barash (1977) provides a good general review of different reproductive strategies having unequal sex ratios. Trivers and Willard (1973, as cited by Barash 1977) proposed that sex ratios may vary in response to different environmental pressures. An unusual case of sex ratio variation was reported by Robertson (1972) for the labrid Thalassoma bifasciatum where individuals change sex from female to male as they progress in a size related dominance hierarchy. Regarding *Campostoma*, an r - selected species, numerical abundance of females probably serves to enhance reproductive output.

Growth Increments

Growth, or increase in body tissue per unit time, of most fish inhabiting temperate latitudes is typified by rapid increases of length in the first year of life, or all age class 0 plus part of age class I, followed by lesser increases with successive years of life (see life history summaries in Carlander 1969). Factors influencing growth are numerous, often interdependent, and are summarized in Lagler et al. 1962; several chapters in Gerking 1967; Weatherly 1972. An obvious factor affecting growth is food supply, which for *Campostoma* in this study, is essentially unlimited; thus in this respect growth conditions are ideal.

Seasonal growth increments were determined for Elk River and Roan Creek and are listed in Table 7. The post yolk sac larva length of 9 mm TL (Hogue et al. 1976) was used to estimate growth increments for age classes 0 and I.

The period of greatest growth in both sexes of *Campostoma* occurred during the first summer and fall of life. The growth increment of 40.5 (Table 7) for the April 1978 males from Elk River is interpreted as the result of small sample size rather than increased growth. With few exceptions, males grew faster than females in both Elk River and Roan Creek. Higher male growth rates was also reported by Miller (1962).

Length-Weight Relationship

The length-weight relationship is generally described by the formula:

$$W = aL^n$$

where W = weight, L = length, and a and n are constants determined from the length-weight regression (Carlander 1969). For most fish the value n is modally around 3.0 indicating a cubic relationship between volume and length. Values of n which are higher than 3.0 generally indicate an increase in plumpness with an increase of length, whereas values of n less than 3.0 indicate the opposite.

Length-weight regressions and their respective logistic equations were calculated for the five study streams; the regression lines are in Figures 11 - 15, and the equations are listed in Table 8. Differences in the length-weight regressions between sexes for each stream are in Table 9. Differences in length-weight regressions between streams, sexes combined and within sexes, are in Table 10.

Comparison of length-weight regressions between streams yielded some interesting results. North and South Indian Creeks, both tributaries of the Nolichucky River (Figure 1, p. 3), were the only streams with no significant difference between regression slopes, sexes combined (Table 10). Variation of regression slopes between the study streams appears to be due to males as females from Roan Creek, Doe Creek, North Indian Creek, and South Indian Creek had no significant difference between slopes (Table 10). Within each study stream, no significant slope difference between sexes occurred (Table 9). One might expect a difference in length-weight regressions between sexes to occur resulting from increased weight of females during the protracted spawning season;

however, males also increased weight during spawning due to increased musculature.

Schmulbach (1957) determined the length-weight relationship for 342 Campostoma. His logistic equation is similar to those generated in this study (Table 8). Carlander (1969) stated that the regression equation reported by Swingle (1965) was probably not valid based on Swingle's high condition factor, C(TL) = 2.62, for small specimens, but Carlander incorrectly reported Swingle's equation as Log W = 3.72 + 2.39 TL. Swingle's logistic equation is correctly listed in Table 8. No striking differences in the length-weight relationships of Campostoma anomalum determined in this study were evident when compared to other cyprinids surveyed by Carlander (1969).

Ponderal indices or condition factors were not determined for this study. The K value reported by Schmulbach (1957) for Campostoma ranging from 34 to 102 mm TL, age classes and sexes combined, was 2.06. He found a slight decrease in K values for larger specimens, however, the range of values for all age classes was only 0.28.

V. REPRODUCTION

Epigametic Characters

The males of Campostoma a. anomalum, as well as other subspecies and species of Campostoma, exhibit extreme states of seasonal sexual dimorphism, and moderate states of sexual dichromatism. No other North American cyprinid exceeds Campostoma in its degree of sexual dimorphism although the genus Nocomis rivals it (see Lachner and Jenkins 1971, figures 10-11). The nuptial dress of Campostoma has been thoroughly figured and described elsewhere (Jordan and Evermann 1896, p.206; Hubbs and Cooper 1936, plate 10; Burr and Smith 1976; Smith 1979; Pflieger 1975, p. 38).

However, to aid in understanding of reproduction, these epigametic traits and their relative chronology of development in C. a. anomalum are discussed (refer to Figure 16). Nuptial males possess large cephalic tubercles in front and above the eyes, and usually a pair of large tubercles just above the dorsal margin of the opercle. Additional smaller cephalic tubercles overlie the cranium posterior to the eyes, often forming a pentagonal pattern. The larger cephalic tubercles are generally directed laterally or posteriorly. Somatic tubercles occur, usually one per scale, dorsally and dorsolaterally from the nape to the caudal peduncle. These somatic tubercles are often retrose. Tubercles also occur on the thickened anterior dorsal fin rays, and on the dorsal, leading rays of the caudal fin. Uni- or biserial rows of tubercles occur on the anterior half of the pectoral fin and are attached to the rays. Small excrescenses occur ventrolaterally on preopercle and opercle margins as well as on the branchiostegal rays. The physiognomy of male Campostoma also changes. The dorsal and dorsolateral musculature between the nape and dorsal fin becomes enlarged, giving a slight humped-back appearance. White, fleshy extensions of the upper and lower lips develop, resembling flattened barbels. Epigametic pigmentary characters are the occurrence of medially developed black bands in all fins except the caudal, which develops a prominent caudal spot. A yellow to orangish wash develops basally in all fins, especially the dorsal and pectoral.

Females do not develop tubercles, excrescenses, enlarged musculature, or fleshy appendages. Dark bands and chromatic pigments occur, but are much less intense than in males. Gravid females appear rotund owing to swollen abdomens. Genital papillae are variable, but are slightly more enlarged in females than males in specimens over 60 mm SL.

Development of epigametic characters varies greatly by season and age class. Tuberculate males appear as early as December and were available until late June. The large cephalic tubercles develop first and are followed by the smaller cephalic and somatic tubercles. Somatic tubercles develop in anterior to posterior and dorsal to lateral directions. Age class I to IV males develop tubercles during the spawning season. There is no explicit correlation between tuberculation and gonadal morphology (see Gonadal Development).

Spawning Times and Temperatures

Campostoma exhibited a protracted spawning period. Spawning lasted from April to June with the greatest reproductive effort occuring in mid-April. Similar periods of spawning activity were reported by Crevecoeur (1907), Hankinson (1919), Smith (1935), Schmulbach (1957), Lennon and Parker (1960), and Miller (1962). Temperatures recorded during the spawning season in this and other studies ranged from 10.8 to 26.8° C (Table 11). Temperatures recorded during peak spawning activity in this study ranged from 12.0 to 14.2° C. The studies from which spawning periods and temperatures were abstracted ranged latitudinally from New York to Tennessee; however, no cline in spawning seasonality or temperature regimes was evident.

Spawning Habitat

Within the study area *Campostoma* were observed spawning over small to medium gravel substrates in shallow runs (up to 0.5 m deep; ca. 0.1 - 0.4 m/sec velocity). Spawning substrates were generally silt free and patchily distributed in the five study streams. No stream had large concentrations of gravel, however, the paucity of small areas of erosional substrates is typical of streams in the Blue Ridge. Gravel substrates were generally associated with the mouths of tributaries and the heads or tails of riffles. Granny Lewis Creek, a tributary of South Indian Creek, had the largest concentration of gravel substrates among the observed portions of the study streams.

In addition to observations within the study area, *Campostoma* were observed spawning in a similar habitat in the Duck River, Coffee County, Tennessee.

Equivalent spawning habitats have been reported by numerous authors. Miller (1962), who compiled the most exhaustive study of spawning behavior in *Campostoma*, felt that potential spawning habitats were more preferable if pools were adjacent to the spawning site (for use as cover). Since runs are intermediate currents between riffles and pools, the above preferred situation would always be likely, thus leaving gravel substrates in runs the salient spawning habitat requirements. Studies of *Nocomis* reproduction have also demonstrated a gravel substrate preference by spawning *Campostoma*. It has long been documented that certain cyprinids, including *Campostoma*, spawn in association with various species of the genus *Nocomis* (Cope 1868, Raney 1947, Lachner 1952). *Campostoma* utilize the gravel mound nests of *Nocomis* in spawning, and will concurrently spawn with *Nocomis*, sometimes resulting in various hybrid combinations (Schwartz 1972). Lachner (pers. comm.) pointed out that within a given section of stream where *Nocomis* are spawning, their nests represent local concentrations of gravel.

Spawning Aggregations

Campostoma is a gregariously spawning species. Aggregations varying in size descend upon suitable habitats to perform the spawning ritual. The largest observed spawning aggregation of *Campostoma* was estimated to contain 400 individuals and the smallest about 50. Miller (1962) observed an aggregation of over 1000 females in a pool adjacent to a spawning shoal. The snorkeling observation of ca. 400 individuals in Clarks Creek had an estimated sex ratio of 4:1 (male to female). The females were peripherally situated around a central concentration of males and intermingled with the males only occasionally. Similar configuration of sexes were reported by Smith (1935) and Miller (1962).

The localization of *Campostoma* for spawning, whether into smaller or larger streams, does not constitute a true "spawning migration." Vernal movements into small creeks for spawning were reported by Hankinson (1919) and Smith (1935), and postspawning movements into larger streams by Trautman (1957). Miller (1962) suspected that spawning movements were highly localized (in his study streams) due to abundant spawning habitat. Spawning aggregations in this study were observed in both smaller streams (Clarks Creek and Granny Lewis Creek) and in a moderate size stream (Elk River). In all cases, aggregations were associated with concentrations of gravel substrates.

Bait poachers collecting *Campostoma* for sale take advantage of vagile concentrations and purportedly capture up to 2000 fish in a single effort.

Pit Construction and Maintenance

Campostoma males excavated shallow pits in gravel, and maintained them through a more or less continuous process of gravel removal. Pit sizes varied. The pit size appeared to be a function of substrate size and cohesiveness, and of the size of the excavating male. Pits excavated in small, homogenous gravel had dimensions of about four to six cm deep and up to 10 cm in diameter. Pits excavated in larger, heterogeneous gravel tended to be shallower with varying diameters, a few up to 15 cm. Larger males appeared to dig larger pits, although supportive data was lacking. Miller (1962) also described a variety of pit sizes ascribing differences to substrates, but did not associate larger pits with larger males.

Pit excavation and maintenance are one in the same process since currents continually erode the pit margin, redepositing gravel in the pit. The process of pit maintenance is essentially composed of two distinct activity patterns: the actual removal of gravel from the pit, and the "pit-maintenance" posture. The latter was intimately associated with territoriality and possibly spawning. Miller (1962) described three methods of gravel removal while the author observed two. The most frequently observed method of gravel removal was mouth-held transport. The least frequent and apparently least successful method was a nudging of gravel with the snout followed by uplifting of the head and anterior body. In both methods the gravel was immediately deposited at the pit periphery. The "pit-maintenance" posture was assumed when males were not actively excavating pits. The *Campostoma* males oriented against the current in a head down position, assuming an angle of about 30-45°. The head of the pit-excavating male was usually several cm above the substrate, either over the pit or downstream just below it. The "pit-maintenance" posture was sustained by a slow, lateral undulation of the body.

Pit Territoriality

Males that were excavating pits or sustaining pit-maintenance postures (pit-males) rigorously defended their pits against intrusion by other males (non-pit males). Non-pit males of all sizes frequently violated the territorial space of pit-males, resulting in agonistic behavior. In fact, the frequency of aggression was occasionally so high that the spawning shoal resembled an aquatic battlefield. Hankinson

(1919 p.138) observed "The fish frequently give chase to each other, often with such heedlessness that they throw themselves on shore...." Although emperical data is lacking for this study, it appeared that territorial encounters constituted a large portion of the spawning activities. Indeed, Miller (1962) found that 45.8% and 40.7% of nest related activities from two creeks were agonistic behavior.

A non-pit male usually initiated an agonistic encounter by coming too close to an active pit or pit-male. The pit-male would usually dart from the pit towards the intruding non-pit male. At this point several things could happen: (a) the pit-male could chase the non-pit male off without contact; (b) the pit-male could chase the non-pit male off only after contact (usually frontally or laterally directed head butting); (c) the non-pit male could usurp the pit from the former pit-male. Only the first two situations were observed during this study while Miller (1962) observed all three. Furthermore, Miller (1962) described intention movements displayed by the pit-male in the above first situation. In this case the pit-male would dart a short distance towards the intruding non-pit male and stop, often preforming modified reduced movements associated with head butting. Considering the large cephalic tubercles of male _Campostoma_, the benefit of ritualized combat is obvious.

During periods of intense spawning activity, any pit momentarily vacated by a pit-male was immediately occupied by an adjacent non-pit male. Males temporarily occupying a pit (prior to being challenged by the returning pit-male) often proceeded to excavate it.

Spawning

The majority of energy spent in reproduction is in preparation, as the spawning act is brief, lasting only a few seconds. In response to some cue, females dashed singly into the spawning aggregation's central concentration of males, selected a pit-male, entered the pit, and spawned. While in the pit females apparently flexed their abdomens ventrally to exude ova. The pit-male and any adjacent males quickly followed the female into the pit to release milt. The pit-males had the first opportunity to release gametes, albeit a brief one. Females left the pit nearly as fast as they entered it, usually leaving a mass of spawning males behind.

The spawning sequence observed is similar to that reported by Smith (1935), Miller (1962), and others. Of particular interest are the cues to which a female responds to initiating her nuptial dash, and the factors governing selection of a particular male. The pit, the pit maintenance posture, and the sexual dimorphism and dichromatism of the male certainly signal a state of spawning readiness. Miller (1962) speculated that the pit could be as important as the pit-male in stimulating the females spawning dash. Spawning likelihood probably increases (up to a given limit) as the number of signals of spawning readiness increases. Neither observation or literature reports reveal any cues to factors governing mate selection in Campostoma. It has been shown that females of certain species differentiate qualitative attributes of reproductively ready males. Female Drosophilia melanogaster yellow mutants discriminate between males on the basis of wing beat frequency (Bastock and Manning 1955), and female canaries respond to male song diversity by building nests faster and laying larger clutches (Kroodsma 1976).

