

## Demographic characteristics of female mottled sculpin, *Cottus bairdi*, in the Coweeta Creek drainage, North Carolina

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### Synopsis

We quantified: (1) growth rate, (2) length-mass relationships, (3) size- and age-specific fecundity, (4) egg size-frequencies, and (5) size- and age-specific egg diameter relationships for reproductively active female *C. bairdi* from one of the southern-most extant populations of this species (Coweeta Creek drainage, North Carolina). Gravid females were collected during February and March in 1993–1995, and 1998. *Cottus bairdi* reached an age of 7+ and 79 mm standard length. The youngest and smallest gravid female collected was a 41 mm 1+ individual. Mature 1+ females were not uncommon and we collected 21 during our study. All females older than age 2 were mature. Mean fecundity for *C. bairdi* at Coweeta was 71 eggs (range 9–166 eggs). We found significant positive relationships between fecundity and female length, weight and age. Female length and weight also significantly affected mean egg diameter, although the relationship was not linear. Neither female size or age significantly affected mean maximum egg diameters. Female *C. bairdi* from the Coweeta Creek drainage possess a unique suite of reproductive characteristics that may represent adaptations to the local selective regime or ecophenotypic variation.

### Introduction

The mottled sculpin, *Cottus bairdi* (Girard 1850), is a benthic species that inhabits moderate to high gradient streams and rivers (Jenkins & Burkhead 1994), low gradient coastal plain streams (Rohde & Arndt 1981), and the rocky shallows of lakes (Jenkins & Burkhead 1994), across the northern United States and southern Canada. These habitats comprise a wide range of environmental conditions and indicate that *C. bairdi* is capable of substantial ecological flexibility. In fact, not only does this species have an extremely broad geographical distribution, but where present, frequently is the numerically dominant fish species (Smith 1922, Hahn 1927, Bailey 1952, Zarbock 1952, Ludwig & Norden 1969, DeHaven et al. 1993, Freeman et al. 1988, Grossman et al. 1998). Despite *C. bairdi*'s wide distribution, most life history information has come from northern and

western populations (Hann 1927, Bailey 1952, Patten 1970, Ludwig & Norden 1969, Simon & Brown 1943, Zarbock 1952, Downhower & Brown 1980), although one Delaware (Rohde & Arndt 1981) and two southeastern populations (Tennessee and North Carolina) have been examined (Nagel 1980, Freeman et al. 1988, DeHaven et al. 1993).

Our current knowledge of *C. bairdi* indicates that this species exhibits variability in its demographic and reproductive characteristics. For example, populations in Tennessee and Delaware are composed almost entirely of individuals less than three years of age (Nagel 1980, Rohde & Arndt 1981), whereas three to five year old sculpin represent a significant proportion of northern and western populations (Ludwig & Norden 1969, Bailey 1952 & Zarbock 1952). Fecundity also varies markedly among populations, with mean annual fecundities ranging from 55 to 68 in Tennessee

(Nagel 1980) to 629 in Wisconsin (Ludwig & Norden 1969). Nonetheless, the breeding behavior of this species appears to be similar to most other Cottidae, wherein males guard nest cavities under flat objects (e.g., cobbles) and females enter the nest cavity and lay eggs on the underside of the object covering the cavity (Breder & Rosen 1966, Downhower & Brown 1980). Multiple females may lay their eggs in one nest and there is size-assortative mating in one Ohio population (Downhower & Brown 1980).

For the past 18 years we have been studying one of the southernmost populations of *C. bairdi*, located in the Coweeta Creek drainage of western North Carolina. *Cottus bairdi* is the most abundant fish in these streams, where it also displays high population stability despite substantial environmental fluctuations (i.e., frequent droughts and floods, Freeman et al. 1988, Grossman et al. 1990, 1995a, 1998). The vast majority of adult *C. bairdi* have small home ranges (<2.5 m<sup>2</sup>, Petty 1998), and microhabitat choice for this species is most strongly affected by the local distribution of prey rather than the physico-chemical characteristics of the habitat (Petty & Grossman 1996). Recent studies demonstrate that *C. bairdi* is not strongly affected by either predators or competitors (Grossman et al. 1995b, 1998, Petty & Grossman 1996); instead, population regulation appears to be most strongly influenced by density-dependent interactions between large and small adults (Petty 1998).

We have previously quantified several aspects of the reproductive ecology of *C. bairdi* in the Coweeta drainage. For example, this species spawns during April and gravid females are present several months prior to the onset of the reproductive season (Dehaven et al. 1993, G. Grossman personal observation). Microsatellite DNA analysis of 62 clutches from 24 nests has shown that Coweeta females lay a single clutch of eggs in one nest (Fiumera et al. 2001). In this report we examine several undescribed aspects of the demography and reproductive biology of female *C. bairdi* in the Coweeta drainage, specifically: (1) growth rates and length-mass relationships, (2) size- and age-specific fecundity, (3) egg diameter frequency distributions, and (4) size and age-specific egg diameter relationships.

## Methods and materials

We collected *C. bairdi* from Ball Creek and Shope Fork, fourth order tributaries of Coweeta Creek, located in

the Blue Ridge physiographic province of the southern Appalachian Mountains. These streams are typical of relatively undisturbed habitat in the region (Swank & Crossley 1987). Our study sites were located on the USDA Forest Service Coweeta Hydrologic Laboratory in Otto, NC, and general site descriptions have been given in several previous papers (Grossman & Freeman 1987, Petty & Grossman 1996, Grossman et al. 1998, and Thompson et al. 2001).

