Demography of the Hellbender Cryptobranchus alleganiensis in the Ozarks

CHRIS L. PETERSON
1635 Lee Street, Springfield, Mo. 65803

DEAN E. METTER
Department of Biological Sciences, University of Missouri, Columbia 65211

BRIAN T. MILLER
Department of Zoology, Washington State University, Pullman 99164

and

ROBERT F. WILKINSON and MILTON S. TOPPING
Department of Biology, Southwest Missouri State University, Springfield 65804

ABSTRACT: Hellbenders *Cryptobranchus alleganiensis* were sampled by mark-recapture in four rivers: *C. a. bishopi* in the Spring River, Arkansas, and Eleven Point River, Missouri, and *C. a. alleganiensis* in the Gasconade and Big Piney rivers, Missouri. Densities ranged from 0.9-6.1 hellbenders per 100 m^2, biomass from 66-418 kg per ha. Growth of hellbenders decreased linearly as a function of total length in all populations. Spring River hellbenders exhibited the greatest length-specific growth, Eleven Point River hellbenders the least. Females exhibited a greater length-specific mass than males in all populations. Fecundity was a positive linear function of female body length. The mean number of eggs produced per female was 480, 450, 429 and 365 by the Spring River, Gasconade, Big Piney and Eleven Point river females, respectively. Age-specific production of ova was also greatest by Spring River females because of greater growth and consequent larger body size. It was least by Eleven Point River females.

INTRODUCTION

Cryptobranchus alleganiensis is a large aquatic salamander with two subspecies. The hellbender *C. a. alleganiensis* inhabits swift rocky streams from southern New York to northern Georgia and W through Tennessee and the Ohio River Valley to four N-flowing streams in the Ozarks (Dundee, 1971); the Meramec, Gasconade, Big Piney and Niangua rivers. The Ozark hellbender *C. a. bishopi* is known from the Spring River in Arkansas (Dowling, 1957) and from the Current, Eleven Point and North Fork rivers in Missouri (Firschein, 1951), all S-flowing, heavily spring-fed streams.

The hellbender is a habitat specialist because its success is dependent on a constancy of dissolved oxygen, temperature and flow found in swift water areas (Williams *et al.*, 1981). Thus the hellbender may serve as an indicator species for cool, unaltered streams. Smith and Minton (1957) reported that the range of the hellbender was rapidly decreasing because of human modification of stream habitat. In particular, impoundment, channelization, siltation, acid mine drainage and thermal pollution have reduced habitat for hellbenders (Dundee, 1971; Nickerson and Mays, 1973a). The status of the hellbender is uncertain in at least six states; it is endangered in two, and may have been extirpated in Illinois (Williams *et al.*, 1981). Although stable populations exist in the Ozarks (Nickerson and Mays, 1973a), demographic data exist only for Niangua and North Fork river populations (Nickerson and Mays, 1973a; Taber *et al.*, 1975; Topping and Ingersol, 1981; Peterson *et al.*, 1983). Therefore, the objective of this study was to provide information by mark-recapture on the population dynamics of four other populations to serve as a reference for future evaluation of the status of the hellbender in the Ozarks. The populations studied were *Cryptobranchus alleganiensis bishopi* in the Spring and Eleven Point rivers and *C. a. alleganiensis* in the Gasconade and Big Piney rivers.

Study Sites

The Spring River has its origin at Mammoth Spring less than 1 km S of the Missouri-Arkansas border in Fulton County. The spring has an average discharge of 34 million liter/hr. Collection site 1 was ca. 7 km downstream from the spring. Site 2 was within the town of Mammoth Spring ca. 1 km downstream from the spring.

The flow of the Eleven Point River is nearly doubled by the 29 million liter/hr average discharge from Greer Spring. Site 1 was about 20 km downstream from the spring, site 2 about 7 km downstream. Both sites were surrounded by Mark Twain National Forest in Oregon County, Missouri.

The Gasconade River was the largest river sampled and the warmest during summer. Unlike the other sites, its shorelines were muddy, and smooth bedrock areas were heavily covered by algae during summer. Site 1, the only collection site, was ca. 6 km N of Waynesville, Missouri, in Pulaski County.

