SOME ASPECTS OF THE INTESTINAL HELMINTHS OF THE MUSKRAT (ONDATRA ZIBETHICUS LINNAEUS) IN NEWFOUNDLAND

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Some aspects of the intestinal helminths of the Muskrat (*Ondatra zibethicus* Linnaeus) in Newfoundland

A thesis
presented to
The Department of Biology
Memorial University of Newfoundland

In partial fulfillment
of the requirements of the Degree
Master of Science

by

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July 1980

ABSTRACT

One hundred and fourteen muskrats (*Ondatra zibethicus* (Linnaeus 1776)) were collected between September 1977 and January 1979 from three regions in insular Newfoundland, and were examined for helminths. Eleven species were found (7 Digenea, 2 Cestoda and 2 Nematoda). *Diplostomum mergi* Dubois 1932 were recovered from a mammal for the first time.

Adult and immature muskrat showed differences in the prevalence and intensity of infection and the adults also had larger concurrent infections (Table 3, Figures 3 and 4). In only one case, namely *Hymenolepis evaginata* Barker and Andrews 1915, was a parasite species more prevalent in one sex (the males).

All commonly occurring helminth species showed seasonal peaks in prevalence and intensity of infection, except for *Quinqueserialis quinqueserialis* Barker and Laughlin 1911 which only showed a seasonal peak in intensity of infection. The seasonal differences were related to the differences in prevalence of infection found between adult and immature muskrat, and to water temperature.

Longitudinal distribution within the alimentary tract was examined and all helminths recovered preferred the proximal 60 per cent of the small intestine, except *Q. quinqueserialis* and *Trichostrongylus calcaratus* Ransom 1911, which preferred the caecum.

A difference in digenean occurrence between areas in insular Newfoundland was related to water pH and hardness. A comparison of the insular fauna of muskrat intestinal helminths was made with previous records throughout North America. An attempt was made to relate helminth occurrence to the zoogeographical distribution of the muskrat and various biotic factors.

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ACKNOWLEDGEMENTS

I wish to acknowledge and thank my supervisor, Dr. W. Threlfall, for his guidance, encouragement and overall help which made this study possible.

Special thanks to Dr. Gordon Bennett for his suggestions and criticisms of manuscript drafts; to Dr. Carl Bursey for help, encouragement and discussions related to cestodes; to Chuck Bourgeois for his valuable comments and criticisms; to Chandra Chinniah and Ken Curnew for help on that adventuresome first field trip; to Dr. Bock Kim and Ruth Cornish for their assistance in the data analysis; Norm Williams for his discussions and criticisms of analytical procedures; Eugene Mercer, Wally Skinner and Oscar Forsey of the Newfoundland Wildlife Division for equipment and help in the field.

Particular thanks to Eugene Fitzgerald for help and suggestions regarding equipment and its care in the field; to Gary Dunphy and Keith Osberg for listening and providing a roof over my head; Dean of Graduate Studies, F.A. Aldrich for his crucial procurement of funds to support 1978's field work; the Principal of the Bonavista Trades and Technology School for

provision of a space to dissect; and especially the many kind citizens of Bonavista, Peter's River and Main Brook whose hospitality can only be experienced.

INTRODUCTION

The fur of the muskrat (*Ondatra zibethicus* L.) is a major revenue source throughout the Holarctic Region. Hence, numerous studies on all aspects of muskrat biology have been undertaken. Except for taxonomic work by Bangs (1913) and Cameron (1950), a summary of summer foods by Lear (1952), and a brief summary of reproductive biology by Curnew (1979) little is known about the muskrat in Newfoundland. A significant decline in the muskrat harvest occurred from 20,396 in 1951-52 to 1456 in 1975-76 (Curnew, 1979). In some areas (e.g. Bay St. Georges) muskrat populations have almost become extinct. Northcott et al (1974) suggest predation by the recently introduced mink (*Mustela vison* Schreber) may be responsible for the decline of the muskrat, while Jennings (1979) showed muskrat to be an important food item of mink in Newfoundland. Hence, there was a need for more information pertaining to the muskrat.

Previous works on muskrat parasites consist largely of surveys and/or descriptions of new parasite species (Appendix 1). Dogiel (1964) stressed the importance of an ecological approach to parasitology, considering both the macro- and micro-environment, with Lavroff (1953), Anderson and Beaudoin (1966), Abram (1968, 1969), Vanatka (1969), Rice and Heck (1975), McKenzie (1977), MacKinnon and Burt (1978) and McKenzie and Welch (1979) utilizing this approach in the study of muskrat parasites. It was felt that insular Newfoundland provided an excellent opportunity to compare the muskrat's helminth fauna to a well-studied continental fauna. Due to its size and habitat variation, it was also hoped to study the parasite fauna of this host in several discrete habitats within the island. The northerly position of the island provided potential for a seasonal comparison of parasites within the context of well-defined seasons. A study was thus initiated to determine the effect of season on helminth infection; to determine if an expected reduced helminth diversity (compared to continental North America) occurred and to look for differences in helminth prevalence and intensity which could be related to habitat differences within the island. In addition, the location of parasites within the host, including the longitudinal distribution within the intestine, was examined.

METHODS AND MATERIALS

Muskrats (114) were collected from three areas in Newfoundland (Figure 1), September 20-30, 1977 from Peter's River (17 specimens); November 6-9, 1977, May 18-31, 1978 and July 14-25, 1978 from Bonavista (20, 15, and 12 specimens respectively); and June 13-15, 1978, August 3-6, 1978, October 1-15, 1978 and December 1, 1978 - January 20, 1979 from Main Brook (15, 12, 16 and 7 specimens respectively).

The collection sites in Bonavista consisted of old beaver ponds and dystrophic bog ponds which were dominated by water lilies (*Nuphar variegatum* Engelm.) and *Potamogeton* spp. One eutrophic pond in Bonavista (euthrophication being man-induced) was choked with horsetails (*Equisitem fluviatile* L.), water lilies and *Potamogeton*. The pond banks were densely vegetated with *Myrica gale* L. Adjacent habitat consisted of barrens dominated by ericaceous species and lichens and/or forest or tree clumps dominated by white spruce (*Picea glauca* (Moench)) and black spruce (*P. mariana* (Mill.) BSP.). The underlying bedrock consisted of siltstone, arkose, conglomerate, slate, and acidic to intermediate volcanic rocks.

FIGURE 1

Sampling areas:

1. Main Brook
2. Peter's River
3. Bonavista


NEWFOUNDLAND
1
2
3

Muskrat habitat in Peter's River consisted of a series of oxbows and shallow marshes (0.2 - 0.4m deep) adjacent to and connected with the river. Marshes were dominated by horsetails, sedge (*Carex* spp.) and water lilies. The stream edges were vegetated with water lilies, *Potamogeton*, and horsetails. The banks were characterized by grasses (*Poa* spp.), *M. gale* and alder (*Alnus* spp.). Surrounding forest supported balsam fir (*Abies balsamea* (L.) Mill.), white spruce and aspen (*Populus tremuloides* Michx.). The underlying bedrock consisted of sandstone, conglomerate, acidic to mafic volcanic rocks, greywacke, shale and limestone.

Main Brook sites consisted of streams, old beaver ponds and junctions between slow-moving streams and ponds. The streams and ponds were choked with horsetails, *Potamogeton*, water lilies and sedges. The beaver ponds were dominated by water lilies and sedges. Streams and ponds were bordered with *M. gale*, alder and forests composed principally of white spruce, with some aspen and birch (*Betula papyrifera* Marsh). The underlying bedrock consisted of limestone, dolomite, quartzite, sandstone, and shale.

Muskrat were trapped with #1 Oneida leghold, #110 Connibear or live traps. May and July specimens from Bonavista were examined fresh; remaining specimens were deep frozen and stored for later examination. Collection of the October and December-January muskrat samples from Main Brook were by a trapper; from Peter's River by Newfoundland Wildlife personnel and the author; and the remaining specimens by the author.

The alimentary tract, heart, lungs, diaphragm, liver, gall bladder, spleen, kidneys and bladder were examined with a dissecting microscope. The alimentary tract was divided into several parts, namely the esophagus, stomach, small intestine, caecum and colon. The small intestine was initially sub-divided into four equal sections in the first 57 muskrats. To further differentiate longitudinal patterns of parasite prevalence and intensity, the small intestine from the remaining 57 muskrats was divided into ten equal sections. Sections of the alimentary tract were slit longitudinally, the wall was scraped with a razor blade and contents were flushed with tap water through a screen (250 mm) prior to examination. After sieving, contents were placed in water and subsequently examined under a dissecting microscope. Remaining organs were teased apart under the dissecting microscope, were then squashed between two petri dishes and were re-examined. All helminths were retained.

Trematodes and nematodes were fixed and preserved in 5 percent glycerine in 70 percent ethanol, cestodes from fresh specimens were killed in hot water (70 C) and later were transferred to 5 percent glycerine in 70 percent ethanol. Prior to staining, proglottids were placed in Bouins fixative for 48 hours and subsequently changes of 70 percent ethanol to remove picric acid.

The majority of trematodes were stained in Semichons acetic-carmine with the remainder being stained using a trichrome stain. Cestodes were stained with Ehrlich's haematoxylin or with Semichons acetic-carmine. Scoleces were either mounted in Rubins and measured within 24 hours or were stained in Semichons acetic-carmine. After dehydration, all Platyhelminths (excluding scoleces mounted in Rubins) were cleared in clove oil and were mounted in Canada Balsam. Nematodes were mounted in Rubins.