## Specimen collection and analysis

We used backpack electrofishers to collect gravid female *C. bairdi* during the pre-spawning period (i.e., February–March, see DeHaven et al. 1993), from distinct sections of Shope Fork and Ball Creek. During this period both males and females, and gravid and non-gravid females, are visually distinguishable using external morphological criteria. We selected sites that were visually representative of both streams (minimum length ~ 100 m long, different site in each year) and began sampling in an upstream direction until a minimum of 50 gravid females were collected (almost all females captured were gravid). Sampling yielded the following number of gravid females: (1) 1993–63 females (Shope Fork), (2) 1994–53 females (Shope Fork), (3) 1995–39 females (Shope Fork), and (4) 1998–30 females (Shope Fork) and 21 females (Ball Creek) (these data were pooled). After collection, we placed specimens on ice and returned them to the laboratory, where they were held at –80°C until dissection. Subsequent laboratory analyses indicated that freezing had little or no effect on eggs (no burst or deformed eggs) or ovaries and that fish had not yet begun spawning (none were running-ripe). Because of small sample sizes, we pooled specimens for all analyses; hence, our results represent general trends for this species in the Coweeta drainage.

## Age and growth

Prior to dissection, we thawed specimens at room temperature, blotted them dry, and then measured their standard lengths ( $\pm 1$  mm, SL) and mass ( $\pm 0.001$  g, analytical balance). To age females and calculate growth rates, we removed sagittal otoliths from each specimen. Several investigators working in geographically disparate regions have successfully employed otoliths to age *C. bairdi* (Bailey 1952, Zarbock 1952, Ludwig & Norden 1969, Patten 1970). We immersed otoliths in cedar wood oil and examined them over a

black background using a dissecting microscope at 50x and reflected light. When viewed under reflected light, otoliths displayed a clear pattern of wide translucent and thin opaque bands, and we assumed that a pair of adjacent translucent and opaque bands represented one year's growth (Wootton 1998, Patten 1970). The otolith structure and band pattern that we observed was virtually identical to that illustrated in Patten (1970) for Washington state *C. bairdi*. Consequently, we measured annuli at the outer margin of the opaque band (Grossman 1979, Wootton 1998). A pilot study indicated there were no significant differences between the number of annuli counted on either dorsal or posterior axes of otoliths, or between consecutive readings on the same axis ( $F = 1.33$ ,  $p = 0.25$ ). Nonetheless, it appeared that annuli were slightly more readable along the dorsal otolith axis, hence all final readings were taken at this position. A second reader verified the ages of otoliths that were difficult to read, and the specimen excluded from analyses if both readers did not agree on its age.

We quantified the relationship between length and somatic mass using linear regression and transformed data ( $\log_{10}$ ) (Ricker 1975, Zar 1996). We used von Bertalanffy growth curves to quantify growth patterns of females (Von Bertalanffy 1938). The form of the equation is:

$$SL = L_{\infty}(1 - e^{-k(\text{age}-t_0)})$$

where  $L_{\infty}$  is the theoretical asymptotic length,  $k$  is the Brody growth rate coefficient, and  $t_0$  is hypothetical length at age zero (Ricker 1975). We calculated von Bertalanffy curves using age and length at capture for specimens.

#### *Fecundity and egg diameter measurements*

To estimate fecundity, we removed ovaries from gravid females. We placed ovaries in a vial filled with Gilson's fluid (single lobe for 1993 specimens) for a minimum of three weeks to harden eggs and dissolve ovarian membranes (Bagenal & Braum 1978). We then decanted Gilson's fluid from the vial, poured the eggs into a petri dish and held them in a small volume of water to prevent desiccation. The dish was agitated to evenly distribute eggs across its surface. We counted all eggs using a dissecting microscope set at 8x and reflected light. We adjusted fecundity estimates for 1993 data by doubling the number of eggs obtained from the single lobe examined. We believed this was justified, because there

were no visually apparent size differences between ovarian lobes of our specimens, and other populations do not exhibit significant differences in fecundity between right and left ovarian lobes (Rohde & Arndt 1981).

We used an ocular micrometer in the dissecting microscope (8x) to derive egg diameter frequency distributions for each female by measuring the diameters (i.e. widest axis) of eggs that fell on one side of a line bisecting the petri dish. Eggs were spherical; hence diameter measurements approximate true diameters. If the number of eggs measured on one side of the dish was less than 50% of the total eggs present, we then measured additional eggs on the opposite side of the line until we reached the 50% level. We plotted egg diameter frequency distributions for comparison among size classes of *C. bairdi*. In addition, we calculated the mean egg diameter per female and then used these data to derive a grand mean for each size and age class. Finally, we determined mean maximum egg diameters by taking the largest egg per female and then pooling these data for each size or age-class. We measured mean maximum egg diameters to test for female size effects that were identifiable only through examination of the maximum egg size produced by females rather than the mean.

