LIFE HISTORY PLASTICITY OF THE BLACKTAIL SHINER (*CYPRINELLA VENUSTA*) ACROSS DISTURBANCE GRADIENTS IN ALABAMA STREAMS

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Lemuel Robles Casten

Certificate of approval:

George W. Folkerts
Professor
Biological Sciences

Carol E. Johnston, Chair
Associate Professor
Fisheries and Allied Aquacultures

Russell A. Wright
Associate Professor
Fisheries and Allied Aquacultures

Stephen L. McFarland
Acting Dean
Graduate School

LIFE HISTORY PLASTICITY OF THE BLACKTAIL SHINER (*CYPRINELLA VENUSTA*) ACROSS DISTURBANCE GRADIENTS IN ALABAMA STREAMS

Lemuel Robles Casten

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Lemuel Robles Casten

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Signature of Author

____
Date of Graduation

VITA

Lemuel Robles Casten, was born in Iloilo City, Philippines on February 21, 1975. He attended the University of the Philippines in the Visayas and graduated with a Bachelor of Science degree in Fisheries in 1997. After graduation, he worked as fisheries officer for the International Marinelife Alliance and was research assistant for FishBase and LarvalBase Projects of the WorldFish Center from 1999-2004. While working full-time, he attended the University of the Philippines - Diliman and earned a graduate Diploma in Environmental Science in 2002. On July 2004, he moved to Auburn, Alabama and began graduate school at the Department of Fisheries and Allied Aquacultures of Auburn University on August 2004.

THESIS ABSTRACT

LIFE HISTORY PLASTICITY OF THE BLACKTAIL SHINER (*CYPRINELLA VENUSTA*) ACROSS DISTURBANCE GRADIENTS IN ALABAMA STREAMS

Lemuel Robles Casten

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(B.S., University of the Philippines in the Visayas, 1997)

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Four populations of the blacktail shiner, *Cyprinella venusta* were studied to determine life history parameter variation across disturbance gradients in Alabama streams. Consistent with life history theory, fishes from the degraded site were significantly smaller than fishes from sites with minimal disturbance. Fishes from the degraded site had the smallest size at maturity and the smallest propagule size. Clutch sizes adjusted for standard length (SL) varied among populations. Egg diameters were not related to SL among populations. There was no significant difference in mature egg diameters; however ripening egg diameters differed among populations. There was no difference in gonad mass in females for all spawning months; however, there were differences in gonad mass in males in July. Gonadosomatic index (GSI) peaked in July for both males and females. Reproductive males were still present in September for three populations but all females from all populations had become latent by September, indicating that spawning season has ended. The results of this study suggest that *Cyprinella venusta* has the ability to alter life history parameters in harsh environments and may be a factor contributing to its persistence in habitats where other species are declining.

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INTRODUCTION

The southeastern United States has the richest temperate freshwater fish fauna in the world (Warren and Burr, 1994). However, many southeastern fishes are now imperiled and their populations are declining. The escalating imperilment of fishes is primarily due to widespread decline and loss of habitat which is primarily caused by humans (McKinney and Lockwood, 1999; Warren et al., 2000). The causes of habitat loss and degradation in the Southeast are well known: excessive sedimentation, large and small impoundments, channelization, urbanization and pollution (Moyle and Leidy, 1992; Warren and Burr, 1994; Lydeard and Mayden, 1995; Walser and Bart, 1999; Burkhead and Jelks, 2001).

Anthropogenic activities leading to habitat disturbance have adverse effects on some species whose habitats are highly disturbed. For example, Johnston and Farmer (2004) reported declines in species distribution and abundance from recent surveys of imperiled minnows in Uchee Creek, Chattahoochee River drainage, in Alabama. Species that have declining population sizes may have low tolerance and high sensitivity to environmental changes. However, some species persist in spite of habitat disturbances and may benefit from these perturbations and replace species that are intolerant to these changes by expanding their ranges or niches. Organisms living in disturbed and harsh environments may alter their life history traits to adapt to their changing surroundings. This is referred to as phenotypic plasticity and evolves to allow organisms a greater chance of survival in degraded or harsh environments. Depending on the type of environments they are living in, an organism's genotype may produce different phenotypes when exposed to different environments (Via, 1993; Schlichting and Pigliucci, 1998). The response of the genotype to a given environment is a major component of life history studies and a basis for understanding survival and persistence of organisms.

Life history theory has been used by other investigators to tackle the challenge of predicting the response of different fish species to environmental change because local environment has a strong influence on life history traits of fishes (Van Winkle et al., 1993). A major component of life history studies is to show how a reproductive strategy is adaptive in particular environmental circumstances, and to elucidate the causal mechanisms that produce the observed pattern (Mazzoni et al., 2002).

Life history evolution assumes that different life history components are causally related, so that an increase in a given variable will be associated with a decrease in another variable (Reznick, 1983). Trade-offs in life history components are responses of fish populations to different kinds of environments and disturbances (Balon, 1975; Winemiller and Rose, 1992). An example of this trade-off is an increase in resources devoted to reproduction resulting in decreased growth and survivorship (Stearns, 1992). When fishes start to breed, energy that could have gone to growth will be used in growth of gonads and in other reproductive costs and will result in decreased growth (Diana, 2004).

Reznick and Endler (1982) reported that guppies allocated more resources to reproduction, had a shorter interval between broods, matured earlier and have smaller young when exposed to predation compared to guppies that are predator-free. Johnson (2001) also reported similar findings in the livebearing fish *Brachyrhaphis rhabdophora* that co-occur with predators. Trade-off in growth and reproduction are also reported in plants. Galloway (1995) reported that *Mimulus* flowered earlier and had shorter life spans in unfavorable conditions compared to plants in favorable conditions.

Changes in stream physical and biological characteristics can affect reproductive success. An increase in population density and reduction in food resources may stress fishes, causing reduced fecundity. Reznick and Yang (1993) found out that variation in resource availability influences reproductive allocation, offspring number and offspring size in guppies. Geber (1990) investigated fecundity and growth in the plant *Polygonum arenastrum* and reported that early commitment of meristems to reproduction favors high early fecundity but reduces the number of meristems available for vegetative differentiation which leads to lower growth rate and fecundity later in life. Meristem limitation, like resource limitation, is a proximate mechanism for trade-off between life history traits (Sultan, 2000). Plants respond to local environmental conditions by changing their morphology or physiology in ways that may enhance success in a variable environment (Schlichting, 1986; Sultan, 1987).

Changes in clutch and offspring size may represent adaptations to an unpredictable offspring environment (Kaplan and Cooper, 1984). In this study, clutch and egg sizes varied among populations from different streams and geographical areas and were regulated by environmental factors. Significant variations in clutch size and egg sizes of fishes have been documented (Heins and Rooks, 1984; Heins and Rabito, 1986; Parrish and Heins, 1991; Guill and Heins, 1996; Guill and Heins 2000; Heins, 2000; Machado et al., 2002; Trippel and Neil, 2003). Stearns (1983) found out that *Gambusia affinis* living in streams with higher water fluctuations mature earlier, produced more eggs and had a higher reproductive investment than mosquitofish living in a stable environment.

Rohr (1997) compared two populations of water skink, *Eulamprus tympanum* living in close proximity to each other and separated by 1000 meters in altitude. Age and size at first reproduction differed significantly between the two populations. Females at the lower altitude started to reproduce earlier and at a smaller size than high latitude females. Reproductive output also differed between the two populations with low altitude females producing large litters with small young and high altitude females producing small litters with large young. The total offspring mass a female produced in relation to her body size was significantly smaller in high altitude water skinks, suggesting strong environmental constraints on reproduction compared to low altitude water skinks.

Winemiller (1989) classified life history strategies of fishes into three categories (1) small, rapidly maturing, short lived fishes (opportunistic strategists), (2) larger, highly fecund fishes with longer life spans (periodic strategists), and (3) fishes of intermediate size that often exhibit parental care and produce fewer but larger offspring (equilibrium strategists). Small fishes in a highly stochastic environment spend less time as juveniles, because early maturing organisms have a higher probability of survival to maturity (Bell, 1980). Fishes that mature earlier have higher fitness because their offspring are born earlier and start reproducing sooner (Hamilton, 1966; Stearns, 1992). Small fishes with early maturation, small eggs, small clutches, and continuous spawning are well equipped to repopulate habitats following disturbances or in the face of continuous mortality in the adult stage (Lewontin, 1965; Winemiller and Rose, 1992). This suite of life history traits permits efficient colonization of habitats over relatively small spatial scales (Winemiller and Rose, 1992).

Persistence of species relies upon their continued presence, particularly with respect to potentially devastating forces (Meffe and Minckley, 1987). McMahon (2002) studied the life history adaptations to their environment of the Asian clam, *Corbicula fluminea* and zebra mussel, *Dreissena polymorpha*. He noted that these two species have short life spans, early maturity, rapid growth and high fecundities which allow for rapid re-establishment after their population have been reduced by chance catastrophic environmental events. The persistence of a population suggests that species have broad tolerances to environmental condition (Matthews, 1987; Braaten and Guy, 2002) and that they exhibit life history adaptations derived through phenotypic plasticity (Stearns, 1989).

Documenting life history parameters and response to biotic and abiotic changes can provide insights into the causes of success or failure of species under a particular environmental setting (Schiemer et al., 2003). Increased knowledge of the life histories of a species or group of species provide natural resource managers knowledge of how a species respond to natural or anthropogenic changes (Albanese, 2000) and can be applied to conservation of threatened species.

In the Chattahoochee River drainage, the blacktail shiner, *Cyprinella venusta*, is reported to have persisting populations (Johnston and Farmer, 2004) whereas a sympatric species, the bluestripe shiner, *Cyprinella callitaena*, has been extirpated from much of its native range (Shepard et al., 1995, Johnston and Farmer, 2004). Other species sympatric with *Cyprinella venusta* such as *Notropis buccatus*, *Lythrurus atrapiculus*, *Notropis cummingsae* and *Notropis hypsilepis* were also found to be decreasing in numbers and distribution, and *Nocomis leptacephalus* may be extirpated from the Uchee Creek system (Johnston and Farmer, 2004).

The blacktail shiner, *Cyprinella venusta*, may be persisting in highly disturbed environments due to its life history plasticity. Although some aspects of *Cyprinella venusta* life history have been reported by other researchers (Heins and Dorsett, 1986, Heins and Baker, 1987, Heins, 1990, Baker et al., 1994, Machado et al., 2002), more information is needed on changes in its life history traits as a response to new disturbances in its habitat.

