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Life History Variation in the Yazoo Shiner (Notropis rafinesquei) in Three Mississippi Streams

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Abstract.—We investigated the life history and demographics of *Notropis rafinesquei* (Cyprinidae) in three streams in north Mississippi, USA, over 2 y. Size at maturity (22.5–29.3 mm SL) and the timing and duration of the reproductive period (Apr.–Aug.) were similar among all three streams in both years. We consistently detected two young-of-the-year cohorts, one strong cohort appearing in early summer and the other of varying strength in fall. In contrast, we found striking variation in most other life history traits including female length, body weight, clutch size, ova diameter and sex ratios, despite the close geographic proximity of these populations. Life history traits of all other species in the *Notropis longirostris* clade (*N. ammophilus, N. longirostris* and *N. sabinae*) are similar to *N. rafinesquei*, but like *N. rafinesquei*, vary widely among and within species. The highly plastic nature of reproductive traits in *N. rafinesquei* and other members of the *N. longirostris* clade is likely an important adaptation that allows these animals to maintain large populations in the often physically unstable and unpredictable stream environments of the Gulf Coastal Plain, USA.

Introduction

The Yazoo shiner, *Notropis rafinesquei* (Cyprinidae), is a member of the *N. longirostris* clade including *N. ammophilus, N. longirostris* and *N. sabinae,* each of which occupies a narrow range in the southeastern United States (Suttkus, 1991; Raley and Wood, 2001). *Notropis rafinesquei* is endemic to the upper Yazoo River drainage in Mississippi, including portions of the Coldwater, Tallahatchie, Yalobusha and Yazoo River systems (Ross, 2001). Within its small range, *N. rafinesquei* is often a numerically dominant member of stream fish communities, even in highly degraded streams (Suttkus, 1991; Adams *et al.*, 2004).

Life history information exists for other members of this clade (*e.g., Notropis ammophilus,* Heins *et al.*, 1980; Suttkus and Boschung, 1990; *N. longirostris,* Heins and Clemmer, 1976; Suttkus and Boschung, 1990; *N. sabinae,* Heins, 1981; Suttkus and Boschung, 1990), but little is known about the life history of *N. rafinesquei.* We investigated the life history and demographics of *N. rafinesquei* in three north Mississippi streams over 2 y. We estimated size at maturity, adult body size, longevity, timing and frequency of spawning, clutch size and egg size. Because the study streams vary in their degree of human-induced degradation and because their fish communities show high seasonal variation (Adams *et al.*, 2004), we were particularly interested in how life history traits of *N. rafinesquei* varied among streams and between years.

Study Area

We studied the life history of *Notropis rafinesquei* in three tributaries of the Little Tallahatchie River, upper Yazoo River basin, northern Mississippi (Fig. 1): Buckhorn Creek (Panola Co.; 34°21′04″N, 89°54′47″W), Cypress Creek (Lafayette Co.; 34°26′32″N, 89°17′25″W), and Hotopha Creek (Panola Co.; 34°21′52″N, 89°52′45″W). Cypress and Hotopha Creeks are comparably sized and were channelized for flood control in the 1960s. Both streams are deeply incised and characterized by shifting sand substrate and little

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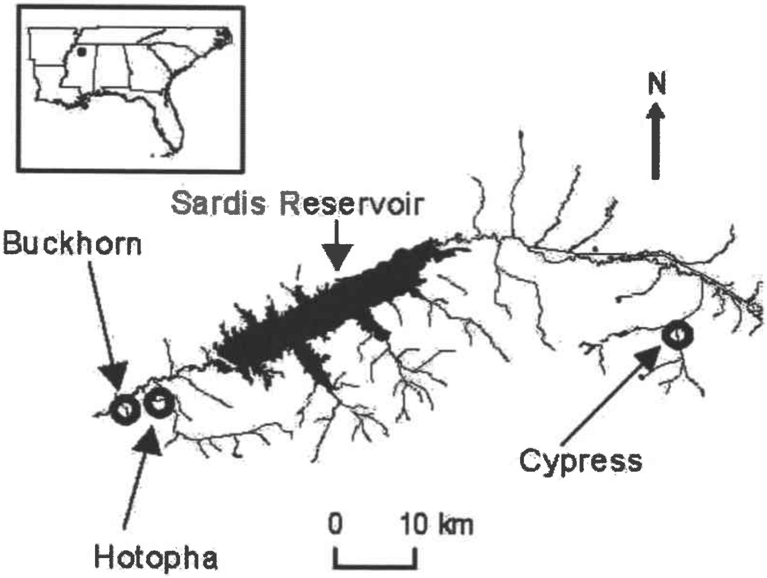


FIG. 1.—Map of the study area in northern Mississippi, USA. Inset map shows location of Mississippi in the eastern United States

canopy cover. Buckhorn Creek is smaller and not channelized, has relatively stable sand and gravel substrate, and is extensively shaded at the study site. For more information on these sites and their watersheds, see Adams *et al.* (2004).

METHODS

We collected *Notropis rafinesquei* approximately monthly from Mar. 1993 to Nov. 1994 by electrofishing and seining. Captured fishes were preserved in 10% buffered formalin. We collected from 29–531 *N. rafinesquei* at each site on each sample date (mean = 140 ± 15.2 SE). In the laboratory, we measured standard length (SL, nearest 0.1 mm) of all individuals and constructed length-frequency histograms of fish from each stream and sample date based on 1– mm size classes. To estimate sex ratios and size at maturity, we dissected all individuals >20 mm SL in May samples from both years and all three streams. By examining gonads, we determined the sex of each individual and classified them as mature or immature. For both years, we used May samples because most mature individuals were reproductively active, and intermediate-sized individuals (20–25 mm SL) were rare later in the spawning season.

We removed ovaries from 15 females from each sample date at each site and classified ovaries as latent, early maturing, late maturing, mature, mature ripening, or ripe, according to Heins and Baker (1993). Collectively, we considered mature, mature ripening and ripe individuals as mature and in spawning condition. We dried the eviscerated bodies and ovaries for 24 h at 100 C then weighed them to the nearest 0.001 g. We expressed relative ovary size as the Gonadosomatic Index [GSI, (ovary weight/total body weight)·100].

