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COMPARATIVE DEMOGRAPHY OF FOUR POPULATIONS OF THE
HELLBENDER, *CRYPTOBRANCHUS ALLEGANIENSIS*, IN THE OZARKS

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COMPARATIVE DEMOGRAPHY OF FOUR
POPULATIONS OF THE HELLBENDER, CRYPTOBRANCHUS
ALLEGANIENSIS, IN THE OZARKS

A Dissertation
Presented to
the Faculty of the Graduate School
University of Missouri-Columbia

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

by

Chris Peterson

Dr. Dean E. Metter

Dissertation Supervisor

May 1985

The undersigned, appointed by the Dean of the
Graduate Faculty, have examined a dissertation entitled

Comparative demography of four populations of the
hellbender, Cryptobranchus alleganiensis, in the Ozarks

presented by Chris Peterson

a candidate for the degree of Doctor of Philosophy

and hereby certify that in their opinion it is worthy
of acceptance

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ABSTRACT

Four Ozark populations of the hellbender, Cryptobranchus alleganiensis, were censused to examine variation in life history among populations of two subspecies. The populations studied were the C. a. bishopi in the Spring River in Arkansas, and the Eleven Point River in Missouri, and the C. a. alleganiensis in the Gasconade and Big Piney Rivers in Missouri. Densities varied from 1.0 to 6.3 hellbenders / 100 m² in different collection sites. Fecundity was positively related to increased length of females in all populations. C. a. bishopi produced more ova at any given size than C. a. alleganiensis females, but differences existed in average adult size among rivers. Stomach contents of females killed for fecundity data indicated that crayfish was the major food item in all populations, although hellbender eggs were eaten in large numbers during spawning by Gasconade females. The number of crayfish caught per unit effort was positively correlated with estimated production by hellbenders in the collection

sites. Growth of hellbenders decreased linearly with increased total length. Growth of adults was greatest in the Spring River followed by hellbenders in the Gasconade, Big Piney, and Eleven Point Rivers. The Eleven Point adults were generally much smaller than adults in the other three rivers. The age-specific fecundity of the Spring River and Gasconade River females was greater than that of the Big Piney and Eleven Point females. Assuming a replacement rate of 1.0, all populations exhibited a Type III survivorship curve. The adult female survivorship in the Spring and Gasconade Rivers may be slightly higher than that of Big Piney and Eleven Point females. It is suspected that differences in age-specific fecundity and possibly survivorship are related to growth. Because hellbenders have been reported to have genetic uniformity throughout their range, it is believed that differences in growth in different populations were due mostly to environmental factors that differed among rivers, perhaps food availability. Demographic comparisons provide little support for the existence of two subspecies in the Ozarks. Where there is suitable habitat, hellbender secondary production is probably at least as great as that of the larger fish species in the rivers.

INTRODUCTION

Cryptobranchus alleganiensis is a large, long-lived salamander. There are two described subspecies. The hellbender, C. a. alleganiensis, inhabits clear, cool streams from southern New York south to northern Georgia and Alabama and west through Tennessee and the Ohio River Valley to north-flowing Ozark streams of the Missouri River drainage (Dundee, 1971). C. a. bishopi, the Ozark hellbender, is known from the Spring River in Arkansas (Dowling, 1957) and from the North Fork of the White, Current, and Eleven Point Rivers in Missouri (Firschein, 1951), all south-flowing streams. Wortham and Nickerson (1971) speculated that the two races became geographically separated in the Tertiary.

Grobman (1943) described the bishopi taxon, noting differences between the two races in size of spiracular openings, dorsal and labial spotting, and development of the lateral line system in the pectoral region. According to Dundee and Dundee (1965), any other morphological differences are slight. Wortham and Nickerson (1971) found that serum protein patterns of C. a. bishopi and C. a. alleganiensis were distinguishable with regard to their electrical migration through polyacrylamide gels. They suggested, as had Grobman (1943), that the two taxa should be treated as separate species. Jerrett and Mays (1973) reported significant differences in erythrocyte size and number, monocyte size, blood pH, and hemoglobin concentration between one population of C. a. bishopi and one population of C. a. alleganiensis. However, Merkle et al. (1977) stated that the bishopi subspecies status was not warranted

on a biochemical basis, but suggested that the taxon should probably be retained because of the above morphological differences. They found only two of 24 presumptive loci were polymorphic in 137 hellbenders from 12 populations, including three populations in the Ozarks. One unique allele occurred in North Fork and Spring River C. a. bishopi in frequencies of 0.28 and 0.35, respectively. At a different locus the other unique allele was present in a Pennsylvania population. The mean proportion of loci heterozygous per individual for a particular population (H) was 0.0 in nine populations. In the other three populations, H was 0.002. Many other urodele populations have greater variability in genetic frequencies than the hellbender. For six Eurycea lucifuga populations in the Ozarks, H values varied from 0.0 to 0.106 ($\bar{H}=0.039$) based on 12 presumptive loci (Merkle, 1975). Shaffer (1983) examined 29 to 32 proteins in seven populations of Ambystoma rosaceum and two populations of A. tigrinum. H levels varied from 0.101 to 0.176 ($\bar{H}=0.139$) for A. rosaceum localities. For the two A. tigrinum samples, H was 0.09 and 0.171. Even in Plethodon ouachitae with its limited range, H values ranged from 0.015 to 0.084 ($\bar{H}=0.055$) among 10 localities based on 23 genetic loci (Duncan and Highton, 1979).

Ecological comparisons of C. a. bishopi and C. a. alleganiensis began with Dundee and Dundee (1965). They found there was an overlap in the breeding season of the two races, but that the Ozark hellbender generally oviposited later and at a smaller initial breeding size. Nickerson and Mays (1973a; 1973b) gathered considerable information about the natural history of C. a. bishopi, mostly from the North Fork River, including population densities, biomasses, food habits,

activity patterns, sex ratios, breeding habits, and differences in size of individuals among populations. Topping and Ingersol (1981) reported that North Fork Ozark hellbenders have a greater length-specific fecundity than C. a. alleganiensis in the Niangua River, Missouri. Coatney (1982) compared the home range of hellbenders in the North Fork with the home range reported for Pennsylvania hellbenders by Hillis and Bellis (1971). Peterson et al. (1983) reported differences between the age and growth of North Fork and Niangua hellbenders from data obtained by Taber et al. (1975) from the latter population. Recently the usefulness of the growth model of Peterson et al. (1983) for Ozark hellbenders was confirmed by resampling the North Fork population and comparing the observed growth of recaptures with predicted growth (Peterson et al., 1985).

Despite the similar genetic frequencies reported by Merkle et al. (1977), some demographic traits (growth, fecundity) are different between subspecies in Missouri. Also, prior sampling by the author and by Nickerson and Mays (1973a) indicated that differences exist in the adult size of hellbenders even in populations within a subspecies. This alone suggests that differences exist in fecundity among populations because fecundity scales with size (Topping and Ingersol, 1981). It is unknown, however, whether differences in demography are as profound among populations within a subspecies as between subspecies. Further, the effects of environmental factors on hellbender life history are unknown. Also, because of the pattern observed by Organ (1961) of greater mortality of the young in increasingly more aquatic species in the salamander genus Desmognathus, the determination of survivorship in the strictly

aquatic hellbender would be useful in examining this concept. Therefore population sizes were estimated, length-specific fecundity and growth relationships measured, and fecundity and life tables constructed for C. a. bishopi in the Spring River, Arkansas, and Eleven Point River, Missouri, and the C. a. alleganiensis in the Gasconade and Big Piney Rivers in Missouri. Maximum and minimum stream temperatures were recorded at approximately monthly intervals during one year to determine if major differences exist in seasonal temperatures among rivers. Also the relative abundance of crayfish was estimated in each collection site after an analysis of stomach contents indicated that crayfish is the major food item of hellbenders in all rivers. Temperatures and relative crayfish abundance among sites were compared because of their possible influence on hellbender growth and thus fecundity.

Finally, annual production by the hellbender was estimated in each of the four rivers because only limited information exists on the secondary production of aquatic salamanders, despite their probable importance as predators in some aquatic systems (cf. Burton, 1977; Neish, 1971). It was hypothesized that Cryptobranchus has a minor role in stream trophic dynamics because Peterson et al. (1983) and Taber et al. (1975) reported that hellbender populations are dominated by slow-growing, long-lived adults.

LITERATURE REVIEW

Wet Weight Biomass and Production

Only a few studies have dealt with the importance of aquatic urodeles in terms of standing crop, even though they may be important predators in some aquatic habitats. Burton (1977) found that 1950 to 2600 adult red-spotted newts, Notophthalmus viridescens, inhabited 1 ha of Mirror Lake, New Hampshire. Assuming an average weight of 3 g for an adult newt (cf. Gill, 1979), the standing crop was 5.8 to 7.8 kg / ha. Neish (1971) estimated a biomass of 37 kg / ha for second-year larvae and neotenus adult Ambystoma gracile throughout a 10-ha lake in British Columbia. Gelbach and Kennedy (1978) presented evidence of dominance of a beaver pond by a single urodele, Siren intermedia. They estimated a biomass of 380 to 570 kg / ha and believed that seven species of insectivorous fish in the pond had a standing crop totaling no more than 420 kg / ha. Their estimate of production by S. intermedia was 290 kg / ha / yr.

Nickerson and Mays (1973b) estimated a biomass of about 450 kg / ha of hellbenders in one riffle in the North Fork River; only suitable diurnal habitat was considered in the estimate of area. If the area of the entire riffle had been considered, the estimate would have been about 105 kg / ha. Peterson et al. (1983) estimated an average hellbender standing crop of 157 and 154 kg / ha for two collection sites in the North Fork based on shoreline to shoreline area. The latter authors speculated that even higher densities existed in the Niangua River. Topping (1981 and personal communication) estimated the production of Niangua hellbenders to be 61 to 714

kg / ha / yr for 10 different sites. Only the limited area where hellbenders could be caught during daylight was considered in these estimates. Other than the production reported for Siren intermedia, Topping's estimates are the only estimates known to the author of production by a truly aquatic salamander. These figures suggest that the hellbender's secondary production may be comparable to many stream fishes.

Waters (1977) reviewed the literature on production of fish in streams and lakes. Estimates of production of the lotic benthic fishes Cottus (3 species) and Etheostoma (2 species) varied from 8 to 431 kg / ha / yr and 23 to 52 kg / ha / yr, respectively. Reported yearly production of stream cyprinids ranged from 0.1 to 915 kg / ha depending on the species and locality. Annual production estimates for brook trout, Salvelinus fontinalis, and rainbow trout, Salmo gairdneri, in different rivers varied from 16 to 300 kg / ha and 28 to 132 kg / ha, respectively. The annual production of brook trout, mottled sculpin (Cottus bairdi), and blacknose dace (Rhinichthys atratulus), the three dominant species in a headwater stream in Virginia, was estimated at three different sites (Neves and Pardue, 1983). Production estimates were 5.4 to 19.3 kg / ha for trout, 5.7 to 10.8 kg / ha for sculpin, and 2.7 to 3.8 kg / ha for dace.

Growth

In most amphibians there appears to be a period of rapid growth preceding attainment of sexual maturity, followed by a period during which growth tends to be intermittent and gradually slows (Porter, 1972). However, growth has been reported to decrease at a constant

rate as a function of length, and thus possibly age, in plethodontids (Houck, 1982; Tilley, 1977), a newt (Efford and Mathias, 1969), and hellbenders (Peterson et al., 1983; Taber et al., 1975).

Flower (1936) stated that Andrias japonicus, the only other extant cryptobranchid, grows very rapidly when young, after which there is a period of very slow growth which may eventually cease if the animal lives long enough. Three A. japonicus suspected of being three or four years old grew 35 to 40 mm in one year in a Vienna zoo. Annual rates of increase in length steadily decreased from these figures, according to Flower (1936). In the case of one individual, growth ceased entirely for the last 12 years. It is unknown whether this growth or lack of growth was strictly age-related or environmentally induced in part.

Nickerson and Mays (1973a) reported that C. a. bishopi grow relatively slowly upon attaining sexual maturity. The maximum growth rate they observed was 20 mm / yr in total length (TL) and 109 g / yr in weight. The growth model of Taber et al. (1975) predicted hellbender growth of 59 mm / yr in length at 1.5 years old decreasing to 1 mm / yr at 30 years old. Five Niangua River hellbenders fed to maximum acceptance levels in the laboratory by Wiggs (1976) exhibited growth similar to that predicted for Niangua hellbenders by Taber et al. (1975). In contrast, the growth regression of Peterson et al. (1983) for North Fork Ozark hellbenders predicted 61 mm / yr of growth in TL at 18 months decreasing to 1 mm / yr at 25 years old. Growth was greater in Niangua hellbenders as indicated by comparison of growth regressions (Peterson et al., 1983).

Growth of hellbender larvae can only roughly be estimated from reports. Eggs hatch in late fall, about six weeks after fertilization, at about 25 to 30 mm TL (Bishop, 1941; Smith, 1907). Larvae 35 to 60 mm in length have been reported to be three to nine months old (Grenell, 1939). One-year-old larvae vary in length between 60 and 90 mm TL (Taber et al., 1975; Grenell, 1939; Smith, 1907). Hellbenders in their second year may be 90 to 130 mm TL (Nickerson and Mays, 1973a; Bishop, 1941; Smith, 1907).

Bishop (1943) reported that metamorphosis occurs when hellbenders are between 100 and 130 mm in length and are about 18 months old. Grenell (1939) stated that gill loss occurs at the end of the second year when larvae have reached a length of at least 120 mm. Goin and Goin (1971) concluded that transformation occurs when hellbenders are 1.5 years old and their length is 125 mm. Nickerson and Mays (1973a) also concluded that 125 mm TL is the approximate size of Ozark hellbenders when they lose their gills.

Age-specific Fecundity and Survivorship

Because of their secretive habits, the analysis of caudate population dynamics is difficult, and many species remain unstudied (Porter, 1972). Difficulties in aging individuals is also a major problem in determining age-specific fecundity and survivorship. Methods of determining age of urodeles have included the examination of skeletal annuli (e. g., Peabody, 1961; Senning, 1940), counting testicular lobes (e. g., Organ, 1961; Humphrey, 1922), the detection of discrete size classes (e. g., Hairston, 1983; Tilley 1973), or mark-recapture studies (Peterson et al., 1983; Tilley, 1980; Taber et

al., 1975). No skeletal growth rings are present in hellbenders (Peabody, 1961), nor have testis lobes been described (cf. Ratcliff, 1965; Branch, 1959). Dundee and Dundee (1965) stated that at least three size groups are present in postmetamorphic hellbenders. However, Taber et al. (1975) were unable to estimate the age of hellbenders in large samples by length-frequency methods. The growth models developed by Taber et al. (1975) and Peterson et al. (1983) were used to produce length-age relationships for hellbenders. However, some bias exists in an age-length key if overlap between successive ages is present (cf. Westrheim and Ricker, 1978) as is the case with old salamanders.

Although the relationship between female body length and fecundity varies among urodeles (Porter, 1972), in general, the size of the female correlates directly with her reproductive capacity (Salthe, 1969). Blanchard (1928) found no correlation between fecundity and size of female Plethodon cinereus in Michigan. Yet Nagel (1977) described a weak correlation between fecundity and body length for the same species in Tennessee, and Lotter (1978) reported a strong correlation between the two variables for P. cinereus in Connecticut. Stebbins (1954) found a slight positive relationship between number of eggs produced and size of female Ensatina up to 70 mm snout-vent length but a decline in eggs produced by larger females. Harrison (1967) found a direct correlation between clutch size and body size in Desmognathus aeneus. Tilley (1968) also described a positive correlation between ova produced and female snout-vent length in four species of Desmognathus but a negative correlation in D. monticola. Although larger D. ochrophaeus females produce larger clutches, fertility rates were uncorrelated with age

(Tilley, 1980), and reproduction was assumed to be an annual occurrence throughout the life of adult Appalachian dusky salamanders. However, fecundity appears to be age-specific in Plethodon jordani; older females produce larger clutches, and individuals at least six years old were assumed to breed in alternate years (Hairston, 1983). Likewise, in the smooth newt, Triturus vulgaris, fecundity increased with increased age (Bell, 1977). Egg production has been reported to be positively correlated with female body length of ambystomatids also (Petranka, 1984; Nussbaum and Tait, 1977), and clutch weight has been positively correlated with female body weight in two hynobiids and one newt (Kuramoto, 1977).

Larger and thus older hellbenders produce greater numbers of eggs (Topping and Ingersol, 1981). Adult females produce eggs annually, although not all ova are laid (Ingersol, 1982). Smith (1907) reported that an average size female C. alleganiensis produces 450 eggs. Bishop (1943) stated that between 300 and 450 eggs are produced by an individual. Swanson (1948) counted eggs from 10 females. The number of eggs varied from 350 to 900 per female, although eggs for two seasons may have been counted. The number of eggs in females dissected by Topping and Ingersol (1981) ranged from 169 eggs by a 408 mm TL individual to 645 eggs produced by a 525 mm TL hellbender.

Although Cagle (1956) pointed out that life tables had not been constructed for any amphibians, Bannikov (1949), as cited by Organ (1961), working with the hynobiid Ranodon sibiricus was able to distinguish five year classes and to calculate age-specific mortality rates by analysis of size-frequency data. Organ (1961) developed male

survivorship curves for five species of Desmognathus based on the number of testis lobes. The more terrestrial the species, the greater was the early survivorship. The more aquatic species had a Type II survivorship curve indicating a constant rate of mortality for males one to four years old (Organ, 1961). Spight (1967) presented a life table for Desmognathus fuscus males in North Carolina from hatching through seven years of age. Again testicular lobes were used in aging. This method was also used by Danstedt (1975) to estimate age-specific survivorship in the same species. Bell (1977) estimated an annual survival rate of about 50% for adult smooth newts, Triturus vulgaris. Female survivorship was a little greater than that of males. Gill (1978) produced a Type II survivorship curve for Notophthalmus viridescens. Male survival was slightly higher than female survival. Tilley (1980), assuming a constant survivorship rate after sexual maturity, calculated a mean generation time of 5.6 years and a longevity of at least 16 years for Desmognathus ochrophaeus. Hairston (1983) calculated a mean generation time of 9.8 years for Plethodon jordani and suggested a life span of as much as 30 years. Thus even rather small urodeles may have a relatively long life span.

Dundee and Dundee (1965) argued that hellbenders live at least seven years, and Nickerson and Mays (1973a) suggested that hellbenders are long-lived. Andrias has lived 55⁺ years in captivity (Flower, 1936), and Cryptobranchus has survived 29 years in captivity (Oliver, 1955). Richmond (1965) hypothesized that hellbender populations are dominated by long-lived adults. Taber et al. (1975) confirmed this speculation for C. a. alleganiensis in the Niangua River, Missouri. They indicated a life span of at least 30 years and suggested that

adult female survivorship is greater than that of mature males. The difference in survivorship between sexes is supported by the one male to four female sex ratio reported by Wiggs (1977) for Niangua hellbenders 15 years old or older. Peterson et al. (1983) in a similar study on C. a. bishopi in the North Fork River reached similar conclusions to those of Taber et al. (1975). Neither study combined fecundity rates with survivorship to estimate mortality between oviposition and sexual maturity.

STUDY AREAS

Spring River

The Spring River has its origin at Mammoth Spring, the second largest spring in the Ozarks (Beckman and Hinchey, 1944). It flows for about 114 km before joining the Black River. The spring is just south of the Missouri-Arkansas border in Fulton County. Nearly all of the drainage area of the spring is in Missouri. The discharge is about 152 million l / hr. Mammoth Spring is inundated by a dam within the town of Mammoth Spring (Ark. Dept. of Pollution Control and Ecology, 1977a; Vineyard and Feder, 1974).

Collection site 1 in the Spring River is located below Dam No. 3 about 7 km downstream from Mammoth Spring at the downstream end of a large island. A trout-raising operation is located on the island and utilizes water from the river for its silos. After settling in lagoons, the water is discharged back into the river just upstream from the collection site. Waste materials in this water include fish metabolic wastes and uneaten fish food (Ark. Dept. of Pollution Control and Ecology, 1977a). The river is still highly influenced by the spring at this point. Water temperatures are cool and fairly uniform throughout the year. Dundee and Dundee (1965) reported that the river for several miles downstream of the spring maintains a temperature of 15 ± 2 °C throughout the year.

Site 2 in the Spring River is located on either side of an island about 1 km downstream from the dam at the spring. The east bank is a residential area. The sewage treatment plant for Mammoth Spring consists of an aerated lagoon and settling pond. The discharge is

chlorinated before entering an unnamed tributary upstream from the collection site (Ark. Dept. of Pollution Control and Ecology, 1977b). The Warm Fork also enters upstream from the collection site. This tributary has about 15 km of permanent flow, mostly in Missouri. Sewage effluent from Thayer, Missouri, enters this creek (Duchrow, 1977). In 1976, fecal coliform and nitrates from municipal discharge into the Spring River were parameters not meeting the Federal Water Pollution Control Act and/or the Water Quality Standards of Arkansas (Ark. Dept. of Pollution Control and Ecology, 1977b).

Eleven Point River

The Eleven Point River has its headwaters in Howell County Missouri. It flows for about 200 km and enters the Spring River near its junction with the Black River. Sixteen major springs contribute substantially to the flow (Vineyard and Feder, 1974). Greer Spring more than doubles the flow of the river and is Missouri's second largest spring. Although large areas of oak-hardwood forests in its headwaters have been converted to pasture, much of its length is in Mark Twain National Forest. The area is sparsely populated.

Duchrow (1977) made a water quality study of the Eleven Point and its major tributaries. The basin was considered unpolluted and unaffected by point sources of pollution. Regression analyses made by Duchrow (1977) for the sampling stations showed a positive relationship between the increase in nutrients and invertebrate species diversity index values. Enriched tributaries normally had higher macroinvertebrate densities. In most cases the tributaries with high species diversity index values had watersheds in which forest had been converted to pasture. However, no sources of pollution or timber clearing were

known to exist from Greer Spring to a sampling station downstream of the hellbender collection sites (Duchrow, 1977). Many springs contribute to the river's flow in this stretch (Vineyard and Feder, 1974).

Site 1 in the Eleven Point River is located about 12 km downstream from Turner's Mill in Oregon County. Site 2 is located about 2 km upstream from Turner's Mill or about 7 km downstream from the Greer Spring Branch. Dundee and Dundee (1965) reported that river temperatures remain below 17 °C for many miles of its course even in midsummer and do not drop below 12.5 °C in midwinter.

