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The reproductive biology of the leech Helobdella stagnalis (Linnaeus) in Utah Lake

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THE REPRODUCTIVE BIOLOGY OF THE LEECH *HELOBDELLA STAGNALIS* (LINNAEUS) IN UTAH LAKE

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INTRODUCTION

Helobdella stagnalis (Linnaeus, 1758), a small, brooding glossiphoniid leech which inhabits lakes and streams of both hard and soft waters, is found on every continent except Australia (Sawyer, 1972). This leech is one of the most common found in Central Utah (Beck, 1954). Sawyer (1972) discussed the distribution of this leech in the United States and gave a complete bibliography on its biology.

The reproductive biology of *H. stagnalis* has been studied in England by Mann (1957). Limited observations on the annual reproductive cycle of *H. stagnalis* in North America have been made by Castle (1900), Gee (1913), and Sawyer (1972). Because of the cosmopolitan distribution of this leech within North America, a detailed description of its reproductive biology seems justified.

The objectives of this study were to describe the reproductive cycle of *H. stagnalis* in Utah Lake and to correlate this cycle with the water temperatures. Utah Lake was chosen as a study site because of the wide range of temperatures the leech encounters during its life cycle. This would allow a closer examination of how temperature effects the annual reproductive cycle of *H. stagnalis*.

MATERIALS AND METHODS

Description of Study Area

Utah Lake is a shallow, eutrophic lake located in Central Utah with an area of 360 km^2. The water is highly turbid, hard and alkaline. The average depth of the lake is approximately three meters. Brown (1969) gives a more complete description of the lake.

The leeches used in this study were collected at a rocky shore area located on the eastern side of Goshen Bay 1.0 km north of the Ludlow sheep stable. The rubble in this area ranges in size from 10 to 30 cm. Under the rubble there is a sand-silt substrate. Lake temperatures range from 30 C in August to 0.5 C in January. The water temperature drops rapidly in the fall and rises quickly in the spring because of the shallowness of the lake. There is usually an ice cover of 10 to 15 cm on the lake from mid-December to late February.

Field and Laboratory Methods

Helobdella stagnalis were collected from the underside of rocks located at the upper shoreline to one meter deep. Collections were made at weekly and bi-weekly intervals through the reproductive period and monthly at the other times. The sample size was usually 25-30 with periodic population samples of 80. The leeches were removed from the rocks with forceps and placed in plastic jars containing lake water. The collected animals were relaxed in a chlorobutanol U.S.P. (Chlorotone) solution at room temperature (prepared by placing a few crystals of chlorobutonal in 15 ml of water and then heating until the crystals were dissolved). Relaxation was usually complete in 15 minutes. Once relaxed the length and width were measured and the ventral side was checked for the presence of eggs or young.

Five to 15 leeches from each sample were preserved in Bouin's fixative. The tissues were processed in a regular alcohol, toluene, paraffin series and embedded in Paraplast. Four to six leeches from 26 samples were sectioned at ten micrometers and stained with a standard haematoxylin and eosin series. Only the gonadal region, segments XI through XIX, was sectioned.

Continuous water temperatures were recorded at the study site with an underwater Ryan thermograph. A 23 kg cement weight, molded to enclose the thermograph, was used to anchor the thermograph in water one meter deep.

RESULTS

Annual Reproductive Cycle of Utah Lake

Field observation data on the reproductive cycle are summarized in Table 1. On June 15, 1970, 70% of the adult leeches (those that had overwintered) collected were carrying young and the remainder were clear. The average number of young per carrying leech was seven. On July 3, 1970, 50% were carrying eggs (average number 14) and 33.3% were carrying young; the remainder were clear. On July 16, 1970, 30% were carrying young (average number 3) and 3.3% were carrying eggs (average number 4). The August and September 1970 samples showed very little reproductive activity. The highest amount of brooding in these two months was on September 2, 1970, when 3.3% of the leeches were found carrying eggs and 3.3% were carrying young. From October 1970 to March 1971 no brooding activity was observed on the overwintering adult leeches.