The objective of this study is to determine factors that make *Cyprinella venusta* successful in a stochastic environment. The persistence of *Cyprinella venusta* could be due to: (1) the generalist nature of this fish, in which case its life history metrics would remain unchanged across habitat disturbance regimes, (2) the ability to alter life history parameters in response to disturbance. Alternatives that will not be investigated in this study are alteration in the biotic environment such as changes in predation or competition, which could allow persistence or even an increase in *Cyprinella venusta* abundance or distribution.

METHODS

Study species

The blacktail shiner, *Cyprinella venusta* belongs to the family Cyprinidae and can be easily identified by a well developed caudal spot, dorsal fins darkly pigmented, anal and caudal fin yellow, and all fins with milky white edges. It has a slender body form that is elongate to moderately deep. The head is moderately large, with a sharp snout and a terminal, large, and oblique mouth (Mettee et al., 1996). Breeding males usually have numerous tubercles on their head. Blacktail shiners are one of the bigger minnows belonging to the genus *Cyprinella* with a maximum standard length of about 155 mm (Boschung and Mayden, 2004) and a maximum age of 4 years (S.T. Ross, unpubl. data, in Ross, 2001).

This species is abundant all throughout its range. It is found in Gulf drainages from the Suwanee River, Georgia and Florida, west to the Rio Grande, Texas. In the Mississippi River basin (mostly in the former Mississippi embayment), it occurs from southern Illinois to Louisiana and west in the Red River drainage to western Oklahoma. This species prefers habitats of sandy pools and runs of small to medium rivers and also creeks and rocky pool runs (Page and Burr 1991).

Blacktail shiners are crevice spawners and nest sites are defended by males. Spawning is from late March to early October, and is most intense from April to early

September (Heins and Dorsett, 1986). Females reach sexual maturity at 42 mm SL and may produce clutches numbering from 139-459 eggs, which measure 0.97 to 1.34 mm in diameter (Page and Burr, 1991). This species is known to be a surface feeder because terrestrial insects have been found to be part of their diets. Feeding variations are noted depending on season, from steady feeding throughout the day to peaking just prior to sunset (Page and Burr, 1991).

The blacktail shiner has three recognized subspecies, *Cyprinella venusta venusta*, *Cyprinella venusta cercostigma* and *Cyprinella venusta stigmatura*. This fish is also known to hybridize with *Cyprinella whipplii*. Delco (1960) and Smith (1979) reported hybrid swarms with *Cyprinella lutrensis*.

Study Sites

Four sites from Chattahoochee River drainage were chosen for this study (Fig. 1). Sites chosen in Uchee Creek are in County Road 39 and Highway 169 and will be referred to as Uchee Creek 39 and Uchee Creek 169 hereafter. Blacktail shiners were collected from Uchee Creek 39 (300 meters upstream of County Road 39 Old Bridge, Russell Co., AL, 32°20’42”N, 85°3’16”W), and Uchee Creek 169 (200 meters upstream of Hwy 169 Bridge, 1 mile from Parkmanville, Russell Co., AL, 32°22’42”N, 85°10’53”W), Moffits Mill (shoal area) in Little Uchee Creek (Lee Co., AL, 32°30’24”N, 85°10’48”W) and Wacoochee Creek (300 meters upstream of County Road 379 Bridge, Lee Co., AL, 32°37’21”N, 85°8’0”W). Except for the larger Moffits Mill, all three streams are similar in size. The sites ranged from relatively pristine (Wacoochee Creek) to intermediate (Uchee Creek 169 and Moffits Mill) to highly degraded (Uchee

Creek 39). Each site represents unique habitat characteristics with different species associations.

The four sites under study are found in two physiographic provinces, the Piedmont Plateau and the Coastal Plain. Separating the two provinces is a transition zone called the Fall Line, which is characterized by falls and rapids. Wacoochee Creek is in the Piedmont Province, Moffits Mill in Little Uchee Creek lie in the Fall Line and UC39 and UC 169 are both in the Coastal Plain.

Uchee Creek begins in Lee County, Alabama and flows southeast where it joins Little Uchee Creek before entering the Chattahoochee River south of Phenix City. A predominantly Coastal Plain system, the Uchee Creek watershed drains approximately 1200 km^2 of land in east central Alabama (Johnston and Farmer, 2004). Elevation ranges from 50 to 100 meters above sea level and streams in the watershed are low gradient and sluggish with sand, gravel and mud as the predominant substrate, rich in aquatic vegetation and organic matter (Walser 1996).

Uchee Creek, although unimpounded, has shown a decline in species distribution and abundance (Johnston and Farmer, 2004). Reasons for the decline in species populations may be caused by changes in land use causing siltation, deterioration of water quality and recent water draw down for mining and irrigation (Howard, 1997; Walser and Bart, 1999; Johnston and Farmer, 2004). Fish diversity is especially low in mainstem sites where species richness may be as low as 2 species (Johnston and Farmer, 2004).

Uchee Creek 39 was perceived to be the most degraded of the four sites having eroded banks, with gravel and sand substrates, and with sluggish to fast flows. Riparian areas along the site are not in good condition. There was obvious clear cutting in the area. Uchee Creek 169 is a typical Coastal Plain stream with sandy gravel and mud substrates with sluggish flows. The riparian area is rich in vegetation and snags are present in the stream. Though Uchee Creek is heavily influenced by agricultural activity, this site remains relatively undisturbed. Because of the presence of both disturbed and relatively unchanged sites within the watershed, both sites along Uchee Creek are an excellent site for this study.

Little Uchee Creek drains 212 km^2 of Piedmont and Coastal Plain and increases in elevation from 50 to 100 meters above sea level. The Fall Line cuts across Little Uchee Creek. The tributaries have high gradient reaches with large falls and fast rapids. Moffits Mill on Little Uchee Creek, lies directly on the Fall Line and is characterized by a large shoal and fast flows. Most fish were collected just bellow the Fall Line.

Just north of Little Uchee Creek is Wacoochee Creek in the Piedmont Plateau. The total drainage for the Wacoochee Creek watershed is 85 km^2 and elevation range from 50 to 100 meters above sea level with low to moderate gradient. No major impoundments are found in the stream system (Walser and Bart, 1999). The site chosen in this creek is 300 meters upstream from the County Road 379 bridge. The water is clear and flows are sluggish. Substrate types are sand and gravel. The riparian zone is forested and no disturbance was observed along the banks.

Field and Laboratory Data Collection

Cyprinella venusta were collected monthly from May to November 2005 using a backpack shocker and seine in four streams along the Chattahoochee River drainage. From May to July, sampling frequency was twice a month because this is the time when *Cyprinella venusta* actively spawn. Sampling was conducted once a month from August to November. Samples from May to September were used to quantify life history parameters. May to November samples were used to determine sex ratios and age.

All available habitats preferred by *Cyprinella venusta* were sampled from each site. This allowed for the collection of representative number of *Cyprinella venusta* inhabiting variable habitats. At each site, stream temperature, stream velocity, water depth, substrate, turbidity, vegetation type and woody debris was recorded. Site coordinates was taken using GPS unit and entered in ArcMap (2005).

Fish collected were anesthetized using tricaine methanesulfonate (MS 222), and fixed in neutral 10% buffered formalin before processing. Fishes were sexed and measured to the nearest 0.01 mm standard length (SL) with dial calipers. Female fishes were chosen at random from each sampling site. Ovaries were removed from each specimen to assess gonad stage. Clutch size, gonad mass, egg size, egg mass, gonadosomatic index, and size at maturity were determined for each fish examined.

Ovarian condition of females was categorized using the classification of Heins and Baker (1993): (1) latent (LA), (2) early maturing (EM), (3) late maturing (LM), (4) mature (MA), (5) ripening (MR), and (6) ripe (RE). Ovarian stages that were MA, MR, and RE were considered reproductive and LA, EM, and LM females were considered non-reproductive (Heins and Baker, 1993). Reproductive condition of males was determined by visual examinations of testes. Mature males have large and opaque testes. Males that have small and transparent testes were considered latent.

Seasonal change in gonad mass for both sexes was determined using the gonadosomatic index (GSI). Gonads and eviscerated specimens were air dried for 2 hours (Johnston and Knight, 1999) and weighed to the nearest 0.0001 grams. GSI was calculated by dividing dry gonad mass by dry somatic mass (mass of eviscerated specimen) and multiplying by 100 (Johnston and Knight, 1999).

Clutch size and egg size (diameter) for each clutch was determined following Heins and Baker (1993). Clutch size was quantified by counting the number of all mature eggs in mature (MA) and ripening (MR) females. Ripe (RE) females were not used because they may have already spawned before sampling collection and will not represent complete clutches.

Size estimates of eggs in each clutch were obtained by measuring the diameter of ten randomly chosen eggs from the clutch. Because eggs were not spherical in preserved specimens, egg diameters were estimated by averaging measurements to the nearest 0.05 mm of the maximum and minimum dimensions. Mean egg mass was quantified by dividing total dry clutch mass by clutch size.

Size at maturity was determined for each sex by assessing samples collected during the reproductive season. Sexually mature females were those classified as EM, LM, MA, MR, and RE. Latent (LA) individuals were considered sexually immature. Mature males were determined by visual inspection of testes as noted earlier.

Statistical Analyses

Sex ratio was determined for each population by using pooled fish from monthly collections. Deviations from the expected 1:1 sex ratio were determined using a chi-square test. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to test for life history parameter differences among populations followed by Tukey posthoc tests for pairwise comparison between population means. Differences among populations in standard length (SL) were tested for significance using ANOVA. Differences among populations in clutch size, gonad mass, egg size, egg mass and GSI were tested using ANCOVA using SL as covariate. Linear regression was conducted to determine the relationship of life history parameters to SL, and correlations in life history parameters of females were determined using Pearson's correlation analysis.

All values were $\log_{10}$ transformed prior to analysis and tested for normality and homogeneity of slopes to satisfy the assumptions of statistical analysis. All analysis was conducted using SAS (SAS Institute, 2003) and SPSS 11.0 (SPSS Inc., 2005) and considered significant at $P \leq 0.05$.

