TIME AND DURATION OF SPAWNING BY SMALLMOUTH BASS (MICROPTERUS DOLOMIEUI) IN THE NEW RIVER DRAINAGE

by

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(ABSTRACT)

The influence of physical parameters on spawning times of smallmouth bass and subsequent growth of young-of-the-year was studied via the otolith ageing technique. Daily rings on the sagittae of young-of-the-year smallmouth bass were first formed the day of swim-up, and continued to be formed until growth was significantly reduced in the fall. Daily age estimates of young-of-the-year smallmouth bass collected from one unregulated section of the New River, two regulated sections of the New River, and two tributary streams of the New River were used to back-calculate spawning dates. Growth rates of young-of-the-year declined as fish got older. Smallmouth bass spawned early in the spawning season did not initially grow as rapidly as those spawned later. Spawning occurred from late-April through

mid-July, 1982, at mean daily water temperatures ranging from 12.5 to 23.5 C. Frequency distributions of spawning dates were nearly identical among study sites, as were hydrological events. A major flood in June separated the spawning season at all study sites into two distinct periods. Discriminant functions were developed from four water temperature variables that differentiated between daily stream conditions prior to the spawning season and daily stream conditions during the spawning season. Mean daily water temperature was the most important of the four variables in differentiating between groups of conditions.

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INTRODUCTION

Forty-three percent of all freshwater anglers in the United States fished streams and rivers in 1980, and effort directed toward the black basses (*Micropterus* spp.) comprised forty-nine percent of all freshwater fishing effort expended (United States Fish and Wildlife Service 1983). The smallmouth bass (*Micropterus dolomieui* Lacepede) commonly inhabits warmwater streams throughout much of North America (Scott and Crossman 1973) and is readily available to many freshwater anglers. Due to its large size and sporting qualities, the smallmouth bass is generally regarded as a desirable species by the fishing public, who annually expend considerable amounts of money pursuing it. Andrews (1975) surveyed anglers on 72 km of the Mountain Fork River, a smallmouth bass stream in Oklahoma, and estimated that the capitalized value was $82,709/km based solely on fishermen expenditures.

In Virginia, the Shenandoah River has long held a reputation for high quality smallmouth bass fishing. Excessive mercury levels necessitated banning the consumption of fish from the South Fork of the Shenandoah in 1977. Kauffman (1980) estimated that local communities lost over $432,000 in revenue in the following year due to decreased fishing pressure, a substantial loss to this rural

area. Considering the number of anglers utilizing streams and rivers, the availability and desirability of smallmouth bass, and the cases of the Mountain Fork and Shenandoah rivers, the economic value of smallmouth bass fisheries is significant.

Protection and management of smallmouth bass stocks are necessary to maintain and increase their present value. In recent years, diversion and regulation of warmwater streams has risen rapidly (Parker and Krenkel 1969), often resulting in degradation of smallmouth bass resources. Smith (1979) has implicated siltation, fluctuating water levels, and general deterioration of water quality as factors contributing to the decline of smallmouth bass populations in Illinois. Regulation of the Columbia River, Washington, for hydroelectric power generation and flood control has resulted in a variety of detrimental effects on the reproductive success of its smallmouth bass stock (Montgomery et al. 1980). Almost every conceivable alteration of warmwater streams and their associated fisheries has been accepted with little or no thought of adverse impacts to the resource (Fajen 1981). Early recognition of factors affecting smallmouth bass stocks and implementation of management plans based on such knowledge can help us avoid further losses of smallmouth bass fisheries.

Reproductive activities of fish are often disrupted by habitat alterations; however, few conclusive studies regarding the timing of smallmouth bass reproduction in lotic systems and the relative influences of environmental factors have been conducted. Knowledge of the reproductive timing of smallmouth bass and the manner in which the environment affects this timing is needed to understand variations in the spatial and temporal patterns of smallmouth bass biomass, production, and yield (MacLean et al. 1981). Such understanding is vital to sound management plans designed to enhance smallmouth bass fisheries. For these reasons, coupled with the paucity of literature regarding smallmouth bass reproduction in large rivers, the present study has concentrated on the influences of physical parameters on the time and duration of spawning by smallmouth bass in the New River drainage.

Determination of the time and duration of smallmouth bass spawning previously has been accomplished through observation of active nests (Cleary 1956; Pflieger 1966; Surber 1970; Neves 1975), gonadal indices (Robbins and MacCrimmon 1977; Vogele 1981), and occurrence of larvae in the drift (Potter et al. 1978). Each of these methods has serious drawbacks for determination of smallmouth bass spawning time and duration for this study. Stream systems, especially large rivers, are extremely difficult to sample

(Gale and Mohr 1978; Campbell 1979) due to highly mobile fish populations, sampling problems associated with current, and fluctuations in water level and turbidity. Heavy precipitation during the smallmouth bass spawning season can eliminate the opportunity to visually observe nesting due to high turbidity. Collection of representative samples of adults for gonadal examination throughout the spawning season is difficult during times of either very high or very low water levels, and gonadal-somatic indices are of limited usefulness when there is an extended spawning season. Occurrence of smallmouth bass larvae and juveniles in stream drift can be of relatively short duration (Potter 1978), and the effort required to obtain sufficient numbers of fish by drift sampling is often impractical.

For these reasons, I decided to employ the otolith ageing technique of Pannella (1971) to determine the time and duration of spawning by smallmouth bass. Although the otolith ageing technique has not been applied to smallmouth bass, the high correlations between the number of growth rings on the sagittae (the largest otoliths) of other centrarchids and their daily ages (Taubert and Coble 1977; Miller and Storck 1982) suggests that daily growth rings are probably laid down on the sagittae of smallmouth bass. If so, precise estimates of smallmouth bass spawning dates can be obtained from the daily ages of young-of-the-year

smallmouth bass collected during and after the spawning season. Estimates of spawning dates can be made by subtracting the age (in days) of young-of-the-year smallmouth bass from the date of collection. This in turn permits the influences of physical parameters on the time and duration of spawning to be evaluated. Use of the otolith ageing technique assumes (1) growth rings on the sagittae of smallmouth bass are laid down with a daily periodicity, (2) the age of first daily ring formation is known, (3) ring formation continues on a daily basis through the sampling period, and, (4) daily rings can be observed and counted. In order to place any confidence in the estimates of spawning dates derived from application of the otolith ageing technique to smallmouth bass, the above assumptions must be verified. Therefore a major portion of this study involved the applicability of the otolith ageing technique to young-of-the-year smallmouth bass.

An additonal benefit of utilizing the otolith ageing technique for determining spawning time and duration is that precise growth rates of young-of-the-year smallmouth bass can be determined. Information on young-of-the-year smallmouth bass growth in the southern portion of its range is lacking, with most intensive studies limited to populations in northern lakes (Beckman 1948; Turner and MacCrimmon 1970; Neves 1973). Furthermore, young-of-the-

year smallmouth bass growth rates are commonly extrapolated from data pertaining to age 1+ or older fish or calculated with the assumption that all young-of-the-year collected on a particular date are of the same age. Both techniques are subject to bias over and above experimental error and can produce misleading results. The otolith ageing technique provides the means to calculate growth rates of individual fish on a daily basis, allowing for much greater accuracy in the determination of growth rates than traditional methods. Given that young-of-the-year growth has been seen to influence smallmouth bass year-class strength (Shuter et al. 1980), precise information on the growth of young-of-the-year smallmouth bass would be of value to fisheries biologists in understanding the population dynamics of southern smallmouth bass stocks.

Specifically, the objectives of this study were to:

(1) Test the assumption that growth rings on the sagittae of young-of-the-year smallmouth bass are daily in occurrence and determine the time of first daily ring formation.

(2) Determine when growth rings on the sagittae of young-of-the-year smallmouth bass cease to be reliable indicators of daily age.

(3) Determine daily instantaneous growth rates of young-of-the-year smallmouth bass from the New River drainage and the effects of spawning time on these growth rates.

(4) Evaluate the influence of photoperiod, temperature, and discharge variables in determining the time and duration of spawning by smallmouth bass in the New River drainage.

LITERATURE REVIEW

The otolith ageing technique

The term otolith refers to any of the three pairs of calcareous structures present in the auditory systems' semicircular canals of teleost fish. In general, the sagitta is the largest followed by the astericus and the lapillus (Pannella 1980). The specific function of otoliths is unclear, although their neural association with the auditory system suggests that they play a role in sound perception (Degens et al. 1969). Experiments reported by Parker (1980) imply that otoliths also aid fish in maintaining their equilibrium in the water column.

Otoliths, primarily sagittae, are useful in determining the yearly ages of fish, separating fish species, and distinguishing between different stocks of the same species (Williams and Bedford 1974). In the early 1970s, Pannella (1971, 1974) provided evidence that the sagittae of many tropical and some temperate fish species exhibit daily growth rings. He suggested, in view of the apparent presence of daily rings on the sagittae of various species inhabiting different depths and climates, that daily rings may be a universal feature of fish sagittae (Pannella 1971).

Pannella's findings generated great interest in the fisheries profession, for, as Brothers et al. (1976) noted,

"The daily increment would appear to be the smallest

> unit of growth that is formed at the supra-molecular level and, as such, is in principle the most natural unit to use for age estimation."

Recently, the daily formation of sagittal rings has been investigated and validated for a host of marine species (Brothers et al. 1976; Ralston 1976; Struhsaker and Uchiyama 1976; Barkman 1978; Wilson and Larkin 1980; Campana and Neilson 1982; Marshall and Parker 1982; Victor 1982; Campana 1983) as well as freshwater species (Taubert and Coble 1977; Schmidt and Fabrizio 1980; Wilson and Larkin 1980; Tanaka et al. 1981; Marshall and Parker 1982; Miller and Storck 1982; Rice 1983), lending credence to Panella's suggestion.

Each daily sagittal ring is composed of two layers, one a calcium carbonate layer and the other proteinaceous (Pannella 1980). Under transmitted light the calcareous layer appears lightly colored while the proteinaceous layer appears dark. Mugiya et al. (1981) and Tanaka et al. (1981) demonstrated that, in laboratory situations simulating natural environmental conditions, the proteinaceous layer is deposited within 3-4 hours after sunrise and the calcareous layer is laid down through the remaining 20-21 hours of the day. This daily periodicity in the formation of alternating calcareous and proteinaceous layers provides for very precise estimates of daily ages of fish (Brothers et al. 1976; Taubert and Coble 1977; Barkman 1978; Wilson and Larkin 1980; Tanaka et al. 1981; Miller and

Storck 1982). However, before the number of rings on sagittae can be used for age determinations the time of first daily ring formation must be known (Brothers et al. 1976; Taubert and Coble 1977), and care must be taken in applying the otolith ageing technique to fishes for which it has not been validated, as the rate of ring formation may not be daily in all species (Geffen 1982). Further, photoperiod (Taubert and Coble 1977; Tanaka et al. 1981), temperature (Taubert and Coble 1977), age of fish (Pannella 1971; Brothers et al. 1976), spawning activity (Pannella 1980), and food ration (Struthsaker and Uchiyama 1976; Tanaka et al. 1981) have been shown to affect the formation of sagittal rings, and the daily periodicity of sagittal ring formation can be disrupted by stressful, extreme environmental conditions (Struthsaker and Uchiyama 1976; Taubert and Coble 1977; Tanaka et al. 1981; Geffen 1982; Victor 1982).

Spawning time and duration

The reproduction of fish is governed by stimuli which ensure synchrony in the readiness of fish to spawn and the availability of favorable environmental conditions for survival of the young (Liley 1969). Under natural conditions, the smallmouth bass undergoes an annual cycle of gonadal recrudescence and regression (Vogele 1981). In temperate centrarchids, the period of gonadal recrudescence

coincides with increasing day length and water temperature (Jones 1946; Kaya and Hasler 1972), while the period of regression varies with different environmental conditions, stocks, and species (Kaya and Hasler 1972; Siler and Clugston 1975). As such, the timing of reproduction through the annual cycle of gonadal development is crude, with the actual process of spawning occurring within a relatively brief time period when appropriate environmental conditions prevail (Schwassmann 1971).

Several factors have been implicated in triggering smallmouth bass spawning and determining the length of the spawning season; principal among these is water temperature. Spawning generally occurs in the spring following rising water temperatures in the range of 15 to 21 C (Surber 1939; Cleary 1956; Clady 1975; Neves 1975; Robbins and MacCrimmon 1977; Shuter et al. 1980), although it has been reported at temperatures as low as 13.3 C (Vogele 1981) and as high as 26.7 C (Reynolds 1965). Normal development of smallmouth bass eggs occurs within the range of 15.0 to 25.0 C (Kerr 1966), and eggs maintained at 18.3 C have been acclimated to temperatures ranging from 11.7 to 25.0 C within one half hour without apparent harm (Webster 1948). These observations support Cleary's (1956) contention that temperature thresholds for smallmouth bass spawning are variable. However, this variation in observed temperature

thresholds is likely related to the thermal history of the fish. Shuter et al. (1980) have observed that, during periods when water temperatures exceeded 15 C, the accumulation of approximately 25 degree-days greater than 10 C was necessary to initiate spawning and that accumulation of approximately 150 degree-days greater than 10 C generally terminated spawning activities in northern populations. These findings allowed Shuter et al. (1980) to accurately predict the northern limit of the geographic distribution of smallmouth bass from annual temperature regimes in northern lakes.

Duration of smallmouth bass spawning seasons appear to be inversely related to the rate of water temperature increase (MacLean et al. 1981; Vogele 1981). Renesting of smallmouth bass is commonly reported (Surber 1943; Cleary 1956; Henderson and Foster 1957; Pflieger 1966; Coble 1975; Vogele 1981) and generally has been attributed to nest failures caused by a rapid drop in water temperature (Shuter et al. 1980). Pflieger (1966) and Neves (1975) have observed renesting following drops in water temperature despite previous nesting success. In an Oklahoma hatchery, female smallmouth bass have spawned seven times in a single season (Inslee 1975). Sanderson (1958) examined the ovaries of several smallmouth bass collected from one pool on the same day during the spawning season and found that all

ovaries contained eggs in various stages of maturation. These observations indicate that renesting and repeated spawning may be a basic reproductive strategy of smallmouth bass, as suggested by Pflieger (1966).

Although the importance of water temperature in regulating smallmouth bass reproduction is undeniable given the animal's poikilothermic nature, hydrological variables, either in conjunction with temperature or by themselves, have been implicated as major determinants of spawning times in stream systems. Upstream movements of smallmouth bass prior to spawning have been highly correlated with discharge (Robbins and MacCrimmon 1977), and elevated water levels have provided access to previously unavailable spawning habitat (Henderson and Foster 1957). Reynolds (1965) observed spawning activity in an Iowa stream at a temperature of 26.7 C during a time of stable stream flow and suggested that water levels may be more important than temperature in triggering smallmouth bass spawning.

Smallmouth bass nests are built in areas of minimal current (Pflieger 1966; Coble 1975) where they will be protected in times of moderate flooding (Winemiller and Taylor 1982). Important criteria in selection of smallmouth bass nest sites include current, depth, and distance from escape cover (Pflieger 1966), all of which can be affected by changes in water level. Surber (1943) reported that both

stable stream flows and reduction in turbidity levels were necessary before smallmouth bass would commence spawning in the Shenandoah River, Virginia, and that when these conditions were met spawning occurred simultaneously in several streams with similar hydrological profiles. Both Pflieger (1975) and Becker et al. (1981) have concluded that it is not so much the direction of water fluctuations, but rather the combination of the magnitude and timing of water fluctuations that determine smallmouth bass spawning time and duration in stream systems.

The precise determinations of spawning times obtained in this study coupled with daily records of environmental conditions should provide needed insight into what factors are most important in determining the spawning time and duration of smallmouth bass. If so, management strategies for riverine smallmouth bass stocks can be improved through increased knowledge of the resource and documented justification of policies.

METHODS

Laboratory validation

Validation of the otolith ageing technique's applicability to smallmouth bass was performed under laboratory conditions to verify the daily periodicity of sagittal ring formation and to determine the time of first daily ring formation. Approximately 250 smallmouth bass eggs were removed from a nest in the South Fork of the Roanoke River on 26 May, 1982. The eggs were maintained under a 16-hour light/8-hour dark daily cycle and a temperature range of 20-22 C. Eggs hatched 3 days after collection and larvae swam-up (rose off the nest) and began feeding 7 days after hatching. Larvae were raised under a 16 hour light/8 hour dark regime within a temperature range of 17-23 C and fed live *Artemia* nauplii to satiation twice daily at 0800 and 2000 hours. Starting the day of swim-up, 10 or 11 larvae were removed from the culture every other day between 2000 and 2200 hours and frozen in water until their sagittae could be prepared for ageing. Sampling was terminated fifteen days after swim-up due to a mass mortality.

The left and right sagittae were removed from thawed fish approximately 6 months after freezing with the aid of a dissecting scope, polarizing lenses, and fine (0.05 mm tip diameter) jeweler's probes. After scraping off as much of

the saccular membrane as possible, sagittae were embedded in thermoplastic cement on standard (25 x 75 mm) microscope slides with their dorso-ventral axis parallel with the slide. All sagittae were randomly numbered to reduce bias when counting rings. Random numbers were assigned by sequentially numbering labels for microscope slides, randomly selecting a label for each slide after each fish's sagittae were mounted, and recording what label number each fish had received. All sagittae were measured at their greatest width to the nearest 0.01 mm with an ocular micrometer.

Rings were counted in the posterior half of sagittae under 400-1000X phase-contrast transmitted light by two different methods. Method 1 was based on identification and counting procedures of sagittal rings described by Pannella (1971), Brothers et al. (1976), Taubert and Coble (1977), and Wilson and Larkin (1980). Method 2 was recommended by S.J. Miller (Illinois Natural History Survey, personal communication), who felt that this method was a useful precaution against reading prolarval rings which rarely follow the daily pattern of postlarval rings. Method 1 consisted of counting any clearly defined pair of alternate light and dark bands as one daily ring. Method 2 required measuring the sagittal radius (the distance between the nucleus and the outermost posterior edge) at the time of

swim-up. On the day of swim-up, the radius of 18 sagittae from 9 reared fish averaged 0.07 mm (standard deviation = 0.004 mm); hence, 0.07 mm was used as the sagittal radius at the time of swim-up for ring counts by Method 2. Any clearly defined pair of light and dark bands occurring past this radius was counted as one daily ring.

When possible, both sagittae from each fish were read three times each by the two methods previously described. No two readings of any one sagitta were made in consecutive order. Ring counts were recorded by label number, and after 10-20 sagittae had been read, individual fish were identified by label number. Results of appropriate ring counts were then recorded for that fish. The mean of the three ring counts per sagitta was rounded to the nearest whole number and used in subsequent analyses.

The relationship between the mean number of rings from three ring counts of individual sagittae and that particular fish's known age in days after swim-up was determined separately for both reading methods using Theil-Sen linear regression procedures (Hollander and Wolfe 1973). Theil-Sen procedures were employed due to unequal sample sizes between different sampling days, a situation which tends to disrupt bivariate normal distributions. The null hypothesis that the slopes of these regressions were equal to one, as would be expected if the relationship between sagittal rings and

daily ages was 1:1, was tested by Kendall's test for bivariate association (Hollander and Wolfe 1973). Confidence intervals for the Theil-Sen estimates of the slopes were obtained by Hodges-Lehman estimators (Hollander and Wolfe 1973).

The null hypothesis that the y-intercepts of the Theil-Sen regressions were equal to zero, as would be expected if no sagittal rings were present the day of swim-up, was tested by the Wilcoxon signed ranks procedure (Hollander and Wolfe 1973) on estimates of the y-intercept. These estimates were obtained by applying the known age in days and the mean number of sagittal rings counted on individual sagittae to the Theil-Sen regressions determined separately for the two methods of counting; ie.,

$$Y = D - BX$$

where,

Y = an estimate of the y-intercept,

D = the known age in days from swim-up,

B = the slope of the appropriate Theil-Sen regression, and,

X = the appropriate mean number of sagittal rings.

Confidence intervals on the y-intercepts were then estimated using Hodges-Lehman estimators.

Study sites

Three study sites on the New River and one study site

on each of three tributary streams to the New River were chosen for collection of young-of-the-year smallmouth bass to accomplish objectives 2, 3, and 4 of this study. Choice of study sites was based on the occurrence of smallmouth bass, the availability of suitable smallmouth bass spawning habitat, and the site's proximity to United States Geological Survey gauging stations. An effort was made to choose study sites with dissimilar hydrologic and temperature profiles so that generalized relationships between physical variables and the time and duration of spawning by smallmouth bass could be examined (Table 1; Appendix 1). The study sites chosen with the above criteria were as follows: New River approximately 4 km northwest of Galax, Virginia; New River approximately 3 km southeast of Eggleston, Virginia; New River approximately 6 km southeast of Meadow Creek, West Virginia; Big Reed Island Creek approximately 3 km south of Farris Mines, Virginia; Little River approximately 6 km east of Snowville, Virginia; and Walker Creek approximately 1 km southeast of Poplar Hill, Virginia (Fig. 1).

The New River exhibits marked hydrological changes from its origin in North Carolina to its confluence with the Gauley River in West Virginia. Near Galax the river is characterized by an unregulated flow regime and long, shallow riffles and runs. The bordering terrain is piedmont

Table 1. Physical characteristics of study sites in the New River drainage.

