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The Rocky Road to Eastern Hellbender (Cryptobranchus a. alleganiensis) Recovery in Ohio: An Evaluation of Habitat in Ohio's Streams

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ABSTRACT.—Determining habitat characteristics that influence the contemporary distribution of species is imperative for effective conservation planning. The Eastern Hellbender (*Cryptobranchus a. alleganiensis*) reaches its Midwestern northern range limit in Ohio, U.S.A.Most previous studies have focused on habitat within the mountainous core of the species' range. We assessed physical and chemical habitat characteristics across the extant range of the Hellbender in Ohio. Physical habitat characteristics were similar to habitat across the range. Hellbenders occupied stream segments typically in contact with steep hillsides that are the source of large shelter rocks. Stream substrate consisted of large boulders and cobble and contained moderate proportions of gravel and sand. Both water temperature (max =← 29.4–33.0 C) and conductivity (range = 284–1323 μS/cm) were elevated in Ohio streams. Historic alterations to streams in combination with distinct hydrologic regimes and geology have resulted in habitat characteristics not commonly reported elsewhere. This may have contributed to Hellbender populations being dominated by large adults. Developing an understanding of the role habitat structure and perturbations play in egg and larval survival is critical for the implementation of effective conservation strategies.

INTRODUCTION

Understanding the factors that influence the distribution and abundance of species is imperative for effective conservation planning and natural resource management. Freshwater habitats represent less than 1% of the Earth's surface, but provide critical habitat for nearly 6% of all species and are often threatened by persistent anthropogenic environmental degradation (Dudgeon *et al.*, 2006; Strayer and Dudgeon, 2010). Despite significant improvement in water quality in the United States due to the Clean Water Act, particularly in urban and suburban environs (Andreen, 2013), freshwater mussels, freshwater fish, and amphibians remain three of the most imperiled taxonomic groups in the United States (Strayer, 2006; Corey and Waite, 2008; Jelks *et al.*, 2008). Many species in these taxonomic groups are cryptic or not easily surveyed, resulting in little available information to inform causalities for decline and subsequent conservation efforts. Even with the critical need for information to guide conservation efforts, including the often complex and synergistic causal factors for declines, freshwater ecosystems remain some of the most poorly studied (Abell, 2002).

Freshwater ecosystems are affected by a variety of interacting factors, including historical land uses and associated legacy impacts, point source and nonpoint source pollution, and

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widespread habitat degradation and alteration. Lotic ecosystems, such as rivers, streams, and creeks, are negatively impacted through direct effects, such as those caused by dams, channelization, and fossil fuel extraction and transportation, and indirect effects, such as riparian land use changes (Abell *et al.*, 2016). In-stream and riparian habitat alterations may shift hydrologic regimes, resulting in a reduction of substrate heterogeneity in addition to increased sediment and nutrient input (Allan, 2004; Carpenter *et al.*, 2011; Maloney and Weller, 2011). For example, deforestation of riparian habitat is linked to increased water temperature, increased sedimentation rates, and increased conductivity (Pugh *et al.,* 2016; Pitt *et al.,* 2017; Jachowski and Hopkins, 2018). Changes to both the chemical and physical environment negatively impact lotic biodiversity, including mussels, fish, and amphibians. However, the resulting individual and population-level impacts may not be immediately observable, if fitness effects or mortality are delayed. This is particularly pertinent for long-lived species with late maturity (Wheeler *et al.,* 2003). Unfortunately, this "extinction debt" may only become observable with long-term monitoring and at a time when the causes for decline may no longer be discernable (Gibbons *et al.,* 2000; Wheeler *et al.,* 2003). Given the potential chronic and acute impacts of historic and contemporary alterations to riparian and lotic habitat, understanding the current distribution and associated chemical and physical habitat characteristics is imperative for understanding underlying mechanisms for declines and future conservation planning.

Eastern Hellbenders (*Cryptobranchus alleganiensis alleganiensis*) are large, long-lived, late-maturing, fully-aquatic salamanders endemic to the Eastern United States. The historic range of the Hellbender included portions of the Missouri River, Mississippi River, Ohio River, Tennessee River, and Susquehanna River drainages. In Ohio Hellbenders are restricted to the Ohio River drainage (Lipps, 2013). Although once widespread, the range of the Hellbender has contracted and many extant populations have declined over the last several decades (Nickerson and Mays, 1973; Williams *et al.,* 1981; Freake and DePerno, 2017), including estimated 80% declines in Ohio streams from the mid-1980s to mid-2000s (Lipps, 2013). Frequently hypothesized causes of declines include habitat alteration, water quality degradation, and disease (Bodinof *et al.,* 2011; Burgmeier *et al.,* 2011). Recent studies have found strong relationships between decreases in forest cover at local and landscape scales with the presence, recruitment, and declines of Hellbender populations (Pugh *et al.,* 2016; Nickerson *et al.,* 2017; Pitt *et al.,* 2017; Jachowski and Hopkins, 2018). Often these declines in forest cover were associated with increases in conductivity and water temperature (Pitt *et al.,* 2017; Jachowski and Hopkins, 2018). However, it was noted by Jachowski *et al.* (2016) that historical factors should not be ignored when inferring distributional patterns, particularly given the often-delayed responses of long-lived, late-maturing species to habitat alterations.