Results

Sex Ratio

A total of 698, 531, 439 and 282 fish from Uchee Creek 39, Uchee Creek 169, Moffits Mill and Wacoochee Creek, respectively, were dissected and sexed to determine deviations from the expected 1:1 sex ratio. The sex ratio (male:female) for Uchee Creek 39 did not depart from 1:1 ratio (χ^2 = 0.098, df = 1, *P* = 0.325), while deviations from 1:1 ratio were found in the other three populations with skewness towards females. There was a significant difference in sex ratio at Uchee Creek 169 (0.8:1) (χ^2 = 6.556, df = 1, *P* = 0.010) and a highly significant departure from the expected 1:1 sex ratio in Moffits Mill (0.7:1) (χ^2 = 19.702, df = 1, *P* = 0.0001), and Wacoochee Creek (0.6:1) (χ^2 = 17.376, df = 1, *P* = 0.0001).

Standard Length (SL)

Females.---ANOVA showed that female sizes differed significantly among populations (ANOVA: F = 22.88, df = 3, *P* = 0.0001). Wacoochee Creek females (mean = 71.0 mm) were significantly larger than females from the other three populations and were almost 10 mm larger than the smallest mean female size from Uchee Creek 39 (mean = 61.7 mm). There were no significant differences in mean size among Moffits Mill (mean = 64.6 mm) and Uchee Creek 169 (mean = 62.2 mm), and Uchee Creek 169 and Uchee Creek 39 females (Table 1).

Males.---ANOVA showed that there was a significant size difference among populations (ANOVA: F = 5.03, df = 3, P = 0.003). Males from Uchee Creek 169 were largest. Uchee Creek 39 had the smallest sized males. Males from Uchee Creek 169 (mean = 88.0 mm) were significantly larger than Uchee Creek 39 (mean = 80.1 mm) and Moffits Mill (mean = 82.5 mm). There was no significant size difference between Wacoochee Creek (mean = 85.1 mm) and Uchee Creek 169 males.

There was a significant size difference when both males and females were combined (ANOVA: F = 7.97, df = 3, P < 0.0001). Pairwise comparison of SL between populations showed that the SL of Wacoochee Creek fishes are different from the other three populations. Fishes from Wacoochee Creek were largest (mean = 72.9 mm SL) and Uchee Creek 39 fishes were smallest (mean = 65.7 mm SL). SL for Moffits Mill and Uchee Creek 169 were 69.2 mm and 67.9 mm respectively.

Size at maturity

A total of 2311 female fish were examined to determine size at maturity for each population (Fig. 2). Females with EM, LM, MA, MR, RE ovarian stage were considered sexually mature. Females from Uchee Creek 39 showed the smallest size at maturity at 38.2 mm SL. Moffits Mill females showed the largest size at maturity at 46.4 mm SL. Uchee Creek 169 and Wacoochee Creek females were sexually mature at 44.4 mm SL and 41.1 mm SL, respectively.

A total of 128 males were judged as mature basing on gross examination of testes and presence of breeding tubercles. The smallest mature male from Uchee Creek 39 was 66.1 mm SL, 65.1 mm SL from Uchee Creek 169, 60.1 mm SL from Moffits Mill, and 72.8 mm SL from Wacoochee Creek (Fig. 3).

Demographics

Length-frequency histograms for blacktail shiner populations in the Chattahoochee River drainage exhibits 4 age classes. All samples were collected from May to November 2005. Samples were pooled to create length frequency histograms (Fig. 4). Basing on the histograms, Uchee Creek 39 fishes exhibit 2 age groups: 0 – 1 year old (≤ 55.0 mm SL, 47.1% of population) and 2 year old (≥ 55.1 mm SL, 52.9% of the population). Uchee Creek 169 has 3 age groups: 0 – 1 year old (≤ 40.0 mm SL, 27.8% of population), 2 year old (≤ 65.0 mm SL, 27.8% of population) and 3 years old (≥ 65.1 mm SL, 44.4% of population). Moffits Mill exhibits 3 age groups: 0 – 1 year old (≤ 25.0 mm SL, 11.8% of population), 2 year old (≤ 65.0 mm SL, 47.1% of population) and 3 years old (≥ 65.1 mm SL, 41.2% of population). Data from Wacoochee Creek shows 4 age groups: 0 – 1 year old (≤ 30.0 mm SL, 11.1% of population), 2 year old (≤ 60.0 mm SL, 33.3% of population), 3 year old (≤ 95.0 mm SL, 38.9% of population) and 4 year old (≥ 95.1 mm SL, 16.7% of population). These length frequency histograms provide an estimate of age classes of the four populations.

The presence of only two age classes at Uchee Creek 39 maybe related to the fact that fishes from Uchee Creek 39 are smaller than populations with at least three age classes.

Clutch Size

Clutch size peaked in May and June and started to decrease as spawning season progressed and as eggs were being spawned (Fig. 5). All populations showed significant positive regressions of clutch size on SL (F = 435.64, $P < 0.0001$) (Table 2). Within populations, there was a significant correlation between clutch size and standard length for all populations (Pearson's: $P < 0.0001$). Since female SL was not uniform in all populations, I adjusted clutch size for SL in the analysis of data. Among populations, there were significant difference in SL-adjusted mean clutch size for May (ANCOVA: F = 3.21, df = 3, $P = 0.0266$), June (ANCOVA: F = 4.30, df = 3, $P = 0.0069$), July (ANCOVA: F = 4.79, df = 3, $P = 0.0035$). Pairwise comparisons of populations showed significant differences in May between clutch sizes of Moffits Mill and Uchee Creek 169. For June, clutch sizes between Moffits Mill and Uchee Creek 169; and Uchee Creek 169 and Uchee Creek 39 showed significant differences. July comparisons showed clutch sizes from Moffits Mill and Uchee Creek 169; and Uchee Creek 169 and Wacoochee Creek were significantly different. When all females were pooled for all months, there was a significant clutch size difference among populations (ANCOVA: F = 4.31, n = 408, $P = 0.0053$). Pairwise comparisons showed Moffits Mill and Uchee Creek 169; and Uchee Creek 169 and Wacoochee Creek clutch sizes were different. Clutch size for Uchee Creek 39 range from 63-776 eggs (mean = 281); 61-653 eggs (mean = 252) for Uchee Creek 169; 81-673 eggs (mean = 300) for Moffits Mill; and 73-1515 eggs (mean = 302) for Wacoochee Creek (Table 3).

Gonad Mass

Female gonad mass showed no significant difference among populations for all spawning months (ANCOVA: F = 2.10, df = 3, P = 0.1002). Gonad mass peaked in June for all populations and gonad mass was lowest in August (Fig. 6). The largest gonad mass was recorded in Moffits Mill in June at 0.1790 grams and the lowest gonad mass recorded was 0.0562 grams in Uchee Creek 169 in August. When all females were pooled, the mean gonad mass for Uchee Creek 39 was 0.1079 grams, 0.1043 grams for Uchee Creek 169, 0.1242 grams for Moffits Mill, and 0.1219 grams for Wacoochee Creek (Table 4). Within populations, gonad mass was highly correlated to SL, clutch size and GSI for May, June and July (Pearson's: $P < 0.05$).

Male gonad mass showed significant differences among populations only in July (ANCOVA: F = 2.38, df = 3, P = 0.01). Population comparisons in July showed that gonad mass of Uchee Creek 39 males was significantly smaller than gonad mass from Uchee Creek 169 males (Fig. 7). There were no significant differences among other populations. All males when combined did not show significant differences in gonad mass among populations (F = 1.13, df = 3, P = 0.3393). Males from Uchee Creek 39 have the smallest gonad mass and males from Moffits Mill have the largest. Male mean gonad mass for Uchee Creek 39 was 0.017101 grams; 0.023468 grams for Uchee Creek 169; 0.023468 grams for Moffits Mill; and 0.022700 grams for Wacoochee Creek (Table 5).

Egg diameter

Females showed distinct groups of early maturing (EM), late maturing (LM), mature (MA), mature ripening (MR) and ripe (RE) eggs. Only MA and MR egg classes were measured and analyzed in this study. Due to a limited number of females with clutches having RE eggs, RE egg measurements were not included in statistical analysis. Obtaining ripe eggs from field caught samples is rare especially in minnows (Heins, personnal observation, see Machado et al., 2002), and this hold true for this study.

Mature Egg Diameter.---Among populations, there were no significant difference in mature egg diameters for all months and all females combined (F = 0.71, df = 3, $P = 0.5467$). The range for mature egg diameter for Moffits Mill was 0.78-1.23 mm (mean = 0.94), 0.80-1.17 mm (mean = 0.96) for Uchee Creek 169, 0.79-1.24 mm (mean = 0.94) for Uchee Creek 39, and 0.78-1.21 mm (mean = 0.94) for Wacoochee Creek population (Table 6). There was no significant relationship between regressions of mature egg diameter with SL for all populations ($P > 0.05$), however, when all females were pooled, there was a positive relationship between mature egg size and SL (F = 123.00, $P < 0.0001$). Mature egg diameters were not significantly correlated with SL for all populations and were smaller than ripening eggs.

Ripening Egg Diameter.---Ripening egg diameter was not correlated with SL or clutch size among females within populations. There was no significant relationship between regressions of ripening egg diameter with SL for all populations ($P > 0.05$) but when all females were pooled, there was a positive relationship between ripening egg diameter and SL (F = 387.60, $P < 0.0001$). ANCOVA showed significant differences among populations during the peak spawning months of June (ANCOVA: F = 3.87, n = 95, $P = 0.0155$) and July (ANCOVA: F = 5.91, n = 125, $P = 0.0014$). Pairwise comparison between populations showed that Wacoochee Creek egg diameters were significantly bigger than Uchee Creek 39 in June and Uchee Creek 169 egg diameters were significantly bigger than ripening egg diameters from the other three populations in July. There was a significant difference in ripening egg diameters when all females were pooled (ANCOVA: F = 3.07, n = 195, $P = 0.0290$). Uchee Creek 39 females have the smallest eggs and Uchee Creek 169 females have the biggest ripening eggs among populations (Table 7). The range of ripening eggs for Uchee Creek 39 was 0.94-1.18 mm (mean = 1.04 mm); 0.93-1.31 mm (mean = 1.08 mm) for Uchee Creek 169, 0.93-1.19 mm (mean = 1.06 mm) for Moffits Mill and 0.96-1.19 mm (mean = 1.06 mm) for Wacoochee Creek.

