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Distribution, Food and Life History of Tiger Salamanders in Devils Lake, North Dakota

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DISTRIBUTION, FOOD AND LIFE HISTORY
OF TIGER SALAMANDERS IN DEVILS
LAKE, NORTH DAKOTA

by

Gary L. Buchli

B. S., Jamestown College, 1964

A Thesis

Submitted to the Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the Degree of

Master of Science

Grand Forks, North Dakota

February
1969

This Thesis submitted by Gary L. Buchli in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

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Title DISTRIBUTION, FOOD AND LIFE HISTORY OF TIGER
SALAMANDERS IN DEVILS LAKE, NORTH DAKOTA

Department Department of Biology

Degree Master of Science

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Date Jan. 21, 1969

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ABSTRACT

Food, growth, distribution, migration, metamorphosis, neoteny, and breeding habits of Ambystoma tigrinum diaboli Dunn were studied in Devils Lake, North Dakota. Salamanders were captured in gill and frame nets, and growth and metamorphosis were followed on specimens caged in the lake. Food habits were ascertained from stomach analyses and migrating adults were caught in gill nets and trench-barrier traps.

Salamander adults breed readily in Devils Lake and display a sex ratio of 13 females to 10 males. The population appears to consist of larvae, neotenus gilled forms, and adults. Adults leave the lake in fall and return in spring; larvae are present from time of egg hatching until late summer when they change to adults or "neotenic"; neotenus forms are apparently present at all seasons unless eradicated by winter kill. Breeding by neotenus forms was neither verified nor refuted; females had eggs in the body cavity in the fall of 1967 and had lost them before ice melt in 1968. Major growth occurs during the first summer after hatching, but neotenic continued growth at a much slower rate during the second summer. Both larvae and neotenic metamorphosed into adults. Metamorphosis of neotenic could be induced by penning them in the lake or removing them to

tanks and aquaria. Amphipods were the major food item of all 3 categories. Gastric and intestinal nematodes and cestodes were the only parasites found.

INTRODUCTION

Tiger salamanders are members of the family Ambystomidae which includes 11 species distributed throughout North America (Noble, 1931). Ambystoma tigrinum has been divided into 6 to 8 subspecies; Ambystoma tigrinum diaboli Dunn is the subspecies found in Devils Lake. Its type locality is Devils Lake and the type specimens are in the Museum of Zoology, University of Michigan (No. 50156). Common names include gray tiger salamander, yellow salamander, and Devils Lake salamander.


Ambystoma tigrinum diaboli adults have a ground color of light olive with scattered black spots on the back and sides. Larvae are yellow brown, darker dorsally and generally unmarked or very faintly marked.


Devils Lake salamanders were first mentioned by Pope (1908) who erroneously called them Cryptobranchus allegheniensis. This faux pas was corrected by Young (1912) who placed them in the species Amblystoma tigrinum and they were named Ambystoma tigrinum diaboli by Dunn in 1940. Distribution of Ambystoma tigrinum and A. t. diaboli appears in Figure 1.

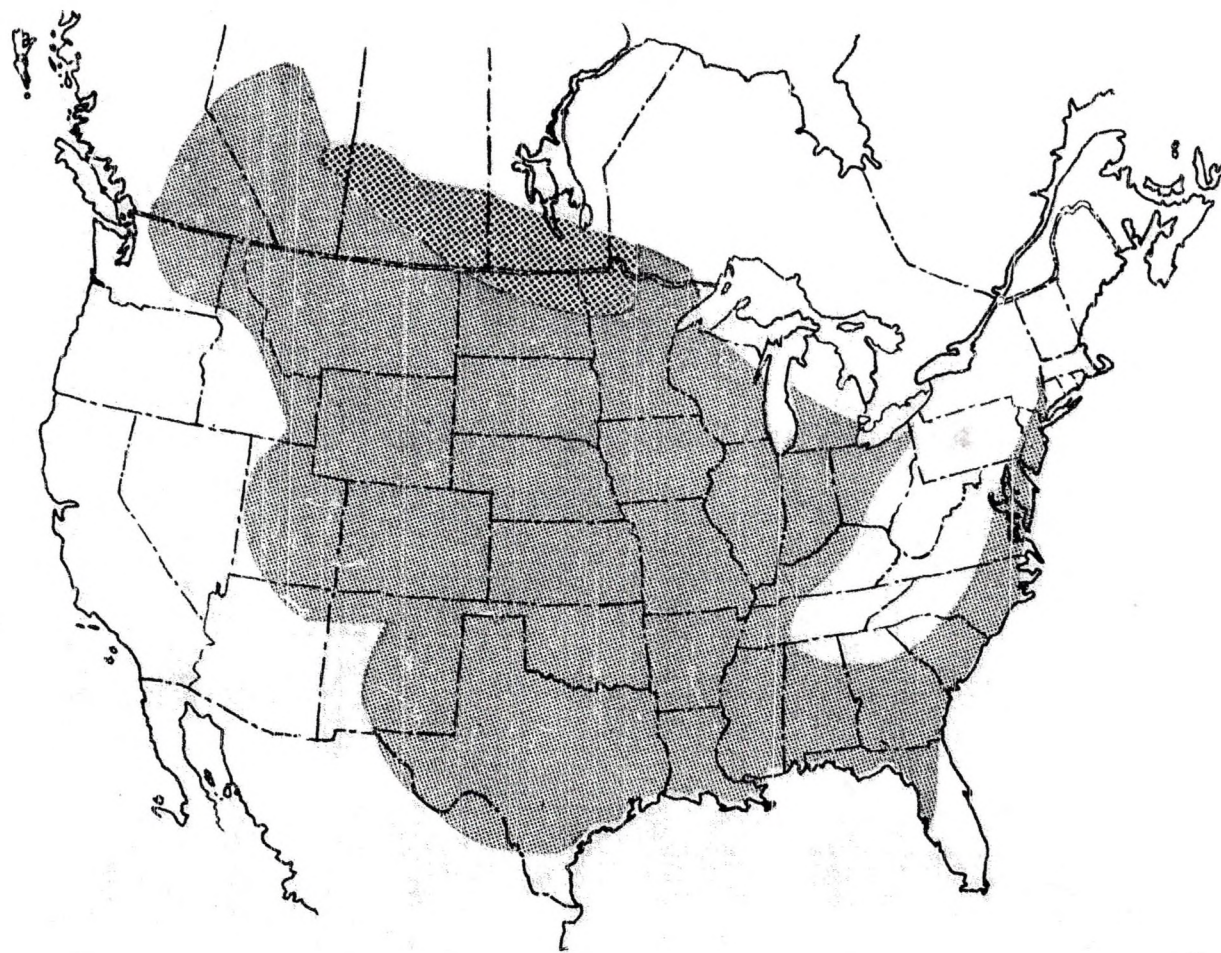
Tiger salamanders (Ambystoma tigrinum) are secretive

FIGURE 1

DISTRIBUTION OF Ambystoma tigrinum AND A.t. diaboli
(After Bishop, Handbook of Salamanders, 1943)

 Ambystoma tigrinum

 A.t. diaboli



and essentially burrowing amphibians that live underground most of their adult lives. They are quite slimy and harmless except for the alkaloid secretions of glands which upon repeated contact may produce severe irritation and edema of human skin. The genus Ambystoma is characterized by neotenic life forms in which individuals become sexually mature before metamorphosis as described by Osborn (1900, 1901), Powers (1903, 1907), Noble (1931), Slater (1934, 1937), Graf et al. (1939), Dunn (1940), Bishop (1943, 1944), Reese and Smith (1951), De Marco (1952), Levi and Levi (1955), Prosser and Brown (1962), Craig (1962), Larson (1965), and Larson (1968).

Adults of this genus prefer damp, dark places, and frequently inhabit animal burrows, cellars, window wells, rotting wood, decomposing vegetation, ponds and lakes. They feed on land and in water upon any animal small enough for them to ingest.

