TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

TABLE OF CONTENTS (continued)

ACKNOWLEDGEMENTS

I am especially grateful to Doctors S. U. Qadri, A. H. Clarke, and R. M. Reed for their encouragement and advice during the course of this investigation and for their suggestions and criticisms in the preparation of this dissertation.

I wish to acknowledge the assistance of Dr. S. Walters in the statistical treatment of the data and of Dr. I. Ahmad in computer programming procedures. Thanks are also due to Dr. R. K. S. Lee and his technicians for identifying the algae specimens. Mr. F. Wayne Grimm kindly showed me the location of Carp Pond. The financial support came from grants awarded to S. U. Q. by the National Research Council of Canada (Grant No. A 2386) and the Department of Environment (Grant No. HIK).

Finally, I am grateful for the many contributions of my wife, Elizabeth. Her patience and understanding are sincerely appreciated.

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

This dissertation reports comparative studies carried out on populations of Musculium securis (Prime, 1851) from two temporary forest ponds, a river, and a permanent pond. The taxonomy, anatomy, life history, ecology, food habits, and distribution of the species were investigated from May 1970 to May 1973.

Calyculae (or caps) on the shells have a predictable seasonal occurrence. It is proposed that a calyculus on a shell provides a valid taxonomic characteristic of the genus Musculium.

The anatomy of M. securis appears to be similar to that of other sphaeriids but the development of brood sacs differs markedly. A new technique called back-calculation of brood sacs, was developed to determine the number of litters produced. The structure of the byssus which attaches larvae to the gill of parents, is also described.

Samples were collected at least once a month for three years from a temporary pond and a river and at monthly intervals for one year from another temporary pond and a permanent pond for studies of the life history of the species. Analyses of the life history samples showed that there are intraspecific variations in growth, seasonal gonad activity, number of brood sacs and larvae per sac, sizes of litters produced, number of litters produced, birth period, and longevity. Intrapopulation variations in life history are more pronounced in temporary aquatic habitats than in permanent aquatic habitats. Interpopulation transplants of M. securis indicate that growth and fecundity may be adaptively modified in the river habitat.

Usually fifteen clams were maintained in laboratory growth dishes containing soil, leaves, and water. It is shown that the soil provides

food organisms while leaves probably provide nutrients (e.g. calcium) in elemental form. Laboratory and field experiments showed that such factors as temperature, soil texture, tree foliage, different soils, sulfate, road salts, pulp and paper wastes, population density, interspecific competition, and parasitism affect the growth and/or reproductive capacity of M. securis.

Analyses of the intestines of M. securis showed that phytoplankton, especially diatoms, are ingested. Food ingestion is most active during the summer months.

The significance of litter size in M. securis is discussed. It is proposed that surplus recruitment (i.e. production of more young than the carrying capacity of a habitat) may be an important mechanism in maintaining population densities at carrying capacity. It is shown that recruitment is a function of larval viability and of the number of litters produced.

The North American distribution and range extension of M. securis are also described. Evidence is given to suggest that some waterfowl species may be important dispersal agents of M. securis. The distribution of the species in various habitats is also discussed.

RESUME

Le présent travail se rapporte à des études comparées de populations de Musculium securis (Prime, 1851) trouvées respectivement dans deux étangs situés dans un milieu forestier, une rivière et un étang permanent. On traite de la taxonomie, de l'anatomie, de l'histoire naturelle, des habitudes alimentaires et de la distribution de l'espèce. Ces travaux ont été faits de mai 1970 à mai 1973.

La formation d'un renflement ("calycula") au sommet des coquilles est prévisible sur une base saisonnière. On croit que la présence d'un tel renflement sur une coquille constitue un critère taxonomique valable pour le genre Musculium.

L'anatomie de M. securis paraît semblable à celle d'autres sphaeriidés mais le développement des sacs marsupiaux est différent. Une nouvelle technique qu'on pourrait appeler calcul à rebours ("back-calculation") des sacs marsupiaux a été mise au point pour déterminer le nombre de pontes produites. La structure du byssus qui attache la larve aux branchies des parents est également décrite.

Pendant trois ans, des échantillons furent prélevés une fois par mois dans un étang temporaire et un étang permanent dans le but d'étudier l'histoire naturelle de l'espèce. L'étude de ces échantillons a révélé l'existence de variations intraspécifiques dans la croissance, l'activité saisonnière des gonades, le nombre de poches incubatrices et des larves qu'elles contiennent, la période d'éclosion et la longévité. Pour ce qui est de l'histoire naturelle proprement-dite, les variations sont plus marquées chez les populations occupant un habitat temporaire par opposition aux populations qui occupent un habitat permanent. La croissance

et la fécondité de M. securis peuvent être modifiées suite à des transplantations dans une rivière.

