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Spawning ecology of the American brook lamprey, *Lampetra appendix*

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Synopsis

We observed spawning American brook lamprey, *Lampetra appendix*, in coldwater streams in Minnesota to assess various aspects of their spawning behavior and spawning habitat requirements. Spawning occurred during April and May, at water temperatures ranging from 8.7 to 15.5°C. Average adult lamprey length and mass differed significantly among streams, but there were no significant differences in length or mass between males and females. Overall sex ratio was 1:1, although one stream had significantly more males than females and one stream held significantly more females. Lampreys spawned in groups of 2–14 individuals, averaging 4.2 adults per nest across all streams. Nests were constructed in gravel and cobble substrate just upstream of riffles, spaced at an average density of three nests m^{-2}. The typical nest was 16 cm in diameter in water 31 cm deep with a bottom current velocity of 14 cm s^{-1}, and was excavated to a depth of 4 cm below the stream bottom; however, some nest characteristics varied significantly in a few streams. Nests were larger in streams with larger spawning groups, deeper water, and slower current velocities. American brook lamprey exhibited spawning behaviors and spawning habitat requirements similar to those of other species of lamprey in North America.

Introduction

Water pollution, stream habitat degradation, bait collecting activities, and sea lamprey control programs have negatively impacted many populations of American brook lamprey, *Lampetra appendix*, throughout the species range in eastern North America (Vladykov 1949, 1973, Manion & Purvis 1971, Eddy & Underhill 1974, Trautman 1981, Cochran et al. 1993). These problems have led to the need for special protection of the species in many localities (Johnson 1987).

Despite the wide geographic distribution of this nonparasitic lamprey (Page & Burr 1991) and scientific studies that date back a century or more (e.g., Gage 1893, Dean & Sumner 1897, Young & Cole 1900), there is surprisingly little information on the spawning ecology of American brook lamprey (see reviews by Hoff 1988, Cochran et al. 1993). Continuing threats to *L. appendix* and its habitats necessitate a more comprehensive examination of the species' spawning ecology in a region where many of the lamprey populations still appear healthy (Mundahl 1998, Lyons et al. 2000). Information from this study, when combined with data on the habitat requirements of American brook lamprey larvae (Beamish & Lowartz 1996), will enable resource managers to protect the habitats needed by this species throughout its range.

Methods

Study area

In southeastern Minnesota, American brook lampreys inhabit streams and small rivers that often originate on cultivated glacial plains before descending through steep, wooded valleys leading to the Mississippi River (Eddy & Underhill 1974, Waters 1977, Phillips et al. 1982, Omernik & Gallant.[1]) Historically, intensive agricultural development within the region, in combination with steep topography, rapid snowmelt, and torrential rains, led to greatly increased soil erosion, severe flooding, and widespread stream sedimentation (Waters 1977, Thorn et al. 1997). Expanding land conservation practices during the past several decades have led to improved stream habitats (Waters 1977, Thorn et al. 1997), and today more than 130 of these streams (1145 stream km) are managed for brown, *Salmo trutta*, brook, *Salvelinus fontinalis*, and rainbow trout, *Oncorhynchus mykiss* (Thorn et al. 1997, Minnesota Department of Natural Resources (MDNR).[2]) Historical and recent collection records indicate that American brook lamprey have been found in 48 streams in nine drainage basins within this region (MDNR[3], N. Mundahl, unpublished data). Based on these records and recommendations of natural resources agency personnel, fishermen, and land owners, we selected lamprey populations in 14 streams in four drainages for investigation. These streams varied dramatically in drainage area, stream size, habitat, and suspected lamprey population size. We examined some streams for spawning lamprey each spring during three successive years, whereas others were studied only one or two of the years because of protracted spawning periods and time constraints.

