

Population Status of Hellbender Salamanders (*Cryptobranchus alleganiensis*) in the Allegheny River Drainage of New York State

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ABSTRACT.—Studies that document changes in long-lived species are valuable in determining how demographic and environmental changes are affecting populations. This study documents apparent declines in Eastern Hellbender (*Cryptobranchus alleganiensis*) populations over the last 20 years in the Allegheny River drainage of New York State. We compared current mark–recapture data to similar data collected in the 1980s at eight sites using a comparable method of capture (rock turning). In addition, we employed several other methods of capture including trapping, bank searching, and night lighting. Despite these extra efforts, the number of Hellbenders captured was less than the number captured historically. Hellbenders were extirpated from a single site and the ecological density (number of individuals per 10 m² of habitable area) decreased in several other sites relative to the 1980s. Current and historical populations contained more mature adults than juveniles, but we found more Hellbenders <20 cm total length at five sites compared to the 1980s study. The sex ratio changed from predominantly female in the 1980s to predominantly male currently. Eggs in nests were found in both studies, although little is known about egg or larval survival and overall recruitment. Although demographic issues such as reproduction and recruitment may be contributing to Hellbender declines in the Allegheny drainage, these do not appear to have changed drastically from the 1980s. Other possible causes of decline include factors such as land use changes, introduced species, or some other environmental issue.

The Eastern Hellbender (*Cryptobranchus alleganiensis*) is a large, long-lived, aquatic salamander that inhabits cool, clean rivers and streams. It is widely believed that the Hellbender is declining throughout much of its range (Nickerson and Mays, 1973; Trauth et al., 1992; Wheeler et al., 2003; Briggler et al., 2007a). Much of the evidence for this decline comes from comparing recent population data to anecdotal reports of past abundance, although several investigators have compared their results to previously published data. Trauth et al. (1992) observed only 20 Hellbenders in the Spring River in Arkansas, where 370 animals were tagged only 10 years earlier (Peterson et al., 1988). Wheeler et al. (2003) reported an average decline of 77% in both subspecies of Hellbenders in Missouri over a 22-year period. Recent searches of Butternut Creek in New York yielded one Hellbender after several years of regular searches in areas where they were abundant as recently as 1999 (A. Breisch, pers. comm.). However, few other studies have provided quantitative evidence of Hellbender declines.

Hellbender declines could be driven by either environmental factors, demographic factors, or a combination of both. Environmental factors

include habitat degradation (Nickerson and Mays, 1973; Wheeler et al., 2003), chemical pollution, siltation (Briggler et al., 2007a), and over collection (Nickerson and Mays, 1973; Trauth et al., 1992; Nickerson and Briggler, 2007). Land use changes, including road construction, stream relocation, and dam construction, have been important factors in shaping the current habitat of the Allegheny Drainage.

Demographic factors may include lack of recruitment or high adult mortality. Many reports indicate finding Hellbender populations heavily skewed toward larger size classes (Bothner and Gottlieb, 1991; Blais, 1996; Wheeler et al., 2003; Humphries and Pauley, 2005). However, larvae and juveniles <20 cm total length are particularly hard to find. It could be that rock turning, the most common search technique for Hellbenders, is simply an ineffective method for finding these size classes (Peterson et al., 1983; Nickerson et al., 2003; Foster et al., 2008). Little is known about nest success or larval survival. In addition, factors such as introduced predators or disease could affect survivorship at all life stages. Hellbenders may be affected by nonnative fish species, which have been introduced for sport fishing in many streams (Gall, 2008). Negative impacts on survival, growth, and habitat use resulting from such introductions have been reported for several amphibian species, including the Long-

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Toed Salamander (*Ambystoma macrodactylum*) and the Northwestern Salamander (*Ambystoma gracile*; Tyler et al., 1998). Chytrid fungus (*Batrachochytrium dendrobatidis*), which has been implicated in declines of many amphibian species (Collins and Storfer, 2003), recently has been detected in wild Hellbender populations (Briggler et al., 2007b). High adult mortality has been attributed to direct harvesting of Hellbenders by commercial collectors. Nickerson and Briggler (2007) found that over 500 Hellbenders were harvested from the North Fork of the White River in Missouri over a 30-year period. Many of these were taken for scientific study or the pet trade. Kern (1984) stated that natural bait anglers were the most devastating predators in Indiana's Blue River.

