THE UNIVERSITY OF MANITOBA

ADAPTIVE STRATEGIES OF THE CENTRAL MUDMINNOW, UMBRA LIMI (KIRTLAND) IN SOUTHERN MANITOBA

by

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A DISSERTATION

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ABSTRACT

The variation in the environmental factors encountered, the habitat occupied and preferred, patterns of activity, aspects of growth, reproduction and food consumption by the central mudminnow, Umbra limi were studied to illustrate the mudminnow's adaptations to the spatial and temporal pattern of its environment.

Mudminnows inhabit and show a preference for areas with cover which is consistent with their morphological, behavioural and physiological adaptations. Mudminnows showed variations in time of activity. Crepuscular, nocturnal and diurnal activities were observed at different times and places.

Enhanced survival of females is one of the life history strategies exhibited by mudminnows. Females (age 2+) were usually larger and more abundant than males. Age at first maturity was two for females and one for males. Time of spawning varied between years in the streams studied and some females did not spawn at all in 1979. Delayed spawning (particularly in smaller females) may be an important survival strategy in a variable environment. Larger females produced more eggs so that a strategy of increased growth in females may be selected. Gonad development in females occurred largely in winter when a piscivorous diet was observed. Variability in growth rates resulted in overlap in lengths which increased as the fish aged. All are indicative of a generalized life history strategy.

Feeding occurred in the vegetated areas of streams. Benthic, mid-water, surface and organisms attached to vegetation were included in the diet. Mudminnows were euryphagic carnivores and ate aquatic and terrestrial invertebrates and fish (which became more important as the temperature dropped). Utilization of all available food resources was accomplished by increased diet diversity with increased fish size, reduction in apparent overlap by a different microhabitat occupied by year classes and use of abundant food items (e.g. zooplankton and Chironomidae larvae by age 0 and 1 fish), the opportunistic strategy of switching to new resources as they became available, incorporation of allochthonous material in the diet, and feeding at different times.

The central mudminnow responds to a heterogeneous environment by specializing in habitat and generalizing in time of activity, life history and feeding strategies.

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INTRODUCTION

The central mudminnow, *Umbra limi* (Kirtland) reaches the northern limit of its range in southern Manitoba (Scott and Crossman 1973) and although much is known of its biology in southern populations (Westman 1941; Peckham and Dineen 1957; Jones 1973) little, apart from the work of Keast (Keast and Webb 1966; Keast 1966, 1968, 1970) is known from northern areas of its distribution. In addition, most researchers place little importance on the role of adaptive strategies in *U. limi*'s response to its environment. Gee (1980, 1981), one exception, discussed adaptive strategies in respiratory patterns and hydrostatic functions of the swimbladder of mudminnows.

At the northern end of its range, *U. limi* is found in the headwaters of small, slow-moving streams characterized by seasonal variation of temperature, oxygen, pH, conductivity, water velocity, presence of cover and availability of food. Adaptive strategies for such a variable environment should include the ability to occupy a broad niche in terms of either space, resources utilized or time (Mayr 1963; Selander 1966; Keast 1970, 1977).

The purpose of this study was to describe on a seasonal basis the variation in the environmental factors encountered by *U. limi*, the habitat occupied and preferred, patterns of activity, aspects of growth, reproduction and food consumption by *U. limi*. Such information would provide an understanding of the mudminnow's adaptations to the spatial and temporal pattern of its environment.

METHODS

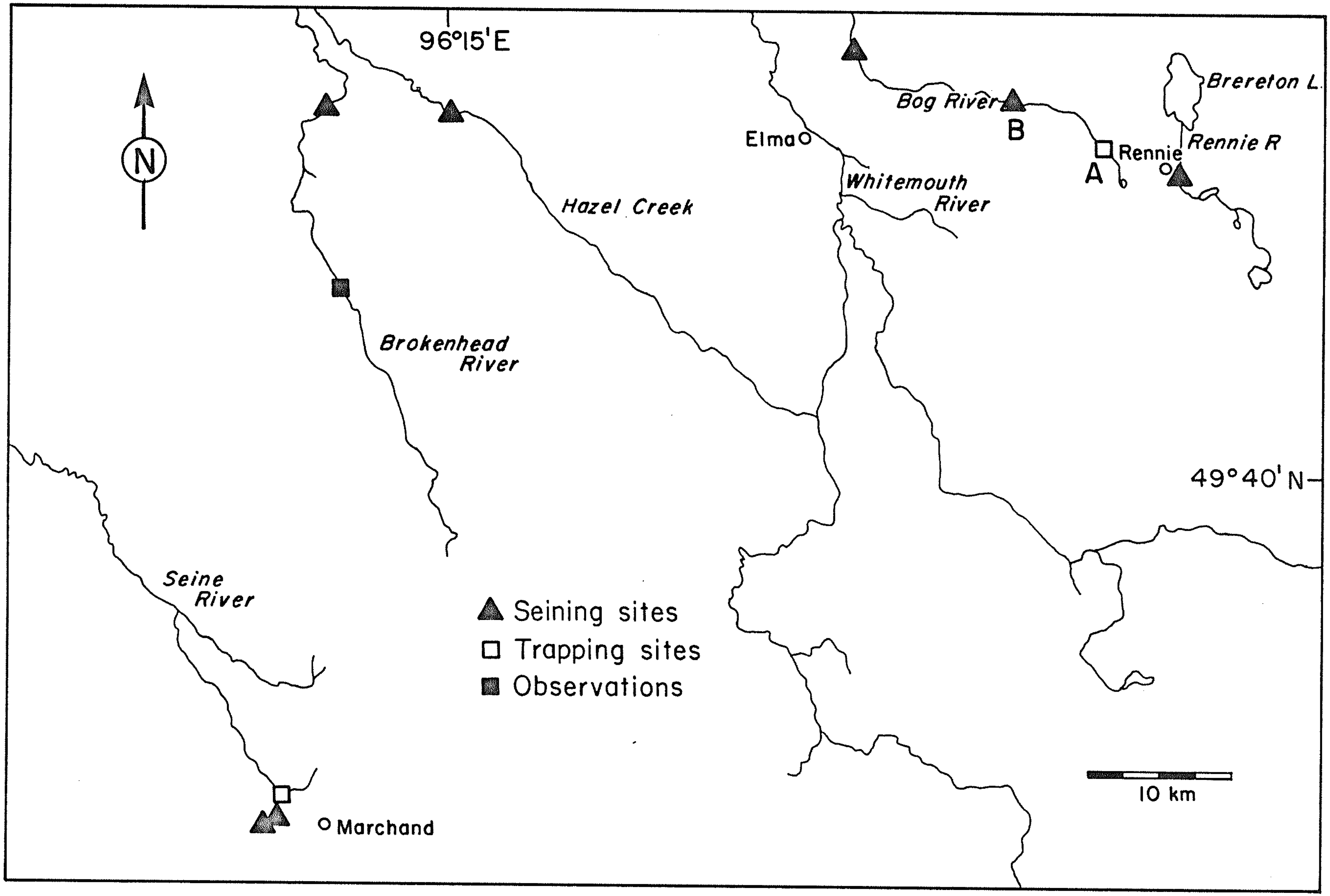
Study Area.

Measurements of environmental variables and collections of fish were made from streams in the Red River, Brokenhead and Winnipeg River drainage systems (Fig. 1) from April 1978 to August 1979. The Seine River was sampled intensively in 1978, the Rennie River in 1979 and the Bog River in both years. Variables measured included; dissolved oxygen (YSI model 54 oxygen meter), salinity, conductivity, temperature (YSI model 33 SCT meter) and pH (measured in the laboratory with a Corning Model 7 pH meter and a Corning triple purpose electrode). Water velocities were measured by timing a floating object over a 1-m interval at each collection site. Stream characteristics such as depth, substrate, percent of the area with cover and the type of cover were described for each collection in addition to the area sampled.

Fish Collections.

A 2.0-m X 1.4-m two-man seine with 2-mm square mesh and a heavily weighted lead line was used in sampling fish to describe distribution and abundance of mudminnows in particular environments and to provide collections of fish for age, reproduction and diet analysis. Collections were categorized into two environments: vegetated margins and pools and unvegetated or sparsely vegetated channels. In sparsely vegetated areas the net was hauled quickly upstream and raised within

Figure 1: River systems and sampling sites where mudminnows were collected in 1978 and 1979 in southern Manitoba.



96°15'E
Brereton L.
Bog River
B
Elma
Rennie
Rennie R
A
Whitemouth
River
Hazel Creek
Brokenhead
River
49°40'N
Seine
River
Seining sites
Trapping sites
Observations
10 km
Marchand

the same habitat. Vegetated areas along the stream edges were encircled by the net. The substrate within the net was disturbed by vigorous kicking, driving fish out of the substrate and vegetation as the net was hauled to shore and lifted. Collections were made through relatively uniform habitat and were repeated where necessary to ensure thorough sampling (removal of all mudminnows within the seined area). An attempt was made to remove at least 10 mudminnows per sample for feeding analysis at each site. Shallow water was sampled using a dip net to collect fry.

All fish collected were initially anaesthetized in <1% phenoxyethanol to prevent regurgitation of stomach contents and then preserved in 10% formalin for up to seven days after which they were transferred to 70% isopropanol to facilitate handling.

A 2.5-cm stretched mesh gill net (7.6m X 2.4m) was used to sample fish in deep water in the Seine River. The number and length of fish were recorded and the stomach contents of _Esox lucius_ Linnaeus were preserved in 10% formalin.

Collections were made under the ice during winter and early spring of 1979 using floating plastic minnow traps (length 43cm; diameter 21cm) set in the Bog River. Attempts to sample in other areas were unsuccessful. Traps were sunk by attaching several lead weights where water level permitted, otherwise they were left to float beneath the ice. Traps were not baited and most were left up to four hours. Fish were preserved as previously described. Trap collections were used for feeding analysis only during winter and early spring when fish could not be collected by seining. Trapping was carried out during the summer to demonstrate seasonal changes in distribution in the Seine and Bog Rivers. Fish were preserved as previously described (early summer 1978) or captures were noted and fish were released.

The seasonal sampling regime was defined as: spring, 1 March to 31 May; early summer, 1 June to 30 June; midsummer, 1 July to 31 July; late summer, 1 August to 31 August; autumn, 1 September to 30 November; winter, 1 December to 28 February.

Attempts were made to observe *U. limi* under field conditions using a face-plate and snorkel. These attempts were generally unsuccessful because of the dense vegetation, the cryptic colouration of the fish and their secretive behaviour.

Habitat Preference.

