

# Distribution of the Ribbon Leech in North Dakota

CHRISTOPHER M. PENNUTO<sup>1</sup>  
and MALCOLM G. BUTLER

Department of Zoology, North Dakota State University, Fargo, ND 58105

**ABSTRACT**—The distribution of the ribbon leech, *Nepheleopsis obscura*, was examined in the Central Lowland and Missouri Coteau regions of North Dakota. The leech was found in 12 of 38 ponds sampled during a two-year period. Leeches were trapped with throated metal cans and burlap sacks baited with frozen fish parts. Leech occurrence was positively correlated with maximum depth, mean conductivity, and percent littoral rock cover. Leech occurrence was not correlated with surface area or latitude. Ponds containing *N. obscura* were characterized by maximum depths greater than or equal to 1.0 m, mean conductivity values between 500 and 2300 uS/cm<sup>2</sup>, and some measurable littoral rock cover. Investigations concerning all life cycle attributes of leech populations should be pursued in North Dakota to assist resource managers in establishing harvest policy for this important bait source.

**Key words:** *Nepheleopsis obscura*, conductivity, maximum depth, prairie wetlands, ribbon leech

The ribbon leech (*Nepheleopsis obscura* Verrill; Hirudinea: Erpobdellidae) is an important fish bait in the upper Midwest prized by walleye and bass anglers. This leech occurs in ponds throughout the North Central and northern Rocky Mountain states in the U.S. and Canada (Herrmann 1970a, Klemm 1985). Collins et al. (1981) suggested that Type III and IV wetlands with a silty bottom and no sport fish are ideal leech habitats in Minnesota. This leech has a semelparous, but potentially iteroparous, life cycle and attains a maximum fresh weight of 150-1200 mg, depending on geographic region (Davies and Everett 1977, Davies 1978, Linton et al. 1983b, Peterson 1983, Baird et al. 1986). When foraging, *N. obscura* is a non-parasitic, opportunistic predatory and scavenging leech (Davies and Everett 1975, Collins et al. 1981, Anholt 1986, Pennuto pers. observ.). It is susceptible to desiccation and is not easily transported by biotic vectors (Davies et al. 1982). Although there are some biogeographic studies relating leech distribution to the chemical features of the environment (Beck 1954, Mann 1955, Scudder and Mann 1968, Herrmann 1970b, Klemm 1977, Hovingh 1986), there are few studies addressing how the physical aspects of the environment relate to distribution and there are no studies on leech distribution within North Dakota.

In response to rising demand for this species as a fish bait, the Minnesota Department of Natural Resources has developed intensive pond culture techniques and monitors trapping gear to reduce periodic bait shortages (Peterson and Hennagir 1980, Peterson 1982). Annual sales of this species contribute significant income to

<sup>1</sup> Present address: Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045

bait harvesters in upper Midwest states (Peterson and Hennagir 1980, Pennuto 1989). These economic incentives have led to detailed studies on the life history and habitat requirements of *N. obscura* in Minnesota (Collins et al. 1981, Peterson 1983), but the state of North Dakota has not initiated such examinations. Pennuto (1989) reported that this leech is widely used by anglers in North Dakota and that bait retailers, as a group, purchased approximately 75% of their leeches from sources outside of North Dakota. The purpose of this study was to examine the distribution and habitat requirements of *Nephelopsis obscura* in North Dakota to aid resource managers in establishing harvest policy.