On April 17, 1971, weekly sampling started and continued through August 1971. In the May 1, 1971, sample 59% of the leeches were carrying eggs; the remainder were

TABLE 1

SUMMARY OF FIELD DATA FROM JUNE 15, 1970, TO NOVEMBER 24, 1971

Date of Sample	Mean Water Temp. C	% Carrying Eggs	Av. No. of Eggs	% Carrying Young	Av. No. of Young	% Clear
June 15, 1970	19.5	0	0	70	7	30
July 3	25.8	50	13.6	33.3	10.5	16.7
July 16	26.7	3.3	4	30	3	66.7
August 19	31.7	0	0	0	0	100
Sept. 2	30.1	3.3	20	3.3	4	93.4
Oct. 10	4.5	0	0	0	0	100
Nov. 6	3.5	0	0	0	0	100
Dec. 4	3.5	0	0	0	0	100
Jan. 15, 1971	1.5	0	0	0	0	100
Feb. 27	1.0	0	0	0	0	100
March 30	7.5	0	0	0	0	100

TABLE 1 (continued)

Date of Sample	Mean Water Temp. C	% Carrying Eggs	Av. No. of Eggs	% Carrying Young	Av. No. of Young	% Clear
April 17	12.5	0	0	0	0	100
May 1	13.0	59	10.5	0	0	41
May 6	14.1	95	17.4	0	0	5
June 2	18.6	0	0	80	12	20
June 14	20.0	0	0	50	--	50
June 21	21.4	80	--	20	--	0
June 29	18.4	70	--	30	--	0
July 8	22.2	8	--	46	9.7	46
July 14	24.2	0	0	53	--	47
August 20	25.3	3.3	--	0	0	96.7
Sept. 13	20.5	0	0	0	0	100
Oct. 2	10.5	0	0	0	0	100
Nov. 24	3.9	0	0	0	0	100

clear. Ninety-five percent were carrying eggs in the May 6, 1971, sample (average egg count of 17.4); the rest were clear. Embryogenesis continued through May and by June 2, 1971, 80% of the population was carrying an average of 12 young. None of the leeches in this sample were carrying eggs. On June 14, 1971, 50% of the leeches were carrying young and 50% were clear.

In the June 21, 1971, sample, 80% of the overwintering adult leeches were bearing a second brood of eggs and 20% were still carrying young from the first brood. By June 29, 1971, 70% of the overwintering leeches were bearing eggs and 30% had young attached. On July 8, only 8% were carrying eggs and 46% were carrying young (average number 9.7). Forty-six percent were clear. On July 14, 53% were carrying young and the rest were clear. At this point, the overwintering adult leeches which had produced two broods began dying off and almost disappeared from the population by the August 13, 1971, sample (see Fig. 1). The young of the two broods could be separated from the adult overwintering leeches by total length, width and pigmentation. The young leech when it released from the parent was between 3.5 and 4.0 mm in length. The majority of overwintering leeches were between 7.0 and 8.0 mm in length.