The Big Piney River empties into the Gasconade River ca. 42 km downstream from the Gasconade River collection site. Collection sites in the Big Piney River were about 90 km upstream from the confluence: site 1 about 3 km upstream from the Highway 32 bridge between Licking and Success in Texas County, site 2 ca. 1 km downstream from the bridge.

Methods

From May 1980 to September 1982, hellbenders were caught during daylight hours by turning rocks. Uncovered hellbenders were grabbed by hand and placed in muslin or net bags. Swim masks were worn to aid visibility. Animals were anesthetized with tricaine; total length (TL) was measured to the nearest mm; and mass was measured to the nearest g with a pan-equipped, triple-beam balance. Marking was accomplished by branding. Arabic numerals ca. 3 cm long were made of small-diam wire. The numerals were heated with a propane torch, and the hellbenders were branded on the venter with a three-digit number. External determination of sex was made from late July into November, a period extending approximately 2 months before and after the reported breeding season. Males could be identified at this time by swelling around the cloaca and females by the absence of such swelling and egg-distended abdomens (Smith, 1912). Hellbenders were released in the area of capture within 3 hr. No collections were made in winter or early spring.

Population size for each collection site was estimated with the Jolly-Seber model as described by Begon (1979). Leslie's (1958) test was performed to test the assumption that all individuals are equally catchable. Roff (1973) argued that Leslie's test is incapable of distinguishing whether subgroups, such as sexes and age classes, differ in catchability. Therefore, tests of whether male and female hellbenders were equally catchable or had similar survival rates were also performed on each population as described by Begon (1979). Similar tests were made on three length classes for each population after pooling recapture data on both sexes. These tests can be used to examine differences in capture probabilities alone by assuming a constant survival probability. Alternatively, if the capture probabilities are assumed constant, the test is for constancy of survival probability (Begon, 1979). The average estimate of population size for each site was used to estimate density. Area was measured from shoreline to shoreline and not just where cover items were present. Estimates of natality and immigration (B_i) and probability of survival and lack of emigration (P_i) were also estimated from the Jolly-Seber analyses. Monthly survival rate ($MSR = P_i^{1/\text{intersample period}}$) was calculated as described by Tilley (1980).

Relative abundance of hellbenders was estimated in different sites by catch per unit effort by one of us. Timed samples were made only when visibility was good, the river was not in flood, and the temperature was not extremely cold.

Fecundity was determined by collecting females before a single spawning season. Ovaries were removed, and the ova to be laid that year were counted. Least squares regression was used to determine the relationship between reproductive potential and body size. Comparisons of fecundity-TL regressions of different populations were made as described by Zar (1984).

Length-specific growth rates of hellbenders for each population were estimated from recapture data. Mean monthly growth was regressed on initial TL by assuming a constant growth rate during the intercapture period. Due to the possibility of measurement error in both variables, Bartlett's (1949) regression method was used to describe the growth-TL and mass-TL relationships. Simpson *et al.* (1960) described methods for comparing coefficients of two Bartlett regressions. Growth increments within a single season were rejected to minimize the effect of marking and measurement error on growth. To maintain independence, only initial and final TLs were used to estimate growth of animals captured more than once.

The growth-TL regressions were integrated to generate equations relating age to TL as described by Van Devender (1978). If age at any specific size is known, the constant of integration can be calculated, and thus age can be estimated from TL. Age-specific fecundity was then estimated based on the fecundity-TL and age-TL relationships.