Egg Mass

Mature Egg Mass.---Mature Egg mass was not correlated with SL for all populations. Within populations, egg mass was highly correlated with gonad mass and GSI during spawning months for all populations. Monthly comparisons among populations showed significant differences only in August (ANCOVA: F = 3.97, df = 3, *P* = 0.0138). Mature egg mass for Uchee Creek 39 females was significantly smaller than the other three populations in August (Table 8). When all females were pooled for all months, ANCOVA showed no significant difference in mature egg mass (ANCOVA: F = 0.55, n = 213, *P* = 0.6476). Mean mature egg mass for each population was 0.00031 grams, 0.00034 grams, 0.00033 grams, and 0.00033 grams for Uchee Creek 39, Uchee Creek 169, Moffits Mill, and Wacoochee Creek, respectively.

Ripening Egg Mass.---Ripening egg mass was highly correlated to GSI for all populations during spawning peaks (Pearson's: *P* < 0.05) and there was a significant correlation to gonad mass for all populations in July. ANCOVA showed no significant difference among populations when all females were combined (ANCOVA: F = 0.98, n = 195, *P* = 0.4047). Moffits Mill mean ripening egg mass (0.00053 grams) was highest among populations and Uchee Creek 39 showed the lowest ripening egg mass (0.00048 grams). Mean ripening egg mass for Uchee Creek 169 was 0.00051 grams and 0.00052 grams for Wacoochee Creek (Table 9).

Gonadosomatic index (GSI)

Females.---There were no significant difference in GSI among populations for all months and all females combined. GSI peaked in July for all populations and dropped after July (Fig. 8). Females in all populations have become latent by September indicating spawning season has ended. Moffits Mill (mean = 5.8) showed the highest GSI and Uchee Creek 169 females showed the lowest GSI (mean = 4.9). Uchee Creek 39 and Wacoochee Creek have mean GSI values of 5.3 and 5.2 respectively (Table 10). The range of GSI values for Uchee Creek 39 was 4.1 – 6.5, the range for Uchee Creek 169 was 3.4 – 6.6, Moffits Mill has a range of 4.1 – 7.0, and GSI range for Wacoochee Creek was 2.5 – 6.5. GSI peaked in July for all populations, and then made a huge drop after its peak month.

Males.---GSI peaked in July and the values dropped after the peak month showing a pattern similar to female GSI (Fig. 9). ANCOVA showed significant differences in GSI for July and August. Pairwise comparison for July showed that Uchee Creek 169 GSI (0.8 grams) was significantly higher than Wacoochee Creek (0.5 grams) and Uchee Creek 39 (0.4 grams) (F = 3.24, df = 3, P = 0.0330). For August, Moffits Mill GSI was significantly higher than the other three populations (F = 3.20, df = 3, P = 0.0455). Pooled males showed no significant difference in GSI. Mean GSI for Uchee Creek 39 was 0.3, Uchee Creek 169 (0.3), Moffits Mill (0.4) and Wacoochee Creek (0.4). The range of GSI values for Uchee Creek 39 was 0.1 – 0.4; 0.1 – 0.8 for Uchee Creek 169; 0.1 – 0.6 for

Moffits Mill, and 0.0 – 0.5 for Wacoochee Creek. A zero GSI was taken from September samples. Reproductive males were still present during September for three populations (Uchee Creek 39, Uchee Creek 169, Moffits Mill), however Wacoochee Creek males have become latent a month earlier (Table 11).

DISCUSSION

This study found significant differences in life history parameters of fish in close proximity but from sites with varying physical properties. Specifically, differences in size at maturity, clutch size, and egg size among the four populations were found. Variations in life history parameters may be phenotypic responses to biotic or abiotic factors. Alternatively, the variations observed could also be genetic.

Females from Uchee Creek 39 have smaller sizes at maturity than the other three populations. Temperature has been known to be a major factor affecting growth and metabolism of organisms (Houde 1989), and temperature may be the main factor responsible for variation in size at maturity as water temperature in Uchee Creek 39 is one to two C° warmer than water temperature of the other three streams. Another factor that may have contributed to variations in size at maturity is an organism's response to environmental cues. Uchee Creek 39 has been documented to be *Cyprinella venusta* dominated (Johnston and Farmer, 2004), and in combination with warmer temperature and resource competition, blacktail shiners from this population are expected to increase their reproductive investment by maturing earlier so they can reproduce sooner. However, the effect on size at maturity of temperature cannot be assumed with assumed plastic growth rate, blacktail shiners may exhibit a wide range of sizes at maturity.

Based on length frequency histograms, blacktail shiners from the Chattahoochee River drainage have a life span of 2 – 4 years. Uchee Creek 39, which has only 2 age class, may reflect smaller-sized, mature fishes in that stream. Perceived as degraded, fishes from this site will likely mature faster and reproduce sooner, and probably most will die after their second year. In contrast, more than half (55.6%) of the individuals in Wacoochee Creek are 3 - 4 year olds which explains the bigger samples caught in the site.

Variations in sizes at maturity and growth represent phenotypic plasticity resulting from proximate interactions with the environment (Stearns, 1992). Most stream fish inter-population studies (Heins and Baker, 1987; Heins, 1991; Guill and Heins, 1996; Heins, 2000; Machado et al., 2002) found strong evidence that differences in life history parameters were caused by environmental components. The differences observed in life history parameters among populations in the Chattahoochee River drainage may be due to available food resources and fish biodiversity between streams. Data from past surveys showed that fish biodiversity was lowest in Uchee Creek 39 (less than 10 species) (Johnston and Farmer, 2004) and was dominated by *Cyprinella venusta* that may lead to intense intraspecific competition. Although not documented in this study, I suspect that habitat use and food competition will greatly affect growth of blacktail shiners in Uchee Creek 39. In other streams with higher fish diversity, because of resource segregation, I hypothesize that there will be less habitat and food competition for blacktail shiners, as the other species will have different habitat and diet preferences. Studies have documented food and habitat segregation in sympatric species minimizing competition for resources by feeding on different types of food at different places in the water column in different habitats (Moyle, 1973; Mendelson, 1975). Furthermore, Grossman and Freeman (1987) observations on microhabitat use in stream fishes reported that aggression between heterospecifics was rare and there was more intense aggression towards conspecifics. Habitat and food competition between *Cyprinella venusta* individuals may explain in part the difference in growth rates between populations. Vertical segregation permits species with different diet preference a partitioning of food resources (e.g. benthic, midwater and surface feeders).

Sex ratio can provide information on demography and can be useful in assessing reproductive potential in fish populations (Vicentini and Araújo, 2003). Skewed sex ratio observed in Uchee Creek 169, Moffits Mill and Wacoochee Creek may have resulted from variable factors such as environmental stability or harshness resulting to mortality between sexes (Hoenig and Hewitt, 2005) or habitat use and conspecific aggressions (Grossman and Freeman, 1987). During spawning periods, males may become aggressive and hostile to other males in competing for mates and protecting their territory, which may have resulted in increased mortality in males. Heins (1990) documented spawning behaviour of *Cyprinella venusta* males using video and direct observations and reported that there is a higher degree of violent encounters with conspecific males than other

Cyprinella species. This reproductive behaviour of the blacktail shiner, especially aggression of males towards conspecific males may have resulted in the smaller ratio of males to females. Sex ratio can also provide information on growth and lifespan of fishes in a population (Schultz, 1996). It is likely that the skewed ratio from the three populations of *Cyprinella venusta* likely resulted from unequal longevity of males and females. Future studies on the blacktail shiner life history warrants growth and longevity comparisons between populations.

Variation in clutch and egg sizes among populations indicates that *Cyprinella venusta* is altering life history parameters depending on its stream environment. Environmental heterogeneity can select for phenotypic plasticity (Levins, 1968; Via, 1993) and the differences observed in CS among populations may have resulted from habitat, food, or maybe genetic difference. Heins and Dorsett (1986) and Heins and Baker (1987) reported clutch size of 139-459 eggs from the Gulf Coastal Plain. Clutch sizes from this study showed a range of 61-1515 eggs which has a significantly broader range than recent studies. This difference in clutch sizes demonstrates life history adjustments within different environments supporting the hypothesis that *Cyprinella venusta* persists because it can alter reproductive allocation.

Roff (1992) considered egg sizes to be less phenotypically plastic than clutch size. In this study, mature egg diameters did not show significant differences among populations, however, ripening egg diameters were variable among populations between spawning months. As typical with cyprinids, *Cyprinella venusta* exhibits multiple egg size classes, a characteristic of multiple clutch spawners (Mayden, 1989; Boschung and Mayden, 2004; Heins and Dorsett, 1986; Heins and Baker, 1987) and egg size was not correlated with SL (Heins and Dorsett, 1986; Heins and Baker, 1987; this study). Heins and Dorsett (1986) reported egg diameters for Coastal Plain populations as 0.97-1.34 mm and Heins and Baker (1987) reported egg diameters ranging from 0.88-1.21 mm for 16 populations in southern United States. Egg diameters for this study (MA and MR combined) range from 0.78-1.31 mm which is consistent with other populations studied for this species. Egg size difference in populations may represent differences in stream discharge with a higher discharge and run-offs results to higher offspring mortality (Schlosser, 1985; Heins and Baker, 1987; Machado et al., 2002). To compensate for higher mortality in streams with high discharges, fishes will develop bigger eggs, and larvae from larger eggs will have larger body size and greater swimming strength than larvae developed from smaller eggs. Larvae from bigger eggs attained a bigger size faster and increase the chances of survival. In this study, the sites perceived to have a high discharge and faster flows are Uchee Creek 39 and Moffits Mill and theoretically eggs from these populations will be bigger, however Uchee Creek 169 eggs were bigger in this study and might be caused by other environmental influences such as greater amount of food, a more stable habitat allowing females to produce larger eggs. Uchee Creek 169 is an area with minimal disturbance, and if there are more food resources in this stream, blacktail shiners will spend less time and energy foraging and in the process will have more time and energy for other functions such as growth and reproduction. Larger eggs may also be due to genetic factors and future life history studies coupled with a genetic component will allow researchers to determine additional factors causing life history variations.

Cyprinella venusta are known to spawn from April to early September (Heins and Dorsett 1986). In this study however, we were not able to get samples from April and was not able to determine the exact time spawning starts among the four populations. Although this study was not able to document the start of spawning season in the four sites, basing from mature and ripening ovaries extracted from May samples for all populations, it can be said that spawning may have started in late March or early April. Again, temperature is an important determinant of fish spawning period and egg development at a regional scale (Brett 1970; Clarkson and Childs, 2000). Fishes from Chattahoochee populations, although have different stream temperature have probably same spawning period that lasted till August for females. Same spawning schedule among females could be due to smaller geographic scale as in contrast to regional scale differences in spawning period. Results in this study indicated that males from three populations have extended spawning season until September. The start of spawning schedules for each population could be documented better if samples were taken prior to the spawning season.