In early spring salamanders leave their winter burrows and journey to lakes and ponds to breed. Courtship display takes place in the water and is followed by male deposition of a spermatophore which is picked up by the cloacal lips of the female.

Numerous general reports about salamanders are available but there is a paucity of information on the Devils Lake population. Food habits, growth rates, distribution, emigration and immigration, neoteny, and breeding

have not been investigated. This study was undertaken to collect information on these characteristics before the water level of Devils Lake is raised by Garrison Diversion. Such data would be significant as a basis for future studies after water levels have been raised as well as indicating salamander dynamics in the present highly mineralized waters.

MATERIALS AND METHODS

Salamanders were captured with $5\frac{1}{2}$ x 75', $3/4$ " stretch mesh gill nets, and 3 x 4', $\frac{1}{2}$ " bar mesh frame nets. The latter were available only at intervals. Growth studies were conducted on salamanders in a holding pen sunk into a Ruppia bed in Creel Bay.

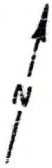
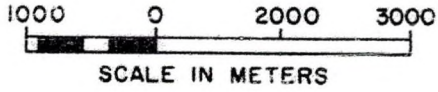
Devils Lake appears to have 3 major ecological divisions: Creel Bay, Main Bay littoral, and Main Bay limnetic zones. Collection stations were established in all three divisions as shown in Figure 2, and characterized as to depth, vegetation and sediment (Table I). Nets were set at each station every 5th day during sampling periods. Captured salamanders were taken to the laboratory where they were killed, sexed, measured, and weighed. Stomachs were removed and preserved for later analysis of contents. Parasites of the stomachs and small intestines were saved for later identification. Weights were recorded in grams and dimensions in millimeters. The following measurements were made where applicable:

1. total length
2. maximum height of tail
3. maximum height of dorsal fin
4. maximum diameter of head
5. distance between pupils
6. distance between external nares
7. length of 1st, 2nd, and 3rd gills




FIGURE 2

LOCATIONS OF MAJOR ECOLOGICAL DIVISIONS
OF LAKE AND THE SAMPLING STATIONS

DEVILS LAKE
NORTH DAKOTA



LEGEND

-  CREEL BAY (AREA I)
-  MAIN BAY LITTORAL REGION (AREA II)
-  MAIN BAY LIMNETIC ZONE (AREA III)
- SAMPLING STATION

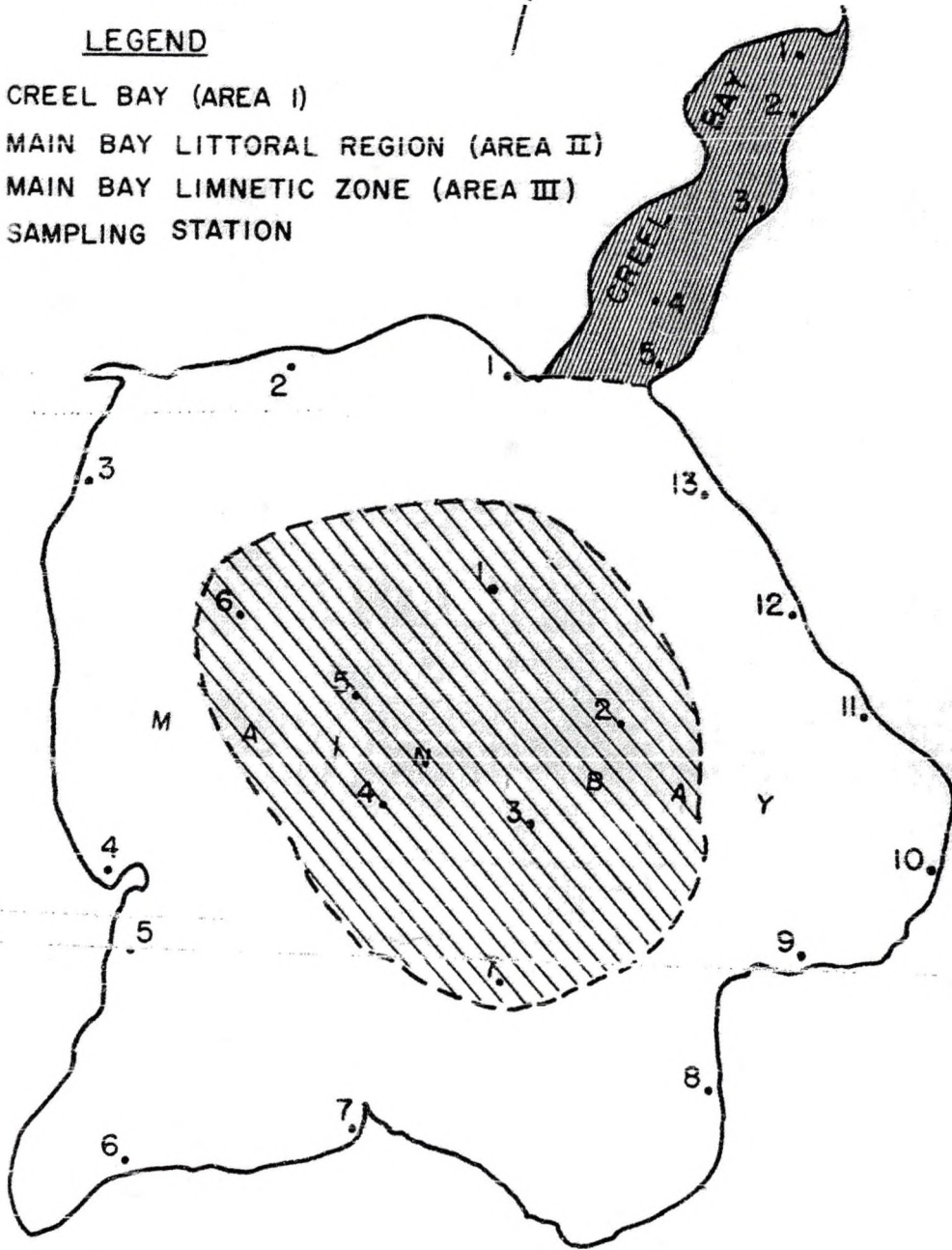


Table I

SEDIMENT, VEGETATION AND DEPTH
AT INDIVIDUAL STATIONS

	Depth	Vegetation	Bottom
Area I			
Station 1	1.5m	Ruppia	ooze
Station 2	.5m	Ruppia	ooze
Station 3	1.0m	Ruppia	sandy
Station 4	2.4m	none	ooze
Station 5	1.0m	Ruppia	sandy
Area II			
Station 1	2.5m	none	rocky
Station 2	1.5m	algae	sandy
Station 3	1.5m	Ruppia	clay
Station 4	2.0m	Ruppia	ooze
Station 5	1.4m	Ruppia	ooze
Station 6	2.0m	algae	rocky
Station 7	2.5m	algae	rocky
Station 8	2.0m	algae	ooze
Station 9	2.3m	algae	sandy
Station 10	2.0m	Ruppia	sandy
Station 11	1.3m	algae	ooze
Station 12	1.2m	algae	rocky
Station 13	2.2m	algae	rocky
Area III			
Station 1-7	3.4m	none	Marl and clay

To follow changes in metamorphosis, larvae were placed in the holding pen and these measurements were periodically taken:

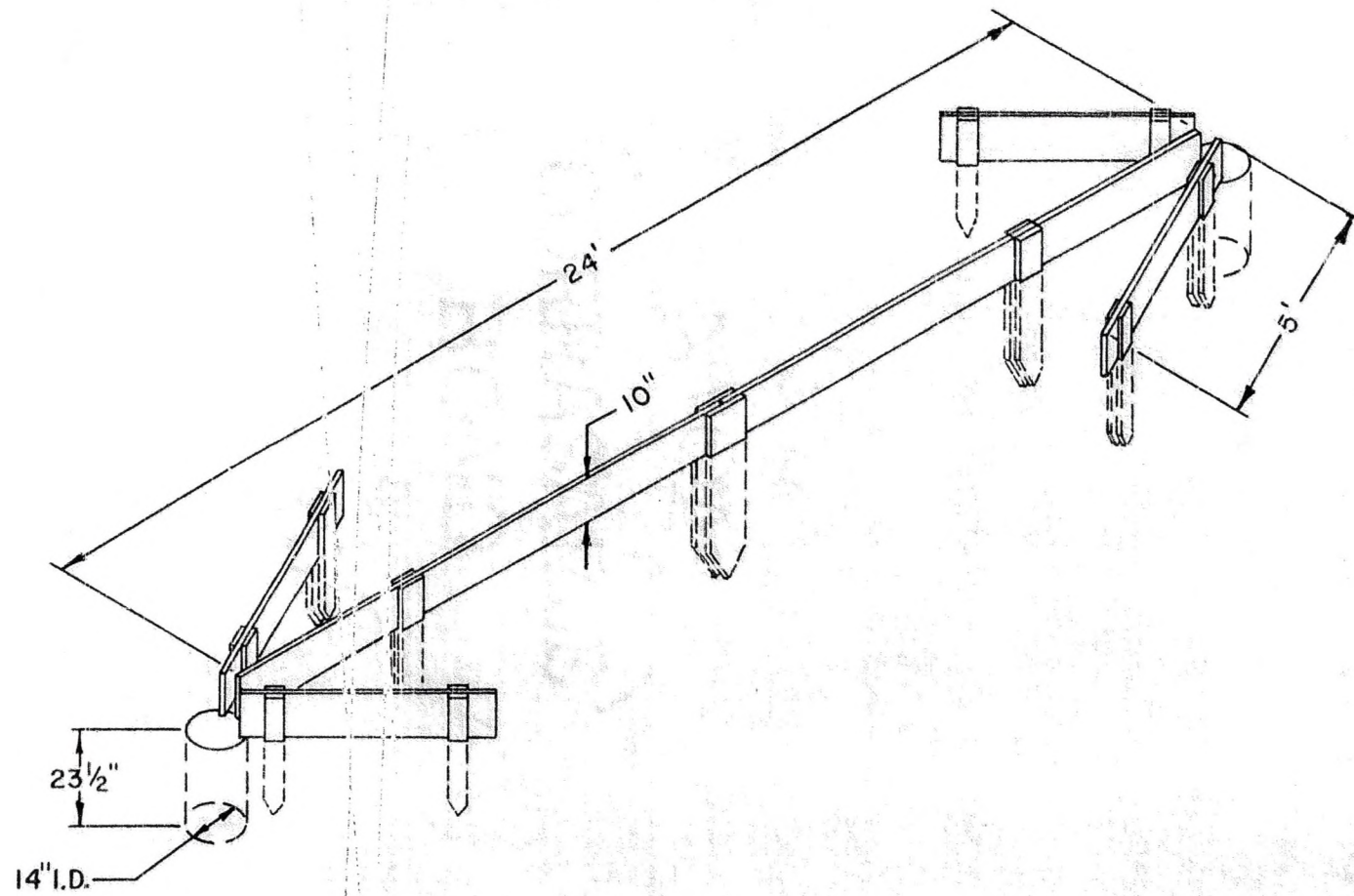
1. total length
2. weight
3. height of tail at vent from dorsal body line to most dorsal portion of tail
4. height of tail from the bottom of the vent to the most dorsal portion of the tail
5. maximum width of head
6. length of dorsal fin from tip of tail to its most anterior extension
7. interorbital length
8. length of longest gill (most dorsal)
9. distance from middle of orbit to side of head

Stomachs taken from 133 adults and 182 larvae were fixed in 10% formalin and stored in 70% ethanol. Ingested organisms were identified and the number of each form recorded. A survey of food organisms in the lake was made by use of hand seines and a fine mesh tow dredge.

Immigrating adult salamanders were collected with a gill net positioned with weights on shore and floats in a few inches of water. An emergent trap (Figure 3) was successfully employed in capturing adults leaving the lake. It was placed 20' from and at a 90° angle to the shoreline. Salamanders emigrating from the lake encountered this barrier and in attempting to bypass it they traveled to the ends of the barrier where they were captured in containers 23½" in depth.

Cestodes and nematodes were killed in hot water, preserved in AFA and stored in 70% ethanol. They were

FIGURE 3
EMERGENT TRAP



stained with hematoxylin and mounted in balsam. Nematodes were dehydrated through graded alcohols; 85, 95, and 100%, followed by clearing with carbo-xylol. Cuticles were punctured to prevent "vacuum opacity" in balsam.

PRESENTATION OF DATA

Lake Conditions

Devils Lake (Figure 2) covers about 7,000 acres. The maximum depth of Main Bay was 3.4 m in 1967, and its average depth between 3 and 3.4 m; Creel Bay had a maximum depth of 3.2 m near Main Bay, but its average depth was less than 1.5 m. The lake is fully exposed to winds that keep the water well mixed from surface to bottom during open water seasons. Most of the bottom of Main Bay is a mixture of marl and silt with varying amounts of sand, but Creel Bay and some shallow areas of Main Bay are covered with decomposing organic matter. Some materials contributing to organic deposits, which attain a thickness of 1.5 m in northern Creel Bay, originate in sewage effluents from the city of Devils Lake. Ruppia maritima L. occurs to a depth of 2 m and is most concentrated in Creel Bay. Large masses of Cladophora glomerata Kuetzing were usually associated with Ruppia. Enteromorpha prolifera Fl. Dan. grew attached to rocks along the shore from early June until freeze up. All plants attained their greatest biomass in late August.

The lake was frozen from November 22, 1967 until

April 12, 1968. Maximum thickness of the ice was approximately 1 m on Main Bay and somewhat less on Creel Bay.

Devils Lake is a highly mineralized, saline water body (Pope, 1908; Abbot, 1924; Swenson and Colby, 1955; Anderson, 1966). Oxygen is a major concern and its persistence under ice cover varied markedly during the winter of 1966-67 and 1967-68. It had disappeared completely by April 1, 1967, but during the following winter its minimum concentration was 7.0 ppm (Anderson, personal communication).

Salamander Population

Salamander Life Forms

Salamanders were considered to be larvae from the time of hatching until metamorphosis or development of definitive external sexual characters. Individuals developing secondary sexual characters without metamorphosis were considered neotenus. Some of these later changed to adults by losing their gills. Neoteny was attained at the end of the first summer, but many individuals maintained this condition through the second summer and changed only by becoming larger.

Three life forms give Devils Lake salamanders a high biotic potential. Severe winter conditions resulting in oxygen depletion kills neotenus forms over-wintering in the lake. Adults over-wintering on land insure continuance of the species when they return to the lake in the spring. If oxygen depletion does not occur the neotenus over-winter successfully and may become adults. It has been confirmed that Ambystoma tigrinum diaboli have previously over-wintered in a lake (Breckenridge, 1944).

All neotenus were killed in the 1966-67 winter, and only adults and young of the year inhabited the lake during 1967. Some of the larvae became adults and others developed into neotenus forms the first year. Neotenus readily changed to adults if their environment was altered by

confinement in a pen. What advantage the neotenus stage offers to the general population is obscure. It could be argued that their occupancy of the lake reduces competition among terrestrial stages and allows a greater net production of salamanders. However, eradication by winter kill, and exposure to aquatic predators under normal lake conditions, would appear to offset any advantages attributable to continued recourse to the lake food supply.

Seasonal and Spatial Distribution

Total catch of salamanders per working period appears in Table II. Sex ratio was 10 males per 16.3 females. Only adults were found from June 15 to July 15, 1967 when larvae first appeared in Area I. Larvae become very abundant in July catches, which netted the largest total of salamanders. The largest catch in July was a frame net haul of 304 salamanders in 24 hours. Larson (1968) reports the capture of nearly 6,000 salamanders with a hoop net in 72 hours.