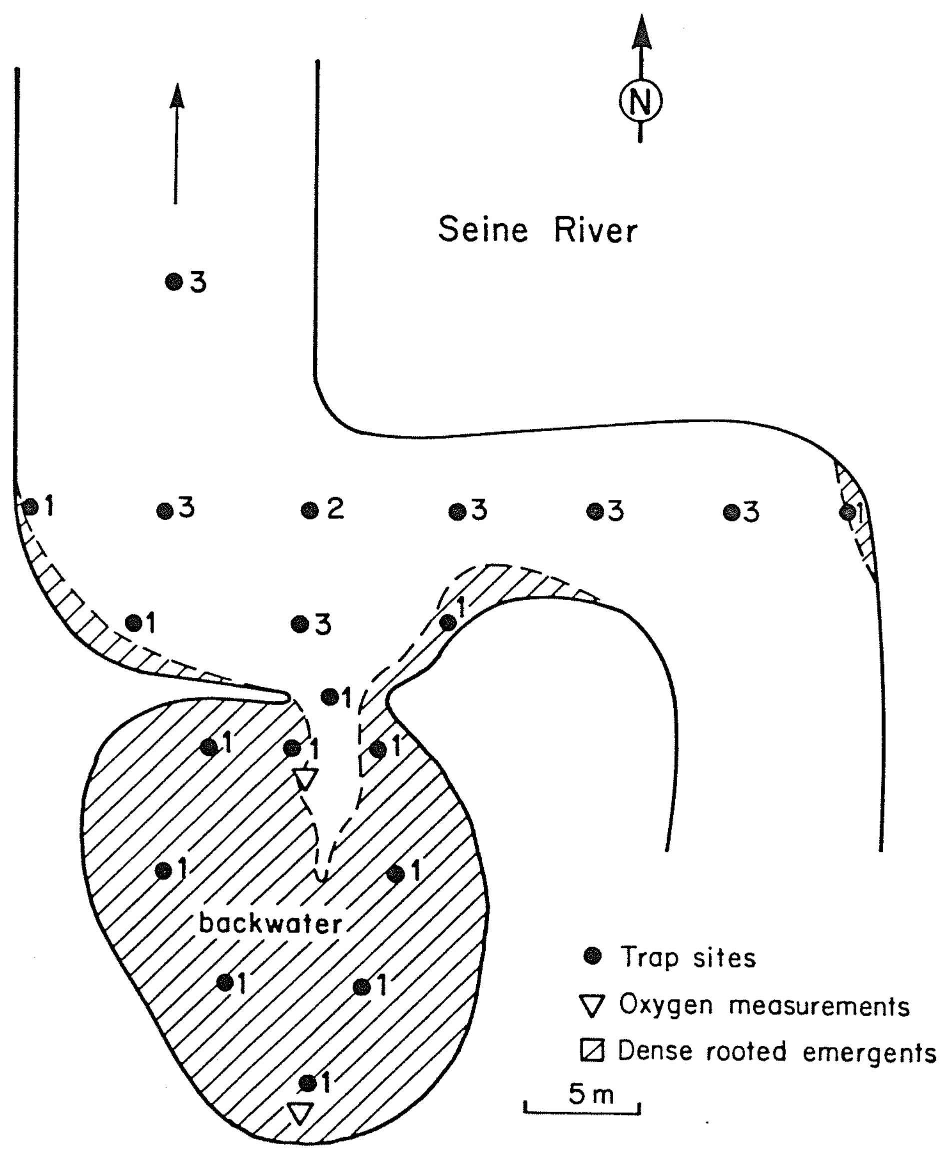
Laboratory experiments were carried out to assess habitat preference by *U. limi*. Fish were collected from the Bog River in late autumn 1979, held for two months prior to observation and tested in the laboratory at $25^{\circ}C$ under a photoperiod of 12L:12D. Observations were carried out in six aquaria (90cm X 45cm X 45cm) each of which was surrounded by black barriers and illuminated by an overhead light source (100-W bulb positioned 0.5m above the water surface). Fish were viewed through a slot (0.5m X 5.0cm) in the front panel. Initial observations were made in aquaria with no vegetation. Then four to six strands of *Myriophyllum* sp., collected from the Bog River, were tied to a lead weight and six to nine of these bundles were spaced evenly in one half of the aquarium as vegetation, the other half was left bare. Fish were introduced into the centre of the aquaria and were observed every 6min for 1h, after a 10-min and 24-h acclimation period as well as after 7-days (for groups of fish). Observations on choice of habitat were made on individual fish (52 fish in total) and fish held in groups of 10 (6 groups of 10 fish). The criterion used to assess choice of habitat for Cole's closed sequential test design (Cole 1962) was 8 of 10 observations within one habitat for the single fish and for groups of 10 fish, 8 of the 10 fish in one area. The number of observations in each area was also tested using a chi-square analysis.

Diurnal Activity.

To obtain information on time of activity, six series of collections were made over 24h at 4-h intervals in 1978 using minnow traps set in areas of the Bog and Seine Rivers. Frequency of capture was used as an index of time of activity.

The Seine River site had a protected backwater with access to the main river (Fig. 2). The river edge, the area near the backwater mouth and the backwater itself supported a mixed aquatic plant community including rooted emergents (e.g. *Typha* sp.) rooted non-emergents (e.g. *Myriophyllum* sp.) and floating plants (e.g. *Lemna* spp.). Vegetation was surveyed and its seasonal progression noted. Traps were set in the river and backwater in early and late summer 1978. For comparison with the Seine River, trapping was carried out during midsummer 1978 in the Bog River which had a much less diverse plant community (4 species were abundant as compared to 16 in the Seine River), confined to a smaller area along the river edge. Fish were either preserved as previously described (early summer 1978) or total lengths were measured and fish were released (mid- and late summer 1978).

Figure 2: A diagram of the trapping site on the Seine River, Manitoba. Points represent trap placement with numbers indicating the number of traps at each site. Direction of flow is marked by an arrow.



N
Seine River
3
1
3
2
3
3
3
1
1
3
1
1
1
1
1
1
1
backwater
1
1
1
1
Trap sites
Oxygen measurements
Dense rooted emergents
5 m

Age, Growth, Condition and Reproduction.

Total length, weight, sex and gonad weight were recorded for all *U. limi* collected and preserved. To age fish, otoliths were dryed and then cleared in benzyl benzoate for 15min to 12h and while still in the clearing solution, were examined through a dissecting microscope with reflected light against a dark background. Age was determined for a subsample (1197 fish) of the fish collected (2836 fish) following the interpretation of Jones and Hynes (1950). Estimated age for the remaining fish was based on these data in conjunction with length frequency information. For this study age change-over was said to occur at the New Year (age 0 fish became age 1 fish on 1 January 1979, etc.). Fry and age 0 fish are interchangeable terms.

Growth for each age class was calculated from mean lengths throughout all seasons. Coefficient of condition for age classes and sexes was calculated using Hile's (1936) index (Appendix 1). Percent sexual development (Appendix 1) was calculated (Luoma and Gee 1980) and sex ratios compared. Eggs were counted from samples of gravid females collected in 1978 and 1979.

Feeding Biology.

Time of feeding activity on both a seasonal and diurnal basis was investigated during several 24-h seining periods. Seasonal changes in feeding were indicated by the change in percent of fish with empty and full and distended stomachs. The change in the ratio of stomach content to body weight ($x10^3$) with time was the measure of diurnal feeding activity.

Diet was studied for age classes 0,1 and 2+ . Data for both years and all streams were combined. Hynes' (1950) point method was used to assess the importance of food items consumed. Each stomach was assessed seperately. Points were allotted to the stomach based on fullness (distended, 30; full, 20; 3/4 full, 15; 1/2 full, 10; 1/4 full, 5; trace, 2). These points were then subdivided amongst the various food items based on the estimated percent volume of each item present in the stomach. In some cases <1 point was assigned to minor quantities of small items. Points were then totalled for each item and presented as the percentage of the total points for each age group. Stomach samples were identified to Family for the Insecta (Borror et al. 1976; Merritt and Cummins 1978; Usinger 1956) and to Order for all others (Borror et al. 1976; Pennak 1953). Overlap in diet was calculated using Morisita's (1959) index as modified by Horn (1966) (Appendix 1). Diversity was calculated using MacArthur's index (1972) (Appendix 1).

RESULTS

Habitat Description.

The headwater regions sampled were generally narrow (<10m wide), shallow (<2m deep) meandering prairie streams with high humus content. Flow rate was irregular, rising sharply during spring flooding (max 60cm/s) and approaching 0 cm/s in mid- to late summer when vegetation impeded the flow (0 to 25 cm/s). In winter no flow was detectable.

Fig. 3 illustrates the progression of vegetational change typical of all sites. Submerged terrestrial vegetation in areas flooded by runoff was the major vegetated habitat observed in the spring. Undercut banks provided cover for fish particularly in areas of the Seine River. During early and midsummer aquatic vegetation started to develop in the main stream and became more dense along the stream margins. In the Bog River *Sparganium* sp. and *Myriophyllum* sp. were the dominant forms of aquatic vegetation. Overhanging terrestrial vegetation provided cover along the river edges. The plant community of the Seine River was more diverse particularly in and around the backwater. By late summer the water level had risen approximately 20 cm, in part due to the construction of a beaver dam near the trapping site (Seine River). Water flow was reduced and some terrestrial vegetation was submerged. The vegetation which had extended into deeper water in midsummer began to

Figure 3: Seasonal progression of vegetation in the Bog River, Manitoba at site A in spring(A), early summer(B), midsummer(C) and late summer (D). Note traps set in midsummer.


A
B
C
D

die back. Submerged portions of Valisnaria sp., Potomageton sp. and Nuphar sp. began to deteriorate while floating leaves formed a dense surface cover. In the backwater there were dense mats of rotting vegetation covered with a thick layer of Lemna spp. This deterioration occurred later in the Bog River.

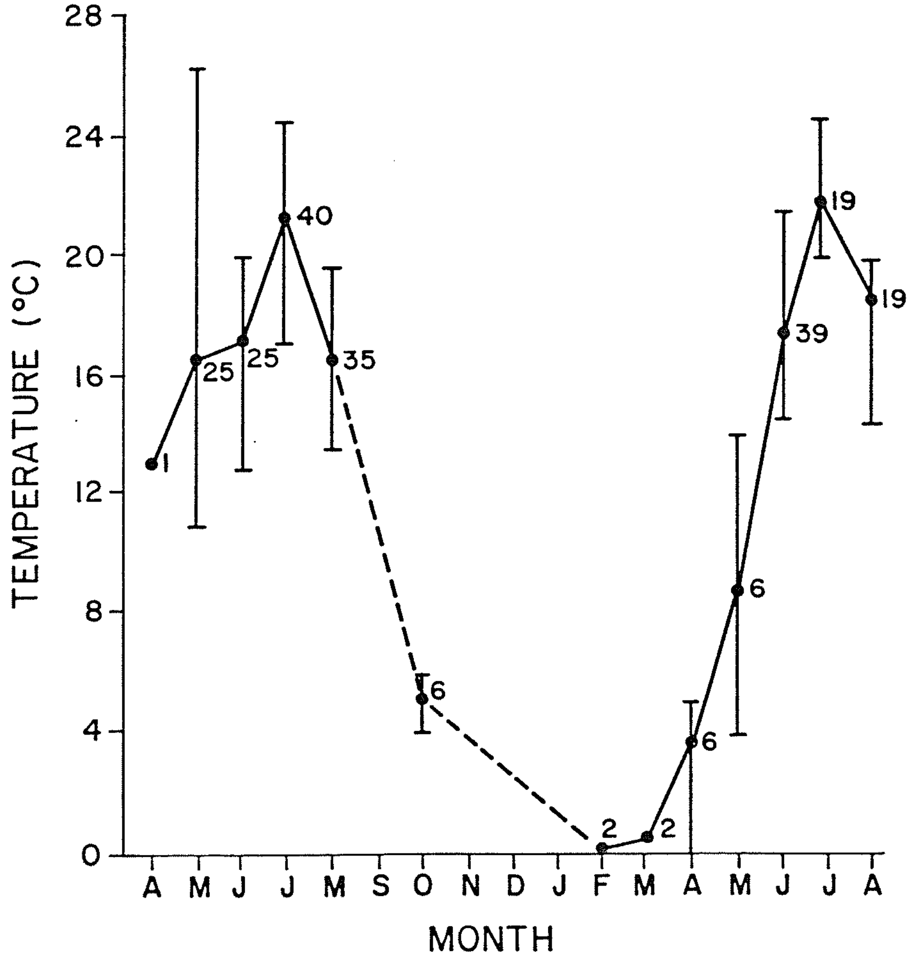
U. limi were subjected to large variations in seasonal temperatures (Fig. 4). Surface water temperature (sub-ice in winter) averaged $<5^{o}C$ for six months of the year and ice-cover extended from late October 1978 until late April 1979 in most of the areas studied.

During the spring when water flow increased the pH in the streams was moderately acidic (6.5), increased only slightly through midsummer (6.7) and by late summer the streams were slightly basic (7.2). The pH increased in the fall to 7.9 and continued to increase under ice-cover to 8.5 by March.

Conductance varied between streams and throughout the seasons. Low values correspond to input from meltwater in the spring and from precipitation in the fall. Values increased under ice-cover in winter and during the summer months. Mean values of conductance (µmos) were calculated for the Seine River (406.4), Brokenhead River (384.0), Hazel Creek (257.1), Rennie River (95.1) and Bog River (90.9) at the study sites.

Seasonal as well as diurnal changes in oxygen concentrations were apparent in habitats occupied by U. limi. During the spring when flow rate was high and vegetative production was low, oxygen levels were high (60 to 93% saturation). During the summer months the effects of

Figure 4: Mean monthly water temperatures ($\pm$ range and number of observations) for all study sites combined. The period of infrequent sampling is indicated by a dashed line.



