associated with an appropriate rectus capitus musculature. Such a correlation among extant snakes might greatly facilitate interpretation of fang evolution in Tertiary forms, where, understandably, the dentition is seldom preserved.

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Age and Growth of the Ozark Hellbender (*Cryptobranchus alleganiensis bishopi*)

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Length-specific growth rates of Ozark hellbenders, *Cryptobranchus alleganiensis bishopi*, from the North Fork of the White River, Missouri, were calculated by regression from the growth of marked and recaptured hellbenders. Growth rates declined steadily after transformation from a predicted 61 ± 7 mm total-length increase per year at 18 months to about 1 mm annual increase at 25 years of age. Male and female hellbenders grew at similar rates. The growth model provides a means to estimate age based on length and predicts longevity in excess of 25 years. Statistical analysis indicated a significant difference in the length-growth and length-weight relationships of Ozark hellbenders from the North Fork and *C. a. alleganiensis* from the Niangua River, Missouri. Despite an apparently similar or greater density of hellbenders, growth is greater in the Niangua population.

The hellbender, *Cryptobranchus alleganiensis,* is a large primitive, aquatic salamander. There are two described subspecies. *C. alleganiensis alleganiensis* inhabits clear, rocky streams from southern New York south to Georgia and northeastern Mississippi and west to north-flowing Ozark streams of the Missouri River Drainage and possibly southeast Kansas (Dun-

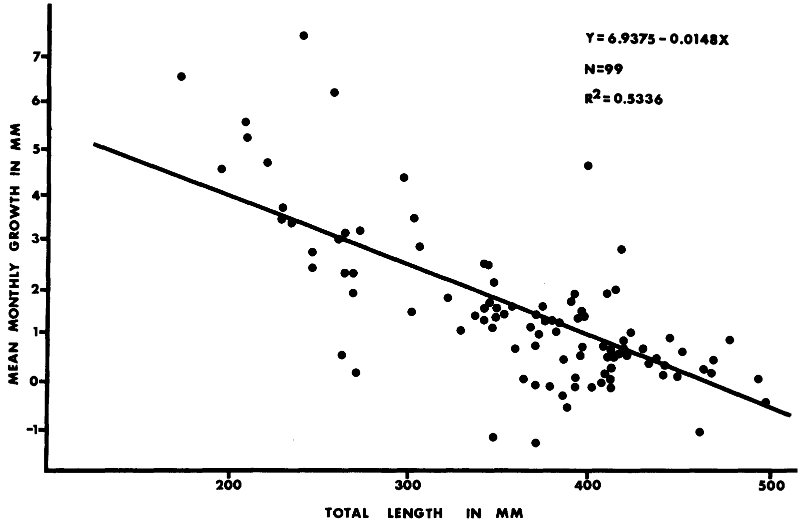

Fig. 1. Length-specific monthly growth rates of 99 hellbenders with Model II regression line.

dee, 1971). *C. a. bishopi,* the Ozark hellbender, is known from the Spring River in Arkansas (Dowling, 1957) and, in Missouri, from the south-flowing North Fork of the White, Current and Eleven Point rivers. Wortham and Nickerson (1971) speculate that the two subspecies have been geographically separated since the Tertiary.

Longevity and growth of the Ozark hellbender in the North Fork of the White River were studied to gather information about age and to compare that information with the data collected by Taber et al. (1975) for age and growth of *C. a. alleganiensis* in the Niangua River, Missouri. This was accomplished by marking and recapture over a 1.5-year period. Length-specific growth rates were calculated from the growth of recaptured animals, and a length-age relationship was developed by adding annual growth increments successively to a length at known age.

Materials and Methods

Three large riffles and adjacent pools of a 4.6-km section of the North Fork River, Ozark County, Missouri, approximately 12 km upstream from Norfork Lake were studied from May 1977 to Nov. 1978. This habitat has been described by Nickerson and Mays (1973a, b). In general, the North Fork is a typical spring-fed Ozark stream.