Study site	Longitude and latitude	Length (m)	Average width (m)	Mean daily* discharge (m^3/s)	Gradient (m/km)	Predominant substrate
New River near Galax	81° 58' 00'' 36° 40' 30''	1880	163	43	0.4	sand and cobble
New River near Eggleston	80° 37' 00'' 37° 15' 30''	1357	200	95	1.2	bedrock and cobble
New River near Meadow Creek	80° 55' 30'' 37° 48' 00''	1428	207	221	1.6	cobble and silt
Big Reed Island Creek	80° 43' 30'' 37° 53' 00''	2142	50	11	2.4	bedrock and boulder
Little River	80° 32' 00'' 37° 01' 30''	1047	39	9	2.0	silt and sand
Walker Creek	80° 44' 00'' 37° 11' 00''	785	14	8	3.2	bedrock and cobble

* 1982 water year

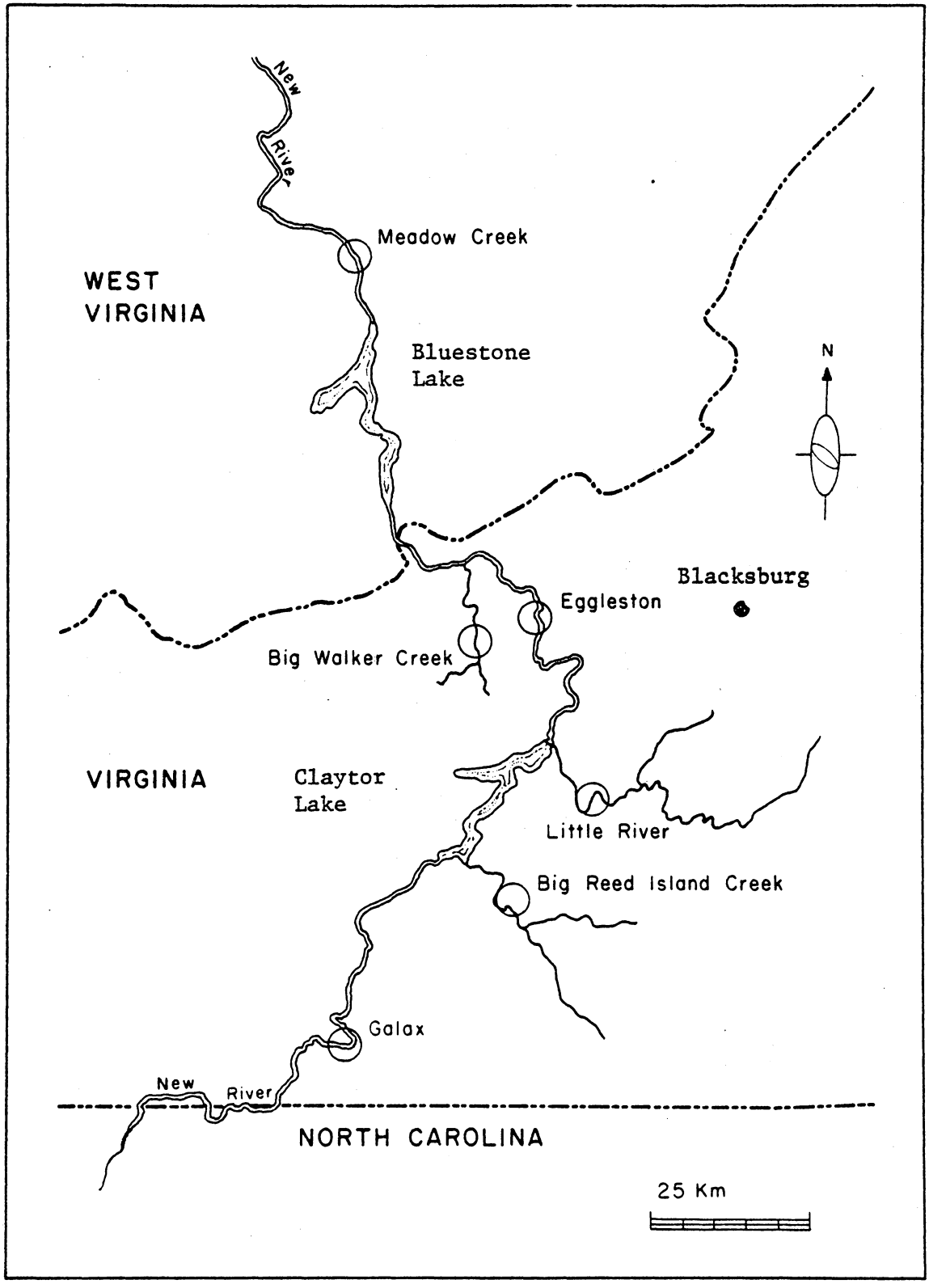


Figure 1. Study sites in the New River drainage.

with low gradient slopes and agricultural lands predominating. The New River near Eggleston is subject to highly variable discharge rates due to releases from Applachian Power Company's Claytor Lake hydroelectric dam, which are timed with peak power demands. Successive series of ledges create numerous plunge pools, while riffle areas are relatively scarce. Banks are characterized by steep sided, undeveloped woodlands. Near Meadow Creek, the New River is influenced by releases from the U. S. Army Corps of Engineers' Bluestone Lake dam. Discharge rates do not fluctuate as widely as those below Claytor Lake; however, flood control needs and recreational use demands frequently dictate variable release schedules. Repeated series of short riffles, long runs, and deep pools are common. Streamside slopes are often severe (>20%) with exposed rock faces.

The three tributary study sites are all free flowing. The study site on Big Reed Island Creek is dominated by long, shallow runs and infrequent deep pools. Banks are generally steep and undeveloped. Long runs and short riffles typify the Little River study site. Extensive agricultural lands adjacent to both banks contribute to the relatively high sediment load in the Little River. The study site on Walker Creek is characterized by long deep runs interrupted by short, shallow riffles. Bordering

terrain varies from limited floodplain agricultural land to steep rock slopes.

Field collections

Each study site was visited at least twice monthly from May through October of 1982 for collection purposes, although collections were not always feasible due to high water and turbidity levels (Appendix 2). Different sampling gear types were employed in the collection of young-of-the-year smallmouth bass due to the difficulties encountered in collecting fish less than 30-40 mm in total length, changes in gear selectivity as young-of-the-year bass grew, and differences in water depth and substrate between study sites. Generator-driven backpack and boat electrofishing units (pulsed D.C.), and seining with a 6.1 x 1.2-m, 0.04-cm stretch mesh seine were ineffective in collecting young-of-the-year smallmouth bass less than 30 mm in total length. Direct dip net (mesh size 2 mm) capture was the only method found suitable and required lengthy time periods to spot and capture individual fish. At this stage in their development, young-of-the-year smallmouth bass are very difficult to approach and associate closely with overhanging cover where seining is ineffective. Backpack and boat electrofishing were also ineffective in capturing small young-of-the-year fish due to their response to electric shock, which can best be described as total immobilization.

Young-of-the-year smallmouth bass rarely exhibited a galvanotaxic response to pulsed direct current.

Dip nets and backpack electrofishing were used during collections previous to the time most young-of-the-year attained a length of 30-40 mm. Upon reaching a length of 30-40 mm, young-of-the-year smallmouth bass became susceptible to backpack electrofishing, probably due to a lessened propensity to associate closely with overhanging cover. From this time until sampling was terminated, backpack electrofishing was the sampling method consistently used in the New River near Eggleston, the Little River, and Walker Creek and accounted for the vast majority (83%) of young-of-the-year collected from these sites.

The New River sites near Galax and Meadow Creek are characterized by unobstructed and more uniform substrates than other study sites and were generally sampled by boat electrofishing or seine. Boat electrofishing accounted for 94% of young-of-the-year collected from the New River near Galax, and seining accounted for 76% of young-of-the-year collected from the New River near Meadow Creek. Over a four-month period, only eight young-of-the-year were collected from Big Reed Island Creek; consequently, collections at this study site were discontinued in late September and the study site was excluded from any analyses. For all collections an effort was made to collect 15 or more

young-of-the-year. However, it was only after the young-of-the-year had attained a length of 50-60 mm that this goal was consistently achieved.

Upon collection, all fish were placed on ice and transported to the laboratory where they were measured to the nearest 0.1 mm and weighed to 0.01 g. After measurements were completed all fish were individually packaged, labeled, and frozen until their sagittae could be excised and prepared for determination of daily ages.

Sagittae preparation

Sagittae of young-of-the-year smallmouth bass less than 15 mm in total length were cleaned of the sacculus and mounted in thermoplastic cement on standard microscope slides with their dorso-ventral axis parallel with the slide. Both sagittae from each fish were mounted on the same slide. Each slide was assigned a random number as described for laboratory fish to reduce bias in ring counts.

Due to the time involved in sagittae preparation and reading (approximately 20 minutes per sagitta), it was desirable to prepare and read only one of the two sagittae per fish. Comparison of the mean number of sagittal rings from three ring counts on the left and right sagittae of fifteen randomly selected fish from each of four size categories (40.0-49.9, 50.0- 59.9, 60.0-69.9, and 70.0-79.9 mm; Appendix 3) by Wilcoxon signed-ranks tests revealed no

significant difference in the mean number of sagittal rings counted on right versus left sagittae at the P=0.05 level (Table 2). Campana and Neilson (1982) similarly found that mean ring counts between the left and right sagittae of starry flounder (Platichthys stellatus) did not significantly differ. Hence, only one sagitta from collected fish was randomly numbered as described for laboratory fish, prepared, and read three times by Method 1.

Sagittae from young-of-the-year smallmouth bass greater than 15 mm total length required more preparation to distinguish individual sagittal rings. The preparation techniques of Taubert and Coble (1977) and Miller and Storck (1982) were applied to sagittae of young-of-the-year spotted bass (Micropterus punctulatus) collected from the New River near Meadow Creek to gain familiarity with these procedures before attempting to prepare and age young-of-the-year smallmouth bass. Sagittal rings were poorly defined, and those rings occurring in the posterior edge of the sagittae were not consistently exposed. However, good results were obtained when slight modifications of the published methods were employed.

Specifically, sagittae were mounted in thermoplastic cement with their convex (proximate) side face downward on a standard microscope slide and aligned so that their nucleus and outermost posterior edge formed a plane parallel with

Table 2. Results of Wilcoxon-signed-ranks tests on the null hypothesis that the mean number of rings on right and left sagittae of smallmouth bass do not differ.

Size category (mm)	N	P
40.0-49.9	15	0.98
50.0-59.9	15	0.99
60.0-69.9	15	0.07
70.0-79.9	15	0.33

that of the slide. Sagittae were then ground with wet number 600 sandpaper until a flat plane parallel with the slide was achieved. The thermoplastic cement was heated and the sagittae turned over. The sagittae were then ground until the nucleus was clearly exposed when viewed under 100X. At this point, my method differed from those of Taubert and Coble (1977) and Miller and Storck (1982), who recommended grinding until the nucleus is just barely exposed and then etching the sagittae in 1% hydrochloric acid for 15 to 45 seconds. Once the nucleus was clearly exposed, I buffed the sagittae with a felt pad, heated the thermoplastic cement, and turned the sagittae over again. Sagittae prepared in this manner exhibited well defined sagittal rings, and those rings occurring in the posterior edge were consistently exposed when viewed under 200-400X phase-contrast transmitted light. No etching in acid was necessary, which resulted in a substantial saving of time. Following preparation one sagitta from each fish was read three times by Method 1.

Ring formation in older fish

The time when sagittal rings ceased to be reliable indicators of daily ages was estimated by three methods. Collections of young-of-the-year smallmouth bass were continued into January, 1983 at two study sites, the New River near Eggleston and Walker Creek, to ensure that young-

of-the-year with very slow growth rates were represented.

The first method consisted of plotting the mean number of rings counted on individual sagittae and collection dates for each study site. These plots were then examined for departures from linearity. The second method involved identifying the three fish from each collection that exhibited the maximum range in their three individual ring counts from their mean ring counts. These three maximum ranges per collection were then averaged and plotted by collection date. These plots were also examined for departures from linearity. Finally, notes were taken during counts regarding the degree to which crowding of rings affected my ability to distinguish individual rings. The collection date and study sites were then determined when counts were completed and randomly numbered sagittae were identified.

Results of the three methods just described were compared and used to determine a time of year when ring counts ceased to be reliable indicators of daily age. All fish collected after this time were then eliminated from further analyses involving daily ages.

Growth

Growth rates of young-of-the-year smallmouth bass estimated in this study were based on total length and daily ages from swim-up. Length-weight relationships were

developed for all study sites to transform growth in length to growth in weight (Ricker 1975). Total lengths and age in days from swim-up of individual smallmouth bass were fitted to von Bertalanffy's growth model (von Bertalanffy 1938) for each study site, as availability of von Bertalanffy growth parameters might be of value in future studies. Von Bertalanffy's growth equation takes the form of

$$lt = Li\ (1 - e^{-k(t-to)})$$

where,

lt = total length at age t (mm),

Li = asymptotic length (mm)

k = Brody's growth coefficient

t = age in days from swim-up, and,

to = hypothetical age at which the fish was zero length.

Individual instantaneous growth rates were calculated for all fish in the following manner:

$$G = [\log_e (li/lo)] / t$$

where,

G = instantaneous daily growth rate,

li = total length at time of collection (mm),

lo = total length at time of swim-up (mm), and,

t = the number of days between time of collection and time of swim-up (d).

Total length at time of swim-up was determined from 17

fish collected from a nest containing approximately 500 larvae in the New River near Eggleston on 30 June, 1982. About half of the larvae had risen from the nest and half still remained in the gravel. Both groups of larvae appeared to be approximately the same length, which indicates that they were all of the same brood. The 17 fish collected were all hovering above the nest, and their mean total length was 8.4 mm (standard deviation = 0.3). This length at swim-up was within 0.6 mm of lengths that have previously been reported (Meyer 1970; Wallace 1972), and so 8.4 mm was used as lo in the calculation of instantaneous growth rates.

The Julian date of swim-up for individual fish was assumed to be the mean of that fish's sagittal ring counts rounded to the nearest whole number, subtracted from the Julian date it was collected. Only two study sites, the New River near Meadow Creek and Walker Creek, were chosen to assess the effect of spawning time on growth since very few young-of-the-year spawned early in the year were collected from other study sites. Identification of early versus late-spawned fish was based on an examination of frequency distributions of swim-up dates at each study site. Frequency distributions of swim-up dates showed a bi-modal pattern at both study sites, indicating two distinct spawning periods. The few fish that swam-up between the

early and late modes were excluded from any comparisons of early and late-spawned fish.

Instantaneous growth rates of individual fish and that particular fish's age in days after swim-up were plotted and indicated that growth rate was inversely related to age. Therefore, instantaneous growth rates of early and late-spawned fish could not be compared on any particular collection date due to age discrepencies. Consequently, Theil-Sen linear regressions were separately developed for early and late-spawned fish, with instantaneous growth rates as the response variable, and age in days from swim-up as the independent variable. Confidence intervals on the Theil-Sen estimates of slopes were derived from Hodges-Lehman estimators. Confidence intervals on the y-intercepts were derived by the same methodology used in the Theil-Sen regressions of sagittal rings and daily ages of laboratory fish. The estimates and confidence intervals of the slopes and y-intercepts of early versus late spawned fish were then compared.

Spawning time and duration

Spawning date frequencies for each study site were constructed from estimates of the dates on which individual young-of-the-year smallmouth bass had been spawned. Spawning dates were estimated in the following manner:

SD = SUD - 7 - I

where,

SD = the Julian date of spawning,

SUD = the Julian date of swim-up,

7 = the number of days required between hatching and swim-up, and,

I = the number of days required between egg fertilization and hatching.

Julian dates of swim-up were estimated as described for growth comparisons of early and late spawned fish. The number of days required between hatching and swim-up was assumed to be a constant 7 days, based on the range of swim-up times reported in the literature (Meyer 1970; Inslee 1975; Vogele 1981). The number of days required between egg fertilization and hatching was estimated by regression of Webster's (1948) data concerning hatching times in relation to temperature. The specific relationship (R^2=0.99; P<0.01) developed for a temperature range from 12.8 to 25.0 C was

$$Y = 3442.66\ X^{-2.299}$$

where,

Y = the number of days required for hatching, and,

X = water temperature (C).

This relationship corresponded closely with other field data (Table 3). As water temperatures at all study sites varied daily, the grand mean of mean daily water temperatures for the five days preceeding the estimated date

Table 3. Days (d) required for smallmouth bass egg hatching and fry swim-up in relation to temperature.

Source	T(C)	hatch(d)	hatch(d)[1]	swim-up(d)
Tester 1930	12.2-22.8			12[2]
Webster 1948	25.0	2.17	2.11	
	23.9	2.25	2.34	
	21.7	2.92	2.92	
	21.1	3.25	3.11	
	19.4	3.75	3.77	
	18.3	4.08	4.32	
	15.6	6.25	6.23	
	15.0	6.96	6.82	
	12.8	9.83	9.78	
Pflieger 1966	15.2-18.2	4	4.37-6.61	
	17.2-19.5			8-11[2]
	12.2-22.8			12[2]
Meyer 1970	21.1			6[3]
Turner and MacCrimmon 1970	15.2-18.2	4	4.37-6.61	
	17.2-19.5			8-11[2]
Wallace 1972	23.0	1.75-1.88	2.55	
Inslee 1975	18.3-23.3			3-7[3]
Neves 1975	16.0-20.0	5-4	3.52-5.88	
	19.0	3.9	3.96	
Vogele 1981	14.4-15.6	7	6.23-7.49	
	17.8-18.6	5	4.16-4.60	
	15.3-16.4			8[3]
	18.3-23.3			6[3]

[1] predicted from regression of Webster's (1948) data.
[2] indicates time from egg fertilization to swim-up.
[3] indicates time from hatching to swim-up.

of hatching was applied to the regression of Webster's data for estimation of the number of days required from egg fertilization to hatching.

Spawning date frequencies were compared among study sites by Kolmogorov-Smirnov tests for general distributions (Hollander and Wolfe 1973).

Relative importance of physical variables

Photoperiod data were obtained from the United States Naval Observatory's estimates of sunrise and sunset times for Roanoke, Virginia. These data were not corrected for deviations among study sites as any variation would be due solely to topographical variation. As it was not known where smallmouth bass had spawned at each study site, it was impossible to correct for topographical variation.

Temperature data were obtained from continuously recording Ryan thermographs placed at all study sites prior to spawning. At two study sites, the New River near Eggleston and Walker Creek, temperature data were lost for 29 days (10 June-9 July) and 24 days (26 June-20 July) because of vandalism and an oversight in handling, respectively. Missing temperature data for the New River near Eggleston were estimated by developing a least squares regression of mean daily temperatures of the New River near Eggleston and mean daily temperatures of the New River near Galax. The relationship developed ($R^2 = 0.90$; $P<0.01$) was

$Y = 1.095 + 0.870X$

where,

Y = mean daily water temperature (C) for the New River near Eggleston, and,

X = mean daily water temperature (C) for the New River near Galax.

Mean daily water temperatures, minimum daily water temperatures, and maximum daily water temperatures for the New River near Eggleston on any day for which data were missing were then estimated by applying the same variables values at the New River near Galax on that day to the regression. Missing mean daily water temperatures, minimum daily water temperatures, and maximum daily water temperatures for Walker Creek were estimated from Big Reed Island Creek in the same manner. The relationship between mean daily temperatures of Walker Creek and Big Reed Island Creek ($R^2 = 0.94$; $P<0.01$) was

$Y = 3.430 + 0.821X$

where,

Y = mean daily water temperature (C) for Walker Creek, and,

X = mean daily water temperature (C) for Big Reed Island Creek.

Daily discharge data were obtained from the United States Geological Survey offices located in Marion,

Virginia, and Charleston, West Virginia.

Stepwise discriminant analysis (Sarle 1982) was used to assess the relative importance of thirteen physical variables in defining three groups of stream conditions associated with spawning. Stepwise discriminant analysis is a standard statistical procedure used when a large set of variables are suspected to be important in characterizing one or more groups of conditions. The variables that are identified by stepwise discriminant analysis as most important in characterizing the groups are those that exhibit the greatest variability among the groups.

The physical variables examined included two photoperiod variables (number of hours between sunrise and sunset and the rate of change in the number of hours between sunrise and sunset), eight water temperature variables (mean daily water temperature, the rate of change in mean daily water temperature, minimum daily water temperature, the rate of change in minimum daily water temperature, maximum daily water temperature, the rate of change in maximum daily water temperature, the daily accumulation of degree days greater than 15 C, and the rate of change in the daily accumulation of degree days greater than 15 C), and three discharge variables (mean daily discharge, the ratio of mean daily discharge and water year 1982 mean annual discharge, and the rate of change in the ratio of mean daily discharge and

water year 1982 mean annual discharge). These photoperiod, temperature, and discharge variables were selected for study for two reasons. One is that they have been shown to be or have been implicated as important in determining spawning times of fish in previous studies. The other is that, with the exception of the photoperiod variables, they are useful in quantifying stream conditions.

All rates of change are the algebraic differences between any particular day's variable value and that of the same variables value on the previous day. The daily accumulation of degree days greater than 15 C was based on mean daily water temperatures and defined as the sum of the number of degrees greater than 15 C for all days previous to and including any particular day of 1982.

The three groups chosen for analyses were thought to represent three different sets of stream conditions that influenced smallmouth bass spawning. The groups were: (1) daily conditions for approximately one month prior to the spawning season at each study site; (2) daily conditions when spawning did occur during the spawning season at each study site; and, (3) daily conditions when spawning did not occur during the spawning season at each study site. Each study site's spawning season was defined as the period between the first and last estimated spawning dates, inclusive of those dates. Each group's data set consisted

of daily measurements of the thirteen physical variables previously described for all days that were associated with the appropriate group.

All variables for the three groups were lagged one and two days, applied to the stepwise discriminant analysis, and results compared with those of unlagged variables. Daily measurements of physical variables from New River sites, tributary sites, and all sites combined were also pooled by group to aid in the determination of reproductive generalities associated with the physical variables examined.

Four of the original variables were then selected for use in developing discriminant functions (Goodnight 1982), designed to differentiate between the three groups of daily stream conditions detailed previously. Choice of these four variables was based on the percent variation in the groups of daily conditions they accounted for, as indicated by R^2 values, and the frequency with which the stepwise discriminant analyses identified them as important factors in differentiating among the three groups. The selection of only four variables was due to sample size constraints in association with discriminant analysis.

The effectiveness of the four variables in differentiating among the three groups was evaluated with a standard cross-validation technique in multivariate analysis

(Diaconis and Efron 1983). This technique consisted of randomly splitting the daily measurements of physical variables for the three groups for each study site in half, taking one half of the data from each study site (calibration data set) and developing discriminant functions from it, applying the discriminant functions obtained to the other half of the data (test data set) to classify daily observations by groups, and calculating the percent of misclassified observations. The data for each study site were randomized by sequentially picking numbers corresponding to the Julian dates covered by the three groups from a table of random digits (Jessen 1978) until half the total number of Julian dates had been selected. Those dates were then used to develop the discriminant functions and the remaining dates used to test them.

RESULTS

Laboratory validation

A total of 82 fish (164 sagittae) were sampled from the day of hatching to fourteen days after swim-up. Average sagittal widths ranged from 0.12 mm the day of swim-up to 0.24 mm fourteen days after swim-up (Table 4). Thirty-three of the 164 sagittae sampled were severely fragmented and 12 were considered unreadable, hence a total of 45 sagittae were dropped from the analyses. All sagittae sampled prior to swim-up were fragmented. Fragmentation was thought to be the result of a power failure during which samples had thawed and later refrozen. S.J. Miller (Illinois Natural History Survey, personal communication) has frozen larval largemouth bass (Micropterus salmoides) in water with no adverse effects to their sagittae; hence, the mechanical stress of freezing, thawing, and refreezing was probably responsible for fragmentation of sagittae. Sagittae were considered unreadable when saccular membrane obscured rings.

The estimate of the slope obtained from regression of mean ring counts by Method 1 and known daily ages of fish was not significantly different ($P=0.13$) from one (Table 5). This indicates that sagittal rings were formed on a daily basis. The null hypothesis that the y-intercept of the above relationship was equal to zero was rejected ($P<0.01$). The estimate of the y-intercept indicated that the first

Table 4. Average widths and standard deviations (S) of laboratory fish sagittae in relation to the number of days after swim-up.

Days after swim-up	N	Average width (mm)	S
0	18	0.12	0.01
2	6	0.13	0.01
4	21	0.18	0.01
6	16	0.20	0.01
8	11	0.21	0.01
10	20	0.21	0.01
12	16	0.23	0.01
14	11	0.24	0.01

Table 5. Estimates of the slope and y-intercept with 95% confidence intervals (in parentheses) for the relationship between the mean number of rings and known age in days from swim-up by counting method.

	Method 1[1]	Method 2[2]
slope	0.970 (0.900-1.000)	0.875 (0.808-0.950)
y-intercept (d)	0.420 (0.350-0.500)	0.500 (0.400-0.500)

[1] counting all clearly defined rings beyond the discontinuous zone.

[2] excluding any rings found with 0.07 mm of the nucleus.

daily ring had been formed by approximately 12 hours after swim-up.

The estimate of the slope obtained from regression of mean ring counts by Method 2 and known daily ages significantly ($P<0.01$) differed from one. The slope was estimated to be less than one, which suggests that more than one day was required for the formation of one sagittal ring. The null hypothesis that the y-intercept of the relationship between mean ring counts and daily ages was equal to zero was rejected ($P<0.01$), and the estimate of the y-intercept indicated that the first daily ring had been formed by approximately 12 hours after swim-up.