## METHODS

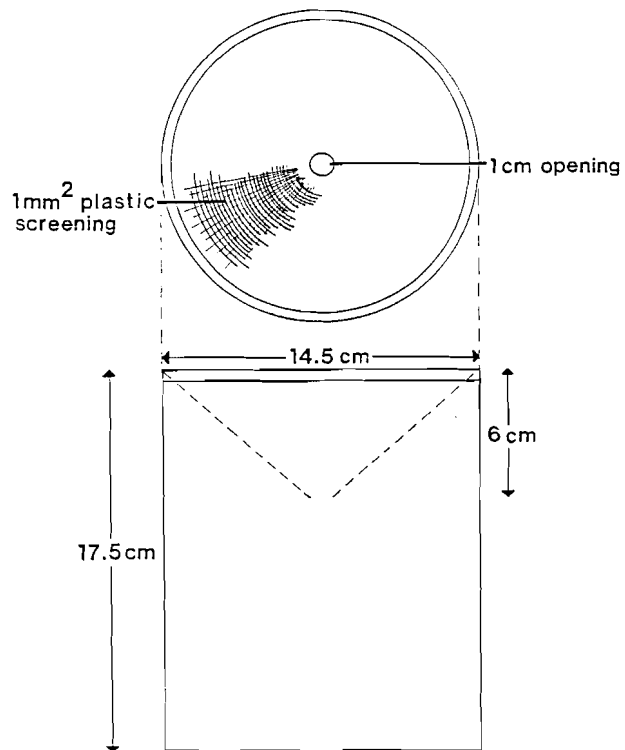
The distribution of *N. obscura* was studied in the Central Lowland and Missouri Coteau regions of North Dakota. Sites were selected by scanning Federal Highway Aid Maps for clusters of ponds such that at least two sites could be sampled in one day. Twenty-six and nineteen ponds were sampled in May/June and August of 1986 and 1987, respectively, for the presence of ribbon leeches, with seven of the sites sampled in both years. Although other leech species were found in many of the ponds surveyed, all uses of the term "leech" or "leeches" in this paper refer only to the ribbon leech *N. obscura*.

We determined leech presence using two trapping devices and by visually inspecting the undersides of rocks. The two trapping methods were a metal funnel trap and a burlap sack. Funnel traps were 17.5 cm tall and 14.5 cm in diameter. The funnel was made of 1-mm mesh plastic window screen with an apex opening of 1 cm (Fig. 1). Burlap sacks measured 90 x 30 cm with a mesh of approximately 1 mm. A funnel trap and a burlap sack constituted a trap pair. Seven trap pairs were baited with frozen fish parts and placed at 50-m intervals in littoral areas at depths less than or equal to 1 m. We deployed trap pairs at dusk and retrieved them at dawn. Leeches captured were counted, narcotized with hot water, and preserved in 4% formalin solution. Identification was made using the keys of Klemm (1985).

Funnel traps have been used by previous researchers to assess *N. obscura* populations (Peterson 1982, Bendell and McNicol 1991) and may be size selective, underestimating smaller size classes. We feel the combination of funnel traps and burlap sacks and visual inspection for cocoons were adequate measures to indicate leech presence.

We recorded maximum water depth, specific conductance, percent littoral rock cover, temperature, and surface area for each site. Maximum depth was determined by sounding with a weighted line calibrated at 0.5-m intervals. Specific conductivity was measured in the lab with a Beckman RB3 Solu Bridge conductivity meter. One water sample was taken from the littoral zone of each site and kept on ice until taken to the lab. Mean conductivities represent the average of May and August readings. Percent littoral rock cover was measured using a 0.5-m<sup>2</sup> weighted hoop divided into four quarters. The hoop was thrown blindly over the shoulder to within 1 m from the shore at each of seven trap pair locations. The area within the hoop occupied by stones greater than 5 cm in diameter was estimated to the nearest 5% by visual inspection. The seven measurements were then averaged for each pond. Temperature was measured in an unvegetated, near-shore area using a hand-held thermometer. Lake area was estimated from 7.5-minute topographic maps digitized on a Houston Instruments Hipad.

We used a Chi-square test to determine if the physical variables influenced the occurrence of *N. obscura*. Expected frequencies were calculated based on the percent



**Figure 1.** Dimensions of standard leech trap. Traps were baited with fresh fish parts placed in the bottom of the can and left overnight in  $\leq 1$  m of water.

occurrence of each variable in the study area. Classes were grouped if expected frequencies did not equal at least five. Correlations among variables were determined by Spearman's rank correlation (Sokal and Rohlf 1981). Because we sought only to determine the relative abundance of leeches, we pooled the number of leeches captured to represent the number per trap pair within a pond. The number captured per pond is a total of seven trap pairs.