Many of these recent studies have occurred in populations within the core of the Hellbender range in the Blue Ridge and Ridge and Valley physiographic regions (Nickerson *et al.*, 2002; Pugh *et al.*, 2016; Freake and DeParno, 2017; Jachowski and Hopkins, 2018) where metamorphic geology, forested land cover, and high topographic relief result in fairly clear, cool, low nutrient waters with larger substrates (Scott *et al.*, 2002). Similarly, populations in the Ozark Highlands of Missouri, where streams are fed by massive springs (Vineyard and Feder, 1982), have been the focus of intensive study (Nickerson and Mayes, 1972; Nickerson *et al.*, 2003; Briggler *et al.*, 2007; Nickerson *et al.*, 2017). In contrast, Ohio streams with extant Hellbender populations are found mostly in the foothills of the Appalachians, in the Western Allegheny Plateau (WAP) physiographic region composed of horizontally bedded sedimentary rock. The WAP is a lower, warmer, less steep, and less

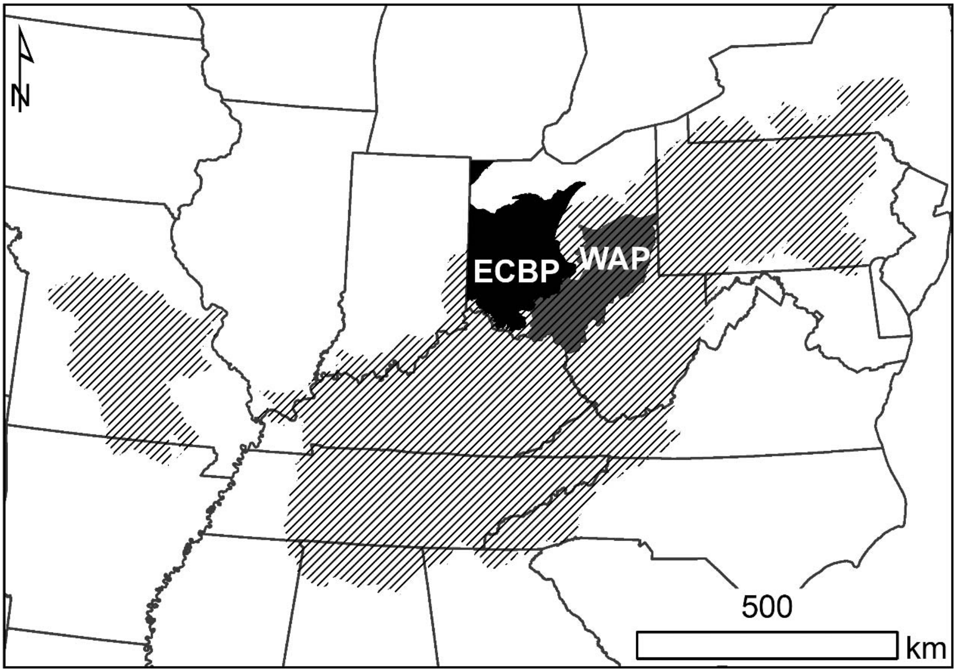

FIG. 1.—Map of the range of the Hellbender (hatched) and the location of the Western Allegheny Plateau (WAP) physiographic region in Ohio (gray shading) where all but one of the streams with extant Hellbender populations are located. The species is thought to be extirpated from the Eastern Corn Belt Plains (ECBP) in western Ohio (black)

densely forested region compared to those to the east (Woods *et al.*, 1999), but with greater relief and forest cover than the Eastern Corn Belt Plains to the west, where Hellbender populations have been extirpated (Fig. 1; Lipps, 2013). These characteristics result in streams in the WAP generally being more eutrophic and having greater variability in flow regimes and water quality parameters than what is commonly reported from other Hellbender research sites. Similar to other portions of the range, extensive in-stream, riparian area, and watershed alterations have occurred. Recently, unconventional hydraulic fracturing ("fracking") has dramatically increased infrastructure development in much of the extant range of the Hellbender in Ohio. In 2015 Ohio had an estimated 225,683 km of pipelines mostly transporting oil, gas, and products from 54,771 producing oil and gas wells (American Petroleum Institute, 2017), with most new construction being focused in the Marcellus and Utica shale gas plays, corresponding with the WAP in eastern Ohio.

Pfingsten (1990) conducted the first state-wide surveys for Eastern Hellbenders in Ohio during the mid-1980s, during which he provided initial descriptions of Hellbender habitat in the state, including water temperature, pH, turbidity, and depth, as well as general habitat descriptions. Given the estimated 80% declines in Hellbender populations in Ohio since this initial survey (Lipps, 2013) and the continued anthropogenic alterations within occupied watersheds and riparian corridors, understanding landscape, local, and chemical habitat characteristics is imperative for future conservation planning. Here, we present descriptions and measures of Eastern Hellbender habitat in Ohio and discuss how distinct differences from habitat elsewhere in the range present unique challenges for the continued persistence of populations and development of conservation plans in the state.

METHODS

From 2011–2019 we conducted surveys for Eastern Hellbenders in stream segments across the range of extant populations in Ohio. Survey methods varied by year. From 2011–2016 surveys consisted of rock turning in concert with snorkeling with a dive light. Due to concerns with potential destruction of habitat associated with rock turning (Horchler, 2010; Pike *et al.,* 2010), from 2017–2019 we conducted surveys by snorkeling and peering under large rocks with dive lights. The primary purpose of these surveys was to locate nest sites for the collection of eggs for an ongoing head-start and repatriation program in the state. The presence of eggs was determined using an egg collecting hook. If eggs were present, they were collected for inclusion in the head-start program. Detections of Hellbenders from these surveys were used to define occupied streams and watersheds for measuring habitat characteristics.

We measured landscape characteristics for both occupied streams and associated watersheds. For occupied streams we determined the upstream catchment area and percent forest cover within the defined catchment. Both upstream catchment area and percent forest cover were determined using StreamStats v4.0 (Ries *et al.,* 2017). Upstream catchment and riparian forest cover have been shown to be important for maintaining stream water quality (Pugh *et al.,* 2016; Pitt *et al.,* 2017; Jachowski and Hopkins, 2018). Percent forest cover was determined in StreamStats based upon the 2011 National Land Cover Database.