Helminth occurrence was recorded as prevalence (percent of hosts infected) and intensity (average number of helminths per infected individual). Digeneans were identified using Schnell (1970) Olsen (1937) Beaver (1937), Skrjabin (1964 a, b) and Dubois (1953); cestodes with Schmidt (1970) Hughes (1941) and Rauch (1948); and nematodes utilizing Read (1949 a, b) Skrjabin (1960) Skrjabin et. al. (1970) and Webster (1966). A brief summary on the status as a muskrat parasite in Newfoundland is given for each helminth species, and on the taxonomy of such where this bears specific relevance to the present study, without being unnecessarily repetitious of what exists in the literature.

Sex of the muskrats were determined by the morphology of the reproductive structures (Taber, 1971). Aging (immature or adult) followed criteria established by Errington (1939) and Baumgartner and Bellrose (1943).

Contingency tests (2 x k) were used to determine whether significant differences occurred in the prevalence of infection with parasites, as related to host age, sex, area and season (spring, summer, fall, and winter). A one-way Anova (analysis of variance) was used to determine if the site of occurrence of each species differed within the host alimentary tract (excluding esophagus) and Student-Newman-Keuls *a posteriori* pair-wise comparisons were used to determine group mean differences between sections of the alimentary tract. Differences in frequency of occurrence of concurrent infections with parasites between male and female and adult and immature muskrats in each area were tested, utilizing a G-test (Sokal and Rohlf, 1973).

Analyses of water pH, and concentrations of calcium and total hardness for each sampling site were performed using a water analysis kit, (Lamotte Chemical Products Company, Chestertown, Maryland, U.S.A.).

RESULTS AND DISCUSSION

Eleven species of helminths were recovered - 7 Trematoda, 2 Cestoda and 2 Nematoda from 82 percent of the muskrats (Table 1, Figure 2). Fifty-seven percent of the Bonavista muskrats were infected with at least one of *Quinqueserialis quinqueserialis* (Barker and Laughlin 1911), *Plagiorchis proximus* Park 1936, *Hymenolepis evaginata* Barker and Andrews 1915, an anoplocephalid, *Capillaria michiganensis* Read 1949 and *Trichostrongylus calcaratus* Ransom 1911. One hundred percent of the muskrats from Peter's River were infected with one or more of *Q. quinqueserialis*, *P. proximus* and *H. evaginata*. One hundred percent of Main Brook muskrats were infected with one or more of *Q. quinqueserialis*, *P. proximus*, *Echinostomum revolutum* (Froelich 1802), *Echinoparyphrium contiguum* Barker and Bastron 1915, *Echinoparyphrium recurvatum* (Von Linstow 1873), *Diplostomum mergi* Dubois 1932, a paramphistomatid, *H. evaginata*, *C. michiganensis* and *T. calcaratus*.

TREMATODA

Q. quinqueserialis was found to occur most frequently with the highest intensity of infection (Table 1). The

Table 1 - Prevalence and Intensity of Infection with Parasites of Muskrats From Three Regions of Newfoundland

PARASITE	Nfld. (114)[+] a*	b*	c*	Bonavista (47) a	b	c	Peter's River (17) a	b	c	Main Brook (50) a	b	c
Quinqueserialis quinqueserialis	64	560	1-4855	10	8	1-22	100	278	69-943	100	723	97-4855
Plagiorchis proximus	51	334	1-4388	2	-	1	76	83	1-444	88	410	1-4388
Echinostoma revolutum	6	-	-	-	-	-	-	-	-	14	-	-
Echinoparyphium contiguum	4	-	-	-	-	-	-	-	-	8	-	-
Echinoparyphium recurvatum	5	-	-	-	-	-	-	-	-	12	-	-
Echinostomes (Total)	7	892	2-4135	-	-	-	-	-	-	16	892	2-4135
Diplostomum mergi	9	14	1-38	-	-	-	-	-	-	20	14	1-38
Paramphistomatid	1	-	4	-	-	-	-	-	-	2	-	4
Digenea (Total)	65	904	1-6598	15	7	1-22	100	341	73-949	100	1221	97-6598
Hymenolepis evaginata	59	13	1-110	26	5	1-28	65	1	1-6	88	21	1-110
Anoplocephalid	1	-	1	2	-	1	-	-	-	-	-	-
Cestodes (Total)	59	13	1-110	26	5	1-28	65	1	1-6	88	21	1-110
Capillaria michiganensis	38	65	1-692	23	44	1-264	-	-	-	64	73	1-692
Trichostrongylus calcaratus	11	22	1-166	19	28	1-166	-	-	-	6	2	1-3
Nematodes (Total)	39	65	1-692		-	1-264	-	-	-	66	73	1-692

\+ Host Sample Size
*a. Percent of Hosts Infected (Prevalence)
*b. Average Number Helminths/Infected Host (Intensity)
*c. Range

FIGURE 2

Total number of species of Digenea, Cestoda and Nematoda collected from three areas of Newfoundland.

Areas:

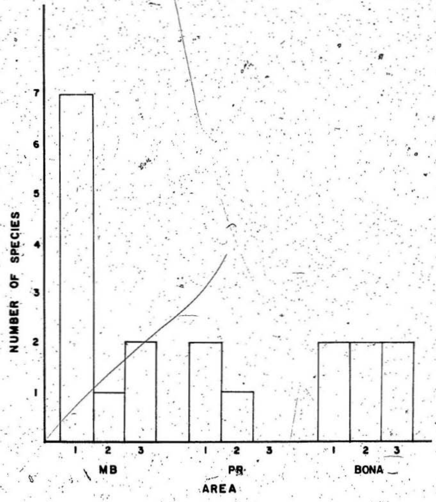
MB - Main Brook

PR - Peter's River

BONA - Bonavista

Parasite Groups:

1. Digenea
2. Cestoda
3. Nematoda


NUMBER OF SPECIES
1
2
3
4
5
6
7
1
2
3
MB
1
2
3
PR
1
2
3
BONA
AREA

preferred site of infection was the caecum (100 percent of infected muskrat) whereas the colon and small intestine were infected in 52.1 percent and 31.5 percent of the muskrats respectively. These showed an increased prevalence from small intestine section (S.I.S.) five to S.I.S. 10 (Table 2). Three minute immature specimens were found in the stomach of one muskrat. The literature indicates *Q. quinqueserialis* to be a characteristic helminth of the muskrat throughout its native North American range and that it has been introduced with the muskrat into Eurasia.

P. proximus was second only to *Q. quinqueserialis* in prevalence and third in intensity of infection (Table 1). It was found throughout the small intestine (concentrated principally from S.I.S. four to six; rarely in the stomach and caecum (3.5 and 1.8 percent of infected muskrats respectively). The probable synonomy of a number of species within the genus *Plagiorchis* as indicated by the work of Angel (1959), Fedorova (1969), Sharpilo and Sharpilo (1972) and Blankespoor (1974) due to variation of characters previously considered taxonomically important is herein acknowledged. Although Olsen (1937) used Shulz

Table 2 - Prevalence and Intensity of Infection by *Quinqueserialis quinqueserialis* in the Alimentary Tract of Muskrats thus infected from Newfoundland.

Site of Occurrence	Percent Infected	Mean Intensity (Range) of Infection/Infected Host
Stomach	1	3(3)
Intestine 1	-	
Intestine 2	-	
Intestine 3	-	
Intestine 4	-	
Intestine 5	2	1(1)
Intestine 6	6	1(1-2)
Intestine 7	18	2(1-5)
Intestine 8	18	2(1-5)
Intestine 9	20	6(1-26)
Intestine 10	26	4(1-19)
Caecum	100	542(1-4847)
Colon	52	15(1-98)

and Skorzow's (1935) subgeneric designations and the position of the oral sucker, both having since been shown to be unreliable, after an exhaustive examination of the literature, I have used Olsen (1937) to determine the specimens from this study to be *P. proximus* by excluding dichotomies based on these taxonomic characters.

Differentiation between the genera *Echinostoma* Rudolphi 1809 and *Echinoparyphrium* Dietz 1909 was after Beaver (1937), using the relative length of uterus and/or arrangement of cephalic spines. Specific designation in both genera was based on number and arrangement of cephalic spines and by using Skrjabin (1964b). Infections with echinostomes often included immature specimens in which the uterus was not developed and in which spines were missing, making generic or specific diagnosis suspect. These were recorded as immature echinostomes. Longitudinal distribution in the gut, to be discussed subsequently, was restricted to a composite of the echinostomes found.

Three species of echinostomes were identified to the specific level, namely *Echinostoma revolutum*, *Echinoparyphrium contiguum* and *Echinoparyphrium recurvatum*, all restricted to muskrat collected from Main Brook. Only two species of helminths had a lower prevalence than the echinostomes during this study (Table 1). However, in four (50 percent of infected hosts) echinostomes constituted a major infection (157, 1004, 1841, and 4135 echinostomes respectively). Site of infection ranged from the stomach to colon, with primary concentration restricted to S.I.S. 1-5.

Diplostomum mergi was found only in muskrat from Main Brook (Table 1). Measurements closely approximate those of Skrjabin (1964 a, b). All specimens were adult and gravid. Site of infection was restricted to S.I.S. 1-6 with one exception being a single specimen recovered from the colon.