TEMPERATURE (°C)
28
24
20
16
12
8
4
0
1
25
25
40
35
6
2
2
6
6
39
19
19
A M J J M S O N D J F M A M J J A
MONTH

temperature and vegetation were evident. Areas of dense vegetation had higher concentrations of oxygen during the day (up to 139% O_2 saturation) and lower concentrations at night (down to 2% O_2 saturation). Extremes were greater in vegetated areas than in unvegetated areas and the surface waters were generally higher in oxygen than deeper water. During the autumn percent saturation of oxygen continued to show diurnal fluctuations (from 8% to 95%). Winter levels were low (2.9% to 14.3% O_2 saturation) and in previous years (1976-1977) dropped to the point that winterkill occurred (J.H. Gee personal communication).

Distribution and Abundance.

During spring, flooded stream margins, meltwater channels and ditches became accessible to gravid female and ripe male *U. limi*. Few mudminnows were found in the main channel. They moved up meltwater channels where spawning may have occurred and in some cases were 10m from the river. These areas were inhabited as long as water remained, usually for several weeks. In Hazel Creek however, *U. limi* remained in the drainage ditches along an abandoned highway until late summer when they presumably moved into the main stream.

In early summer mudminnows were captured in the main stream, along its edges and extending out from the backwater mouth in the Seine River. All fish were captured in traps set on the bottom in water from 25 to 110cm and all captures were made in vegetation. More intensive trapping was done in late June. Vegetation had developed further in the main stream and was much more dense than during the initial trapping. Mudminnows were collected from surface and midwater traps only at night. Activity had increased in all areas including the backwater during the night and in general was more extensive than in spring.

Encroachment of vegetation into deeper water became more evident in mid- to late summer with the distribution of mudminnows expanding to cover these areas. In midsummer, trapping was carried out in the Bog River. U. limi were largely found in vegetated areas and along edges with overhanging vegetation.

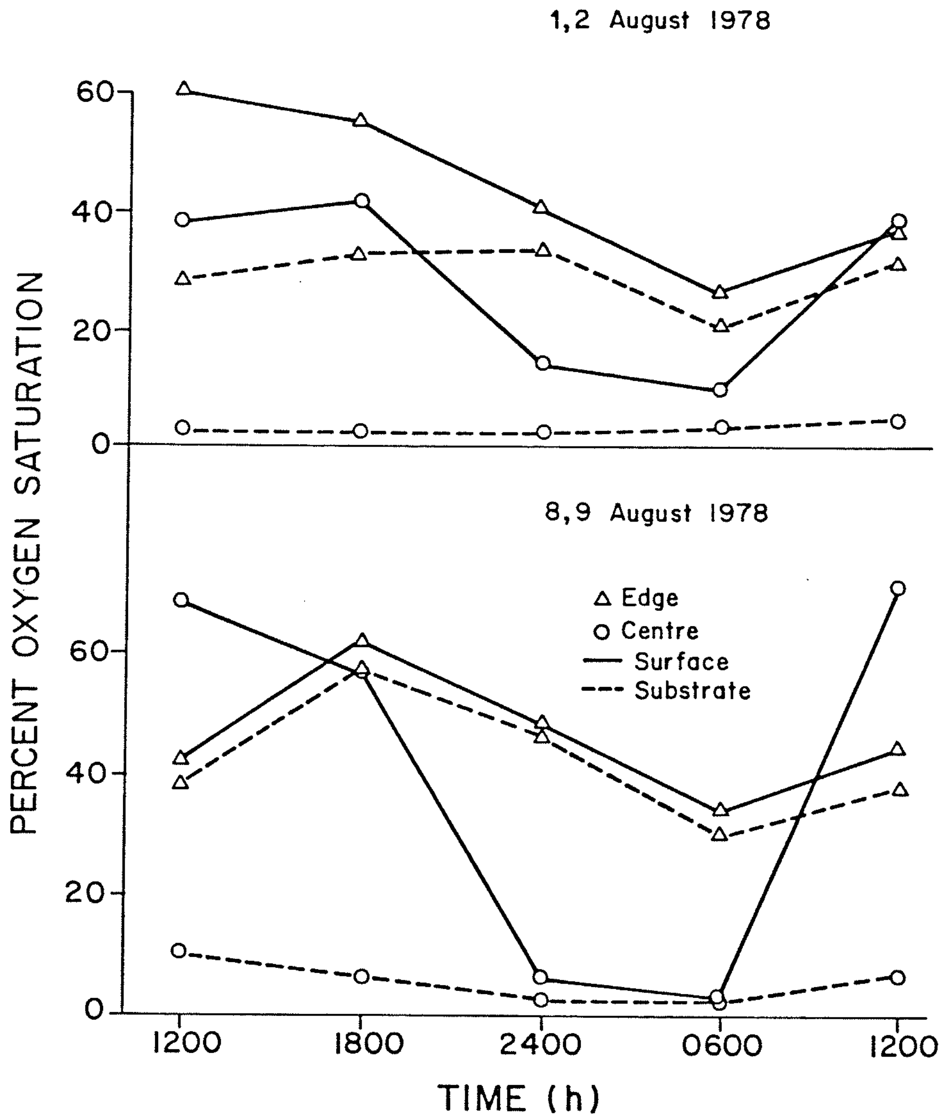
By late summer in the Seine River activity was found only in the backwater area. Oxygen concentrations were recorded over a 24-h period during this trapping session (Fig. 5). In dense vegetation oxygen dropped sharply at dusk and increased at dawn at the surface but remained low throughout at the substrate. Trap mortalities occurred in the backwater during the night when the traps were completely submerged.

A migration of U. limi fry was observed in the Brokenhead River in midsummer 1978. Fry swam along the edges of the river through the dense vegetation with upstream progress impeded by two cement culverts under a road. The fry swam through the culverts where a current of 30cm/s was recorded, directly into the edge vegetation at the upstream end. This was the only case where fry were not found in dense vegetation and when a number of mudminnows were found in moderate current.

During autumn U. limi moved into deeper water and in winter, congregations of fishes were found in isolated pools along the course of the streams. Occasionally U. limi were found frozen in the ice.

Densities of U. limi were calculated throughout the sampling period in the two habitats studied (Table 1). Overall mean densities in vegetated margins and pools was 1.83 fish/m^2 and in unvegetated channels

Figure 5: Diurnal fluctuations in oxygen concentration (% saturation) at the Seine River trap site in August 1978.



1,2 August 1978
8,9 August 1978
Edge
Centre
Surface
Substrate
PERCENT OXYGEN SATURATION
60
40
20
0
1200
1800
2400
0600
1200
TIME (h)

Table 1. Distribution and abundance of mudminnows from all seine net collections made in 1978 and 1979.

Season	Vegetated margins and pools		Unvegetated channels	
	Area sampled (m^2)	Density (no./m^2)	Area sampled (m^2)	Density (no./m^2)
Spring	507.5	0.7	184.0	0.1
Early summer	172.0	2.4	183.0	0.8
Midsummer	185.0	3.0	201.0	0.1
Late summer	262.0	2.3	156.0	0.3
Autumn	160.8	2.6	-	-

was 0.32 fish/m^2 . Mudminnows were always significantly more abundant in vegetated margins and pools ($P<0.005$) than in unvegetated channels.

In the Seine River, fry were collected in dense vegetation in the backwater areas. Occasionally seine hauls contained fry although many may have been overlooked in the debris collected in the nets. A small inflow stream in a backwater of the Bog River yielded several U. limi fry on 4 July 1979. Close to the backwater large U. limi were collected in 10cm of water. Further upstream fry alone were found in water 3cm deep and several were found in 1cm of water. In the main stream fry were found along the edge in dense vegetation.

In general mudminnows were found in shallow water, 98.5% were seined from water less than 1m deep and 67.9% were seined from water less than 0.5 m deep in close association with vegetation.

Habitat Preference.

Observations of mudminnow behaviour were recorded in conjunction with habitat preference experiments. When introduced into a bare aquarium U. limi swam to the bottom and remained motionless, sometimes after a short period of frenzied activity. Smaller fish remained inactive longer than larger ones and fish tested singly remained inactive longer than when in groups. Fish were observed in the lower half of the aquarium for most of the observation period (90% of the observations on single fish and 85% of the observations on groups of 10 fish).

U. limi were always observed more often (> 65%) in vegetation in the laboratory preference experiments (Table 2), however from Cole's sequential analysis, single fish showed a preference for vegetation after a 10-min acclimation, but no preference after 24h. Groups of fish showed a preference for vegetation after 10min, 24h and 7 days.

Table 2. Habitat preference exhibited by mudminnows in laboratory experiments for single fish (A) and groups (B), N is the number of observations, PX and PY the percent of observations in and not in vegetation respectively.

	Acclimation	N	PX	PY	Cole's test	
					Results	trials
A.	10-min	52	72.3	27.7	Vegetation	14
	24-h	48	68.3	31.7	No preference	44
B.	10-min	60	69.5	30.5	Vegetation	25
	24-h	60	74.0	26.0	Vegetation	19
	7-d	60	72.0	28.0	Vegetation	13

Diurnal Activity.

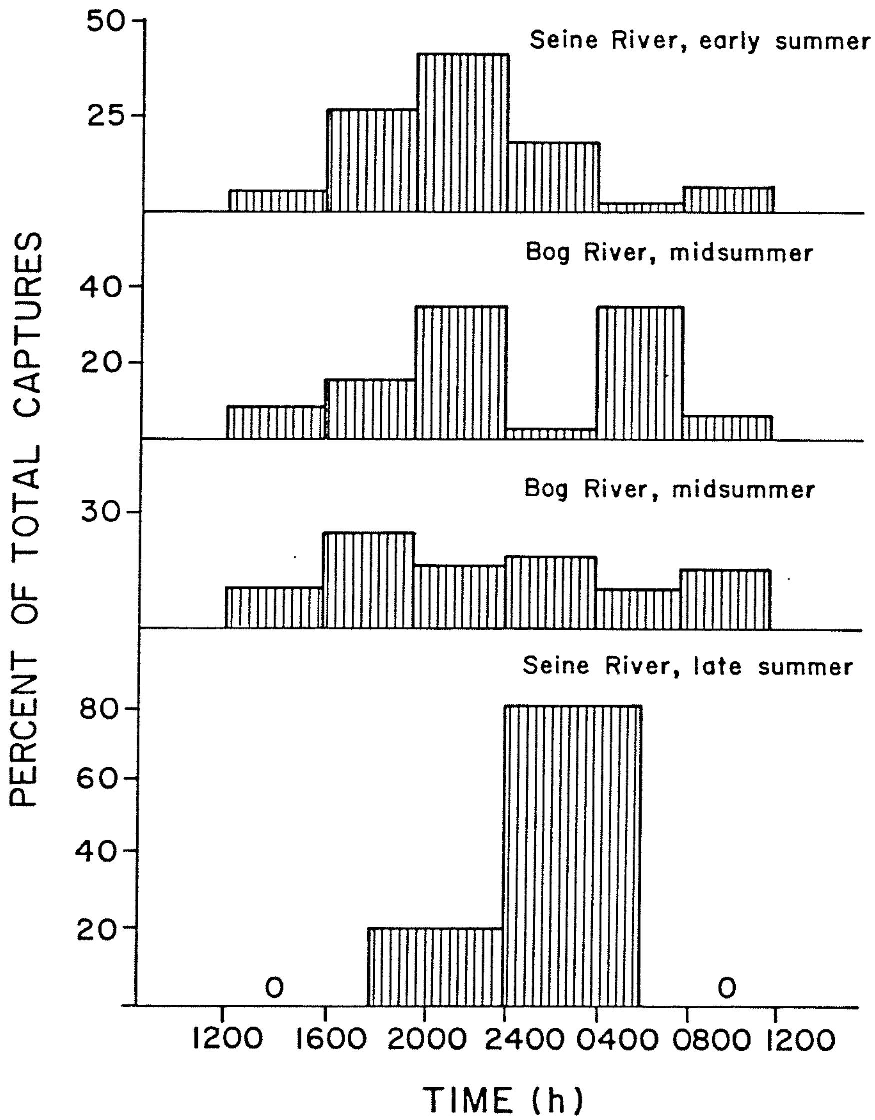
During early summer *U. limi* showed greatest activity from evening through to early morning (Fig. 6) regardless of moon phase. Two different activity periods were observed during midsummer on the Bog River. Crepuscular activity was observed during the new moon (Fig. 6) but a more uniform activity pattern was observed during the full moon (Fig. 6). In the Seine River in late summer *U. limi* also showed high levels of activity from 2400h to 0600h (Fig. 6). In winter activity was low but by March activity had increased as indicated by greater capture success in traps.

