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HABITAT DIFFERENCES AFFECTING AGE CLASS DISTRIBUTIONS OF THE HELLBENDER SALAMANDER, *CRYPTOBRANCHUS ALLEGANIENSIS*

MAX A. NICKERSON[1,*], KENNETH L. KRYSKO[1], AND RICHARD D. OWEN[1]

ABSTRACT – Hellbender salamander (*Cryptobranchus alleganiensis*) populations have received considerable attention over the last few decades and recent studies show declines. We compared *C. alleganiensis* populations and habitat characteristics of the Little River (LR) in the Great Smoky Mountain National Park (GSMNP) of Tennessee, with those of the North Fork of the White River (NFWR), Missouri. We also compared the results of two different sampling methods for obtaining small individuals < 20 cm total length (TL) and gilled larvae. There was no significant difference in the frequency of larvae and adults in LR population There were highly significant differences in the frequency of larvae and adults in the NFWR population and in the proportion of larvae and adults between LR and NFWR. The stream bottom substrate, especially the deep gravel beds of the NFWR, provided a more secure larval habitat than in the LR. We believe this secure larval habitat was a major factor in maintaining large adult populations in NFWR. The less secure larval habitat within the LR makes larvae more susceptible to capture, and coupled with reduced crayfish populations, translates to fewer adult *C. alleganiensis*. Larvae were more efficiently collected by skin-diving than wading and turning rocks in these habitats. With the exception of the LR population, which is composed of 48% gilled or gilled size larvae, all recorded populations are almost entirely composed of adult and sub-adult age groups and small larvae, especially gilled larvae are either uncommon or unknown.

INTRODUCTION

A population's history is reflected in the structure of its age classes, geographic distribution, size, sex ratios, populations structure, gene flow, gene frequencies, and birth and death rates. Population variability arises from changes in the intensity at which environmental factors affect these variables (Zug 1993). It is important to understand which habitat characteristics affect these variables to understand a population's ecology. By studying a species in variable habitats; i.e., with different abiotic and biotic variables, it may be possible to better understand population structure and perhaps infer a species response to different environmental factors.

Hellbender salamanders (*Cryptobranchus alleganiensis*) populations have shown substantial declines from previously known popula-

[1]Florida Museum of Natural History, Division of Herpetology, University of Florida, PO Box 117800 Gainesville, FL 32611-7800. *Corresponding author - maxn@flmnh.ufl.edu.

tion parameters (Wheeler et al. 2003). In the past three decades, there have been numerous mark and recapture studies to obtain information about population numbers, density, growth rates, and basic natural history. However, almost no studies have remarked on habitat, especially as it relates to larval and small *C. alleganiensis* (Nickerson 2003). In 1969 and 1970, Nickerson and Mays (1973a, 1973b) used skin-diving (wet suit, snorkel, face mask, fins or shoes, and sometimes weighted belts) technique to conduct intensive surveys of *C. alleganiensis* populations within a 4.6 km section of the North Fork of White River (NFWR), Missouri. These initial studies included population estimates and structure, biomass, water quality, diet, individual movement, and summated much of what was known about this species. After these initial studies, Nickerson and colleagues visited NFWR annually (1971–1980) using skin-diving to study activity patterns, reproductive events, re-establish removed animals, and obtain samples for genetic, hematological, and hepatic enzyme research (Merkle et al.1977; Nickerson 1980; Nickerson and Tohulka 1986; Noeske and Nickerson 1978; Roerig et al. 1980; Taketa and Nickerson 1973a, 1973b). The NFWR population included all size classes, however, larvae were rarely observed (Nickerson and Mays 1973a). Other Ozark streams surveyed using skin-diving between 1971 and 1986 included the Current River, Eleven Point River, Niangua River, Meramec River, Piney River, and Spring River.