D. mergi is a new host and class (Mammalia) record, although two other members of the Diplostomatidae (*Alaria mustelae* Bosma 1931 and *Fibracola crater* (Barker and Noll 1915) Dubois 1938 have been found in muskrat in North America. *D. spathaceum* (Rud 1819) was recovered from muskrat in Kazakhistan S.S.R. (Gvozdev, 1969). *D. mergi* has been recorded only twice from North America (Bain and Threlfall, 1977) in Hooded Mergansers (*Lophodytes cucullatus* L. 1758) from

Ontario and Dubois (1969) in Red-breasted Mergansers (*Mergus serrator* L. 1758) from Alaska. Six specimens of *D. mergi* were also recovered from an otter (*Lutra canadensis* Schreb. 1776) taken from Main Brook during the winter of 1979.

Four immature specimens of a Digenean from the colon of one muskrat from Main Brook resembled closely the genus *Wardius*.

CESTODA

H. evaginata was second only to *Q. quinqueserialis* in prevalence (Table 1). Site of attachment was principally S.I.S. 4-6 with decreasing proximal and distal frequencies. *H. evaginata* has been commonly associated with the muskrat throughout North America.

One cestode with a few immature proglottids was recovered in a muskrat from Bonavista. Although generic and specific identification cannot be definitely stated, taxonomic characters suggested *Aprostatandrya macrocephala* (Douthitt, 1915).

NEMATODA

C. michiganensis was the fourth most prevalent parasite (Table 1). Measure of the present specimens agreed with Read (1949 b) and Webster (1966). Site of occurrence was principally S.I.S. 1-4. This finding is the first one east of Ontario in Canada.

T. calcaratus was recovered from 11 percent of the muskrats autopsied (Table 1). Nineteen percent of Bonavista and six percent of Main Brook muskrat were infected.

DIFFERENCES IN PARASITE INFECTION RELATED TO HOST SEX AND HOST AGE

The prevalence of *H. evaginata* in males was significantly higher (X^2 $p < 0.05$) than prevalence in female muskrat in both Bonavista and Main Brook, but was not significant for intensity of infection (X^2, $p > 0.05$). Within seasons this difference was significant in the fall only. Because muskrat are sexually inactive in the fall testosterone could be involved. However McKenzie (1977) found a higher prevalence of an *Hymenolepis* spp. in female muskrats. Hence the difference may simply be due to sampling or due to not rejecting a false hypothesis (i.e. Type II error).

No other significant differences in parasite

prevalence or intensity of occurrence (X^2, $p > 0.05$) were found between sexes in Newfoundland. McKenzie (1977) found a higher prevalence of *C. michiganensis* in female muskrats. Abram (1968) indicated a higher prevalence of helminth infection in female muskrat in freshwater ponds. *H. evaginata* was absent from his muskrats.

Studies by various researchers have shown a relationship between host sex and helminth infection e.g. Harley (1958) and Dunsmore (1966) in experimental infections of rats and a natural infection of the European Rabbit (*Oryctolagus cuniculus* (L.)) respectively. Dobson (1961a, b, 1964, 1966 a, b, c) working with *Nematospiroides dubius* (Baylis) in rats; Esch (1967) with experimental and natural infections of *Taenia multiceps* Lecke, 1780 in mice and jackrabbits (*Lepus californicus* Gray 1837) respectively; and Leiby and Kritsky (1974) with *Echinococcus multilocularis* Leuckart 1863 in deer mice (*Peromyscus maniculatus* (Wagner)) all related host sex differences in infections to host hormonal differences associated with sex. No significant differences (G, $p > 0.05$) were found with concurrent infections (hosts infected with two or more species or parasite) between male and female muskrats.

The prevalence and intensity of infection by *C. michiganensis* in adult muskrats was significantly higher (X^2, $p < 0.05$; F, $p < 0.05$) than in immature muskrats. *T. calcaratus* and *D. mergi* both occurred only in adult muskrat and *Q. quinqueserialis* and *P. proximus* generally had a lower prevalence of occurrence in immature muskrat. Anderson and Beaudoin (1966) found adult muskrats had a higher prevalence of *Q. quinqueserialis*, while Abram (1968) and Vanatka (1969) found a higher prevalence in adult muskrats from a freshwater habitat, in contrast to Abram (1968) who detected no differences in animals from tidal marshes.

The difference noted in Main Brook animals infected with *C. michiganensis* is probably related to exposure to the parasite. This proposal is further strengthened by the pattern of concurrent infections found in adult versus immature muskrats from both Bonavista and Main Brook (Table 3, Figures 3, 4). A significant difference (G, $p < 0.05$) in concurrent infections was found between adult and immature muskrats in both localities.

In Bonavista, concurrent infections of two or

Table 3 - Prevalence of Concurrent Infections with Helminths in Bonavista and Main Brook, Newfoundland

Number of Species	BONAVISTA				MAIN BROOK			
	ADULT		IMMATURE		ADULT		IMMATURE	
	1*	2+	1	2	1	2	1	2
0	11	34.3	9	60.0	0	0	0	0
1	12	37.5	6	40.0	1	2.9	0	0
2	7	21.9	0	0	1	2.9	4	28.6
3	2	6.3	0	0	1	2.9	9	64.3
4	0	0	0	0	19	54.2	1	7.1
5	0	0	0	0	10	28.5	0	0
6	0	0	0	0	3	8.6	0	0

* Number of Hosts Infected

\+ Percentage of Hosts Infected

FIGURE 3

The proportion of immature (N = 15) and adult muskrats (N = 32) from Bonavista infected with 0-3 species of helminths.

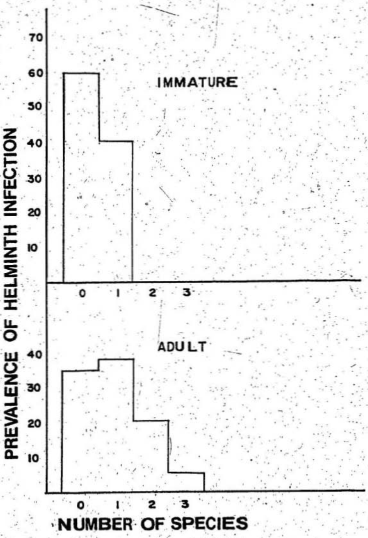
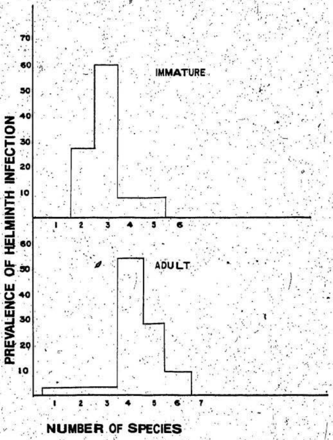

PREVALENCE OF HELMINTH INFECTION
70
60
50
40
30
20
10
IMMATURE
0
1
2
3
ADULT
40
30
20
10
0
1
2
3
NUMBER OF SPECIES

FIGURE 4

Proportion of immature (N = 15) and adult (N = 35) muskrats from Main Brook infected with 1-6 species of helminths.



PREVALENCE OF HELMINTH INFECTION
70
60
50
40
30
20
10
IMMATURE
1 2 3 4 5 6
60
50
40
30
20
10
ADULT
1 2 3 4 5 6 7
NUMBER OF SPECIES

three species occurred in 28 percent of adult muskrats. Immature muskrats harboured a maximum of one helminth species (Figure 3). In Main Brook, concurrent infections of four to six helminth species occurred in 91 percent of adult and 71.4 percent of immature muskrat (Figure 4). The small sample from Peter's River showed a similar trend with 80 percent of adults harbouring concurrent infections of three species compared to 29 percent of immature muskrats. In Main Brook, the helminth species generally found in adults but not immature muskrats were *C. michiganensis* and *D. mergi*; in Bonavista, *C. michiganensis*.

SEASONAL OCCURRENCE OF HELMINTHS

Seasonality of intestinal helminths in vertebrates has been related to a variety of factors, primarily external to the host. For fish, water temperature, its effect on the parasites, the intermediate hosts, and on movement and feeding behaviour of the fish occurs regularly in the literature e.g. Bauer (1958), Pennycuick (1971), Burreson and Olson (1974), Anderson (1976), Eure (1976 a, b) and Komarova (1976). In birds migration (if it occurs) is important e.g.

Belopolskaya (1956), Bakke (1972) and Kornyushin (1973), although not a prerequisite e.g. Threlfall (1965) and Nesterov (1973). In light of the muskrat's proximity to migrant waterfowl this is an important consideration. For other mammals seasonality has also been related to the macroenvironment e.g. Hansson (1974), Leiby and Kritsky (1974) and Gibbs et. al. (1977), being most thoroughly documented for domestic species (Michel, 1976).