Gasconade River

The Gasconade River has its headwaters in Wright County in south-central Missouri, and it flows northeast for about 440 km to its junction with the Missouri River. It is subject to frequent and severe flooding (U.S.G.S. and Mo. Div. of Geol. Surv. and Water Res., 1967). Much of the upper portion of the Gasconade Basin is used extensively for crop farming; however, in the hilly sections dairy farming is predominant. Although towns are located in the basin, a 1973 report indicated no improvements were needed in waste treatment in the area (Mo. Water Pollution Bd., 1973). Although there are many springs flowing into the river, according to Dundee and Dundee (1965), the Gasconade is a larger stream than the south-flowing hellbender rivers, and thus spring waters are not as effective in modifying its temperatures. They recorded summer temperatures of 25 °C, and they speculated that winter temperatures were perhaps colder than in the south-flowing streams.

Site 1, the only collection site in the Gasconade River, is a long stretch about 1 km upstream from the highway 17 bridge in Pulaski County near Waynesville. Shorelines are generally muddy, and smooth bedrock areas are heavily covered with algae in summer. Following heavy rains this stretch remains turbid with low visibility, sometimes for many days. The sewage treatment plant at Waynesville discharges into Roubidoux Creek which joins the Gasconade at the highway 17 bridge downstream from the collection site.

Big Piney River

The Big Piney River is located in the Gasconade Basin and flows into the Gasconade in Pulaski County 42 km downstream from the Gasconade collection site. The river originates in Texas County and flows through Fort Leonard Wood in Pulaski County. The middle portion of the stream runs through National Forest. No water treatment problems were noted at Fort Leonard Wood downstream from the collection site, nor at Houston, the only town upstream that could much affect the collection sites (Mo. Water Pollution Bd., 1973). However, water quality reports have indicated violation of dissolved oxygen standards due to municipal discharge from the town of Cabool in the headwaters of the Big Piney River (Mo. Clean Water Comm. Plan. Sec., 1982; 1980), but probably this did not affect the collection sites. As is typical of Ozark streams, the Big Piney River is exceptionally clear; turbidities were less than 7 ppm except immediately following heavy rains when measured by Fleener et al. (1974).

Site 1 in the Big Piney is located about 2.5 km upstream from the highway 32 bridge between Licking and Success in Texas County. Site 2 is located about 0.5 km downstream from the bridge at a privately

operated campground.

MATERIALS AND METHODS

Hellbenders were caught during daylight hours by turning rocks in the collection sites. Uncovered hellbenders were grabbed by hand and placed in muslin or net bags. Swim masks were worn to aid visibility. The animals were anesthetized in a solution of tricaine (ethyl-m-amino-benzoate). A standard fish board was used to measure total length (TL) to the nearest mm. Because Taber et al. (1975) reported a highly significant linear correlation between snout-vent and TL in both male and female hellbenders, TL was measured rather than snout-vent length because TL could be obtained with more facility and with as much accuracy. Animals were weighed to the nearest g with a pan-equipped, triple-beam balance. Marking was accomplished with a branding technique described by Clark (1971) and employed successfully by Peterson et al. (1983), Wiggs (1977), and Taber et al. (1975). Arabic numerals about 2 cm in length were made of small diameter wire. The numerals were heated with a propane torch connected to a bunsen burner, 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 two months before and after the breeding season. Males were identified at this time by swollen cloacal glands (Reese, 1904) and females by egg-distended abdomens and the absence of cloacal swelling (Smith, 1907). After these data were recorded, the hellbenders were released in the area of capture. No collections were made in winter or early spring.

Maximum-minimum thermometers were placed under rocks near the bank of each river: site 1 in the Spring and Gasconade Rivers, site 2 in the Big Piney, and near Turner's Mill in the Eleven Point River.

Thermometers were checked approximately once a month from fall 1980 to fall 1981, although flooding occasionally prevented readings, particularly in the Gasconade River. Thermometers were also checked in the North Fork River at the highway H bridge in Ozark County, and in the Niangua River about 1 km downstream from Bennett Spring State Park because growth and fecundity data gathered on hellbenders in those two rivers by Peterson et al. (1983), Topping and Ingersol (1981), and Taber et al. (1975) were compared with data collected in this study.

Population size for each collection site was estimated with the Jolly-Seber model (Jolly, 1965; Seber, 1965) as described by Begon (1979) and Caughley (1977). This model assumes that the capture of an individual does not affect the probability of subsequent recaptures and that all previously captured or uncaptured animals are equally catchable (Jolly and Dickson, 1983; Seber, 1982). The form and nature of the statistical tests used to test these assumptions are described by Begon (1979). Population size of site 1 in the Big Piney was also estimated by a frequency of capture method as described by Caughley (1977). This method assumes there are no losses during the study but does not make the equal-catchability assumption. It requires multiple recaptures of individuals.

Length-fecundity relationships were developed by collecting females before the spawning season and counting the eggs to be laid that year: the enlarged yolk-laden ova of both ovaries. The females were transported on ice from the collection site to the laboratory before killing with tricaine or by freezing. Ovaries were removed and placed in 10% formalin before oocytes were counted. Bartlett's (1949) method as described by Simpson et al. (1960) was used to describe the relationship

between TL, the independent variable, and the number of eggs per female, the dependent variable. Davies (1971) provided a Fortran program for this method, and Simpson et al. (1960) described methods for testing for the significance of the slope and for deviations from linearity, for constructing confidence limits for the slope and y-intercept, and for comparing two regression lines. If there are errors in the independent variable, least squares regression provides biased, inconsistent estimators for the relationship between the variables unless target values of the independent variable are set or unless severe assumptions can be imposed on the problem (Neter and Wasserman, 1974). Although the least squares equation is still suitable for prediction (Bartlett, 1949), Ricker (1973) has suggested that when both variables are subject to natural variability and measurement error the functional relationship is best described by the geometric mean regression, Wald's regression or the Nair-Bartlett regression. Because Bartlett's method was used successfully on hellbenders (cf. Peterson et al., 1985) and is easy to apply, this regression method was used whenever measurement error could exist in the independent variable.

Length-specific growth rates of hellbenders for each population were estimated from recapture data. Mean monthly growth was regressed on initial TL. Growth increments within a single season were rejected to minimize the effect of marking and measurement error on growth. Only initial and final TLs were used to estimate growth of animals recaptured more than once to maintain independence. As described by Van Devender (1978), the length-growth equations were integrated to yield an equation relating age to TL.

Fecundity tables, life tables, and cohort biomass were determined from a sample of females caught within ± 2 months of the breeding season. A stationary age distribution for each population was assumed. Females were aged based on TL. The number of females in the zero age class was estimated by summing the products of the number of females in each age class and the expected number of eggs produced per female (estimated from the length-fecundity relationships). Survivorship was calculated by dividing the zero age class, taken from the fecundity tables, into the number of females alive in each age class. The average age at egg laying or mean generation time was calculated by multiplying the interval midpoint age times the number of zygotes produced per female times the survivorship for each age class and summing all the products (cf. Leslie, 1966). Female cohort biomass was determined from the life tables and the estimated number of females in the collection sites. Average weight at death of the females was estimated from length-weight regressions.

Annual secondary production of females was estimated by the summation-removal method (cf. Waters, 1977) from the female cohort biomass (assuming a stable age distribution). Production : biomass ratios were calculated by multiplying site biomass estimates by the average female proportion of the population and dividing the product into the production estimate. Yearly production was also estimated based on the product of biomass and an estimate of instantaneous growth: $\ln(\text{weight of heaviest individual} / \text{ovum weight}) / \text{hypothesized age of oldest individual}$.

RESULTS

Population Size

Initial marking mortality. The recapture data (Table 1) were used to estimate population size, recruitment, and survivorship rates by the Jolly-Seber method. To test the assumption that marking does not increase mortality, a chi-square test may be used (Begon, 1979). Of the r_i individuals captured and released on day i , some will have been caught and marked in samples prior to day i and some will not. If the chances of dying are increased by the initial marking, then the individuals which were marked for the first time on day i will be under-represented in subsequent samples. Chi-squares and their degrees of freedom may be summed for different sampling periods.

Because methods were the same, the effect of capturing and marking on mortality should be similar for different populations unless the size of individuals being branded is a factor. Therefore the test of whether marking increases mortality was conducted only on the population where individuals were observed to be smallest, the Eleven Point River population (Table 2). Although the chi-square value for the third sampling period is significant at $\alpha = 0.1$, the overall value indicates that being caught and marked for the first time did not affect the mortality of Eleven Point hellbenders significantly.

Random sampling. Leslie's (1958) test for random sampling as outlined by Begon (1979) and Caughley (1977) was performed on recapture data for each population except, due to insufficient data, the Eleven Point hellbenders (Table 3). Also the Spring River data are not quite adequate for this test. Of G individuals (should exceed 20) caught on or before day j and on or after day $j+t$, g_i individuals will be caught

Table 1. Summary of the capture-recapture data.

Study interval	Population	No. of collection sites	No. of individuals captured	No. recaptured at least once	Total recaptures
24 May 1980- 21 Aug. 1982	Spring	2	370	92	119
26 July 1980- 4 Sept. 1982	Eleven Point	2	211	55	68
21 July 1980- 26 Sept. 1982	Gasconade	1	293	126	240
31 May 1980- 24 July 1982	Big Piney	2	334	135	227
Totals		7	1208	408	654

Table 2. Chi-square test of whether initial marking has an effect on the mortality of Eleven Point hellbenders.

Sample	χ^2	df	$\alpha = 0.1$	$\alpha = 0.5$
2	0.39	1	ns	ns
3	2.95	1	*	ns
4	2.09	1	ns	ns
overall	5.43	3	ns	ns

Table 3. Leslie's (1958) approximate chi-square test comparing the expected binomial variance of recapture frequencies, if sampling is random, with the variance of the observed recapture frequencies.

Population	No. known alive between time i and $i+j$	No. of samples between i and $i+j$	No. of individuals captured (0-3 times) between i and $i+j$				χ^2	α	ns
			0	1	2	3			
Spring	15	3	10	3	2	0	19.72	ns	ns
Eleven Point	4 ^a	3							
Gasconade	35	3	12	11	11	2	47.39	*	ns
Big Piney	22	3	5	13	5	1	20.22	ns	ns

^a Leslie suggests that number known alive should exceed 20

on day i (should be at least three day i) between j and $j+t$. If the catchability is constant, the recapture frequencies will form a binomial distribution. This hypothesis can be tested by comparing the observed variance of recapture frequencies with the expected binomial variance. This approximate chi-square test is run with $\sum g_i - 1$ degrees of freedom. There is no indication that sampling was not random in the three populations tested at the 0.05 significance level, although the Gasconade value exceeds the critical value at the 0.1 level.

Roff (1973) argued that Leslie's test is incapable of distinguishing whether subgroups, such as sex and age classes, differ in catchability. Thus, because data are insufficient to obtain reliable density estimates directly on different subgroups, tests of whether male and female hellbenders were equally catchable and/or had similar survival rates were performed on each population (Table 4). Similar tests were made on three life stages: animals were classified as juveniles-young adults, adults, or old adults based on TL (Table 5). These tests can be used to test for 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). These tests can be made with single-mark-recapture data or multiple-mark-recapture data. Considering the longevity of hellbenders (Peterson et al., 1983; Taber et al., 1975), the single-mark-recapture data (only for samples within the same year) should provide information on equal catchability nearly exclusive of survivorship differences in the subgroups. Only

Table 4. Chi-square tests of whether the survival-rates and/or the catchabilities of males and females are the same. The test is repeated for each sample period, and the chi-square values and degrees of freedom are summed as suggested by Begon (1979). Only samples within the same calendar year are considered in the single capture-recapture tests to decrease survivorship effects.

Population	Multiple capture-recapture			Single capture-recapture		
	χ^2	df	Significance	χ^2	df	Significance
Spring	0.51	1	ns	0.04	1	ns
	1.76	1	ns	0.18	1	ns
	0.53	1	ns	0.22	2	ns
	1.07	1	ns			
Eleven Point	3.87	4	ns			
	2.35	1	ns	1.81	1	ns
	0.02	1	ns			
	2.37	2	ns			

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 4 cont. Chi-square tests of whether the survival-rates and/or the catchabilities of males and females are the same. The test is repeated for each sample period, and the chi-square values and degrees of freedom are summed as suggested by Begon (1979). Only samples within the same calendar year are considered in the single capture-recapture tests to decrease survivorship effects.

Population	Multiple capture-recapture			Single capture-recapture		
	χ^2	df	Significance	χ^2	df	Significance
Gasconade	0.47	1	ns	0.68	1	ns
	0.16	1	ns	0.15	1	ns
	0.00	1	ns	2.23	1	ns
	6.54	1	**	—	—	—
	2.23	1	ns	3.06	3	ns
Big Piney	—	—	—	—	—	—
	9.40	5	*	—	—	—
	1.59	1	ns	0.30	1	ns
	5.38	1	**	—	—	—
	1.00	1	ns	—	—	—
—	—	—	7.97	3	**	

*, **, *** P < 0.1, 0.05, 0.01 respectively

Table 5. Chi-square tests of whether the survival-rates and/or the catchabilities of juveniles-young adults, adults, and old adults are the same. The test is repeated for each sample period, and the chi-square values and degrees of freedom are summed as suggested by Begon (1979). Only samples within the same calendar year are considered in the single capture-recapture tests to decrease survivorship effects.

Population	Multiple capture-recapture			Single capture-recapture		
	χ^2	df	Significance	χ^2	df	Significance
Spring	3.48	2	ns	5.09	2	*
	3.39	2	ns	0.94	2	ns
	1.68	2	ns	4.77	2	*
	1.45	2	ns	3.38	2	ns
	1.15	2	ns	0.59	2	ns
	1.36	2	ns	0.41	2	ns
	0.60	2	ns	15.18	12	ns
	0.96	2	ns			
	14.07	16	ns			

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 5 cont. Chi-square tests of whether the survival-rates and/or the catchabilities of juveniles-young adults, adults, and old adults are the same. The test is repeated for each sample period, and the chi-square values and degrees of freedom are summed as suggested by Begon (1979). Only samples within the same calendar year are considered in the single capture-recapture tests to decrease survivorship effects.

Population	Multiple capture-recapture		Single capture-recapture			
	χ^2	df	Significance	χ^2	df	Significance
Eleven Point	3.30	2	ns	2.00	2	ns
	0.39	2	ns	1.01	2	ns
	1.82	2	ns	3.01	4	ns
	0.13	2	ns			
	5.64	8	ns			

*, **, *** P < 0.1, 0.05, 0.01 respectively

Table 5 cont. Chi-square tests of whether the survival-rates and/or the catchabilities of juveniles-young adults, adults, and old adults are the same. The test is repeated for each sample period, and the chi-square values and degrees of freedom are summed as suggested by Begon (1979). Only samples within the same calendar year are considered in the single capture-recapture tests to decrease survivorship effects.

Population	Multiple capture-recapture		Single capture-recapture	
	χ^2	df Significance	χ^2	df Significance
Gasconade	5.46	2 *	3.61	2 ns
	2.14	2 ns	8.33	2 **
	5.53	2 *	2.33	2 ns
	0.96	2 ns	0.80	2 ns
	0.38	2 ns	2.34	2 ns
	1.25	2 ns	1.36	2 ns
	4.72	2 *	18.77	12 *
	1.44	2 ns		
	21.88	16 ns		

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 5 cont. Chi-square tests of whether the survival-rates and/or the catchabilities of juveniles-young adults, adults, and old adults are the same. The test is repeated for each sample period, and the chi-square values and degrees of freedom are summed as suggested by Begon (1979). Only samples within the same calendar year are considered in the single capture-recapture tests to decrease survivorship effects.

Population	Multiple capture-recapture			Single capture-recapture		
	χ^2	df	Significance	χ^2	df	Significance
Big Piney	3.37	2	ns	2.90	2	ns
	3.43	2	ns	6.61	2	**
	1.12	2	ns	1.28	2	ns
	4.72	2	*	3.78	2	ns
	2.04	2	ns	7.99	2	**
	3.29	2	ns	11.06	2	***
	7.28	2	**	33.62	12	***
	11.06	2	***			
	36.31	16	***			

*, **, *** P < 0.1, 0.05, 0.01 respectively

in the Big Piney population did males and females differ significantly in survivorship and/or catchability. Also only in the Big Piney were individuals of different life stages significantly different with regard to catchability.

Population size, recruitment, and survival rates. Besides the estimates of population size provided by the Jolly-Seber model (Table 6), estimates for the first and last collection periods were made by the method described by Caughley (1977). Due to difficulties with equal catchability of subgroups in the Big Piney, population size for site 1, where there were multiple recaptures of individuals, was also estimated by a frequency of capture model that does not require random sampling but assumes no losses. Goodness-of-fit tests of the frequency of capture of individuals to a zero-truncated Poisson, negative binomial, and geometric distribution were made by chi-square tests. The best fit of the observed frequency of capture was to the geometric distribution ($\chi^2=4.26$, $P>0.10$) yielding a population estimate of 806 hellbenders. The average estimate for site 1 by the Jolly-Seber method was 161 hellbenders.

The recruitment estimates (A_i) include animals that have entered the population through natality or immigration. The average of the A_i for each collection site indicates little increase or decrease in numbers during the study period. The observed rate of increase can be estimated by the slope of the least squares regression of the natural logarithm of the population estimate versus time (Caughley, 1966). For all collection sites but site 1 of the Eleven Point (Fig. 1), which has a significant negative slope ($t=3.96$, $P<0.05$), the slopes are not significantly different from zero (all $t<1.96$).

Table 6. Jolly-Seber estimates of population size (N), number of individuals entering population between time i and $i + 1$ (A), probabilities that an individual present at time i will still be present at time $i + 1$ (P), and their standard errors (SE). Monthly survival rates (MSR) are the n th roots of the corresponding P_i 's, where $n =$ the number of months between time i and $i + 1$.

Population	Interval									
	Interval length (i to i+1) (months)	N	SE	A	SE	P	SE	MSR	SE	MSR
Spring	0-1	—	459.4 ^a	—	—	—	—	—	—	—
Site 1	1-2	0.6	463.8	97.8	-177.7	500.8	1.213	0.276	1.380	—
	2-3	0.6	384.8	79.7	409.2	1252.4	1.361	0.377	1.671	—
	3-4	1.2	933.0	226.2	-187.2	541.4	0.638	0.186	0.688	—
	4-5	3.0	408.0	95.9	-88.6	365.2	0.772	0.302	0.917	—
	5-6	8.0	226.4	78.8	202.2	1077.5	1.096	0.581	1.012	—
	6-7	0.8	450.4	188.8	-11.2	89.1	0.534	0.337	0.456	—
	7-8	1.4	229.3	116.8	—	—	—	—	—	—
	8-9	11.3	228.9 ^a	—	—	—	—	—	—	—
	\bar{X} and $SE_{\bar{X}}$		420.4	72.6	24.4	96.5	0.936	0.137	1.021	—
Site 2	0-1	—	120.3 ^a	—	—	—	—	—	—	
	1-2	0.7	121.3	113.2	—	—	—	—	—	
	2-3	0.6	55.2	24.9	22.6	64.5	0.808	0.512	0.701	
	3-4	1.3	67.2	34.7	—	—	—	—	—	
	4-5	2.0	67.3 ^a	—	—	—	—	—	—	
\bar{X} and $SE_{\bar{X}}$			86.3	14.3	—	—	—	—	—	

^a Estimate calculated by method described by Caughley (1977).

Table 6 cont. Jolly-Seber estimates of population size (N), number of individuals entering population between times i and $i + 1$ (A), probabilities that an individual present at time i will still be present at time $i + 1$ (P), and their standard errors (SE). Monthly survival rates (MSR) are the n th roots of the corresponding P_i 's, where n = the number of months between time i and $i + 1$.

Population	Interval		N	SE	A	SE	P	SE	MSR
	(i to i+1)	length (months)							
Eleven Point	0-1	—	170.7 ^a	—	—	—	—	—	—
Site 1	1-2	1.8	171.9	54.5	0.7	49.4	0.676	0.246	0.804
	2-3	10.0	117.0	33.5	-3.7	15.5	0.451	0.190	0.923
	3-4	3.0	49.1	19.0	—	—	—	—	—
	4-5	9.0	48.9 ^a	—	—	—	—	—	—
	\bar{X} and $SE_{\bar{X}}$	—	—	111.5	27.4	-1.5	2.2	0.564	0.112
Site 2	0-1	—	110.2 ^a	—	—	—	—	—	—
	1-2	1.9	111.1	35.8	-5.6	24.6	0.702	0.250	0.830
	2-3	10.0	72.4	25.0	—	—	—	—	—
	3-4	13.2	72.3 ^a	—	—	—	—	—	—
\bar{X} and $SE_{\bar{X}}$	—	—	91.5	11.1	—	—	—	—	—

^a Estimate calculated by method described by Caughley (1977).

Table 6 cont. Jolly-Seber estimates of population size (N), number of individuals entering population between times i and $i + 1$ (A), probabilities that an individual present at time i will still be present at time $i + 1$ (P), and their standard errors (SE). Monthly survival rates (MSR) are the n th roots of the corresponding P_i 's, where n = the number of months between time i and $i + 1$.

Population	Interval length (i to i+1) (months)	Interval					MSR		
		N	SE	A	SE	P		SE	
Gasconade	0-1	—	96.8 ^a	—	—	—	—	—	
Site 1	1-2	0.6	100.4	6.3	88.8	73.0	1.021	0.102	1.035
	2-3	0.7	191.2	16.9	196.1	377.8	1.100	0.182	1.146
	3-4	1.9	406.5	63.8	-66.7	155.0	0.707	0.158	0.833
	4-5	1.6	220.5	41.4	80.2	221.8	0.720	0.214	0.814
	5-6	9.2	238.9	57.3	-33.2	125.0	1.112	0.290	1.012
	6-7	0.5	232.5	28.2	42.0	105.9	1.118	0.231	1.250
	7-8	0.8	302.0	54.8	-6.9	28.0	0.594	0.176	0.521
	8-9	10.0	164.7	40.8	—	—	—	—	—
	9-10	2.0	162.7 ^a	—	—	—	—	—	—
	\bar{X} and $SE_{\bar{X}}$			211.6	29.4	42.9	33.5	0.910	0.086

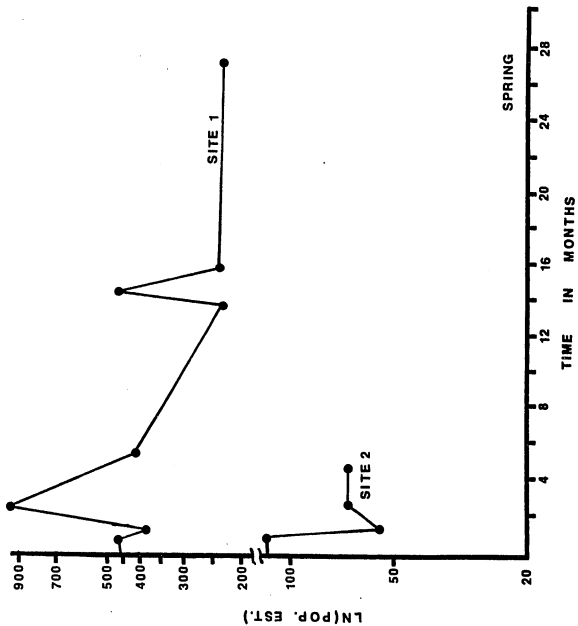
^a Estimate calculated by method described by Caughley (1977).