In the mid-1980s, a mark-recapture study was conducted that surveyed Eastern Hellbender populations at eight sites in the Allegheny drainage and provided estimates of population size, ecological density, size class structure, and sex ratio (Bothner and Gottlieb, 1991; Gottlieb, 1991). Our study was designed to provide a comparison to these previous investigations. Our primary objective was to revisit the eight sites previously surveyed and determine whether changes in the population size and structure have occurred within the past 20 years. We also employed additional search methods in an attempt to locate portions of the population that may not have been sampled in the previous study. Ultimately, we aimed to determine, using both qualitative and quantitative measures, whether Hellbender populations in southwestern New York State have changed.

MATERIALS AND METHODS

Study Sites.—This study was conducted at eight sites in the Allegheny River drainage in New York State (Fig. 1). Each of these study sites historically has supported populations of Hellbenders, which were described in terms of population size and demographic structure (Bothner and Gottlieb, 1991; Gottlieb, 1991). To the greatest extent possible, we worked within the sites previously defined although information about the exact starting and ending points for each site was scant. To ensure that sites were included in their entirety, we searched all continuous habitable area at a site. Habitable area was essentially a stream reach containing suitable cover rocks (>30 cm in diameter; as per Gottlieb, 1991).

Study sites varied in size (Table 1), but all included areas of fast-flowing water and contained numerous large cover rocks. Land use surrounding the sites varied, with three sites near agricultural land, two bordering residential properties, and three near industrial or

commercial sites (including a municipal garbage dump and a decommissioned wastewater treatment facility). Water depth rarely exceeded 1 m in most areas within the study sites. More detailed site descriptions are found in Foster et al. (2008) and Gottlieb (1991). During the present study, mark-recapture (see below) was conducted only under near-baseflow conditions when streams were clear, which included most of the 2004–05 study period. In the 1980s, mark-recapture events took place under similar stream flow conditions (J. Gottlieb, pers. comm.).

Mark-Recapture Study.—Population surveys were conducted between late August and October of 2004 and 2005. This corresponds to the Hellbender breeding season in New York, during which time breeding males can be identified by swelling around the cloaca, and females may be identified by the swollen appearance of the abdomen (Smith, 1907). The time between mark and recapture events ranged from two to four weeks, depending on weather. Surveys were conducted at Sites 1–4 in 2004. Surveys were conducted at Sites 5–8 and repeated for Sites 1, 3, and 4 in 2005.

Hellbenders were located by lifting the upstream ends of suitable rocks at each study site. A peavey or cant hook was used to provide leverage when needed. Suitable rocks were defined as those at least 30 cm in diameter (as per Gottlieb, 1991) and not requiring the use of multiple leverage devices for lifting. Sexes of all Hellbenders present under a rock were recorded. Every attempt was made to restore each rock to its original position.

Hellbenders were captured by grasping them behind the head and maneuvering them into a trout net. Total length and standard (snout-vent) length were recorded for each animal using a measuring trough made from PVC pipe. Masses were obtained using Pesola spring scales. All mature Hellbenders (30 cm or greater total length) and some larger juveniles were tagged by inserting a PIT (passive integrated transponder) tag subcutaneously at the base of the tail on the left side. Digital photos were taken of each animal. For Hellbenders too small to be PIT tagged, photos, measurements, and descriptions of unique markings were used for comparison to any untagged juveniles. Ages of immature Hellbenders were determined using a variety of morphological characteristics, including gill, gular fold, and lateral fold morphology and total length (Bishop, 1941).

For the purposes of this study, each site was treated independently, both because the level of isolation of a given site was unknown and to facilitate comparison with historical data. Population size estimates for each site were calculated using Chapman's correction of the Lin-