We estimated clutch size by counting all mature ova from a maximum of five mature or mature ripening females on each sample date when such individuals were present. We did not estimate clutch size for ripe individuals because some had likely already released eggs, resulting in biased estimates for these individuals. We measured the diameter (nearest 0.0001 mm) of three mature ova from all mature females in each sample at each site. Because ova were not spherical, we expressed the diameter of each ovum as the average of three measurements taken from different axes.

DATA ANALYSIS

We used a two-step analytical approach to examine variation in life history traits among streams and years. For a given trait, we pooled observations from all sample dates within each stream × year combination, and then initially tested a full model including all potential factors related to variation in the trait (*e.g.*, stream, year, and stream × year interaction). When a trait was not significantly different for a given factor and there was no interaction between factors, we did not further explore that factor. For example, if length was not significantly different among years, we pooled years for any further analyses (*e.g.*, differences among streams). We explored the effect of a factor in greater detail when a variable differed significantly among levels of the factor or when there was a significant interaction between factors. We transformed data as necessary to achieve normality and homogeneity of variance; specific transformations used are stated with the results of each analysis.

We examined differences in body size among streams and years using lengths of mature females only to avoid potential confounding effects of the appearance of variable and often large numbers of young-of-the-year (YOY) fishes during the summer and fall. We tested for differences in mean $\log_{10}$ SL of mature females among streams and between years using a two-factor analysis of variance. We tested for differences in length-weight relationships and length-specific weight among streams with analysis of covariance (ANCOVA) using $\log_{10}$-transformed weight and $\log_{10}$ SL as the covariate.

We tested for stream and year differences in mean $\log_{10}$ clutch size and mean ova diameter separately, using two-factor analysis of variance. We used linear regression to examine relationships between clutch size and $\log_{10}$ SL in 1993 and 1994 and ova diameter and $\log_{10}$ SL in all three streams.

RESULTS

Size and weight.—We collected *Notropis rafinesquei* ranging in size from 10.0–41.8 mm SL, but length differed among streams and years. Maximum length was greater in Buckhorn and Cypress Creeks (41.8 and 41.7 mm SL, respectively) than in Hotopha Creek (38.0 mm SL), but was similar within streams (<1.0 mm difference between years in all streams). There was a significant stream × year interaction (ANOVA: $F_{2,293} = 12.34$, $P < 0.0001$, $\log_{10}$ SL) with regard to the effect of these variables on mean length of mature females across the study (Fig. 2). In 1993 mean length of mature females differed among all three streams (ANOVA: $F_{2,147} = 35.67$, $P < 0.0001$, $\log_{10}$ SL) and showed a gradient of decreasing body size from Cypress to Hotopha Creek. In 1994 there was no significant difference in mean length among streams.

Slopes of relationships between length and weight of mature females were not different among streams but differed among years (ANCOVA: $F_{1,112} = 11.78$, $P < 0.001$, both variables $\log_{10}$ transformed). In 1993 length-specific weight differed among all three streams (Fig. 3, ANCOVA: $F_{2,55} = 8.25$, $P < 0.001$) and showed a gradient decreasing from Cypress to Hotopha Creek, similar to the pattern for mean length. In 1994 there was no significant difference in length-specific weight among the three streams (Fig. 3).

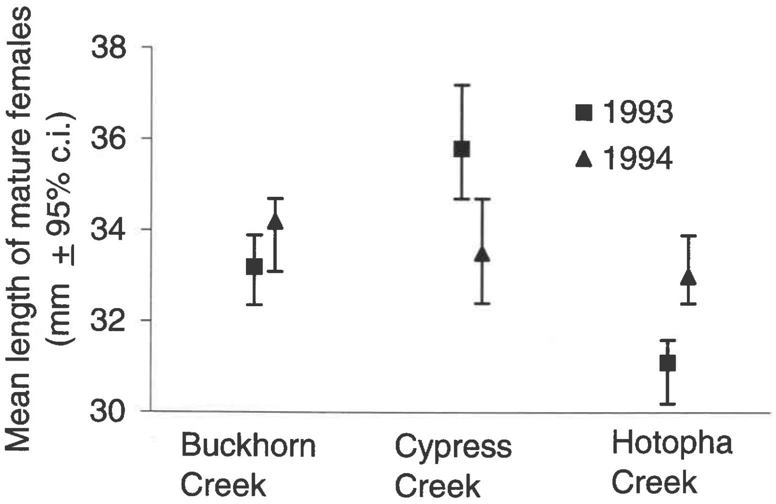


FIG. 2.—Mean standard length of mature female *Notropis rafinesquei* in three north Mississippi streams in 1993 and 1994. Means and confidence intervals are back-transformed from $\log_{10}$ transformed data. For 1993 all means are significantly different from each other

Size at maturity and longevity.—Fish reached sexual maturity at approximately the same size in all three streams (Table 1). Maximum size of immature individuals varied little among streams (28.7–29.3 mm SL), but minimum size at maturity was slightly larger in Buckhorn Creek than in Cypress and Hotopha creeks. Length-frequency distributions suggest that fish live up to 2 y in Buckhorn and Cypress creeks, but only 1.5 y in Hotopha Creek. In Buckhorn and Cypress creeks, two distinct cohorts of adult fish were present prior to spawning (Feb.–May), presumably representing fishes recruited in the previous two years (Fig. 4). The largest cohort disappeared by Jul., but the smaller cohort persisted until the following spring. In Hotopha Creek only a single cohort was present early in the year, presumably representing fishes recruited in the previous year, but this cohort disappeared by fall (Fig. 4).

Sex ratios.—Sex ratios differed among streams (3 × 2 *G*-test: $G = 15.16$, df = 2, $P < 0.001$). After applying the Bonferroni correction for multiple testing, the sex ratio did not differ from 1:1 in Buckhorn Creek (25F:15M, G = 2.527, df = 1, P = 0.317) or Hotopha Creek (71F:47M, $G = 4.92$, df = 1, P = 0.082), but was male-biased in Cypress Creek (24F:48M, $G = 8.16$, df = 1, P = 0.013). Within streams, we were unable to test for differences in sex ratios between years because of low sample sizes.