Disparities and similarities between results of the two counting methods are related to the age of individual fish. Mean ring counts by Method 1 were generally greater for older fish (ages greater than 4 days after swim-up) than those of Method 2; however, nearly identical mean ring counts for younger fish (ages less than or equal to 4 days after swim-up) were obtained by the two counting methods (Fig. 2). The disagreement between the two methods in mean ring counts of older fish is believed to be the result of erroneously assuming a radius of 0.07 mm for smallmouth bass sagittae at the time of swim-up. Measurements to determine the radius of sagittae at swim-up were made from fish sampled at 2200 h of the day of swim-up, about 16 hours

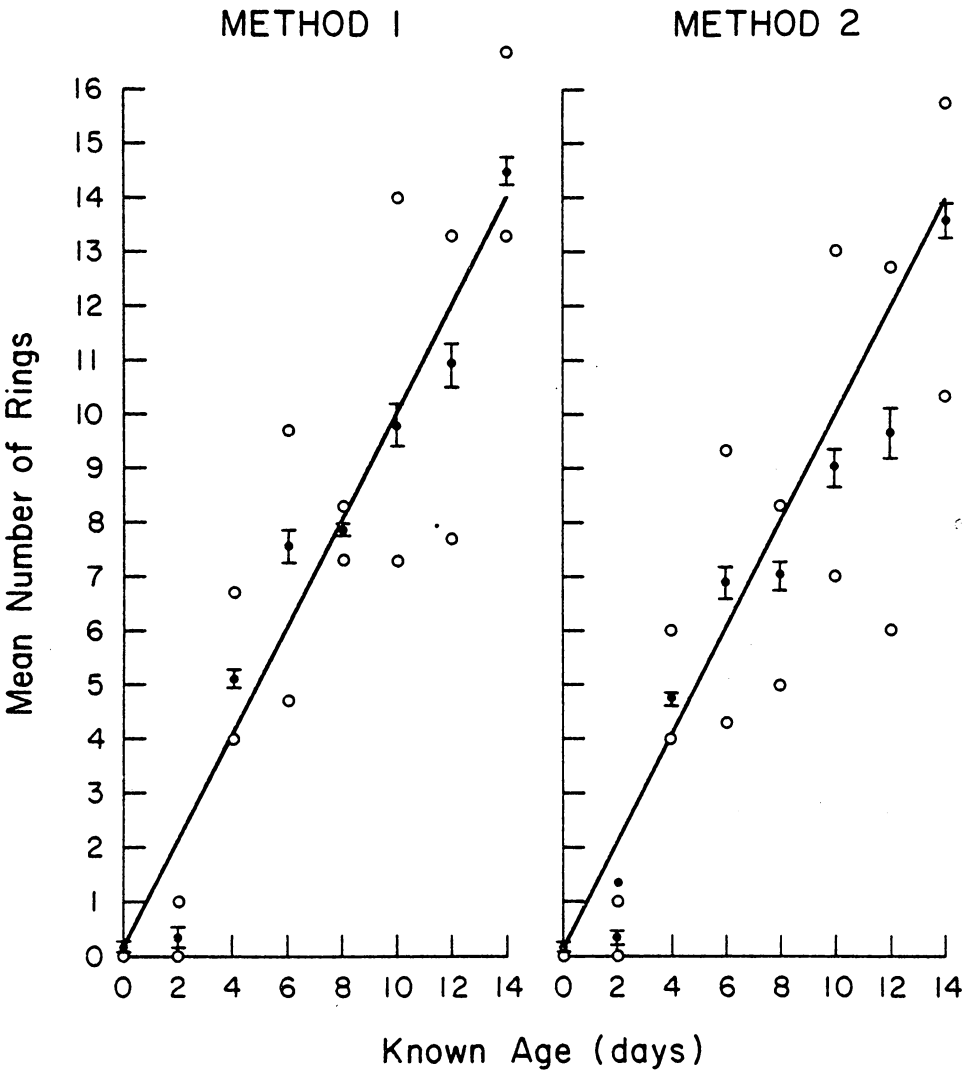


Figure 2. Relationships between mean number of sagittal rings and known age of fish after swim-up for counting methods 1 and 2. Bars represent one standard error from the mean of any sampling day's counts and circles denote the range in mean counts.

after dawn. Given that the first daily proteinaceous layer is laid down at dawn and that the calcareous layer was forming through the rest of the day, my measurements of the radius of sagittae sampled 16 h after dawn would not have been representative of the true radius of sagittae prior to deposition of the first daily ring. During ring counts I frequently observed one ring at approximately 0.06 to 0.07 mm from the nucleus, as would be expected if I had overestimated the radius of sagittae at swim-up. These rings were excluded from ring counts by Method 2 but included in ring counts by Method 1. Since ring counts by both methods were similar for younger fish, this resulted in a lower slope estimate for Method 2 than Method 1. Therefore, the estimate of the slope obtained by Method 1 more accurately reflects the relationship between mean ring counts and known daily ages and supports the assumption that sagittal rings are formed on a daily basis.

It is not known why similar ages were determined for younger fish by the two counting methods. Nonetheless, this situation certainly contributed to the similarity in the estimates of the y-intercepts obtained by the two methods. This was due to the fact that regression lines developed for both methods were restricted to similar mean ring count values for younger fish. Although the difference in the y-intercept estimates is inconsequential, greater confidence

is placed in the estimate obtained from ring counts by Method 1 for the same reasons Method 1's slope estimate is more accurate than that of Method 2.

Ring formation in older fish

Sagittal rings ceased to be reliable indicators of daily ages of young-of-the-year smallmouth bass around early November. Plots of the mean number of rings counted on individual sagittae and collection date showed that around early November a sharp departure from linearity occurred (Fig. 3). This departure is probably due to either greatly reduced growth or lack of growth that affected my ability to distinguish individual sagittal rings or caused resorbtion of sagittal material.

Average deviations in ring counts for the three fish per collection that exhibited the maximum deviations exceeded 5 rings on only one collection date (Fig. 4). This was an odd case where the three fish exhibited maximum deviations of 5, 6, and 10 rings from the mean of their three individual ring counts. Deviations of 5 rings or more occurred in only eleven readings from a total of 436 sagittae used in the analyses. On most collection dates, maximum deviations were between 2 and 3 rings. There was no evidence of a sharp increase in mean deviations as the sampling year progressed and fish got older. This method offered no insight as to when sagittal rings ceased to be

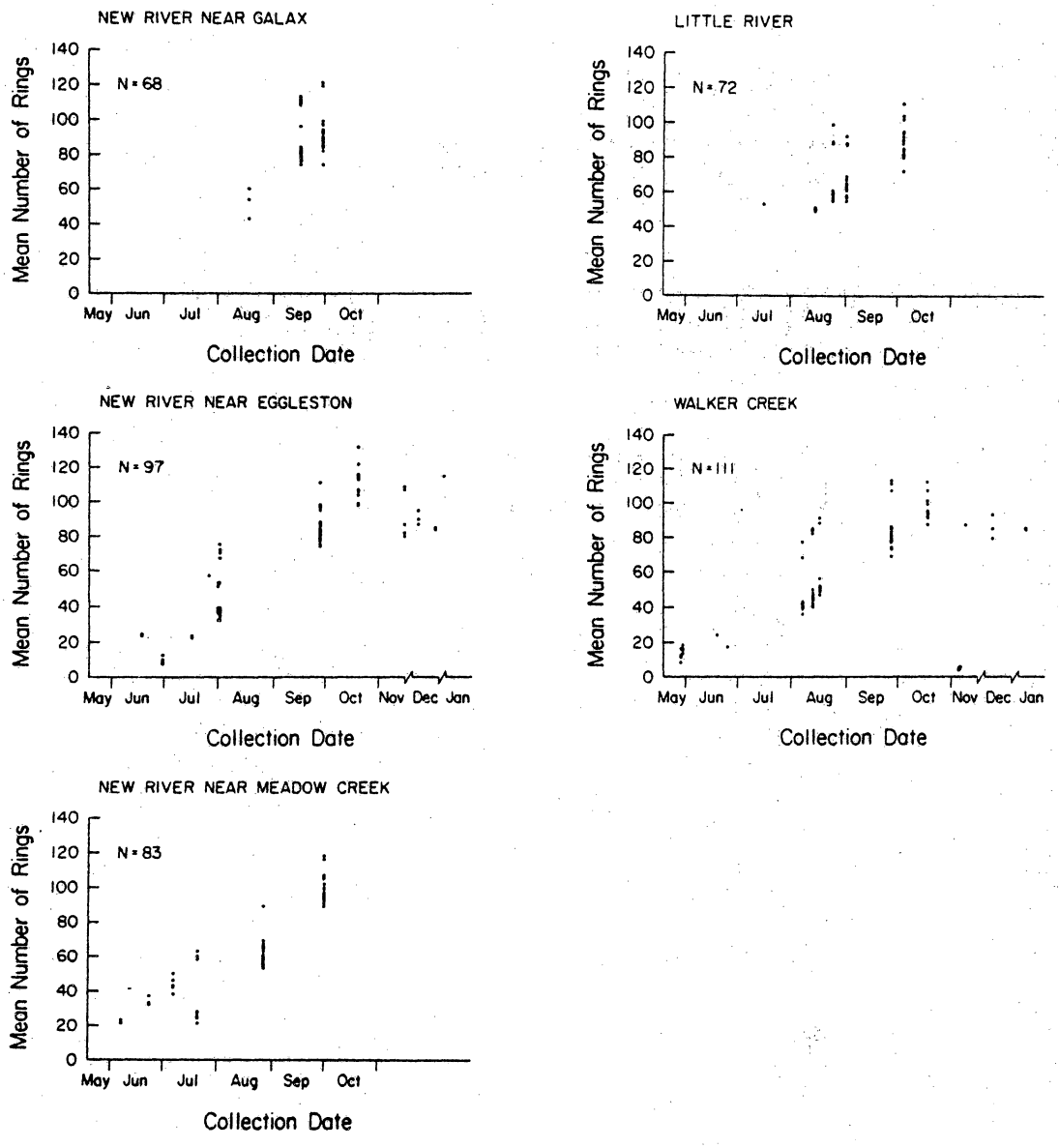


Figure 3. Mean number of rings counted on individual sagitta by collection date and study site.

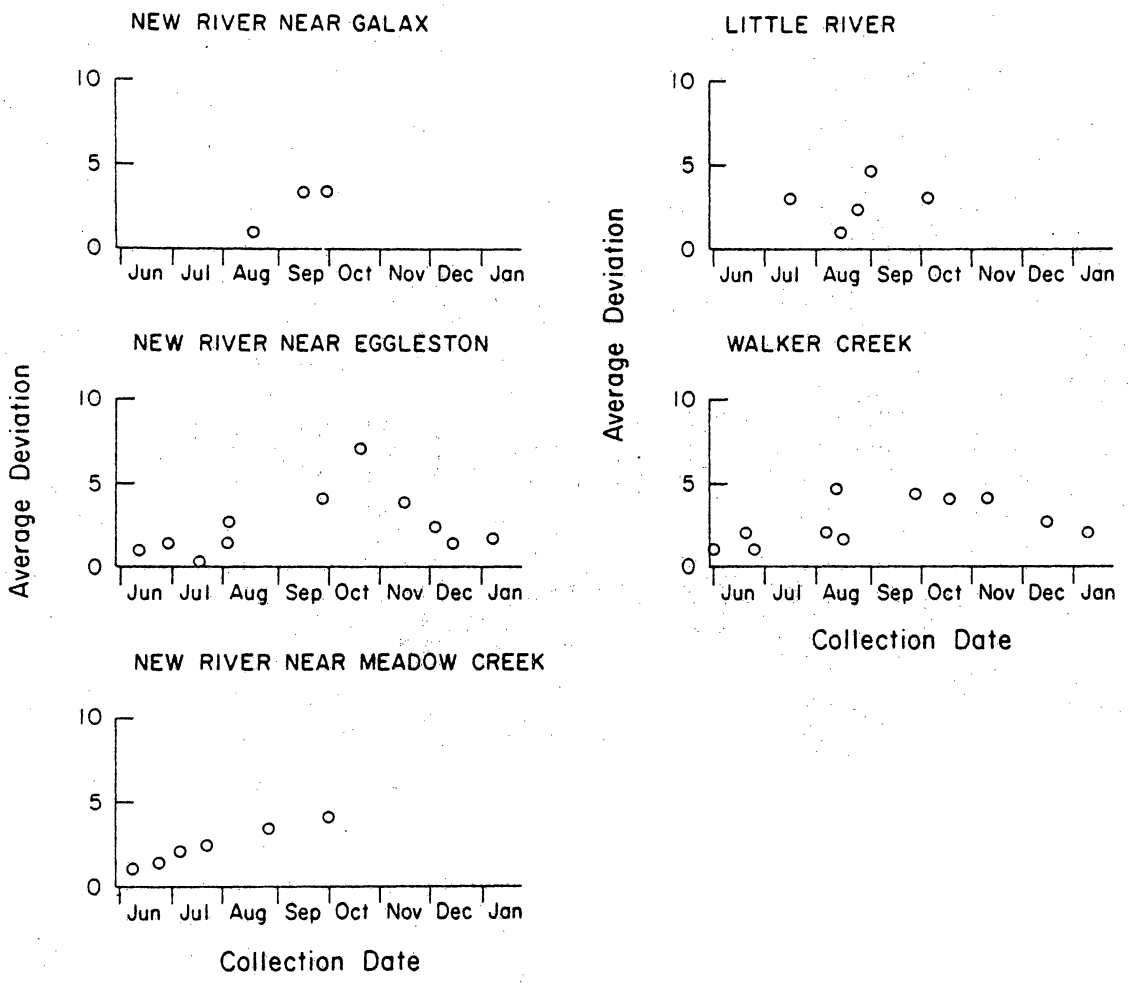


Figure 4. Average deviations in the range of individual sagittal ring counts from their mean for the three fish per collection that exhibited the greatest deviations.

reliable indicators of daily ages. However, it does provide an index of the precision of sagittal ring counts for worst-case conditions.

Crowding of rings in the posterior edge of sagittae was noted during ring counts when reading sagittae from fish collected between late October 1982 and January 1983, again indicating reduced or lack of growth during this time. Individual rings in the posterior edge of sagittae from fish collected in late October could be distinguished by slowly varying the microscope's focus. However, when dealing with sagittae from fish collected in early November through early January, this technique only resulted in viewing intersecting, indistinguishable rings.

Based on plots of mean ring counts and collection dates and microscope observations, age determinations of fish collected after November 1, 1982, were considered unreliable. Such fish were eliminated from any further analyses involving daily ages.

A few age 1+ fish (ages verified from scale samples) were collected and exhibited a distinct annulus on their sagittae. Viewed from the nucleus to the posterior edge of sagittae, annuli were characterized by widely separated rings merging into progressively more crowded rings, terminating in a dark, solid band. Beyond the band, rings were closely crowded and progressively became widely

separated. All age 1+ smallmouth bass collected were excluded from any analyses.

Growth

Instantaneous growth rates of young-of-the-year smallmouth bass (Appendix 4) ranged from 0.018 to 0.064 per day. Growth rates declined as fish got older.

Length-weight relationships (Table 6) developed for young-of-the-year smallmouth bass from the New River drainage were similar among study sites. The slopes of these relationships approximated three, indicating that first year growth of smallmouth bass was isometric.

Von Bertalanffy growth parameters (Table 7) derived from fish collected at the New River near Galax and the Little River were not representative due to collecting most of these fish during a relatively brief (one to two month) time period when they differed only slightly in length or age. This resulted in an approximate linear relationship between length and age that extended the area over which the von Bertalanffy growth curve was developed and contributed to the extremely wide confidence intervals on the parameter estimates. Fish from the New River near Eggleston, the New River near Meadow Creek, and Walker Creek were collected more uniformly over time and represented a wide range of lengths and ages. Consequently, von Bertalanffy parameters were probably representative of population growth at these

Table 6. Length-weight relationships (base 10 logarithm) for young-of-the-year smallmouth bass in the New River drainage.

Study site	Estimated regression line
New River near Galax	log W (g) = -4.73 + 2.92 log L (mm)
New River near Eggleston	log W (g) = -4.62 + 2.85 log L (mm)
New River near Meadow Creek	log W (g) = -4.79 + 2.92 log L (mm)
Little River	log W (g) = -4.92 + 3.02 log L (mm)
Walker Creek	log W (g) = -4.56 + 2.81 log L (mm)

Table 7. Von Bertalanffy growth parameter estimates with 95% confidence intervals (in parentheses) for young-of-the-year smallmouth bass in the New River drainage.

Study site	N	Li	k	to
New River near Galax[1]	290	(-843,1423)	0.003 (-0.013,0.019)	-12 (-82,58)
New River near Eggleston	98	(86,110)	0.016 (0.011,0.021)	3 (0,7)
New River near Meadow Creek	129	(92,168)	0.011 (0.005,0.017)	0 (-8,7)
Little River[1]	113	(-10,236)	0.011 (-0.014,0.035)	5 (-40,51)
Walker Creek	102	(84,121)	0.012 (0.008,0.017)	0 (-4,4)

[1] not representative due to a limited range of ages.

study sites.

Comparisons of the relationships between instantaneous growth rates and daily ages of young-of-the-year smallmouth bass spawned early and late in the season at the New River near Meadow Creek and Walker Creek showed considerable overlap in the confidence intervals of the slopes, but not in the y-intercepts (Table 8). The similarity between slope estimates indicates that instantaneous growth rates of both early and late spawned fish declined in the same manner as fish got older (Fig. 5).

The y-intercepts of smallmouth bass spawned early in the season were less than those of smallmouth bass spawned later. Therefore, growth rates of early-spawned fish were initially less than those of late-spawned fish. This suggests that young-of-the-year spawned early in the season encountered conditions less conducive to growth than those spawned later. However, plots of length by age from swim-up seemed to indicate that by the end of the first growing season, both early and late-spawned fish were approximately the same size in Walker Creek (Fig. 6).

Spawning time and duration

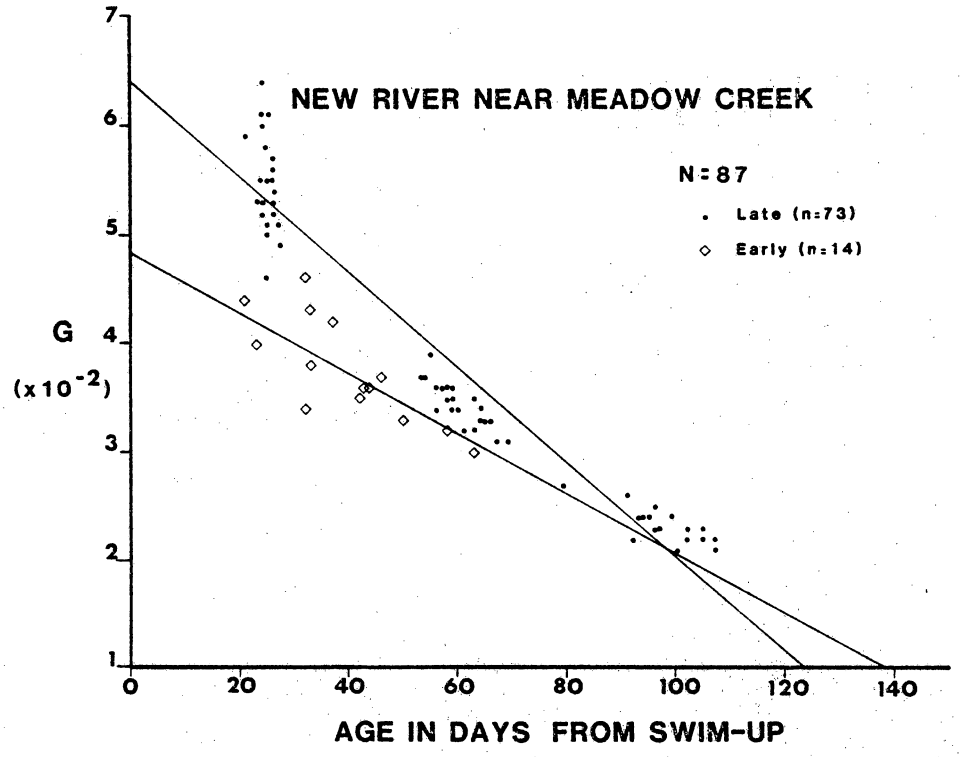
Smallmouth bass spawned in the New River drainage between 29 April and 20 July, 1982, with most spawning activity in mid-June (Figs. 7-11). Water temperatures on days when spawning occurred ranged from 12.5 C to 23.5 C.

Table 8. Estimates of the slope and y-intercept with 95% confidence intervals (in parentheses) for the relationship between instantaneous growth rates (G) and daily age from swim-up for fish spawned early and late in the season.

	New River near Meadow Creek			
	Early		Late	
slope	-2.8	(-4.4,-1.9)	-4.4	(-4.8,-4.0)
y-intercept (G)	0.048	(0.047,0.050)	0.064	(0.063,0.065)
R[1]		-0.81		-0.96

	Walker Creek			
	Early		Late	
slope	-2.5	(-6.7,-1.4)	-3.0	(-3.2,-2.8)
y-intercept (G)	0.042	(0.039,0.046)	0.050	(0.050,0.050)
R		-0.90		-0.92

[1] Spearman's rank correlation coefficient.



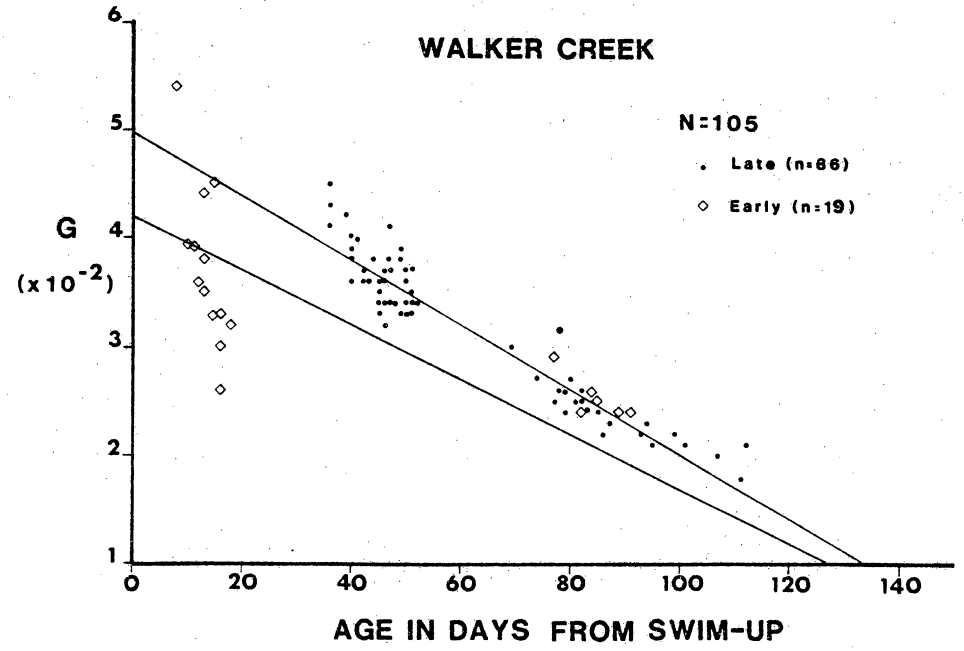


Figure 5. Instantaneous growth rates (G) and age in days after swim-up for young-of-the-year smallmouth bass collected from the New River near Meadow Creek and Walker Creek.