Hellbenders were caught during daylight hours by turning rocks in shallow riffles and shoreline areas, usually 1 m or less in depth, and in a few pools to 2 m in depth. A standard fish board was used to measure total length (TL) to the nearest millimeter. Since Taber et al. (1975) found a highly significant linear relationship between snout–vent length and TL in both male and female hellbenders, TL rather than snout–vent length was measured because TL could be obtained more accurately. Animals were weighed to ±1 g using a pan-equipped triple beam balance. For greater accuracy and to facilitate measurements, the animals were first anesthetized in a weak solution of tricaine (ethyl-m-aminobenzoate, Sigma Co.). Marking was accomplished using a branding technique described by Clark (1971) and utilized successfully on hellbenders by Taber et al. (1975). Sex was recorded when external determination was possible. During late summer through the fall breeding season, males can be identified by swollen cloacal glands and females by egg-distended abdomens. The presence of these characteristics was used as criterion of sexual maturity.

Model II regression in which both variables are subject to error was used to determine the relationship between initial total length (TL_0) and growth (Bartlett, 1949; Davies, 1971). Although many individuals were recaptured more than once, only initial and final length measurements were used to determine growth. Growth during recapture intervals of less than

60 days was rejected due to the growth increment being small compared to measurement error and possible effects of handling.

Length-growth relationships for males and females were compared using Bartlett's three group method as illustrated by Simpson, Roe and Lewontin (1960). This method was also used to compare the length-growth relationships of the North Fork River population and the Niangua River population using data collected by Taber et al. (1975). Though subject to criticism (e.g., Ricker, 1973), Bartlett's method was employed because 1) reasonable doubt exists as to an optimal Model II strategy (Sokal and Rohlf, 1981; Jolicoeur, 1975) and 2) computational methods have been developed to compare slopes and intercepts of regressions determined by this method (Davies, 1971; Simpson et al., 1960).

Estimates of population size for two collection sites in the North Fork were made by the Petersen method and by the method described by Jolly (1965) using multiple-mark-and-recapture data.

Results and Discussion

During the study 744 hellbenders were marked. Forty-five were identified as males and 24 as females. A total of 180 hellbenders was recaptured at least once, and 99 were recaptured with more than 60-day intervals. The smallest recapture was 172 mm TL_0. The longest recaptured hellbender was 501 mm TL_0, and the longest animal caught measured 551 mm TL. No individual was recaptured more than four times.

Comparison of growth in length of recaptured males (N = 12) and recaptured females (N = 12) indicated no significant difference in slope ($t_{[9]} = 0.091$; $P > 0.5$), but a significant difference in their y-intercepts ($t_{[9]} = 7.602$; $P < 0.001$). However, the sample sizes were small and Taber et al. (1975), who sexed considerably more hellbenders, indicated that the sexes grow at about the same rate. Therefore, the two sexes were pooled together with unsexed animals to yield a sample of 99 recaptured hellbenders for determining monthly length-specific growth rates (Fig. 1). Analysis of deviations from linearity ($t_{[96]} = 0.340$; $0.5 > P > 0.2$) indicated that monthly growth was a highly significant decreasing linear function of TL:

$$\Delta TL_{(mm)}/\text{month} = 6.9375 - 0.0148\ TL_{0(mm)}.$$

An ellipse as the boundary of a 95% joint confidence region for the intercept and slope was determined using the method described by Bartlett (1949). The slope is indicated to be between −0.0103 and −0.0193 and the intercept between 6.648 and 7.227.

