A COMPARISON OF THE LIFE-CYCLE OF *HELOBDELLA STAGNALIS* (LINN. 1758) (HIRUDINOIDEA) IN TWO DIFFERENT GEOGRAPHICAL AREAS IN CANADA

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INTRODUCTION

*Helobdella stagnalis* (Linn.) is a widely distributed species of freshwater leech recorded from every continent except Australia (Sawyer 1972). With the exception of the Yukon it has been recorded from all Provinces and Territories in Canada (Davies 1973) and is also abundant throughout the northern United States of America (Sawyer 1972). Despite its widespread and common occurrence few studies have been made of the life-history of *H. stagnalis*. In Great Britain the life-history has been studied by Mann (1957a) and Learner & Potter (1974). In North America the only study is that of Tillman & Barnes (1973) in Utah Lake, Utah. This paper on the life-history, growth and age structure of *H. stagnalis* in British Columbia and Alberta is the first study in Canada.

SITE DESCRIPTIONS

Marion Lake is situated in south-western British Columbia 50 km east of Vancouver on the southern slopes of the Coast Mountains. The lake is 800 m long and at its maximum 200 m wide. The greatest depth is 7 m with a mean of 2·4 m. The lake bottom consists primarily of soft mud with a sparse covering of *Vallisineria* spp. in the shallow water and *Isoetes occidentalis* Henders. in water below 2 m. A more detailed description of Marion Lake appears in Efford (1967).

Newsome Pond is situated in south-eastern Alberta 5 km west of Calgary in the prairie-foothills transition zone with a typical knob and kettle topography (Legget 1961). The pond has been enlarged by the construction, in 1958, of an earth dike at the eastern and is presently 80 m long with a maximum width of 75 m. The maximum depth of water is 3 m with a mean of 1·5 m. The substratum is mostly soft mud with a high proportion of organic vegetable material. About 10% of the shore is stony, the rest consisting of soft mud which has a vigorous macrophyte (*Scirpus* sp.) growth in the summer.

METHODS

The collections of *Helobdella stagnalis* from Marion Lake were in part incidental to collections made for other components of the benthos relating to an International Biological Program project. The lake was divided into a grid of 106 squares each 1300 m² and the data presented represents collections made from those squares sampled regularly at four-weekly intervals during the whole of 1969 and May to October inclusive 1970 (Fig. 1). Collections were taken from the soft substrate using a Hargrave (1969) sampler

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(0.15 m$^3$). After collection the leeches were preserved in 70% ethanol and weighed. Learner & Potter (1974) showed that no significant change in weight occurred after preservation in ethanol, an observation confirmed in this study.

At Newsome Pond during the ice free periods leeches were collected at four-weekly intervals from the underside of the stones and rocks of the littoral zone using a 60-min unit time basis. This technique has been successfully used for many freshwater invertebrate population studies (Macan 1950; Mann 1955; Reynoldson 1966) and has been reviewed in detail by Kono (1953). During the periods of ice cover eight samples from the deep water zone were taken with an Ekman dredge (0.23 m$^3$) at randomly selected locations through holes cut in the ice, while during the ice free periods a dinghy was used. In the laboratory the leeches from the dredge samples were separated from the mud using a sieve and water spray. After the removal of excess moisture, the $H$. stagnalis collected were narcotized in carbonated water (Davies 1972) to determine the reproductive state and then returned within four days to the pond. Each month a sub-sample of three to five animals were sacrificed to determine the precise number of cocoons or young attached to the parents. The concentration of some of the major inorganic ions for Marion Lake appears in Efford (1967) while the water temperature data based on monthly means at 0.5–4.0 m are shown in Table 1.

At Newsome Pond on each sampling, pH, conductivity, dissolved oxygen concentration and alkalinity were measured in the field and a water sample taken for analysis of total hardness, calcium, sulphate and chloride in the laboratory. Water temperature at 1.0 m was continuously monitored with a recording thermograph (Table 2).