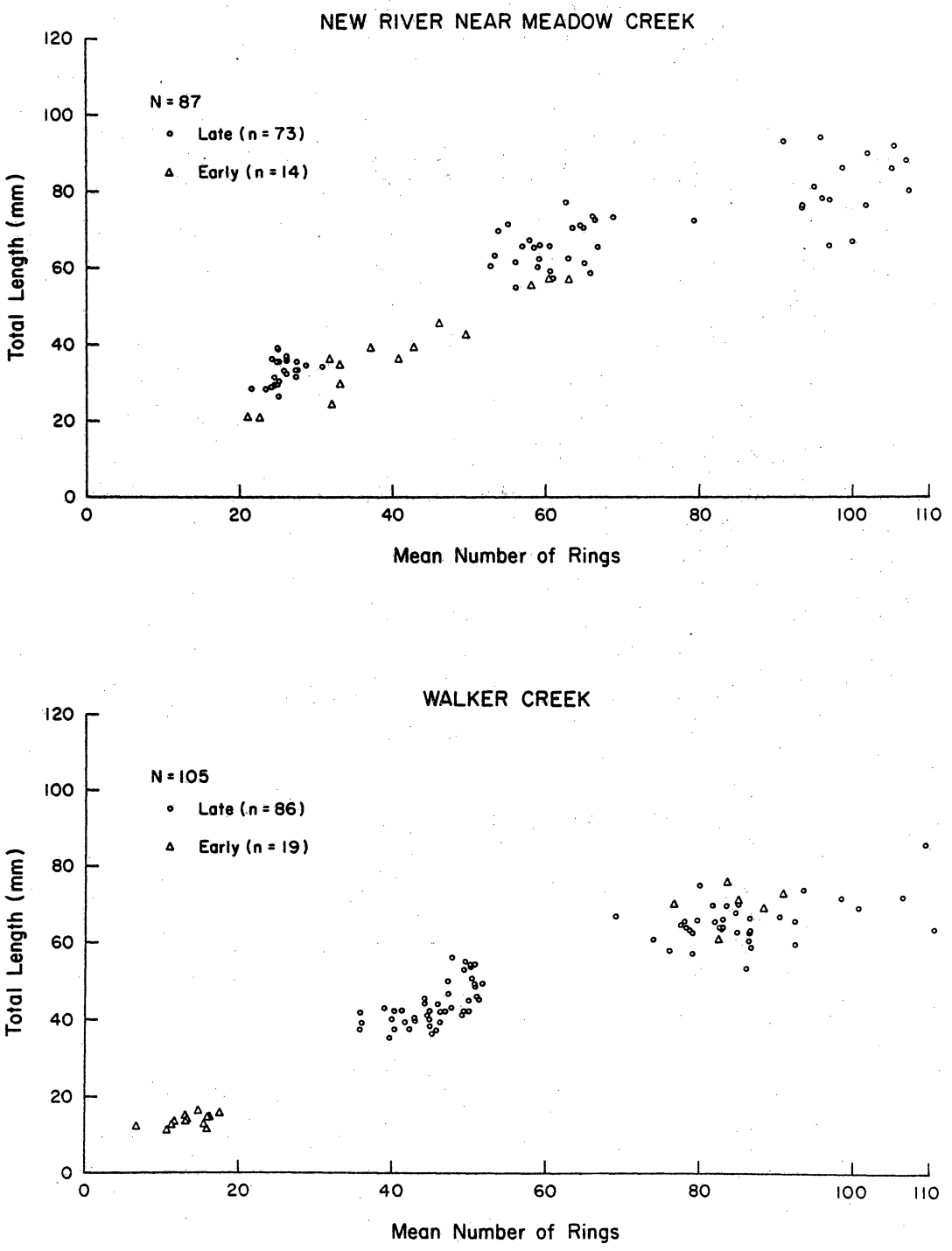


Figure 6. Total length and mean number of sagittal rings of young-of-the-year smallmouth bass collected from the New River near Meadow Creek and Walker Creek.

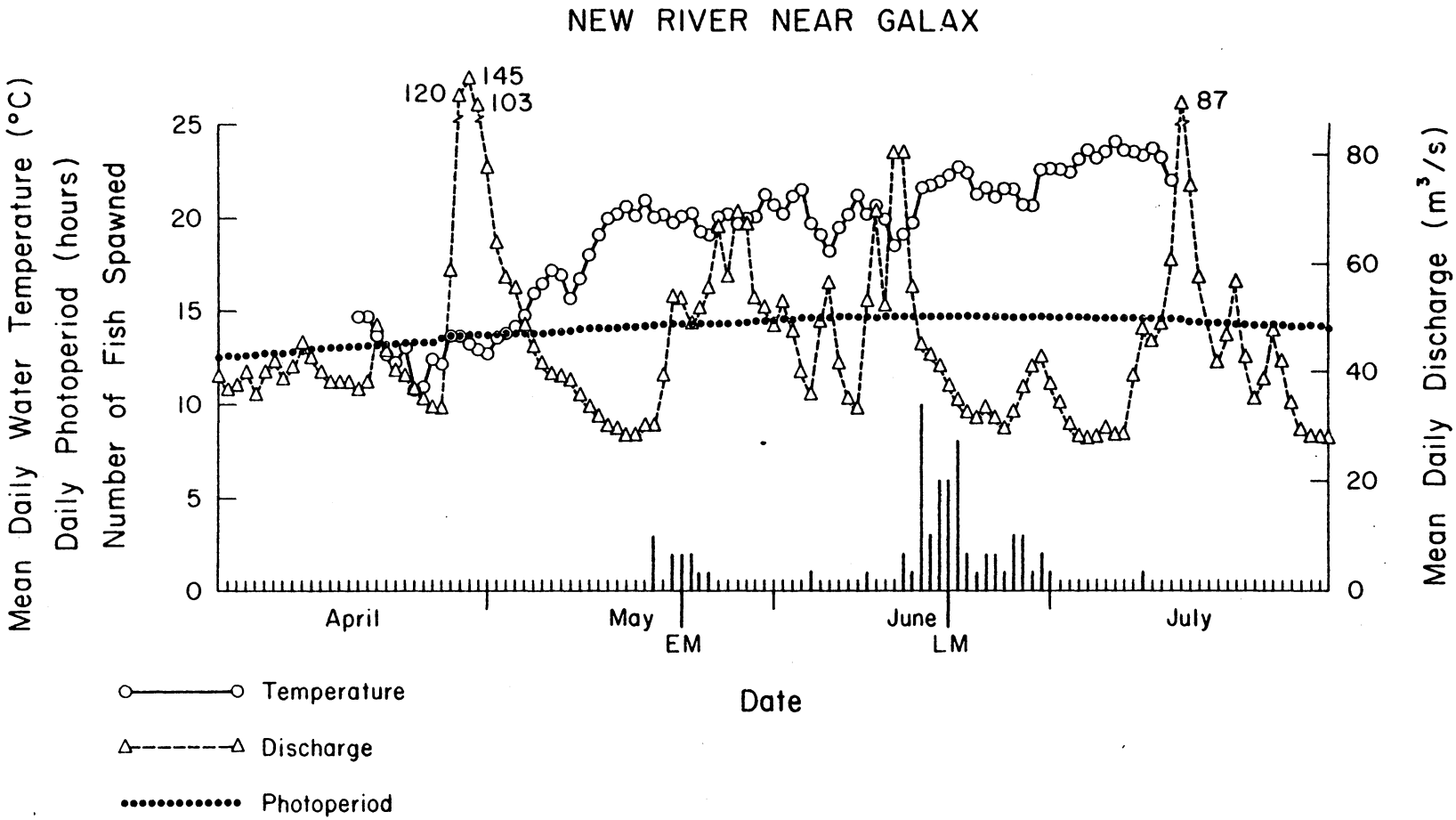


Figure 7. Photoperiod, temperature, and discharge profiles of the New River near Galax and number of collected fish spawned by date. EM indicates the median spawning date of the early spawning period and LM indicates the median spawning date of the late spawning period.

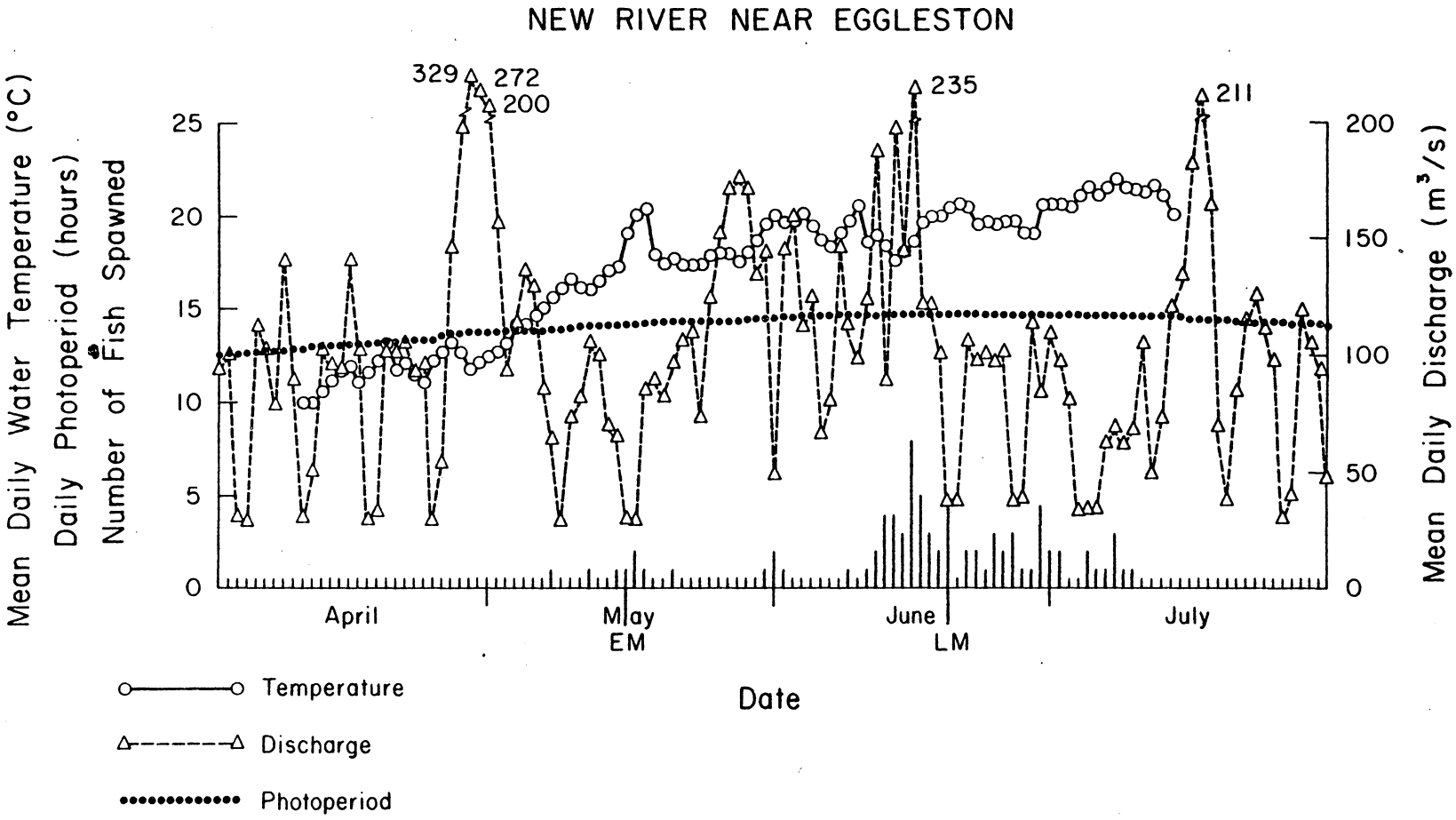


Figure 8. Photoperiod, temperature, and discharge profiles of the New River near Eggleston and number of collected fish spawned by date. EM indicates the median spawning date of the early spawning period and LM indicates the median spawning date of the late spawning period.

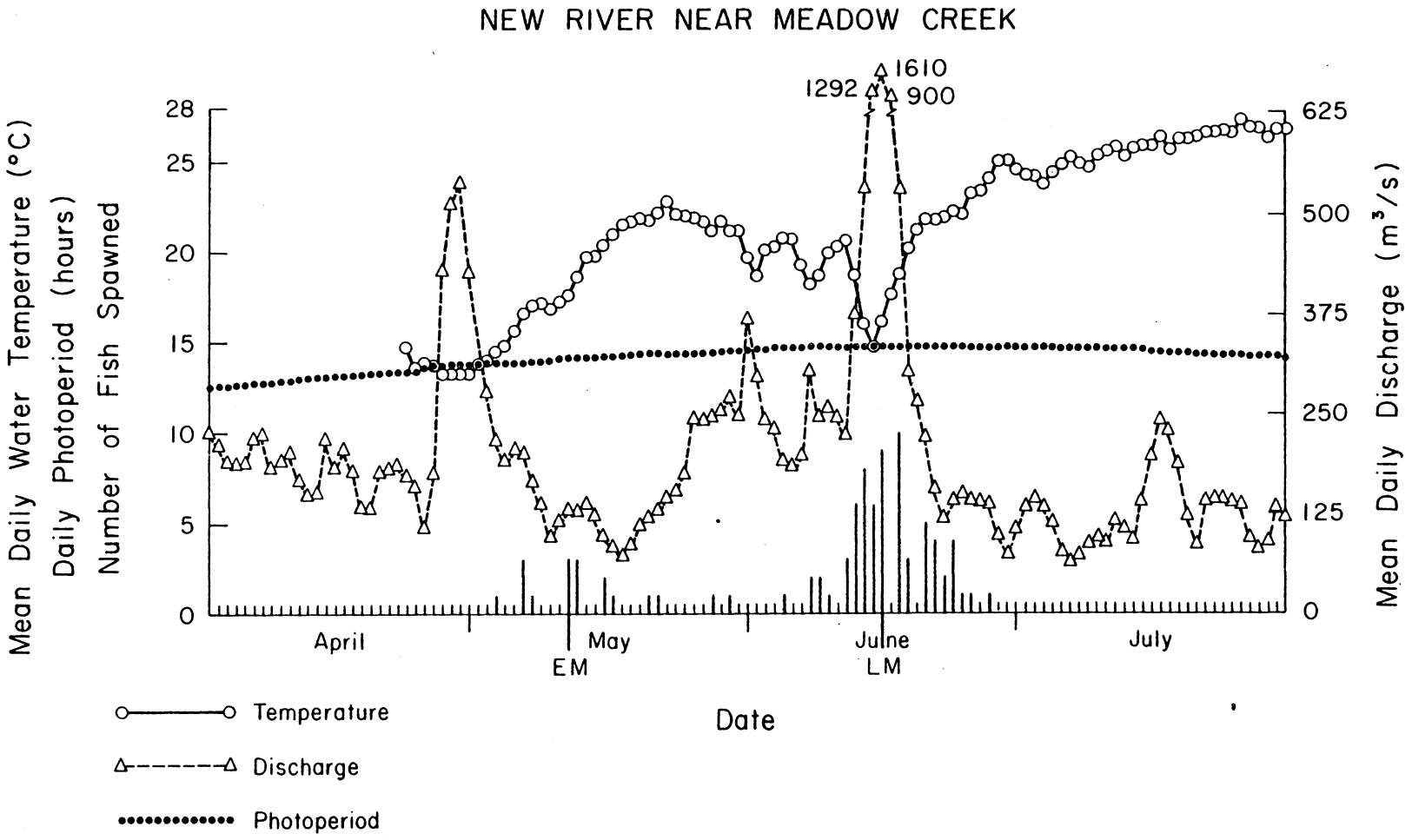


Figure 9. Photoperiod, temperature, and discharge profiles of the New River near Meadow Creek and number of collected fish spawned by date. EM indicates the median spawning date of the early spawning period and LM indicates the median spawning date of the late spawning period.

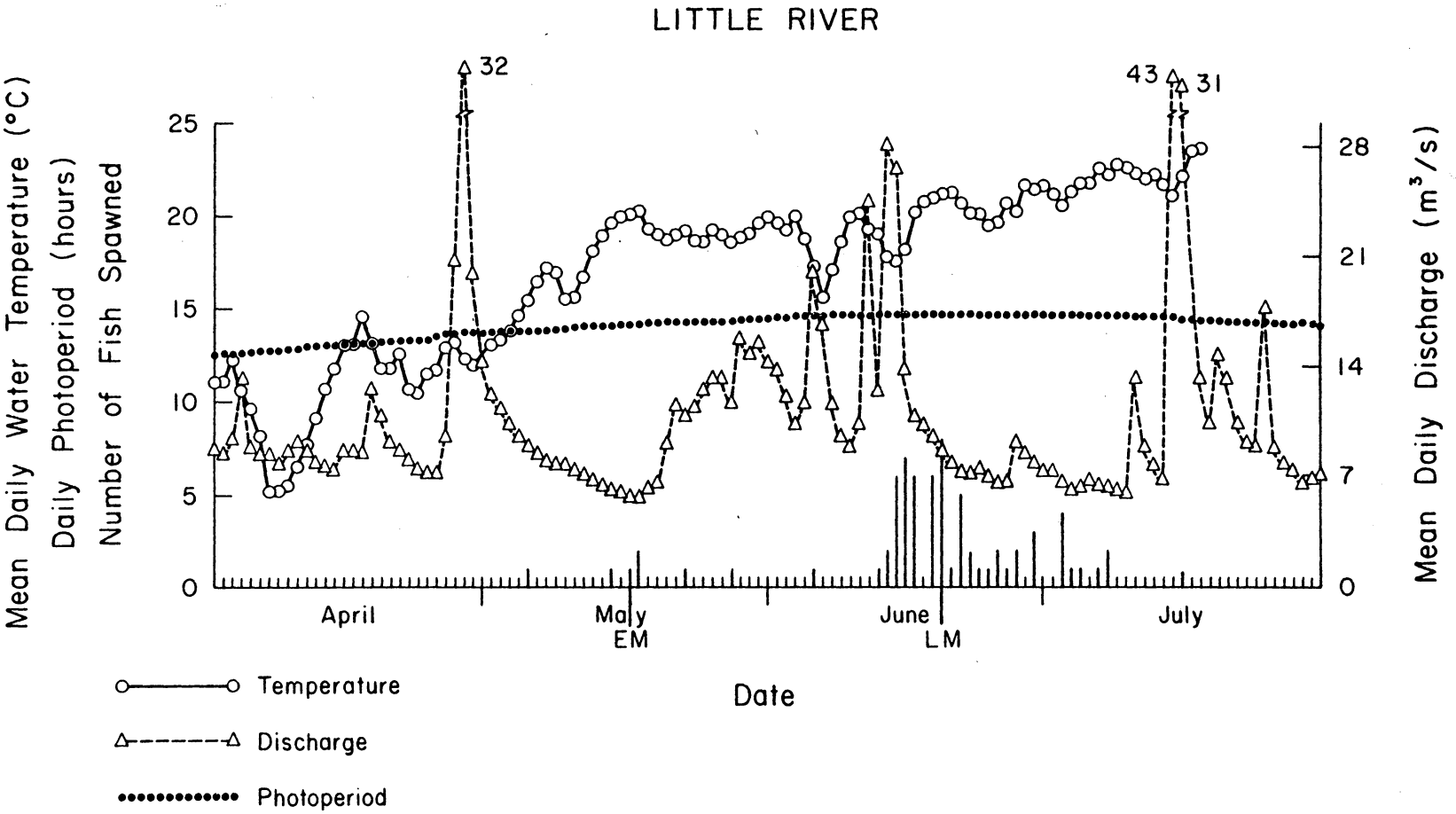


Figure 10. Photoperiod, temperature, and discharge profiles of the Little River and number of collected fish spawned by date. EM indicates the median spawning date of the early spawning period and LM indicates the median spawning date of the late spawning period.

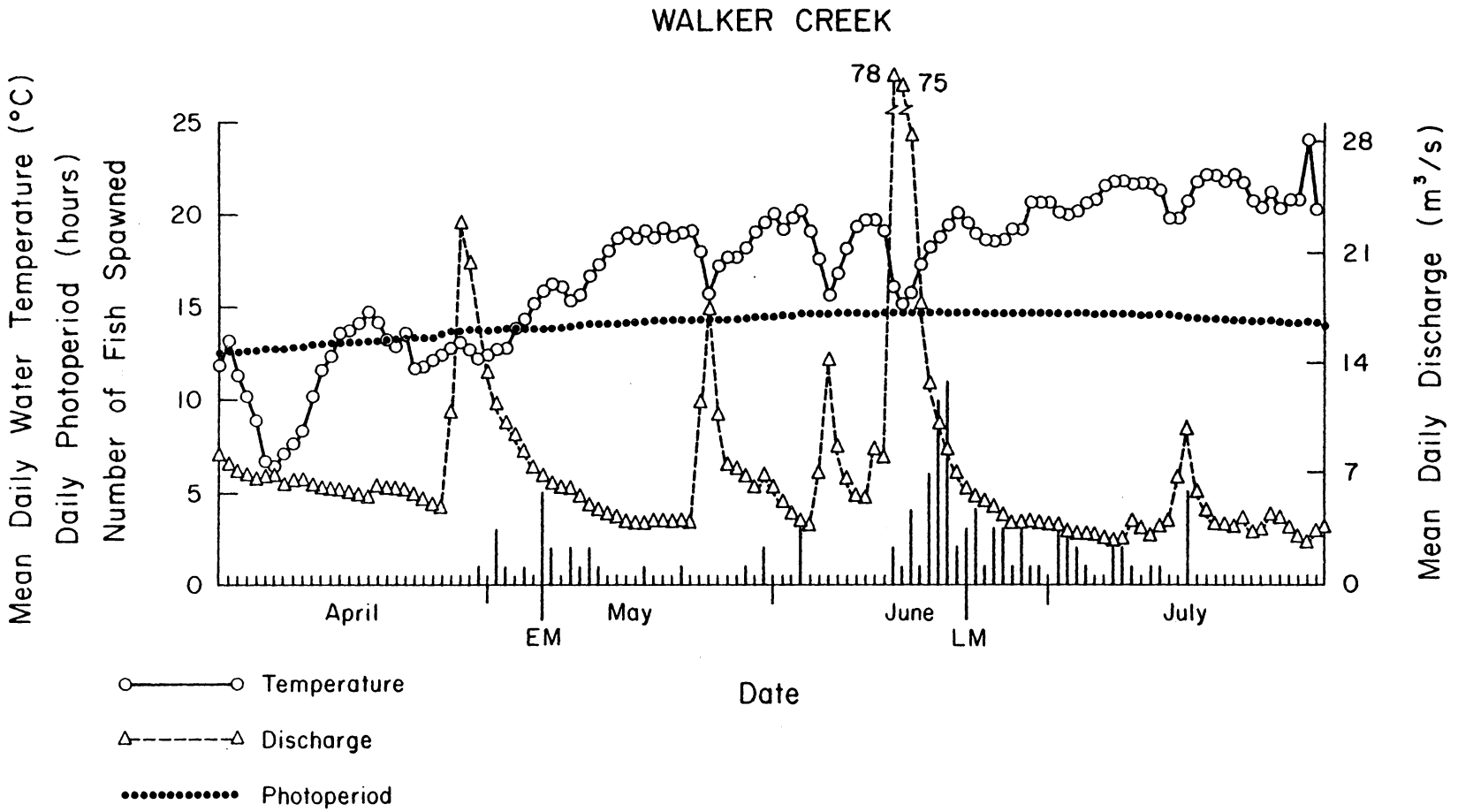


Figure 11. Photoperiod, temperature, and discharge profiles of Walker Creek and number of collected fish spawned by date. EM indicates the median spawning date of the early spawning period and LM indicates the median spawning date of the late spawning period.