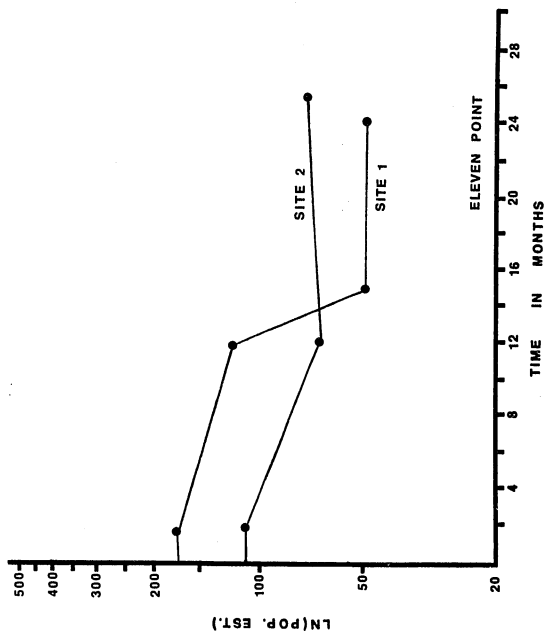
Table 6 cont. Jolly-Seber estimates of population size (N), number of individuals entering population between times i and $i+1$ (A), probabilities that an individual present at time i will still be present at time $i+1$ (p), and their standard errors (SE). Monthly survival rates (MSR) are the n th roots of the corresponding P_i 's, where n = the number of months between time i and $i+1$.

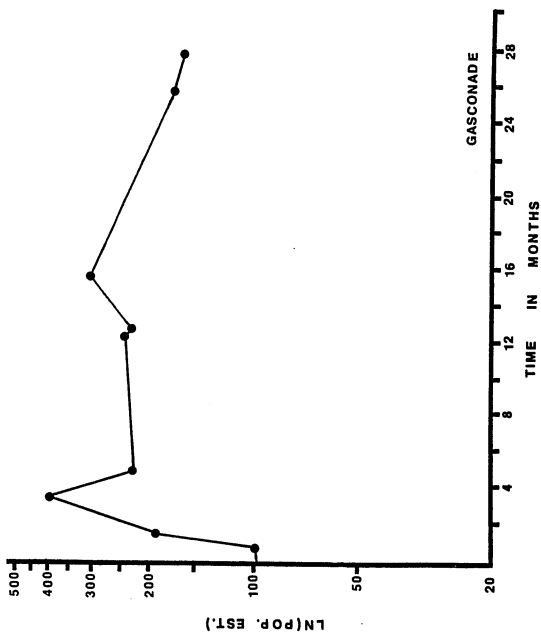
Population	Interval		N	SE	A	SE	P	SE	MSR
	Interval length (i to i+1) (months)	length (months)							
Big Piney	0-1	—	160.3 ^a	—	—	—	—	—	—
	1-2	0.2	154.1	16.8	64.7	84.3	0.800	0.122	0.328
	2-3	1.5	187.9	24.9	17.0	36.3	0.842	0.152	0.892
	3-4	0.6	175.2	26.3	34.9	65.9	0.669	0.150	0.512
	4-5	1.3	152.1	29.0	70.2	23.0	1.191	0.401	1.144
	5-6	9.5	251.3	74.1	6.4	29.1	0.459	0.138	0.921
	6-7	2.1	121.8	17.8	-11.8	42.0	1.100	0.347	1.046
	7-8	10.2	122.2	27.0	—	—	—	—	—
	8-9	0.6	122.2 ^a	—	—	—	—	—	—
\bar{X} and $SE_{\bar{X}}$ Site 2	0-1	—	160.8	13.8	30.2	13.3	0.844	0.111	0.807
	1-2	0.6	69.6 ^a	—	—	—	—	—	—
	2-3	10.7	71.4	19.7	-5.2	18.0	0.720	0.258	0.578
	3-4	1.9	46.2	10.1	68.2	496.6	1.250	0.116	1.021
	4-5	10.6	126.0	114.9	—	—	—	—	—
\bar{X} and $SE_{\bar{X}}$	—	—	126.4 ^a	—	—	—	—	—	—
	—	—	87.9	16.2	31.5	36.7	0.985	0.265	0.800

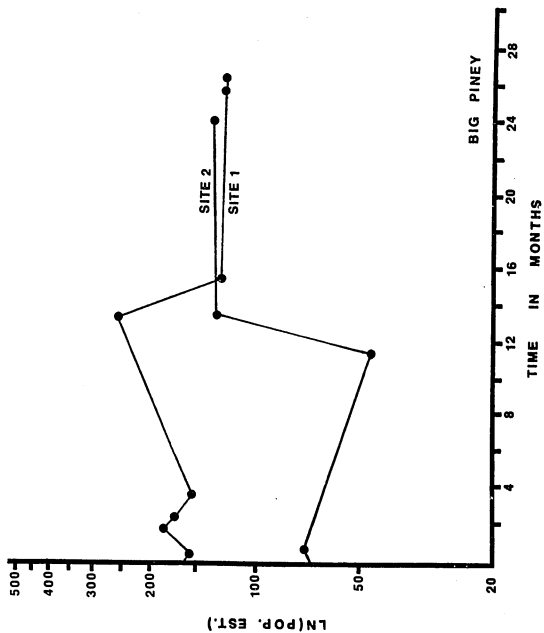
^a Estimate calculated by method described by Caughley (1977).

Figure 1. Natural logarithm (LN) of the estimated number of hellbenders during the study period for each collection site from Table 6.









Estimates of probability of survival (P_i) from time i to $i+1$ do not distinguish between actual mortality and emigration from the site. Due to sampling error, the P_i may exceed one. Monthly survival rate (MSR) was calculated as $P_i^{-\text{interval length}}$ as described by Tilley (1980). A comparison of MSRs for all sites of the Big Piney, Gasconade, and Spring River populations was made by ANOVA after a test of equal variance was made using Hartley's test ($H=4.19$, $r=3$, $n=7.3$, $P>0.05$) as outlined by Neter and Wasserman (1974). No significant difference ($F=0.143$, $P>0.05$) in mean MSRs was indicated. The Eleven Point population was excluded from the comparison due to the paucity of estimates. An average MSR of 0.8974 ($SD=0.3014$) was calculated from the pooled MSRs, including those of the Eleven Point sites. The annual survivorship rate was then estimated as 0.2728 for hellbenders from all collection sites of all populations.

Densities and biomass. Relative abundance was estimated in the different populations by determining the number of hellbenders caught per time (Table 7). Timed samples were made only when visibility was good, the river was not in flood, and temperatures were not extremely cold. From the average wet weight of an individual caught from each collection site (Table 8) and the average population estimate (Table 6), site biomass was calculated (Table 9). There is a significant correlation between absolute density of hellbenders (no./100 m^2) and mean relative density (catch/hr) estimates (Table 9), except for the Gasconade population ($r=0.867$, $P<0.05$, exclusive of the Gasconade estimates).

Table 7. Average number of hellbenders caught per hour.

Population	Site	No. of timed samples	Average catch time (hours)	Average no. of hellbenders caught per hour	SD	Range
Spring	1	6	2.47	9.02	1.98	6.43-12.00
	2	3	2.17	3.81	1.67	2.40-5.65
Eleven Point	1	3	1.14	8.40	3.12	6.46-12.00
	2	2	0.83	8.75	1.77	7.50-10.00
Gasconade	1	3	1.69	13.21	3.12	11.08-16.80
	1	3	1.28	7.64	2.55	5.05-10.15
Big Piney	1	3	1.28	7.64	2.55	5.05-10.15
	2	2	1.00	12.75	4.24	9.75-15.75

Table 8. Average weight of hellbenders from each collection site.

Population	Site	No. of individuals	Average weight (grams)	SD
Spring	1	310	970.8	304.2
	2	60	769.2	208.7
Eleven Point	1	121	214.0	125.5
	2	90	340.6	109.7
Gasconade	1	241	597.6	189.6
Big Piney	1	254	486.7	172.3
	2	80	531.5	181.5

Table 9. Density and biomass of hellbenders

Population	Site	Area (m ²)	No. of estimates	Average estimate	SD	No. per 100 m ²	Site biomass		Catch/hour	
							kg	kg/ha	mean	SD
Spring	1	10,300	9	420	218	4.1	407.7	396	9.02	1.98
	2	9,000	5	86	32	1.0	66.2	74	3.81	1.67
Eleven Point	1	2,600	5	112	61	4.3	24.0	92	8.40	3.12
	2	1,500	4	92	22	6.1	31.3	209	8.75	1.77
Gasconade	1	21,400	10	212	93	1.0	126.7	59	13.21	3.12
Big Piney	1	7,000	9	161	42	2.3	78.4	112	7.64	2.55
	2	1,400	5	88	36	6.3	46.8	334	12.75	4.24

Population Composition

Except in the Spring River where there was an unequal adult sex ratio, adult females appeared to be more common than adult males, at least from late July into November when hellbenders can be sexed externally (Table 10). In the Gasconade and Spring Rivers the populations were dominated by large, long-lived adults. Only one juvenile in the latter river and two in the former were captured during late summer to fall during three years, but 200⁺ adults were captured in each river during those samples. Only in the Eleven Point was a substantial proportion (25%) of the population composed of immature individuals. Further, of the approximately 1200 hellbenders marked during this study, only one larval or gilled specimen was observed. This individual from the Big Piney measured 77 mm TL and was approximately 10 months old from time of spawning.

Pecundity

Paired comparison of ovary oocyte number. All externally sexed females were ripe but one. The number of developing eggs in the right ovary was compared with those of the left ovary for each population by a two-way ANOVA without replication (Sokal and Rolf, 1973) after no significant difference was found in the variance of ova number in right and left ovaries (Table 11). A significantly greater number of ova in the right ovary was indicated for the Eleven Point and Gasconade animals, but no significant difference between ovaries in the Spring and Big Piney females.

Size at maturity. Size at sexual maturity seems to differ among populations. From external identification Eleven Point females mature at about 300 mm TL while Big Piney females do not mature

Table 10. Number and percent of juveniles, adult males, and adult females in samples where all adults were sexed externally and chi-square tests of whether the ratio of adult males and females is significantly different from 1:1 for each sample and for the total number of individuals (adult males and females) in those samples (excludes recaptures).

Date	Spring River						Total no. of individuals in samples		
	Juveniles		Males		Females		M	F	
	No.	%	No.	%	No.	%			
9-10 Aug. 1980	0	0.0	40	44.4	50	55.6	128	119	0.33 ^{ns}
8-9 Nov. 1980	0	0.0	42	56.0	33	44.0			1.08 ^{ns}
31 July 1981	0	0.0	17	54.8	14	45.2			0.29 ^{ns}
12 Sept. 1981	0	0.0	22	51.2	21	48.8			0.02 ^{ns}
21 Aug. 1982	1	2.6	17	43.6	21	53.8			0.42 ns
		$\bar{X} = 0.5$		$\bar{X} = 50.0$		$\bar{X} = 49.5$			2.13 ns

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 10 cont. Number and percent of juveniles, adult males, and adult females in samples where all adults were sexed externally and chi-square tests of whether the ratio of adult males and females is significantly different from 1:1 for each sample and for the total number of individuals (adult males and females) in those samples (excludes recaptures).

Date	Eleven Point River						Total no. of individuals in samples		χ^2
	Juveniles		Males		Females		M	F	
	No.	%	No.	%	No.	%			
26-27 July 1980	23	26.4	23	26.4	41	47.1	54	86	7.31***
20-21 Sept. 1980	19	25.3	24	32.0	32	42.7			1.14 ^{ns}
18 Oct. 1981	9	47.4	2	10.5	8	42.1			3.60*
4 Sept. 1982	0	0.0	9	31.0	20	69.0			4.17**
	\bar{X}	24.8	\bar{X}	25.0	\bar{X}	50.2			13.98***

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 10 cont. Number and percent of juveniles, adult males, and adult females in samples where all adults were sexed externally and chi-square tests of whether the ratio of adult males and females is significantly different from 1:1 for each sample and for the total number of individuals (adult males and females) in those samples (excludes recaptures).

Date	Gasconade River						Total no. of individuals in samples			
	Juveniles		Males		Females		M	F	χ^2	
	No.	%	No.	%	No.	%				
28 Sept. 1980	0	0.0	22	34.4	42	65.6	6.25**	95	131	5.74**
15 Nov. 1980	0	0.0	5	20.0	20	80.0	9.00***			
5 Sept. 1981	1	1.8	21	36.8	35	61.4	3.50*			
28 Sept. 1981	1	1.4	36	50.0	35	48.6	0.01 ^{ns}			
27 July 1982	0	0.0	28	39.4	43	60.6	3.17*			
26 Sept. 1982	0	0.0	12	35.3	22	64.7	2.94*			
		$\bar{X} = 0.5$		$\bar{X} = 36.0$		$\bar{X} = 63.5$	24.87***			

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 10 cont. Number and percent of juveniles, adult males, and adult females in samples where all adults were sexed externally and chi-square tests of whether the ratio of adult males and females is significantly different from 1:1 for each sample and for the total number of individuals (adult males and females) in those samples (excludes recaptures).

Date	Big Piney River						Total no. of individuals in samples		χ^2
	Juveniles		Males		Females		M	F	
	No.	%	No.	%	No.	%			
5-6 Aug. 1980	14	17.1	26	31.7	42	51.2	81	114	5.58**
13 Sept. 1980	1	2.1	19	40.4	27	57.5			1.39 ^{ns}
30 Aug. 1981	1	2.0	22	44.9	26	53.1			0.33 ^{ns}
19 Sept. 1981	1	2.9	16	45.7	18	51.4			0.12 ^{ns}
24 July 1982	1	2.6	14	35.9	24	61.5			2.63 ^{ns}
	\bar{X}	= 5.3	\bar{X}	= 39.7	\bar{X}	= 54.9			8.24*

*, **, *** $P < 0.1, 0.05, 0.01$ respectively

Table 11. A comparison of the number of developing ova in right and left ovaries by analysis of variance.

Population	N	Left ovary		Right ovary		F value	
		Mean no. of ova	SD	Mean no. of ova	SD	Variance ratio	Paired comparison
Spring Eleven Point	15	283.3	71.1	293.2	103.5	2.119 ^{ns}	0.428 ^{ns}
	15	135.8	39.9	153.1	41.5	1.082 ^{ns}	15.096**
Gasconade	16	179.9	54.0	194.1	64.7	1.436 ^{ns}	4.605*
Big Piney	16	156.9	54.8	162.9	51.2	1.146 ^{ns}	0.953 ^{ns}

*, **, *** $P < 0.05, 0.01, 0.001$ respectively

until a size of about 370 mm. Due to the few number of juveniles, size at maturity could not be determined for Spring River and Gasconade River females. All females dissected from the Eleven Point were mature. The smallest of these was 323 mm TL. One 353 mm female from the Big Piney was immature, the next smallest individual dissected, 387 mm TL, was mature. No female less than 400 mm was dissected from either the Spring or Gasconade Rivers.

TL-fecundity relationships. Fecundity is positively related to female length in all populations (Table 12 and Fig. 2). The Gasconade females and the Big Piney females exhibit similar TL-fecundity relationships as do the two C. a. bishopi populations (Table 13); however, the latter two were not pooled in further comparisons because of the disparity in size of Spring River and Eleven Point females. The TL-fecundity regressions calculated for North Fork and Niangua River females by Topping and Ingersol (1981) were included in the comparisons. The females of the three C. a. bishopi populations produce more eggs at any specific size than the females of the three C. a. alleganiensis populations. All possible comparisons were not made because of the increasing possibility of error due to chance alone with each further test. Moreover, further comparisons would provide little more information about the relationships between the regressions, especially because sample sizes are similar.

Spawning. Thirteen of 15 Big Piney females killed 19 September 1981 were spent. On 26 September 1981, egg strings were protruding from the cloaca of a few captured Gasconade females, and an egg string was found under a rock. Seven Spring River females were

Table 12. Regression of fecundity (F) on total length (TL) using Bartlett's (1949) method as described by Simpson et al. (1960). The 95% confidence limits for the slope and y-intercept, respectively, are shown in parentheses.

Population	N	Mean TL (mm)	SD	Mean clutch size	SD	Regression equation	r ²	t value		
								nonlinear component	slope differing from zero	
Spring	15	480	51	576	168	F=2.3374TL-545.2915 (0.85-3.64) (-608--482)	0.614	0.398 ^{ns}	3.223**	
Eleven Point	15	365	33	289	80	F=1.8405TL-382.9678 (0.64-2.87) (-404--362)	0.673	0.807 ^{ns}	2.972*	
Gasconade	16	450	36	374	116	F=2.4066TL-709.0420 (1.03-3.54) (-746--672)	0.691	0.714 ^{ns}	3.321**	
Big Piney	16	429	31	320	107	F=2.7258TL-849.8760 (1.47-4.10) (-887--813)	0.618	0.479 ^{ns}	4.583***	

*, **, *** P < 0.05, 0.01, 0.001 respectively

Figure 2. TL-fecundity regressions. C. a. bishopi populations: Spring River (S,●), Eleven Point (EP,●). C. a. alleganiensis populations: Gasconade (G,◆), Big Piney (BP,♠). Line lengths represent the approximate range of adult female sizes for each population.

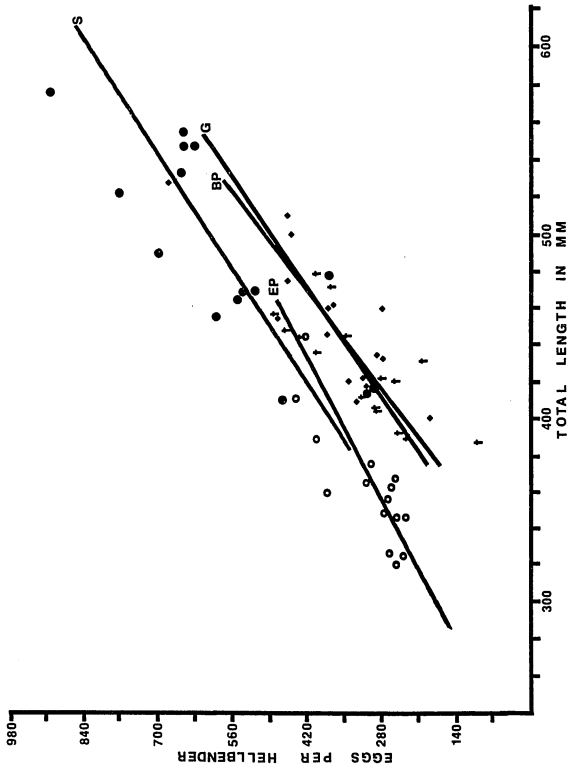


Table 13. T-tests of the significance of the difference between slopes and y-intercepts of the regressions of fecundity on total length as described by Simpson et al. (1960). Regressions for Niangua and North Fork River populations are from Topping and Ingersol (1981).

Test	Variances		Slopes		Elevations		Conclusions	
	N	F	t	t	t	t	variances	slopes elevations
Gasconade vs. Big Piney	16;16	1.030 ^{ns}	-0.012 ^{ns}	1.889 ^{ns}	equal	equal	equal	equal
Gasconade and Big Piney vs. Niangua	32;9	2.779 ^{ns}	0.091 ^{ns}	-6.199 ^{***}	equal	equal	equal	different
North Fork vs. Spring	12;15	1.110 ^{ns}	-0.032 ^{ns}	-3.302 [*]	equal	equal	equal	different
North Fork vs. Gasconade and Big Piney	12;32	1.247 ^{ns}	-0.058 ^{ns}	-17.342 ^{***}	equal	equal	equal	different
North Fork vs. Eleven Point	12;15	1.073 ^{ns}	-0.243 ^{ns}	24.048 ^{***}	equal	equal	equal	different
Spring vs. Gasconade and Big Piney	15;32	1.998 ^{ns}	-0.109 ^{ns}	-44.483 ^{***}	equal	equal	equal	different
Spring vs. Eleven Point	15;15	1.719 ^{ns}	0.025 ^{ns}	0.736 ^{ns}	equal	equal	equal	equal

^a Comparison made after a double natural logarithmic transformation to equalize variances
*, **, *** P < 0.05, 0.01, 0.001 respectively

collected 12 December 1984; all were ripe. Two males were producing milt.

Stomach Contents

Crayfish remains were the most frequently found items in stomachs, except for the females collected near the height of the Gasconade breeding season (Table 14). In 10 of the 13 Gasconade females killed that day, hellbender eggs were found in the stomach, generally in large numbers, though they could not be counted. Only four of the 15 Big Piney females contained eggs in the stomach at or after spawning; five of the 15 contained crayfish remains. Food items regurgitated in capture and transport were not considered. It is unknown how widespread regurgitation was in capture, but it was minimal during transport on ice.

