# POPULATION STRUCTURE OF THE HELLBENDER (*CRYPTOBRANCHUS ALLEGANIENSIS*) IN A GREAT SMOKY MOUNTAINS STREAM

Kirsten A. Hecht-Kardasz[1], Max A. Nickerson[2], Michael Freake[3],
and Phil Colclough[4]

## ABSTRACT

The hellbender (*Cryptobranchus alleganiensis*) is an imperiled salamander that has experienced population declines in many parts of its range. Young hellbenders, particularly larvae, have rarely been found in the wild. In 2000, a short study in Little River in Great Smoky Mountains National Park, Tennessee, discovered a population of *C. alleganiensis* where larvae were regularly encountered and few adults were observed. However, the 2000 study was limited in scope, and additional research was needed to accurately describe the overall hellbender population structure. Three additional studies of *C. alleganiensis* in the same section of Little River occurred from 2004–2010. This paper analyzes the results of all four studies conducted between 2000–2010 to examine trends in the hellbender population structure within Little River, and to provide reference data for future monitoring efforts in the park. From 2000–2010, a total of 533 captures, including 33 recaptures, occurred with larvae representing a quarter of overall captures. Adults were more abundant than suggested by the 2000 study, but individuals representing larger size classes were still relatively rare. Although the structure of the sampled population varied among years, larvae were relatively abundant except following years of extreme stream flow events, suggesting that turbulent current may be an important influence on the population structure of Little River's hellbender population.

**Key Words:** hellbender, *Cryptobranchus alleganiensis*, Great Smoky Mountains, amphibian population, salamanders, population structure, size structure.

[1]School of Natural Resources and Environment, University of Florida, Gainesville, FL 32611-6455 USA <kirstenhecht@ufl.edu>
[2]Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-7800 USA <maxn@flmnh.ufl.edu>
[3]Department of Natural Sciences and Mathematics, Lee University, Cleveland, TN 37320-3450 USA <mfreake@leeuniversity.edu>
[4]Knoxville Zoological Gardens, 3500 Knoxville Zoo Drive, Knoxville, TN 37914-4416 USA <pcolclough@knoxville-zoo.org>

---

Hecht-Kardasz, K. A., M. A. Nickerson, M. Freake, & P. Colclough. 2012. Population structure of the hellbender (*Cryptobranchus alleganiensis*) in a Great Smoky Mountains stream. Bulletin of the Florida Museum of Natural History 51(4):227–241.

## INTRODUCTION

Size, age, or life stage structures are integral components to understanding population dynamics and can give more insight into population status than population size estimates alone (Alexander 1958; Downing 1980; Gillespie 2010). In species of conservation concern, demographic composition can indicate overall population stability and lead to more accurate predictions regarding future population trends (Crowder et al. 1994). A population composed primarily of older individuals may be at risk of decline or extirpation due to low recruitment (Alexander 1958; Downing 1980). A population with few older individuals, but many young individuals could indicate population growth, high adult mortality, or a failure to recruit young life stage classes into adults (Alexander 1958; Downing 1980). Understanding population structure is also important because demographic rates can vary among different segments of the population (Crowder et al. 1994; Dobson & Oli 2001).

In aquatic environments, organisms often adapt life strategies that can cause differences in demographic rates among age or life stage classes (Duellman & Trueb 1986; Pough et al. 2004). Many species, including fish, aquatic insects, and amphibians, develop complex life cycles or ontogenetic shifts in habitat use and diet, which are believed to be adaptations for increasing survival in a stressful environment (Werner & Gilliam 1984; Foster et al. 1988; Giller & Malmqvist 1998). These types of shifts can serve as a form of refugia, limiting intra-specific competition and predation (Werner & Gilliam 1984; Colley et al. 1989; McGrath et al. 2007). While these adaptations may help reduce individual mortality, they can also make studying population dynamics more complicated. The difficulties associated with studying organisms with complex life cycles or ontogenetic shifts have caused knowledge gaps in the field of amphibian population ecology.

Although many amphibian populations are declining worldwide (Alford & Richards 1999; Vié et al. 2009), population dynamics and demographics of many species remain unstudied (Duellman & Trueb 1986; Alford & Richards 1999; Swanack et al. 2009; Gillespie 2010). As obtaining amphibian population and life history data that accurately considers all life stage classes can be problematic due to complex life cycles and ontogentic shifts, data are often lacking for specific size or life stage classes (Swanack et al. 2009; Gillespie 2010). Larval and juvenile classes can be difficult to study because they are generally cryptic, small, and sometimes use different habitats than other life stages (Gillespie 2010). The resulting gaps in population structure data have hindered researchers from fully comprehending the scope of amphibian declines (Lips 2011). The failure to elucidate potential mechanisms affecting individual amphibian populations has limited mitigation efforts (Alford & Richards 1999; Gillespie 2010). Once population declines occur, information is even more difficult to obtain as individuals become rare (Gillespie 2010).

One amphibian species with few studies regarding its basic demographics and population dynamics is the hellbender salamander, *Cryptobranchus alleganiensis* (Daudin 1803). A member of the giant salamander family Cryptobranchidae, this long-lived (at least 29 years), large (740 mm), aquatic species resides primarily in cool, oxygen-rich streams in the eastern United States (Nickerson & Mays 1973a). There are currently two accepted subspecies: the eastern hellbender, *Cryptobranchus alleganiensis alleganiensis* (Daudin 1803) which ranges from Missouri to New York, and the Ozark hellbender, *Cryptobranchus alleganiensis bishopi* (Grobman 1943) found only in Missouri and Arkansas (Nickerson & Mays 1973a). Currently listed as near threatened on the International Union for Conservation of Nature (IUCN) red list (Hammerson & Phillips 2004), hellbender populations appear to be declining in many parts of its range (Trauth et al. 1992; Wheeler et al. 2003; Briggler et al. 2007; Foster et al. 2009; Nickerson et al. 2009; Burgmeier et al. 2011). The exact cause or causes of declines remain difficult to elucidate, but siltation, disease, collection, species introductions, and habitat loss are just some of the cited problems facing this species (Trauth et al. 1992; Hiler et al. 2005; Briggler et al. 2007; Nickerson & Briggler 2007; Nickerson et al. 2009). Due to these declines, the hellbender is protected at the state-level throughout most of its range, and was recently added to CITES appendix III and the federal endangered species list (Anonymous 2011).

Despite the conservation interest in *Cryptobranchus alleganiensis*, data regarding the population dynamics of this species remain sparse. Many hellbender localities lack data regarding population size, status, and demographics. Population studies have primarily focused on snapshot estimates of population size or adult population structure. Few studies have examined growth rates, fecundity, and survivorship in hellbenders and those that have were restricted to a few localities in Missouri (Taber et al. 1975; Topping & Ingersol 1981; Peterson et al. 1988). Existing examples may not be representative for hellbenders across their range, particularly for the eastern subspecies.

Limited historical data from a few studied drainages in New York and Missouri have given better insight into long-term hellbender population trends and indicated that some populations were declining and shifting in overall structure (Wheeler et al. 2003; Foster et al. 2009). Comparisons of historical and recent data in Missouri populations suggested that in declining hellbender populations, size class distributions shifted towards larger individuals, possibly indicating inadequate recruitment (Wheeler et al. 2003). Foster et al. (2009) noted shifts in the sex ratio towards a male-biased population in the declining hellbender populations of New York's Allegheny River drainage. In both of these studies, few young individuals < 20 cm (i.e. larvae and small subadults) were sampled. It remains uncertain whether these size classes were largely absent from the population or inadequately sampled perhaps due to their association with interstitial spaces in gravel beds (Nickerson & Krysko 2003). Regardless, little is known about larval hellbenders, and few studies include data on larvae.