RESULTS

Equal catchability.—A total of 1208 hellbenders were marked in the four populations (Table 1). Based on the recapture data, there was no significant indication from Leslie's (1958) test that sampling was not random in the Spring ($\chi^2 = 19.7$, df = 14, $0.25 > P > 0.10$), Gasconade ($\chi^2 = 47.4$, df = 35, $0.10 > P > 0.05$) and Big Piney ($\chi^2 = 20.2$, df = 23, $0.50 > P > 0.25$) rivers. There were insufficient Eleven Point River data to employ Leslie's test. In the Big Piney River, females were significantly ($\chi^2 = 8.0$, df = 3, $0.05 > P > 0.025$) more catchable or had higher survivorship than males, unlike in the other three rivers (all $P > 0.05$). Also, larger individuals were significantly ($\chi^2 = 36.3$, df = 8, $P < 0.001$) more catchable or had higher survivorship only in the Big Piney River. In site 1 of that river, several large females were captured numerous times, one individual in nine of 10 samples. These large females resulted in the significant chi-square values in both tests.

Population gains and losses.—The average B_i estimates indicate that populations increased due to immigration in all sites but the Eleven Point River (Table 2). Natality was not a significant factor, since only one larva (77 mm TL and ca. 10 months old from the Big Piney River) was captured. The average P_i estimates were lowest for the Eleven Point River sites. However, this partly reflects the generally longer intersample periods for that river, as evident from the mean MSR estimates. The mean MSR for

TABLE 1.—Summary of the capture-recapture data

River	Number of individuals captured	Number recaptured at least once	Total recaptures
Spring	370	92	119
Eleven Point	211	55	68
Gasconade	293	126	240
Big Piney	334	135	227
Totals	1208	408	654

site 1 in the Spring River slightly exceeds one; therefore sampling error was present.

A comparison of MSRs among populations, except those of the Eleven Point River (due to few estimates), was made by analysis of variance. This followed an approximate test of equal variance using Hartley's test ($H = 4.2$, $P > 0.05$) as described by Neter and Wasserman (1974). Assuming a normal distribution, no significant difference ($F = 0.14$, $P > 0.50$) in MSRs was indicated among the three populations. Therefore an average MSR of 0.90 (SE = 0.06) was calculated from the pooled MSRs, including those of the Eleven Point sites. The estimated annual survival rate was 0.28 ($= 0.90^{12}$) for hellbenders from all collection sites. This estimate is based on loss due to emigration as well as mortality.

Density, relative abundance and biomass.—Absolute density estimates ranged from ca. 1-6 hellbenders per 100 m^2 among the different sites (Table 3). Density of hellbenders and mean catch per unit effort were significantly correlated, except for the Gasconade River population ($r = 0.85$, $0.05 > P > 0.01$, exclusive of the Gasconade estimates). The average mass of an individual in the Spring River was much larger than in the other rivers, particularly compared to the Eleven Point River animals. Therefore biomass per ha was highest in site 1 of the Spring River even though the density was as high or higher in three other sites.

Length of females at sexual maturity.—Based on distension of the abdomen by eggs, Eleven Point River females matured at ca. 300 mm TL, while Big Piney River females did not mature until about 370 mm TL. All females dissected from the Eleven Point River were gravid. The smallest of these was 323 mm TL. One 353-mm-TL female from the Big Piney River was immature; the next smallest individual dissected, 387 mm, was mature. Length at sexual maturity could not be estimated for Spring River and Gasconade River females due to the small number of juveniles captured. During late summer and autumn, less than 1% of the individuals captured were juveniles in the Spring and Gasconade rivers compared to 5% in the Big Piney River and 25% in the Eleven Point River. No female less than 399 mm TL was dissected from the Spring or Gasconade rivers.

Growth.—In the Spring and Eleven Point river populations, growth data of the sexes were pooled because of insufficient data to produce significant growth-TL regressions for adult males and females separately (Fig. 1). The slopes of all growth regressions shown are negative and significantly different (all $P < 0.05$) from zero. However, the regression of the Big Piney River males includes a significant nonlinear component ($0.05 > P > 0.02$).