All species found in the present study showed seasonal peaks for both prevalence and intensity of infection in both Bonavista and Main Brook (Table 4, Figures 5-8). In Main Brook, *Q. quinqueserialis* showed no variation in prevalence of occurrence (remained constant at 100 percent) whereas intensity of occurrence increased from spring to summer, declining in the fall and winter. This difference in intensity of occurrence was significant (F, $p < 0.05$). In Bonavista, the occurrence of *Q. quinqueserialis* was too infrequent to detect trends. The high prevalence of occurrence in Main Brook is not unexpected since the cercariae encyst on vegetation and therefore are available to the host throughout the year. The summer

Table 4.- Seasonal Prevalence and Intensity of Infection with Helminths in Muskrats from Bonavista and Main Brook, Newfoundland

	SPRING				SUMMER				FALL				WINTER			
	Bonavista (15)[a]		Main Brook(15)		Bonavista(12)		Main Brook(12)		Bonavista(20)		Main Brook(16)		Bonavista(0)		Main Brook(7)	
SPECIES	1[b]	2[c]	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Quinquaserialis quinqueserialis	-	-	100	614	8	*	100	1236	25	2	100	497	-	-	100	590
Plagiorchis proximus	-	-	93	727	-	-	83	287	-	-	75	75	-	-	100	299
Diplostomum mergi	-	-	33	4	-	-	33	6	-	-	6	*	-	-	-	-
Echinostomes	-	-	20	67	-	-	8	345	-	-	19	10	-	-	14	263
Hymenolepis evaginata	13	2	87	11	50	2	83	27	20	*	88	19	-	-	100	16
Capillaria michiganensis	20	3	87	87	42	40	83	62	15	*	38	13	-	-	43	4
Trichostrongylus calcaratus	40	4	7	*	17	16	17	*	-	-	-	-	-	-	-	-

a. Sample size

b. Prevalence

c. Intensity

* Intensity Less Than 1 Helminth/Host

FIGURE 5

Seasonal prevalence of helminth infection in Bonavista muskrats

Species:

C. *Capillaria michiganensis*

H. *Hymenolepis evaginata*

Q. *Quinqueserialis quinqueserialis*

T. *Trichostrongylus calcaratus*

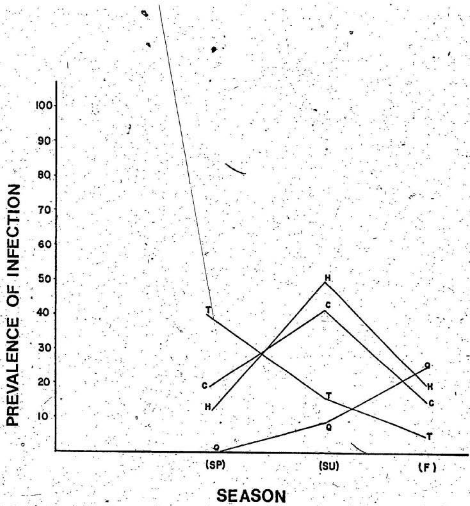

PREVALENCE OF INFECTION
100
90
80
70
60
50
40
30
20
10
T
C
H
Q
(SP)
(SU)
(F)
SEASON

FIGURE 6

Seasonal prevalence of helminth infection in Main Brook muskrats.

Species:

C. *Capillaria michiganensis*

D. *Diplostomum mergi*

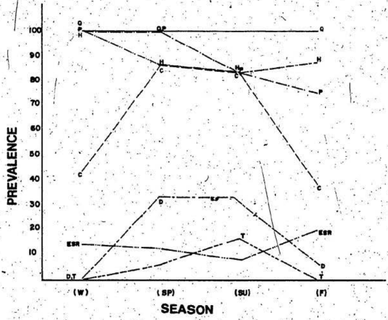
ESR. Echinostomes

H. *Hymenolepis evaginata*

P. *Plagiorchis proximus*

Q. *Quinqueserialis quinqueserialis*

T. *Trichostrongylus calcaratus*



PREVALENCE
SEASON
(W)
(SP)
(SU)
(F)
100
90
80
70
60
50
40
30
20
10
ESR
D,T

FIGURE 7

Seasonal intensity of helminth infection in Bonavista muskrats

Species:

CM. *Capillaria michiganensis*

HE. *Hymenolepis evaginata*

QQ. *Quinqueserialis quinqueserialis*

TC. *Trichostrongylus calcaratus*

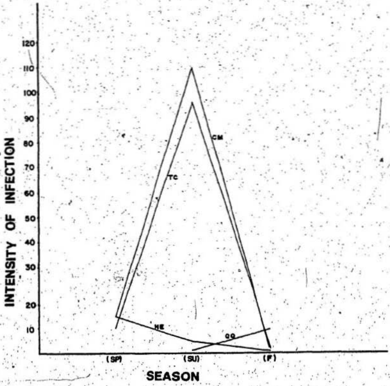

INTENSITY OF INFECTION
120
110
100
90
80
70
60
50
40
30
20
10
CM
TC
HE
CO
(SP)
(SU)
(F)
SEASON

FIGURE 8

Seasonal intensity of helminth infection in Main Brook muskrats.

Species:

CM. *Capillaria michiganensis*

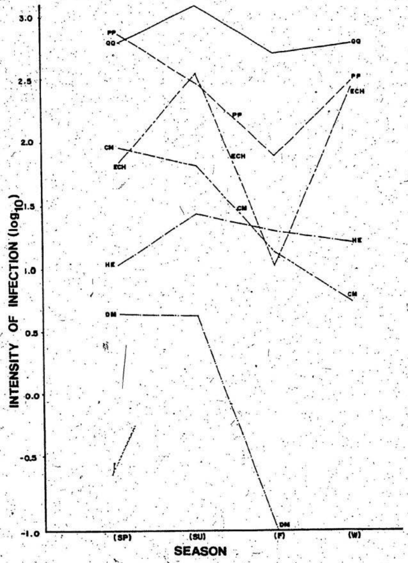
DM. *Diplostomum mergi*

ECH. Echinostomes

HE. *Hymenolepis evaginata*

PP. *Plagiorchis proximus*

QQ. *Quinqueserialis quinqueserialis*



INTENSITY OF INFECTION (log10)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
PP
QQ
ECH
CM
HE
DM
(SP)
(SU)
(F)
(W)
SEASON

peak may be a reflection of rising water temperature in spring facilitating successful hatching of eggs and renewed intramolluscan development. Erlandson (1972) related egg hatching and intramolluscan development of larval digeneans to the effect of water temperature.

Plagiorchis proximus showed peaks of prevalence and intensity of occurrence in the spring followed by a small decline in prevalence in the summer, associated with a sharp decline in intensity of infection through summer and fall. Intensity of infection from the small winter sample indicated a probable increase. The differences in prevalence and intensity of occurrence were significant (X^2, $p < 0.05$; F, $p < 0.05$). The metacercariae encyst in dragonfly, mayfly, naiad and chironomid larvae which can attach to vegetation. Hence the muskrat probably ingest the parasite while feeding on vegetation.

D. mergi showed peaks of prevalence and intensity of occurrence during spring and summer respectively. With the exception of a single worm, this species was absent from fall and winter samples. The differences in prevalence and intensity of occurrence were significant X^2, $p < 0.05$; F, $p < 0.05$). The life-cycle of *D. mergi* is not known, but is probably similar to that of other species of the genus *Diplostomum* where the cercariae penetrate fish and develop into metacercariae in the optic region. This suggests that the muskrat eat fish. Fish scales were found in one muskrat which was infected with *D. mergi*. Curnew (pers. comm.), Smith (1938), Bondar (1950) and Errington (1963) all indicate that muskrat will eat fish. From the occurrence of *D. mergi*, fish consumption appeared to be only seasonal. That *D. mergi* is available at other times is indicated by its probable occurrence in fish and its occurrence in an otter taken from Main Brook in the winter of 1979.

H. evaginata showed peaks of prevalence and intensity of occurrence during the summer in Bonavista, whereas in Main Brook prevalence peaked in winter (although sample size was small) and intensity of infection peaked in summer. The differences in prevalence and intensity of occurrence were significant (X^2, $p < 0.05$; F, $p < 0.05$). The life cycle of *H. evaginata* is unknown, although Penner (1940) suggested an arthropod intermediate host. This would indicate a temperature-related cause for the peak in intensity of occurrence.

C. michiganensis showed peaks of prevalence and intensity of occurrence in the spring in Main Brook and in the summer in Bonavista. In both areas a marked decline in intensity of infection had occurred by autumn. These differences in prevalence and intensity of occurrence were significant (X^2, $p < 0.05$; F, $p < 0.05$). Since the life cycle of *C. michiganensis* is unknown, and, because species in the genus *Capillaria* have life-cycles which are both direct or which involve an intermediate host, a specific hypothesis as to its seasonal occurrence cannot be forwarded. The sharp decline in intensity of infection in adult muskrat associated with the absence of *C. michiganensis* from immature muskrat (immature muskrat could potentially become infected upon leaving the nest in mid-late June, assuming forageing behaviour of immature muskrats does not deviate from that of the adults) suggest a short period of occupancy within the definitive host as well as a restricted annual period for potential infection.

T. calcaratus showed a peak in prevalence of occurrence in spring and summer for Bonavista and Main Brook respectively, whereas the peak in intensity of infection in both areas occurred in summer. These differences in prevalence and intensity of occurrence were significant (X^2, $p < 0.05$; F, $p < 0.05$). The life-cycle is unknown and, like *C. michiganensis*, it is absent from immature muskrats.

Other helminths did not occur frequently enough to enable discussion relative to seasonal occurrence. From Tables 3 and 4 and Figures 3-8 it becomes evident that for Newfoundland muskrat the difference in concurrent parasite infection is related to the seasonal occurrence of *D. mergi* and *C. michiganensis*. The young muskrats apparently become infected with *Q. quinqueserialis*, *P. proximus* and *H. evaginata* soon after leaving the nest. Although probably available, *D. mergi* is not ingested throughout the year. Intensity of infection by *Q. quinqueserialis* and *P. proximus* increases so that by winter the intensity of infection in young muskrats approximates that found in adults. The small winter sample (7) precluded testing this statistically.

Seasonal occurrence of muskrat parasites was first documented in the U.S.S.R. by Lavroff (1953) who found peak helminth prevalence and intensity of infections and concurrent infections to be in the summer. Vanatka (1969) observed a seasonal difference between spring and fall helminth infections in Czechoslovakia. Abram (1968), working in Maryland, U.S.A. found variation in the seasonal peak in helminths from both fresh water and tidal water habitats.