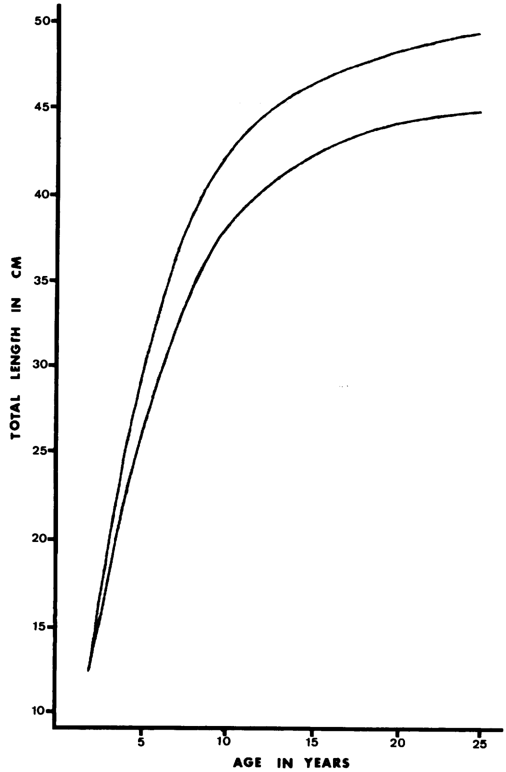

Fig. 2. Length-age relationship derived from growth rates of the regression equation of Fig. 1. Annual growth increments were successively added to a 1.5-year length of 125 mm. The area between the curves includes the 95% confidence region.

A length-age curve was generated from the length-growth equation in the manner described by Taber et al. (1975). Nickerson and Mays (1973a) report that Ozark hellbenders lose their gills at about 125 mm TL, and Goin and Goin (1971) state that hellbenders lose their gills when they are about 1.5 years old at which time they are approximately 125 mm TL. Hence, the length characteristic of particular age classes was determined in this study by adding successive annual growth increments to 125 mm (Fig. 2). Annual growth, also considered to be a function of length, was calculated by summing monthly growth rates.

Maximum and minimum sizes calculated from the 95% confidence region for the slope and

TABLE 1. COMPARISON OF SLOPES (± STANDARD ERRORS) AND INTERCEPTS FOR LOG-TRANSFORMED LENGTH-WEIGHT RELATIONSHIPS OF MALES, FEMALES AND TOTAL RECAPTURES USING MODEL I AND MODEL II (RICKER'S GM AND BARTLETT'S THREE GROUP METHODS) REGRESSION ANALYSIS.

		Model I		Model II			
				Ricker's GM method		Bartlett's three group	
	N	b ($\pm s_b$)	a	v ($\pm s_v$)	u	b ($\pm s_b$)	a
Males	45	2.849 (±0.1294)	−4.809	2.973 (±0.1294)	−5.125	2.831 (±0.1467)	−4.762
Females	24	2.531 (±0.3862)	−3.956	3.112 (±0.3862)	−5.473	3.210 (±0.6356)	−5.729
Recaptures	121	2.940 (±0.0546)	−5.009	3.000 (±0.0546)	−5.161	2.967 (±0.0649)	−5.076

intercept of the regression relationship are shown by the curves in Fig. 2. At about 38 cm TL, growth rates have diminished to the point that variation among equal-aged animals introduces uncertainty into the determination of year classes from lengths. However, the curves suggest that the largest specimens encountered (Fig. 1) were probably over 25 years old, and indicate a maximum length of about 47 cm TL. Oliver (1955) reported that the hellbender has been kept in captivity for 29 years, and Taber et al. (1975) believe that both sexes of *C. a. alleganiensis* in the Niangua River may live more than 30 years. The growth model of Taber et al. (1975) predicts a maximum length of about 54 cm, although 3.8% of the population studied during the fall was longer. Of 1,132 hellbenders marked by Taber et al. (1975) and 405 by Wiggs (1977), the longest Niangua hellbender measured 610 mm TL. Of the animals captured in the North Fork, 2.3% were longer than 47 cm. The longest *C. a. bishopi* reported from Missouri, one of about 2,000 captured in the North Fork River in a study by Nickerson and Mays (1973a) and 744 in this study, was 551 mm TL.