Quinze mollusques furent gardés en laboratoire dans des contenants renfermant de la terre, des feuilles et de l'eau. On a démontré que le sol fournit des organismes qui servent à la nutrition alors que les feuilles sont une source de produits alimentaires sous forme d'éléments (e.g. calcium). Des expériences en milieu naturel et en laboratoire démontrent que la croissance et la capacité de reproduction de M. securis sont affectées par des facteurs tels que: la température, la texture et les type de sols, le feuillage des arbres, les sulfates, les sels de calcium et de sodium ("road salts"), les déchets de l'industrie des pâtes et papiers, la densité de la population, la compétition interspécifique et le parasitisme.

L'analyse des contenus intestinaux a révélé que M. securis ingère du phytoplancton et plus spécialement des diatomées. L'ingestion de nourriture atteint son maximum durant les mois d'été.

On assume que la production d'un excédent de jeunes M. securis est un mécanisme important servant à maintenir la densité des populations au niveau de la capacité de support. Cet excédent est fonction de la viabilité des larves et du nombre de pontes.

On décrit la distribution de M. securis en Amérique du nord. Certains indices portent à croire que certains oiseaux aquatiques pourraient être des agents importants de dispersion pour M. securis. La distribution de l'espèce dans différents habitats est aussi discutée.

INTRODUCTION

Within a 50 km radius of Ottawa, Ontario there are at least 26 of the 34 North American species of Sphaeriidae. Twenty of these species occur in the Ottawa River. Sphaeriidae are omnipresent, occurring everywhere from roadside ditches to deep-water lakes and rivers. They are a major food source for such vertebrates as waterfowl (Anderson, 1959; Rogers and Korschgen, 1966; Gale, 1969) and fish (Gale, 1969; Smith, MS1973). Some species may be considered ecological indicators since they occur in only certain aquatic habitats. For example, Sphaerium occidentale is usually found in temporary forest ponds rich in calcium carbonate while Sphaerium nitidum and Pisidium conventus are most common in deep and/or cold, oligotrophic waters.

The purpose of this study is to provide information on the taxonomy, anatomy, life history, ecology, food habits, and distribution of Musculium securis. The species was chosen for study because (1) it is the only species of Musculium for which the life history has not been fully described, (2) it occurs in a variety of habitats permitting comparative ecological studies, and (3) it is abundant in the Ottawa area.

There has been much debate over the validity of the genus Musculium Link, 1807. Prior to 1960, most taxonomists used three genera (Sphaerium, Musculium, and Pisidium) to describe 128 species. Herrington (1962), on the basis of shell characters, then revised the North American Sphaeriidae and reduced the number of genera to two (Sphaerium and Pisidium) and the number of species to thirty-four. New taxonomic keys have since been published by Burch (1971) and Clarke (1973) but only Clarke has challenged Herrington's (op. cit.) revision; Clarke (op. cit.) uses Musculium as a separate taxon (a subgenus of Sphaerium) and proposes a new subgenus,

Herringtonium, for S. occidentale. However, Heard (1973), in a comparative study of Sphaeriidae, maintains that Musculium is a valid genus on the basis of several aspects of life history.

The anatomy of M. securis has not been studied previously but the literature contains several anatomical descriptions of other sphaeriids (Poyarkoff, 1910; Gilmore, 1917; Monk, 1928; Ohdner, 1929; Okada, 1935a, 1935b, 1935c, 1936, 1938). In this study, particular attention is paid to the development of brood sacs because it is much different from that described by Okada (1935b) for Musculium heterodon. Also, the structure of byssal stalks is given since there are no descriptions in the literature.

Life history studies of sphaeriids are numerous (Gilmore, 1917; Thiel, 1924; Monk, 1928; Foster, 1932; Thomas, 1963; Heard, 1963, 1965, 1973; Mitropolskji, 1965; Ladle and Baron, 1969; Gale, 1969) but only Heard (1973) has given a brief description of the life history of M. securis. Studies showing the variation of aspects of the life history of sphaeriids within and between habitats are uncommon in the literature.

Many investigators have attempted to relate the abundance of sphaeriid species, including M. securis, to organic pollution but with conflicting results (Richardson, 1928; Carpenter, 1928; Baker, 1922; Purdy, 1930; Ellis, 1937; Gaufin and Tarzwell, 1952; Ingram et al, 1953; Wurtz, 1956; Mackie and Qadri, 1973). Aside from the few studies on substrate relations of sphaeriids (Meier-Brook, 1969; Gale, 1969), other studies on the ecology of sphaeriids have received little attention.

There are only a few food habit studies of sphaeriids in the literature. The most detailed study was done by Gale (1971) on Musculium transversum. O'Malley (1924) and Mitropolskji (1966) have studied the food habits of Sphaerium striatinum and Sphaerium corneum, respectively.

Herrington (1962), Heard (1962b, 1963) and Clarke (1973) have given only brief descriptions of the distribution of M. securis. Since these descriptions, many new localities have been reported in the literature and museum records. In an attempt to explain the dispersal of sphaeriids, many authors (Kew, 1893; Boycott, 1936, Baker, 1945; Ohdner, 1951) suggest that insects, frogs, salamanders, and aquatic birds are important dispersal agents. Few (Judd, 1966; Baker, 1927) describe factors that limit the distribution of sphaeriids.

