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THE UNIVERSITY OF ALBERTA

EFFECTS OF THERMAL EFFLUENT ON THE POPULATION DYNAMICS OF *PHYSA GYRINA* SAY (MOLLUSCA: GASTROPODA) AND ITS HELMINTH PARASITES AT WABAMUN LAKE, ALBERTA

by

© CHANDRA SEKHAR SANKURATHRI

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Effects of thermal effluent on the population dynamics of *Physa gyrina* Say (Mollusca: Gastropoda) and its helminth parasites at Wabamun Lake, Alberta" submitted by Chandra Sekhar Sankurathri, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Effects of thermal effluent on the population dynamics of *Physa gyrina* (Mollusca: Pulmonata), its larval helminth parasites, and populations of *Chaetogaster l. limnaei* and *C. l. vaghini* were studied at Wabamun Lake, Alberta, from May 1971 to August 1973.

Thermal effluents increased the rate of development and growth of *P. gyrina*, and allowed continuous reproductive activity throughout the year. These changes, and the increased period of growth of aquatic macrophytes, resulted in increased population densities of *P. gyrina* in the heated area. Temperatures below 10° or small amounts of vegetation can apparently control the population of *P. gyrina* in the winter.

Thermal effluents provided the necessary conditions to maintain trematode transmission throughout the year, increased the prevalence of certain parasites, especially metacercarial stages, and enhanced parasite populations in definitive hosts during the winter.

Thermal effluents eliminated or reduced *C. l. limnaei* (which are highly sensitive to temperature above 24° C) and *C. l. vaghini* from *P. gyrina* during the summer. These oligochaetes are sensitive to high temperatures and may be good indicators of thermal pollution.

Chaetogaster l. limnaei is a very effective agent of biological control for trematodes with free-living larval stages. The elimination of *C. l. limnaei* from *P. gyrina* in the heated area during the summer resulted in higher metacercarial infections.

The *Physa gyrina*-trematode-chaetogaster system is a complex one, in which water temperature plays a central modifying role. The entire

system, its components, and especially *Chaetogaster l. limnaei* and *C. l. vaghini*, show potential as ecological indicators of thermal pollution.

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INTRODUCTION

Thermally altered aquatic environments are becoming commonplace throughout the world. Rapidly increasing demands on energy requirements are promoting the exploitation of energy sources of all types. Hence thermal electricity generating plants, using both fossil and nuclear fuel, are being built increasingly rapidly. These bring with them the problem of disposal of "waste" heat from condenser coolers.

For the last few years there has been much concern among biologists regarding the effects of thermal effluents from power plants on the aquatic habitats important for fish and other aquatic organisms. Problems stemming from these effects will be exacerbated by the ever increasing demands on both power and recreational facilities due to population growth. Increased exposure of populations and communities of aquatic organisms to thermal discharges can thus be anticipated when natural water systems are utilized as a cooling source. Hence a critical need exists to understand how thermally affected (or altered) environments function biologically.

The biological effects of thermal discharges on aquatic ecosystems are many and diverse. They may range from direct lethal effects of high temperatures to subtle changes in behavior, metabolism, performance, community structure, food chain relationships, and genetic selection (Cairns 1968).

Reviews dealing with thermal effects (Coutant 1968, 1969, 1970, 1971, Coutant and Goodyear 1972, Coutant and Pfuderer 1973, 1974) indicate

the amount and variety of studies conducted. Most of these studies have dealt with the effects of heated water on estuaries, rivers and large lakes. Few deal with relatively shallow eutrophic lakes, particularly in northern latitudes, such as that of Edmonton.

Lake Wabamun, approximately 65 kilometers (40 miles) west of Edmonton, is such a lake and was chosen as the site for a long-term interdisciplinary program, initiated in 1968, with Dr. J. R. Nursall, Department of Zoology, as the principal investigator. The preliminary results of various studies of this program were given by Gallup (1971). So far studies dealing with phytoplankton (Wheelock 1969), rotifers (Horkan 1971), epiphytic algae (Klarer 1973) and submerged macrophytes (Allen 1973) have been completed and other studies are in the process of completion. This program provided an excellent background for work on snails and their parasites and an unique opportunity to test the usefulness of parasites as indexes of ecological changes.

Over a half century ago Ward (1919) recognized that the small organisms are the most powerful biological tools for pollution studies and he said:

> As a means for determining the suitability of the water body for the existence of fish life and its favorableness for the multiplication of fish species, it is better to study the small organisms rather than the fish themselves. The fish are evidently less subject than are the smaller organisms to the control of the immediate environment and better able to change continuously their position, as well as to undergo for a limited period unfavorable conditions without really adapting themselves to the situation.

The points Ward made for small organisms apply particularly well to larval helminth parasites and their invertebrate hosts.

It is generally accepted that the parasite fauna in an aquatic ecosystem is determined by the interaction of various biotic and abiotic

forces (Dogiel 1964). This suggests that ecological changes in the habitat or the organisms living there will be reflected in the parasite fauna and that parasites may therefore be good ecological indicators.

The potential value of parasites as biological tags or ecological indicators has been recognized for some time. Parasite tags have been used in studying the continental origin of high seas salmon stocks in the Pacific (Margolis 1956). A parasitic copepod, *Sphyrion lumpi*, has provided information about the degree of discreteness of western North Atlantic red fish stocks (Templeman 1950, Perlmutter 1953). Sproston and Hartley (1941) have used another parasitic copepod (*Lernaeocera branchialis*) to identify the inshore and offshore whiting and pollock in European waters.

Parasitological data were used as auxiliary sources of information about the biology of Pacific salmons by Margolis (1965). Sindermann (1961a) has used larval cestodes (trypanorhynchs), a fungus parasite (*Ichthyosporidium hoferi*), larval anisakid nematodes and a myxosporidian (*Kudoa clupeidae*) to provide the information that there were no major migrations or movements between herring populations from Gulf of Maine and Gulf of St. Lawrence. Parasitological evidence was also used to support the changes in feeding habits of the Atlantic argentine (*Argentina silus*) by Scott (1969). Similarly, Gibson (1972) has used parasites as markers to trace three populations of flounders in the U.K. and Olson and Pratt (1973) have used parasites as indicators of English sole nursery grounds in Yaquina Bay, Oregon.

The study of parasites can be of great significance to establish the effects of ecological changes in a habitat. Esch (1971) studied the

parasite fauna of molluscs and fish of an oligotrophic lake compared with that of an eutrophic lake. To explain the distribution of parasites, he proposed a trophic hypothesis, based on the nature of predator-prey relationships in the two types of habitats. Earlier, Wisniewski (1955, 1958) suggested that a characteristic trait of eutrophic ecosystems is that the parasites of fish are mostly larval forms which culminate their life cycles in fish-eating birds and mammals.

The above-mentioned studies suggest that parasite faunas are influenced by changes in the habitat and hence that parasites may be a good measure of the general ecological conditions. Among other uses, studies on parasites may be useful in assessing the impact of environmental pollutants. Study of Arai and Kussat (1967) showed that domestic and industrial effluents discharged into the Bow River at Calgary affected the distributional patterns of two acanthocephalan parasites, *Octospinifer macilentus* and *Neoechinorhynchus cristatus*, in catostomid fishes, presumably by exclusion of their arthropod intermediate hosts.

There have been few published reports on the effects of thermal effluents on the population structure and species diversity of adult helminth parasites. Esch and Gibbons (1970) showed that thermal pollution dramatically increased the growth of the yellow bellied turtle, *Pseudemys scripta*. They also suggested that thermal pollution did not change the quality of the enteric parasite fauna, but did change the population structure of a few species of parasites (*Camallanus* sp., *Spiroxys* sp., *Neoechinorhynchus* spp.). Bourque and Esch (1973) found that thermally altered conditions have resulted in decreased parasite species diversity in *P. scripta*, but increased numbers of parasites per host. Trematodes were adversely affected, but certain species of

acanthocephalans increased in heated areas. Eure and Esch's (1973) study on largemouth bass (*Micropterus salmoides*) has shown that thermal effluents resulted in a larger number of helminth parasites than in the fish from the unaffected areas. In order to understand the reasons for these changes in the species diversity and population structure of parasites and their mode of transmission in a habitat, studies should also be conducted on the intermediate hosts (or invertebrate fauna) along with the definitive hosts.

Many helminth parasites have indirect life cycles with invertebrates as obligatory intermediate hosts. Among the various invertebrates, molluscs constitute an important link in the circulation of parasites. They are obligatory first intermediate hosts of most of the Digenea, second intermediate hosts of many digeneans and intermediate hosts of some cestodes and nematodes. All of the known molluscan hosts belong to the Gastropoda, Scaphopoda and Pelecypoda (Wright 1971). Most of the aquatic intermediate hosts of trematodes are benthic and slow moving. They do not generally undergo elaborate diurnal migrations, although some do make seasonal offshore migrations during the winter, which seem to be temperature dependent (DeWitt 1955, Sindermann 1961b, Rowan 1966, Morris 1970). Because of their population sizes and their status as permanent residents, gastropods would be especially suitable to use in assessing the impact of environmental pollutants, including thermal effluents.

Of all the gastropods collected at Wabamun Lake, only *Physa gyrina* Say was present in large numbers in both the heated and unaffected areas of the lake. Moreover, these pulmonate molluscs were present throughout the year in the heated area, and they have a varied and interesting

parasite fauna. Background information on the ecology of *Physa gyrina* has been provided by the studies of DeWitt (1954a, b, c, 1955) at Michigan and by Clampitt (1970) at Iowa. Hence *P. gyrina* was selected as the main object of this study to investigate how a thermally altered habitat can influence the biology of a snail and its parasites.

Poikilothermic animals are profoundly affected by temperature in many ways. Probably no other single factor has a greater effect upon their general biology. Temperature influences the speed of development, the duration of life, the fecundity, and the behavior of animals (Andrewartha 1971). Molluscs and their parasites are no exception to this rule. *Physa gyrina* oviposit only when the water temperature is raised to at least 10° C (DeWitt 1955, Clampitt 1970), and embryonic development (DeWitt 1954a) and growth (DeWitt 1955, Clampitt 1970) are faster at higher temperatures. Temperature has similar influences on other species of freshwater molluscs, like *Aplexa hypnorum* and *Lymnaea palustris* (McCraw 1970), *Lymnaea stagnalis appressa* (Vaughn 1953), *Helisoma trivolvis* (Morris 1970), and *Lymnaea truncatula* (Heppleston 1972).

Of the various groups of helminths, digenetic trematodes probably provide the best material for a study of the effects of thermal effluents on the transmission of parasites. Most trematodes have complex life cycles and almost all the larval stages, both free-living and parasitic, are influenced by environmental conditions, especially temperature (Wright 1971). Temperature is important in determining the rate of development of the intramolluscan stages of digenetic trematodes and hence in the timing of events in their life cycle (Smyth 1966, Wright 1971).

Most trematode eggs have to be embryonated in water; the duration of embryonation and the emergence of miracidia are dependent on the water temperature. Development of eggs was inhibited below 10° C in the case of *Bulbophorus confusus* (Fox 1965), *Bunodera sacculata* and *B. luciopercae* (Cannon 1971), *Cotylurus erraticus* (Olson 1970), *Fasciola hepatica* (Rowcliffe and Ollerenshaw 1960), *Fascioloides magna* (Friedl 1961), *Neodiplostomum intermedium* (Pearson 1961), and *Spirorchis scripta* (Holliman 1971). The rate of development and hatching of miracidia was shown to be dependent on temperature in *Bunodera sacculata* and *B. luciopercae* (Cannon 1971), *Spirorchis scripta* and *S. parvus* (Holliman 1971) and *Strigea tarda* (Mathias 1925).

Considerable information is available on the effect of temperature on the longevity of miracidia. Olíver and Short (1956) and Farley (1962) showed that the longevity of *Schistosomatium douthitti* miracidia was decreased as the temperature of the water was increased. They also became moribund below 5° C (Farley 1962). Mobility of *Schistosoma mansoni* miracidia was directly related to the temperature (DeWitt 1955); they were immobile at 10° C. Miracidia of *Phyllodistomum folium* were also immobile below 10° C (Pigulevski 1953).

The rate of infection of snails with *Schistosoma mansoni* miracidia was increased as the temperature increased (Stirewalt 1954). At 10° C very low infections of snails have been established with miracidia of *S. haematobium* (Chu et al. 1966) and *S. mansoni* (DeWitt 1955, Purnell 1966). When bivalves were exposed to miracidia of *Phyllodistomum* spp. at 4-8° C, very low infections resulted (Ubelaker and Olsen 1970).

Larval development in the intermediate hosts is directly related to water temperature in all the major groups of helminths including

trematodes (Stirewalt 1954, Foster 1964, Watertor 1968, Nice and Wilson 1974). Kendall (1965) observed that larvae of *Fasciola hepatica* develop very slowly at 10° C and the larval development in the snails was inhibited below 10° C (Kendall and McCullough 1951, Nice and Wilson 1974). Kendall (1965) also found that the pattern of development may be temperature-dependent: in infections maintained at 20.7° C no daughter rediae were produced, but in infections maintained at 4-5° C for 4½ hours daily, daughter rediae were produced instead of cercariae. A similar phenomenon has been reported by Dinnik and Dinnik (1956) in *Fasciola gigantica* infections.

Cort (1922) observed that the temperature of the environment has a very significant effect on the number of cercariae emerging from the infected snails. Cercariae of *F. hepatica* did not emerge from *Lymnaea truncatula* at temperatures below 9° C (Kendall and McCullough 1951). Fox (1965) has indicated that cercariae of *Bulbophorus confusus* did not emerge below 12° C and Gumble et al. (1957) have observed that cercariae of *Schistosoma japonicum* failed to emerge below 10° C.

Very few *S. mansoni* cercariae penetrated into the definitive host at 10° C (DeWitt 1965, Purnell 1966). Olson (1966) has suggested that the number of *Cotylurus erraticus* cercariae which penetrate the fish hosts at 10° C was very low.

The time required for development of infective metacercariae of *C. flabelliformis* in lymnaeids was correlated inversely with temperature (Campbell 1973). He also noticed that at 12-14° C, development never passed the precystic stages in most snails.

Temperature may also regulate the growth and maturation of adult digeneans in poikilothermic definitive hosts. Watertor (1968) has

suggested that adult *Telorchis bonnerensis* in *Ambystoma tigrinum* grew faster at higher temperatures, and that there was no growth at 10° C. Similarly the rate of attaining sexual maturity and the rate of migration of *Gorgoderina vitelliloba* to the urinary bladder of *Rana temporaria* increased as the temperature increases (Mitchell 1973).

In brief, temperature influences various stages in trematode life cycles. It affects the development of eggs, miracidial activity and longevity, miracidial penetration into the snail hosts, larval development in the snail hosts, development of cercariae, emergence of cercariae, penetration of cercariae into intermediate (or definitive) hosts and growth and migration of adult digeneans in poikilothermic animals. The available evidence suggests that temperatures below 10° C are not suitable for transmission and/or development of most trematodes. However, most of this information has been obtained from laboratory studies. Thus far very few studies have provided appropriate data from natural conditions, especially at the latitude of Edmonton.

The population dynamics of trematodes depend not only on host populations and the physical factors of the environment, but also on the abundance of some natural enemies.

Many miracidia probably are killed in attempts to penetrate insusceptible snails (Chernin 1968, Chernin and Perlstein 1969). Miracidia are also killed by mosquito larvae and excretions of a planarian (Chernin and Perlstein 1971), predation by a rhabdocoel (Holliman and Mecham 1971), and are damaged by Hydrozoa (Mattes 1949).

Enemies of the intramolluscan stages are microsporidian hyperparasites (Schäller 1959, 1960, Canning and Basch 1968, Lie et al. 1970) and antagonistic larval stages of other trematodes (Heyneman and Umathevy

1967, Lie et al. 1968, Basch 1970, Lie 1972). Lim and Heyneman (1972) reviewed the aspects of inter-trematode antagonism in the view of its possible role in the biological control of trematode infections of economic importance.

Laboratory tests show that guppies, *Lebistes reticulatus*, prey actively on cercariae (Oliver-Gonzalez 1946, Rowan 1958, Pellegrino et al. 1966) and Rowan (1965) and Pellegrino (1967) concluded that guppies play an important role in limiting the schistosome infections of vertebrate hosts in nature.

However, the most important enemy is apparently an oligochaete, *Chaetogaster limnaei*, which lives in association with various freshwater snails and may prey upon free-swimming trematode larvae (Khalil 1961, Michelson 1964).

Chaetogaster limnaei (von Baer 1827) is commonly found on the surface and in the mantle cavity of freshwater gastropods, and the relationship is usually described as commensalism. Gruffydd (1965a) recognized two subspecies: *Chaetogaster limnaei limnaei* which inhabits the outer surface of the snail, and *C. l. vaghini* which lives in the renal organ. *Chaetogaster l. limnaei* is generally considered to be a commensal and feeds on planktonic organisms (Vaghin 1946, Khalil 1961, Gruffydd 1965b), while *C. l. vaghini* lives in the kidney, feeds on the renal cells of the snail, and is considered to be parasitic (Stephenson 1930, Vaghin 1946, Gruffydd 1965b).

Although the general biology and population dynamics of *C. l. limnaei* were studied by Gruffydd (1965a, b) and the behavior was studied by Buse (1972), most publications concerning *C. l. limnaei* deal with the significance of the fact that it will eat and destroy trematode

miracidia and cercariae. Mrazek (1917), Wagin (1931), Buckland (1949), Ruiz (1951) and Khalil (1961) believed that *C. l. limnaei* may be an important factor in controlling trematode infections. Ruiz (1951) and Khalil (1961) showed an inverse relationship between the degree of infection of trematodes and the number of *C. l. limnaei* harbored by the molluscan host. Gruffydd (1965a) observed that fair numbers of cercariae were eaten by *C. l. limnaei* and Shigina (1970) determined that 11.7-51.0% of the total food of *C. l. limnaei* was composed of cercariae. Wajdi (1964) noticed *C. l. limnaei* feeding on *Schistosoma mansoni* miracidia and Michelson (1964) suggested that snails with these oligochaetes may be refractory to experimental trematode infections.

As *C. l. limnaei* can occur in high prevalence and intensity among snail populations, Wagin (1931) concluded that they may be useful as agents of biological control in trematode infections of economic importance. However, there are no published reports indicating that they have ever been so employed.

Chaetogaster l. vaghini was reported from the kidney of gastropods by Lankester (1869), Vaghin (1946), Michelson (1964), Gruffydd (1965a, b) and Buse (1971). The general biology and population dynamics have been studied by Gruffydd (1965a, b) and Buse (1971). Buse (1972) also studied their behavior in relation to the gastropod host.

Even though both subspecies of these oligochaetes have been studied in detail in the United Kingdom, nothing is known about the effects of either temperature or thermal effluent on their biology. Because of their potential importance to trematode life cycles, the biology of these annelids was added to the study of *P. gyrina* and its helminth parasites.

Physa gyrina, its parasites and commensal oligochaetes constitute an integrated system, in which all three major components may be affected either directly or indirectly by temperature. Hence, this system was chosen as the object of a study with the following objectives:

1. To establish the effects of thermal effluent on the population dynamics of *P. gyrina*.

2. To determine the effects of thermal effluent on the helminth fauna of *P. gyrina*.

3. To establish the effect of thermal effluent on the dynamics of *Chaetogaster l. limnaei* and *C. l. vaghini*.

4. To determine the role of *C. l. limnaei* in controlling the trematode infections.

5. To test whether this system, or any of its components, can be used as ecological indicators of thermal pollution.

GENERAL METHODS

SNAIL COLLECTIONS

Hairston et al. (1958) have pointed out that no uniform method for the quantitative study of snail populations, useful in all situations, has been developed. The selection of a suitable technique depends on the objectives of the study, ecology of the snail concerned, nature of the habitat and the facilities available. In this study, two techniques were used to assess the relative densities of snail populations.

1. Snails Collected per Unit Time

This method, described by Olivier and Schneiderman (1956), measures the density of a snail population by the number of snails that can be collected in a given area in a unit of time. It was first used by Vaughn et al. (1954); various modifications were used subsequently by many other investigators, including Webbe (1962), Howard and Walden (1965), Sodeman (1973) and Sturrock (1973). Repeated counts have shown a reasonable statistical reliability. This method was rated as the best sampling technique for estimating aquatic snail populations by the World Health Organization (1965).

In this study, the number of snails that could be collected with a dipnet during one half minute was used as an index to the population density ("density index"). The dipnet had a nylon millimeter-mesh bag mounted loosely on a triangular metal frame, 40 cm wide by 40 cm long.

Samples were obtained from a boat at rest by scraping the vegetation within 1-2 feet of the surface. When no vegetation was available, the bottom was scraped for 30 seconds. The dipnet was emptied into a white plastic plate, any snails or egg masses present were counted, and the whole sample was returned to the lake. A small sample of 20-25 snails was then collected for parasitological examination, then the boat was moved to another site in the same general area and another sample taken. Usually 6 to 8 samples were made at each sampling time. When the snail populations were sparse, 10 to 12 counts were made. Sampling sites were chosen randomly, but from different regions within the sampling area.

Olivier and Schneiderman (1956) have showed that the variances between snail counts made by two men using this technique in the same place were much greater than day to day variances for one man. Therefore, to minimize sampling error, all samples were taken by myself, using the same equipment.

This method is rapid, can be repeated (to give variance estimates) and does not unduly distufb the habitat or the snail populations. Egg masses, which are attached to vegetation or other solid substrates, and snails measuring less than 1 mm, which may pass through the net or may be located in protected locations in the vegetation, are probably underrepresented in these counts. This technique was adopted as the standard index method, and was used from May 1971 through August 1973.

2. Snails Collected per Unit Vegetation

After using the above technique to assess snail population densities for one year it was obvious that the heated area contained more dense vegetation and more snails than the control area. To assess the

relationship between the amount of vegetation and the abundance of the snails, the number of snails present per unit weight of vegetation was determined.

Approximately 50 to 100 grams of vegetation was collected, taking care to minimize the disturbance to the snails attached to the vegetation, and returned to the laboratory in a plastic bag. The vegetation was washed into a large porcelain tray and allowed to settle for a few minutes. Many snails, including most of the young ones, came to the surface of the water and were collected. The vegetation was checked macroscopically for snails, especially hatchlings (< 3 mm long), and egg masses. Then the water in the tray was carefully emptied and the remaining snails and egg masses were collected. The vegetation was blotted to remove excess water, weighed to the nearest gram, and the number of snails and egg masses per 100 grams of vegetation was calculated.

This technique was used through most of one growing season, from May 1972 to October 1972.

EXAMINATION FOR PARASITES

At each sampling time, a total of approximately 100 to 200 *Physa gyrina* was collected from each area (as indicated earlier), transported to the laboratory, washed, then isolated in half-pint milk bottles containing approximately 50 cc of dechlorinated water. The water in the bottle was checked with a dissecting scope for emerged cercariae, and the bottle was checked for recently encysted metacercariae, two or three times per day. Occasionally other gastropods were also collected from

the study areas and observed for larval helminths. No quantitative data was obtained on species other than *P. gyrina*, but qualitative information on the larval parasites was collected.

Snails that had not shed cercariae after two or three days were crushed and examined for chaetogasters, early larval stages and metacercariae. The following data were collected on each snail crushed: length of the shell (to the nearest millimeter), number and type of germinal sacs (sporocysts or rediae), state of development of germinal sacs, number and kind of metacercariae, number of *Chaetogaster l. limnaei* and *C. l. vaghini*, and any other relevant information.

Snails that did release cercariae were kept alive in the laboratory for a few days so that the cercariae could be obtained for morphological studies and laboratory experiments. After obtaining the desired material, the snails were crushed and examined as above.

Larval stages were studied using both live and preserved specimens. Living forms were studied unstained or stained with neutral red or Nile blue sulphate. Cercarial measurements were obtained on live specimens and on those fixed according to the method of Talbot (1936). Three drops of saturated aqueous solution of neutral red were added to 50 cc of water containing cercariae. The cercariae were allowed to stain for 5 minutes, then an equal volume of boiling 10% formalin was added while stirring. The cercariae were fixed in a relaxed position with their tails attached. In so far as possible, identification of the larval stages was confirmed by comparison with known material from experimental infections and by completion of life cycles.

Parasitized and control snails were relaxed in 5° C cold water

with a few menthol crystals for 30 minutes, shells were removed and the bodies fixed in Bouin's for sectioning. After fixation, these specimens were dehydrated in ethanol, embedded in paraffin wax, and sectioned at 7 μ. Sections were stained with Ehrlich's haematoxylin and eosin.

EXPERIMENTAL INFECTIONS

Snails used in the experimental infections were raised in the laboratory and were maintained at 19° to 20° C in glass aquaria with some gravel and soil. Water in the aquaria was continuously aerated and filtered through glass wool and activated charcoal. Snails were fed exclusively on fresh lettuce. Once a month a teaspoonful of calcium carbonate was added to each aquarium. The water was replenished every two or three months.

Snails used in the experimental infections were 3 to 7 mm long. Snails were exposed individually to a known number of miracidia of *Echinoparyphium recurvatum* or *Echinostoma revolutum* in a stender dish. *Notocotylus urbanensis* eggs, teased from mature flukes collected from local muskrats, were embryonated at room temperature in a stender dish for three days; a few snails were allowed to feed on the contents of the dish for 15 to 20 minutes.

Metacercarial infections with *Echinoparyphium recurvatum*, *Echinostoma revolutum* and *Cotylurus douglasi* were obtained by exposing 10 to 15 laboratory-reared *Physa gyrina* in 200 cc of water containing 200-300 cercariae. Cercariae usually penetrated the snails within two hours. Snails exposed to cercariae of echinostomes were crushed after 24 hours to obtain the metacercariae. Snails exposed to *Cotylurus*

douglasi were maintained at room temperature in glass aquaria for two months. A few were examined every week to note the development of tetracotyles. Metacercariae of *Notocotylus urbanensis* were collected from pieces of lettuce kept for two or three days in the bottle along with the infected snails. Planarians (*Dugesia tigrina*) used to obtain metacercariae of echinostomes were collected from the lake, checked under a dissecting scope for metacercarial infections, then exposed to cercariae using the same methods as for snail infections.

Young spottail shiners and sticklebacks used in the experiments were collected from the lake when they first appeared during June. They were brought to the laboratory, and maintained in glass aquaria. A sample was examined for larval parasites and found to be negative; the remainder were later exposed to the cercariae of *Ornithodiplostomum ptychocheilus*. The exposed fish were grouped into three groups of five each and examined for metacercariae after one, two and three weeks.

Unfed, one to two day old chicks, purchased from a hatchery, were given metacercariae *per os*, by pipette or in a gelatin capsule. After infection, they were fed mashed turkey starter. They were necropsied 7 to 10 days after infection.

The mallards and scaup used in this study were raised in the laboratory from eggs collected from nests of wild birds. They were fed *ad libitum* on a mash diet.

Those challenged with schistosome cercariae were one to two weeks old. The cercariae of *T. cameroni* from naturally infected snails were used for experimental infections. Approximately equal numbers of cercariae from two or more snails were used in order to increase the

chances that both males and females were present. The mallard ducklings to be infected were held with their feet suspended in the vessel containing the cercariae for 30 to 40 minutes. Some cercariae were also pipetted into the mouth. In the case of schistosome challenge, bird feces were collected 10-14 days postchallenge, diluted with water in a special flask designed to hatch eggs of schistosomes (McMullen and Beaver 1945), and looked for free-swimming miracidia. After the 14th day the ducks were necropsied and searched for adult schistosomes.

When challenged with other trematode metacercariae, the ducks were 6-8 weeks old and were starved for three hours prior to administering metacercariae *per os*. Then they were fed *ad libitum* on a mash diet. Birds challenged with metacercariae of *C. douglasi* and *N. urbanensis* were necropsied after 7 days.

Hamsters (L.S.H. strain) and rats used were males, 3 to 4 weeks old, fed on *ad libitum*, Teklad Mouse-Rat diet of Teklad Inc., Norman, Illinois. They were deprived of food for three hours before infection. The parasites were administered *per os*, by pipette or in gelatin capsules. These animals were necropsied 7-10 days postinfection.

Specific details of the other experimental methods are described in their respective sections.

STUDY AREAS

GENERAL DESCRIPTION

Wabamun Lake is located about 65 km (40 miles) west of Edmonton, at 114° 35' W; 53° 32' N and at an altitude of 723 m above sea level. It is situated in the cold, temperature climatic region, characterized by having long, bright, and moderately warm summer days and bright, cold, dry winter weather (Kendrew and Currie 1955). It is located in the Boreal Parkland Transition vegetation zone (Moss 1955). The lake bedrock is composed of late Cretaceous and early Tertiary sandstones and shales, with numerous coal seams (Rutherford 1928). The surface drainage area is small, with no significant inlet rivers or streams, and so the lake levels are maintained by precipitation and probably subsurface flow (Nursall and Gallup 1971). It is a popular resort and fishing lake, and is also used as a source of condenser cooling water for two thermal power plants.

Wabamun is a moderately large lake, with a surface area of 82.5 km^2 and maximum dimensions of 19.2 by 6.6 km, but is relatively shallow, with a mean depth of 5.4 m. Other morphometric features (Table 1) are those given by Nursall and Gallup (1971); contours of the lake are shown in Figure 1.

Physiographical and topographical features of this lake are discussed in detail by Wheelock (1969) and Horkan (1971). Ice first appears on the lake during November and generally increases in thickness until it reaches about 70 cm (Horkan 1971). As in other lakes of this

Table 1. Morphometry of Lake Wabamun (from Nursall and Gallup, 1971)

Elevation	723 m
Area (A)	82.5 km^2
Volume (V)	ca. 0.455 km^3
Length (L)	19.2 km
Maximum breadth	6.6 km
Mean breadth (b)	4.3 km
Maximum depth (Zm)	11.6 m
Mean depth ($\bar{z}$)	5.4 m
Shore length (L)	57.3 km
Shoreline development (DL)	1.83
Area of surface drainage	372.4 km^2

Note: The symbols used are those of Hutchinson, 1957.