We quantified the relationship between fecundity and female size and age by testing for significant correlations between these parameters using linear, non-linear, and polynomial regression (SAS Institute 1985, Zar 1996). We calculated regression equations for these variables to facilitate comparisons with other populations of *C. bairdi*. We then performed a stepwise multiple regression (SAS Institute 1985) using all three variables (e.g., age, mass and length) to identify the independent effects of these parameters (correlated parameters are automatically dropped using this algorithm) on fecundity. We also determined age-specific, length-specific, and mass-specific fecundities. Prior to analyses, we used a square root transformation to normalize fecundity data because they were not normally distributed (Shapiro-Wilkes  $W = 0.0197$ ,  $p < 0.05$ ). Because we were interested in testing for intergroup differences (e.g., ages and sizes), we converted length and mass data from continuous variables to categorical variables by grouping fish into 5 mm length classes and 1.0 g somatic mass classes, respectively. We then tested the null hypothesis of no significant differences in mean fecundity among length, somatic mass, or age classes using Bonferroni tests for unplanned comparisons (Sokal & Rohlf 1995). Bonferroni tests control

for experiment-wide error rates. Identical statistical analyses were used to test for significant size and age-related differences in mean female egg diameter and mean female maximum egg diameter. We were unable to test for significant inter-year differences in fecundity, mean female egg diameters or mean female maximum egg diameters because of significant inter-year differences in both the size and age composition of females (ANCOVA). All statistical analyses were performed using SAS (SAS Institute 1985) with  $p = 0.05$ .

Finally, we plotted fecundity-length regressions for both Coweeta *C. bairdi* and other populations of this species and then compared these regressions visually. Statistical comparisons of regression equations were precluded because neither the original data nor variance estimates were published in these papers.

## Results

### Age and growth

Reproductively active female *C. bairdi* reached a maximum age and length of 7 years and 79 mm respectively. Length (X) and mass (Y) were highly correlated for females ( $Y = 0.20X - 6.86$ ,  $N = 158$ ,  $p < 0.001$ ,  $r^2 = 0.88$ ), and this relationship was linear. Annulus formation in females occurred during April and May (G. Grossman et al. unpublished data), hence fish had almost completed an additional year of growth. The Von Bertalanffy growth curve (Figure 1) indicated that females grew rapidly until age 3 at which point growth leveled off.

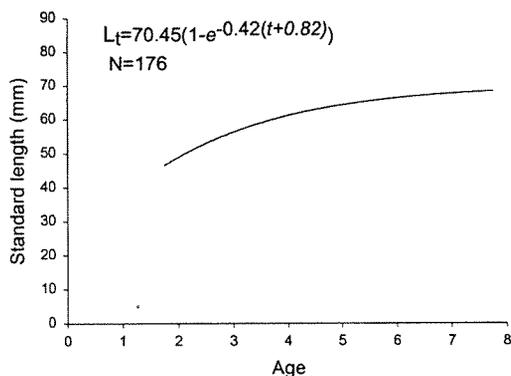


Figure 1. Brody-von Bertalanffy growth curve for gravid female *C. bairdi* from the Coweeta drainage.

### Sexual maturity, fecundity and egg diameter frequency distributions

The youngest and smallest gravid female was age 1+ and 41 mm in length. We collected 21 gravid females that were age 1+, two of which were 41 mm in length. Fecundity of *C. bairdi* ranged from 9 to 166 eggs, and was significantly correlated with female length, somatic mass, and age (Figure 2). Use of a non-linear model did not improve the fit of these relationships. Step-wise multiple regression demonstrated that all three variables contributed significantly to female fecundity, however partial  $r^2$  values showed that female mass had a much stronger effect than either female length or age (regression equation [partial  $r^2$  values]: fecundity =  $8.393 \text{ mass} [0.706] + 0.985 \text{ length} [0.007] - 2.500 \text{ age} [0.009]$ ,  $n = 175$ ,  $p < 0.0001$ ). Mean ( $\pm$ SE) fecundity for females sampled from the Coweeta population was 71 ( $\pm 2$ ) eggs. Bonferroni tests indicated that longer, heavier and older females generally were more fecund than their smaller, lighter, or younger counterparts (Tables 1–3), although adjacent classes frequently did not differ significantly from one another.

Comparisons of length-fecundity relationships for Coweeta *C. bairdi* with those for other populations, indicated that although the slopes of these relationships were generally similar their elevations clearly differed (Figure 3). These data suggest that there may be a latitudinal cline in fecundity for *C. bairdi* with Delaware, Washington and Wisconsin populations being more fecund than Coweeta and Tennessee populations.

Egg size-frequency distributions were similar among females of different size classes (Figure 4), although females in the 40 mm size class appeared to have distributions shifted towards smaller eggs. Bonferroni tests showed that females between 55 and 64 mm in length had significantly larger mean egg diameters than at least one size group of smaller females (Table 1), whereas all females weighing more than 3 g had significantly larger mean egg diameters than lighter females (Table 2). Age-specific comparisons yielded a single significant difference, with 3 year old females having significantly greater mean egg diameters than 1+ fish (Table 3). Multiple regression analysis indicated that female mass and age significantly affected both mean and mean maximum egg diameters of *C. bairdi*, but neither mass nor age explained biologically significant amounts of variation in the data (regression equation [partial  $r^2$