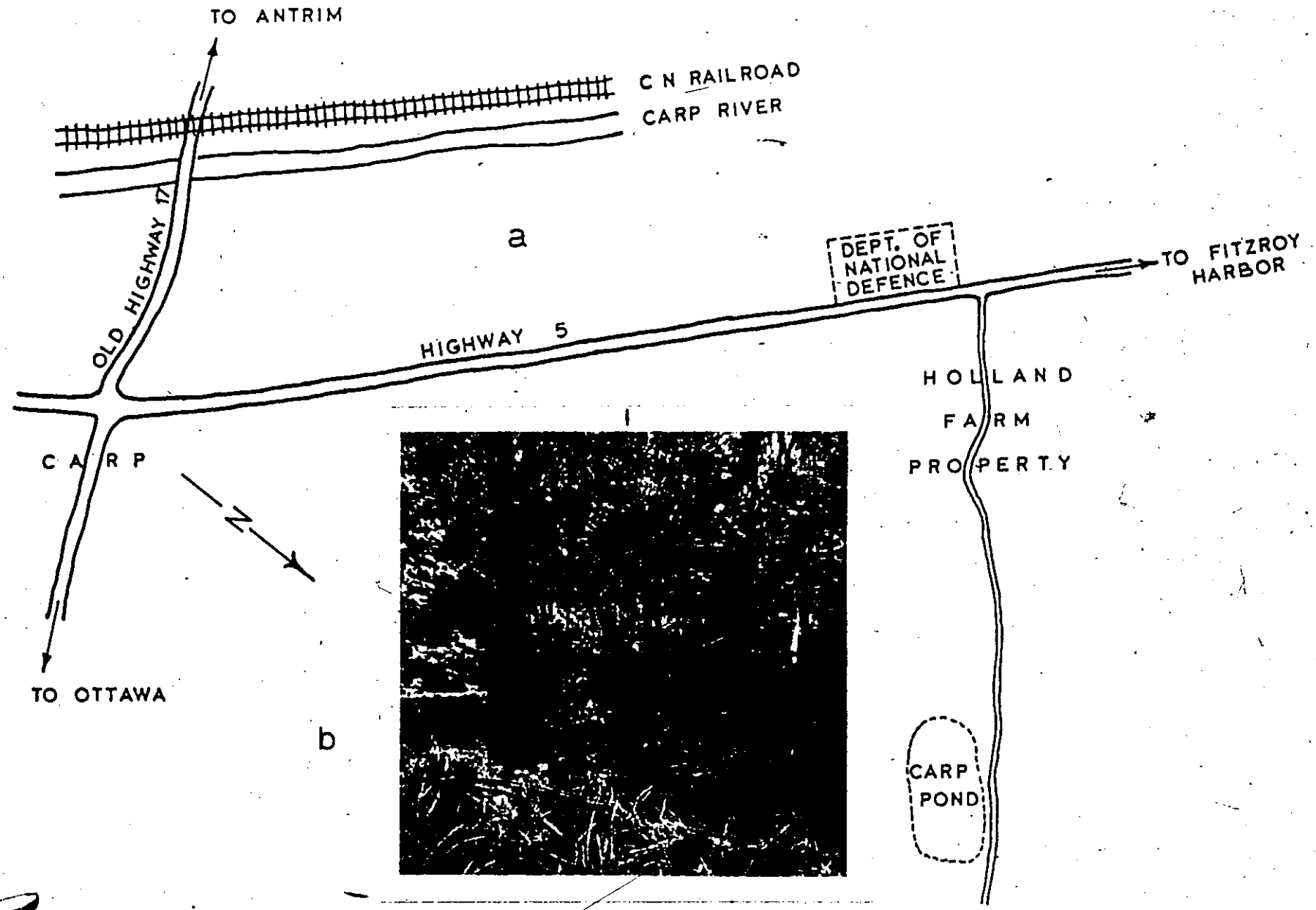
DESCRIPTION OF STUDY AREAS

For comparative life history and ecological studies of M. securis, four habitats containing the species were located within a 46 km radius of Ottawa; two are temporary forest ponds, one a river bed, and the fourth a permanent pond.

One temporary pond is located in a deciduous forest near Carp, Ontario and is called "Carp Pond" for the purposes of this study. It is situated on a tongue of the Canadian Shield (Wilson, 1956) and can be reached by travelling 1.1 km on Highway No. 5, North-west from Carp, Ontario and then going 1.6 km north on a narrow dirt road through Mr. Holland's farm property (Fig. 1a). The pond is approximately 100 x 150 m with a maximum depth of 1 m. White elm (Ulmus americana), black willow (Salix nigra), and red maple (Acer rubrum) are the dominant tree species in the pond (Fig. 1b). Less common trees include red oak (Quercus borealis), trembling aspen (Populus tremuloides), and white cedar (Thuja occidentalis). The top layer of soil has a black humus layer of decaying leaves and twigs. The pond is usually dry by the end of July or early August.