HELMINTH DISTRIBUTION WITHIN HOST

Individual species of parasites have been found to occur in, and actively seek, specific sites within the host (Ulmer, 1971; Holmes, 1973) with helminths favouring the gastro-intestinal tract (Mettrick and Podesta, 1974). Most helminths previously recorded from the muskrat (and all in the present study) occur in the gastro-intestinal tract. Two possible factors influencing the site where a parasite is found are immunological effects and interactions between the worms. Although the present study cannot point to causal mechanisms it can show the distribution pattern of helminths found in muskrat from Newfoundland.

The prevalence and intensity of infection of each helminth species recovered (excluding *T. calcaratus* which occurred only in the caecum) were plotted against site of occurrence along the alimentary tract (Figures 9, 10). A significant difference (F, $p < 0.05$) was found between the different sections of the alimentary tract with respect to the total number of *P. proximus, Q. quinqueserialis, D. mergi, H. evaginata,* and *C. michiganensis.* No significant differences (F, $p > 0.05$) were found between different sections of the alimentary tract and the total number of echinostomes in each section.

Figures 9 and 10 indicate the proximal 60 percent of the small intestine was preferred by all helminth species found except *Q. quinqueserialis* and *T. calcaratus* which prefer the caecum. A separation of preferred sites can be seen in the three common species found in the small intestine *(P. proximus, H. evaginata* and *C. michiganensis).* From Figure 10, as the number of *C. michiganensis* declines (A3), the number of *P. proximus* increases. As *P. proximus* begins declining (A5) the number of *H. evaginata* peaks. The amount of longitudinal overlap between these three species is large, and can be attributed, in part, to the variation in the number of worms in individual infections.

FIGURE 9

Prevalence/infected host of helminth distribution along the alimentary tract of 57 Newfoundland muskrats.

Species:	Section of Alimentary Tract:
CM. *Capillaria michiganensis*	A1. Stomach
DM. *Diplostomum mergi*	A2. Small Intestine 1
ECH. Echinostomes	A3. Small Intestine 2
HE. *Hymenolepis evaginata*	A4. Small Intestine 3
PP. *Plagiorchis proximus*	A5. Small Intestine 4
QQ. *Quinqueserialis quinqueserialis*	A6. Small Intestine 5
	A7. Small Intestine 6
	A8. Small Intestine 7
	A9. Small Intestine 8
	A10. Small Intestine 9
	A11. Small Intestine 10
	A12. Caecum
	A13. Colon

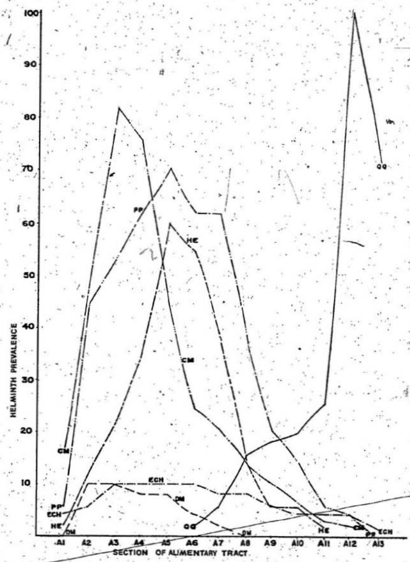

HELMINTH PREVALENCE
SECTION OF ALIMENTARY TRACT
A1 A2 A3 A4 A5 A6 A7 A8 A9 A10 A11 A12 A13
10 20 30 40 50 60 70 80 90 100
CM
PP
ECH
HE
DM
QQ

FIGURE 10

Intensity/infected host of helminth distribution along the alimentary tract of 57 Newfoundland muskrats.

Species:

CM. *Capillaria michiganensis*

DM. *Diplostomum mergi*

ECH. Echinostomes

HE. *Hymenolepis evaginata*

PP. *Plagiorchis proximus*

QQ. *Quinqueserialis quinqueserialis*

Section of Alimentary Tract:

A1. Stomach

A2. Small Intestine 1

A3. Small Intestine 2

A4. Small Intestine 3

A5. Small Intestine 4

A6. Small Intestine 5

A7. Small Intestine 6

A8. Small Intestine 7

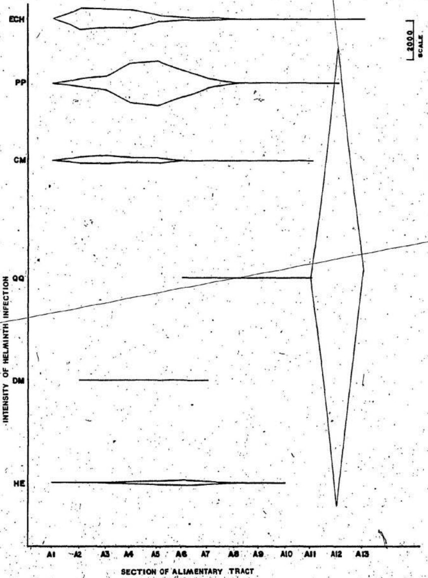
A9. Small Intestine 8

A10. Small Intestine 9

A11. Small Intestine 10

A12. Caecum

A13. Colon



ECH
PP
CM
QQ
DM
HE
INTENSITY OF HELMINTH INFECTION
2000
SCALE
A1
A2
A3
A4
A5
A6
A7
A8
A9
A10
A11
A12
A13
SECTION OF ALIMENTARY TRACT

The wide range of occurrence and overlap between species in conjunction with 'preferred' sites of peak occurrence indicates selective site segregation (Holmes, 1973). Whether concurrent infections produce competitive exclusion or interactive site selection cannot be determined. High intensity of echinostome occurrence associated with low intensity of *P. proximus* occurrence suggested competitive exclusion between these two species, but the sample size was too small (3) for definitive conclusions. *H. evaginata* proglottids were generally reduced in size in large infections (greater than 10 worms) as was noted by Halvorsen (1976).

The various concurrent infection combinations found and the frequency with which they occurred were recorded in Table 5. It is clear that concurrent infections of three species (particularly *P. proximus*, *Q. quinqueserialis*, and *H. evaginata*) and four species (particularly *P. proximus*, *Q. quinqueserialis*, *H. evaginata* and *C. michiganensis*) were found most frequently. A concurrent infection combination with five species (*P. proximus*, *Q. quinqueserialis*, *D. mergi*, *H. evaginata* and *C. michiganensis*) was found in 60 percent of the muskrat infected with *D. mergi*. The one and two species infections were found principally in hosts from Peter's River and Bonavista and were a reflection of a lower muskrat helminth diversity in those areas.

Table 5. Summary of Helminth Species Combinations from the Alimentary Tract of Newfoundland.

Number of Species	Species Found Together	Sample Size	Percent of Total Sample Size
6	PP, QQ, ECH, DM, HE, CM	2	2.1
6	PP, QQ, ECH, PAR, HE, CM	1	1.1
5	PP, QQ, HE, CM, TC	3	3.2
5	PP, QQ, DM, HE, CM	6	6.4
5	PP, QQ, ECH, HE, CM	2	2.1
4	PP, QQ, DM, CM	1	1.1
4	PP, QQ, DM, HE	1	1.1
4	PP, QQ, ECH, CM,	1	1.1
4	PP, QQ, ECH, HE	1	1.1
4	PP, QQ, HE, CM	15	16.0
4	PP, QQ, ECH, CM	2	2.1
4	QQ, ECH, HE, CM	1	1.1
3	PP, QQ, CM	3	3.2
3	PP, QQ, HE	16	17.0
3	PP, HE, TC	1	1.1
3	QQ, ECH, HE	1	1.1
3	HE, ANO, CM	1	1.1
3	HE, CM, TC	1	1.1
2	PP, QQ	6	6.4
2	QQ, HE	3	3.2
2	QQ, CM	1	1.1
2	HE, CM	5	5.3
2	HE, TC	1	1.1

Table 5. continued

Number of Species	Species Found Together	Sample Size	Percent of Total Sample Size
1	QQ	7	7.5
1	HE	2	2.1
1	CM	4	4.3
1	TC	6	6.4

KEY

ANO - Anoplocephalid

CM - *Capillaria michiganensis*

DM - *Diplostomum mergi*

ECH - Echinostome

HE - *Hymenolepis evaginata*

PAR - Paramphistomatid

PP - *Plagiorchis proximus*

QQ - *Quinqueserialis quinqueserialis*

TC - *Trichostrongylus calcaratus*

The intensity of infection by helminths of Main Brook muskrat was the highest recorded to date in the literature. However, no evidence of pathological damage was found and no correlation between adult host size (g) and intensity of infection was found. With the exception of isolated reports of cestode occlusion of the intestine, and acanthocephalan-induced damage (McKenzie, 1977) the literature gives no evidence of helminths causing damage to muskrats.

GEOGRAPHICAL DISTRIBUTION OF MUSKRAT PARASITES

Newfoundland is believed to have emerged from the last glaciation within the past 8,000 to 10,000 years. It is probable that repopulation by mammals occurred across the Strait of Belle Isle from populations in Labrador. The barrier of the Strait of Belle Isle is believed to have prevented Newfoundland being populated by such native Labrador mammals as the woodchuck (*Marmota monax L.*) and the red squirrel (*Tamiasciurus hudsonicus L.*). Likewise one would expect a lower helminth diversity for Newfoundland muskrat than for muskrat on the adjoining mainland. Such an insular reduction is a general theorem of zoogeography (Darlington, 1957; Udvardy, 1971). The helminth fauna which now exists in Newfoundland muskrat would have reached the island with the original "pioneer" population of muskrats or through hitch-hiking with avian hosts in the case of helminths which are not host-specific. Reduction of helminth diversity on the island would be a consequence of:

1. Helminth absence from muskrat which dispersed to the island.
2. Helminth absence from either resident or migrating avian host.
3. Absence of necessary intermediate host(s).