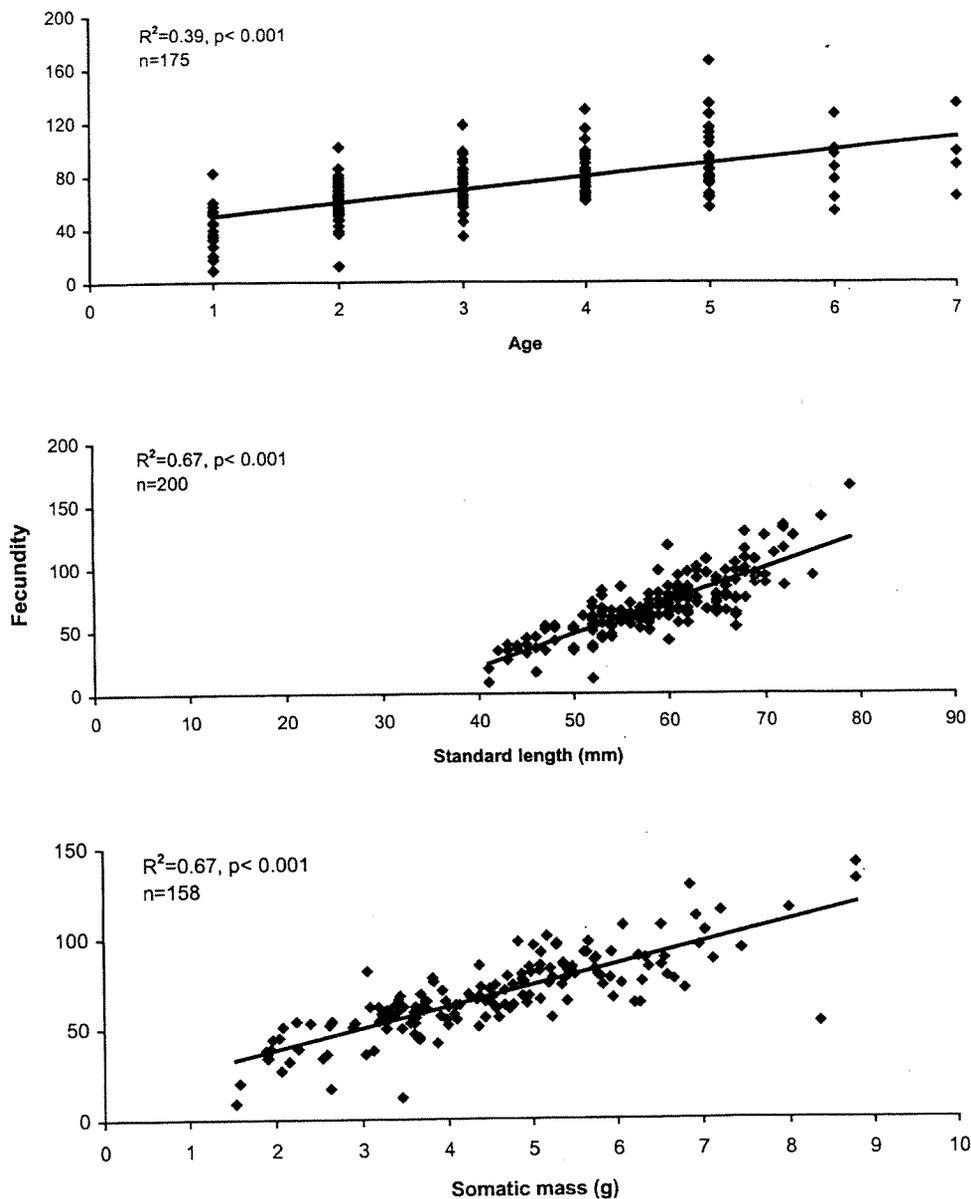


Figure 2. Relationships between fecundity (Y) and female age ( $Y = 9.94x + 39.48$ ), length ( $Y = 2.64x - 84.54$ ), and mass ( $Y = 11.88x + 14.62$ ).

values]: mean egg diameter =  $0.069 \text{ mass} [0.028] - 0.067 \text{ age} [0.037]$ ,  $n = 175$ ,  $p < 0.027$ ; mean maximum egg diameter =  $0.085 \text{ mass} [0.032] - 0.087 \text{ age} [0.057]$ ,  $n = 175$ ,  $p < 0.017$ ). Concomitantly,

univariate Bonferroni tests indicated that neither size nor age had a significant effect on mean maximum egg diameter (Tables 1–3, all  $p > 0.05$ ). The largest egg diameter observed was 3.4 mm.

Table 1. Bonferroni results for the test of significant differences in fecundity and mean egg diameter among length classes. Estimates of back-transformed fecundity with the same superscript are not significantly different.

Length group, mm (N)	Mean fecundity $\pm$ S.E.	Mean egg diameter, mm $\pm$ S.E. (range)	Mean maximum egg diameter, mm $\pm$ S.E. (range)
41–44 (8)	30 $\pm$ 3.7 <sup>a</sup>	1.9 $\pm$ 0.06 <sup>a</sup> (1.7–2.2)	2.3 $\pm$ 0.08 <sup>a</sup> (2.0–2.6)
45–49 (13)	43 $\pm$ 3.0 <sup>a,b</sup>	2.0 $\pm$ 0.07 <sup>a,b</sup> (1.6–2.5)	2.4 $\pm$ 0.08 <sup>a</sup> (1.7–2.8)
50–54 (35)	54 $\pm$ 2.3 <sup>b</sup>	2.2 $\pm$ 0.04 <sup>a,b,c</sup> (1.6–2.6)	2.6 $\pm$ 0.04 <sup>a</sup> (2.2–3.2)
55–59 (45)	65 $\pm$ 1.5 <sup>c</sup>	2.3 $\pm$ 0.04 <sup>b,c</sup> (1.5–2.8)	2.6 $\pm$ 0.05 <sup>a</sup> (1.8–3.2)
60–64 (48)	79 $\pm$ 2.1 <sup>d</sup>	2.4 $\pm$ 0.04 <sup>c</sup> (1.7–3.0)	2.8 $\pm$ 0.04 <sup>a</sup> (1.8–3.4)
65–69 (38)	84 $\pm$ 2.7 <sup>d</sup>	2.2 $\pm$ 0.05 <sup>a,b,c</sup> (1.5–2.7)	2.6 $\pm$ 0.06 <sup>a</sup> (1.8–3.3)
70–79 (13)	119 $\pm$ 6.6 <sup>c</sup>	2.1 $\pm$ 0.11 <sup>a,b,c</sup> (1.6–2.7)	2.5 $\pm$ 0.11 <sup>a</sup> (2.0–3.1)

Table 2. Bonferroni results for the test of significant differences in fecundity among somatic mass classes. Estimates of back-transformed fecundity with the same superscript are not significantly different.