Lekking

The social organization of *Campostoma* spawning behavior is very similar to lek mating strategies found in birds and mammals. Whether any fishes spawning behavior conforms to the term "lekking" is controversial, and is discussed, but not clearly resolved, by Loiselle and Barlow (1978). It is the author's opinion that *Campostoma* lek, as they exhibit the array of behaviors associated with lekking except that zygote formation and partial development of the offspring occurs at the lek. The latter constraints are merely products of oviparity. Furthermore, there is no reason why the selective pressures associated with formation of lek mating strategies could not occur aquatically.

Intersubspecific Variation

The preceeding discussion of reproductive parameters compared observations between *Campostoma a. anomalum* (this study) and *C. a. pullum* (other studies). It is not known, nor deducible from this study, whether any of the differences observed result from subspecific variation.

Gonadal Development

The gonads of both sexes are located next to the kidneys at the dorsal wall of the abdominal cavity. In the young of both sexes, the gonads are small, white to opaque straps of tissue that are often embedded in the dark abdominal peritoneum. As development of the males proceeds towards sexual maturity, the testes first enlarge in width and thickness, then eventually become weakly to moderately convoluted in spawning specimens. As females mature, ovaries change from straps to tapered cylinders (all immature ova) to roughly funnel-shaped, as the ova mature in a posterior-anterior direction. Most specimens of both sexes, when possessing mature gonads, also exhibited an array of secondary sexual characters (see <u>Epigametic Characters</u>). A small number of aberrant specimens occurred in all study streams during the spawning season. Some small, nontuberculate age class I males possessed large testes and exuded milt; some large, tuberculate age class III-IV males possessed small testes; some large females were observed with small strap-like ovaries. These ovservations indicate that in some specimens, epigametic characters develop independently of gonadal development. The contrary was reported by Wiley and Collette (1970) in their summary of physiological literature discussing tubercle and other secondary sexual character formation.

Seasonal Variation in Gonadal Development

The most frequently used method of analyzing seasonal changes in gonadal states is the gonosomatic index of Vladykov (1956). Gonosomatic indices are usually determined for only females; males are generally treated by description (Tarter 1969; Fava and Tsai 1974; Heines and Clemmer 1976; Mathur and Ramsey 1974; Page 1975; Burr and Page 1978; and numerous others). However, studies by Larimore (1957) and Cambell and Branson (1978) analyzed and compared both sexes gonosomatically. Due to the large numbers of specimens examined in this study (4,161), and since all but 224 specimens were sexed, an alternative method, the "gonad index means", was devised to depict seasonal changes in gonadal states of development in both sexes (see MATERIALS AND METHODS). The gonad index means method is useful when large numbers of specimens are available as it reflects the reproductive development of a sampled population. The results of these indices are in Figures 17 - 21.

The following conclusions are drawn from the figures cited above:

1. Differences in relative states of gonadal development exist between each sex for each month examined.

2. Within each study stream, both sexes varied in a synchronous manner.

3. The greatest differences between sexes occurred during the reproductive season (April to June).

4. Peak gonadal development coincided with peak reproductive activity (mid-April based on observations).

5. Maximal values of the gonad index means were similar at all stations, except North Indian Creek, where both sexes exhibited depressed values.

The above conclusions represent typical observations of seasonal gonadal variation of fishes inhabiting temperate latitudes except for conclusion number three. If both sexes were indexed equally, it would be expected that gonadal response to the spawning season would be similar. The differences between sexes during the spawning season could be the result of a protracted spawning season, where a large portion of the population (age classes I-IV) are in various states of elevated gonadal development, and where there exists disproportionate sex ratios (females greater than males). When males and females were compared using gonosomatic indices (Larimore 1957; Campbell and Branson 1978), both sexes exhibited peak values during spawning. However, large differences in magnitude of values between males and females existed due to the lower ratios of testes weight/body weight in males. The gonosomatic index better reflects energetic input into reproduction in terms of percent tissue increase. Ovary weights were examined by Schmulbach (1957) for *C. a. pullum* and found to range from 10 to 35% body weight (size ranges 45 to 108 mm SL) during the spawning season.

It has been shown in fishes and other vertebrates that mediation of environmental stimuli is accomplished by neurosecretory organs which release gonadotropic hormones (Hoar 1966; Hoar and Randall 1969; Prosser 1973). In temperate latitudes the two most important environmental factors influencing the onset of reproduction are photoperiod and temperature.

Fecundity

Fecundity is generally defined as the reproductive potential of a species, and in fishes it is often analyzed in terms of a females age, size, and condition (Lagler et al. 1962). Fecundity has also been shown to vary with temperature, latitude, race, and other factors as summarized and discussed by Bagenal (1967) and Bagenal and Braum (1971). This study follows Bagenal's (1966) definition of fecundity as the number of ripe ova present just prior to a given spawning. Ova maturity has been determined based on ova shape (James 1946) and on ova size and color (Heines and Clemmer 1976). It was obvious from examination of ovaries from *Campostoma* females collected during the spawning season that several developmental stages were present. These ova stages were distinguished primarily by color with the largest ova appearing bright yellow-orange. The successively smaller ova ranks appeared pale yellow, then opaque whiteish, and finally transparent and minute in size. Size ranges of the round, mature ova were 1.1-1.9 mm maximum diameter (based on 20 ova). Fecundity was analyzed by statistical correlation rather than least squares regression as both length and ova number were considered to be independent variables. The results of correlation analysis are listed in Table 12, and the scattergrams are depicted in Figures 22 - 26. The probability that r was significantly different from zero varied from low (Doe Creek) to very high (Elk River). The ova count ranges for all study streams are listed in Table 13.

Ova count ranges of *Campostoma a. anomalum* were very similar to those of *C. a. pullum* as reported by Schmulbach (1957). *Campostoma* appears intermediate in fecundity when compared to other North American Cyprinidae. *Campostoma* is considerably more fecund than the small, annual species *Notropis maculatus* (Cowell and Barnett 1974) and *N. longirostris* (Heines and Clemmer 1976). Carlander's (1969) tome summarized the literature from which the following comparisons are made. *Campostoma* is generally more fecund than smaller cyprinids living two or more summers (e.g. *Notropis rubricroceus*, *N. volucellus*, *Pimephales notatus*), but was about the same as other smaller species, *N. hudsonius* and *Rhinichthys atratulus*. When compared to eastern North American cyprinids of similar to larger sizes, *Campostoma* was more fecund than *Nocomis leptocephalus*, *N. micropogon*, and *N. bigguttatus*, but about the same as *Semotilus atromaculatus*. In comparison to larger, pelagic spawning western cyprinids, *Gila bicolor* and *G. robusta*, *Campostoma* was considerably less fecund. The introduced cyprinid, *Cyprinus carpio*, perhaps the most fecund of all fishes in North America, is up to 700 times more fecund than *Campostoma*.

It is obvious when considering the range of spawning behaviors, presence or absence of parental care, spawning habitat, latitudes of occurrence, size, age, and other characteristics of the above species, that factors affecting fecundity are numerous and interdependent.

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APPENDIX

Table 1. Localities of the regularly sampled study stations.

Elk River above Watauga Reservoir at second bridge on Co. Rt. 2520, 16.3 air km (10.2 mi) E center Hampton, Carter Co., TN.
Roan Creek at mouth Forge Creek off St. Rts. 34-421, 3.7 air km (2.3 mi) SSE center Mountain City, Johnson Co., TN.
Doe Creek off Co. Rt. 2374, 2.5 rd km (1.5 mi) NE junction Co. Rts. 2374-2576, Johnson Co., TN. (Prior to flooding 1977).
Doe Creek off Co. Rt. 2374, 1.1 rd km (0.7 mi) NE junction Co. Rts. 2374-2576, Johnson Co., TN. (after flooding 1977).
North Indian Creek off unnumbered Co. Rt., 6.4 air km (4.0 mi) NNE center Erwin, Unicoi Co., TN.
South Indian Creek off Rts. 19W-23 at mouth Granny Lewis Creek, 9.1 air km (5.7 mi) SSW center Erwin, Unicoi Co., TN.

Table 2. Physical characteristics of the study streams. Data collected during a period of low to moderate stream flow.

Station	Length km(mi)	Width* m(ft)	Mean Gradient m/km(ft/mi)	Discharge m^3/sec(ft^3/sec)	Drainage Area km^2(mi^2)
Elk River: in Tenn.	22.4(14)	12.8(42)	16.3 (85.7)	1.10 (38.85)	75.7 (29.2)
Total	44.8(28)	--	33.9(178.6)	--	120.5 (46.5)
Roan Creek	49.6(31)	11.0(36)	10.4 (54.8)	1.21 (42.74)	285.2(42.74)
Doe Creek	22.4(14)	11.0(36)	20.4(107.1)	1.73 (61.17)	114.7 (44.3)
North Indian Creek	28.2(17.5)	7.0(28)	16.2 (85.7)	0.98 (34.58)	156.0 (60.2)
South Indian Creek	25.7(16)	17.7(58)	17.8 (93.8)	3.33(117.65)	209.5 (80.9)

*Mean width at study station.

Table 3. Alimentery canal contents of *Campostoma a. anomalum* from the five study streams. (+ = present, - = absent).

Stream	Elk River	Roan Creek	Doe Creek	N. Indian Creek	S. Indian Creek
No. Specimens	19	14	10	12	11
% Full ($\overline{X}$ estimate)	97	91	100	95	100
Algae					
Ulothrix sp.	+	+	+	+	+
Diatoms					
Navicula sp.	+	+	+	+	+
Fragilaria sp.	+	+	+	+	+
Insects					
Plecoptera					
Brachyptera sp.	-	+	-	-	-
Diptera					
Chironomidae	+	+	+	+	+
Other					
cycloid scales	-	+	-	-	-
fish eggs	-	-	-	+	-
Detritus	+	+	+	+	+
Sand	+	-	+	+	+

Table 4. Age class size ranges in mm SL of *Campostoma a. anomalum* from Elk River and Roan Creek. (M = male, F = female)

Stream	Elk River					Roan Creek				
	Size Range	%		$\bar{X}$		Size Range	%		$\bar{X}$	
Age Class	Sept. 1977	M	F	M	F	Sept. 1977	M	F	M	F
0	30-60	34.5	55.4	47.3	45.7	30-60	19.7	24.4	47.3	45.3
I	61-85	4.5	2.9	70.0	71.8	61-100	13.0	30.5	81.3	83.1
II	86-110	0.16	2.1	97.5	93.7	101-125	8.3	1.6	113.3	107.5
III	111-120	0.16	--	121.3	--	126-135	1.6	--	128.4	--
	Jan. 1978					Feb. 1978				
I	25-65	18.2	11.4	49.9	55.5	55-80	33.3	52.6	69.0	68.2
II	66-90	20.5	27.3	76.4	80.0	81-100	10.3	2.6	87.2	83.4
III	91-105	4.5	9.1	97.5	96.9	101-120	1.3	--	116.8	--
	April 1978					April 1978				
I	25-70	28.9	28.9	56.3	44.6	35-70	26.0	20.2	54.6	55.1
II	71-100	11.3	22.7	81.6	84.5	71-105	7.3	36.4	91.2	87.8
III	101-120	2.1	2.1	111.3	102.6	106-140	5.6	2.9	121.1	113.9
IV	121-170	4.1	--	151.8	--	141-160	1.2	--	147.4	--
	June 1978					June 1978				
0	9-40*	54.5+		30.0+		9-35*+	--		--	
I	41-75	16.1	22.7	61.5	61.7	36-70	16.3	39.3	59.7	58.3
II	76-100	2.4	3.4	82.7	83.2	71-105	7.7	32.1	80.6	89.2
III	101-110	0.24	--	106.3	--	106-130	4.1	1.0	117.0	112.5

* Lower extreme from Hogue et al. (1976)
\+ 224 unsexed age class 0
*+ Hypothetical range

Table 5. Sex ratios of _Campostoma a. anomalum_ by season and age class from Elk River and Roan Creek. (M = male, F = female)

Stream	Elk River			Roan Creek		
	Male N	Female N	Sex Ratio(M:F)	Male N	Female N	Sex Ratio (M:F)
Age Class	Sept. 1977			Sept. 1977		
0	215	345	1:1.61	62	140	1:2.26
I	28	18	1:0.64	42	139	1:3.31
II	1	11	1:11	26	31	1:1.19
III	1	3	1:3	5	5	1:1
	Jan. 1978			Feb. 1978		
I	8	5	1:0.63	26	41	1:1.58
II	9	16	1:1.78	8	2	1:0.25
III	2	4	1:2	1	--	--
	April 1978			April 1978		
I	28	50	1:1.79	135	105	1:0.78
II	11	2	1:0.18	40	189	1:4.73
III	2	--	--	29	15	1:0.52
IV	4	--	--	6	--	--
	June 1978			June 1978		
0	*--	--	--	--	--	--
I	66	93	1:1.41	32	76	1:2.38
II	10	15	1:1.5	15	63	1:4.20
III	1	--	--	8	2	1:0.25

* 224 unsexed age class 0

Table 6. Sex ratios of *Campostoma a. anomalum* from all samples for the five study streams. (M = male, F = female)

Stream	Male N	Female N	Ratio (M:F)
Elk River	514	709	1:1.38
Roan Creek	676	965	1:1.43
Doe Creek	167	163	1:0.98
North Indian Creek	187	197	1:1.05
South Indian Creek	271	312	1:1.15

Table 7. Mean growth increments (length) by age class and season of Campostoma a. anomalum from Elk River and Roan Creek. (M = male, F = female)

Stream	Elk River		Roan Creek	
	Sept. 1977		Sept. 1977	
Age Class	M	F	M	F
0	38.3	36.7	38.3	36.3
I	22.7	26.1	34.0	37.8
II	27.5	21.9	32.0	24.4
III	23.8	--	15.1	--
	Jan. 1978		Feb. 1978	
I	40.9	46.5	60.0	59.2
II	26.5	24.5	18.2	15.2
III	21.1	16.9	29.6	--
	April 1978		April 1978	
I	47.3	35.6	45.6	46.1
II	25.3	39.9	36.6	32.7
III	29.7	18.1	29.9	26.1
IV	40.5	--	26.3	--
	June 1978		June 1978	
0	21+	--	--	--
I	31.5	31.7	29.7	28.3
II	21.2	21.5	20.9	30.9
III	23.7	--	36.4	23.3

+ 224 unsexed age class 0

Table 8. Length-weight logistic equations for <u>Campostoma</u> <u>a</u>. <u>anomalum</u> from this and other studies.