## RESULTS

Ribbon leeches occurred in 12 of the 38 sites examined in 1986 and 1987 (Table 1). Seven sites were sampled in both years, but in only six locations was a population of *N. obscura* detected in both years. Leech occurrence was positively correlated with maximum depth, mean conductivity, and inversely correlated with percent littoral rock cover, but was independent of surface area and latitude (Table

Table 1. Physical characteristics of all sites sampled in 1986 and 1987.

SITE	MAX DEPTH (m)	AREA (ha)	MEAN COND (uS) <sup>b</sup>	% ROCK	MEAN TEMP (C) <sup>c</sup>	MEAN # <i>N. obscura</i> <sup>d</sup> CAPTURED	
						June	August
St Mary's	2.25	20.94	1300	60	19.5		
Moon	12.00	38.81	660	50	19.0		
Sweet	1.25	5.86	3100	10	20.5		
Blacks	0.50	1.10	3000	10	21.5		
MNW <sup>a</sup>	2.00	10.92	1300	90	20.0	22.0 (6.09)	0.6 (0.43)
MSE <sup>a</sup>	1.50	18.14	1100	42	20.5	35.6 (11.33)	21.9 (7.14)
Jensen <sup>a</sup>	2.50	12.92	1000	75	23.5	2.9 (1.61)	0.0
Eckert <sup>a</sup>	2.00	22.52	1400	66	20.0	56.1 (10.37)	0.3 (0.29)
A1	0.75	49.94	8000	0	17.0		
A2	0.50	52.91	8800	0	16.0		
A3	0.75	42.30	9100	40	17.0		
Strt1	2.25	2.15	2000	70	21.5		
Strt2	2.50	0.51	400	0	20.5		
Strt3	1.00	1.56	700	0	19.0		
Strt4	1.00	0.34	400	0	20.5		
3MNB	1.25	3.11	500	2	22.0	35.1 (11.77)	0.4 (0.43)
Skogmo	3.00	7.39	2100	50	20.5		
WPA	1.00	0.72	2600	0	18.5		
Farm	1.00	13.29	4800	30	18.5		
Road	1.00	2.85	3100	40	22.0		
Church <sup>a</sup>	5.25	29.25	700	47	20.0	585.3 (47.71)	56.9 (15.0)
Bend <sup>a</sup>	2.25	6.13	600	15	24.5	46.9 (12.99)	24.7 (6.68)
Beaver	1.00	5.96	1625	10	22.5		
Fish	2.50	26.03	1300	15	18.0		
Clear	1.75	0.16	500	10	19.0		
Hshoe <sup>a</sup>	1.50	1.28	800	46	20.5	0.0	0.5 (0.34)
Curve	1.00	2.61	1200	0	18.5		
Mpond	1.75	2.32	2500	0	24.5		
1156	2.50	79.81	2500	0	20.5		
LA	1.25	10.69	2300	0	22.5		
LB	1.00	4.80	3100	30	21.0		
Mc2	2.10	2.63	2300	35	24.5	131.3 (22.02)	13.9 (6.42)
1641	2.00	3.27	1000	42	24.0	70.3 (7.96)	10.4 (3.69)
Mc1	0.75	0.46	2500	0	23.0		
HS	1.75	8.12	1200	59	20.5		
HE	1.25	4.67	1400	41	21.5	128.4 (32.45)	44.4 (15.3)
HN	1.75	6.71	700	47	20.5		
HW	1.75	3.46	1400	42	21.5	97.9 (44.66)	2.9 (1.65)