In 2000, a short survey of the hellbender population in Little River, Tennessee, yielded 33 individuals, of which 48% (n = 16) were larval sized (< 130 mm) (Nickerson et al. 2002). This percentage was in stark contrast to those recorded for other hellbender populations (e.g., Peterson et al. 1988; Wheeler et al. 2003; Foster et al. 2009). Furthermore, the proportion of adult hellbenders to larvae within Little River was the lowest of any studied river system (Nickerson et al. 2003). However, the findings of Nickerson et al. (2002) were limited by small sample size and reduced search hours. Additional data were needed to confirm the differences in population structure in Little River from those in well-studied streams. We compiled and analyzed data from surveys conducted in Little River from 2004–2010 with the results of Nickerson et al. (2002) in order to investigate the size structure of the hellbender population in Little River, provide reference data for this site, and to investigate long-term trends in population structure.

## MATERIALS AND METHODS

### STUDY SITE

To better elucidate the structure of Little River's hellbender population within Great Smoky Mountains National Park, skin-diving surveys were conducted within the 3 km section investigated by Nickerson et al. (2002). Little River, located in the Blue Ridge Physiographic Province of eastern Tennessee, originates on the north slope of Clingmans Dome, the highest topographical point in both the state and Great Smoky Mountains National Park. Draining ~980 km$^2$, Little River flows through the park and several small towns before joining the Tennessee River. Human disturbance, including farming and logging related activities, historically occurred within the present boundary of Great Smoky Mountains National Park (Mast & Turk 1999). Many forests remain in successional stages following the cessation of widespread logging activity in 1939 (Madden et al. 2004). Few large-scale landscape alterations have occurred after 1950 in the park area adjacent to Little River, but human recreational use is common. Spanning 2,108 km$^2$, Great Smoky Mountains National Park is the most visited national park in the United States and receives over 9 million visitors each year

(Madden et al. 2004). Little River attracts tourists year-round including a large number of swimmers, snorkelers, and inner tube users during the warmer months, and fishermen throughout the year (pers. obs.). Building temporary rock dams, disturbing rocks, and kayaking are other frequent activities in the stream (pers. obs.).

Little River's exposed bedrock of Late Precambrian Elkmont and Thunderhead metamorphosed sandstone has eroded over time leaving great numbers of dense rounded boulders, cobble, and gravel in the streambed (Mast & Turk 1999). Macroscopic in-stream vegetation was rare during the 2000–2010 survey period. Elevation within the study area ranged from 327–407 m. Surrounding upland habitat was comprised primarily of pine and river cove hardwood forest (Madden et al. 2004). Scenic TN 73, constructed on the site of the former logging railroad that ran along Little River, had several concrete/gravel parking lots and pull-offs providing walking access to Little River. The river was difficult to access near some pull-offs because of steep boulder-covered slopes.

### Field Sampling Methods

Diurnal skin-diving surveys were conducted in Little River between June and October of 2004–2010 in order to locate *Cryptobranchus alleganiensis*. Skin-diving was chosen as the survey method due to its success in locating all size classes of hellbenders (Nickerson & Mays 1973a; Nickerson & Krysko 2003; Nickerson et al. 2003). During 2000, and most occasions in 2008–2010, the amount of time each individual surveyor spent searching for hellbenders was recorded. Surveyors worked upstream, against the current, to prevent visibility issues from displaced sand and silt. Rocks and other potential shelters were mostly hand turned towards the surveyor to limit disturbance to the streambed particles, but studies conducted by Lee University utilized log peaveys to lift large rocks. Rocks were replaced in their original position and orientation. Encountered hellbenders were captured by hand and taken to the river bank for data collection and tagging.

The total length (TL) and snout-vent length (SVL) of each hellbender was measured in millimeters (mm) with the aid of a ruled, modified PVC pipe. Mass was recorded in grams using an Ohaus® CS2000 compact digital scale (accuracy ±1.0 g; Ohaus Corporation, Parsippany, NJ, USA), DYMO® Pelouze SP5 digital scale (accuracy ±1.0 g; DYMO, Norwalk, CT, USA), or Pesola® spring scale (accuracy ±0.3%; Pesola AG, Baar, Switzerland). Sex was recorded if it could be determined based on the swelling of male cloacal glands in August and September (Nickerson & Mays 1973a). Biomark 9 mm and 12.5 mm Passive Integrated Transponder (PIT) tags (Destron-Fearing, South Saint Paul, MN, USA) were injected dorsal-laterally near the base of the tail in adult and most subadult individuals. Individuals as small as 140 mm TL were tagged, but no standardized minimum hellbender size for injection was used across studies. PIT tag injection needles were disinfected in a 70% ethanol solution between each use. New Skin® liquid bandage (Prestige Brands, Inc., Irvington, NY, USA) was applied at injection sites. From 2008–2010, unique individual combinations of Visible Implant Elastomer (VIE) (Northwest Marine Technology, Inc., Shaw Island, WA, USA) were injected posterior to the limbs on the ventral side of 48 individuals too small for PIT tag injection. New VIE injection needles were used daily, and needles were disinfected with rubbing alcohol wipes between uses. Individuals were returned to their capture site following data collection. GPS localities were recorded using an eTrex® Legend and GPSMAP® 76CSx (Garmin International, Inc., Olathe, KS, USA).

### Data Analysis

Mean mass and TL of hellbenders sampled across all years was calculated. Histograms of annual and combined *Cryptobranchus alleganiensis* size class distribution in Little River were constructed based on individual TL. All histograms used 25 mm intervals. Recaptured hellbenders were only represented once in the combined histogram, but we only eliminated individuals recaptured within a single year from the yearly histograms. To determine if the size distribution of Little River's hellbenders was statistically different from a representative sampled population, our hellbender TL data were compared to data from one of most well-studied hellbender streams, the North Fork of the White River, Missouri (Nickerson & Mays 1973b). Data from the 1969 North Fork of the White River population were used for this comparison because the population has since experienced substantial declines (Wheeler et al. 2003; Nickerson & Briggler 2007), and these data are the best available baseline. To reduce potential bias from unmarked individuals in Little River, data from only the two years with the largest sample sizes that were not directly impacted by flooding (2006 and 2008) were used for analysis. Data were tested against the North Fork of the White River historical data using two-sample boot-strap Kolmogorov-Smirnov tests. The ks.boot function, from R Package "Matching" (Sekhon 2011), tested whether probability densities for TL data from the two rivers were the same. The significance level for these tests was set at $\alpha = 0.05$.

Size classes may not always correlate with life stage classes, so hellbenders were also divided into life stage classes based on individual total length. Based on previous research, individuals < 125 mm in TL, both gilled and non-gilled, were classified as larvae (Bishop 1941; Nickerson & Mays 1973a). Previous *Cryptobranchus alleganiensis* studies suggested that size at sexual maturity differs among sex and locality, but generally ranges from 300–390 mm TL (Dundee & Dundee 1965; Taber et al. 1975; Peterson et al. 1988). While sex could not be determined for most animals captured during this study period, one small individual of 285 mm TL was verified as sexually mature during late summer because of a swollen cloaca. Due to this capture as well as the general lack of larger adults in Little River, sexual maturity was estimated at 275 mm TL for this analysis. All individuals measuring 125–275 mm TL were considered subadults. Finally, search effort was calculated as the number of person hours required to locate one hellbender. Data analyses were completed using Microsoft Excel for Mac (2008) and R (version 2.12.2; R Development Core Team 2008).