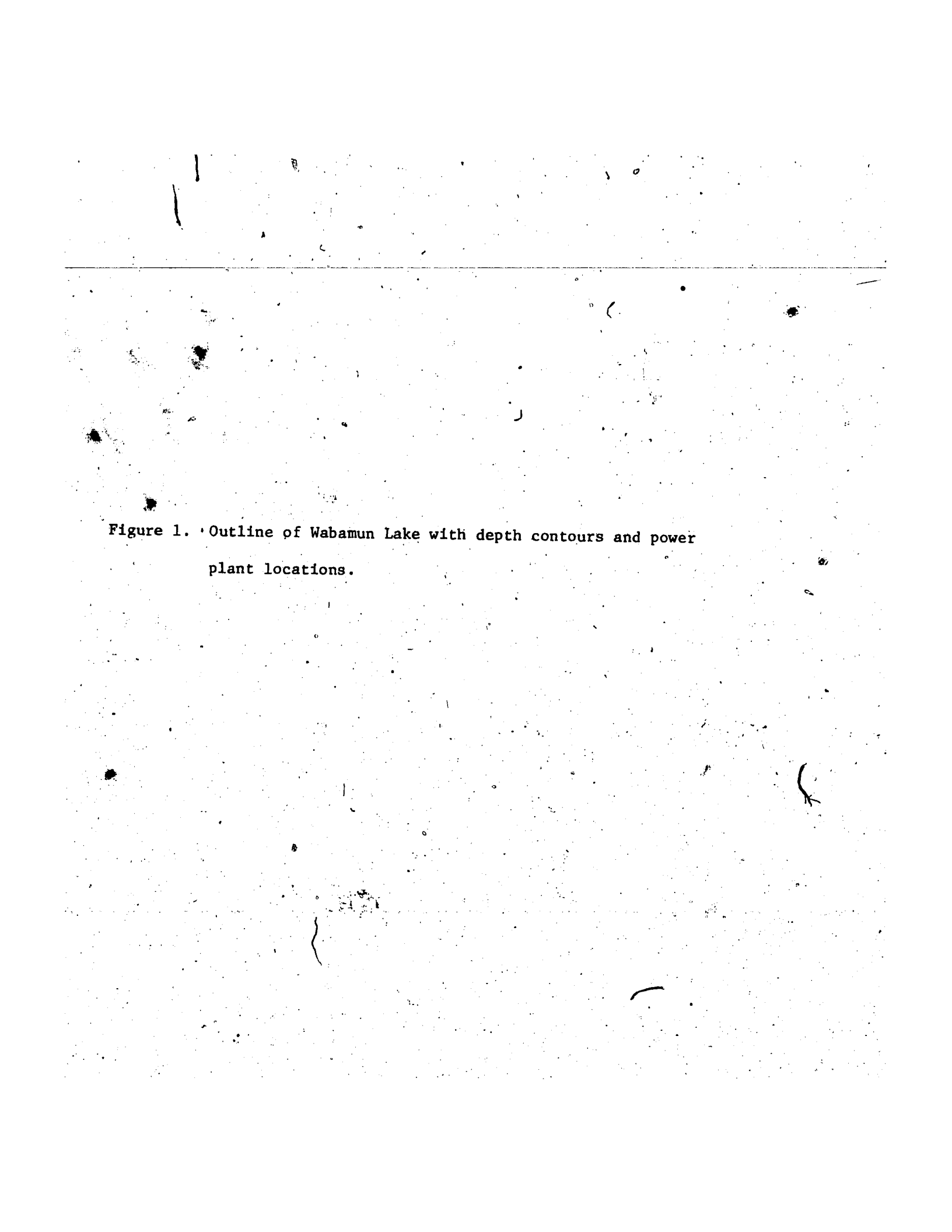
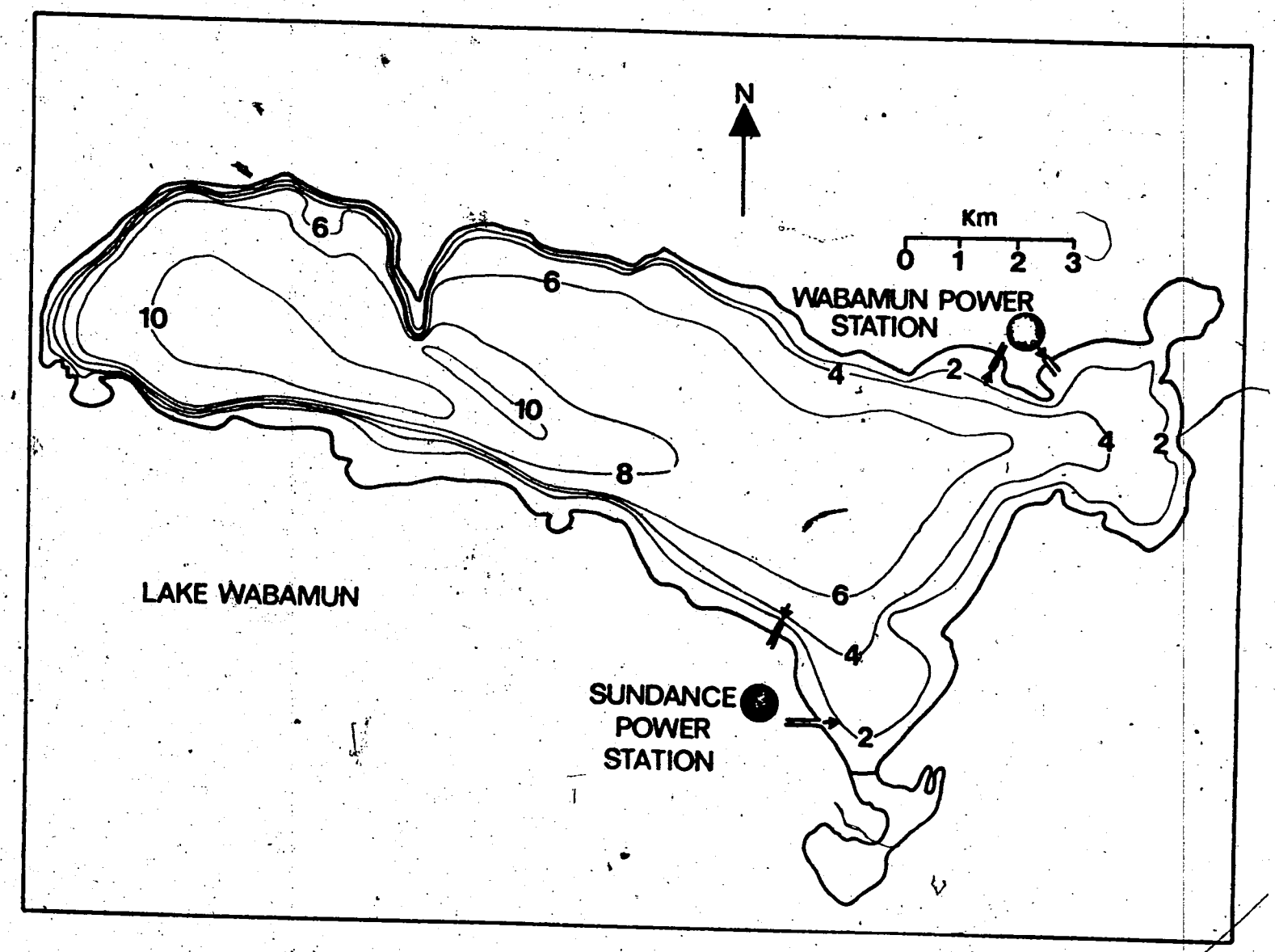


Figure 1. Outline of Wabamun Lake with depth contours and power plant locations.


N
Km
0 1 2 3
WABAMUN POWER STATION
LAKE WABAMUN
SUNDANCE POWER STATION
6
10
6
10
8
4
2
4
2
6
4
2

area, the period of ice cover lasts about six months, and the lake remains ice-free for the rest of the year. However, a variable area remains ice-free during the winter due to the addition of heated water from the two power plants. Therefore, unlike others in the area, this lake (or at least a portion of it) can be described as an open system all year (Nursall 1969). Because of this open water, Lake Wabamun is inhabited by a variety of waterfowl during the winter.

The presence of extensive coal deposits lying both to the north and to the south of the lake has resulted in the establishment of the two coal-fired electrical generating plants. Both power plants draw in lake water for cooling the condensers. This heated water is then discharged directly back into the lake. The locations of the two power plants are shown in Figure 1.

The first power plant, the Wabamun plant, came into operation during 1956 with an initial capacity of 75 megawatts, but it was gradually increased to its present capacity of 600 Mw by March 1968. The second plant, located at Sundance, was commissioned during 1970 with a maximum capacity of 300 Mw in phase 1.

The amount of water used to cool the condensers varies seasonally. The Wabamun station draws about 300,000 Imp. gal/min in summer (May to October) and about 150,000 Imp. gal/min during winter (Nursall and Gallup 1971). The heat discharged is sufficient to raise temperatures of the cooling water about 8° C in summer and 14° C in winter (Nursall and Gallup 1971), and represents about 65 percent of the energy produced by burning coal (Allen 1973).

The heated effluent causes localized temperature stratifications whose intensity, depth and extent are determined by local weather

conditions (Gallup and Hickman 1973, 1975). In winter, the thermal effluents keep an extensive area of the lake ice-free; the shape and extent of the ice-free area depends on the influence of wind and currents (Nursall et al. 1972).

Submerged and emergent vegetation is concentrated along the shallower edges of the lake. The species composition and distributional patterns have been discussed in detail by Wheelock (1969), Horkan (1971) and Allen (1973). Wheelock (1969) also gave a detailed account of phytoplankton. An epiphytic algal community attached to *Scirpus validus* has been extensively studied by Klarer (1973), Hickman and Klarer (1974a, b), Klarer and Hickman (1974). The epipelic and epipsammic algal community was investigated by Hickman (1974), and Allen (1973) and Allen and Gorham (1973) studied the growth of submerged macrophytes at Wabamun Lake. Studies on rotifers and macroinvertebrate communities have been conducted by Horkan (1971) and Gallup et al. (1973), respectively. A list of species of phytoplankton, zooplankton, submerged aquatic plants and fish is given by Gallup and Hickman (1975).

The vertebrate fauna is mostly composed of fishes, birds and muskrats. Among fishes, *Catostomus commersonii*, *Coregonus clupeaformis*, *Culaea inconstans*, *Esox lucius*, *Etheostoma exile*, *Lota lota*, *Notropis hudsonius* and *Perca flavescens* were common. The avian fauna is mostly comprised of aquatic birds, which use the lake as a breeding/staging area. The important species are mallards (*Anas platyrhynchos*), blue-winged teal (*Anas discors*), shovelers (*Spatula clypeata*), lesser scaup (*Aythya affinis*), common goldeneye (*Bucephala clangula*), white-winged scoter (*Melanitta deglandi*), American coot (*Fulica americana*), various grebes (*Podiceps* spp.), gulls (*Larus* spp.), and common tern (*Sterna*

hirundo). Muskrats (*Ondatra zibethica*) are moderately common in the lake.

After surveying several potential sampling sites, three sampling sites were selected. One site ("control" area) is near the intake canal, the other two ("heated" areas) are near the discharge canal of the Wabamun plant, which lie on opposite sides of a promontory called Pt. Allison (Fig. 2).

CONTROL AREA

This is a shallow area with a maximum depth of 1.5 m, situated east of the inlet canal (Fig. 2). This study area is almost identical to the inlet canal study area of Klarer (1973) and Klarer and Hickman (1974) which lies west of the inlet canal. This study area was covered with ice from about mid-November to mid-April, and was ice-free for the rest of the season. Surface temperatures were usually within ±1.0° C of those obtained by Klarer (1973). This difference is negligible when compared to the variations within the same day or between various days (Horkan 1971). Klarer (1973) and Klarer and Hickman (1974) reported that their study area was isothermal and showed no oxygen stratification, due to its extreme shallowness. These conditions appeared to be true of my area as well. The surface temperatures from this area are given in Figure 3.

At the time of spring breakup there was no green emergent or submerged vegetation; it began to appear during May, increased gradually during the summer to a high density during August (Fig. 4A), then died back until there were no green macrophytes present at the time of

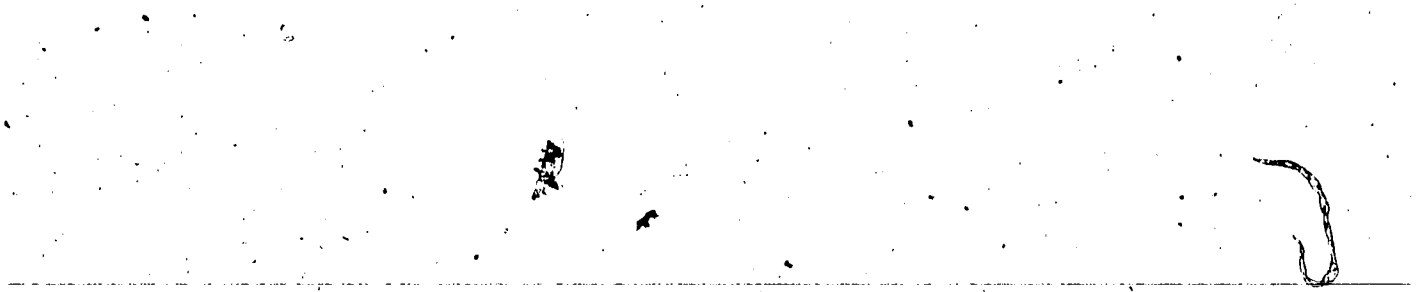
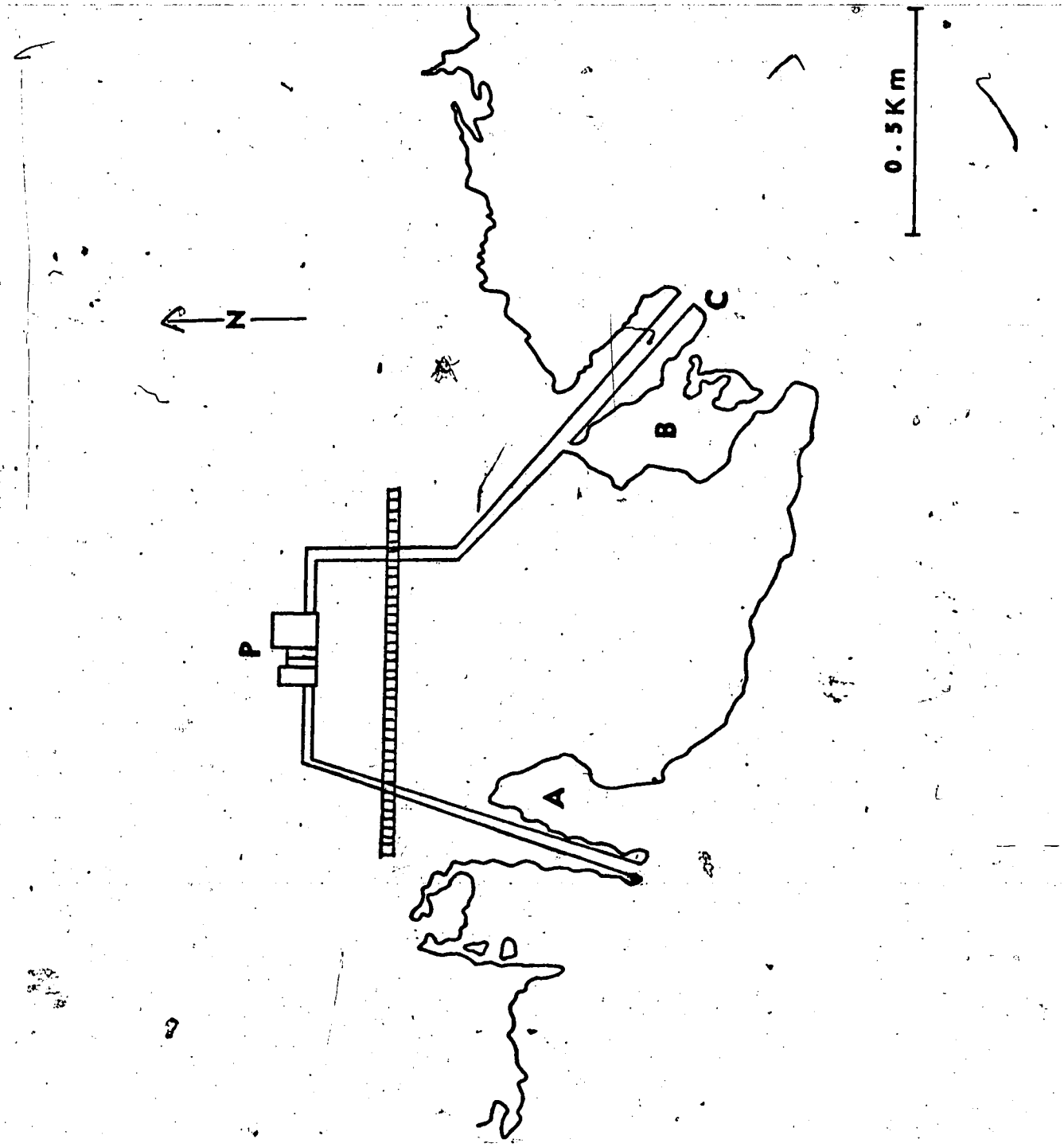


Figure 2. Study areas of Wabamun Lake.

A - control area

B, C - Heated areas

P - Wabamun Power plant


0.5Km
N
C
B
P
A

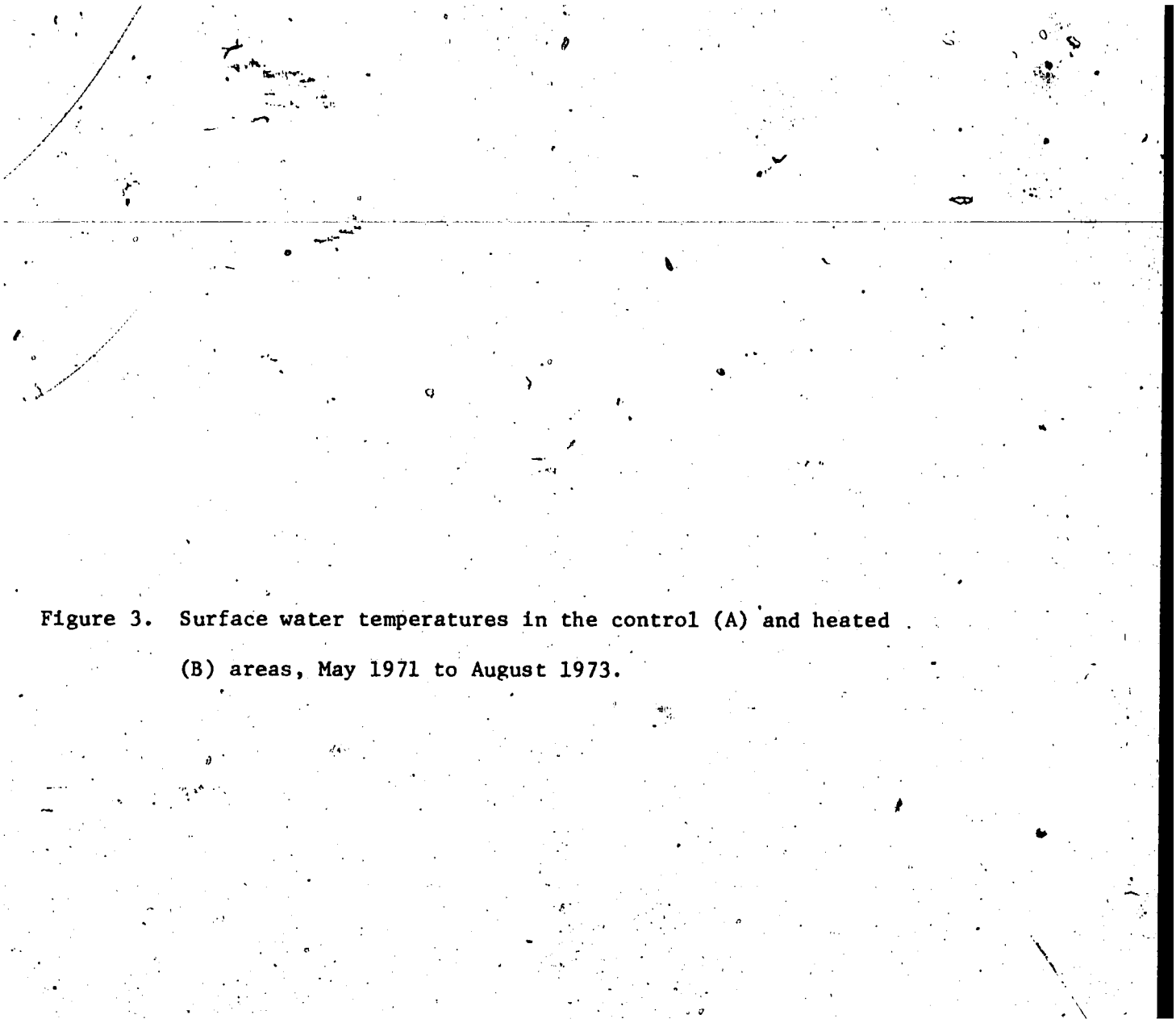
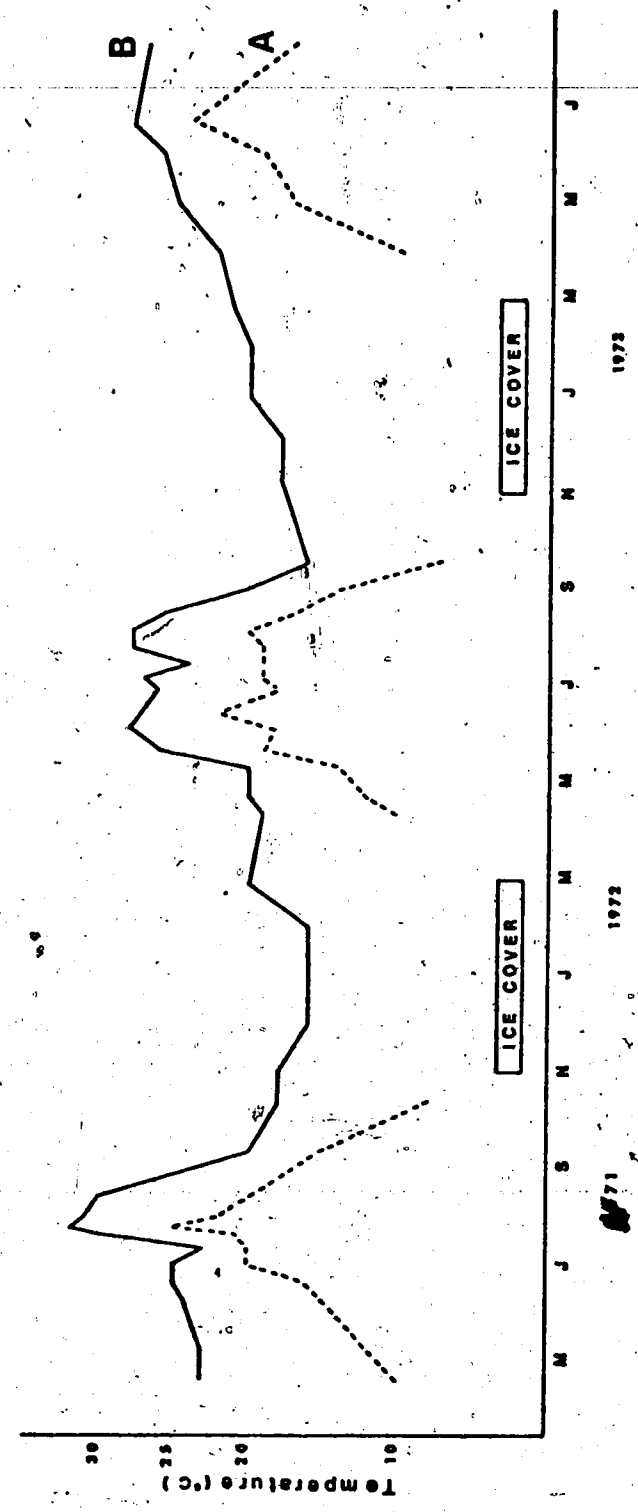


Figure 3. Surface water temperatures in the control (A) and heated (B) areas, May 1971 to August 1973.


B
A
ICE COVER
ICE COVER
1973
1972
1971
Temperature (°C)
30
20
10
M
J
S
N
J
M
M
J

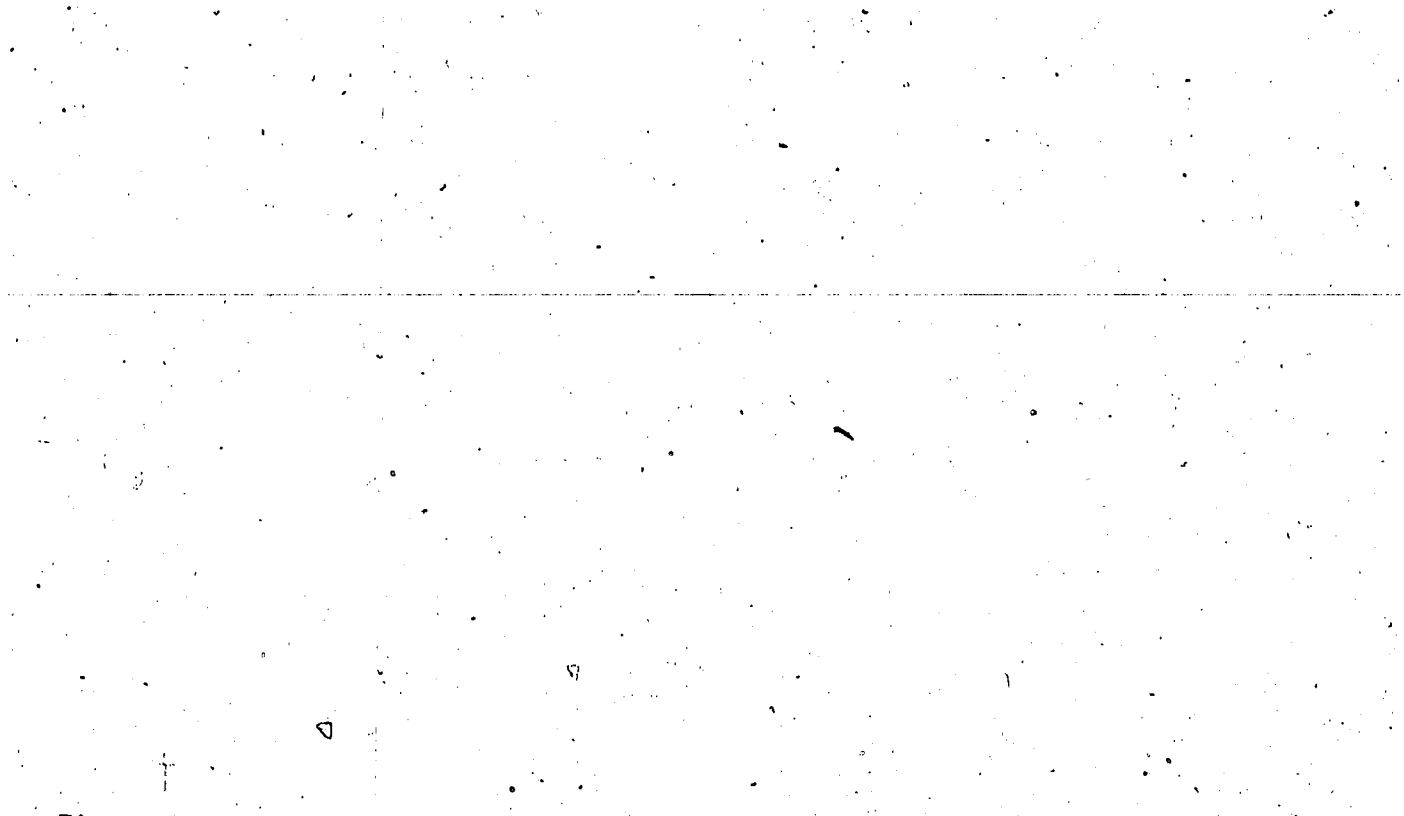
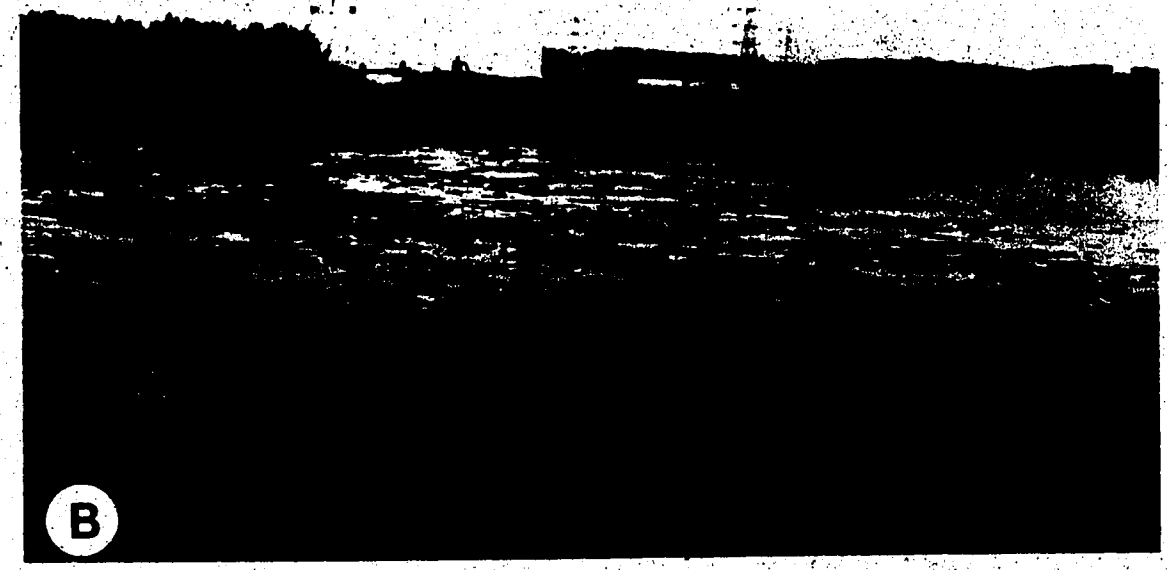


Figure 4. Control area (A) and heated area (B) showing the abundance of aquatic macrophytes during August.