Spawning lamprey and habitat assessments

During the spring spawning periods (late April–early May) in 1995–1997, we made visual counts of adult American brook lamprey within the spawning habitat. Sections (up to 2 km) of streams where lamprey were known to spawn were walked each year until groups of spawning lamprey were located. In most streams examined, spawning lamprey were located in only one or a few riffle areas, with no spawning activity observed outside of these areas. In some streams, lamprey used the same spawning area(s) each year, whereas in others lampreys used different areas in different years.

We made repeated scans from various vantage points along the stream banks and/or while wading within the stream to tally the individuals actively involved in spawning activity (nest construction and/or spawning), as well as the number of nests present within the spawning area. We observed spawning groups only long enough to count the number of spawners, and spawners within a particular nest were only counted once on a given visit. If spawning groups were obscured by water surface disturbances, submerged vegetation, or woody debris, we temporarily displaced lamprey from the spawning nest by hand into a large dip net held immediately downstream from the nest in order to count them. Special care was taken to search for spawning lamprey around and under all instream objects and undercut banks. After counting, lamprey were returned to the point of capture. This procedure captured all lamprey within a given nest, and, judging from their immediate return to spawning activities when released, had no observable effect on spawning behavior.

In 1997, all spawning lamprey that we observed were collected by hand net to facilitate sex determination and measurements. We determined sex of all individuals from each spawning group by examination of external sex characteristics (male genital papillae, female with obvious egg masses and/or swollen base of second dorsal fin; Cochran et al. 1993). Lamprey were anesthetized (tricaine methanesulfonate, MS-222), weighed (0.1 g wet mass), measured (mm TL), and released after a recovery period.

We assessed physical habitats at each location where spawning adult lampreys or their nests were located. The sizes of bottom substrates within and adjacent to nests were measured with a ruler, and water temperature and dissolved oxygen concentration were measured with a YSI oxygen/temperature meter. Water depth and bottom current velocity (Marsh–McBirney Flowmate current meter) were measured at each spawning nest. In addition, we measured the total area of spawning habitat being used (rectangular

[1]Omernik, J.M. & A.L. Gallant. 1988. Ecoregions of the upper midwest states. EPA/600/3-88/037, USEPA, Corvallis.

[2]MDNR 1998. Trout fishing access in southeastern Minnesota. MDNR, St. Paul. 101 pp.

[3]MDNR 1995. Known locations for American brook lamprey (*Lampetra appendix*) in Minnesota, January 1995. MDNR Nat. Herit. Nongame Res. Progr., St. Paul. 26 pp.

area just encompassing all nests clustered within a single riffle or portion of a riffle), distances between adjacent nests (distance between nearest edges), and nest dimensions (width, length, depth below surrounding substrate). All nests, whether or not they were in immediate use, were measured.

Results

Spawning lamprey

We observed adult American brook lamprey spawning, excavating nests, or swimming within spawning areas in 14 streams during 1995–1997 (Table 1). Numbers of lamprey observed per stream each year ranged from 1 to 69, averaging 16 individuals. Spawning lamprey were observed during all 3 years in some streams (e.g., North Branch Whitewater River), but during only a single year at others (e.g., South Branch Whitewater River) despite repeated visits during each year.

Lamprey were observed both as individuals (loners excavating nests or swimming through the spawning area) and as active spawners (Table 1). Active spawners comprised over 75% of all lamprey observed, although loners were encountered more frequently than spawners in some streams. Active spawners were observed in groups ranging in size from a single spawning pair to 14 individuals. Of the 62 spawning groups observed, 20 (32%) contained only two individuals, 31 (50%) held three to five spawners, and 11 (18%) contained six or more lamprey. Average spawning group size in each stream ranged from 2.0 to 9.8,

Table 1. Numbers of American brook lamprey observed as lone individuals, active spawners, and mean (range) spawning group sizes during 1995–1997 spawning seasons.