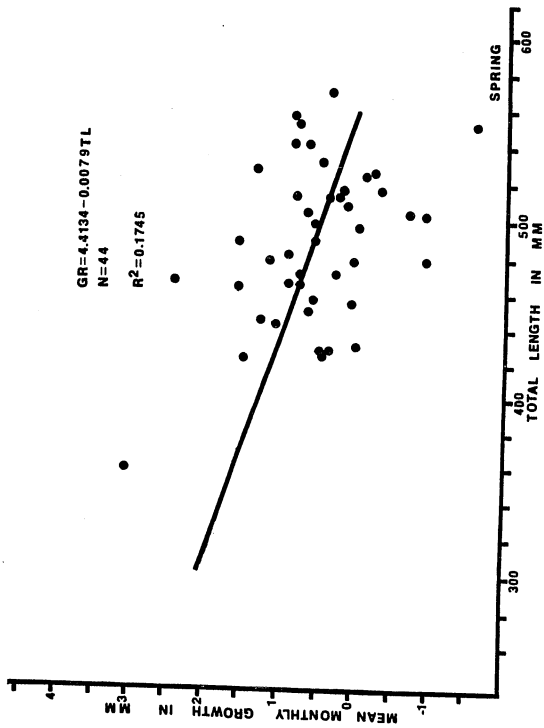
Growth and Size Comparisons

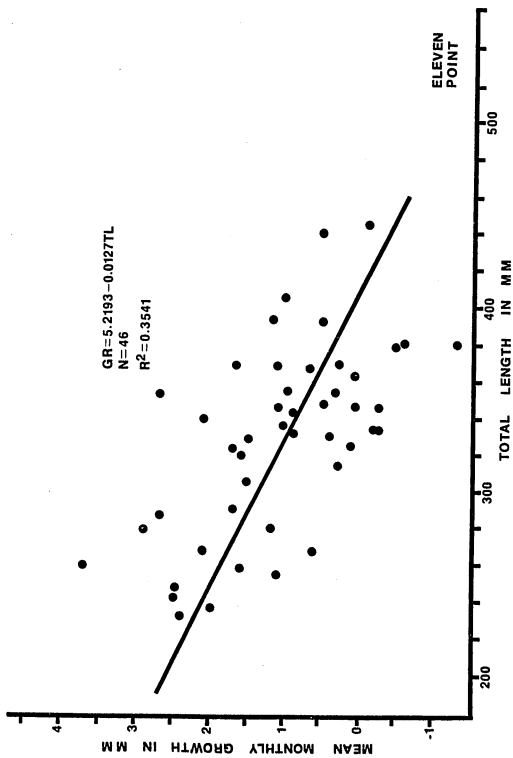
Growth. Growth of the sexes was pooled in the Spring and Eleven Point populations because of insufficient data to produce significant regressions for adult males and females separately. However, in the Gasconade and Big Piney populations, adult males and females could be treated separately (Fig. 3). The slopes of all regressions shown of growth versus length are negative and significantly different from zero (Table 15). Because of nonlinearity, a logarithmic transformation was performed on the TLs of Gasconade males. There was a significant difference in the y-intercepts of Gasconade males and females ($t = -6.22$, $P < 0.001$) but not slopes ($t = 0.03$, $P > 0.05$). Similarly, females are generally longer than males in the Big Piney River; slopes are not significantly different ($t = 0.07$, $P > 0.05$), but elevations are significantly different ($t = 7.52$, $P < 0.001$).

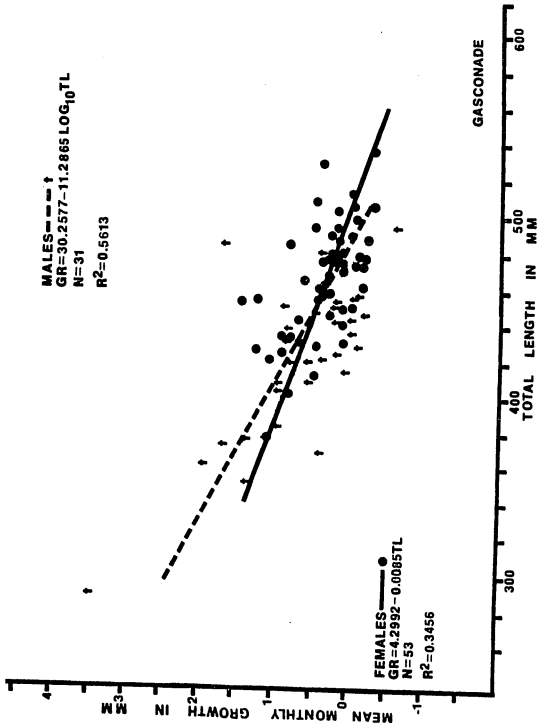
Table 14. Contents of stomachs of hellbenders killed for information on fecundity.

Population	No. of stomachs examined before/just after spawning	No. of stomachs with crayfish remains before/just after spawning	Average no. of pairs of chelae per stomach (SD) before spawning	No. of stomachs with fish remains	No. of stomachs with hellbender eggs	No. of stomachs with pebbles/bits of foliage	No. of empty stomachs
Spring	15/0	15/—	2.7(1.5)	1	—	3/1	0
Eleven Point	15/0	14/—	1.9(1.1)	2	—	1/0	1
Casconade	11/13	6/3	0.6(0.7)	0	10	0/1	6
Big Piney	15/15	7/5	0.9(1.3)	1	4	4/1	13

Figure 3. Length-growth regressions for Spring River, Eleven Point, Gasconade, and Big Piney hellbenders. Only the Eleven Point regression includes juvenile growth. Sexes are pooled for the Spring River and Eleven Point regressions.







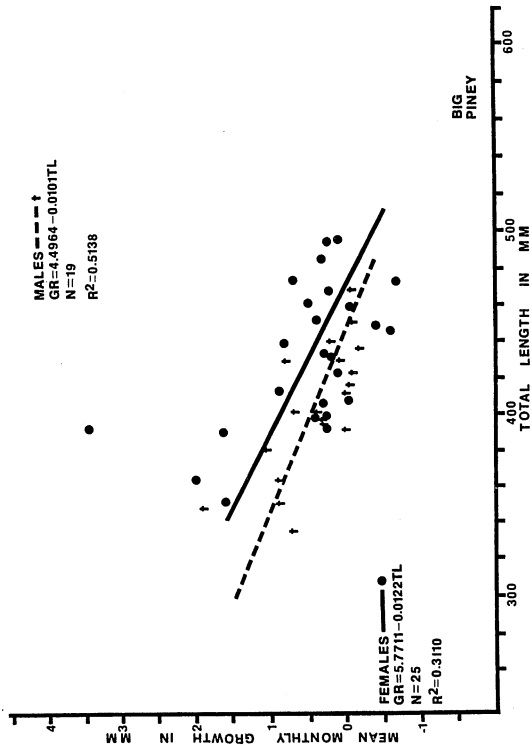


Table 15. Regression of growth (GR) on total length (TL) using Bartlett's (1949) method as described by Simpson et al. (1960). The 95% confidence limits for the slope and y-intercept, respectively, are shown in parentheses.

Population	Sex	N	Regression equation	r ²	t value	
					nonlinear component	slope differing from zero
Spring	Both	44	GR=0.0079TL+4.4134 (-.0038--.0159) (4.31-4.69)	0.174	1.71 ^{ns}	-2.52*
Eleven Point	M	11	GR=0.0200TL+7.3704 (-.0012--.0395) (6.80-7.94)	0.464	-2.06 ^{ns}	-2.42*
	Both	46	GR=0.0127TL+5.2193 (-.0072--.0184) (4.96-5.48)	0.354	0.428 ^{ns}	-4.54***
Gasconade	M	31	GR=11.2865LogTL+30.2577 (-5.78--16.27) (30.06-30.46)	0.561	1.76 ^{ns}	-4.96***
	F	53	GR=0.0085TL+4.2992 (-.0051--.0121) (4.20-4.39)	0.346	1.60 ^{ns}	-4.87***
Big Piney	M	19	GR=0.0101TL+4.4964 (-.0038--.0159) (4.31-4.69)	0.512	1.65 ^{ns}	-3.20**
	F	25	GR=0.0122TL+5.7711 (-.0035--.0207) (5.47-6.07)	0.311	2.06 ^{ns}	-2.84**

*, **, *** P < 0.05, 0.01, 0.001 respectively

To compare the regression coefficient estimates of the TL-growth relationships (Table 16), each growth was divided by the standard deviation of the growths for a particular regression to equalize variances (Murphy, 1973). The Big Piney and Gasconade growth equations used in the comparisons are those of the females. Data for the growth equations of the North Fork and Niangua hellbenders are from Peterson et al. (1983) and Taber et al. (1975), respectively. The regressions for the Big Piney, Gasconade, and Spring Rivers are not influenced by juvenile growth because no juveniles were recaptured or because there was differential growth of the sexes. Thus they are not as likely to be as steep as the growth lines of the other three populations which are influenced by juvenile growth (Fig. 4). Because slopes are significantly different in only one test, but elevations are different in all tests, growth per size among adults is greatest in the Niangua population followed by the Spring River, Gasconade, North Fork, Big Piney, and Eleven Point hellbenders. All possible comparisons were not made for reasons given previously with regard to length-fecundity comparisons.

Length-weight relationships. A power function was fitted to the length-weight data of recaptured adults of both sexes (Table 17). The Big Piney females exhibit a significant nonlinear component; however, the measure of the amount of variation in weight explained by the regression on TL, the coefficient of variation, is large. Between sexes there are no significant differences in the slopes of the length-weight relationships but significant differences in the y-intercepts. This suggests that females are larger than males in the Eleven Point and Spring Rivers as in the Big Piney and

Table 16. T-tests of the significance of the difference between slopes and y-intercepts of the regressions of growth on TL as described by Simpson et al. (1960). Data for the Niangua and North Fork regressions are from Taber et al. (1975) and Peterson et al. (1983). Growths were transformed by division of the growths by their standard deviation to equalize variances. The Gasconade and Big Piney regressions are those of the females only.

Test	N	Variances		Slopes		Elevations		Conclusions	
		F	t	t	t	variances	slopes	elevations	
Spring vs. Niangua	44;260	1.297 ^{ns}	1.184 ^{ns}		-13.076 ^{***}	equal	equal	different	
Spring vs. Gasconade	44;53	1.272 ^{ns}	0.619 ^{ns}		-27.955 ^{***}	equal	equal	different	
Gasconade vs. North Fork	53;99	1.384 ^{ns}	3.419 ^{***}		—	equal	different	—	
Niangua vs. North Fork	260;99	1.357 ^{ns}	0.857 ^{ns}		9.706 ^{***}	equal	equal	different	
Big Piney vs. Gasconade	25;53	1.018 ^{ns}	0.285 ^{ns}		-18.730 ^{***}	equal	equal	different	
Big Piney vs. North Fork	25;99	1.389 ^{ns}	1.010 ^{ns}		-15.767 ^{***}	equal	equal	different	
Eleven Point vs. Big Piney	46;25	1.019 ^{ns}	0.083 ^{ns}		7.684 ^{***}	equal	equal	different	

*, **, *** P < 0.05, 0.01, 0.001 respectively

Figure 4. A comparison of the length-growth regressions of hellbenders: Spring River (S), Eleven Point (EP), Gasconade females, (G), Big Piney females (BP), Niangua (N), North Fork (NF). Lines for the Niangua and North Fork hellbenders are from Peterson et al. (1983). C. a. bishopi are represented by dashed lines, C. a. alleganiensis by solid lines.

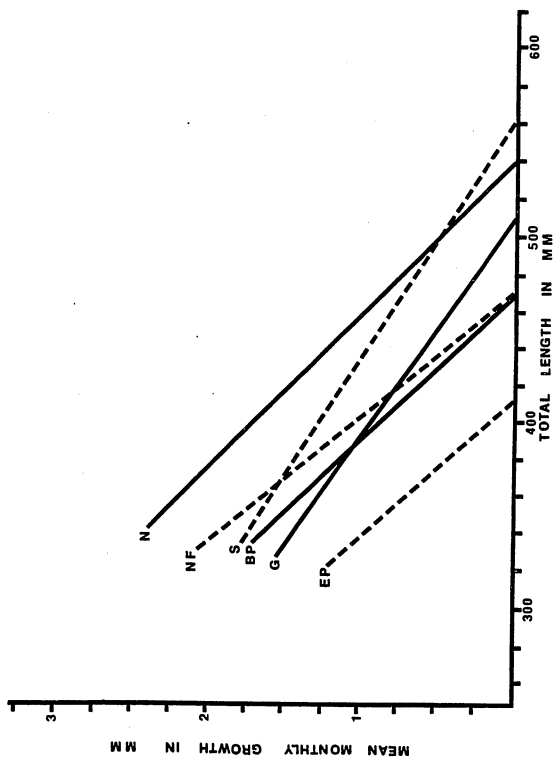


Table 17. Regression of the logarithm of weight (WT) on the logarithm of total length (TL) of recaptured hellbenders using Bartlett's (1949) method as described by Simpson et al. (1960) and a comparison of the regression coefficients between sexes of each population.

Population	Sex	N	Regression equation	r ²	nonlinear differing component from zero	t value	
						slope	slopes elevations
Spring	M	38	WT=0.0000532TL ² .6998	0.756	-1.834 ^{ns}	5.151***	-0.022 ^{ns}
	F	36	WT=0.0000005TL ³ .4675	0.716	-1.530 ^{ns}	7.041***	34.024***
Eleven Point	M	12	WT=0.0000282TL ² .7764	0.931	-0.185 ^{ns}	4.352**	-0.005 ^{ns}
	F	27	WT=0.0000160TL ² .8770	0.911	-0.455 ^{ns}	4.264***	2.355*
Gasconade	M	39	WT=0.0000492TL ² .7003	0.905	-0.013 ^{ns}	7.777***	-0.049 ^{ns}
	F	68	WT=0.0000129TL ² .9048	0.800	0.086 ^{ns}	10.228***	11.819***
Big Piney	M	31	WT=0.0000436TL ² .7027	0.838	0.677 ^{ns}	7.298***	-0.035 ^{ns}
	F	50	WT=0.0000011TL ³ .3121	0.877	-2.196*	11.179***	30.388***

*, **, *** P < 0.05, 0.01, 0.001 respectively

Gasconade Rivers.

Maximum size. The average maximum TL or asymptotic length predicted by each length-growth regression is the x-intercept. Unlike the Spring and Eleven Point populations, a significant difference in growth of sexes was detected in the Gasconade and Big Piney populations. Thus asymptotic length can be predicted for each sex in the latter two rivers (Table 18). The asymptotic length was substituted into the length-weight relationships to estimate an average maximum weight.

Environmental Factors Influencing Growth

Temperature. The heavily spring-influenced streams, the Spring and Eleven Point Rivers, remained fairly stenothermal and exhibited similar temperatures (Figs. 5, 6, and 7). However, growth of hellbenders was about the most disparate in these two rivers. The North Fork, also highly influenced by springs, showed less variation in temperatures than the Big Piney and Gasconade, remaining warmer in winter and cooler in summer like the other south-flowing streams. The Niangua River exhibited rather wide variation despite temperature recordings being made only about 4 km downstream from Bennett Springs, the fourth largest spring in Missouri (Vineyard and Feder, 1974).

Relative crayfish abundance. Catch per unit effort of crayfish was determined when conditions were "good" (Table 19) as described for catch per unit effort of hellbenders. Crayfish of all sizes and species (Orconectes spp.) were captured. The North Fork hellbender biomass is from Peterson et al. (1983). No information on hellbender biomass is available from the site of collection

Table 18. Predicted average maximum total length (TL) from length-growth regressions in Table 15 and the expected weight (WT) from length-weight regressions in Table 17 compared with the longest and heaviest individuals captured.

Population	Average predicted maximum size		Longest observed individual		Heaviest observed individual	
	TL (mm)	WT (g)	TL (mm)	WT (g)	TL (mm)	WT (g)
Spring						
Male	559 ^a	1392	600	1656	600	1656 ⁺
Female		1593	596	1872	578	2110 ⁺
Eleven						
Point						
Male	411 ^a	510	444	565	444	565
Female		530	446	784	446	784
Gasconade						
Male	480	723	515	857	487	858
Female	506	923	548	1154	543	1584
Big Piney						
Male	445	627	502	953	502	953
Female	473	797	523	878	476	1018

^aNo significant difference was detected in the growth of the sexes

⁺Only individual that weighed more than 2110 g, the maximum the triple-beam balance could measure

Figure 5. Maximum and minimum temperatures and current temperature when thermometers were checked for the Spring (.), Eleven Point (●), Gasconade (◆), and Big Piney (†) Rivers from fall 1980 to fall 1981.

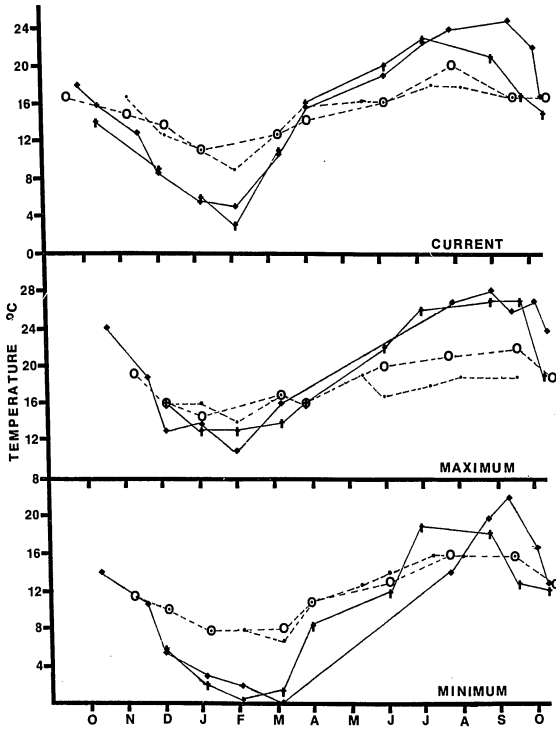


Figure 6. Maximum and minimum temperatures for the cold season months, November through March 1980-81. Vertical lines are the range, crossbars the mean, and boxes represent ± 1 standard deviation. C. a. bishopi rivers: Spring (S), Eleven Point (EP), North Fork (NF). C. a. alleghaniensis rivers: Gasconade (G), Big Piney (BP), Niangua (N).

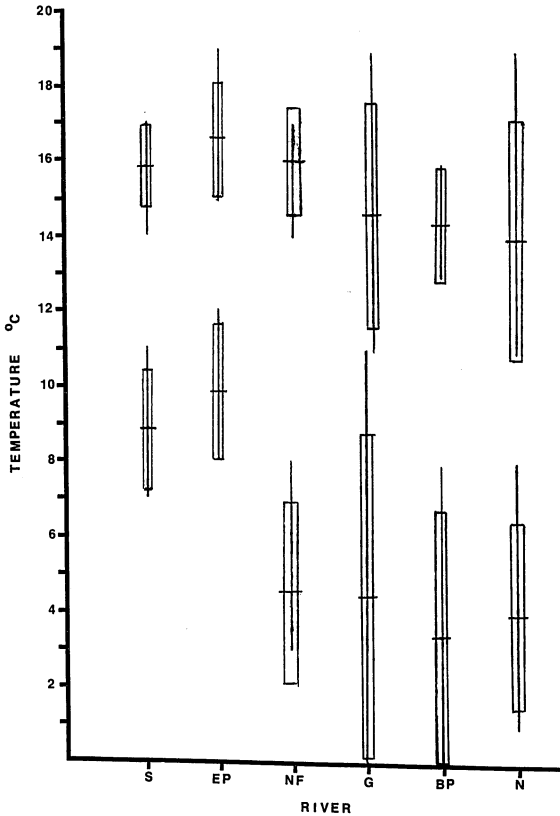


Figure 7. Maximum and minimum temperatures for the warm season months, April through October, 1981. Vertical lines are the range, crossbars the mean, and boxes represent ± 1 standard deviation. C. a. bishopi rivers: Spring (S), Eleven Point (EP), North Fork (NF). C. a. alleghaniensis rivers: Gasconade (G), Big Piney (BP), Niangua (N).

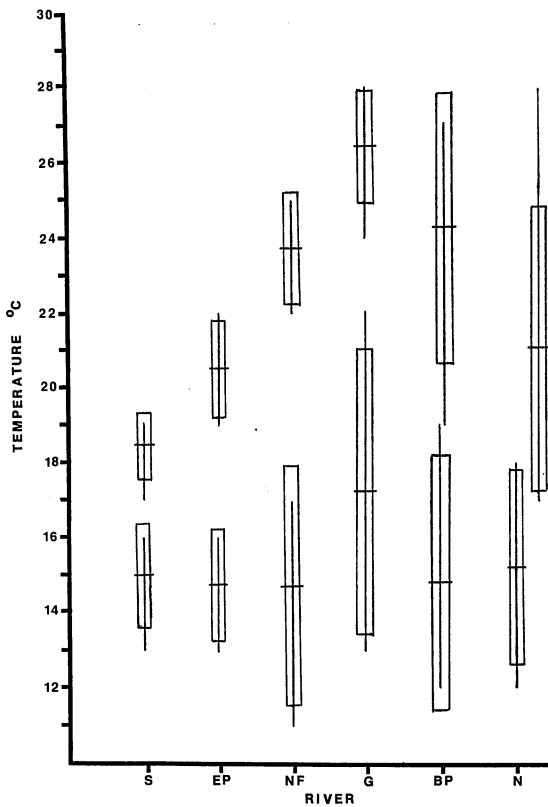


Table 19. Catch per unit effort of crayfish (*Orconectes spp.*) made only during summer. Hellbender biomass is from Table 9, except the North Fork datum is from Peterson et al. (1983).

Population	Site	Average catch		Man-hours	Hellbender biomass (kg/ha)
		per hour	weight(g) no.		
Spring	1	1792	177	1.0	396
	2	888	127	1.0	74
Eleven Point	1	1100	102	0.9	92
	2	729	92	1.0	209
North Fork	1	1510	180	1.0	157
Gasconade	1	349	50	1.3	59
Big Piney	1	1165	88	1.0	112
	2	923	153	1.1	334
Niangua	-	2721	182	1.0	---

of crayfish in the Niangua; however, catch per time indicates a dense population: an average of 17.2 hellbenders were captured per hour based on 1.9 hours of effort, a greater catch than in any other river. By wet weight the crayfish catch correlation with hellbender biomass is not significant ($r=0.534$, $P>0.1$), but the number of crayfish caught per hour is weakly correlated with standing crop of hellbenders ($r=0.657$, $0.1>P>0.05$). If the average estimate of hellbender biomass made by Topping (personal communication) for 10 Niangua collection sites (871 kg / ha) is divided in half as an approximate measure of biomass for the entire area of the sites (not just diurnal habitat) and paired with the Niangua crayfish catch in Table 19, the result is a correlation coefficient significantly different from zero for weight of crayfish caught per hour versus hellbender biomass ($r=0.730$, $P<0.05$) as well as number of crayfish caught per hour versus hellbender biomass ($r=0.731$, $P<0.05$).

To determine the error that could be involved in the crayfish catch, three other collectors besides the author worked site 1 in the Eleven Point concurrently for approximately one hour. For the four efforts the mean and standard error of the number of crayfish caught per hour was 114.4 and 11.2 crayfish, respectively. The mean and standard error of the crayfish weight caught per hour was 1119.2 and 142.1 g, respectively. This suggests that catch per unit effort may be a useful method for assessing relative crayfish abundance.