During 2000, portions of Abrams Creek, Big Creek, Cataloochee Creek, Cosby Creek, Deep Creek, Fighting Creek, Little Pigeon River, Little River (LR), Middle Prong of Little River, Noland Creek, Oconaluftee River, and West Prong of Pigeon River in the Great Smoky Mountains National Park (GSMNP) of Tennessee and North Carolina were surveyed to assess the distribution and ecological status of *C. alleganiensis*. *Cryptobranchus alleganiensis* was found in three of these streams. However, the LR was the only stream where substantial numbers were found, including numerous adult size classes and larvae (Nickerson et al. 2002).

The primary purpose of this paper is to compare the habitats and selected population characteristics of *C. alleganiensis* from LR with those of the NFWR. Furthermore, we attempt to determine what habitat characteristics might cause the observed differences in population structure between these two streams. Additionally, we compare the results of two sampling techniques (skin-diving versus wading and turning) to determine their effectiveness in sampling galled larvae and small individuals < 20 cm total length (TL). We contrast thee results of the initial NFWR studies conducted in 1969 and 1970 (Nickerson and Mays 1973a, 1973b) using skin-diving with those studies using the wading and turning technique.

MATERIALS AND METHODS

In the GSMNP, diurnal skin-diving surveys were conducted between 1015 and 1805 hrs from 21 August to 15 October 2000. Survey crews typically consisted of four individuals, three of whom would be in the water surveying and one out of the water providing support, recording data, carrying equipment, and tagging. Underwater surveying was accomplished by direct observation coupled with turning rocks and other objects via skin-diving. *Cryptobranchus alleganiensis* were weighed to the nearest gram with an Ohaus CS-2000 compact scale. TL and snout-vent length (SVL) to anterior portion of vent, were measured to the nearest mm using a standard meter stick. Biomark Passive Integrated Transponder (PIT) tags were inserted with a 10 ml syringe and a 12 gauge needle within connective tissue adjacent to the vertebral column just caudad and lateral to the hind limb attachment. Habitat characteristics examined include stream substrate, relief, water quality, and food resources. Dissolved oxygen (DO) was measured with a Hanna Hi 9142 oxygen meter, conductivity and pH were measured with a Hanna Watercheck pH and TDS reader. Both Hanna instruments were standardized between site readings using Orion perpHect buffers. Elevations, latitudes, and longitudes were taken with a Garmin GPS 12. All elevations were then corrected with topographic maps.

The NFWR survey methodology differed from the GSMNP survey by sampling between 0900 and 1830 hrs from 9 June to 7 August 1969 and 0700 to 1730 hrs between 4 June to 20 August 1970. There were either 3 or 4 members in the survey crew and a boat was used to transport equipment. Water quality was measured with Hach Kit chemical methods. *Cryptobranchus alleganiensis* were tagged with mammalian ear tags or Floy T-tags and weighed with an Ohaus triple beam scale (Nickerson and Mays 1973a, 1973b).

Because of ringed crayfish, *Orconectes neglectus chaenodactylus* are the major diet of non-larval *C. alleganiensis* (Nickerson and Mays 1973a), crayfish populations in LR were subjectively compared to those of NFWR by recording the frequency of crayfish exposed after turning rocks. The presence or absence of crayfish was recorded from 100 rocks turned in riffles at each of four survey sites in LR. In 1969, Nickerson (unpubl. data) turned 100 rocks in each of four riffles within the NFWR research section to determine relative frequency of the crayfish populations. Crayfish populations were considered low (0–30% of rocks revealed crayfish), moderate (31–60% of rocks revealed crayfish), or high (≥ 60% of rocks revealed crayfish).

Chi-square Tests for independence were performed to determine significance in frequency of larvae versus adults within and among

GSMNP and NFWR populations. All statistical tests were performed using Statistical Analysis System (SAS Institute Inc., version 6.12) with $\alpha = 0.05$.