A


B

freeze-up. In the summer the macrophyte species were varied and composed of *Potamogeton filiformis, P. richardsonii, P. zosteriformis, Ceratophyllum demersum, Nuphar variegatum, Myriophyllum exalbescens, Utricularia vulgaris* and *Chara* sp.

During the open season, this area was inhabited by large numbers of a variety of macroinvertebrates comprising several species of insect larvae, corixids, cladocerans, and the amphipods *Gammarus lacustris* and *Hyalella azteca*. The molluscan fauna was composed of moderate numbers of *Physa gyrina, Lymnaea stagnalis, Helisoma trivolvis* and very few *Lymnaea elodes (palustris), Helisoma anceps* and *Valvata tricarinata*. There were small numbers of spottail shiners and perch. During the summer, many waterfowl of a variety of species were noted. A few muskrats were noticed, especially during fall.

HEATED AREA

The two sampling sites in the heated area are shallow (maximum depth 1.5 m), one situated immediately west of the outlet canal (B in Fig. 2). The heated water from the outlet canal flows directly into this area through a break in the canal wall. The other site (C in Fig. 2) is near the opening of outlet canal into the lake and is similar to the outlet canal area of Klarer (1973) and Klarer and Hickman (1974). However, since the two sampling sites in the heated area were identical in most features, during the later part of the study, sampling was restricted to the first site (B in Fig. 2). This site is referred to throughout the rest of this thesis as the "heated area."

The surface temperatures of this area are illustrated in Figure 3.

The minimum surface temperatures recorded were 16° and 18° C during the winters of 1971 and 1972, respectively; the maximum temperatures were 31°, 27° and 28° C during 1971, 1972 and 1973, respectively. As this area is so shallow, isothermal conditions and no oxygen stratification can be expected (Klarer 1973, Klarer and Hickman 1974).

In this area the macrophyte populations began to appear in March, increased through the early summer, reaching a high density (Fig. 4B) by June. They continued to be dense up to November, decreased slightly during December, then almost disappeared for two or three months. A few green submerged plants were present during this period. The composition of the aquatic macrophytes was much different from that of the control area. The dominant species were *Potamogeton pectinatus* and *Elodea canadensis*, both of which were absent in the control area. Besides these two dominants, there were smaller numbers of *P. filiformis*, *P. vaginatus*, *Ceratophyllum demersum*, *Myriophyllum exalbescens* and *Chara* sp. *Potamogeton richardsonii*, *P. zosteriformis*, *Nuphar variegatum* and *Utricularia vulgaris* were never found in this area.

The heated area contained fewer macroinvertebrates and the snail species composition was quite different from that of the control area. Large numbers of *P. gyrina*, *L. elodes* and *V. tricarinata*, moderate numbers of *H. anceps* and very few *L. stagnalis* and *H. trivolvis* were present. Gallup et al. (1973) showed similar differences in the benthic fauna of heated and normal areas of the lake. There were large numbers of spottail shiners and perch. This area harbors large numbers of waterfowl throughout the summer, and during the winter, the waterfowl present were restricted to this area only. A few muskrats were sighted, mostly during the winter.

To summarize: the heated area and the control area were similar in their physico-chemical characteristics, except temperature (Klarer 1973, Klarer and Hickman 1974); the species composition of macrophytes and their phenology was different (Allen 1973); and the composition of the benthic fauna was very different between the two areas (Gallup et al. 1973).

POPULATION DYNAMICS OF *PHYSA GYRINA*

Physa gyrina was found only in areas with shallow water (maximum 1.5 m) and was usually associated with submerged macrophytes, although in the winter the snails in the heated area occupied a variety of other habitats.

RELATIVE DENSITIES

The density index (average number of snails collected per half minute) in each collecting time is shown in Figure 5. (In this figure, and throughout the body of the text, the data from the two study sites sampled in 1971 in the heated area have been combined. The data are separated in Appendix II.) In the control area, the population density could be monitored only during the ice-free period. It followed a fairly consistent seasonal pattern, with very few snails just after spring break-up, increasing in density as the season progressed, reaching a relatively stable level by July, which continued through the last sampling before freeze-up. The maximum density index in the control area was only 32; the median value was 16.8 snails.

In the heated area, *P. gyrina* was present throughout the year. Irreguiar fluctuations were superimposed on a fairly constant seasonal pattern, with few snails (indexes less than 15) during the winter months (December through March), peak populations (indexes of 140-180) during the summer months (June through August) and moderate populations (indexes of 40-80 in the fall).

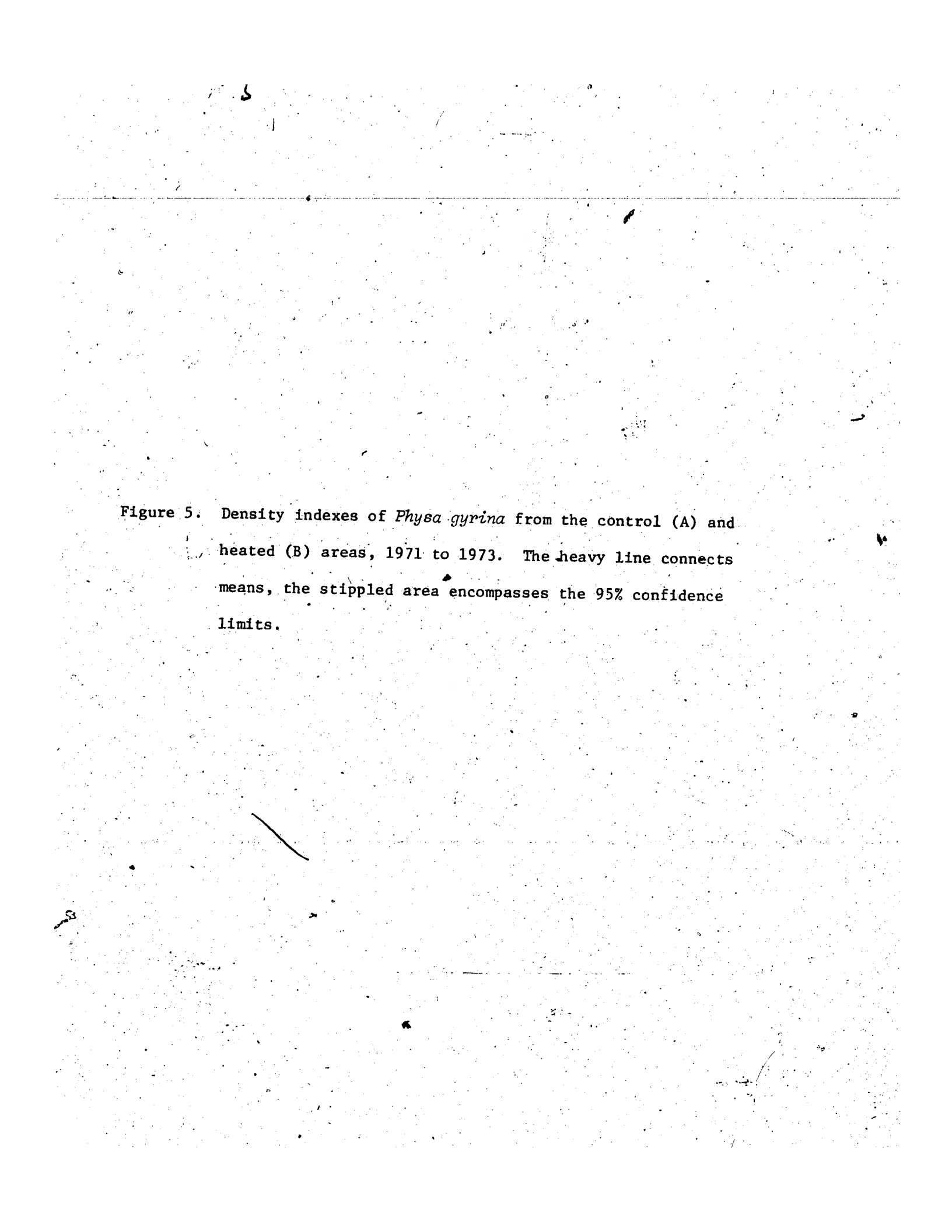
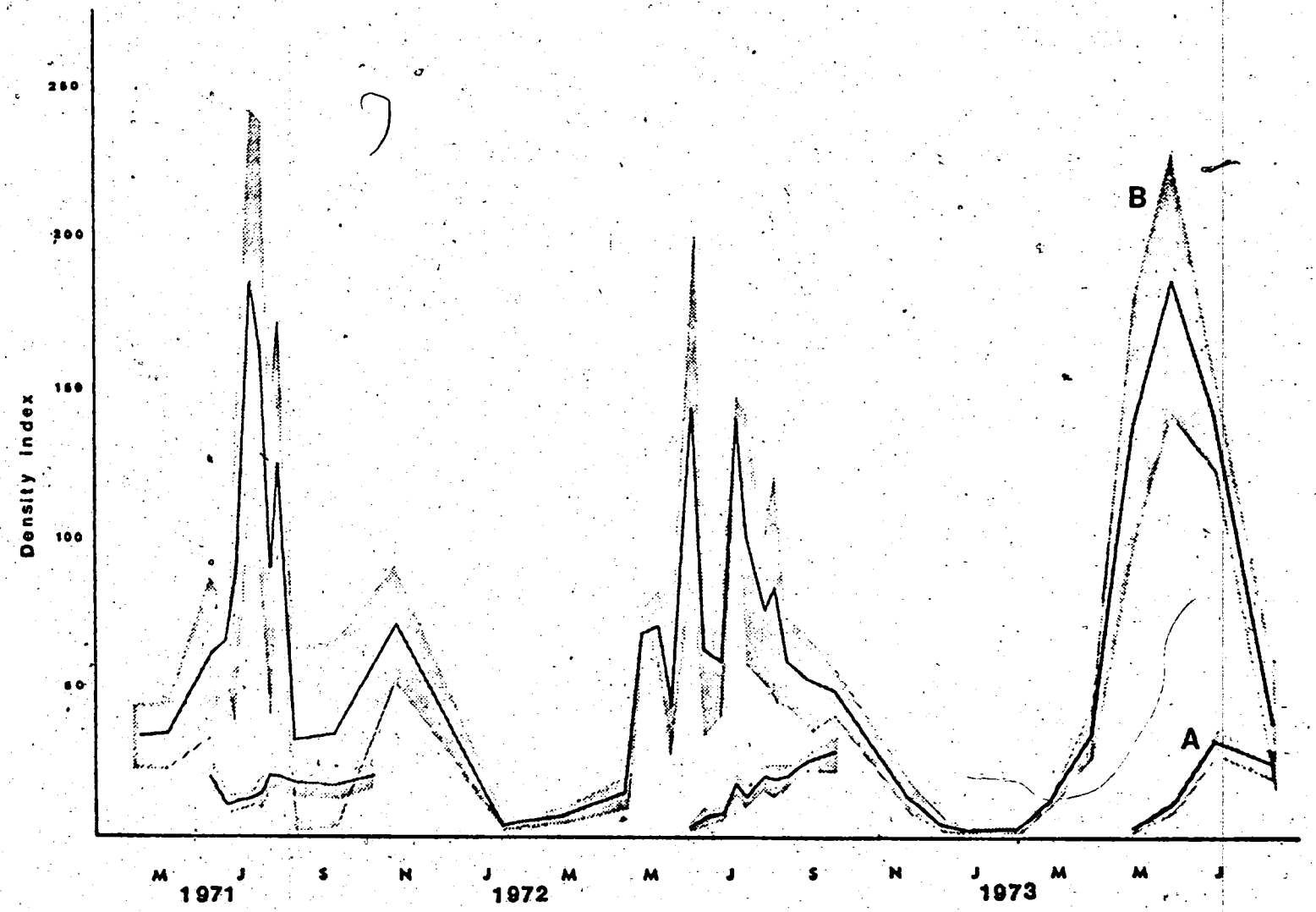


Figure 5. Density indexes of *Physa gyrina* from the control (A) and heated (B) areas, 1971 to 1973. The heavy line connects means, the stippled area encompasses the 95% confidence limits.


Density Index
250
200
150
100
50
B
A
M
J
S
N
J
M
M
J
S
N
J
M
M
J
1971
1972
1973

Population densities were always significantly higher than in the control area at the same time. The maximum density index was 183 per half minute; the median value from May through October was 68.3.

The patterns described above roughly parallel the patterns of abundance of submerged macrophytes. In particular, the lower densities of *P. gyrina* in the heated area during the winters correspond to periods when submerged macrophytes were very sparse. During that period, snails were restricted to the little vegetation present or were present on dead floating leaves or root systems of *Scirpus* or other floating objects.

These observations suggest that the number of snails present may be a function of the abundance of submerged macrophytes. To test this hypothesis, the number of snails per 100 grams vegetation was determined at each sampling period during the summer of 1972. The results (Fig. 6) do not support the hypothesis, but show that the number of snails per unit vegetation was always much higher in the heated area than in the control area. The relative differences between the numbers per unit vegetation in the two areas were roughly similar to the differences between the numbers collected per unit time. Even though the vegetation in the control area was fairly dense in August, the number of snails per 100 g vegetation was only 90, roughly 1/3 the number in the heated area at the same time, and considerably less than the maximum density of 842 in the heated area during June.

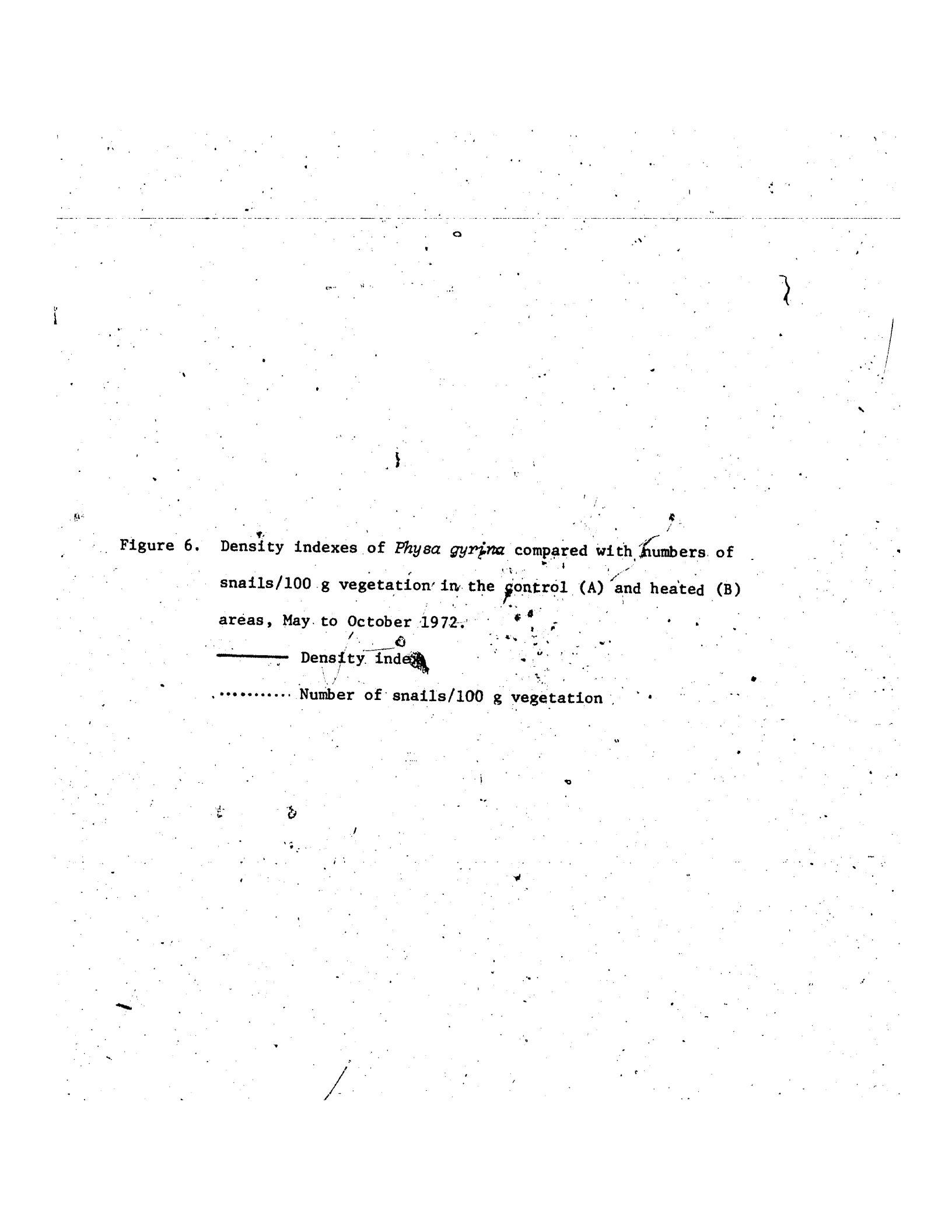
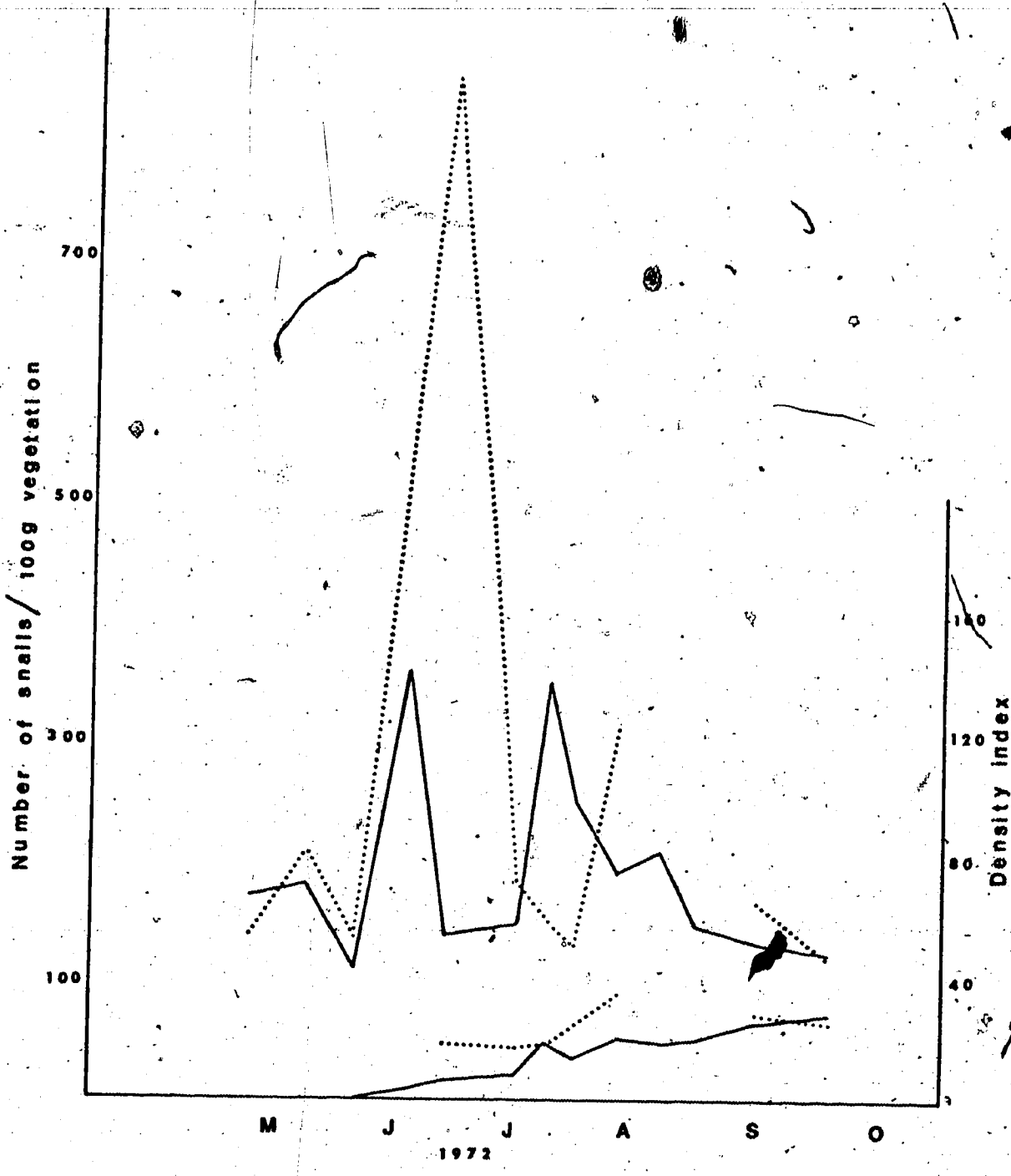


Figure 6. Density indexes of *Physa gyrina* compared with numbers of snails/100 g vegetation in the control (A) and heated (B) areas, May to October 1972.

——— Density index

..... Number of snails/100 g vegetation


700
500
300
100
Number of snails/ 100g vegetation
160
120
80
40
Density index
M
J
J
A
S
O
1972

POPULATION STRUCTURE

In the laboratory, *P. gyrina* begin ovipositing after they reach approximately 7 mm in shell length. Therefore, field-collected snails with shells greater than 7 mm were considered mature, and those with shells 7 mm or shorter were considered immature. Snails with shells 3 mm or less in length were considered hatchlings (cf. Sturrock, 1973).

The overall size-frequency distribution for *P. gyrina* in the control area (Fig. 7) shows a preponderance of immatures, whereas in the heated area it shows a preponderance of mature snails. Figure 7 also shows the larger size range and the higher proportion of larger snails in the heated area.

Seasonal age structures also differed between areas. In the control area, there were very few snails immediately after spring break-up; most were immatures. There were no egg masses or hatchlings (Fig. 8). The subsequent pattern can be seen best in the data from 1971. The proportion of immatures dropped and that of mature snails increased through July, due to the growth of overwintered snails (as evidenced by the changing size distributions in Fig. 9). These mature snails oviposited, then died out by early August (Figs. 8 and 9). They were replaced by hatchlings which appeared in June or July and reached peak populations in late July and August, starting a new population wave of immatures in late July and August and mature snails in September and October. However, egg masses were found only in September of 1971, when the proportion of mature snails was high.

The population structure of *P. gyrina* during 1972 was basically similar to that in 1971, with a few minor changes. The May sample

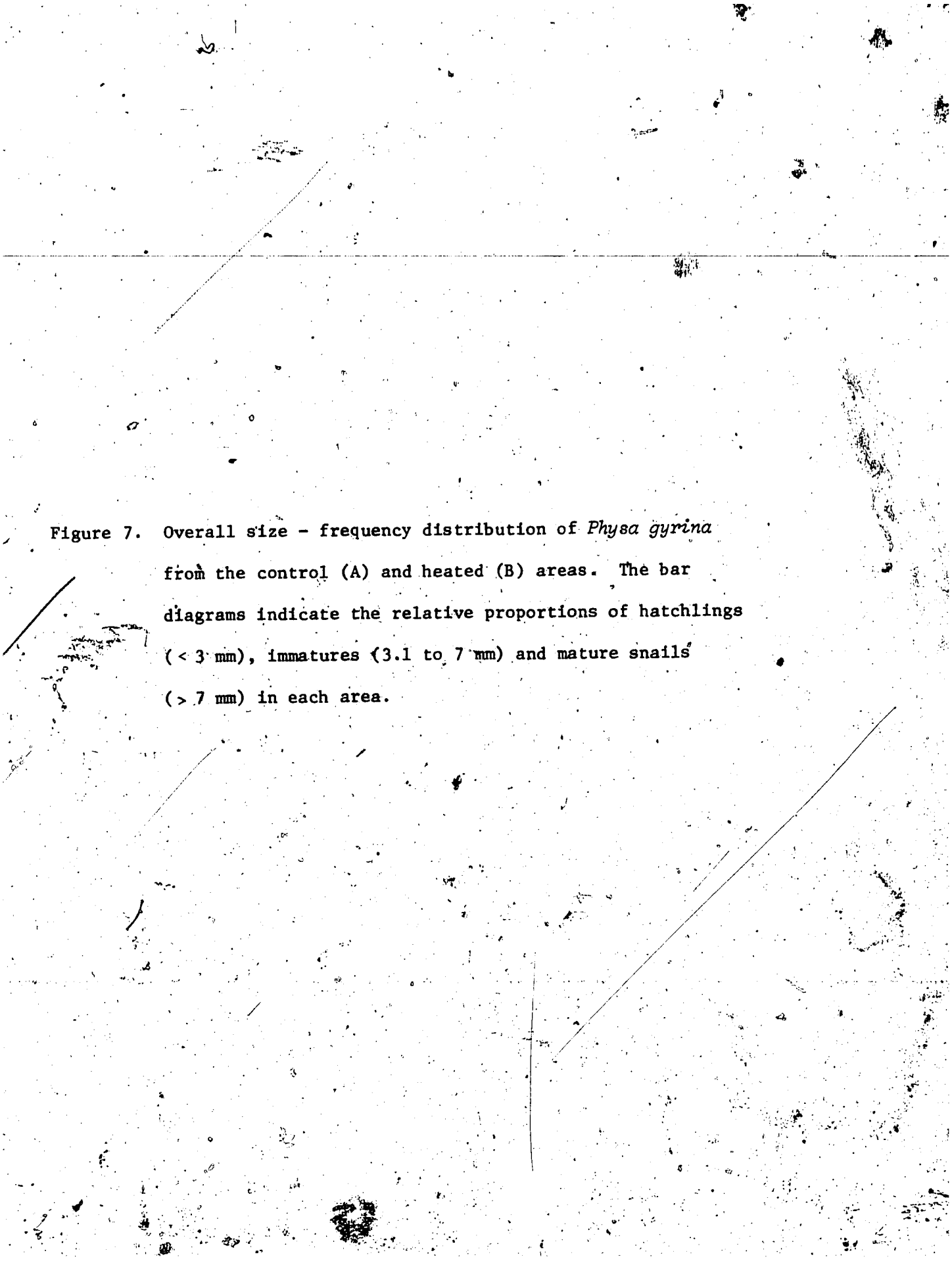
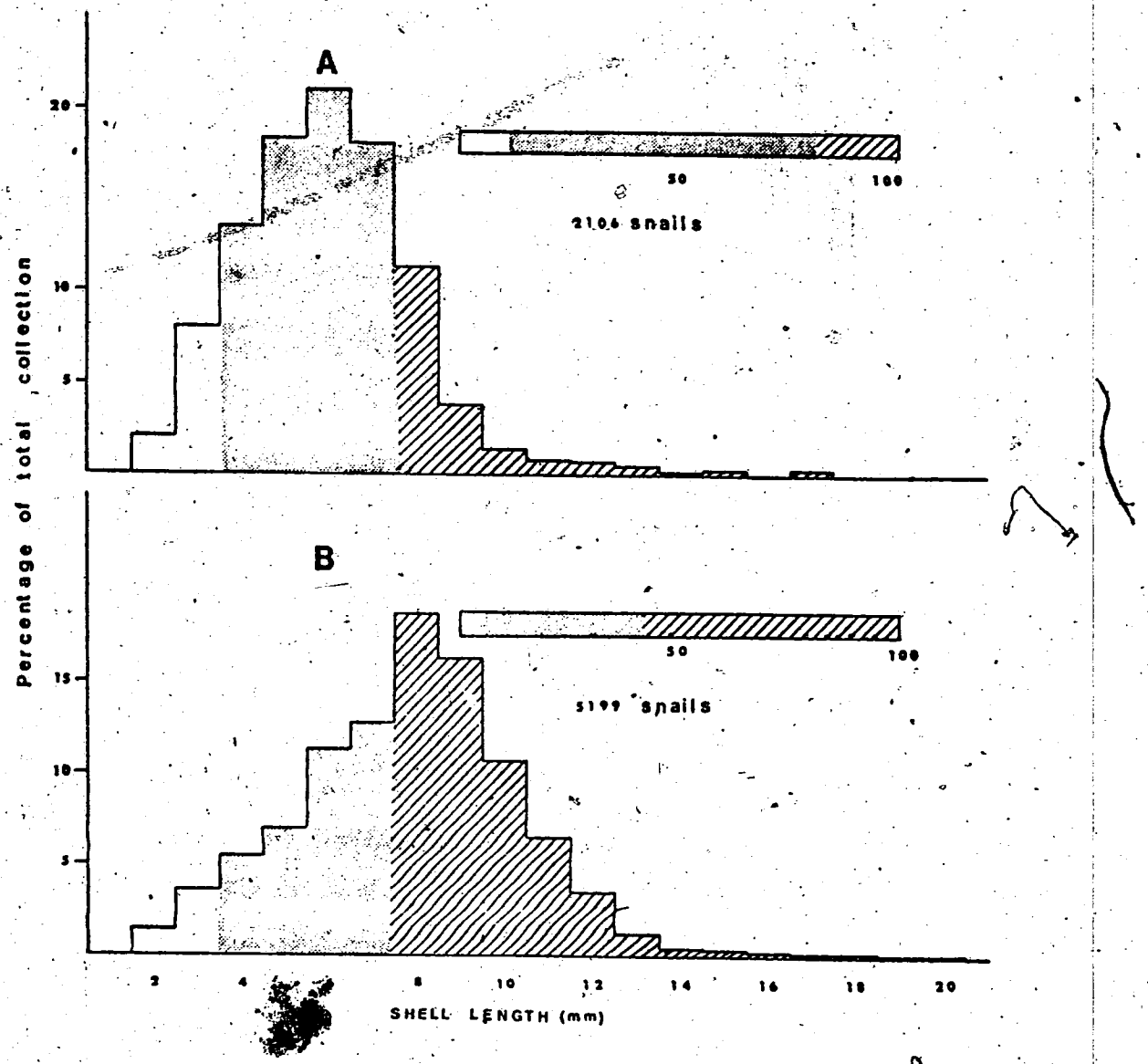


Figure 7. Overall size - frequency distribution of *Physa gyrina* from the control (A) and heated (B) areas. The bar diagrams indicate the relative proportions of hatchlings (< 3 mm), immatures (3.1 to 7 mm) and mature snails (> 7 mm) in each area.