Year/stream	Loners	Spawners	Number of spawning groups	Spawning group size
1995				
Badger Creek	0	17	?	
Beaver Ck.(Win. Co.)		1	0	
M. Br. Whitewater	1	0		
N. Br. Whitewater	2	12	3	4.00 (2–5)
Pine Ck.	12	15	4	3.75 (2–5)
Rupprecht Ck.	0	69	7	9.86 (4–14)
S. Br. Whitewater	1	17	5	3.40 (2–5)
1995 totals	17 (11.6%)	130 (88.4%)		5.95 (2-14)
1996				
Badger Ck.	0	2	1	2.00
Beaver Ck.(Hou. Co.)		1	0	
Canfield Ck.	3	7	2	3.50 (2–5)
Etna Ck.	1	0		
Forestville Ck.	4	19	4	4.75 (4–7)
N. Br. Whitewater	5	2	1	2.00
Rupprecht Ck.	4	0		
S. Br. Root R.	1	4	1	4.00
S. Fk. Zumbro R.	1	0		
1996 totals	20 (37.0%)	34 (63.0%)		3.78 (2–7)
1997				
Badger Ck.	4	0		
Canfield Ck.	0	12	3	4.00 (2–8)
N. Br. Whitewater	13	11	4	2.75 (2–5)
Pine Ck.	12	32	7	5.47 (2–7)
Salem Ck.	5	27	7	3.86 (2–5)
S. Br. Root R.	4	14	5	2.80 (2–4)
S. Fk. Zumbro R.	6	21	8	2.63 (2–4)
1997 totals	44 (23.6%)	117 (72.7%)		3.44 (2–8)

Percentages compare relative numbers of loners and spawners.

but varied significantly among streams only during 1995, and only because of the large spawning groups in Rupprecht Creek (1995 ANOVA $F = 9.58$, $p = 0.001$; 1996 ANOVA $F = 0.92$, $p = 0.533$; 1997 ANOVA $F = 1.59$, $p = 0.197$). Spawning group size varied significantly among years (ANOVA $F = 6.25$, $p = 0.003$) when Rupprecht Creek data were included, but not when they were excluded (ANOVA $F = 0.20$, $p = 0.817$). Spawning group size did not differ within the same creek over time (North Branch Whitewater River: ANOVA $F = 0.81$, $p = 0.496$; Pine Creek: $t = 0.79$, $p = 0.226$). Overall, spawning group size during the 3 years averaged 3.55 individuals across all streams except Rupprecht Creek (4.26 individuals including Rupprecht Creek).

The overall ratio of male to female lamprey collected in 1997 was 1:1 (76 males:78 females). In the 34 spawning groups observed, 13 had equal numbers of males and females, 12 had more females than males, and nine had more males than females. Sex ratios (male:female) within spawning groups ranged from 5:1 to 1:4. Only Salem Creek had a sex ratio of active spawners significantly different from 1:1 (Table 2), with females outnumbering males 3:1. All loners at North Branch Whitewater River, South Branch Root River, and South Fork Zumbro River were males, whereas they were all females at Pine Creek. Inclusion of loners skewed the sex ratio significantly in favor of males in North Branch Whitewater River (Table 2).

Total length and wet mass of spawning lamprey varied significantly (two-factor (site × sex) ANOVAs: both $p < 0.001$) among the streams examined in 1997 (Table 2). Differences were most apparent between South Fork Zumbro River and Pine Creek populations, with Pine Creek lamprey averaging 19% longer and 73% heavier than Zumbro River specimens (Figure 1, Table 2). Average female lengths and masses were slightly less than those of males at most sites, although neither length nor mass differed significantly (two-factor ANOVAs: both $p > 0.05$) between sexes.

Although there were slight variations in both slopes and intercepts for the length–mass regressions of spawning lamprey collected from six different streams (Table 3), regressions were not significantly different (ANCOVA: $p > 0.05$). Consequently, a single length–mass regression was calculated for lamprey from all streams combined (Table 3).

