

Reproductive characteristics of female longnose dace in the Coweeta Creek drainage, North Carolina, USA

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Abstract – We examined the reproductive characteristics of 38 female longnose dace (*Rhinichthys cataractae*) from one of the southernmost populations of this species during two sampling periods in 1999 (ES= March 1999, LS=June 1999). Our data indicated that ES fish had not spawned, whereas LS fish had begun spawning. The smallest mature female captured was 56 mm SL (age 1+). Mean potential fecundity differed significantly between ES (mean \pm 1 SD=1832 \pm 572 oocytes) and LS (mean \pm 1 SD=775 \pm 415 oocytes) specimens. Potential fecundity was positively correlated with both standard length and somatic mass for both ES and LS specimens. Oocyte diameter frequency histograms indicated that ES specimens possessed two modes of oocytes, whereas LS fish contained two or three modes. Female longnose dace appeared to spawn more than once during a reproductive season. Oocyte number varied substantially both among individuals within periods and between periods. The number of Mode II oocytes in ES fish was positively correlated with both length and somatic mass. Female longnose dace appeared potentially capable of spawning 6+ clutches per year. GSI values for longnose dace ranged from a high of 21.4% (LS specimen) to 2.4% (ES specimen). Regression analysis demonstrated that there was no evidence of differential reproductive effort between longnose dace of different size in this population.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Studies of variation in life-history characteristics of species may yield substantial insights into the manner in which natural selection operates within natural populations (Roff 1992). In fishes, life history studies show that traits such as age and size at maturity, number of clutches per year, clutch size and ova size all may vary both within and among populations (Roff 1992). Life-history studies are particularly useful if they involve species that occur in a variety of habitat types, because this increases the probability that these populations will be subjected to distinct selective pressures. The longnose dace (*Rhinichthys cataractae*, Valenciennes 1842) is such a species; it has the broadest natural geographic range of any

North American cyprinid (see references in Thompson et al. 2001) and occupies habitats ranging from coldwater streams to cold northern lakes (Etnier & Starnes 1993). Consequently, we assessed several reproductive parameters for one of the southernmost populations of longnose dace and compared our results with data from a population inhabiting Lake Michigan (Brazo et al. 1978).

Despite its wide distribution, little is known about the basic biology of longnose dace. This species is small (maximum length <225 mm) and reaches an age of 5 years in streams (Gerald 1966; Kuehn 1949). Females typically achieve greater length than males by age 3 (Gerald 1966; Kuehn 1949). We have conducted a series of studies on the ecology of longnose dace in the Coweeta Creek drainage of North Carolina (Freeman et al. 1988;

DeHaven et al. 1992; Grossman & Ratajczak 1998; Grossman et al. 1998; Thompson et al. 2001), where this species is the second most abundant benthic species. In the Coweeta drainage, adult longnose dace preferentially occur on the bottom in deep, erosional microhabitats, whereas juveniles and young-of-year inhabit the water-column in shallow depositional areas (Grossman & Ratajczak 1998). Spawning of longnose dace typically occurs over pits in loose gravel substrata (Bartnik 1970). DeHaven et al. (1992) established that female longnose dace in the Coweeta drainage reproduce between May and July, although the exact date was unknown.

We have examined several life-history characteristics of longnose dace. First, we quantified ovarian mass, potential fecundity and clutch size for longnose dace and determined whether these characteristics were related to female length and mass. Second, we quantified oocyte and ova diameter distributions and assessed whether this species was group synchronous and spawned more than once during the reproductive season. Finally, we compared these characteristics for dace captured before and during the spawning period, as well as to the data of Brazo et al. (1978) for Lake Michigan longnose dace.

Material and methods

Study site and sampling procedures

We collected longnose dace from a fifth-order stream (Coweeta Creek) and two of its fourth-order tributaries (Shope Fork and Ball Creek) in the Coweeta Creek drainage of western North Carolina (Blue Ridge province – southern Appalachian Mountains). These streams, typical of relatively undisturbed lotic habitats in this region, have been described in detail elsewhere (Petty & Grossman 1996; Grossman et al. 1998; Thompson et al. 2001); hence we will provide just a brief description here. Our collection sites represented typical longnose dace habitat in the drainage: reaches with moderate gradient and riffle – run – pool development dominated by erosional substrata. The riparian flora was dense and included primarily rosebay rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) (Grossman et al. 1998). Most sampling occurred on the USDA Forest Service Coweeta Hydrologic Laboratory (Otto, North Carolina). Additional physiognomic information about the watershed and region can be found in Swank & Crossley (1987).