Source	Equation
Current Study	
Elk River	Log W = -4.8322 + 3.0829 Log L
Roan Creek	Log W = -4.3672 + 2.8513 Log L
Doe Creek	Log W = -4.6390 + 2.9874 Log L
North Indian Creek	Log W = -4.0299 + 2.6578 Log L
South Indian Creek	Log W = -4.1192 + 2.6884 Log L
Other studies	
Schmulbach (1957)	Log W = -4.5402 + 2.9180 Log L
Swingle (1965)	Log W = -3.02 + 2.39 TL

Table 9. Confidence intervals of slope and y-intercept between sexes for length-weight regressions for the five study streams. Intervals of slope and y-intercept tested at .01 level, t /2 = 2.576, df = . Interval overlap indicates no difference between regressions.

	slope	stream	y-intercept
		Elk River	
Male	2.8321 -- 3.4190		-5.4275 -- -4.3741
Female	2.7932 -- 3.2746		-5.1767 -- -4.3254
		Roan Creek	
Male	2.6394 -- 3.0989		-4.8266 -- -3.9796
Female	2.6435 -- 3.0218		-4.6799 -- -3.9812
		Doe Creek	
Male	2.7533 -- 3.2869		-5.6898 -- -3.4776
Female	2.4445 -- 3.4087		-5.2315 -- -3.8261
		North Indian Creek	
Male	2.4270 -- 2.7188		-4.1498 -- -3.6046
Female	2.6693 -- 2.9365		-4.5403 -- -4.0455
		South Indian Creek	
Male	2.3319 -- 2.9927		-4.6571 -- -3.4600
Female	2.4113 -- 3.0470		-4.7971 -- -3.6140

Table 10. Results of analysis of covariance between the length-weight regressions of Campostoma a. anomalum. Slopes are: b_1 = Elk River, b_2 = Roan Creek, b_3 = Doe Creek, b_4 = North Indian Creek, b_5 = South Indian Creek. Only the subsets of slopes having no significant difference at $F_{\alpha}(4,\infty) = .01$ are shown.

Slope Subsets	SS among b's*	SS crit*
Sexes combined		
b_4 b_5	0.005	0.397
Males		
b_2 b_4	0.394	0.510
b_3 b_5	0.327	0.510
Females		
b_1 b_2	0.261	0.302
b_2 b_3 b_4 b_5	0.086	0.302

* Sokal and Rohlf (1969, p.457-8)

Table 11. Spawning duration and temperature ranges of _Campostoma anomalum_ listed from north to south.

Source	Locality	Duration	Temperature °C
Smith (1935)	New York	Mar. - June	10.8-18.4
Miller (1962)	New York	Apr. - June	14.6-24.0
Hankinson (1919)	Illinois	Mar. - May	18.4-26.8
Schmulbach (1957)	Illinois	Mar. - June	12.9-18.4
Current Study	Tennessee	Apr. - June	12.0-16.2

Table 12. Results of length-mature ova number correlations for Campostoma a. anomalum for the five study streams.

Stream	r	$P_r = 0$
Elk River	.902	.0001
Roan Creek	.768	.0001
Doe Creek	.639	.01
North Indian Creek	.808	.0001
South Indian Creek	.725	.001

Table 13. Numbers of ova (immature and mature) from *Campostoma a. anomalum* from the five study streams (right ovary only).

Stream	N	Size Range mm SL	Ova No. Range	$\bar{X}$	SD
Elk River	30	62-130	427-2110	1128.3	513.94
Roan Creek	30	60-123	305-2424	804.5	697.31
Doe Creek	19	60-128	206-2416	1062.2	704.41
N. Indian Creek	18	60-112	380-1801	718.5	513.63
S. Indian Creek	15	62-124	183-1758	1010.5	533.96

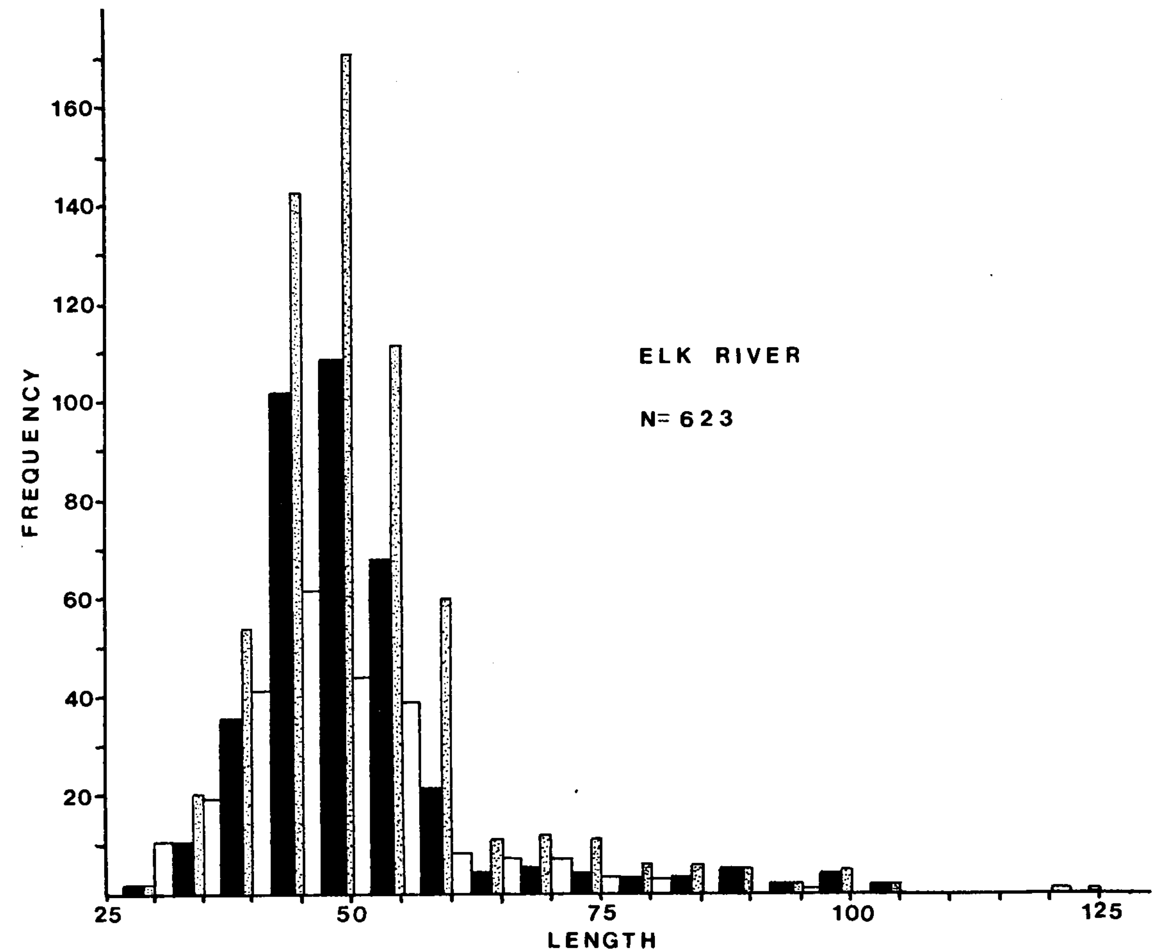

Figure 3. Length frequency distribution of Campostoma a. anomalum in Elk River, September 1977. (open bar = male, closed bar = female, stippled bar = total)

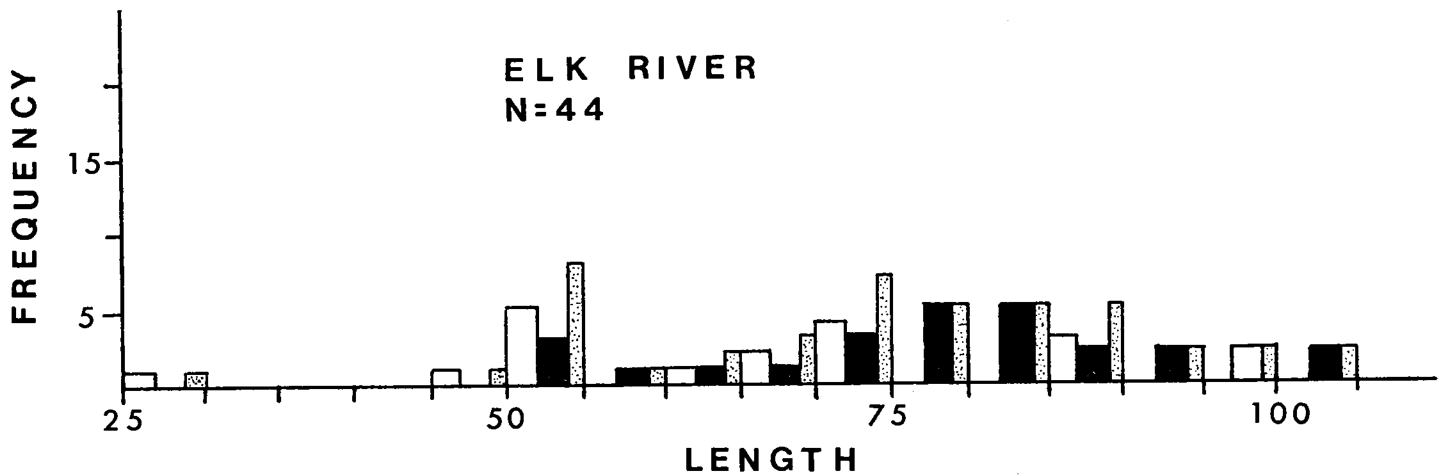

Figure 4. Length frequency distribution of Campostoma a. anomalum in Elk River, January 1978. (open bar = male, closed bar = female, stippled bar = total)

Figure 5. Length frequency distribution of Campostoma a. anomalum in Elk River, April 1978. (open bar = male, closed bar = female, stippled bar = total)

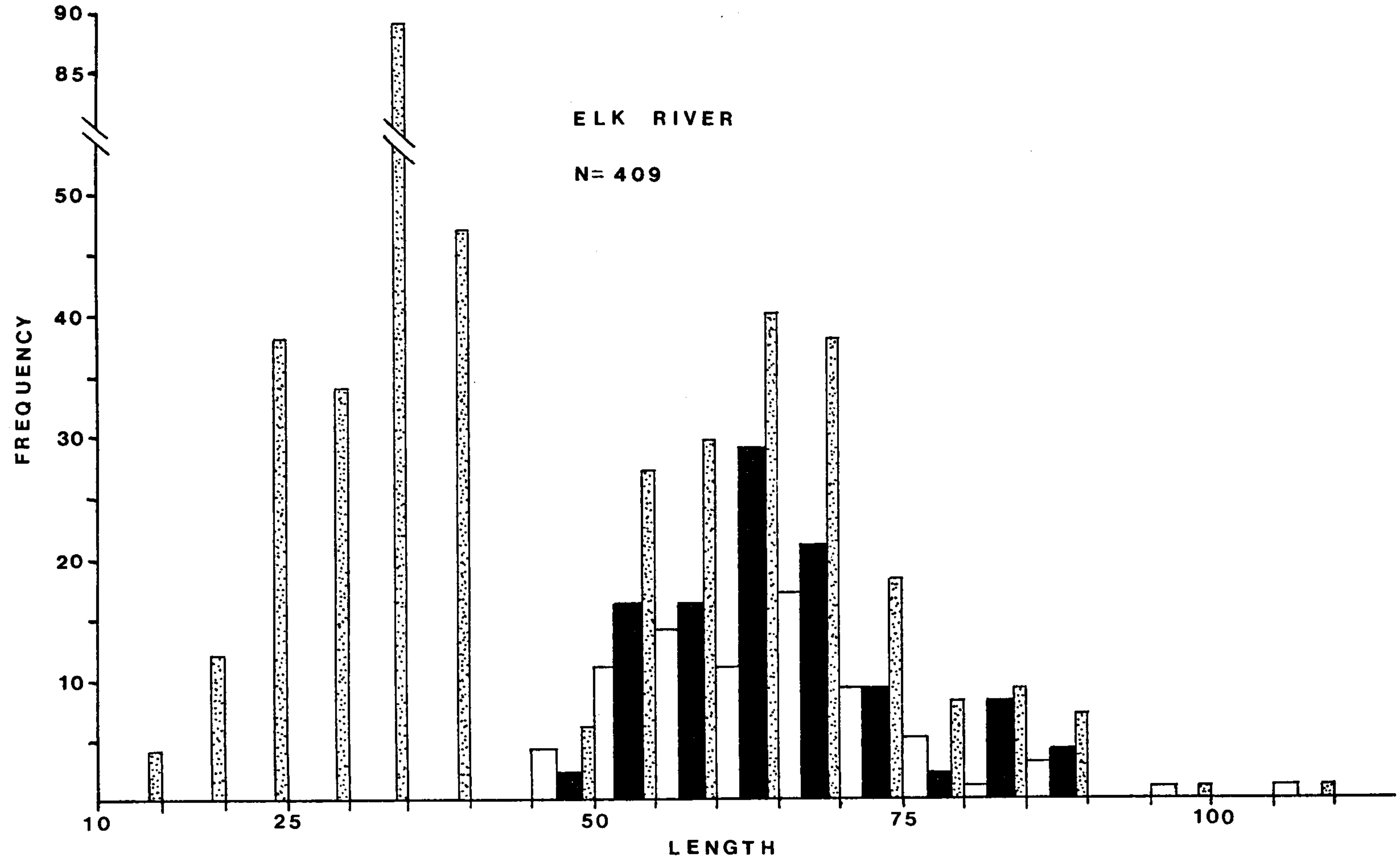

Figure 6. Length frequency distribution of Campostoma a. anomalum in Elk River, June 1978. (open bar = male, closed bar = female, stippled bar = total)