Age, Growth, Condition and Reproduction.

Length-frequency histograms were constructed for fish from each of the four streams (Fig. 7). Hazel Creek fish showed a bimodal frequency distribution, an indication of a missing year class (age 1 fish were scarce during 1978). The Seine, Rennie and Bog River fish had length frequency distributions which differed from Hazel Creek but were similar to each other.

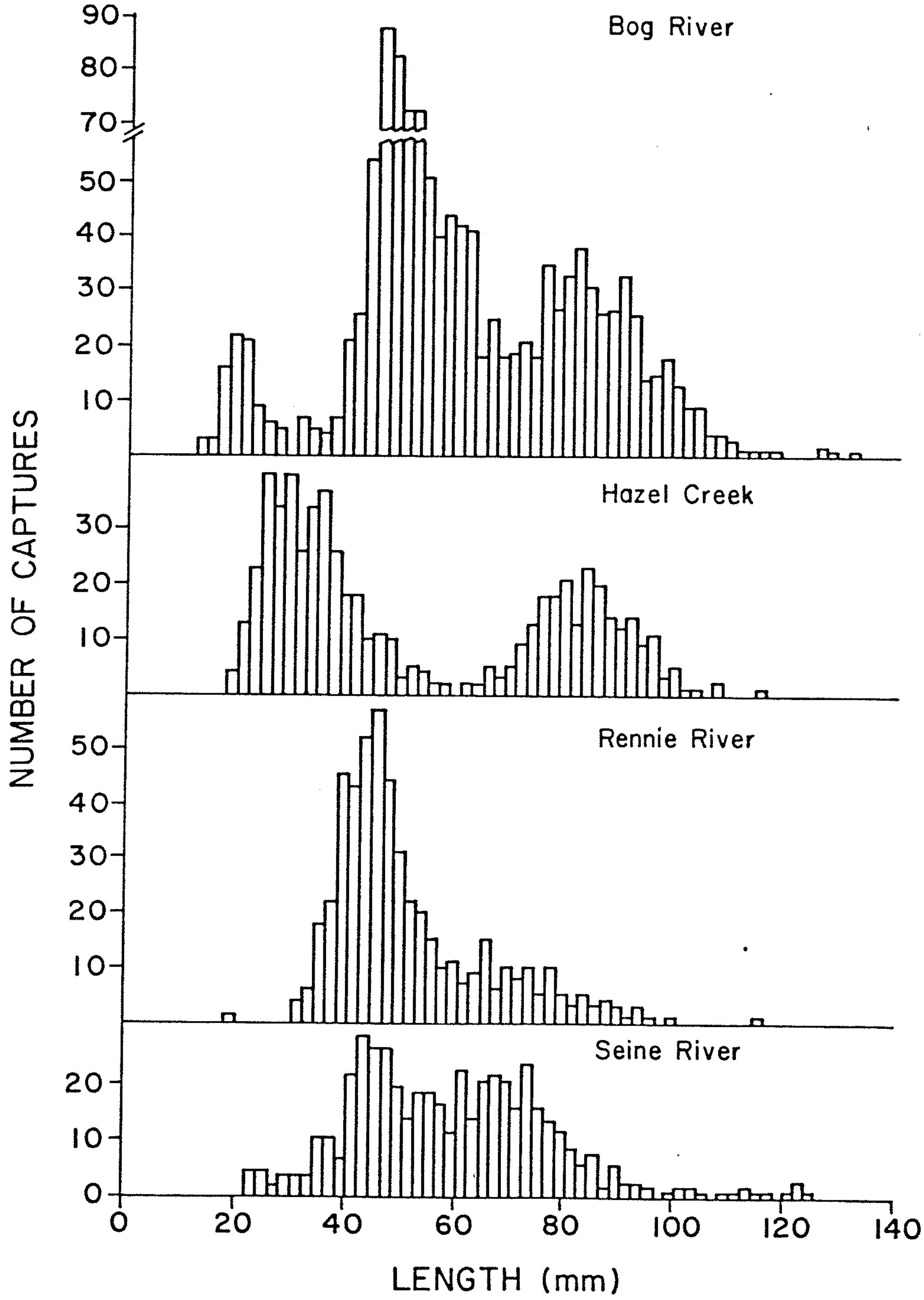
There was little difference in mean lengths between male and female mudminnows of age 0 and 1 (Table 3). In the Bog River and Hazel Creek, age 2 females were larger than age 2 males. In all four streams females were larger than males in the age 3 group. Small sample sizes and high variability in length of 4+ fish mask any size differences between sexes.

Figure 6: Diurnal fluctuations in activity as measured by capture success (percent of total captures) from minnow traps.



Seine River, early summer
Bog River, midsummer
Bog River, midsummer
Seine River, late summer
PERCENT OF TOTAL CAPTURES
50
25
40
20
30
80
60
40
20
0
0
1200
1600
2000
2400
0400
0800
1200
TIME (h)

Figure 7: Length-frequency histograms for each stream from combined data for 1978 and 1979.



Bog River
Hazel Creek
Rennie River
Seine River
NUMBER OF CAPTURES
LENGTH (mm)
90
80
70
50
40
30
20
10
0
20
40
60
80
100
120
140

Table 3. Mean lengths (mm) of mudminnows calculated for each stream. N is the number of observations, standard deviation (S.D.), in parenthesis, follows the mean.

Age	Sex	Bog River			Hazel Creek			Rennie River			Seine River		
		Mean (mm)	S.D.	N	Mean (mm)	S.D.	N	Mean (mm)	S.D.	N	Mean (mm)	S.D.	N
0	♀	23.3	(5.9)	36	31.2	(6.3)	147	-	-	0	41.2	(7.6)	73
	♂	23.3	(5.0)	36	30.5	(5.6)	170	24.4	(14.4)	2	41.1	(8.2)	76
1	♀	50.6	(7.5)	349	47.2	(4.5)	20	45.2	(7.0)	203	58.7	(9.4)	109
	♂	50.1	(7.4)	304	47.8	(4.9)	22	44.4	(6.0)	191	58.8	(9.8)	108
2	♀	78.9*	(12.5)	165	80.8*	(9.1)	31	64.6	(6.0)	30	75.8	(6.0)	65
	♂	75.5*	(8.6)	141	75.7*	(6.0)	78	65.7	(7.2)	28	76.3	(6.9)	35
3	♀	92.6*	(10.3)	130	89.0*	(7.0)	61	79.2	(6.9)	23	97.9	(10.7)	16
	♂	83.3*	(6.4)	35	84.7*	(8.0)	49	76.6	(6.6)	14	90.7	(8.1)	8
4	♀	93.1	(7.1)	4	93.6	(1.8)	2	87.7	(10.2)	15	120.2	(5.1)	6
	♂	100.4	(10.7)	4	91.7	(1.0)	1	76.1	(4.8)	3	108.3	(5.5)	3

* Significant difference between male and female lengths (P<0.05) as determined by a F-test.

Time of sampling may have resulted in some of the observed differences between streams. For example, in Hazel Creek and the Seine River the majority of age 0 fish were collected in the fall after the growing season whereas Bog River age 0 fish were collected throughout the summer growing season and were consequently smaller.

Growth curves for mudminnows in each stream have similar patterns (Fig. 8). Growth was greatest in the age 0 and 1 fish while in older fish any growth was obscured by variation in length. Growth continued throughout the year including in the cold water period ($< 5^{o}C$), from late fall to early spring.

The coefficient of condition was highly variable throughout the sampling period (Table 4). There was a tendency for females to have slightly lower values (in 15 of 19 cases) than males except in Hazel Creek. Coefficient of condition was greatest in the Seine and Bog Rivers followed by the Rennie River and then Hazel Creek mudminnows.

The ratio of males to females was greatest in age 0 fish for all streams combined and was lowest in 3+ fish (Table 5). Differences between streams were evident. In Hazel Creek fish, age 2 males outnumbered females 2.5 to 1. The highest ratio of females to males (3.5:1) was exhibited by 3+ fish in the Bog River.

The Bog River collections were chosen as representative of sexual development of U. limi in southern Manitoba from 1978 and 1979 (Fig. 9).

Figure 8: Growth curves for each stream with vertical bars representing standard deviations.

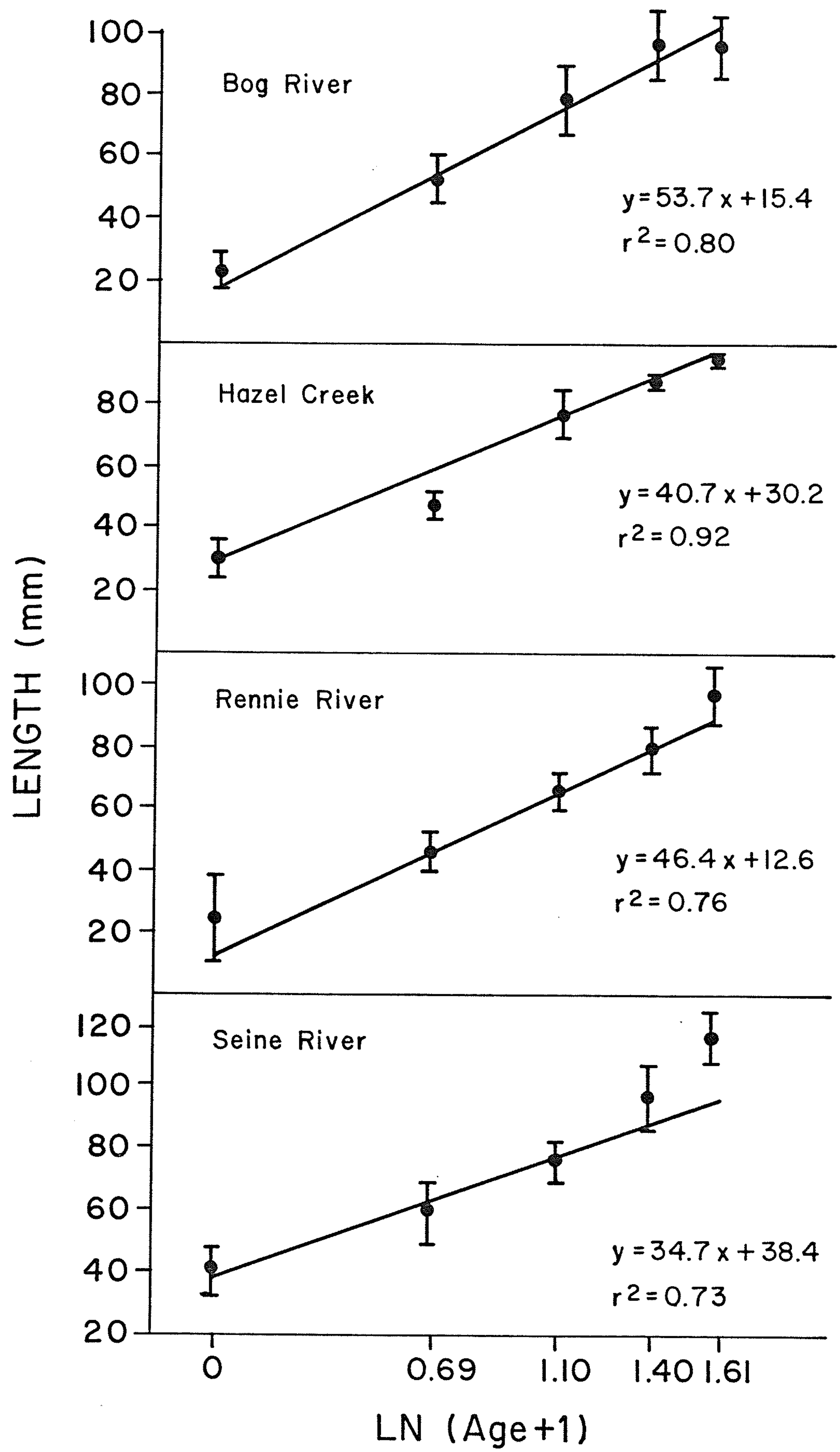

Bog River
y=53.7x+15.4
r2=0.80
Hazel Creek
y=40.7x+30.2
r2=0.92
Rennie River
y=46.4x+12.6
r2=0.76
Seine River
y=34.7x+38.4
r2=0.73
LENGTH (mm)
LN (Age+1)
0
0.69
1.10
1.40
1.61
20
40
60
80
100
120

Table 4. Mean coefficient of condition (Hile 1936) for N observations. Standard deviation (S.D.), in parenthesis, follows the mean.