Spawning habitat

We observed American brook lampreys spawning during late-April and early-May in southeastern Minnesota (Table 4). Spawning activities were observed during morning and afternoon hours (9:30–16:00 h). We made no attempts to determine

Table 2. Mean (± SD) total length and wet mass, and sex ratios of adult American brook lamprey collected from streams in southeastern Minnesota, 1997.

Stream	Sex	Spawners only	Spawners + loners	Total length (mm)	Wet mass (g)
Badger Creek	F	0	3	151 (12)	8.1 (3.2)
Canfield Creek	F	5	5	ND	ND
	M	5	4	ND	ND
N. Br.	F	5	5*	177 (7)	11.6 (2.3)
Whitewater R.	M	6	17	185 (10)	11.9 (1.8)
Pine Creek (2.1)	F	13	25	192 (12)	15.1
	M	19	19	198 (9)	15.7 (2.3)
Salem Creek	F	21*	24*	171 (13)	10.3 (2.8)
	M	6	8	166 (10)	9.2 (1.9)
S. Br.	F	7	7	174 (8)	12.0 (2.0)
Root R.	M	7	10	179 (9)	11.6 (1.5)
S. Fk.	F	9	9	162 (10)	8.8 (2.3)
Zumbro R.	M	12	18	165 (10)	9.0 (1.6)

Sex ratios are shown for both active spawners only and spawners and loners combined. Asterisks indicate samples with sex ratios significantly different from 1:1 (chi-square, $p < 0.05$). ND = not determined.

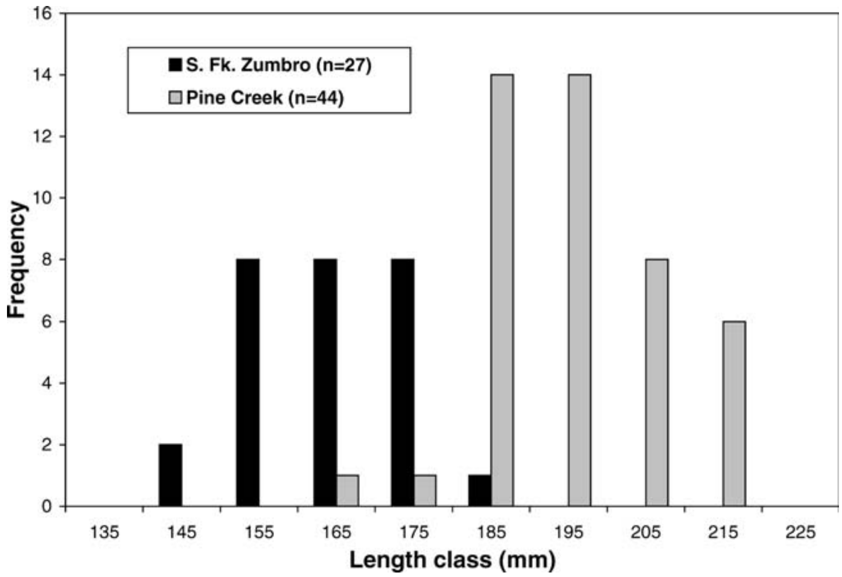

Figure 1. Total length-frequency distributions (10-mm size classes) of American brook lamprey adults during spawning, April 1997, in the South Fork Zumbro River and Pine Creek.

Table 3. Length–mass relationships for adult American brook lamprey during spawning in six streams in southeastern Minnesota, spring 1997.

Stream	n	Regression	r^2
Badger Creek	3	lnW = −24.4 + 5.26 lnTL	0.929
N. Br. Whitewater R.	22	lnW = −10.9 + 2.56 lnTL	0.687
Pine Creek	44	lnW = −10.5 + 2.51 lnTL	0.746
Salem Creek	32	lnW = −14.9 + 3.35 lnTL	0.872
S. Br. Root River	17	lnW = −8.4 + 2.10 lnTL	0.581
S. Fk. Zumbro River	27	lnW = −13.2 + 3.02 lnTL	0.806
All sites combined	145	lnW = −13.1 + 2.99 lnTL	0.883

Regressions are based on the natural logarithms of wet body mass (g, lnW) and total length (mm, lnTL).