Eastern Hellbender "populations" in Ohio are largely restricted to bends in rivers adjacent to steep hillsides (Pfingsten, 1990; Lipps, 2013). We define a stream segment as a portion of a stream that is occupied by Hellbenders. These occupied segments exist as disjunct patches that are intervened by long stretches of unoccupied stream consisting of deep runs, pools, and riffles lacking large rocks. Within stream segments, we assessed both substrate quality and water quality. To assess substrate, we conducted Wolman Pebble Counts (zig-zag pebble count) within the segment of occupied habitat (Bevenger and King, 1995). A pebble count consists of traversing the occupied stream segment in a zig-zag from bankfull width to bankfull width, beginning at the downstream end. An observer takes three steps and then blindly touches the substrate material nearest their front foot. This substrate is then measured using a gravelometer or determined to be bedrock, hardpan, sand, or silt. This pattern is continued until a minimum of 100 substrate measurements are collected. We then calculated and plotted proportions from smallest substrate (silt) to largest substrate (>724 mm boulders). Elevated amounts of fine sediments (silt and sand) are associated with degraded habitats and reduced habitat suitability for Hellbenders (Pugh *et al.,* 2016), possibly due in part to filling of interstitial spaces in gravel beds thought to be important for larvae (Nickerson *et al.,* 2003). Streams were categorized as occupied, unoccupied-but-suitable, or unoccupied-and-unsuitable. Habitat suitability was determined by the presence or absence of >724 mm boulders and boulder slabs that serve as shelter rocks for adult Eastern Hellbenders.

When a Hellbender was captured or observed, we collected local habitat data including shelter rock size, water depth, and predominate substrate under and around the rock. Using a tape measure, we measured the size of the shelter rock under which Hellbenders were observed along two axes, the longest axis and the axis perpendicular to the longest axis. Shelter rock surface area was calculated as the product of the two axis measurements. Water depth was measured using a tape measure from the stream bed directly in front of the shelter rock entrance to the surface of the water. Substrate immediately surrounding rocks was categorized as bedrock, boulder, cobble, gravel, sand, or silt and the proportion observations for each substrate was calculated. Up to four substrates could be recorded in association which each occupied rock.

Previous studies have hypothesized that water chemistry, in particular conductivity (Pugh *et al.,* 2016; Pitt *et al.,* 2017; Jachowski and Hopkins, 2018), may play a significant role in determining the status of Hellbenders populations across their range. Beginning in 2015, we measured temperature (C), pH, conductivity (μS/cm), and dissolved oxygen (DO; mg/L) as local measures of water quality. Measures of pH and conductivity were collected with an ExTech EC500 meter (ExTech, Nashua, NH) and DO and temperature were measured using an ExTech DO600 meter (ExTech, Nashua, NH). In all instances, measures were taken in flowing water within the occupied stream segment.

RESULTS

Between 2011 and 2019, we observed 237 Hellbenders in 25 stream segments in 11 streams. Larval and juvenile Hellbenders were only observed in two stream segments from 2011–2019. Population structure observed in all other stream segments consisted of large adults. During the same period, fertilized nests were collected in 14 of 25 occupied stream segments. We used these observations to define stream segments and watersheds for habitat descriptions and analysis. Ninety-two percent (23/25) of occupied stream segments were located adjacent to steep topography and nearly all were located within bends in rivers.

We determined upstream catchment area and percent forest cover for 25 upstream catchments, representing all known occupied stream segments in Ohio. Upstream catchment area for occupied stream segments ranged from 84 km^2 to >2400 km^2 (Table 1). Percent forest cover in the upstream catchment showed extreme variation ranging from as low as 18.8% to as high as 83% ($\bar{x} = 50.2$; SD = 14.4) (Table 1).

In 2011, 2015, and 2016, we conducted Wolman Pebble Counts at 22 occupied, eight unoccupied, and nine unoccupied-but-suitable stream segments in six Ohio streams. There is some overlap in 95% confidence intervals for unoccupied and occupied sites; however, substrate in unoccupied stream segments generally had greater proportions of smaller substrates, such as silt, sand, and gravel, and lacked large boulders and shelter rocks (Fig. 2). In contrast, substrate in occupied and suitable stream segments consisted of much lower percentages of smaller substrates and greater percentages of large boulder (362–724 mm) and shelter rocks (>724 mm) (Fig. 2). Very large shelter rocks were detected in all but one occupied Hellbender stream segments, but boulders between 362–724 mm were detected in all occupied stream segments.

At locations where Hellbenders were observed, water depth varied from 12–122 cm ($\bar{x}$ =← 44.94; SD = 20.12; Median = 41). Depth measurements varied by stream, but also due to recent weather conditions and season. For example, during the late summer, we often observed streams with low flow, even interstitial at times, and shallow water depth; however, in early-spring and early-fall when persistent rain occurs, water depths are greater, even within the same stream stretch. In total, we measured 97 shelter rocks under which Hellbenders were observed. There are fewer rock measurements than observed animals, as some rocks were not measured, and Hellbenders often used the same rock across years and will also use bedrock openings. The smallest rocks under which Hellbenders were observed were approximately 60 cm x 50 cm, but most (85.6%) were 100 cm along at least one axis (Fig. 3A). In general, we did not find males guarding eggs under rocks < 100 cm along both

TABLE 1.—The total catchment area and percent forest for 25 sites within 11 streams with extant Eastern Hellbender populations in Ohio. Catchments within the same stream are in order from upstream to downstream