Age	Sex	Bog River		Hazel Creek		Rennie River		Seine River	
		Mean S.D.	N	Mean S.D.	N	Mean S.D.	N	Mean S.D.	N
0	♀	1.07(0.13)	36	0.86(0.15)	147	- -	0	0.90(0.12)	73
	♂	1.05(0.13)	36	0.85(0.17)	170	1.19(0.33)	2	0.95(0.13)	76
1	♀	0.88(0.14)	349	0.95(0.09)	20	0.89(0.11)	203	0.96(0.09)	109
	♂	0.92(0.15)	309	0.92(0.11)	22	0.91(0.12)	191	0.93(0.10)	108
2	♀	0.93(0.15)	165	0.91(0.08)	31	0.90(0.12)	30	1.00(0.10)	65
	♂	0.95(0.17)	141	0.92(0.11)	78	0.88(0.16)	28	1.07(0.09)	35
3	♀	0.98(0.19)	130	0.95(0.17)	61	0.92(0.12)	23	1.01(0.10)	16
	♂	0.99(0.15)	35	0.94(0.11)	49	0.98(0.14)	14	1.13(0.08)	8
4	♀	0.95(0.15)	4	0.99(0.03)	2	0.92(0.10)	15	1.13(0.04)	6
	♂	1.11(0.12)	4	1.36(-)	1	1.02(0.18)	3	1.24(0.09)	3
Combined*		0.94(0.17)	1239	0.89(0.15)	581	0.90(0.12)	511	0.98(0.12)	501

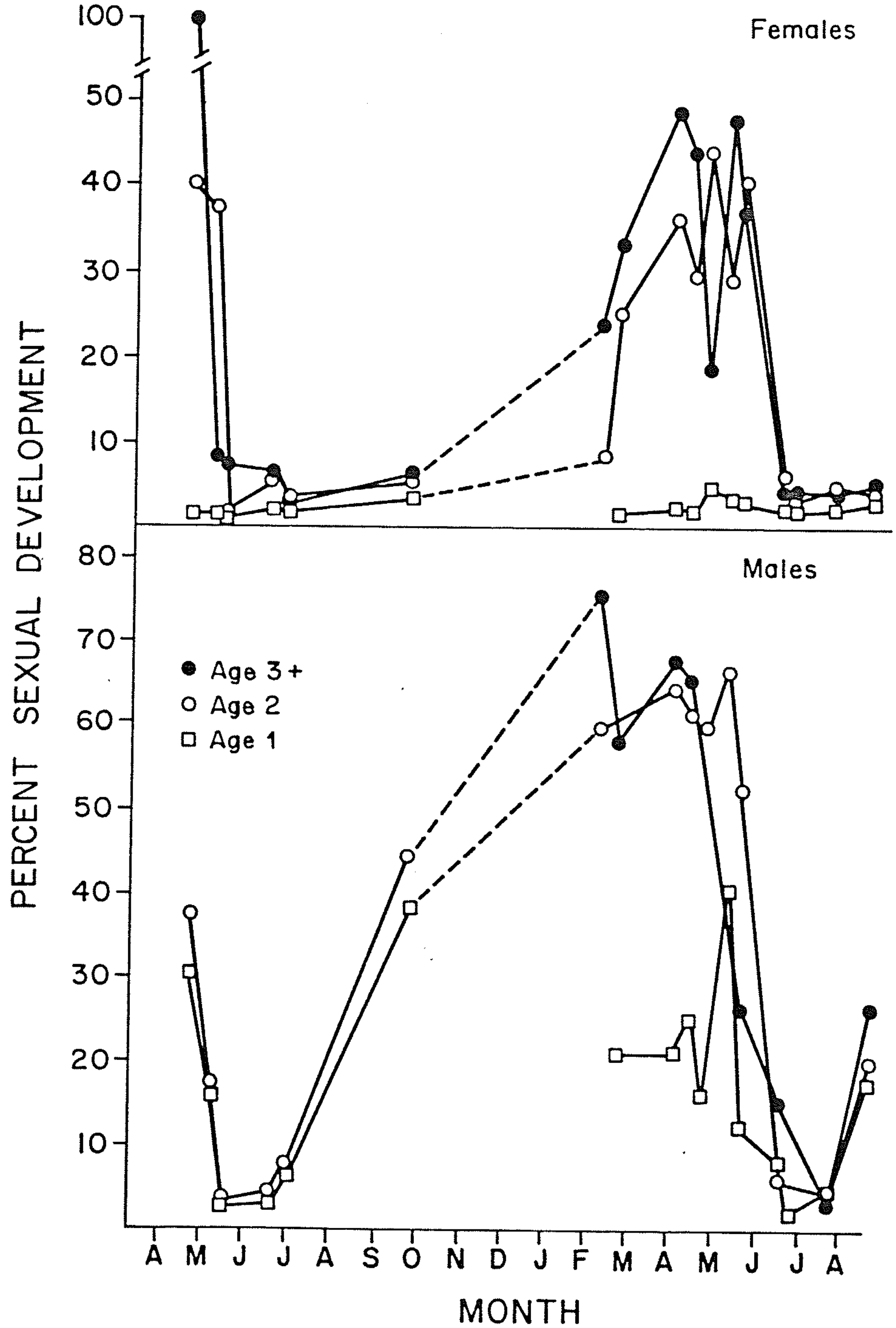
* Note combined data may include individuals not included in data seperated by sex.

Table 5. Sex ratios, the number of females captured for every 100 males, in 1978 and 1979, where N is the total number of fish.

Age	Bog River		Hazel Creek		Rennie River		Seine River		Combined	
	♀	N	♀	N	♀	N	♀	N	♀	N
0	100	72	83	318	-	2	100	147	91	539
1	110	651	91	42	110	394	100	217	110	1304
2	120	306	40 *	108	110	59	190 *	100	100	573
3+	350 *	176	120	97	190 *	53	190	32	220 *	358

* Significant difference from a random distribution ($P \leq 0.05$) as determined by a chi-square test.

Figure 9: Percent sexual development of Bog River mudminnows during 1978 and 1979. Each point represents the mean value calculated from fish collected and preserved on that day.



Females
Males
Age 3+
Age 2
Age 1
PERCENT SEXUAL DEVELOPMENT
MONTH
A M J J A S O N D J F M A M J J A

The overall trends were similar between all sites studied although values of percent sexual development varied slightly.

Spawning occurred in the first three weeks of May in 1978. Culmination of spawning occurred by the last week in June 1979. No gravid females were found later than 26 May 1978 from any sampling site. In 1979 the first spent female was found on 5 June. Some females were found in midsummer 1979 with eggs still visible but much reduced in size within the gonads. Age 1 females were not included in the breeding population, however some males of this age appear to be capable of spawning. Young of the year first appeared on 7 June 1978 in the Seine River and on 10 June 1979 in the Bog River.

Gonadal development in males reached an intermediate stage by late summer and autumn indicating that only partial development occurred during the winter months (Fig. 9). Females however, showed little development over the summer and fall periods and much greater development during winter.

There is a positive relationship between the number of eggs (total for both ovaries) and the length of the fish (Fig. 10). Fewer gravid females were captured in 1978 (mean no. eggs 695.9 S.D.= 383.7) than in 1979 (mean no. eggs 999.3 S.D.= 504.4).

Feeding Biology.

The percentage of empty stomachs was highest in winter (33%) and remained at a consistently low level (5-11%) from early summer to fall (Fig. 11). The percentage of full and distended stomachs (Fig. 11) was high in winter and early summer and low in spring.

Figure 10: The relationship between number of eggs and length (mm) of gravid female mudminnows.

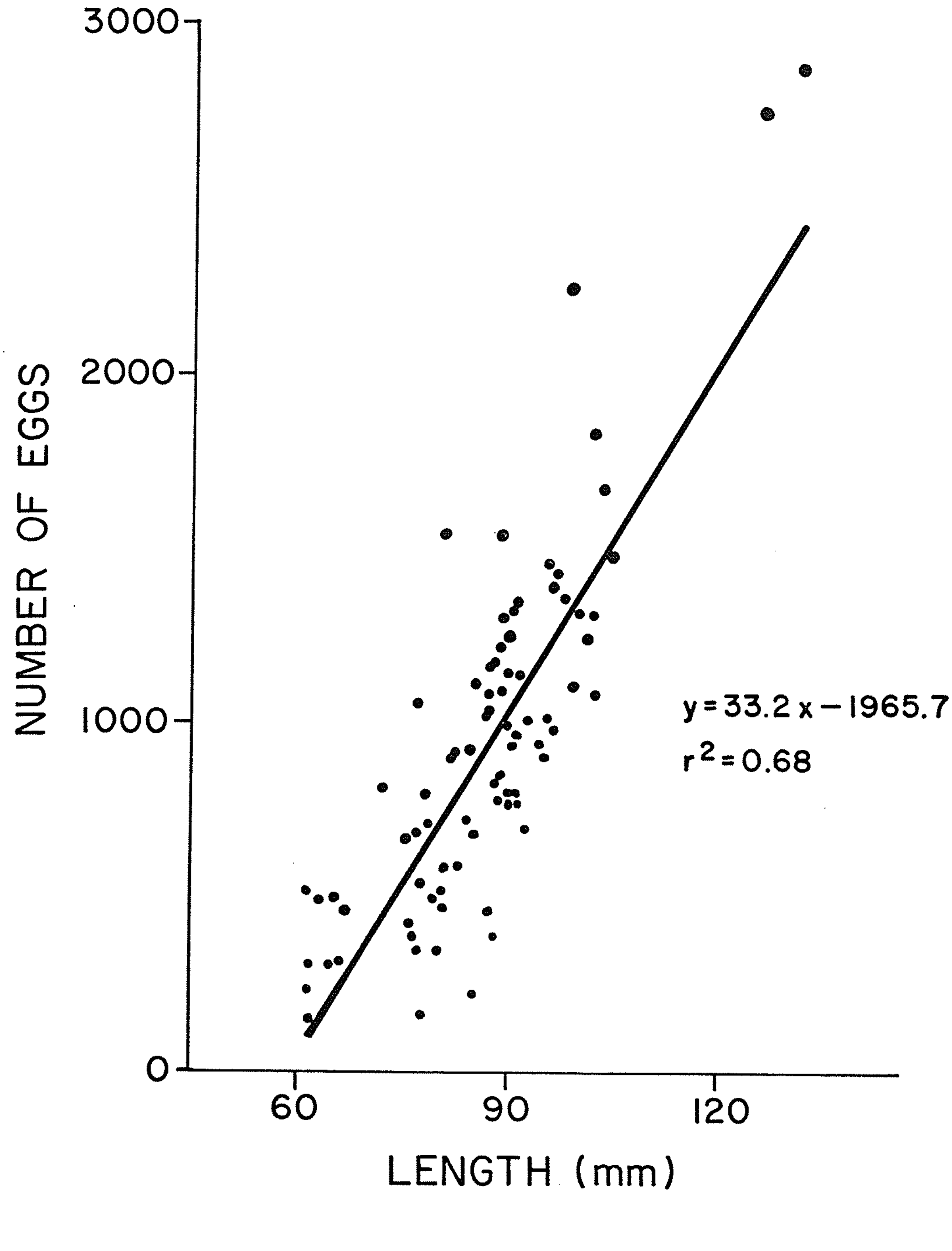
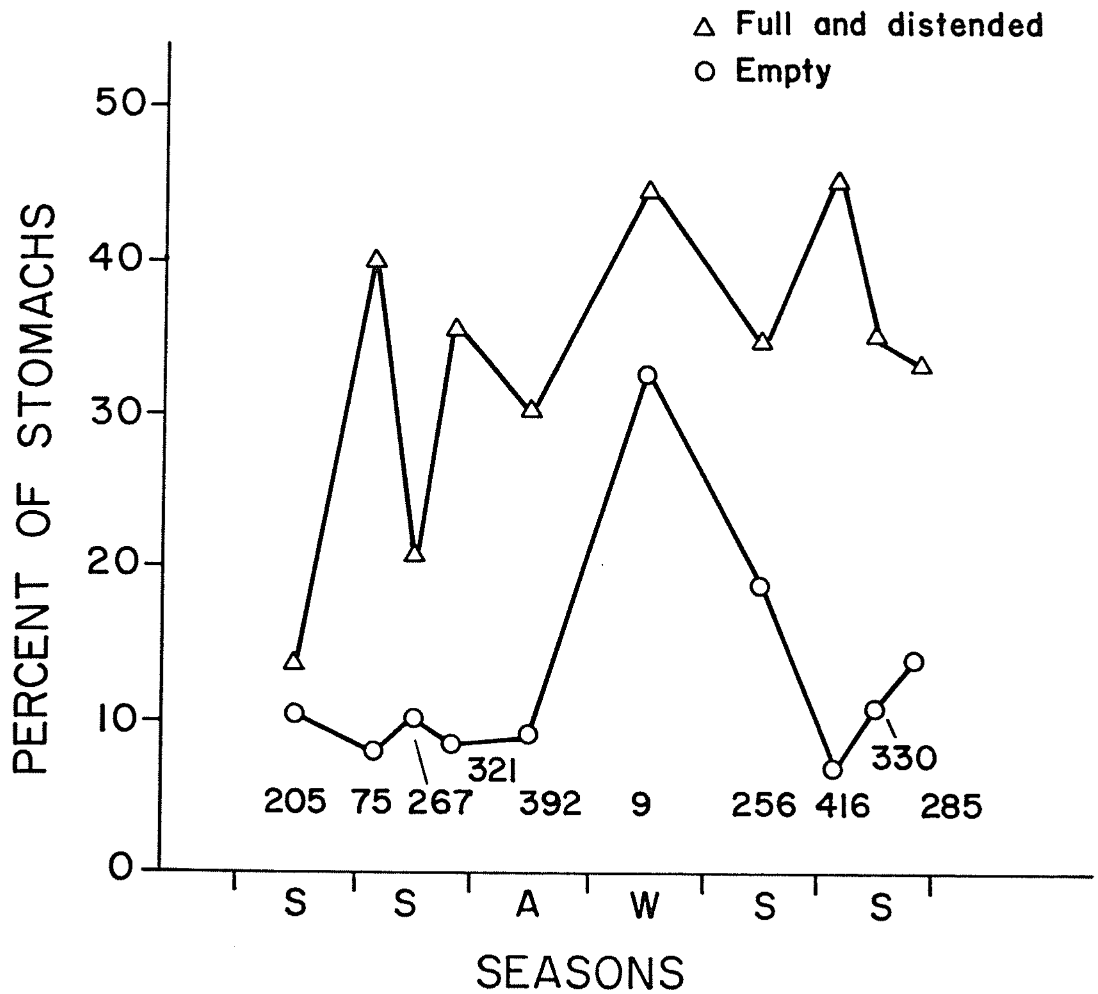