The spawning season was divided into two distinct spawning periods at each study site, as indicated by otolith ages. Median spawning dates for young-of-the-year spawned early in the season varied among study sites and ranged from 6 May to 21 May, a 16-day interval. The low numbers of early-spawned fish collected may have contributed to the wide range in median spawning dates for this spawning period. Median spawning dates for late-spawned fish were very similar among study sites, ranging from 15 June to 21 June, a 7-day interval. It appeared that a major flooding event in mid-June was responsible for delineating the two spawning periods at most study sites, with early spawning activities ceasing at the onset of flooding and late spawning activities beginning when water levels began to recede (Figs. 7-11).

Frequency distributions of spawning dates among most study sites did not differ greatly (Table 9). Only one study site, the New River near Meadow Creek, differed significantly ($P<0.05$) from other study sites. Probability levels of less than 0.01 were consistently exhibited in comparisons of the New River near Meadow Creek's frequency distribution of spawning dates with those of other study sites. The late spawning period of the New River near Meadow Creek study site occurred slightly earlier in the year than at most other study sites, and spawning at this

Table 9. Probabilities (P) of Kolmorogov-Smirnov tests of the null hypothesis that the spawning date frequency distributions between study sites do not differ.

Study sites	New River			
	Eggleston	Meadow Creek	Little River	Walker Creek
New River				
Galax	0.13	<0.01	0.66	0.09
Eggleston		<0.01	0.45	0.20
Meadow Creek			<0.01	<0.01
Little River				0.19

study site was sharply curtailed in late June while at other study sites spawning continued intermittently into July (Figs. 7-11).

Relative importance of physical variables

Daily conditions approximately one month prior to the spawning season at each study site were generally very dissimilar from those of the spawning season (Tables 10-14). Mean photoperiod and temperature variables were generally lower for the group of days prior to the spawning season than for the groups of days when spawning did and did not occur during spawning season. However, discharge variables and all variables' rates of change did not appear to differ greatly. Daily conditions when spawning did and did not occur during the spawning season at each study site did not differ greatly in terms of group mean photoperiod, temperature, and discharge variables nor in their rates of change. This suggests that spawning on any particular day of the spawning season was determined by very subtle differences in the physical variables studied or other factors not investigated.

Results of initial trial runs of stepwise discriminant analysis to assess the relative importance of photoperiod, temperature, and discharge variables in distinguishing between the three groups of daily conditions indicated that the number of hours between sunrise and sunset was a very

Table 10. Group means and standard deviations (S) of the New River near Galax study site's photoperiod, temperature, and discharge variables. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

	Group 1			Group 2			Group 3		
Variable*	N	Mean	S	N	Mean	S	N	Mean	S
Photo	30	13.76	0.29	26	14.62	0.16	28	14.59	0.10
d Photo	30	0.03	0.01	26	0.00	0.16	28	0.00	0.02
Temp	30	15.33	3.08	26	21.13	1.22	28	21.23	1.69
d Temp	30	0.21	0.88	26	-0.03	0.83	28	0.08	0.73
Min	30	13.62	2.84	26	19.90	1.17	28	19.78	1.51
d Min	30	0.17	1.18	26	0.04	0.72	28	0.09	0.80
Max	30	17.38	3.48	26	22.88	1.54	28	22.89	2.24
d Max	30	0.28	1.28	26	0.10	1.21	28	0.09	1.38
D-days	30	7.30	12.30	26	195.00	86.28	28	191.39	103.23
d D-days	30	1.43	2.10	26	6.15	1.32	28	6.07	1.68
pFlow	30	1.16	0.65	26	1.00	0.27	28	1.06	0.35
d pFlow	30	0.00	0.38	26	0.00	0.18	28	0.02	0.24
Flow	30	49.63	27.75	26	42.72	11.48	28	45.66	1.50

*Variable name descriptions

Photo = the number of hours between sunrise and sunset (h).
d Photo = the rate of change in the number of hours between sunrise and sunset.
Temp = mean daily water temperature (C).
d Temp = the rate of change in mean daily water temperature.
Min = minimum daily water temperature (C).
d Min = the rate of change in minimum daily water temperature.
Max = maximum daily water temperature (C).
d Max = the rate of change in maximum daily water temperature.
D-days = the daily accumulation of degree-days greater than 15 C.
d D-days = the rate of change in the daily accumulation of degree-days greater than 15 C.
p Flow = the ratio of mean daily discharge and water year 1982 mean annual discharge.
d pFlow = the rate of change in the ratio of mean daily discharge and water year 1982 mean annual discharge.
Flow = mean daily discharge (m^3/s).

Table 11. Group means and standard deviations (S) of the New River near Eggleston study site's photoperiod, temperature, and discharge variables. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

	Group 1			Group 2			Group 3	
Variable*	N	Mean	S	N	Mean	S	N	Mean	S
Photo	27	13.44	0.29	38	14.58	0.22	26	14.42	0.02
d Photo	27	0.04	0.01	38	0.00	0.02	26	0.02	0.02
Temp	27	12.32	1.29	38	19.67	1.49	26	18.42	1.47
d Temp	27	0.19	0.60	38	0.15	0.76	26	0.02	0.70
Min	27	11.54	1.43	38	18.51	1.43	26	17.65	1.32
d Min	27	0.20	0.82	38	0.17	0.85	26	0.00	0.50
Max	27	13.07	1.43	38	21.16	1.87	26	19.44	1.80
d Max	27	0.18	0.89	38	0.18	1.13	26	0.00	1.05
D-days	27	0.00	0.00	38	140.24	78.46	26	68.46	59.50
d D-days	27	0.00	0.00	38	4.74	1.55	26	3.38	1.55
pFlow	27	1.21	0.74	38	0.99	0.52	26	1.09	0.45
d pFlow	27	0.00	0.55	38	0.02	0.54	26	-0.02	0.33
Flow	27	114.74	70.00	38	95.89	47.24	26	103.16	42.31

*Refer to Table 10. for variable name descriptions.

Table 12. Group means and standard deviations (S) of the New River near Meadow Creek study site's photoperiod, temperature, and discharge variables. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

	Group 1			Group 2			Group 3		
Variable*	N	Mean	S	N	Mean	S	N	Mean	S
Photo	10	13.60	0.10	29	14.50	0.30	27	14.37	0.28
d Photo	10	0.04	0.01	29	0.01	0.01	27	0.02	0.01
Temp	10	13.69	0.49	29	19.73	2.55	27	20.02	2.21
d Temp	10	-0.05	0.40	29	0.21	0.95	27	0.19	0.68
Min	10	12.90	0.70	29	18.71	2.62	27	19.13	2.40
d Min	10	-0.10	0.97	29	0.21	1.03	27	0.13	0.95
Max	10	14.40	0.39	29	20.74	2.53	27	20.94	2.18
d Max	10	-0.05	0.28	29	0.22	1.24	27	0.15	0.98
D-days	10	0.00	0.00	29	145.03	88.78	27	100.81	72.94
d D-days	10	0.00	0.00	29	4.79	2.46	27	5.00	2.13
pFlow	10	1.41	0.72	29	1.39	1.61	27	0.91	0.44
d pFlow	10	0.04	0.49	29	0.02	0.98	27	-0.05	0.38
Flow	10	311.64	157.86	29	307.37	356.04	27	201.81	96.85

*Refer to Table 10. for variable name descriptions.

Table 13. Group means and standard deviations (S) of the Little River study site's photoperiod, temperature, and discharge variables. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

	Group 1			Group 2			Group 3		
Variable*	N	Mean	S	N	Mean	S	N	Mean	S
Photo	29	13.29	0.32	30	14.58	0.22	36	14.41	0.26
d Photo	29	0.04	0.01	30	0.00	0.02	36	0.02	0.02
Temp	29	11.01	2.77	30	20.15	1.66	36	18.99	1.68
d Temp	29	0.12	1.14	30	0.03	0.70	36	0.21	0.79
Min	29	9.67	2.90	30	19.08	2.64	36	17.65	1.87
d Min	29	0.16	1.47	30	0.07	0.90	36	0.21	0.91
Max	29	12.33	2.84	30	21.38	1.70	36	20.53	2.28
d Max	29	0.10	1.31	30	0.00	0.93	36	0.17	1.12
D-days	29	0.00	0.00	30	171.03	82.39	36	90.69	72.66
d D-days	29	0.00	0.00	30	5.17	1.66	36	4.03	1.66
pFlow	29	1.16	0.59	30	1.05	0.61	36	1.13	0.42
d pFlow	29	-0.01	0.47	30	-0.04	0.50	36	0.02	0.31
Flow	29	10.32	5.23	30	9.34	5.47	36	10.12	3.76

*Refer to Table 10. for variable name descriptions.

Table 14. Group means and standard deviations (S) of the Walker Creek study site's photoperiod, temperaure, and discharge variables. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

	Group 1			Group 2			Group 3	
Variable*	N	Mean	S	N	Mean	S	N	Mean	S
Photo	30	13.00	0.34	43	14.46	0.34	40	14.42	0.26
d Photo	30	0.04	0.01	43	0.01	0.02	40	0.01	0.02
Temp	30	11.48	2.34	43	18.47	2.60	40	18.77	2.19
d Temp	30	0.13	1.08	43	0.17	0.75	40	0.23	1.33
Min	30	10.17	2.51	43	17.06	2.66	40	17.48	2.22
d Min	30	0.15	1.54	43	0.16	0.92	40	0.05	0.85
Max	30	12.75	2.27	43	19.90	2.77	40	20.01	2.33
d Max	30	0.01	1.18	43	0.24	0.92	40	-0.01	1.36
D-days	30	0.00	0.00	43	125.35	90.67	40	107.48	96.90
d D-days	30	0.00	0.00	43	3.65	2.33	40	3.90	2.05
pFlow	30	0.87	0.46	43	1.15	1.84	40	0.73	0.38
d pFlow	30	0.04	0.29	43	-0.03	1.56	40	-0.02	0.32
Flow	30	7.32	3.91	43	9.69	15.51	40	6.15	3.20

*Refer to Table 10. for variable name descriptions.

important factor at most study sites in differentiating between the three groups (Table 15). It is believed that the importance of photoperiod was an artifact of the analyses due to relatively minor changes in photoperiod variables on a day-to-day basis compared to the daily changes in temperature and discharge variables. This was especially true on days centered about the median dates of spawning for the late spawning period. These days coincided with the summer solstice, when for nine consecutive days there was no measured change in the values of photoperiod variables. Therefore, a fairly large portion of the days when spawning did occur was associated with a constant photoperiod value while temperature and discharge variable values were fluctuating. As such, the number of hours between sunrise and sunset was the variable which offered the most utility to the stepwise discriminant analyses in differentiating between the three groups of daily conditions.

It hardly seems possible that smallmouth bass in these streams would use the number of hours between sunrise and sunset as their primary environmental cue for spawning, given the rapidly fluctuating temperature and discharge conditions of the New River drainage. Further, photoperiod variables cannot account for the observed interruption of spawning during the June flood. Therefore, the two

Table 15. Variables identified by stepwise discriminant analyses as important sources of variation between daily conditions prior to the spawning season and daily conditions when spawning did and did not occur during the spawning season.

Study site	Variable*	R^2	P
New River near Galax	Photo	0.80	<0.01
	d D-days	0.23	<0.01
	Max	0.08	0.04
New River near Eggleston	Temp	0.84	<0.01
	D-days	0.24	<0.01
	Photo	0.10	0.01
	d Temp	0.06	0.08
	Flow	0.05	0.13
New River near Meadow Creek	Photo	0.56	<0.01
	D-days	0.48	<0.01
	p Flow	0.17	<0.01
	d Photo	0.17	0.07
Little River	Photo	0.81	<0.01
	d D-days	0.30	<0.01
	D-days	0.16	<0.01
Walker Creek	Photo	0.79	<0.01
	Max	0.08	0.01
	Min	0.06	0.04
	D-days	0.04	0.08

*Refer to Table 10. for variable name descriptions.

photoperiod variables initially included in the stepwise discriminant analyses were considered spurious and excluded from further analyses.

Stepwise discriminant analyses of the relative importance of water temperature and discharge variables in distinguishing between the three groups of daily stream conditions indicated different variables were important in determining when spawning occurred at different study sites (Table 16). The relative importance of variables in distinguishing between the three groups of daily stream conditions did not appreciably change when variables were lagged one and two days at any study site, indicating that any one day's stream conditions were highly dependent on what conditions were like one and two days previously.

Results from pooling data from the three New River study sites (Table 17), the two tributary study sites (Table 18), and all study sites (Table 19) varied, but when examined in relation to results from individual study sites, certain generalities became apparent.

Mean daily water temperature accounted for greater than 50% of the variation among the three groups in fifteen of the twenty-four different analyses. Minimum daily water temperature was also implicated as an important variable, accounting for greater than 50% of the variation among groups in six analyses. Maximum daily water temperature

Table 16. Variables identified by stepwise discriminant analyses as important sources of variation between daily conditions prior to the spawning season and daily conditions when spawning did and did not occur during the spawning season.

New River near Galax			New River near Eggleston			New River near Meadow Creek			Little River			Walker Creek		
Variable*	R^2	P	Variable	R^2	P	Variable	R^2	P	Variable	R^2	P	Variable	R^2	P
						No lag								
Min	0.69	<0.01	Temp	0.84	<0.01	Max	0.54	<0.01	Temp	0.78	<0.01	Temp	0.64	<0.01
d Min	0.10	0.01	D-days	0.24	<0.01	d D-days	0.32	<0.01	D-days	0.15	<0.01	pFlow	0.09	<0.01
D-days	0.09	0.02	d Temp	0.10	0.01	Temp	0.21	<0.01	d D-days	0.06	0.05	D-days	0.07	0.02
Max	0.08	0.04				Flow	0.12	0.02	d Temp	0.05	0.09	d pFlow	0.04	0.13
Temp	0.08	0.05				D-days	0.08	0.08						
d Max	0.07	0.07				Min	0.07	0.14						
						One day lag								
Min	0.72	<0.01	Temp	0.79	<0.01	Max	0.48	<0.01	Temp	0.79	<0.01	Temp	0.62	<0.01
d Min	0.12	<0.01	D-days	0.24	<0.01	d D-days	0.25	<0.01	D-days	0.14	<0.01	Flow	0.11	<0.01
d D-days	0.09	0.02	d D-days	0.11	<0.01	Temp	0.19	<0.01				D-days	0.07	0.02
d Max	0.08	0.05	d Min	0.10	0.01	D-days	0.11	0,03				d pFlow	0.05	0.07
Max	0.07	0.07	d Temp	0.08	0.02									
			Min	0.07	0.06									
						Two day lag								
Min	0.75	<0.01	Temp	0.81	<0.01	Max	0.43	<0.01	Temp	0.80	<0.01	Temp	0.61	<0.01
d Min	0.12	<0.01	d D-days	0.35	<0.01	d D-days	0.25	<0.01	D-days	0.14	<0.01	Flow	0.08	0.01
Max	0.07	0.06	D-days	0.17	<0.01	Temp	0,15	<0.01	Max	0.08	0.02	D-days	0.08	0.01
Temp	0.06	0.10	Min	0.10	0.01	D-days	0.09	0.06				d pFlow	0.04	0.14
			d Min	0.08	0.03									

*Refer to Table 10. for variable name descriptions.

Table 17. Results of applying pooled New River study site temperature and discharge variables to stepwise discriminant analysis.

No lag			One day lag			Two day lag		
Variable*	R^2	P	Variable	R^2	P	Variable	R^2	P
Min	0.65	<0.01	Min	0.65	<0.01	Min	0.65	<0.01
d D-days	0.07	<0.01	d D-days	0.08	<0.01	d D-days	0.07	<0.01
D-days	0.06	<0.01	D-days	0.06	<0.01	D-days	0.07	<0.01
d Min	0.05	<0.01	d Min	0.04	<0.01	d Min	0.05	<0.01
Flow	0.02	0.07	d Temp	0.02	0.05	Flow	0.02	0.07
d Temp	0.02	0.09				d Temp	0.02	0.09

*Refer to Table 10. for variable name descriptions.

Table 18. Results of applying pooled tributary study site temperature and discharge variables to stepwise discriminant analysis.

No lag			One day lag			Two day lag		
Variable	R^2	P	Variable	R^2	P	Variable	R^2	P
Temp	0.70	<0.01	Temp	0.69	<0.01	Temp	0.68	<0.01
D-days	0.08	<0.01	D-days	0.09	<0.01	D-days	0.09	<0.01
pFlow	0.05	<0.01	pFlow	0.06	<0.01	pFlow	0.08	<0.01
Flow	0.04	0.02	Flow	0.04	0.02	Flow	0.05	<0.01
d D-days	0.02	0.10				d pFlow	0.04	0.01
						d Min	0.02	0.12

*Refer to Table 10. for variable name descriptions.

Table 19. Results of applying all study site's pooled temperature and discharge variables to stepwise discriminant analysis.

No lag			One day lag			Two day lag		
Variable*	R^2	P	Variable	R^2	P	Variable	R^2	P
Temp	0.63	<0.01	Temp	0.63	<0.01	Temp	0.62	<0.01
D-days	0.06	<0.01	D-days	0.05	<0.01	D-days	0.06	<0.01
pFlow	0.03	<0.01	pFlow	0.03	<0.01	pFlow	0.04	<0.01
Max	0.02	0.01	Max	0.02	0.02	Max	0.02	<0.01
d Min	0.02	0.03	d pFlow	0.01	0.08	d D-days	0.01	0.04
			d Min	0.01	0.10	d Min	0.01	0.10

*Refer to Table 10. for variable name descriptions.

accounted for greater than 50% of the variation among the three groups in only one analysis (New River near Meadow Creek; no lag). Since maximum daily water temperature is correlated with both mean daily water temperature and minimum daily water temperature (Appendix 5), it was decided to select mean daily water temperature and minimum daily water temperature to help develop the discriminant functions. The rate of change in the daily accumulation of degree-days greater than 15 C accounted for greater than 25% of the variation among groups in four analyses. The daily accumulation of degree-days greater than 15 C accounted for greater than 10% of the variation between groups in seven analyses and was the only variable identified as important in all analyses. Therefore the daily accumulation of degree-days greater than 15 C and its rate of change were also selected to build the discriminant functions.

Unlagged variables were used to develop the discriminant functions because lagging had not explained any additional variation between the three groups of daily conditions. Data from all study sites were pooled to reduce the effects of peculiarities associated with individual study sites and to develop more generally useful discriminant functions.

Use of mean daily water temperature, minimum daily water temperature, the daily accumulation of degree-days

greater than 15 C, and the rate of change in the daily accumulation of degree-days greater than 15 C to develop discriminant functions from the calibration data set resulted in the following functions:

(1) $Y = -68.3367 + 12.6216\ X1 - 1.8597\ X2 + 0.0254\ X3 - 12.6730\ X4$

(2) $Y = -93.7860 + 13.8552\ X1 - 1.3765\ X2 + 0.0227\ X3 - 13.3676\ X4$

(3) $Y = -93.3542 + 13.9536\ X1 - 1.5260\ X2 + 0.0354\ X3 - 13.6437\ X4$

where,

Y = a decision value

X1 = mean daily water temperature (C),

X2 = minimum daily water temperture (C),

X3 = the daily accumulation of degree-days greater than 15 C, and,

X4 = the rate of change in the daily accumulation of degree-days greater than 15 C.

Function (1) was developed from daily conditions prior to the spawning season. Functions (2) and (3) were developed from daily conditions when spawning did and did not occur during the spawning season, respectively. Given a data set of X1, X2, X3, and X4, a decision as to which of the three groups of daily conditions the data set is most characteristic of is made by applying the data set to all

three functions. The function from which the largest Y value is obtained is the group of daily conditions the data set best characterizes.

Applying the calibration data set's group mean values (Table 20) for the four water temperature variables to the discriminate functions indicates that mean daily water temperature is the most important variable in determining the magnitude of Y values. This is due to the combination of: (1) mean daily water temperature being assigned a much larger coefficient relative to that of minimum daily water temperature, while absolute values of the two variables did not differ greatly; (2) the extremely small coefficient assigned to the daily accumulation of degree-days greater than 15 C, negating the influence of its large absolute values relative to those of mean daily water temperature; and, (3) mean daily water temperatures exhibiting large absolute values relative to those of the rate of change in the daily accumulation of degree-days greater than 15 C, while coefficients of the two variables were similar in magnitude. This is true for all functions, since the proportions of all coefficients are about the same between functions. Further, coefficient signs are identical between functions. Only mean daily water temperature and the daily accumulation of degree-days greater than 15 C were assigned positive coefficients; hence, these variables are the only

Table 20. Group means and standard deviations (S) of the calibration data set's four temperature variables. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

Variable*	N	Mean	S
Group 1			
Temp	64	12.97	2.77
Min	64	11.76	2.68
D-days	64	2.3	8.0
d D-days	64	0.4	1.3
Group 2			
Temp	83	19.64	2.33
Min	83	18.45	2.67
D-days	83	152.5	92.9
d D-days	83	4.7	2.2
Group 3			
Temp	77	19.53	2.12
Min	77	18.40	2.04
D-days	77	110.0	94.0
d D-days	77	4.5	2.1

*Refer to Table 10. for variable name descriptions.

ones which can increase Y values. Absolute values of the latter variable rapidly increased over the spawning season, and so increasingly contributed to larger Y values. However, even at the upper end of its range of values, the daily accumulation of degree-days greater than 15 C contributed little to the magnitude of Y values relative to mean daily water temperature. Therefore, it appears mean daily water temperature was the most important variable in differentiating between the three groups of daily conditions associated with spawning times.

When the test data set was applied to the discriminant functions, more than 90% of the days prior to the spawning season were correctly classified and approximately 65% of the days when spawning did and did not occur during the spawning season were correctly classified (Table 21). Overall correct classification for the three groups of daily conditions was approximately 72%, with most incorrect classifications occurring between days when spawning did and did not occur during the spawning season.

Based on the percentages of correctly classified daily conditions, the discriminant functions developed were judged to be useful in distinguishing between the three groups of daily conditions. Therefore, the following discriminant functions were developed by pooling the calibration and test data sets in an attempt to refine the above functions:

Table 21. Results of applying the test data set to the discriminant functions developed from the calibration data set. Group 1 represents daily conditions prior to the spawning season and groups 2 and 3 represent daily conditions when spawning did and did not occur during the spawning season, respectively.