Unfortunately, in the absence of comparable data from Labrador, this comparison cannot be made.

The foregoing results on the occurrence of muskrat helminths in Newfoundland (cf. Tables 1 and 3; Figures 2-4) indicate a reduction in helminth diversity as one moves in the direction of the expected dispersal of muskrat in Newfoundland i.e. eastwards. The most noteworthy difference was the virtual absence of digeneans from Bonavista. In an effort to explain the anomalous distributions, the water pH and calcium and total hardness concentrations were measured for the sampling areas. These were related to the $\log_{10}$ average number of digeneans, cestodes and nematodes from all muskrats from each of Bonavista, Peter's River and Main Brook (Table 6, Figures 11-13). The data presented suggest a link between pH, calcium and total hardness concentrations and the occurrence of digeneans. From a chemical perspective, increased acidity necessarily implies reduced carbonate concentrations. Since calcium is found in association with carbonate, calcium would not be expected, and is not found, in Bonavista. This would imply a limiting factor to the presence of aquatic molluscs. A limitation on the number of aquatic molluscs implies a limitation for digeneans.

Only one mollusc was noted in nearly two months of muskrat sampling in Bonavista, whereas in Main Brook, where pH was basic and calcium and total hardness concentrations were comparatively high, molluscs were noted to be abundant. I suggest the low pH in Bonavista limits mollusc and hence digenean occurrence.

Hunter (1964), discussing physiological ecology in freshwater molluscs, states "throughout the world- other environmental factors being equal - harder fresh waters [i.e. those with greater Ca and total hardness concentrations] undoubtedly support more molluscs than low calcium waters". In Britan, Hunter (1964)

Table 6 - Water Chemical Characteristics (pH, Calcium and Total Hardness Concentrations in p.p.m.) for Bonavista, Peter's River and Main Brook, Newfoundland compared to Log_{10} Average Infection of Digeneans, Cestodes and Nematodes Recovered from Muskrat in these areas.

Area	Log_{10} $\bar{X}$ infection with Helminths/Muskrat Collected		pH Mean (Range)	Calcium Mean (Range)	Total Hardness (Range)
Bonavista	Digenea	0.04	5.92		
	Cestoda	0.13	(5.5-6.0)	<2	<2
	Nematoda	1.22			
Peter's River	Digenea	2.53	6.92	10.5	44
	Cestoda	1.29	(6.5-7.0)	(9-12)	(40-50)
	Nematoda	0			
Main Brook	Digenea	3.09	7.47	38.3	71.8
	Cestoda	1.26	(6.5-8.0)	(25-60)	(45-112)
	Nematoda	1.67			

FIGURE 11

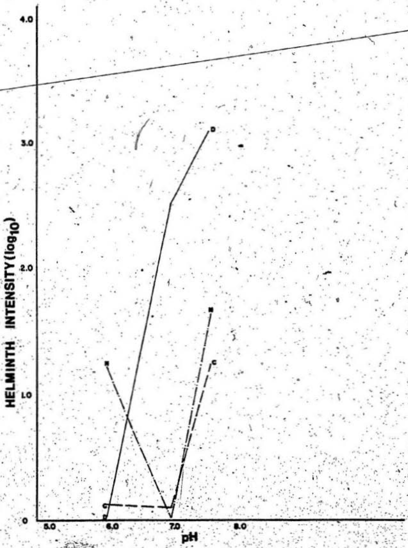
pH plotted against intensity of Newfoundland muskrat helminth infections (Log_{10}).

Parasite Groups:

C. Cestoda

D. Digenea

N. Nematoda



HELMINTH INTENSITY (log10)
4.0
3.0
2.0
1.0
0
5.0
6.0
7.0
8.0
pH
D
H
C

FIGURE 12

Calcium (Ca.) concentration (p.p.m.) plotted against intensity of Newfoundland muskrat helminth infections (Log_{10}).

Parasite Groups:

C. Cestoda

D. Digenea

N. Nematoda

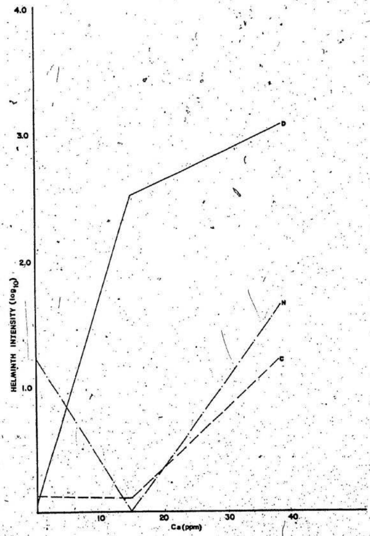

4.0
3.0
2.0
1.0
HELMINTH INTENSITY (log_{10})
D
H
C
10
20
30
40
Ca (ppm)

FIGURE 13

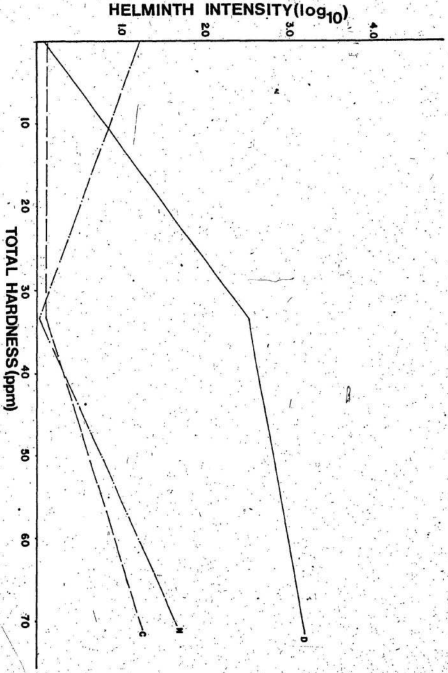
Total hardness concentration (p.p.m.) plotted against intensity of Newfoundland muskrat helminth infections (Log_{10}).

Parasite Groups:

C. Cestoda

D. Digenea

N. Nematoda



HELMINTH INTENSITY(log10)
1.0
2.0
3.0
4.0
TOTAL HARDNESS (ppm)
10
20
30
40
50
60
70
C
N
D

correlated mollusc distribution to calcium content of the water and noted few molluscs were found to live at pH lower than 6.0. Green (1971) found low calcium levels associated with low pH, and in a multivariate analysis of bivalves in central Canada, found 45 percent of the variation in molluscs was associated with calcium variation. Ökland (1969) found few molluscs in Norwegian Lakes with pH less than 6.0, such lakes possessing low calcium concentrations. A decreased frequency was found for all gastropods in sphagnum bogs and most species favoured a high concentration of total hardness. Scioli (1964) related low abundance of molluscs to low pH. Fischthal (1953) indicated scarcity of of molluscs is related to acid dissolving or corroding of carbonate shells. Hence ample evidence exists in the literature to support my hypothesis.

Peter's River was intermediary between Bonavista and Main Brook both for pH and water hardness. *Q. quinqueserialis* and *P. proximus* were abundant but the echinostomes were absent. Waterfowl do frequent Peter's River hence the absence of echinostomes could be a function of there being no suitable intermediate host(s).

Differences in the occurrence of muskrat parasites related to habitat or between regions have been noted before (Chandler, 1941; Anderson and Beaudoin, 1966; Abram, 1968; Rice and Heck, 1975; and MacKinnon and Burt, 1978) and can be detected from the results of Knight (1951), Sweatman (1952), Lavroff (1953), Dunagan (1957) and Vanatka (1969). However only Chandler (1941) and Abran (1968) give satisfactory supporting evidence to explain the differences they found.

Four of the Digenea (*Echinostoma revolutum*, *Echinoparyphrium contiguum*, *Echinoparyphrium recurvatum*, and *D. mergi*) found in Main Brook were probably transplanted to Newfoundland by avian hosts. These particular helminth species, as well as *T. calcaratus*, exhibit what Noble and Noble (1976) describe as ecological specificity wherein the parasite is capable of living in a foreign host if not isolated by an ecological barrier. Since Main Brook is on the edge of a waterfowl migration corridor to Labrador, the area is probably reseeded with echinostomes each spring and, possibly, fall. *Q. quinqueserialis*, *P. proximus* and the paramphistomatid species (if it is *Wardius zibethicus* Barker and East, 1915) *H. Evaginata*, *C. michiganensis* the echinostomes and *T. calcaratus* are all characteristi of the muskrat. With the possible exception of *T. calcaratus,* and the echinostomes these species may be categorized as possessing phylogenetic specificity (Noble and Noble, 1976). Hence, from the foregoing discussion, the occurrence of helminths in Newfoundland muskrat is, among other things, a function of the host's and/or helminth's zoogeographic distribution.

The concept of ecological or physiological specificity is more clearly demonstrated for the composite of North American and holarctic muskrat helminths. A summary of North American intestinal helminths was compiled (Appendix 3) by subdividing the continent in accordance with Hagmeier's (1966) mammal provinces. As shown, the greatest diversity of helminths are found in the Illinoan Province. Many of these are what may be labelled as ecological parasites. This diversity is likely a reflection of:

1. This region being at the junction of the Atlantic and Mississippi migration flyways.
2. This region is the junction of the North American grassland, boreal and temperate ecosystems.
3. This region possesses the 'best' muskrat habitat in North America (as described by Errington, 1963)

shown both by the high density of muskrat and the restriction of most muskrat epizootics to this region.