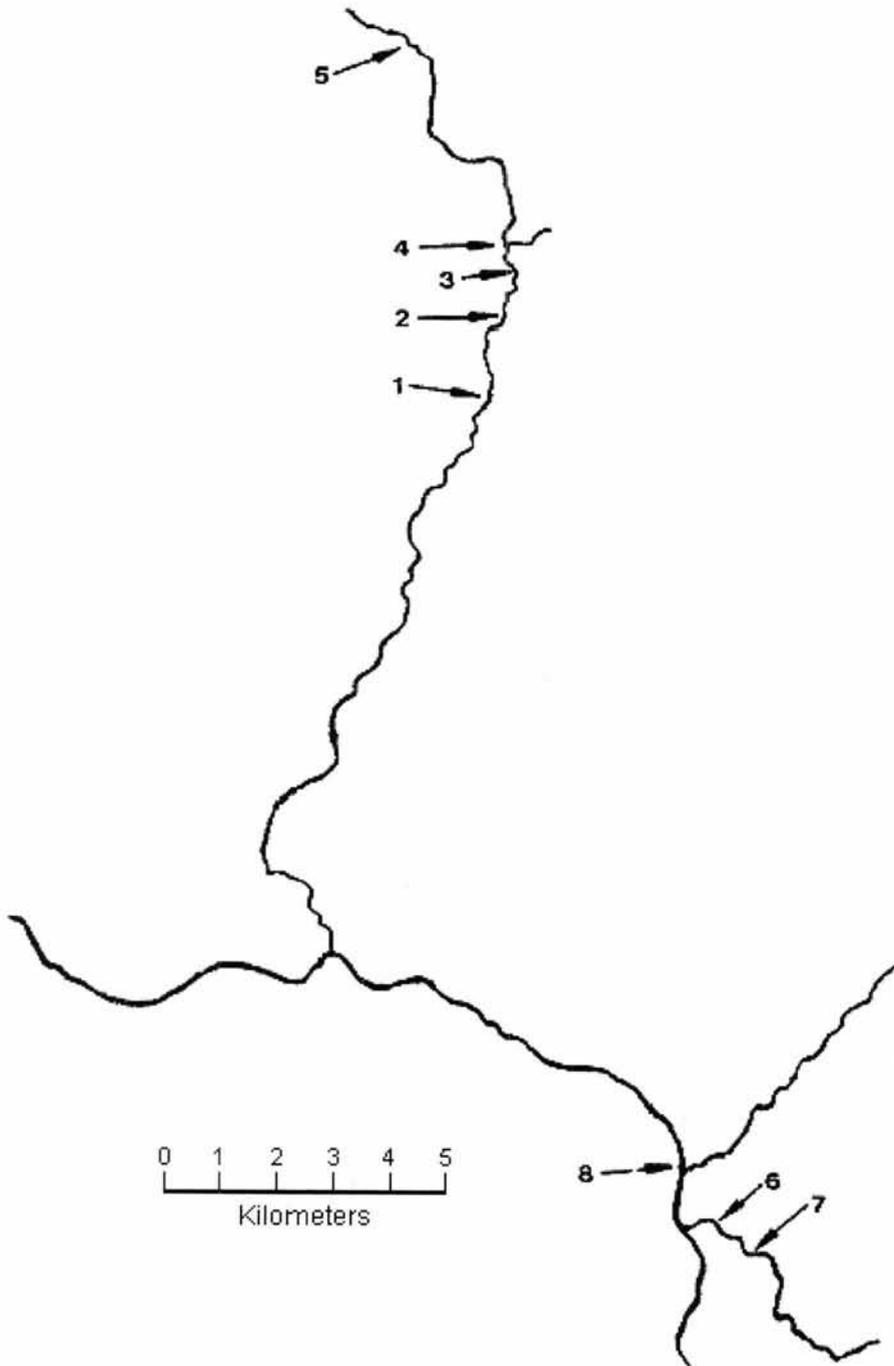


FIG. 1. Line map indicating study site locations in the Allegheny River Drainage (modified from Bothner and Gottlieb, 1991). Names of rivers and tributaries are omitted to protect the remaining animals at these sites.

coln-Petersen estimator

$$\hat{N}_C = \left(\frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} \right) - 1,$$

where n_1 is the number of marked individuals,

n_2 is the number of individuals captured in the second capture event, and m_2 is the number of marked individuals that were recaptured (Amstrup et al., 2005). Standard error of population estimates was calculated using the equation

TABLE 1. Estimates of Hellbender population size for eight sites in the Allegheny River Drainage during the 1980s (modified from Gottlieb, 1991) and in 2004–05. Population size estimates in 2004–05 were calculated using Chapman's correction of the Lincoln-Petersen estimator (Amstrup et al., 2005).