Mass group, g (N)	Mean fecundity $\pm$ S.E.	Mean egg diameter, mm $\pm$ S.E. (range)	Mean maximum egg diameter, mm $\pm$ S.E. (range)
1.00–1.99 (8)	32 $\pm$ 4.1 <sup>a</sup>	1.9 $\pm$ 0.06 <sup>a</sup> (1.7–2.2)	2.3 $\pm$ 0.08 <sup>a</sup> (2.0–2.6)
2.00–2.99 (14)	43 $\pm$ 3.2 <sup>a</sup>	2.1 $\pm$ 0.07 <sup>a</sup> (1.7–2.6)	2.5 $\pm$ 0.08 <sup>a</sup> (2.0–3.2)
3.00–3.99 (41)	58 $\pm$ 1.9 <sup>b</sup>	2.3 $\pm$ 0.04 <sup>b</sup> (1.9–2.8)	2.7 $\pm$ 0.04 <sup>a</sup> (2.4–3.2)
4.00–4.99 (38)	68 $\pm$ 1.6 <sup>c</sup>	2.3 $\pm$ 0.04 <sup>b</sup> (1.9–3.0)	2.7 $\pm$ 0.04 <sup>a</sup> (2.3–3.4)
5.00–5.99 (32)	83 $\pm$ 1.9 <sup>d</sup>	2.4 $\pm$ 0.03 <sup>b</sup> (2.1–2.8)	2.9 $\pm$ 0.04 <sup>a</sup> (2.5–3.3)
6.00–6.99 (17)	88 $\pm$ 4.3 <sup>d</sup>	2.4 $\pm$ 0.05 <sup>b</sup> (1.9–2.7)	2.8 $\pm$ 0.05 <sup>a</sup> (2.5–3.1)
7.00–7.99 (4)	100 $\pm$ 5.9 <sup>d</sup>	2.5 $\pm$ 0.16 <sup>b</sup> (2.1–2.7)	3.0 $\pm$ 0.13 <sup>a</sup> (2.6–3.1)

Table 3. Bonferroni results for the test of significant differences in fecundity among age classes. Estimates of back-transformed mean fecundity with the same superscript are not significantly different.

Age group (N)	Mean fecundity $\pm$ S.E.	Mean egg diameter, mm $\pm$ S.E. (range)	Mean maximum egg diameter, mm $\pm$ S.E. (range)
1 (20)	43 (4.0) <sup>a</sup>	2.0 $\pm$ 0.06 <sup>a</sup> (1.7–2.6)	2.4 $\pm$ 0.06 <sup>a</sup> (2.0–2.9)
2 (55)	60 (2.0) <sup>b</sup>	2.2 $\pm$ 0.04 <sup>a,b</sup> (1.5–2.7)	2.6 $\pm$ 0.04 <sup>a</sup> (1.7–3.2)
3 (37)	72 (2.6) <sup>c</sup>	2.4 $\pm$ 0.05 <sup>b</sup> (1.7–3.0)	2.8 $\pm$ 0.05 <sup>a</sup> (2.0–3.4)
4 (27)	84 (4.0) <sup>c,d</sup>	2.3 $\pm$ 0.06 <sup>a,b</sup> (1.6–2.8)	2.6 $\pm$ 0.07 <sup>a</sup> (1.8–3.3)
5 (26)	98 (6.1) <sup>d</sup>	2.2 $\pm$ 0.06 <sup>a,b</sup> (1.5–2.6)	2.6 $\pm$ 0.06 <sup>a</sup> (2.1–3.1)
6 (7)	98 (9.3) <sup>c,d</sup>	2.0 $\pm$ 0.13 <sup>a,b</sup> (1.6–2.6)	2.5 $\pm$ 0.14 <sup>a</sup> (2.1–3.1)
7 (4)	96 (15.0) <sup>c,d</sup>	2.1 $\pm$ 0.26 <sup>a,b</sup> (1.6–2.7)	2.3 $\pm$ 0.29 <sup>a</sup> (1.8–3.1)

## Discussion

Our results demonstrate that female *C. bairdi* in the Coweeta Creek drainage reached an age of 7+ years, and grew slowly after age three. Female size and age significantly affected both fecundity and mean egg diameter. Most females reached reproductive maturity at 2+ years of age, however, some females were mature at age 1+. Finally, mean clutch size estimates (mean

$\bar{x}$  = 66 eggs per clutch) for *C. bairdi* nests from the Coweeta drainage (Fiumera et al. unpublished data) closely matched our estimate of mean fecundity (mean = 71), which also suggests that our fecundity data are reasonable measures of mean annual fecundity.