Catchment ID	Catchment area (km^2)	% Forest in upstream catchment
CRCR1	95.82	58.2
CRCR2	137.52	55.9
CRCR3	138.56	55.9
CRCR4	175.86	58.1
KOKR1	859.87	28.8
KOKR2	1227.65	31.8
MORI	2486.39	33.6
NFCA	84.17	46.6
SFCA1	88.31	44.2
SFCA2	92.98	45.0
MSCA1	178.97	46.1
MSCA2	323.75	50.0
MSCA3	347.06	51.2
MSCA4	388.50	54.5
PACR	2315.45	18.8
SACR	1432.26	71.1
SBCR	678.58	83.2
WFLB1	202.80	38.4
WFLB2	271.95	45.0
WFLB3	274.54	45.1
WFLB4	282.31	45.5
WFLB5	287.49	45.8
YECR1	170.16	63.9
YECR2	252.78	68.3
YECR3	380.73	69.4

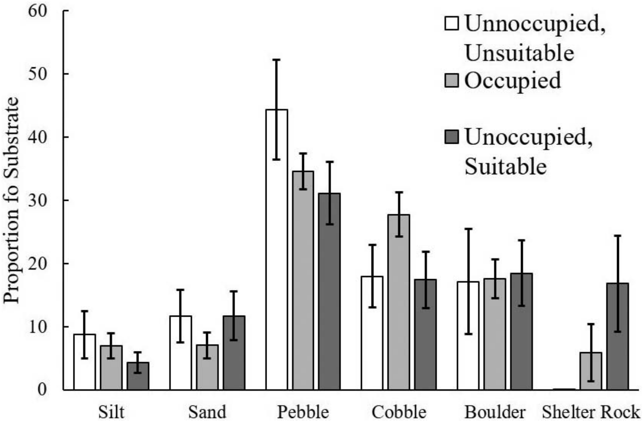

FIG. 2.—Percentages of substrate from Wolman Pebble Counts for unoccupied but unsuitable (n = 8), occupied habitat (n = 22), and unoccupied but suitable habitats (n = 9). The bars represent mean proportion with 95% confidence intervals

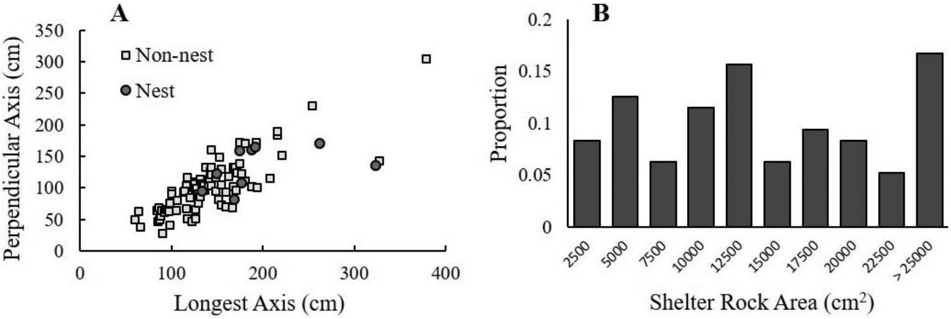

FIG. 3.—Measurements of 97 rocks under which Hellbenders were observed during surveys from 2011–2019. Shelter rocks were measured on the longest axis and the axis perpendicular to the long axis (**A**). These measurements were used to calculate shelter rock surface area (**B**)

perpendicular axes (Fig. 3A). Shelter rock size varied from 2508 cm^2 to 115,595 cm^2, but the most frequently used shelter rocks were between 5000 cm^2 and 15,000 cm^2 (52%; Fig. 3B). The most common substrates near occupied rocks were cobble and sand, which were both observed at nearly 60% of occupied rocks (Fig. 4). Bedrock, sand, and silt were all observed at between 25–30% at occupied rocks (Fig. 4). Boulder was the least commonly observed associated substrate.

We collected water quality data a total of 56 times in 29 stream segments encompassing all known occupied stream segments and watersheds. All measures of water quality were variable both within and among stream segments and watersheds (Table 2). In fact, within a single stream stretch pH varied as much as 1.25 (WFLB1; Table 2) and conductivity by nearly 400 μS/cm (MSCA4). The highest conductivity measured within an occupied stream segment was 1323 μS/cm (MSCA4), downstream of a coal slurry impoundment discharge. In contrast, the lowest measured conductivities were 284 μS/cm and 289 μS/cm (SACR and

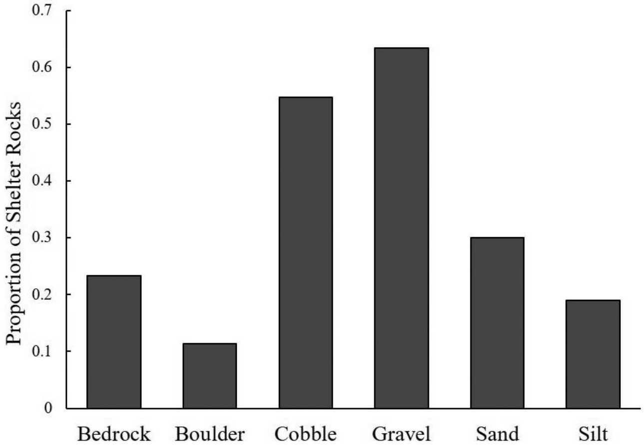

FIG. 4.—Proportion of occupied shelter rocks where bedrock, boulder, cobble, gravel, sand, and silt were observed as the predominate substrates

TABLE 2.—Water quality measurements for individual stream stretches including DO (mg/L), pH, conductivity (µS/cm), Temperature (C). Measurements were taken June–September. Also included are whether or not a stream stretch is occupied by Hellbenders and whether or not fertilized eggs have been observed from 2015–2019