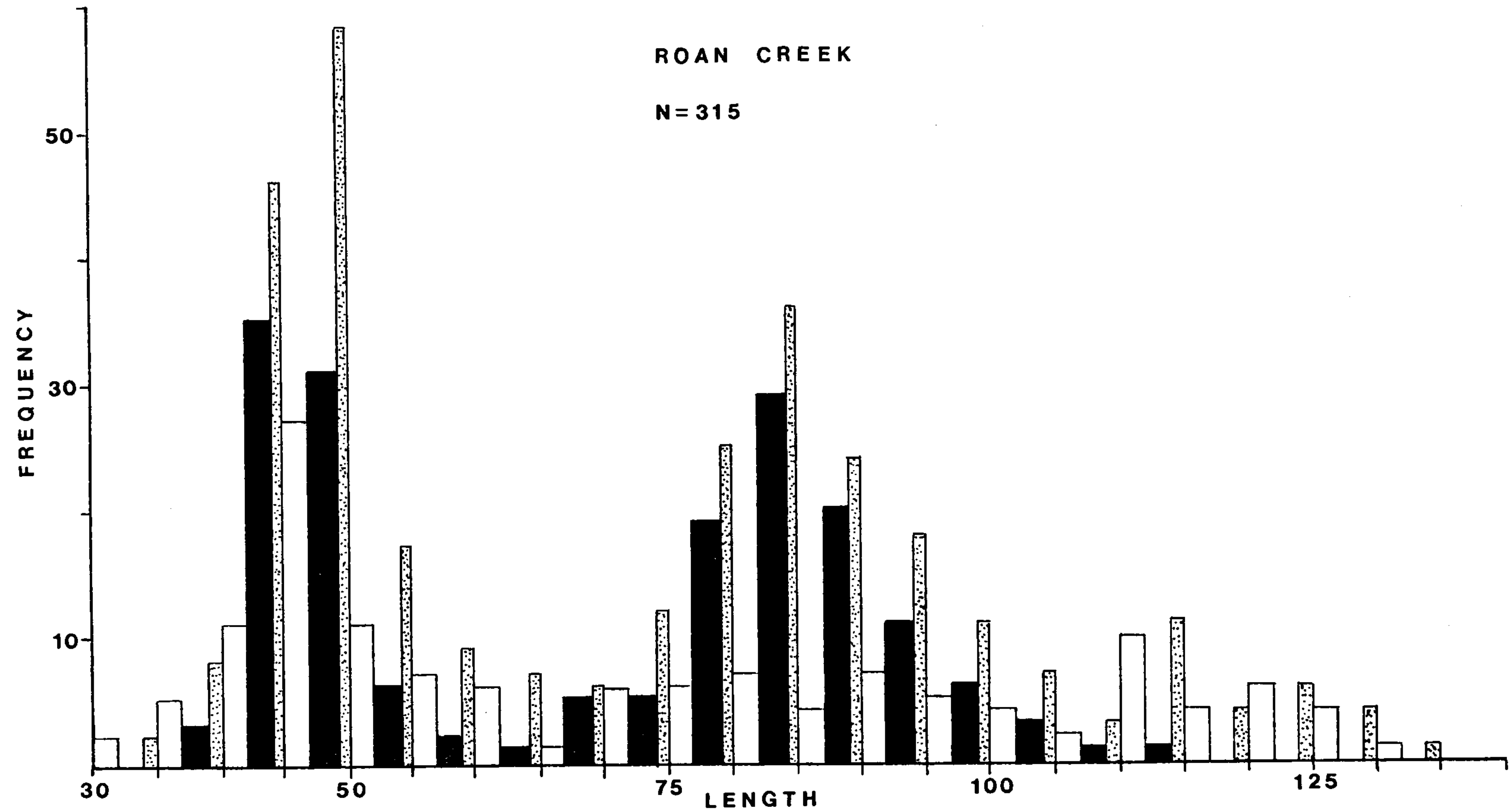

Figure 7. Length frequency distribution of Campostoma a. anomalum in Roan Creek, September 1977. (open bar = male, closed bar = female, stippled bar = total)

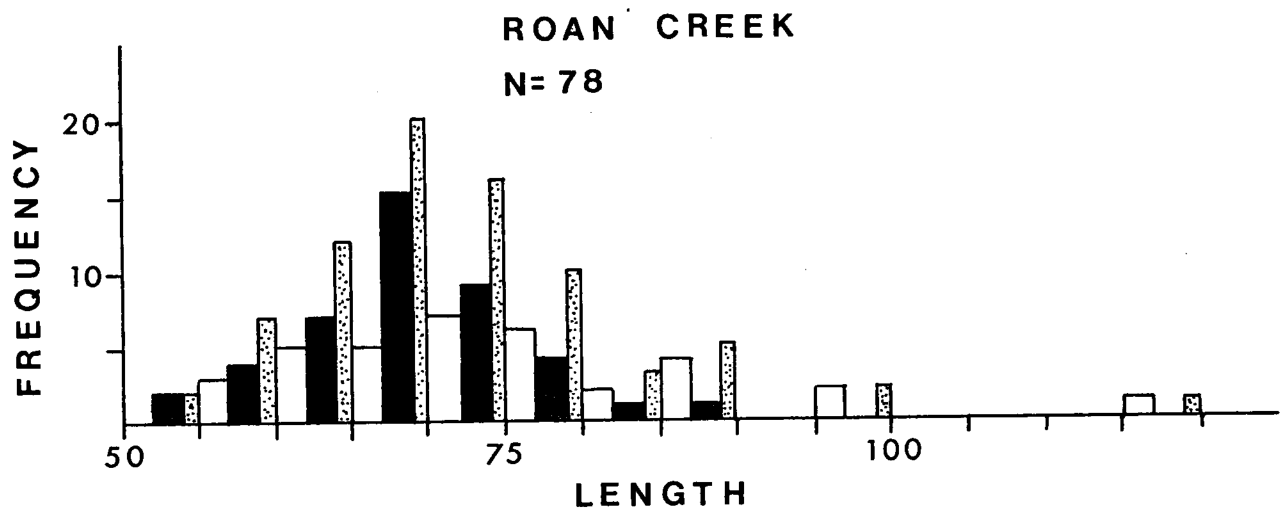

Figure 8. Length frequency distribution of Campostoma a. anomalum in Roan Creek, February 1978. (open bar = male, closed bar = female, stippled bar = total)

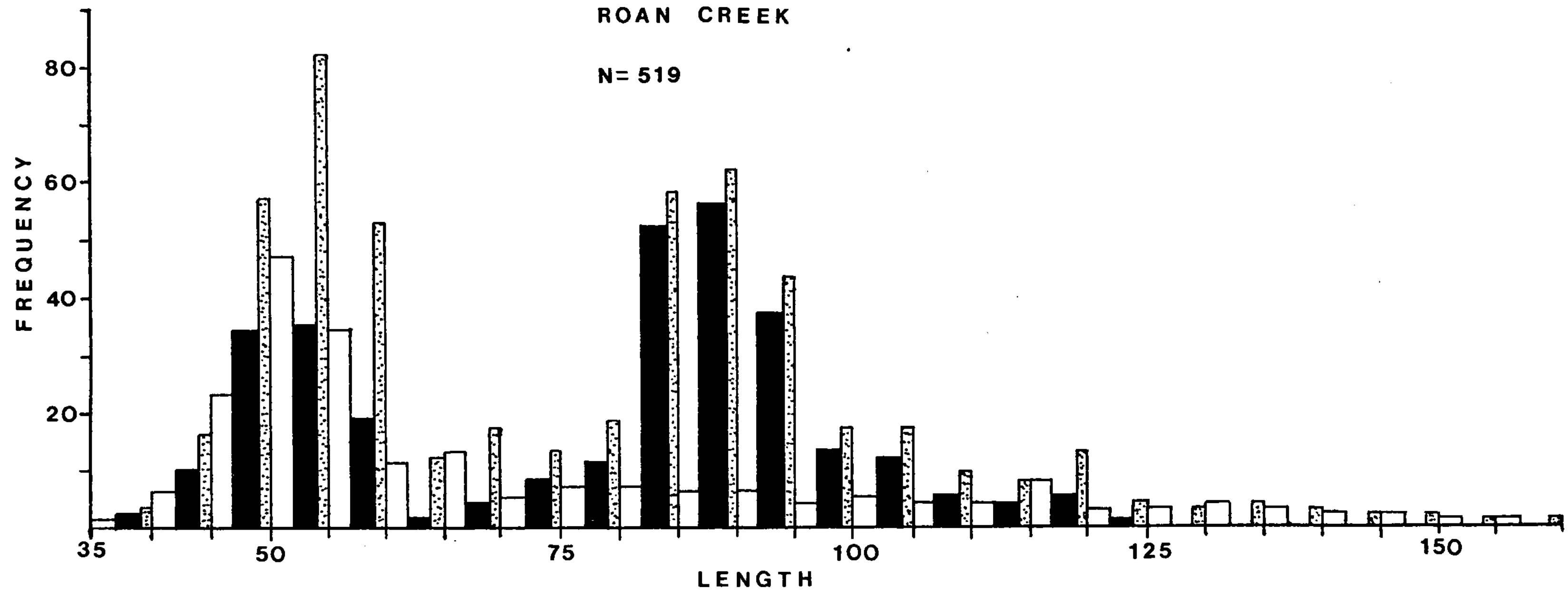

Figure 9. Length frequency distribution of <u>Campostoma</u> <u>a</u>. <u>anomalum</u> in Roan Creek, April 1978. (open bar = male, closed bar = female, stippled bar = total)

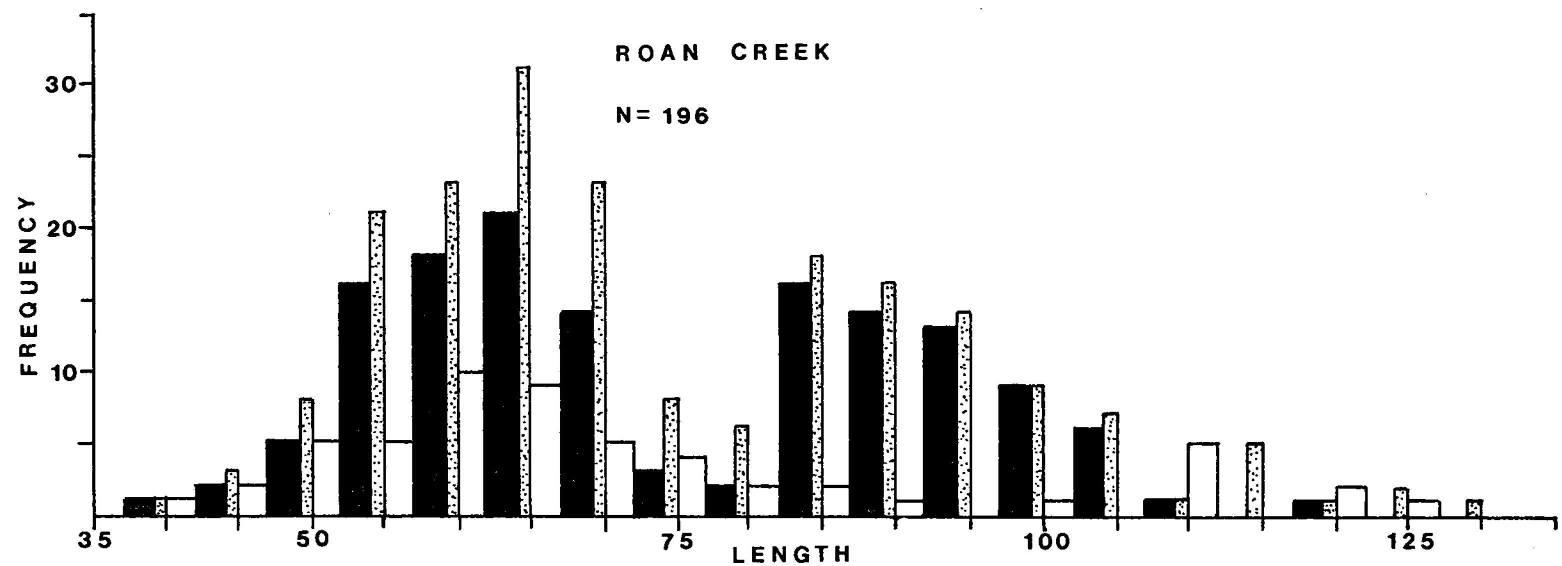

Figure 10. Length frequency distribution of Campostoma a. anomalum in Roan Creek June 1978. (open bar = male, closed bar = female, stippled bar = total)

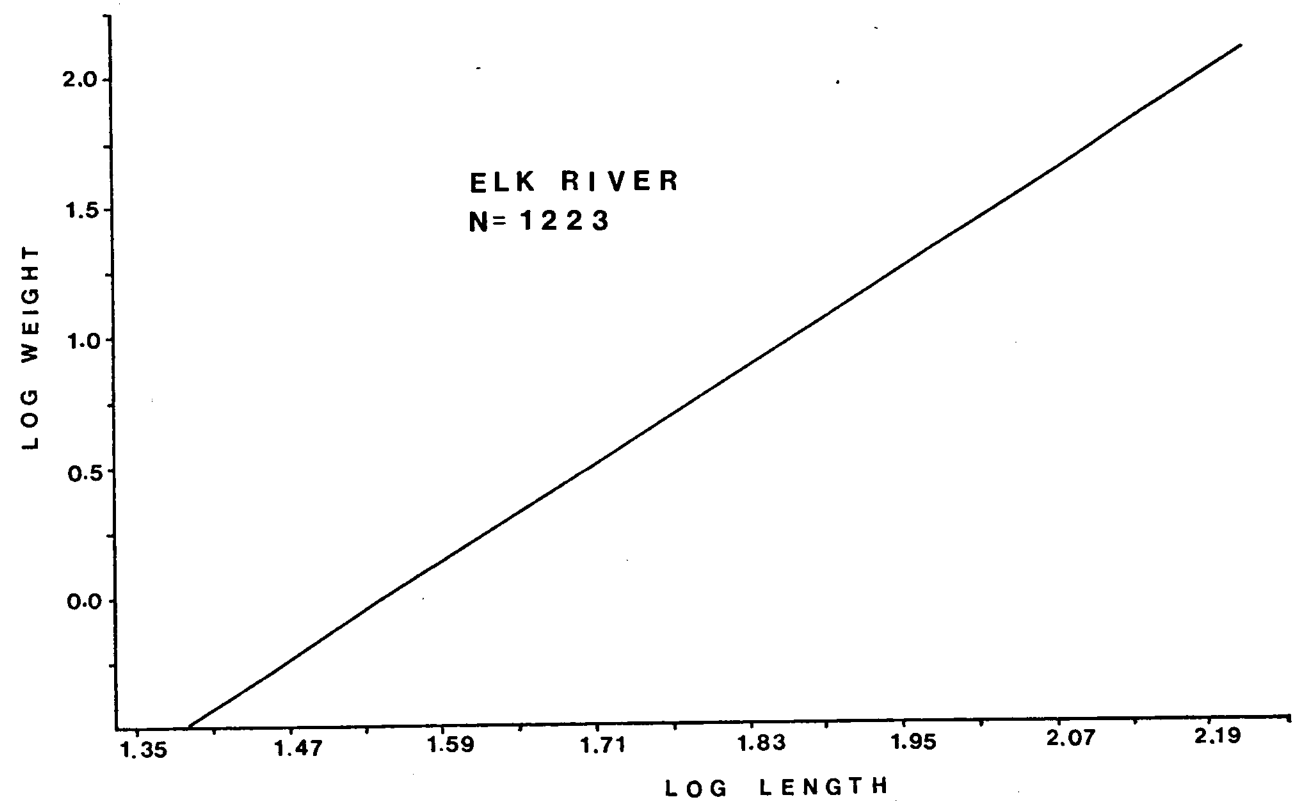

Figure 11. Length-weight regression of _Campostoma a. anomalum_ from Elk River. (all samples combined)