A life span of 7+ years exceeds the maximum age reported for all other populations of *C. bairdi*. In contrast, *C. bairdi* attains a maximum age of 2+ years in Delaware and probably Tennessee

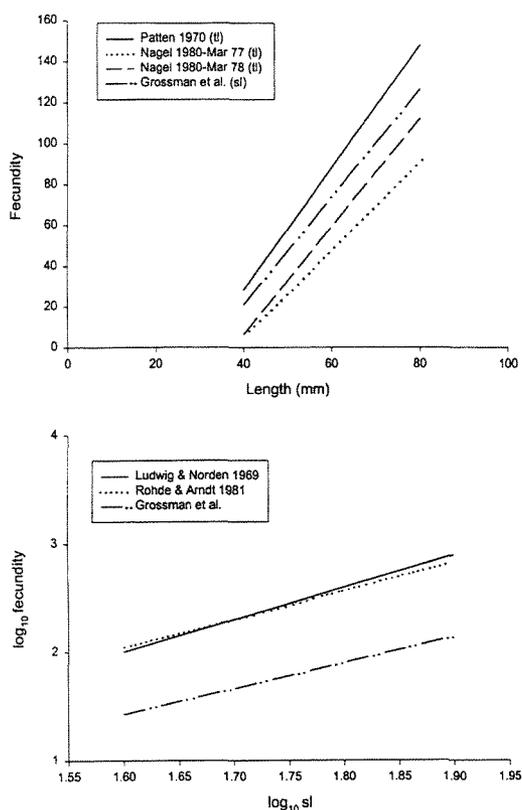


Figure 3. Comparisons of published length-fecundity with data for Coweeta *C. bairdi*. The upper panel depicts regressions based on total length and the lower panel regressions based on standard length. See the cited papers for details regarding the regressions.

(Nagel 1980, Rohde & Arndt 1981), 3+ years in Wisconsin (Ludwig & Norden 1969), 4+ years in Washington (Patten 1971), and 5+ years in Montana and Utah (Zarbock 1952, Bailey 1952). Peaks in length-frequency histograms for Coweeta *C. bairdi* generally agreed with mean lengths of age classes 0+, 1+, and 2+ (G. Grossman unpublished data), and hence, support the contention that bands counted on otoliths were annuli rather than growth checks. Nonetheless, due to high overlap in length among age classes and sex-specific differences in growth rates (unpublished data) it is difficult to match lengths of older *C. bairdi* (i.e., >age 3) to peaks in length frequency histograms (Bailey 1952, Zarbock 1952, Ludwig & Norden 1969, Nagel 1980, Rohde & Arndt 1981). It is likely that annulus formation for specimens in this

study would have occurred just after samples were collected, because *C. bairdi* collected in late April and early May 2000 had either completed, or were in the process, of annulus formation (G. Grossman et al. unpublished data). Annulus formation in northern populations of this species occurs in late winter or spring (Zarbock 1952, Patten 1970).

The reproductive characteristics of *C. bairdi* at Coweeta display both similarities and differences when compared to other populations of this species. For example, regardless of location, reproduction in *C. bairdi* appears to be population synchronous and occur over an approximately 30 day period (Bailey 1952, Downhower & Brown 1980, Nagel 1980, Rohde & Arndt 1981). Unlike other populations in which females mature in their third year of life (Hahn 1927, Bailey 1952, Ludwig & Norden 1969, Patten 1970), some Coweeta females matured in their second year of life (i.e. 1+). Females in both Delaware and Tennessee populations also mature in their second year of life (Nagel 1980, Rohde & Arndt 1981) as do two other cyprinids (*Clinostomus funduloides* and *Rhinichthys cataractae*) syntopic with *C. bairdi* in Coweeta Creek (DeHaven et al. 1992). Substantial evidence suggests that female *C. bairdi* deposits all of their eggs in one clutch. First, there were few immature oocytes in ovaries. Second, genetic analyses of 24 nests containing 62 clutches of eggs from an adjacent site, failed to reveal a single instance of a female depositing more than one clutch of eggs or of a female spawning in multiple nests (Fiumera et al. 2001). Finally, the mean number of eggs per clutch (i.e., 66) (Fiumera et al. 2001) was strikingly similar to the mean fecundity of females reported here (i.e., 72). These data strongly suggest that females in the Coweeta drainage deposit a single clutch per year and that our fecundity estimates measure annual fecundity for this species. Similar conclusions based on ancillary data have been reported for other populations of *C. bairdi* (Bailey 1952, Patten 1970, Downhower & Brown 1980, Nagel 1980).

There is a widespread trend for fecundity in *C. bairdi* to be positively correlated with length (Bailey 1952, Patten 1970, Ludwig & Lange 1975, Nagel 1980, Rohde & Arndt 1981) and in some cases, with mass (Rohde & Arndt 1981). Fecundity also may be positively correlated with female age (Ludwig & Norden 1969), although this relationship typically is weaker than those for fecundity and female length or mass (Rohde & Arndt 1981, Nagel 1980, Patten 1970). All of these trends were observed in Coweeta *C. bairdi*. Fecundity-length relationships (i.e., regression slopes)