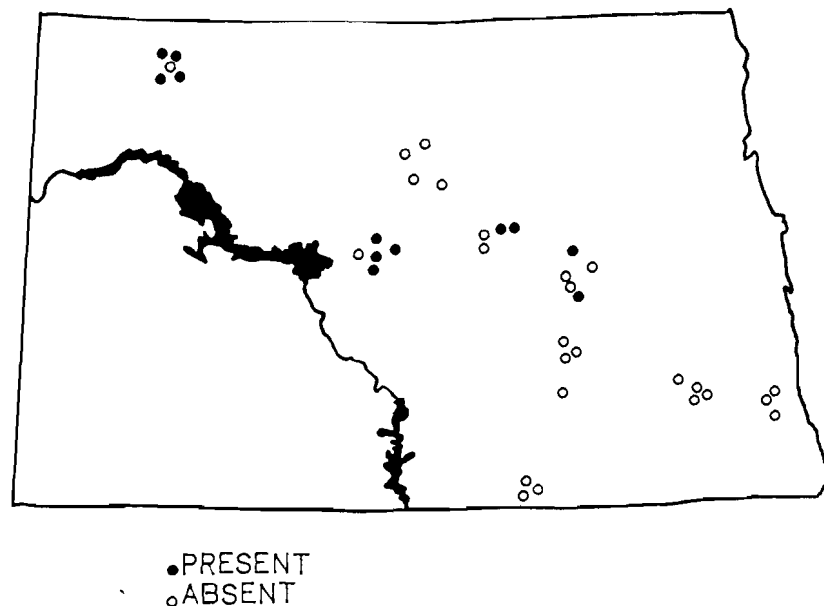
<sup>a</sup> Sites sampled in both years. <sup>b</sup> Average of May and August conductivity readings. <sup>c</sup> Average of May/June and August littoral temperature. <sup>d</sup> Average number of *N. obscura* captured in seven trap pairs (see text) per site during the May/June and August sampling period. Mean number  $\pm$  1 S.E.

2). Leech distribution appeared clumped in four local areas (Fig. 2). This clumping is probably an artifact of the site selection procedure, which ensured that at least two locations could be sampled on each date.

Maximum depth had a significant influence on the occurrence of *N. obscura* ( $\chi^2 = -38.214$ ,  $P < 0.001$ ), and occurrence was restricted to sites with a maximum depth greater than 1 m (Table 1). Leeches were present in 12 of 25 sites with maximum depths greater than 1 m. Of the 13 sites with maximum depths greater than 1 m, but not containing leeches, at least five sites (Skogmo, Fish, Clear, HN, HS) might be expected to support leech populations based on the other variables

**Table 2.** Chi-square statistics resulting when leech presence is tested for independence with respect to the listed variable.

Variable	$\chi^2$	df	n	P
Mean conductivity ( $\mu\text{S}/\text{cm}^2$ )	9.623	1	38	<0.01
Maximum depth (m)	-38.214	1	38	<0.001
Percent littoral rock cover	5.788	1	38	<0.05
Surface area (ha)	-0.032	1	38	n.s.



**Figure 2.** Distribution of sites sampled in North Dakota in 1986 and 1987 for the presence of the leech *Nephelopsis obscura*.

measured. Maximum depth for all sites had a mean of 1.9 m, while the maximum depths for sites with and without leeches averaged 2.1 and 1.8 m, respectively (Table 3). Maximum depth was inversely correlated with mean conductivity and positively correlated with percent littoral rock cover ( $r_s = -0.388$ ,  $P < 0.02$ ;  $r_s = 0.532$ ,  $P < 0.001$ ; respectively; Table 4).

Leech occurrence was positively correlated with mean conductivity ( $\chi^2 = 9.623$ ,  $P < 0.01$ ), and occurrence was restricted to sites with a mean conductivity between 500 and 2300  $\mu\text{S}/\text{cm}^2$ . Leeches were present in 12 of 24 sites with mean conductivities in this range (Table 1). Of the 12 sites with appropriate conductivity values but not containing this leech, five sites (Skogmo, Clear, Fish, HN, HS) appeared to be acceptable habitats for *N. obscura* in reference to the other variables measured. Mean conductivities for all sites had an average of 2340  $\mu\text{S}/\text{cm}^2$ , while sites with and without leeches had mean conductivities of 1125 and 2901  $\mu\text{S}/\text{cm}^2$ , respectively (Table 3). Specific conductance was inversely correlated with maximum depth ( $r_s = -0.388$ ,  $P < 0.02$ ; Table 4).