Site	Site Area (m ²) (% habitable)		Estimated <i>N</i> (± 95% CI)	
	1980s	2004–05	1980s	2004–05
1	424 (2)	2355 (2)	3.0 (2.9)	5.0 (0)
2	1208 (2–3)	12,240 (2)	6.0 (2.0)	26.0 (14.4)
3	806 (2–5)	4512 (1)	5.0 (2.7)	0
4 ^a	624 (10)	3640 (5)	23.3 (19.1)	39.0 (35.1) 11.9 (2.3)
5	6048 (8–10)	8901 (6)	40.4 (19.6)	51.0 (28.3)
6	2082 (6–8)	11,666 (1)	24.2 (17.4)	11.0 (5.9)
7 ^b	1592 (6–8)	4554 (3)	52.0 (12.6) 58.5 (27.3)	23.4 (6.7)
8	14,003 (3–5)	15,741 (3)	45.2 (14.6)	23.0 (10.4)

^aSurveyed in 2004 and in 2005.

^bSurveyed in 1985 and in 1988.

$$SE(\hat{N}_C) = \sqrt{\frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2(m_2 + 2)}}$$

The 95% confidence interval was calculated for each population estimate (Amstrup et al., 2005). The 1980s study did not employ Chapman's correction on the Lincoln-Petersen estimator (Bothner and Gottlieb, 1991; Gottlieb, 1991).

Although the study sites were in the same locations as those searched in the 1980s, the study area within each site differed from the historical study sites (Table 1). Site length was measured down the center of the stream, and width was measured at the beginning, center, and end of each site. Area was calculated as the site length multiplied by the average of the three width measurements. Percent habitable area was estimated visually for each site.

To compare across sites and historical data, we estimated Hellbender ecological density (number of individuals/10 m² of habitable area) at each site. Standard errors on the ecological density estimates were calculated from the delta method (Williams et al., 2002) as follows

$$SE_{ED} = \sqrt{\left(\frac{10}{HA}\right)^2 \times SE_{pop}^2}$$

where *HA* is habitable area in m² and *SE_{pop}* is the standard error on the population estimate. Confidence intervals were then calculated using

$$N\left(\frac{10}{HA}\right) \pm 1.96(SE_{ED}),$$

where *N* is the population estimate.

Total length can be used as an estimator of age (Taber et al., 1975). Size classes were assigned according to the manner of Bothner and Gottlieb (1991) to facilitate comparison

between the data sets. Past and present size class distributions of Hellbenders captured at all eight sites combined were compared using a chi-square goodness-of-fit test. Because of the small number of juveniles captured in the 1980s, the two smallest size classes were combined for the chi-square test resulting in five size classes. Sex ratios between the two studies also were compared using a chi-square test.

Other Search Methods.—Because rock turning is of limited use under certain conditions (Foster et al., 2008), additional methods of capturing Hellbenders were employed to capture portions of the population that may not have been accessible in the previous study (Bothner and Gottlieb, 1991; Gottlieb, 1991). Hellbenders captured using these methods were not included in any statistical comparisons with Gottlieb's study because different methods of capture may not be comparable. Traps were set during the summer of 2005 at all sites. A description of traps is provided in Foster et al. (2008). Traps were set approximately 20 m apart in habitable areas with sufficient water depth to cover the entire trap (0.25 m minimum). In areas that contained habitat not accessible by turning rocks, such as rock ledges or large, unliftable rocks, and in areas too deep to be searched by hand, traps were set more densely (up to every 5 m). Traps were baited with White Sucker (*Catostomus commersonii*) and set with the entrance facing downstream. Traps were checked daily in all sites. Bait was changed every other day in Site 8, which was the first site trapped. Based on the results in that site, we decided to increase to daily bait changes for the other sites.

In an effort to locate smaller size classes, areas of potential habitat along the bank were searched. Habitable bank sites were defined as having substrate larger than 70 mm in diameter (Foster et al., 2008). At each site, habitable

TABLE 2. Number of Hellbenders captured using methods other than rock turning classified by size class in centimeters. Bank searches and trapping are described in text and in Foster et al. (2008). Other search methods include two Hellbenders caught night lighting and one Hellbender captured by rock turning outside of the study season.

Capture method	Size class in cm						
	<11	11–20	21–30	31–40	41–50	51–60	>60
Bank searches	0	7	5	1	1	0	0
Trapping	0	1	1	2	8	5	2
Other methods	0	0	0	1	2	0	0
Total	0	8	6	4	11	5	2

stretches of bank were divided into 1-m wide quadrants extending up to 4 m into the stream. We randomly selected 5% of these quadrants to conduct searches. Searching involved turning or agitating all substrate particles in the quadrant. Nets were held downstream to catch juveniles that were swept away in the current.