To compare the growth-TL relationships of different populations, each estimate of individual growth was transformed by dividing by the standard deviation of all growths for that particular regression because of significant differences in variances. Growth equations of the Gasconade and Big Piney rivers used in the comparisons were of the females. Slopes were not significantly different (all $P > 0.05$) between any pair of populations, but all y-intercepts were significantly different (all $P < 0.001$). Spring River hellbenders exhibited the greatest length-specific growth followed by the Gasconade and Big Piney River hellbenders. Eleven Point River hellbenders exhibited the least amount of length-specific growth. The results of this analysis correlate well with the results of the analysis of average mass of individuals in each river. Body length was also greatest in the Spring River; 74% of the individuals captured exceeded 450 mm TL (maximum 600 mm TL). In contrast, only 4% of the Eleven Point River hellbenders exceeded 400 mm TL (maximum 446 mm TL). In the Gasconade River, 43% were longer than 450 mm TL (maximum 548 mm TL). In the Big Piney River, 18% exceeded 450 mm TL (maximum 523 mm TL).

A common logarithmic transformation was made on mass and TL of recaptured hellbenders from each population to determine the relationship between the two variables for adults of each sex (Table 4). The Big Piney River females had a significant nonlinear component; however, 88% of the variation in mass was explained by the regres-

TABLE 2.—Average Jolly-Seber estimates of population size ($\overline{N}$), number of individuals entering population between samples ($\overline{B}_i$), and probabilities that an individual will not die or emigrate between samples ($\overline{P}_i$). Mean monthly survival rates ($\overline{MSR}$) were calculated from the nth roots of corresponding P_i values, where n was the number of months between samples. The number of estimates of B_i, P_i, and MSR for each site was one less than the number of population size estimates, except for site 2 in the Spring River

Spring	Site	Number of population estimates	$\overline{N}$	$SE_{\overline{N}}$	$\overline{B}_i$	$SE_{\overline{B}_i}$	$\overline{P}_i$	$SE_{\overline{P}_i}$	$\overline{MSR}$	$SE_{\overline{MSR}}$
Spring	1	7	442	90	24	96	0.94	0.14	1.02	0.18
	2	3	81	20	23*	—	0.81*	—	0.70*	—
Eleven Point	1	3	113	36	−2	2	0.56	0.11	0.86	0.06
	2	2	92	20	−6*	—	0.70*	—	0.83*	—
Gasconade	1	8	232	32	43	34	0.91	0.09	0.94	0.09
Big Piney	1	7	166	17	30	13	0.84	0.11	0.81	0.13
	2	3	81	24	32	37	0.98	0.26	0.80	0.22

*Represents one estimate

sion on TL. There were no significant differences in the slopes of the mass-TL regressions between sexes of the same population, but there were significant differences in the y-intercepts. Females were generally heavier than males at any specific TL.

Age estimation. — An age-TL key for Eleven Point River hellbenders was generated by integrating the growth equation of Figure 1:

$$\text{Age}_{(months)} = (1/-0.0127)\ln(5.2193 + (-0.0127)\text{TL}_{(mm)}) + 120.$$

Approximate age and TL at metamorphosis, 18 months (Bishop, 1943) and 125 mm (Nickerson and Mays, 1973a), were used to calculate the constant of integration (120). Eleven Point River females attained sexual maturity at about 300 mm TL and were approximately 7-8 years old. Because females matured ca. 7-8 years old in the Niangua

TABLE 3. — Density of hellbenders at seven sites in the Ozarks

River	Site	Area (m^2)	Number per 100 m^2	Average mass of an individual ± SE (g)	Biomass (kg/ha)	Average number of hellbenders caught per hour ± SE
Spring	1	10,300	4.3	971 ± 17	418	9.0 ± 0.8
	2	9000	0.9	769 ± 27	69	3.8 ± 1.0
Eleven Point	1	2600	4.3	214 ± 11	92	8.4 ± 1.8
	2	1500	6.1	341 ± 12	208	8.8 ± 1.2
Gasconade	1	21,400	1.1	598 ± 12	66	13.2 ± 1.8
Big Piney	1	7000	2.4	487 ± 11	117	7.6 ± 1.5
	2	1400	5.8	532 ± 20	309	12.8 ± 3.0