A
B
20
10
5
15
10
5
50
100
2104 snails
5199 snails
Percentage of total collection
2
4
8
10
12
14
16
18
20
SHELL LENGTH (mm)

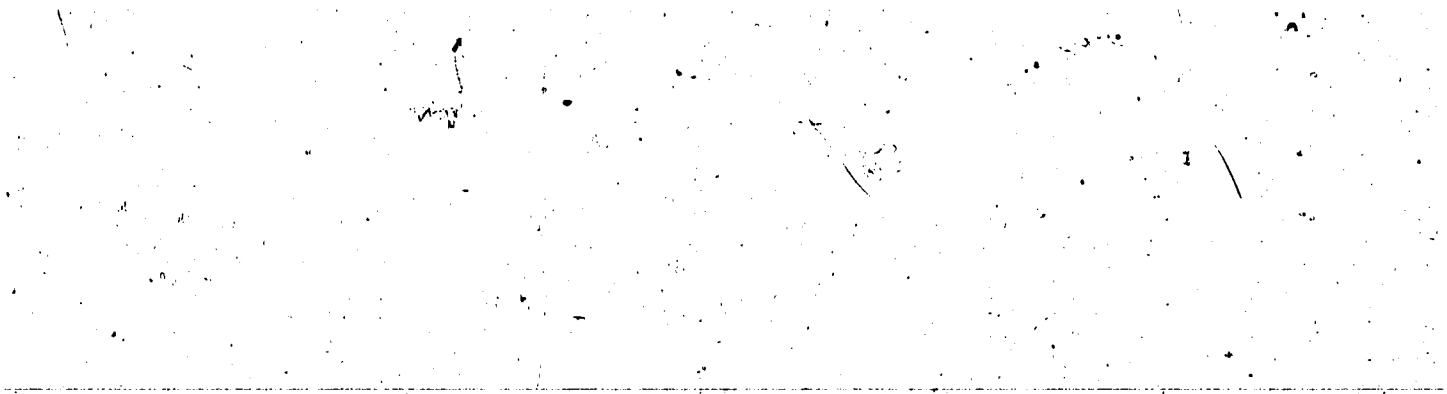


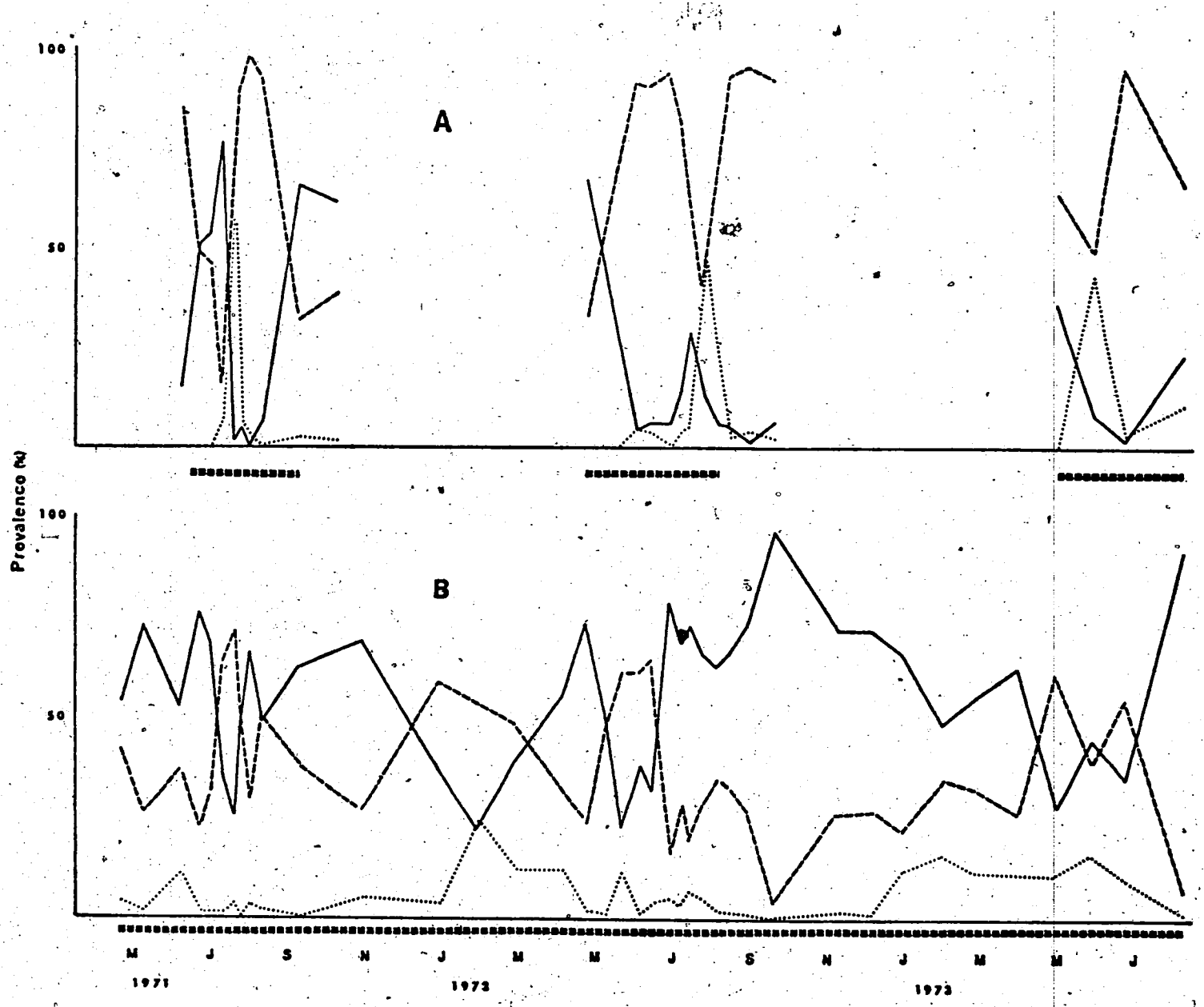
Figure 8. Seasonal changes in the population structure of *Physa gyrina* from the control (A) and heated (B) areas, May 1971 to August 1973.

■■■■■■■■ Egg masses

····· Hatchlings

– – – – – – Immatures

——————— Matures


100
50
A
Prevalence (%)
100
50
B
M
J
S
N
J
M
M
J
S
N
J
M
M
J
1971
1972
1973

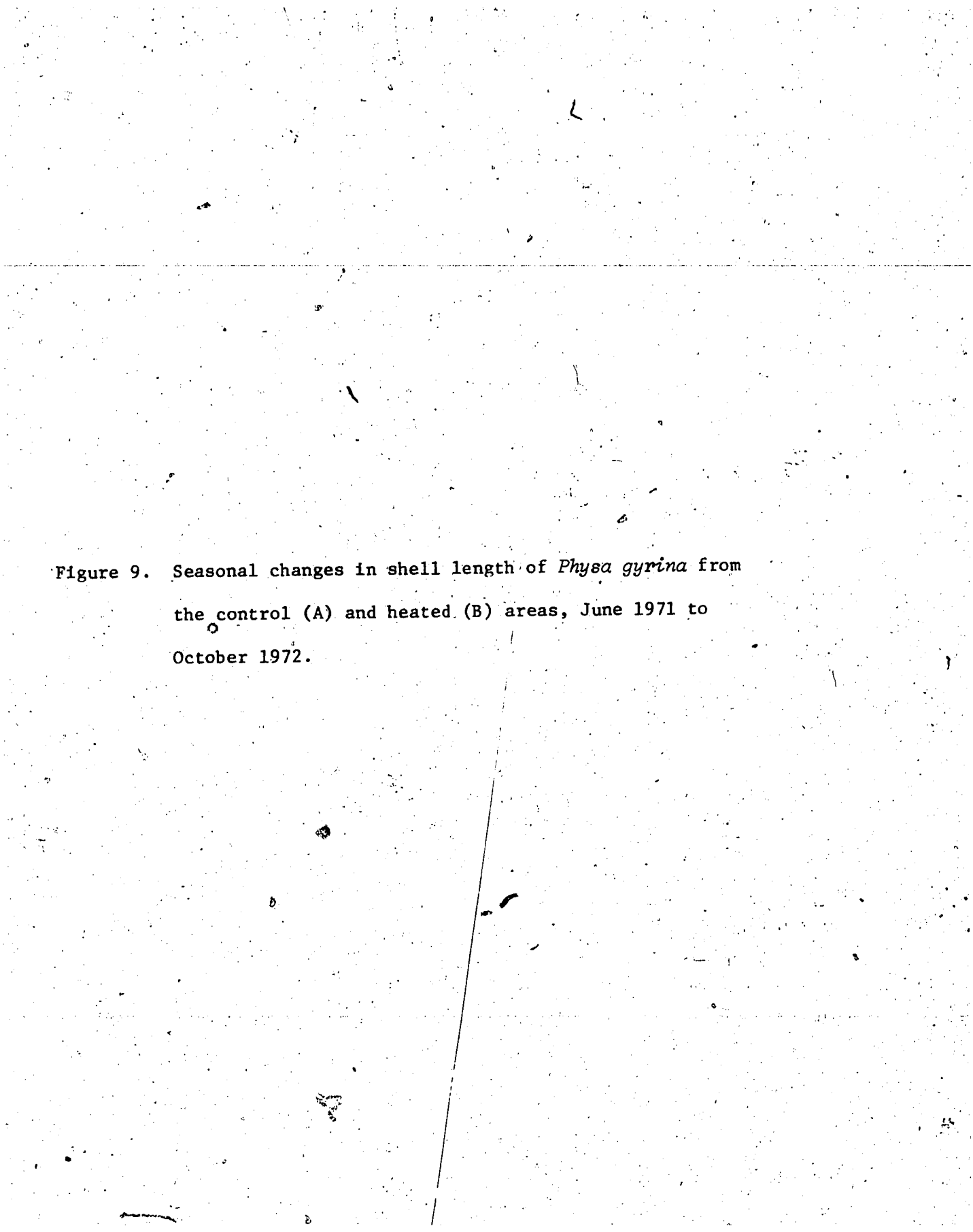
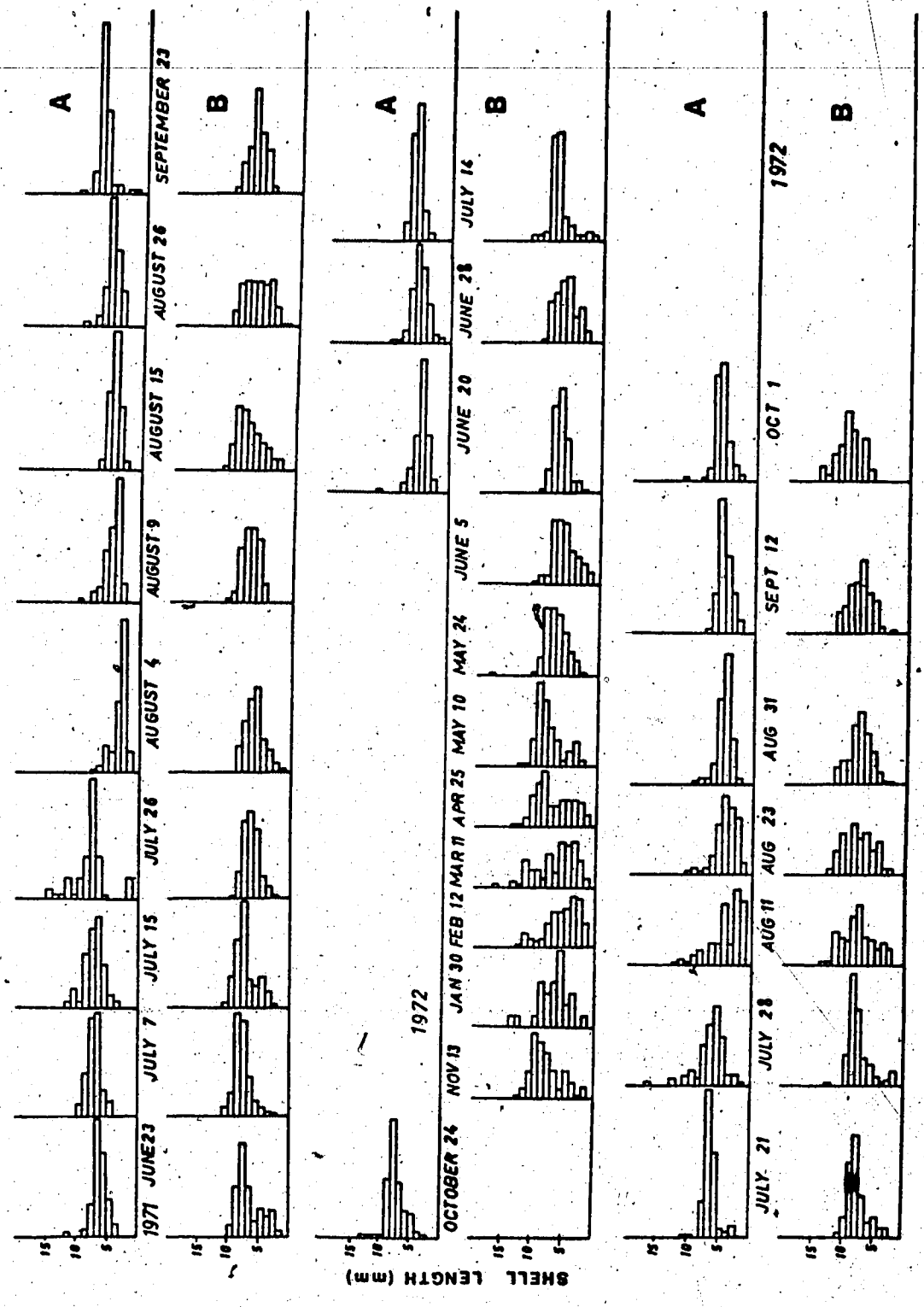


Figure 9. Seasonal changes in shell length of *Physa gyrina* from the control (A) and heated (B) areas, June 1971 to October 1972.


A
B
1971
JUNE 23
JULY 7
JULY 15
JULY 26
AUGUST 4
AUGUST 9
AUGUST 15
AUGUST 26
SEPTEMBER 23
OCTOBER 24
NOV 13
JAN 30
FEB 12
MAR 11
APR 25
MAY 10
MAY 24
JUNE 5
JUNE 20
JUNE 28
JULY 14
1972
JULY 21
JULY 28
AUG 11
AUG 23
AUG 31
SEPT 12
OCT 1
15
10
5
SHELL LENGTH (mm)
0 20%

suggests that more mature snails overwintered; however, that sample was based on a very small number of snails (6). The larger, later samples suggest that the major proportion of the overwintered snails were immatures. The rate of maturation of the overwintered immatures was somewhat slower, and the rate of maturation of the new generation was definitely slower (Fig. 9), so that mostly immature snails were present at freeze-up. The pattern during 1973 was harder to discern due to the fewer samples; except for the earlier peak of appearance of hatchlings (in June), it appeared to be basically similar to 1971.

In the heated area, the population structure of *P. gyrina* showed little consistent seasonal pattern; egg masses, hatchlings, immatures and mature snails were present throughout the year (Fig. 8) and a wide range of sizes were present at each sampling period (Fig. 9). The only seasonal pattern suggested by the data is the greater proportion of larger snails during the cooler part of the year (October to April or May).

EFFECTS OF TEMPERATURE ON THE DEVELOPMENT OF *P. GYRINA* EGGS

Snails measuring over 8 mm were collected in the field, brought to the laboratory and isolated in half-pint milk bottles containing dechlorinated water at room temperature (20°). Egg masses isolated immediately after they were deposited were maintained at different temperatures (from 5 to 35° C) in dechlorinated water, and observed daily until the young snails broke through the external membrane of the egg mass.

The results are shown in Table 2. Between 15 and 31°, the time required for embryonation and hatching was inversely related to the incubation temperature. At 10° development was very slow and only a few hatched, while at 5° or below and 32° or above there was no development at all. In addition, eggs that had been maintained at 5° for three months failed to resume development when moved to room temperature.

In addition, *P. gyrina* transferred to temperatures of 10° C in the laboratory did not oviposit.

DISCUSSION

There are probably two reasons for the close association between *P. gyrina* and submerged macrophytes: the availability of food and the air-breathing habit of the snails. *Physa gyrina* feeds on a variety of materials like dead and decaying vegetation (DeWitt 1955), diatoms, algae and small crustaceans (Clampitt 1970). Such food items would be more available on submerged macrophytes than on the mud bottom of the study area.

Like some other pulmonates, *P. gyrina* must come to the surface of the water periodically to get air (Clampitt 1970). Submerged macrophytes would provide an avenue for this ascent, and the subsequent descent through the water column. Such an avenue of descent may be essential for hatchlings to escape the surface tension.

It is clear from the counts of snails per unit vegetation that the amount of macrophytes present during the summer does not regulate the population of *P. gyrina* in either the control or the heated area. Nevertheless, because of such close association with submerged macrophytes

Table 2. Time (days) to hatching for eggs of *Physa gyrina* at different temperatures

Temperature (° C)	No. of egg masses	No. of days to hatching	
		First hatch	50% hatching
5	6	No development for 3 months	
10	10	65	-
15	12	20-22	24-25
20	13	16-17	17-18
25	8	8- 9	9-10
28	9	6	6- 7
30	7	4	4- 5
31	8	3	3- 4
32	5	No development	
35	6	No development	

populations of *P. gyrina* may be limited by the very small amount of vegetation present in the control area just after break-up, or in the heated area in the winter. This suggestion is supported by the findings of Gallup et al. (1973), who showed that mechanical harvesting of aquatic macrophytes in Wabamun Lake significantly reduced summer populations of *P. gyrina*.

The population dynamics of *P. gyrina* in the control area were basically similar to those described for the same species from other north temperate regions by DeWitt (1955) and Clampitt (1970). The two basic features common to all three studies are the overwintering by immature and mature snails in deep water with a migration back into shallow water during spring and the annual cycle with a summer population turnover.

The absence of eggs for 1-2 months prior to freeze-up, the absence of eggs or hatchlings immediately after break-up, and the inability of eggs to survive prolonged exposure to 5° C in the laboratory all indicate that, in the control area of Wabamun Lake, *P. gyrina* overwinters only as immature or mature snails. These snails apparently did not overwinter in the study area. In each year, there was a moderate population in the study area at the last sampling period before freeze-up, but few, or no, snails immediately after break-up (shown best in the data for 1972, Fig. 5). The repopulation of the control area was by overwintered snails, and took place before the appearance of eggs and hatchlings. The source of these snails was not investigated, but it seems likely that they migrated from the deeper waters offshore, as in *P. gyrina* elsewhere (Cheatum 1934, DeWitt 1955, Clampitt 1970) or in another pulmonate, *Helisoma trivolvis*, in Alberta

(Morris 1970). The repopulation appeared to coincide with the appearance of aquatic macrophytes (Appendix III).

The summer population overturn appears to be due to a combination of three factors: postreproductive mortality of mature snails, conditions necessary for oviposition, and the rate of development and growth of eggs and young snails. The first is evidenced by the disappearance of most of the mature *P. gyrina* shortly after hatchlings appeared in the collections. It is a common feature among semelparous organisms, and has been reported for *P. gyrina* by both DeWitt (1955) and Clampitt (1970). The midsummer disappearance of the mature snails, especially in 1971, suggests that the reproductive season for individuals is considerable shorter than the four to five month season for this species.

The other two factors appear to be directly related to water temperature. DeWitt (1967) suggested that egg production in physids is stimulated by temperature, but not photoperiod, and that *P. gyrina* oviposit only when the temperature of the water is raised to at least 10-12 C (DeWitt 1955). In the control area, the temperature of the water was above 12-14 C, and hence provided the necessary conditions for oviposition, only from May to September.

The minor variations in the reproductive activity in the control area during the three summers appear to be directly related to water temperatures. The continuation of warm water temperatures late into September in 1971, apparently allowed the relatively large population of mature snails to oviposit at that time. Similarly, the early break-up and rapid temperature rise during the spring of 1973 was apparently responsible for the early reproductive activity, resulting in a peak of

hatchlings in June, at least a month earlier than in the other years.

As evidenced by the laboratory experiments, the rate of embryonation and hatching is directly related to water temperature, as reported earlier by DeWitt (1954a). The rate of growth of *P. gyrina* and other gastropods is also directly related to water temperature (e.g., DeWitt (1955), Clampitt (1970) for *P. gyrina*; McCraw (1970) for *L. palustris*; Heppleston (1972) for *L. truncatula*, and Shiff (1964b) for *Bulinus (Physopsis) globosus*). The data from this study agree. There was no significant growth over winter, as evidenced by the similar mean lengths and size distributions of the populations at freeze-up and break-up (Appendix I, Fig. 9). The rate of growth of immature snails into the mature size classes was slower during the cooler summer of 1972, resulting in very few mature snails by freeze-up. The faster growth rate in 1973 appeared to be due to the early spring and generally warmer conditions that summer.

To summarize, the pattern of the *P. gyrina* population in the control area appeared to be as follows: The population overwintered as mature or immature snails off the control study area, presumably in deeper water, and migrated back into the area as the macrophytes developed. The mature snails oviposited and died; their numbers were replaced, then augmented, by the growth and maturation of overwintered immatures. The peak of oviposition, and hence the peak in numbers of hatchlings and the maximum population size, depended on the relative numbers of mature and immature snails overwintering and on the rate of growth of the immature snails, determined by spring and early summer temperatures. The postreproductives died, and the new generation grew at a rate depending on the

late summer and fall temperatures, with some fall oviposition if conditions were particularly favorable.

The population dynamics in the heated area are quite different. Growth and reproductive activity was continuous, not seasonal, as attested by the presence of mature snails, egg masses and hatchlings throughout the year. As a result, the population at all times of the year consists of several broadly overlapping generations. These findings corroborate those of Agersborg (1932) who found that *P. gyrina* in warm waste waters in Illinois grew and oviposited continuously throughout the year.

Although growth and reproduction continued throughout the year, there was a definite annual cycle of population size, with maximal populations in summer and very few snails during the winter. The low populations during the winter were correlated with, and presumably due to, the absence of aquatic macrophytes. The population build-up during the spring seems to be mainly due to the reproductive activity. It was not clear what happened to the majority of the *P. gyrina* at the time of the early winter population crash. However, there was some evidence to suggest that they might have drifted off the study area along with dead, floating vegetation. Despite the dense stand of aquatic macrophytes in the heated area during the summer, there was never much dead or decomposing vegetation in the area during the winter. The absence of any large quantities of dead macrophytes in the shallow area suggests that the dead vegetation might have drifted along with the current of water flowing through the study area from the outlet canal and/or by wind action. The *P. gyrina* associated with the macrophytes would presumably drift off with it.

During the summer, the higher temperatures produce earlier hatching,

a faster growth rate, and earlier maturity and oviposition--in general, a shorter generation time. This short generation time, and the overlapping generations produced by the continuous reproduction, allow the rapid build-up of the populations to very high densities whenever there was sufficient vegetation present. Agersborg (1932) also suggested that the conditions in the warm waste water resulted in higher population densities of *P. gyrina*, and Shiff (1964a, c) showed that higher temperatures increased the intrinsic rate of natural increase of *Bulinus globosus*.

The data suggest that the population dynamics of *P. gyrina* are controlled by two major factors: rate of reproduction, and the amount of aquatic macrophytes present. The latter apparently sets a ceiling, which effectively limits the populations of *P. gyrina* during the winter (extending into spring and early summer in the control area). During the summer, the ceiling is apparently high enough so that rate of reproduction of the *P. gyrina* population takes over as the primary control. Since the thermal effluents at Wabamun Lake have marked effects on both the rate of reproduction of *P. gyrina* and the amount of aquatic macrophytes, they have markedly altered the regular pattern of *P. gyrina* populations and have provided the necessary conditions to build up very high population densities during the summer.

HELMINTH PARASITES

A total of 7,305 *Physa gyrina*, 2,106 from the control area and 5,199 from the heated area, were examined for larval helminth parasites between May 1971 and August 1973. The results are summarized in Table 3. Four species of trematodes were found in the control area, seven in the heated area. Among the seven species of trematodes, *Echinoparyphium recurvatum*, *Ornithodiplostomum ptychocheilus*, and *Apatemon gracilis* are reported from *P. gyrina* for the first time.

The seasonal prevalences of total infections with germinal sacs (rediae or sporocysts), and the total metacercarial infections in the two areas are shown in Figure 10. The two measures show entirely different patterns and levels of infection in the two areas.

In the control area, infections with germinal sacs increased in prevalence through the early summer, reaching peaks of 35-50% in July, then declined to relatively low levels (10% or less). Metacercarial infections in the control area were generally low; none were present immediately after break-up, they gradually appeared in low proportions during the summer, reaching peaks of 15-20%, and declined towards the end of the summer (Fig. 10).

In the heated area, infections with germinal sacs were present throughout the year, but showed a typical seasonal pattern of low levels from May to September (less than 5% except in 1971), and significantly higher levels during the winters (20-40%). These higher levels almost reached the summer peak levels of infections in the control area. Although the prevalence of germinal sac infections was low during the

Table 3. Overall prevalence of helminth parasites in *Physa gyrina* collected from Wabamun Lake, 1971-1973

	Control		Heated	
No. examined	2,106		5,199	
Infected with:	n	%	n	%
Echinoparyphium recurvatum				
Cercariae*	175	8.3	354	6.8
Metacercariae	94	4.5	3,632	69.9
Notocotylus urbanensis				
Cercariae	68	3.2	72	1.4
Metacercariae	33	1.6	49	0.9
Cotylurus douglasi				
Cercariae	3	0.1	10	0.2
Metacercariae	13	0.6	1,749	33.6
Ornithodiplostomum ptychocheilus				
Cercariae*	0		3	0.1
Apatemon gracilis				
Cercariae*	0		2	0.1
Trichobilharzia cameroni				
Cercariae	5	0.2	16	0.3
Trichobilharzia physellae				
Cercariae	0		2	0.1
Sporocysts (unidentifiable)	3	0.1	2	0.1
Total snails infected with germinal sacs	252	12.0	52	8.8
Total snails infected with metacercariae	137	6.5	3,943	75.8

*New host record.

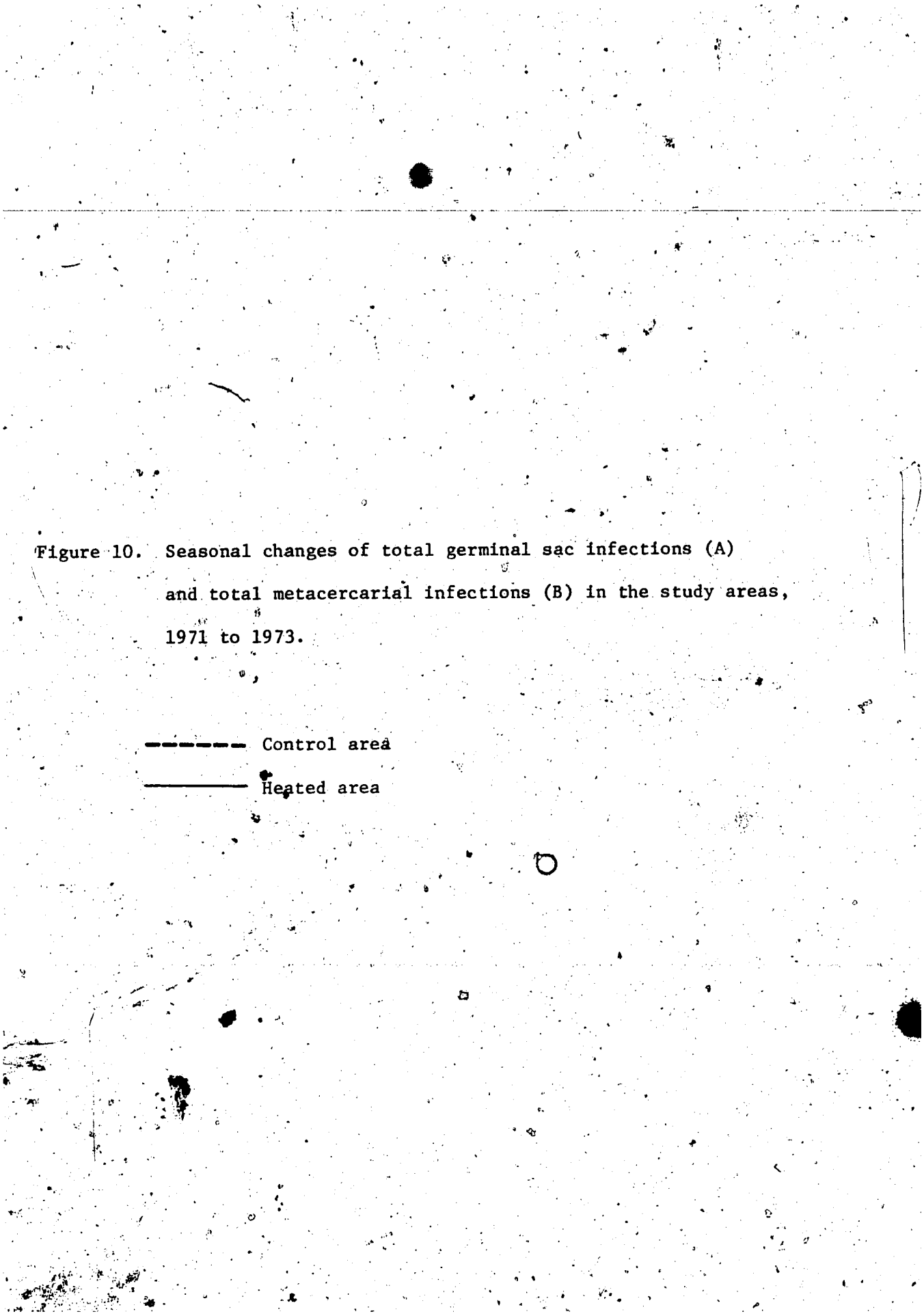
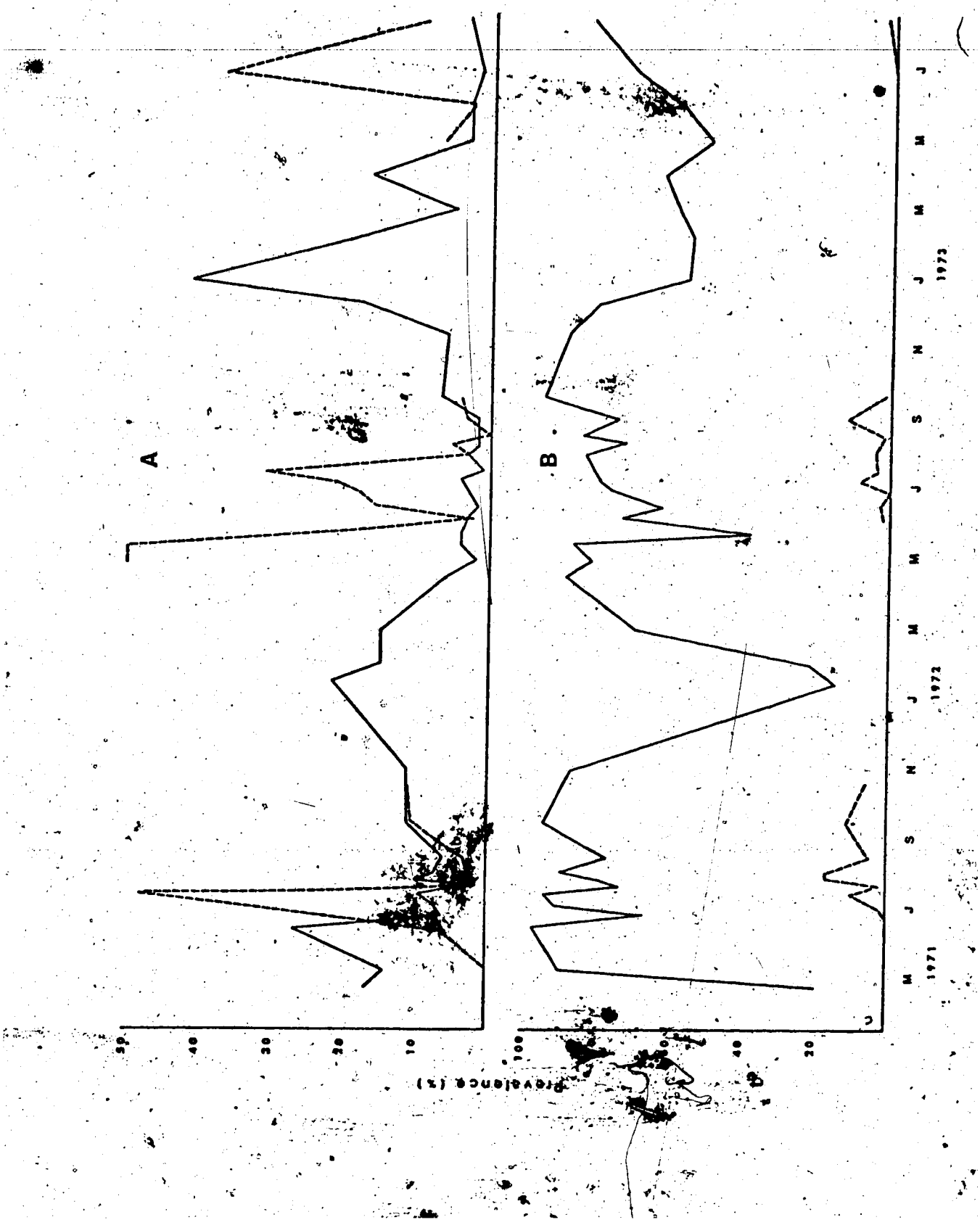


Figure 10. Seasonal changes of total germinal sac infections (A) and total metacercarial infections (B) in the study areas, 1971 to 1973.