Timing of spawning.—Seasonal patterns of ovary development and GSI both indicated a protracted spawning period for *Notropis rafinesquei.* In all streams and in both years, the percentage of females with mature ovaries rose sharply in spring when water temperatures reached 17–21 C, exceeded 80% by Apr., and remained at or above this level until Aug. (Fig. 5). During this period, the percentage of females with mature ovaries was 100% on multiple sample dates. This percentage began to decline sharply in Aug., and by Sept. no females in our samples had mature ovaries, even though temperatures remained above 17 C until Oct. in all streams in both years. Ovaries remained latent throughout the winter. Annual variation in GSI showed a pattern similar to ovary development but was more variable during the spawning season (Fig. 5). Although GSI remained high overall from

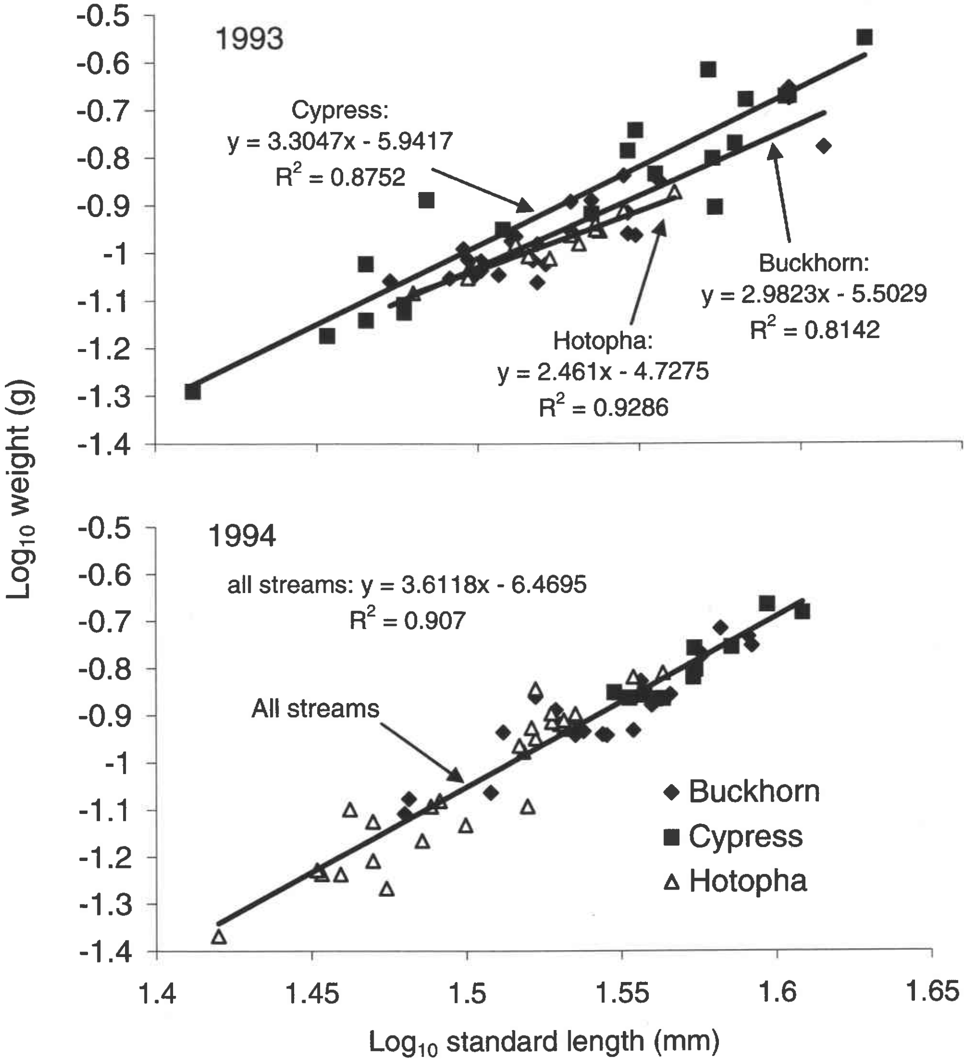


FIG. 3.—Length-weight relationships for mature female *Notropis rafinesquei* in three north Mississippi streams in 1993 and 1994. All regression lines are significant at $P < 0.0001$

Apr. to Aug., peaks in GSI were evident in all three streams during this period. In particular, Buckhorn Creek showed both an early and a late peak in GSI during the spawning season.

In most cases, YOY fish first appeared in Jun. and Jul. and made up a distinct cohort that was prominent in all streams for the remainder of the year (Fig. 4). Fishes from this summer cohort were 10–20 mm SL by Jul.–Aug., and reached 20–30 mm SL by Sept.–Oct. The summer cohort was usually strong and made up a large percentage of the total population by late summer. The single exception to this pattern was in Cypress Creek in 1994, when the summer cohort was weak and consequently was difficult to detect unequivocally in later samples (Fig. 4).

TABLE 1.—Size at maturity for *Notropis rafinesquei* (both sexes combined) in three north Mississippi streams in 1993 and 1994

Size class (mm, SL)	% mature	N
Buckhorn Creek		
<26.8	0	10
26.8–28.7	71	17
>28.7	100	13
Cypress Creek		
<22.5	0	3
22.5–29.1	69	29
>29.1	100	54
Hotopha Creek		
<23.0	0	31
23.0–29.3	62	74
>29.3	100	13