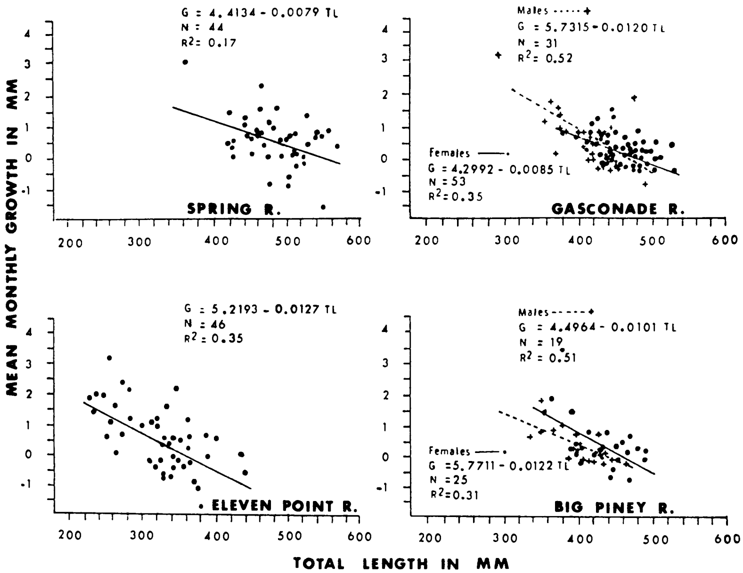

Fig. 1. — Growth-TL regressions from recapture data. Growth data of the sexes were pooled in the Spring and Eleven Point river populations. Only the Eleven Point River regression includes juvenile growth

TABLE 4.—Regression of the logarithm of mass (WT) on the logarithm of TL of recaptured hellbenders and a comparison of the regression coefficients between sexes of each population

					t value			
Population	Sex	N	Regression equation	r^2	Nonlinear component	Slope differing from zero	Slopes	Elevations
Spring	M	38	LogWT = 2.6998LogTL-4.2738	0.76	-1.84^{ns}	5.15***		
	F	36	LogWT = 3.4675LogTL-6.3243	0.72	-1.53^{ns}	7.04***	-0.02^{ns}	34.02***
Eleven Point	M	12	LogWT = 2.7764LogTL-4.5495	0.93	-0.18^{ns}	4.35**		
	F	27	LogWT = 2.8770LogTL-4.7956	0.91	-0.46^{ns}	4.26***	-0.01^{ns}	2.36*
Gasconade	M	39	LogWT = 2.7003LogTL-4.3808	0.90	-0.01^{ns}	7.78***		
	F	68	LogWT = 2.9048LogTL-4.8896	0.80	-0.09^{ns}	10.23***	-0.05^{ns}	11.82***
Big Piney	M	31	LogWT = 2.7027LogTL-4.3603	0.84	-0.68^{ns}	7.30***		
	F	50	LogWT = 3.3121LogTL-5.9576	0.88	−2.20*	11.18***	-0.04^{ns}	30.39***

*, **, *** represent $P<0.05$, 0.01, 0.001, respectively; ns represents $P>0.05$

River (Taber *et al.*, 1975) and in the North Fork River (Peterson *et al.*, 1983), this age was also assumed for the other three populations in this study. Length at maturity was ca. 370 mm for Big Piney River females. This length also was assumed for the Spring and Gasconade river females. Thus 84 months and 370 mm TL were used to generate the following age-TL relationships from the integrated growth equations for the Spring, Gasconade and Big Piney river adult females, respectively:

$$\text{Age}_{(months)} = (1/-0.0079)\ln(4.4134 + (-0.0079)\text{TL}_{(mm)}) + 134,$$

$$\text{Age}_{(months)} = (1/-0.0085)\ln(4.2992 + (-0.0085)\text{TL}_{(mm)}) + 101,$$

$$\text{Age}_{(months)} = (1/-0.0122)\ln(5.7711 + (-0.0122)\text{TL}_{(mm)}) + 103.$$

The age and TL at metamorphosis were not used to calculate the integration constant because the growth equations for the latter three populations did not include juvenile growth as did the Eleven Point River equation. Thus the metamorphic reference point was considered beyond the scope of the regression models. Mean monthly growth suggested that the largest hellbenders in each population were more than 25 years old.