We collected longnose dace on five occasions in 1999: on March 17 (early spring=ES) and on June 1, 3, 4, and 8 (late spring=LS). We sampled a total

of 1050 m of stream using a DC backpack electrofisher and retained 162 specimens >40 mm SL. Sampling began at the downstream end of a site and progressed upstream. Specimens were placed on ice and returned to the laboratory, where they were held in a freezer at -10°C for later analysis. There was no visible evidence that freezing damaged ovaries or oocytes (i.e., deformed or lysed ovaries or oocytes).

Laboratory analysis

Prior to dissection, specimens were thawed, rinsed and blotted dry, measured (± 1 mm standard length [SL], measuring board) and weighed (± 0.01 g, electronic balance). (All further references to length refer to SL.) Our dissections yielded 38 females with what appeared to be mature gonads (i.e., containing visually detectable oocytes or ova) and 124 fish that were either immature or spent females or males. We then removed ovaries from the mature females and weighed their ovaries to the nearest 0.001 g with an electronic balance. The ovaries were then placed in Gilson's fluid (Bagenal 1978). We held ovaries in Gilson's fluid for 3 to 6 months and agitated them regularly to dissolve ovarian tissue and harden oocytes (Bagenal 1978). Because we do not know whether some oocytes had been ovulated, we refer to both oocytes and ova as oocytes.

We made potential fecundity and oocyte diameter measurements by first placing oocytes in a dish with a small amount of water. Holding oocytes in water did not significantly affect diameter measurements (unpublished data). We defined potential fecundity as the total number of oocytes present in the ovary at the time of capture, and we counted oocytes using a dissecting microscope at $\times 50$ magnification. Longnose dace appear to spawn all or most of their oocytes during the spawning season (see Results) and there was little evidence of resorption such as darkening, deformation of the oocyte, or deterioration of the cell membrane. We measured oocyte diameters at the widest point of an oocyte using a calibrated ocular micrometer and dissecting microscope at $\times 50$ magnification. Because oocytes were almost always spherical, this measurement method accurately reflected true oocyte diameters. Oocyte diameter measurements were recorded to the nearest 0.04 mm.

Immersion in Gilson's fluid produced almost complete digestion of ovarian tissue for 12 of 40 specimens; however, 15 ovaries retained sufficient ovarian tissue to require manual dissection of oocytes from the remaining tissue. Nevertheless, there were no visually apparent losses of oocytes in these

specimens, and we estimated fecundity for these individuals by counting all oocytes in the ovary. Unfortunately, the 13 remaining specimens displayed little digestion of ovarian tissue by Gilson's fluid, and consequently, were used only for analysis of reproductive effort. These 13 specimens were LS fish, and their mean size did not differ significantly from the remaining 27 specimens used in all other analyses (i.e., there was no size bias produced by deleting these fish).

For the 12 fish with complete digestion of ovarian tissues, we derived potential fecundity estimates by randomly subsampling oocytes using an eight-section sample splitter (Petty & Grossman 1996). Complete enumeration of oocytes for three specimens with lengths bracketing the size range of specimens in the sample demonstrated that three subsamples were needed to yield asymptotic potential fecundity estimates (sample estimation technique of Grossman 1986). Therefore, we based oocyte counts and diameter measures for the remaining nine specimens on extrapolations from three of eight subsamples from the ovary. We obtained complete oocyte diameter frequency distributions for the 12 fish with complete digestion of ovaries and quantified maximum oocyte diameters by measuring oocytes for all 27 specimens used in fecundity analysis. Maximum oocyte diameters were based on ten randomly selected oocytes from the most mature clutch (henceforth maximum oocyte diameter).