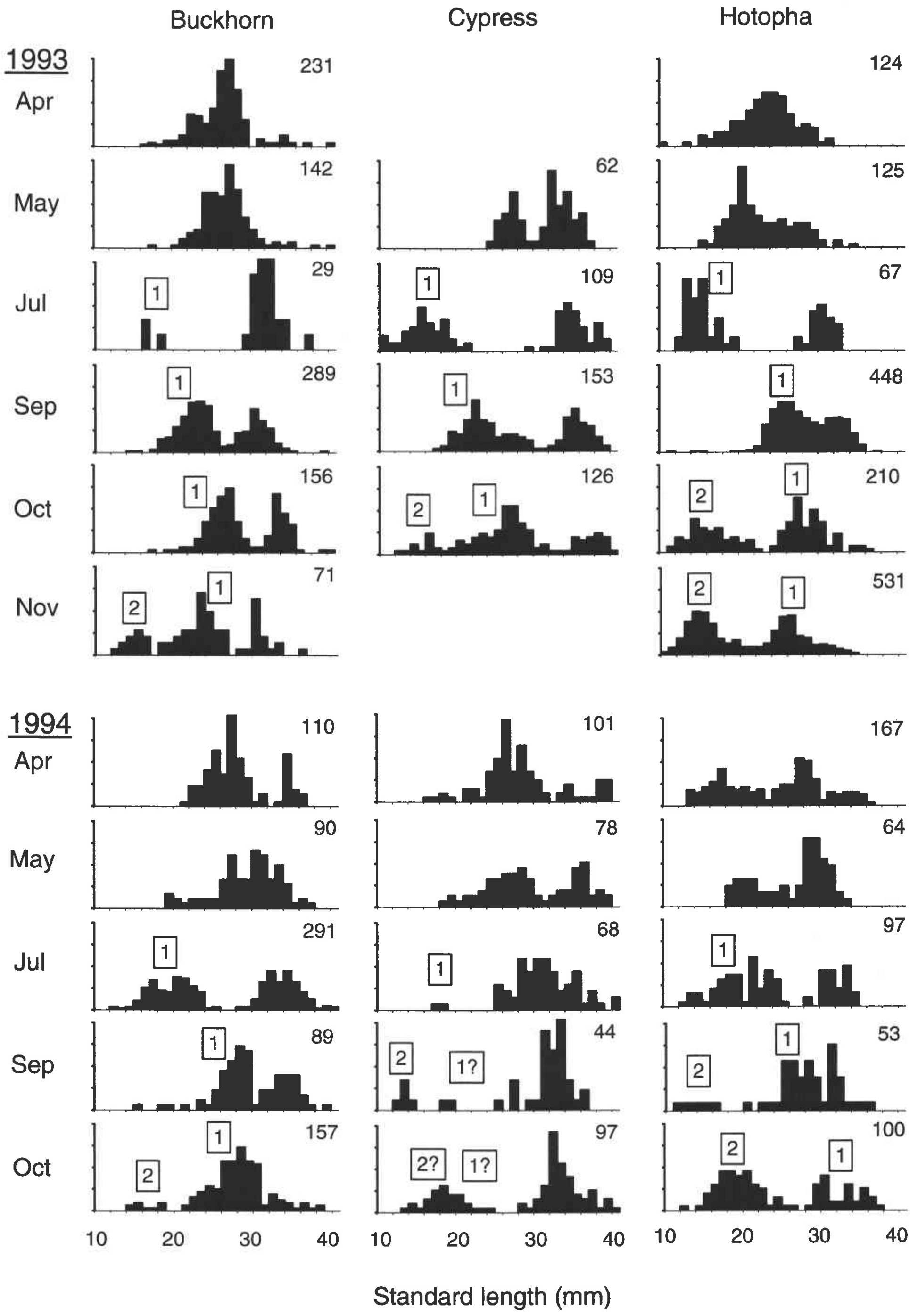
A second distinct cohort of YOY fish appeared from Sept. to Nov. in all streams and in both years (Fig. 4). Fishes from this fall cohort were about 10–20 mm SL by the end of the year. The relative strength of the fall cohort varied widely. The fall cohort made up a small percentage of the total population in both years in Buckhorn Creek and in 1993 in Cypress Creek. In contrast, the fall cohort was strong in Hotopha Creek in both years (Fig. 4).

Clutch characteristics.—Clutch size ranged from 13–305 across all individuals in the study. Mean clutch size was higher in 1994 (mean = 108.2, 95% confidence interval = 91.5–128.0) than 1993 (mean = 81.5, 95% c.i. = 68.1–97.6), but did not differ among streams (ANOVA: year, $F_{(1,105)} = 5.99$, $P < 0.05$; stream and stream × year not significant). Slopes of the relationship between clutch size and length differed for 1993 and 1994 (ANOVA: year × $\log_{10}$SL, $F_{(1,107)} = 9.83$, $P < 0.01$), but there was a significant positive relationship in both years. Length explained little of the variation in clutch size in 1993, but in 1994 length was a relatively good predictor of clutch size (Fig. 6).

Diameter of mature ova ranged widely from 0.2119–1.0617 mm. Mean ova diameter differed among streams but not among years (mean ± SE, for combined years: Buckhorn = 0.841 ± 0.008, Cypress = 0.809 ± 0.012, Hotopha = 0.768 ± 0.008; ANOVA: stream, $F_{(2,262)} = 19.57$, $P < 0.0001$; year and stream × year interaction not significant). Ova diameter differed among all three streams (Tukey's HSD test, $P < 0.05$) and showed a gradient of decreasing size from Buckhorn to Hotopha Creek in both years (Fig. 7). Ova diameter was positively related to fish length in Buckhorn and Cypress Creeks, but was negatively related to length in Hotopha Creek (Fig. 8). Despite significant relationships between length and ova diameter in all three streams, length explained little of the variation in ova diameter ($R^2 = 0.057$–0.200, Fig. 8).

DISCUSSION

Life history variation in Notropis rafinesquei.—We found striking spatial and temporal variation in reproductive characteristics of three populations of *Notropis rafinesquei*, despite their close geographic proximity. Relatively few patterns were similar among or within streams and between years. Size at maturity and the timing and duration of the reproductive period (Apr.–Aug.) were similar among all three streams in both years. During the


Buckhorn
Cypress
Hotopha
1993
Apr
231
124
May
142
62
125
Jul
1
29
1
109
1
67
Sep
1
289
1
153
1
448
Oct
1
156
2
1
126
2
1
210
Nov
2
1
71
2
1
531
1994
Apr
110
101
167
May
90
78
64
Jul
1
291
1
68
1
97
Sep
1
89
2
1?
44
1
2
53
Oct
1
2
157
2?
1?
97
2
1
100
10
20
30
40
10
20
30
40
10
20
30
40
Standard length (mm)

reproductive period, one or two peaks in GSI and a high percentage of females with mature ovaries occurred in both years in all streams. We also consistently detected two young-of-the year cohorts, one strong cohort appearing in early summer and the other of varying strength in the fall.