Fecundity.—The regression coefficients of all regressions of number of ova on TL were positive and significantly different (all $P<0.05$) from zero (Fig. 2). The slopes of the fecundity-TL relationships of all four populations did not differ significantly ($F=0.27$, $P>0.50$); however, there was a significant difference in y-intercepts ($F=15.4$, $P<0.001$). A multiple range comparison indicated that the elevations of the regressions of Spring River and Eleven Point River hellbenders were not significantly different ($q=0.03$, $P>0.50$). Also, the y-intercepts of the fecundity-TL regressions of Gasconade and Big Piney river females were not significantly different ($q=0.11$, $P>0.50$). However, the elevations of Spring River and Eleven Point River hellbenders were significantly higher (all $P<0.001$) than those of Gasconade and Big Piney river fe-

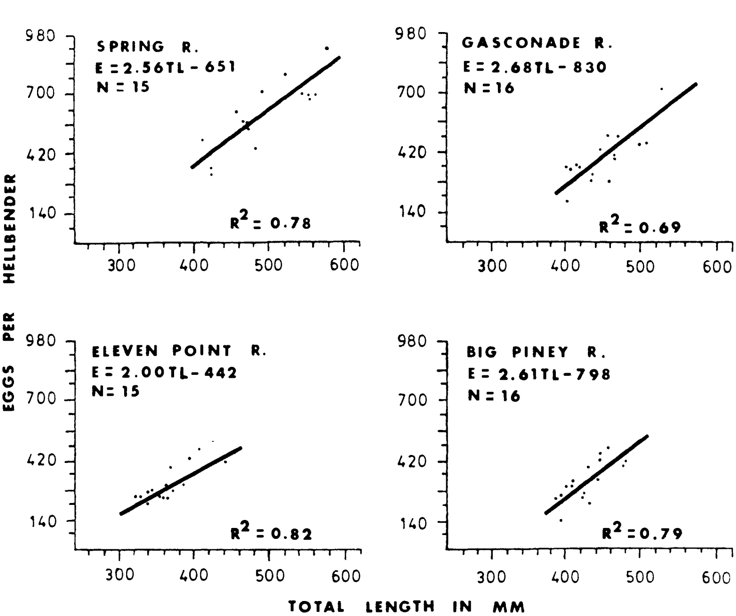

Fig. 2.—Fecundity-TL regressions

males. Thus at any specific length, *Cryptobranchus alleganiensis bishopi* females generally produced more ova than *C. a. alleganiensis* females.

For the dissected females, the average number (and range) of ova produced was 480 (296-908) by the Spring River females, 365 (215-452) by the Eleven Point River females, 450 (159-687) by the Gasconade River females and 429 (95-481) by the Big Piney River females. Age-specific fecundity was also greatest by the Spring River hellbenders and least by the Eleven Point River females (Fig. 3).

DISCUSSION

Peterson (1987) reported significant unequal catchability of hellbenders in the Niangua River in a study of movement over a 2-month period. However, he replaced hellbenders under the rock of capture and also attempted to reposition the cover. This was not done in this study. Further, the intersample period averaged 3 days in the former study, whereas intersample periods were mostly longer than 2 weeks in this investigation. This may explain why similar unequal catchability was not indicated by Leslie's (1958) test in this study. However, the capture of several large females numerous times in site 1 in the Big Piney River resulted in significant chi-square values for testing differential subgroup catchability or survival. The high chi-square values were probably due to nonrandom sampling of sexes and length classes rather than differential subgroup survival over the relatively short study period (compared to the life span of hellbenders). If this is true, it also provides support for Roff's (1973) contention that Leslie's test is inadequate for determining whether subgroups are equally catchable.