**Table 3.** Summary statistics of all sites sampled for the presence of *N. obscura* in 1986 and 1987.

	VARIABLE	n	mean	S.D.	MIN	MAX
	Latitude	38	47.18	0.679	46.14	48.39
ALL	Max depth	38	1.92	1.894	0.50	12.00
SITES	Conductivity <sup>a</sup>	38	2340.00	2254.013	400.00	9100.00
	Rock cover	38	28.26	26.151	0.00	90.00
	Area	38	13.33	17.991	0.16	79.81
	Latitude	12	47.60	0.574	47.09	48.39
LEECH	Max depth	12	2.11	1.063	1.25	5.25
PRESENT	Conductivity <sup>a</sup>	12	1125.00	488.324	500.00	2300.00
SITES	Rock cover	12	45.25	23.860	2.00	90.00
	Area	12	9.86	9.105	1.28	29.25
	Latitude	26	46.99	0.623	46.14	48.38
LEECH	Max depth	26	1.84	2.189	0.50	12.00
ABSENT	Conductivity <sup>a</sup>	26	2901.00	2526.000	400.00	9100.00
SITES	Rock cover	26	20.42	23.642	0.00	70.00
	Area	26	14.94	20.841	0.16	79.81

<sup>a</sup> average of May and August conductivity readings.

**Table 4.** Summary of Spearman's rank correlations ( $r_s$ ) of physical and chemical variables measured in all sites sampled in 1986 and 1987 (n=38).

	LA	MD	AC	PR	SA
Latitude	1.000	0.215	-0.249	0.356*	-0.119
Maximum depth		1.000	-0.388*	0.532***	0.237
Average conductivity			1.000	-0.123	0.350*
% rock cover				1.000	0.312
Surface area					1.000

LA = latitude, MD = maximum depth, AC = average of May and August conductivity readings, PR = percent littoral rock cover, SA = surface area. \* $P < 0.05$ , \*\*\* $P < 0.001$ .

Leech presence was positively correlated with percent littoral rock cover ( $X^2=5.788$ ,  $P < 0.05$ ; Table 2), with leeches occurring only in sites with some measurable near-shore rock cover. Leeches were present in 12 of 27 sites with measurable near-shore rock cover. Of the 15 sites with measurable rock cover but not containing leeches, five sites (Skogmo, Fish, Clear, HN, HS) were expected to contain leeches based on the other variables measured. Littoral rock cover for all sites averaged 28%, while rock cover for sites with and without *N. obscura* had means of 45 and 20%, respectively (Table 3). Percent littoral rock cover was correlated with latitude and maximum depth ( $r_s=0.376$ ,  $P < 0.05$ ;  $r_s=0.532$ ,  $P < 0.001$ ; Table 4).

Leeches never occurred in sites with latitudes lower than 47°. This trend is probably a sampling artifact, because *N. obscura* has been reported from areas in the midwest as far south as Iowa (Klemm 1985). However, within the geographic area sampled, the more southern sites had less littoral rock cover than the northern sites, and latitude was correlated with percent littoral rock cover ( $r_s=0.376$ ,  $P < 0.05$ ; Table 4).

Lake surface area had no influence on leech presence ( $X^2= -0.032$ ,  $P > 0.05$ ; Table 3) and was correlated with mean conductivity ( $r_s=-0.350$ ,  $P < 0.05$ , Table 4).

## DISCUSSION

The occurrence of *N. obscura* was influenced by maximum depth and its correlate, mean conductivity. Leeches occurred only in sites with maximum depths greater than 1 m and low conductivities. In shallow wetlands, salt concentrations increase as waters evaporate, water may evaporate completely, water may freeze solid in winter, and anoxic conditions may persist in both summer and winter (Bach 1951, Barica and Mathias 1979, Davies and Baird 1988). Laboratory studies have correlated leech mortality and reproductive failure with high conductivity levels

(Reynoldson and Davies 1976, Linton et al. 1983a, 1983b). Other field studies have correlated leech distribution with conductivity or total dissolved solids (Scudder and Mann 1968, Herrmann 1970b, Reynoldson and Davies 1976, 1980). The upper conductivity value associated with leeches in this study exceeds previously recorded conductivity limits, but the lower value is within reported limits. Sites with conductivity values greater than 2300  $\mu\text{S}/\text{cm}^2$  were the most numerous in this study and are probably reflective of the majority of North Dakota prairie wetlands. Wetlands with maximum depths greater than 5 m do not experience evaporation and salt concentration problems to the same extent as shallow wetlands, but may offer conditions favorable for sport fishes. Collins et al. (1981) suggest that *N. obscura* will seldom occur in sites with predatory fish such as yellow perch (*Perca flavescens*), esocids, and centrarchids; thus, sites deep enough to support these fishes may not be good leech habitats.