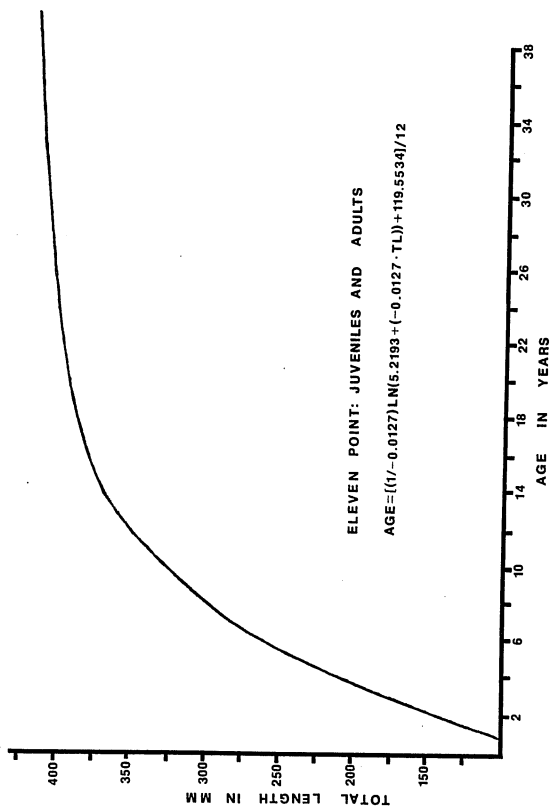
Age

The length-growth regressions can be integrated to generate an equation relating age in months to TL in mm. If age at any specific size is known, the constant of integration can be calculated. For the Eleven Point hellbenders, age and size at metamorphosis, 18 months and 125 mm TL according to Goin and Goin (1971), was used to calculate the constant. This reference point was also used by Peterson et al. (1983) and Taber et al. (1975) for their growth models. The length-age curve in Fig. 8 was then generated from this length-age equation: $Age_{(months)} = (1/-0.0127) \ln(5.2193 + (-0.0127)TL_{(mm)}) + 119.5534$. Reaching sexual maturity at about 300 mm TL, Eleven Point females are approximately seven to eight years old.

Because juvenile growth was not measured in the other three populations, transformation size and age was considered too far beyond the scope of the growth regression to be useful. Therefore size and age at sexual maturity for females was estimated to calculate the integration constant for the Spring, Gasconade, and Big Piney populations. Because maturity for females is attained when about seven to eight years old in the Eleven Point and also in the North Fork and Niangua populations (Peterson et al., 1983; Taber et al., 1975), this age is assumed for the other three populations. Size at maturity is about 370 mm TL for Big Piney females. This size is also assumed for the Gasconade and Spring River females because their growth is slightly less than that of the Niangua females which mature when about 38 to 39 cm TL (Ingersol, 1982; Taber et al., 1975). Thus 84 months and 370 mm TL were used to

Figure 8. Length-age curve for Eleven Point hellbenders.

The line is the integral form of the regression in Fig. 3 with the integration constant calculated by substitution of the estimated size (125 mm TL) and age (18 months) at metamorphosis, according to Goin and Goin (1971). Division by 12 changes age from months to years.



generate length-age curves (Fig. 9) from the following equations

for the Spring, Gasconade, and Big Piney adult females, respectively:

$$\text{Age}_{(\text{months})} = (1/-0.0079)\ln(4.4134 + (-0.0079)\text{TL}_{(\text{mm})}) + 134.5120,$$

$$\text{Age}_{(\text{months})} = (1/-0.0122)\ln(4.2992 + (-0.0085)\text{TL}_{(\text{mm})}) + 100.8715,$$

$$\text{Age}_{(\text{months})} = (1/-0.0122)\ln(5.7711 + (-0.0122)\text{TL}_{(\text{mm})}) + 102.7547.$$

Age-specific Fecundity and Survivorship

Fecundity tables. Because the method of aging is crude, intervals of less than five years were not considered for aging the adult females sampled for age-specific fecundity information (Table 20). The number of females of the zero age class was estimated by summing the products of columns two and four for each age interval, then dividing by two. This method assumes that all eggs are laid and fertilized and that the sex ratio at conception is 1:1.

Although fecundity increases with size and thus age as evident from the length-fecundity relationships (Fig. 2), the greatest number of eggs laid each year by the population is produced by the young adults. This is because fewer animals are alive in each subsequent five-year age interval. This is particularly so in the Eleven Point, less so in the Gasconade and Spring Rivers where the populations are dominated to a greater degree by older animals. The number of female zygotes produced per female varies among populations for females of similar age (column 6). An approximate Hartley's test indicated no significant difference in the variance of the female zygotes produced per female among populations ($H=2.522$, $r=4$, $n=5.25$, $P>0.05$). A single factor ANOVA did indicate a significant difference in the means of the number of female zygotes

Figure 9. Length-age curve for adult females: Spring River (S), Eleven Point (EP), Gasconade (G), Big Piney (BP). The lines represent the integral form of the regressions in Fig. 3. Except for the Eleven Point, the integration constant was calculated by substitution of the estimated size (370 mm TL) and age (84 months) at sexual maturity.

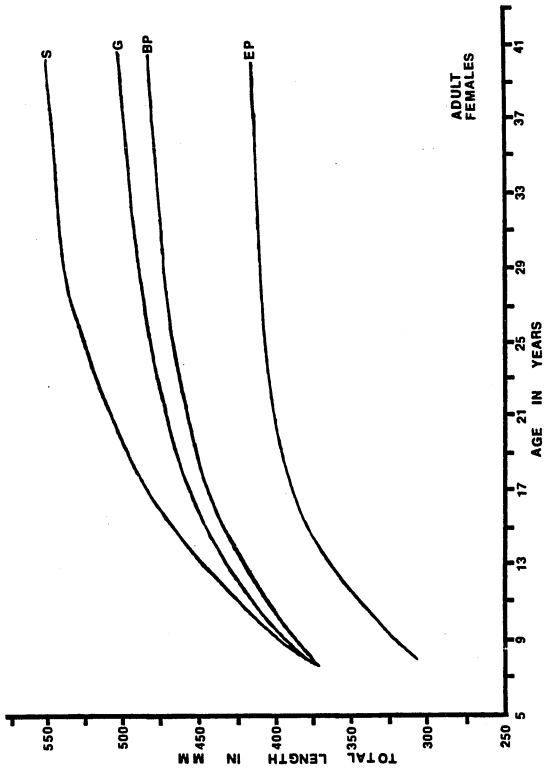


Table 20. Number of female zygotes produced per female over age intervals for all ages from sexual maturity to hypothesized oldest age.

Spring River						
Age in years (interval)	Sampled frequency of females late summer to fall 1980	Expected TL in mm from age-length relationship	Expected no. of eggs produced per female from length-fecundity relationship	Product of column 2 and column 4	No. of female zygotes per female, column 4 + 2	
0	29,170 ^a	—	—	—	—	—
11.5 (7-16)	39	435	471	18,369	235.5	
19 (17-21)	22	498	619	13,618	309.5	
24 (22-26)	13	521	673	8,749	336.5	
29 (27-31)	6	535	705	4,230	352.5	
41.5 (32-51)	18	551	743	13,374	371.5	
				<u>58,340 + 2 = 29,170^a</u>		

^aAssumes a 1:1 zygote sex ratio and that all eggs are laid and fertilized

Table 20 cont. Number of female zygotes produced per female over age intervals for all ages from sexual maturity to hypothesized oldest age.

Age in years (interval)	Eleven Point River				Product of column 2 and column 4 + 2
	Sampled frequency late summer to fall 1980	Expected TL in mm from age-length relationship	Expected no. of eggs produced per female from length-fecundity relationship	No. of female zygotes per female, column 4	
0	8,329 ^a	—	—	—	—
9 (7-11)	38	320	206	7,828	103
14 (12-16)	17	368	294	4,998	147
19 (17-21)	7	391	337	2,359	168.5
24 (22-26)	1	402	357	357	178.5
29 (27-51)	3	410	372	1,116	186
				16,658 + 2 = 8,329 ^a	

^aAssumes a 1:1 zygote sex ratio and that all eggs are laid and fertilized

Table 20 cont. Number of female zygotes produced per female over age intervals for all ages from sexual maturity to hypothesized oldest age.

<u>Gasconade River</u>						
Age in years (interval)	Sampled frequency of females late summer to fall 1980	Expected TL in mm from age-length relationship	Expected no. of eggs produced per female from length- fecundity relationship	Product of column 2 and column 4	No. of female zygotes per female, column 4 \div 2	
0	17,975 ^a	—	—	—	—	—
9 (7-11)	28	395	242	6,776	121	
14 (12-16)	19	439	347	6,593	173.5	
19 (17-21)	14	466	412	5,768	206	
24 (22-26)	10	482	451	4,510	225.5	
29 (27-31)	7	491	473	3,311	236.5	
41-5 (32-51)	18	502	499	8,992	249.5	
				35,950 \div 2 = 17,975 ^a		

^aAssumes a 1:1 zygote sex ratio and that all eggs are laid and fertilized

Table 20 cont. Number of female zygotes produced per female over age intervals for all ages from sexual maturity to hypothesized oldest age.

Big Piney River						
Age in years (interval)	Sampled frequency of females late summer to fall 1980	Expected TL in mm from age-length relationship	Expected no. of eggs produced per female from length-fecundity relationship	Product of column 2 and column 4	No. of female zygotes per female, column 4 \div 2	
0	15,024 ^a	—	—	—	—	
9 (7-11)	37	396	230	8,510	115	
14 (12-16)	27	436	339	9,153	169.5	
19 (17-21)	14	455	390	5,460	195	
24 (22-26)	3	464	415	1,245	207.5	
39 (27-51)	13	472	437	5,681	218.5	
				30,049 \div 2 = 15,024.5 ^a		

^a Assumes a 1:1 zygote sex ratio and that all eggs are laid and fertilized.

produced per female among the four populations ($F=13.41$, $P<0.001$). The test is not totally conclusive because of the slightly different age classes in each population.

Even though for a particular size the Eleven Point and Spring River females produce similar numbers of eggs (Table 13), the age-specific production is much greater by the Spring River females. This is because their growth is greater than that of the Eleven Point animals. Likewise, the age-specific production of eggs by Gasconade females is greater than that of Big Piney females.

Life tables. Survivorship was determined from the sample of females utilized in the fecundity tables and aged based on TL (Table 21). Therefore a stable age distribution was assumed for each population, i. e., survivorship and fecundity rates were assumed to have been constant, as well as rate of increase (assumed equal to zero in this case), for at least a few generations. Survivorship follows the pattern of Deevey's (1947) Type III survivorship curve with high mortality of the young but relatively high survival rates for adults in all populations (Fig. 10). An approximate Hartley's test indicated no significant difference in variances of the survivorship rates (column 6 figures) among the four populations ($H=2.18$, $r=4$, $n=5.25$, $P>0.05$). ANOVA indicated no significant difference in the means of the survivorship rates ($F=0.701$, $P>0.05$).

Female Cohort Biomass and Production

From 74,363 eggs, half the annual fecundity of the estimated 250 adult Spring River females in the two collection sites, about 186 kg of salamander biomass are produced over about 51 years in the Spring River (by one cohort), or approximately 15 g / yr wet

Table 21. Age-specific survivorship of females. Replacement rate is assumed to equal 1.0.

Spring River						
Age in years (interval)	Sampled frequency of females late summer to fall 1980	No. surviving as a fraction of zygotes	Proportion dying during age X to X+1	Mortality rate	Survivorship rate	
0	29, 170 ^a	1.0000000	0.9986630	0.9986630	0.0013370	
11.5 (7-16)	39	0.0013370	0.0005850	0.4375467	0.5624533	
19 (17-21)	22	0.0007520	0.0003063	0.4073138	0.5926862	
24 (22-26)	13	0.0004457	0.0002400	0.5384788	0.4615212	
29 (27-31)	6	0.0002057	0.0000514	0.2498788	0.7501215	
41.5 (32-51)	18	0.0001543	—	—	—	
Mean Generation Time = 23.3 years						

^aFrom fecundity table

Table 21 cont. Age-specific survivorship of females. Replacement rate is assumed to equal 1.0.

Eleven Point River						
Age in years (interval)	Sampled frequency of females late summer to fall 1980	No. surviving as a fraction of zygotes	Proportion dying during age X to X+1	Mortality rate	Survivorship rate	
0	8,329 ^a	1.000000	0.9954376	0.9954376	0.0034320	
9						
(7-11)	38	0.0045624	0.0025213	0.5526258	0.4473742	
14						
(12-16)	17	0.0020411	0.0012007	0.5882612	0.4117388	
19						
(17-21)	7	0.0008404	0.0007203	0.8570919	0.1429081	
24						
(22-26)	1	0.0001201	0.0000481	0.4004996	0.5995004	
39						
(27-51)	3	0.0000720	—	—	—	
						Mean Generation time = 14.2 years

^aFrom fecundity table

Table 21 cont. Age-specific survivorship of females. Replacement rate is assumed to equal 1.0.

		<u>Gasconade River</u>				
Age in years (interval)	Sampled frequency of females late summer to fall 1980	No. surviving as a fraction of zygotes	Proportion dying during age X to X+1	Mortality rate	Survivorship rate	
0	17,975 ^a	1.0000000	0.9984423	0.9984423	0.0015577	
9 (7-11)	28	0.0015577	0.0005007	0.3214354	0.6785646	
14 (12-16)	19	0.0010570	0.0002781	0.2631031	0.7368969	
19 (17-21)	14	0.0007789	0.0002226	0.2857876	0.7142124	
24 (22-26)	10	0.0005563	0.0001669	0.3000180	0.6999820	
29 (27-31)	7	0.0003894	0.0001391	0.3572162	0.6427838	
41.5 (32-51)	18	0.0002503	—	—	—	
			Mean Generation Time = 23.4 years			

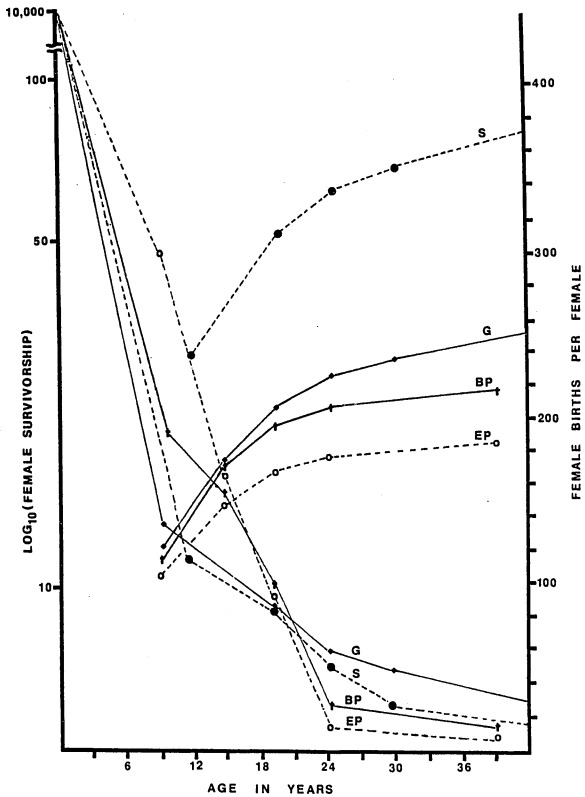
^aFrom fecundity table

Table 21 cont. Age-specific survivorship of females. Replacement rate is assumed to equal 1.0.

Big Piney River						
Age in years (interval)	Samples frequency of females late summer to fall 1980	No. surviving as a fraction of zygotes	Proportion dying during age X to X+1	Mortality rate	Survivorship rate	
0	15,024 ^a	1.0000000	0.9975373	0.9975373	0.0024627	
9 (7-11)	37	0.0024627	0.0006656	0.2702725	0.7297275	
14 (12-16)	27	0.0017971	0.0008653	0.4814980	0.5185020	
19 (17-21)	14	0.0009318	0.0007321	0.7856836	0.2143164	
24 (22-26)	3	0.0001997	0.0000266	0.1331998	0.8668002	
39 (27-51)	13	0.0001731	—	—	—	—
				Mean Generation Time = 18.6 years		

^aFrom fecundity table

Figure 10. Age-specific survivorship of a cohort of 10,000 females based on Table 21 and age-specific fecundity from Table 20: Spring River (S), Eleven Point (EP), Gasconade (G), Big Piney (BP).



weight from each clutch of female zygotes is consumed by predators and decomposers (Table 22). Similarly, for the Eleven Point, it is about 7 g / yr per clutch of females. For the Gasconade and Big Piney populations, 7 g and 9 g of female biomass per year per clutch, respectively, are consumed. This production is highly influenced by the great early mortality as evident from the first value in the Ix column in all populations. The relatively large biomass value for the Spring River is due to the greater growth rate (Fig. 4) and particularly the large fecundity of the Spring River females (Figs. 2 and 10).

If a species produces a new generation each year so that overlapping cohorts are present and the population has a stable age distribution, then annual production for any one year would be equal to one cohort production (Waters, 1977). Thus the sum of the weights of individuals dying between all age intervals in Table 22 represents the annual production of female hellbenders (P) calculated by the summation-removal method in the area of the collection sites (Table 23). Yearly production in all collection sites was also calculated based on an estimate of instantaneous growth (P').

As might be expected because of the influence of biomass in their calculation, the correlation between production estimates (P') and number of crayfish caught per hour in each site (Fig. 11) is significant ($r=0.821$, $P<0.05$), but no significant correlation exists with weight of crayfish caught per hour ($r=0.647$, $P>0.1$). Again, if production for site 1 in the North Fork (calculated by the instantaneous growth method) and half of Topping's (1981 and personal communication) average estimate of production by *Niangua* hellbenders

Table 22. Biomass furnished to the system's predators and decomposers from a cohort of females. The number of adult females alive is the combined estimate of female population size for the two collection sites based on Tables 9 and 10.

Spring River										
Age interval (years) x	No. alive Nx	Expected weight from length-weight relationship (grams) Wx	Weight increment between intervals (grams) Gx	Average individual growth per year (grams) Gx	No. dying between intervals Dx	Average weight at death (grams) Ix	Total weight of individuals dying between intervals (grams) Tx			
0	74,363	0.1 ^a	—	—	—	—	—			
7-16	100	668	668	58	74,263	1.0	74,263			
17-21	56	1,067	399	53	44	891.4	39,222			
22-26	33	1,248	181	36	23	1,173.7	26,995			
27-31	15	1,369	121	24	18	1,303.0	23,454			
32-51	46	1,516	147	12	15	1,481.7	22,226			
					74,363		186,159			

^a Approximate weight of an egg before laying

$Ix = Wx-1 + ((Nx/Nx-1) \cdot Gx)$; $Tx = Dx \cdot Ix$ from Spight (1967)

Table 22 cont. Biomass furnished to the system's predators and decomposers from a cohort of females. The number of adult females alive is the combined estimate of female population size for the two collection sites based on Tables 9 and 10.

Eleven Point River										
Age interval (years) x	No. alive Nx	Expected weight from length-relationship (grams) Wx	Weight increment between intervals (grams) Gx	Average individual growth per year (grams) Gx	No. dying between intervals Dx	Average weight at death (grams) Ix	Total weight of individuals dying between intervals (grams) Tx			
0	14,626	0.1 ^a	—	—	—	—	—			
7-11	59	258	258	29	14,567	1.1	16,024			
12-16	26	386	128	26	33	314.4	10,375			
17-21	11	459	73	15	15	416.9	6,254			
22-26	2	498	39	8	9	466.1	4,195			
27-51	4	527	29	2	2	509.6	1,019			
							14,626			

^a Approximate weight of an egg before laying

IX = Wx-1 + ((Nx/Nx-1) · Gx); Tx = Dx · Ix from Spight (1967)

Table 22 cont. Biomass furnished to the system's predators and decomposers from a cohort of females. The number of adult females alive is the estimate of female population size for the collection site based on Tables 9 and 10.

<u>Cascadia River</u>												
Age interval (years)	No. alive	Expected weight from length-weight relationship (grams)	\bar{W}_x	No. x	Weight increment between intervals (grams)	Gx	Average individual growth per year (grams)	No. dying between intervals	Dx	Average weight at death (grams)	Ix	Total weight of individuals dying between intervals (grams)
x	Nx											Tx
0	25,110	0.1 ^a										
7-11	39	450			450		50	25,071		0.8		20,057
12-16	26	611			161		32	13		557.3		7,245
17-21	20	727			116		23	6		700.2		4,201
22-26	14	802			75		15	6		779.5		4,677
27-31	10	846			44		9	4		833.4		3,334
32-51	25	902			56		4	10		881.0		8,810
												48,324

^a Approximate weight of an egg before laying

$I_x = W_x - 1 + ((N_x/N_{x-1}) \cdot G_x)$; $T_x = D_x \cdot I_x$ from Spight (1967)

Table 22 cont. Biomass furnished to the system's predators and decomposers from a cohort of females. The number of adult females alive is the combined estimate of female population size for the two collection sites based on Tables 9 and 10.

Big Piney River									
Age interval (years) x	No. alive Nx	Expected weight from length-weight relationship (grams) Wx	Weight increment between intervals (grams) Gx	Average individual growth per year (grams)	No. dying between intervals Dx	Average weight at death (grams) Ix	Total weight of individuals dying between intervals (grams) Tx		
0	21,702	0.1 ^a	—	—	—	—	—		
7-11	54	443	443	49	21,648	1.2	25,978		
12-16	39	609	166	33	15	562.9	8,444		
17-21	20	702	93	19	19	656.7	12,477		
22-26	4	749	47	9	16	711.4	11,382		
27-51	19	792	43	3	4	789.8	3,159		
					21,702		61,439		

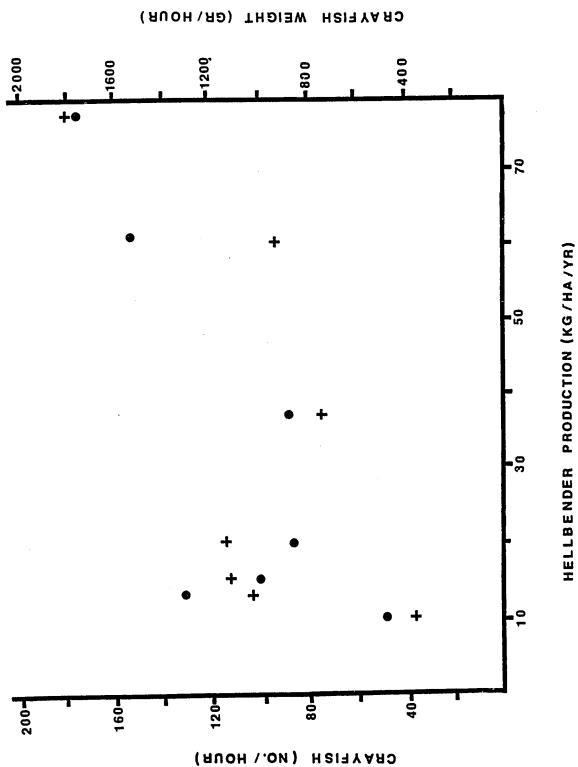
^a Approximate weight of an egg before laying

$I_x = W_x - 1 ((N_x/N_{x-1}) \cdot G_x)$; $T_x = D_x \cdot I_x$ from Spight (1967)

Table 23. Production of females (P) by the summation-removal method assuming a stable population and production of both sexes (P') by the instantaneous growth method, both are in kg / ha / yr. The denominators of the production : biomass ratios are the estimated biomass of females (B) in the population based on data in Tables 9 and 10 and estimated biomass of all hellbenders (B') in the site from Table 9.