The differences in life history parameters among four *Cyprinella venusta* populations in Alabama streams are a typical reaction norm for fishes responding to their highly variable environments. In life history theory, in order for fishes to increase their survival in unpredictable environments, fishes adjust their life history parameters by maturing earlier so they can reproduce sooner, have smaller body sizes as they invest more on reproduction instead of growth, produce many but smaller propagules so the chances that one or few of their offspring survives and continue their lineage. *Cyprinella venusta* has a strategy consistent with opportunistic life history strategy (see Winemiller and Rose, 1992) and is the major reason for its persistence in disturbed environments; a trait which not all fishes has which might be a major factor for some species declines.

Although this opportunistic strategy of high fecundity, high population doubling time and the ability to colonize new habitats, fishes that exhibit this strategy are still in danger of extirpation due to habitat loss and degradation, even minor anthropogenic disturbance can pose a major impact to these fishes. In cyprinids and other opportunistic strategists, although not commercially exploited, should still be a major conservation focus as most of these species have declining populations. Cyprinids are important link in the aquatic food chain as they serve as food resources for larger piscivores (Winemiller and Rose, 1992).

Life history studies provide resource managers insights on what species are able to persist or decline in a certain environmental condition. Information from these studies can prevent population declines and extinctions in organisms. Habitat protection and monitoring should be a priority of fisheries managers and conservation biologists in order for species to increase survival and persistence.

CONCLUSION

This study found variation in life history parameters of *Cyprinella venusta* among four populations in a single drainage system. These variations in life history traits are a result of adaptive phenotypic plasticity in response to unpredictable heterogeneous environment. The results of this study are consistent with other inter-population studies on the blacktail shiner. The significant life history trait differences among the four populations show life history adjustments supporting the hypothesis that *Cyprinella venusta* persists because it can alter its life history metrics across habitat disturbance regimes.

The results of this study will help in understanding species extinctions, species persistence and stream homogenization. With widespread environmental disturbance, the species that are tolerant to biotic and abiotic changes will persist and perhaps even expand their ranges. Since this species persists in degraded habitats, and given its high tolerance to environmental stress, this species may be a conservation threat to similar imperiled species by displacing them in their native habitats. Thus, stream homogenization occurs when environmental changes promote invasion and expansion of tolerant species and the reduction of other species (McKinney and Lockwood, 1999). Another cause of conservation concern is loss of genetic integrity through hybridization. Species of *Cyprinella* are known to hybridize when coming in contact with closely similar species. *Cyprinella venusta* has been known to hybridize with *Cyprinella callitaenia*, *Cyprinella whipplii* and hybrid swarms has been reported with *Cyprinella lutrensis.* (Boschung and Mayden, 2004). Genetically mixed populations will lose their distinctness due to the loss of genetic variation and may decrease their fitness resulting to a decline in populations. The ability to alter and adjust life history traits can make *Cyprinella venusta* a successful invasive species and may cause genetic damage among populations. Fisheries managers should be aware of the consequence and impact of species invasion if we are to preserve diversity among stream habitats.

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TABLE 1. MEAN STANDARD LENGTH (SL IN mm) OF *Cyprinella venusta* DURING THE SPAWNING SEASON FROM FOUR POPULATIONS IN THE CHATTAHOOCHEE RIVER DRAINAGE. Numbers in parentheses are standard deviations. Means with same letters are not significantly different. UC 39 = Uchee Creek 39, UC 169 = Uchee Creek 169, MM = Moffits Mill, WC = Wacoochee Creek

Population	Mean (±SD)		
	Female	Male	Female/Male combined
UC 39	61.7(±8.3)[a] n=119	80.1(±8.0)[a] n=38	65.7(±11.4)[a] n=157
UC 169	62.2(±7.6)[ab] n=93	88.0(±8.6)[b] n=31	67.9(±13.4)[a] n=124
MM	64.6(±7.0)[b] n=114	82.5(±7.9)[a] n=45	69.2(±10.9)[a] n=159
WC	71.0(±11.5)[c] n=82	85.1(±11.4)[b] n=14	72.9(±12.4)[b] n=96
F value	22.8	5.03	7.97
P-value	0.0001	0.003	< 0.0001

TABLE 2. STATISTICS FOR CLUTCH SIZE-STANDARD LENGTH RELATIONSHIPS FOR FOUR POPULATIONS OF *Cyprinella venusta*. All values were $\log_{10}$ transformed prior to analysis.

Population	n	Intercept	Slope	r^2	*P*-value
UC 39	119	-2.88130	2.94766	0.5229	< 0.0001
UC 169	93	-3.33040	3.17116	0.506	< 0.0001
MM	114	-2.09781	2.53000	0.3374	<0.0001
WC	82	-2.40643	2.70475	0.4789	< 0.0001

TABLE 3. MONTHLY SL-ADJUSTED MEAN CLUTCH SIZES FOR EACH POPULATION OF *Cyprinella venusta*. Numbers in parentheses are standard deviations. Means with same letters are not significantly different.

Population	May	June	July	August	All months combined
UC 39	366(±117)[bc]	388(±149)[a]	286(±101)[ab]	170(±64)[a]	281(±145)[ab]
n	25	24	32	38	119
UC 169	327(±107)[b]	318(±125)[b]	254(±110)[a]	136(±83)[a]	252(±124)[a]
n	22	28	24	19	93
MM	412(±143)[c]	396(±133)[a]	316(±100)[b]	155(±70)[a]	300(±140)[b]
n	25	26	38	25	114
WC	345(±117)[bc]	390(±124)[ab]	324(±80)[b]	137(±87)[a]	302(±129)[b]
n	25	17	31	9	82
F value	3.21	4.30	4.79	1.54	4.31
P-value	0.0266	0.0069	0.0035	0.2104	0.0053

TABLE 4. MONTHLY MEAN GONAD MASS OF FEMALES (g) FOR EACH POPULATION OF *Cyprinella venusta*. Standard deviation in parentheses.

Population	May	June	July	August	All months combined
UC 39	0.1289(±0.060)	0.1646(±0.148)	0.1166(±0.066)	0.0588(±0.037)	0.1079(±0.114)
n	25	24	32	38	119
UC 169	0.1268(±0.057)	0.1335(±0.108)	0.1142(±0.093)	0.0562(±0.061)	0.1043(±0.088)
n	22	28	24	19	93
MM	0.1338(±0.140)	0.1790(±0.132)	0.1457(±0.090)	0.0663(±0.037)	0.1242(±0.096)
n	25	26	38	25	114
WC	0.1349(±0.146)	0.1697(±0.169)	0.1275(±0.143)	0.0566(±0.141)	0.1219(±0.139)
n	25	17	31	9	82
F value	0.06	1.91	1.46	0.43	2.1
P-value	0.9807	0.1336	0.2294	0.7313	0.1002

TABLE 5. MONTHLY MEAN GONAD MASS OF MALES (g) FOR EACH POPULATION OF *Cyprinella venusta*. Standard deviation in parentheses.

Population	May	June	July	August	September	All months combined
UC 39	0.0298(±0.005)	0.0172(±0.01)	0.0230(±0.021)	0.0109(±0.007)	0.0054(±0.003)	0.0171(±0.016)
n	4	12	13	6	3	38
UC 169	0.0338(±0.024)	0.0169(±0.02)	0.0536(±0.042)	0.0116(±0.007)	0.0068(±0.006)	0.0207(±0.020)
n	4	6	9	6	6	31
MM	0.0245(±0.017)	0.0295(±0.015)	0.0362(±0.028)	0.0246(±0.022)	0.0090(±0.005)	0.0235(±0.022)
n	9	5	13	11	7	45
WC	0.0322(±0.004)	0.0211(±0.007)	0.0260(±0.006)	0.0106(±0.016)	0	0.0227(±0.009)
n	2	3	7	2	0	14
F value	0.38	0.79	4.76	2.38	0.49	1.13
P-value	0.7699	0.5128	0.0066	0.0998	0.6238	0.3393

TABLE 6. MEAN MATURE EGG DIAMETER (mm) OF *Cyprinella venusta* FROM FOUR POPULATIONS IN THE CHATTAHOOCHEE RIVER DRAINAGE. Standard deviation in parentheses.

Population	May	June	July	August	All months combined	Range
UC 39	1.00(±0.12)	0.96(±0.08)	0.90(±0.05)	0.90(±0.08)	0.94(±0.08)	0.79-1.24
n	16	10	16	19	61	
UC169	1.01(±0.07)	0.98(±0.05)	0.92(±0.06)	0.93(±0.12)	0.96(±0.08)	0.80-1.17
n	13	14	13	9	49	
MM	0.94(±0.12)	0.94(±0.06)	0.92(±0.04)	0.98(±0.07)	0.94(±0.08)	0.78-1.23
n	12	14	20	14	60	
WC	0.99(±0.10)	0.99(±0.07)	0.91(±0.05)	0.89(±0.06)	0.94(±0.09)	0.78-1.21
n	12	8	16	6	42	
F value	1.11	1.40	0.25	2.39	0.71	
P-value	0.3529	0.2575	0.8593	0.0816	0.5467	

TABLE 7. MEAN RIPENING EGG DIAMETER (mm) OF *Cyprinella venusta* FROM FOUR POPULATIONS IN THE CHATTAHOOCHEE RIVER DRAINAGE. Numbers in parentheses are standard deviations. Means with same letters are not significantly different.

Population	May	June	July	August	All months combined	Range
UC 39	1.08(±0.08)	1.03(±0.06)[a]	1.02(±0.05)[a]	1.05(±0.08)	1.04(±0.06)[a]	0.94-1.18
n	9	14	16	18	57	
UC169	1.08(±0.06)	1.07(±0.04)[ab]	1.10(±0.09)[b]	1.06(±0.06)	1.08(±0.06)[b]	0.93-1.31
n	9	14	11	10	44	
MM	1.06(±0.06)	1.08(±0.06)[ab]	1.02(±0.05)[a]	1.08(±0.05)	1.06(±0.06)[b]	0.93-1.19
n	13	12	18	11	54	
WC	1.09(±0.07)	1.11(±0.05)[b]	1.04(±0.04)[a]	1.02(±0.04)	1.06(±0.07)[b]	0.96-1.19
n	13	9	15	3	40	
F value	0.52	3.87	5.91	0.84	3.07	
P-value	0.6732	0.0155	0.0014	0.4812	0.0290	

TABLE 8. MEAN MATURE EGG MASS (g) DURING SPAWNING MONTHS FOR *Cyprinella venusta*. Means with same letters are not significantly different. Standard deviation in parentheses.