Data and statistical analysis

We conducted all statistical analysis using Statistical Analysis Software (SAS Institute 1982). When data were not normally distributed, they were transformed by \ln with the exception of potential fecundity – length relationships, which were transformed by \log_{10} . The latter transformation was required for comparison with the results of Brazo et al. (1978), who presented regression equations in this format. To determine the relationship between potential fecundity and fish size, we regressed potential fecundity against somatic mass (i.e., total mass – ovarian mass) and \ln (potential fecundity) against \ln length.

We compared the number of oocytes in each oocyte diameter mode (I, II, and III) for ES and LS longnose dace using the 12 specimens for which complete oocyte diameter measurements were obtained. We assumed that modes in oocyte diameter distributions approximated a normal distribution and then separated modes at either breaks in the distributions, or at the midpoints of overlapping tails. When oocyte diameter distributions possessed overlapping tails, we assigned 50% of the

oocytes in the midpoint diameter class to each of the overlapping modes. We used linear regression to determine the relationship between the number of oocytes in each diameter mode and somatic mass, and \ln length, and tested for significant differences in these relationships between ES and LS fish using analysis of covariance (ANCOVA) with length as the covariate.

We calculated potential clutch size from LS longnose dace because these specimens either had what appeared to be a relatively intact clutch (i.e., contained a group of large, relatively normally distributed oocytes) or had just spawned a clutch (i.e., contained no or few oocytes larger than Mode II, see Results). In addition, there was little evidence of resorption (see above). Consequently, we chose the two LS fish (84 mm and 98 mm, SL) that had intact clutches and estimated clutch size as the mean number of Mode III oocytes in these specimens. We recognize that our calculations may underestimate the "true" number of eggs in a clutch, if clutches are partially spawned (Heins & Baker 1993).

We used linear regression to quantify the relationship between \ln (ovarian mass) and \ln length. We determined whether mature ES and LS females exhibited differential reproductive effort (i.e., \ln ovarian mass) using ANCOVA, with \ln length as a covariate (ES: $n=7$, LS: $n=31$). In addition, we tested for non-isometric relationships between ovarian mass (y) and somatic mass (x) and ovarian mass (y) and length (x) using nonlinear regression ($y=x^m + b$). We determined whether relationships were non-isometric by using a t -test to determine whether the exponents (i.e., slopes) of these equations differed significantly from one (mass) or three (length) respectively. We also determined whether the somatic mass – length relationship was isometric (slope=3) using the above method.

We determined reproductive effort using the gonadosomatic index (GSI=ovarian mass/(total mass – ovarian mass) \times 100) (deVlaming et al. 1982).

Results

Mean length did not differ significantly between ES (80 ± 8 mm) and LS (77 ± 13 mm) specimens used in potential fecundity analysis (t -test, $P=0.56$, $n=25$). The smallest female with mature ovaries was 56 mm SL (age 1+, Grossman & Rajtaczak, unpublished data) with a somatic mass of 3.0 g, and the largest was 106 mm SL with a somatic mass of 16.6 g.

Mean (\pm SD) potential fecundity for ES fish was 1832 ± 572 oocytes (range 1155–2534), whereas for LS fish it was 775 ± 415 oocytes (range 246–1653).

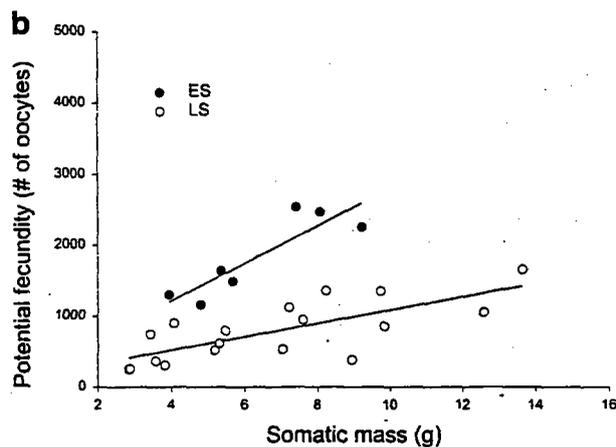
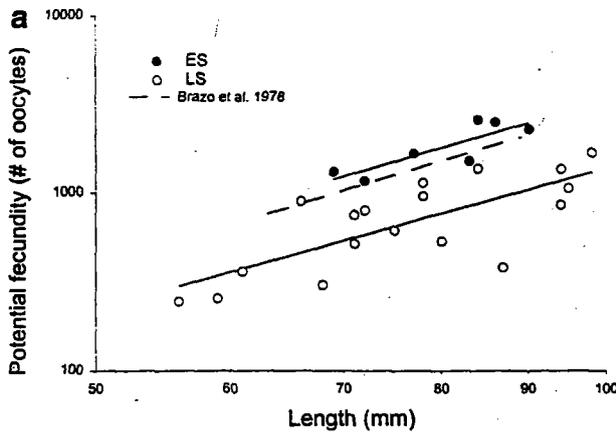