3000
2000
1000
0
NUMBER OF EGGS
60
90
120
LENGTH (mm)
y = 33.2 x − 1965.7
r² = 0.68

Figure 11: Seasonal feeding patterns as measured by the percent of empty and full and distended stomachs over the study period. Sample sizes are recorded for each period.



Full and distended
Empty
PERCENT OF STOMACHS
0
10
20
30
40
50
205
75
267
321
392
9
256
416
330
285
S
S
A
W
S
S
SEASONS

Further analysis of winter samples (Chilton *et al.* in prep.) from this area corroborate the level of winter feeding.

Variation in time of feeding occurred (Fig. 12). In midsummer mudminnows fed at dawn and dusk in the Bog River and at midday and late evening in the Rennie River (Fig. 12). In early summer 1979 Bog River mudminnows fed at dawn and dusk at site B, while at site A they fed prior to sunrise and then showed a much larger feeding peak in the morning (Fig. 12). On the same day Rennie River mudminnows exhibited a continuous feeding pattern over 24h. Mudminnows in midsummer 1979 showed dusk and late morning peaks in feeding (Fig. 12). Site A had higher levels of feeding throughout the morning. Rennie River mudminnows decreased feeding at night. In late summer 1979 (Fig. 12) lowest feeding occurred near midnight in Rennie River and site B on the Bog River. At site A, the lowest period of feeding was later. In autumn 1978 levels of feeding were compared for three streams at night and during the day (Table 6). Seine River *U. limi* had the highest level of feeding followed by Hazel Creek and Bog River fish. Seine River and Hazel Creek fish had higher levels of feeding during the day than at night whereas in the Bog River there was little diurnal variation.

The diet of mudminnows in this study varied considerably in content over the seasons (Table 7). They consumed crustaceans, aquatic and terrestrial insects and fish. Occasionally plant material (seeds) was found in the stomach contents. Material such as sticks and pebbles was labelled as debris and appeared to be ingested incidentally. Minor food items were combined in a single category (other).

Figure 12: Feeding periodicity as measured by the ratio of stomach content weight to body weight ($x10^3$) over time.

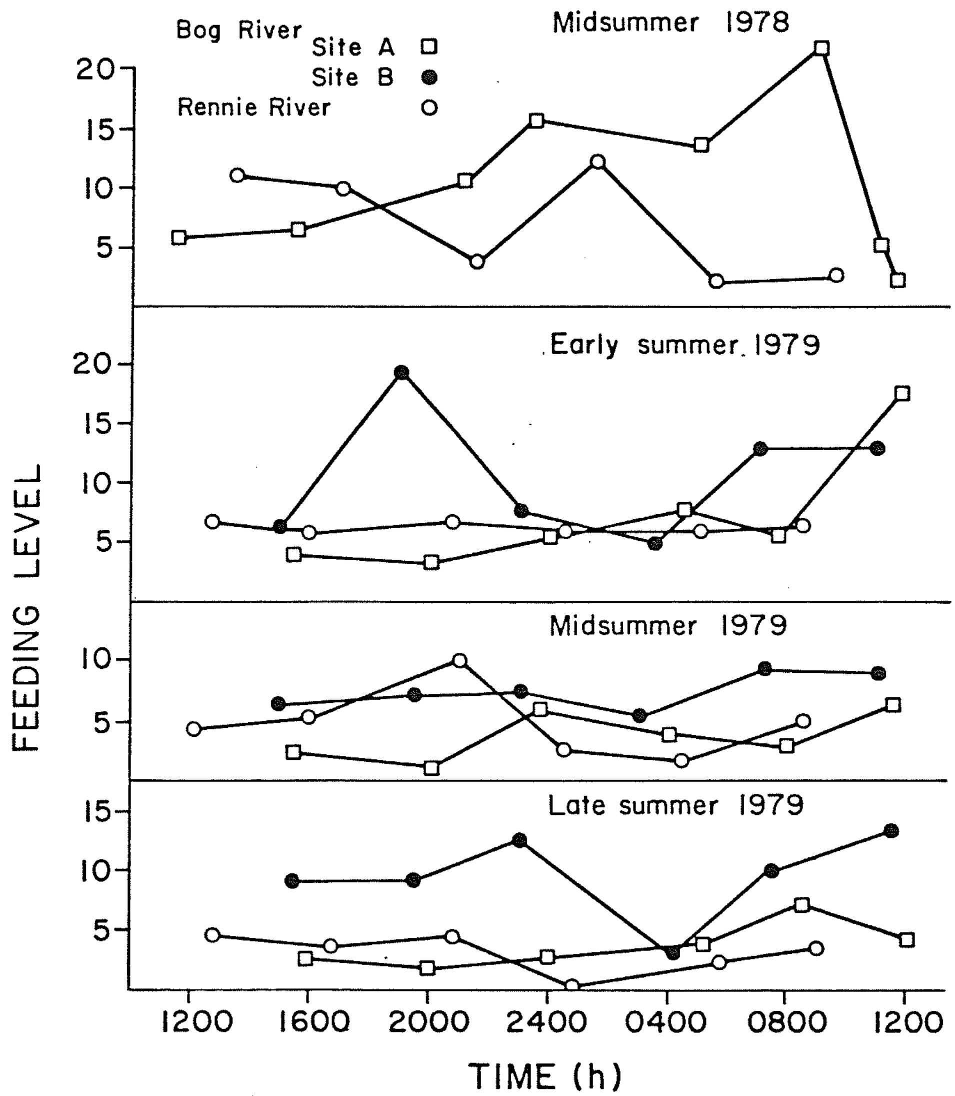

Bog River
Site A
Site B
Rennie River
Midsummer 1978
Early summer 1979
Midsummer 1979
Late summer 1979
FEEDING LEVEL
20
15
10
5
1200
1600
2000
2400
0400
0800
1200
TIME (h)

Table 6. Feeding activity, the levels and diurnal changes found in autumn 1978 during a full moon. The mean ratio of stomach content weight to body weight ($x10^3$) was the measure of feeding.

River	Day	Night
Bog River	3.7	3.0
Hazel Creek	8.7	4.9
Seine River	19.3	17.0

Table 7. Seasonal changes in diet based on importance of items calculated from combined data.

Season	Winter		Spring		Early summer			Midsummer			Late summer			Autumn		
Age Group	1	2+	1	2+	0	1	2+	0	1	2+	0	1	2+	0	1	2+
No. Fish	1	8	317	146	32	326	136	71	362	164	296	187	93	173	48	201
% Empty	0	37.5	15.5	13.7	6.2	7.1	8.1	9.9	6.1	18.4	6.8	11.2	17.2	2.9	0	15.9
Food Items																
Aquatic																
Hirudinea				1.9			18.2			7.4		1.2			2.3	1.5
Mollusca			2.7	5.2	1.4	5.2	7.7	1.3	6.2	7.3	2.5	7.0	17.0	2.2	1.1	23.0
Cladocera			1.0		3.8	7.8	2.6	10.2	4.6		21.2	5.9	4.0	19.4	21.2	5.1
Ostracoda			17.1	6.0	16.6	19.1	4.3	10.4	7.2	1.5	15.1	9.3	1.3	10.6	7.1	10.7
Copepoda			11.9	1.4	7.5	11.7	2.6	13.6	3.6		5.1	1.0		7.6	6.5	1.0
Amphipoda			3.8	7.1	8.0	8.5	1.3	9.9	1.1	1.3	8.7	1.1	3.1	28.0	3.7	8.9
Ephemeroptera	100		1.0	6.0		5.4	2.4	1.9	1.3	1.0	1.4	1.9	4.6	6.7	14.5	
Odonata			1.8	7.8		4.7	1.7	5.4	2.3	5.3	5.5	4.2	3.8	6.7	13.0	12.3
Corixidae				1.2		1.2			1.1	6.5		4.0	3.9			9.6
Coleoptera			3.6	8.3	17.8	5.4	6.6	2.6	9.0	6.3	4.6	15.5	15.7	3.5	13.0	8.5
Trichoptera			5.3	2.6		2.5	24.5	3.5	7.9	6.4	1.8	5.5	7.4		1.1	4.0
Chironomidae			11.9	6.6	35.1	15.4	4.3	29.3	28.3	5.9	25.5	25.2	13.9	9.8	8.5	3.9
Diptera(other)			10.2	11.5	4.1	4.9	2.1	2.2	5.0	5.0	2.2	1.5		2.7	1.2	
Minor items		2.1	7.2		2.9		2.4		3.7	1.0	1.0	2.3				
Fish		97.9		10.3			5.6		1.1	5.7			3.2		1.0	3.0
Terrestrial																
Combined			18.1	15.8	1.3	1.0	8.3	3.0	12.4	31.1	1.2	9.4	9.4		2.1	1.1
Miscellaneous																
Plant material			1.8					1.0		1.6						2.1
Debris						1.3	1.3		1.0	1.5			6.1		1.5	1.4
Unidentifiable				2.1			2.1	3.6	1.4	1.7	2.3	1.7	1.0			
Other			2.6	6.2	1.5	3.7	0.8	2.1	2.8	3.5	1.9	3.3	5.6	2.8	2.3	3.9

Terrestrial invertebrates were found in the diet of mudminnows from spring through to autumn. Oligochaeta were the most important terrestrial items in spring, early and midsummer and were ingested by 1 and 2+ fish. Aranae were found in 1 and 2+ fish in spring and midsummer. Homoptera, principally aphids and leaf hoppers were consumed in mid- and late summer by 1 and 2+ *U. limi*. Terrestrial Coleoptera were eaten in autumn by age 1 fish. Lepidoptera larvae were eaten in spring and midsummer mostly by 2+ fish. Diptera (larvae, pupae and adults) were eaten by 0 and 1 fish from spring through late summer. During the summer months age 1 and 2+ mudminnows ate Hymenoptera (Formicidae and small wasps). Chilopoda were found in the diet of 2+ fish in the spring.