From Group	Classified into group 1	2	3
1			
no.	58	0	5
percent	92.1	0.0	7.9
2			
no.	3	52	24
percent	3.8	65.8	30.4
3			
no.	3	28	53
percent	3.6	33.3	63.1

(1) $Y = -51.3789 + 10.3774\ X1 - 2.2302\ X2 + 0.0132\ X3 - 9.3270\ X4$

(2) $Y = -73.8687 + 11.4660\ X1 - 1.8203\ X2 + 0.0126\ X3 - 9.7498\ X4$

(3) $Y = -73.8026 + 11.4749\ X1 - 1.8682\ X2 + 0.0229\ X3 - 9.9050\ X4$

The relation of these functions to temperature variables, groups of daily conditions, and the manner in which a decision is made as to which group a data set would best characterize are the same as previously described for the calibration data set. Since these functions were developed with a sample size double that used to develop those of the calibration set, they are probably more precise in characterizing daily conditions associated with smallmouth bass spawning than the calibration data sets functions. This can be verified by testing both sets of functions against an independent data set and comparing the percentages of correctly classified observations obtained from the two sets of functions.

Stepwise discriminant analysis was applied to the pooled data to evaluate the relative importance of each of the four variables in distinguishing between the three groups of daily conditions. Mean daily water temperature and the daily accumulation of degree-days greater than 15 C accounted for approximately 63 and 6 percent of the

variation between groups, respectively. The rate of change in the daily accumulation of degree-days greater than 15 C and minimum daily temperature accounted for relatively little (2 and 1 percent respectively) of the variation between the three groups. This indicates that the latter two variables' usefulness in characterizing the three groups by themselves was minimal. These results agreed with the evaluation of the relative importance of the above four variables to the calibration data set's functions. In both cases, mean daily water temperature was identified as the most important variable in characterizing smallmouth bass spawning times.

DISCUSSION

Laboratory validation

The close correlation between the number of rings on smallmouth bass sagittae and daily ages after swim-up obtained from Method 1 indicates that rings were deposited with a daily periodicity. This was in agreement with results of the three previous studies of sagittal ring formation in centrarchids. Under laboratory conditions Taubert and Coble (1977) found that rings on the sagittae of pumpkinseed (*Lepomis gibbosus*), bluegill (*L. macrochirus*), and green sunfish (*L. cyanellus*) were laid down on a daily basis. Similarly, Miller and Storck (1982) found that the number of sagittal rings was linearly related to the daily ages of largemouth bass (*Micropterus salmoides*). Schmidt and Fabrizio (1980) also provided evidence of daily sagittal ring formation in a wild population of largemouth bass. Results of the present study and those mentioned above support Pannella's (1971) suggestion that sagittal rings in many, if not all, fish are deposited on a daily basis.

Mean ring counts of sagittae from laboratory fish generally exhibited a wide range of values. One source of variation was the exact time of swim-up by individual larvae. Approximately 80% of the reared larvae had risen and were actively swimming at 0700 h the day of swim-up.

When the fish were next checked at 2000 h the day of swim-up, all larvae were actively swimming. Consequently, some of the variation in mean ring counts may be due to variation in swim-up time.

Another source of variation may have been my inability to consistently differentiate between daily and subdaily rings. Fourteen sagittae from laboratory fish were sent to S. J. Miller (Illinois Natural History Survey) to verify my identification of daily and subdaily rings. He noted that these sagittae had poorly defined, indistinct daily rings compared to those of largemouth bass. Sagittae from larval smallmouth bass collected in the field exhibited more prominent rings than those of laboratory fish, suggesting that some aspect of laboratory rearing contributed to poorly defined rings. Therefore, much of the variation in mean ring counts on any particular day was probably due to poorly defined daily rings which resulted from laboratory conditions.

Formation of the first daily ring in smallmouth bass occurred the day of swim-up. This was consistent with observations on other species; ie., the first daily ring is formed when larvae first begin exogenous feeding. Daily ring formation begins when northern anchovy (Engraulis mordax) complete yolk-sac absorption (Brothers et al. 1976), when sockeye salmon (Oncorhynchus nerka) emerge from redds

(Wilson and Larkin 1980), and when mozambique mouth-brooders (Tilapia mossambica) leave the female's mouth (Taubert and Coble 1977). For centrarchids, the time of first daily ring formation was the day of swim-up in pumpkinseed, bluegill, and green sunfish (Taubert and Coble 1977) and largemouth bass (Miller and Storck 1982). Previous observations and the present study support the hypothesis that initiation of daily sagittal ring formation is dependent on exogenous feeding.

Ring formation in older fish

Plots of the number of rings on sagittae and collection date for fish from the New River near Eggleston and Walker Creek indicated that cessation of ring formation occurred in early November. This was also the time when extensive crowding of rings in the posterior edge of sagittae began to affect my ability to distinguish individual rings. Struthsaker and Uchiyama (1976) and Taubert and Coble (1977) have observed that reduced growth rates result in extensive crowding of sagittal rings. These observations indicate that early November marked the end of the first growing season for smallmouth bass in the New River drainage in 1982.

The above observations agree with results of winter simulation experiments by Taubert and Coble (1977) on green sunfish. They found that ring formation stopped when fish

were exposed to temperatures around 10 C. The grand mean of mean daily temperatures of the New River near Eggleston and Walker Creek from 16 October to 31 October were approximately 14 and 10 C, respectively. In early November (1 November to 15 November) the grand mean of mean daily temperatures had dropped to approximately 11 and 8 C, respectively. Young-of-the-year smallmouth bass cease feeding and become lethargic at temperatures below roughly 10 C (Oliver et al. 1979); therefore, it seems likely that water temperature effects on growth determine the time of year when sagittal rings cease to be reliable indicators of daily ages.

Taubert and Coble (1977) found in their winter simulation experiments that green sunfish formed annuli when fish subjected to temperatures less than 10 C were returned to temperatures of about 25 C. Taubert and Tranquilli (1982) have verified annulus formation in the sagittae of largemouth bass. Annuli of smallmouth bass closely resembled those of green sunfish and largemouth bass as described by Taubert and Coble (1977) and Taubert and Tranquilli (1982), respectively.

Using scanning electron microscopy techniques, Brothers et al. (1976) have found that sagittal rings continue to be formed on a daily basis throughout the winter in striped bass (Morone saxatilis). However, Taubert and Coble (1977),

using light microscopy techniques similar to those of this study, stated that daily sagittal ring formation stopped in green sunfish under simulated winter conditions. Use of electron microscopy may have revealed the presence of very tightly packed rings within the annuli of smallmouth bass, indicating that daily ring formation continued throughout winter. If no rings were present in annuli, ring formation must have stopped or resorbtion of sagittae must have occurred during winter, as suggested by Pannella (1980).

Potential biases in ageing

The methods used to estimate daily ages of smallmouth bass possessed three major sources of potential bias; (1) estimation of daily ages beyond swim-up from ring counts; (2) estimation of the number of days required from hatching to swim-up; and, (3) estimation of the number of days required from egg fertilization to hatching.

Potential bias associated with estimation of daily ages beyond swim-up from ring counts has several components. Prolarval and subdaily rings occurred in the sagittae of young-of-the-year collected from the New River drainage study sites. Prolarval rings were always contained within a discontinuous zone about the nucleus and became obscured as fish aged. Subdaily rings were indistinct and exhibited a much narrower proteinaceous layer than those of daily rings. Both prolarval and subdaily rings were easily identified;

therefore, counting of these rings could not have severely biased estimates of instantaneous growth rates or spawning dates.

The degree of grinding of sagittae is very important in the determination of daily ages. If sagittae are not ground sufficiently, rings in the posterior edge are not exposed. If sagittae are ground excessively, rings in the posterior edge can be obliterated. Both situations result in the underestimation of daily age in fish. I modified Taubert and Coble's (1977) and Miller and Storck's (1982) grinding techniques to consistently expose rings in the posterior edge of sagittae, and as noted in the Methods section, the modifications produced the desired results. Excessive grinding of sagittae did occur occasionally and was readily apparent. Over-grinding resulted in discontinuous rings in the posterior edge of sagittae. Further, the posterior edge itself would exhibit patchy, opaque areas (not to be confused with the opaque areas of sagittae described by Taubert and Coble (1977) and Miller and Storck (1982)). Such sagittae were discarded and the remaining left or right sagitta from the same fish was prepared and read. On no occasion did both sagittae from any one fish have to be discarded due to excessive grinding. Therefore, my grinding technique was not considered a source of bias.

The occurrence of numerous rings in the sagittae of

older fish resulted in a wider range in ring counts per sagitta than those of younger fish. Hence, the precision of age determinations declined as fish got older. This has also been observed by Taubert and Coble (1977) and Miller and Storck (1982). It seems unlikely that there was any consistent bias towards underestimating or overestimating the ages of older fish in this study given that (1) ring counts necessarily followed a circuitous path from the nucleus to the posterior edge; (2) no two readings of any one sagitta were made in consecutive order; and, (3) the outermost rings in the posterior edge of sagittae from fish collected in October could be distinguished with variable focusing. Therefore, ring counts in older fish with numerous rings were less precise but not biased in any particular direction.

Another potential source of bias in my estimation of daily ages is the assumption that the time required from hatching to swim-up was seven days. Precise information as to the relationship between the number of days required from hatching to swim-up and temperature has not been reported for smallmouth bass. Shuter et al. (1980) observed smallmouth bass larvae rising off nests seven days after hatching at temperatures ranging from 17.3 to 20.5 C. Temperatures in the New River drainage during times of spawning activity were generally within this range at all

study sites; therefore, bias associated with the assumption that seven days were required between hatching and swim-up was considered to be minor.

The final source of bias in the methods used to estimate daily ages involves the time required from egg fertilization to hatching. Regression of Webster's (1948) data concerning the number of days required from egg fertilization to hatching for smallmouth bass and water temperature indicated a highly significant ($R^2=0.99$; $P<0.01$) relationship. Shuter et al.'s (1980) plot of this relationship shows that between 16 and 22 C, there is only a difference of three days in incubation time. Since water temperatures during spawning were generally within this range, age estimates were probably not unduly biased by my estimates of the time required between fertilization and hatching.

In conclusion, the methods used to estimate the daily ages of young-of-the-year smallmouth bass possessed several sources of potential bias. As there is no evidence that any of the potential biases exhibited any consistent directional trend, ages are not thought to have been consistently underestimated or overestimated. Therefore, instantaneous growth rates and spawning date estimates were probably representative of young-of-the-year growth and the time and duration of spawning by smallmouth bass in the New River

drainage.

Growth

As it is difficult to compare and interpret length-weight relationships and von Bertalanffy growth parameters, these relationships were primarily developed for future reference to biologists concerned with smallmouth bass in the southern portion of its range. Length-weight relationships did not differ very much from those reported by Beckman (1948), Turner and MacCrimmon (1970), and Neves (1973) for young-of-the-year smallmouth bass from northern populations.

Von Bertalanffy growth parameters are generally derived from the incremental increases in fish lengths over the sampling period. However, such an approach could not be taken in this study because of variation in the times individual fish were spawned. Von Bertalanffy growth parameters for young-of-the-year smallmouth bass have not been previously reported, hence comparisons with other smallmouth bass populations is impossible. The similarity among parameters developed for the New River near Eggleston, the New River near Meadow Creek, and Walker Creek and their narrow confidence intervals indicate that these parameters provide reasonable descriptions of young-of-the-year smallmouth bass growth in these waters.

The small sample sizes of smallmouth bass spawned early

in the year and the clumped age distributions they exhibited necessitate cautious interpretation of comparisons between growth of young-of-the-year spawned early and late in the year. However, I feel confident in the accuracy of the regressions developed due to the relatively narrow confidence intervals on the y-intercepts, the similarity of results obtained from the New River near Meadow Creek and Walker Creek study sites, and the environmental conditions which prevailed during the spawning season.

Based on y-intercept estimates and associated confidence intervals of the relationships between instantaneous growth rates and daily ages, it appears that early-spawned fish did not grow initially as rapidly as those spawned later. This may well have been due to a major flooding event which peaked on 13 June at the New River near Meadow Creek and 15 June at Walker Creek, approximately five weeks after the median dates of early spawning at both study sites. Larimore (1975) conducted extensive laboratory experiments which simulated flood conditions and showed that young-of-the-year smallmouth bass are increasingly susceptible to displacement with progressively greater water velocities, turbulence, and turbidity levels. Surber (1939) reported that high water and turbidity levels were responsible for an almost complete loss of young-of-the-year smallmouth bass in a Virginia stream, and Larimore and

Duever (1968) have attributed losses of entire year-classes of smallmouth bass to floods occurring when young-of-the-year were less than 25 mm in total length. Cleary (1956) has further noted that fingerling smallmouth bass may have difficulty in obtaining food following flooding events.

Young-of-the-year smallmouth bass subjected to the flooding of mid-June in the New River drainage were undoubtedly exposed to conditions that fish spawned later in the season did not experience. Since growth rates of smallmouth bass spawned early in the season were slower than those of fish spawned later, it appears that flooding may significantly impact growth of young-of-the-year smallmouth bass.

Spawning time and duration

Previous studies of smallmouth bass reproduction have shown great variability in both the time and duration of smallmouth bass spawning. Spawning has been reported to occur between April (Surber 1943; Pflieger 1966; Montgomery et al. 1980) and August (Henderson and Foster 1957), with the duration of the spawning season lasting from less than one week (Surber 1943; Turner and MacCrimmon 1970) to over four months (Henderson and Foster 1957). Further, there does not appear to be any consistent trends in spawning time or duration in regards to latitude or lentic versus lotic waters.

The spawning season of smallmouth bass in the New River drainage extended from mid-May through mid-July at most study sites in 1982, and two distinct spawning periods occurred at all study sites. This was similar to the time and duration of smallmouth bass spawning in an Ozark stream (Pflieger 1966). Although there were differences in the median dates of early spawning periods between study sites, median dates of the late spawning periods were very similar. Surber (1943) noted that smallmouth bass spawning occurred within a one week period in different Virginia and West Virginia streams, as Pflieger (1966) has in Missouri. As hydrologic events were synchronous throughout the New River drainage, and absolute values of temperature and discharge variables varied between study sites during any particular time period, it appears that spawning was greatly influenced by the pattern of fluctuations in daily conditions.

Relatively few young-of-the-year bass were collected that had been spawned during the early spawning period compared to those that were spawned during the later spawning period. As mentioned previously, a major flooding event and associated drop in water temperature occurred between the two spawning periods at most study sites. Cleary (1956), Pflieger (1975), and Clark and Mancini (1980) have implicated flooding as the cause for smallmouth bass spawning seasons being broken into two distinct spawning

periods. Rapid drops in water temperature, as occurred during New River drainage flooding, have been held responsible for smallmouth bass nest desertion (Rawson 1945; Henderson and Foster 1957; Vogele 1981) and increased egg (Rawson 1945; Cleary 1956) and larval mortality (MacLean et al. 1981).

The low numbers of smallmouth bass collected from the early spawning period may reflect high mortality of eggs and young during the June flood. This possibility suggests that frequency distributions of spawning dates may be more representative of survival of young-of-the-year smallmouth bass than of the actual number of spawnings that occurred on any day. At all study sites, very few young-of-the-year spawned early in the season were collected. If frequency distributions of spawning dates are indeed indicative of survival, flooding appears to result in low survival of those young-of-the-year spawned prior to flooding, at least when flooding occurs early in the spawning season. However, other hypotheses regarding the low numbers of young-of-the-year collected from the early spawning period cannot be ruled out.

For instance, Robbins and MacCrimmon (1977) have repeatedly seen larger smallmouth bass moving into spawning areas before smaller individuals, and Doan (1940) and B. J. Shuter (University of Toronto, personal communication) have

observed larger smallmouth bass spawning earlier in the year than smaller individuals. Surveys of the New River in the areas of Eggleston and Meadow Creek (Austen 1984) have indicated that smaller (less than 305 mm) smallmouth bass dominate the populations at these study sites. Although there is evidence that spawning stock size has little influence on the reproductive success of smallmouth bass (Pflieger 1975), it is possible that relatively few young-of-the-year were collected from the early spawning period due to less spawning activity during this time.

At one study site, the New River near Meadow Creek, spawning occurred during times of rising water levels, inclusive of the June flood, as well as times of receding water levels. This may be due to the fact that most of the fish sampled from the New River near Meadow Creek were collected from one large, deep pool. Pflieger (1975) has noted that rises in water levels occurring during the spawning season are only detrimental to smallmouth bass reproductive success if they cause extensive scouring of the stream bottom. During times of rising water levels, a greater proportion of total discharge is moving near the surface of the water column in deeper water than shallow (Hynes 1970), and so deepwater substrate is less susceptible to scouring than that of shallow water. Hence, nests in deeper water are better protected from turbulence by

increased discharge than nests in shallow water. Smallmouth bass in the New River near Meadow Creek certainly had more access to deeper waters than those at other study sites and may have utilized these waters for spawning. This would be consistent with Pflieger's (1966) observations that smallmouth bass nests in larger streams are generally deeper than those of smaller streams. If smallmouth bass in the New River near Meadow Creek did spawn in deeper waters than fish at other study sites, one would expect enhanced survival of their young spawned during times of rising water levels, as apparently occurred at the New River near Meadow Creek.

MacLean et al. (1981) and Vogele (1981) have noted that the duration of the smallmouth bass spawning season is inversely related to the rate at which water temperatures rise. Such a relationship was also observed in this study. The spawning season of smallmouth bass in the New River near Meadow Creek was of shorter duration than those of other study sites and was sharply terminated in late June. Water temperatures at this study site rose more rapidly during the spawning season than at other study sites. A water temperature of approximately 24 C was reached by late June, and temperatures remained above this value for the next several weeks. Robbins and MacCrimmon (1977) have observed that a potamodromous stock of smallmouth bass abandoned its

spawning area when temperatures reached 25 C, a temperature near which spawning in the New River near Meadow Creek was sharply curtailed.

The spawning season of Walker Creek began sooner and ended later in the year than at any other study site. Water temperature of Walker Creek also rose more gradually over the spawning season than those of other study sites. Pflieger (1966) has suggested that smallmouth bass spawning will continue so long as temperature is within a range suitable for spawning. As the above mentioned studies and the present study pertain to smallmouth bass spawning over a wide range of latitudes, environments, and stocks; the rate at which water temperature increases seemingly exerts a dominant influence in determining the duration of smallmouth bass spawning seasons.

Relative importance of physical variables

Previous investigations of the relationships between smallmouth bass reproduction and physical conditions of streams have been largely a matter of casual observation and conjecture, although extensive studies have been conducted for smallmouth bass in northern lakes (Shuter et al. 1980). The present study is the first to quantitatively assess the relative importance of physical variables which influence smallmouth bass spawning times in stream systems. Although this study was confined to the 1982 spawning season and a

limited area of the smallmouth bass' range, the general relationships between physical variables and spawning times found in this study should apply to similar streams, as the study sites represent a variety of stream conditions that smallmouth bass commonly inhabit.

While photoperiod is acknowledged as an important factor in smallmouth bass reproduction, it is not believed to have exerted much influence in determining when spawning occurred. Prior to the summer solstice, the number of hours between sunrise and sunset increased by approximately two to four minutes each day. Increased daylength stimulates production of gonadotropic hormones which promote gonad maturation; however, other environmental factors also govern gonad maturation. For example, temperature affects the rates at which gonadotropic hormones are produced and released (Crim 1982). Given that photoperiod's influence on the reproductive timing of fish can be moderated by other environmental changes, such moderation must be especially pronounced in rapidly fluctuating environments. Temperature and discharge conditions of the streams studied often exhibited great day-to-day variation, which leads to the conclusion that photoperiod was a priming factor in determining when spawning occurred and temperature or discharge variables acted as releasing factors. Therefore the remainder of this discussion will be solely concerned

with the influence of temperature and discharge variables on smallmouth bass spawning.

Different temperature and discharge variables were identified as important in differentiating between the three groups of daily conditions at different study sites. This was not surprising, since study sites were chosen to represent a variety of environmental conditions that smallmouth bass inhabit. Variables that are identified by stepwise discriminant analysis as important are those which exhibit the maximum variation between the groups of observations. Since there were inherent differences in the variation of temperature and discharge variables among study sites, variables identified as important in differentiating between the three groups of daily conditions at any one study site would not necessarily be identified as important at other study sites. For this reason, application of pooled data from all study sites to stepwise discriminant analysis was considered the best assessment of the relative importance of temperature and discharge variables in determining smallmouth bass spawning times.

Results of these analyses indicated that only water temperature variables were important in differentiating between the three groups of daily conditions, with mean daily water temperature being identified as the most important. Identification of only temperature variables was

the result of temperature variables undergoing a progressive quantitative change due to the warming of waters over time. Discharge variables did not undergo any such trend over time; identical discharge variable values were often associated with all three groups of daily conditions. Therefore, only temperature variables were identified as important in differentiating between the three groups of daily conditions as they exhibited greater variability among groups than discharge variables. The smallmouth bass is considered a warmwater, fairly tolerant species and as such should be most responsive to extreme variations in its physical environment. As temperature variables exhibited the most variation among the three groups of daily conditions, temperature probably exerted a dominant influence in determining spawning times.

Although no discharge variables were identified by the stepwise discriminant analysis as important in differentiating between the three groups of daily conditions, they should not be considered unimportant in influencing smallmouth bass spawning times. The early and late spawning periods at most study sites began when water levels were receding following flooding events (Figs. 7-11). Pflieger (1975) has stated spawning always follows flooding in Missouri streams and that flooding will interrupt the spawning season, as seen in this study.

Discharge and temperature variables of the streams studied were so highly correlated that it is difficult to defend one set of variables as more important than the other in determining smallmouth bass spawning times. Probably the relationships between discharge, temperature, and spawning are analagous to those alluded to by Shuter et al. (1980) concerning wind direction, temperature, and spawning of smallmouth bass in northern lakes. Offshore winds produce upwellings which bring cold, hypolimnetic water into littoral spawning areas, interrupting smallmouth bass spawning. When offshore winds die down, the shallow littoral areas are warmed by the sun and spawning is reinitiated. Similarly, rising water levels during flooding in the New River drainage were generally associated with falling water temperatures and cessation of spawning activity. After floods peaked and water levels receded, water temperatures rose and spawning again commenced. Therefore, it seems that the interaction of discharge and temperature variables, not the sole influence of either one, determined smallmouth bass spawning times.

As noted previously, the discriminant functions were more than 90% successful in identifying daily conditions prior to the spawning season over a variety of different stream systems. This was expected, given the large differences in group mean temperature variable values

between daily conditions prior to the spawning season and those of the spawning season. However, the functions were only about 65% successful in differentiating between days when spawning did and did not occur during the spawning season. Several factors may be responsible for this outcome. One is the sampling methodology employed to collect young-of-the-year bass. Many days where no spawning occurred were classified as days on which spawning should have occurred by the discriminant functions. These days were generally bracketed by days when spawning had occurred, which suggests that spawning did occur but no fish spawned on these days were collected. This in turn implies that the sampling effort was not intensive enough and larger sample sizes should have been obtained.

It is also possible that size-selectivity of gear type biased frequency distributions of spawning dates. This seems unlikely for the New River near Eggleston and Walker Creek, as collections from these study sites represented a wide range of fish lengths and ages. It also seems unlikely to have occurred in collections of fish from the Little River, for as sampling progressed the population of young-of-the-year at this study site was obviously being depleted. However, most of the fish collected from the New River near Galax and Meadow Creek were collected during a relatively brief time period with one gear type. Therefore size-

specific gear selectivity may have contributed to the number of incorrect classifications occurring on days when spawning did and did not occur during the spawning season.