Fig. 1. (a) Comparison of potential fecundity - length regressions for ES and LS longnose dace (note \log_{10} scale). We included the data of Brazo et al. (1978) for comparison. Regression equations follow: ES - $\ln(\text{potential fecundity}) = 2.74(\ln \text{ length}) - 1.97$ ($R^2 = 0.71$, $P < 0.02$, $n = 7$); LS - $\ln(\text{potential fecundity}) = 2.50(\ln \text{ length}) - 2.07$ ($R^2 = 0.55$, $P < 0.0005$, $n = 18$). Data for ES and LS longnose dace are based on standard length, whereas data for Brazo et al. (1978) are based on total length. We did not record total length for Coweeta longnose dace. (b) Potential fecundity - mass regressions for ES and LS longnose dace. Regression equations follow: ES - $\text{potential fecundity} = 263(\text{somatic mass}) + 157$ ($R^2 = 0.77$, $P < 0.009$, $n = 7$); LS - $\text{potential fecundity} = 94(\text{somatic mass}) + 143$ ($R^2 = 0.54$, $P < 0.0006$, $n = 18$).

Five LS longnose dace appeared to have spawned most of their oocytes and had fecundities less than 400 oocytes (range 246-381). Potential fecundity was positively related to: 1) standard length (Fig. 1), 2) somatic mass (Fig. 1) and 3) total mass (Fig. 2). Both Coweeta and Lake Michigan populations of longnose dace exhibited similar relationships between potential fecundity and length and mass (Fig. 1, 2).

Oocyte - diameter frequency histograms indicated that ES specimens contained two modes of oocytes (Fig. 3A), whereas LS fish frequently had three modes (Fig. 3B). Some LS specimens ap-

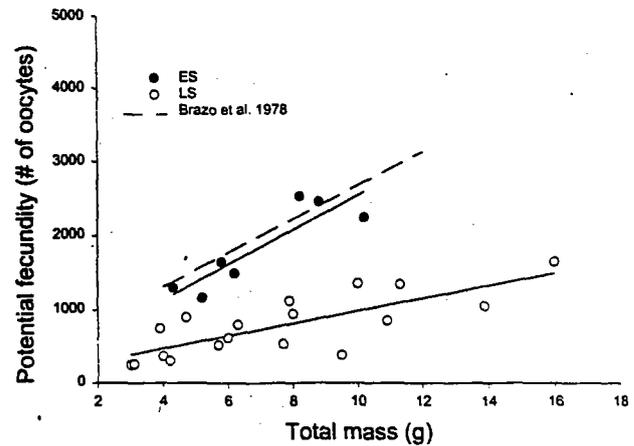


Fig. 2. Comparison of potential fecundity - total mass relationships for ES and LS longnose dace from Coweeta and Lake Michigan (Brazo et al. 1978). Regression equations follow: ES - $\text{potential fecundity} = 236(\text{total mass}) + 195$ ($R^2 = 0.78$, $P < 0.009$, $n = 7$); LS - $\text{potential fecundity} = 94(\text{total mass}) + 143$ ($R^2 = 0.60$, $P < 0.0002$, $n = 18$).