Other reproductive traits varied between years, among streams, or interacted between these factors, and in most cases, this variation showed no consistent pattern over the course of the study. For example, mean female length and length-specific weight varied among streams in 1993 but not in 1994. Mean clutch size differed between years, but was similar among streams, while ova diameter differed among streams, but was similar between years. Other reproductive characteristics such as sex ratios and the relationship between length and clutch size also showed seemingly haphazard patterns of variation.

The highly plastic nature of reproductive traits in *Notropis rafinesquei* suggests that females make life-history trade-offs in response to highly variable stream environments (vis-à-vis Winemiller and Rose, 1992). Because of widespread stream channelization and resulting massive channel erosion and incision, most streams in north-central Mississippi today are characterized by highly unstable sand substrates and extremely flashy hydrographs (Adams *et al.*, 2004). Despite the highly degraded condition of these streams, *N. rafinesquei* is one of the most abundant and widespread fish species in streams in this region (Shields *et al.*, 1994, 1998; Adams *et al.*, 2004). Further, in a previous study of fish assemblage dynamics in our three study streams, *N. rafinesquei* was one of the few species that did not vary significantly in abundance among streams or over time (Adams *et al.*, 2004), illustrating its ability to adapt well to the high variability imposed by these systems.

The only consistent pattern of variation evident in this study was that values for several traits were lower in Hotopha Creek than in the other two streams. Over both years, maximum fish length was lowest in Hotopha Creek and, although fish size did not differ among streams in 1994, both mean length and length-specific weight were lowest in Hotopha Creek in 1993. Similarly, over both years, mean ova diameter was smallest and ova diameter declined with increasing fish size in Hotopha. In contrast, ova diameter was related positively to fish size in Buckhorn and Cypress Creeks. Reductions in somatic growth and reproductive investment may represent trade-offs necessary to ensure female survival during periods of low resource availability or other stressors (Winemiller and Rose, 1992; McCann and Shuter, 1997). In two populations of *Notropis cummingsae*, reduced lipid reserves were associated with lower monthly growth, smaller ovaries and a shorter spawning season and were interpreted as evidence of reduced resource availability (Shultz, 1999).

Smaller body and ova size in Hotopha Creek may be indicative of the particularly stressful environment imposed by this stream. Mean water temperature across all sample dates was substantially higher in Hotopha Creek (21.2 C) than in Buckhorn (18.9 C) and Cypress Creeks (18.6 C). Temperatures above 30 C were observed on three dates in Hotopha Creek (maximum recorded, 36 C), but temperatures in Buckhorn and Cypress Creeks never exceeded 29 C. Mean fish richness was lower in Hotopha (13.6 species·sample^{-1} ± 0.8 SE)

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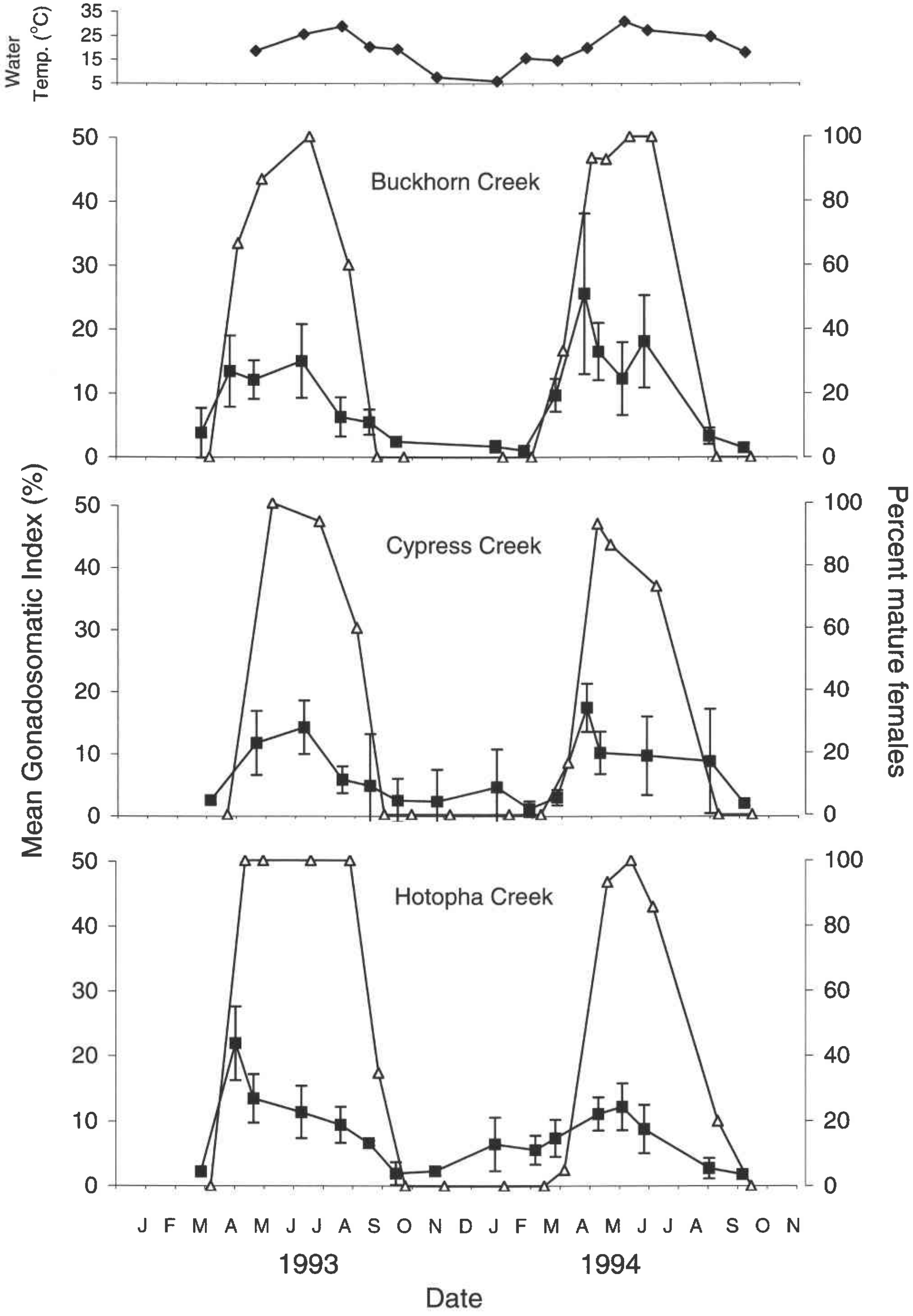
Fig. 4.—Monthly length-frequency histograms for *Notropis rafinesquei* in three north Mississippi streams in 1993 (top) and 1994 (bottom). Some months are not plotted; Apr. and Nov. data were not available for Cypress Creek. The y-axis is the percentage frequency; each y-axis tick mark represents 5%. Numbers in the upper right corner of each graph are sample sizes. Boxed numbers label the first and second young-of-the-year cohorts produced in each year. Question marks for Cypress Creek, 1994, indicate a weak first cohort that was difficult to detect in fall samples