RESULTS

There were substantial elevational and relief differences between the LR and NFWR sites. LR sites ranged from 330–394 m in elevation, and relief within stream sampling sections was sometimes substantial. Ozark streams on the Salem Plateau rarely have local relief > 30 m (Thornbury 1965) and the NFWR site ranged from ca.198–202 m. We were unable to determine the elevation or relief effects on distribution.

There are major habitat differences in stream bottom substrate between LR and NFWR. LR sites typically have metamorphic rock streambeds with scattered piles of dense metamorphic rock, and some scattered accumulations of sand, gravel, and igneous rocks. Metamorphic formations erode into fragments, typically with rounded surfaces. Often the shallow, scattered gravel have limited interstitial spaces filled with sand. NFWR featured sections with large gravel beds, including chert with piles of dolomite, limestone, and some sandstone rocks on a limestone/dolomite streambed. Limestone formations typically erode into flat fragments. The interstices within the deep gravel beds within riffles were typically not filled with sand.

Water quality data from LR sites were: pH 6.9–7.4, DO 7.1–10.4 ppm, and water temperatures 8.5°–20 °C. Comparable year-round water quality data from what appears to be optimal habitat for *C. alleganiensis* in NFWR includes: pH 7.6–9.0, DO 8.4–13.6 ppm, $C0_2$ levels from immeasurable to 6.5 ppm, alkalinity 122–289 ppm, and water temperatures 9.8°–22.5 °C (Nickerson and Mays 1973a). Rock turning data characterized the LR crayfish populations as low (11%, range 9–13%), while the NFWR had high (62%, range 56–67%) crayfish populations.

There was no significant difference in frequency of gilled or gilled-size larvae (< 13 cm TL) versus adults encountered in LR ($\chi^2 = 0.03$, df = 1, P = 0.86). Sixteen of 33 *C. alleganiensis* were gilled or gill-size larvae ranging from 5.8–13.0 cm TL (mean = 10.1 cm), and 22 *C. alleganiensis* measured ≤ 20 cm TL. However, there was a significant difference in frequency of gilled larvae and adults encountered in NFWR ($\chi^2 = 725.5$, df = 1, P < 0.001). The initial 1969, 1970, plus 11 March 1972 NFWR surveys yielded only 10 gilled larvae (< 13.0 cm TL) within a sample of 765 *C. alleganiensis* (Nickerson and Mays 1973a, Nickerson unpubl. data). These gilled larvae ranged from 10.5 to 13.0 TL cm (mean = 12.0 cm). There was also a significant difference in the proportion of larvae and sub-adults and adults (≥ 20 cm TL) encountered between LR and NFWR ($\chi^2 = 208.7$, df = 1, P < 0.001).

DISCUSSION

A comparison of water quality data from LR and NFWR reveals both areas are cool, well-oxygenated, and typically alkaline streams. It is not known if the slightly acidic conditions recorded in LR might negatively affect *C. alleganiensis* populations. Adult *C. alleganiensis* have very unique physiological and biochemical respiratory characteristics (Taketa and Nickerson 1973a, 1973b) and some amphibians are sensitive to mild acidic conditions (Vatnik et al. 1999). The presence of sulfide-rich rocks within GSMNP has decimated fish and salamander populations downstream from road construction sites (Huckabee et al. 1975). Any degradation, even minor abrasion of the surfaces of these sulfide-rich rocks, could make these rocks inhospitable or dangerous to underneath or nearby *C. alleganiensis*.

The LR crayfish population is quite small as compared to the NFWR population. Historically, crayfish populations in NFWR have been characterized as abundant (Price and Payne 1984). Year-round benthic surveys revealed high density crayfish populations from 1969–1971 (H.R. Cooper, pers. comm.). Raymond W. Boucher began studying crayfish while earning his PhD at the University of Tennessee-Knoxville (1972) and by 1977 noticed that crayfish in the Tennessee streams draining non-carbonate areas such as the Blue Ridge province (LR site) often have smaller populations than those draining carbonate areas such as the Ridge and Valley, Highland Rim, and Nashville basin provinces to the west (R.W. Bouchard, pers. comm.).