Two aspects of smallmouth bass biology may also have contributed to misclassifications of days when spawning did and did not occur during the spawning season. Robbins and MacCrimmon (1977) and B. J. Shuter (University of Toronto, personal communication) have suggested that the appearance of larger smallmouth bass in spawning areas earlier in the year may be due to different temperature thresholds between size classes. If larger smallmouth bass spawned earlier in the year and at lower temperatures than smaller fish in the New River drainage, the discriminant functions developed from pooled data represent generalized relationships between spawning times and water temperature. Therefore, some incorrect classifications of days when spawning did and did not occur during the spawning season may be due to variation in the response of individual fish to water temperatures.

Another aspect of smallmouth bass biology which may account for the discriminant functions' moderate success in distinguishing between days when spawning did and did not occur during the spawning season is the occurrence of repeated spawning by individual fish. Thirty-six hours have been reported to elapse between successive spawnings within one nest, and under semi-natural conditions, females can

spawn at least three times within a spawning season (Beeman 1924). Since eggs in various stages of maturation occur in smallmouth bass at any one time during the spawning season (Sanderson 1958; Vogele 1981), it may be that a resting period only loosely associated with daily temperature conditions is required between successive spawnings of any one fish. This would certainly account for the lowered ability of the discriminant functions to identify days when spawning did and did not occur within the spawning season.

The discriminant functions developed may be useful to fisheries managers dealing with regulated smallmouth bass streams. Given adequate data bases, hydrologists can predict seasonal water temperatures of streams from historical discharge and meteorological data (Theurer and Voos 1982). By simulating different discharge release schedules, various stream temperature regimes can be predetermined. Applying these temperature regimes to the discriminant functions, their effects on the spawning time and duration of smallmouth bass can be compared and evaluated. Knowledge of the effects of various discharge release schedules on smallmouth bass reproduction may be used to manipulate the spawning time and duration of smallmouth bass in regulated streams and enhance reproductive success. However, the discriminant functions should only be used to distinguish between stream conditions

prior to spawning seasons and stream conditions during spawning seasons. The predictive abilities of the discriminant functions (>90% correct classifications) are sufficient for this purpose, but not for differentiating between days when spawning will and will not occur during a spawning season (65% correct classifications). Further investigation of the relationships between smallmouth bass reproductive success and year-class strength in stream systems and the effects of flow regulation on other biota of stream communities is needed to take appropriate advantage of the discriminant functions' application as described above.

Results of this study emphasize the interrelationships which exist among smallmouth bass spawning times, subsequent growth of young-of-the-year, and environmental conditions in stream systems. Water temperature seems to exert the most influence in determining when spawning occurs, although discharge rates also affect spawning activities. Termination of spawning may occur despite water temperatures remaining within a range conducive to spawning and is probably due to rapid drops in water temperature which accompany major flooding, although extreme flooding may cause physical damage to eggs, larvae, and nests.

Flooding may also affect growth of young-of-the-year. Oliver et al. (1979) and MacLean et al. (1981) have found

that overwinter survival of young-of-the-year smallmouth bass is affected by the size of fish, with smaller individuals being more suceptible to overwinter mortality. Young-of-the-year bass spawned before major flooding did not appear to differ greatly in size from those spawned after major flooding at the end of the growing season. This was probably due to a combination of their initial advantage in size and a longer growing season. Year-class strength of smallmouth bass is largely determined by the end of the first winter of life (Shuter et al. 1980). Prolonged high, relatively cool discharges resulting from abnormally cold or wet weather or flow regulation could delay spawning, reduce the length of the growing season, and result in reduced year-class strength due to increased overwinter mortality.

Recommended improvements in methodology

Within the exploratory framework of this study, the discriminant analysis approach proved valuable in differentiating among different groups of daily conditions associated with smallmouth bass spawning. However, refinement should be attempted and can best be accomplished through several courses of action designed to promote efficiency and reduce the potential biases present in the estimation of daily ages of fish.

Depending on the physical characteristics of the streams to be studied, a standardized methodology should be

used to collect young-of-the-year bass. Standardization of collection methods should reduce size-selective bias. Young-of-the-year should be collected within a short time period after all spawning is finished. This is is necessary to reduce the effort required to obtain samples which are representative of all spawning dates. Collections should also coincide with the time that young-of-the-year are growing rapidly. During times of rapid growth, sagittal rings are easily counted, and the lack of crowding of rings in the posterior edge of sagittae enables the most precise estimates of daily ages from the time of swim-up. Sample sizes of at least 100 fish per study site should assure confidence in statistical procedures.

Controlled laboratory experiments are needed to determine the relationship between the number of days from hatching to swim-up under a variety of water temperatures. Such experiments have not been performed and would provide an index of the variability in swim-up times in relation to temperature.

Spawning date estimates obtained from the otolith ageing technique should be compared with an independent method, e.g., nest observations. This would aid in determining if the methodology used to estimate spawning times in this study was more representative of the frequency of spawning on any date or survival of young-of-the-year.

These refinements should enable more precise characterization of daily conditions associated with smallmouth bass spawning. They should also allow for further evaluation of the discriminant functions developed in this study, and enhance their applicability.

SUMMARY

(1) From the day of swim-up until fourteen days after swim-up, sagittal ring formation in smallmouth bass was daily in occurrence. The first daily ring was formed the day of swim-up.

(2) The otolith ageing technique was applicable to young-of-the-year smallmouth bass collected prior to November 1, 1982. Reduced growth rates, apparently resulting from low water temperature, caused crowding of sagittal rings and determined when sagittal rings ceased to be reliable indicators of daily ages.

(3) Age estimates of young-of-the-year, obtained from the otolith ageing technique, had several sources of potential bias, none of which appeared to exhibit any consistent directional trends.

(4) Instantaneous growth rates declined as young-of-the-year got older. Smallmouth bass spawned early in the spawning season did not initially grow as rapidly as those spawned later.

(5) Spawning occurred from late-April through mid-July, 1982, at mean daily water temperatures ranging from 12.5 to 23.5 C.

(6) Frequency distributions of spawning dates were nearly

identical among study sites, as were hydrological events. Spawning activities were interrupted by flooding in June and resumed when water levels were receding.

(7) Four water temperature variables were found to be useful in characterizing daily stream conditions prior to the spawning season and when spawning did and did not occur during the spawning season. Mean daily water temperature was the most important of these temperature variables.

(8) Discriminant functions were developed which were 72% successful in identifying days on which spawning apparently did and did not occur. The functions may be useful in predicting smallmouth bass spawning times in southern streams.

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Appendix 1. Monthly mean daily water temperatures (C) and discharge rates (m^3/s) for the year of study (1982) and monthly mean discharge rates for the ten years (1971-1981) previous to the year of study.

New River near Galax

Month	1982				1971-1981	
	Mean daily water temperature	Range	Mean daily discharge	Range	Mean daily discharge	Range
January			66	16-252	76	8-764
February			88	37-312	72	20-523
March			66	39-135	113	28-869
April	11.7	10.9-14.8	50	33-145	93	28-594
May	18.6	13.6-21.4	46	29-70	81	26-826
June	21.0	18.3-22.8	44	29-80	74	28-381
July	23.3	22.0-24.2	41	27-87	48	18-107
August	22.2	20.2-23.8	30	21-62	38	12-124
September	18.9	14.4-21.9	26	19-64	43	14-174
October			19	13-59	59	18-619
November			16	13-20	68	17-1613
December			27	11-62	65	13-292

Appendix 1. cont.

New River near Eggleston

Month	1982 Mean daily water temperature	1982 Range	1982 Mean daily discharge	1982 Range	1971-1981 Mean daily discharge	1971-1981 Range
January			138	36-537	160	24-1230
February			204	56-787	150	25-2343
March			157	73-263	226	26-514
April	11.8	10.0-13.3	106	29-329	196	28-1457
May	17.1	12.8-20.5	101	30-177	169	25-1093
June	19.6	17.2-20.8	111	37-235	148	24-1278
July	21.3	20.6-22.2	88	32-211	97	28-1409
August			63	26-112	76	26-1431
September			50	26-139	84	29-1062
October	15.6	9.8-21.9	41	25-192	115	21-243
November	9.9	7.0-14.5	34	23-51	127	22-235
December	6.8	3.7-10.8	53	23-143	131	3-1125

Appendix 1. cont.

New River near Meadow Creek

Month	1982				1971-1981	
	Mean daily water temperature	Range	Mean daily discharge	Range	Mean daily discharge	Range
January			329	80-1250	343	38-1431
February			574	169-1573	344	61-1448
March			486	228-1110	500	94-1605
April			221	106-542	428	74-1528
May	19.0	13.7-22.8	177	70-369	332	64-1570
June	20.5	14.8-25.1	328	72-1610	255	53-1795
July	25.7	24.2-27.3	123	64-234	141	42-1267
August	24.0	22.8-25.8	101	55-193	105	29-537
September	23.2	21.9-26.0	62	39-145	107	30-1170
October			69	35-432	177	38-1593
November			64	50-109	218	18-1480
December			154	70-528	279	33-1656

Appendix 1. cont.

Big Reed Island Creek

Month	1982				1971-1981	
	Mean daily water temperature	Range	Mean daily discharge	Range	Mean daily discharge	Range
January	1.1	0.0-3.6	13	3-62	16	2-207
February	0.8	0.0-3.8	18	8-87	14	4-138
March	6.4	2.8-9.7	14	10-26	20	4-150
April	9.8	4.1-13.8	14	9-46	20	5-189
May	16.6	12.1-18.6	13	8-29	17	4-155
June	18.8	14.8-20.9	14	8-47	15	3-135
July	21.5	19.8-22.8	14	6-57	10	3-35
August	20.4	17.9-22.8	8	5-23	8	2-45
September	15.8	12.8-19.8	7	4-7	10	3-223
October	11.4	5.6-17.8	7	3-81	12	4-181
November	6.4	2.2-11.5	4	4-6	12	4-76
December	3.8	0.0-11.4	5	2-15	14	3-102

Appendix 1. cont.

Little River

Month	1982 Mean daily water temperature	1982 Range	1982 Mean daily discharge	1982 Range	1971-1981 Mean daily discharge	1971-1981 Range
January			13	2-61	14	2-256
February			17	6-85	13	4-127
March	9.9	3.2-10.0	14	8-29	20	4-127
April	10.5	5.1-14.6	10	7-32	19	5-156
May	17.9	12.4-20.3	9	6-15	15	4-166
June	19.3	15.8-21.8	11	6-27	13	3-77
July	22.1	20.7-23.6	10	6-43	9	2-26
August	21.7	19.0-24.3	6	4-17	7	2-19
September	18.0	14.1-21.4	4	3-5	9	2-232
October	12.9	7.2-18.9	4	2-36	11	4-150
November	9.4	3.7-12.2	4	3-5	11	4-104
December	5.7	1.6-11.9	5	2-15	12	3-82

Appendix 1. cont.

Walker Creek

Month	1982				1971-1981	
	Mean daily water temperature	Range	Mean daily discharge	Range	Mean daily discharge	Range
January			16	3-30	18	1-183
February			24	9-101	16	2-154
March	8.0	3.2-11.8	20	8-48	24	4-186
April	11.6	6.4-14.8	8	5-20	19	5-256
May	17.2	12.4-20.0	6	4-17	14	2-110
June	18.7	15.3-20.6	12	4-76	9	2-77
July	21.1	19.8-22.2	4	3-10	5	1-20
August	20.5	18.8-21.8	3	2-8	3	1-19
September	15.8	14.1-20.4	2	1-2	3	1-44
October	12.8	7.9-17.5	2	1-6	7	1-84
November	7.8	4.2-12.1	2	1-2	10	1-79
December	6.0	0.9-11.8	4	1-17	13	1-115

Appendix 2. Field collection sampling dates, gear type*, effort**, and number of fish collected by study site.

New River near Galax				New River near Eggleston				New River near Meadow Creek			
Date	Gear type	Effort	Number collected	Date	Gear type	Effort	Number collected	Date	Gear type	Effort	Number collected
6/11	bp	1.5	0	5/20	dn	3.0	0	6/7	dn	1.0	2
7/1	bp	1.0	0	6/3	dn	1.5	0	6/23	bf	1.0	1
									sn	2.0	4
7/17	bp	0.0	0	6/13	dn	1.0	0	7/6	sn	4.5	5
7/21	bp	0.0	0	6/18	dn	1.5	3	7/21	sn	1.0	28
8/4	bp	0.0	0	6/26	dn	1.0	0	8/5	bp	0.5	0
8/18	bp	0.0	4	6/28	bp	1.5	0	8/27	sn	1.0	27
					dn	0.5	1				
9/17	bf	3.0	42	6/30	sn	3.5	0	9/8	bp	1.0	0
					dn	0.5	17				
9/30	bf	4.0	32	7/17	sn	3.0	8	10/1	bf	0.5	20
					dn	2.0	3				
				7/20	dn	1.5	0				
				8/1	sn	1.0	8				
					dn	1.0	2				
				8/2	sn	1.5	17				
				8/17	bp	2.0	26				
				9/4	bp	1.0	0				
				9/28	bp	1.0	15				
				10/20	bp	1.0	15				
				11/1	bp	2.0	0				
				11/16	bp	1.5	6				
				12/4	bp	2.0	4				
				12/14	bp	2.0	4				
				1/8	bp	1.0	3				

*bf = boat electrofishing
bp = backpack electrofishing
dn = dip net
sn = seine

**rounded to the nearest half-hour

Appendix 2. cont.

Big Reed Island Creek				Little River				Walker Creek			
Date	Gear type	Effort	Number collected	Date	Gear type	Effort	Number collected	Date	Gear type	Effort	Number collected
6/4	dn	0.0	0	6/4	dn	0.0	0	5/30	dn	0.5	10
6/16	dn	1.0	0	6/16	dn	1.0	0	5/31	dn	0.5	30
7/8	dn	1.0	0	7/2	dn	1.0	0	6/6	dn	1.0	0
7/14	sn	1.0	0	7/14	sn	1.5	0	6/20	dn	1.0	1
7/16	sn	1.5	0	7/16	sn	5.0	1	6/25	dn	1.5	2
8/8	bp	1.0	0	7/29	sn	2.0	0	7/9	bp	1.5	0
8/24	bp	2.5	0	8/14	bp	1.5	3	7/22	bp	1.0	0
					sn	1.0	1				
9/9	bp	3.5	5	8/24	bp	3.5	32	8/7	bp	1.0	14
9/11	bp	3.0	3	9/1	bp	2.5	21	9/3	bp	0.0	0
				9/22	bp	0.5	0	9/28	bp	1.0	27
				10/4	bp	2.5	21	10/19	bp	2.0	15
								11/9	bp	1.5	3
								11/30	bp	1.0	0
								12/14	bp	1.5	3
								1/8	bp	1.0	2

Appendix 3. Mean number of rings on the left and right sagittae of smallmouth bass used in Wilcoxon-signed-ranks tests on the null hypothesis that the mean ring counts of left and right sagittae do not differ.

Size category (mm)							
40.0-49.9		50.0-59.9		60.0-69.9		70.0-79.9	
Left	Right	Left	Right	Left	Right	Left	Right
40.0	41.7	47.3	49.7	64.7	60.7	82.0	83.0
44.3	41.0	50.7	49.0	80.0	77.3	110.7	108.7
43.0	44.7	50.3	48.7	83.0	81.6	80.3	77.3
49.7	50.0	79.3	79.0	85.0	88.7	74.7	77.3
49.3	49.7	53.0	53.3	74.3	70.7	84.0	78.7
35.7	34.7	63.0	64.3	81.0	75.3	87.0	86.0
39.0	38.3	56.7	61.0	79.0	81.0	80.0	81.3
37.0	36.7	58.0	59.7	92.3	93.7	97.0	96.0
38.7	36.7	62.7	62.7	64.7	61.0	80.7	82.7
38.3	39.0	67.3	66.7	86.0	81.0	98.7	102.0
37.0	37.3	63.3	65.3	79.3	74.3	88.7	91.7
39.0	39.3	57.7	54.7	74.3	76.0	83.7	86.0
37.0	37.3	69.0	68.3	86.3	83.3	85.0	85.3
35.3	36.7	64.0	62.3	81.7	83.0	74.0	74.3
51.3	50.0	61.3	60.0	82.7	82.7	95.3	98.7

Appendix 4. Length, weight, mean number of sagittal rings, and instantaneous growth rates (G) of young-of-the-year smallmouth bass by study site and collection date.

New River near Galax

Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})
8/18	48.7	1.46	43.3	41	9/17	79.3	6.67	77.3	29
	49.4	1.63	53.7	33		84.6	7.83	79.3	27
	55.3	2.23	60.3	31		91.0	10.02	109.7	22
	56.3	2.29	54.3	35		65.0	3.75	79.3	26
9/17	67.9	3.99	80.7	26		80.1	6.86	81.0	28
	72.7	6.02	78.3	28		64.5	3.32	83.3	25
	65.8	4.22	74.0	28		70.2	3.87	84.0	25
	70.8	5.12	82.7	26		78.8	6.95	113.0	20
	86.2	8.80	112.7	21		78.4	7.15	83.7	27
	77.0	5.99	79.7	28		67.9	4.66	84.3	25
	74.4	5.37	83.7	26		61.4	3.11	80.0	25
	67.6	4.40	81.7	25		61.6	3.04	79.0	25
	66.1	3.83	79.3	26		55.8	2.20	79.3	24
	60.7	3.20	75.7	26		63.1	2.20	76.7	26
	72.8	4.96	83.7	26		72.8	3.17	81.3	27
	79.0	6.34	83.3	27		69.8	4.88	81.7	26
	80.0	7.73	107.7	21		63.6	4.79	78.3	26
	70.0	4.83	84.3	25		69.7	3.35	82.0	26
	62.1	3.29	81.0	25		93.5	4.12	110.7	22
	79.4	6.84	82.7	27		111.7	18.53	95.7	27
	78.9	6.50	82.3	27		99.1	14.19	109.7	22
	66.0	4.10	84.0	24		100.6	13.16	108.7	23
	70.0	4.82	82.3	26		98.7	13.30	112.0	22

Appendix 4 continued.

New River near Galax

Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})
9/30	70.0	4.38	73.7	29	9/30	73.2	4.71	93.3	23
	82.6	6.87	93.7	24		74.5	5.16	87.0	25
	74.7	5.27	87.7	25		73.8	5.27	99.0	22
	71.2	4.62	86.0	25		70.3	4.45	88.7	24
	88.1	8.61	119.3	20		76.4	5.39	unreadable	
	79.2	6.44	92.0	24		80.3	6.35	85.3	26
	70.0	4.66	85.7	25		85.2	7.64	94.3	25
	75.8	5.31	82.0	27		80.0	7.05	84.3	27
	70.1	4.26	87.3	24		95.1	9.98	unreadable	
	81.0	6.95	99.3	23		98.2	8.17	84.0	29
	88.2	8.45	97.0	24		94.3	9.47	120.7	20
	70.5	4.34	90.3	24		111.4	16.92	unreadable	
	75.1	5.49	90.7	24					

Appendix 4. continued.

New River near Eggleston

Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})
6/18	17.0	0.07	24.3	29	8/02	42.2	0.98	37.0	44
	16.6	0.08	23.3	30		49.5	1.64	39.0	44
	13.8	0.06	22.7	22		40.6	1.01	38.0	41
6/30	8.3	0.01	*	*		44.6	1.11	37.0	45
	8.2	0.01	*	*		45.1	1.13	35.3	48
	8.4	0.01	*	*		37.4	0.71	35.3	43
	9.1	0.01	*	*		37.0	0.65	31.7	46
	8.5	0.01	*	*		42.9	1.02	36.3	45
	8.4	0.01	*	*		37.1	0.62	32.0	46
	8.8	0.01	*	*		37.1	0.64	33.7	44
	8.6	0.01	*	*		40.5	1.00	36.3	44
	8.3	0.01	*	*		48.4	1.39	53.3	33
	8.3	0.01	*	*		50.5	1.73	71.7	25
	8.3	0.01	*	*		49.8	1.46	38.3	47
	8.0	0.01	*	*		63.0	2.91	67.3	30
	8.4	0.01	*	*		61.8	2.90	70.0	28
	8.1	0.01	*	*		65.0	3.90	75.3	27
	8.8	0.01	*	*	8/17	54.8	2.11	0	0
	8.4	0.01	*	*		55.6	2.17	0	0
	8.5	0.01	*	*		54.5	2.12	0	0
7/17	27.5	0.23	21.7	54		52.2	1.87	0	0
	30.1	0.33	22.0	58		57.1	2.25	0	0
	28.9	0.34	23.0	54		51.4	1.82	0	0
8/01	43.8	1.00	37.0	45		56.8	2.22	0	0
	39.1	0.68	36.3	43		47.9	1.46	0	0
	32.4	0.39	32.0	42		52.4	1.92	0	0
	49.1	1.29	38.7	45		54.8	1.83	0	0
	57.1	2.06	53.0	36		43.3	1.06	0	0
	43.8	1.04	38.3	43		51.5	1.81	0	0
	38.6	0.65	37.3	41		56.5	2.15	0	0
	35.8	0.56	37.3	39		56.4	2.41	0	0
	37.4	0.64	32.3	47		49.2	1.53	0	0
	59.1	2.44	51.0	38		54.6	2.00	0	0

* rising fish

0 unreadable

Appendix 4 continued.

New River near Eggleston

Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})
8/17	59.7	3.03	0	0	9/28	89.2	9.07	82.0	29
	66.8	3.65	0	0		100.8	11.27	unreadable	
	62.1	3.11	0	0		101.2	12.72	121.0	20
	73.1	4.80	0	0	10/20	73.8	5.76	99.3	22
	66.7	3.95	0	0		69.0	4.85	106.3	20
	63.2	3.17	0	0		70.4	4.95	107.0	20
	70.5	4.16	0	0		69.2	5.03	98.3	22
	76.6	5.62	0	0		67.0	4.61	114.0	18
	74.6	5.05	0	0		72.8	5.32	104.0	21
	82.4	6.04	0	0		78.5	6.66	116.3	19
9/28	74.1	5.17	74.7	29		80.1	7.31	115.0	20
	82.3	6.88	83.3	27		89.4	9.91	122.3	19
	74.7	5.30	84.0	26		76.5	6.21	115.7	19
	69.2	4.49	81.0	26		75.5	5.76	113.0	19
	57.4	2.75	78.7	24		80.4	7.19	99.0	23
	55.6	2.39	77.0	25		86.3	8.61	114.0	20
	70.7	3.58	84.3	25		88.0	8.78	114.0	21
	64.1	3.54	86.0	24		95.9	11.96	131.7	18
	67.2	3.54	86.3	24	11/16	72.5	5.21	82.0	
	67.1	3.80	79.3	26		77.7	6.30	87.3	count
	69.9	4.01	78.0	27		78.4	5.24	107.7	to
	68.9	4.22	74.3	28		85.2	7.99	107.3	crowding
	71.0	4.81	87.7	24		89.0	9.08	109.7	
	72.5	5.20	87.0	25		87.6	7.91	unreadable	
	77.6	5.72	87.0	26	12/04	68.6	3.90	88.3	
	77.7	6.34	79.7	28		98.5	10.89	unreadable	
	62.4	4.29	86.3	23		65.4	3.68	89.7	
	67.9	3.92	81.7	25		75.9	5.49	95.3	
	61.8	3.44	82.7	24	12/14	76.3	5.15	unreadable	
	72.0	4.61	unreadable			74.1	4.09	83.7	
	71.5	4.63	80.0	37		98.6	10.03	85.0	
	71.6	4.97	97.0	22		79.6	6.08	85.0	
	79.1	6.62	98.0	23	1/08	74.0	5.86	81.7	
	70.9	4.56	80.7	26		75.1	5.19	74.0	
	81.0	7.14	95.0	24		89.7	7.69	84.3	
	86.3	7.79	82.3	28					

Appendix 4. continued.