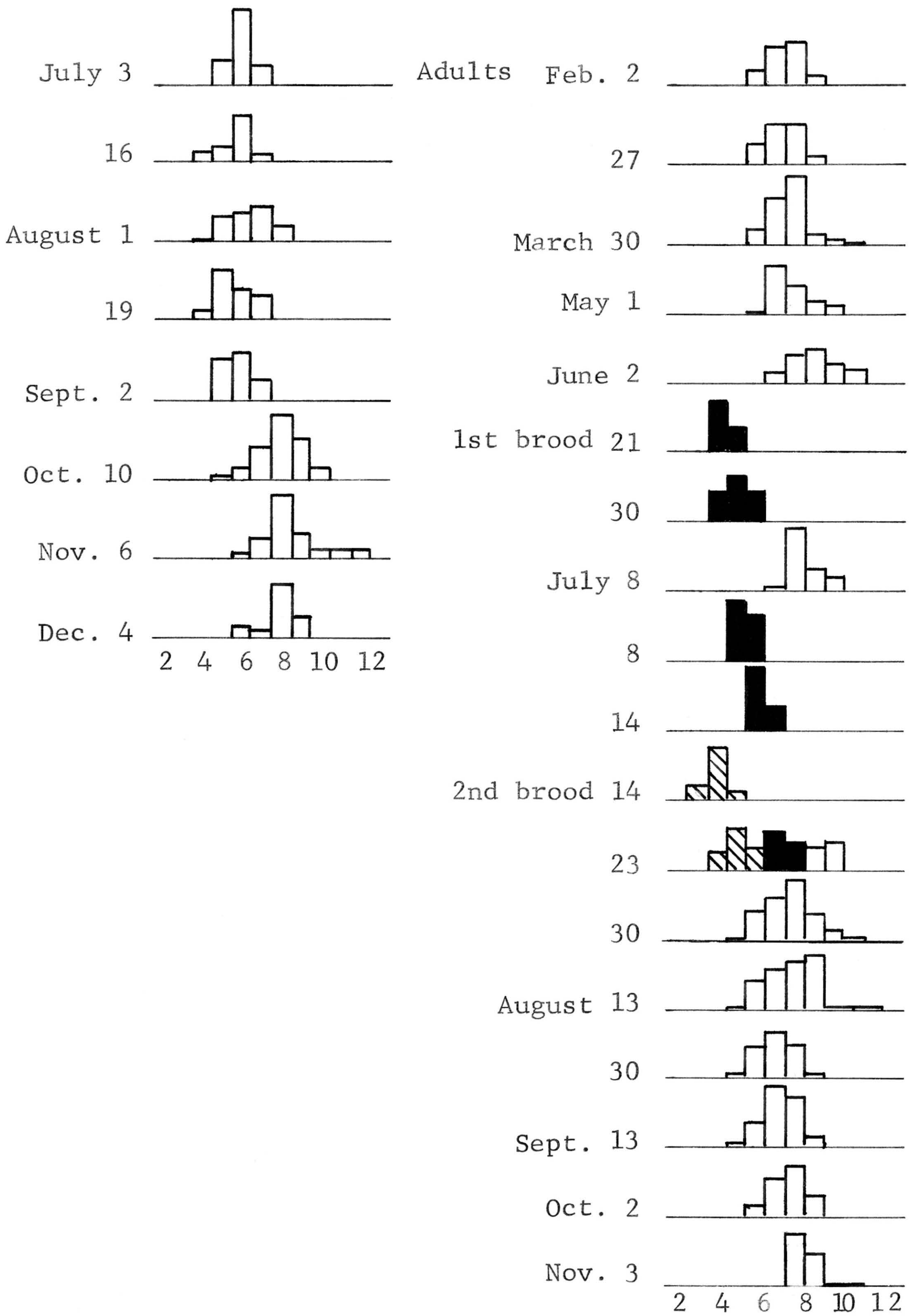


Fig. 1. Length distribution of <u>Helobdella stagnalis</u> in millimeters July 1970 to November 1971.

There is also a distinct width difference across the widest point. The young leech at time of release is about 1 mm across, whereas the overwintering leech is around 3 mm across. Young leeches are quite transparent with little pigmentation. The overwintering leech has yellow and brown pigment granules on the dorsal surface, which gives it a darker appearance.

No eggs or young were ever found on the young leeches of the first and second broods in June or July. In the August 20, 1971, sample, 3.3% of the new broods were carrying eggs. No brooding activity was observed through November 1971, when the study concluded.

Histological Data

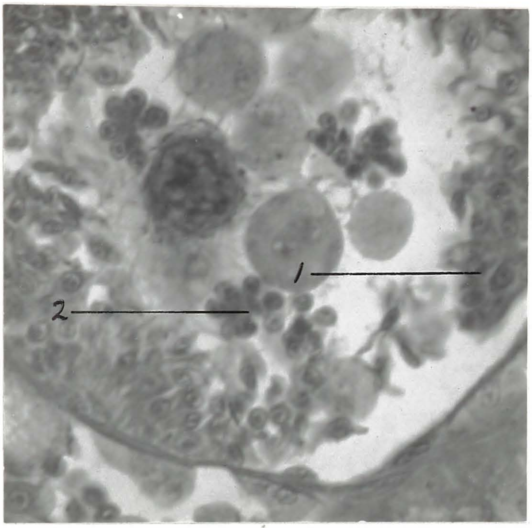
Staging of gonads

The staging of the gonads of H. stagnalis follow closely the work of Hagadorn (1962) and Malecha (1970). In staging the testes, five stages were used. Stage 1: individual cells are proliferating from the germinal lining. Stage 2: 8 to 16 cell stage. The spermatogonia have a clustered berry appearance. Stage 3: 32 to 64 cell stage with spermatocytes attached to a cytoplasmic mass called the cytophore. Stage 4: 128 cell stage with spermatids or mature sperm still attached to cytophore. Stage 5: the spermatozoa have been released from the cytophore and the cytophore is now free in the testes. The stages of spermatogenesis are shown in Figure 2.