Several factors may affect the validity of the length-growth relationship and thus the length-age curve. Variation in environmental factors may have been involved. Handling and branding, as suggested by Taber et al. (1975), likely retards growth to a variable and unknown degree, and Van Devender (1978) in a study of the growth ecology of *Basiliscus* indicated that the use of initial length rather than average length in the length-growth relationship may underestimate size at all ages (though resulting in a greater r^2 value). Thus the length-age curve (Fig. 2) may need to be elevated slightly. Further, even though the data indicate only decreasing growth as length increases, it seems unlikely that a single straight line accurately describes growth at all sizes. The length-growth relationship predicts negative growth for animals longer than 469 mm, but this is probably due to the difficulty in determining accurately the growth of large animals because they grow so slowly. Possibly the growth of these older animals would more accurately be described by a curve approaching the zero-line asymptotically beyond 469 mm.

Although Nickerson and Mays (1973a) found a 1:1 ratio of males to females in the North Fork, considerably fewer female hellbenders (N = 24) were identified than males (N = 45) in this study. However, due to the difficulty in identifying females externally, particularly smaller individuals, little can be said about the exact sex ratio from our data.

Length-weight relationships were calculated for North Fork males, females, and recaptured animals using common log-transformed initial measurements. The length-weight relationship for males was

$$W_{(g)} = 0.0000173\ L_{(mm)}^{2.8309}\ (R^2 = 0.9187)$$

while the relationship for females was

$$W_{(g)} = 0.0000019\ L_{(mm)}^{3.2104}\ (R^2 = 0.6619)$$

and the relationship for all recaptures (N = 121) was

$$W_{(g)} = 0.0000084\ L_{(mm)}^{2.9667}\ (R^2 = 0.9604).$$

There was no significant difference between the slopes of the length-weight relationships of males and females ($t_{[63]} = 0.217$; $0.9 > P > 0.8$), although their intercepts did differ ($t_{[63]} = 45.54$; $P < 0.001$) with females being heavier. The relationship for all recaptures was intermediate. Similarly, Taber et al. (1975) found no significant difference between the sexes in the rate at which weight increased as a function of length, although females were slightly heavier than males at all lengths. Finally, these length-weight relationships also were analyzed by Model I and

Ricker's GM method of Model II regression analysis (Ricker, 1973). Model I analysis indicated highly significant linear predictive equations using the log-transformed data (i.e., for males $F_{[1,43]} = 484.8$, for females $F_{[1,22]} = 42.95$, and for recaptures $F_{[1,119]} = 2{,}899$). The slopes, standard errors of the slopes and y-intercepts for each of the methods are given in Table 1.

Absolute and percentage annual weight increments of North Fork hellbenders were calculated from the length-age curve using the length-weight formula for recaptures. Although percentage weight gain decreases exponentially with age, absolute weight gain is greatest at about four years of age. This contrasts with the Niangua hellbenders in which weight gain seems to be greatest when the animals are about seven years old (Taber et al., 1975).

Sexual maturity for most males from the North Fork is apparently attained at about 256 to 300 mm TL (4–5 years old) while most females are mature at about 330 to 380 mm TL (7–8 years old). However, it is more difficult to determine at what age females first attain sexual maturity externally. Taber et al. (1975) suggested that most Niangua male hellbenders are sexually mature at about 300 mm (5 years old) and most females at about 380 mm TL (7–8 years old). The minimum and maximum lengths for sexually identifiable North Fork males were 240 and 461 mm, respectively, and for females, 297 and 501 mm TL. Because males and females apparently grow at about the same rate, the greater maximum lengths reported by Collins (1974) for female hellbenders may be due to more females living longer than males rather than to a difference in growth. This is supported by the four females to one male ratio reported by Wiggs (1977) for Niangua hellbenders 15 years old or older (450 mm TL or longer).