Population	May	June	July	August	All months combined
UC 39	0.00031(±0.00022)	0.00033(±0.00014)	0.00034(±0.00014)	0.00035(±0.00009)[a]	0.00031(±0.00015)
n	16	10	16	19	61
UC 169	0.00031(±0.00022)	0.00031(±0.00012)	0.00037(±0.00012)	0.00039(±0.00008)[b]	0.00034(±0.00015)
n	13	14	13	9	49
MM	0.00022(±0.00022)	0.00030(±0.00008)	0.00040(±0.00014)	0.00039(±0.00018)[b]	0.00033(±0.00015)
n	12	14	20	14	60
WC	0.00034(±0.00022)	0.00035(±0.00009)	0.00031(±0.00013)	0.00037(±0.00016)[b]	0.00033(±0.00015)
n	12	8	16	6	42
F value	2.63	0.73	1.78	3.97	0.55
P-value	0.0609	0.5414	0.1545	0.0138	0.6476

TABLE 9. MEANS FOR RIPENING EGG MASS (g) DURING SPAWNING MONTHS FOR *Cyprinella venusta*. Standard deviation in parentheses.

Population	May	June	July	August	All months combined
UC 39	0.00045(±0.00018)	0.00052(±0.00022)	0.00050(±0.00015)	0.00043(±0.00016)	0.00048(±0.00019)
n	9	14	16	18	57
UC 169	0.00050(±0.00018)	0.00053(±0.00018)	0.00062(±0.00034)	0.00044(±0.00012)	0.00051(±0.00019)
n	9	14	11	10	44
MM	0.00045(±0.00018)	0.00070(±0.00018)	0.00054(±0.00016)	0.00049(±0.00012)	0.00053(±0.00018)
n	13	12	18	11	54
WC	0.00048(±0.00019)	0.00065(±0.00021)	0.00048(±0.00013)	0.00053(±0.00007)	0.00052(±0.00020)
n	13	9	15	3	40
F value	0.14	2.55	1.21	0.62	0.98
P-value	0.9357	0.0683	0.3152	0.6064	0.4047

TABLE 10. GONADOSOMATIC INDEX (GSI) OF *Cyprinella venusta* FEMALES DURING SPAWNING MONTHS. Standard deviation in parentheses.

Population	May	June	July	August	All months combined
UC 39	5.2(±4.3)	5.6(±3.3)	6.5(±3.7)	4.1(±2.2)	5.3(±3.5)
n	25	24	32	38	119
UC 169	5.1(±2.6)	4.7(±2.6)	6.6(±4.1)	3.4(±1.6)	4.9(±3.2)
n	22	28	24	19	93
MM	6.0(±4.0)	6.5(±3.4)	7.0(±3.2)	4.1(±1.8)	5.8(±3.4)
n	25	26	38	25	114
WC	4.9(±3.3)	5.2(±3.4)	6.5(±3.4)	2.5(±2.2)	5.2(±3.4)
n	25	17	31	9	82
F value	0.54	2.35	0.18	2.53	1.87
P-value	0.6560	0.0775	0.9121	0.0625	0.1339

TABLE 11. MONTHLY GSI MEANS FOR THE FOUR POPULATIONS OF *Cyprinella venusta* MALES. Means with same letters are not significantly different. Standard deviation in parentheses.

Population	May	June	July	August	September	All months combined
UC 39	0.4(±0.2)[a]	0.3(±0.2)[a]	0.4(±0.3)[a]	0.3(±0.2)[a]	0.1(±0.1)[a]	0.3(±0.2)[a]
n	4	12	13	6	3	38
UC 169	0.4(±0.2)[a]	0.3(±0.2)[a]	0.8(±0.3)[b]	0.2(±0.1)[a]	0.1(±0.1)[a]	0.3(±0.2)[a]
n	4	6	9	6	6	31
MM	0.4(±0.2)[a]	0.4(±0.2)[a]	0.6(±0.3)[ab]	0.5(±0.2)[b]	0.1(±0.1)[a]	0.4(±0.3)[a]
n	9	5	13	11	7	45
WC	0.5(±0.3)[a]	0.5(±0.3)[a]	0.5(±0.2)[a]	0.2(±0.1)[a]	0.0	0.4(±0.3)[a]
n	2	3	7	2	0	14
F value	0.26	0.76	3.24	3.20	0.1	1.37
P-value	0.8497	0.5277	0.0330	0.0455	0.9066	0.2539

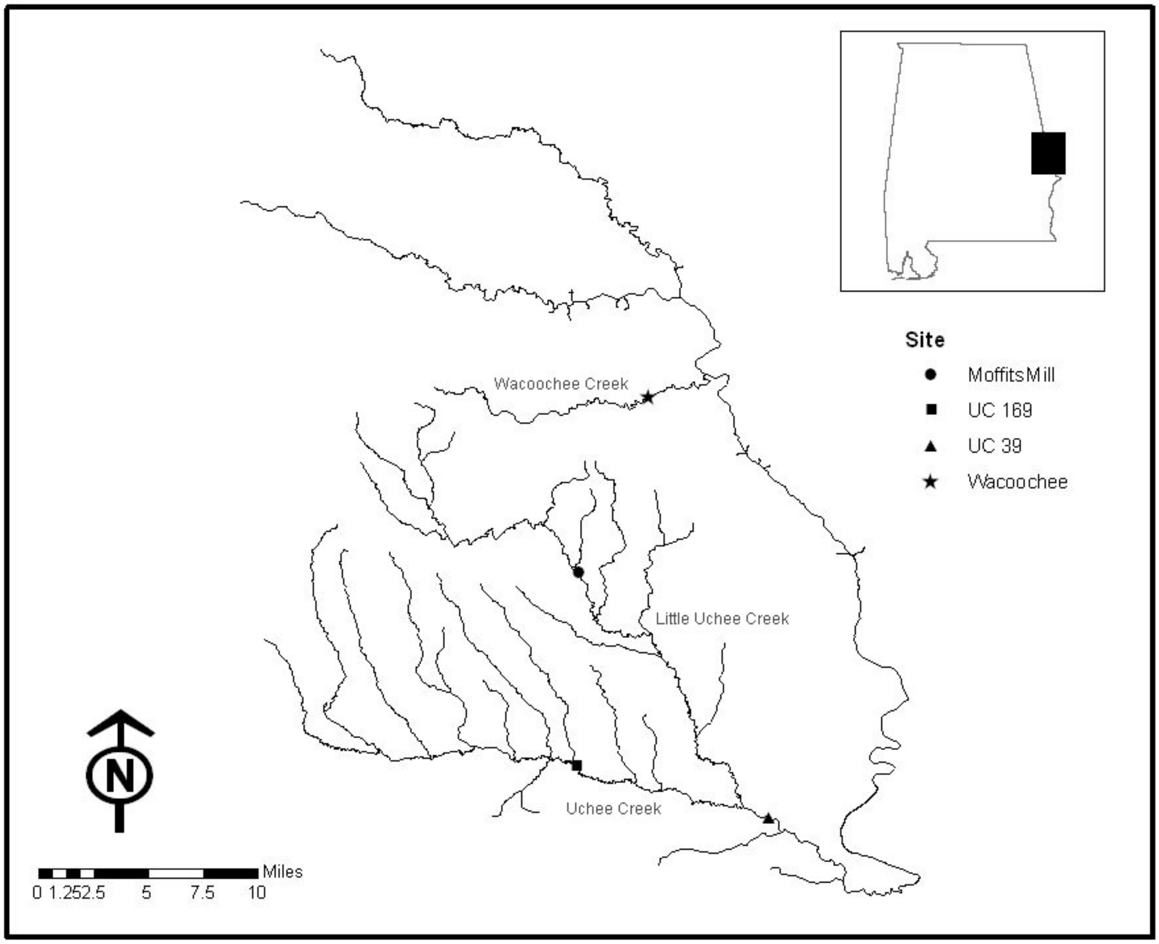

Fig. 1. Sampling localities of *Cyprinella venusta* populations within the Chattahoochee River drainage in Alabama, USA.

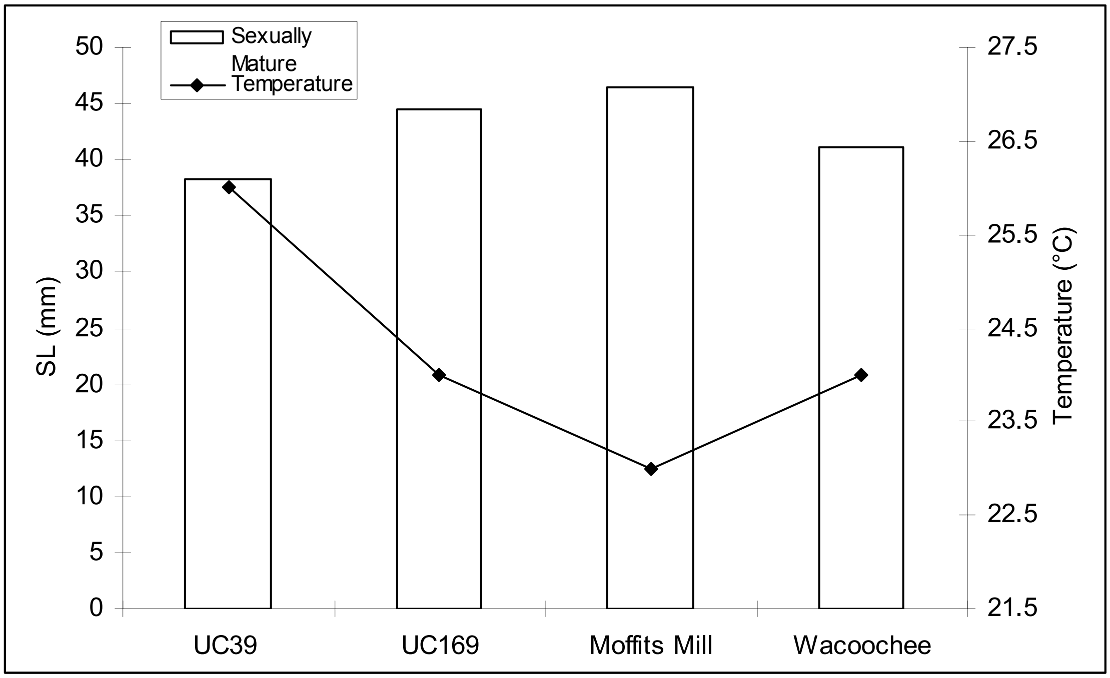

Fig. 2. Size at maturity of *Cyprinella venusta* females. Females with early maturing (EM) ovarian stages were considered sexually mature. A total of 2311 females were examined to determine size at maturity. Solid line represents mean temperature for each site.