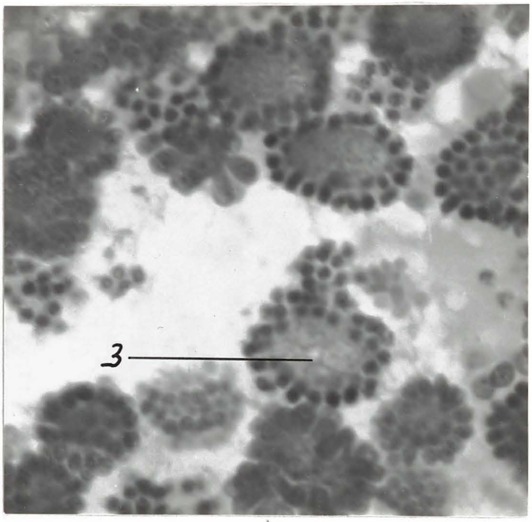
Oogenesis was divided into three stages. Stage 1: no differentiated cells in the ovarian strand. Stage 2: prospective ova larger than other cells of the ovarian strand. Stage 3: accumulation of yolk in the maturing oocytes. Stage E: the beginning of embryogenesis with the eggs on the ventral side of the leech. The stages of oogenesis are shown in Figure 3. For a complete description of the reproductive system see Castle (1900).

Results of histological sections

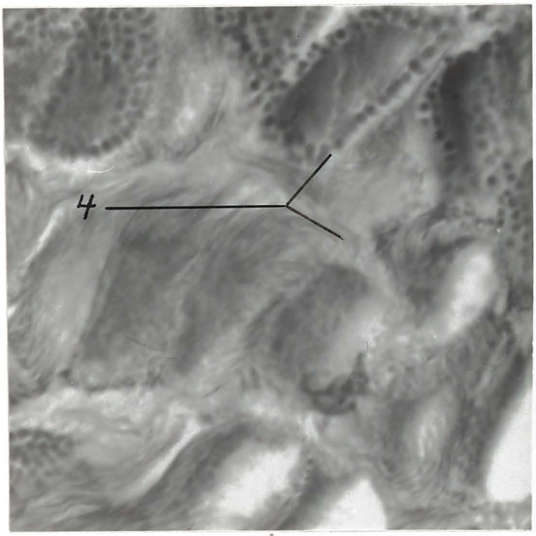
A summary of histological results is found in Table 2. On August 19, 1970, the ovaries were in Stage 2 of oogenesis and the testes in Stage 2 and 3 of spermatogenesis. The water temperature at this time was 31.7 C. By the December 4, 1970, sample, spermatogenesis had gone through Stage 5 and mature sperm were filling the seminal vesicle. The ovaries still remained in Stage 2 of oogenesis. During this period, August 19 to December 4, 1970, the mean water temperature dropped about 27 C.



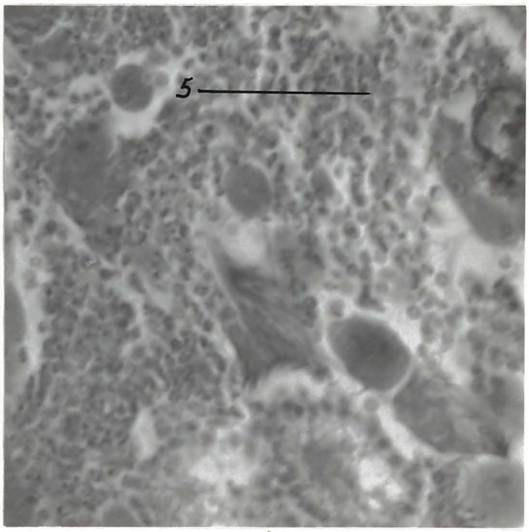
Stage 1 and 2 (400 x)



Stage 3 (400 x)