There were five sites in the study that had all measured variables within the acceptable range for leech presence, yet did not contain leeches. Two of these sites (Clear and Fish) were recently constructed water retention ponds (M. Callow, USFWS, pers. commun.) and would not be expected to contain this leech because of inadequate time for dispersal. Two other sites not containing leeches, HN and HS, were located within 5 km of other leech-containing sites. However, the locations sampled within HN and HS were adjacent to recent road-grading activity. Localized siltation may have diminished the availability of tube-dwelling chironomids, a primary food item for *N. obscura* (Davies et al. 1978, Davies et al. 1981). A reduced food supply may have led *N. obscura* to forage elsewhere within the habitat and thus escape capture. The remaining site (Skogmo) was located in an area where five other ponds were sampled, and none of these contained the leech. All sites in this particular area had elevated conductivity levels and were shallow. Skogmo may represent an isolated, spring-fed wetland with tolerable water chemistry, but little potential for leech colonization due to its location and the poor dispersal capability of this leech.

Distributional surveys provide habitat managers with information on environmental variables important for species occurrence. However, managers need to be aware of other ecological aspects of target species to avoid the possibility of overharvest. In North Dakota, information was lacking on the habitat requirements for *N. obscura*, an important bait resource. Prairie wetlands in North Dakota are numerous and often located on public lands. Thus, leech harvesters may be successful in locating leech habitats in North Dakota, but further information crucial to regulation and management are needed. For example, although we might be able to identify habitats expected to contain leeches, we need to understand what factors within a given site influence the population size, individual growth rate, and long-term persistence of a population. Further investigations concerning all life cycle attributes of North Dakota leech populations are encouraged before harvesting policy is considered by resource managers.



## ACKNOWLEDGMENTS

We express thanks to the Zoology Department of North Dakota State University for covering transportation costs during this study. We also thank A. McMillan and G. Walsh for assistance in constructing leech traps.

## LITERATURE CITED

- Anholt, B. 1986. Prey selection by the predatory leech *Nepheleopsis obscura* in relation to three alternative models of foraging. *Can. J. Zool.* 64:649-655.
- Bach, R.N. 1951. Some aspects of North Dakota's surface waters. North Dakota Game and Fish Department, Bismarck.
- Baird, D.J., L.R. Linton, and R.W. Davies. 1986. Life-history evolution and post-reproductive mortality risk. *J. Anim. Ecol.* 55:295-302.
- Barica, J., and J.A. Mathias. 1979. Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. *J. Fish. Res. Board Can.* 36:980-986.
- Beck, D.E. 1954. Ecological and distributional notes on some Utah Hirudinea. *Proc. Utah Acad. Sci. Arts Lett.* 31:73-78.
- Bendell, B.E., and D.K. McNicol. 1991. An assessment of leeches (Hirudinea) as indicators of lake acidification. *Can. J. Zool.* 69:130-133.
- Collins, H., L.L. Holmstrand, and J. Denny. 1981. Bait leech: its nature and nurture. *Univ. Minn. Sea Grant Ext. Super. Adv. Notes No.* 12.
- Davies, R.W. 1978. Reproductive strategies shown by freshwater Hirudinoidea. *Verh. Int. Verein. Limnol.* 20:2378-2381.
- Davies, R.W., and D.J. Baird. 1988. The effects of oxygen regime on the ecology of lentic macroinvertebrates. *Verh. Int. Verein. Limnol.* 23:2033-2034.
- Davies, R.W., and R.P. Everett. 1975. The feeding of four species of freshwater Hirudinoidea in Southern Alberta. *Verh. Int. Verein. Limnol.* 19:2816-2827.
- Davies, R.W., and R.P. Everett. 1977. The life history, growth, and age structure of *Nepheleopsis obscura* Verrill, 1872 (Hirudinoidea) in Alberta. *Can. J. Zool.* 55:620-627.
- Davies, R.W., L.R. Linton, and F.J. Wrona. 1982. Passive dispersal of four species of freshwater leeches (Hirudinoidea) by ducks. *Freshwater Biol.* 1:40-43.
- Davies, R.W., F.J. Wrona, and R.P. Everett. 1978. A serological study of prey selection by *Nepheleopsis obscura* Verrill (Hirudinoidea). *Can. J. Zool.* 56:587-591.
- Davies, R.W., F.J. Wrona, L.R. Linton, and J. Wilkialis. 1981. Inter- and intra-specific analysis of the food niches of two sympatric species of Erpobdellidae (Hirudinoidea) in Alberta, Canada. *Oikos* 37:105-111.
- Herrmann, S.J. 1970a. Systematics, distribution, and ecology of Colorado Hirudinea. *Am. Midl. Nat.* 83:1-37.
- Herrmann, S.J. 1970b. Total residue tolerances of Colorado Hirudinea. *Southwest Nat.* 15:261-273.