peared to be spent or contained only one or two small clutches (Fig. 4). For ES fish, the medians of Mode I oocytes ranged from 0.26 to 0.40 mm and medians for mode II oocytes varied from 0.72 to 0.92 mm. Medians for LS fish (Mode I oocytes: 0.28-0.36 mm; Mode II oocytes: 0.68-0.76 mm) were similar to those for ES specimens with the exception of Mode III oocytes (1.10-1.36 mm), which only were present in LS fish. The maximum recorded oocyte diameter for longnose dace was 1.6 mm. There were significantly fewer Mode I oocytes in LS specimens (mean \pm SD = 207 ± 162) than in ES specimens (mean \pm SD = 569 ± 303) (ANCOVA, $P < 0.005$, $n = 5, 7$), and we observed an identical result (LS < ES) for Mode II oocytes (LS: mean \pm SD = 440 ± 344 ; ES: 1231 ± 370) (ANCOVA, $P < 0.0001$, $n = 5, 7$). The number of Mode II oocytes in ES fish was positively correlated with both \ln length ($R^2 = 0.66$, $P < 0.03$, $n = 7$) and somatic mass ($R^2 = 0.81$, $P < 0.0006$, $n = 7$). Most LS specimens contained very low numbers of Mode I oocytes (Fig. 3, 4), which suggests that longnose dace may spawn all or the great majority of their oocytes in a given year. Consequently, potential fecundity estimates for ES fish may be accurate estimates of "true" fecundity for longnose dace, especially given that there is little evidence of substantial resorption or oocyte production during spawning (see below). Finally, given that LS samples contained individual longnose dace that had either two or three modes of oocytes, it unlikely that this species is a group synchronous spawner.

Because oocyte diameter distributions showed a decline in oocytes between ES and LS specimens

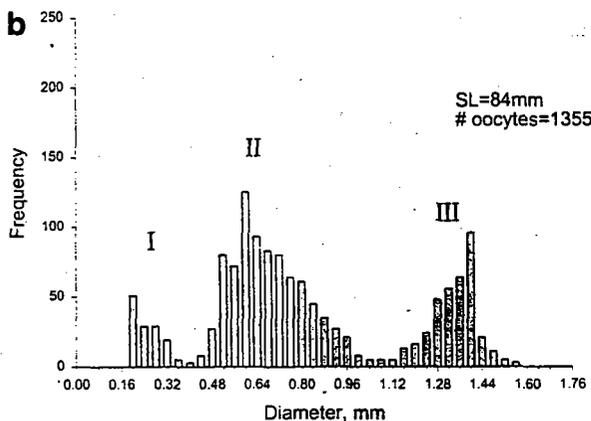
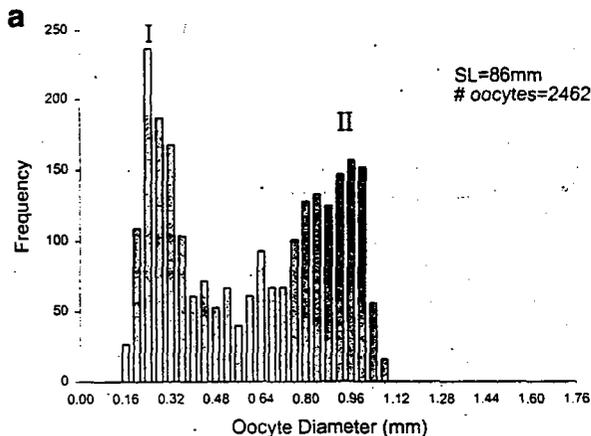


Fig. 3. Oocyte diameter distributions for typical ES (a) and LS (b) longnose dace. We used dace of similar length to control for size effects.

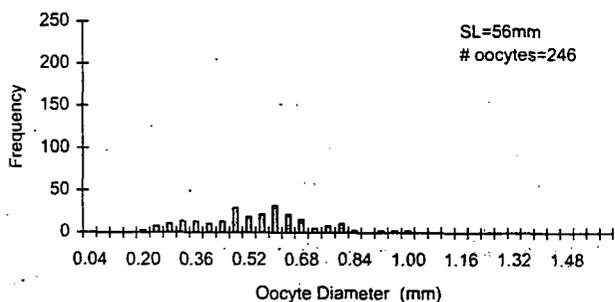


Fig. 4. Oocyte-diameter distributions representative of longnose dace that have almost completed spawning (i.e., one or two small clutches remaining).