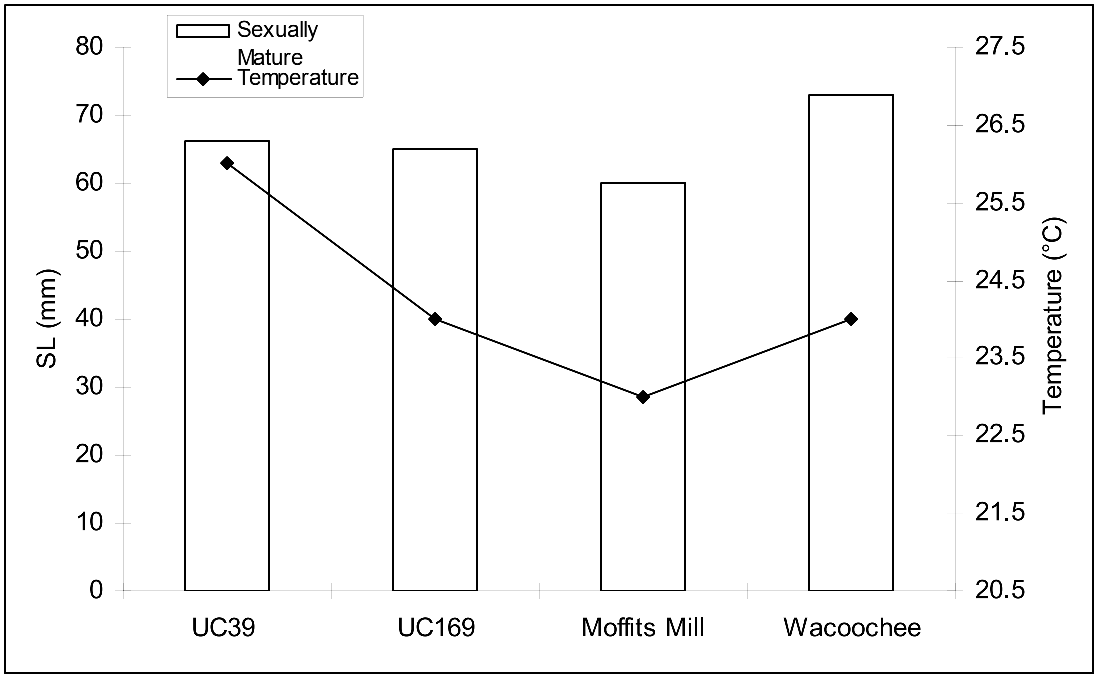

Fig. 3. Size at maturity of *Cyprinella venusta* males (n=128). Solid line represents mean temperature for each site.

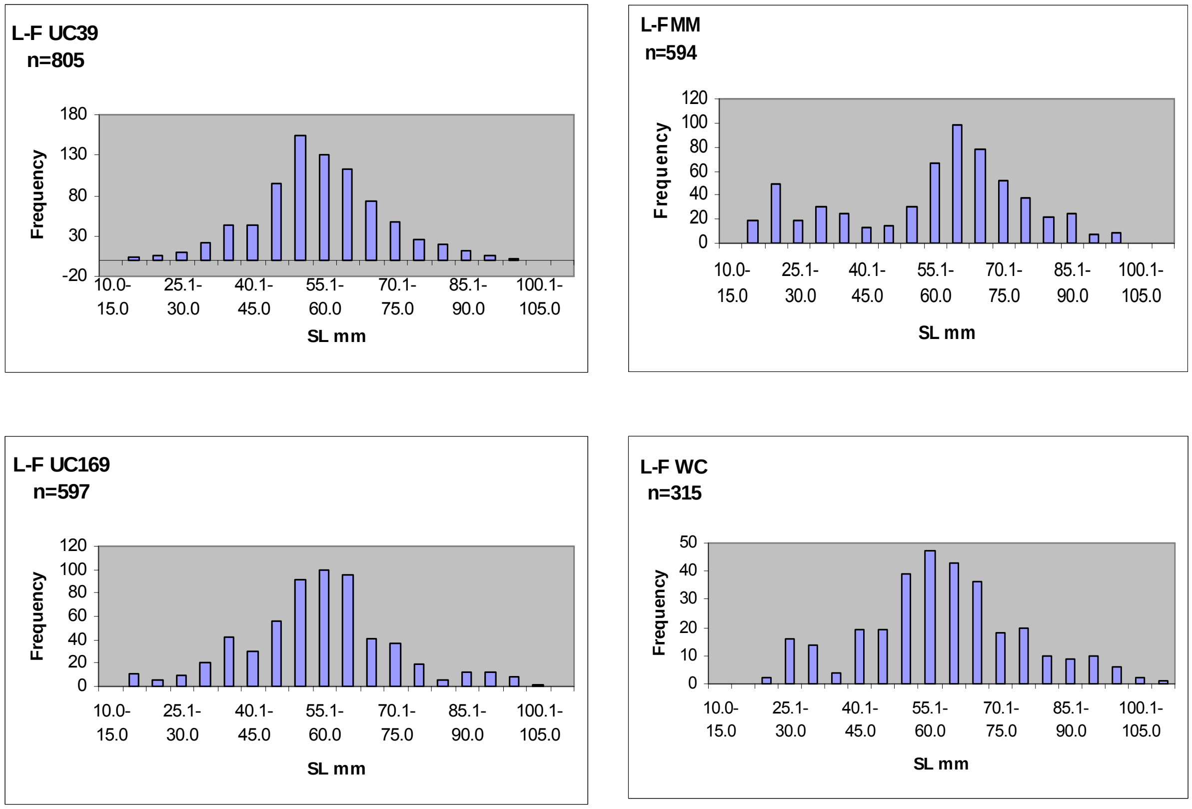

Fig. 4. Length-frequency histograms for *Cyprinella venusta* taken from four populations along the Chattahoochee River drainage from May to November 2005.

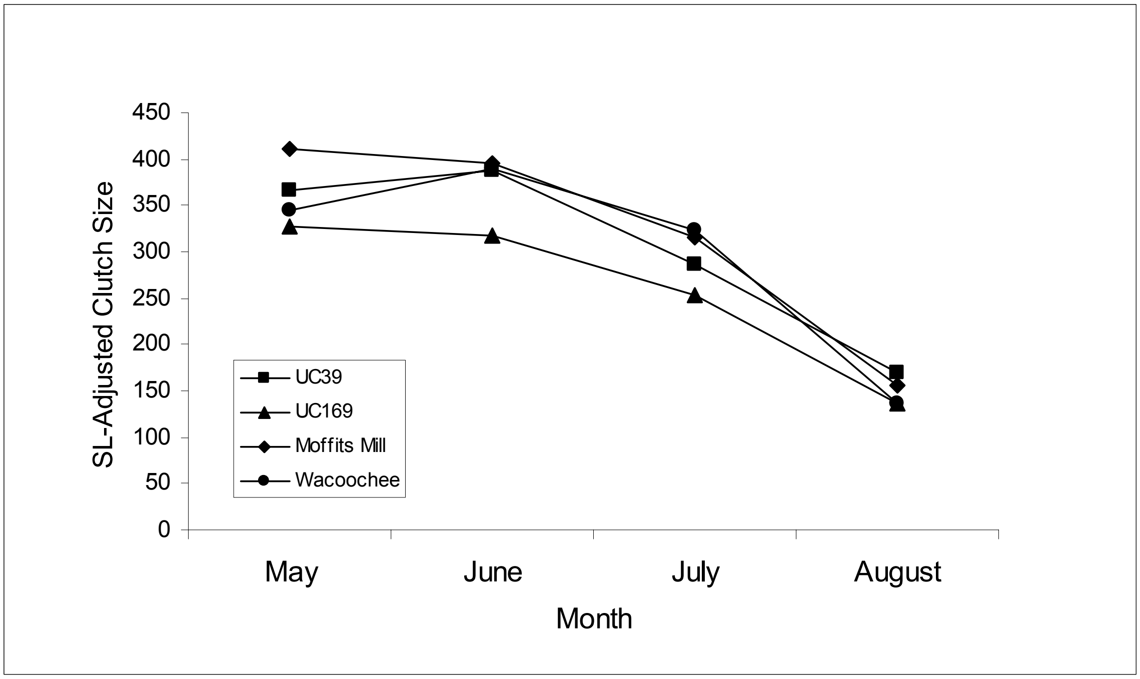

Fig. 5. Monthly changes in SL-adjusted mean clutch size of *Cyprinella venusta* from four sites in the Chattahoochee River drainage. Clutch sizes peaked in May to June and starts to drop as eggs were being spawned (F = 4.31, n = 408, *P* = 0.0053).