------ Control area

——————— Heated area


A
B
C
D
Prevalence (%)
40
30
20
10
100
80
60
40
20
M J S N M J 1971
M J S N M J 1972
M J 1973

summer in the heated area, the actual number of infected snails per square meter is greater than in the control area or the heated area during the winter. Because of sparse snail populations in the control area and in the heated area during the winter a relatively larger area was sampled to obtain fewer snails, whereas a very small area was sampled to obtain a larger sample of snails in the heated area during the summer.

Metacercarial infections in the heated area were considerably higher than infections with germinal sacs in the heated area or infections of either type in the control area (Fig. 10, Table 3). Fluctuations were irregular, but included decreases in prevalence during the winters.

The overall proportion of germinal sac to metacerial infections was very different in the two areas; in the control area it was 1:0.6, whereas in the heated area it was 1:11.8.

Concurrent infections of *P. gyrina* with more than one species of germinal sacs were very sparse; only four double infections were found, all involving *E. recurvatum*, the most common species.

Only two concurrent infections with metacercariae of *E. recurvatum* and those of *C. douglasi* were found in the control area, but such concurrent infections were very common (28.7% of all the snails) in the heated area (significantly more than expected; X^2, 1 d.f. = 375.2; $p << 0.001$).

In each area, the total prevalence of germinal sacs, the prevalence of each of the two common species (*E. recurvatum* and *N. urbanensis*), and the prevalence of metacercarial infections increased significantly with increased size (age) of the snails (Fig. 11), suggesting no age resistance in *P. gyrina* to these helminth infections.

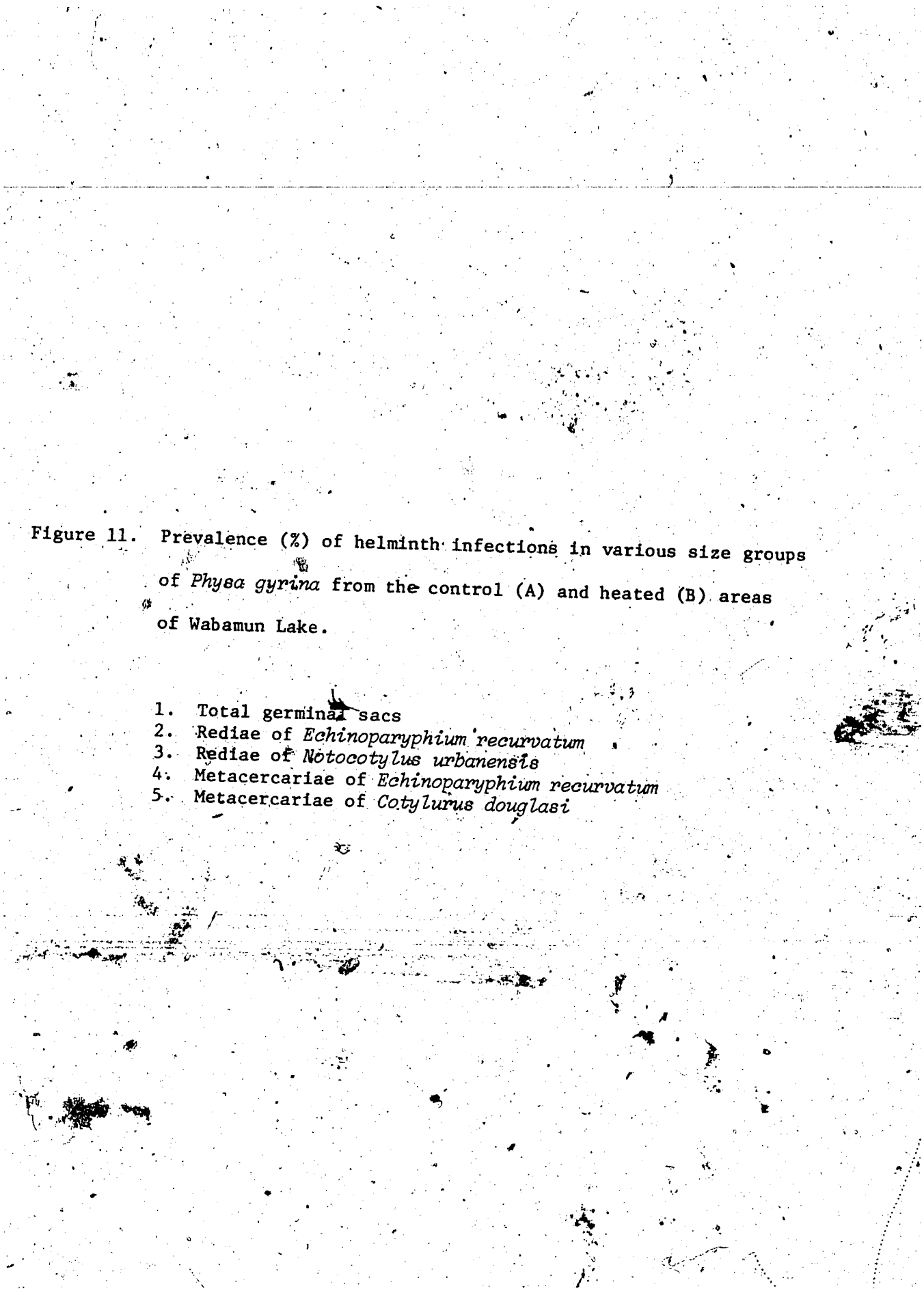
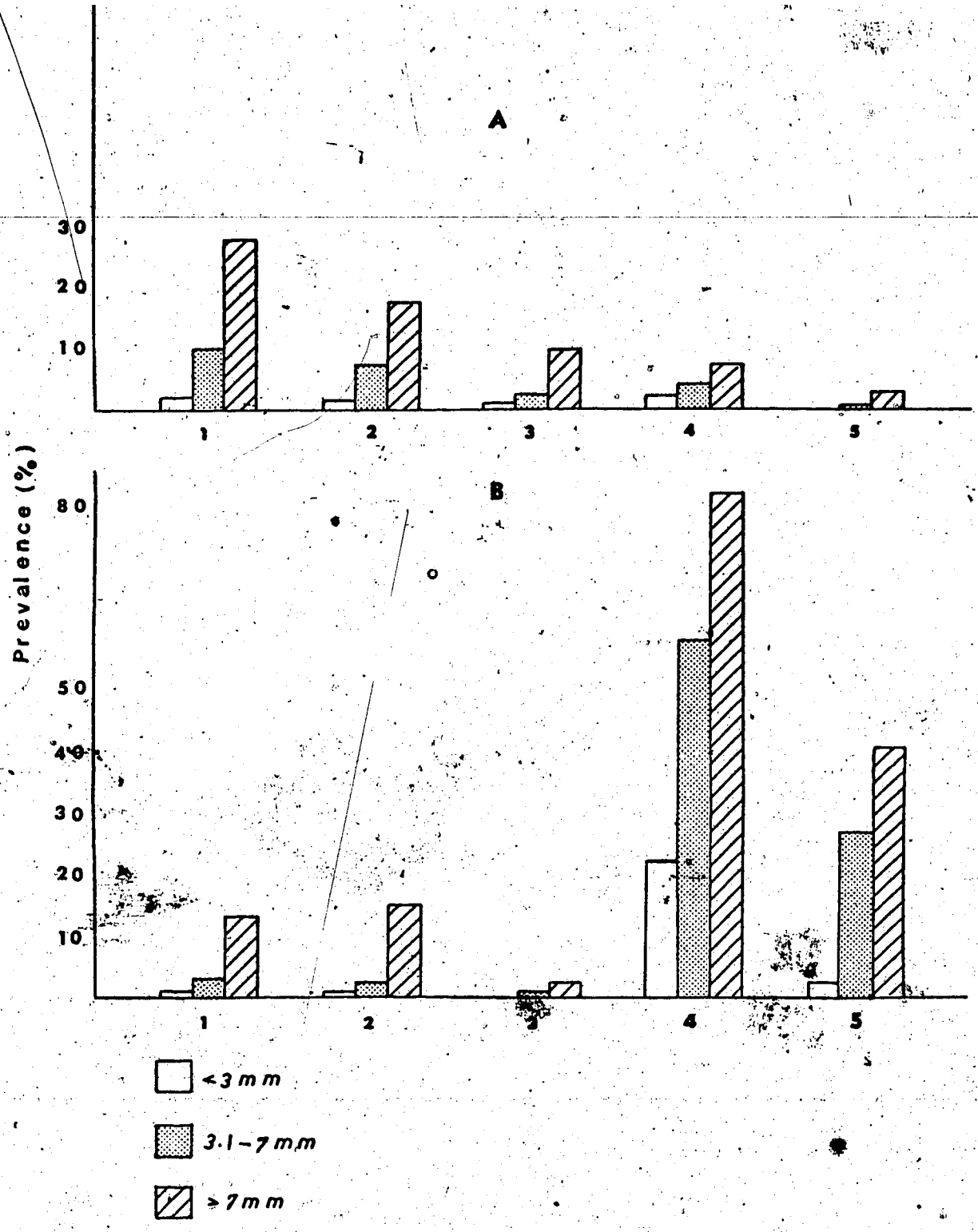


Figure 11. Prevalence (%) of helminth infections in various size groups of *Physa gyrina* from the control (A) and heated (B) areas of Wabamun Lake.

1. Total germinal sacs
2. Rediae of *Echinoparyphium recurvatum*
3. Rediae of *Notocotylus urbanensis*
4. Metacercariae of *Echinoparyphium recurvatum*
5. Metacercariae of *Cotylurus douglasi*


A
30
20
10
1
2
3
4
5
B
Prevalence (%)
80
50
40
30
20
10
1
2
3
4
5
< 3 mm
3.1 – 7 mm
> 7 mm

Larval trematodes found in other species of snails from the study areas are listed in Table 4. None of the larval stages present in *P. gyrina* were present in other gastropods except the germinal sacs of *A. gracilis* (rare in *L. elodes*) and possibly the metacercariae of *E. recurvatum* (see species account below).

EFFECTS OF TEMPERATURE ON LARVAL STAGES

Effect of Temperature on Hatching of *E. recurvatum* Eggs

Eggs of *E. recurvatum* were teased from mature flukes collected from laboratory-infected animals, usually chicks. Some eggs were also collected by maintaining live echinostomes in 0.85% NaCl at room temperature for 4 to 5 hours. Eggs were washed two or three times in dechlorinated water, then incubated in stender dishes in dechlorinated water at 5, 10, 15, 20, 25, 28 and 30° C and examined daily to determine the time required for the emergence of miracidia.

At water temperatures between 15 and 28°, the time required to hatch miracidia was inversely related to the temperature (Table 5). At or below 10° there was no development for three months. At 30° less than 25% of the eggs hatched.

Effect of Temperature on the Emergence of Cercariae

The normal time of cercarial emergence at room temperature (19-20° C) was determined for field-collected snails infected with 6 species of cercariae. Half-pint milk bottles containing the infected snails were transferred from room temperature to a lower test temperature one hour prior to the usual time of cercarial emergence. The bottles were examined for emerged cercariae after one, two and three hours. If

Table 4. Larval helminth parasites of other gastropods from Wabamun Lake

Snail hosts	Larval helminths*	Prevalence**	
		Control area	Heated area
Helisoma trivolvis	*Petasiger* sp.	rare	-
	Tylodelphyis sp.	rare	-
	Zygocotyle lunata	common	-
Lymnaea elodes	*Apatemon gracilis*	-	rare
	Echinostoma revolutum	-	common
	E. revolutum metacercariae	-	common
	Notocotylus attenuatus	-	common
	Unidentified cotylurid	-	rare
	Unidentified plagiorchid (Sp. A)	-	common
Lymnaea stagnalis	*Notycotylus attenuatus*	common	-
	Unidentified strigeid	common	-
Valvata tricarinata	*Ichthyocotylurus erraticus*	rare	common
	Sanguinicola lophophora	absent	rare
	Unidentified plagiorchid (Sp. B)	absent	rare
	Echinostome metacercariae	absent	rare

*Germinal sacs, unless otherwise stated.

**rare < 3.0%; common > 3.0%.

Table 5. Time (days) to hatching for eggs of *Echinoparyphium recurvatum* at different temperatures

Temperature (° C)	No. of eggs	Number of days to release miracidia	
		Minimum	50%
5	60	No development for 3 months	
10	35	No development for 3 months	
15	40	28-29	29-31
20	60	11-12	12-13
25	50	9-10	10-11
28	45	7- 8	8- 9
30	35	7	*

*Less than 25% hatched.

positive, the snails were returned to room temperature, and the experiment was repeated the following day, at a lower temperature. If the snails did not shed cercariae, they were left at the test temperature for an additional 10-12 hours to test for any delayed release of cercariae.

The results are summarized in Table 6. In five of the six species cercariae emerged in apparently undiminished numbers down to 15°; at 14° all five species emerged, but in markedly reduced numbers; at 13° or lower, no cercariae emerged. The cercariae of *T. cameroni*, however, emerged in large numbers down through 12°, with reduced numbers emerging even at 5° C.

SPECIES ACCOUNTS

The identification features, basic life cycles, general prevalence and seasonal fluctuations of each of the trematode species found in *P. gyrina* are given below in separate species accounts.

Echinoparyphium recurvatum (Linstow, 1873) Lühe, 1909

The taxonomy of the *E. recurvatum-E. flexum* complex is unclear. Najarian (1961) states that *E. recurvatum* can be distinguished from *E. flexum* by the following characters: miracidium with two pairs of eyespots, as opposed to one pair; three pairs of gland openings at the oral sucker of cercaria, as opposed to four pairs; and the absence of a seminal receptacle, as opposed to its presence. In addition, "one of the most characteristic features of the adult of *E. flexum* is the protrusibility of the acetabulum . . ." (Najarian 1954) and he also suggested that it is characterized by 17-25 indentations along the edge of the ventral sucker.

In the present study, these characters could not be used, or gave

Table 6. Effect of temperature on the emergence of cercariae

		Number of snails shed cercariae at Temperature (°C)									
	n	20	18	17	16	15	14	13	12	10'	5
Physa gyrina											
Echinoparyphium recurvatum	12*	12	12								
	6			6	6	6	6**	0	0	0	0
Notocotylus urbanensis	8*	8	8								
	4			4	4	4	4**	0	0	0	0
Cotylurus douglasi	4*	4	4								
	2			2	2	2	2**	0	0	0	0
Trichobilharzia cameroni	8*	8	8								
	4			4	4	4	4	4	4	4**	4**
Lymnaea elodes											
Echinostoma revolutum	6*	6	6								
	3			3	3	3	3**	0	0	0	0
Plagiorchid (sp. A)	6*	6	6								
	3			3	3	3	3**	0	0	0	0

*Sample was subdivided into two groups from 17° and below and used simultaneously at two temperatures.

**Only few cercariae emerged.

conflicting results. The appearance of the eyespots depended on the amount of pressure on the coverslip. With light pressure, there was one pair of banana-shaped eyespots, similar to those described for *E. flexum* by Najarian (1954). With increased pressure, the single pair resolved into two pairs. These pairs had two different arrangements, one for each of the two strains described below (Fig. 12). The arrangement of the "snail strain" is similar to that described for *E. recurvatum* by Rasin (1933). I could not be sure of the number of gland openings at the oral sucker of enough cercariae to be able to evaluate it as a taxonomic character. It may be valid, but would be very difficult to use. The acetabulum in my live specimens was protrusible, but devoid of indentations along the edge. Live adults, serial sections and permanent mounts were studied, but no definite seminal receptacle was found.

In addition, during the present study, two types of "*E. recurvatum*" cercariae were observed from *P. gyrina*. The major difference between them was their specificity to different second intermediate hosts in the laboratory, planarians (*Dugesia tigrina*, apparently a new host record) or snails. The "planarian strain" can also be distinguished from the "snail strain" by morphological and behavioral features. The former are characterized by a longer tail, shorter body, and shorter ventral sucker (Table 7). They began to emerge from the snails somewhat earlier (8 as opposed to 10 AM), but emergence times overlapped broadly (8 AM to 4 PM as opposed to 10 AM to 5 PM). The reaction towards light and the general swimming patterns are similar in both types of cercariae, but they differed in their resting position; "planarian strain" cercariae always concentrated in the upper layers of the water column, whereas "snail strain" cercariae always settled at the bottom of the container.

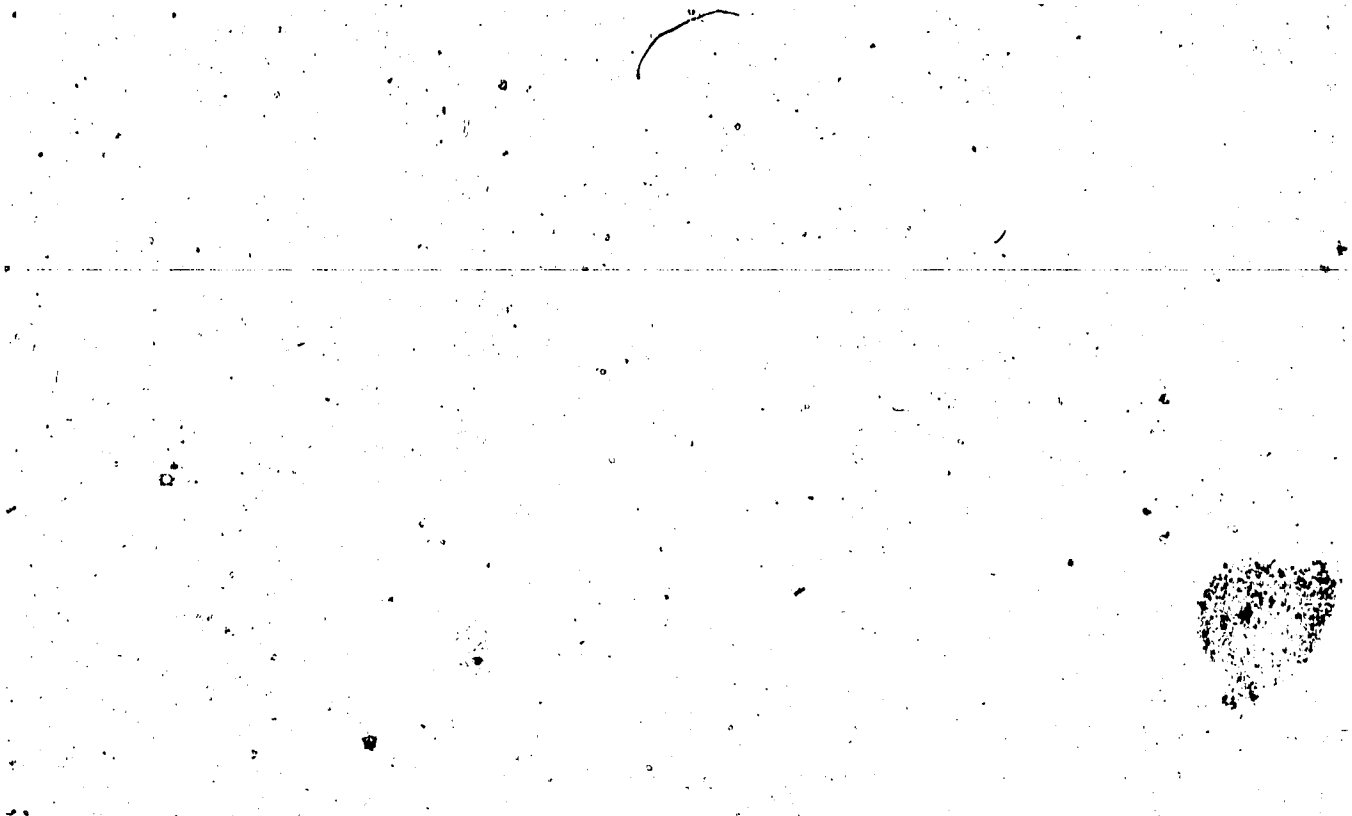


Figure 12. Eyespots of miracidia of planarian (A) and snail (B) strains of *Echinoparyphium recurvatum* (approximately to the scale shown).


A
B
0.1 mm

Table 7. Measurements (mean in microns ± S.E.) of snail and planarian strains of *Echinoparyphium recurvatum* cercariae fixed in hot 5% formalin

	Snail strain	Planarian strain
n	30	30
Body length	384 ± 5.2	323 ± 7.8
Body width	164 ± 2.4	158 ± 2.6
Length of tail	466 ± 5.4	524 ± 6.4
Width of tail	55 ± 0.9	50 ± 0.7
Length of oral sucker	54 ± 0.4	52 ± 0.4
Width of oral sucker	51 ± 0.4	50 ± 0.5
Length of ventral sucker	63 ± 1.3	49 ± 1.2
Width of ventral sucker	69 ± 1.0	70 ±
Length of pharynx	27 ± 0.3	28 ± 0.3
Width of pharynx	15 ± 0.2	16 ± 0.3

At least 100 metacercariae from planarians were fed to each of two hamsters and two chicks. The chicks were examined 6-7 days after exposure, and harbored only 4 and 5 mature *E. recurvatum*. The hamsters were examined 10 days after exposure; they harbored a total of 110 worms, all mature, over 3 mm in length, and containing 30-35 well-developed eggs.

At least 100 metacercariae from snails were fed to each of 10 chicks, 2 mallards, 2 hamsters and 2 rats; adults were obtained from all the hosts infected. However, only 18 adults were recovered from the hamsters 10 days after exposure; they averaged only slightly over 1 mm in length; only 4 were mature, and they contained only one or two small eggs. Specimens obtained from the other hosts were fully grown and contained 20-30 eggs on the 7th day. Except in the hamsters, the adults from the two strains were morphologically indistinguishable.

As indicated earlier, under moderate to strong coverglass pressure, the eyespots of the miracidia of the two strains differed markedly (Fig. 12).

Data on the relative proportions of the snails infected with the two strains were available only from January 1973 on; the proportions were roughly equal: 2 "snail" to 5 "planarian" strain in the control area during the summer of 1973, and 8 "snail" to 5 "planarian" strain in the heated area from January to August 1973.

All these observations, plus the insusceptibility of local *L. elodes* and *L. stagnalis* (both recorded as first intermediate hosts of *E. recurvatum* elsewhere, McDonald 1969) to laboratory infection with miracidia derived from local *E. recurvatum*, strongly substantiate Odening's (1965) suggestion that *E. recurvatum* is a complex species with many local strains ("races") (with *E. flexum* one of these strains), or

alternatively, a species complex with many local sibling species, and may explain why the literature on the larval stages is so confusing.

Complex species, with their multiplicity of local races (and races of their molluscan hosts) are common occurrences in trematodes (Wright 1971). Usually, they are similar morphologically, but differ markedly in some of their biological characteristics, such as growth rate, egg production, maturation time or pathological effects on their hosts. These intraspecific variations are determined by the basic ecology of the host-parasite relationships. Since the developmental physiology of populations of parasites is closely geared to that of their molluscan hosts, every host population exerts a selective influence over its parasites (Wright 1971). Such intraspecific variations are well marked in some cases, such as *Schistosoma japonicum* (Hunter et al. 1952, DeWitt 1954, Hsü and Hsü 1959), *S. haematobium* (LeRoux 1954, Wright 1967, Paperna 1968, Webbe and James 1972) and *S. intercalatum* (Wright et al. 1972).

All of these parasites are medically important and therefore have received a great deal of attention. Similar differences between strains of many other parasites, which have not received the same attention, are to be expected. The only available example not of medical importance is the larval complex of *Posthodiplostomum minimum*. Four different cercariae have been described (Bedinger and Meade 1967); experimentally, each of them produced metacercariae, and adults, identified as those of *P. minimum*. Host specificity of *P. minimum* metacercariae to either cyprinids or centrarchids has been reported by several people (reviewed by Avault and [illegible] 1965); because of their specificity, Hoffman (1958a) proposed two subspecies, *P. m. minimum* for the minnow line, and *P. m. centrarchi*

for the centrarchid line. Avault and Smitherman (1965) found that the "centrarchid strain" is not only specific to the particular family, but also showed varying degrees of infectivity to individual species within the family.

Adults of *P. minimum* mature quickly (in 32 hours--Miller 1954) and presumably have a short life span (4-5 weeks is usual for such strigeids), features which Wright (1971) suggests increase the chances of intraspecific divergence by reducing genic exchange between populations. In this case, at least, the short life span and intraspecific variation are accompanied by a lack of host specificity in the adults. The susceptible hosts include 4 classes and 15 orders of vertebrates (Ulmer 1961, Palmieri 1973).

The larval complex of *E. recurvatum* appears to be similar to that of *P. minimum*. The cercariae (and miracidia) of the obvious strains differ more than the adults, and the most obvious difference is a differential specificity to second intermediate hosts. *Echinoparyphium recurvatum* is also similar to *P. minimum* in having a short life span (4-5 weeks) and in being infective to a wide variety of birds and mammals (McDonald 1969). The adults are morphologically similar, but, unlike those of *P. minimum*, appeared to differ biologically, at least in their development in hamsters.

The ecological differences between the two local strains of *E. recurvatum* are intriguing, and suggest that they are undergoing a process of divergence towards the formation of isolated local host-parasite compatibilities (cf. Paperna 1968), one completing the life cycle through *Physa gyrina* and waterfowl (snail strain), and the other through *Dugesia tigrina* and muskrats (planarian strain).

Stunkard (1957) commented that "the problem of intraspecific

variation in parasitic flatworms are formidable, but not insuperable." It is quite evident that more information must be obtained in order to fully understand the ecological host-parasite relationships of the strains of *E. recurvatum*.

The taxonomic problems with echinostomes do not end with the recognition of two local strains of *E. recurvatum*. Encysted echinostome metacercariae are difficult to identify; they must be excysted and their collar spines examined or fed to experimental hosts. Three to four hundred of the metacercariae from about 20 *P. gyrina* were fed to laboratory-reared chicks; only *E. recurvatum* were recovered, suggesting that *E. recurvatum* was at least the predominant species present. However, *Echinostoma attenuatum*, which also has 45 collar spines, with 5 corner spines, is a common parasite of local coots (Colbo 1965). A limited number of observations on infections derived from eggs from adults in coots indicate that both redial and metacercarial stages of *E. attenuatum* will develop in *P. gyrina*, but that the metacercariae did not develop to adults in chicks. Metacercariae identified here as *E. recurvatum* may, therefore, include some *E. attenuatum* (or other species).