and LS samples included specimens ranging from almost spent to those containing high numbers of Mode II oocytes, it is clear that individual longnose dace spawn repeatedly within a given spawning season. Estimates of potential clutch size for the two LS fish with intact clutches were 400 (98 mm SL specimen) and 365 (84 mm SL specimen) oocytes, respectively. If we assume that: 1) all oocytes in an ovary are spawned during a single repro-

ductive season, 2) few new oocytes are produced by females during the reproductive season (supported by the low number of Mode I oocytes in LS fish), 3) there is little resorption of oocytes (supported by the lack of these oocytes in samples, and 4) clutch size remains relative constant, then we can estimate the potential number of clutches spawned by female longnose dace by dividing the maximum number of oocytes observed in ES fish (2534 oocytes, 84 mm SL specimen) by mean clutch size (382 oocytes). This calculation yielded a potential of 6.6 clutches spawned by female longnose dace per year.

Reproductive effort varied among longnose dace; however, mean \ln ovarian mass values did not differ significantly between ES ($n=7$) and LS ($n=31$) specimens (ANCOVA, $P>0.71$). Gonadosomatic index values for longnose dace ranged from 2.4% (ES specimen) to 21.4% (LS specimen). Regression analysis demonstrated that there was no evidence of differential reproductive effort between longnose dace of different size. Nonlinear regressions of \ln (ovarian mass) - \ln length for ES ($y = -16.85 * x^{3.71}$, $R^2=0.88$, $P<0.0002$, $n=31$) and LS ($y = -14.31 * x^{3.15}$, $R^2=0.51$, $P<0.0002$, $n=31$) specimens possessed slopes that did not differ significantly from isometric relationships (i.e., slope=3, t -test, all $P>0.05$). We obtained a similar result for \ln (ovarian mass) - \ln (somatic mass) regressions for ES ($y = -2.84 * x^{1.25}$, $R^2=0.96$, $P<0.0001$, $n=7$) and LS ($y = -2.65 * x^{1.10}$, $R^2=0.50$, $P<0.0001$, $n=31$) (i.e., slope=1, t -test, all $P>0.05$) specimens. The relationship between \ln (somatic mass) and \ln length also did not differ significantly for that predicted by isometric growth (ES: $y = -11.22 * x^{2.98}$, $R^2=0.91$, $P<0.0009$, $n=7$; LS: $y = -10.20 * x^{2.77}$, $R^2=0.94$, $P<0.0002$, $n=31$) (i.e., slope=3, t -test, all $P>0.05$).

Discussion

Our data indicate that female longnose dace began spawning between March and June during 1999 in the Coweeta Creek drainage. Nevertheless, given results for potential fecundity (ES>LS) and oocyte frequency distributions (Mode III present only in LS fish), the inception of spawning probably was closer to June than March. This pattern is similar to that observed in our previous work (DeHaven et al. 1992), which used Relative Gonadal Index values (Erickson et al. 1985) and histological classification of longnose dace ovaries to indicate the onset of spawning. Longnose dace in other geographical regions also spawn between May and July (Bartnik 1970; Brazo et al. 1978). Female longnose dace in the Coweeta drainage were capable of reaching maturity in their second year of

life (G. Grossman et al., unpublished data), as were longnose dace inhabiting Lake Michigan (Brazo et al. 1978). Reaching maturity in the second year of life is not uncommon in cyprinids and has been observed in both European and North American species (Mills 1987; Heins & Rabito 1986, 1988; Velasco et al. 1990; Fernandez-Delgado & Herrera 1995a; Gotelli & Pyron 1991; Aparicio & De Sostoa 1998).

Potential fecundity for ES longnose dace in the Coweeta drainage ranged from 1155 to 2534 oocytes, and these values appear to represent reasonable estimates of total annual potential fecundity for longnose dace. We based this conclusion on the fact that 1) oocyte diameter distributions and potential fecundity data for LS fish suggested that the great majority of oocytes were spawned during a given spawning season, 2) there were few signs of oocyte resorption (i.e., atretic oocytes), and 3) oocyte diameter distributions provided little evidence that production of substantial numbers of new oocytes (i.e., large numbers of Mode I oocytes) occurred during the spawning season. Our lack of data from post-spawning period specimens, however, renders this conclusion tentative. An unusual life-history characteristic of longnose dace is that the great majority, if not all, oocytes were spawned during the 1999 reproductive season. This conclusion is supported by the fact that we collected females that did not have visually apparent oocytes in their ovaries in LS samples (females with as few as 250 eggs were visually identifiable). This pattern appears to be uncommon among members of the Cyprinidae (Rinchard & Kestemont 1996).