Watershed	Stream stretch	DO (mg/L)	pH	Conductivity (µS/cm)	Temperature (C)	Occupied?	Fertilized nest?
CRCR	CRCR1	6.46	7.93	613	-	Yes	Yes
	CRCR1	8.77	7.6	644	-	Yes	Yes
	CRCR2	8.38	8.45	780	26.3	Yes	No
	CRCR2	8.88	8.71	686	24.7	Yes	No
	CRCR2	9.18	8.32	880	24	Yes	No
	CRCR2	9.76	8.85	1018	22.1	Yes	No
	CRCR3	9.49	8.27	863	23.2	No	No
	CRCR4	9.46	8.78	1072	23.3	No	No
	CRCR5	8.85	8.84	683	24.5	Yes	Yes
	CRCR5	8.96	8.36	773	24.6	Yes	Yes
	CRCR5	8.21	8.43	831	26.8	Yes	Yes
	CRCR5	10.5	8.67	976	20.6	Yes	Yes
	CRCR5	11.83	8.88	978	18.3	Yes	Yes
KOIN	KOIN	8.95	8.93	521	24.1	Yes	No
KORC	KORC	8.77	8.41	502	25.1	No	No
KOZU	KOZU	8.31	8.41	523	26.5	Yes	Yes
KOZU	KOZU	8.96	8.73	480	24.2	Yes	Yes
MORI	MORI	11	-	572	19.6	Yes	Yes
MSCA	MSCA1	9.12	8.32	781	-	Yes	No
	MSCA1	10.13	8.36	784	-	Yes	No
	MSCA1	10.05	8.37	786	-	Yes	No
	MSCA2	11.13	8.31	545	-	Yes	No
	MSCA3	8.88	8.11	816	24.7	No	No
	MSCA4	8.44	8.16	660	26	Yes	No
	MSCA4	8.38	8.3	1053	26.3	Yes	No
	MSCA5	9.89	8.47	1101	21.8	Yes	No
	MSCA6	8.44	8.31	1095	26.1	Yes	Yes
	MSCA6	8.99	8.71	1323	24.4	Yes	Yes
	MSCA7	8.91	7.84	827	24.7	No	No
NFCA	NFCA	8.85	8.23	534	24.9	Yes	No
	NFCA	8.44	8.18	613	26.1	Yes	No
PACR	PACR	9.52	8.81	435	22.7	Yes	No
SACR	SACR	9.8	8.2	284	21.9	Yes	Yes
SBCR	SBCR	8.76	7.83	482	24.7	Yes	Yes
SFCA	SFCA1	7.4	8.33	392	29.4	Yes	Yes
	SFCA1	9.76	8.25	398	21.8	Yes	Yes
	SFCA2	7.83	8.35	289	28	Yes	Yes
	SFCA2	10.76	8.32	369	20	Yes	Yes
	SFCA2	10.88	7.92	377	19.8	Yes	Yes
WFLB	WFLB1	11.59	8.51	673	-	Yes	Yes
	WFLB1	9.46	8.32	570	23.3	Yes	Yes
	WFLB1	9.68	-	577	22.3	Yes	Yes
	WFLB1	9.34	7.07	409	23.8	Yes	Yes
	WFLB2	9.89	8.05	476	22.2	Yes	Yes
	WFLB3	11.06	-	694	19.5	Yes	Yes
	WFLB4	10.75	7.99	622	20.4	Yes	Yes
	WFLB4	11.32	-	647	19.1	Yes	Yes

TABLE 2.—Continued

Watershed	Stream stretch	DO (mg/L)	pH	Conductivity (μS/cm)	Temperature (C)	Occupied?	Fertilized nest?
YECR	YECR1	9.89	7.97	325	22.2	Yes	Yes
	YECR1	9.23	8.53	445	23.9	Yes	Yes
	YECR1	11.57	8.48	414	18.8	Yes	Yes
	YECR1	11.63	8.41	416	19.1	Yes	Yes
	YECR1	8.52	8.89	484	25.46	Yes	Yes
	YECR2	8.8	-	384	25	Yes	No
	YECR2	9.07	8.36	570	24.3	Yes	No
	YECR3	9.56	8.37	467	22.9	Yes	No

SFCA2, respectively). More commonly, conductivity fluctuated from 350–650 μS/cm in occupied stream segmentss (Table 2). Temperature within stream segments was variable and regularly fluctuated dependent upon recent weather and time of year (Table 2). The highest temperature recorded in an occupied stream segment during this study was 29.4 C (Table 2).

DISCUSSION

Eastern Hellbender populations in Ohio have declined by an estimate 80% since the mid-1980s when the first statewide survey was conducted, with many local populations now functionally extirpated (Pfingsten, 1990; Lipps, 2013). Extant populations are often small, consisting of only large (and presumably old) individuals with little to no recruitment occurring. The rapidity of declines and rapid extirpation of many populations is disconcerting, particularly given the significant improvement in water quality across much of the known range in Ohio. Since the early 2010s, researchers have continually monitored populations in Ohio in order to track Hellbender occurrences and assess landscape and local habitat characteristics. Understanding habitat characteristics is essential for understanding mechanisms driving population declines and the development of effective conservation and management plans. Both physical and chemical habitat characteristics play large roles in defining habitat for this species. The importance of physical and chemical habitat has been effectively studied in many portions of the range, but do not effectively or adequately define the conditions associated with Hellbender habitat in northern portions of the Ohio River watershed.