Table 4. Water temperatures (ranges with sample sizes in parentheses) associated with American brook lamprey behaviors during the spawning season.

Year	Temperature range (°C)			Spawning dates	Spawning time	DO (mg l^{-1})
	Hiding under rocks	Swimming upstream	Excavating/ spawning			
1995	7.9–8.6 (3)	13.9 (1)	13.0–15.5 (5)	4/25–5/11	1400-1630	–
1996	6.9–10.6 (2)	9.9–12.6 (3)	10.5–14.3 (5)	4/28–5/9	0930–1600	–
1997	4.4 (1)*	12.9 (1)	8.7–14.9 (7)	4/21–4/29	1000–1500	10.5–15.6

Dates and time of day when active spawning was observed and dissolved oxygen (DO) concentrations during spawning also are shown.
* Buried in fine sediments with ammocoetes.

peak spawning times, nor to determine whether spawning occurred at night. Spawning occurred at water temperatures between 8.7 and 15.5 °C, with dissolved oxygen concentrations of 10.5 to 15.6 mg l^{-1} (Table 4). In the absence of active spawning, adult lamprey often were observed swimming upstream or hiding beneath rocks and other large objects, both behaviors occurring at water temperatures at or slightly cooler than those present during spawning (Table 4). In mid-April at a water temperature of 4.4°C, adult lampreys in Pine Creek were observed to remain buried in fine stream sediments in association with ammocoetes (presence determined by electrofishing).

American brook lampreys usually constructed nests in shallow water at the upstream ends of riffles in gravel (<2 cm diameter) and cobble (2–8 cm diameter) areas with accelerating current (gradient of change between pool and riffle). Nests were shallow, circular or oval depressions created by both sexes. Violent body undulations were used to move fine sediments, whereas large gravel and cobble (up to 5 cm diameter) were moved individually with the aid of the oral disc. Lampreys in some streams, most notably Rupprecht Creek, dug through approximately 5 cm of silt and fine sand to construct nests in underlying gravel. In other streams (e.g., Badger Creek) where gravel and cobble apparently were buried too deeply by sand and silt, lamprey spawned in the crevices between larger (30–32 cm diameter) rocks that served as riprap to protect road bridge abutments.

The majority (95.1%) of the 265 lamprey nests we observed were constructed in the open, but 13 nests in six streams (in four drainages) were constructed either partially or completely concealed beneath overhanging rocks, logs, or debris. Concealed nests comprised 7.6% (range = 2.9–15.6%) of all nests observed in these six streams. In three of these streams (Pine, Rupprecht, North Branch Whitewater), concealed nests were constructed beneath logs and sticks during two separate spawning seasons. Woody debris was the most abundant form of cover in these streams, especially Rupprecht Creek, where beaver were active. The other three streams (South Branch Root, Canfield, Salem) had much less instream woody debris, but had an abundance of limestone slab rocks, which served as cover for all concealed lamprey nests in these systems. Concealed nests were observed only during one year in these three streams.

We examined the specific stream areas used by lamprey for spawning in eight streams in either 1995 or 1997. Only one to four spawning areas were located in each stream, and the total areas actually containing nests in each stream were small, ranging from 0.5 to 30.9 m^2 (Table 5). Nests generally were spaced 30–60 cm apart at the head of the spawning riffles. Although mean spacing differed significantly among streams (Kruskal–Wallis: $H = 14.70$, $p = 0.040$), this difference was the result of greater spacing only at North Branch Whitewater River (Kruskal–Wallis without N. Br. Whitewater: $H = 8.09$, $p = 0.232$). Nest densities were highly variable, but not significantly different (Kruskal-Wallis: $H = 8.19$, $p = 0.316$) among streams (Table 5), averaging three nests m^{-2}.