Echinostome metacercariae were also recovered from *L. elodes* and *V. tricarinata* from the heated area. When fed to chicks, those from *L. elodes* produced only *Echinostoma revolutum* adults, never *E. recurvatum*. Too few metacercariae were recovered from *V. tricarinata* to attempt laboratory infections. Their identity is unknown. In the laboratory, *H. anceps*, *H. trivolvis* and *V. tricarinata* were readily infected with metacercariae of *E. recurvatum*, but only a few encysted in *L. elodes* and none in *L. stagnalis*.

At Wabamun Lake, redial and cercarial stages of *E. recurvatum* were recovered only from *P. gyrina*, never from other species of molluscs. Adults of *E. recurvatum* have been reported from almost all the species of local ducks, and from muskrats (University of Alberta, unpublished records). All 15 muskrats taken in winter from Wabamun Lake were infected, with a mean intensity of 52, whereas only 1% of 238 muskrats taken from Big Island Lake, east of Edmonton, were infected, with a mean intensity of 3. Among the mallards, 92% of the 12 taken during the winter at Wabamun Lake were infected, with a mean intensity of 226, and a maximum intensity of 1,650. Mallards collected during the summer in other lakes in Alberta had a prevalence of 21% (n = 33), with a mean intensity of 20, and a maximum intensity of 50. The population of *E. recurvatum* from the mallards collected during the winter at Wabamun Lake was comprised of one-day old to fully mature digeneans containing eggs.

The overall prevalence of *E. recurvatum* rediae in the control area (8.3%) was significantly higher (X^2, 1 d.f. = 4.8; $p < 0.05$) than in the heated area (6.8%) (Table 3). The overall prevalence figures are somewhat misleading, however, because of vastly different seasonal distributions of *E. recurvatum* redial infections in the two areas (Fig. 13). In the control area, redial infections were absent at spring break-up, reached a peak prevalence (approximately 30%) during July, then essentially vanished.

In the heated area, the rediae of *E. recurvatum* were present throughout the year, their prevalence was low during the summer (except in 1971), but considerably higher during the winter. The maximum prevalence was 33% during January 1973. In the heated area, infections during the winter were in all stages of development. Most were releasing cercariae,

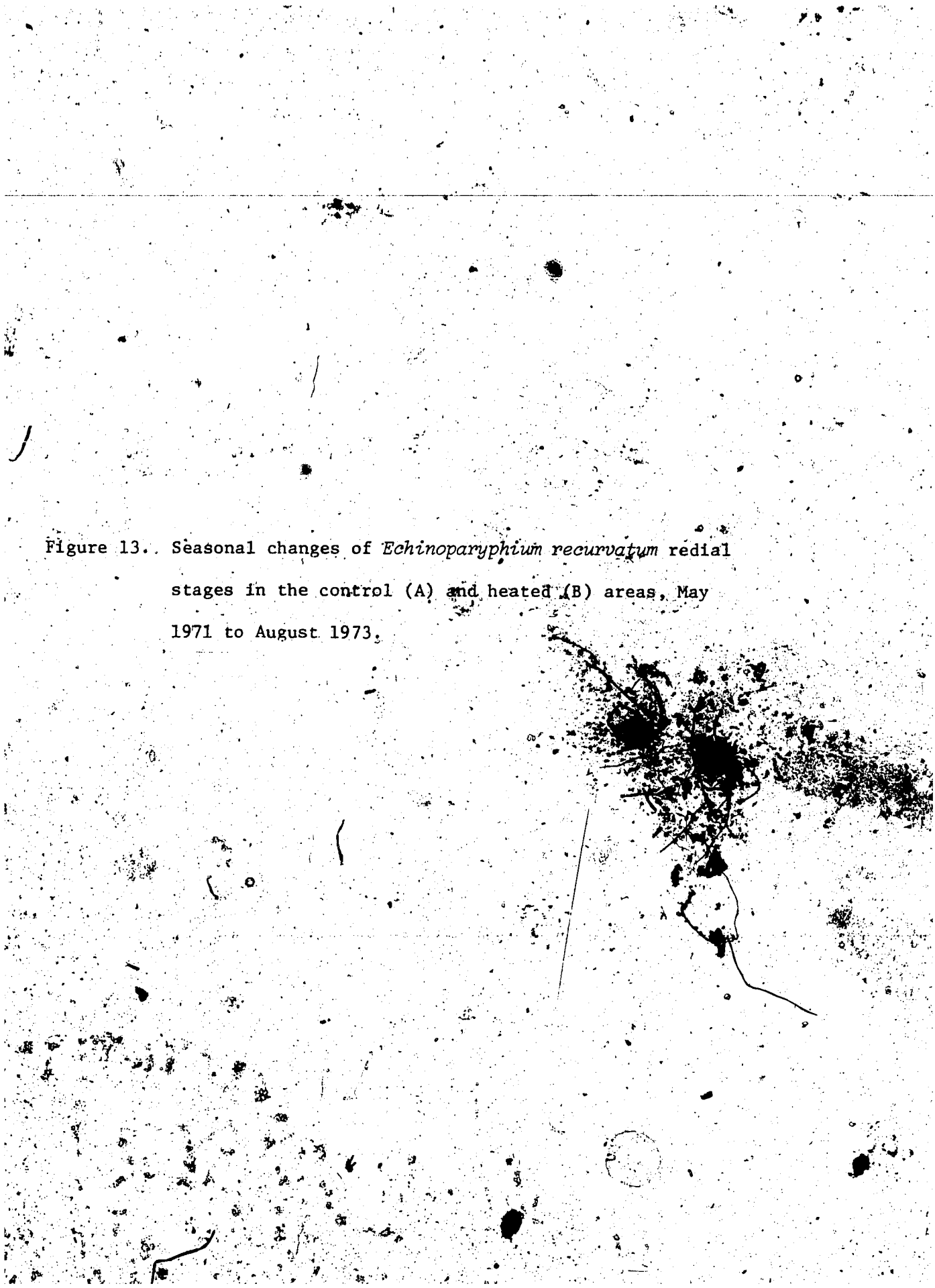
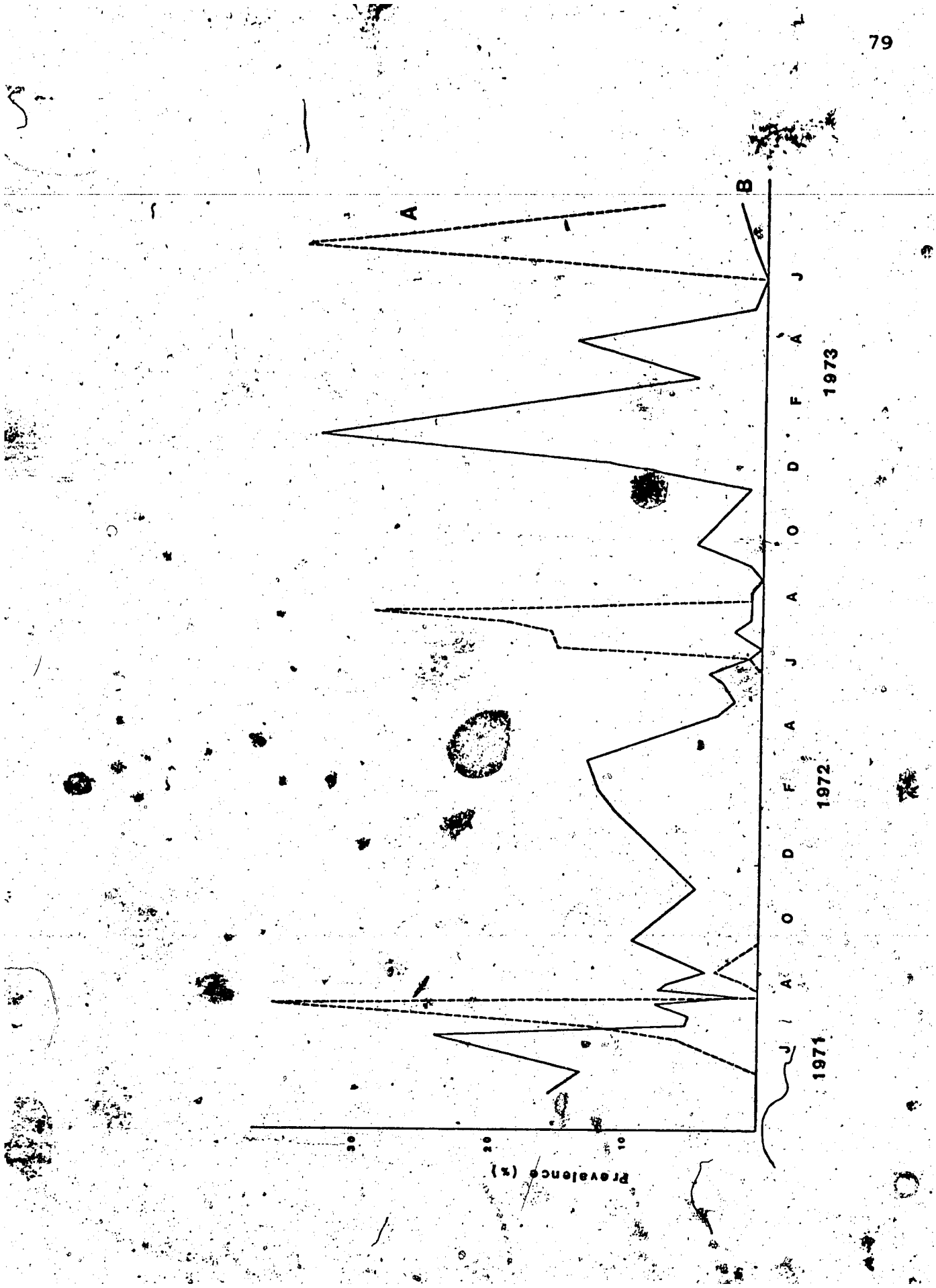


Figure 13. Seasonal changes of *Echinoparyphium recurvatum* redial stages in the control (A) and heated (B) areas, May 1971 to August 1973.


A
B
Prevalence (%)
30
20
10
J I A O D F A J A O D F A J
1971
1972
1973

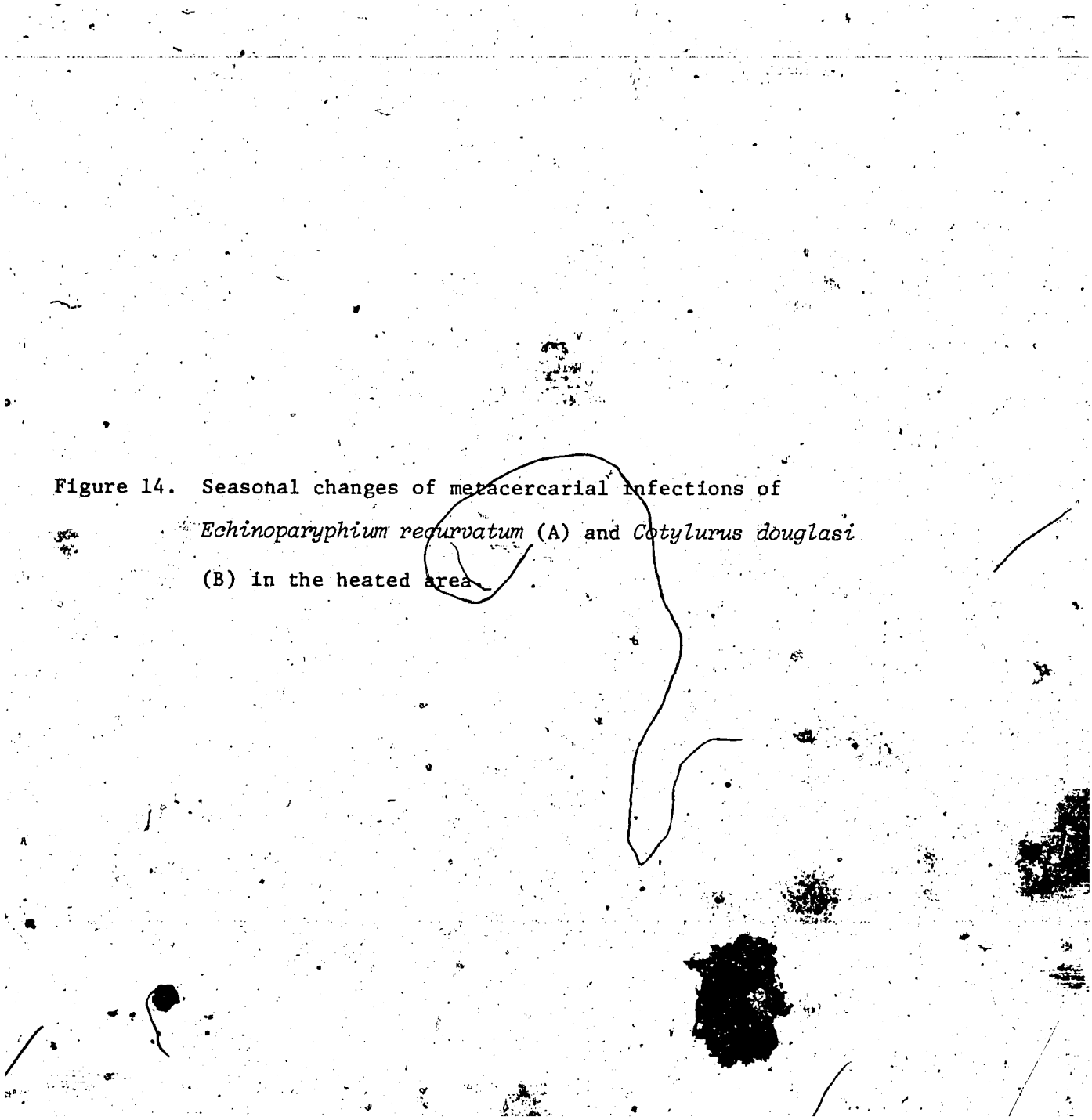
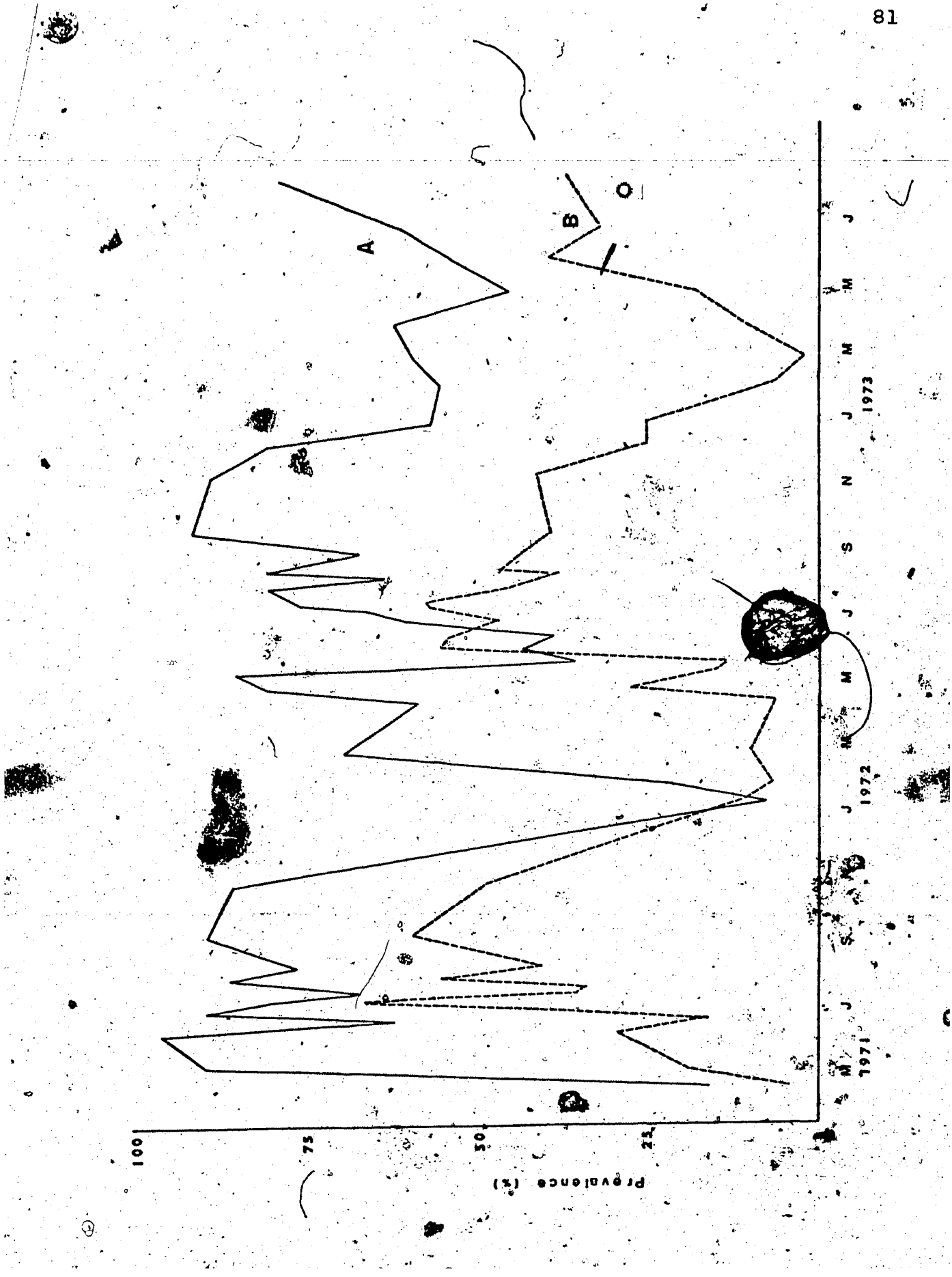


Figure 14. Seasonal changes of metacercarial infections of *Echinoparyphium recurvatum* (A) and *Cotylurus douglasi* (B) in the heated area.


A
B
C
100
75
50
25
Prevalence (%)
M
J
S
N
J
M
M
J
S
N
J
M
M
J
1971
1972
1973

but some were of very young rediae, and others were in very young snails, presumably those hatched during the winter.

Snails infected with echinostome metacercariae were very scarce in the control area (Fig. 10, Table 3), with a mean intensity of 3.3. Even though there were significant numbers of redial infections in the control area, they were not followed by significant numbers of metacercarial infections. No metacercarial infections were present in the control area at the time of freeze-up.

In the heated area, metacercarial infections were found in a large proportion of the snails (68.2%), and the mean intensity was also high (18.8). Metacercarial infections were also found in young snails, which presumably hatched during the winter.

Notocotylus urbanensis (Cort, 1914) Harrah, 1922

Cercariae of this species were identified by differentiating them from the closely related *N. attenuatus*, by the position of the excretory tubules (joining anterior to the median eyespot) and their specificity to *P. gyrina*, not lymnaeids, as pointed out by Herber (1955) and Acholonu and Olsen (1967). This identification was verified by exposing 2 chicks, 2 mallards, 2 hamsters and 2 rats to metacercariae obtained in the laboratory from snails shedding these cercariae. One immature *N. urbanensis* was obtained, from a mallard 3 days after infection.

The adults of this monostome are normally parasitic in muskrats (Herber 1955, McDonald 1969). All 15 muskrats collected during the winter from Wabamun Lake harbored *N. urbanensis*, with a mean intensity of 38. In contrast, 238 muskrats collected from Big Island Lake had only 4% prevalence with a mean intensity of 2 (University of Alberta unpublished results).

Larval stages of this trematode were recovered only from *P. gyrina*. They were the second most abundant of the germinal sac stages, and were found in 3.2% of the snails from the control area, significantly more (X^2, 1 d.f., = 27.05; $p < 0.001$) than the 1.4% from [illegible] area (Table 3). Snails releasing cercariae, but not oth[illegible]ably had notocotylid metacercariae encysted on their shells.

There was no clear seasonal pattern of infections in the control area. A few snails with redial infections were collected immediately after break-up (the high prevalence during May 1972 was due in part to a small sample size--6 snails). Redial stages were present in variable numbers throughout the summer up to the time of freeze-up (Fig. 15).

In the heated area, infections were present throughout the year, and the seasonal [illegible] was more or less similar to that of *E. recurvatum* infections, with [illegible]valences during the summer and higher prevalences during the winter. Early redial infections were found in some snails during the winter, especially in young snails, presumably hatched during the winter.

Cotylurus douglasi (Cort, 1917), n. comb.

The cercariae of this species of strigeid were easily identified to the *Cotylurus* type, based on the cercarial characters (4 penetration glands situated in front of the ventral sucker, between the caecae; flame cells 2 x [(2 + 2) + (2 + 2 + [2])] = 20), and t[illegible]ture of the metacercariae (encysted in pulmonates; pear-shaped body) as pointed out by Niewiadomska (1971). The cercarial measurements were generally similar to those of *Cercaria douglasi* Cort 1917 (Table 8), except for minor differences in the lengths of the tail stem and furcae and the size of the

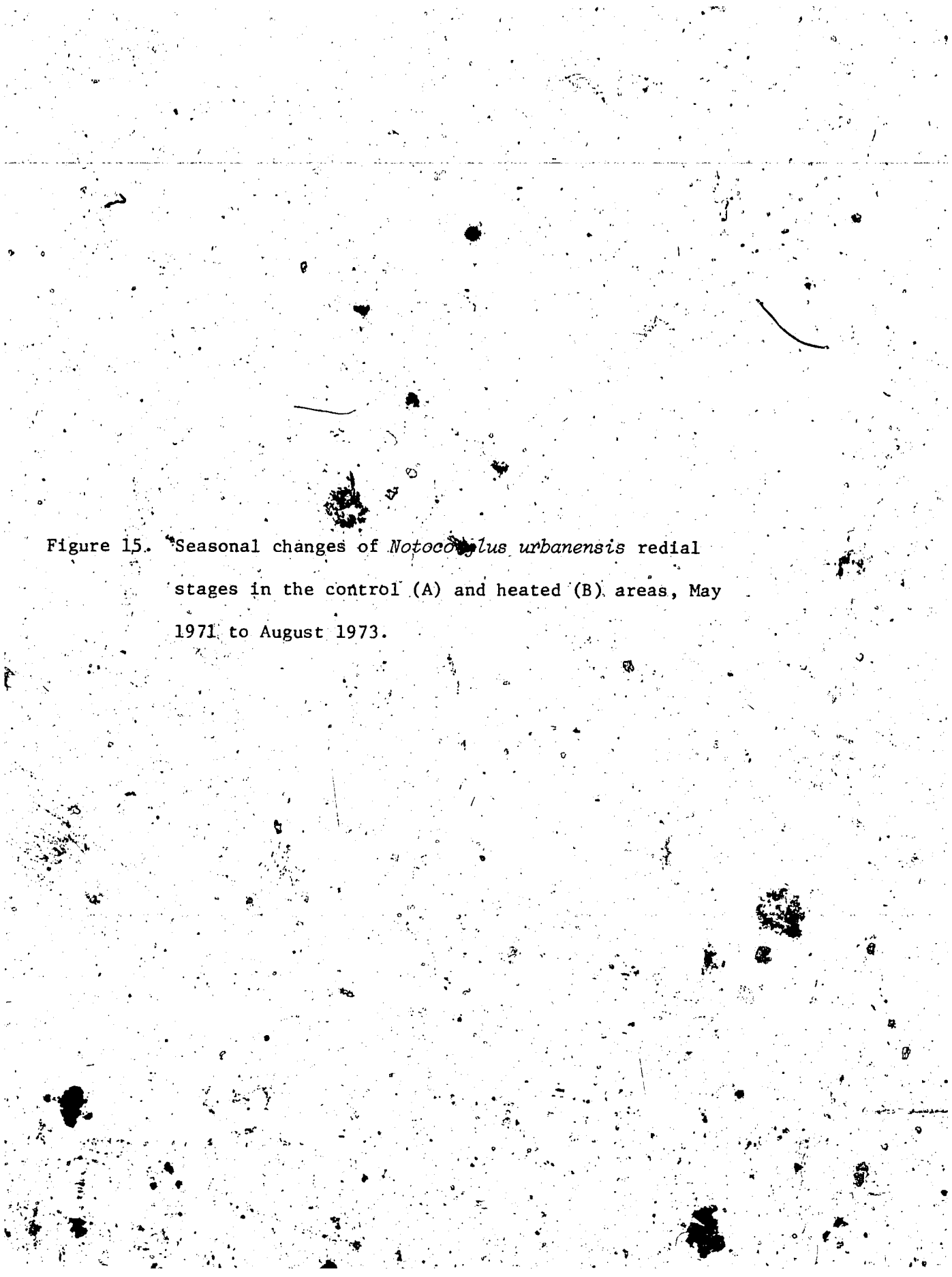


Figure 15. Seasonal changes of *Notocotylus urbanensis* redial stages in the control (A) and heated (B) areas, May 1971 to August 1973.

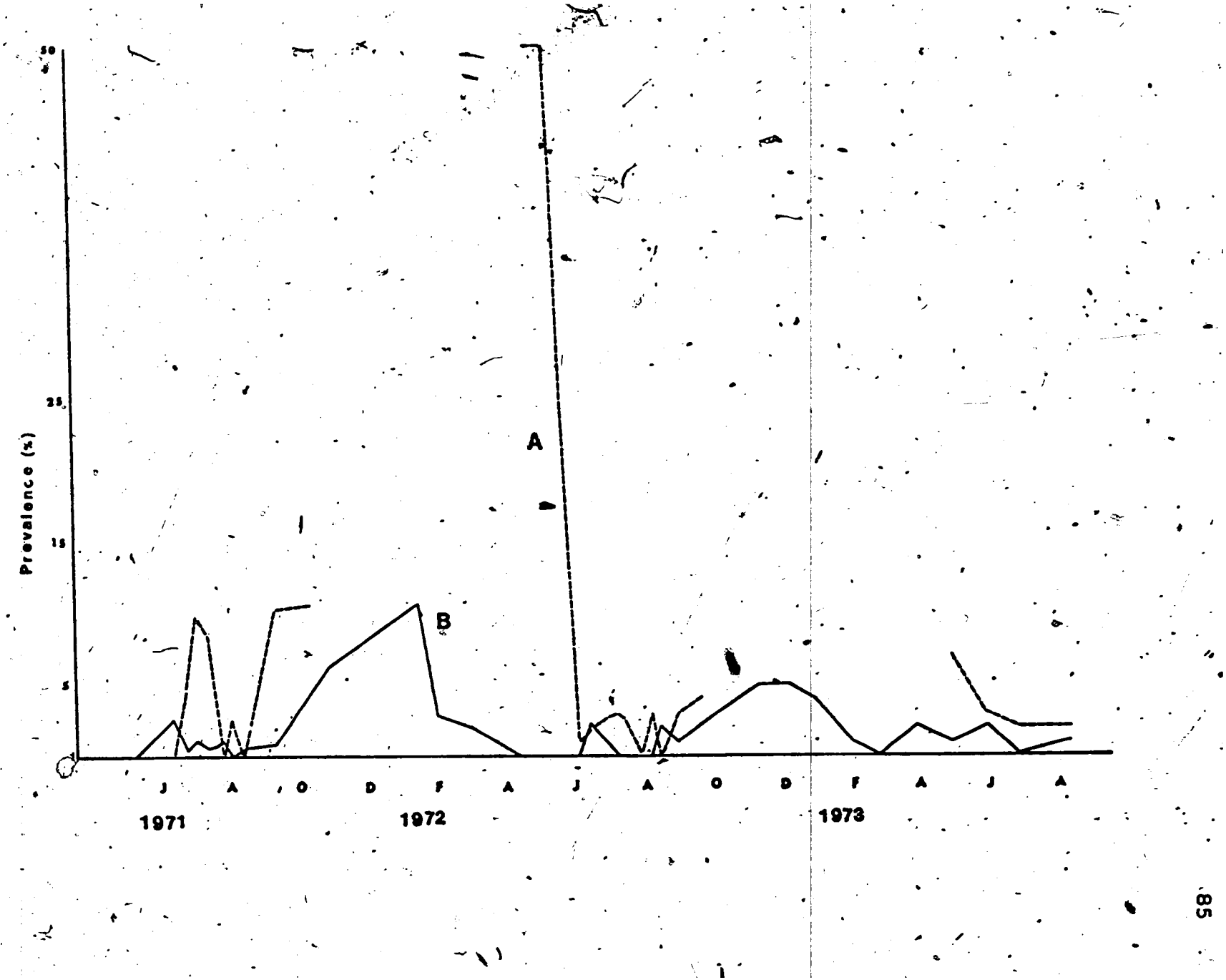

Prevalence (%)
50
25
15
5
A
B
J
A
O
D
F
A
J
A
O
D
F
A
J
A
1971
1972
1973

Table 8. Measurements (mean in microns ± S.E.) of cercariae of *Cotylurus douglasi*

	Present study	Olivier and Cort (1941)
n	30	50
Body length	205 ± 1.7	198 ± 2.0
Body width	58 ± 2.0	38 ± 0.3
Tail stem length	138 ± 1.2	184 ± 0.5
Tail stem width	44 ± 0.6	32 ± 0.3
Furcal length	165 ± 1.1	207 ± 1.0
Furcal width	18 ± 0.6	-
Length of oral sucker	43 ± 0.6	35 ± 0.4
Width of oral sucker	29 ± 0.5	18 ± 0.1
Length of ventral sucker	32 ± 0.4	-
Width of ventral sucker	32 ± 0.4	23 ± 0.1

suckers. *Cercaria douglasi* has been described from physids, including *P. gyrina*, in Michigan (Olivier and Cort 1941). They indicated that the germinal sacs of *C. douglasi* are specific to physids and that cercariae will develop into tetracotyles only in members of the Physidae, in contrast with the related *Cotylurus flabelliformis*, which is specific to lymnaeids only (Cort et al. 1941). The adult of *C. douglasi* is not known. *Cotylurus douglasi* constitutes a new combination.

In the laboratory, these cercariae readily penetrated *P. gyrina* and developed into tetracotyles (metacercariae) in 6 weeks at room temperature. Tetracotyles did not develop in lymnaeids. *Physa gyrina*, but none of the other snails examined, were also found naturally infected with the tetracotyles.