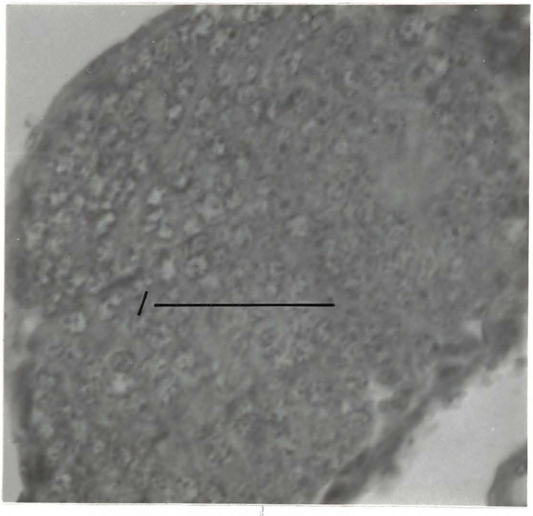


Stage 4 (400 x)

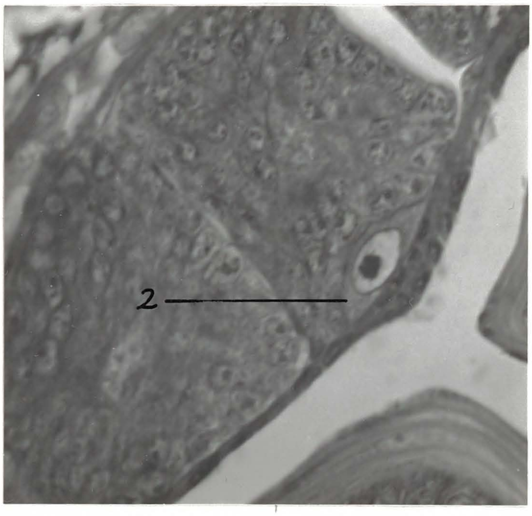


Stage 5 (400 x)

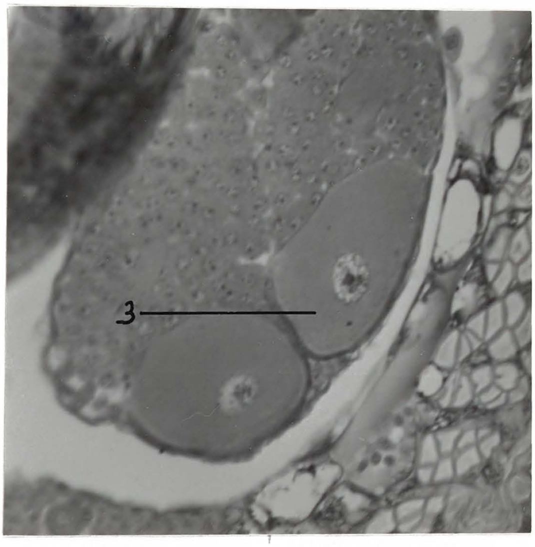
Fig. 2. Cross sections of testes showing stages of spermatogenesis.



Stage 1 (400 x)



Stage 2 (400 x)



Stage 3 (160 x)

Fig. 3. Cross sections of ovaries showing stages of oogenesis.

TABLE 2

RELATIONSHIP OF THE STAGES OF SPERMATOGENESIS AND OOGENESIS TO TEMPERATURE AND TO EACH OTHER

Date of Sample	Mean Temp. of Water C	Stages of Spermatogenesis	Most Prominent Stages of Spermatogenesis	Stage of Oogenesis
August 19, 1970	31.7	2, 3	2, 3	2
Sept. 2	30.1	2, 3	3	2
Oct. 10	4.5	4	4	2
Nov. 6	3.5	2, 3, 4	4, 5	2
Dec. 4	3.5	3, 4, 5	5	2
Jan. 15, 1971	1.5	1, 3, 5	1	2
Feb. 27	1.0	1, 2, 3	1	2
March 30	7.5	1, 2	1	3
April 10	11.4	1, 2	1	3
April 17	12.5	1,2	1	3
April 24	11.6	1, 2	1	3

TABLE 2 (continued)

Date of Sample	Mean Temp. of Water C	Stages of Spermatogenesis	Most Prominent Stages of Spermatogenesis	Stage of Oogenesis
May 1	13.0	1, 2, 3	2	3
May 6	14.1	2, 3	3	3, E
May 13	15.5	2, 3, 4	3	1, E
May 22	13.7	2, 3, 4	4	1, E
May 27	19.5	2, 3, 4	4	2, E
June 2	18.6	2, 3, 4	4	2, E
June 9	19.2	2, 3, 4, 5	4, 5	2
June 14	20.0	2, 3, 4, 5	4, 5	2
June 21	21.4	2, 3, 4, 5	2	3, E
July 8	22.2	1, 2, 3	2	1, E
July 14	24.2	1, 2, 3	3	1, E
July 30	26.1	2, 3, 4	3, 4	1
August 6	26.1	2, 3, 4	4	1

For the period December 4, 1970, to February 27, 1971, the most prominent stage of spermatogenesis present was Stage 1. The most prominent stage of oogenesis present was Stage 2. The mean water temperature ranged from 1.5 C on December 15-31 to 2.9 C on February 15-28. The lake was frozen over from mid-December 1970 until the first week of February 1971.