Table 5. Mean ($\pm$SD) spacing (distance to nearest nest, cm) and density (number of nests m^{-2}) of American brook lamprey spawning nests in eight streams in southeastern Minnesota, April–May 1995 and 1997.

Stream	Spacing	n	Density	n
Pine Creek	47	2	1.641	2
Rupprecht Creek	56(19)	6	3.481 (5.004)	4
S. Br. Whitewater R.	63(33)	12	1.317	2
N. Br. Whitewater R.	107(49)	6	0.360	1
Trout Valley Creek	63(23)	3	4.336 (1.759)	3
Beaver Creek	37	2	5.455	1
Salem Creek	39(20)	7	5.385	1
S. Br. Root River	39(22)	6	2.000	2
Overall means	59(35)		3.003 (2.829)	

Samples sizes are labeled as n.

Mean water depths and bottom current velocities at spawning nests differed significantly (ANOVA: both $p < 0.001$) among study streams (Table 6), but most nests were constructed in waters <35 cm deep with bottom current velocities <20 cm s^{-1}. Most nests were <16 cm in diameter and dug to a depth of 4 cm below the stream bottom (Table 6). Nest length, width, and area differed significantly (ANOVA: all $p < 0.001$) among streams, but depth below stream bottom did not (ANOVA: $p = 0.905$). Nests constructed in deeper water were larger in area than those in shallow water (simple linear regression: $r^2 = 0.24$, $p < 0.001$), and there was a tendency for larger nests to occur in areas of reduced current ($r^2 = 0.03$, $p = 0.055$). Nest depressions were slightly shallower in faster currents ($r^2 = 0.05$, $p = 0.026$), but larger nests were not dug out deeper than smaller nests ($p = 0.10$). The average number of spawners at a site was not related to average nest width ($p = 0.418$), but number of spawners was positively correlated with average

Table 6. Mean (SD, n) dimensions, water depths, and bottom current velocities for American brook lamprey nests in 12 streams in southeastern Minnesota, April–May 1995–1997.

Stream	Nest dimensions					Bottom current velocity (cm s^{-1})
	Length (cm)	Width (cm)	Area (cm^2)	Depth below stream bottom (cm)	Water depth (cm)	
Canfield Ck.	19 (–,2)	21 (–,2)	321 (–,2)	4 (3,3)	23 (7,11)	13 (7,11)
Salem Ck.	14 (4,12)	16 (4,12)	178 (66,12)	4 (1,12)	20 (8,24)	14 (8,24)
S. Fk. Zumbro R.	16 (3,9)	17 (3,9)	212 (67,9)	4 (1,11)	28 (11,26)	14 (7,26)
N. Br. Whitewater R.	15 (4,24)	14 (4,24)	172 (55,24)	4 (1,24)	34 (4,49)	16 (7,49)
S. Br. Root R.	14 (6,11)	15 (4,11)	182 (110,11)	4 (2,11)	18 (5,18)	13 (7,18)
Pine Ck.	13 (4,18)	11 (3,18)	117 (67,18)	5 (1,11)	26 (8,23)	21 (9,20)
S. Br. Whitewater R.	13 (4,15)	15 (3,15)	164 (78,15)	4 (1,15)	34 (12,26)	13 (5,26)
Rupprecht Ck.	28 (10,14)	19 (7,14)	493 (327,14)	4 (–,1)	55 (5,29)	13 (6,23)
Trout Valley Ck.	14 (3,7)	21 (8,7)	250 (144,7)	5 (1,7)	28 (12,7)	5 (2,7)
Beaver Ck.	14 (3,3)	16 (2,3)	174 (58,3)	5 (1,3)	15 (0,3)	8 (6,3)
Etna Creek	–	–	–	–	18 (-,1)	18 (–,1)
Forestville Ck.	–	–	–	–	23 (8,11)	16 (9,11)
Overall means	16 (7)	16 (5)	213 (172)	4 (1)	31 (14)	14 (8)

nest length ($r^2 = 0.78$, $p = 0.004$) and average nest area ($r^2 = 0.70$, $p = 0.010$).