All the experimental animals (1 chick, 2 mallards, and 3 scaup) were negative three days after challenge with tetracotyles. Even though adults were not obtained experimentally, there are some indications suggesting that the larval stages of *C. douglasi* are probably those of *Cotylurus hebraicus* Dubois, 1934. *Cotylurus hebraicus* is fairly common in this area in waterfowl, and were found in the few mallards collected at Wabamun Lake during the winter (University of Alberta, unpublished results). As most of the species of *Cotylurus* are known to have a short life span in the definitive hosts (Basch 1969), these infections must have been acquired during that winter, when the only common cotylurid tetracotyles I know of were those of *C. douglasi*. However, this presumed identity can be confirmed only by completing the life cycle in experimental hosts.

Sporocysts of this trematode were found sporadically in *P. gyrina*. In the control area, only 3 infected snails were found, all during the

summer of 1971. In the heated area, infections were present sporadically in each summer, but were absent during the winters.

Infections with tetracotyles were negligible in the control area, but were the second most abundant parasite in the heated area (Table 3), where they were present in about one-third of the snails, with a mean intensity of 3.8. They were present throughout the year, although the prevalence of tetracotyles during the winter (January to April) was considerably lower (about 9% of the snails) (Fig. 14), and they were found only in the larger snails; no tetracotyles were found in young snails hatched during the winter.

Ornithodiplostomum ptychocheilus (Faust, 1917) Dubois, 1936

Cercariae of this species can be separated from those of the related, sympatric genus, *Posthodiplostomum*, by the absence of pigmented eye spots. They developed into a neascus type of metacercariae in spottail shiners, but not in sticklebacks. Such metacercariae were very common in spottail shiners in Wabamun Lake; specimens fed to chicks produced adults of *O. ptychocheilus* (R. Leong, pers. comm.).

The life cycle of this digenean was described by Hoffman (1958b); adults are parasitic in mergansers and other fish-eating birds (McDonald 1969). *Physa gyrina* and *Notropis hudsonius* are new host records.

Only three infections with the sporocysts of this species were found, all in the heated area during the summer.

Apatemon gracilis burti (Miller, 1933), Dubois and Rausch, 1960

The cercariae were identified by the morphological and behavioral features described by Stunkard et al. (1941). Germinal sacs were originally described from *H. trivolvis* and *L. humilis*; the infections in

P. gyrina constitute a new host record.

These cercariae normally develop into tetracotyles in leeches (cercariae recovered in this study did not encyst in *L. elodes* and *P. gyrina*); adults are parasitic in a variety of waterfowl (McDonald 1969), and are commonly encountered in local ducks (University of Alberta, unpublished records). Only two infections were found, both in the heated area during the summer of 1973.

Trichobilharzia cameroni Wu, 1953

Cercariae were identified as those of *T. cameroni* because of their general behavior and especially their behavior towards light. Measurements were slightly smaller than, but generally similar to, those given by Wu (1953).

The life cycle of this species was described by Wu (1953); adults are probably parasitic in waterfowl. However, all 6 mallards exposed to cercariae in the laboratory were negative by both fecal examination and necropsy.

Snails infected with this schistosome were rarely found in the control area, and only during July and August. In the heated area, the prevalence was low, but infected snails were present throughout the year. There was a slight, but significant, increase of prevalence from 0.3% during the summer to 1% during the winter (X^2, 1 d.f. = 4.17; $p < 0.05$). Some very young snails, which hatched during the winter, also harbored sporocysts of this trematode.

Trichobilharzia physellae (Talbot, 1936), McMullen and Beaver, 1945

Identification was based on the morphology and general behavior of the cercariae as given by Cort and Talbot (1936). These cercariae have

been reported previously from physids including *P. gyrina*, and the adults are parasitic in waterfowl (McDonald 1969). The larval stage of this avian schistosome were found only twice, both in the heated area during the winter of 1972.

DISCUSSION

Trematodes in almost all bodies of water in Alberta show a seasonal pattern of transmission. This seasonal pattern is most obvious in the trematode fauna of grebes (Gallimore 1964), coots (Colbo 1965), lesser scaup and ruddy ducks (Graham 1966). In general, the trematodes of these waterfowl showed peak populations in the spring and fall. The spring population appears to be derived from infections in overwintered intermediate hosts (not apparent in the data from the control area in this study, but apparent in other unpublished records, University of Alberta). Eggs from this population give rise to infections in the new season's young snails, from which the fall population is derived. Obviously there is no transmission to snails during the period of ice cover.

Definitive hosts which are active under the ice, such as fish and muskrats, probably acquire trematode infections during the winter from already available infective stages. However, because of the effects of temperature on the development of eggs and early germinal sacs of various trematodes, these infections are apparently not transmitted to snails during the winter. For example, Tedla and Fernando (1969) showed peak prevalences and intensities of *Bunodera luciopercae* in yellow perch during the winter. However, Cannon (1971) showed that the eggs of *B. luciopercae* did not develop at 4°. Therefore, temperature alone may be responsible for

interrupting the transmission of trematodes to snails during the winter. In brief, trematode transmission in the temperate regions is interrupted during the winter and resumed in the spring.

In contrast, the transmission of most helminths clearly continued uninterrupted throughout the year in the heated area. The germinal sacs of *E. recurvatum*, *N. urbanensis*, *T. cameroni* and *T. physellae* were present and actively shedding cercariae in the winter, and transmission between vertebrate hosts and intermediate hosts appeared to be continuous through the year. The effect of the thermal effluents in keeping water temperatures at 15° or above throughout the winter appears to be critical in keeping these life cycles going.

Germinal sacs of the three strigeids, *C. douglasi*, *O. ptychocheilus* and *A. gracilis*, were not present during the winter. The last two were rare, and their absence during the winter may be due to the smaller number of snails examined (1,181 from November to April versus 4,018 from May to October). However, the interruption of the life cycle of *C. douglasi* was apparently real, as evident by the lack of new tetracotyle infections and the decline in the general prevalence of tetracotyle infections in *P. gyrina* during the winter. It is not clear why the life cycle of *C. douglasi* was interrupted during the winter. If *C. douglasi* and *C. hebraicus* are in fact the same, definitive hosts (and indeed, infected definitive hosts) were present during the winter. It may be that the specific requirements for transmission of this species to its snail host are different from those of the other trematodes.

Light has been shown to be essential for hatching of the eggs of *Fasciola hepatica* (Rowan 1956, 1957), and Erasmus (1972) concluded that it is an important factor in influencing the hatching of other operculate

eggs. The eggs of *C. douglasi* (and other strigeids?) may require more light to hatch than the other trematodes of this study. In addition, the host-finding behavior of miracidia can be broken down into four phases: a dispersal phase, selection of the general environment of the snail, random search, and a short-range attraction to the snail host (Wright 1959, Cable 1972, and others). The photic responses of the miracidia appear to be involved primarily in the first two phases; these responses are closely tied to the responses of the snail host (Wright 1971, Cable 1972). Takahashi et al. (1961) found that the phototaxis of miracidia of *Schistosoma japonicum* depended upon an interaction between the intensity of the light and the ambient temperature. They responded positively to any light intensity at 15°; only to intensities of 2000 lux or less at 20°; and only to intensities of 50 lux or less at 30°. Some similar (but unknown) interactions between temperature and light might produce, in miracidia of *C. douglasi*, responses inappropriate to finding the general location of the *P. gyrina*.

In addition to suitable temperatures (and other physical conditions), populations of definitive hosts are essential to keep the life cycles of trematodes going. Of the four species of trematodes with active life cycles in the winter, three are parasitic in waterfowl, and two in muskrats. Muskrats are normally active throughout the year, whether there is open water or not. Waterfowl are not. The presence of open water at Wabamun Lake allows some waterfowl to overwinter there. Because of the progressively more limited open area during the winter, all the waterfowl present are squeezed into a more and more restricted area. This helps to build up higher densities of helminths, partly by concentrating the eggs of helminths, enhancing the contact between the snail hosts and miracidia,

and partly by enhancing transmission from snails to waterfowl. As a result, the definitive host populations, both waterfowl and muskrats, in the open areas of Wabamun Lake during the winter showed a considerable increase in the general prevalence and intensity of trematodes.

The presence of dense populations of parasites, especially *E. recurvatum* and schistosomes, can be detrimental to the overwintering populations of waterfowl, particularly the mallards. Their population at Wabamun Lake gradually declined as the winter progressed, undoubtedly due to unfavorable conditions, presumably including declining food sources. The mean emaciation index (Cornwell and Cowan 1963) of overwintering mallards was .79 (suggesting malnutrition), in contrast to .9 in mallards taken during June to August (B. Calverly, pers. comm.). The lowest emaciation indexes were .66 and .67, in mallards which harbored 1,181 and 1,650 *E. recurvatum* respectively, considerably greater than numbers of this trematode found in other local dabblers (University of Alberta, unpublished records), and may be sufficient to cause pathology. Soulsby (1955) indicated that several mute swans killed by large numbers (actual numbers not given) of *E. recurvatum* were characterized by emaciation, a marked absence of internal fat, diarrhoeic feces, and a marked catarrhal enteritis. Similarly, Annereaux (1940) indicated a severe inflammation of the intestinal mucosa associated with only 267 adult *E. recurvatum* in the duodenum of a domestic turkey. Other records of pathology and mortality of waterfowl attributed to this echinostome have been reviewed by McDonald (1969).

In addition, because of the available open water at Wabamun Lake, early arriving waterfowl in this area might go to Wabamun Lake where they may be exposed immediately to high concentrations of infective stages of

trematodes. Infections picked up at Wabamun Lake might be directly detrimental to these birds, or the infections might be carried to surrounding bodies of water, enhancing parasite stocks there to the detriment of the young birds produced later. At present there is no evidence, for or against, such an overall enhancement of parasites in the general region.

The lower prevalence of germinal sac infections in the heated area during the summer is of equal interest. Several factors may be involved. Ewers (1964) found that the prevalence of trematode infections varied with the density of snails; the prevalence in dense populations (>20 snails/sq. ft.) was significantly lower than that in less dense snail populations (< 20 snails/sq. ft.). The same number of successful miracidia (or eggs) will obviously give a lower prevalence in a more dense snail population, purely through dilution by more uninfected snails.

The longevity of miracidia is reduced by higher temperatures (Oliver and Short 1956, Farley 1962), this might also be contributing to a lower infection rate by reducing the chances of contact with the snail hosts.

In addition, during the summer, the waterfowl and muskrats are spread all over the lake through their territorial activity, thereby reducing the concentration of helminth eggs in the heated area.

A third feature of interest is the pattern of metacercarial infections in relation to the number of germinal sac infections. Metacercarial infections in the control area were very low despite the relatively high level of germinal sac infections. The same pattern was present in the heated area during the winter, whereas during the summer, the reverse was true--there were high levels of metacercarial infections despite low levels of germinal sac infections. Najarian (1954) found

that a single naturally infected snail released 900 to 1,300 cercariae of *E. flexum* per day for at least 5 days. At that rate, even the very low rates of *E. recurvatum* infection in snails in the heated area during the summer would be sufficient to saturate the snail population with metacercariae (as was the case). Therefore, it is the low prevalence of metacercarial infections in the control area, and in the heated area during the winter, despite the higher prevalence of germinal sac infections, that must be explained. The most likely explanation is the apparent protective action of *Chaetogaster l. limnaei*, which will be discussed in the following section.

CHAETOGASTERS

Both types of chaetogasters were present in both study areas. *Chaetogaster l. limnaei* was present on the head, foot and in the mantle cavity of *P. gyrina* and other gastropods (*H. anceps, H. trivolvis, L. elodes, L. stagnalis, Ferrissia* sp., *Gyraulus* sp. and *V. tricarinata*) (Fig. 16A). *Chaetogaster l. vaghini* was found in the kidney of *P. gyrina, L. elodes* and *H. trivolvis*. Concurrent occurrences were common, especially in the heated area.

Chaetogaster l. vaghini was rare in the control area, infecting only 0.9% of the snails. In the heated area, it was moderately abundant (32.9% overall), but its prevalence varied considerably. There was an apparent seasonal variation, with relatively high prevalences during the winter (30-70%) declining during the summer and reaching values close to zero in late summer (Fig. 17). Chaetogasters of this subspecies appeared to have no significant interactions with other parasites of the snail.

Chaetogaster l. limnaei, in contrast, was very abundant in the control area, occurring on 92.7% of the snails with a mean intensity of 10.1 annelids/snail. There was a considerable decrease in its prevalence in August 1971, but not in any other period (Fig. 18). In the heated area, it was only moderately abundant, occurring (overall) on 36.6% of the snails with a mean intensity of 3.6 annelids/snail. This subspecies was even more seasonal in abundance than *C. l. vaghini*; during the winter (October through May), the mean prevalence was 70%, with a mean of 5.0 annelids/snail, whereas during the summer (June through September) the

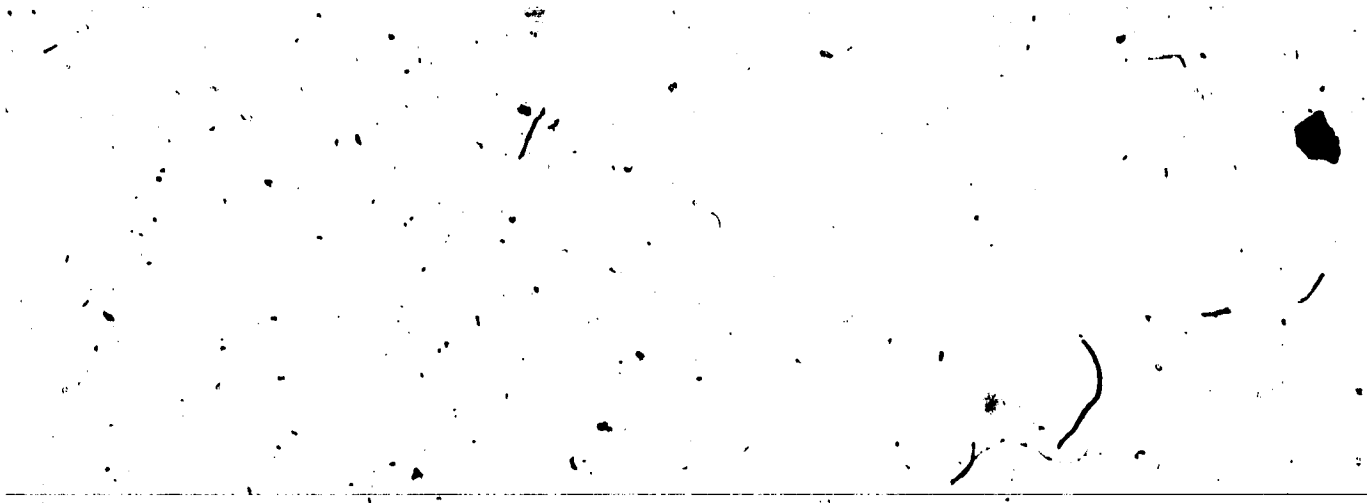
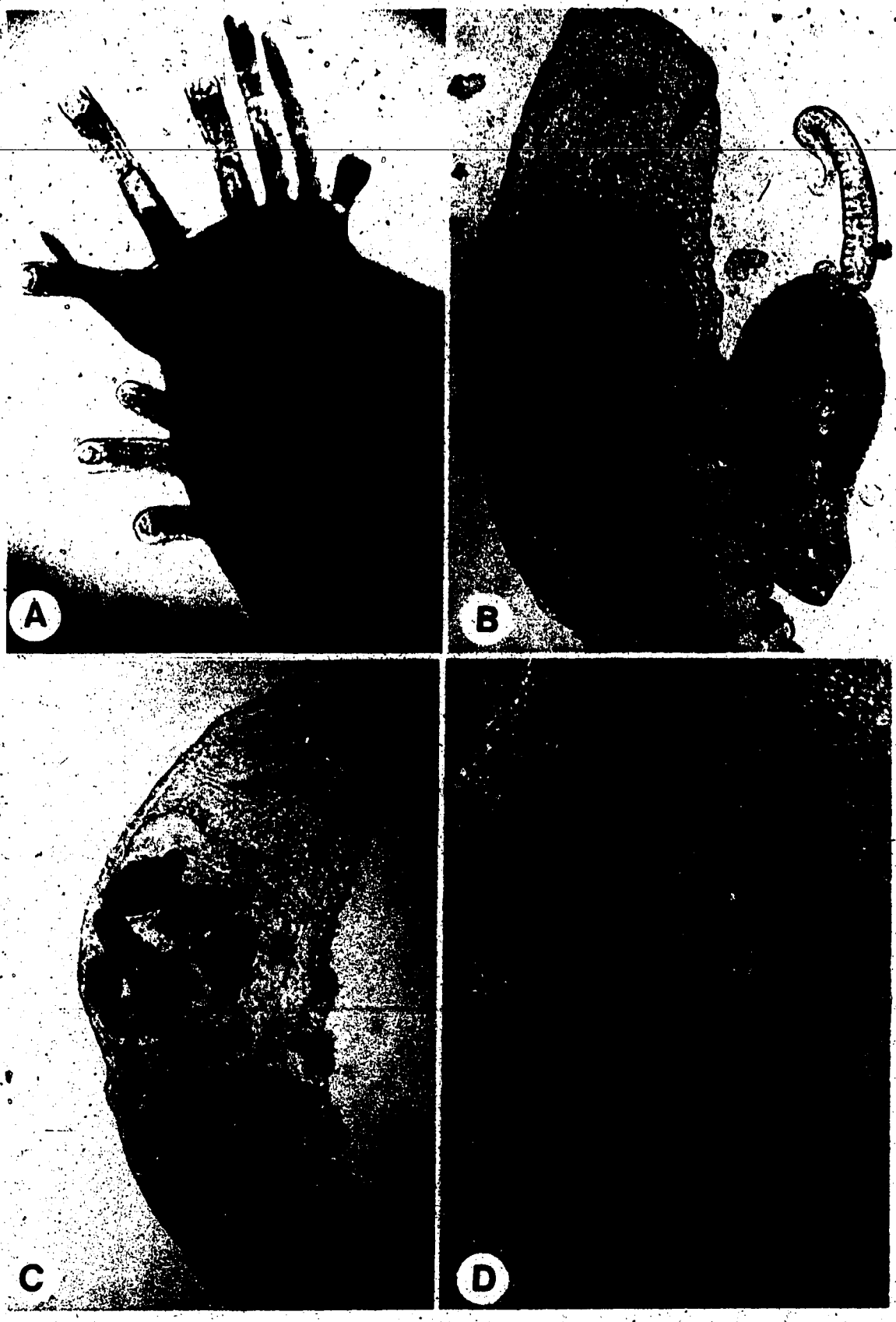


Figure 16. *Physa gyrina* harboring *Chaetogaster l. limnaei* (A); *Chaetogaster l. limnaei* containing ingested cercariae of *Echinoparyphium recurvatum* (B), and *Cotylurus* sp. (C, D).


A
B
C
D

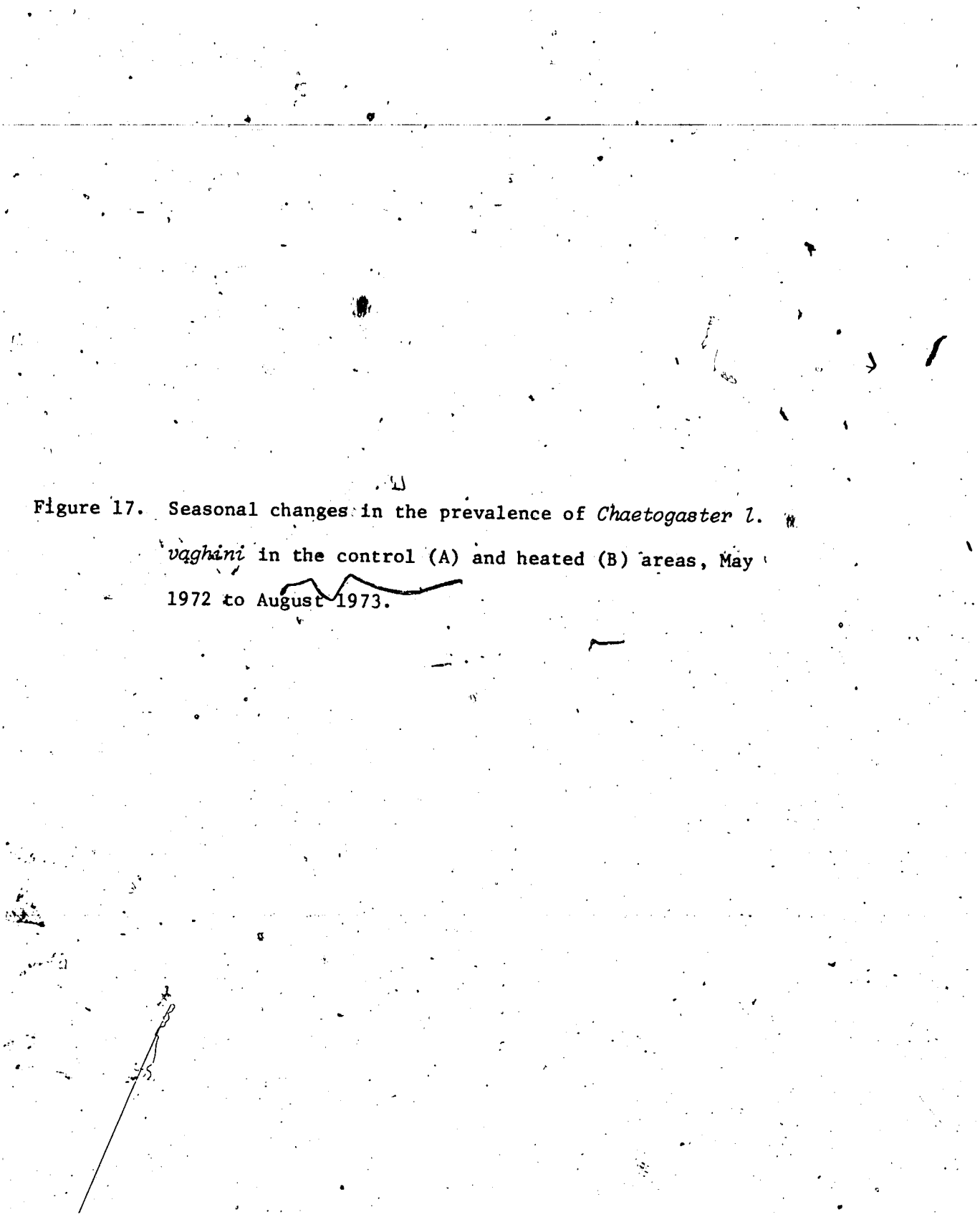
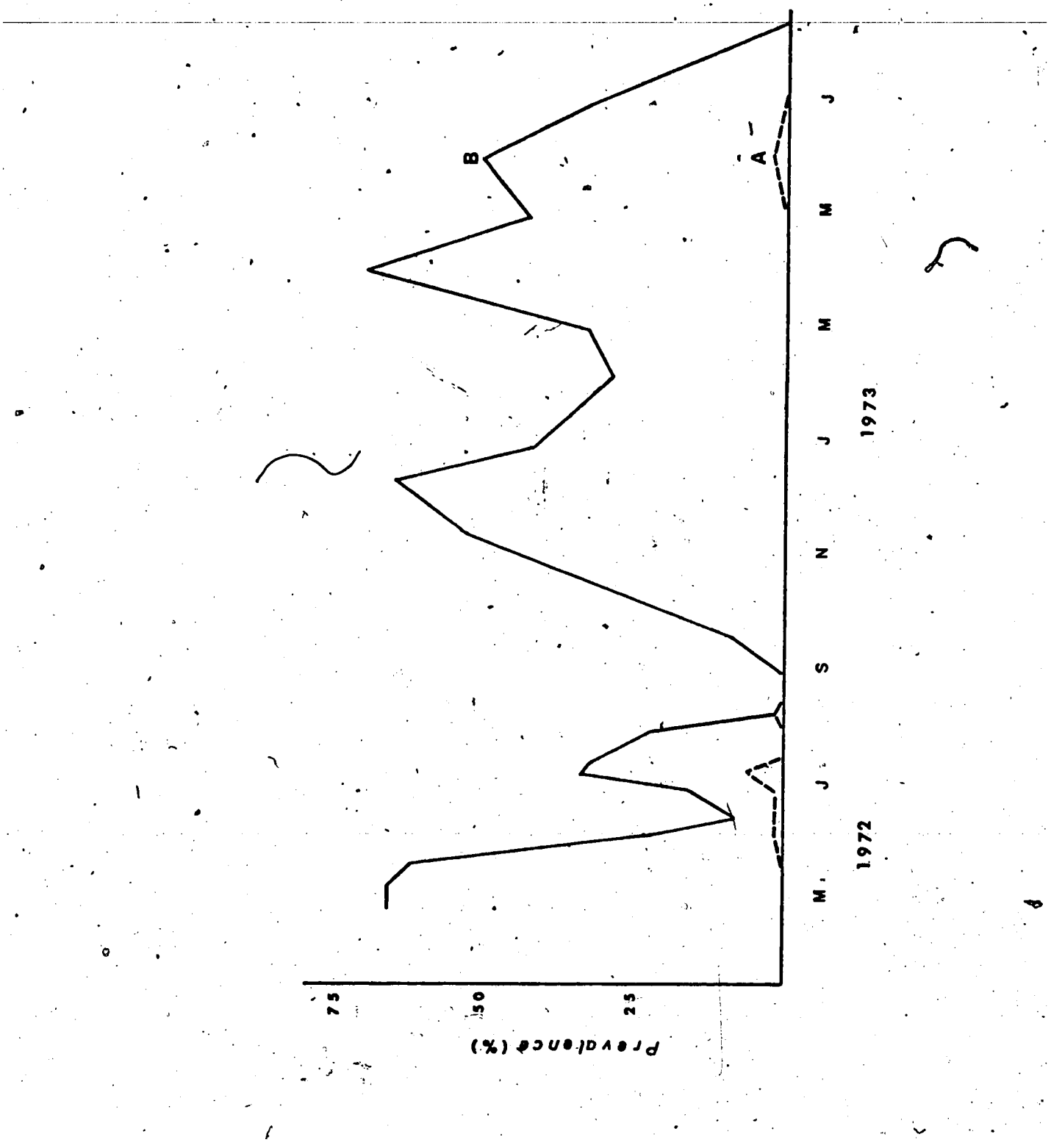


Figure 17. Seasonal changes in the prevalence of *Chaetogaster l. vaghini* in the control (A) and heated (B) areas, May 1972 to August 1973.


Prevalence (%)
75
50
25
M
J
S
N
J
1972
M
M
J
J
1973
A
B

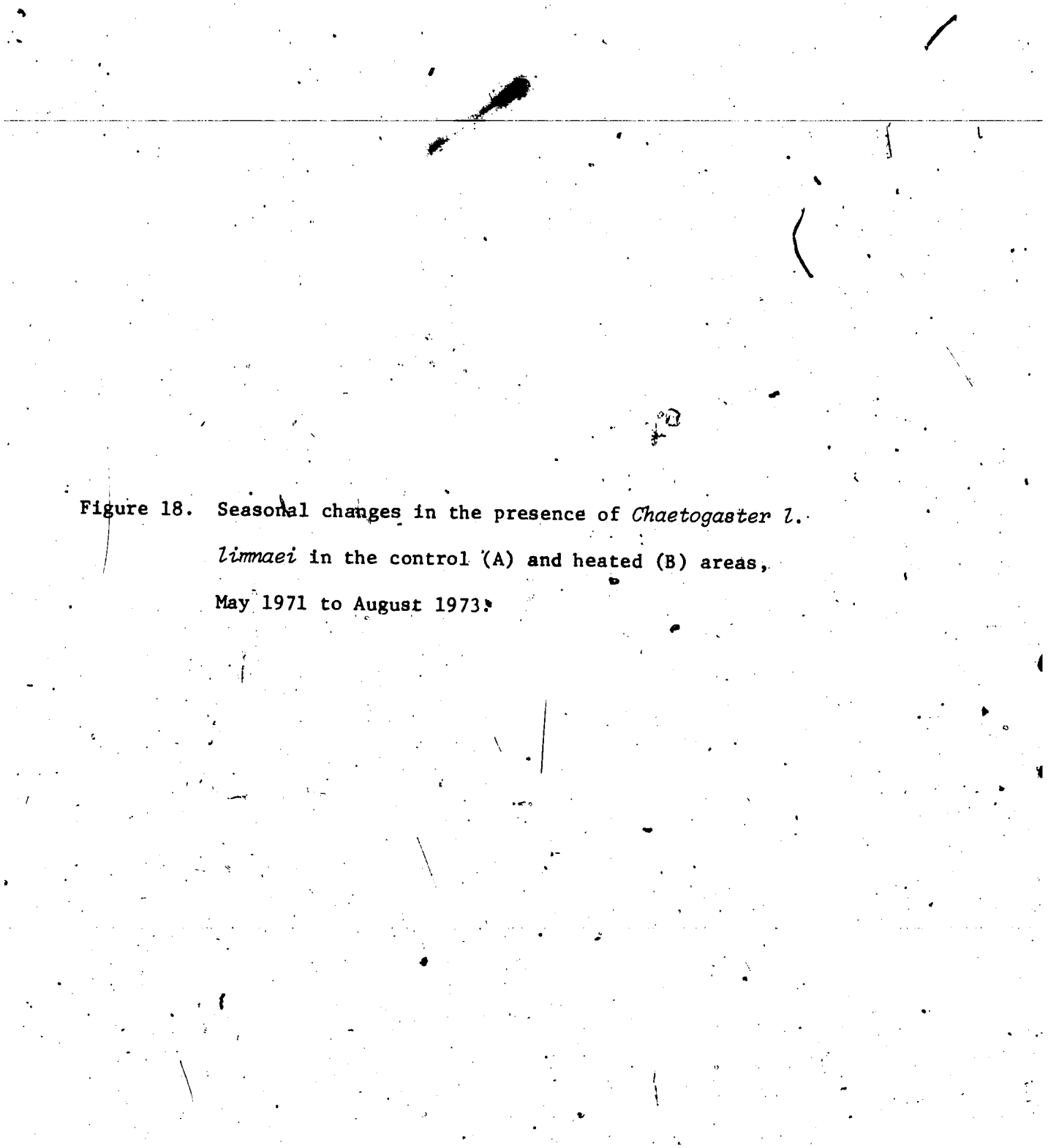
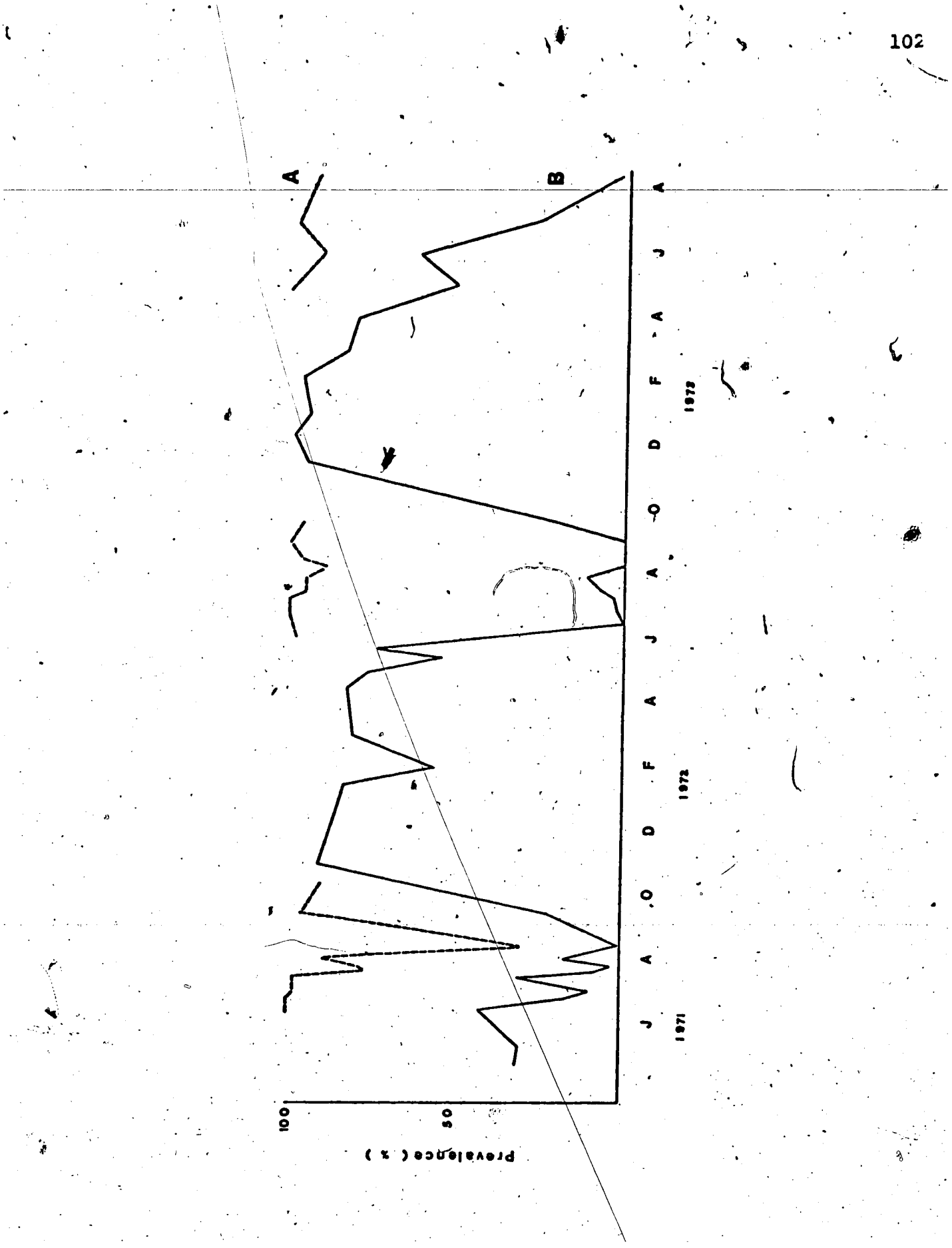


Figure 18. Seasonal changes in the presence of *Chaetogaster l. limnaei* in the control (A) and heated (B) areas, May 1971 to August 1973.