## RESULTS

During 2000–2010, there were 533 total hellbender captures (168 larvae, 159 subadults, and 206 adults) including 33 recaptures of 27 individuals. Three hundred fifty-six individuals were tagged. Sex was determined for 38 individuals (23 males; 15 females). In 2000, search effort to collect one hellbender was 2.54 hrs (n = 33; Nickerson et al. 2002). During additional surveys by the University of Florida from 2008–2010, search effort varied annually [2008 = 3.43 hrs/hellbender (n = 32); 2009 = 5.01 hrs/hellbender (n = 6); 2010 = 2.50 hrs/hellbender (n = 80)] and was 2.88 hrs/hellbender across all three years (n = 118). Mean TL (±SD) for hellbenders across all years in Little River (n = 500) was 218.1 mm (±130.1). Mean mass (±SD) of hellbenders of all size classes (n = 494) was 115.1 g (±142.5), but was influenced by the large number of larval individuals. Mean mass (±SD) of adults (n = 183) was 266.6 g (±128.3). All three life stage classes were well represented over the study period, and 25% of the total captured individuals were classified as larvae. A sharp decline from the 50–75 mm TL size class to the 75–100 mm TL size class was noted, suggesting low survival of hellbenders between the first and second year (Fig. 1). Size class distribution varied among years, but larvae were generally abundant in the population samples (Fig. 2). Hellbender size class distributions from Little River in 2006 (n = 113) and 2008 (n = 117) were statistically different from the 1969 North Fork of the White River population (n = 478; Fig. 3) based on results of Kolmogorov-Smirnov bootstrap tests ($D = 0.584$, $p < 0.001$; $D = 0.284$, $p < 0.001$, respectively).

## DISCUSSION

An understanding of the overall population structure, particularly over time, was needed to verify that the Little River population was in fact unique in its larval component from the majority of studied populations. Overall, the population in Little River over the last decade appears stable with regular recruitment of young individuals and representation of all size classes. Our results were consistent with the results of Nickerson et al. (2002) as larvae represented a significant proportion of the sampled hellbender population both overall and in individual years. Although we captured more adult *Cryptobranchus alleganiensis* since the original study by Nickerson et al. (2002), the general trend of capturing few large adults over 450 mm TL remained. Over the 10 year study period, we captured fewer adults in every size interval, particularly > 475 mm, than were captured in the North Fork of the White River in 1969 (Fig. 4). It remains unclear, however, whether these observations represent true differences in population structure or differences in detectability.

Studies in the Little River suggest that larval-sized hellbenders primarily utilize cobble and boulders for shelter (Nickerson et al. 2003; Freake & Hecht unpubl. data). Unlike rivers where larvae have been located within gravel beds (Nickerson et al. 2003), larval hellbenders in the Little River can be readily sampled using standard skin-diving methods. Researchers in other localities have not normally used methods to search additional habitats where larval hellbenders might be located (Nickerson & Krysko 2003; Foster et al. 2009). A recent study in the Allegheny River drainage of New York found that despite a decrease in the density of *Cryptobranchus alleganiensis* at study sites within the last 20 years, more individuals

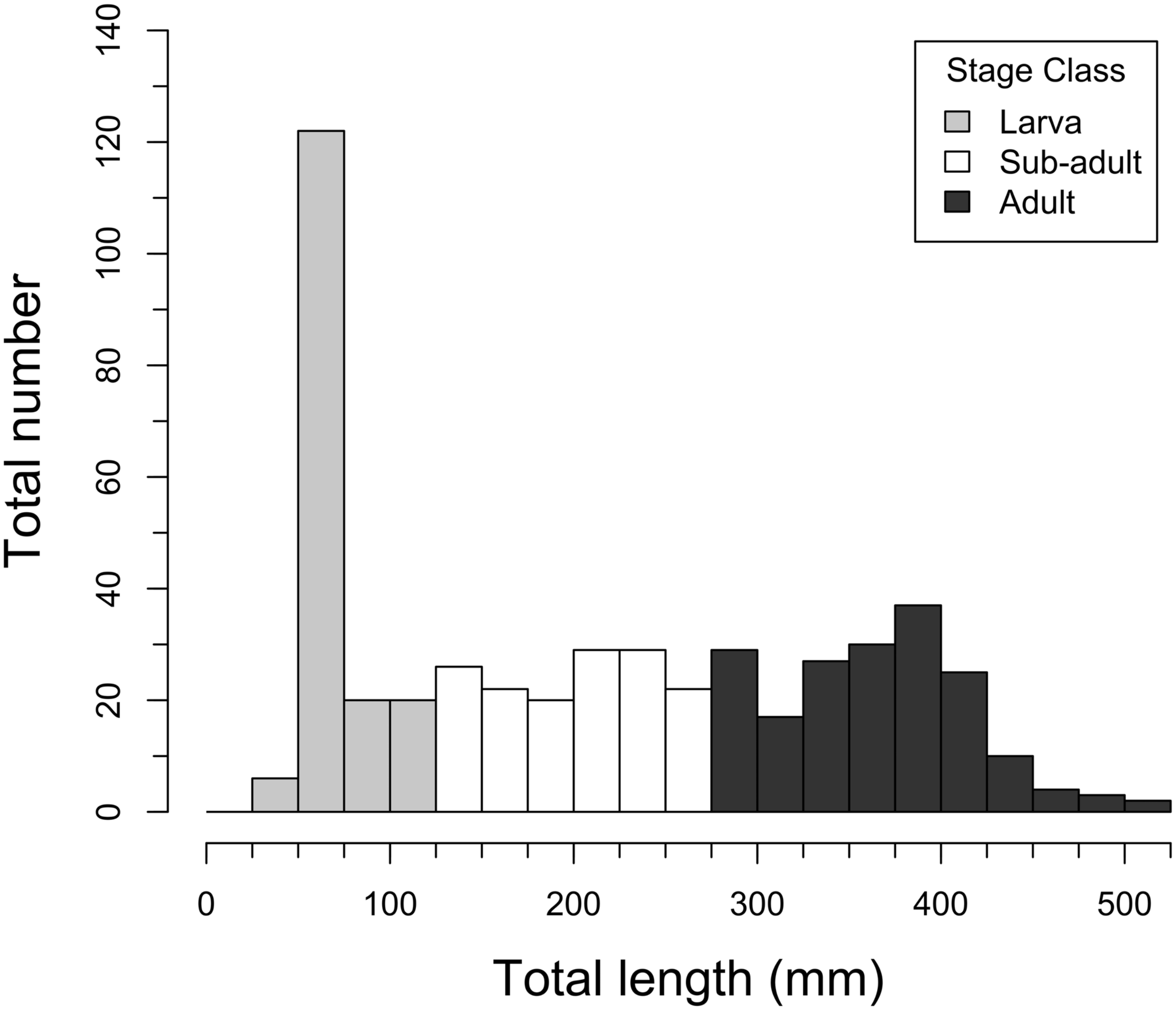

**Figure 1.** Size distribution of captured hellbenders (*Cryptobranchus alleganiensis*) from 2000–2010 in the Little River, Tennessee (n=500).

< 20 mm were captured recently than in the 1980s presumably because of methods specifically targeting these size classes (Foster et al. 2009). It is also unclear how deep larvae may reside within gravel beds in other localities so many larvae may not be accessible even with methods specifically targeting their habitat. Larval hellbenders could potentially be present in some other localities, but not adequately represented in the sample due to low detectability rates. Larger adults may also avoid detection in Little River. Due to the density of rocks and the presence of very large boulders that could not be lifted, individuals may have been missed during surveys. In addition, deep pools > 3 m in depth, which *C. alleganiensis* sometimes inhabit in other rivers (Green 1933; Nickerson & Mays 1973a), were not surveyed.

Recent studies conducted in other localities within the Blue Ridge Province have also produced young *Cryptobranchus alleganiensis* (Maxwell 2009; Groves & Williams 2011; Burgmeier et al. 2011; Freake unpubl. data). Approximately 21% of hellbenders captured during surveys in the Hiwassee River of the Cherokee National Forest

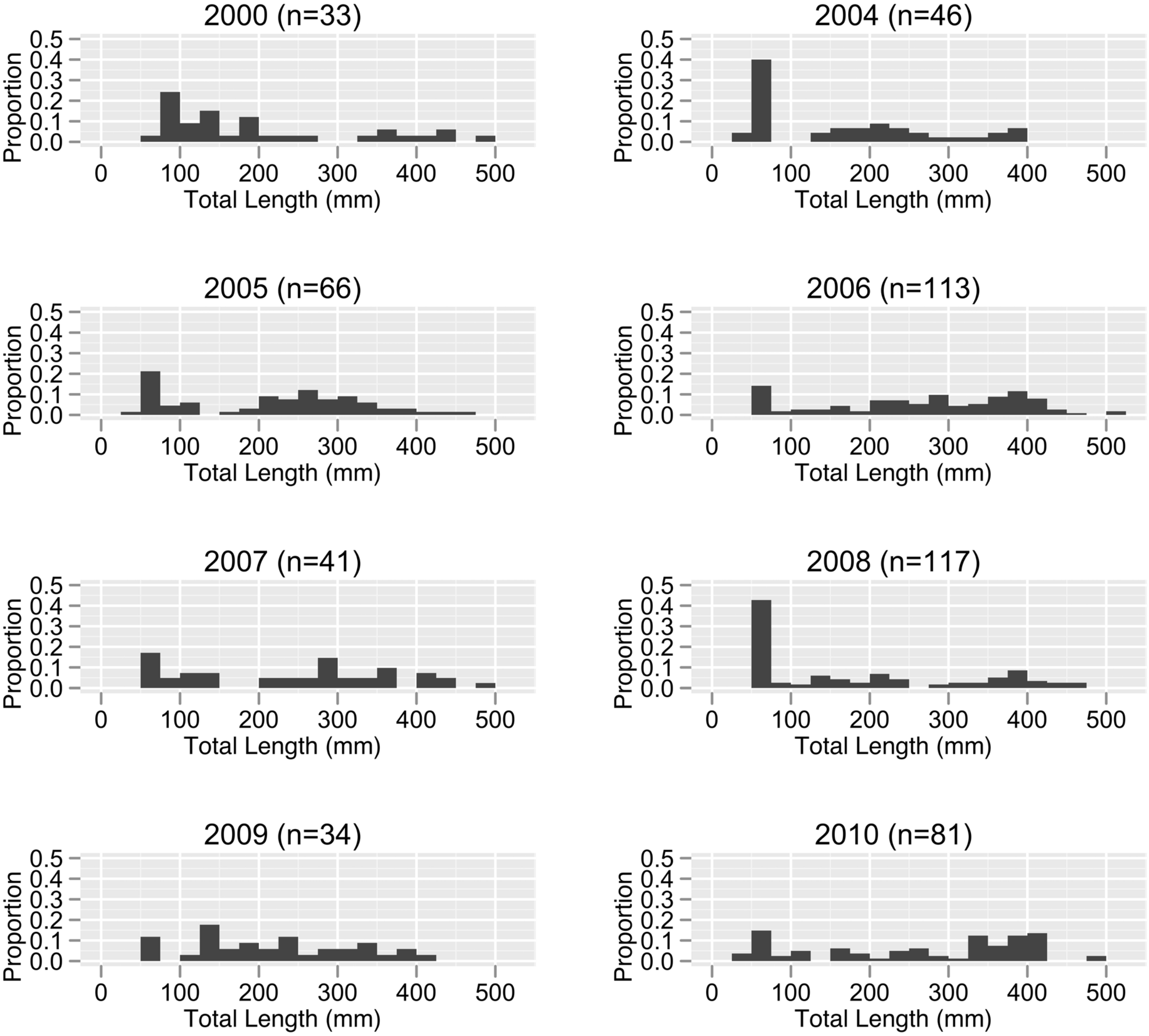

**Figure 2.** Yearly size distribution of captured hellbenders (*Cryptobranchus alleganiensis*) from 2000–2010 in the Little River, Tennessee.

in Tennessee were larval-sized individuals (Freake unpubl. data). Short surveys of the Pigeon River in North Carolina's Blue Ridge region produced 3 larvae out of only 6 individuals captured (Maxwell 2009). Larvae were located in northern Georgia and other western North Carolina populations (Burgmeier et al. 2011; Groves & Williams 2011). These Blue Ridge populations also do not appear to be impacted by disease and/or serious abnormalities (Groves & William 2011; Gonynor et al. 2011; Souza et al. 2012) as in other regions (Miller & Miller 2005; Hiler et al. 2005, Nickerson et al. 2009).

Due to geology, topography, and history, the Blue Ridge Province, which has the highest proportion of interior forest habitat in the Southern Appalachian region, remains 80% forested (SAMAB 1996a, 1996b). Relatively

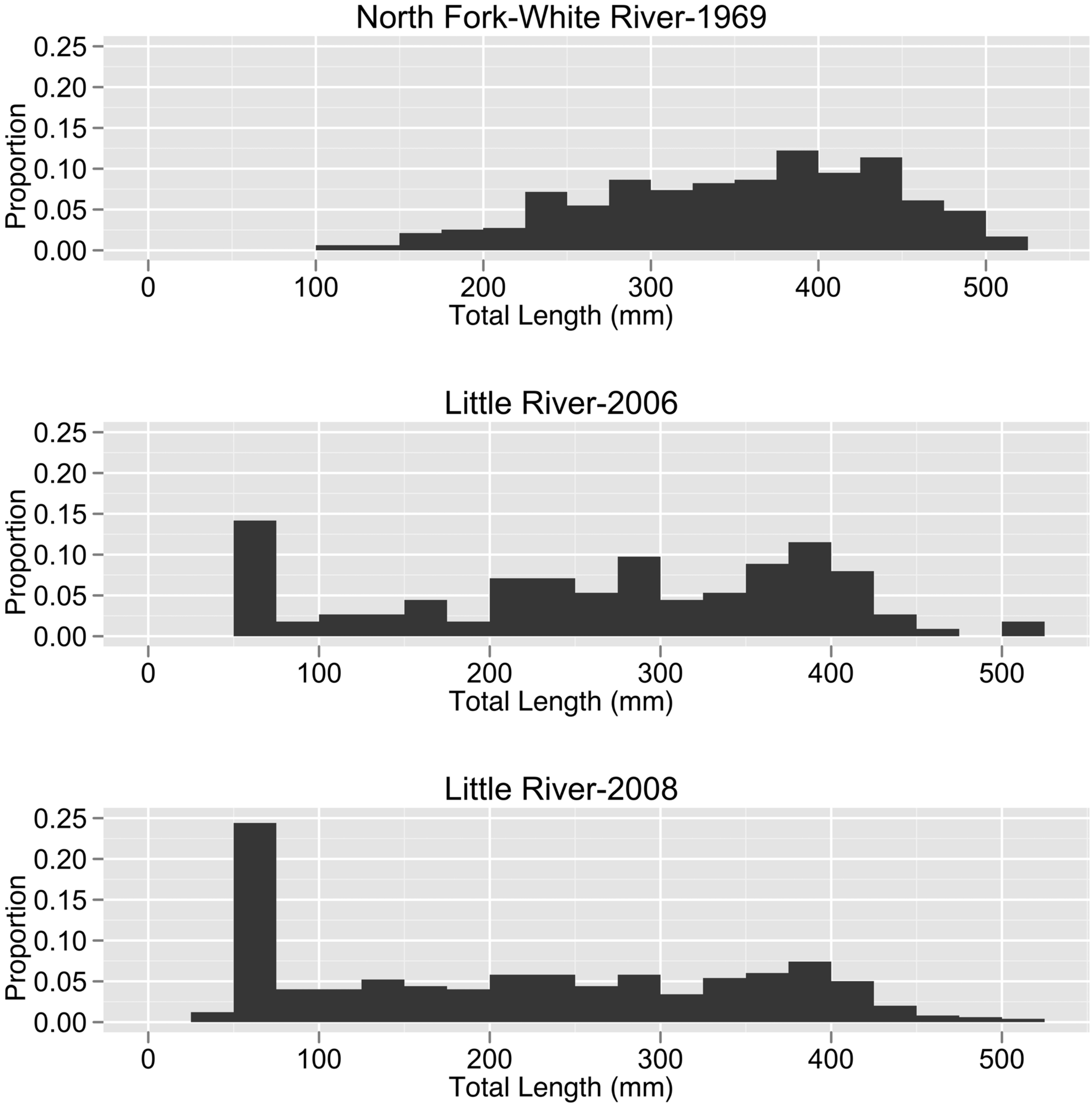

**Figure 3.** Comparison of hellbender (*Cryptobranchus alleganiensis*) size class distributions sampled from the Little River, Tennessee in 2006 (n=113) and 2008 (n=117), with the North Fork of the White River, Missouri in 1969 (n=478).

large portions of the Blue Ridge, including the greatest concentration of public lands in the eastern United States, are now protected due to aesthetics and ecological value (SAMAB 1996a, 1996b; Fig. 5). Therefore, the abundance of larvae seen throughout the Blue Ridge Province may be partially due to the decrease in factors which have been suspected in hellbender declines such as siltation, channelization, agriculture, mining, and pollution (Dundee 1971; Nickerson and Mays 1973a; Bury et al. 1980). Recent studies by Groves and Williams (2011) noted a negative correlation between human development and hellbender densities, but the finding was not statistically significant. Many historically studied hellbender populations in West Virginia's Appalachian Plateau and Valley and Ridge regions appear to be declining, except for some located in the protected Monongahela National Forest (Keitzer 2007). This supports the hypothesis that human disturbance,

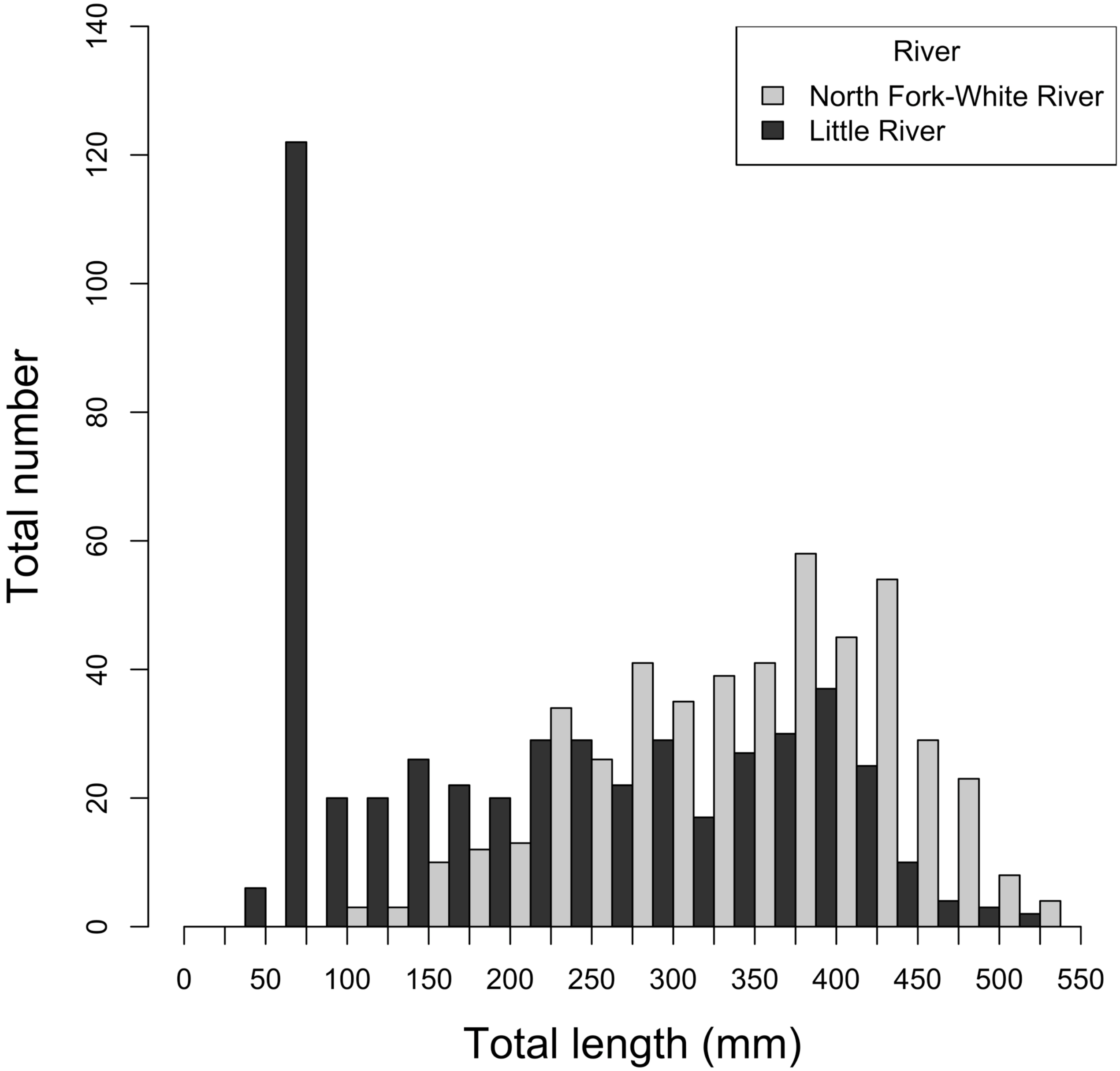

**Figure 4.** Size class distribution of hellbenders (*Cryptobranchus alleganiensis*) captured in the Little River, Tennessee from 2000–2010 (n=500) and the North Fork of the White River, Missouri in 1969 (n=478).

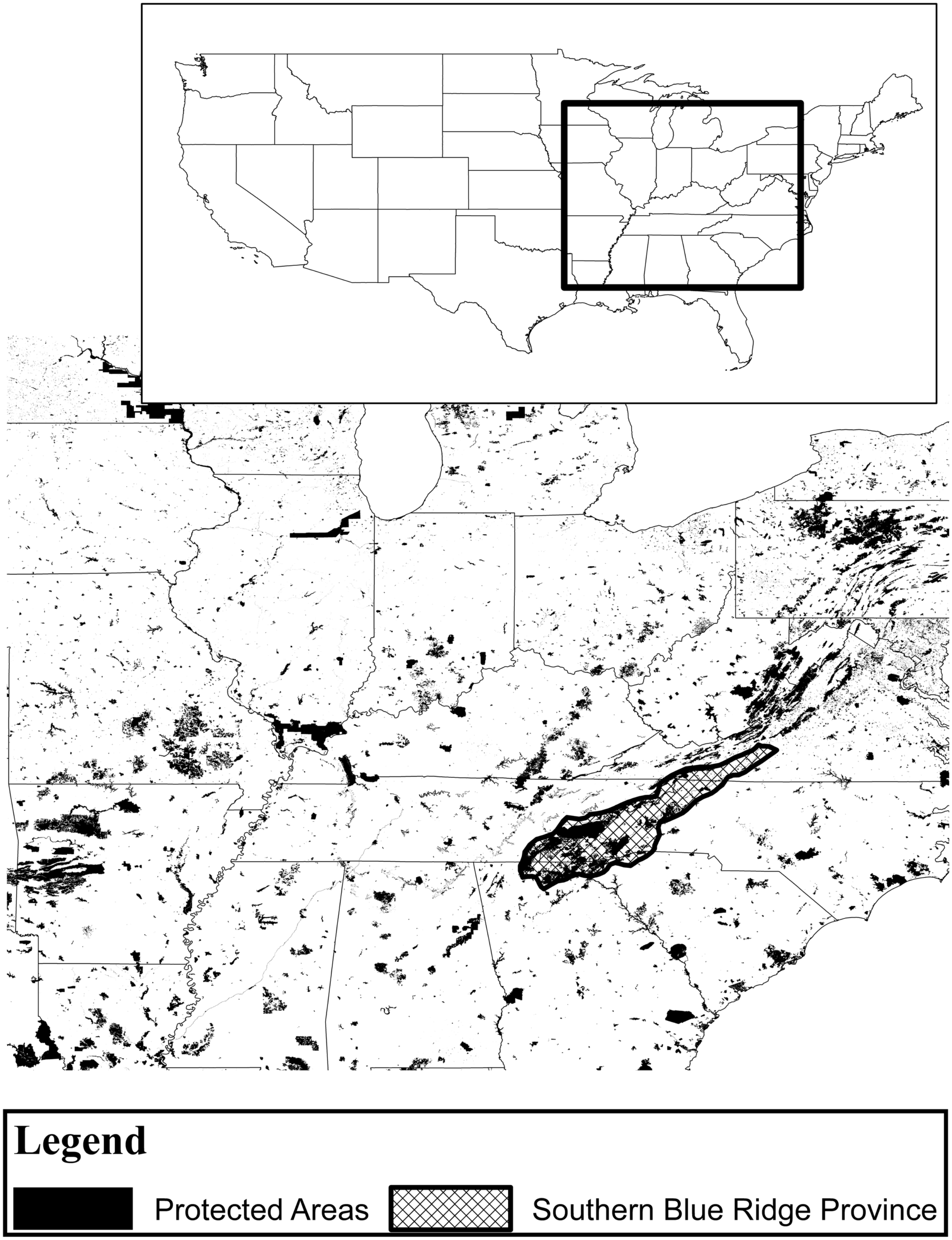

**Figure 5.** Map of the eastern United States showing protected areas in the southern Appalachian and Ozark regions (Modified from Fenneman and Johnson 1946; U.S. Geological Survey 2011).

rather than geology alone, may be a major influence on hellbender populations.

Life stage classes were relatively well represented throughout the study period, but many size classes were absent or low in abundance in the individual years. Water regimes can influence the population structure of stream-dwelling amphibians by affecting mortality and recruitment (Metter 1968; Duellman and Trueb 1986). Flooding has been suspected as a source of mortality in hellbenders (Trauth et al.1992; Humphries 2005; Miller & Miller 2005; Nickerson et al. 2007), but its influence on population dynamics remains unclear. Nickerson et al. (2007) noted that following flooding of the Middle Prong of Little River in 2003, no individuals were captured within the stream the following year despite previously finding four larvae in only eight hours of searching. Second year larvae were also absent from the main portion of Little River in 2004. In 2005, no individuals 125–150 mm TL were captured, and only three individuals measuring 150–200 mm TL were found. Additional small-scale flooding events in 2009 correlated with a missing size class (small subadults from 125–150 mm TL) the following year.

Nickerson et al. (2007) examined the potential impacts of flooding on hellbenders in the Middle Prong of Little River, and cited USGS stream flow readings from station 03497300 beginning in 1997. An examination of peak stream flow data taken at the station within Little River prior to 1997 revealed an extreme flooding event in 1994, where peak stream flow was over 750 $m^3/s$ (Fig. 6). Unfortunately no data on *Cryptobranchus alleganiensis* populations in Little River are available prior to 2000 to illuminate the effects of this flood on hellbender population structure. However, data from the Great Smoky Mountain National Park's fisheries division found no young of year brown trout (*Salmo trutta*) and few young of year rainbow trout (*Oncorhyncus mykiss*) following the 1994 flooding, suggesting that other taxa were affected by the flooding (Kulp pers. comm.). It is therefore possible that this extreme flooding event also had a substantial impact on the hellbenders in Little River, potentially contributing to the lack of large individuals seen in the river today.

As individual growth rates of *Cryptobranchus alleganiensis* slow with age (Taber et al. 1975; Peterson et al. 1988) and no growth studies are available for the Little River population, it is difficult to follow cohorts through time based on the available data. However, two size classes (125–150 mm; 300–325 mm), possibly correlating to flooding events in 2003 and 2009 (Fig. 6), were under-represented in Little River's 2010 size class distribution (Fig. 2). Water regimes may be an important influence on hellbender recruitment in Little River, leading to long-term impacts on the population structure. Potential reductions in recruitment following flooding events could be related to larval *C. alleganiensis* habitat use within Little River. Nickerson et al. (2003) hypothesized that larval hellbenders in Little River were forced to use less secure shelters due to the lack of interstitial spaces within the gravel beds.

While turbulent current may influence size structure of the *Cryptobranchus alleganiensis* population in Little River, additional factors could also be affecting this population. Nickerson et al. (2003) suggested that the habitat used by larvae within Little River, in conjunction with relatively small crayfish populations, might explain the hellbender population structure. The relatively unsecure habitat of larval hellbenders in Little River may increase mortality by escalating predation risk and competition with both conspecifics and other organisms, leading to reduced recruitment to the adult stage. In addition, the studied portion of Little River appears to have relatively low densities of crayfish (Nickerson et al. 2003; Hecht & Freake unpubl. data), which could affect the size structure of adults by reducing overall growth potential or increasing mortality. Most adults captured in Little River appeared relatively thin, and the average mass of adult *C. alleganiensis* was less than reported in other localities (Nickerson & Mays 1973a; Burgmeier et al. 2011), but the impacts of this trend remain unclear.

While additional study may be needed to confirm the factors influencing Little River's hellbender population, the overall population appears to be stable and reproducing. Long-term monitoring of the population structure will help confirm whether the lack of large adults in the last 10 years is a result of the flooding event in 1994 or is instead related to other factors, such as the reduced crayfish population in Little River. Following new cohorts after flooding events in Little River will also increase our understanding of the effects of stream flow on *Cryptobranchus alleganiensis* populations. Predictions of more frequent intense precipitation events due to climate change (Bates et al. 2008) may lead to an increase in flooding events in some hellbender streams. Flooding induced mortality may therefore become an important consideration in future hellbender conservation efforts.

## ACKNOWLEDGMENTS

Thank you to Dr. Marcy Souza, The Great Smoky Mountains Institute at Tremont, Dr. Perran Ross, Dr. Mary Christman, Dr. Ken Dodd, the Williams Lab at Purdue University, and all volunteers for assistance on this project. We would also like to acknowledge Paul Super, Keith Langdon, and the National Park Service. Financial support for this research was provided by the Great Smoky Mountains Conservation Association: Carlos C. Campbell Fellowship, The Reptile and Amphibian Conservation Corp (RACC), the Cryptobranchid Interest Group: Jennifer Elwood Conservation Grant, U.S. Geological Survey (U.S. Department of Interior), Max Allen's Zoological Gardens, and the Arkansas State Faculty Grant. Research was conducted under permits from the National Park Service (GRSM-2009-SCI-0061, GRSM-2009-0056, GRSM-2008-SCI-0052, GRSM-00-131), scientific collecting permits from the Missouri Department of Conservation, University of Florida, IACUC (#A560), and University of Florida ARC Protocol (#017-08WEC).

## LITERATURE CITED

Alexander, M. M. 1958. The place of aging in wildlife management. American Scientist 46(2):123–137.

Alford, R. A., & S. J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30:133–165.

Anonymous. 2011. Endangered and threatened wildlife and plants; endangered status for the Ozark hellbender salamander. Federal Register 76(194):61956–61978.

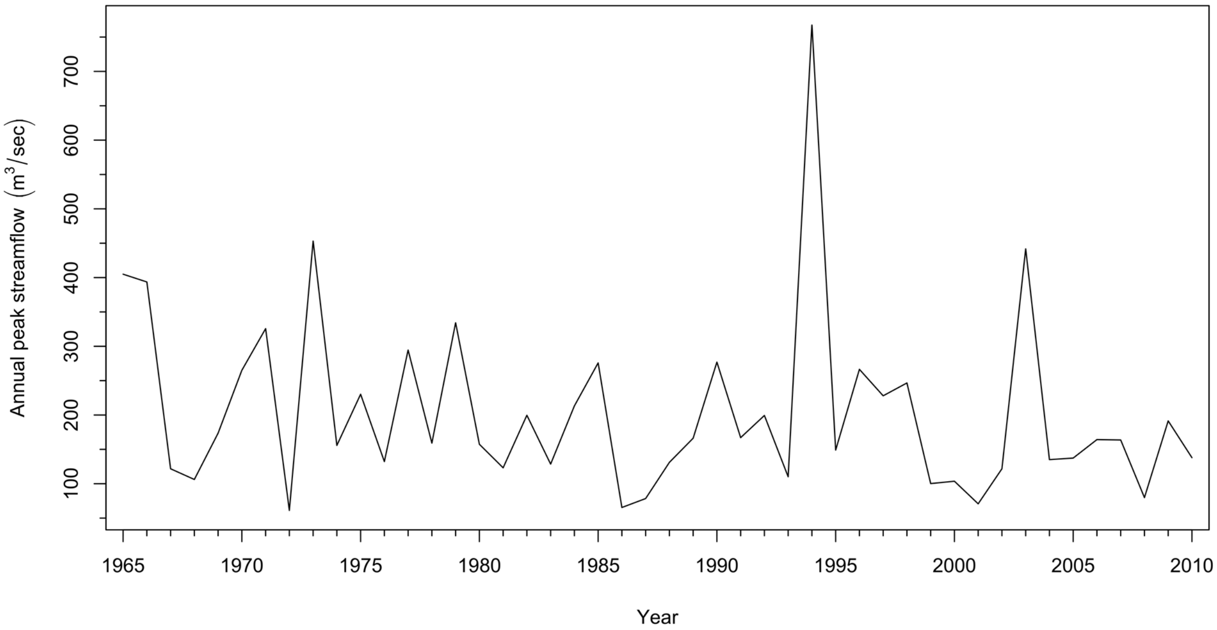

**Figure 6.** Peak streamflow of water years 1965–2010 at Little River, Tennessee, USGS station within the Great Smoky Mountains National Park (Modified from U.S. Geological Survey 2001).

Bates, B. C., Z. W. Kundzewicz, S. Wu, & J. P. Palutikof, eds. 2008. Climate Change and Water. Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva, Switzerland, 210 p.

Bishop, S. C. 1941. The Salamanders of New York. New York State Museum Bulletin. The University of the State of New York, Albany, 365 p.

Briggler, J., J. Utrup, C. Davidson, J. Humphries, J. Groves, T. Johnson, J. Ettling, M. Wanner, K. Traylor-Holzer, D. Reed, V. Lindgren, & O. Byers, eds. 2007. Hellbender Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota, 118 p.

Burgmeier, N., S. D. Unger, T. M. Sutton, & R. N. Williams. 2011. Population status of the eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*) in Indiana. Journal of Herpetology 45(2):195–201.

Bury, R. B., C. K. Dodd Jr., & G. M. Fellers. 1980. Conservation of the Amphibia of the United States: a review. Resource Publication 134, U.S. Fish and Wildlife Service, Washington, 34 p.

Colley, S. W., W. H. Keen, & R. W. Reed. 1989. Effects of adult presences on behavior and microhabitat use of juveniles of a desmognathine salamander. Copeia 1989(1):1–7.

Crowder, L. B., D. T. Crouse, S. S. Heppell, & T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4(3):437–45.

Dobson, F. S., & M. K. Oli. 2001. The demographic basis of population regulation in Columbian ground squirrels. The American Naturalist 158(3):236–247.

Downing, R. L. 1980. Vital Statistics of Animal Populations. Pp. 247–266 *in* S. D. Schemnitz, Ed. Wildlife Management Techniques Manual. The Wildlife Society, Inc., Bethesda, Maryland.

Duellman, W. E., & L. Trueb. 1986. Biology of Amphibians. McGraw–Hill Book Company, New York, 670 p.

Dundee, H. A. 1971. *Cryptobranchus alleganiensis*. Catalogue of American Amphibians and Reptiles. SSAR:101.1–101.4.

Dundee, H. A., & D. S. Dundee. 1965. Observations on the systematics and ecology of *Cryptobranchus* from the Ozark Plateaus of Missouri and Arkansas. Copeia 1965(3):369–370.

Fenneman, N. M., & D. W. Johnson. 1946. Physical divisions of the United States: U.S. Geological Survey. Retrieved from http://water.usgs.gov/GIS/metadata/usgswrd/physio.html.

Foster, R. L., A. M. Mcmillan, & K. J. Roblee. 2009. Population status of hellbender salamanders (*Cryptobranchus alleganiensis*) in the Alleghany River Drainage of New York State. Journal of Herpetology 43(4):579–588.

Foster, S. A., V. B. Garcia, & M. Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74(4):577–585.

Giller, P. S., & B. Malmqvist. 1998. The Biology of Streams and Rivers. Oxford University Press, Inc., New York, 296 p.

Gillespie, G. 2010. Population age structure of the spotted tree frog (*Litoria spenceri*): insights into population declines. Wildlife Research 37:19–26.

Gonynor, J. L., M. J. Yabsley, & J. J. Jensen. 2011. A preliminary survey of *Batrachochytrium dendrobatidis* exposure in hellbenders from a stream in Georgia, USA. Herpetological Review 42(1):58–59.

Green, N. B. 1933. *Cryptobranchus alleganiensis* in West Virginia. Proceedings of the West Virginia Academy of Sciences 7:28–30.

Groves, J. D., & L. A. Williams. 2011. In search of the hellbender in North Carolina. CONNECT Magazine, March 2011.

Hammerson, G., & C. Phillips. 2004. *Cryptobranchus alleganiensis*. In IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. Retrieved from http://www.iucnredlist.org.

Hiler, W. R., B. A. Wheeler, & S. E. Trauth. 2005. Abnormalities in the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*) in Arkansas: a comparison between two rivers with a historical perspective. Journal of

Arkansas Academy of Science 59:88–94.

Humphries, W. J. 2005. C*ryptobranchus alleganiensis* (hellbender). Displacement by a flood. Herpetological Review 36(4):428.

Keitzer, S. C. 2007. Habitat preferences of the eastern hellbender in West Virginia. M.S. Thesis. Marshall University, Huntington, West Virginia. 64 p.

Lips, K. R. 2011. Museum collections: mining the past to manage the future. Proceedings of the National Academy of Sciences 108(9):9323–9324.

Madden, M., R. Welch, T. R. Jordan & P. Jackson. 2004. Digital Vegetation Maps for the Great Smoky Mountains National Park. Final Report to U.S. Department of Interior, National Park Service, Great Smoky Mountains National Park, Gatlinburg, Tennessee, 44 p.

Mast, M. A., & J. T. Turk. 1999. Environmental characteristics and water quality of hydrologic benchmark network stations in the eastern United States, 1963–95. U.S. Geological Survey Circular 1173–A, 158 p.

Maxwell, N. J. 2009. Baseline survey and habitat analysis of aquatic salamanders in the Pigeon River, North Carolina. M.S. Thesis. University of Tennessee, Knoxville. 55 p.

McGrath, K. E., E. T. H. M. Peters, J. A. J. Beijer, & M. Scheffer. 2007. Habitat-mediated cannibalism and microhabitat restriction in the stream invertebrate *Gammarus pulex*. Hydrobiologia 589:155–164.

Metter, E. 1968. The influence of floods on population structure of *Ascaphus truei* Stejneger. Journal of Herpetology 1(1):105–106.

Miller, B. T., & J. L. Miller. 2005. Prevalence of physical abnormalities in eastern hellbender (*Cryptobranchus alleganiensis alleganiensis*) populations of middle Tennessee. Southeastern Naturalist 4(3):513–520.

Nickerson, M. A., & J. T. Briggler. 2007. Harvesting as a factor in population decline of a long-lived salamander; the Ozark hellbender, *Cryptobranchus alleganiensis* Grobman. Applied Herpetology 4:207–216.

Nickerson, M. A., & K. L. Krysko. 2003. Surveying for hellbender salamanders, *Cryptobranchus alleganiensis* (Daudin): a review and critique. Applied Herpetology 1:37–44.

Nickerson, M. A., K. L. Krysko, & R. D. Owen. 2002. Ecological status of the hellbender (*Cryptobranchus alleganiensis*) and the mudpuppy (*Necturus maculosus*) salamanders in the Great Smoky Mountains National Park. Journal of the North Carolina Academy of Science 118(1):27–34.

Nickerson, M. A., K. L. Krysko, & R. D. Owen. 2003. Habitat differences affecting age class distributions of the hellbender salamander, *Cryptobranchus alleganiesnsis*. Southeastern Naturalist 2:619–629.

Nickerson, M. A., & C. E. Mays. 1973a. The Hellbenders: North American Giant Salamanders. Milwaukee Public Museum, Milwaukee, 106 p.

Nickerson, M. A., & C. E. Mays. 1973b. A study of the Ozark hellbender, *Cryptobranchus alleganiensis bishopi*. Ecology 54(5):1164–1165.

Nickerson, M. A., A. L. Pitt, & M. D. Prysby. 2007. The effects of flooding on hellbender salamander, *Cryptobranchus alleganiensis* Daudin, 1803, populations. Salamandra 43(2):111–117.

Nickerson, M. A., A. L. Pitt, & J. T. Tavano. 2009. Decline of the Ozark hellbender (*Cryptobranchus alleganiensis bishopi*) in the North Fork of White River, Ozark County, Missouri: a historical habitat perspective. A final report submitted to the Saint Louis Zoological Park and the Reptile and Amphibian Conservation Corps. Reptile and Amphibian Conservation Corps, Gainesville, Florida, 53 p.

Peterson, C. L., D. E. Metter, B. T. Miller, R. F. Wilkinson, & M. S. Topping. 1988. Demography of the hellbender *Cryptobranchus alleganiensis* in the Ozarks. American Midland Naturalist 119:291–303.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, & K. D. Wells. 2004. Herpetology, 3rd Edition. Pearson Education, Inc., Upper Saddle River, New Jersey, 726 p.

R Development Core Team (2008). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.R-project.org.

Sekhon, J. S. 2011. Multivariate and propensity score matching software with automated balance optimization: the matching package for R. Journal of Statistical Software 42(7):1–52.

Southern Appalachian Man and the Biosphere (SAMAB). 1996a. The Southern Appalachian Assessment Social/Cultural/Economic Technical Report. Report 4 of 5. U.S. Department of Agriculture, Forest Service, Southern Region. Atlanta, 208 p.

Southern Appalachian Man and the Biosphere (SAMAB). 1996b. The Southern Appalachian Assessment Terrestrial Technical Report. Report 5 of 5. U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, 248 p.

Souza, M. J., M. J. Gray, P. Coclough, & D. L. Miller. 2012. Prevalence of infection by *Batrachochytrium dendrobatidis* and *Ranavirus* in eastern hellbenders (*Cryptobranchus alleganiensis alleganiensis*) in eastern Tennessee. Journal of Wildlife Diseases 48(3):560–566.

Swanack, T. M., W. E. Grant, & M. R. J. Forstner. 2009. Projecting population trends of endangered amphibian species in the face of uncertainty: a pattern-oriented approach. Ecological Modelling 220:148–159.

Taber, W. E., R. F. Wilkinson Jr., & M. S. Topping. 1975. Age and growth of hellbenders in the Niangua River, Missouri. Copeia 1975(4):633–639.

Topping, M. S., & C. A. Ingersol. 1981. Fecundity in the hellbender, *Cryptobranchus alleganiensis*. Copeia 1981(4):873–876.

Trauth, S. E., J. D. Wilhide, & P. Daniel. 1992. Status of the Ozark hellbender, *Cryptobranchus bishopi* (Urodela: Cryptobranchidae) in the Spring River, Fulton County, Arkansas. Proceedings of the Arkansas Academy of Science 46:83–86.

U.S. Geological Survey. 2001. National Water Information System data available on the World Wide Web (Water Data for the Nation). USGS 03497300 Little River above Townsend, TN. Retrieved from http://waterdata.usgs.gov/usa/nwis/uv?03497300.

U.S. Geological Survey, Gap Analaysis Program (GAP). 2011. Protected Areas Database of the United States (PADUS), version 1.2. Retrieved from http://gapanalysis.usgs.gov/PADUS

Vié, J.-C., C. Hilton-Taylor, & S. N. Stuart, eds. 2009. Wildlife in a Changing World – An Analysis of the 2008 IUCN Red List of Threatened Species. IUCN: Gland, Switzerland, 180 p.

Werner E. E. & J. E. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

Wheeler, B. A., E. Prosen, A. Mathis, & R. F. Wilkinson. 2003. Population declines of a long-lived salamander: a 20+ year study of hellbenders, *Cryptobranchus alleganiensis*. Biological Conservation 109:151–156.