RESULTS

$Helobdella stagnalis$ lays its egg in transparent thin-walled cocoons which after deposition are covered by the body of the parent. The eggs develop attachment organs and adhere to
Table 1. Mean monthly water temperatures (°C) at depths of 0.5–4.0 m in Marion Lake, British Columbia

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<td>18</td>
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<td>14</td>
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<td>9</td>
<td>15</td>
<td>17</td>
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Table 2. Selected limnological characteristics of Newsome Pond, Alberta

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<thead>
<tr>
<th>Mean temp. (°C) at 1 m</th>
<th>1972</th>
<th>1973</th>
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<td></td>
<td>0.5</td>
<td>0.9</td>
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<tr>
<td>pH</td>
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<td>7</td>
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<tr>
<td>Dissolved oxygen (mg/l)</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Alkalinity (mg/l)</td>
<td>344</td>
<td>380</td>
</tr>
<tr>
<td>Hardness Ca++ (mg/l)</td>
<td>181</td>
<td>207</td>
</tr>
<tr>
<td>Total (mg/l)</td>
<td>330</td>
<td>259</td>
</tr>
<tr>
<td>Sulphate (mg/l)</td>
<td>8</td>
<td>8.5</td>
</tr>
<tr>
<td>Chloride (mg/l)</td>
<td>16</td>
<td>20</td>
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the ventral body wall of the parent. After hatching from the egg the young attach themselves again to the parent’s ventral body wall by the posterior sucker until their final liberation several weeks later (Mann 1961). The size structure and reproduction condition, as judged by the presence of attached eggs or young, of *H. stagnalis* from Marion Lake are shown in Fig. 2.

While none of the overwintering population carried eggs in January 1969, by February 11% of the population (mean weight 7.2 mg) carried eggs and in March 88.9% (mean weight 9.1 mg) carried either eggs or young. In April the appearance of a large proportion (43.2%) of small (0.5–1.0 mg) individuals indicated the liberation of young from the parents, a process completed in May when 47.4% of the population were in the 1–3 mg

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Fig. 2. The seasonal changes in the population size structure of *Helobdella stagnalis* from Marion Lake, British Columbia. The histograms are based on milligram weight categories and only those useful in interpreting the life-cycles are included. Hatched areas indicate brooding animals. Total sample size for each month shown in parentheses: (a) January 1969 (58); (b) March 1969 (36); (c) April 1969 (44); (d) May 1969 (56); (e) June 1969 (42); (f) July 1969 (50); (g) August 1969 (73); (h) September 1969 (30); (i) October 1969 (36); (j) May 1970 (41); (k) June 1970 (30); (l) July 1970 (22); (m) August 1970 (62); (n) September 1970 (53).
weight categories. By June the population consisted primarily of smaller leeches (mean weight 4.8 mg), while the parents (mean weight 12.3 mg) made up only 8.3 of the population. In June 38.1% of the offspring from the first generation carried eggs and in July 66.6% (mean weight 5.3 mg) carried either eggs or young. In July 14% of the population represented a new group of recently liberated young (0.5–1.0 mg) and another group of recently liberated young (29.8%) appeared in August. The samples from September (mean weight 4.6 mg) to December (mean weight 6.3 mg) showed a population made up of the offspring of the second generation produced in June/July with few if any of the parent population having survived.
Fig. 3. The seasonal changes in the population size structure of *Helobdella stagnalis* from Newsome Pond, Alberta. The histograms are based on milligram weight categories and only those useful in interpreting the life-cycles are included. Hatched areas indicate brooding animals. Total sample sizes shown in parentheses: (a) April 1972 (60); (b) May 1972 (24); (c) June 1972 (339); (d) July 1972 (72); (e) August 1972 (77); (f) September 1972 (34); (g) May 1973 (122); (h) June 1973 (257); (i) July 1973 (81); (j) September 1973 (43).
A similar pattern was shown in summer 1970. In May, 51.2% of the population was in the 1-4 mg weight range clearly representing the young liberated in April and May from the overwintering parent population (mean weight 8.05 mg). Recently liberated young (0.5-1.0 mg) also appeared in July and August when they made up 14.5% and 28.4% respectively. The samples from September and October showed a population consisting of the offspring (mean weight 4.9 mg) of the second generation with only 7.8% of the population in the 10-11 mg weight categories representing the survival of the parent population.