Two nocturnal surveys also were completed, one each at Sites 2 and 5. These sites were chosen because of their accessibility and clear, shallow water conditions. Each survey began approximately one hour after dusk and lasted for three hours. This was similar to surveys described by Humphries and Pauley (2000) and encompassed the period of maximum daily activity occurring shortly after dark (Noeske and Nickerson, 1979). Nocturnal surveys were conducted by four searchers, two with spotlights and two with nets. Searches were performed by walking upstream using a one million candle-power spotlight to scan the stream bottom. Mesh bags containing White Sucker were set at several points in the stream to entice Hellbenders out from under the rocks. Any Hellbenders seen were captured using a trout net.

RESULTS

We searched a considerably larger area than the previous study (Table 1). The mark-recapture portion of this study covered a total area of 63,609 m², compared to 26,787 m² searched in the 1980s (Bothner and Gottlieb, 1991; Gottlieb, 1991). The rock turning portion of our study involved over 300 person hours. Additional methods included 627 trap nights and 55 person hours of bank searches (Foster et al., 2008).

Population Size and Ecological Density.—Hellbenders were present in seven of the eight historically populated sites. A total of 159 Hellbenders was captured and marked or otherwise identified. This compared to 219 Hellbenders reported by Gottlieb (1991). Of the 159 animals, 36 were located using methods not employed in the historical survey (Table 2).

All animals recaptured were in their site of original capture except one female, which was captured >1 km upstream from the site of first capture.

Current population sizes ranged from zero at Site 3 to 49 at Site 5. Site 3, which historically held only a small population of Hellbenders, was found to be unoccupied in both 2004 and 2005 (Table 1). No Hellbenders were found at Site 1 in 2004, but five were caught during the second capture event in 2005. All sites were occupied in the 1980s and population sizes ranged from 3 at Site 1 to 58 in Site 7 (Table 1).

Although estimated population size increased in three sites compared to the 1980s estimates, ecological density decreased in all sites but one (Fig. 2). In the present study, ecological density estimates ranged from 0–2 Hellbenders/10 m² of habitable area. In the 1980s study, estimated ecological density ranged from <1 to 6 Hellbenders/10 m² of habitable area.

Size Class Distribution.—Overall size class distribution varied significantly between the past and present mark-recapture studies ($\chi^2 = 17.393$, $P < 0.005$), although both were dominated by older, larger animals (Fig. 3). Juveniles were more commonly encountered in the present study than in the 1980s study. We also found two gilled larvae, although none were captured in the 1980s study. Trapping resulted in the addition of a larger size class (>60 cm total length) and the capture of two juveniles. Bank searches yielded one gilled larva and 10 juveniles. All of these were in the 11–20 or 21–30 cm size classes.

Comparing rock turning methods only, current size class structure varied between sites, and size class structure appears to have changed in all sites since Gottlieb's survey (Fig. 4). The smallest Hellbenders (<14 cm) were present only at Sites 2 and 4 during the present survey, and this class was absent from all sites in the 1980s. Mature Hellbenders were more numerous in most sites for both surveys. Site 1 was the exception, containing only immature Hellbenders in the 2004–05 survey.

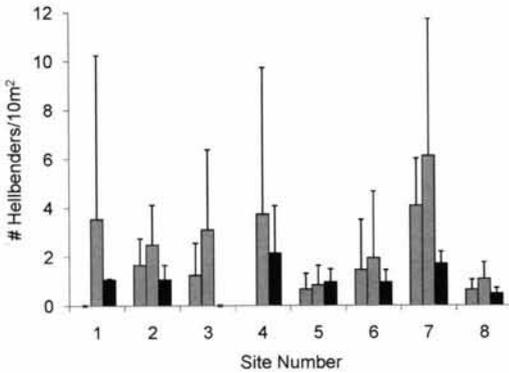


FIG. 2. Ecological density estimates for sites in the Allegheny River Drainage. Gray bars indicate samples from 1983–85 and 1988 (estimated from Gottlieb, 1991). Where there were two or more possible estimates, the first bar shows the lowest, and the second bar shows the highest. Black bars are samples taken for this study in 2004–05. Density estimates were calculated using Chapman's correction of the Lincoln-Petersen estimator (Amstrup et al., 2005). Error bars indicate 95% CI on the density estimates (see text).

Site 2 was the only site where all size classes were represented in the current study.