The annual survival rate (calculated from the mean MSR for all rivers) seems low for such a long-lived animal, particularly since most of the individuals captured were adults. Although the P_i are not significantly affected by unequal catchability (Begon, 1979), sampling error was a problem. Further, the MSR estimates were undoubtedly influenced by emigration. The sites had no natural upstream or downstream boundaries, and Peterson (1987) reported that dispersal occurred in a local population in the Niangua River. Also, in three of the rivers, the number of hellbenders marked was more than the average estimate of population size. Thus movement from the sites was

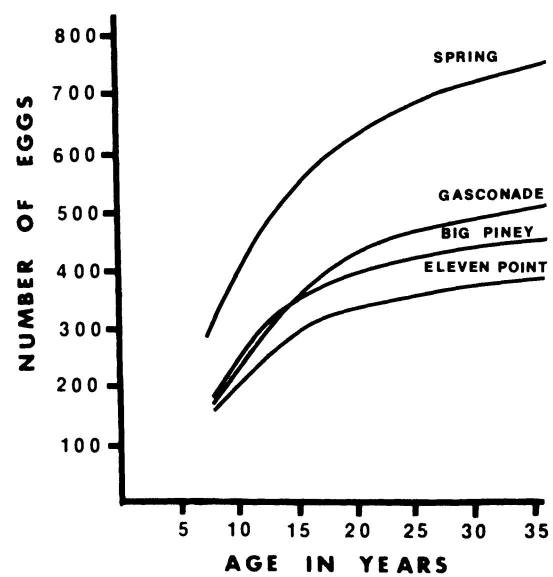

Fig. 3.—Age-specific fecundity

probably a large component of the MSR estimates and resulted in a low estimate of annual survival rate.

The average catch per unit effort for all but one site correlated significantly with the absolute density estimates. This provides credibility for the Jolly-Seber estimates except in the Gasconade River site. In contrast to the other sites, the Gasconade River site had very large stretches of slab rock and generally wide, muddy shorelines where hellbenders were not found. These areas were considered in the absolute density estimates, however. Where large rocks occurred, hellbenders were numerous. This was responsible for the large catch per unit effort, as shorelines were not searched and the smooth bedrock stretches were passed over quickly.

Peterson *et al.* (1983) estimated average hellbender densities of 5.0 and 4.9 per 100 m^2 for two sites in the North Fork River. The first estimate was for the same location, approximately, worked by Nickerson and Mays (1973b). The latter authors estimated a population size of 269 hellbenders for the site by the Petersen method compared to an average of 239 hellbenders by the former authors using the Jolly-Seber model. This is not a large difference considering the many problems associated with mark-recapture estimation of population size (Caughley, 1977). On the basis of these studies, the estimate of five hellbenders per 100 m^2 has some credibility, and the estimates of 1-6 hellbenders per 100 m^2 in Table 3 seem reasonable. Even if the density estimates are rough, it is certain that the four rivers contain a large number of hellbenders.

Females matured at different TLs in the Eleven Point and Big Piney rivers. Females matured at ca. 330-380 mm TL in the North Fork River (Peterson *et al.*, 1983). Taber *et al.* (1975) believed Niangua River females matured at ca. 380 mm. Ingersol (1982) dissected both juvenile and adult Niangua River females and found none less than 390 mm TL that was mature. This contrasts with the smallest mature Eleven Point River female dissected (323 mm TL). The smallest mature female measured by Smith (1912) was 350 mm TL. Dundee and Dundee (1965) stated that *Cryptobranchus alleganiensis bishopi* females matured at ca. 238 mm snout-vent length or 330 mm TL and that *C. a. alleganiensis* females in Missouri attained maturity when about 247 mm snout-vent length (TL not reported). Males mature at a shorter TL than females (Smith, 1912; Dundee and Dundee, 1965) and at a younger age (Taber *et al.*, 1975; Peterson *et al.*, 1983).

It is difficult to detect significant differences in the growth of sexes from recapture data because adults can be sexed externally only for a few months each year. Differences in the growth of sexes was detected in *Cryptobranchus alleganiensis alleganiensis* populations but not in *C. a. bishopi* populations. However, mass-TL regressions of all four populations suggest that female growth exceeded that of males. Similar differences in the mass-TL relationships of the sexes were indicated for Niangua (Taber *et al.*, 1975) and North Fork (Peterson *et al.*, 1983) river hellbenders. The generally greater length-specific mass of females may in part reflect the growth of ova.