Fig. 1a A free-hand sketch of the route to Carp Pond from Carp, Ontario.

Fig. 1b A photograph of Carp Pond as it appears in the summer months when water is present.


TO ANTRIM
C N RAILROAD
CARP RIVER
OLD HIGHWAY 17
a
DEPT. OF NATIONAL DEFENCE
TO FITZROY HARBOR
HIGHWAY 5
HOLLAND FARM PROPERTY
CARP
N
TO OTTAWA
b
CARP POND

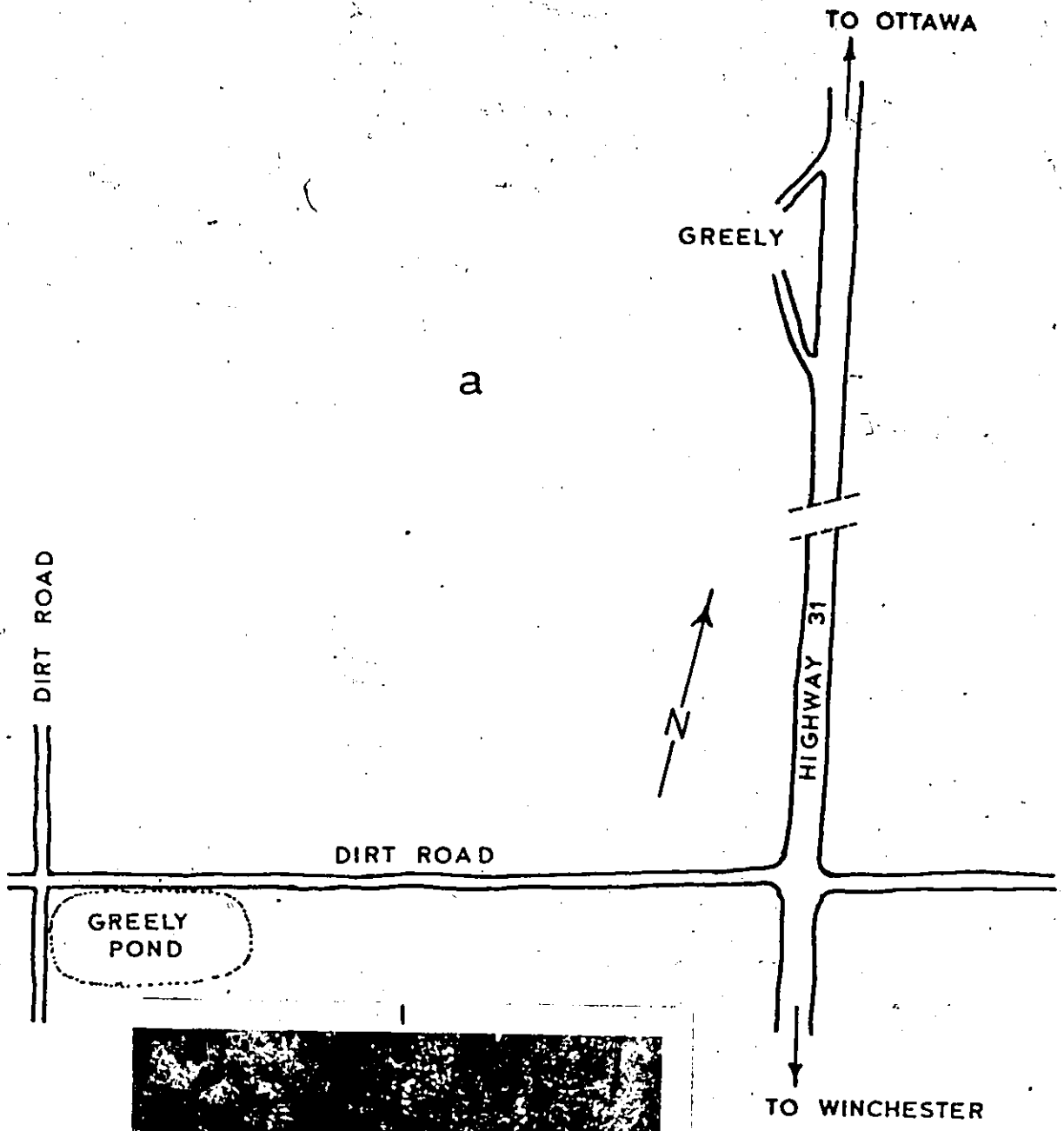
Musculium securis was the most abundant invertebrate. Other common species include the gastropods, Helisoma anceps, Gyraulus parvus, Physa gyrina, and Lymnaea elodes, among Amphipoda (Hyalella azteca), Isopoda (Asellus sp.), Anostraca (Eubranchipus sp.), Diptera (Chrionomidae, Culicidae), and Trichoptera. Black ducks (Anas rubripes) were seen feeding and breeding in the pond every summer during the study period (May 1970 to May 1973).