Forest cover is an important predictor of the occupancy of Hellbender populations and deforestation may in fact be a primary driver for declines due to ecological cascades for both the Ozark Hellbender (*Cryptobranchus alleganiensis bishopi*) and Eastern Hellbender (Nickerson *et al.,* 2017; Jachowski and Hopkins, 2018). We found upstream catchment forest cover to be variable in occupied streams, ranging from 18–80%, with more than half of catchments having less than 50% forest cover. Pugh *et al.* (2016) used occupancy modeling to model stream habitat characteristics at multiple spatial scales and found that when upstream catchment forest cover decreased toward 70%, predicted occupancy neared 0. Pitt *et al.* (2017) failed to detect Hellbenders when conductivity was greater than 300 μS/cm and increased conductivity was strongly correlated with decreases in canopy cover within the watershed and riparian buffer. In addition to conductivity, Nickerson *et al.* (2017) also found an increase in small substrates, such as silt and sand, due to losses of riparian forest cover.

Ohio has a long history of deforestation for conversion to agriculture, housing, roads, fossil fuel extraction, and the timber industries resulting in a loss of nearly 90% of historic forests by the early 1900s. This precipitous decline was followed by decades of land protection and reforestation. Today, there is approximately 30% statewide forest cover (Balser, 2020), with much of the reforestation having occurred within the extant range of the Eastern Hellbender. In Southwest Virginia, Jachowski and Hopkins (2018) found that in comparison to sites with mostly forested catchments, those with 50% upstream catchment forest cover had smaller populations, showed little to no recruitment, and consisted of nearly all adults, conditions which are present in nearly all extant Ohio populations (N. Smeenk and G. Lipps, pers. obs.). While not the direct mechanism for declines, it appears as though both historic and contemporary loss of forest cover are resulting in cascading effects on in-stream habitat and water quality, similar to those observed by Nickerson *et al.* (2017) in Missouri.

Substrate is a critical component of habitat for the persistence of Hellbender populations in streams. Moderate proportions of gravel, cobble, and boulder are often components of suitable Hellbender streams, as they provide the appropriate micro-habitat to support all life-stages (Nickerson *et al.,* 2003; Nickerson *et al.,* 2017). Stream segments occupied by Hellbenders in Ohio were composed of approximately 43% gravel, 24.5% cobble, and 7% shelter rocks. In contrast, in unoccupied stream segments, we found much greater proportions of small substrates, including up to 30% silt and sand. In Indiana, Burgmeier *et al.* (2011) found 39% gravel substrate and approximately 6% shelter rock, a finding consistent with results from this study. While other studies do not report exact percentages, increased proportions in fine substrates are negatively associated with Hellbender presence, while increases in substrate size are positively associated with Hellbender presence (Pugh *et al.,* 2016). The mechanism(s) by which fine substrates contribute to declining Hellbender populations remains unclear, but given the lack of recruitment, the degradation of substrate may be a proximate cause of declines (Wheeler *et al.*, 2003; Lipps, 2013). The effects of silt on larval behavior and availability of interstitial refugia are worthy of further study (McAdam, 2011). Increases in the proportion of pebbles and other fine substrates are directly attributable to decreases in forest cover and other in-stream alterations (Nickerson *et al.,* 2017; Jachowski and Hopkins, 2018). Despite low percentages of small fines in most of the streams we surveyed, shallow layers of silt were nearly universally distributed in the stream in conjunction with deeper deposits along the margins. Further, water clarity in many streams was frequently poor during the 2016–2018 surveys. Given that overall forest cover has not significantly changed since the mid-1980s, these changes in siltation and water clarity are likely a result of increased fossil fuel extraction in the region, which often involves in-stream construction in addition to the clear-cutting and excavation of pipeline easements traversing adjacent steep and highly erodible hillsides (Fig. 5; G. Lipps, pers. obs.). For example, through a public records request, we learned of one company self-reporting 72 water quality violations in one watershed occupied by Hellbenders; many of these involved slipping hillsides in recently constructed pipeline right-of-ways, undoubtedly resulting in increases of sediment transport. Further, at least five of the 11 occupied streams have been crossed by new pipeline construction since our work began, some by multiple lines.

In Ohio, most Hellbenders were detected in runs with a water depth of 45 cm, but were also observed at depths as shallow as 13 cm and as deep as 122 cm. Burgmeier *et al.* (2011) found a strong association with runs averaging a depth of 66.6 cm. They also observed four individuals using adjacent deep pools, in which it seems likely that overwintering occurred. While Hellbenders very likely use adjacent pools in Ohio streams, these habitats are logistically difficult to survey and are often used during times when surveys are not

FIG. 5.—Occupied Hellbender habitat in Ohio consists of stream stretches with large rocks for shelter. Columbiana County, OH (**A**). Infrastructure related to the oil and gas boom has resulted in new pipeline construction and hillside clearing which can be a considerable source of sediment entering streams. Jefferson County, OH (**B**)

conducted. Water depth and flow are seasonably variable. Flow regimes in most Ohio Hellbender streams can be described as flashy, resulting in periods of low flow interspersed with periods of high flow (Engleke and Roth, 1981). In smaller watersheds, we frequently observe little flow and shallow water during the late summer, often resulting in shallow warm pools hydrologically connected through interstitial flow. In contrast, flows in larger streams are consistent with less interannual variation in depth and flow. These conditions differ greatly from those in other portions of the range in which streams are spring-fed and hydrology remains more consistent (Whiting and Stamm, 1995).