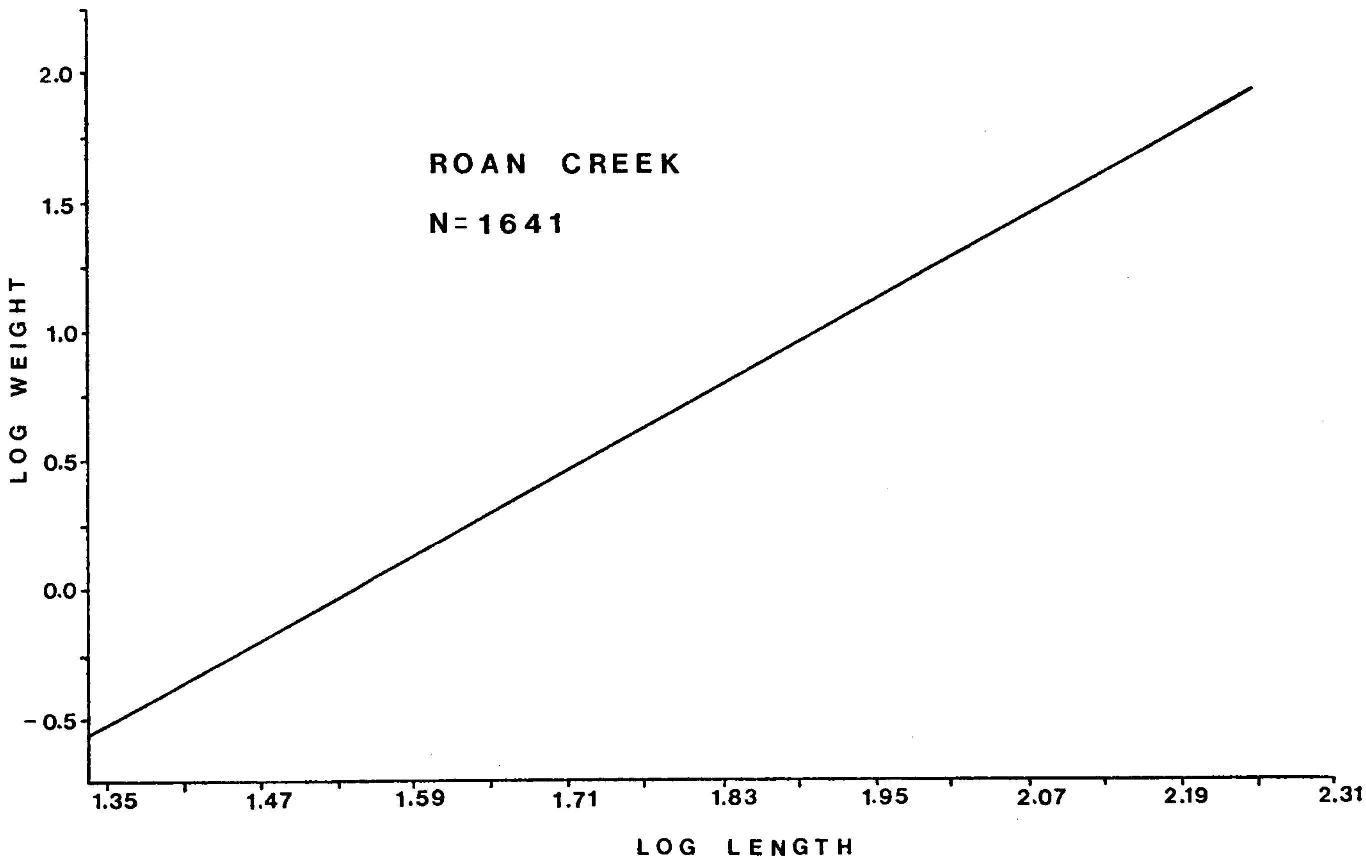

Figure 12. Length-weight regression of *Campostoma a. anomalum* from Roan Creek. (all samples combined)

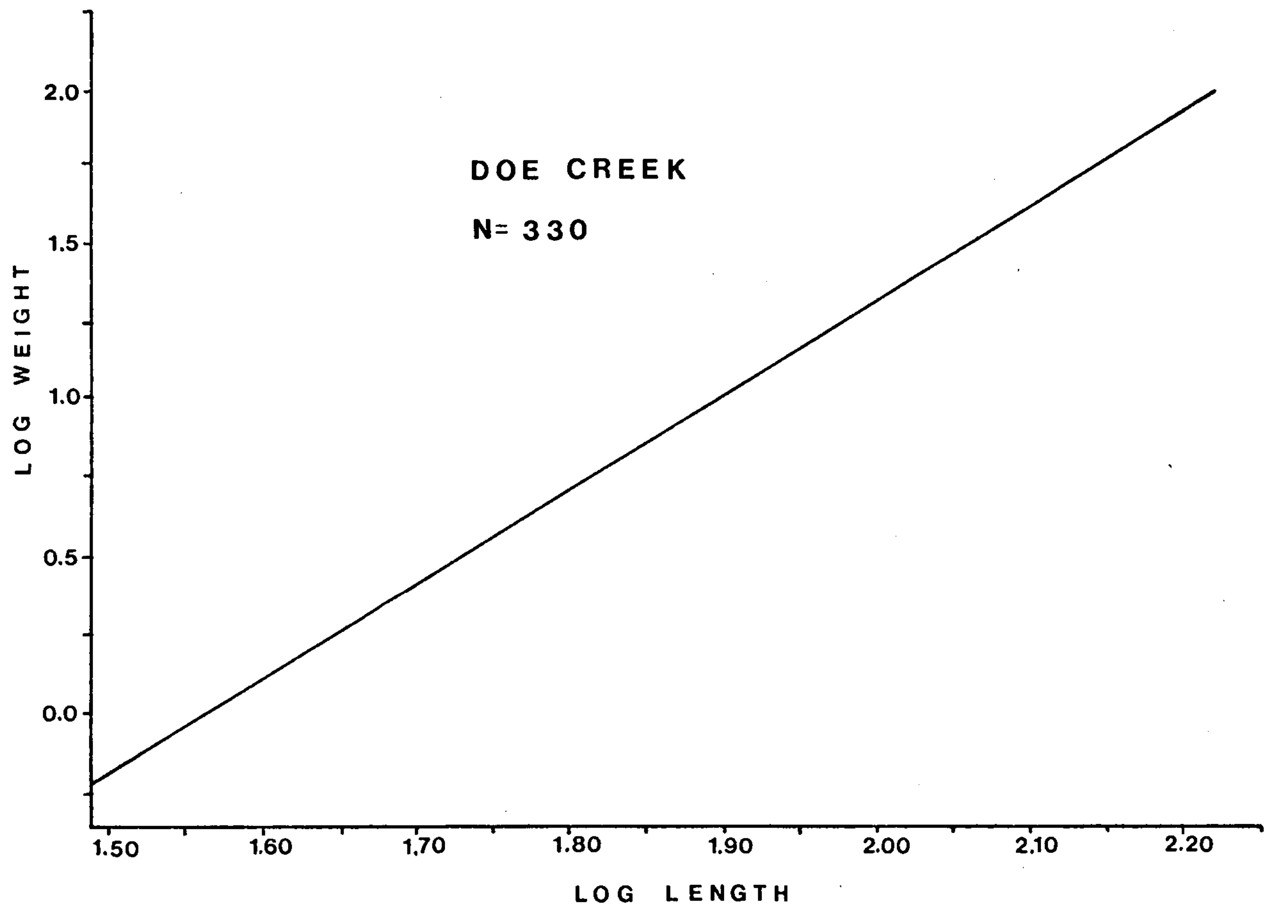

Figure 13. Length-weight regression of _Campostoma a. anomalum_ from Doe Creek.(all samples combined)

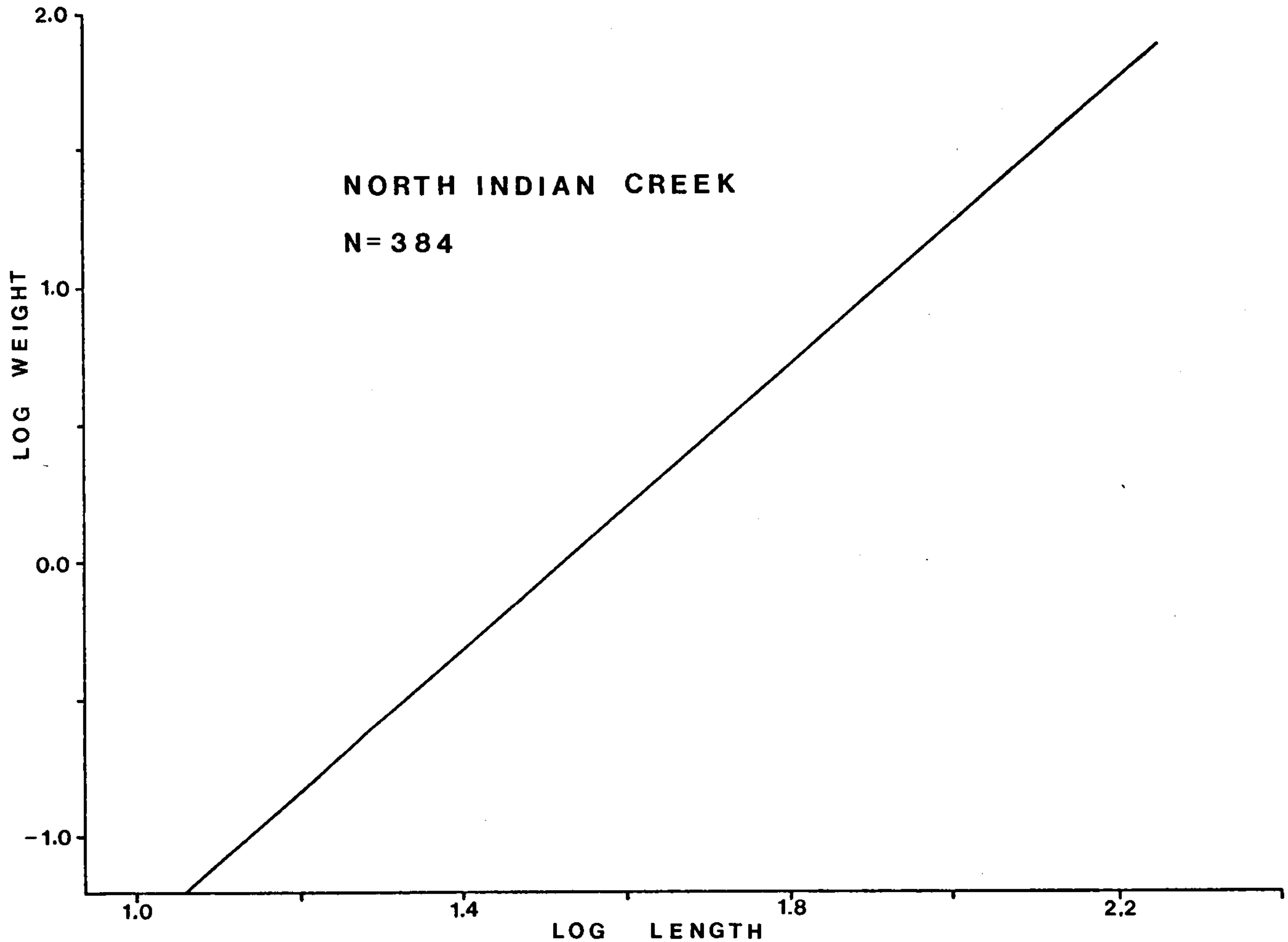

Figure 14. Length-weight regression of *Campostoma a. anomalum* from North Indian Creek. (all samples combined)

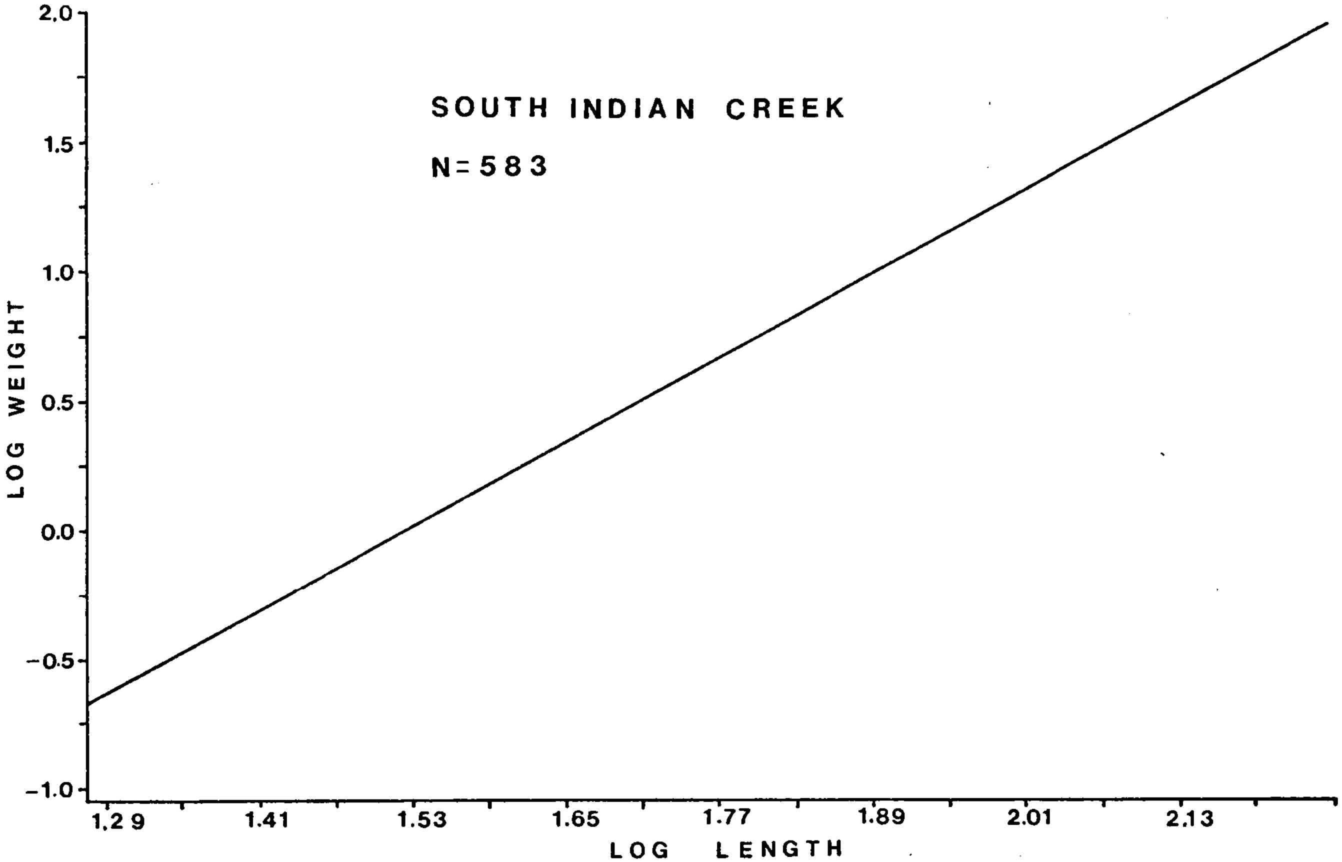

Figure 15. Length-weight regression of _Campostoma a. anomalum_ from South Indian Creek. (all samples combined)