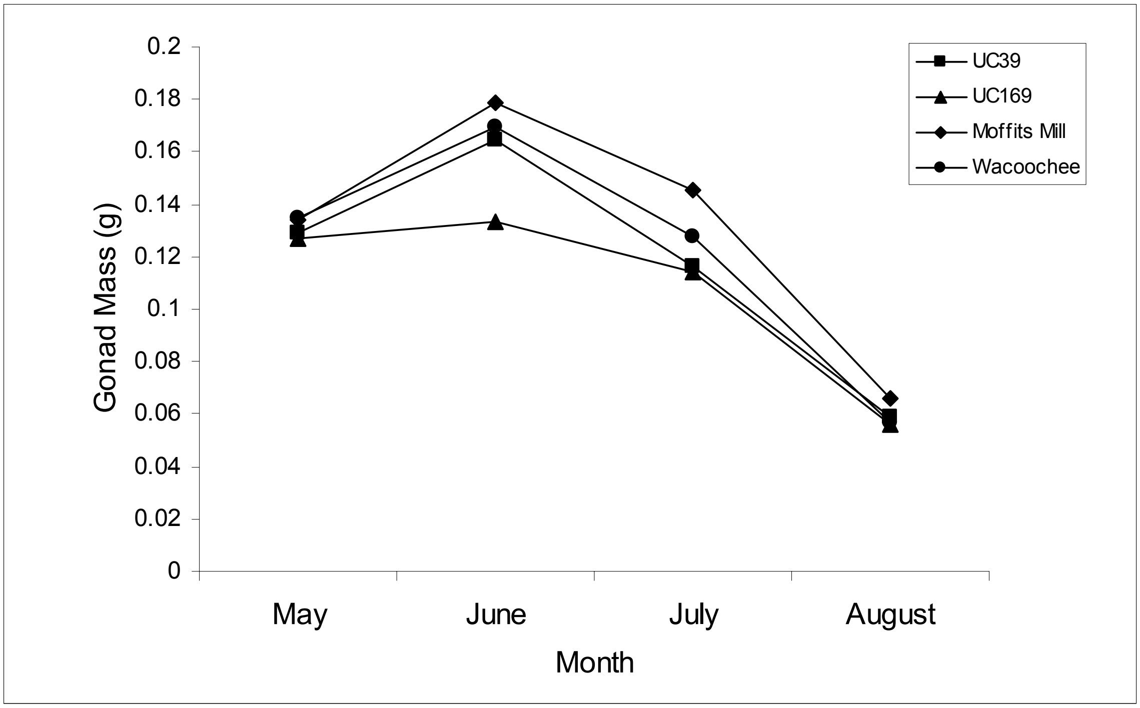

Fig. 6. Monthly variation in mean gonad mass of *Cyprinella venusta* females from the Chattahoochee River drainage. Gonad mass peaked in June for all populations (F = 2.1, n = 408, *P* = 0.1002).

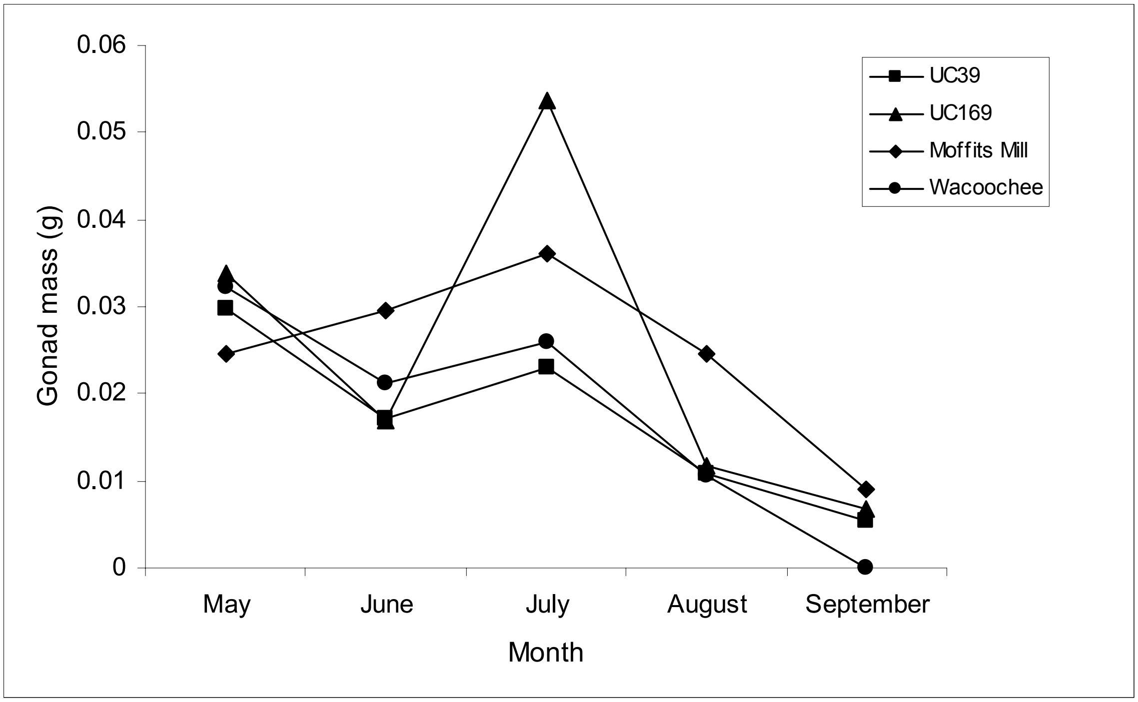

Fig. 7. Monthly variation in mean gonad mass of *Cyprinella venusta* males from the Chattahoochee River drainage. Significant differences of gonad mass only in July. Gonad mass from Uchee Creek 39 males was significantly smaller than the gonad mass of Uchee Creek 169 males. n = 128.

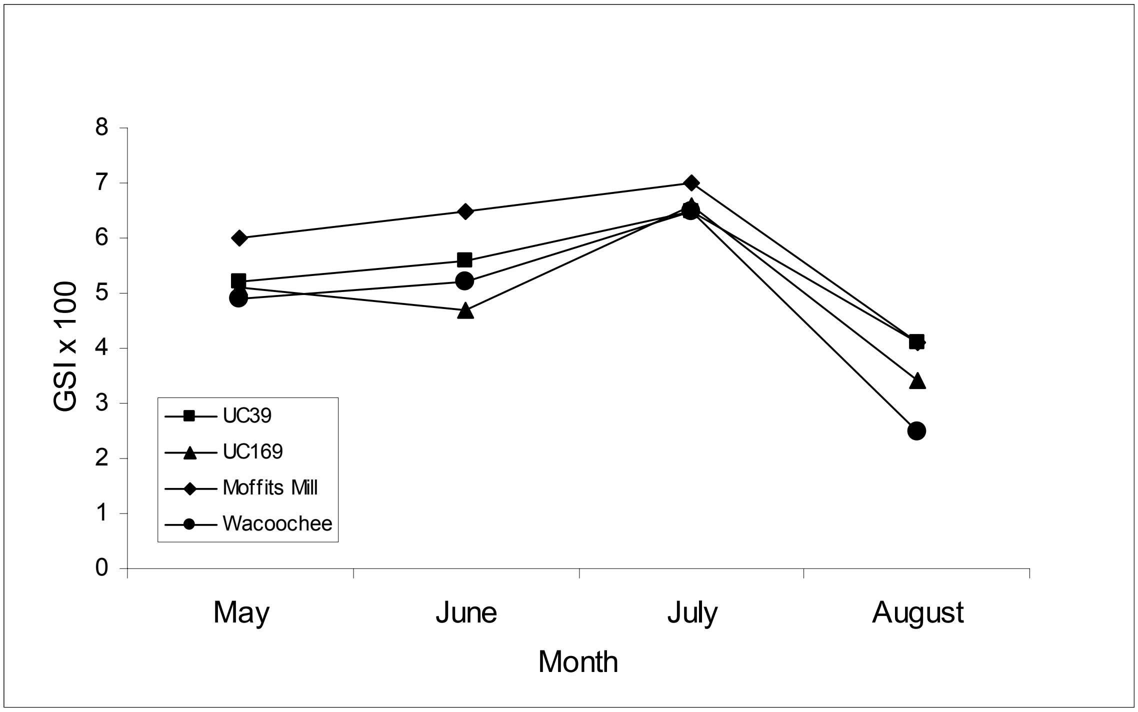

Fig.8. Monthly variation in gonadosomatic indices (GSI) of female *Cyprinella venusta* from four sites in the Chattahoochee River drainage. There were no significant differences in monthly GSI for all populations in all spawning months (F = 1.87, n = 408, *P* = 0.1339).

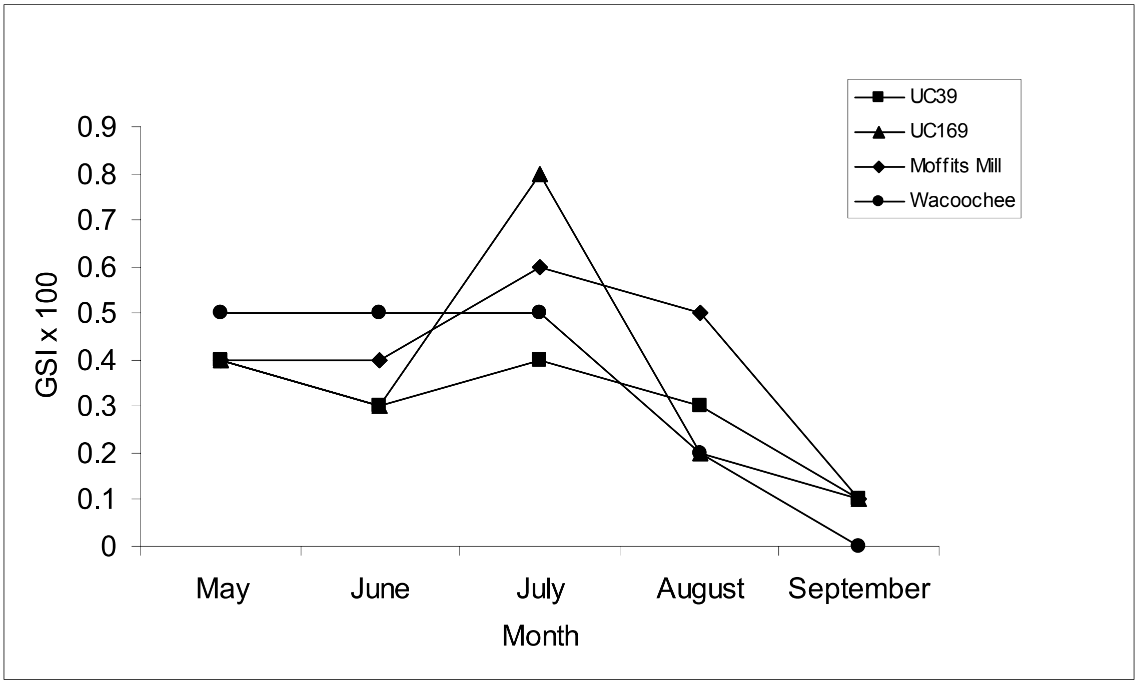

Fig. 9. Monthly variation in gonadosomatic indices of *Cyprinella venusta* males from four sites in the Chattahoochee River drainage. Uchee Creek 169 GSI was significantly higher than Wacoochee Creek and Uchee Creek 39 in July. GSI for Moffits Mill was significantly higher than the other three populations in August. All other months shows no significant differences in GSI for all populations. Wacoochee Creek males were latent by September. n = 128.