Discussion

Spawning American brook lamprey observed in Minnesota during this study generally were similar in size to those reported in other localities (Table 7). However, apart from the giant form of *L. appendix* reported in Michigan by Manion & Purvis (1971), none were as large as specimens collected from Pine Creek (mean TL = 195 mm).

Table 7. Average total lengths of adult American brook lamprey from locations throughout its range in North America.

Location	Total length (mm)	References
Alaska	155	Heard (1966)
Delaware	127	Rohde et al. (1976)
Kentucky	151	Branson (1970)
Massachusetts	104	Hoff (1988)
Michigan	154, 286	Manion & Purvis (1971)
Minnesota	151, 164, 170, 177, 183, 195	This study
New Hampshire	116	Sawyer (1960)
Ontario	164	Lanteigne et al. (1981)
	179	Kott (1971)
	188	Kott (1974)
Quebec	143	Vladykov (1951)
Tennessee	162, 186	Seagle & Nagel (1982)
Wisconsin	160	Cochran et al. (1993)

The reason for the larger size of adult American brook lamprey in Pine Creek in unknown, although it may be the result of habitat very favorable for growth of lamprey ammocoetes (larvae) (Kott 1971), or from a growth period for larvae longer than the typical 5 years (Seagle & Nagel 1982).

Sex ratios of adult American brook lamprey continue to be a puzzle. Although some studies have reported that males may outnumber females by factors of two to five, or even more (Dean & Sumner 1897, Kott 1971, Cochran et al. 1993), others report a 1:1 ratio (Seagle & Nagel 1982, this study). In general, however, males tend to dominate the spawning populations of *L. appendix* and other species of lampreys (e.g., Applegate,[4] Hardisty 1960, see review by Cochran et al. 1993). No previous study has reported a significant preponderance of females during spawning, as was observed in this study in Salem Creek. It has been suggested that sex ratios of both parasitic and nonparasitic lampreys may be linked to population size, with large populations dominated by males and small populations having more balanced sex ratios (Wigley 1959, Hardisty 1961). If this is true, Minnesota's *L. appendix* populations with 1:1 sex ratios, and especially those with more

[4]Applegate, V.C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Fish. Rep. 55. 237 pp.

females than males, may be at risk because of low numbers. Low densities and missing age classes of ammocoetes are characterisitic of many populations of American brook lamprey in Minnesota (N. Mundahl, unpublished data), lending further support to the hypothesis that these populations may be threatened.

American brook lampreys are typical group spawners, with several males attending each female (Eddy & Underhill 1974). From three to 30 spawners have been reported sharing a single nest (Hoff 1988, Young & Cole 1900, Cochran et al. 1993). In the present study, spawning groups ranged from 2 to 14 individuals, but fewer than 20% of these groups contained more than five lamprey. By contrast, 70% of the spawning groups observed by Cochran et al. (1993) in Wisconsin contained six or more lamprey. Only Rupprecht Creek in Minnesota, with four of seven spawning groups comprised of more than 10 lamprey each, had relatively large spawning groups. The low number of spawners per nest in Minnesota is unusual, and appears more typical of those of parasitic sea lampreys (*Petromyzon marinus*, spawning group size range of two to six lamprey; Manion & McLain[5]) and chestnut lampreys (*Ichthyomyzon castaneus*, spawning group size five or less; Cochran & Gripentrog 1992). Other non-parasitic brook lampreys in North America (e.g., southern brook lamprey *Ichthyomyzon gagei* and northern brook lamprey *Ichthyomyzon fossor*) also tend to spawn in large groups (spawning group size two to 45 and eight to 10, respectively; Cochran & Gripentrog 1992). As with the low sex ratios, low numbers of spawners per nest in many Minnesota streams may be suggestive of small populations of *L. appendix* in these systems. In fact, spawning group size in Minnesota was similar to that reported for a Massachusetts population of *L. appendix* (Hoff 1988), where the species is on the state threatened species list (Johnson 1987, Hoff 1988). Alternatively, spawning group size may be low if spawning habitats are abundant and substrates allow for easy nest construction (but see below).