Water Temp. (°C)
35
25
15
5
Buckhorn Creek
Cypress Creek
Hotopha Creek
Mean Gonadosomatic Index (%)
50
40
30
20
10
0
Percent mature females
100
80
60
40
20
0
J F M A M J J A S O N D J F M A M J J A S O N
1993
1994
Date

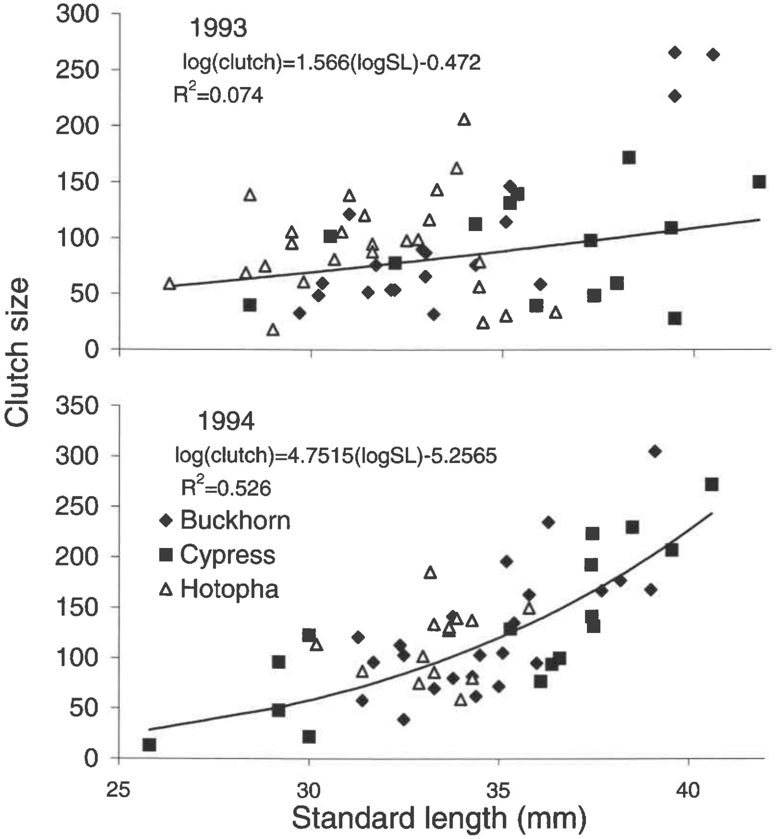


FIG. 6.—Relationships between length and clutch size for *N. rafinesquei* in three north Mississippi streams in 1993 and 1994. For each year, data are pooled among all three streams. Regression lines were created by plotting the back-transformed predicted clutch size for each observed value of length, computed using the regression equation for a particular year

than the similarly-sized Cypress Creek (22.8 ± 1.6 species), and comparable to the much smaller Buckhorn Creek (15.3 ± 0.5 species) (Adams *et al.*, 2004). Further, fish species dominance and annual turnover (May to May) were highest in Hotopha Creek, reflecting a depauperate and unstable community (Adams *et al.*, 2004). Together, life history, environmental and fish assemblage attributes suggest that Hotopha Creek represents an extreme environment for fishes due at least in part to the effects of channelization and the slow pace by which the stream has recovered from this insult (Shields *et al.*, 1994).

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Fig. 5.—Percentage of females with mature ovaries (open triangles) and mean gonadosomatic index for female *Notropis rafinesquei* in three north Mississippi streams in 1993 and 1994. For GSI, error bars are 95% confidence intervals. Water temperatures are averages among the three streams on each sample date

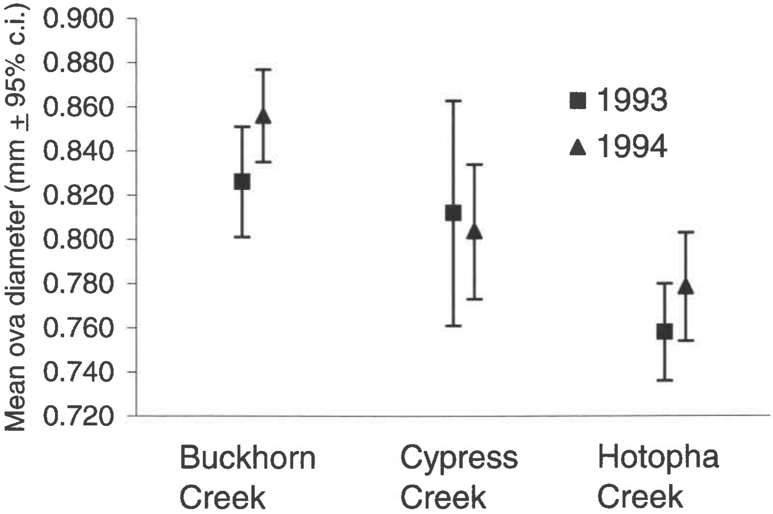

FIG. 7.—Mean ova diameter for *Notropis rafinesquei* in three north Mississippi streams in 1993 and 1994

Life history characteristics of the Notropis longirostris clade.—All members of the *Notropis longirostris* clade are adapted to living in shallow, shifting sand-bottom streams (Hubbs and Walker, 1942; Moriarty and Winemiller, 1997; Williams and Bonner, 2006). At least some species, in addition to *N. rafinesquei,* can adapt to the degraded habitats that result from channelization and incision. For example, *N. ammophilus* is one of the numerically dominant cyprinids in channelized streams in the Tombigbee River drainage (Shields and Hoover, 1991) and *N. longirostris* rapidly colonizes shallow, recently dredged areas of streams (Ross, 2001).