From March 1 to May 1, 1971, the testes remained in Stages 1 and 2 of spermatogenesis and the ovaries in Stage 2 until March 30. Rapid yolk accumulation in the oocytes occurred from March 30 to May 1, 1971. The diameter of the maturing oocyte on March 30, 1971, was 0.06-0.07 mm; on April 10, 0.10-0.11 mm; April 24, 0.24-0.25 mm; and on May 1, 0.29-0.30 mm. On May 1, the eggs were being pushed out of the ovaries into the brood pouch representing the first brood of young leeches. The mean water temperature ranged from 0.6 C on March 1-15 to 10.9 C on April 16-30.

From May 1 to June 14, 1971, the testes passed through all five stages of spermatogenesis and mature sperm were in the seminal vesicle at the end of this period. This was the second generation of sperm produced by the overwintering adults. During this same time, the ovaries showed little activity--remaining in Stages 1 and 2. Fifty percent of the first brood of young were released from the adults by June 14. The mean water temperatures for this period ranged from 15.5 C from May 1-30 to 19.3 C from June 1-15.

From June 21 to July 8, 1971, the testes remained in Stage 2 of spermatogenesis while the ovaries passed through Stage 3 of oogenesis. These eggs were the second generation produced by the overwintering leeches. The mean water temperatures ranged from 21.4 C from June 16-31 to 21.9 C from July 1-15.

It took four months for the first generation of sperm to form and six weeks for the second generation. Yolk accumulation took one month in the first generation of oocytes and one to two weeks in the second generation.

From July 8 to August 6, 1971, spermatogenesis went through Stages 3 and 4 and oogenesis stayed in Stage 1. The mean temperature for this period was approximately 25 C. The gonads were not sectioned after August 6, 1971.

Population Measurement Data

For length distribution data see Figure 1. From October through December 1970, the majority of the overwintering adult population was 6-9 mm in length. The range was from 4-12 mm. In the February 1971 samples, the range of length distribution was reduced as all adult leeches were from 5-9 mm long with two-thirds being between 6 and 8 mm. From March 30 until May 1, 1971, the majority of the adult leeches were in the 6-8 mm length classes. From June 2 until August 6, 1971, the majority of adult leeches were between 7 and 10 mm. The adults ranged in length from 5-11 mm for the period of March 30, 1971, to August 13, 1971, at which time they died. When released from adult overwintering leeches, young leeches were between 3.5 and 4.0 mm in length. By October 2, 1971, the majority of the first and second brood of leeches were in the 6-9 mm length classes.

DISCUSSION

Annual Reproductive Cycle

The annual reproductive cycle of Helobdella stagnalis in Utah Lake is considerably different from the cycle in Whiteknights Lake, Reading, Berkshire, England (Mann, 1957). Mann reported that the overwintering leeches produced a brood of young in May and then died in June. Over 50% of the new brood matured and reproduced in July and August and died after reproduction. The next year's overwintering leeches were composed of June leeches which did not mature and July to August leeches produced by mature June brood leeches. The overwintering leeches in Utah Lake have a first brood of young in May which release from the adults in mid-June. Then the same adults bear a second brood of young in late June and early July. The adults died after the second brood of young. Very few first and second brood leeches mature and reproduce that same summer. The leeches from the first and second brood then become the next year's overwinter population.

There are probably several reasons why the reproductive cycle of Helobdella stagnalis differs in the two localities. It may be a water temperature difference during the breeding season. This idea will be discussed in a later section. Mann (1957) included no temperature data in his study. A second reason may be adaptation. Since H. stagnalis is so wide spread, isolation may have occurred in various areas and a reproductive cycle developed that fits the environment of the leech. Numerous reproductive cycles may be present in H. stagnalis. If this were true, the cosmopolitan H. stagnalis could possibly be more than a single species.