Sex Ratio.—The sex ratio across all sites differed significantly from the historical sex ratio ($\chi^2_1 = 9.28$, $P < 0.005$). In the 1980s, approximately 55% of all Hellbenders sexed were female (0.8 males to 1 female), compared to only about 36% of Hellbenders sexed in 2004 and 2005 (1.8 males to 1 female; Fig. 5). The percentage of females decreased at all sites.

DISCUSSION

In the approximately 20 years since the last population estimates were made in the Allegheny River drainage, Hellbender numbers appear to have declined. Despite an expanded search area and the use of additional capture methods, we found fewer Hellbenders overall than the previous survey (Bothner and Gottlieb, 1991; Gottlieb, 1991). In addition, we documented decreased ecological density in several of the study sites, and observed significant changes in size class distribution and a more male-biased sex ratio.

The largest decrease in ecological density occurred at Site 3, where despite two seasons of rock turning, 40 trap nights, and nine person hours of bank searches no Hellbenders were found (Table 1; Fig. 2). Suitable habitat for all age classes was present at this site (Foster et al., 2008). Furthermore, the female Hellbender that was captured at two sites had to travel through this site. Most other sites appear to have

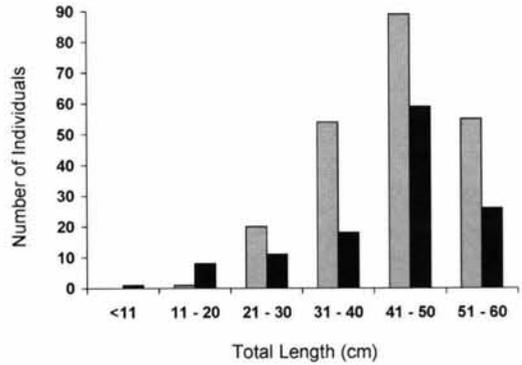


FIG. 3. Size class distribution of Hellbenders captured in the Allegheny River Drainage during the fall seasons of 2004 and 2005, compared to historical data from Hellbenders captured during the fall seasons of 1983–85 and 1988 (Bothner and Gottlieb, 1991; Gottlieb, 1991). The size distributions differ significantly between the two time periods ($\chi^2_4 = 17.393$, $P < 0.005$). Grey bars = 1983–85 and 1988; black bars = 2004–05.

declined as well, although the extent of decline is difficult to quantify because of the extremely large confidence intervals around the 1980s estimates (Bothner and Gottlieb, 1991; Gottlieb, 1991). Chapman's correction of the Lincoln-Petersen estimator was not employed in that study, although its use may have reduced the standard errors on these estimates and allowed more meaningful comparison. Despite the overlap between confidence intervals, we believe that the decline is real, as supported by the reduction in total numbers of Hellbenders caught, even with the increased search areas and use of additional capture methods in our study.

Both studies were potentially affected by assumptions of the Lincoln-Petersen estimator, some of which may be violated when turning rocks to sample Hellbenders. The assumption of equal catchability may not have been met in some sites. Hellbenders beneath unliftable rocks or in deep water are not likely to be captured using this method. However, any violations of the equal catchability assumption because of habitat features would have been similar in both the 1980s and the present study and should not affect the validity of comparisons between them. Additionally, the assumption of a closed population may have been violated by the movement of a single female Hellbender between sites in 2004. The closed population assumption has been considered reasonable for Hellbenders because adult mortality is generally low, hatching occurs outside the sampling period, and numerous studies show that Hellbenders have small home ranges and