The size structure and reproductive condition of *H. stagnalis* in Newsome Pond are shown in Fig. 3. In April 1972 the overwintering population consisted of leeches of mean weight 5.4 mg, which by May had increased to 9.0 mg with 50% brooding young. In June a new group of recently liberated young (0.5-1.0) mg formed 68% of the total population, while 78% of the parent population still carried young. The July and August data showed an increase in weight to 2.2 mg and 4.2 mg respectively and a reduction in the proportion of the parent population from 40% of the total in July to 10% in August. This trend in growth of offspring and reduction in numbers of parents continued through
September and October so that the overwintering population consisted only of the offspring. The 1973 data are similar with recently liberated young appearing in the population in June followed by their growth and the gradual reduction of the parent population. In August, the last sampling date, the data showed a population with a similar weight frequency structure to that of the previous September.

For those months when eggs or young were brooded by the parents but no young had been liberated, in Marion Lake the mean number of eggs or young carried in March was $17.2 \pm 1.83$ ($P = 0.05$) and in June $19.7 \pm 1.42$ ($P = 0.05$). In Newsome Pond in May each parent carried a mean number of $21.3 \pm 5.96$ ($P = 0.05$) eggs or young.

The exact time of copulation in Marion Lake and Newsome Pond is unknown, but two *H. stagnalis* collected in January 1973 from Newsome Pond and kept individually in the laboratory at $18^\circ C$ both produced viable eggs within several days. This indicates copulation occurred prior to January and presumably in the fall, an inference substantiated in Table 3 based on *H. stagnalis* collected from Chestermere Lake, 10 km west of Newsome Pond.

Table 3. Viable cocoon production by *Helobdella stagnalis* collected in the winter from Chestermere Lake, Alberta and maintained in the laboratory for thirty days in individual containers at $20^\circ C$

<table>
<thead>
<tr>
<th>Date collected</th>
<th>No. collected</th>
<th>% producing cocoons</th>
<th>% mortality</th>
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<tr>
<td>November 1969</td>
<td>32</td>
<td>40.6</td>
<td>6.3</td>
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<tr>
<td>December 1969</td>
<td>25</td>
<td>76.0</td>
<td>16.0</td>
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<tr>
<td>January 1970</td>
<td>18</td>
<td>88.9</td>
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At Newsome Pond during the periods of ice cover (January–March and November–December) while *H. stagnalis* were captured in the Ekman dredges taken in water deeper than 2 m, none were found on the shore. In March the shore was ice free and in April the whole lake was ice free but *H. stagnalis* were not found on the shore until the May sampling. Subsequent sampling during the summer showed *H. stagnalis* on the shore and very few in the deeper waters. A similar pattern of events was observed in the 1973 sampling programme.

Shore collections were not taken in Marion Lake but from April to November 83.4% of the *H. stagnalis* collected were in water less than 2 m while during the remaining periods 93.2% were collected from water deeper than 2 m.

DISCUSSION

Great similarity in life cycle pattern occurs between Marion Lake and Whiteknights Lake, England (Mann 1957a). In Whiteknights Lake the two generations of young are produced in May and July/August both some four to six weeks later than in Marion Lake. Essentially all the first generation of young reproduces the same summer in Marion Lake with the overwintering population consisting entirely of the second generation. Mann (1957a) records only 60–70% of the May generation reproducing the same summer so that the overwintering population consists of survivors of both the first and second generations.

The liberation of young from the parents of Whiteknights Lake and their appearance in the population occurs over a short period of two to four weeks compared to Marion Lake where the same event occurred over a period of four to eight weeks. Analysis of the data from each of the two groups of squares sampled in Marion Lake (Fig. 1) separately
shows the same extended period of young liberation occurs in both regions of the lake indicating a general reduced synchrony of reproduction.