A synthesis of life history characteristics of the *Notropis longirostris* clade reveals a number of commonalities among clade members and highlights the extent to which plasticity in life history traits is a general feature of this group (Table 2). All clade members are small-bodied, short-lived, protracted spawners with high percentages of mature females and high GSI values throughout the reproductive period. The occurrence of a strong early summer YOY cohort followed by an early fall cohort of varying strength also appears to be characteristic of all clade members and is likely related to the two peaks in GSI documented in most populations. Relationships between clutch size and length and ova size and length both show high variability within and among species. For example, no ova size-length relationship was detected in seven of eight populations of *N. longirostris,* but in other species, the predictive strength of the relationship varied from moderately strong (*N. ammophilus*) to weak (*N. rafinesquei*) (*see* Table 2).

All members of the clade can be characterized as opportunistic strategists along a continuum of fish reproductive strategies (Winemiller and Rose, 1992; McCann and Shuter, 1997). Defining characteristics of opportunistic strategists include small body size, early maturation, no parental care, and low fecundity per spawning event coupled with frequent spawning. The protracted spawning period is one of the most pervasive life history

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Fig. 8.—Length-ova diameter relationships for *Notropis rafinesquei* in three north Mississippi streams. For each stream, data were pooled for 1993 and 1994. Regression lines were created by plotting the predicted ova diameter for each observed value of length, computed using the regression equation for a particular stream

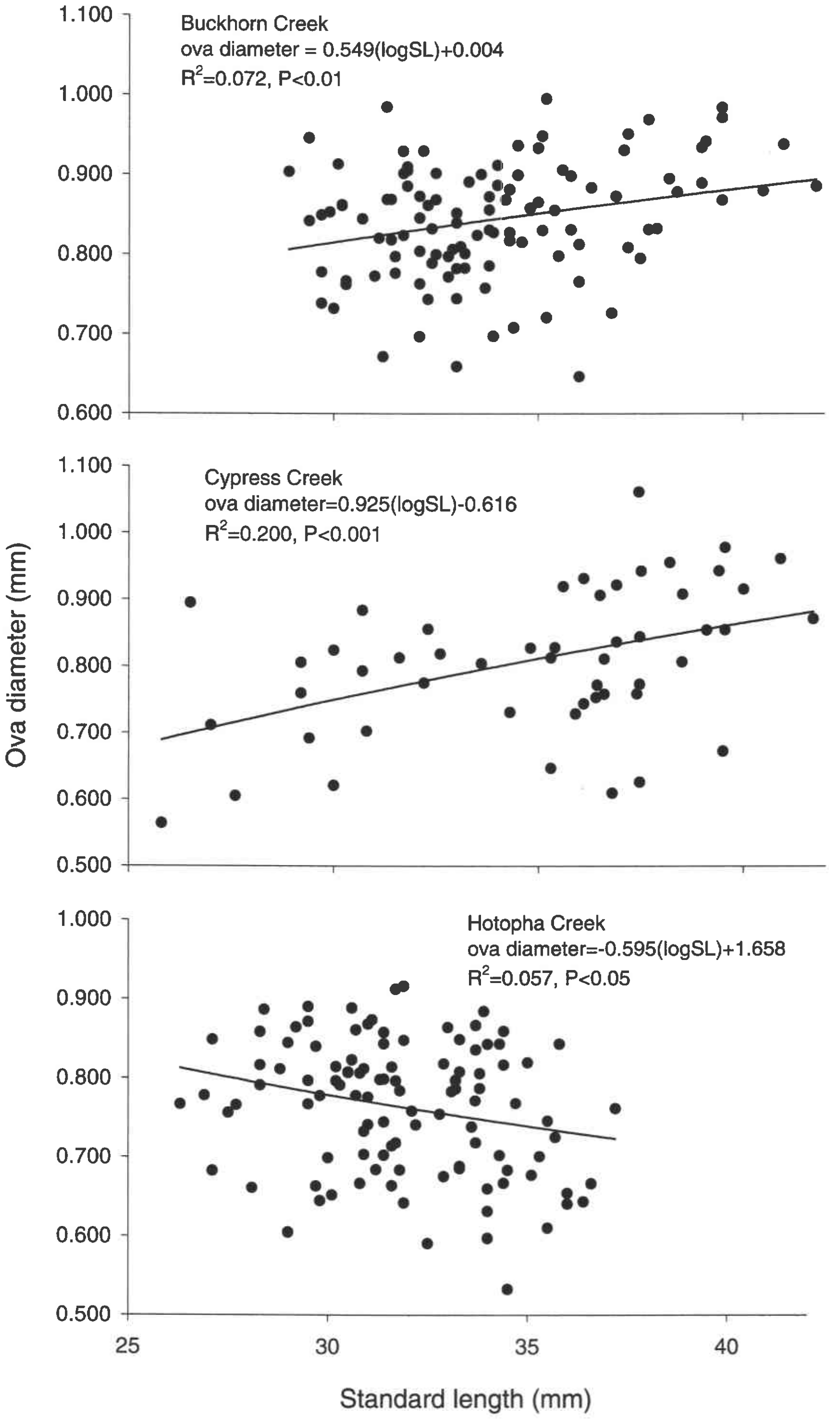
Buckhorn Creek
ova diameter = 0.549(logSL)+0.004
R2=0.072, P<0.01
Cypress Creek
ova diameter=0.925(logSL)-0.616
R2=0.200, P<0.001
Hotopha Creek
ova diameter=-0.595(logSL)+1.658
R2=0.057, P<0.05
Ova diameter (mm)
1.100
1.000
0.900
0.800
0.700
0.600
0.500
25
30
35
40
Standard length (mm)