Adults started leaving the lake in large numbers in August, 1967. Neotenus forms which had developed from young of the year remained in the lake but were not taken in nets set under ice during the winter of 1967-68; they were captured again early in the spring of 1968.

Total gill net catch by area and station appears in Table III. Five hundred and thirty-three (533) adults, larvae and neotenuics were taken from Area I; Area II yielded 263 of all 3 categories; Area III only 20 larvae.

Table II

TOTAL CATCH OF SALAMANDERS FOR ALL STATIONS
6/15/67 - 10/13/68

Month	Type of Net	Adults		Larvae and Neotenic Forms		Total
		Males	Females	Males	Females	
6/15-6/30/67	gill frame	58	72	0	0	130
		-	-	-	-	-
7/1-7/31/67	gill frame	76	104	115	212	507
		193	241	282	593	1309
8/2-8/15/67	gill frame	6	5	68	100	179
		12	17	165	237	431
9/13/67	gill frame	-	-	-	-	-
		2	0	2	3	7
9/28/67	gill frame	-	-	-	-	-
		0	0	2	3	5
11/4/67-4/1/68	gill frame	0	0	0	0	0
		-	-	-	-	-
4/19/68	gill frame	-	-	-	-	-
		0	0	15	27	42
5/15/68	gill frame	-	-	-	-	-
		7	12	14	24	57
6/20/68	gill frame	-	-	-	-	-
		3	9	8	12	32
7/21/68	gill frame	-	-	-	-	-
		1	4	23	39	67
8/20/68	gill frame	-	-	-	-	-
		2	3	17	22	44
10/13/68	gill frame	-	-	-	-	-
		0	0	8	24	32
Total		358	467	721	1296	2842

Table III

TOTAL GILL NET CATCH - AREA I, II, III
6/15/67 - 10/13/68

Station No.	Adults		Larvae and Neotenic Forms		Station Totals
	Males	Females	Males	Females	
Area I					
1	12	19	69	79	179
2	18	29	32	48	127
3	18	29	29	42	118
4	31	26	17	11	85
5	11	9	0	4	24
Total	90	112	147	184	533
Area II					
1	6	6	0	25	37
2	2	2	0	5	9
3	12	10	3	4	29
4	4	7	3	4	18
5	3	8	0	16	27
6	7	8	0	5	20
7	3	5	10	7	25
8	0	0	7	20	27
9	4	8	2	7	21
10	1	3	0	3	7
11	5	6	0	8	19
12	0	2	0	4	6
13	3	4	1	10	18
Total	50	69	26	118	263
Area III					
1	0	0	1	3	4
2	0	0	1	1	2
3	0	0	0	2	2
4	0	0	1	0	1
5	0	0	0	0	0
6	0	0	4	3	7
7	0	0	3	1	4
Total	0	0	10	10	20

Population Dynamics

An enormous food supply and paucity of predators may contribute to the development of a large population of tiger salamanders in Devils Lake. Pope (1908) reported a cormorant rookery in Main Bay and a few pelicans all feeding on salamanders. Pelicans still visit the lake occasionally, but the cormorant rookery no longer exists. Carnivorous fish which may rapidly deplete salamander populations (Levi and Levi, 1955) have been virtually absent from the lake since 1889. Recent plantings of pike (Esox lucius L.) have had a short life and their predation of salamanders has been of little consequence.

Salamanders seemingly prefer shallow areas with considerable detritus and rooted plants. Creel Bay with extensive weed beds has the largest concentration of salamanders, Main Bay littoral regions are deeper, have less vegetation and support fewer salamanders. The limnetic area of Main Bay, which is devoid of attached plants, yielded only larvae that were young of the year and swam almost as well as fish.

Dimensions and Weights

A process to determine the age of salamanders has not yet been devised. This may be the first time measurements and weights have been recorded for a wild population of known age. A size differential was observed between adults and the two neotenus forms, i.e., those with 1 or 2

summers growth (Table IV). Samples for the neotenic of one summers growth and for adults were selected from the total catch while the 32 second summer neotenic represent the total catch of this form. The largest adult measured 312 mm and weighed 210 grams; the largest neotenic form, 325 mm and 247 grams. These measurements are somewhat larger than previously recorded. Young (1912) reported that adult Devils Lake salamanders ranged in length from 250 to 285 mm. Dunn (1940) lists the largest adult as 287 mm and the largest "larval form" as 312 mm; however, the largest larval form according to Larson (1968) was 385 mm in length. This neotenic may have resulted from more than 2 seasons growth. The smallest larvae taken in this study measured 90 mm. Sample size of previous investigations has been considerably smaller than for the present study and may explain some of the size discrepancies that exist.

Adults ranged from 190 to 312 mm (average 258 mm) in length. Bishop (1943) described extremes of adult size (based on 15 specimens) as ranging from 119 mm to 282 mm in length with an average of 190 mm. The average total length of adult females measured 5 mm less than the 261 mm adult males. A t-test showed no significant difference between male and female lengths. Adults ranged from 60 to 210 grams (average 127 grams) in weight. The average weight of adult females was 134 grams or 17 grams more than the adult male average. A significant difference existed between weights

Table IV

AVERAGE DIMENSIONS AND WEIGHTS OF ADULTS AND
NEOTENOUS FORMS OF 1 AND 2 SUMMERS GROWTH

Measurements	Neotenus Forms One Summers Growth n=121	Neotenus Forms Two Summers Growth n=32	Adults Age Unknown n=321
Maximum height of tail	38	40	25
Maximum height of dorsal fin	7	7	0
Maximum diameter of head	43	46	31
Distance between external nares	12	14	10
Distance between pupils	24	24	20
Length 1st gill (most dorsal)	42	44	0
Length 2nd gill	33	36	0
Length 3rd gill	23	28	0
Total length	222	302	258
Weight	118	219	126

of males and females at the 99% level.

Food Habits

Principle organisms used as food each month in descending order of preference were amphipods, cladocerans, hemipterans, trichopterans and dipterans (Figures 4, 5, 6, and 7). Anostracans were consumed for only a few weeks in the spring. Other groups eaten were beetles, sticklebacks, larval salamanders and snails in descending order. Table V lists organisms found in salamander stomachs.

Hemipterans were eaten by adults, larvae, and neotenus forms but the latter two utilize them to a greater extent. Odonata are preyed on by adults more than by larvae and neotenus; dipterans are utilized more by the gilled stages. Adults utilize trichopterans but very few are ingested by other life stages (Figures 4, 5, 6, and 7). Sand grains were found only in adult stomachs. This may indicate that adults feed on the bottom and gilled forms at some distance above the bottom. Salamanders in captivity snap at any moving objects when hungry and often catch each other by a leg or tail. Cannibalism occurs in captive and wild populations.

Metamorphosis and Neoteny

Young of the year larvae metamorphosed into adults or changed to neotenus in August 1967. Neotenus forms were not present until they developed from these larvae.