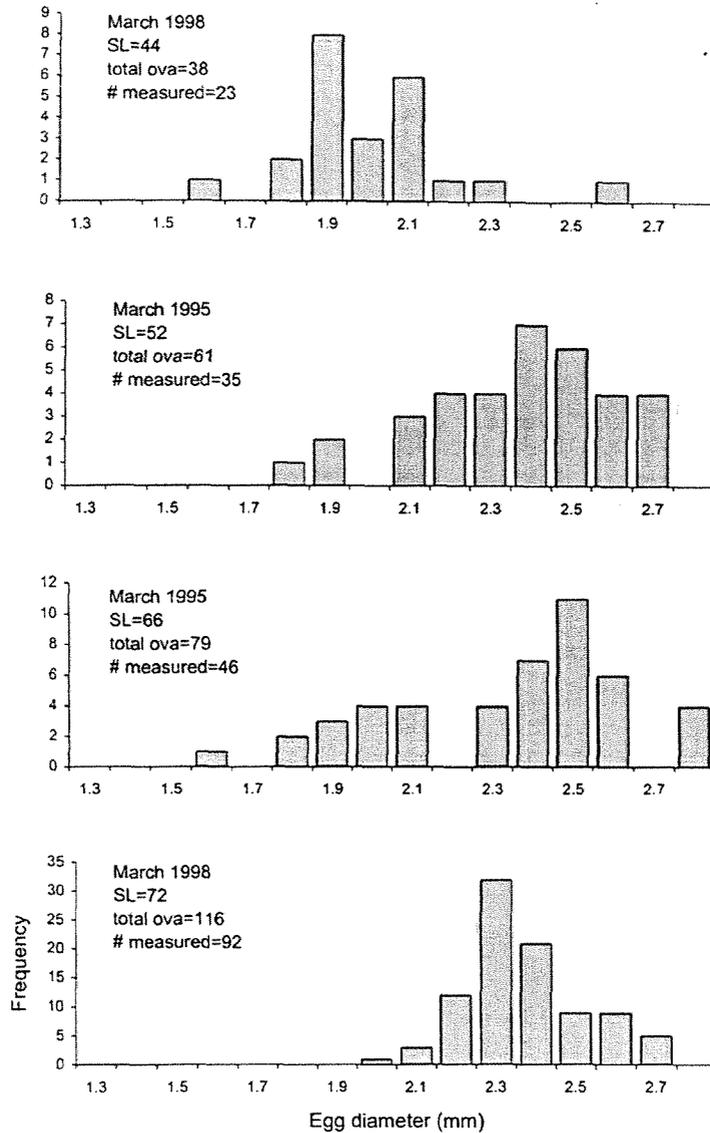


Figure 4. Egg diameter frequency distributions for representative females in different size classes (10 mm intervals).

appeared to be similar for populations from Delaware, Tennessee, North Carolina (Coweeta), Washington and Wisconsin, although length-specific fecundities (i.e., elevations) differed substantially among populations. In addition, the magnitude of these differences were greatly under-represented by our comparison of published regression equations, because data for the most fecund populations were not available (Bailey 1952,

Ludwig & Lange 1975). Clearly, even for fishes, there are very large (ten-fold) inter-population differences in fecundity for *C. bairdi* (Wootton 1998), although the conspecific status of some of these populations currently is being questioned (D. Neely personal communication).

Univariate analyses indicated that female length, mass, and age, significantly influenced mean egg

diameters, although this was not true for mean maximum egg diameters. Interestingly, females with the largest mean egg diameters were intermediate in length and age, whereas the female mass – egg diameter relationship was a step function (i.e., females larger than 3 g had significantly larger mean egg diameters than all lighter females). Step-wise multiple regression analysis also produced significant relationships between female size and age, and egg diameters, however, these results appeared to have little biological significance. There are few published data on relationships between female size or age and egg diameters for *C. bairdi*, so the generality of these findings is unknown. Rodhe & Arndt (1981) also found a positive correlation between female length and diameters of mature ova. Finally, extant egg diameter data suggest that northern (Hahn 1927, Simon & Brown 1943, Ludwig & Norden 1969) and eastern (Rodhe & Arndt 1981) populations have smaller egg diameters than both Tennessee (Nagel 1980) and Coweeta populations. This pattern is the opposite of the fecundity trend, which suggests that there may be a trade off between egg size and number in *C. bairdi*.

The Coweeta drainage is a fluctuating environment in which drought can alternate with high flows (Grossman et al. 1995a, Grossman & Ratajczak 1998). In this environment, *C. bairdi* has a long life span, matures early, has low to intermediate fecundity, and produces large eggs. Although female size had a strong effect on the reproductive characteristics of this species, age effects were less pronounced. Given the size and age structure of this population, and the frequency with which gravid females are found, it is probable that females reproduce multiple times during their lifetime. Our results, combined with previous studies, suggest that populations currently assigned to *C. bairdi* exhibit substantial demographic plasticity. It seems likely that much of the variation among populations represents adaptation to local selective pressures, or ecophenotypic variation, rather than evolutionary constraints. Comparative life history studies of *C. bairdi* and other widely ranging species should increase our understanding of how local selective pressures influence the demography and ecology of fishes.