Learner & Potter (1974) claim that their results from Eglwys Nunydd, Wales indicate a similar life cycle to that described by Mann (1957a). However, as the sample sizes of the critical periods of the life-cycle are so low their evidence for two generations per year is tenuous.

In Denmark, Bennike (1943) records *Helobdella stagnalis* brooding eggs or young from April to August and concluded that this extended five-month reproductive season indicated the production of at least two generations of young. Similar circumstantial evidence of two generations of young can be deduced from Iceland (Bruun 1938), Central Europe (Herter 1937), Poland (Wilkialis 1970), Iran (Bennike 1940), Canada (Moore 1964) and U.S.A. (Castle 1900; Moore 1912; Gee 1913; Thut 1969; Sawyer 1972).

Zschokle (1900) recorded that *H. stagnalis* at the higher altitudes of the Swiss Alps had a brooding season of only one month suggesting that only a single generation of young is produced per year. Similar evidence for a single generation of young can be deduced from Canada (Moore 1966) and U.S.A. (Sapkarev 1968; Hilsenhoff 1967). The data presented from Newsome Pond, Alberta is the first fully documented case of *H. stagnalis* producing only a single generation per year.

Tillman & Barnes (1973) describe a very different life-cycle for *H. stagnalis* in Utah Lake, where the overwintering population produces two broods of young, the first in May and the second in June before post-productive mortality. The conclusions of Tillman & Barnes are drawn from field and laboratory observations as well as histological data on gonad development. Two peaks of egg brooding in early May and late June are reported but data on the seasonal changes in population structure are not presented for analysis. Whether these two peaks of egg brooding represents two broods of young produced by the overwintering population or simply two separate generations as described for Marion Lake and Whiteknights Lake (Mann 1957a) is questionable. In Utah Lake 940 day-degrees occur between the hatching of the ova of the first generation and the production of ova for the second generation. This compares with 1000 day-degrees in Eglwys Nunydd (Learner & Potter 1974) and 1064 day-degrees in Marion Lake. This indicates that the first brood in Utah Lake had time to mature and produce a second generation.

The question of whether *H. stagnalis* from Utah Lake does indeed produce two broods compared with the usual single brood requires further investigations. If the conclusions drawn by Tillman & Barnes are substantiated then the question of whether or not they observed the same species as other investigators must be examined.

At Marion Lake and Newsome Pond the young liberated from the parents ranged from 0.5-1.0 mg; the range in size of reproductively mature animals was 4-15 mg while the overwintering population ranged from 5-10 mg. These figures are in close agreement with Mann (1957a). Strangely Learner & Potter (1974) present their size classes in terms of the diameter of the posterior sucker although a formula for conversion to fresh weight is given. After conversion it is clear that the population size structure in Eglwys Nunydd is very different. The liberated young range from 0.002-0.026 mg; mature reproductive animals range from 1.4-13.6 mg while most of the overwintering population are in the 1.5-2.5 mg weight categories. It is not possible to compare the Tillman & Barnes (1973) data as they use body length rather than weight for their size categories.

The time of copulation (sperm transfer) in Newsome Pond is suggested to occur in the fall with egg production the following May. Examination of the gonad development data presented in Tillman & Barnes (1973) also indicates that copulation in Utah Lake may
also occur in the late autumn. In November and December they showed the testes containing mature spermatozoa while during January to April only individual cells proliferating from the germinal lining were present in the testes. The advantage of autumn copulation by the overwintering population is that full and immediate advantage of the productive season commencing with the increase in spring water temperatures can be taken. In Newsome Pond with eggs present on the parents in April unless copulation occurred the previous fall, it would have to occur under ice at water temperatures of 0.5-1.0°C. There is no evidence to indicate when the overwintering individuals in Marion Lake copulate although clearly the second generation of young must be the result of summer copulation.