We found local habitat characteristics to be similar to those from other studies. The most frequently observed substrates associated with Hellbender locations were gravel, cobble, and sand (Fig. 4). While we did not assess substrate use relative to availability, these results are consistent with those reported in Indiana, where 79% of Hellbender locations were associated with gravel (Burgmeier *at al.,* 2011). Missouri streams with high proportions of larvae contained deep cobble and gravel beds, suggesting that these may be necessary for successful recruitment and maintaining large adult populations (Nickerson *et al.,* 2003). It also seems plausible that this association with smaller substrates results in greater embeddedness and stability of shelter rocks, many of which are annually occupied (Lipps, 2013).

Hellbenders rely on large heavily embedded shelter rocks for all life-stages, with the possible exception of larvae. While Hellbenders most frequently use shelter rocks, we also observed Hellbenders in bedrock openings with some regularity. The smallest shelter rocks under which we observed Hellbenders were approximately 60 cm x 50 cm, but most shelter rocks were 100 cm along at least one axis. Similar to Burgmeier *et al.* (2011), we observed Hellbenders using shelter rocks between 5000 cm^2 and 15,000 cm^2 greater than 50% of the time. Shelter rocks from both Indiana (Burgmeier *et al.,* 2011) and this study were generally larger than those observed in North Carolina (Rossell *et al.,* 2013). Differences in shelter rock size may relate to differences in geology, but it should also be noted that Hellbenders in North Carolina (Male = 37.7 cm TL and Female = 38.4 cm TL; Rossell *et al.,* 2013) were generally smaller than those observed in Ohio (Male = 49.6 cm TL and Female = 50.3 cm TL; N. Smeenk and G. Lipps, unpub. data), resulting in a reliance on smaller shelter rocks than dictated by Hellbender size in Ohio. It is also possible that Hellbenders use smaller rocks where population densities and competition for shelter rocks is greater.

TABLE 3.—Comparison of water quality parameters from this study and previous studies for Hellbender occupied sites throughout their range

State	DO (mg/L)	pH	Conductivity (μS/cm)	Temperature (C)	
OH	6.5–11.8	7.1–8.9	284–1323	18.3–29.4	This study
OH	-	6.0–9.2	-	0.0–33.0	Pfingsten (1990)
TN	7.1–10.4	6.9–7.4	-	8.5–20.0	Nickerson *et al.* (2003)
MO	8.4–13.6	7.6–9.0	-	9.8–22.5	Nickerson *et al.* (2003)
WV	7.3–9.6	5.8–7.0	29–53	14.8–20.0	Keitzer *et al.* (2013)
IN	6.8–15.0	7.5–8.7	150–660	0.0–25.9	Burgmeier *et al.* (2011)
PA	-	-	78–277	-	Pitt *et al.* (2017)

Hellbenders are often described as sensitive to water quality due to their general reliance on cutaneous respiration and frequent occurrence in clear, cool, fast flowing streams across much of their range. While the link to parameters, such as conductivity, is not well understood, Hellbenders show a preference for lower water temperatures (Hutchison and Hill, 1976). This is likely due to their relatively limited cutaneous gas exchange abilities, in addition to their limited aerobic activity capabilities and slow recovery (Hutchison and Hill, 1976; Ultsch and Duke, 1990). Additional water quality parameters, including conductivity, pH, and DO, are often linked to the persistence of Hellbender populations. We measured pH from 7.07–8.93 and DO from 6.46–11.83 mg/L in occupied stream segments in Ohio, generally corresponding to supersaturated DO concentrations. Measurements for both pH and DO were variable within streams due to both contemporary and historical alterations within watersheds, such as the presence of coal slurry pond outflow and mine drainage. These impacts did not usually result in degraded biological indices (*e.g.*, Index of Biotic Integrity, Ohio EPA (2015)) downstream of the inputs (Ohio EPA, pers. comm.). Measures of pH and DO from occupied Ohio streams are all well within the measures from other portions of the range (Table 3). However, we observed much greater measures of both conductivity and temperature than previous studies (Table 3). In fact, every measure of conductivity from this study was greater than the predicted limit for occupancy from across the range (WV: 53 μS/cm [Keitzer *et al.* 2013]; PA: 277.4 μS/cm [Pitt *et al.* 2017]), with the exception of Indiana, where the maximum conductivity reported was 660 μS/cm (Burgmeier *et al.,* 2011). The mechanism through which conductivity affects Hellbenders is not well understood. Conductivity may vary across the range naturally due to regional geology, leading to local adaptation of Hellbender populations to differing levels of conductivity (Pitt *et al.,* 2017). Geographic variability in baseline conductivity appears likely, given the regional variability previously observed (Table 3). Baseline estimates in the WAP of Ohio are thought to be between 195–244 μS/cm (Cormier *et al.*, 2018). We never recorded conductivity within this range in any occupied Ohio streams, suggesting that conductivity across the Hellbender range in Ohio is significantly elevated above baseline estimates. Pitt *et al.* (2017) found conductivity to be the strongest predictor of Hellbender population occupancy and hypothesized that increased conductivity may inhibit sperm motility, resulting in reduced recruitment in extant populations. This supposition is not supported by our findings in which fertile nests with developing embryos were collected in stream stretches with conductivity ranging from 283–1323 μS/cm (Table 2; $\mu = 609.3$; SD $= 237.9$). However, despite the presence of fertile nests in many stream segments and watersheds, most populations in Ohio lack recruitment and persist as populations consisting of large old individuals (N. Smeenk and G. Lipps, pers. obs.). This suggests that while conductivity may not limit sperm motility, it may affect egg and/or larval development and survival. Further, while conductivity may naturally vary geographically, it is widely considered an effective measure of anthropogenic impacts within watersheds, such as riparian forest loss (Jachowski and Hopkins, 2018). Such anthropogenic impacts have also been linked to increased water temperatures.