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#### References cited

- Bagenal, T.B. & E. Braum. 1978. Eggs and early life history. pp. 165–201. *In*: T.B. Bagenal (ed.) *Methods for Assessment of Fish Production in Fresh Waters*, Blackwell Scientific, Oxford.
- Bailey, J.E. 1952. Life history and ecology of the sculpin *Cottus bairdi punctulatus* in southwestern Montana. *Copeia* 1952: 243–255.
- Breder, C.M. & D.E. Rosen. 1966. *Modes of reproduction in fishes*. Natural History Press, Garden City. 941 pp.
- Dehaven, J.E., D.J. Stouder, R. Ratajczak, T.J. Welch & G.D. Grossman. 1993. Reproductive timing of three fish in a southern Appalachian stream. *Ecol. Freshwat. Fish* 1: 104–111.
- Downhower, J.F. & L. Brown. 1980. Mate preferences of female mottled sculpins, *Cottus bairdi*. *Anim. Beh.* 28: 728–734.
- Freeman, M.C., M.K. Crawford, J.C. Barrett, D.E. Facey, M.G. Flood, J. Hill, D.J. Stouder & G.D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. *Can. J. Fish. Aquat. Sci.* 45: 1949–1958.
- Girard, C. 1850. *Contributions to the natural history of the freshwater fishes of America. I. A monograph of the cottids*. Smithsonian Institution Contribution to Knowledge 3: 1–80.
- Grossman, G.D. 1979. Demographic characteristics of an intertidal bay goby (*Lepidogobius lepidus*). *Env. Biol. Fish.* 4: 207–218.
- Grossman, G.D., J.F. Dowd & M.C. Crawford. 1990. Assemblage stability in stream fishes: a review. *Environ. Manage.* 14: 661–671.
- Grossman, G.D. & M.C. Freeman. 1987. Microhabitat use in a stream fish assemblage. *J. Zool. Soc. (London)* 212: 151–176.
- Grossman, G.D., J. Hill, & J.T. Petty. 1995a. Observations on habitat structure, population regulation, and habitat use with respect to evolutionarily significant units: a landscape approach for lotic systems. *Amer. Fish. Soc. Symp.* 17: 381–391.
- Grossman, G.D., R. Ratajczak, Jr. & M. C. Crawford 1995b. Do rock bass (*Ambloplites rupestris*) induce microhabitat shifts in mottled sculpin (*Cottus bairdi*). *Copeia* 1995: 343–353.
- Grossman, G.D. & R.E. Ratajczak, Jr. 1998. Long-term patterns of microhabitat use by fish in a southern Appalachian stream from 1983 to 1992: effects of hydrologic period, season, and fish length. *Ecol. Freshwat. Fish* 7: 108–131.

- Grossman, G.D., R.E. Ratajczak, Jr., M. Crawford & M.C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol. Monogr.* 68: 395–420.
- Hahn, H.W. 1927. The history of the germ cell of *Cottus bairdi* Girard. *J. Morph. Physiol.* 43: 427–497.
- Jenkins, R.E. & N.M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda. 1080 pp.
- Ludwig, G.M. & E.L. Lange. 1975. The relationship of length, age, and age-length interaction to the fecundity of the northern mottled sculpin, *Cottus b. bairdi*. *Trans. Amer. Fish. Soc.* 105: 64–67.
- Ludwig, G.M. & C.R. Norden. 1969. Age, growth, and reproduction of the northern mottled sculpin (*Cottus bairdi bairdi*). Milwaukee Public Museum Occasional Paper 2: 1–67.
- Nagel, J.W. 1980. Life history of the mottled sculpin, *Cottus bairdi*, in northern Tennessee (Osteichthyes: Cottidae). *Brimleyana* 4: 115–121.
- Patten, B.G. 1970. Spawning and fecundity of seven species of northwest American cottus. *Amer. Midl. Nat.* 85: 493–506.
- Petty, J.T. 1998. Mottled sculpin in a dynamic landscape: linking environmental heterogeneity, individual behaviors, and population dynamics in a southern Appalachian stream. Ph.D. Dissertation, University of Georgia, Athens. 156 pp.
- Petty, J.T. & G.D. Grossman. 1996. Patch selection by mottled sculpin (Pisces: Cottidae) in a southern Appalachian stream. *Freshwat. Biol.* 35: 261–276.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Department of the Environment, Fisheries, and Marine Service, Ottawa. 382 pp.
- Rohde, F.C. & R.G. Arndt. 1981. Life history of a coastal plain population of the mottled sculpin, *Cottus bairdi* (Osteichthyes: Cottidae), in Delaware. *Brimleyana* 7: 69–94.
- SAS Institute. 1985. SAS user's guide; statistics. Cary 956 pp.
- Simon, J.R. & R.C. Brown. 1943. Observations on the spawning of the sculpin. *Copeia*. 1943: 41–42.
- Smith, B.G. 1922. Notes on the nesting habits of *Cottus*. *Pap. Mich. Acad. Sci. Arts & Letters* 2: 212–224.
- Sokal, R.R. & F.J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd edn. Prentice-Hall, Upper Saddle River. 880 pp.
- Swank, W.T. & D.A. Crossley. 1987. *Forest hydrology and ecology at Coweeta*. Springer-Verlag, New York. 469 pp.
- Thompson, A., J.T. Petty & G.D. Grossman. 2001. Multi-scale effects of resource patchiness on foraging behaviour and habitat use by longnose dace, *Rhinichthys cataractae*. *Freshwat. Biol.* 46: 145–161.
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Hum. Biol.* 10: 181–212.
- Wootton, R.J. 1998. *Ecology of teleost fishes*. Chapman & Hall, London. 392 pp.
- Zar, J.M. 1996. *Biostatistical analysis*, 3rd edn. Prentice-Hall, Upper Saddle River. 931 pp.
- Zarbock, W.M. 1952. Life history of the Utah sculpin, *Cottus bairdi semiscaber* (Cope), in Logan River, Utah. *Trans. Amer. Fish. Soc.* 81: 249–259.