FIGURE 4

AVERAGE NUMBER OF ORGANISMS PER STOMACH

JUNE 16-29, 1967

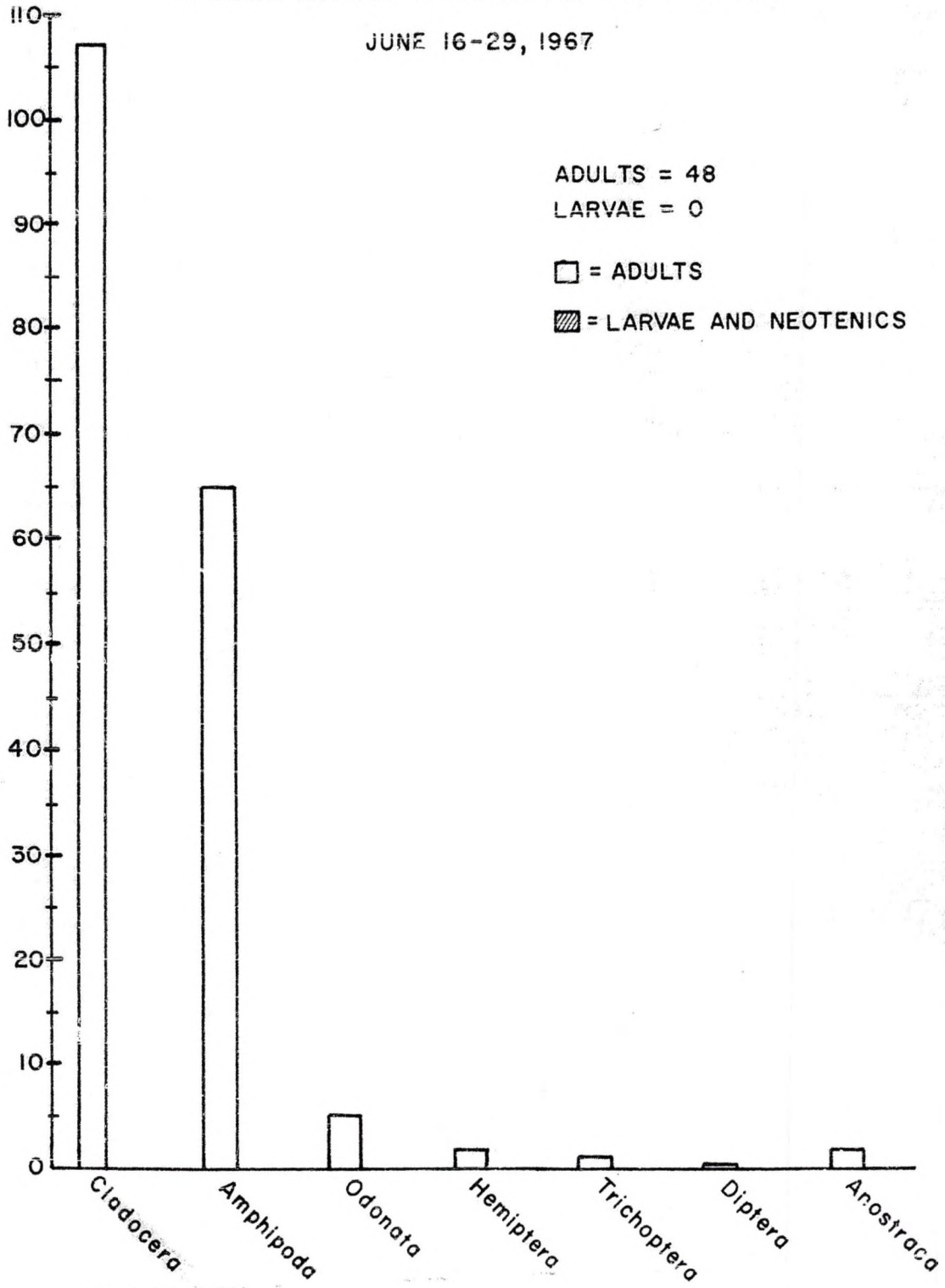


FIGURE 5

AVERAGE NUMBER OF ORGANISMS PER STOMACH

JULY 2-31, 1967

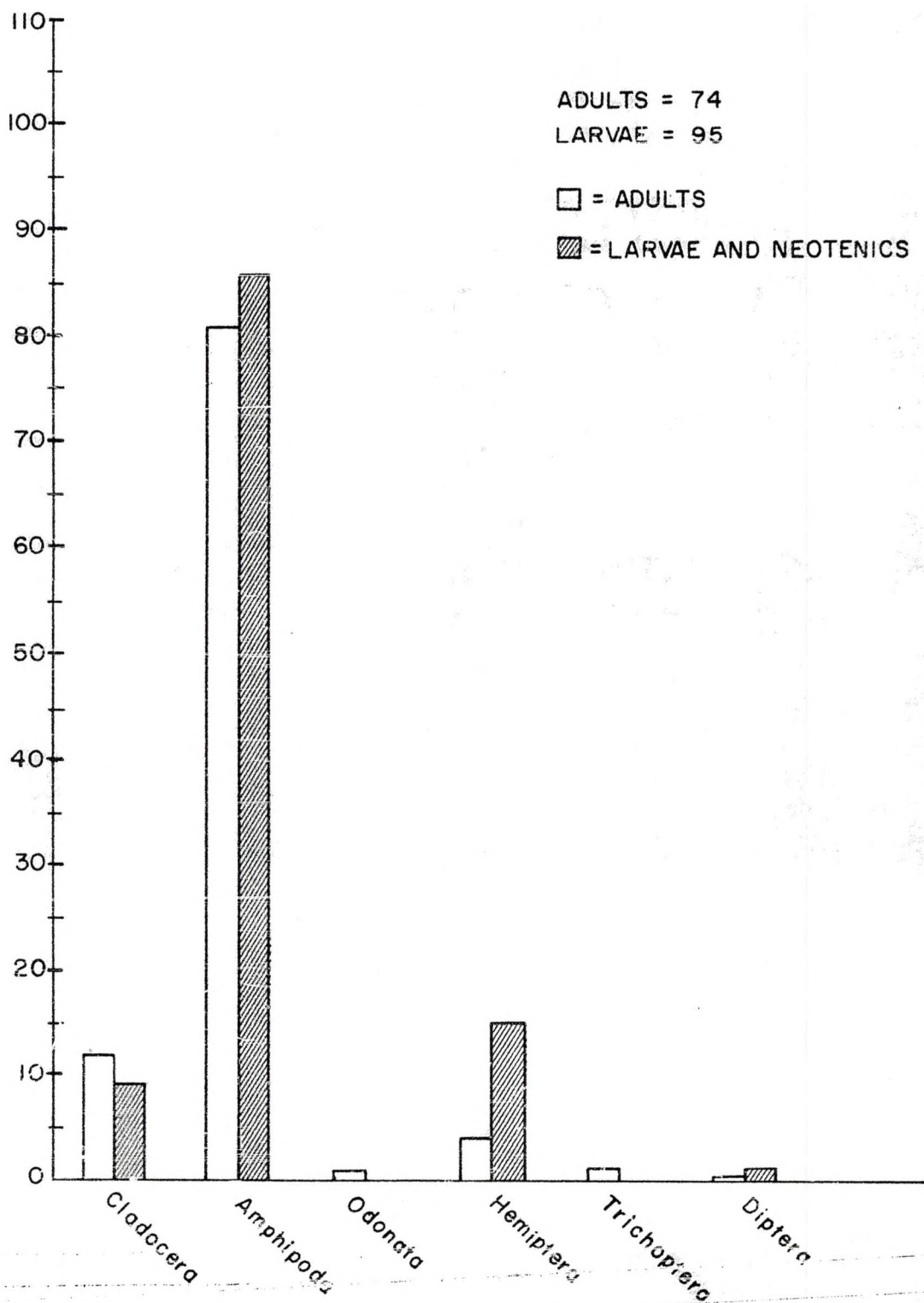


FIGURE 6

AVERAGE NUMBER OF ORGANISMS PER STOMACH

AUGUST 8-31, 1967

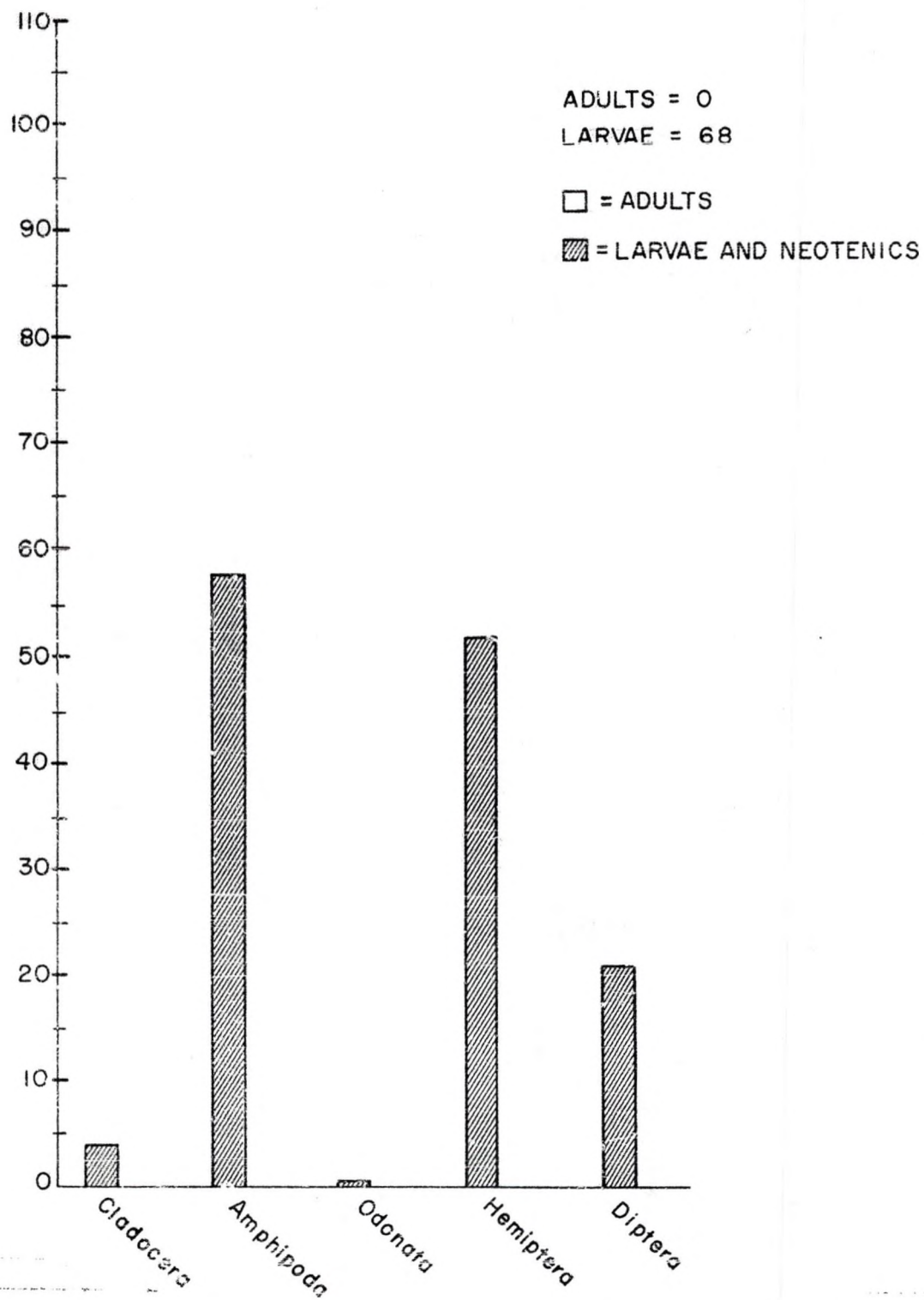


FIGURE 7

AVERAGE NUMBER OF ORGANISMS PER STOMACH

JUNE 6-30, 1968

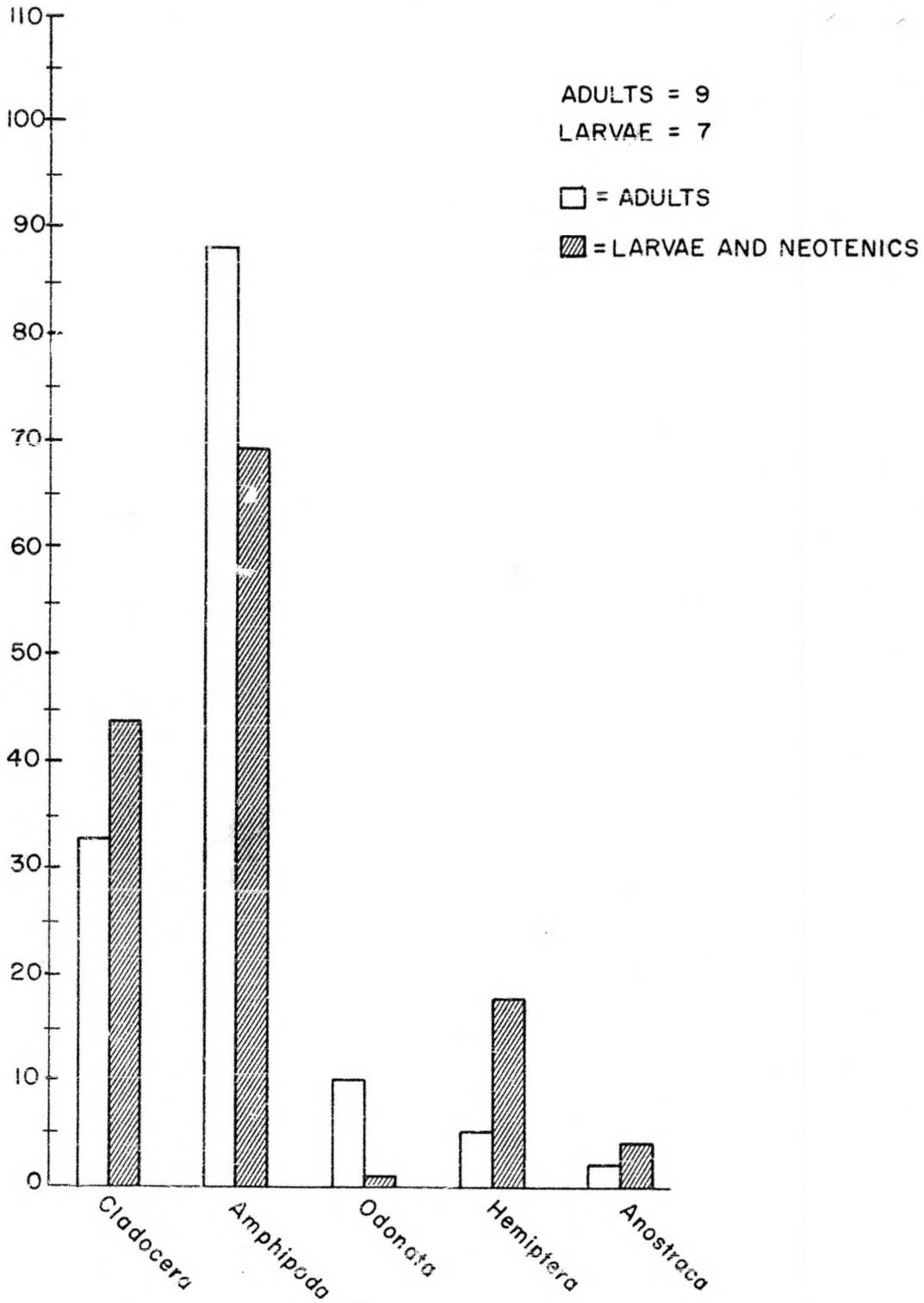


Table V

ORGANISMS FOUND IN SALAMANDER STOMACHS

Order	Family	Genus	Species	Authority
Cladocera	Daphnidae	<u>Moina</u>	<u>hutchinsoni</u>	Brehm
Trichoptera	Leptoceridae	<u>Triaenodes</u>	---	---
		<u>Oecetis</u>	species a	Ross
	Phryganeidae	---	---	---
Coleoptera	Dytiscidae	<u>Agabus</u>	<u>disintegratus</u>	Crotch
	Hydrophilidae	<u>Enochrus</u>	---	---
Anostraca	Branchinectidae	<u>Branchinecta</u>	---	---
Gastropoda	Physidae	<u>Aplexa</u>	---	---
Odonata	Coenagrionidae	<u>Enallagma</u>	<u>civile</u>	Hagen
Gasterosteiformes	Gasterosteidae	<u>Eucalia</u>	<u>inconstans</u>	(Kirtland)
Diptera	Chironomidae	<u>Chironomus</u>	<u>decorus</u>	Johannsen
		<u>Tanypus</u>	<u>stellatus</u>	Coquillett

They were the only salamanders remaining in the lake after the adults emigrated, and they survived the 1967-68 winter in large numbers. They were not caught under the ice, but readily entered nets after ice melt in April 1968. Neotenus forms evidently did not survive the winter of 1966-67. Their bodies were found in large windrows on shore in the spring of 1967 (Anderson, personal communication). This is contrary to Larson's (1968) view that winter conditions do not affect salamanders.