A
B
100
50
Prevalence (%)
J A O D F A J A O D F A J A O D F A
1971
1972
1973

mean prevalence was 15%, with a mean of 3.0 annelids/snail (Fig. 18).

Periods of declining or low chaetogaster populations in the heated area corresponded to periods in which water temperatures were high (24° or above--Figs. 3 and 18). The major decrease in *C. l. limnaei* in the control area in August 1971 followed the only period of high water temperature that summer. Because of these observations, the relationship between high temperatures and survival of *C. l. limnaei* was tested in the laboratory.

Field-collected snails with chaetogasters were put in 1% ethyl carbomate (urethane); within 5 to 10 minutes all the *C. l. limnaei* were free from the snails. The chaetogasters were pipetted into another stender dish and washed with dechlorinated water. Known numbers were added to individual snails in separate dishes. Within a few minutes they were settled on the snail. These snails with chaetogasters were allowed to acclimate at room temperature for one day.

The snails with known numbers of *C. l. limnaei* were maintained in half-pint milk bottles at different temperatures from 5 to 30° C in lake water along with a small piece of fresh lettuce. The snails were checked every day, the number of chaetogasters present recorded, and the water replaced with fresh lake water. The experiments were continued until all the oligochaetes were eliminated.

The results suggest that temperatures above 24° are not favorable for survival (Table 9). At 5 to 20°, chaetogasters survived for up to 2 months without any decrease in their numbers, whereas at temperatures of 24° and above, the annelids abandoned the snails at a rate directly related to the temperature. At temperatures of 25° or more, all annelids left within a week. All annelids which abandoned the snails died within

Table 9. Survival time (days) for *Chaetogaster l. limnaei* on *Physa gyrina* at different temperatures

Temperature (° C)	No. of oligochaetes	Number of days	
		Maximum	50% survival
5	80	*	*
10	80	*	*
15	75	*	*
20	100	*	*
24	80	20-25	15-17
25	60	4- 6	2- 3
26	80	4- 6	2- 3
28	80	2- 3	1
30	60	1- 2	1

*Experiments terminated at 60 days, with no loss of oligochaetes.

a few hours, without attempting to reestablish on the same or other snail.

As observed previously, *C. l. limnaei* actively feed on a variety of cercariae. Cercariae of *E. recurvatum*, *Echinostoma revolutum*, *N. urbanensis*, *T. cameroni* and several strigoid cercariae were observed in the intestine of *C. l. limnaei*. Figure 16B-D shows *C. l. limnaei* containing cercariae of *E. recurvatum* and *Cotylurus* sp. Up to 6-8 of the smaller cercariae, such as those of *Cotylurus* spp., *A. gracilis* or *Ichthyocotylurus erraticus*, but only 1-2 of the larger cercariae, such as those of *E. recurvatum* or *N. urbanensis*, could be ingested over a short time. These observations led to a series of experiments on the effect of *C. l. limnaei* on invading trematode larvae.

Chaetogaster l. limnaei were obtained as described above. In one set of experiments, individual control snails, with no chaetogasters, or those with 5, 10 or 15-20 *C. l. limnaei*, were isolated in stender dishes, then exposed to known numbers of miracidia or cercariae of *E. recurvatum*.

In the second set of experiments, all control snails, and all those with the same number of chaetogasters, were put in a single dish and a known number of miracidia or cercariae of *E. recurvatum* were added. (This experiment was also run using cercariae of *Echinostoma revolutum*.)

Snails exposed to miracidia were kept in stender dishes at room temperature and checked for developing rediae 7-10 days after exposure. Snails exposed to cercariae were kept in dishes and checked for metacercariae after 24 hours.

In the experiments using miracidia of *E. recurvatum*, the number of miracidia which had successfully penetrated and developed was inversely, and significantly (X^2, 3 d.f. = 9.04; $p < 0.05$) related to the number of *C. l. limnaei* present (Table 10). The protective action was significantly

Table 10. Influence of *Chaetogaster l. limnaei* on the rate of infection of *Physa gyrina* exposed to *Echinoparyphium recurvatum* miracidia.

	Isolated snails				Grouped snails			
No. of *C. l. limnaei*	0	5	10	15-20	0	5	10	15-20
No. of snails exposed	20	20	20	20	20	20	20	20
No. of miracidia used	20	20	20	20	20	20	20	20
No. of successful miracidia	9	4	5	1	10	2	1	0
Percentage of successful infections	45	20	25	5	50	10	5	0

Table 11. Influence of *Chaetogaster l. limnaei* on the rate of infection of *Physa gyrina* exposed to cercariae of *Echinoparyphium recurvatum*

	Isolated snails				Grouped snails			
No. of *C. l. limnaei*	0	5	10	15-20	0	5	10	15-20
No. of snails exposed	20	20	20	20	20	20	20	20
Total no. of cercariae used	100	100	100	100	100	100	100	100
Total no. of encysted metacercariae	88	76	59	35	92	49	26	11

Table 12. Influence of *Chaetogaster l. limnaei* on the rate of infection of grouped *Physa gyrina* exposed to cercariae of *Echinostoma revolutum*

No. of *C. l. limnaei*	0	5	10	15-20
No. of snails exposed	20	20	20	20
Total no. of cercariae used	100	100	100	100
Total no. of encysted metacercariae	65	17	7	5

improved when the snails were grouped (X^2, 3 d.f. = 23.05; $p < 0.001$). Only one of 40 snails was infected when there were 15 or more oligochaetes per snail.

The number of cercariae which penetrated and encysted was also inversely related to the number of the oligochaetes present (Tables 11, 12). Again, the protective action was greater when the snails were grouped than when isolated (Table 11).

Observations made during these tests, and at other times, indicated that the protection provided by the chaetogasters was due only partially to ingestion of the invading cercariae. The chaetogasters also appeared to obstruct the cercariae and prevent their penetration into the snails. The anterior ends of the oligochaetes protrude into the water surrounding the snail (shown in Fig. 16A) and are in constant motion, as though searching. Cercariae approaching the oligochaetes are sometimes captured by them, but more frequently, the cercariae escape and swim in the opposite direction. However, in the experiments, cercariae repeatedly attempted to reach the snail. Some were eventually successful, others were ingested by the oligochaetes, while still others were eventually found dead at the bottom of the container, possibly due to the exertion of their repeated unsuccessful attempts to reach the snail. Dead cercariae were observed only in the dishes containing snails with chaetogasters, especially when there were 10 or more oligochaetes. Dead cercariae were never observed in the controls.

DISCUSSION

The seasonal dynamics of *Chaetogaster l. limnaei* in the heated area were closely related to the water temperature. The maximum critical temperature is about 24°; higher temperatures are lethal for these oligochaetes. The revival of the *C. l. limnaei* population corresponds to the reappearance of lower temperatures. Because of its sensitivity, *C. l. limnaei* would seem to be an excellent organism to use as an indicator of thermal pollution. However, its populations recover fairly rapidly, which might tend to reduce its usefulness.

Chaetogaster l. vaghini showed a similar seasonal pattern, also related to water temperature, in the heated area. However, the most striking feature is the almost complete lack of *C. l. vaghini* infections in the control area. The seasonal pattern suggests that *C. l. vaghini* is somewhat more tolerant of warm water than is *C. l. limnaei*. If this is accompanied by a lower tolerance to lower temperatures, *C. l. vaghini* may be a useful indicator of thermal pollution. Unfortunately, the thermal relations of *C. l. vaghini* were not investigated in the present study, and further investigation of the possible use of this oligochaete as an indicator is needed.

Several authors (reviewed in the introduction) have shown that, in the laboratory, the predatory activity of *C. l. limnaei* can reduce the rate of infection of snails by miracidia or cercariae of various trematodes. My observations agree. In the laboratory these oligochaetes are very active, and can capture even the cercariae of *N. urbanensis*, which usually encyst on a substratum within 3-5 minutes after emergence. The food of *C. l. limnaei* consists mainly of planktonic organisms (Gruffydd 1965b);

they probably feed on any free-swimming organisms available, especially those in close contact with the snail.

The predatory activity is important, but my laboratory observations suggest that the obstructive behavior of *C. l. limnaei*, which has not been reported previously, is also important. This obstructive behavior of these oligochaetes may be due to their unsuccessful feeding activity. This obstructive action may be of even greater significance in the field, where because of the unlimited area, larvae which are repelled may not be able to make repeated attempts to penetrate the same snail.

Previous studies have shown the effectiveness of *C. l. limnaei* in the laboratory. The present study provides the first field data on the regulatory importance of these oligochaetes. The protective action of *C. l. limnaei* is evident from the very low metacercarial infections whenever *C. l. limnaei* were prevalent, and also by the differences in the seasonal pattern of redial infections of *E. recurvatum* and *N. urbanensis* in the control area. There were no redial infections of *E. recurvatum* after August (despite suitable temperatures and other favorable conditions), whereas *N. urbanensis* redial stages were present right up to freeze-up. The chaetogasters controlled the infections with the echinostome, in which the snail is infected by penetration by the miracidium, but did not control the infections with the monostome, in which the snail is infected by eating the eggs.

Over the past ten years there has been an increasing interest in the biological control of snail-borne diseases (reviewed by Berg 1973). The field data and laboratory experiments of the present study strongly suggest that *C. l. limnaei* can regulate trematode infections in field populations of snails.

A review of publications dealing with various larval trematode infections in snail populations suggests that the importance of *C. l. limnaei* may have been overlooked. The results of various surveys show considerable variation in the total prevalence of germinal sac infections, ranging from 0.5% (McCoy 1929) to 95.5% (Cort et al. 1937). Data on the abundance of chaetogasters would be very useful in interpreting these variations in the data obtained from field samples (and perhaps also from laboratory experiments, since chaetogasters are common in many laboratory snail colonies). More information is needed, especially from field data, correlating the abundance of *C. l. limnaei* and larval trematode infections in various snail populations.

SUMMARY AND CONCLUSIONS

It is obvious that the *Physa gyrina*-trematode-*Chaetogaster l. limnaei* system is very complex. Each of the major components interacts with the others, and those interactions are modified by many external factors, either directly or indirectly. The most important of these external factors are temperature, light, vegetation and the populations of definitive hosts. The interactions are summarized in Figure 19.

Interactions between the three major components determine the main characteristics of the system. Increases in the snail populations obviously increase the populations of chaetogasters and of trematodes by providing more susceptible hosts; increases in chaetogaster populations generally decrease trematode populations, by preventing new infections; and increases in trematode populations decrease snail populations, by affecting the fecundity, and probably the longevity, of the infected snails.

These basic characteristics are modified by several external factors. Light may influence miracidial behavior, thereby affecting parasite populations; however, the main effect of light on the system (other than through its heat-producing radiation) appears to be through its effects on vegetation, particularly the low limits on vegetation in winter. The vegetation affects the system primarily by setting low limits to the snail populations when vegetation is scarce. The size of the definitive host populations influences parasite populations by affecting rates of transmission to the snails; some also reduce snail populations through direct predation. High parasite populations appear to have detrimental effects on some definitive hosts.

Figure 19. Interactions within the *Physa gyrina* - trematode - *Chaetogaster l. limnaei* system, and the major extermal factors influencing that system in Wabamun Lake, Alberta (for explanation see text).

■■■■■■■■ Interactions between primary components

———————— Direct effects on primary components

- - - - - - - Indirect effects

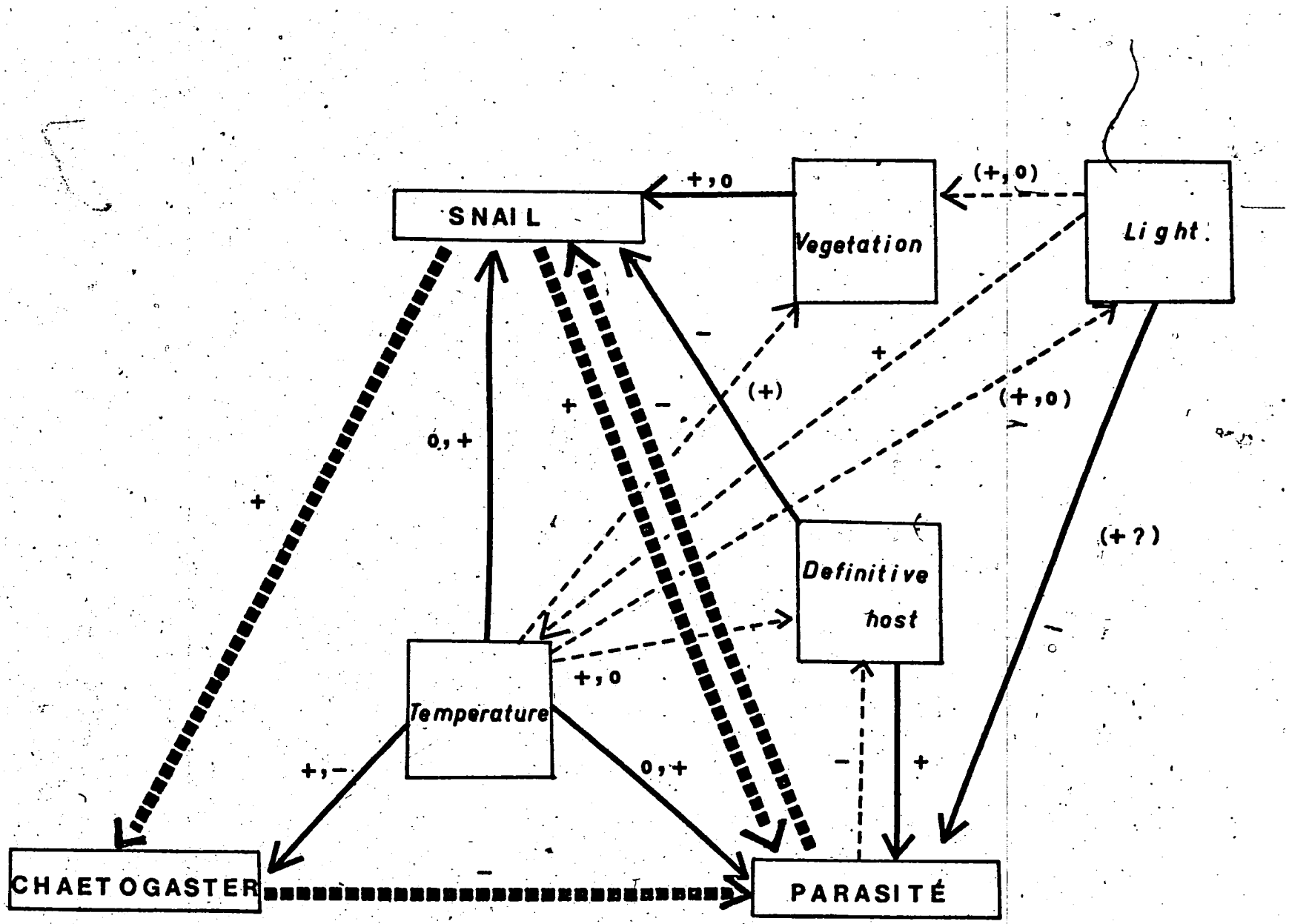
\- Negative effect on the component

\+ Positive effect on the component

o Alteration of that component has no effect either before or after a positive influence

? Suggesting the possible relationship

() Influences not investigated in this study


SNAIL
Vegetation
Light
Definitive host
Temperature
CHAETOGASTER
PARASITÉ
+,0
(+,0)
(+)
(+,0)
(+?)
0,+
+,0
+,−
0,+

The central role of temperature as a modifying factor in the system is well shown in Figure 19. Temperature exerts a direct influence, not only on all three components of the system, but also on the other three major external modifying factors. There is a threshold effect in its action on snail and parasite populations; the threshold for both is approximately 10° C. Its crucial action on chaetogasters is a ceiling effect, essentially eliminating the annelids at temperatures above 24° C. The major influence of temperature on definitive populations, light, and vegetation in this system is through provision of ice-free areas during the winter.

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Appendix I. Summarized data on collections of *Physa gyrina* from the control area, 1971-1973

Date	Snail density index: No. of samples	Snail density index: Mean ± S.D.	No. of snails examined	Length of shell (mm): Mean ± S.E.	Length of shell (mm): Range	Number of snails infected: *E. revolutum* rediae	*E. revolutum* metacercariae	*E. urbanensis* rediae	*C. douglasi* sporocysts	*C. douglasi* metacercariae	*P. cameroni* sporocysts	Unident. sporocysts	*C. l. limosa*	*C. l. vaghini*
23-6-71	8	19.5 ± 6.9	110	6.58 ± 0.12	4-12	7		0	0	0	0	0	110	
8-7-71	8	11.1 ± 3.1	78	7.53 ± 0.12	5-10	10		4				1	78	
15-7-71	8	12.2 ± 3.5	50	7.78 ± 0.22	4-12	12		5	0	1		0	49	
26-7-71	8	13.1 ± 2.4	61	8.45 ± 0.35	2-15	22	5	5	2	1		0	60	
4-8-71	7	15.1 ± 6.1	90	3.71 ± 0.13	2- 8	0	2	0	1	0		0	68	
9-8-71	6	20.3 ± 3.9	80	4.91 ± 0.14	3-10	0	17	2		1		1	63	
15-8-71	8	19.9 ± 3.9	80	5.07 ± 0.09	3- 7	1	17	0		0		1	71	
26-8-71	8	17.5 ± 3.7	60	5.83 ± 0.15	4-10	2	4	0		1		0	18	
23-9-71	6	16.8 ± 4.2	85	7.58 ± 0.13	2-11	0	11	9		1			82	
24-10-71	6	19.7 ± 3.9	102	7.55 ± 0.15	3-13	0	2	11		5			92	
10-5-72	10	0.1 ± 0.3	4	7.5 ± 0.64	6- 9	0		2					4	0
24-5-72	10	0.1 ± 0.3	2	10.0 ± 3.0	7-13	0		1					1	0
5-6-72	15	0 -	0					0					0	0
20-6-72	10	3 ± 2.7	88	5.25 ± 0.13	3-12	1	0	1		1			86	1
28-6-72	8	6.31± 4.2	112	5.66 ± 0.12	2-10	17	3	2		0			111	1
14-7-72	8	7.6 ± 2.5	110	6.32 ± 0.08	4- 8	17	0	3		0			110	1
21-7-72	6	18.3 ± 3.4	100	6.63 ± 0.12	3-11	19	7	3		1			100	6
28-7-72	6	14 ± 3.8	80	6.85 ± 0.26	2-17	23	2	2		1			76	0
11-8-72	6	20 ± 3.4	100	4.67 ± 0.26	2-13	1	4	0		0	2		95	0
23-8-72	6	19.2 ± 5.6	100	4.83 ± 0.17	2-11	1	3	3		0	1		90	1
31-8-72	6	20.2 ± 3.7	100	5.42 ± 0.11	3-10	0	1	0		0	0		96	0
12-9-72	6	24.8 ± 2.0	100	5.52 ± 0.10	3- 8	0	12	3		0			100	0
1-10-72	6	28 ± 5.6	100	6.23 ± 0.11	3-12	0	2	4		0			96	0
14-5-73	10	1 ± 1.2	14	7.85 ± 0.74	o-17	0		1					14	0
21-6-73	15	10.8 ± 3.2	100	4.28 ± 0.22	2-13	0		3					91	2
8-7-73	6	32 ± 4.0	100	4.72 ± 0.09	3- 8	34		2			2		99	0
21-8-73	8	24.2 ± 6.7	100	6.06 ± 0.22	3-13	8	2	2					93	0

Appendix II. Summarized data on collections of *Physa gyrina* from the heated areas, 1971-1973

	Snail density index			Length of shell (mm)		Number of snails infected											
Date	No. of samples	Mean ± S.D.	No. of snails examined	Mean ± S.E.	Range	*E. revolutum* rediae	*E. revolutum* metacercariae	*H. urbanensis* rediae	*C. douglasi* sporocysts	*C. douglasi* metacercariae	*O. ptychocheilus* sporocysts	*A. pusilla* sporocysts	*T. cameroni* sporocysts	*T. physellae* sporocysts	Unidentified sporocysts	*C. I. ilmani*	*C. I. vaghini*
5-5-71	8	19.6 ± 8.4	104	7.94 ± 0.29	3-14	17	19			6			1			31	
	6*	25 ± 7.1	63	8.98 ± 0.32	4-13	9	8			1			1			21	
21-5-71	8	27.9 ± 7.8	78	8.97 ± 0.27	3-15	8	58			10						24	
	7*	43 ± 9.2	112	8.03 ± 0.20	2-13	17	131			26						34	
23-6-71	8	79.9 ± 21.2	179	6.93 ± 0.16	2-10	38	173	7		60	1					73	
	7*	36 ± 9.9	92	6.95 ± 0.27	3-12	27	189			18						41	
8-7-71	8	74.9 ± 20.4	130	8.15 ± 0.12	3-11	2	109			27						23	
	8*	54 ± 12.9	131	6.64 ± 0.16	2-12	12	52	1		15						24	
15-7-71	8	110 ± 64.9	123	7.70 ± 0.15	3-11	8	114	3	1	49						16	
	6*	62 ± 15.9	107	7.44 ± 0.15	2-11	4	91			44						5	
26-7-71	8	209 ± 59.1	124	6.93 ± 0.12	3-10	6	90			87			1			11	
	7*	153 ± 46.3	130	8.26 ± 0.20	3-14	14	114		2	80						68	
4-8-71	8	216 ± 48.6	107	6.44 ± 0.14	2-9	1	88	1		45	1					2	
	6*	81 ± 18.2	112	7.47 ± 0.21	2-12	2	59	1		37						17	
9-8-71	8	123 ± 34.8	114	7.41 ± 0.12	5-11	11	104	2		44			1			2	
	6*	44 ± 10.6	114	7.62 ± 0.18	4-11	6	68	1	1	33						5	
15-8-71	6	152 ± 55.6	120	8.09 ± 0.19	3-12	10	110		2	62						0	
	6*	98 ± 17.5	112	7.94 ± 0.17	3-11	5	90			67						40	
26-8-71	8	63.9 ± 17.2	116	7.38 ± 0.21	2-15	6	103	1		56			2			0	
	10*	6 ± 3.2	33	7.21 ± 0.44	3-11	0	10			5						1	
25-9-71	6	57.3 ± 11.7	117	7.83 ± 0.12	5-11	11	104	1		70			1			26	
	10*	0															
13-11-71	6	80.5 ± 17.8	130	8.12 ± 0.22	2-13	7	107	5		60						117	
	6*	60 ± 15.6	114	8.59 ± 0.18	3-12	5	103	11		60						105	
30-1-72	12	3.2 ± 3.2	27	7.04 ± 0.50	2-14	3	2	3		3						21	
12-2-72	10	5 ± 4.3	100	5.70 ± 0.27	2-13	12	22	3		7						51	
11-3-72	10	7.3 ± 4.1	100	6.95 ± 0.32	2-17	13	69	2		10						81	
25-4-72	10	14.9 ± 6.7	150	7.52 ± 0.23	2-14	5	87			10					1	125	
10-5-72	8	66.9 ± 8.5	100	8.44 ± 0.21	3-13	2	80			27						76	66
24-5-72	8	69.6 ± 15.4	100	7.51 ± 0.20	3-19	3	85		1	15						54	66
5-6-72	6	43 ± 14.8	100	6.23 ± 0.19	2-11	4	35			13						74	63
20-6-72	6	142 ± 55.2	100	7.06 ± 0.12	3-10	1	43			55	1		1			31	23
28-6-72	6	54.8 ± 19.9	100	6.56 ± 0.17	3-10	0	38	2		54						0	8
14-7-72	6	58.2 ± 15.9	100	7.96 ± 0.18	2-12	2	60	1		47						2	16
21-7-72	6	138 ± 8.9	100	7.73 ± 0.16	3-11	1	66		2	56			1			3	34
28-7-72	6	99.3 ± 39.5	100	7.86 ± 0.20	2-13	1	75			57						7	32
11-8-72	6	75.3 ± 22.9	100	8.21 ± 0.26	3-14	1	80		1	45					1	11	22
23-8-72	6	82.3 ± 35.6	100	8.40 ± 0.24	3-13	1	63	1		38						0	1
31-8-72	6	57.8 ± 14.2	100	8.24 ± 0.18	3-12	0	80	2		46						0	0
12-9-72	6	52 ± 15	100	8.58 ± 0.18	3-12	1	67	1		43						0	0
1-10-72	6	48.2 ± 8.2	100	10.53 ± 0.19	7-15	5	91	2		39						21	9
24-11-72	8	14.4 ± 6.4	100	9.37 ± 0.27	3-14	1	88	5		41						95	54
20-12-72	8	4.4 ± 3.7	100	8.48 ± 0.18	3-12	12	80	5		25			1			99	66
13-1-73	12	1.6 ± 1.4	60	8.35 ± 0.40	2-13	20	34	4		15			2	2		56	40
16-2-73	10	1.9 ± 1.7	100	8.29 ± 0.46	2-20	17	53	1		7			1			97	29
8-3-73	8	11.9 ± 3.2	100	8.16 ± 0.37	2-18	5	59			2						84	33
12-4-73	8	34.3 ± 17.7	100	8.03 ± 0.31	2-14	14	42	2		11			2			81	70
14-5-73	8	135 ± 48.7	100	6.11 ± 0.23	2-13	1	45	1		18			1			51	43
12-6-73	6	183 ± 41.6	100	6.31 ± 0.22	2-11	0	53	2		39		1				42	51
8-7-73	6	141 ± 18	100	6.59 ± 0.21	3-11	1	61			32		1				27	33
21-8-73	8	37.5 ± 26.6	100	10.6 ± 0.21	3-14	2	78	1		37						2	0

* = second sampling area.

Appendix III. Raw data for estimating the number of snails/100 g vegetation

Date	Control area		Heated area	
	Wt. of vegetation sampled (g)	No. of snails	Wt. of vegetation sampled (g)	No. of snails
10-5-72	No vegetation		90	121
24-5-72	No vegetation		46	95
5-6-72	No vegetation		91	120
20-6-72	Too sparse vegetation		39	197
28-6-72	165	79	48	406
14-7-72	150	66	59	106
21-7-72	170	78	113	170
28-7-72	120	72	85	110
11-8-72	140	126	26	74
23-8-72	Too dense vegetation		Too dense vegetation	
31-8-72	Too dense vegetation		Too dense vegetation	
12-9-72	135	94	80	130
1-10-72	122	77	72	86