4. This region possesses an abundance of marshes, sluggish streams, ditches and rich vegetation, providing a diversified habitat for intermediate hosts and other definitive hosts.

Radial movement away from the Illinoin Province is accompanied by a reduction of helminth diversity. Errington (1963) noted that (with the possible exception of the Artimesian, Louisianian and Alleghenian provinces) the quality of muskrat habitat declines. Also, other factors listed above as being related to the Illinoian helminth diversity take on different relative importances which in general translates into a less diverse habitat for muskrat helminths. From Appendix 3 we see helminth diversity declines.

More specifically, from Appendix 3 the concept of ecological and physiological specificity is reinforced. In addition to helminth species already listed, ecological specificity may be seen for *Metorchis conjunctus* Cobbold 1860, *Alaria mustelae* Bosma 1931, *Fibracola crater* Barker and Noll 1915, *Echinochasmus schwartzi* Price 1931, *Paragonimus kellicotti* Ward 1908, *Aprostatandrya macrocephala*, *Ascaris lumbricoides* L. 1758, *Reticularia ondatrae* Chandler 1941 and *Trichurus opaca* Barker and Noyes, 1915. Physiologic specificity appears to be additionally exhibited by *Notocotylus fillamentis* Barker 1915, *N. urbanensis* Cort 1914, *Nudacotyle novicia* Barker 1916, *Ribeiroia ondatrae* Price 1931, *H. ondatrae* Rider and Macy 1947, *H. oregonensis* Neiland and Senger 1952, and *C. ransomia* Barker and Noyes, 1915. A paucity of information makes it impossible to comment on the other species listed.

Of the helminths found in North America only three are found in the muskrat in Eurasia. Of these *Q. quinqueserialis* and *P. proximus* were probably introduced with the muskrat to Europe while *E. revolutum* may either have accompanied the muskrat or were aquired from the Eurasian population which existed previously. Genera represented in North America e.g. *Plagiorchis*, *Echinostoma*, *Hymenolepis* and *Capillaria* are represented in the muskrat in Eurasia by other different species as indicated in Andreiko et al. (1963), Podkolzina (1967), Sey (1967), Gvozdev (1969), Vanatka (1969), Machinskii and Semov (1972), Zakariev (1972) and Shuteev (1977).

The genus *Aprostatandrya,* found in only four North American studies of muskrat parasites is found commonly in Eurasia (Andreiko et. al. 1963; Gvozdev, 1969; Vanatka, 1969; and Machinskii and Semov, 1972). Sey (1967) categorized helminths of muskrat in Hungary into:

1. Species found in phylogenetically closely related species acquired in Europe - 66 percent.
2. Species common to vertebrate hosts - 22 percent.
3. Species which survived introduction with the host - 12 percent.

Categories 1 and 3 correpond roughly with phylogenetic specificity while category 2 corresponds with ecologic specificity.

Throughout its holarctic range the muskrat has been accompanied by *Q. quinqueserialis* and *P. proximus*. The versatility of these two species is probably related to their having intermediate hosts which are distributed throughout the holarctic zone. These species have likely been transported by the muskrat throughout its range and hence their occurrence in Newfoundland muskrats is not surprising. *E. revolutum,* by contrast, is probably picked up by the muskrat from already existing populations.

Hence intestinal helminth parasites from Newfoundland muskrats generally do not vary in relation to host sex. Two species (*D. mergi* and *T. calcaratus*) vary in relation to host age and larger concurrent infections occur in adult muskrats. Seasonal variation generally occurs. Intestinal helminth occurrence in Newfoundland and throughout the muskrat's native and introduced holarctic range can be related to physiological or ecological specificity by the helminths.

SUMMARY

1. Eleven species of intestinal helminths (7 Digenea, 2 Cestoda, and 2 Nematoda) were recovered from 114 muskrats collected from three regions of insular Newfoundland. Ten species of intestinal helminths (7 Digenea, 1 Cestoda, and 2 Nematoda) were collected from 50 Main Brook muskrats; six species (2 Digenea, 2 Cestoda, and 2 Nematoda) were collected from 47 Bonavista muskrats; and three species (2 Digenea and 1 Cestoda) were collected from 17 Peter's River muskrats.

2. *Diplostomum mergi* was recovered from a mammal for the first time.

3. Only *Hymenolepis evaginata* was found to be more prevalent in one sex (i.e. male) than in the other sex.

4. Prevalence and intensity of infection by *Capillaria michiganensis* in adult muskrats was significantly higher (X^2, $p < 0.05$; F, $p < 0.05$) than in immature muskrats. *D. mergi* and *Trichostrongylus calcaratus* occurred only in adult muskrats. Adult muskrats also had larger concurrent infections.

5. Seasonal peaks in prevalence and intensity of infection was shown by all species except *Quinqueserialis quinqueserialis* and *T. calcaratus* which preferred the

caecum. The three commonly occurring helminth species found in the small intestine of Newfoundland muskrats, namely *C. michiganensis*, *P. proximus*, and *H. evaginata* exhibited a separation of preferred sites of occurrence. The number of these species of worms found in different infections, along with various combinations of concurrent infections found, tended to mask this separation.

7. A difference in digenean occurrence between areas within insular Newfoundland was related to water pH and hardness. An attempt was made to relate the zoogeographical distribution of helminths to the distribution of the muskrat and various other biotic factors, including the concept of environmental versus physiological specificity of parasites.

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Appendix 1 - Topical Summary of Publications Related to Helminths of Muskrat

Taxonomy	Life Cycle	Survey	Ecology	Disease
Barker and Laughlin (1911)	Penner (1940)	Leidy (1888)	Lavroff (1953)	Knight (1951)
Barker (1915)	Penn (1942a)	Warwick (1936)	Anderson & Beaudoin (1966)	Lord (1952)
Barker (1916)	Read (1949)	Olsen (1939)	Abram (1968, 1969)	
Price (1932)		Goble (1942)		
Olivier (1938)		Penn (1942b)	Vanatka (1969)	
Chandler (1941)		Rauch (1946)	Rice & Heck (1975)	
Ameel (1942)		Edwards (1949)	McKenzie (1977)	
Rider and Macy (1947)		Chandler (1950)	MacKinnon & Burt (1978)	
Doerkson (1969)		Meyer and Reilly (1950)	McKenzie & Welch (1979)	
		Ball (1952)		
		Byrd (1952)		
		Sweatman (1952)		
		Gilford (1954)		
		Burnett (1956)		
		Connell & Corner (1957)		
		Dunagan (1957)		
		Senger & Bates (1957)		
		Shaldbin (1960)		
		Andreiko (1963)		
		Sey (1966)		
		Beckett & Gallicchio (1967)		
		Grundmann & Tsai (1967)		
		Podkolzina (1967)		

Appendix 1 - continued

Taxonomy	Life Cycle	Survey	Ecology	Disease
		Sey (1967)		
		Cromer (1968)		
		Gvozdev (1969		
		Gash & Hannah (1972)		
		Harley (1972)		
		Machinskii & Semov (1972)		
		Zakariev (1972)		
		Jilek (1977)		
		Shuteev (1977)		

Appendix 2 - Average number ($\bar{X}$), S.E. and Range of Helminth Numbers Found in Sections of the Alimentary Tract of Newfoundland Muskrat.

Diplostomum mergi

Section	$\bar{X}$	S.E.	Range
Stomach	0		
Small Intestine 1	1.43	0.88	0-38
Small Intestine 2	0.24	0.16	0-8
Small Intestine 3	0.71	0.45	0-19
Small Intestine 4	0.06	0.03	0-1
Small Intestine 5	0	0	-
Small Intestine 6	0	0	-
Small Intestine 7	0	0	-
Small Intestine 8	0	0	-
Small Intestine 9	0	0	-
Small Intestine 10	0	0	-
Caecum	0	0	-
Colon	0.02	0.02	0-1

Plagiorchis proximus

Section	$\bar{X}$	S.E.	Range
Stomach	3.10	2.98	0-152
Small Intestine 1	15.80	7.63	0-359
Small Intestine 2	29.00	7.81	0-269
Small Intestine 3	72.94	27.24	0-1198
Small Intestine 4	82.27	38.96	0-1913
Small Intestine 5	51.57	19.48	0-916
Small Intestine 6	21.10	5.16	0-134
Small Intestine 7	4.35	1.77	0-61
Small Intestine 8	2.94	1.94	0-96
Small Intestine 9	3.86	3.39	0-173
Small Intestine 10	2.37	2.22	0-113
Caecum	0	0	-
Colon	0.10	0.10	0-5

Appendix 2 - continued

Quinqueserialis quinqueserialis

Section	X̄	S.E.	Range
Stomach	0.04	0.28	0-2
Small Intestine 1	0	0	-
Small Intestine 2	0	0	-
Small Intestine 3	0	0	-
Small Intestine 4	0	0	-
Small Intestine 5	0.02	0.02	0-1
Small Intestine 6	0.08	0.05	0-2
Small Intestine 7	0.31	0.13	0-5
Small Intestine 8	0.45	0.15	0-5
Small Intestine 9	1.20	0.60	0-26
Small Intestine 10	1.08	0.48	0-19
Caecum	724.45	148.58	0-4847
Colon	10.71	2.99	0-98