The rounded surfaces of many GSMNP metamorphic rocks appear to be less suitable undersurfaces for *C. alleganiensis.* The lack of *C. alleganiensis* under round rocks has also been noted by Petranka (1998). Round rocks allow more light to penetrate under the rock's margins, relative to similar-sized flat limestone rocks of the NFWR. In LR round rocks are coupled with a lack of gravel cover and depth and could be a significant factor in *C. alleganiensis* ecology. *Cryptobranchus alleganiensis* exhibits positive thigmotaxis, negative phototaxis, is typically nocturnal, and has well developed dermal light sense, especially in the tail (Pearse 1910; Reese 1906). The tail of *C. alleganiensis* is often positioned near the margin of its cover rock and may serve as the initial light receptor for exposure. Its positive thigmotaxis may be somewhat dependent on the amount of light present and photo-negativity may be reduced during the reproductive season (Nickerson and Mays 1973a).

Cryptobranchus alleganiensis populations within NFWR were among the largest recorded, having been estimated at 428 individuals/km and densities in riffles from 1 individual/6–7 m^2 to 1 individual/13–16 m^2 (Nickerson and Mays 1973a). In comparison with

NFWR, the LR population was much smaller. NFWR skin diving capture rate of individuals/hour ranged from 1,200–1,800% above that of LR (Nickerson et al. 2002). Unlike any other known population of *C. alleganiensis*, larvae were common in LR as 16 of 33 (48%) were gilled or gilled size (< 13.0 cm TL). Larvae were found under rocks in riffles, and pools 10 cm to 2.5 m deep. Most larvae were found under small rocks, within interstices of small accumulations of gravel, and sometimes gravel mixed with twigs. Many were found near stream margins, but some were found under large rocks that could barely be turned at depths up to 2.5 m. The bottom substrate in LR lacks the large, deep gravel beds and substantial areas of flat cover rocks characteristic of NFWR. The lack of these features may force larvae into less secure sites making them more susceptible to capture in GSMNP.

In the 1969, 1970, and 2 March 1971 NFWR surveys, the greatest diversity of *C. alleganiensis* age classes occurred in limestone rock piles on gravel beds (Nickerson and Mays 1973a). Population samples from one riffle (riffle 2–3) primarily composed of rock piles on deep gravel beds differed substantially from samples from a large pool with only a small section of similar habitat. While 17 of 245 *C. alleganiensis* from the riffle were < 16 cm TL, the pool sample of 151 individuals had no *C. alleganiensis* < 16 cm TL. Nine gilled larvae were collected in riffle areas with substantial gravel beds partially covered with limestone rocks, and eight of these were in the riffle between stations 2 and 3 (riffle 2–3) in the NFWR research site (Nickerson and Mays 1973a). Three non-gilled larvae 13.4–13.5 cm TL were also found in riffle 2–3 during the 1969–1970 surveys.

The relative abundance of individuals within age groups may change temporally for a population, making it difficult to make comparisons between different sampling methods. The utility of the wading and turning method for finding small < 20 cm *C. alleganiensis* was questioned by Peterson et al. (1983) and Nickerson and Krysko (2003). Finding larval *C. alleganiensis* in Ozark streams has been a challenge, as only three gilled larvae were found out of 1,132 *C. alleganiensis* in a survey of the Niangua River from 1971–1973 (Taber et al. 1975). Peterson et al. (1983) found relatively few *C. alleganiensis* < 20 cm TL and no gilled larvae among 744 *C. alleganiensis* in NFWR from 1977–1978. Peterson et al. (1988) found only one larva out of 1,208 *C. alleganiensis* from four other Ozark rivers from 1980–1982.