Table 2.—Summary of reproductive characteristics of members of the *Notropis longirostris* clade. Sources: *Notropis sabinae,* Heins (1991), Williams and Bonner (2006); *N. longirostris,* Heins and Baker (1992), Heins and Clemmer (1976), Heins (1991), S. Ross, pers. comm.; *N. ammophilus* (Heins *et al.*, 1980); and *N. rafinesquei,* this study. Note: *N. longirostris* likely contains two putative species (Wiley and Titus, 1992)

	N. sabinae (four populations)	*N. longirostris* (eight populations)*	*N. ammophilus* (one population)	*N. rafinesquei* (three populations)
Maximum length (mm SL)	47–49	48**	45	38.0–41.8
Mean length mature females (mm SL)	37.7–38.2	33.8–46.2	34.6	31.1–35.8
Minimum length female with mature ova (mm SL)	32–33	28**	24	22.5–29.3
Maximum longevity (years)	1.5–2.5	1–2.5**	1.5–2.0	1.5–2.0
Sex ratio different from 1:1?	No	No**	No	No (two populations) Yes (one population)
Timing of spawning (range in temperature)	Apr.–Oct. (17–27 C, air)	late Feb.–Oct.** (17–29 C, water)	Apr.–early Oct. (18–26 C, air)	Apr.–late Aug. (17–33 C, water)
Number of peaks and range of GSI (%) during spawning season	One or two peaks 3.7–8.5	Two peaks 2.4–6.4**	One peak 6.9–13.3	One or two peaks 5.9–25.6
Appearance of 'fall' cohort?, month	Yes, Oct.–Jan.	Yes, Oct.–Nov.**	Yes, Sept.–Oct.	Yes, Sept.–Oct.
Clutch size (range in female size, mm SL)	113–423 (35.4–47.8)	15–129 (30.8–44.0)**	99–323 (30.9–40.8)	13–305 (25.8–41.7)
Clutch size-length relationship [Log(clutch) = slope log(SL) – intercept]	Slope: 3.1953 Intercept: −2.8297 $R^2 = 0.53$	Slopes: 1.6725 to 4.3565 Intercepts: −5.1351 to −0.6836 $R^2 = 0.478–0.814$	Slope: 3.9294 Intercept: −3.8379	Slopes: 1.566 to 4.752 Intercepts: −5.527 to −0.472 $R^2 = 0.074–0.526$
Predicted single clutch size for 33.9 mm SL female	114.8	34.0–82.8	149.6	84.0–103.3
Mean mature ova diameter (mm)	0.72	0.84–0.95	0.80	0.77–0.84
Ova diameter-length relationship	Positive $R^2 = 0.167$	Positive (one of eight populations) $R^2 = 0.296$, no relationship in other populations	Positive $R^2 = 0.510$	Positive (two populations) $R^2 = 0.072–0.200$ Negative (one population) $R^2 = 0.057$

* Includes two separate samples from Catahoula Creek, Jourdan River (1970–1972, Heins and Clemmer, 1974, 1976; Heins, 1991) that are treated as separate populations.

** Data from Catahoula Creek only, 1970–1972.

characteristics of the *Notropis longirostris* clade. Protracted spawning in fishes is hypothesized to provide survival insurance, increase mean fitness and stabilize populations in variable environments (Garvey *et al.*, 2002). Although some reproductive traits vary substantially among species, all members of the *N. longirostris* clade appear to occupy a similar region of the opportunistic life history space which allows them to cope well with the highly variable stream habitats in which they occur.

Overall, *Notropis rafinesquei* showed smaller maximum lengths, maturity at smaller size, and much higher GSIs relative to other clade members. In addition, *N. rafinesquei* was the only clade member that had a negative ova size-length relationship and sex ratios that deviated from 1:1 (Table 2). At this time, we cannot determine with certainty the significance of differences in these traits among species. However, the extreme values seen for *N. rafinesquei* could indicate that this species experiences resource limitation to a greater extent than other clade members. More severe resource limitation for *N. rafinesquei* could be caused by regional differences in the general severity of stream degradation, similar to local differences among our study streams that may have resulted in smaller body size and ova size in Hotopha Creek. Inter-populational differences in mature egg size of *N. longirostris* have been associated with regional environmental differences (Heins, 1991). Despite strong east-west genetic divergence among those populations (Raley and Wood, 1999; Wiley and Titus, 1992), egg size showed a north-south gradient not congruent with patterns of genetic variation; this strongly suggests that variation in egg size is a phenotypic response to local conditions (*e.g.*, stream discharge, Heins, 1991; Heins and Baker, 1992). Streams in our north Mississippi study area have experienced a degree of degradation that is exceptional even within the context of the Gulf Coastal Plain, a region known for its highly altered streams and endangered aquatic ecosystems (Shields *et al.*, 1994; Noss *et al.*, 1995; Shankman, 1999). Consequently, the extremely harsh and variable conditions in these streams may challenge even a highly adaptable animal like *N. rafinesquei* and may be manifested in lowered investment in somatic growth relative to other clade members.

Reproductive plasticity within the opportunistic life history strategy is likely an important mechanism by which *Notropis rafinesquei*, other members of the *N. longirostris* clade (*e.g.*, Heins, 1991; Heins and Baker, 1992), and perhaps many *Notropis* (*e.g.*, Schultz, 1999; Roberts *et al.*, 2006), are able to maintain large populations in physically unstable and unpredictable environments. Both regional and local environmental variability likely influences availability of resources for reproduction. In our study, size at maturity and spawning time were similar among populations suggesting a response to regional factors. Even though our study encompassed only two years, other traits varied widely among streams and years suggesting responses to highly variable local conditions. This high degree of reproductive plasticity makes it difficult to characterize reproductive traits of these and many other fishes based on one or a few samples. Ideally, the sample time frame and geographic scope should be wide enough to encompass the wide range of variation inherent in these animals.

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