Water temperatures in occupied stream stretches from this study regularly exceed those from previous studies by 3.4 C, with temperatures exceeding 29.0 C in some stream stretches. Previously, Pfingsten (1990) also captured Hellbenders in Ohio streams with measured water temperatures of 30.0 C and 33.0 C. These temperatures far exceed the mean preferred temperature of 20.21 C for individuals acclimated to 25.0 C (Hutchison and Hill, 1976). Previous studies report maximum temperatures of 20.0–22.5 C (Table 3). The greater water temperatures frequently observed in Ohio streams likely results in increased thermal stress, exacerbated by both limited gas exchange abilities and limited aerobic abilities in concert with slow recovery (Ultsch and Duke, 1990). Hellbenders do have functional lungs for breathing atmospheric oxygen, allowing survival of hypoxia for 5–11 d (Ultsch and Duke, 1990). During much of the year, Hellbenders are relatively inactive; however, from August–September, females are actively searching for mates and males are actively protecting shelter rocks, resulting in increased aerobic activity during what are usually the warmest stream conditions of the year. From mid-September to November, females retreat to shelter rocks, while males actively protect nests and care for eggs. During unseasonably warm falls, this may result in extreme aerobic output for males as they protect and aerate eggs. These activities increase oxygen demands for males, resulting in frequent forays to breathe atmospheric oxygen as well as a physiological demand for increased caloric intake. On multiple occasions, we have observed the consumption of entire egg clutches by males, occasionally coupled with the abandonment of shelter rocks (N. Smeenk and G. Lipps, pers. obs.). Hellbenders are known to exhibit filial cannibalism, in which "diseased" eggs are consumed (Unger and Williams, 2017; Settle *et al.*, 2018), but the consumption of entire clutches has not been previously reported. Given the low density of Hellbenders in Ohio streams and potential Allee effects resulting in frequently observed lower egg counts caused by fewer clutches per nest (250–300 eggs), this may mean that in any given year nearly all fertile eggs are consumed by guarding males.

In general, we observed physical habitat characteristics to be consistent with those reported from across the range of the species. Hellbenders in Ohio use stream segments in river bends adjacent to steep topography. Within stream segments they use large shelter rocks generally found in conjunction with cobble, gravel, and sand. However, due to significant historic removal of forests and fossil fuel extraction activities, Ohio streams exist in an apparent permanently altered state. These historic alterations, in addition to differences in river hydrology and geology, have resulted in habitat characteristics not reported elsewhere in the range. Both conductivity and water temperature in this study are substantially higher than measures from other portions of the range. Conductivity in Ohio streams is likely naturally higher than other regions due to underlying geology and other factors (Pitt *et al.,* 2017), but are still elevated from expected baseline estimates ranging from 195–244 μS/cm (Cormier *et al.*, 2018). Additionally, the natural hydrology of many occupied streams in Ohio results in extremely variable flashy flows (Engleke and Roth, 1981), which, during the winter months, results in large ice flows that we have observed to move, alter, and bury shelter rocks. Furthermore, reliance on precipitation and overland flow results in low flow, lower DO, and higher temperatures during the late summer in some occupied stream stretches. This suggests Hellbenders in Ohio may be adapted to such conditions. Given models suggesting higher stream temperatures as a result of climate change (Mohseni *et al.*, 1999), coupled with changes to precipitation regimes in the Midwest (Wuebbles and Hayhoe, 2004), Ohio Hellbender populations represent either the first portion of the range to likely become extirpated or the most genetically important portion of the range due to local adaptations to higher stream temperatures.

Forest cover is perhaps the single most important habitat characteristic in determining occupancy and persistence of Hellbender populations (Pugh *et al.,* 2016; Nickerson *et al.,* 2017; Pitt *et al.,* 2017; Jachowski and Hopkins, 2018). Few occupied stream segments in Ohio have contemporary upstream catchment forest cover greater than 60%. Jachowski and Hopkins (2018) found forest cover of <60% is strongly linked to increased water temperatures, increased conductivity, increased pH, and higher proportion of pebble substrate. Further, they found significant relationships between population structure and forest cover in which low forest cover resulted in an adult biased size structure, suggesting these factors are directly linked to recruitment (Jachowski and Hopkins, 2018). Taken together with their findings, the patterns of low forest cover, increased water temperature and conductivity, and adult biased size structures we observed in nearly all Ohio streams, suggest that legacy effects of deforestation and fossil fuel extraction have resulted in an extinction debt that was not previously observable due to a lack of historic surveys. Observed population structures in combination with observed physical and chemical habitat characteristics suggest that forest cover is a primary driver of conditions observed across the range of the species in Ohio. In most occupied Ohio streams, adult habitat is prevalent, but suspected larval habitat (interstitial spaces of gravel beds [Nickerson *et al.,* 2003]) has been significantly altered by increased deposition of fines and small substrates. While any effective conservation strategy will involve increasing forest cover to minimize contemporary depositions of small substrates, these legacy effects of silt present a difficult, if not insurmountable obstacle to the goal of eventually ending the "intensive population management" (Lacy, 2010) that is currently required for the persistence of Hellbenders in nearly all occupied streams in Ohio.

The continued persistence of the Hellbender in Ohio is fraught with uncertainty. While adult survival remains high and reproduction naturally occurs in Ohio streams, natural recruitment is rare or absent. Given the on-going lack of recruitment, current captive rearing and release programs provide a stopgap measure to ensure the short-term persistence of the species in Ohio streams, but do little to alleviate concerns related to egg and larval survival. As a long-lived species, the short-term may be measured in decades, but further research is merited to investigate factors related to the success of wild nests and survival and habitat use of larval Hellbenders. A more complete understanding of these life-stages appears critical to the implementation of effective conservation and management plans that will result in self-sustaining populations throughout Ohio.

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