Aquatic invetebrates were generally the most important diet items for *U. limi* (Table 7). Nematodes were found only in age 2+ fish in early summer and at that time only contributed to 1% of the diet. Hirudinea were important items for 2+ fish (up to 18.2% in early summer) in spring, early and midsummer. They also appeared in late summer and autumn in age 1 fish. Mollusca were found in all age groups in spring through autumn. Gastropoda were most important although Pelecypoda were eaten as well. Cladocerans were important in the diet of age 0 fish, less so in age 1 fish and were of even less importance in 2+ fish. Ostracoda were eaten by all age classes. Copepoda were usually consumed by age 0 and 1 fish. Amphipoda were ingested by all ages in spring through autumn. Hydracarina were found in stomachs of 1 and 2+ fish from spring to late summer. Collembola were consumed by age 1 fish only in the spring. Ephemeroptera were eaten by all ages. Age 1 fish ate the naiads in all seasons, 2+ fish in all but autumn and winter and age 0 fed on them only in midsummer, late summer and autumn. The majority of Ephemeroptera were Baetoidea naiads although occasionally Ephemeridae and Heptageniidae naiads were found. Both Anisoptera and Zygoptera naiads were consumed by _U. limi_. Age 0 fish started feeding on them in midsummer, 1 and 2+ fish started in the spring. Both Ephemeroptera and Odonata naiads were occasionally found as newly-hatched individuals within a mass of eggs. Corixidae, Notonectidae, Belostomatidae and Saldidae nymphs and adults were eaten, although only Corixidae were common. They occurred in 2+ fish from spring to autumn and in age 1 fish from midsummer to autumn. Neuroptera naiads were ingested occasionally. Coleoptera were consumed by 2+ fish from spring to autumn, and age 0 fish from early summer to autumn. Haliplidae, Dytiscidae, Hydrophilidae larvae and adults, Noteridae, Hydraenidae adults, Gyrinidae, Sphaeridae and Helodidae larvae were identified in the stomach contents. Dytiscidae and Haliplidae were the most important Coleoptera consumed by _U. limi_. Trichoptera larvae were important items in the diet of 1 and 2+ fish from spring to autumn. Age 0 fish consumed Trichoptera in mid- and late summer. Trichoptera cases were often found in the stomach contents. Hydroptilidae larvae were consumed during the summer. Diptera larvae and pupae were important in the diet of all ages. Tipulidae, Pyschodidae, Dixidae, Chaoboridae, Culicidae, Ceratopogonidae, Simuliidae, Stratiomyidae, Tabanidae, Empididae, Dolichopodidae, Syrphidae, Sciomyzidae and Ephydridae were the families combined under the category Diptera. Chironomidae, the most important family of dipterans in the diet (particularly of age 0 and 1 fish) were most important in the summer months.

Fishes were important components in the diet of 2+ *U. limi*. Smaller fish (age 1) were collected with fry and eggs in their stomachs. The larger mudminnows ate *Culaea inconstans* (Kirtland), cyprinids or small *U. limi* (occasionally). Several species of cyprinids were collected with *U. limi* and may have been included in the diet (*Chrosomus eos* Cope, *C. neogaeus* (Cope), *Semotilus margarita* (Cope) and *Pimephales promelas* Rafinesque. There were 38 mudminnows found to have eaten fish, fry or eggs and only five of these were male. Most fish were consumed in autumn, winter and early spring.

Overlap in diet varied between 0.0 and 0.85 between age groups (Table 8). The greatest overlap was between age 0 and 1 fish. Little overlap occurred between 0 and 2+ fish although it increased from early summer to autumn. Between age 1 and 2+ fish overlap was greatest (0.72) in late summer and was relatively high (0.60) in spring.

Diet overlap calculated between seasons was used as a measure of the change in diet which occurred through the year (Table 9). Diet of age 0 fish was similar during the summer months and only changed slightly in autumn. Age 1 mudminnows showed a similar trend. The diet of age 2+ fish was variable throughout the seasons.

Diversity of diet was lowest in winter (Table 10). Age 0 fish had the lowest diversity in diet items. Age 1 fish had high diversity in mid- and late summer diet as did 2+ fish. Age 2+ fish were also diverse feeders in spring.

Table 8. Overlap in diet (Morisita 1959 as modified by Horn 1966). Overlap can vary from 0 to 1, indicating completely different to completely overlapping diets respectively.

Age groups Compared	Winter	Spring	Early Summer	Mid-Summer	Late Summer	Autumn
0 vs. 1	-	-	0.77	0.85	0.76	0.70
0 vs. 2+	-	-	0.21	0.24	0.44	0.52
1 vs. 2+	0.00	0.60	0.33	0.48	0.72	0.47

Table 9. Overlap in diet (Morisita 1959 as modified by Horn 1966) between seasons for all sites combined.

Seasons Compared	Ages		
	0	1	2+
Autumn vs. winter	-	0.13	0.05
Winter vs. spring	-	0.01	0.20
Spring vs. early summer	-	0.79	0.42
Early summer vs. midsummer	0.89	0.73	0.60
Midsummer vs. late summer	0.91	0.93	0.47
Late summer vs. Autumn	0.76	0.51	0.66

Table 10. The diversity in mudminnow diet as measured by MacArthur's (1972) empirical measure of diversity, a larger number indicates greater diversity.

Age	Winter	Spring	Early Summer	Mid-Summer	Late Summer	Autumn
0	-	-	5.6	7.9	7.0	6.6
1	1.0	10.5	10.7	10.8	11.8	10.0
2+	1.0	20.5	8.7	13.8	14.2	12.8

DISCUSSION

U. limi occurs in a heterogeneous environment in southern Manitoba and responds to it by specializing in habitat and generalizing in time of activity, aspects of growth, reproduction and feeding strategies.

Environmental Heterogeneity.

Small slow-moving streams in north temperate locations are more variable in their physical and chemical characteristics than deeper bodies of water (Hynes 1970). In winter, ice cover may last for many months and small streams may freeze down to the substrate with free water remaining under stones and in deeper pockets (Hynes 1970). Snow cover on ice acts as an insulator modifying ice-cover, reducing light intensity and photosynthesis and ice prevents entry of oxygen from the air (Hynes 1970). As a result dissolved oxygen in the stream may drop to critical levels. Water depth is reduced and temperatures are depressed. In the spring fluctuations in water levels may be great, increasing water flow and flooding areas bordering the stream. Diurnal temperature variations occur along with an overall temperature increase. During the ice-free period seasonal fluctuations occur in cover, water velocity, water level, temperature and dissolved oxygen content. High temperatures and critically low levels of dissolved oxygen may occur during the summer when water flow is reduced and dense aquatic vegetation is present.

Certain environmental factors may be critical to the survival and reproductive success of _U. limi_. Winter water levels and dissolved oxygen concentrations affect survival. Reproductive success entails some optimal combination of factors which may include water velocity, temperature and photoperiod in the spring whereas summer survival may be reduced when water temperatures exceed a critical level.

Habitat.

Mudminnows occupy still waters throughout their range with an abundance of submerged or partially submerged vegetation and muddy bottoms (Gill 1903; Adams and Hankinson 1928; Peckham and Dineen 1957; Keast 1970).

Mudminnows prefer a habitat with cover. The body form of _U. limi_ is foreshortened, tubular and the entire body is thick (Keast and Webb 1966). They are slow swimmers with the ability to move in sudden bursts of speed attested to by their fin placement, thickened caudal peduncle and rounded fins (Keast and Webb 1966). _U. limi_ may rest on the bottom or hang in midwater, maintaining postion by gentle undulations of the extended pectoral fins. Forward movement is usually slow with a minimum of turbulence (Keast 1970) and they are best designed for movement through vegetation where speed is less important than maneuverability. Their cryptic colouration and secretive behaviour are compatible with areas of cover. Behavioural and physiological bouyancy control and airbreathing mechanisms (Gee 1980, 1981) are best suited to conditions consistent with those found in the vegetated areas studied.

Mudminnows can and do use a variety of cover when dense aquatic vegetation is not available. In spring the inundated terrestrial vegetation was occupied to avoid the strong current in the main channel and to provide an area for reproduction. In some areas, after water levels declined and aquatic vegetation was no longer present, undercut banks and overhanging terrestrial vegetation provided the necessary cover. In autumn, leaf litter may in some instances conceal U. limi (J.H. Gee personal communication).

Fry were confined to very shallow water which may have resulted in a spatial segregation from older mudminnows and may have resulted from predator pressure (Keast 1978).

From habitat selection experiments, mudminnows showed preference for vegetated areas except in the case of single U. limi after 24-h acclimation. In this instance the percentage of observations in vegetation are similar to that found in other experimental treatments (all are significant at $p<0.005$ using chi-square analysis). The result may be an artifact of Cole's test analysis (Type II error) or may actually indicate no preference after suitable acclimation in a situation where disturbance is eliminated. Mudminnows may be able to adapt to a different habitat when the confining infuences of competition, predation and environmental factors such as current are reduced. Keast (1966) found Umbra limi to be randomly distributed between the shallow weedy ponds and clear deeper sections of Jones Creek in southern Ontario. U. limi were included in the diet of S. atromaculatus (Mitchill) (Keast 1966) and E. americanus vermiculatus LeSueur (Crossman 1962; Keast 1966), the former confined to the weedy areas, the latter in both, but in greater abundance in the clear areas. Current was also found to be low (Keast 1966). In this situation competition for food resources would seem to be of paramount importance in influencing the habitat occupied by *U. limi*. Molluscs, a semi-exclusive diet item of *U. limi* (Keast 1966) were much more abundant in clear ponds which would explain the occurrence of *U. limi* in this area (Keast 1966).

Movement between patches of suitable habitats occurs. The observed migration of fry in the Brokenhead River was one instance and similar movements have been reported in the literature (Westman 1941; Peckham and Dineen 1957; Jones 1973). Movements into flooded vegetation where spawning occurs in the spring have also been recorded (Adams and Hankinson 1928; Westman 1941; Peckham and Dineen 1957; Jones 1973). Indirect evidence exists for colonizing migrations into areas where winterkill has occurred. Presence of a fish population in Hazel Creek following extensive winterkill in 1976-1977 is one such example.

In general mudminnows specialize in their selection of habitat. Mudminnows are found in greatest abundance in the weedy margins of streams and lakes, protected from the current and with suitable cover. Mudminnows may be randomly distributed when conditions permit (Keast 1966) but this is more an exception than a rule. An element of generalization occurs in habitat selection as the variety of cover used by mudminnows is broad, including aquatic vegetation, inundated terrestrial vegetation, overhanging banks and terrestrial plants and leaf litter.

<u>Diurnal Activity.</u>

Mudminnows showed variable activity patterns indicating an idiocratic flexibility. Activity as defined in this study probably included feeding activity and other movements. Factors influencing activity include predators, competitors and availability of food resources. In the Seine River mudminnow movement was confined to the vegetated areas and was greatest at night. *E. lucius*, a predator, may have influenced this pattern as few mudminnow competitors were present in the area. In the Bog River, where no aquatic predators were found (in all streams non-aquatic predators were present), the periods of greatest activity corresponded to times when activity was low for cyprinids and *C. inconstans*, both potential competitors. Migration of zooplankton and diurnal activity of some invertebrates (Hynes 1970) may provide for differing availability of food resources and would influence patterns of activity related to feeding. Other movements such as for the purpose of breathing atmospheric oxygen would be restricted to specific areas where conditions of low dissolved oxygen concentrations occurred. Several times such conditions were observed in the Seine River and activity was highest at night when dissolved oxygen concentrations were low. Whether the patterns of activity relate to feeding or some other factor, mudminnows are able to respond with an inherent plasticity.

Growth and Reproduction.