The second temporary forest pond was found south of Greely, Ontario and is called "Greely Pond" for the purposes of this study. It can be located by travelling 6.4 km south on Highway 31 from Greely, Ontario and then 1.0 km west on a dirt road (Fig. 2a). The pond lies south of this dirt road and is approximately 300 x 300 m in area. Willows (Salix spp.), trembling aspen, white elm, and red maple are the most common tree species within the pond (Fig. 2b). The maximum depth of the pond is 0.8 m. A thick black layer of humus with decaying leaves and twigs composes the top soil. Sphaerium occidentale and M. securis are the most abundant invertebrates with the former being approximately twice as numerous as the latter. Other common benthos includes P. gyrina, L. elodes, H. azteca, Asellus sp., Chironomidae and Trichoptera. Black ducks are usually seen feeding and breeding in the pond during the summer months. Greely Pond was studied from June 1972 to May 1973.

The third population was found in Britannia Bay of the Ottawa River near Ottawa, Ontario (Fig. 3a). Britannia Bay lies on the fringe of the Canadian Shield. Larger populations of M. securis occur in the mud of the 3-4 m depths than in the fine sand of the 0-3 m depths where other sphaeriids (Musculium transversum and Sphaerium striatinum) predominate.

Fig. 2a A free-hand sketch of the route to Greely Pond from Greely, Ontario.

Fig. 2b A photograph of Greely Pond as it appears in the summer months when water is present.


TO OTTAWA
GREELY
a
DIRT ROAD
HIGHWAY 31
N
DIRT ROAD
GREELY POND
TO WINCHESTER

b

Unlike the other habitats, Britannia Bay has many fish species including catfish (Ictalurus punctatus), brown bullheads (Ictalurus nebulosus), sauger (Stizostedion canadense), walleye (Stizostedion vitreum), and pike (Esox lucius). Many species of waterfowl, including mallards (Anas platyrhynchos platyrhynchos), black ducks (A. rubripes), greater scaups (Aythya marila), and Canada geese (Branta canadensis) frequent Britannia Bay to feed. Britannia Bay (Fig. 3b) was studied from May 1970 to November 1972.

The fourth habitat studied is a large permanent pond called Lac Bourgeois. It is situated in the Gatineau Hills of the Canadian Shield, north of Hull, Quebec. The pond is surrounded by a hardwood forest composed mainly of maples (Acer spp.) and oak (Quercus spp.) trees. Having a contagious distribution in Lac Bourgeois, M. securis is almost confined to a small area, 4 x 8 m, along the east shore in the shade of several small willow (Salix sp.) trees. The pond is approximately 200 x 450 m in area with a maximum depth of 3 m. The substrate consists of a thick layer of decomposing plant material which gives the pond a "false bottom" effect. A large beaver house is located in the middle of the pond. Black ducks often frequent Lac Bourgeois to feed during the summer months. The pond was studied from October 1971 to September 1972.

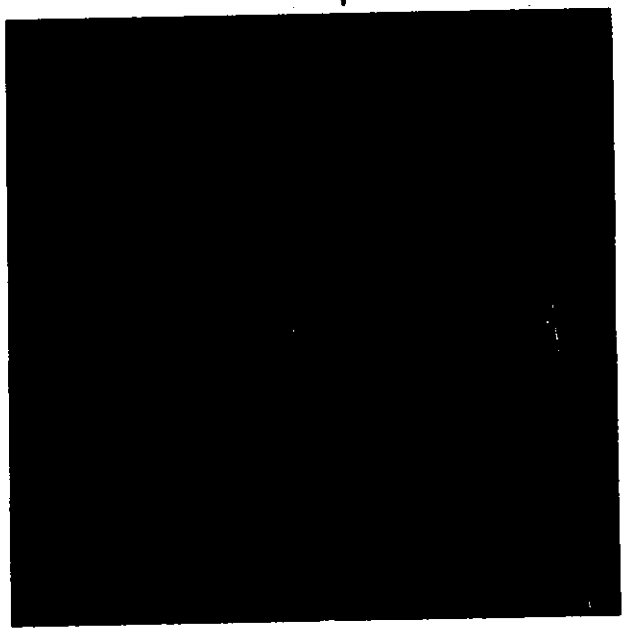
DESCRIPTION OF MUSCULIUM SECURIS

Taxonomy

Characters diagnostic of M. securis and a taxonomic key may be found in Herrington (1962). Herrington (op. cit.) describes the species as "Sphaerium securis Prime"; Cyclas securis Prime (1851), Cyclas sphaerica

Fig. 3a The location of Britannia Bay in relation to the city of Ottawa.