[5]Manion, P.J. & A.L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–1965. Great Lakes Fish. Comm. Tech. Rep. 16. 35 pp.

Most North American lampreys spawn in spring or early summer when water temperatures rise to the 10 to 24°C range (Hardisty & Potter 1971). The American brook lamprey spawns between March and early-June (earlier at lower latitudes) at water temperatures between 6.7 and 20.6°C (see reviews by Seagle & Nagel (1982), Cochran et al. (1993)). Minnesota spawners (mid-April to early-May, 8.7 to 15.5°C) fall within this range. Water temperature also likely controls the time of day when most spawning occurs, with the daily rise and fall of stream temperatures in spring stimulating spawning activity during late-morning and afternoon hours and suppressing it at other times.

Information on nests of American brook lamprey often is anecdotal, with little quantification. Nests are usually described as shallow, gravel-filled pits or pockets at the upper ends of riffles, and oval to circular in outline (Vladykov 1949, Hoff 1988). Reports of nest size are highly variable (Scott & Crossman 1973, Rohde et al. 1976, Hoff 1988), likely a reflection of available substrate size, spawning group size, and possibly water depth and current velocity. Nests of the much larger sea lamprey are far greater (approximately two to three times) in diameter than those of *L. appendix* (Manion & McLain[5]), but apparently nests of both species are found in similar-sized substrates at similar water depths (<50 cm) and are excavated to the same extent (25–50 mm below the sediment surface) (Manion & McLain,[5] Hoff 1988, Cochran & Gripentrog 1992, this study).

Nests of *L. appendix* tend to be clustered within the spawning habitat (Young & Cole 1900, this study). Hoff (1988) reported nests spaced 3 m apart, but the present study found nests clustered much more closely together (60 cm), with nest densities in some areas exceeding 5 m^{-2}. This may imply that high-quality spawning habitat is rare in many of the streams examined, forcing lamprey to construct and spawn in nests very close together. However, lack of spawning habitat logically also might result in more lamprey sharing a single nest, a scenario not played out in the present study. Selective forces may be at work here, with males expending more energy by excavating separate nests, but then having more exclusive access to females attracted to those nests. Obviously, further examination of this aspect of lamprey spawning ecology is warranted.

American brook lamprey have been observed previously constructing nests and spawning beneath cover objects such as rocks, logs, and stumps (Young & Cole 1900, Cochran & Gripentrog 1992, Cochran et al. 1993). In this study, sheltered nests (including one completely covered by an arched piece of broken, pale-blue plastic partially embedded in the sediment) were observed in six of 14 streams where nests were located, comprising 3–15% of all nests examined in those streams. The incidence of shelter use by spawning American brook lamprey, although now known to occur in several localities, apparently is not as common as it is in other species of lamprey, especially southern brook lamprey (Cochran & Gripentrog 1992). It has been hypothesized that lampreys may use cover objects to spawn in deep, swift waters where spawning would not be possible otherwise, or to protect themselves from some types of predators (Cochran & Gripentrog 1992). In Minnesota streams, sheltered spawning was most common in Rupprecht Creek, where nests were found in waters nearly twice as deep as those in other streams.

This study has demonstrated that many of the physical and biological factors associated with spawning by American brook lampreys are very consistent and predictable. The physical habitat needed for spawning by this species is very similar to that of many other species of lamprey in North America, making it simpler for resource managers who may be faced with protecting habitats for several different species of lampreys. In addition, this study may serve notice of the potentially small and/or declining populations of American brook lamprey in Minnesota and the possible need for future protection of this species in this region.

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