Population	Site	P	P/B	P'	P'/B'
Spring	1	96.5	0.49	77.3	0.20
	2		2.61	14.0	0.19
Eleven Point	1	92.4	1.59	15.9	0.18
	2		0.71	36.7	0.18
Gasconade	1	22.6	0.59	11.2	0.19
Big Piney	1	73.1	1.14	20.3	0.18
	2		0.38	60.4	0.18

Figure 11. The relationship between hellbender production (P') in Table 23 and average crayfish catch per hour in Table 19 for each of the seven collection sites. Crayfish number per hour (●). Crayfish weight per hour (◆).



are paired with crayfish catch in Table 19 for the two rivers, both correlations are significant: weight of crayfish caught versus hellbender production ($r=0.770$, $P<0.02$) and number of crayfish caught versus hellbender production ($r=0.733$, $P<0.05$).

DISCUSSION

Population Size

Equal catchability. According to Caughley (1977), mark-recapture experiments are divided into two classes: (1) those experiments involved with movement, growth rate, age-specific fecundity, or age-specific mortality and (2) those involved with estimating population size, rate of increase, rate of loss and gain, or rate of harvesting. The two classes differ in that in the former the behavior and number of animals in the unmarked segment of the population is irrelevant to estimating parameters, whereas in the second class of investigations, equal catchability of all individuals, marked and unmarked, is crucial to the accuracy of the estimates (Caughley, 1977). The design of this study was made with the last three components of the first class of experiments in mind. As many salamanders as possible were captured, and this may be contrary to random sampling. A mark-recapture model robust to unequal catchability has been developed for open populations (Pollock, 1982), but it requires considerably more sampling periods than are available from this study. However, since a mark-recapture study is time-consuming and expensive, it seems reasonable to gain all possible benefits from it as long as results are viewed with proper caution and the assumptions are tested.

Although no population exhibited highly significant departures from random sampling (Table 3), the Gasconade results were borderline in interpretation, insufficient data were available from the Eleven Point for Leslie's test, the Spring River data were

less numerous than desirable, and the Big Piney hellbenders differed significantly in catchability with regard to sexes and age classes (Tables 4 and 5). Thus all estimates resulting from the Jolly-Seber analyses must be viewed with caution.

Eberhardt (1969) listed three causes for unequal catchability: (1) a property inherent in the individual, such as behavior near a capturing device, (2) the result of learning, becoming capture-prone or capture-shy, and (3) a property depending on the relative opportunity of capture. As stated by Tilley (1980), it seems unlikely that salamanders will exhibit unequal catchability because of learning, but Beukema (1970) showed that the catchability of pike decreased considerably after being hooked previously, at least when using artificial bait. Some hellbenders, at least at certain times, do swim away quickly when their cover is removed making capture difficult. Whether this is an inherent property of some individuals or just expressed by all or most hellbenders only at certain times is unknown. The relative opportunity of capture does present a problem. Although hellbenders move about within a riffle (Coatney, 1982; Hillis and Bellis, 1971), there is some evidence that individuals may spend much of their time under the same cover during daylight hours (Coatney, 1982). Thus a hellbender that spends much time under an easily accessible, easily turned rock would more likely be captured by the hand-grabbing method than a hellbender that spends much time in a deep pool under slab rock or a boulder too large to be moved. In the Big Piney, site 1, several old large females were captured numerous times, one individual in nine of the ten samples, and resulted

in the large chi-square values in Tables 4 and 5. It could be that these large females that probably could defend their cover from other hellbenders spent much diurnal time under large flat, turnable rocks which were accessible and never bypassed, a rock that seemed very likely to shelter a hellbender. Therefore there exist some difficulties in the design of the investigation for population size estimation, and a few of the assumptions made by the Jolly-Seber method are questionable. However, according to Begon (1979), no actual mark-recapture study ever satisfies all assumptions in the very finest detail. Rather than rejecting all mark-recapture models because of this and deny any information, it is better to take a utilitarian view that the assumptions are valid so long as they do not lead to results which are so unreliable as to be useless. Begon (1979) stated that if the equal catchability assumption is violated the population size will be underestimated. Survivorship will also be underestimated (Carothers, 1973). But even with a statistically significant indication of unequal catchability, the bias in survivorship may be lower than that due to sampling variation and thus of little practical significance (Carothers, 1979). Further, Carothers (1979) stated that this points out the difficulty in relying only on significance tests to determine the appropriateness of mark-recapture models to a particular data set. Thus the estimates in Table 6 may at least be a minimum estimate of the numbers of hellbenders, and the effect on survivorship by possible nonrandom sampling may be negligible, despite Caughley's (1977) assertion that unequal catchability is the greatest source of error in mark-recapture studies.

There is significant evidence that Big Piney subgroups were not sampled randomly (Tables 4 and 5). Thus, because there were multiple recaptures of individuals in site 1, frequency of capture models were compared to the observed frequency of recaptures to estimate the number of hellbenders in the site. Although Caughley (1977) refers to these methods as crude and insensitive, he stated that at least one of the three is liable to be a good fit. However, Wilbur and Landwehr (1974) believed that the frequency of capture models have very limited value based on their work with painted turtles.

The estimate of 806 hellbenders by the geometric distribution frequency of capture model seems too large, nearly 12 hellbenders per 100 m², especially in comparison to the catch per unit effort. This would indicate that only about 6 to 10% of the population was captured during a sample, which does not seem reasonable. The frequency models assume no losses which is somewhat unrealistic just considering mortality.

Losses and gains to the population. The additions to the population (Table 6) probably do not reflect natality, as so few juveniles were captured. More likely the variation in the population estimates is due to sampling error as indicated by the standard errors, than to mortality or movement, although these are probably involved. Regression of the natural logarithm of the population size on time indicates little increase or decrease in all sites but one during the study. That one, site 1 in the Eleven Point, probably did not undergo a decrease in numbers of hellbenders, as no reason is known why such a decrease should occur. The slope

of the regression was negative probably because of the few number of estimates plus sampling error.

The average annual survivorship rate for all collection sites (0.27) determined from the pooled monthly survival rates (MSRs) is very low compared to the survivorship indicated in the life tables for adult females. This may be due partly to the influence of juvenile survivorship on the MSRs. The difference may be mostly due to sampling error and dispersal movements because the survivorship rates (P_i) are influenced by emigration as well as mortality. The sites are not closed by natural boundaries, and movements of several hundred meters upstream or downstream by a few hellbenders have been reported (Wiggs, 1977; Nickerson and Mays, 1973a). From Table 1 it is obvious that many hellbenders captured once were never seen again, as is true of all hellbender mark-recapture studies (Peterson et al., 1983; Taber et al., 1975; Nickerson and Mays, 1973a; Hillis and Bellis, 1971). Further as reported by Wiggs (1977), in the same site worked previously many times, unbranded hellbenders are captured each time. This suggests that there are many more hellbenders on the sites at one time than the Jolly-Seber estimates would indicate, which may be true if nonrandom sampling is a large problem, or it may be that emigration and immigration are important factors in local populations. Possibly both are involved. Thus the large estimate by the frequency of capture method for site 1 in the Big Piney may reflect a large hidden portion of the population and thus a poor sampling of each collection site, long-distance movements, or just the inexactness of the method.

Densities. Despite possible sources of error, such as differing current rates, depths, temperatures, visibilities, and, possibly, intensiveness of collecting in different streams, the relative abundance estimates, catch per unit effort, correlate well with absolute density estimates of hellbenders. This provides credibility for the Jolly-Seber estimates except in the Gasconade. In comparison to the other sites, the Gasconade site has very large stretches of slab rock with generally wide, muddy shorelines where hellbenders are not found during the day, but these areas were considered in the absolute density estimates. Where there are large rocks, however, hellbenders are numerous. This is responsible for the large catch per unit effort, as shorelines were not searched and the smooth bedrock stretches were passed over quickly.

Nickerson and Mays (1973b) reported a density of 1 hellbender / $6-7 \text{ m}^2$ to 1 / $13-16 \text{ m}^2$ for one riffle in the North Fork River. However, only the area where hellbenders were found during daylight hours (the area where large rocks were present) was considered in the density estimates. In contrast, Peterson et al. (1983) estimated a density of 5.0 and 4.9 hellbenders / 100 m^2 for two collection sites in the North Fork. Shoreline to shoreline area was considered in the estimates. Although there is merit in estimating only the area where hellbenders are located diurnally, slab rock and shoreline areas may be feeding areas at night (Beck, 1965). Also shoreline to shoreline area is less subjectively measured.

Hillis and Bellis (1971), based on a calculated mean activity radius of 10.5 m and a median activity radius of 6.0 m, estimated that the average circular home range of hellbenders in French Creek, Pennsylvania, was 346 m^2 and the median home range was 113 m^2 . Coatney (1982) estimated a mean elliptical home range of 90 m^2 for North Fork hellbenders. Because the estimates of density range from 1.0 to 6.3 hellbenders per 100 m^2 in different sites (Table 9), home ranges likely overlap as reported by (Coatney, 1982). However, one hellbender followed by Coatney had a home range of just 18 m^2 based on two weeks of telemetry data. It is uncommon to find more than one hellbender under a single rock (Nickerson and Mays, 1973a; Hillis and Bellis, 1971). However, Bishop (1941) reported finding three male hellbenders, a mass of hellbender eggs, and one Necturus under a single rock that measured just less than 1 m in width and length. While he was observing, a fourth male tried to enter the nest. Certainly if many large rocks are piled next to each other, several hellbenders sometimes can be uncovered in a few square meters during daylight hours. Coatney (1982) suggested that hellbenders whose home ranges overlap will not be in the area of overlap at night at the same time, at least in midsummer before the breeding season.

Population Composition

Adults. External sexing of adults during late summer to fall is valid: 84 hellbenders were sexed externally as females and then dissected for fecundity and stomach contents; all were female. Adult females, except in the Spring River, seem to be more numerous than adult males (Table 10). But the data for

the Big Piney is ambiguous because females are more catchable than males.

Reports of sex ratios for hellbenders vary from population to population and even from one time to another. Smith (1912) reported a male to female ratio of 2:1 to 3:1 based on several years of data. However, he found a higher proportion of females than males in "nonbreeding" areas during the summer and an equal number of the sexes during the breeding season. Hillis and Bellis (1917) reported a ratio of 1.58 males to 1 female. These two studies were made in Pennsylvania. In Missouri, Nickerson and Mays (1973a) reported male to female ratios based on midsummer collections for three rivers: North Fork, 1:1; Eleven Point, 1:2.45; Niangua, 1.3:1. Wiggs (1976) found a 1:1 ratio in the Niangua, but a report of 1 male to 1.6 females was made also for the Niangua and a ratio of 1:4 for hellbenders 15⁺ years of age (Wiggs, 1977).

It seems reasonable that males, particularly older males are less numerous in some populations because adult male age-specific survivorship may be less than that of females (Peterson et al., 1983; Taber et al., 1975). Although differences in length-specific growth have not been detected between sexes in the North Fork (Peterson et al., 1983), Niangua (Taber et al., 1975), Spring, and Eleven Point Rivers, the growth of females is greater than that of males in both the Gasconade and Big Piney Rivers. Further, length-specific weight is greater for females in all the populations above, at least during midsummer to fall. It may be that the

females' larger size may deter predation to a greater extent, resulting in the greater number of females found in this study and possibly greater survivorship. If such reasoning is correct, why there exists an equal sex ratio in the Spring River is unknown. The predators of adults are probably the same: large catfish (Minton, 1972; Barbour, 1971), common water snakes, Nerodia sipedon (Rhoads, 1895), turtles (Surface, 1913, as cited by Nickerson and Mays, 1973a), other hellbenders (Wiggs, 1976; Nickerson and Mays, 1973a), and perhaps mink, Mustela vison.

Juveniles. Other populations of hellbenders have been reported to be dominated by adults (Peterson et al., 1983; Taber et al., 1975; Hillis and Bellis, 1971), as in this study. Only a small number of larvae have been captured in other studies. Nickerson and Mays (1973a) captured about 2000 hellbenders in the North Fork River; eight of them were larvae. Taber et al. (1975) marked over 1100 Niangua hellbenders but only three larvae were captured. No larvae were captured by Peterson et al. (1983) who marked over 700 hellbenders in the North Fork. Undoubtedly the eggs and larvae and even the young subadults are subject to considerable predation. This agrees with the large young mortality in the life tables. Further, cannibalism of the eggs and young has been suggested to be an important factor in maintaining population stability (Mays and Nickerson, 1971).

Richmond (1965) stated that in those species that have great longevity and spend most of their lives as reproductive adults any stable or even slowly expanding population will consist almost entirely of mature animals. Further, he noted that such populations

are characterized by a very slow population turnover, an annual reproductive potential vastly greater than the annual replacement, and a high mortality of the young. Richmond (1965) argued that this is true of some turtles and suggested that this may be true of the hellbender. His speculation has been affirmed by this study and previous ones.

Pecundity

Paired comparison of ovary oocyte number. No reason is known why the right ovary of Eleven Point and Gasconade females should contain more developing ova than the left ovary. Topping and Ingersol (1981) found that one ovary of both Niangua and North Fork females contained more oocytes than the other. They did not indicate whether the right or left ovary systematically contained a greater number of developing eggs.

Size at maturity. Female hellbenders appear to mature at different lengths in different populations. Eleven Point and Big Piney females mature at about 300 mm and 370 mm TL, respectively. Females seem to mature at a size between 330 and 380 mm TL in the North Fork (Peterson et al., 1983). Taber et al. (1975) believed Niangua females mature at about 380 mm. Ingersol (1982), who dissected both juvenile and adult females from the Niangua, found none less than 390 mm TL that was mature. The smallest mature female measured by Smith (1912) was 350 mm TL. Dundee and Dundee (1965) stated that C. a. bishopi females mature at about 238 mm snout-vent length or 330 mm TL based on females from three rivers and that C. a. alleganiensis females in Missouri attain maturity when about 247 mm snout-vent length. Males mature at a smaller

size than females (Peterson et al., 1983; Taber et al., 1975; Dundee and Dundee, 1965; Grenell, 1939; Smith, 1912).

TL-fecundity relationships. Despite a similar size-specific production of eggs (Table 13), the actual fecundity of Spring River females was much larger than that of Eleven Point females (Fig. 10). This is because growth is much greater in the former (Fig. 4), and fecundity increases with TL (Fig. 2). Similarly, but to a lesser degree, Gasconade females produce more eggs than Big Piney females. Comparisons of the regressions, including those of Topping and Ingersol (1981), indicate that length-specific fecundity is greater in C. a. bishopi than Missouri C. a. alleganiensis (Table 13 and Fig. 2). Assuming, of course, that fecundity is influenced by the genotype directly, this difference in fecundity points to genetic differences between the subspecies, as all populations vary environmentally. Topping (personal communication) had postulated that the greater North Fork female size-specific fecundity over that of Niangua females might be an adaptation that has been selected because of the smaller size of North Fork hellbenders. Otherwise, the latter would have a much reduced reproductive capacity in comparison to the larger Niangua females. However, the greater growth of the Spring River C. a. bishopi would seem a contradiction to the idea of selection for increased fecundity in smaller C. a. bishopi over that of larger C. a. alleganiensis. Yet if the environment does play an important role in the growth measured in this study, the large growth of Spring River hellbenders may be related to an enrichment of that stream in the past few decades because of development by humans.

Warren et al. (1964) found that the continuous enrichment of stream flow by a few mg / l of sucrose could increase the benthos and lead to a sevenfold or more increase in trout production. Thus the nutrient enrichment of the Spring River, as mentioned in the description of the study areas, might be an important factor in the growth and fecundity of Spring River hellbenders.

Spawning. According to Dundee and Dundee (1965), there is no complete separation of the spawning seasons of the two subspecies, but for the most part C. a. alleganiensis breed two months earlier. Eastern populations of C. a. alleganiensis do spawn earlier: from late August into September (Huheey and Stupka, 1967; Fitch, 1947; Bishop, 1941; King, 1939; Green, 1933; Smith, 1907), except in Alabama where breeding occurs in late September through early October (Mount, 1975). Spawning of C. a. alleganiensis in the Niangua River occurs from September into early October according to Ingersol (1982). However Dundee and Dundee (1965) reported collecting two ripe Niangua females on 14 November 1954. On the same date they collected females in the Gasconade River that had ova 2 mm or less in diameter. It is possible that these females were spent, and the observed oocytes were to be laid in subsequent seasons. Nickerson and Mays (1973a) observed egg laying by C. a. bishopi in the North Fork on 13 September 1970 and 6 October 1973. Males were observed expelling milt on 3 November 1971, and one decomposing female was ripe. Dundee and Dundee (1965) reported that peak size of ova of Spring River C. a. bishopi is attained in late October, and Ratcliff (1965) reported that Spring River hellbenders breed in October. Baker (1963) stated that mature

sperm were present in the testes of Spring River males in early September; however, on 1 December the testes were considerably enlarged and full of sperm. On 15 December no sperm were present, and the gonads were reduced in size. It is thus unclear whether the ripe condition of Spring River females collected on 12 December in this study is unusual.

Topping and Ingersol (1981) reported that Niangua females may lay only 76% of their large ovarian eggs, and some females, approximately 27.5% (Ingersol, 1982), do not lay any eggs in a particular year but resorb all of them. They suggested that the resorption of eggs might be a trait of other hellbender populations because of the genetic uniformity described by Merkle et al. (1977). Whether this occurs is unknown. The two ripe (in contrast to 13 spent) Big Piney females killed 19 September may not have been going to spawn, but this date is early in the breeding season for most hellbenders in the Ozarks. Smith (1912) also found hellbenders with eggs that appeared to be degenerating. Swanson (1948) killed five females in December, but none had more than five ova left from the past spawning season.

Stomach Contents

Crayfish remains were the most frequently found food items in stomachs in all previous studies throughout the range of Cryptobranchus; fish remains were the second most frequently found items (Wiggs, 1976; Nickerson and Mays, 1983a; Ferguson, 1961; Swanson, 1948; Bishop, 1941; Green, 1935; Netting, 1929; Smith, 1907; Reese, 1903). Wiggs, (1976) stated that because the digestion of crayfish is slower (about one week, although chelae and chitinous cephalo-

thoraxes may remain in the system for weeks) than of fish (two to five days), the frequency of fish eaten in comparison to crayfish may be two or three times greater than indicated by stomach contents. Still, crayfish were found by Wiggs (1976) as the major stomach item throughout the year with fish a distant second. She speculated this was due to a large population of crayfish in the Niangua River, the occupation of the same microhabitat as hellbenders by the crayfish, and because crayfish were more easily captured by hellbenders than were fish based on laboratory observations. Other food items for adults are varied but apparently minor (cf. Nickerson and Mays, 1973a). Possibly at certain times of the year, there are exceptions, such as lampreys during their spawning (Nickerson et al., 1983) or hellbender eggs as found in this study. Smith (1912) reported that both sexes were voracious eaters of the eggs and that the majority of adults collected during the spawning season had stomachs filled with eggs. Conspecific oophagy has been reported in a number of caudates, and it has been suggested that the significance of such behavior should be studied in urodeles (Kaplan and Sherman, 1980).

Growth and Size Comparisons

Growth models. Growth of individuals is variable so that regressions explain only a relatively small amount of the variance of mean monthly growth as evident from the coefficients of determination (Fig. 4). But similar regressions were developed with similar variability about the regression lines by Peterson et al. (1983) and Taber et al. (1975) for hellbenders in the North Fork and Niangua Rivers, respectively. Two years after marking ended in

the North Fork and six years after branding ended in the Niangua, those populations were sampled, and long-term growth of recaptured individuals was compared to that predicted by the respective regressions. No significant difference in observed TLs and predicted TLs was found for North Fork recaptures. Although final observed and predicted TLs differed significantly for Niangua recaptures, the growth model did predict growth without significant bias. This was true even though individuals were marked as much as 8 to 9 years previously (Peterson et al., 1985). Thus, except possibly the Spring River regression where the coefficient of determination is quite small, the regressions should be useful for predicting growth of individuals. Taber et al. (1975) and Peterson et al. (1983) discussed possible problems with the growth models.

Differences in the growth of sexes was not detected by Peterson et al. (1983) or Taber et al. (1975) nor in the Spring and Eleven Point Rivers in this study. However, the Gasconade and Big Piney females exhibit greater length-specific growth than the males. Based on differences in the length-weight relationships in this study and the studies by Peterson et al. (1983) and Taber et al. (1975), it seems likely that female growth exceeds that of males in all populations in the Ozarks. But the greater elevation of the female length-weight regressions may at least in part reflect the growth of eggs. Because only adults can be sexed and only for a few months of the year, it is difficult to detect possible differences in the growth of sexes. Collins (1974) stated that females more often achieve a greater TL than males, but Bishop (1941) reported that males are often broader and heavier than

females of the same length.

Maximum size. Only the average maximum length is predicted by each regression. The asymptotic length will underestimate the TL of those individuals whose growth is greater than the general trend described by the regression. This is true to a similar degree for hellbenders in the North Fork and Niangua and the growth models of Peterson et al. (1983) and Taber et al. (1975). Growth of hellbenders is likely indeterminate, and the growth of very large individuals is difficult to measure accurately because they grow so slowly. Their growth like many ectotherms may be better predicted by a curve that approaches the zero-line asymptotically than by a single straight line (Peterson et al., 1983).

Population growth comparisons. Due to an inability to measure juvenile growth in the Spring, Gasconade and Big Piney Rivers, the comparisons in Fig. 4 should be viewed with caution. The lack of juvenile growth in the Gasconade is probably responsible for the difference in slopes between the Gasconade and North Fork hellbenders (Table 16). Because of the similar genetic frequencies found by Merkle et al. (1977), it is reasonable that the amount of growth at a specific length differs (elevations different) between most populations (Table 16) because of differing environmental conditions in different rivers. Selection can not be dismissed, however, nor can founder events and drift, especially as gene flow is probably impossible between populations, other than by human intervention, except between the Gasconade and Big Piney hellbenders.