Fig. 3b A photograph of Britannia Bay as it appears in the summer months.



b

N

OTTAWA RIVER

CITY OF OTTAWA

LAC DESCHENES

BRITANNIA BAY

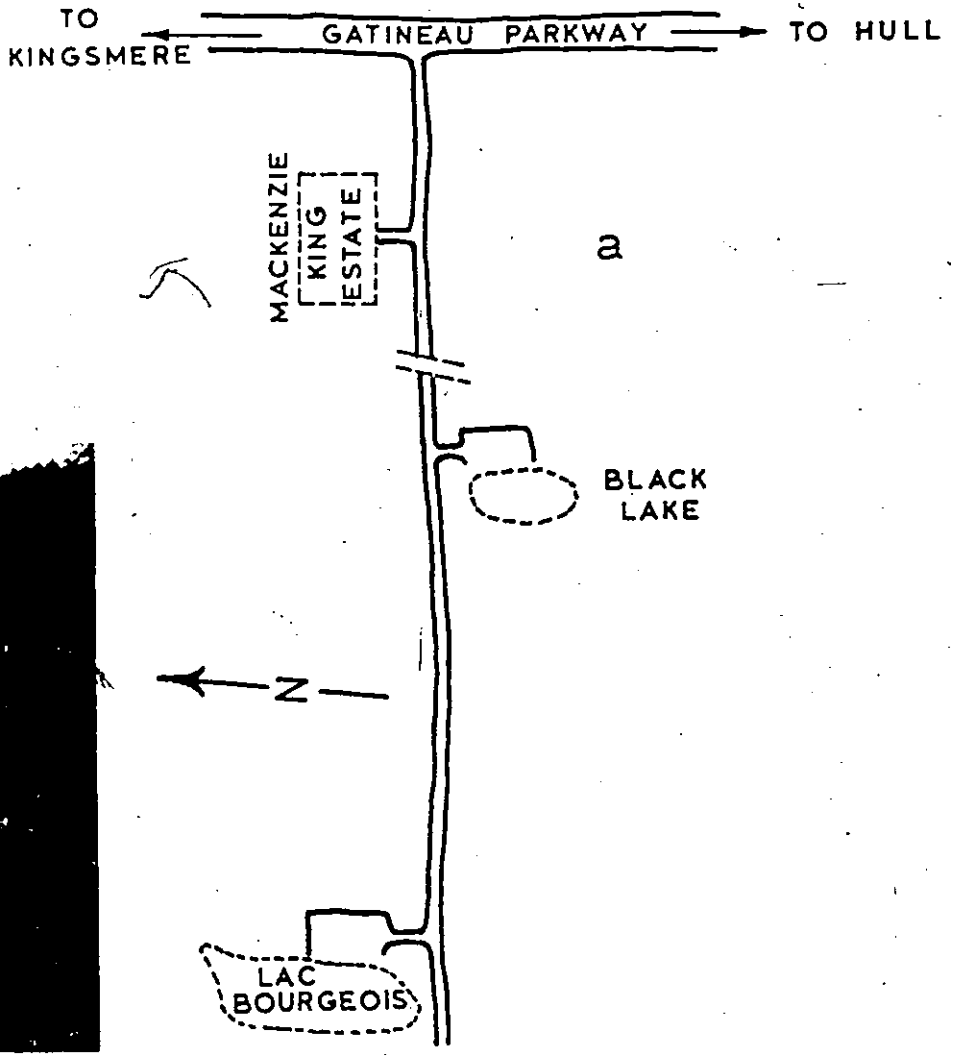
a.

1 Km

811

Fig. 4a A free-hand sketch of the route to Lac Bourgeois from the Gatineau Parkway, Hull, Quebec.

Fig. 4b A photograph of Lac Bourgeois as it appears in the summer months.


TO KINGSMERE
GATINEAU PARKWAY
TO HULL
MACKENZIE KING ESTATE
a
b
BLACK LAKE
N
LAC BOURGEOIS

Anthony, in Prime (1853), Sphaerium securis Prime (1865), Musculium parvum Sterki (1909), and Musculium australe Sterki (1916) are listed as synonyms. After comparing the species to the original description (Prime, 1851), comparisons were made with specimens that were authentically determined by H. B. Herrington.

Neave (1940) states that the genus, Musculium, was originally described by Link (1807). Species now included in this genus are lacustre, partumeium, securis, and transversum. Since Link's (1807) original description there has been much debate over the validity of the genus, Musculium. Herrington (1962) maintains that the characteristics attributed to Musculium (i.e. calyculate beaks and thin shells) are not constant features and often apply equally well to Sphaerium species and consequently does not consider Musculium as a valid genus (or subgenus). However, the present study and Gale (1969) indicate that while calyculate and uncalyculate forms of M. securis and M. transversum do occur, calyculism is predictable and constant under defined ecological conditions. Although not all species of Sphaerium and Musculium have been examined (particularly the type species, S. corneum and M. lacustre, respectively), examinations of the shells of S. striatinum and S. occidentale suggest that only Musculium species have true calyculae while Sphaerium species have "pseudocalyculae" (see p. 18). The calyculate character has recently been used to separate taxa but not at the generic level; Clarke (1973) recognizes Sphaerium and Musculium as subgenera and proposes a new subgenus, Herringtonium, for S. occidentale. Heard (1973), on the other hand, considers Musculium as a valid genus and documents several other differences between Musculium and Sphaerium; (1) proportionately more species of Musculium inhabit temporary ponds, (2) Musculium species

have a higher fecundity than most Sphaerium species, (3) gametogenesis begins during adult life in Musculium species and during larval life in most Sphaerium species, (4) Musculium species have a shorter potential life span than most Sphaerium species, (5) the two siphons are fused for only the basal half in Musculium species but for their entire length in Sphaerium species, and (6) a functional byssus is present in shelled larvae of Musculium species and is absent in most Sphaerium species. The only Sphaerium species that share these six characteristics with Musculium species are S. occidentale and S. corneum. However, as mentioned earlier, the results from the present study indicate that true calyculae are probably absent in these two species.