The role played by neotenuics in production of fertilized eggs in the spring of 1968 is unknown. Egg development in neotenus females paralleled that in female adults in the fall, both having eggs about 2 mm in diameter in the body cavity. However, body cavities of neotenic females were empty of eggs in the spring when adult females had mature eggs up to 8 mm in diameter. If eggs continued development in neotenus females it would appear that they were laid before ice breakup in 1968.

Examination of average measurements for various anatomical features demonstrates that the ultimate result of metamorphosis is a reduction in all dimensions (Table IV). The dorsal fin and gills are absorbed first. Both metamorphosing neotenuics and adults will drown if submerged for 48 hours. Metamorphosis occasions conspicuous external and internal changes in organization, consisting of loss of gills and tail fin, replacement of larval skin by a

glandular one with darker pigmentation, fusion of the operculum with the integument, protrusion of the eyes, and glandular changes in the intestine. Consumption of oxygen increases during metamorphosis (Hopkins and Handford, 1943) and the larvae cease feeding while intestinal changes take place (Wilder, 1925). It is generally accepted that thyroxine promotes metamorphosis in amphibia and that arrested transformation in neotenic forms may not be due to the reduction or absence of this hormone, but rather to continuance of the feedback inhibition of TSH by thyroxine which affects the pituitary through the hypothalamus (Etkin, 1964).

Metamorphosis was initiated in Devils Lake neotemics by removing them from their natural habitat or placing them in cages partially submerged in the lake. This may point up the role of neurosecretory activity of the nervous system in the intergradation of developmental and hormonal responses to stimuli from the environment (Scharrer and Scharrer, 1963). Thus, factors such as crowding, adverse temperature change, starvation, and accumulation of metabolic wastes may stimulate metamorphosis. These adverse conditions which promote metamorphosis would permit the salamander to seek a more favorable environment and therefore are of adaptive value and may be essential for survival (Etkin, 1964).

Breeding Appearance and Breeding

Breeding studies were initiated April 19, 1968. At

this time both sexes displayed striking external sexual characteristics when arriving at the lake. Cloacal areas of the males were greatly enlarged, showing pinkish lips, while the females were heavy with eggs. Fertilized eggs were first found on May 12, 1968 when water temperature at 1 m was 9°C. The eggs were attached to Ruppia in clumps or strings of 5 to 30. By May 28, 1968 most of the eggs had hatched; water temperature was 14°C.

Highly mineralized waters have been considered unfit for the development of amphibian eggs and larvae. However, Taylor (1943) reported a larval Ambystoma living in highly brackish water and subsequent investigations have confirmed that many neotenus forms can exist in such water. Jørgenson et al. (1946) reports that Ambystoma mexicanum balances net up-take of chloride ions by diffusion through the skin and other respiratory surfaces as well as by renal excretion. These physiological adaptations may account for the ability of the tiger salamander to exist in such highly mineralized waters as Devils Lake.

Taylor (1943) suggests that salamanders breed in brackish water but did not present evidence to support this condition. Young (1912) reported that Ambystoma tigrinum occurred both as larvae and adults in the brackish waters of Devils Lake, but pointed out that this species bred only in small fresh water ponds, ditches, and swamps in the immediate area. Breeding did occur in Devils Lake

during April 1968 and fertilized eggs were found during May. Therefore the waters of Devils Lake would appear to be within the tolerance range of conditions affecting reproduction in salamanders. This subspecies had not been reported to breed in highly mineralized saline water prior to this study. Complete courtship behavior of Ambystoma tigrinum has been described by Kumpf (1934).

Emigration and Immigration

Adults began to leave the lake in late August 1967 and continued to do so during favorable weather conditions until October at which time they disappeared from net hauls. Best conditions for migration were rainy nights or cloudy rainy days. In 1968 the mass migration began July 17 and proceeded slowly during periods of rain or heavy dew. The shoreline was often a mass of moving salamanders during August 1968.

Return to the lake began shortly after ice melt in April, 1968. Males arrived first; females were abundant about 10 days later, just before immigration ceased, but the time of their first arrival is unknown.

Migration may be the result of a sensitivity toward certain external stimuli. Baldauf (1952) referring to Ambystoma maculatum indicates the stimuli most important are air temperature of approximately 50°F and high humidity. It appears that if the temperature is optimum the moisture necessary for migration may result from rainfall, snow water

runoff or water vapor. These findings were concomitant with migration during this study except that emigrants and immigrants can move at 32°F. Ambystoma tigrinum diaboli adults, noted for their aquatic adaptability, may spend as many as four months in the lake. They normally exhibit mass emigration 1 or 2 times during the fall. Emigrant numbers were larger than reported by Larson (1968) who considered terrestrial adults to be infrequent. All migration terminates with freeze up. The beginning of migration varies with population dynamics. If neotenic are not present, emigration usually begins in late August; however, if they are present, adults may begin to leave as early as mid-July, suggesting overcrowding as a stimulus. Salamander emigrants take a 90° course from the waters edge, and maintain this bearing regardless of obstacles. Consequently, they are easily trapped by natural or man-made trenches, ditches, and window wells. Salamanders readily dig out of such traps. In leaving Devils Lake, they did not select areas of least resistance but showed some tendency to concentrate along restricted routes.

Parasites

Cestodes found in adult small intestines were identified as Ophiotaenia filaroides La Rue (Plates I and II). This tapeworm has been previously reported from Ambystoma tigrinum in North America (Wardle and McLeod, 1952).

Living within the lumen of the stomachs of some

adults were nematodes of the genus Spiroxys sp. (Plate III). Only female worms were collected making it difficult to identify them to species. Telford and Stevens (1942) reported Spiroxys in A. t. diaboli which were collected in North Dakota.

Larval nematodes were found encysted in the stomach wall, but the immaturity of the specimens made identification impossible.

SUMMARY

1. Devils Lake salamander population consists of larvae, adults and neotenus forms. The larval stage endures from egg hatching through development to adult or neotenic forms. The neotenus stage may persist for 2 or more years or undergo transformation. Adults leave the lake in early or late summer and return to breed the following spring.

2. Neotenuics, the largest life forms, may be found at all times of the year unless eliminated by winter kill.

3. Reproduction by neotenus forms has not been verified or refuted for this population. Eggs began development in neotenus and adult females in the fall. However, adult females exhibited mature eggs in the spring while the neotenus females contained no eggs.

4. Metamorphosis of neotenus forms could be initiated by penning in the lake or removing to aquaria. This suggests a hormonal response to the neurosecretory activity of the nervous system. Environmental factors operating to maintain the neotenus state under natural conditions are unknown.

5. Most numerous food organisms in descending order of use were amphipods, cladocerans, hemipterans,

trichopterans, and dipterans. Salamanders have suffered very little predation because of the absence of sustained populations of game fish.

6. Salamanders are most numerous in weed beds in shallow areas of the lake and least numerous in the limnetic area where only larvae were found. Larvae are more motile and range wider than adults or neotenic.

APPENDIX
Plates I, II, III

EXPLANATION OF SYMBOLS USED IN PLATES

CS...cirrus sac

E....eggs

ES...esophagus

O....ovary

OL...oral lips

S....suckers

T....testis

U....uterus

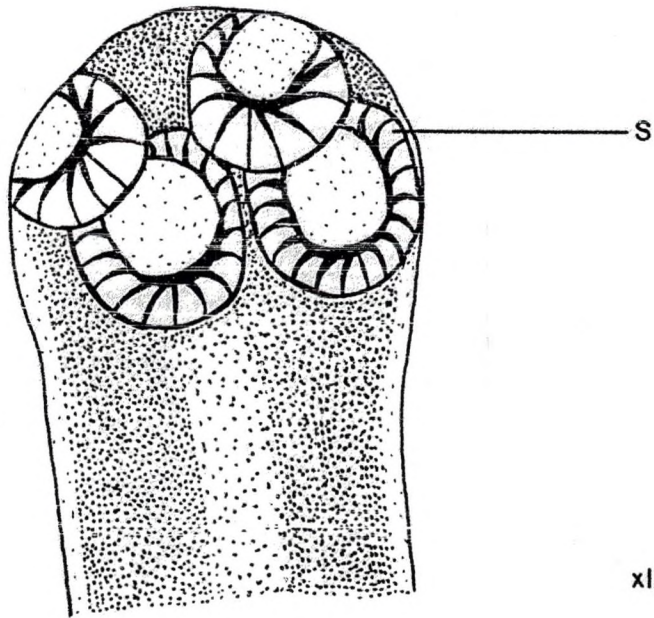
V....vitellaria

PLATE I

Ophiotaenia filaroides

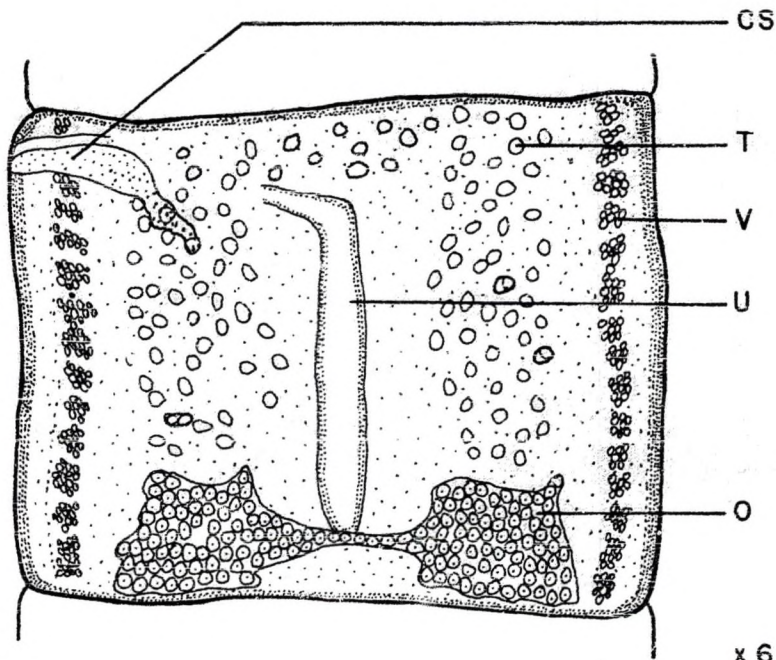
1. scolex
2. mature proglottid

1



x135

2



x65

PLATE II

Ophiotaenia filaroides

gravid proglottid

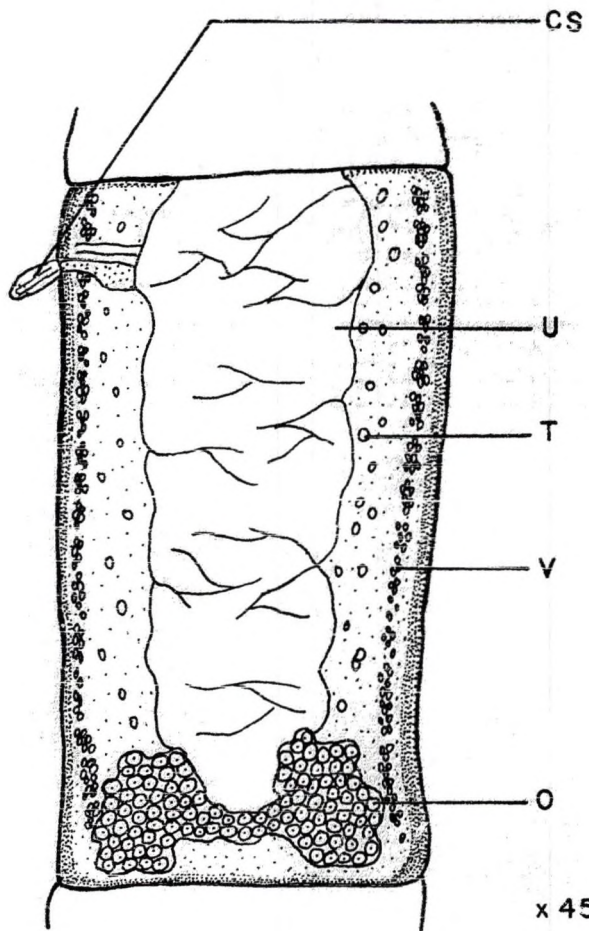
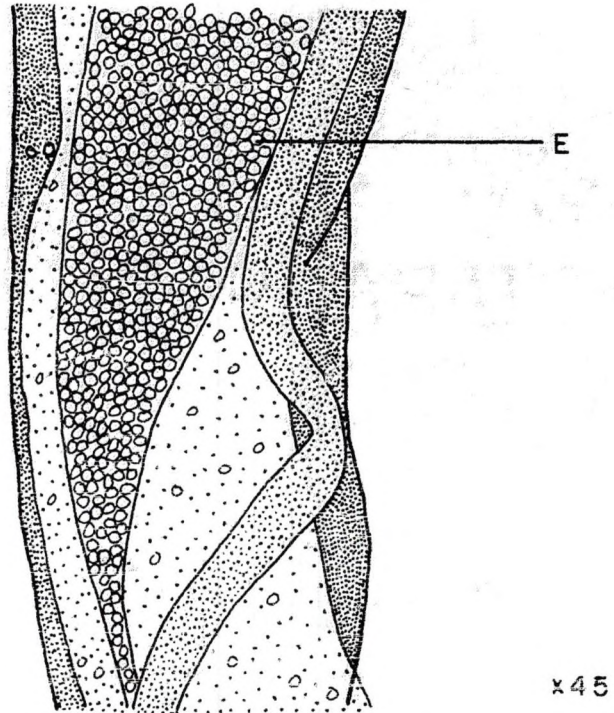
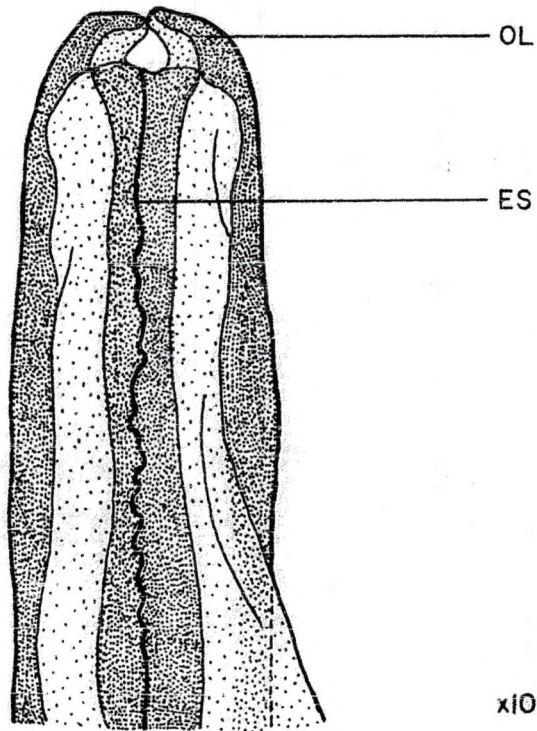


PLATE III

Spiroxys sp.

1. anterior region
2. mid region



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