Histological sections of the gonads confirmed the fact that the same adult leech can, in Utah Lake, produce two broods of young. The sections showed two distinct periods of egg development in the ovaries and three sperm production periods. The purpose of this third sperm production is uncertain since the animals died soon after the release of the second brood. Possibly it is the cyclic nature of the testes to produce sperm anytime the ovaries are inactive, despite the fact that the animal may die without utilizing the sperm. Mann (1957) did not do any histological sectioning to support his data. Length distribution classes showed two separate broods released by the same parent population with the adults disappearing from the population after release of the second brood.

Castle (1900) found that egg laying in H. stagnalis took place in April and May around Cambridge, Massachusetts, and that young individuals matured later in the season. In Denmark, Bennike (1943) found eggs from May 15 to August 23 and young from June 1 to September 11. Bruum (1938) reported that in Iceland the reproduction season of H. stagnalis is from April to September. In Iran, reproductive activities last from February to June (Bennike, 1940). Zschokke (1900) found that in the Alps H. stagnalis had a very short reproductive season lasting from July to early August. This short cycle found in the Alps may imply that only one brood is produced while in the other studies cited indications are that two broods may have been produced because of longer warm water periods (Bennike, 1943). This hypothesis is supported by a preliminary experiment conducted in our laboratory in which overwintering H. stagnalis were kept at 10 C and 20 C to see the effect of temperature on reproductive activities. The ones at 20 C produced two broods while those at 10 C produced only one brood (unpublished data, Barnes and Tillman).

Bennike (1943) feels temperature is the controlling factor in the breeding and distribution of leeches. Castle (1900) found that a rising spring water temperature initiated the breeding activities of _H. stagnalis_. Brooding activities in _H. stagnalis_ from Utah Lake also show a correlation with the rising water temperatures in March and April. It was also observed that the rate of gametogenesis is temperature dependent. The time for the first generation of mature sperm to be produced was four months while the second only took six weeks. During the production of the first generation of sperm, the mean temperature was 11.6 C; and during the production of the second generation, the mean temperature was 16.8 C. Yolk accumulation in the maturing oocytes of the first brood took four weeks (mean water temperature, 10.7 C) and the second brood took approximately two weeks (mean water temperature, 21.4 C). Embryogenesis was also temperature dependent. The second brood developed faster than the first when temperatures were warmer. From the first signs of brood pouches containing eggs until the release of young took approximately six weeks in the first brood. The second brood took only four weeks. Malecha (1970) found spermatogenesis in _Hirudo medicinalis_ to be temperature dependent also.

Preliminary laboratory experiments have shown the importance of temperature in the life cycle of *H. stagnalis*. Several aquaria, each containing 20 overwinter *H. stagnalis*, were kept at temperatures of 20, 10, and 2 C in the laboratory. They were fed earthworms; the light cycle corresponded to the daily photo period for the latitude of Provo, Utah, and was changed weekly. The leeches in the 20 C aquaria produced brood pouches containing eggs in 11 days. The ones at 10 C produced brood pouches containing eggs in 28 days, and those kept at 2 C for five months never produced brood pouches. The leeches kept at 2 C were placed in the 20 C incubator and within 17 days brood pouches containing eggs were observed (unpublished data, Barnes and Tillman). The above experiments are presently being repeated on a larger scale to verify previous results. Temperature is not only important in reproduction but has been shown by Hilsenhoff (1963) to determine the rate of feeding of *H. stagnalis*.

Ovarian and Testicular Activity

The gonads showed an off-on type activity throughout the reproductive cycle. While the testes were active, the ovaries were dormant and vice-versa. Never in any of the histological sections were the ovaries found to have developed beyond Stage 2 while the testes were going through Stages 2-5. The testes never progressed farther than Stage 2 while oogenesis Stage 3 (yolk accumulation) was active. Hagadorn (1962) reported a similar pattern in another glossiphoniid leech Theromyzon rude. He observed that while the initial stages of spermatogenesis were in progress, oogenesis was dormant. It is possible that the function of this off-on cycle is to increase the effectiveness of gamete production by directing the bulk of food energy to one system at a time.