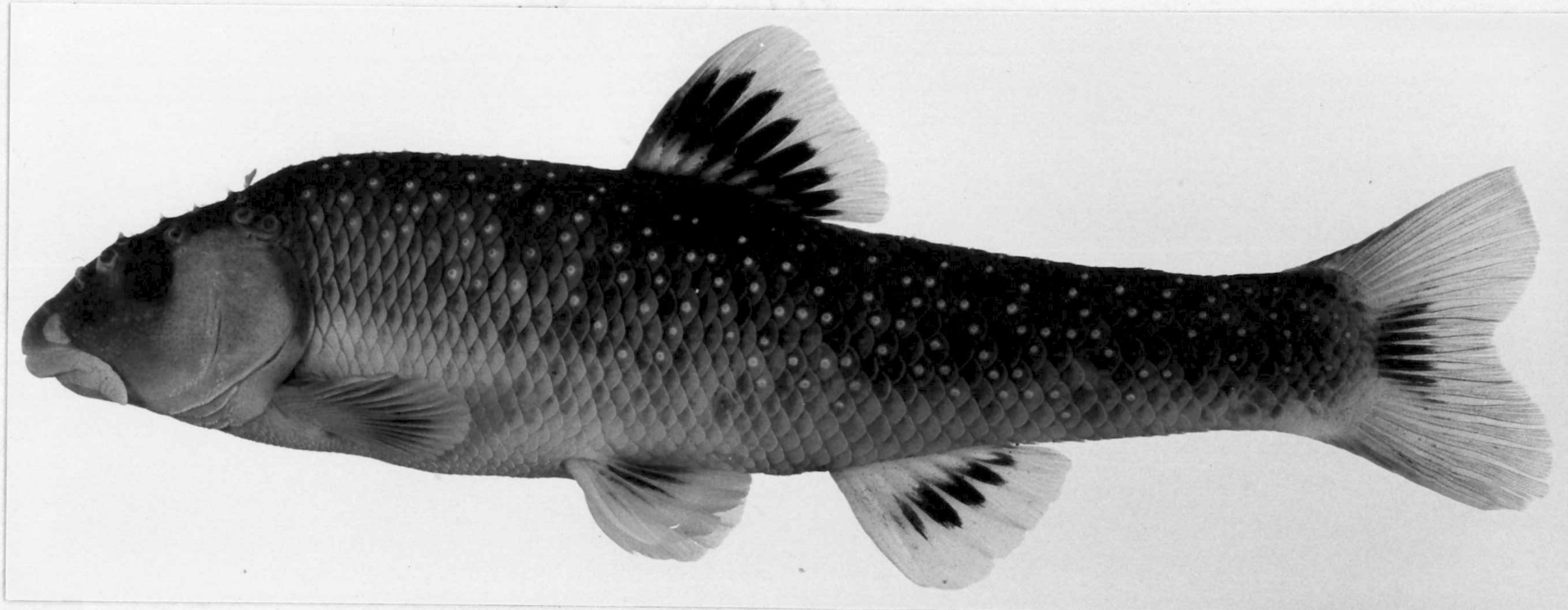

Figure 16. A male Campostoma a. anomalum in nuptial dress.(124.3 mm SL, photograph by Richard T. Bryant)

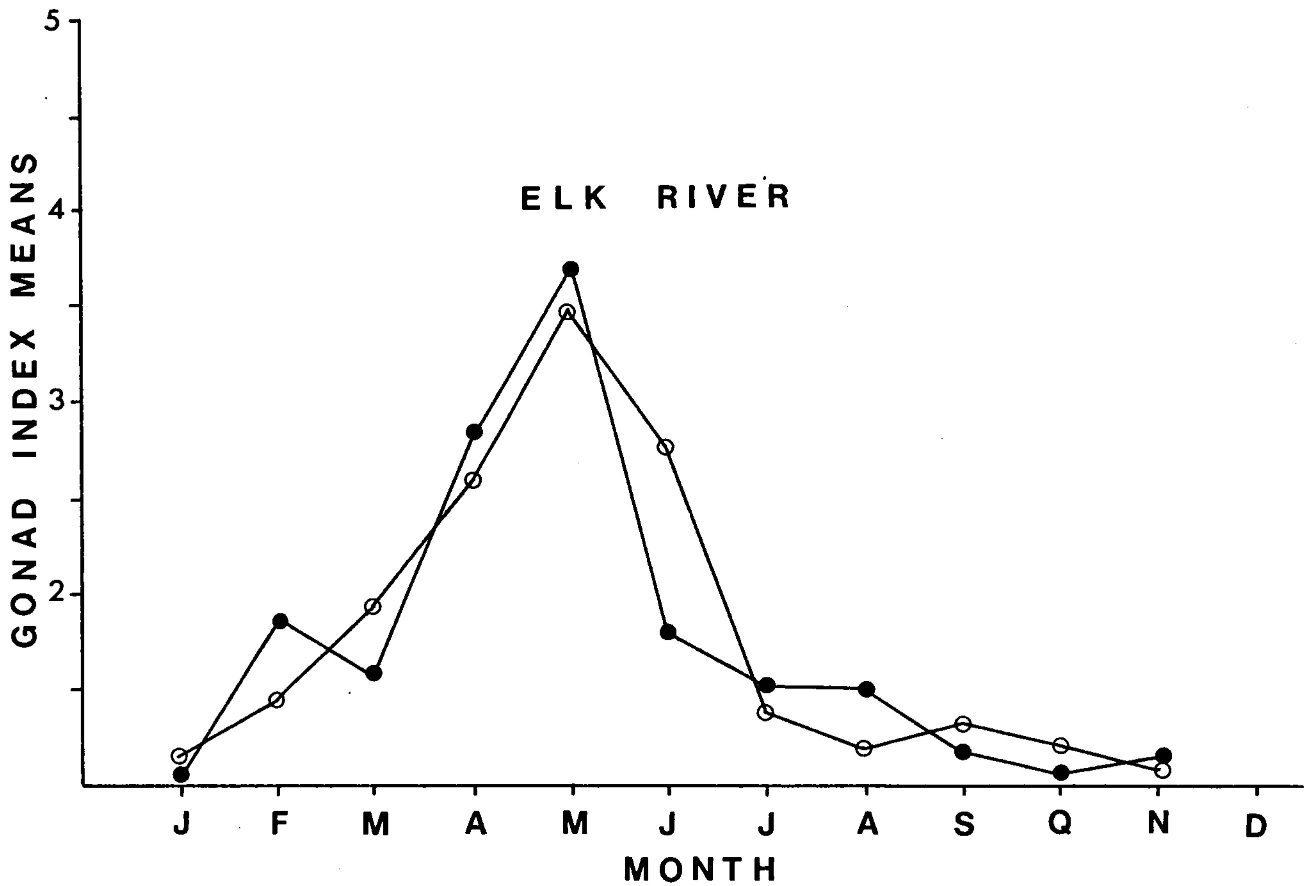

Figure 17. The gonad index means of _Campostoma a. anomalum_ in Elk River. (open circle = male, closed circle = female)

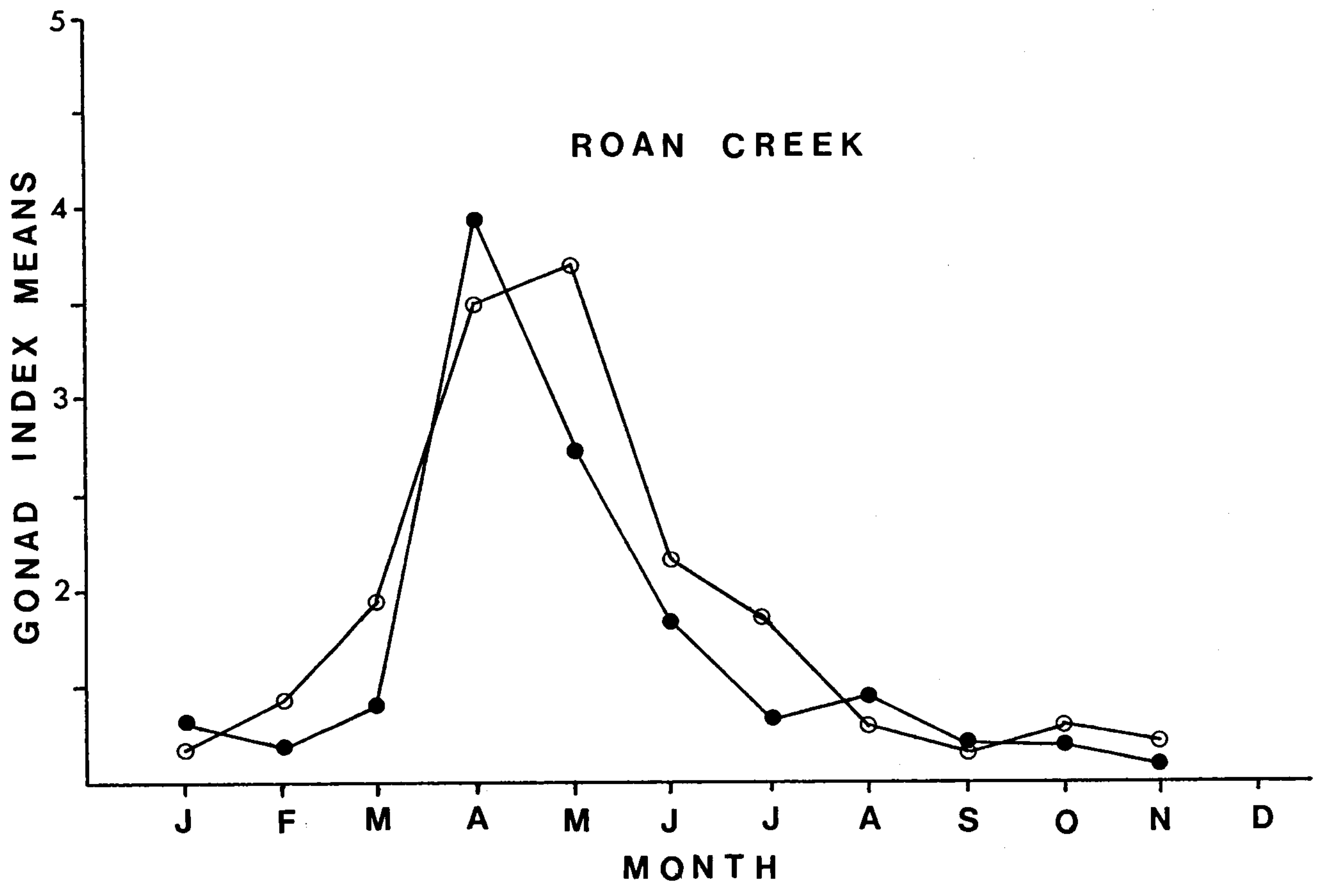

Figure 18. The gonad index means of Campostoma a. anomalum in Roan Creek. (open circles = males, closed circles = females)

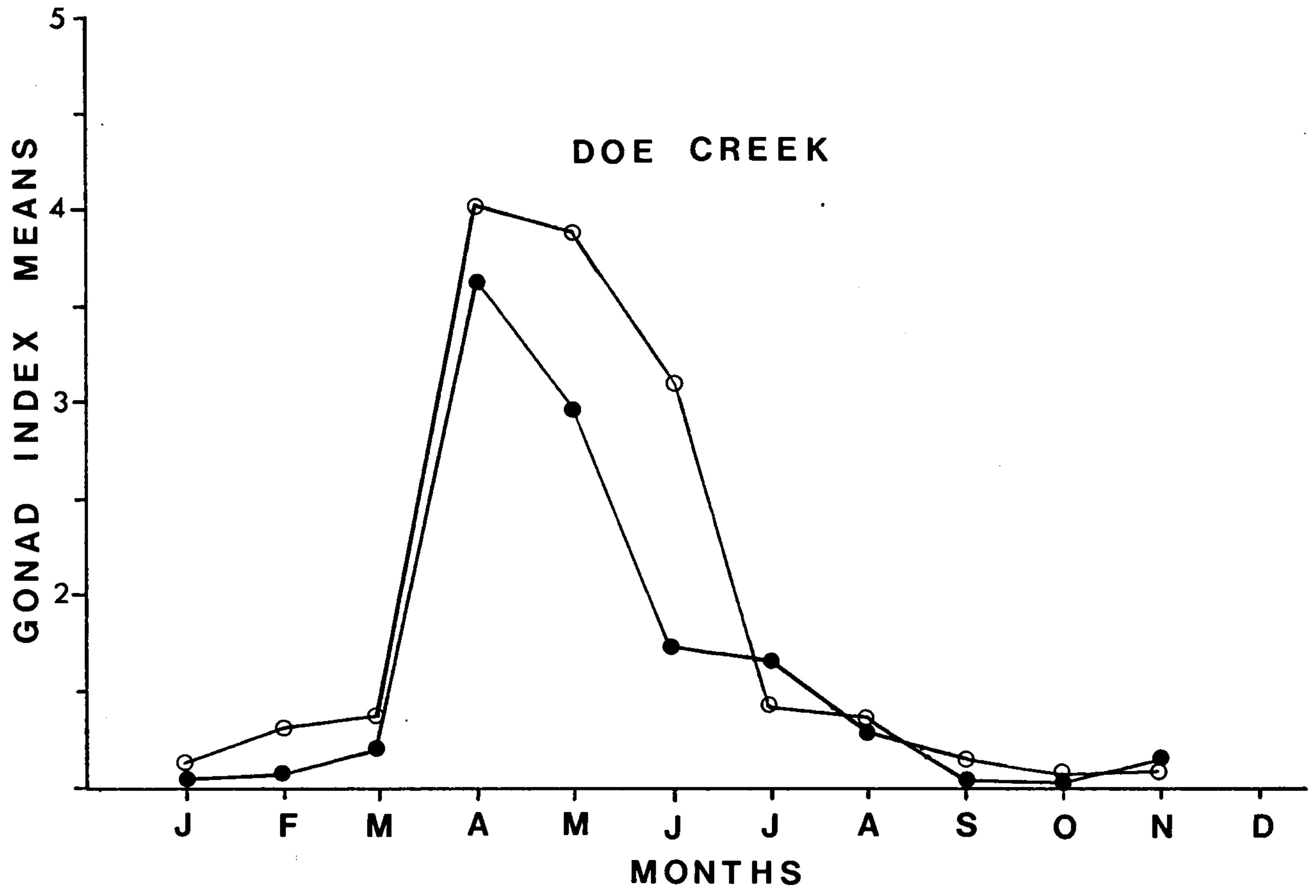

Figure 19. The gonad index means of Campostoma a. anomalum in Doe Creek. (open circle = male, closed circle = female)