The mean number of eggs or young carried per individual *H. stagnalis* in Marion Lake was 17-2 and 19-7 and in Newsome Pond 21-3 compared to the previous records of 31 (16-45) (Castle 1900), 30 (Heinrichs 1905), 13 (Bychowsky 1922), 30 (Berg 1938), 20 (7-37) (Bennike 1943), 20 (17-23) (Moore 1966), 14-5 (6-36) (Thut 1969), 13-17 (Mann 1957a), 16 (14-36) (Wilkialis 1970), 12-6-17-4 (Tillman & Barnes 1973), 14 (2-34) (Learner & Potter 1974), 35-3 (Sawyer 1972). Much of the great variability can be accounted for by the detachment of eggs and particularly young during handling and the inclusion in the calculation of the means of samples taken when a proportion of the young were already liberated. In Newsome Pond in May the mean number of young per individual was 21-3 but in June, when 76% of the population still carried young but liberated young also appeared in the population, this figure had fallen to 7.4±2.54 (P = 0.05). Sawyer (1972) records that in the laboratory one individual produced sixty eggs while his field records give a mean figure of 35-3 suggesting high mortality of eggs between laying and attachment to the parent.

Most authors suggest that temperature is the main factor controlling breeding in leeches (Castle 1900; Bennike 1943; Mann 1957a, b, 1961; Tillman & Barnes 1973; Learner & Potter 1974; Sawyer 1972) and that rising temperature in the spring is the stimulus for reproductive activity. Bennike (1943) reported breeding to start when the water is about 12–13°C, although Herrman (1970) recorded *H. stagnalis* in habitats in Colorado where the midday June water temperature was 5°C. In Marion Lake the first egg-brooding adults appeared in February/March with water temperatures of 1.5–2.5°C in 1969 and 5.0–6.0°C in 1970; eggs first appeared in Newsome Pond in March with water temperatures of 3–5°C. Whether declining temperature in the fall initiates copulatory behaviour in the Newsome Pond population is unknown.

Of the three previous life cycle studies, Mann (1957a) does not include water temperature data. Tillman & Potter (1973) showed that the breeding activity of *H. stagnalis* from Utah Lake was correlated with rising temperature in March and April (0.6–10.9°C) and also observed that the rate of gametogenesis appeared temperature dependent. Learner & Potter (1974) recorded water temperatures of 15.0–18.6°C in their presumed reproductive season of May to September.

A comparison of temperature data between Marion Lake and Newsome Pond shows a maximum for Newsome Pond to be about 25°C with a growing season from late April to the beginning of September. For Marion Lake the maximum temperature is 24°C with a growing season from April to November a difference of 1.5–2.0 months.

The second generation in Marion Lake took only approximately four weeks from appearance of eggs to the release of young and it would therefore appear that there might be time for the production of a second generation in Newsome Pond. However, as *H. stagnalis* in Newsome Pond produces its first generation almost a month later than
Marion Lake, with a similar rate of development the second generation could not be released before the middle of August. This would allow only one month of growth before the middle of August. This would allow only one month of growth before the water temperature falls and an early winter could come while the young are still too small to successfully overwinter. It is therefore likely that the short season in south Alberta is a major factor in preventing the production of a second generation.

In Marion Lake there are 2370 day-degrees between the release of the second generation in July and the cessation of growth in November. This is surprisingly similar to the corresponding figure for Egwys Nunydd and Utah Lake of 2043 and 2520 day-degrees respectively. In Newsome Pond it was assumed that a second brood of young could not be liberated before August and as growth stops in September only 1160 day-degrees are available. This is probably insufficient for the development of the young to reach a size able to survive the rigours of overwintering. It would appear that temperature in terms of length of growing season is at least one of the most important determinants. Indications of only one generation per season come only from regions with comparably short growing seasons.

The growth rates for the Newsome Pond population and the overwintering population in Marion Lake are similar with rapid growth in the summer little growth in the winter and a second period of rapid growth the following spring. In Marion Lake the first generation produced in April showed a continuous period of growth until their death in July (Fig. 4). The Newsome Pond population and the overwintering Marion Lake population curves are very similar to those from Whiteknights Lake (Mann 1957a).