Size of Adult Leech in Relation to Egg Production

Castle (1900) reported the average number of eggs on Helobdella stagnalis was 31. Mann (1957) found an average of 17.2. Bennike (1943) states the average is 20 eggs per leech and Sawyer (1972) found an average of 32 eggs on H. stagnalis in Michigan. The average number of eggs produced in the first brood in Utah Lake was 17.4 and the second brood was 13.6. These variations are probably due to size differences of the leeches from each particular locality. The adult H. stagnalis that Castle (1900) examined were 20-25 mm in total length. Sawyer (1972) reported an increase in egg count with increased length. The adult leeches examined in this study were 6-10 mm in total length. The average number of young attached to the adult leech was always less than the average number of eggs. The first brood average young count was 12 and the second brood average was 9.7.

Comparison of *Helobdella stagnalis* Life Cycle to Other Glossiphoniid Life Cycles

Mann (1957) described the life cycle of *Glossiphonia complanata* in England. He reported the leech to have two broods during the reproductive season. The two broods were produced by different individuals and did not come from the same animal as do the two broods of *H. stagnalis* in Utah Lake. The reproductive cycle of *G. complanata* appears to be temperature initiated in the spring with the first brood appearing in March to April and the second brood in May to June. Results showed the first brood was produced by two-year-old leeches and the second brood by one-year-old leeches. The two-year-old leeches and many of the one-year-old leeches die after reproducing, but some one-year-old leeches overwinter again to breed the next year. *Helobdella stagnalis* in Utah Lake lived one year and died after producing two broods that same year.

Hagadorn (1962) described the reproductive cycle of Theromyzon rude as beginning in May with 25% of the population carrying eggs. This increased to 60% in July and August. Nothing was mentioned as to number of broods or age structure of the leeches. Apparently it has a one-year cycle. It was shown that gametogenesis started with the new generation of leeches the same summer they were brooded. The same was true of new broods of H. stagnalis in Utah Lake; the first stages of spermatogenesis started in July and August.

Adequate Methods for Determining Reproductive Cycles

Temperature is a critical factor in the reproduction of Helobdella stagnalis in Utah Lake and appears to be important in other leeches (Bennike, 1943). It is felt that if future investigations are made on reproductive cycles of leeches, continuous water temperatures should be recorded to see if a relationship exists between the reproductive cycle and the temperature of the environment. Histological sections of the animal's reproductive system are also a necessity to adequately study the reproductive cycle. Samples should be taken weekly during the breeding season so that valid reproductive cycles can be determined. If the traditional monthly samples had been taken of *H. stagnalis* in Utah Lake, it would have been possible to miss entirely the production of the second brood of young. Also, histological sections of neurosecretory cells should be made since their activity can be correlated with reproductive activites (Hagadorn, 1962; Damas, 1966; Malecha, 1970). Sectioning and staining of the neurosecretory cells of *H. stagnalis* will be done in the near future.

CONCLUSIONS AND SUMMARY

The reproductive cycle of *Helobdella stagnalis* in Utah Lake is considerably different from the cycle described by Mann (1957). In Utah Lake the overwintering leeches produce two broods of young. One brood is produced in May and the second in late June. The adult overwintering leeches die after producing the two broods. The average number of young produced in the first brood is greater than in the second brood. The gonads of *H. stagnalis* have an off-on type of activity. When the testes are active, the ovaries are dormant and vice-versa. Two complete cycles of oogenesis take place during the year and three cycles of spermatogenesis. Gametogenesis is temperature dependent with the first generation of sperm taking four months to be produced in the fall and winter months while the second generation of sperm is produced in six weeks during the spring. Egg production and embryogenesis follow a similar pattern.

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THE REPRODUCTIVE BIOLOGY OF THE LEECH *HELOBDELLA STAGNALIS* (LINNAEUS) IN UTAH LAKE

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ABSTRACT

The reproductive biology of the brooding leech *Helobdella stagnalis* (Linnaeus) in Utah Lake was studied for an 18 month period from June 1970 to December 1971. In determining the annual reproductive cycle, the number of adult leeches carrying eggs or young were counted at weekly intervals during the reproductive season and monthly during the rest of the year. Gonadal staging data from histological sections were correlated with the field collection data. It was found that two broods of young were produced by the adult animals during the reproductive season. Continuous water temperatures were recorded at the study site throughout the period of this investigation. Temperature was found to have an effect on the rate of gametogenesis, development, and the number of broods produced. The gonads have an off-on type of activity. When the testes are active, the ovaries are dormant and vice-versa.

COMMITTEE APPROVAL: