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Short note

Population declines of a long-lived salamander: a 20+-year study of hellbenders, *Cryptobranchus alleganiensis*

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Abstract

Accurate assessment of whether long-lived species are stable or declining is challenging. Life history characteristics such as delayed maturity result in relatively slow population responses to perturbations, so data should be collected across a relatively long time span. Because differential effects on age classes can be important, studies should also examine potential changes in the population's age structure. Moreover, multiple populations should be studied to indicate whether changes are regional or are restricted to local populations. We incorporated all three factors (long duration, multiple populations, age structure data) into our study of the conservation status of a long-lived aquatic salamander, the hellbender, *Cryptobranchus alleganiensis*. Over the 20+ years of this study, populations of hellbenders declined by an average of about 77%. This decline was characterized by a shift in size (age) structure, with a disproportionate decrease in numbers of young individuals. The change in density and age structure was consistent for populations in five rivers and for two subspecies (*C. a. alleganiensis* and *C. a. bishopi*), indicating that the decline is not restricted to one or two local populations. For the population with the most extensive data, the decline had clearly begun by the 1980s and there was a significant decrease in body condition over the period of the study. It is not known whether population declines for hellbenders have a single cause or whether each population has experienced independent declines.

Keywords: Hellbender *Cryptobranchus alleganiensis*; Long-lived species; Long-term studies; Amphibian decline; Recruitment

1. Introduction

Long-lived animals offer particularly difficult conservation challenges because their generally slow growth rates, delayed maturity, and low fecundities lead to slow recovery from perturbations (e.g. Congdon et al., 1993, 1994; chapters in Musick, 1999). Long-lived species can experience high variability in juvenile recruitment (Chaloupka and Osmond, 1999), and specific population responses can be strongly dependent on demographic features such as age structure (Punt and Smith, 1999). Therefore, assessing the conservation status of a particular species requires long-term study of changes in population sizes (e.g. Armbuster et al., 1999) and an understanding of whether different life history stages might be differentially affected (Congdon et al., 1994).

In the last decade, there has been particular concern about the apparent widespread decline of many amphibian populations (e.g. Dodd, 1997; Houlahan et al., 2000). Inferences about the extent of amphibian population declines have been hampered by limitations of both the temporal and spatial scales of most available data. Populations can exhibit substantial yearly fluctuations in density (Pechmann et al., 1991; Pechmann and Wilbur, 1994), so monitoring a single population over a short period of time may lead to overestimates of population instability. In Houlahan et al.'s (2000) extensive review of studies of 936 amphibian populations, studies averaged only about 6 years in length. Similarly, Blaustein et al.'s (1994) review found only five species of salamanders that had been monitored for periods of over 10 years, with a maximum time span of

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14 years. The problems associated with the short time-scale of most studies are exacerbated when spatial scale is considered. Although some local populations can dramatically decline (or even go extinct), regional densities can remain relatively stable because other populations in the same area may experience little change or growth during the same time period (Pechmann and Wilbur, 1994; Alford and Richards, 1999). Therefore, conclusions about the conservation status of any taxon are most reliable when they include data from multiple populations.

In this paper, we use relatively robust temporal and spatial sampling scales to assess population stability of a large aquatic salamander, the hellbender (*Cryptobranchus alleganiensis*). Our study examines long-term (20+ years) changes in five local populations (rivers) and two subspecies (*C. a. alleganiensis* and *C. a. bishopi*), including changes in age (size) structure. Hellbenders are somewhat unusual among amphibians in that they are relatively long-lived, with longevity exceeding 20 (Peterson, 1979) to 30 years (Taber et al., 1975).

Hellbenders are habitat specialists, preferring shallow, swift-flowing water with rocky substrates (Smith, 1907; Hillis and Bellis, 1971; Fobes, 1995). The eastern hellbender (*C. a. alleganiensis*) has a relatively wide geographic distribution, ranging from southern New York to northern Georgia and west through Missouri. The distribution of the Ozark hellbender (*C. a. bishopi*) is limited to the Ozark region of Missouri and Arkansas.

Extensive data on population sizes, age (size) structure, and body sizes of hellbenders in Missouri were collected in the 1970s and 1980s (Taber et al., 1975; Merkle et al., 1977; Peterson, 1987; Peterson et al., 1988). The animals used in these studies were branded for later identification. We sampled the same rivers that were previously censused and compared new data from 1998 and 1999 ("late 1990s") to available historical data. Long-term quantitative studies of vertebrates are rare, and the duration of our study is one of the longest that has been reported for amphibians.

2. Methods

Historical data from the 1970s and 1980s were provided by Robert F. Wilkinson and Chris L. Peterson. In May–September of 1998 and 1999, we re-surveyed these historical sites using the same sampling methodology as used by Wilkinson and Peterson.

Gene flow among rivers should be minimal, so we considered rivers to be independent populations. The three populations of *C. a. alleganiensis* were from the Big Piney River (BPR), Gasconade River (GR), and Niangua River (NR). The two populations of *C. a. bishopi* were from the Eleven Point River (EPR) and North Fork River (NFR). We reached sites (4–18 sites per river) either by canoe or by driving to river access points. We sampled the same sites as previous studies when possible, but some previous sites had become unsuitable because of siltation or scouring.

While snorkeling at each site, we slowly rolled the upstream ends of rocks by hand, with the collector positioned downstream. We caught exposed hellbenders by hand and measured them for TL (nearest millimeter) on a standard fish board and mass (nearest gram) using an Ohaus LS2000 portable electronic balance. Snout-vent length (SVL) often is the preferred measure of body size for studies of salamanders because tail length can be quite variable for some species. For hellbenders, there is a strong linear relationship between SVL and TL (Taber et al., 1975), and we used TL instead of SVL in our comparisons because some previous studies only reported TL. Sex was determined only during the breeding season when males have a swollen ring around their cloacae and females have swollen abdomens (Nickerson and Mays, 1973); we could not determine sex during the non-breeding season. After measurements were taken, individuals were released at the site of capture.

Because historical individuals were marked, we were able to insure that each individual was included only once in the data analyses, and thus maintain statistical independence. For the historical data, we used only the first capture that was recorded for an individual (i.e. recaptures were not used). In our late-1990s sample, we recaptured 19 hellbenders that had been marked in earlier studies. Data for these branded animals were removed from the historical sample and used only in the late-1990s sample.

The historical data did not provide mass for some individuals, so data for these animals were used only in TL comparisons. Non-parametric tests were used because some of the data failed to meet assumptions of parametric statistics. Data for each population (river) were analyzed separately.

Depending on the historical data available for each population, we examined potential changes in densities using either Mann–Whitney *U*-tests (early 1980s versus late 1990s) or a Kruskal–Wallis ANOVA (1970s versus 1980s versus 1990s). We used number captured per day in the analysis because the historical data did not record catch-per-unit effort. The number of people collecting on a given day ranged from 2 to 10 during historical censuses (R. Wilkinson and C. Peterson, personal communication) and was usually four for the late-1990s samples. Collection times ranged from 30 min to 2 h per site, but the length of time was not always recorded for historical samples. One of the authors of this study (R. Wilkinson) participated in both historical and late-1990s surveys, and we feel that overall sampling effort was similar for both surveys based on his qualitative assessment.

We compared historical and late-1990s size distributions using Kolmogorov–Smirnov tests. For hellbenders, total length is a good estimator of age, particularly for animals younger than 15 years (Taber et al., 1975; Peterson et al., 1983).

Body condition was based on a regression of the cubed root of mass and TL. The transformation standardized variances and created a more linear relationship between length and mass. The resulting residuals were then compared between the historical and late-1990s samples using Mann–Whitney *U*-tests. Only males were used for the body condition calculations because TL to mass ratios change seasonally for gravid females.

3. Results

3.1. Density

For *C. a. alleganiensis*, historical data for the BPR and GR populations were collected in 1978, 1980, 1981, and 1982 ("1980s" sample). Data for the NR population were more extensive, including data from the early 1970s (1971, 1972, 1973, 1974), 1980s (1979, 1980, 1986, 1988, and 1989) and 1990s (1990, 1991, 1992, 1993, 1994, 1997, and 1998). Overall, populations of this subspecies declined over 80% over the period of this study (Table 1), and this trend was consistent for all three populations. Data for the NR population indicate that the decline in numbers was evident as early as the 1980s.

For *C. a. bishopi*, historical data for the EPR population were collected in 1978, 1980–1982, and historical data for the NFR population were collected in 1977–1980 ("1980s" samples). Between the early 1980s and the late 1990s, populations of Ozark hellbenders declined by around 70% (Table 1). This trend was consistent for both populations, but was only statistically significant for the EPR population. Sample sizes (number of sampling days) for this sub-species were fairly low, so the statistical power of the analysis was limited.

3.2. Body size (age) distributions

For *C. a. alleganiensis*, data for the NR population included the 1970s, 1980s, and 1990s (see earlier). Because the Kolmogorov–Smirnov test allows for comparison of only two samples, the 1980s data for this population had to be combined with either "historical" or "recent" categories. The 1980s data were similar to the 1990s data with respect to density (Table 1). We also compared the three decades of NR size data and found a significant difference among the decades for TL (Kruskal–Wallis: $H=145.48$, $P<0.001$) and mass ($H=103.07$, $P<0.001$). According to non-parametric multi-comparison tests (Zar, 1984), the 1970s hellbenders were significantly smaller than the 1980s and 1990s hellbenders, but data from the 1980s and 1990s were not significantly different. Therefore, we combined the 1980s data and the 1990s data as a "recent" data set for comparisons with the "historical" (1970s) data set for the NR population. For all other populations, the comparison was between 1980s and 1990s samples.

For all three populations of *C. a. alleganiensis*, proportionally fewer individuals were found in the smaller size classes in the more recent samples (Kolmogorov–Smirnov tests: BPR, $D=0.4567$, $P<0.0001$; GR, $D=0.3104$, $P<0.0058$; NR, $D=0.5275$, $P<0.0001$; Fig. 1). For both populations of *C. a. bishopi*, historical samples also contained a significantly greater proportion of small individuals than recent samples (Kolmogorov–Smirnov tests: EPR, $D=0.9958$, $P<0.0001$; NFR, $D=0.2916$, $P<0.005$; Fig. 1).

3.3. Body condition

Sample sizes for comparisons of body conditions were variable and overall numbers were relatively low because data included only individuals that could be accurately identified as males. Sex ratios were identical for our historical and late-1990s data (1M:1.3F).

The following numbers of male hellbenders were used for the three populations of *C. a. alleganiensis*, with data given as historical and late-1990s numbers:

Table 1
Number of hellbenders captured per sampling day ($\bar{x}\pm1$ SE); numbers in parentheses indicate number of sampling days (see text for specific years included in the study)

Population	1970s	1980s	1990s	P[a]
Cryptobranchus alleganiensis alleganiensis				
Big Piney River	–	41.6±5.46 (18)	10.0±2.52 (4)	<0.01
Gasconade River	–	40.2±7.79 (17)	5.6±1.56 (7)	0.05
Niangua River	38.7±3.06 (68)	6.2±1.05 (35)	3.3±0.77 (16)	<0.001
Cryptobranchus alleganiensis bishopi				
Eleven Point River	–	33.5±3.28 (12)	9.0±3.87 (4)	0.01
North Fork River	–	54.9±10.20 (17)	16.7±19.21 (3)	0.15

[a] The *P*-value for the Niangua population if for a Kruskal–Wallis ANOVA and for other populations is for Mann–Whitney *U*-tests.

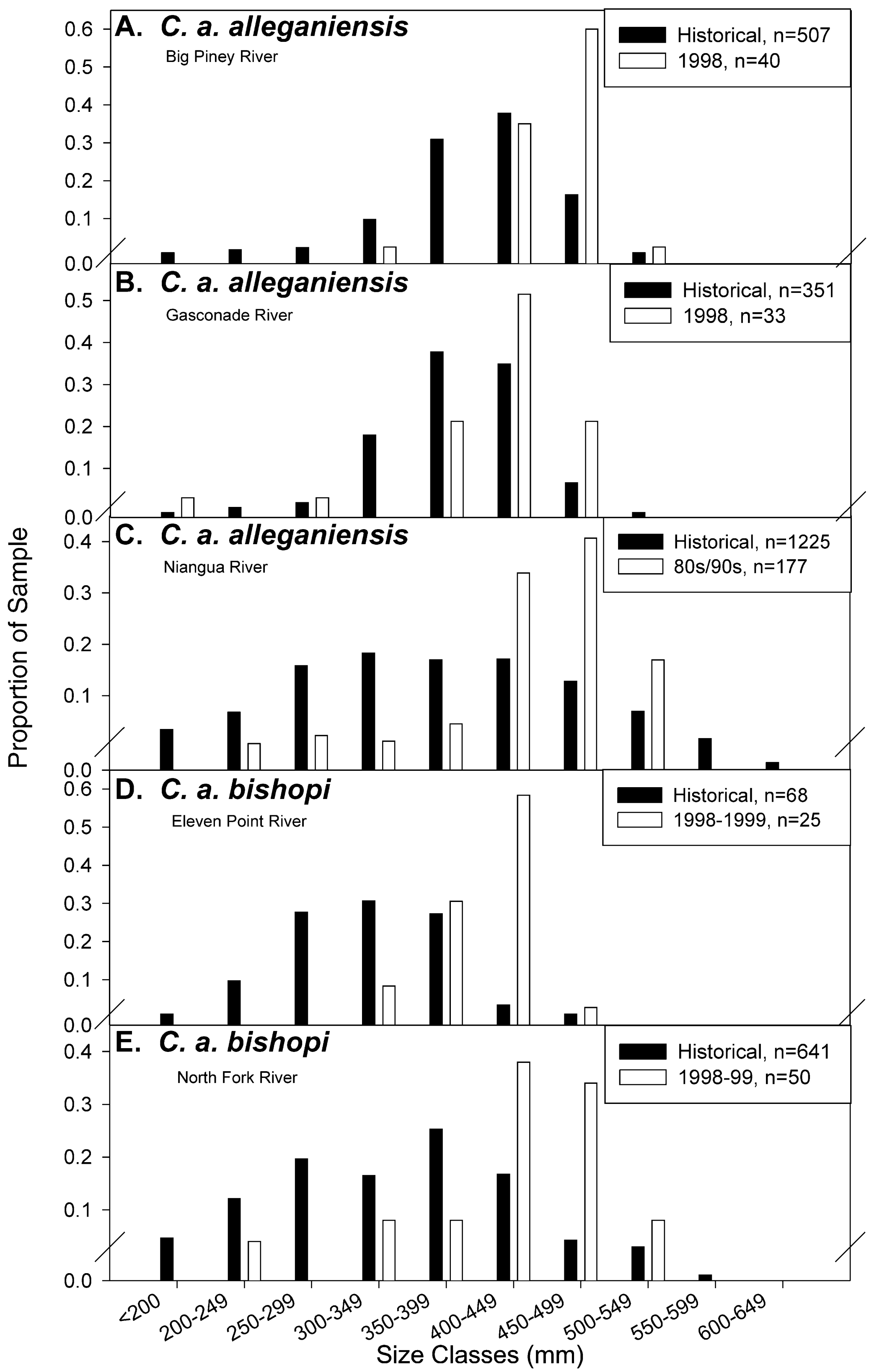

Fig. 1. Comparison of size distributions of historical and 1990s samples from five rivers in Missouri, including eastern (*Cryptobranchus alleganiensis alleganiensis*) and Ozark (*C. a. bishopi*) hellbenders. Diagonal scale break marks are used because of the very small number of individuals at the extreme ends of the distributions. For all rivers, historical distributions were significantly different from the 1990s distributions at the level of $\alpha = 0.05$.

BPR = 129 and 20, GR = 123 and 8, NR = 97 and 36. Only one population (EPR) was used in this comparison for *C. a. bishopi* and the sample sizes were 69 and 20; we were unable to determine sexes for individuals in our sample of the NFR population.