Using the length-age relationship, the age distributions of hellbenders collected in the North Fork were determined, excluding recapture data. From these data the survivorship of metamorphosed Ozark hellbenders was calculated (Fig. 3). They tend to exhibit Deevey's (1947) Type II or diagonal survivorship curve showing a rather constant mortality rate in all age groups. However, the rate of mortality is less for females than for males. Taber et al. (1975) also found that males exhibited a diagonal curve, but the females and the sexed and not sexed hellbenders followed a Type III sur-

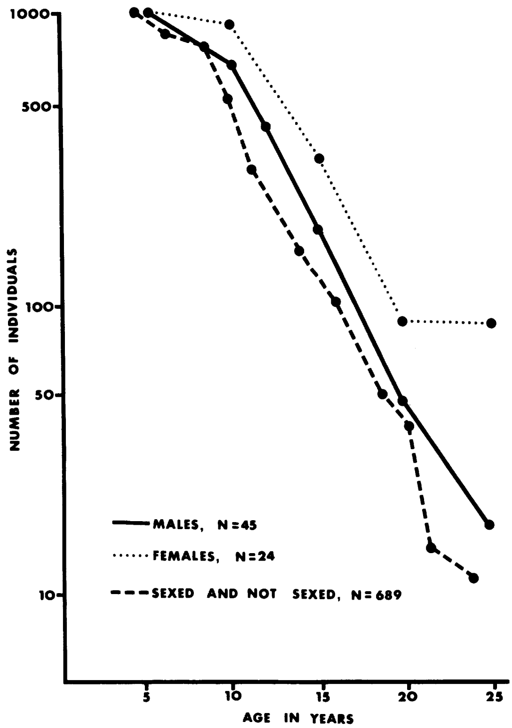

Fig. 3. Survivorship of Ozark hellbenders based on collections from two years.

vivorship curve with relatively high expectation for further life in those animals which survived to relatively older ages.

The survivorship of North Fork hellbenders indicates that the North Fork population is not dominated so much by large, long-surviving salamanders as is the Niangua population. No difference in predation is suspected, however. Further, once hellbenders reach a size of 380 mm TL (9–10 years old for North Fork hellbenders), predation is probably minimal in both rivers.

Initial mortality could not be estimated because relatively few animals less than 200 mm TL were captured, and no gilled specimens were caught. This is probably partly due to inefficiency in the capture technique. However, Taber et al. (1975) suggest that the survivorship features of hellbenders indicate a low rate of egg and larval survival and that the egg-eating and cannibalistic behavior reported by Smith (1907) and Nickerson and Mays (1973a) may be important population control mechanisms. Thus the relatively few small hellbenders captured may reflect the normal population structure

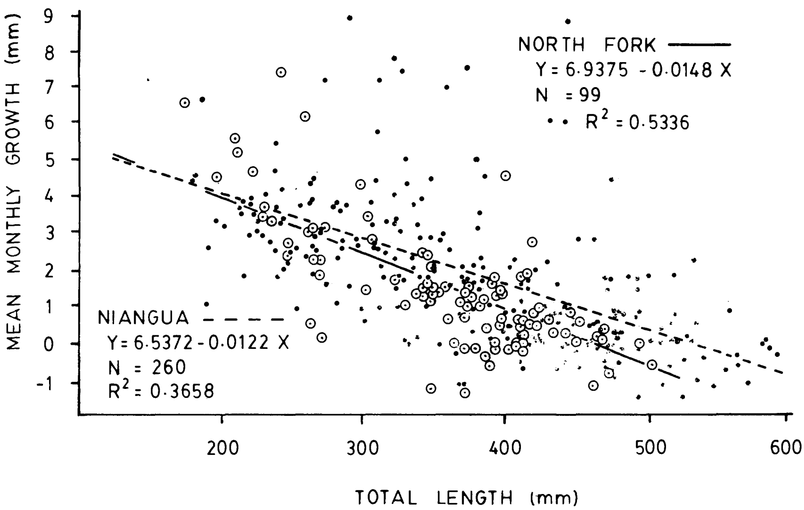

Fig. 4. Comparison of length-growth relationships calculated by Model II regression of transformed hellbenders, *C. a. bishopi* from the North Fork River (open circles) and *C. a. alleganiensis* from the Niangua River (solid circles).