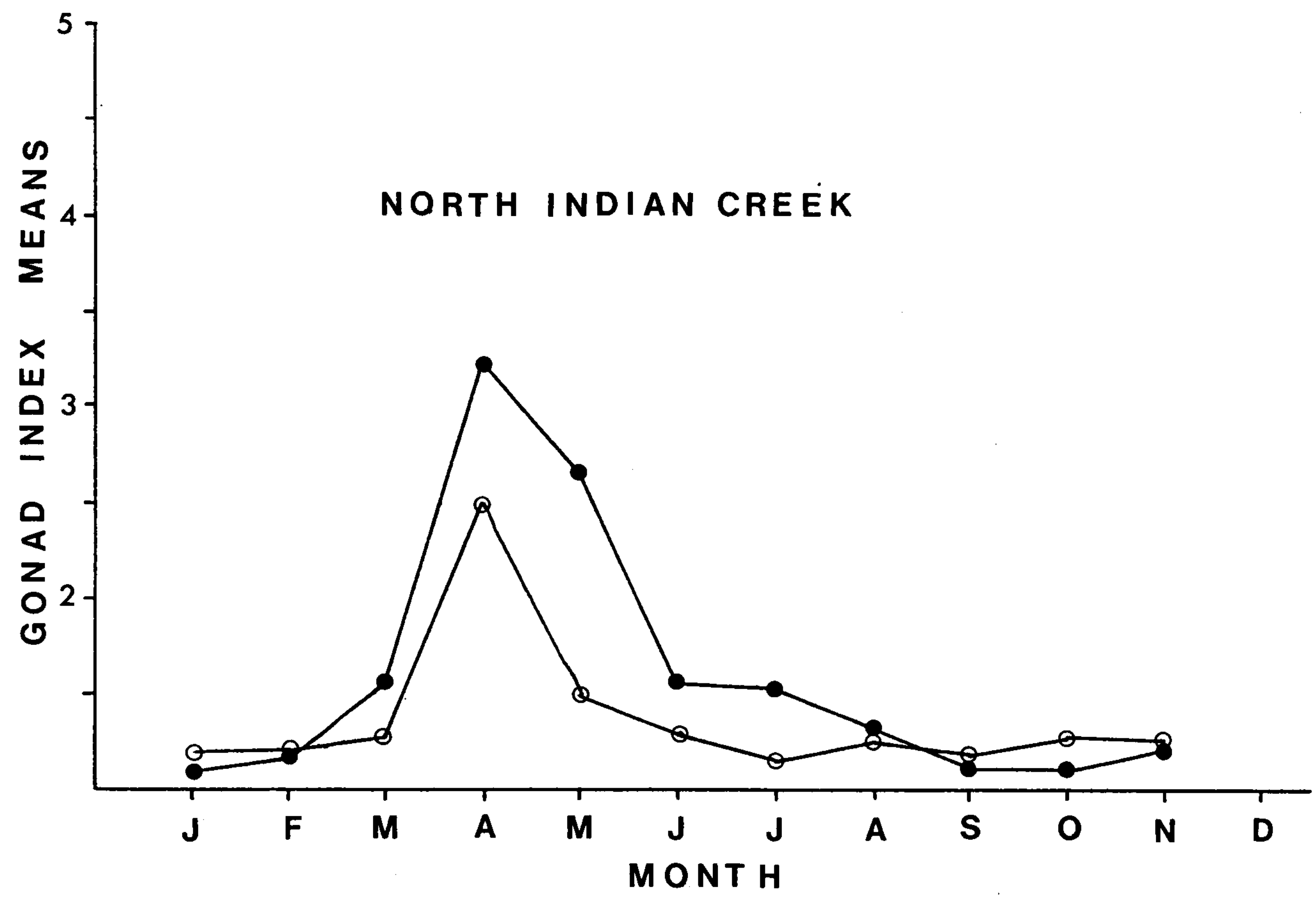

Figure 20. The gonad index means of Campostoma a. anomalum in North Indian Creek. (open circles = males, closed circles = females)

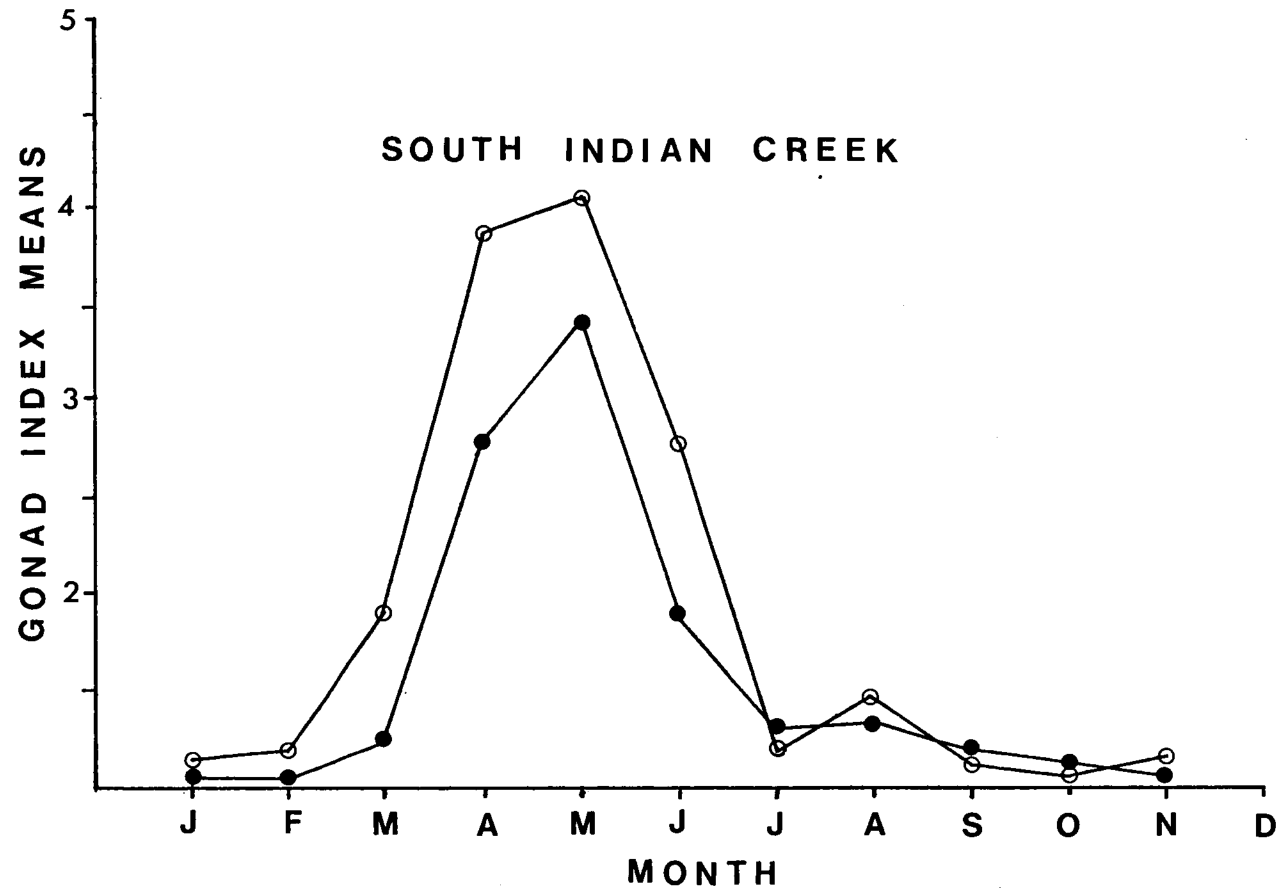

Figure 21. The gonad index means of _Campostoma a. anomalum_ in South Indian Creek. (open circles = males, closed circles = females)

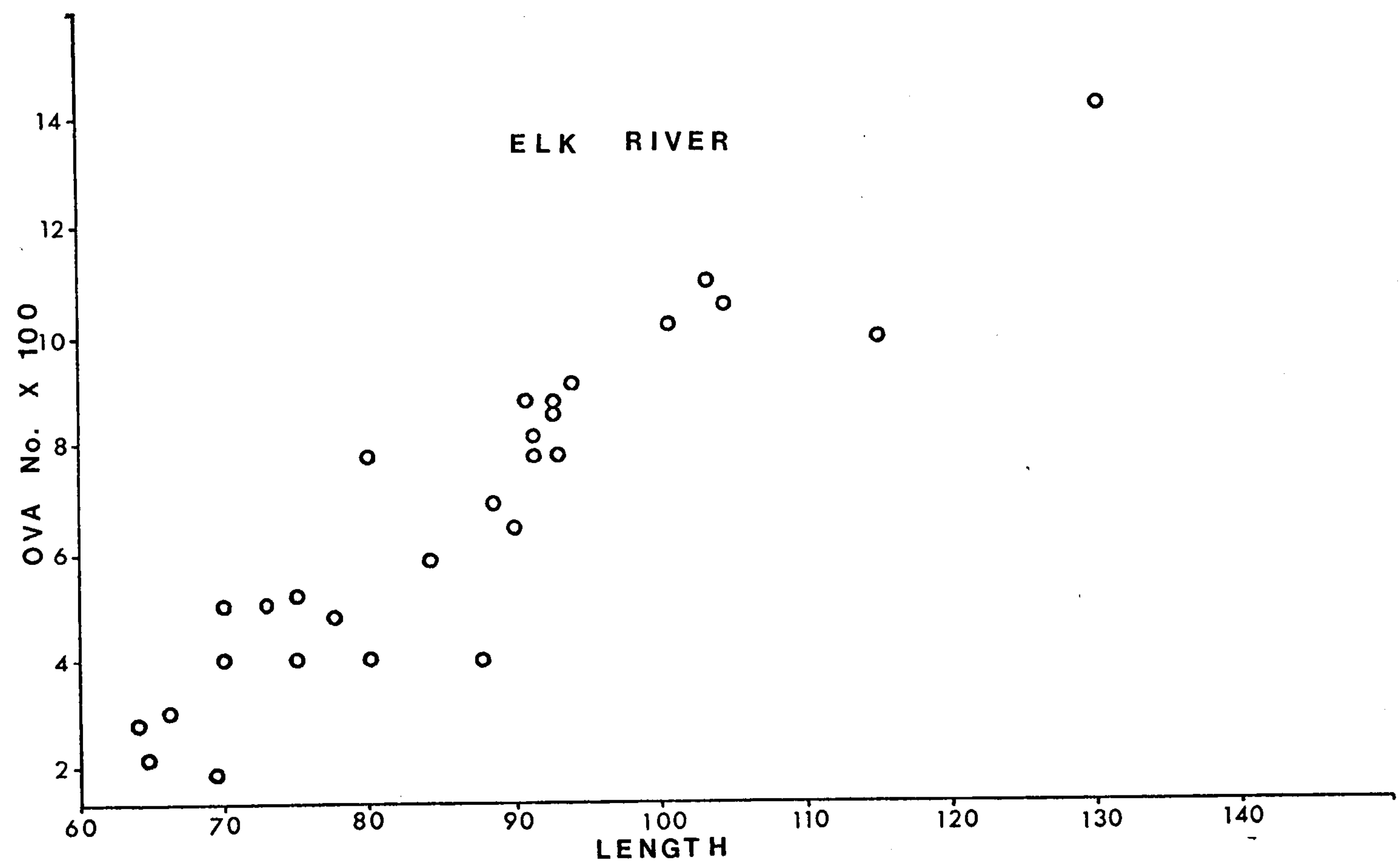

Figure 22. Mature ova-length scattergram of _Campostoma a. anomalum_ from Elk River.