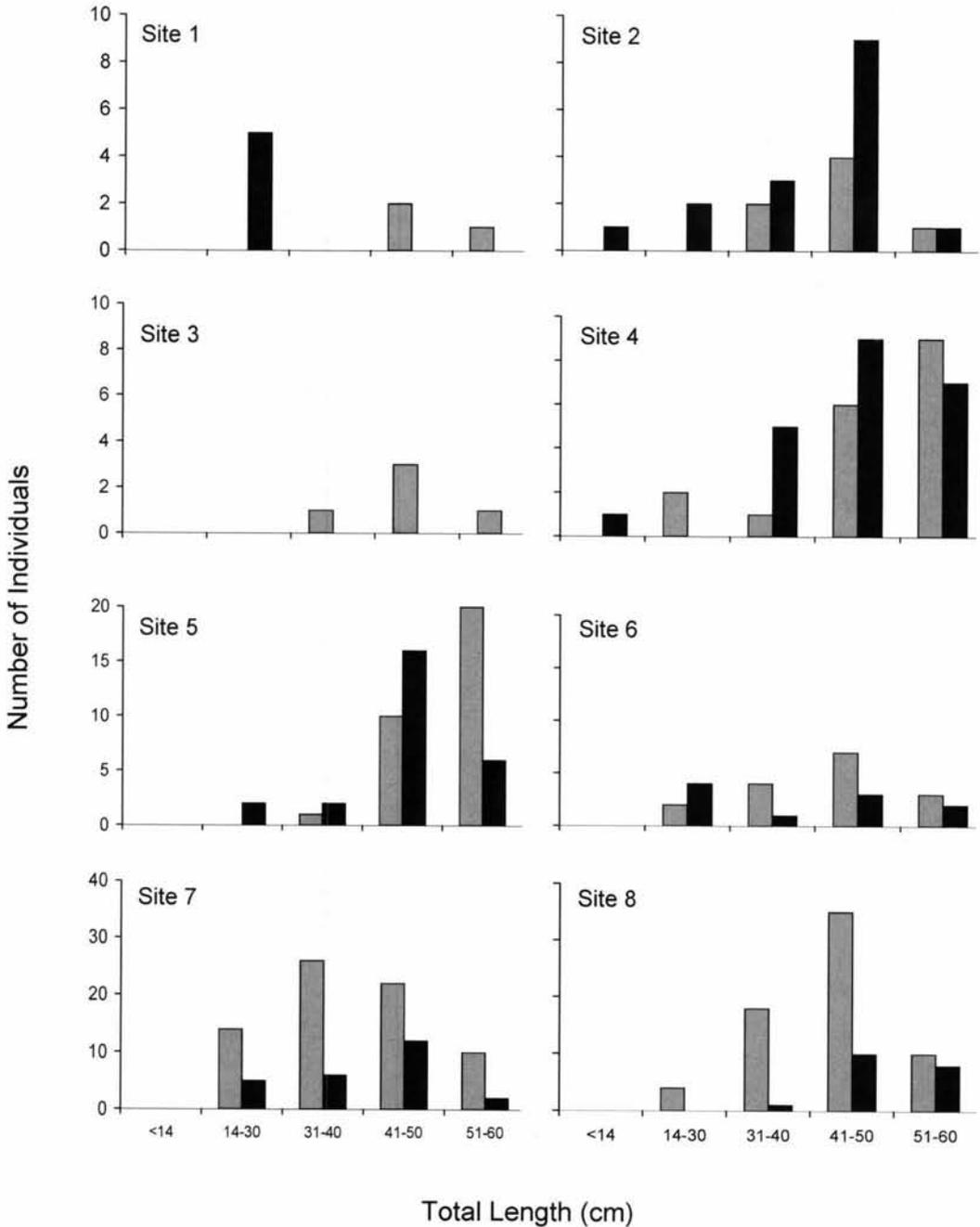


FIG. 4. Size class distribution by site for Hellbenders captured in the Allegheny River Drainage (grey bars = 1983–85 and 1988; black bars = 2004–05). Only data obtained using the rock turning method from both time periods is included, and equal probability of detection was assumed for all sites. Note that Y-axes differ between sites. Size classes are modified from Figure 3 to facilitate comparison with Gottlieb (1991).

do not travel far (Nickerson and Mays, 1973; Peterson, 1987; Blais, 1996; Humphries and Pauley, 2005). Gottlieb (1991) reported no captures outside the site of initial tagging. There is no evidence that this type of movement is

common in this population; therefore, we do not believe it substantially affects our results.

Examination of population structure may provide clues to the factors involved in Hellbender declines. Overall size distribution dif-

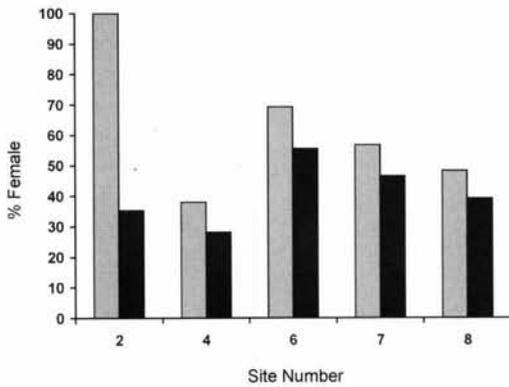


FIG. 5. Percent of individuals identified as female in the 1980s (modified from Gottlieb, 1991) and 2004–05. Sex was not recorded in Site 5 in the 1980s study because sampling occurred outside the breeding season. In the current study, no sexually mature individuals were observed in Site 1, and no Hellbenders were observed in Site 3. Grey bars = 1983–85 and 1988; black bars = 2004–05.