If only adult growth is considered, based on extensive observations of individuals from all six rivers, the comparison of growth in Fig. 4 seems reasonable. The Niangua and Spring River adults attain the largest size followed by the Gasconade hellbenders. The North Fork and Big Piney adults seem similar in size, and the Eleven Point hellbenders are much smaller than the others. This is indicated in the average weight of hellbenders in Table 8. Peterson et al. (1983) determined an average weight of 314 g for North Fork hellbenders based on over 700 individuals. Nickerson and Mays (1973a) calculated an average weight of 671 g for Spring River hellbenders (n=33), 193 g for Eleven Point salamanders (n=31), 365 g for North Fork hellbenders (n=435), and 777 g for Niangua hellbenders (n=30). All but the North Fork animals were measured by the latter authors in the laboratory after regurgitation may have occurred. Juveniles compose a greater proportion of the population in the North Fork (unpublished data) and in the Eleven Point River and thus reduces the estimate of average weight in comparison to the other populations.

Environmental Factors Influencing Growth

Temperature. When food was not limiting, higher growth rates of Bufo boreas have been correlated with an optimum temperature because of the influence of temperature on ingestion rates and conversion efficiencies (Lilywhite et al., 1973). Highton (1962) indicated that the length of the growing season may be involved in the slower growth of slimy salamanders, Plethodon glutinosus, in Maryland as compared to a population in Florida. Temperatures are different among hellbender streams in the Ozarks both summer

and winter, exhibit different ranges of temperatures, and the optimum period of growth may differ slightly between north-flowing rivers and the more southern south-flowing streams. Lowry (1953) found that, in general, smallmouth bass growth was greater in north-flowing Ozark rivers than in south-flowing rivers. Yet no correspondence is noticeable between growth patterns of hellbenders (Fig. 4) and temperature (Figs. 6 and 7). However, any interaction between growth and temperature may be too subtle to detect from the data gathered in this study.

Food availability. Differential availability and quality of food has been suggested as a cause of differential rates of growth in different populations of turtles (Parmenter, 1980; Cagle, 1946) and lizards (Dunham, 1978; Schoener and Schoener, 1978; Andrews, 1976). A lower density population of spadefoot toads, Scaphiopus holbrooki, exhibited greater growth than a more crowded population (Pearson, 1955). Although there is no indication of a linear trend between weight of crayfish caught per hour and hellbender biomass, a weak correlation between hellbender biomass and the number of crayfish caught per hour exists among collection sites. Also a significant correlation was found between hellbender production estimates and the number of crayfish caught (Fig. 11). Further support of a relationship between hellbender production and crayfish production is given by the significant correlations produced when half Topping's (1981) average estimate of Niangua hellbender biomass (and production) is paired with the Niangua crayfish catch and included in the analyses. Even when divided in half, the Niangua average standing crop estimate is larger

than for any other site. Yet the catch per effort of hellbenders in the area where crayfish were caught in the Niangua is higher than for any single catch in any other river. This suggests a high biomass, particularly as hellbender growth may be greatest in the Niangua River (Fig. 4).

No cause and effect is assumed in correlation analysis however. The relationship may be due to a third factor, such as the density of cover items, because both animals hide beneath rocks during the day. Further, with the difficulty in accurately estimating population size, the correlation may be spurious. Also the density of crayfish may vary seasonally. No attempt was made to measure the availability of other food items. At most the analyses indicate that crayfish abundance could be an important environmental factor influencing the growth of hellbenders in different sites and suggest that it would have been beneficial to have obtained sufficient data for growth comparisons within rivers. Further as suggested by Lowry (1953) for smallmouth bass, Missouri fish growth often varies more between portions of the same stream (headwaters compared to lower portions) than between similar habitat types of different streams (Purkett, 1958).

Age

Length-age relationships. Although metamorphosis has been reported to occur at 125 mm TL and 18 months of age, length may vary at transformation just as at sexual maturity between populations. This could lead to an erroneous length-age curve for Eleven Point hellbenders. Bishop (1943) reported that hellbenders transform at 100 to 130 mm TL and 18 months of age. However, even if 100

mm and 18 months is used as the reference point in the integrated equation relating age and TL, the constant of integration changes only from 119 to 126. This produces a length-age curve only about seven months to the right of that in Fig. 8 for Eleven Point hellbenders.

Similarly, whether the actual size at sexual maturity is 360 or 380 mm TL changes the length-age curve for the other three populations by a maximum of ± 9 months. Yet the method of aging is crude, particularly for older animals (cf. Westrhiem and Ricker, 1978) because of the variability of individual growth. Therefore no age class used in the fecundity and life tables is less than a five-year interval, and a very large interval is used for the oldest hellbenders.

The evidence is that maturity is more a function of age than size in hellbenders. Eleven Point females mature when about 7 to 8 years old at about 300 mm TL. North Fork and Niangua females also mature when about 7 to 8 years old, but at a length of about 330 to 380 mm for the former and 380 mm for the latter (Peterson et al., 1983; Taber et al., 1975). According to Wilbur and Collins (1973), amphibian metamorphosis, another life-history transition, is neither size nor age dependent alone, but is predicted best by the differentiation rate. Smith-Gill and Berven (1979) stated that 95% of the variance in the length of amphibian larval periods is accounted for by differentiation rates; only 50% of the variance is explained by growth rates. Nevertheless, Berven and Gill (1983) showed that Rana sylvatica tadpoles from Manitoba metamorphosed at variable sizes but at a constant age. In contrast, a Maryland

population responded with a constant size but variable age at metamorphosis. Policansky (1983) suggested that when platyfish, Xiphophorus maculatus, grow fast there is a minimum age that must be attained before sexual maturity occurs; however, when growth is slow, sexual maturity does not occur until a minimum weight is reached. Policansky (1983) postulated that if reproduction when small costs a lot in terms of survival and later reproduction and if reproductive success increases quickly with increased size, then size should be the trigger, at least in conditions that favor rapid growth. Alternatively, if reproductive success does not increase much with increased size and if mortality of reproductives of all ages is high, then the transition should be determined by age. However, neither of these alternatives seems to fit the life-history traits of Cryptobranchus well. Policansky (1983) did suggest that if the environment is stable in time and space, then there is no difference between age- and size-triggered changes. This is because in such an environment there will be little variation in growth rate for a given genotype, and age and size will be closely correlated. According to Williams et al. (1981), the hellbender is confined to a narrow niche by several adaptations of structure, behavior, and physiology brought about by its evolution in a relatively stable environment. However, Ozark streams differ environmentally at least somewhat with regard to temperature and possibly food availability. Further, hellbender growth is different despite little genetic differentiation among populations. Of course, no two habitats are exactly alike. Even different sites in the same river differ at least slightly in environmental factors and

will differ in time.

If a life history transition is determined by the attainment of a certain age, conditions unfavorable to growth will result in a population of smaller individuals (Policansky, 1983), and individuals will have much lower fecundity if fecundity scales with size (Stearns, 1983a). Stearns (1983a) suggested that organisms should adopt an intermediate course between age-specific or size-specific transitions. He predicted qualitatively how age and length at maturity should change (plastic trajectories) when organisms from different populations subject to differing adult mortality are raised under conditions of food or temperature stress. If organisms have encountered high prematuration rates of mortality, then they should respond to stress by maturing at much smaller sizes with a small delay in maturity. Alternatively, if they have encountered relatively low prematuration mortality rates, then they should respond to stress with a relatively small reduction in size but a larger increase in age at maturity. Stearns' (1983a) trajectory for populations with a high prematuration mortality (m_3 , Fig. 3) is only slightly different than that of the fixed-age trajectory of maturation under "good," "normal," and "poor" environmental conditions. The growth models for the North Fork, Niangua, and Eleven Point populations may be too crude to detect such small differences in age at maturity and thus the populations could show such adaptations. Possibly the Niangua hellbenders with good environmental growth conditions are larger at maturity but slightly younger than the Eleven Point hellbenders experiencing poorer conditions for growth. The North Fork hell-

benders (and presumably the other three populations) are in between with regard to age and length at maturity and environmental conditions. However, the concept is clouded somewhat because Stearns (1983a) referred to prematuration mortality rates at one point, but to adult mortality rates at another, in reference to his plastic trajectories. For hellbenders the two are very different. Considering the homozygosity found in hellbenders by Merkle et al. (1977), such genetic changes may not be possible between populations. Thus age may indeed be the important factor in triggering maturity in all populations studied, while differing growth conditions, such as food availability perhaps, determines the length at transitions. Plasticity has been demonstrated in most life-history traits (Caswell, 1983). Smith-Gill (1983) suggested that plasticity, rather than being a genetic adaptation in many cases in higher organisms, may be a passive response to a variable environment and thus not necessarily adaptive. In fact, such variability may be nonadaptive.

Maximum age. Because the growth of old individuals is so slow, the growth models cannot predict the maximum age of hellbenders. Fifty or more years does not seem unreasonable. Taber et al. (1975) reported that hellbenders live 30⁺ years. One hellbender was maintained in captivity for 29 years (Oliver, 1955), and Flower (1936) stated that six Andrias japonicus, the largest extant salamander, have attained ages between 55 and 60 years in European zoos. It has been speculated that Andrias may live more than a century (Federal Writers' Project, 1939). Even much smaller urodeles have lived long at least in captivity. For example,

Triturus cristatus (Biegler, 1966) and Ambystoma maculatum (Oliver, 1955) have lived 25 years and Salamandra salamandra 43 years (Schmidtler and Schmidtler, 1969). Hairston (1983) suggested that Plethodon jordani has a life span of as much as 30 years under natural conditions. Further, a hellbender marked by Taber et al. (1975) and suspected to be 30⁺ years old in 1972, was recaptured eight years later in apparent good health (Peterson et al., 1985). Robert Wilkinson (personal communication) believes that some hellbenders may attain an age of 75 years.

Age-specific Fecundity and Survivorship

Fecundity tables. Similar to the method used by Organ (1961) to determine the number of individuals in the zero-age class for Desmognathus, eggs were counted and a 1:1 sex ratio at fertilization was assumed. Also, because fertilization is external in hellbenders, it was necessary to assume that all eggs were fertilized to construct the fecundity tables (Table 20). Smith (1912) found few hellbender eggs laid that were not fertilized, and Caughley (1977) stated that vertebrates have a sex ratio so close to 1:1 at birth that the slight preponderance of males can be ignored. However, as mentioned previously, Topping and Ingersol (1981) speculated that as much as 50% of the eggs produced by Niangua females may be resorbed.

Because the greatest number of eggs are produced by the youngest adults (7 to 16 years of age), particularly in the Eleven Point and Big Piney Rivers, it is this segment that would be most advantageously manipulated to control populations. This is especially true because little can be done to improve larval and

juvenile survivorship without raising them away from the river. As long as the young adults survive, the populations should be stable. The removal of old adults or small numbers of the young adults should not affect the population adversely. This is especially true if, as suggested by Taber et al. (1975) and Nicker-son and Mays (1973a), cannibalism and egg-eating are a factor in population control. Because of the number of eggs eaten and because larvae and small juveniles are probably eaten when opportunity permits, it may be that this is the major population control. Although many animals in the rivers would eat the eggs, larvae, and small juveniles, adult hellbenders probably have greater opportunity because of occupying similar cover. Smith (1907) even reported that a captured 12-cm TL larva regurgitated a 6-cm larva. As suggested by Williams et al. (1981), protection of the habitat and prevention of commercial exploitation should allow for viable populations in the Ozarks.

Life tables. The age distributions of females were calculated by sampling within ± 2 months of the birth pulse assuming a stable age distribution and a zero rate of increase. The frequency of the zero-age class is based on fecundity rates. Caughley (1977) lists three primary pitfalls for this type of life table based on a standing age distribution: (1) rate of increase must be known with reasonable accuracy, and this rate must have remained relatively constant for two or three generations; (2) although no absolute judgement on minimum sample size is possible because it depends on the accuracy required, a table based on less than 150 determinations of age is unlikely to be accurate enough for

any purpose when age distribution methods are employed; and (3) some indices of age have wide variances, and although they may be useful for dividing a sample into broad categories, they cannot be used in life table analyses. Information supporting a zero rate of increase has been discussed previously. The number of adults aged ranged from 66 to 99. However, Caughley (1977) presented a life table (Table 8.6) where 120 thar, Hemitragus jemlahicus, were aged. Only the zero-age class estimated from fecundity rates resulted in a sample of more than 150 age determinations. If this is acceptable then certainly the number of age determinations are sufficient in Table 21. It may seem unreasonable that hellbenders can be assigned to the age classes in the life tables with any certainty because of the inexactness of the aging method, particularly in the Spring River sample. But even if hellbenders are grouped into three broad categories, (young adults 7 to 16 years old, adults 17 to 27⁺ years old, and old adults 27⁺ years old), which seems reasonable, the pattern of survivorship for each population would be the same and would still forecast very high early mortality but increasing survivorship after sexual maturity.

All four populations exhibit the Type III survivorship curve, which represents the most extreme type of selection according to Pearl and Minor (1935). This fits the pattern of greater early mortality in a more aquatic urodele. Even the most aquatic species of Desmognathus studied by Organ (1961) exhibited a constant rate of survivorship with age or Type II survivorship curve.

The two populations where growth is less, the Big Piney and the Eleven Point, exhibit slightly less juvenile mortality but slightly greater adult mortality than the other two populations in which growth is greater. Because there may be a bias toward older hellbenders in the Big Piney cohort due to heterogeneous catchability (Table 5), a survivorship curve even more like that of the Eleven Point females may be more realistic. Likewise, age-specific fecundity is less for the Eleven Point and Big Piney females than for the Spring and Gasconade females (Fig. 10). The greater fecundity might be an adaptation that has been selected because of the greater juvenile mortality of Spring and Gasconade River hellbenders. Yet the length-specific fecundity relationships (Fig. 2) strongly suggest that the pattern of fecundity in Fig. 10 is linked with growth. Even the small differences in survivorship that may exist between populations could be tied to growth. The larger Spring and Gasconade hellbenders would probably be less subject to predation than the smaller Big Piney and particularly the Eleven Point hellbenders as adults. Perhaps greater cannibalism and egg-eating because of larger size is a factor in the greater early mortality in the former two populations.

Natural selection has produced a species well adapted to large cool rocky streams having survived in such environments since the Pleistocene (Naylor, 1981). But little genetic variability remains (Merkle et al., 1977). The pattern of survivorship and fecundity differs significantly among hellbender populations. Although Stearns (1980) suggested that contrasts in life-history tactics are more evident at higher taxonomic levels and confirmed

this for squamates (Stearns, 1984), Brown (1983) argued that intraspecific studies can provide greater understanding of the relative importance of the "proximal" causes of life-history variation. These include responses to variation in ecological properties, developmental plasticity, and genetic divergence resulting from selection or drift.

Growth appears to be the important factor causing differences in age-specific fecundity, and possibly survivorship, in different hellbender populations. Probably this is because of the plasticity of growth and the differences in environments in different rivers, such as food availability. According to Stearns (1984, 1983b), patterns of covariance of life-history traits in lizards, snakes, and mammals are strongly influenced by classwide correlations with a single trait, average adult female length; they are further affected by family and genus influences. Thus much of the tendency for traits to covary in the pattern originally thought to have been produced by r- and K-selection can be explained by selection on size alone, followed by coadaptative shifts in life-history traits (Stearns, 1984). Characteristics that compose an organisms' life history are coadapted and modified by selection to solve a particular ecological problem (Stearns, 1976), implying that life-history characteristics have a genetic basis and have evolved under the influence of demographic selection (Berven and Gill, 1983). None the less, small differences in life history between populations should not be attributed to local evolution as a matter of course. In many cases differences may merely be a product

of different environments influencing development passively and may even be nonadaptive (Smith-Gill, 1983). Stearns (1977) pointed out that a large number of studies only document variation in life-history patterns between or within species but then comment on its adaptive significance. Ignoring the variation induced by the environment may lead to false conclusions (Berven, 1982). This is true in reverse also; despite the evidence of similar genetic frequencies in hellbenders, long-term transplant studies must be conducted before these speculations on plasticity can be examined fully.

Hellbender density, growth, and age-specific fecundity and survivorship are about as variable within populations of a subspecies as between subspecies in the Ozarks. Among demographic traits only length-specific fecundity is well segregated between subspecies: a greater length-specific production of ova by all C. a. bishopi populations (Table 13 and Fig. 2). However, even the effect of this characteristic on life history may be masked by differences in growth. It seems unlikely that the difference in demography between the two subspecies in the Ozarks is any more profound than what might be detected between isolated drainages in other parts of the range of Cryptobranchus. Therefore demographic comparisons do not support the existence of subspecies.

Female Cohort Biomass and Production

The zero-age class in Table 22 represents half the expected number of eggs produced annually by females in each population. The high early mortality maintains a relatively low cohort biomass

despite the large number of eggs. It is interesting that the total weight at death is supposedly greater for the Big Piney females than for the Gasconade females. This is due to the greater young mortality in the Gasconade, despite greater fecundity and adult survivorship. Because of the lack of data on juvenile survivorship, the calculated total biomass furnished to the predators and decomposers by a female cohort is possibly a minimum estimate. However, most of the mortality probably does occur in the egg or embryo stage, and not all eggs may be laid. Further, it is possible that a sizeable portion of the biomass is consumed by the hellbenders because of oophagy and cannibalism. The biomass of a male cohort would likely be less because of greater adult mortality (Peterson et al., 1983; Taber et al., 1975) and smaller size than the females.

Topping (personal communication) estimated annual hellbender production by a different measure of instantaneous growth. His estimates for 10 sites in the Niangua River varied from 60.7 to 714 (the next highest was 303) kg / ha with an average of 179 kg / ha. P/B values varied from 0.16 to 0.22. Topping's estimates for the most part are in accord with those made by the summation-removal method in Table 23 if male production is nearly comparable to that of females (and taking into consideration that only diurnal habitat was measured in the Niangua River). This supports the assumption of a stable population made in the construction of the life tables because no such assumption was necessary in Topping's estimates of production. Yet his P/B values are very much in

agreement with the ratios obtained by the instantaneous growth method in Table 23, by which the estimates of yearly production are much less. It may be that those estimates (P') are reduced because of the overestimation of maximum age used as a divisor in the calculations, or because the estimates of density and thus biomass are reduced because of nonrandom sampling. However, such P/B values might be expected because of the longevity of hellbenders. According to Waters (1977), P/B ratios are reasonably constant for given groups of organisms: modes of published annual P/B values are 5.0 for univoltine zoobenthos, 1.2 for stream salmonid fishes (effective life span three years), and 0.6 for warm-water fishes (life span 10 years or more).

If the estimates of production by the summation-removal method are reliable, then hellbenders are likely an important part of the stream trophic dynamics, at least in the areas where suitable habitat exists. Waters (1983) estimated the annual production of trout in a Minnesota stream for 15 years as brown trout, Salmo trutta, replaced brook trout, Salvelinus fontinalis. His estimates of production over that period ranged from 25 to 167, 3 to 45, and 9 to 132 kg / ha / yr for brook, rainbow (Salmo gairdneri), and brown trout, respectively. Covington et al. (1983) estimated annual production of smallmouth bass, Micropterus dolomieu, and rock bass Ambloplites rupestris, at two sites in the Jacks Fork River and two sites in the Current River, both in the Ozarks. Estimates varied from 2 to 16 kg / ha / yr for smallmouth bass and from 6 to 22 kg / ha / yr for rock bass. Production of smallmouth bass was greater in the Jacks Fork, but rock bass production

was greater in the upstream sites on both rivers. At the same sites sampled by Covington et al. (1983), See (1982) estimated production of black redhorse, Moxostoma duquesnei, age three and older: 19.34 to 54.69 kg / ha / yr with the average production greater in the Current River. Along with other production estimates cited previously, these estimates suggest that hellbender production may be of the same order of magnitude of many fish species in the rivers, even if the instantaneous growth estimates of production (P') are used for comparison instead of the higher production estimates made by the summation-removal method (Table 23).

SUMMARY

Estimates of hellbender densities ranged from 1.0 to 6.3 per 100 m² for four different populations and seven collection sites (Table 24). Biomasses based on these estimates (and average weights) varied from 59 to 396 kg / ha wet weight. These may be minimum estimates because of bias produced by unequal catchability. Site areas were measured from shoreline to shoreline and not only where diurnal habitat existed.

Fecundity was positively correlated with female body length in all populations, and *C. a. bishopi* populations exhibited greater length-specific fecundity than *C. a. alleganiensis* populations. Numbers of eggs removed from females that were to be laid during the current breeding season varied from 296 to 908 (\bar{X} =576), 215 to 452 (\bar{X} =289), 159 to 687 (\bar{X} =374), and 95 to 481 (\bar{X} =320) for Spring, Eleven Point, Gasconade, and Big Piney females, respectively.

Crayfish was the most common food item in stomachs in all populations, but large numbers of hellbender eggs were probably eaten during spawning.

No significant linear relationship existed between wet weight of crayfish caught per hour and hellbender production in different collection sites, but a significant positive correlation was found between the number of crayfish caught per hour and hellbender production.

Growth decreases linearly with increased size of hellbenders. Growth of hellbenders is greatest in the Spring River followed

Table 24. Summary of demographic parameters.

Population	Average weight (g)	Density (no./100 m ²)	Biomass (kg/ha)	Production by instantaneous growth method (kg/ha/yr)	Average crayfish catch (no./hr) (g/hr)
<u>C. a. bishopi</u>					
Spring					
site 1	970.8	4.1	396	77.3	177 1792
site 2	769.2	1.0	74	14.0	127 888
Eleven Point					
site 1	214.0	4.3	92	15.9	102 1100
site 2	346.0	6.1	209	36.7	92 729
<u>C. a. alleghaniensis</u>					
Gasconade					
site 1	597.6	1.0	59	11.2	50 349
Big Piney					
site 1	486.7	2.3	112	20.3	88 1165
site 2	531.5	6.3	334	60.4	153 923

Table 24 cont. Summary of demographic parameters.

Population	Population composition average %		Average no. female zygotes produced per female by females aged in years (7-16) (17-26) (27 ⁺)		Type survi- vorship curve	Mean genera- tion time (yrs)	Production of females by summa- tion removal method (kg/ha/yr)		
	juveniles	adult males females	adult males females	aged in years (7-16) (17-26) (27 ⁺)					
<u>C. a. bishopi</u>									
Spring	0.5	50.0	49.5	236	323	362	III	23.3	96.5
Eleven Point	24.8	25.0	50.2	125	174	186	III	14.2	92.4
<u>C. a. alleganiensis</u>									
Gasconade	0.5	36.0	63.5	147	216	243	III	23.4	22.6
Big Piney	5.3	39.7	54.9	142	201	218	III	18.6	73.1

by the Gasconade and Big Piney hellbenders; growth is least in the Eleven Point River. Water quality reports indicate that the Spring River may be nutrient enriched compared to the Eleven Point River.