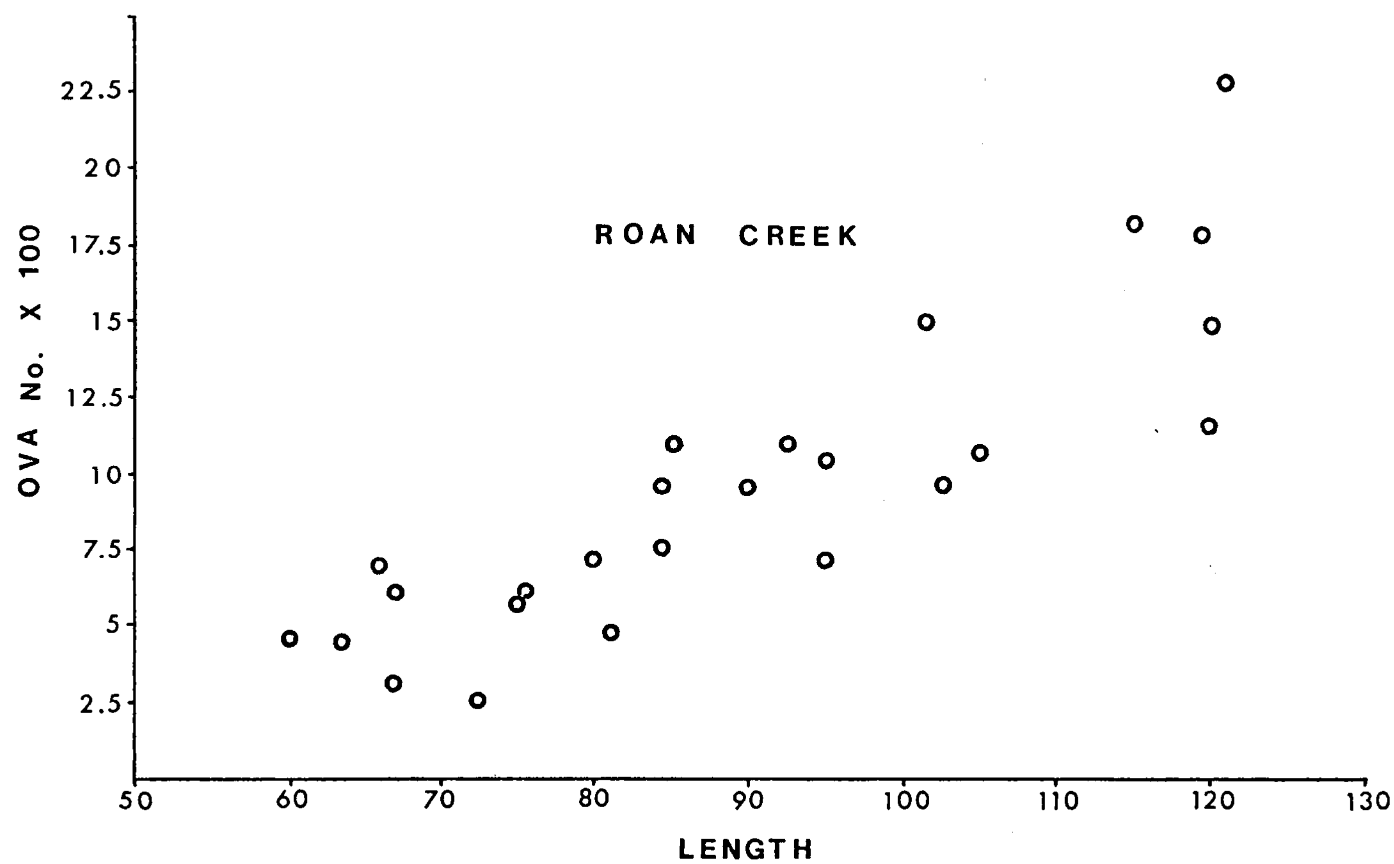

Figure 23. Mature ova-length scattergram of Campostoma a. anomalum from Roan Creek.

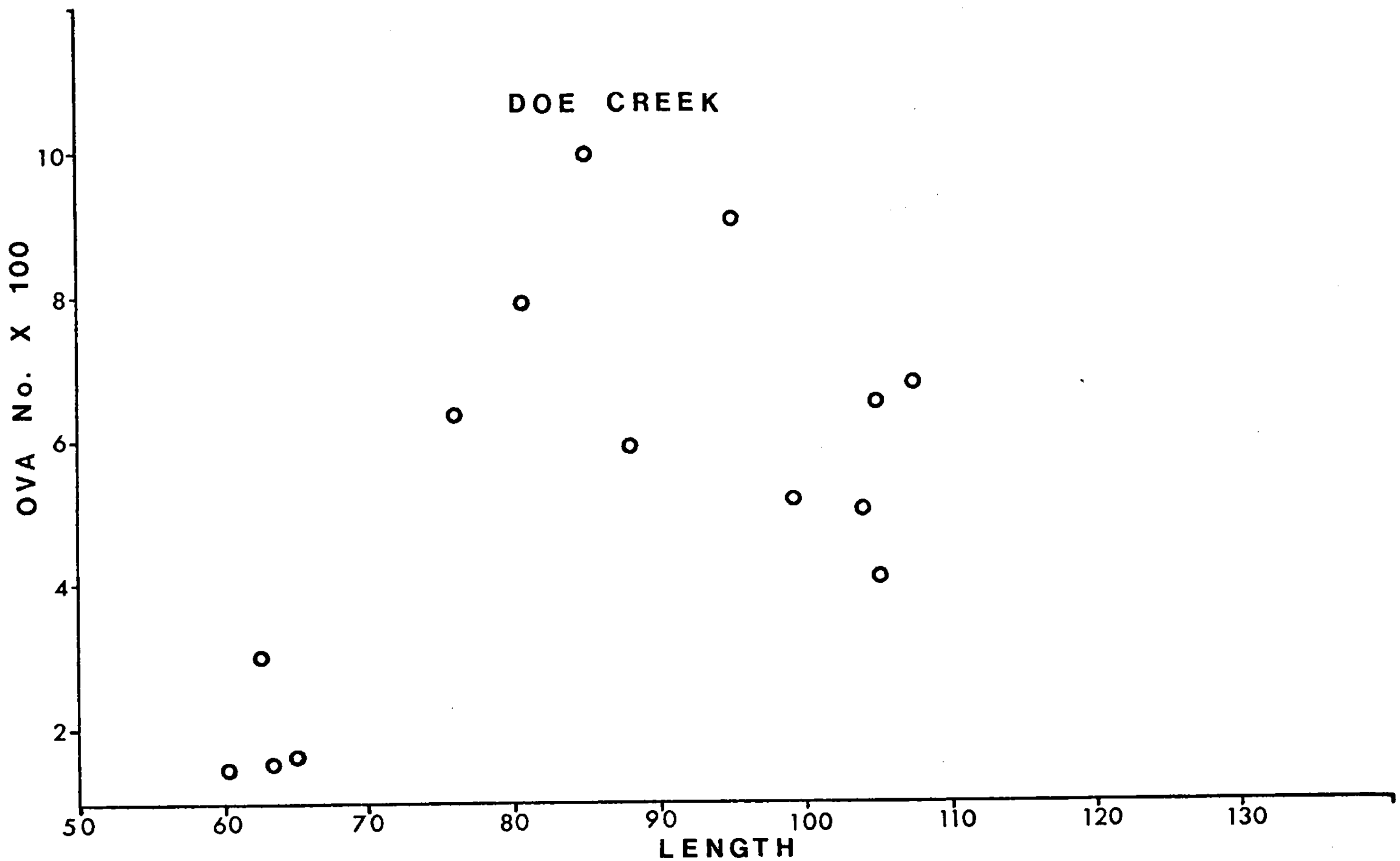

Figure 24. Mature ova-length scattergram of _Campostoma a. anomalum_ from Doe Creek.

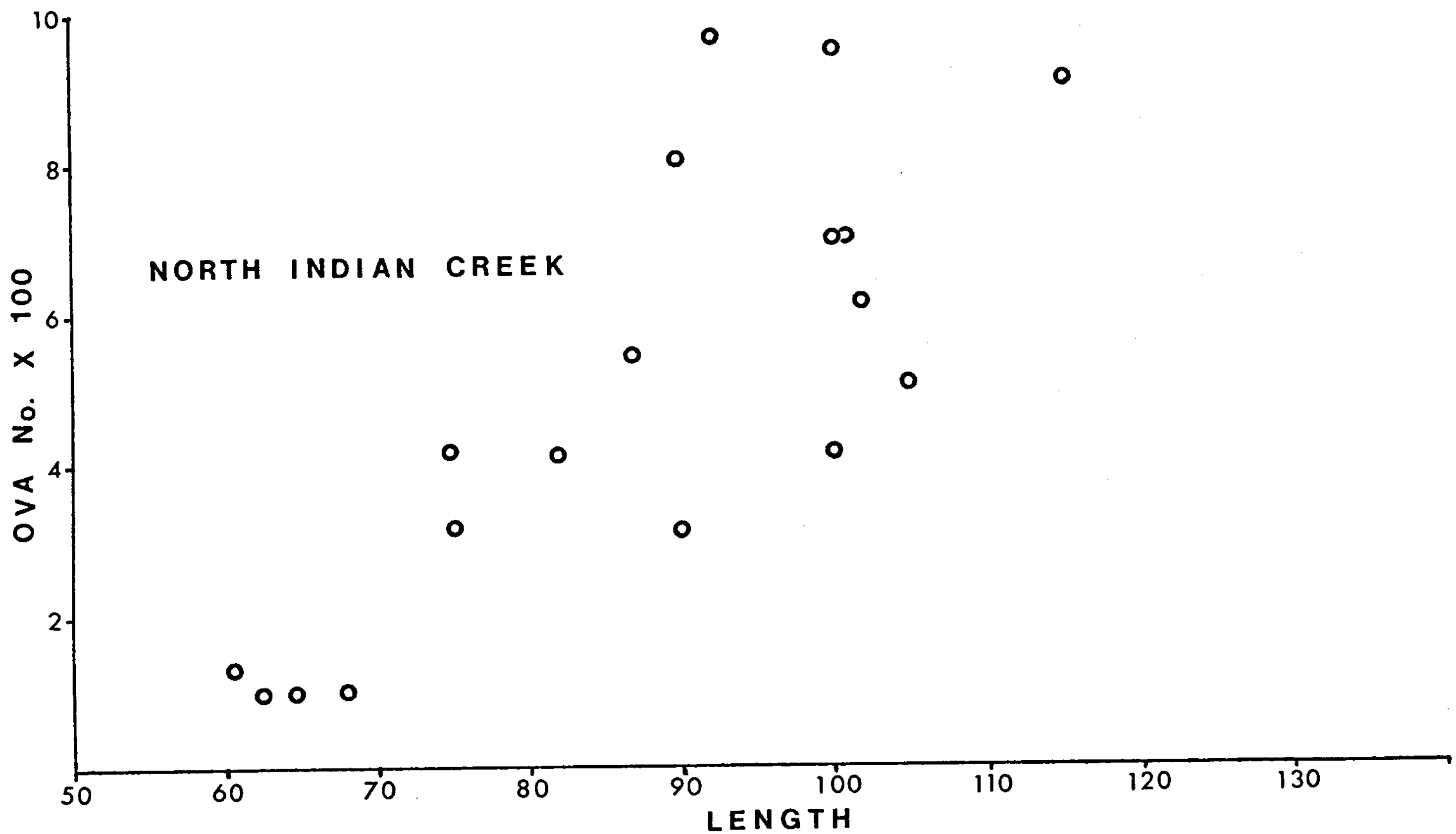

Figure 25. Mature ova-length scattergram of Campostoma a. anomalum from North Indian Creek.

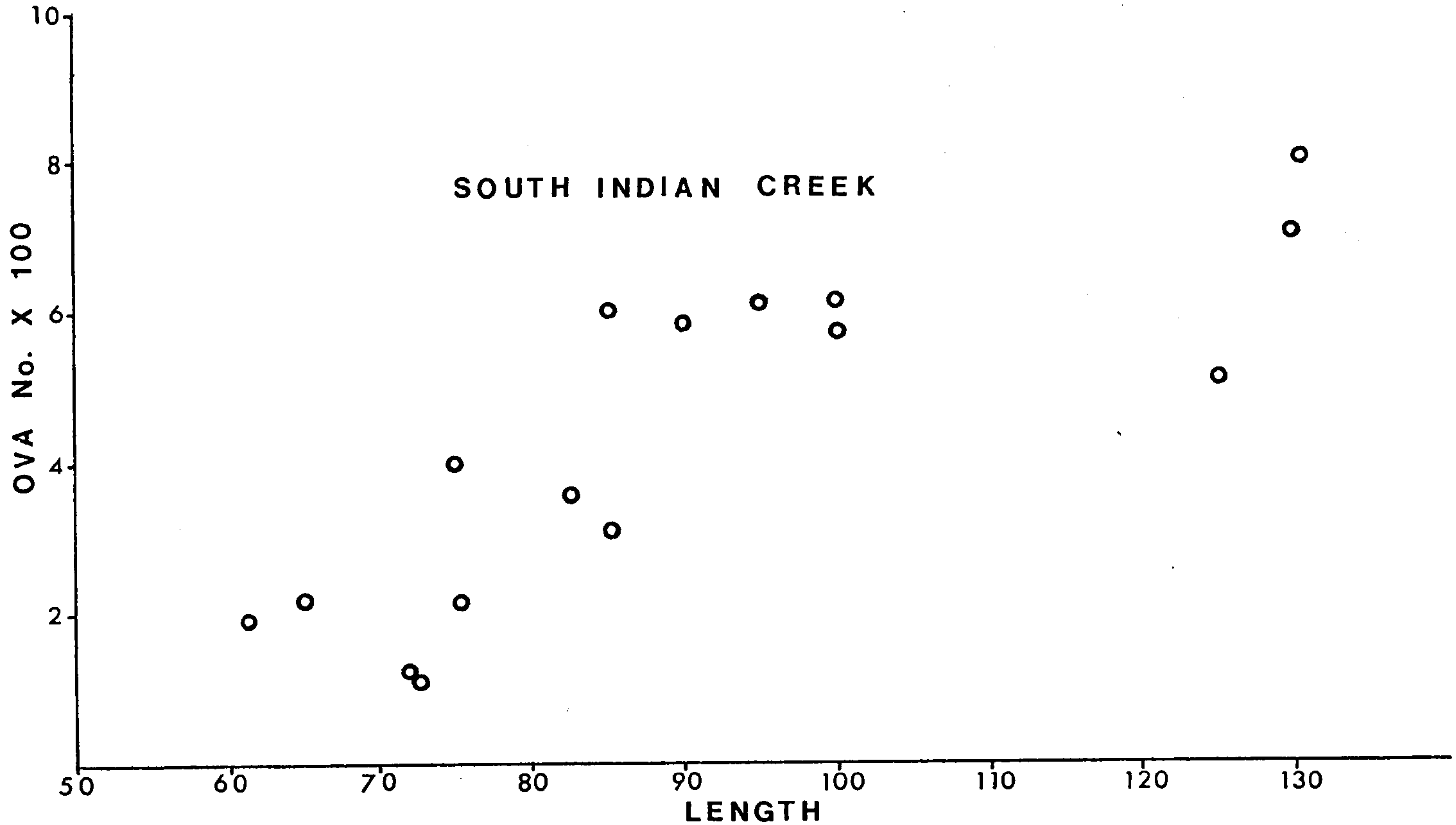

Figure 26. Mature ova-length scattergram of <u>Campostoma</u> <u>a</u>. <u>anomalum</u> from South Indian Creek.

VITA

Noel Martin Burkhead was born in Kansas City Missouri on 25 August 1950. He graduated from Folsom High School, Folsom, California in 1968.

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