Many authors have recorded that, unlike most species of leeches, *H. stagnalis* are often found in deep waters and are not strictly confined to the shallow littoral zone. Sapkarev (1968) found *H. stagnalis* in Lake Mendota, Wisconsin from the shoreline to a water depth of 12 m although the greatest population density was in the 0–1 m zone, especially in the summer and early fall. Thut (1969) found a very definite maximum at 40 m water depth with large numbers from 20–45 m, however, waters shallower than 10 m were not sampled. Berg (1938), Sapkarev (1968), and Okland (1964) all record *H. stagnalis* from profundal depths and Bennike (1943) concluded that in Lake Fures, while most
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commonly encountered in the surf zone (0–1.5 m) from May to September, migration to greater water depths did not occur during the rest of the year; the littoral *H. stagnalis* being killed by winter ice.

In both Newsome Pond and Marion Lake evidence is presented to show that *H. stagnalis* migrates to deeper water in the winter and from deep water to shallow littoral zone in the spring. This migration is most complete in Newsome Pond with no *H. stagnalis* on shore during the winter and markedly increased density in the deeper waters; conversely in the spring after ice melt there are very low densities in the deep waters and high densities on shore. Seasonal movements to and from water deeper than 2 m is shown similarly in Marion Lake. Clearly, studies not including samples of *H. stagnalis* from all water depths are likely to be misleading especially in areas of ice-cover during the winter.

Mann (1957a) states that the small size of *H. stagnalis* as compared to *Glossiphonia complanata* (Linn.) and the related smaller number of eggs, brooded, would place the species at a serious numerical disadvantage in the face of the observed mortality, if it were not for the second generation produced in the summer increasing the number of offspring produced. Mann (1957a) suggested this increased breeding potential was responsible for *Helobdella stagnalis* being the most numerous leech in eutrophic lakes in England.

It is interesting to compare the potential numbers of offspring that may be produced in the three areas. In Whiteknights Lake (Mann 1957a) 169–289 offspring per overwintering adult per year could result compared to 196 in Eglwys Nunnydd (Learner & Potter 1974), 295–388 in Marion Lake and twenty-one in Newsome Pond. If each overwintering parent produces two broods in Utah Lake (Tillman & Barnes 1973), twenty-two offspring will result (twelve from the first brood and 9.7 from the second brood); if, however, two generations are produced, this increases to 116. Reproduction in Marion Lake and Whiteknights Lake is such that it would allow the species to respond quickly to environmental changes and presumably to colonize new areas rapidly. In Newsome Pond reproduction is only just maintaining the population and any deterioration in the environment could cause a significant reduction in population size. This fact might well explain the puzzling unexplained absences and apparent extinctions of *H. stagnalis* from a number of the smaller sloughs sampled in southern Alberta.

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SUMMARY

(1) The life-cycle of the leech *Helobdella stagnalis* was studied in Marion Lake, British Columbia and Newsome Pond, Alberta.

(2) The overwintering population in Marion Lake reproduced in March and then died after the completion of brooding. The spring generation grew rapidly and a second generation of young was produced in July. After summer growth the second generation formed the next overwintering population.
(3) The overwintering population in Newsome Pond reproduced in May and then died after completion of brooding. After summer growth this generation formed the next overwintering population.

(4) It is suggested that copulation in Newsome Pond occurs in the fall with egg production the following spring.

(5) An annual migration between the shore zone and deep water zone occurred in Newsome Pond. During most of the ice free periods *H. stagnalis* were in high densities in the shore zone and in very low densities in the deeper waters. Conversely during periods of ice cover the densities in the deeper waters increased and none were found on shore.

(6) In Marion Lake between April and November 84.4% of the *Helobdella stagnalis* collected were in water less than 2 m deep; during the rest of the year 93.2% were collected from water deeper than 2 m.

(7) The life cycle in Marion Lake is similar to that described previously in England and Wales with two generations per year. The life cycle in Newsome Pond is the first documented example of a single generation being produced per year.

(8) It is suggested that water temperature in terms of growing season is at least one of the most important determinants for the production of only one generation per year in Newsome Pond.

REFERENCES


Life cycle of Helobdella stagnalis


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