For *C. a. alleganiensis*, changes in body condition over time differed among the three populations. Males sampled in the late 1990s were in better condition than historical males in the BPR population (Mann–Whitney *U*-test: $W = 10388.0$, $P = 0.0001$). There was no significant difference between the mean body conditions of historical and late-1990s males in the GR population (Mann–Whitney *U*-test: $W = 8066.0$, $P = 0.6206$), although the sample size was very low for late-1990s males. Males from late-1990s samples of the NR population were in significantly worse condition than historically (Mann–Whitney *U*-test: $W = 6956.0$, $P = 0.02$).

For *C. a. bishopi* (EPR population), there was no significant difference between body conditions for historical and late-1990s males (Mann–Whitney *U*-test: $W = 3062.0$, $P = 0.6761$).

4. Discussion

Over the 20+ years of this study of hellbenders, populations declined by an average of about 77%. This decrease was consistent for all five populations and both subspecies, indicating that the decline is not limited to one or two local populations, but is at least a regional phenomenon. Studies of populations in other areas also report captures of relatively few individuals in recent years (Gates et al., 1985; Bothner and Gottlieb, 1991; Blais, 1996). The limited range of the Ozark subspecies (*C. a. bishopi*) makes it of particularly critical concern. The only river outside of those in our study that has been reported to hold significant numbers of Ozark hellbenders is the Spring River in Arkansas (Peterson et al., 1988) . Recent surveys of the Spring River have yielded relatively few specimens (Trauth et al., 1992; B. Wheeler, personal observation).

In addition to the decline in numbers, there also was a significant shift in age structure for all populations. Even in historical samples, hellbender populations tended to be skewed toward a preponderance of larger, mature individuals. However, in our late-1990s samples, this concentration of older individuals was more pronounced; young (small) individuals made up a significantly smaller proportion of the sample than in previous studies. This lack of recruitment could indicate either reproductive failure or low survival of eggs or young hellbenders. Taber et al. (1975) found a similar, less drastic shift in size distribution in the Niangua River over a 1-year period in the early 1970s. Our data indicate that the shift in age structure for this population was well-established by the early 1980s. Failure to capture young individuals also was reported for a New York population of eastern hellbenders (Blais, 1996).

Populations differed with respect to whether changes in body condition of males had occurred over time, and the direction of changes was not consistent among populations. For two populations (EPR and GR), there was no significant change in condition. Males from the late 1990s samples of the BPR population were in better condition than historically, which we hypothesize is due to competitive release with the apparent decline in numbers freeing up resources for the remaining individuals (e.g. Hairston, 1980). In contrast, males from the late 1990s samples of the NR population were in significantly worse condition than historically, indicating that this population is experiencing stronger negative effects than populations from other rivers.

Effective conservation efforts for hellbenders require a better understanding of the causes of both the overall decline in numbers and the absence of small animals from the populations. Potential causes of amphibian declines were reviewed by Dodd (1997) and include, habitat alteration, climate change, decreased pH, toxic substances and endocrine mimics, UV-B radiation, introduction of predators and competitors, over collection, disease or parasites, and drought or floods. In addition, recent studies have indicated that complex interactions among causal factors may occur (Kiesecker et al., 2001; Relyea and Mills, 2001). For hellbenders, habitat degradation, including increased siltification and eutrophication, clearly has occurred in some areas and probably accounts for at least some of the observed decline. Over the past few decades, there has been substantial development associated with recreational use of rivers and agriculture in the region, suggesting the potential for influences of toxic chemical runoff. Because our results were consistent for all five populations, it is possible that the same causative factors are influencing all populations in the region. However, population-specific perturbations also could occur, which might explain population differences in effects on body condition.

For long-lived organisms, population stability requires relatively high rates of survival of juveniles (Congdon et al., 1993, 1994). Clearly, this requirement has not been upheld for the hellbender populations in our study and low recruitment may explain the rapid decline in overall population numbers. Because long-lived species are slow to recover from perturbations, immediate conservation measures may be required to ensure recovery of this species.

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