During the spring of 1978 conditions appeared to have been ideal for *U. limi* reproduction. Spawning was virtually complete by 26 May. This is one month later than spawning in Indiana (Peckham 1955) and New York (Westman 1941) and about the same time as reported in Minnesota (Jones 1973). In 1979 spawning occurred over an extended period and many females did not spawn at all. It was evident from gonads examined throughout the summer that some individuals resorbed eggs. In a situation where the success of spawning may be questionable it may be energetically feasible or necessary for some individuals (particularly young females) to defer spawning until the following spring when conditions may be more favourable. High water levels and inappropriate temperatures for spawning may have influenced the reproductive success of U. limi in 1979. June (1977) found atresia and resorption of eggs occurred as a responce to adverse conditions encountered during spawning in a variable reservoir. Spawning may be completed within the space of several days when conditions are favourable, however evidence does exist for an extended breeding season as postulated by Applegate (1943) when conditions are less so.

There are conflicting reports concerning age of first maturity in U. limi. In this study males were found to be sexually mature at age 1 and may be capable of breeding at this age. Females first spawn at age 2. Westman (1941) and Applegate (1943) reported male mudminnows and some female mudminnows mature at age 1 whereas Jones (1973) found neither were mature at this age.

Larger and therefore older female U. limi produce greater numbers of eggs than smaller, younger ones, a finding similar to other mudminnow studies (Westman 1941; Peckham 1955; Jones 1973).

Sexual dimorphism in gonadal development is marked. Males appear to have most of their gonadal development completed by autumn, whereas a large proportion of the female gonadal development occurs over winter. In an area where winter conditions are severe this would seem to have few adaptive advantages. Feeding in winter may provide females with an opportunity for fast gonadal development. The introduction of fish as major diet items at this time may provide the energy source. This strategy of ovarian development is similar to that found by Keast (1978) for yellow perch, *Perca flavescens* (Mitchill), which also feeds throughout the winter.

Age 0 and 1 fish are relatively distinct within the population although the first year class is consistently underestimated. Fry were difficult to collect because of their small size and distribution in shallow densely vegetated areas, which probably resulted from predation (Keast 1978). This underestimate of age 0 fish is not common to other studies and differences may exist in the survival strategies of small mudminnows in this area.

Predation may be a factor influencing the population dynamics of Seine River mudminnows. Many small *E. lucius* were collected with mudminnows in their stomachs. The Seine River population had proportionally fewer small mudminnows than other streams.

Competition for food and differences in the the quantity and quality of food resources and habitats available may have resulted in the differences observed in the Bog and Rennie River populations (fewer fry and smaller fish in general were collected in the Rennie River). Differences occurred between all streams in proportion of age groups in the populations, sizes of the age groups and growth rates although large individual variations occurred as well. Such variation in size classes was found in all studies (Westman 1941; Peckham 1955; Jones 1973). The growth curves for mudminnows in southern Manitoba are similar to that found by Peckham (1955) in Indiana.

In 1943, Applegate postulated that the overlap in sizes of mudminnow age classes probably involved slow growth and the tendency for decreasing growth rate with increasing age, the possible existence of an extended breeding season, lack of uniformity of growth and changing environmental conditions. As a result of one or several of these factors an early mergence of size classes was observed (Applegate 1943). This same overlap in size ranges was observed in southern Manitoba as in other studies (Westman 1941; Peckham 1955; Jones 1973). All of the factors reported by Applegate (1943) occurred in the present study.

The coefficient of condition confirmed the variability in growth rates for *U. limi*. The slightly lower values for females may have been related to increased growth rates and the loss of weight at spawning.

As mudminnows age the proportions of females in the population increase. This would suggest that selection for female survival is enhanced. Both Applegate (1943) and Peckham (1955) felt that if an increase in size has a positive selective value then an increased growth rate in females may result in the increased proportion of females in the population.

Mudminnows exhibit generalized life history strategies in terms of growth and reproduction. They are opportunists, utilizing resources when available to enhance survival. The variability in growth, condition, spawning time and reproductive potential (egg number and development of gonads) would be advantageous in a situation where environmental conditions are variable as in southern Manitoba.

Feeding Strategies.

U. limi feed throughout the year although most feeding was concentrated during the period from spring to autumn when water was warm. This was the period when diversity and abundance of invertebrates were greatest in the area studied (Tompkins 1982). Mudminnows achieve optimum conversion of food at 20°C and perform very poorly at 30°C (Keast 1978).

Feeding in winter is generally recognized as having a purely maintenance function (Keast 1970) and in general fish consume much less food and demonstrate digestion rates which are notably reduced (Keast 1970). However, winter feeding appears to be important for U. limi. Keast (1970) described mudminnows as being cold adapted as they showed the highest degree of winter feeding (48-65% of mudminnows examined contained food) and were the only species studied which achieved some length increase at 5°C and 10°C . Winter feeding in U. limi may have ramifications in survival and reproductive success for female mudminnows as described previously. The typical pattern of high levels of feeding in spring followed by a tapering off as the fish's physiological needs are satisfied (Keast 1970) does not hold for mudminnows. U. limi showed a relatively high level of feeding from spring to autumn. Winter starvation, which may result in the typical pattern (Keast 1970) did not occur in this area.

During the warm-water season, U. limi feeding periods were variable with distinct peaks usually occurring twice a day. The time of these peaks varied between sampling sites and seasons and may have resulted from the different faunal constituents (prey and competition) in each situation. The flexibility in U. limi feeding may result from an opportunistic feeding strategy. As a resource becomes accessible (e.g. organisms of appropriate body size) mudminnows may include it in their diet. Some invertebrates show diurnal changes in distribution (Hynes

1970) and thus availability as diet items (Keast and Welsh 1968). Invertebrate drift increases at night and particularly during the period soon after sunset (Hynes 1970). Another explanation for the variable feeding periods is the influence of competition which may be of greater importance in determining the composition of the diet than the habits of the animals actually eaten (Mendelson 1975). In either case differences in feeding period would ensure all potential food organisms are cropped and interspecific contact and competition would be reduced (Keast and Welsh 1968).

Mudminnows have been described as carnivores (Abbot 1870; Gill 1903; Westman 1941; Peckham and Dineen 1957; Keast and Webb 1966), herbivores (Cahn 1927) and omnivores (Forbes 1883; Forbes and Richardson 1907; Pearse 1918; Jones 1973). In southern Manitoba mudminnows are euryphagic carnivores. They feed on aquatic and terrestrial invertebrates during the ice-free period when they are most abundant and switch their diet to aquatic invertebrates and fish during winter.

In analysing their diet mudminnows were subdivided into three age groups; 0, 1 and 2+ fish. Differences were evident between each group and all showed seasonal shifts. Age 0 fish, collected from early summer to fall fed on Chironomidae larvae and crustaceans although changes in the order of importance existed. These changes may reflect changes in the quality of food resources and thus decreased availability of certain items. They may also reflect an increased pressure on the resources by other fishes. Age 1 fish had an intermediate diet between 0 and 2+ fish. They fed heavily on Chironomidae larvae and crustaceans but other items were also important in their diet. The increased niche breadth exploited by age 1 fish (compared to age 0 fish) would increase the variety of food items available to them. Age 2+ fish in general fed on larger items with Chironomidae larvae and crustaceans of lesser importance. Terrestrial invertebrates were important in the diet from spring to autumn and a much greater variety of aquatic invertebrates were also consumed. Fishes became important diet items when the water temperatures were low.

The diet of mudminnows in southern Manitoba had both similarities and differences from that described in other studies. In several cases zooplankton was not considered as an important diet item (Keast 1966; Jones 1973). Keast (1966) did not consider Chironomidae larvae to be important items in the diet of U. limi and described them as predators of small often hard-bodied invertebrates although in another study (Keast 1978) he found Chironomidae (larvae and pupae) and Coleoptera larvae together contributed to 42% of the volume of mudminnow food. Peckham and Dineen (1957) and Westman (1941) described a diet similar to that found here although neither terrestrial invertebrates nor fish were found to be important in the diet in either study. The niche breadth in terms of food resources utilized is broader at the northern end of the mudminnow's range.

Diet overlap, greatest in 0 and 1 fish resulted from the reliance on Chironomidae larvae and various crustaceans by both age classes. The difference in distribution although not complete may reduce the apparent overlap. Mouth size and the ability to handle various food sizes results in partitioning within a resource, a factor not taken into account by indices of overlap. Food overlap may also occur in periods of greatest abundance as in the case of age 1 and 2+ mudminnows feeding heavily on terrestrial items in the spring.

Diet change with season is an important factor in survival. The greatest change occurred between warm- and cold-water periods as mudminnows were limited to fewer food types in winter (Keast 1966). The most obvious change was the appearance of fish in the diet of large mudminnows during the cold-water periods, substantiated by Chilton et al. (in prep.). Fishes have been recorded in the diet but were deemed unimportant in previous studies (Peckham and Dineen 1957; Keast 1966; Jones 1973). Their importance as diet items results from the mudminnow's ability to catch fish when water temperatures are low and large numbers of fishes are confined in small areas along the course of the stream.

Diversity of diet items was least in 0 fish and greatest in 2+ fish. As fish become older and hence larger the absolute size and range of size of food items becomes greater, the prey taxa change and the number of prey items usually decrease (Nikolsky 1963). Foraging areas may change with age and influence diet diversity.

After an examination of the diet of mudminnows in southern Manitoba it became clear that they were able to utilize food items from the benthos, attached to vegetation, in free water and from the surface. Keast (1966) described them as feeding off the bottom and vegetation by stalking prey from a mid-water position (Keast 1978); Peckham and Dineen (1957) as bottom and not surface feeders; and Jones (1973) as feeding on attached or crawling forms. Here, they cover all areas of the water column within their habitat. Utilization of terrestrial insects, important diet items for age 1 and 2+ mudminnows, would reduce the dependence on lower trophic levels in the stream, provide alternate pathways of energy flow and ultimately confer a degree of stability to the community (Reed and Bear 1966).

U. limi's feeding strategy is that of a generalist with a wide range of feeding times, places of feeding and variety of food items consumed. They are opportunistic feeders which are generally more abundant and have greater biomass (Keast 1970) especially in temperate freshwater habitats where there is little chance for specialization (Larkin 1956). This plasticity of food habit seems to permit fish populations to change diet, diversify demands upon resources and reduce competition (Starret 1950).

CONCLUSIONS

According to Keast (1970) some directional rules must be followed in order for a fish species to fit into a complex community. His directional rules were based on adaptations, constraints and the life supporting potential of the system. The morphology of the species and the predictability of the environment were found to be two factors of importance to a species (Keast 1970). The species morphology channels it into a particular role by giving it an advantage. In this way the morphology of the mudminnow gives it an advantage within the vegetated habitat. It is a habitat specialist and this strategy appears in most instances to provide the greatest advantages.

With regard to the predictability of the environment Keast (1970) felt cold temperate environments with abundant rainfall allowed for predictability of life rhythms based on successional seasonal phenomena. That is, fish could rely on invertebrate cycles year after year and partition themselves within the community structure based on this. This is not the case in the small slow-moving streams studied. Over the long term perhaps predictability may exist but for the short term the ability of a species to adapt to fluctuations would seem to be most important. By occupying a broad niche, as the mudminnow does in Manitoba the predictability of the environment is of lesser importance than the variability in the mudminnow's response to it. Mudminnows have adapted to the changing environmental conditions by occupying a broad niche, not in space, but in resources utilized and time.

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Appendix 1

Description of indices referenced in the text.

1. Coefficient of condition from Hile (1936)

$$K = \frac{\text{Weight (g)}}{\text{Length (mm)}} \times 10^5$$

2. Percent sexual development from Luoma and Gee (1980)

$$\%\ \text{S.D.} = \frac{\text{gonad : body weight ratio}}{\text{largest gonad : body weight ratio*}} \times 100$$

* each sex calculated separately

3. Diet overlap from Morisita (1959) as modified by Horn (1966)

$$C = \frac{2 \sum X_i Y_i}{\sum X_i^2 + \sum Y_i^2}$$

X_i = proportion of the ith food item taxon in the diet of X
Y_i = proportion of the ith food item taxon in the diet of Y

4. Diversity from MacArthur (1972)

$$D = \frac{1}{\sum p_i^2}$$

p_i = proportion of the diet contributed by the ith food item taxon