During brief, annual skin-diving surveys from 1971–1980, Nickerson (unpubl. data) continued to find numerous small < 20 cm *C. alleganiensis* within NFWR. For example, on 12 March 1972 in the NFWR research section (riffle 2-3) two of 14 *C. alleganiensis* were gilled larvae of 9.5 cm and 13.0 cm TL; on 2–3 October 1973, four of 38 *C. alleganiensis* were < 20 cm TL; on 15 October 1975, three of 28 *C. alleganiensis* ≤ 20 cm TL; and in March 1977, three gilled larvae were found in separate areas of riffle 2–3 (Nickerson unpubl. data). In contrast, from 1977–1978 no larvae were found in an extensive NFWR study, including this section using the wading and turning method (Table 1, Peterson et al. 1983). The survey method of Peterson et al. (1983:226) was "by turning rocks in shallow riffles and shoreline areas, usually 1 m or less deep, and in a few pools to 2 m deep." Taber et al. (1975:633) "collected from shallow water (to 1.3 m deep) over and near riffles and along some shoreline areas … rocks were turned by hand, often with the aid of a potato rake, and the hellbenders were scooped up in dip nets." At other times a face mask was used to assist visibility (Peterson et al. 1988), and we assume *C. alleganiensis* were also were caught by hand. Nickerson and Mays (1973a, 1973b) and Nickerson and other colleagues in 1969–1980 (Nickerson unpubl. data) used skin-diving gear to survey the entire length of the survey sections from shallow riffles to the bottoms of the deepest pools (2.5 m). Larvae were typically found under smaller rocks than were adults or under smaller rocks that were under larger rocks or within gravel interstices beneath rocks (Fig. 1). Hillis and Bellis (1971) found a correlation between small *C. alleganiensis* and smaller rocks. Larvae were also found in the interstices of gravel in an area of sub-surface percolation within a gravel island in the Eleven Point River, Oregon County, Missouri (H. Barton, pers. comm.). This microhabitat in NFWR is teeming with small invertebrate prey items, provides excellent protection from many predators, and is known to be important to riffle fishes and other salamanders (Cooper 1975, Nickerson and Mays 1973a, Stegman and Minckley 1959).

Cryptobranchus alleganiensis is cannibalistic and known to consume its eggs and smaller hellbenders (Nickerson and Mays 1973a,

Table 1. A comparison of *Cryptobranchus alleganiensis* larvae and adults within Ozark populations (above) and Great Smoky Mountains National Park (GSMNP) surveys (below).

Site	No. of Larvae	No. of Individuals	Years of Study	Reference
NFWR	10	765	1969–70, 1971	Nickerson and Mays 1973a, 1973b; Nickerson unpubl. data, 2 March 1971
Niangua R.	3	1,132	1971–73	Tabor et al. 1975
NFWR	0	744	1977–78	Peterson et al. 1983
Spring, Eleven Point, Gasconade and Big Piney Rivers	1	1,208	1980–82	Peterson et al. 1988
Total	14	3,894		
*GSMNP(LR)	16	33	2000	Nickerson et al. 2000

Smith 1907). Cannibalism has been suggested to be an important factor in maintaining population stability (Nickerson and Mays 1973a). Niangua River male *C. alleganiensis* population survivorship "suggests a low rate of egg and larval survival with numerical domination by mature hellbenders" (Tabor et al. 1975:638). The inability to find larval *C. alleganiensis* has required that life history population tables and growth studies estimate larval sizes for age classes (Peterson et al. 1983, 1988, Tabor et al. 1975). It has been suggested that the "apparent inefficiency in capturing smaller hellbenders may therefore be largely the result of normal population structure" (Peterson et al. 1983:229). However, this seems highly unlikely in the NFWR population since initial estimates indicate 1,143 sub-adult and adult *C. alleganiensis* inhabited the 2.67 km NFWR research section. Within this NFWR section only 10 gilled larvae were found, one gilled larva per 76.5 individuals captured during 1969, 1970, and 2 March 1971 surveys (Nickerson and Mays 1973a, 1973b, Nickerson unpubl. data). The combined Ozark wading and turning surveys yielded 1 larva per 771 *C. alleganiensis* (Table 1). Additionally, 90% of the gilled larvae were found in large deep gravel beds which are difficult to search. Typically only the area under the surface rocks of these gravel beds were examined (Nickerson unpubl. data). These results support the Peterson et al. (1983:229) contention that the lack of larvae found "is probably partly due to the inefficiency in the capture technique" (i.e., wade and turn) in finding small cryptobranchids. Therefore, differences in larval discov-