Age-specific fecundity of hellbenders in different populations is also greatest in the Spring River followed by the Gasconade, Big Piney, and Eleven Point populations. It is believed that differences in growth, due mostly to environmental differences among rivers, highly influences fecundity. Assuming a stationary age distribution, a Type III survivorship curve is exhibited by all populations of the strictly aquatic hellbender. There is little demographic data to support the existence of subspecies.

Estimates of annual production indicate that hellbenders may at least be important in the trophic relationships of the streams in the circumscribed area of suitable habitat.

LITERATURE CITED

- Andrews, R.M. 1976. Growth rate in an island and mainland anoline lizards. *Copeia* 1976:506-604.
- Arkansas Department of Pollution Control and Ecology. 1977a. Arkansas water quality inventory report 1976. Little Rock.
- _____. 1977b. Arkansas water quality inventory report 1977. Little Rock.
- Baker, C.L. 1963. Spermatozoa and spermateleosis in Cryptobranchus and Necturus. *J. Tennessee Acad. Sci.* 38:1-11.
- Barbour, R.W. 1971. Amphibians and reptiles of Kentucky. Univ. of Kentucky Press, Lexington.
- Bartlett, M.S. 1949. Fitting a straight line when both variables are subject to error. *Biometrics* 5:207-212.
- Beck, R. 1965. The great hellbender. *Field and Stream* 69: 65-66, 109-111.
- Beckman, H.C., and N.S. Hinchey. 1944. The large springs of Missouri. *Mo. Geol. Surv. and Water Res.*, Rolla.
- Begon, M. 1979. Investigating animal abundance. Univ. Park Press, Baltimore.
- Bell, G. 1977. The life of the smooth newt (Triturus vulgaris) after metamorphosis. *Ecol. Monogr.* 47:279-299.
- Berven, K.A. 1982. The genetic basis of altitudinal variation in the wood frog Rana sylvatica. I. An experimental analysis of life history traits. *Evolution* 36:962-983.

- Berven, K.A., and D.E. Gill. 1983. Interpreting geographic variation in life-history traits. *Am. Zool.* 23:85-97.
- Beukema, J.J. 1970. Acquired hook-avoidance in the pike Esox lucius L. fished with artificial and natural baits. *J. Fish Biol.* 2:155-160.
- Biegler, R. 1966. A survey of recent longevity records for reptiles and amphibians in zoos. *International Zoo Yearbook* 6:487-493.
- Bishop, S.C. 1941. The salamanders of New York. *New York St. Mus. Bull.* No. 324.
- _____. 1943. Handbook of salamanders. Comstock Publ. Co., Inc., New York.
- Blanchard, F.N. 1928. Topics from the life history and habits of the red-backed salamander in southern Michigan. *Am. Nat.* 62:156-164.
- Branch, H.E. 1959. A laboratory manual of Cryptobranchus alleganiensis Daudin. Vantage Press, New York.
- Brown, K.M. 1983. Do life history tactics exist at the intraspecific level? Data from freshwater snails. *Am. Nat.* 121:871-879.
- Burton, T.M. 1977. Population estimates, feeding habits and nutrient and energy relationships of Notophthalmus v. viridescens in Mirror Lake, New Hampshire. *Copeia* 1977:139-143.
- Cagle, F.R. 1946. The growth of the slider turtle, Pseudemys scripta elegans. *Am. Midl. Nat.* 36:685-729.

- _____. 1956. An outline for the study of an amphibian life history. *Tulane Studies in Zool.* 4:79-110.
- Carothers, A.D. 1973. The effects of unequal catchability on Jolly-Seber estimates. *Biometrics* 29:79-100.
- _____. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. *J. Anim. Ecol.* 48:863-869.
- Caswell, H. 1983. Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. *Am. Zool.* 23:35-46.
- Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47:906-918.
- _____. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York.
- Clark, D.R. 1971. Branding as a marking technique for amphibians and reptiles. *Copeia* 1971:148-151.
- Coatney, C.E., Jr. 1982. Home range and nocturnal activity of the Ozark hellbender. Unpubl. Master's thesis, Southwest Missouri St. Univ., Springfield.
- Collins, J.T. 1974. Amphibians and reptiles in Kansas. Univ. Kansas Pub. Mus. Nat. Hist., Lawrence.
- Covington, W.G., R.E. Marteney and C.F. Rabeni. 1983. Population characteristics of sympatric smallmouth bass and rock bass in the Jacks Fork and Current Rivers, Missouri. *Trans. Missouri Acad. Sci.* 17:27-35.
- Danstedt, R.T., Jr. 1975. Local geographic variation in demographic parameters and body size of Desmognathus fuscus (Amphibia: Plethodontidae). *Ecology* 56:1054-1067.

- Davies, R.G. 1971. Computer programming in quantitative biology. Academic Press, New York.
- Deevey, E.S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.
- Dowling, H.G. 1957. A review of the amphibians and reptiles in Arkansas. Occas. Papers. Univ. Arkansas Mus. 3:1-51.
- Duchrow, R.M. 1977. Water quality of the Current, Jack's Fork, Eleven Point, Little Black and Warm Fork of Spring River Basins of Missouri. Mo. Dept. Conserv., Fish and Wildlife Res. Center, Columbia.
- Duncan R., and R. Highton. 1979. Genetic relationships of the eastern large Plethodon of the Ouachita Mountains. Copeia 1979:95-110.
- Dundee, H.A. 1971. Cryptobranchus and C. alleganiensis. Cat. Am. Amphibians and Reptiles. SSAR:101.1-101.4.
- Dundee H.A., and D.S. Dundee. 1965. Observations on the systematics and ecology of Cryptobranchus from the Ozark Plateau of Missouri and Arkansas. Copeia 1965:369-370
- Dunham, A.E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard Sceloporus merrami. Ecology 59:770-778.
- Eberhardt, L.L. 1969. Population estimates from recapture frequencies. J. Wildl. Manage. 18:403-404.
- Efford, I.E., and J.A. Mathias. 1969. A comparison of two salamander populations in Marion Lake, British Columbia. Copeia 1969:723-736.

- Federal Writers' Project. 1939. Reptiles and amphibians.
R. DeSola (ed.). Albert Whitman and Co., Chicago.
- Ferguson, D. 1961. The herpetofauna of Tishomingo County.
Mississippi, with comments on its zoogeographic affinities.
Copeia 1961:391-396.
- Firschein, I.L. 1951. The range of Cryptobranchus bishopi and
remarks on the distribution of the genus Cryptobranchus.
Am. Midl. Nat. 45:455-459.
- Fitch, F.W. 1947. A record Cryptobranchus alleganiensis. Copeia
1947:210.
- Fleener, G.G., J.L. Funk and P.E. Robinson. 1974. The fishery
of Big Piney River and the effects of stocking fingerling
smallmouth bass. Mo. Dept. of Conservation, Jefferson City.
- Flower, S.S. 1936. Further notes on the duration of life in
animals. II. Amphibians. Proc. Zool. Soc. London 1936:369-394.
- Gehlbach, F.R., and S.E. Kennedy. 1978. Population ecology
of a highly productive aquatic salamander (Siren intermedia).
Southwest. Nat. 23:423-430.
- Gill, D.E. 1978. The metapopulation ecology of the red-spotted
newt, Notophthalmus viridescens (Rafinesque). Ecol.
Monogr. 48:145-166.
- _____. 1979. Density dependence and homing behavior in adult
red-spotted newts Notophthalmus viridescens (Rafinesque).
Ecology 60:800-813.
- Goin, C.J., and O.B. Goin. 1971. Introduction to herpetology.
W. H. Freeman, San Francisco.

- Green, N.B. 1933. Cryptobranchus alleganiensis in West Virginia. Proc. West Virginia Acad. Sci. 7:28-30.
- _____. 1935. Further notes on the food habits of the water dog, Cryptobranchus alleganiensis Daudin. Proc. West Virginia Acad. Sci. 9:36.
- Greenell, R.G. 1939. The morphogenesis of the hypophysis in Cryptobranchus alleganiensis. Anat. Rec. 73:327-340.
- Grobman, A.B. 1943. Notes on salamanders with the description of a new species of Cryptobranchus. Occas. Papers Mus. Zool. Univ. Michigan 470:1-13.
- Hairston, N.G. 1983. Growth, survival and reproduction of Plethodon jordani: trade-offs between selective pressures. Copeia 1983:1024-1035.
- Harrison, J.R. 1967. Observations on the life history, ecology and distribution of Desmognathus aeneus aenus Brown and Bishop. Am. Midl. Nat. 77:356-370.
- Highton, R. 1962. Geographic variation in the life history of the slimy salamander. Copeia 1962:597-613.
- Hillis, R.E., and E.D. Bellis. 1971. Some aspects of ecology of the hellbender, Cryptobranchus alleganiensis alleganiensis, in a Pennsylvania stream. J. Herpetol. 5:121-126.
- Houck, L.D. 1982. Growth rates and age at maturity for the plethodontid salamander Bolitoglossa subpalmata. Copeia 1982:474-478.
- Huheey, J.E., and A. Stupka. 1967. Amphibians and reptiles of Great Smoky Mountain National Park. Univ. Tennessee Press, Knoxville.

- Humphrey, R.R. 1922. The multiple testis in urodeles. Biol. Bull. 43:43-67.
- Ingersol, C.A. 1982. Seasonal reproductive changes in Cryptobranchus alleganiensis. Unpubl. Master's thesis, Southwest Missouri St. Univ., Springfield.
- Jerrett, D.P., and C.E. Mays. 1973. Comparative hematology of the hellbender, Cryptobranchus alleganiensis, in Missouri. Copeia 1973:331-337.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration--stochastic model. Biometrika 52:225-247.
- Jolly, G.M., and J.M. Dickson. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. Can. J. Zool. 61:922-927.
- Kaplan, R.H., and P.W. Sherman. 1980. Intraspecific oophagy in California newts. J. Herpetol. 14:183-185.
- King, W. 1939. A survey of the herpetology of Great Smoky Mountain National Park. Am. Midl. Nat. 21:531-582.
- Kuramoto, M. 1978. Correlation of quantitative parameters of fecundity in amphibians. Evolution 32:287-296.
- Leslie, P.H. 1958. Statistical appendix. J. Anim. Ecol. 27:84-86.
- _____. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (Uria aalge Pont.). J. Anim. Ecol. 35:291-301.
- Lilywhite, H.B., P. Light and P. Chelgren. 1973. The role of behavioral thermoregulation in the growth energetics of the toad, Bufo boreas. Ecology 54:375-383.

- Lotter, F. 1978. Reproductive ecology of the salamander Plethodon cinereus (Amphibia, Urodela, Plethodontidae) in Connecticut. J. Herpetol. 12:231-236.
- Lowry, E.M. 1953. The growth of the smallmouth bass (Micropterus dolomieu Lacepede) in certain Ozark streams of Missouri. Unpubl. Ph.D. dissertation, Univ. of Missouri, Columbia.
- Mays, C.E., and M.A. Nickerson. 1971. A population study of the Ozark hellbender salamander, Cryptobranchus alleganiensis bishopi. Indiana Acad. Sci. 81:339-340.
- Merkle, D.A. 1975. Gene flow and population differentiation in the salamanders Eurycea lucifuga and Cryptobranchus alleganiensis. Unpubl. Ph.D. dissertation, Miami Univ., Oxford, Ohio.
- Merkle, D.A., S.I. Guttman and M.A. Nickerson. 1977. Genetic uniformity throughout the range of the hellbender, Cryptobranchus alleganiensis. Copeia 1977: 549-553.
- Minton, S. 1972. Amphibians and reptiles of Indiana. Indiana Acad. Sci. Monogr. No. 3.
- Missouri Clean Water Commission Planning Section. 1980. Missouri water quality report 1980. Jefferson City.
- _____. 1982. Missouri water quality report 1982. Jefferson City.
- Missouri Water Pollution Board. 1973. Osage and Gasconade Rivers and tributaries. Jefferson City.
- Mount, R.H. 1975. Amphibians and reptiles of Alabama. Auburn Printing Co., Auburn.
- Murphy, J.L. 1973. Introductory econometrics. Richard D. Irwin, Inc., Homewood, Illinois.

- Nagel, J.W. 1977. Life history of the red-backed salamander, Plethodon cinereus, in northeastern Tennessee. *Herpetologica* 33:13-18.
- Naylor, B.G. 1981. Cryptobranchid salamanders from the Paleocene and Miocene of Saskatchewan. *Copeia* 1981:76-86.
- Neish, I.C. 1971. Comparison of size, structure, and distributional patterns of two salamander populations in Marion Lake, British Columbia. *J. Fish. Res. Board Can.* 28:49-58.
- Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois.
- Netting, M.G. 1929. The food of the hellbender Cryptobranchus alleganiensis (Daudin). *Copeia* 1929:23-24.
- Neves, R.J., and G.B. Pardue. 1983. Abundance and production of fishes in a small Appalachian stream. *Trans. Am. Fish. Soc.* 112:21-26.
- Nickerson, M.A., R.E. Ashton and A.L. Braswell. 1983. Lampreys in the diet of hellbender Cryptobranchus alleganiensis (Daudin), and the Neuse River waterdog Necturus lewisi (Brimley). *Herp. Rev.* 14:10.
- Nickerson, M.A., and C.E. Mays. 1973a. The hellbenders: North American "giant salamanders." Milwaukee Public Mus. Publ. in Biol. and Geol. No. 1.
- _____. 1973b. A study of the Ozark hellbender, Cryptobranchus alleganiensis bishopi. *Ecology* 54:1164-1165.
- Nussbaum, R.A., and C.K. Tait. 1977. Aspects of the life history and ecology of the Olympic salamander, Rhyacotriton olympicus (Gauge). *Am. Midl. Nat.* 98:176-199.

- Oliver, J.A. 1955. The natural history of North American amphibians and reptiles. Van Nostrand, Princeton.
- Organ, J.A. 1961. Studies of the local distribution, life history, and population dynamics of the salamander genus Desmognathus in Virginia. Ecol. Monogr. 31:189-220.
- Parmenter, R.R. 1980. Effects of food availability and water temperature on the feeding ecology of pond sliders (Chrysemys s. scripta). Copeia 1980:503-514.
- Peabody, F.E. 1961. Annual growth zones in living and fossil vertebrates. J. Morphol. 108:11-62.
- Pearl, R., and J.R. Miner. 1935. Experimental studies on the duration of life XIV. The comparative mortality of certain lower organisms. Quart. Rev. Biol. 10:60-79.
- Pearson, P.G. 1955. Population ecology of the spadefoot toad, Scaphiopus h. holbrooki (Harlan). Ecol. Monogr. 25:233-267.
- Peterson, C.L., M.S. Topping, R.F. Wilkinson, Jr. and C.A. Taber. 1985. An examination of long-term growth of Cryptobranchus alleganiensis predicted by linear regression methods. Copeia 1985 (in press).
- Peterson, C.L., R.F. Wilkinson, Jr., M.S. Topping and D.E. Metter. 1983. Age and growth of the Ozark hellbender (Cryptobranchus alleganiensis bishopi). Copeia 1983:225-231.
- Petranka, J.W. 1984. Breeding migrations, breeding season, clutch size, and oviposition of stream-breeding Ambystoma texanum. J. Herpetol. 18:106-112.
- Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. Am. Zool. 23:57-63.

- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manage.* 46:752-757.
- Porter, K.R. 1972. *Herpetology*. W. B. Saunders, Co., Philadelphia.
- Purkett, C.A., Jr. 1958. Growth rates of Missouri streamfishes. *Mo. Conservation Comm. D-J Series*, Jefferson City.
- Ratcliff, M.A., Jr. 1965. The male urogenital system in Cryptobranchus. *J. Tennessee Acad. Sci.* 40:52-57.
- Reese, A.M. 1903. The habits of the giant salamander. *Popular Sci. Monthly* 62:526-531.
- _____. 1904. The sexual elements of the giant salamander, Cryptobranchus allegheniensis. *Biol. Bull.* 6:220-223.
- Rhoads, S.N. 1895. Contributions to the zoology of Tennessee. Reptiles and amphibians. *Proc. Acad. Nat. Sci. Philadelphia* 1:376-407.
- Richmond, N.D. 1965. Perhaps juvenile dinosaurs were always scarce. *J. Paleontol.* 30:503-505.
- Ricker, W.E. 1973. Linear regression in fishery research. *J. Fish. Res. Board Can.* 30:409-434.
- Roff, D.A. 1973. An examination of some statistical tests used in the analysis of mark-recapture data. *Oecologia* 12:35-54.
- Salthe, S.N. 1969. Reproductive modes and the number and sizes of ova in the urodeles. *Am. Midl. Nat.* 81:467-490.
- Schmidtler, J.J., and J.F. Schmidtler. 1969. Ein feuersalamander (Salamandra s. terrestris) 43 jahre in gefangenschaft. *Salamandra* 5:71.

- Schoener, T.W., and A. Schoener. 1978. Estimating and interpreting body-size growth in some Anolis lizards. *Copeia* 1978:390-405.
- Seber, G.A.F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249-259.
- _____. 1982. The estimation of animal abundance and related parameters. 2nd ed. Macmillan Publ. Co., New York.
- See, T.C. 1982. Black redhorse population dynamics in the upper Current and Jacks Fork Rivers, Missouri. Unpubl. Master's thesis, Univ. of Missouri, Columbia.
- Senning, W.C. 1940. A study of age determination and growth of Necturus maculosus based on the parasphenoid bone. *Am. J. Anat.* 66:483-494.
- Shaffer, H.B. 1983. Biosystematics of Ambystoma rosaceum and A. tigrinum in northwestern Mexico. *Copeia* 1983:67-78.
- Simpson, G.G., A. Roe and R.C. Lewontin. 1960. Quantitative zoology. Harcourt, Brace, and Co., New York.
- Smith, B.G. 1907. The life history and habits of Cryptobranchus allegheniensis. *Biol. Bull.* 13:5-39.
- _____. 1912. The embryology of Cryptobranchus allegheniensis including comparisons with some other vertebrates. *J. Morphol.* 23:61-157.
- Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. *Am. Zool.* 23:47-55.
- Smith-Gill, S.J., and K.A. Berven. 1979. Predicting amphibian metamorphosis. *Am. Nat.* 113:563-585.

- Sokal, R.R., and F.J. Rolf. 1973. Introduction to biostatistics. W.H. Freeman and Co., San Francisco.
- Spight, T.M. 1967. Population structure and biomass production by a stream salamander. *Am. Midl. Nat.* 78:437-447.
- Stearns, S.C. 1976. Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* 51:3-47.
- _____. 1977. The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* 8:145-171.
- _____. 1980. A new view of life-history evolution. *Oikos* 35:266-281.
- _____. 1983a. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. *Am. Zool.* 23:65-72.
- _____. 1983b. The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. *Oikos* 41:173-187.
- _____. 1984. The effects of size and phylogeny on patterns of covariation in the life history traits of lizards and snakes. *Am. Nat.* 123:56-72.
- Stebbins, R.C. 1954. Natural history of the salamanders of the plethodontid genus Ensatina. *Univ. Calif. Publ. Zool.* 54:47-124.
- Swanson, P.L. 1948. Notes on the amphibians of Venago County, Pennsylvania. *Am. Midl. Nat.* 40:362-371.

- Taber, C.A., R.F. Wilkinson, Jr. and M.S. Topping. 1975. Age and growth of hellbenders in the Niangua River, Missouri. *Copeia* 1975:633-639.
- Tilley, S.G. 1968. Size-fecundity relationships and their evolutionary implications in five desmognathine salamanders. *Evolution* 22:806-816.
- _____. 1973. Life histories and natural selection in populations of the salamander Desmognathus ochrophaeus. *Ecology* 54:3-17.
- _____. 1977. Studies of life histories and reproduction in North American plethodontid salamanders, pp. 1-41. IN: The reproductive biology of amphibians. D. Taylor and S. Guttman (eds.). Plenum Press, New York.
- _____. 1980. Life histories and comparative demography of two salamander populations. *Copeia* 1980:806-821.
- Topping, M.S. 1981. Secondary production in the hellbender, Cryptobranchus alleganiensis alleganiensis. *Trans. Missouri Acad. Sci.* 15:246-247.
- Topping, M.S., and C.A. Ingersol. 1981. Fecundity in the hellbender, Cryptobranchus alleganiensis. *Copeia* 1981:873-876.
- United States Geological Survey and Missouri Division of Geological Survey and Water Resources. 1967. Mineral and water resources of Missouri. U. S. Government Printing Office, Washington, D.C.
- Van Devender, R.W. 1978. Growth ecology of a tropical lizard, Basiliscus basiliscus. *Ecology* 59:1031-1038.
- Vineyard, J.D., and G.L. Feder. 1974. Springs of Missouri. *Mo. Geol. Surv. and Water Res.*, Rolla.

- Warren, C.E., J.H. Wales, G.E. Davis and P. Doudoroff. 1964.
Trout production in an experimental stream enriched with
sucrose. J. Wildl. Manage. 28:617-660.
- Waters, T.F. 1977. Secondary production in inland waters.
Adv. Ecol. Res. 10:91-164.
- _____. 1983. Replacement of brook trout by brown trout over
15 years in a Minnesota stream. Trans. Am. Fish. Soc.
112:137-146.
- Westrheim, S.J., and W.E. Ricker. 1978. Bias in using an age-
length key to estimate age-frequency distributions. J.
Fish. Res. Board Can. 35:184-189.
- Wiggs, J.N. 1976. Food habits, starvation, and growth in the
hellbender, Cryptobranchus alleganiensis. Unpubl. Master's
thesis, Southwest Missouri St. Univ., Springfield.
- Wiggs, R.L. 1977. Movement and homing in the hellbender,
Cryptobranchus alleganiensis, in the Niangua River, Missouri.
Unpubl. Master's thesis, Southwest Missouri St. Univ.,
Springfield.
- Wilbur, H.M., and J.P. Collins. 1973. Ecological aspects of
amphibian metamorphosis. Science 182:1305-1314.
- Wilbur, H.M., and J.M. Landwehr. 1974. The estimation of
population size with equal and unequal risks of capture.
Ecology 55:1339-1348.
- Williams, R.D., J.E. Gates, C.H. Hocutt and G.J. Taylor. 1981.
The hellbender: a nongame species in need of management.
Wildl. Soc. Bull. 9:94-100.
- Wortham, E., and M.A. Nickerson. 1971. A serum protein study of
Ozark Cryptobranchus. Herp. Rev. 3:14.

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