ferred between the studies, with an increase in Hellbenders <20 cm, and decreases in all other size classes (Fig. 3). These overall trends were not consistent between sites, however. In the 1980s, Site 1 contained only a small number of adult Hellbenders (>30 cm). In our study, all Hellbenders captured at this site were in the 14–30 cm size class. At Sites 6, 7, and 8, all size classes >20 cm decreased in number. Sites 2, 4, and 5 (within the same stream) displayed higher numbers of 31–50 cm individuals than were present 20 years ago (Fig. 4). This is consistent with the trend observed by a similar study of Hellbenders in Missouri, in which size classes >40 cm increased over a 20-year period (Wheeler et al., 2003). Despite the apparent increase in the number of juveniles, the small number of larvae found is notable. Gottlieb (1991) reported no larvae <11 cm and only one juvenile <20 cm total length. We captured two larvae in the smallest size class and eight juveniles using comparable techniques. Additional methods resulted in the capture of another eight juveniles (Table 2). Other authors have had success locating larvae by skin-diving (Nickerson et al., 2002, 2003; Pitt and Nickerson, 2005). Additional searches of the Allegheny River drainage using that method could help provide a more complete picture of age structure.

Typically, studies have found more males than females during the breeding season (Smith, 1907; Hillis and Bellis, 1971; Pflugsten, 1990; Blais, 1996). In the 20 years since Gottlieb and Bothner's survey, sex ratios have shifted to a higher proportion of males. Gottlieb (1991)

reported two to four nests each year during his study period with each clutch estimated to have come from a single female based on egg number (as per Bishop, 1941). We found a comparable number of nests (2–3 per year) during our study, all with similar clutch sizes to those reported by Gottlieb (1991). Twice during the course of the 2005 sampling season we witnessed behaviors indicative of mating, including daytime congregations of males with a single female at a potential nest rock and aggressive interactions between males. These observations suggest a reproductively active population, but whether recruitment is sufficient to sustain this population over time needs further exploration.

Although the population characteristics we investigated for Hellbenders in the upper Allegheny drainage appear similar or more favorable compared to the 1980s (i.e., presence of nests, clutch size, size class structure, male-biased sex ratio), the population appears to be declining. Mortality factors for each age class should be identified in future studies. One cause of adult mortality may be anglers using natural baits (Kern, 1984), and anglers in the Allegheny drainage report catching Hellbenders. Another possible source of mortality is predation by fish. Large fish may have the potential to prey on adult Hellbenders (Petranka, 1998), and Muskellunge (*Esox masquinongy*) and Northern Pike (*Esox lucius*) are large predatory fish species present in the Allegheny Drainage. Additionally, predation by nonindigenous fishes, such as the Brown Trout (*Salmo trutta*), could contribute to the mortality of larval and juvenile Hellbenders (Gall, 2008). Impacts of nonnative trout on amphibians are well-documented (Tyler et al., 1998; Collins and Storfer, 2003; Kats and Ferrer, 2003). Interactions between Hellbenders and these and other fish species should be studied to determine their role in Hellbender declines.

Over the past 100 years, the Hellbender habitat in the Allegheny drainage has been substantially altered by land use changes. Perhaps the most significant alteration has been the relocation of stream channels for the construction of roads and railways. In New York, many Hellbender sites are located in "rock generation sites." These are stream areas where erosional forces on the valley wall release large slab rocks into the stream, providing excellent Hellbender habitat. As large rocks on the stream bed are covered by silt and gravel, this erosion process replenishes the Hellbender habitat. Relocation of streams in the Allegheny Drainage has disrupted numerous rock generation sites in areas where Hellbenders have been documented in the past (KJR, unpubl. data).

Although Hellbenders have apparently declined in the New York portion of the Allegheny Drainage, the causes of these declines are not evident in our data. All size classes were present in the drainage, although the smallest size class was only represented in three sites. Reproduction was observed as nesting behaviors, active nests, fertile egg masses, and developing embryos. Whether the current level of reproduction is sufficient to sustain the population at current levels is unknown. Also unknown and in need of further study is the role of fish predation, angler-related mortality, disease, water quality, and food resources in contributing to these declines.

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