Only the average maximum TL (x-intercept) is predicted by the growth-TL equations. This predicted maximum TL will underestimate the TL of those individuals whose growth was greater than the general trend described by the regression. Also, the use of initial TL as the independent variable rather than an average TL for the intercapture period may result in an underestimate of asymptotic size (Van Devender, 1978). Further, the growth of very large individuals was difficult to measure accurately because they grew so slowly. A constant growth rate was assumed during the intercapture period. Although hellbenders eat throughout the year, mass of stomach contents as well as water temperatures may vary seasonally (Wiggs, 1976), so that the assumption is unlikely to be true. However, we do not have sufficient data to analyze seasonal variation in growth. Taber *et al.* (1975) and Peterson *et al.* (1983) measured hellbender growth similarly and discussed other possible problems with the growth model. Despite these potential problems, the growth model was employed because the same model was useful in the prediction of long-term growth of North Fork River hellbenders (Peterson *et al.*, 1985).

Bishop (1943) reported that hellbenders transform (lose their gills) at ca. 100-130 mm TL when 18 months old. However, even if 100 mm and 18 months are used to determine the constant of integration (rather than 125 mm and 18 months) in the age-TL relationship for Eleven Point River hellbenders, the constant changes from 120 to 126, a difference of six months in age estimation. Similarly, the estimate of age changes by a maximum of ± 9 months for the other three populations if either 360 or 380 mm TL is used to calculate the integration constant instead of 370 mm. Yet the method of aging is crude because of the variability of individual growth, particularly for older animals.

Maximum age cannot be predicted from growth; however, a maximum age of 25 or more years is not unreasonable. Taber *et al.* (1975) suggested that some Niangua River hellbenders were over 30 years old. Peterson *et al.* (1985) recaptured nine hellbenders in 1980 that were marked by Taber *et al.* (1975). One of these, because of its size, was suspected to be more than 30 years old when initially captured in 1971. Further, another hellbender marked by the same authors was captured by one of us in 1986 with a legible 15-year-old brand.

Although all adult females produced ova annually, some females may not spawn. Topping and Ingersol (1981) found that some Niangua River females resorbed one season's clutch or a portion of it. They also found that *Cryptobranchus alleganiensis bishopi* from the North Fork River exhibited significantly greater length-specific ova production than *C. a. alleganiensis* from the Niangua River. Thus there seems to be a subspecific difference in length-specific fecundity among hellbender populations in the Ozarks. However, even though for a particular TL the Spring and Eleven Point river females produced similar numbers of ova, the age-specific production of eggs was much greater by the Spring River females. This was a result of the larger size of the latter animals. In fact, the age-specific fecundity of Eleven Point River females was less than that of the *C. a. alleganiensis* females for the same reason.

Despite the difference in length-specific fecundity between subspecies, size and thus growth are responsible for differences in age-specific fecundity among hellbender populations. Merkle *et al.* (1977) found almost no genetic variability within or among hellbender populations of both subspecies. Thus it seems likely that ecological differences are responsible for differences in growth among populations. Seasonal water temperatures and perhaps food availability differ among rivers (Peterson, 1985).

The effect on demography of age-specific fecundity can only be understood when age-specific survivorship is known. Taber *et al.* (1975), Peterson *et al.* (1983) and Peterson (1985) provided survivorship curves, mostly for adult hellbenders, but only by assuming a stable age distribution. Because of the near impossibility of obtaining information for a cohort life table, it may be necessary to determine if the age distribution of hellbenders has remained stable. Caughley (1977) suggested that the rate of increase of a population should have remained relatively constant for at least two or three generations before constructing a time-specific life table. Thus a minimum of 15-20 years is required before the assumption of a stable age distribution can be examined by resampling the standing age distribution of hellbender populations.

Taber *et al.* (1975) suggested that cannibalism of the young and eggs may be an important population control. Thus intraspecific competition may control hellbender densities in the Ozarks rather than extrinsic factors. The hellbender is well-adapted to cool swift rivers; however, little variability exists in the gene pool (Merkle *et al.*, 1977). Therefore it is essential to protect stream habitat from alteration to maintain viable hellbender populations.

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