In view of these findings, I consider Musculium as a valid genus. Prime's (1851) original description was for Cyclas securis; the species is herein referred to as Musculium securis (Prime, 1851).

Development

The development of M. securis is only briefly discussed here because it is similar to that described for other Musculium and Sphaerium species by Heard (1973) and Okada (1935a, 1935b, 1935c, 1936, 1938). Larvae develop within brood sacs attached to the inner gills of the parent. There are five arbitrarily defined, sequential stages of development, viz. embryos, fetal larvae, prodissoconch larvae, extra-marsupial larvae, and adults. Embryos are contained within primary sacs and include that stage of development between the zygote and the completion of gastrulation. Fetal larvae are contained within secondary sacs and include those stages of development between the gastrula and the beginning of shell formation. When the shell begins to form the larvae are known as

prodissoconch larvae and the enveloping brood sac is called a tertiary sac. The tertiary sac eventually ruptures to release the larvae into the suprabranchial chamber of the parent. The larvae at this time are called extra-marsupial larvae. These extra-marsupial larvae are attached to the gill of the parent by a byssal stalk that was secreted during the prodissoconch stage. Eventually the extra-marsupial larvae break free of their byssal stalks and are released by the parent to become adults. Adults include all stages of development from the newborn stage to the gravid parent stage (parents that contain shelled larvae).