New River near Meadow Creek

Date	Length (mm)	Weight (g)	Mean no. of rings	G (10)	Date	Length (mm)	Weight (g)	Mean no. of rings	G (10)
6/07	21.1	0.10	22.7	40	7/21	29.9	0.33	24.3	53
	21.1	0.12	20.7	44		38.6	0.68	24.7	61
6/23	34.6	0.54	33.0	43		55.6	1.90	58.0	32
	36.3	0.62	31.7	46		36.1	0.57	24.0	61
	39.1	0.81	37.0	42		36.1	0.56	26.0	56
	24.8	0.19	32.0	34		33.1	0.50	25.7	53
	29.3	0.32	33.0	38		35.9	0.57	26.0	56
7/06	39.0	0.94	42.7	36	8/27	60.5	2.57	53.0	37
	42.7	1.14	49.7	33		65.4	3.18	60.3	34
	45.7	1.21	46.0	37		69.6	3.86	58.7	36
	38.7	0.83	37.7	40		66.3	3.39	66.7	31
	36.3	0.67	41.7	35		77.6	5.23	63.0	35
7/21	35.6	0.55	24.7	58		63.1	2.60	53.7	37
	28.3	0.29	23.3	53		57.6	2.28	60.7	32
	32.2	0.45	26.0	52		70.4	3.55	63.7	33
	29.7	0.30	24.7	50		73.3	4.24	66.0	33
	34.1	0.48	25.7	54		58.3	2.12	63.7	30
	31.6	0.38	27.3	49		71.6	4.59	64.7	33
	37.0	0.59	26.0	57		60.2	2.40	58.7	34
	35.5	0.57	25.3	58		65.8	3.16	56.7	36
	26.6	0.21	25.0	46		62.9	2.85	62.7	32
	31.7	0.37	24.3	55		65.6	3.23	58.3	35
	33.2	0.44	27.3	51		61.7	2.78	56.0	36
	35.5	0.54	24.3	60		71.8	4.57	55.0	39
	33.4	0.47	25.0	55		72.7	4.52	66.3	33
	34.9	0.45	26.0	55		66.0	3.42	59.0	35
	30.3	0.38	25.0	51		93.0	8.43	88.7	27
	28.5	0.30	21.3	58		76.0	4.62	64.3	34
	38.7	0.64	24.7	61		61.1	2.66	65.0	30
	57.1	2.36	63.0	30		55.3	1.83	56.0	34
	57.2	2.27	60.3	32		62.6	2.75	59.0	34
	38.9	0.69	24.3	64		73.1	4.45	68.7	31
	29.0	0.31	24.0	52		59.3	2.59	60.3	32
						67.3	3.07	57.7	36

Appendix 4. continued

New River near Meadow Creek

Date	Length (mm)	Weight (g)	Mean no. of rings	G (10)	Date	Length (mm)	Weight (g)	Mean no. of rings	G (10)
10/01	93.6	9.71	90.7	26	9/09	65.6	3.52	65.0	
	93.1	9.69	91.0	26		65.4	3.33	74.3	
	88.4	7.57	106.7	22		56.2	2.21	70.3	
	92.1	8.93	105.3	23		54.9	2.02	68.0	
	94.7	9.66	95.7	25		66.8	3.66	75.0	
	86.7	7.44	98.7	24	9/11	53.6	1.92	68.7	
	76.9	5.45	94.0	24		52.4	1.53	69.3	
	76.0	5.77	102.0	22		60.1	2.66	67.7	
	80.2	6.16	107.3	21					
	66.5	3.74	100.3	21					
	66.0	3.56	92.0	22					
	78.8	5.87	97.0	23					
	77.1	5.44	93.3	24					
	72.7	4.69	79.3	27					
	90.1	8.53	101.7	23					
	81.5	6.17	95.0	24					
	78.7	5.81	96.0	23					
	86.1	7.69	105.0	22					
	95.3	9.80	117.7	20					
	108.6	15.41	116.0	22					

Appendix 4. continued.

Little River

Date	Length (mm)	Weight (g)	Mean no. of rings	G_z (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_z (10^{-2})
7/16	40.3	0.96	53.0	30	9/01	50.7	1.51	63.0	28
8/14	40.8	0.88	51.0	31		56.7	2.39	56.7	34
	45.1	1.19	49.7	34		60.0	2.75	62.0	32
	46.0	1.22	49.3	35		51.4	1.82	58.0	31
8/24	45.3	1.35	54.7	31		55.6	2.04	64.0	30
	46.1	1.34	61.3	28		54.9	2.09	67.0	28
	45.4	1.19	56.3	30		51.9	2.01	62.7	29
	40.4	0.86	57.3	28		56.2	2.27	67.3	28
	40.6	0.85	61.0	26		57.8	2.56	63.3	31
	42.6	0.88	58.3	28		52.0	1.84	57.7	33
	43.9	1.07	57.3	29		56.9	2.37	69.0	28
	45.5	1.26	57.3	30		57.3	2.39	64.0	30
	46.5	1.29	59.0	29		58.5	2.42	61.3	32
	45.0	1.08	unreadable			66.7	3.41	87.0	24
	41.8	0.97	58.0	28		67.2	3.71	92.3	23
	41.4	0.95	58.0	28		57.1	2.67	64.7	29
	46.0	1.28	60.0	28		64.8	3.33	64.7	31
	43.5	1.22	58.3	28		80.9	5.94	97.7	23
	42.0	0.96	57.7	28	10/04	60.9	3.11	92.3	22
	43.2	1.04	57.3	29		64.4	3.49	82.7	24
	44.8	1.08	54.7	30		69.6	4.64	85.3	25
	42.2	0.97	61.7	26		52.3	1.97	79.7	23
	46.5	1.23	61.3	28		60.2	3.19	83.7	23
	48.0	1.28	52.0	34		62.6	3.55	103.7	19
	51.0	1.60	59.7	30		64.8	3.79	94.7	22
	50.1	1.47	59.0	30		59.1	3.25	85.0	23
	49.5	1.67	59.7	30		67.0	4.29	92.3	22
	52.9	1.79	58.0	32		73.5	5.36	89.7	24
	52.7	1.77	59.3	31		75.6	5.87	85.0	26
	53.7	2.11	62.0	30		71.6	5.54	102.0	21
	54.2	2.08	60.3	31		68.2	4.74	84.7	25
	52.4	1.84	58.3	32		71.7	4.96	111.3	19
	52.2	1.89	59.3	31		70.3	3.78	87.7	24
	62.2	2.95	89.3	22		74.7	5.93	81.0	27
	71.4	4.68	98.7	22		64.4	3.70	80.3	25
	73.1	4.81	88.7	24		70.2	4.72	87.7	24
						92.7	10.66	unreadable	
						65.9	4.17	71.7	29

Appendix 4. continued.

Walker Creek

Date	Length (mm)	Weight (g)	Mean no. of rings	G (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G (10^{-2})
5/30	12.8	0.05	10.7	38	8/07	35.7	0.60	39.7	36
	13.5	0.04	16.0	30		54.7	2.04	67.7	28
	12.9	0.04	7.7	54		70.4	4.03	77.0	28
	14.3	0.05	16.0	33		42.5	0.94	40.3	40
	13.0	0.04	11.7	36		43.6	0.99	unreadable	
	12.8	0.05	15.7	26	8/13	42.8	1.02	41.3	40
5/31	15.1	0.07	17.6	32		71.8	4.64	85.3	25
	13.3	0.04	13.3	35		42.3	0.94	47.0	34
	16.6	0.08	14.7	45		43.5	0.94	47.7	34
	14.8	0.04	13.3	44		42.9	0.98	45.0	36
	14.2	0.03	16.3	33		46.1	1.14	unreadable	
	13.8	0.03	12.7	38		61.1	2.65	82.3	24
6/20	22.2	0.12	24.3	40		51.0	1.64	unreadable	
6/25	10.7	0.03	12.3	20		36.7	0.80	45.3	33
	11.1	0.02	12.0	23		47.0	1.49	47.3	37
8/07	39.1	0.75	36.0	43		46.0	1.12	46.3	37
	42.0	0.93	35.7	45		45.9	1.13	44.3	38
	43.0	1.03	39.0	42		44.2	1.11	46.0	36
	40.1	0.80	40.0	39		38.8	0.75	45.0	34
	37.9	0.75	42.3	36		37.2	0.71	45.7	32
	37.4	0.74	35.7	41		40.9	0.86	43.0	37
	37.8	0.71	40.3	38		38.3	0.77	unreadable	
	39.2	0.83	41.6	37		40.4	0.80	45.0	35
	44.2	1.14	44.3	38		41.1	0.83	44.7	35
	40.1	0.80	43.0	36		42.9	1.04	50.0	33
						76.1	4.91	84.0	26

Appendix 4. continued.

Walker Creek

Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})
8/17	41.5	1.06	49.0	33	9/28	64.9	3.38	83.0	25
	39.9	0.81	46.3	34		57.6	2.67	79.3	24
	42.9	1.04	49.3	33		63.3	2.98	85.3	24
	50.1	1.76	47.3	38		60.8	2.91	unreadable	
	46.3	1.32	51.0	33		68.1	3.91	85.0	25
	51.0	1.82	50.3	36		54.4	2.14	86.3	22
	49.9	1.66	51.7	34		63.0	3.25	79.3	26
	48.9	1.44	50.7	34		61.3	3.14	74.3	27
	46.6	1.27	unreadable			64.6	3.44	81.0	25
	45.3	1.19	50.0	34		65.7	3.41	73.3	28
	45.9	1.23	51.3	33		63.8	3.20	79.0	26
	47.3	1.51	unreadable			66.7	3.95	83.3	25
	49.3	1.70	50.7	35		67.6	4.17	69.3	30
	54.9	2.27	50.7	37		69.2	3.89	unreadable	
	53.3	1.83	48.7	38		70.4	4.58	82.0	26
	56.4	2.39	49.0	39		65.0	3.91	77.7	26
	54.0	2.05	50.3	37		73.3	5.16	113.0	19
	54.6	2.20	50.3	37		70.5	4.50	83.7	25
	56.7	2.46	47.3	41		74.2	5.28	110.7	20
	69.7	4.30	88.7	24		70.7	4.49	85.3	25
	73.7	5.46	91.3	24		75.5	5.48	80.3	27
9/28	58.1	2.37	76.7	25		83.3	7.13	107.0	21
	60.8	2.93	unreadable			91.3	8.71	111.0	21
	64.7	3.62	83.3	24					
	66.9	4.19	80.0	26					

Appendix 4. continued.

Walker Creek

Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})	Date	Length (mm)	Weight (g)	Mean no. of rings	G_2 (10^{-2})
10/19	61.0	2.90	86.7	23	11/09	68.7	4.01	86.7	
	59.1	2.63	87.0	22		65.7	3.18	unreadable	
	66.4	3.32	92.7	22		66.6	3.42	unreadable	
	67.0	3.34	86.7	24	12/14	69.6	3.75	78.7	
	63.6	2.94	86.7	23		59.0	2.72	84.7	
	67.6	4.01	90.7	23		66.4	3.51	93.3	
	60.3	2.75	95.3	21	1/08	57.4	2.22		
	63.0	3.39	86.7	23		65.1	3.17		
	69.7	4.32	101.0	21					
	74.4	4.63	94.0	23					
	86.3	7.42	112.3	21					
	72.1	4.24	98.7	22					
	66.0	3.08	82.3	25					
	63.9	3.24	110.0	18					
	72.3	4.37	106.7	20					

Appendix 5. Correlation coefficients of photoperiod, temperature, and discharge variables by study site.

New River near Galax
Correlation Coefficients**

Variables*	Photo	d Photo	Temp	d Temp	Min	d Min	Max	d Max	pFlow	d pFlow	Flow	D-days	d D-days
Photo	1.00	-0.35	0.75	0.25	0.68	0.21	0.74	0.19	0.41	0.65	-0.29	-0.14	-0.29
d photo	-0.35	1.00	-0.43	-0.17	-0.40	-0.09	-0.45	-0.21	-0.72	-0.48	0.17	-0.02	0.17
Temp	0.75	-0.43	1.00	-0.31	0.95	0.31	0.97	0.17	0.50	0.94	-0.49	-0.04	-0.49
d Temp	0.25	-0.17	0.31	1.00	0.18	0.57	0.39	0.73	0.08	0.27	-0.12	-0.17	-0.12
Min	0.68	-0.40	0.95	0.18	1.00	0.35	0.86	0.00	0.47	0.87	-0.38	0.01	-0.38
d Min	0.21	-0.09	0.31	0.57	0.35	1.00	0.26	0.10	0.06	0.24	-0.12	-0.04	-0.12
Max	0.74	-0.45	0.97	0.39	0.86	0.26	1.00	0.32	0.52	0.98	-0.58	-0.11	-0.58
d Max	0.19	-0.21	0.17	0.73	0.00	0.10	0.32	1.00	0.06	0.14	-0.11	-0.25	-0.11
pFlow	-0.29	0.17	-0.49	-0.12	-0.38	-0.12	-0.58	-0.11	1.00	0.31	1.00	-0.34	-0.52
d pFlow	-0.14	-0.03	-0.04	-0.17	0.01	-0.39	-0.11	-0.25	0.31	1.00	0.31	-0.01	-0.08
Flow	-0.29	0.17	-0.49	-0.12	-0.38	-0.12	-0.58	-0.11	1.00	0.31	1.00	-0.34	-0.52
D-days	0.41	-0.72	0.50	0.08	0.47	0.06	0.52	0.05	-0.34	0.01	-0.34	1.00	0.62
d D-days	0.65	-0.48	0.94	0.27	0.87	0.24	0.93	0.14	-0.52	-0.08	-0.52	0.62	1.00

* Refer to Table 10. for variable name descriptions.

**Coefficient values greater than 0.22 are significant at P = 0.05.

Appendix 5. Correlation coefficients of photoperiod, temperature, and discharge variables by study site.

New River near Eggleston
Correlation Coefficients**

Variables*	Photo	d Photo	Temp	d Temp	Min	d Min	Max	d Max	pFlow	d pFlow	Flow	D-days	d D-days
Photo	1.00	-0.47	0.71	-0.08	0.74	-0.09	0.61	-0.05	0.60	0.51	0.31	-0.04	0.33
d photo	-0.47	1.00	-0.47	0.00	-0.41	0.03	-0.47	0.02	-0.70	-0.50	0.05	0.11	0.02
Temp	0.71	-0.47	1.00	0.18	0.94	0.13	0.95	0.13	0.66	0.85	-0.09	-0.07	-0.09
d Temp	-0.08	0.00	0.18	1.00	0.11	0.68	0.22	0.85	-0.09	0.11	-0.14	-0.23	-0.17
Min	0.74	-0.41	0.94	0.11	1.00	0.24	0.82	0.04	0.58	0.76	0.01	-0.07	0.02
d Min	-0.09	0.03	0.13	0.68	0.24	1.00	0.08	0.39	-0.09	0.05	-0.16	-0.22	-0.17
Max	0.61	-0.47	0.95	0.22	0.82	0.08	1.00	0.25	0.66	0.84	-0.18	-0.04	-0.18
d Max	-0.05	0.02	0.14	0.85	0.04	0.39	0.25	1.00	-0.09	0.08	-0.10	-0.15	-0.14
pFlow	0.31	0.05	-0.09	-0.14	0.01	-0.16	-0.18	-0.10	1.00	0.43	0.98	-0.10	-0.16
d pFlow	-0.04	0.11	-0.07	-0.23	-0.07	-0.22	-0.04	-0.15	0.43	1.00	0.42	-0.04	-0.10
Flow	0.33	0.02	-0.09	-0.17	0.02	-0.17	-0.18	-0.14	0.98	0.44	1.00	-0.09	-0.16
D-days	0.60	-0.70	0.66	-0.09	0.58	-0.09	0.66	0.09	-0.10	-0.04	-0.09	1.00	0.75
d D-days	0.51	-0.50	0.85	0.11	0.76	0.05	0.84	0.08	-0.16	-0.10	-0.16	0.75	1.00

* Refer to Table 10. for variable name descriptions.

**Coefficient values greater than 0.20 are significant at P = 0.05.

Appendix 5. Correlation coefficients of photoperiod, temperature, and discharge variables by study site.

New River near Meadow Creek
Correlation Coefficients**

Variables*	Photo	d Photo	Temp	d Temp	Min	d Min	Max	d Max	pFlow	d pFlow	Flow	D-days	d D-days
Photo	1.00	-0.61	0.45	-0.13	0.48	-0.09	0.45	-0.13	0.94	0.45	0.31	-0.02	0.31
d photo	-0.61	1.00	-0.29	0.02	-0.30	0.01	-0.28	0.08	-0.68	-0.28	-0.21	-0.10	-0.21
Temp	0.46	-0.29	1.00	0.12	0.98	0.13	0.98	0.09	0.45	0.99	-0.47	-0.02	-0.47
d Temp	-0.13	0.02	0.12	1.00	0.09	0.83	0.12	0.83	-0.05	0.11	-0.40	-0.64	-0.40
Min	0.48	-0.30	0.98	0.09	1.00	0.17	0.94	0.03	0.47	0.97	-0.42	-0.01	-0.42
d Min	-0.09	0.01	0.13	0.83	0.17	1.00	0.08	0.48	-0.05	0.11	-0.29	-0.43	-0.29
Max	0.45	-0.28	0.98	0.12	0.94	0.08	1.00	0.17	0.46	0.98	-0.49	-0.04	-0.49
d Max	-0.13	0.08	0.09	0.83	0.03	0.48	0.17	1.00	-0.05	0.09	-0.37	-0.56	-0.37
pFlow	0.31	-0.21	-0.47	-0.40	-0.42	-0.29	-0.49	-0.37	1.00	0.31	1.00	0.21	-0.47
d pFlow	-0.02	-0.10	-0.02	-0.64	-0.01	-0.43	-0.01	-0.56	0.31	1.00	0.31	-0.07	-0.01
Flow	0.31	-0.21	-0.47	-0.40	-0.42	-0.29	-0.49	-0.37	1.00	0.31	1.00	0.21	-0.47
D-days	0.94	-0.68	0.45	-0.05	0.47	-0.05	0.46	-0.05	0.21	-0.07	0.21	1.00	0.45
d D-days	0.45	-0.28	0.99	0.11	0.97	0.11	0.98	0.09	-0.47	-0.01	-0.47	0.45	1.00

* Refer to Table 10. for variable name descriptions.

**Coefficient values greater than 0.25 are significant at $P = 0.05$.

Appendix 5. Correlation coefficients of photoperiod, temperature, and discharge variables by study site.

Little River
Correlation Coefficients**

Variables*	Photo	d Photo	Temp	d Temp	Min	d Min	Max	d Max	pFlow	d pFlow	Flow	d-Days	d D-days
Photo	1.00	-0.47	0.63	0.03	0.62	0.02	0.51	0.03	0.61	0.41	0.33	0.01	0.22
d photo	-0.47	1.00	-0.45	-0.08	-0.46	-0.03	-0.30	-0.11	-0.71	-0.52	-0.02	-0.15	-0.18
Temp	0.63	-0.42	1.00	0.25	0.88	0.23	0.89	0.14	0.53	0.69	-0.10	0.04	0.26
d Temp	0.04	-0.08	0.24	1.00	0.11	0.75	0.28	0.80	0.02	0.15	-0.27	-0.20	-0.04
Min	0.63	-0.46	0.88	0.15	1.00	0.25	0.72	-0.02	0.52	0.61	-0.03	0.08	0.25
d Min	0.02	-0.03	0.23	0.75	0.25	1.00	0.17	0.38	0.00	0.16	-0.27	-0.14	-0.03
Max	0.51	-0.30	0.89	0.28	0.72	0.17	1.00	0.26	0.40	0.60	-0.15	0.04	0.19
d Max	0.03	-0.11	0.14	0.80	-0.02	0.38	0.26	1.00	0.02	0.06	-0.16	-0.14	-0.04
pFlow	0.33	-0.02	-0.10	-0.27	-0.03	-0.27	-0.15	-0.16	1.00	0.40	0.15	-0.10	-0.32
d pFlow	0.01	-0.15	0.04	-0.20	0.08	-0.14	0.03	-0.14	0.40	1.00	0.10	0.00	-0.10
Flow	0.22	-0.18	0.26	-0.04	0.25	-0.03	0.19	-0.04	0.15	0.10	1.00	0.29	0.29
D-days	0.61	-0.71	0.53	0.02	0.52	0.00	0.40	-0.16	-0.10	0.00	0.29	1.00	0.76
d D-days	0.41	-0.52	0.69	0.15	0.61	0.16	0.60	0.06	-0.32	-0.10	0.29	0.76	1.00

* Refer to Table 10. for variable name descriptions.

**Coefficient values greater than 0.20 are significant at P = 0.05.

Appendix 5. Correlation coefficients of photoperiod, temperature, and discharge variables by study site.

Walker Creek
Correlation Coefficients**

Variables*	Photo	d Photo	Temp	d Temp	Min	d Min	Max	d Max	pFlow	d pFlow	Flow	D-days	d D-days
Photo	1.00	-0.49	0.61	-0.13	0.65	-0.08	0.56	-0.06	0.53	0.51	0.08	0.06	0.08
d photo	-0.49	1.00	-0.60	0.07	-0.58	0.04	-0.61	-0.04	-0.83	-0.67	0.05	-0.09	0.04
Temp	0.61	-0.60	1.00	0.09	0.97	0.13	0.98	0.09	0.67	0.84	-0.31	0.02	-0.31
d Temp	-0.13	0.07	0.09	1.00	0.01	0.59	0.16	0.72	-0.09	0.05	-0.27	-0.33	-0.27
Min	0.65	-0.58	0.97	0.01	1.00	0.18	0.91	-0.02	0.66	0.79	-0.24	-0.04	-0.24
d Min	-0.08	0.04	0.13	0.59	0.18	1.00	0.11	0.32	-0.05	0.07	-0.25	-0.26	-0.25
Max	0.56	-0.61	0.98	0.16	0.91	0.10	1.00	0.21	0.67	0.84	-0.32	0.05	-0.32
d Max	-0.06	-0.04	0.09	0.72	-0.02	0.32	0.21	1.00	-0.04	0.07	-0.22	-0.20	-0.22
pFlow	0.08	0.05	-0.31	-0.27	-0.24	-0.25	-0.25	-0.21	1.00	0.42	1.00	-0.11	-1.41
d pFlow	0.06	-0.09	0.02	-0.33	0.04	-0.26	0.05	-0.20	0.42	1.00	0.42	0.02	0.00
Flow	0.08	0.04	-0.31	-0.27	-0.24	-0.25	-0.32	-0.22	1.00	0.42	1.00	-0.11	-0.41
D-days	0.53	-0.83	0.67	-0.09	0.66	-0.05	0.67	-0.04	-0.11	0.02	-0.11	1.00	0.80
d D-days	0.51	-0.67	0.84	0.05	0.79	0.07	0.84	0.07	-0.41	0.00	-0.41	0.80	1.00

* Refer to Table 10. for variable name descriptions.

**Coefficient values greater than 0.21 are significant at P = 0.05.

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