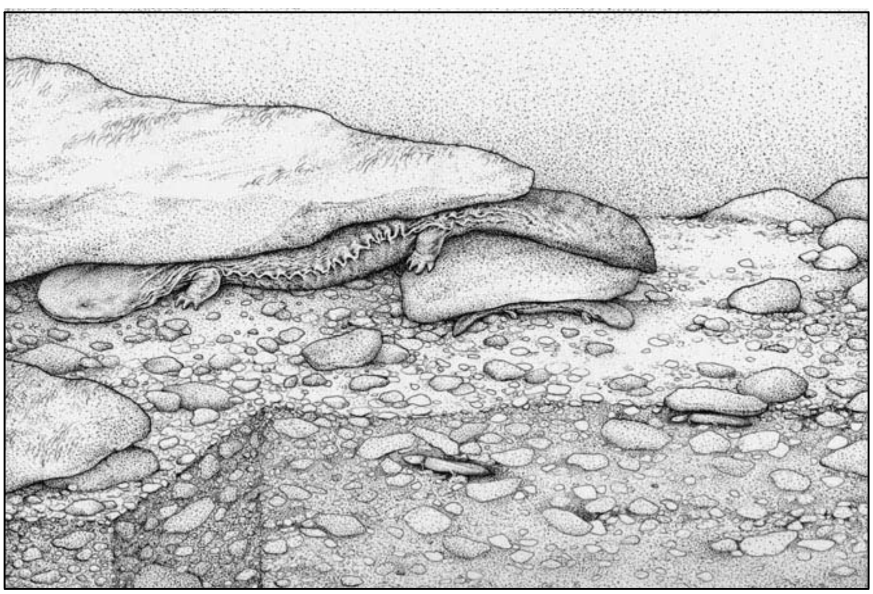

Figure 1. Generalized locations of *Cryptobranchus alleganiensis* in a North Fork White River (NFWR) gravel bed. Note niche partitioning among age classes.

ery may be explained by differences in survey methods (i.e.. skin-diving versus wading and turning) and the cover provided by the large deep gravel beds of the NFWR.

In summation, the NFWR had a large, dense population of *C. alleganiensis,* but far too few larvae were found to support these immense none larval populations. Large dense populations of crayfish provide an abundant food source for the dense sub-adult and adult populations. *Cryptobranchus alleganiensis* larvae found in NFWR were primarily in large, deep, gravel beds and all but two in a single gravel bed within the initial 2.67 km section of the 4.6 km research area. The interstitial spaces in these NFWR gravel beds provide great larval cover and are filled with substantial populations of small, appropriate sized invertebrates for consumption by larvae. In contrast, the LR supports a small, low-density population of *C. alleganiensis*. Gilled larvae were frequently found and represent almost half of the *C. alleganiensis* we captured. Scattered shallow, gravel accumulations are present, but the limited interstitial spaces were often filled with sand. The small population of crayfish supports a small population of sub-adult and adult *C. alleganiensis* skewed toward small individuals < 20 cm TL.

We hypothesize that the stream bottom substrate of NFWR, especially the large deep gravel beds, provided a more secure habitat for larvae than in LR. This larval habitat was presumably a major factor in the maintenance of large adult populations in NFWR. Adult *C. alleganiensis* populations were low in LR relative to NFWR, but larvae were much more susceptible to capture because the stream bottom substrate provided a less secure habitat.

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