(Taber et al., 1975). In a study of the fecundity of hellbenders from the North Fork and Niangua rivers, Topping and Ingersol (1981) found that the reproductive potential is large, further indicating large larval mortality in both populations.

A comparison of the growth relationships calculated by Model II regression of the *C. a. alleganiensis* collected in the Niangua by Taber et al. (1975) and the *C. a. bishopi* from the North Fork is shown in Fig. 4. Although no significant difference was indicated in the slope of the two relationships ($t_{[353]} = 0.598$; $P > 0.5$), a highly significant difference was found in the elevation of the two lines ($t_{[353]} = 2.685$; $P < 0.01$). Thus there seems to be greater growth in Niangua individuals at all sizes and ages. This conclusion is supported by a comparison of the length-weight relationships. Using common log-transformed initial measurements of 121 recaptures from the North Fork and 257 recaptures from the Niangua (Taber et al., 1975), length-weight relationships were found to be significantly different ($P < 0.01$) between the two populations. The rate at which weight increases as a function of length is greater for Niangua hellbenders.

The difference in growth likely results in the different adult size of the salamanders from the two rivers, although greater longevity could be responsible for the larger size of the Niangua hellbenders also. However, there exists little information on this factor, and because the growth of very old salamanders is so small, the life span cannot be determined from growth.

Population sizes, densities and biomasses (based on an average weight of 314.3 g for the 121 recaptures) and their confidence limits for two collection sites in the North Fork are shown in Table 2. The estimate made by the Jolly method is an average of four estimates, while the estimate made by the Petersen method is an average of only three estimates due to one recapture interval of several months. The estimate for the smaller collection site falls within the 95% confidence limits of the population estimate made for the same riffle by Nickerson and Mays (1973b). Using the Petersen method, they estimated the population size of the site to be 269 with 95% confidence limits of 168 and 396. Density was estimated to be one hellbender per 6–7 m² to one per 13–16 m². According to Nickerson and Mays (1973b), only 50–60% of the riffle was suitable "diurnal habitat for taggable sized hellbenders." Thus the density estimated by them is considerably larger than the density estimated in this study where the area of the entire riffle was considered. The riffle biomass estimated by Nickerson and Mays (based on an average weight of 365 g) was 98.2 kg with 95% confidence limits of 61.3–144.5 kg. They also estimated density for a 2.67-km stretch of the river: 428 hellbenders per km with 95% confidence limits of 341 and 573.

TABLE 2. DENSITY AND BIOMASS OF HELLBENDERS FOR TWO COLLECTION SITES IN THE NORTH FORK RIVER BASED ON JOLLY'S METHOD FOR DETERMINING A POPULATION ESTIMATE AND A COMPARISON WITH THE POPULATION ESTIMATE DERIVED USING THE PETERSEN METHOD. The 95% confidence limits are shown in parentheses.

Area m^2	Population estimate		Density #/100 m^2	Riffle biomass	
	Petersen	Jolly		kg	g/m^2
4,827	231 (178–284)	239 (177–301)	5.0 (3.7–6.2)	75.1 (55.6–94.6)	15.7 (11.6–19.5)
12,719	804 (553–1,057)	624 (317–931)	4.9 (2.5–7.3)	196.2 (99.6–292.6)	15.4 (7.9–22.9)

Based on seven collection sites, R. L. Wiggs and K. Barke (pers. comm.) estimated a density of 506 hellbenders per km for a 3.5-km stretch of the Niangua River (using a modified Schnabel method) with 95% confidence limits of 375–677 hellbenders per km. Only "usable area" for hellbenders was considered in the estimate.

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