It is surprising that mass-specific potential fecundity estimates for longnose dace from Coweeta and Lake Michigan (Brazo et al. 1978) were similar, because these populations are likely subjected to very different selective regimes. Potential fecundity and clutch size in Coweeta longnose dace were positively correlated with both length and mass, although these relationships were strongest for ES dace. This difference is likely a result of the fact that LS dace already had begun spawning. Positive correlations between parameters that characterize reproductive effort (e.g., potential fecundity, clutch size, ovary mass, etc.) and body size are common in fishes (Wootton 1979, 1990).

Our data strongly suggest that Coweeta female longnose dace spawned multiple times during the reproductive season, a pattern observed in cyprinid fishes from at least three continents (Abidin 1986; Heins & Rabito 1986, 1988; Heins 1990; Velasco et al. 1990; Fernandez-Delgado & Herrera 1994, 1995a, 1995b; Rinchard & Kestemont 1996;

Aparicio & De Sostoa 1998). Other cyprinids are capable of producing 6+ clutches in a single reproductive season (Heins & Rabito 1986; Aparicio & De Sostoa 1998), although a lower number of clutches (e.g., ~2) appears to be more common in this family (Herrera & Fernandez-Delgado 1992; Fernandez-Delgado & Herrera 1994, 1995a, b). Unfortunately, due to the limited time frame of our collection, we were unable to conclusively determine the number of clutches spawned by Coweeta dace. Oocyte diameter data for longnose dace also showed that oocytes reached maximum size of 1.6 mm, which falls within the range of ripe oocyte sizes reported for other cyprinid fishes (Heins & Rabito 1988; Gotelli & Pyron 1991; Fernandez-Delgado & Herrera 1995b; Rinchard & Kestemont 1996).

Longnose dace have the most widespread geographical range of any native North American cyprinid. Our results, from one of the southernmost populations of this species, demonstrate that longnose dace display life history traits that are common to other cyprinids, including a potential fecundity - body size relationship very similar to a Lake Michigan population of longnose dace. Nevertheless, Coweeta drainage longnose dace also exhibit a life history trait that appears to be uncommon among cyprinid fishes, the ability to spawn the great majority of their oocytes in a single reproductive season. We hope that additional studies will be undertaken on this species to further characterize its life history as well as its phenotypic and genotypic plasticity.

Resumen

1. En dos periodos de muestreo Marzo, 1999 (ES) y Junio 1999 (LS), examinamos las características reproductivas de 38 hembras de una de las poblaciones más sureñas de *Rhinichthys cataractae*. Los datos indicaron que los individuos ES no se habían reproducido mientras que los LS habían empezado ya la puesta.
2. La hembra madura más pequeña capturada midió 56 mm SL (edad 1+). La fecundidad potencial media difirió significativamente entre individuos ES (Media \pm 1 SD = 1832 \pm 572 oocitos) y LS (775 \pm 415 oocitos). La fecundidad potencial estuvo positivamente correlacionada con la longitud estándar y con la masa somática tanto para los individuos ES como para los LS.
3. Histogramas de frecuencia de diámetros de los oocitos indicaron que los individuos ES tenían dos modas mientras que los individuos LS tenían dos o tres modas. Las hembras parecen poner más de una vez durante una estación reproductiva. El número de oocitos varió substancialmente entre individuos en cada periodo tanto como entre periodos. El número de oocitos en la Moda II en individuos ES estuvo positivamente correlacionado con la longitud y con la masa somática. Las hembras parecen potencialmente capaces de producir hasta 6 puestas al año. Los valores de IGS variaron entre 21.4% en individuos LS hasta 2.4% en individuos ES. Un análisis de regresión no mostró evidencia de que el esfuerzo reproductivo fuera distinto entre individuos de diferente tamaño.

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