- Hovingh, P. 1986. Biogeographic aspects of leeches, mollusks, and amphibians in the intermountain region. *Great Basin Nat.* 46:736-744.
- Klemm, D.J. 1977. A review of the leeches (Annelida: Hirudinea) in the Great Lakes region. *Mich. Acad.* 9:397-418.
- Klemm, D.J. 1985. A guide to the freshwater Annelida (Polychaeta, Naidid, and Tubificid Oligochaeta, and Hirudinea) of North America. Kendall/Hunt Publishing Co., Dubuque, IA.
- Linton, L.R., R.W. Davies, and F.J. Wrona. 1983a. The effects of water temperature, ionic content, and total dissolved solids on *Nepheleopsis obscura* and *Erpobdella punctata* (Hirudinoidea: Erpobdellidae) 1. Mortality. *Holarct. Ecol.* 6:59-63.
- Linton, L.R., R.W. Davies, and F.J. Wrona. 1983b. The effects of water temperature, ionic content, and total dissolved solids on *Nepheleopsis obscura* and *Erpobdella punctata* (Hirudinoidea: Erpobdellidae) 1. Reproduction. *Holarct. Ecol.* 6:64-68.
- Mann, K.H. 1955. Some factors influencing the distribution of freshwater leeches in Britain. *Proc. Int. Assoc. Theor. Appl. Limnol.* 12:582-587.
- Pennuto, C. 1989. The bait leech *Nepheleopsis obscura* in North Dakota: an economic assessment. *N.D. Farm Res.* 47:21-23.
- Peterson, D.L. 1982. Management of ponds for bait leeches in Minnesota. *Minn. Dept. Nat. Resour., Div. of Fish and Wildlife, Sec. of Fish. Inv. Rep. No. 375.*
- Peterson, D.L. 1983. Life cycle and reproduction of *Nepheleopsis obscura* Verrill (Hirudinoidea: Erpobdellidae) in permanent ponds of northwestern Minnesota. *Freshwater Invert. Biol.* 2:165-172.
- Peterson, D.L., and F.A. Hennagir. 1980. Minnesota live bait industry assessment study. *Minn. Dep. Nat. Resour. Div. Fish Wildl., Sec. Fish. Inv. Rep. No. 367.*
- Reynoldson, T.B., and R.W. Davies. 1976. A comparative study of the osmoregulatory ability of three species of leech (Hirudinoidea) and its relationship to their distribution in Alberta. *Can. J. Zool.* 54:1908-1911.
- Reynoldson, T.B., and R.W. Davies. 1980. A comparative study of weight regulation in *Nepheleopsis obscura* and *Erpobdella punctata* (Hirudinoidea). *Comp. Biochem. Physiol.* 66:711-714.
- Scudder, G.G.E., and K.H. Mann. 1968. The leeches of some lakes in the Southern Interior Plateau region of British Columbia. *Syesis* 1:203-209.
- Sokal, R.R., and F.J. Rohlf. 1981. *Biometry*, 2nd ed. W.H. Freeman and Co., New York.

Received 21 May 1992. Accepted 22 April 1993.