Echinostomes

Section	X̄	S.E.	Range
Stomach	0.39	0.37	0-19
Small Intestine 1	40.98	30.88	0-1472
Small Intestine 2	34.63	20.73	0-772
Small Intestine 3	36.51	26.67	0-1324
Small Intestine 4	12.43	6.72	0-273
Small Intestine 5	7.53	-	0-165
Small Intestine 6	5.14	3.01	0-124
Small Intestine 7	0.57	0.38	0-16
Small Intestine 8	0.10	0.06	0-3
Small Intestine 9	0.14	0.12	0-6
Small Intestine 10	0.10	0.07	0-3
Caecum	3.67	2.25	0-77
Colon	0.08	0.08	0-4

Appendix 2 - continued

Hymenolepis evaginata

Section	$\bar{X}$	S.E.	Range
Stomach	0.18	0.18	0-9
Small Intestine 1	0.22	0.09	0-3
Small Intestine 2	0.80	0.29	0-11
Small Intestine 3	2.51	0.92	0-40
Small Intestine 4	4.49	1.23	0-51
Small Intestine 5	6.84	2.00	0-82
Small Intestine 6	1.71	0.48	0-16
Small Intestine 7	0.31	0.17	0-8
Small Intestine 8	0.08	0.05	0-2
Small Intestine 9	0.06	0.03	0-1
Small Intestine 10	0	0	-
Caecum	0.02	0.02	0-1
Colon	0	-	-

Capillaria michiganensis

Section	$\bar{X}$	S.E.	Range
Stomach	0.84	0.45	0-17
Small Intestine 1	17.82	5.00	0-201
Small Intestine 2	15.67	4.75	0-202
Small Intestine 3	6.86	2.14	0-76
Small Intestine 4	8.78	6.87	0-350
Small Intestine 5	1.55	0.68	0-21
Small Intestine 6	0.96	0.51	0-18
Small Intestine 7	0.24	0.16	0-8
Small Intestine 8	0.04	0.03	0-1
Small Intestine 9	0.06	0.05	0-3
Small Intestine 10	0.02	0.02	0-1
Caecum	0	0	-
Colon	0	0	-

Appendix 3 - A summary of the zoogeographic occurrence and lifecycle (if known) of intestinal helminths of muskrat in North America

PARASITE SPECIES	MAMMAL PROVINCES: Yukonian	Vancouverian	Montanian	Oregonian	Artimesian	Coloradian	Kansan	Illinoian	Alleghenian	Caralonian	Louisianian	E. Canadian	E. Hudsonian	Areas infected %	Recorded Distribution	Definitive Host	1st Intermediate Host	2nd Intermediate Host
Digenean	x	x	x	x	x	x	x	x	x	x	x	x	x	100		17,26		
Alaria mustelae	x							x	x			x		30.8	N.A.	24	37	
Fibricola crater					x		x	x						23.1	N.A.	10,26,24 30,41	36	
Echinochasmus schwartzi								x		x	x	x		30.8	N.A.	30	?	13
Echinoparyphium contiguum			x		x	x	x	x					x	46.9	N.A.	6,20,35, 41	?	
Echinoparyphium recurvatum								x	x	x		x	x	38.5	C	59	19,23, 36	
Echinostomum revolutum	x	x	x	x	x	x	x	x	x				x	76.9	C	19,36,40 48		
Apophallus brevis								x						7.7	N.A.	12,21	23	43
Phagicola lageniformis											x			7.7	N.A.	49	?	14
Phagicola nanus											x			7.7	N.A.		?	?
Allassogonoporus marginalis								x						7.7	N.A.	32	?	?
Levinseniella brachysoma								x						7.7	HOL	54		
Notocotylus filamentis	x					x	x	x	x					38.5	N.A.	28	?	
Notocotylus urbanensis				x	x			x	x	x				38.5	N.A.	1	36,48	
Nudacotyle novicia								x	x	x	x	x		38.5	N.A.	28	?	
Quinqueserialis quinqueserialis	x	x	x	x	x	x	x	x	x	x		x	x	92.3	N.A.	4,28 55	18	
Paramonostomum pseudalveatum					x					x	x			23.1	HOL	3,5	?	
Metorchis conjunctus								x	x					15.3	N.A.	6,12,20,29 30,39,53	38	
Paragonimus kellicotti								x	x					15.3	N.A.	6,15,25 30,50,53	?	
Wardius zibethicus							x	x	x	x		x	?	46.9	N.A.		19	
Plagiorchis maculosus								x						7.7		48	2	
Plagiorchis microcanthus								x						7.7	PAL	42	48	2
Plagiorchis muris								x						7.7	HOL	32	48	2
Plagiorchis noblei									x					7.7	N.A.	1	48	2
Plagiorchis proximus	x	x	x		x	x		x	x			x	x	69.2	HOL	30,55	48	2
Ribeiria ondatrae				x		x		x	x			x		38.5			?	

PARASITE SPECIES	MAMMAL PROVINCES Yukonian	Vancouverian	Montanian	Oregonian	Artimesian	Coloradian	Kansan	Illinoian	Alleghenian	Caralonian	Louisianian	E. Canadian	E. Hudsonian	Areas Infected %	Recorded Distribution	Definite Host	1st Intermediate Host	2nd Intermediate Host
Urotrema ondatrae								x		x				15.3	N.A.		?	
Diplostomum mergi													x	7.7	HOL	27.47	23	10
CESTODA	x	x	x	x	x	x	x	x	x		x	x	x	92.3				
*Andrya macrocephala**									x				?	15.3	HOL	8,9,16,28,45,51	?	
*Andrya ondatrae**								x						7.7	HOL	8,9,16,28,45,51	?	
Andrya sp.*					x									7.7	HOL	8,9,16,28,45,51	?	
Monococestus americanus								x	x					15.3	N.A.	11,46	42	
Monococestus variabilis								x						7.7	N.A.	11,46	42	
Anomotaenia telescopica							x							7.7	N.A.		?	
Hymenolepis evaginata	x	x	x		x	x	x	x	x		x	x	x	84.6	N.A.	28	2	
Hymenolepis ondatrae				x	x									15.3	N.A.	7	?	
Hymenolepis oregonensis				x				x	x					23.1	N.A.	7	?	
NEMATODA	x	x	x	x	x	x	x	x	x	x	x		x	92.3				
Ascaris lumbricoides					x	x		x	x	x				38.5	C		-	
Capillaria michiganensis					x	x		x	x				x	38.5	N.A.		?	
Capillaria ransomia		x	x				x	x						30.8	N.A.		?	
Heligmosomum longispiculatus								x		x				15.3	N.A.	28		
Longistriata adunca											x			7.7	N.A.	45		
Physaloptera sp.											x			7.7	N.A.	52		
Strongyloides ratti											x			7.7	C	34,45		
Reticularia ondatrae											x			7.7	C	34,45		
Trichostrongylus calcaratus				x			x	x	x				x	38.5	N.A.	49,24,33,44,46		
Tricurus opaca	x	x	x		x	x	x	x	x	x				69.2	N.A.	28,31		

PARASITE SPECIES	MAMMAL PROVINOES: Yukonian	Vancouverian	Montanian	Oregonian	Artimesian	Coloradian	Kansan	Illinoian	Alleghenian	Caralonian	Louisianian	E. Canadian	E. Hudsonian	Areas Infected %	Recorded Distribution	Definite Host	1st Intermediate Host	2nd Intermediate Host
ACANTHOCEPHALA								x						7.7				
Polymorphus paradoxus								x						7.7	N.A.	7		

Key

* Synonomized with *Aprostatandrya macrocephala*

C - Cosmopolitan (many species of definitive hosts throughout the world)

HOL - Holarctic

N.A. - North America

1. *Agelaius phoeniceus*
2. Arthropods
3. *Arvicola riparius*
4. *Arvicola terres*
5. *Branta canadensis*
6. *Canis familiaris*
7. *Castor canadensis*
8. *Citellus* sp.
9. *Cricetellus* sp.
10. *Didelphus marsupialis*
11. *Erithrozon dorsatum*
12. *Felis catus*
13. *Fundulus heteroclitis*
14. *Fundulus pallidus*
15. *Gavia immer*
16. *Geomys* sp.
17. *Gulo gulo*
18. *Gyrulus* sp.
19. *Helistoma* sp.
20. *Homo sapiens*
21. *Larus delawarensis*
22. *Lepus sylvaticus*
23. *Lymnaea* sp.
24. *Marmota monax*
25. *Martes* sp.
26. *Mephitis mephitis*
27. *Mergus* sp.
28. *Microtus* sp.
29. *Mustela furo*
30. *Mustela vison*
31. *Myoptamus coypus*
32. *Myotis* sp.
33. *Oryctolagus* sp.
34. *Oryzomys palustris*
35. *Phasianus colchus*
36. *Physa* sp.
37. *Planorbula* sp.
38. *Pomatiopsis* sp.
39. *Procyon lotor*
40. *Pseudosullinea* sp.
41. *Rattus norvegicus*
42. Rodentia
43. *Salmo salar*
44. *Sciurus* sp.
45. *Sigmodon* sp.
46. *Silvilagus* sp.
47. *Somateria* sp.
48. *Stagnicola* sp.
49. *Sula bassana*
50. *Sus scrofa*
51. *Thomomys* sp.
52. Vertebrate spp. (many)
53. *Vulpes* sp.
54. Wading birds
55. *Zapus hudsonicus*

END

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FIN