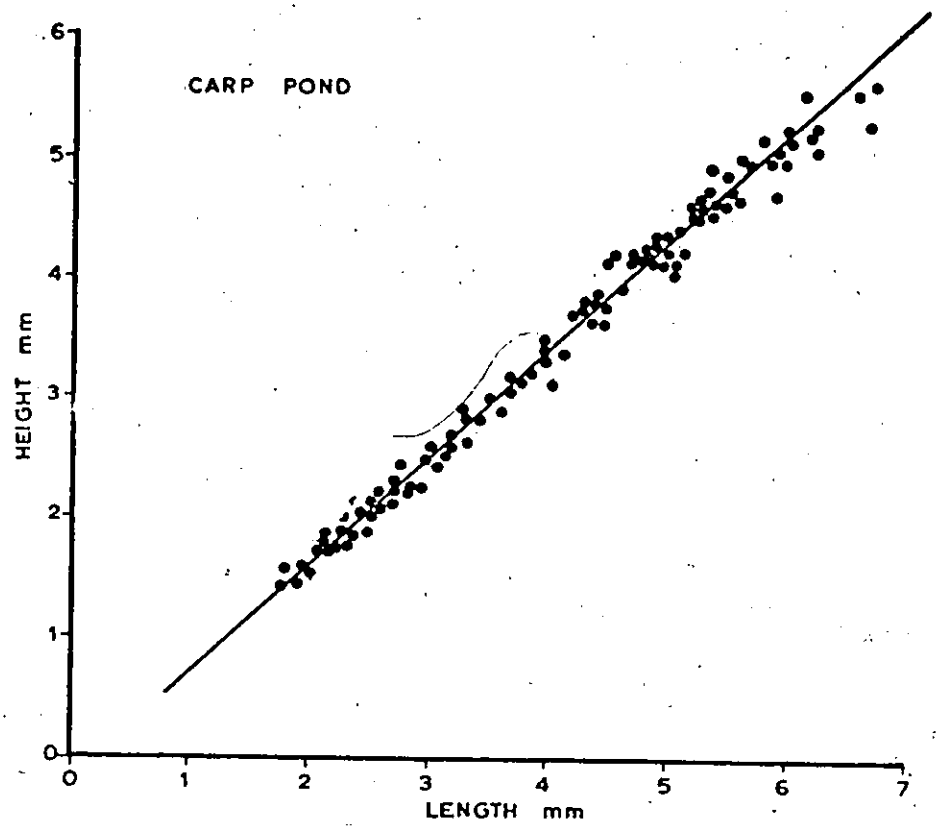
Size and Shell Characteristics

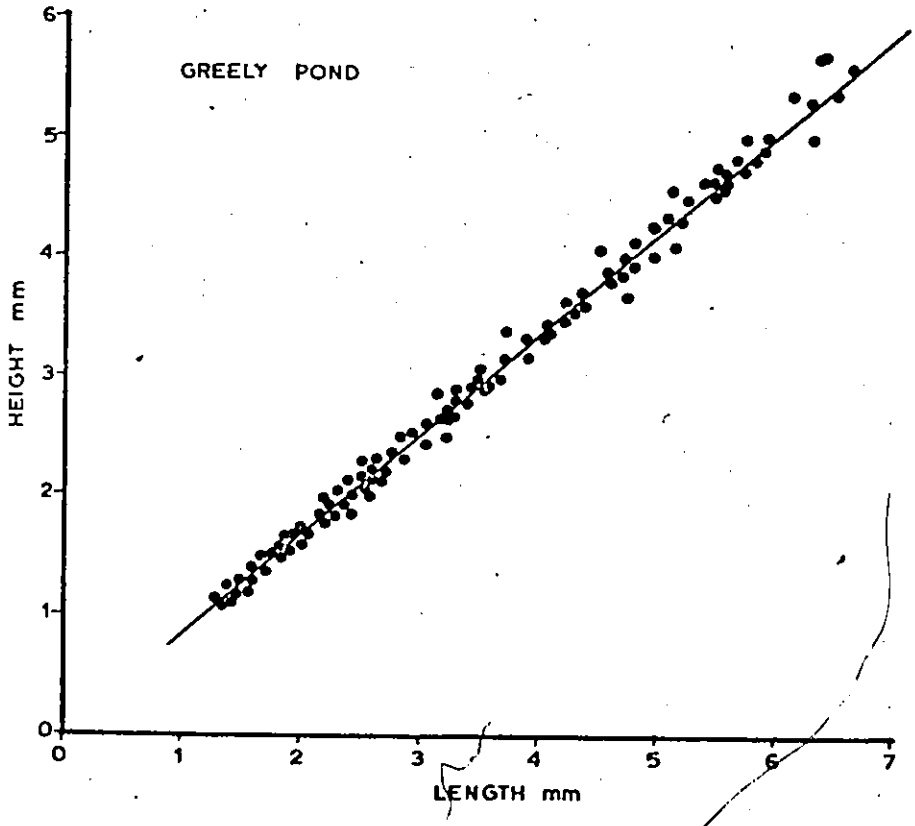
The species can usually be recognized by the steeply sloped, ventral anterior margin, a truncated posterior end, and a rounded anterior end. The dorsal hinge may be straight or slightly curved; if straight, the posterior end is at right angles to it; if curved, the posterior end joins it with a rounded angle. Striae on the shell are distinct and evenly spaced. The shell of pond specimens tend to have a "pitted" appearance while river specimens have a high gloss. Additional variations of M. securis are described in Herrington (1962).

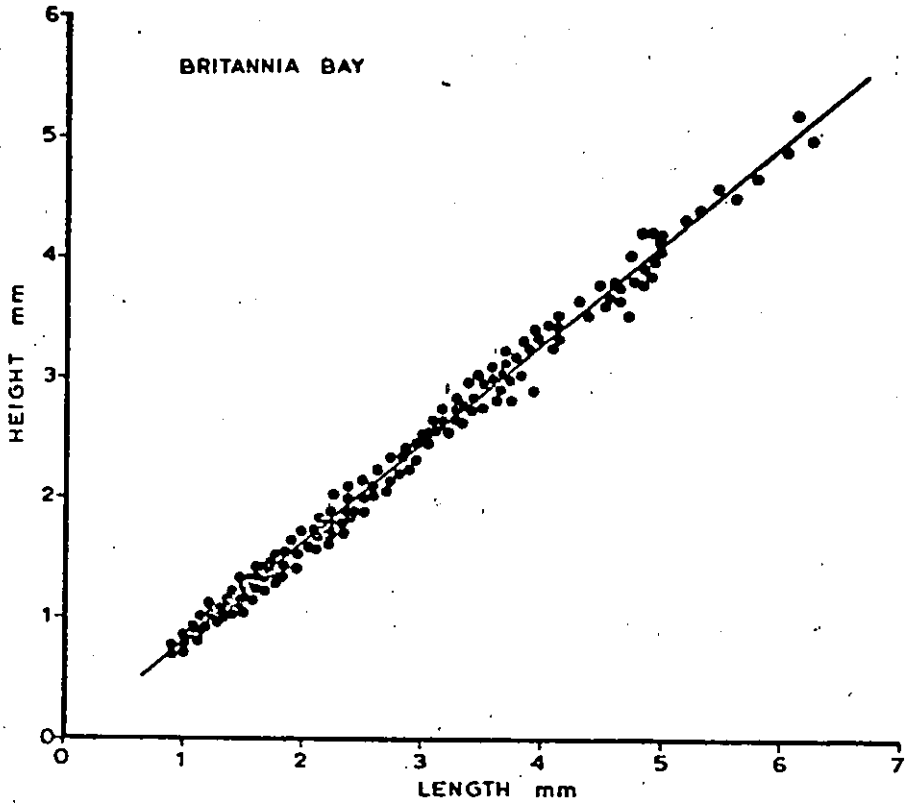
The length-height relationships of shells of M. securis from the four populations are shown in Fig. 5. Individuals of all populations studied have similar ($P < 0.001$) length-height relationships. In general the length is 1.2 times the height.

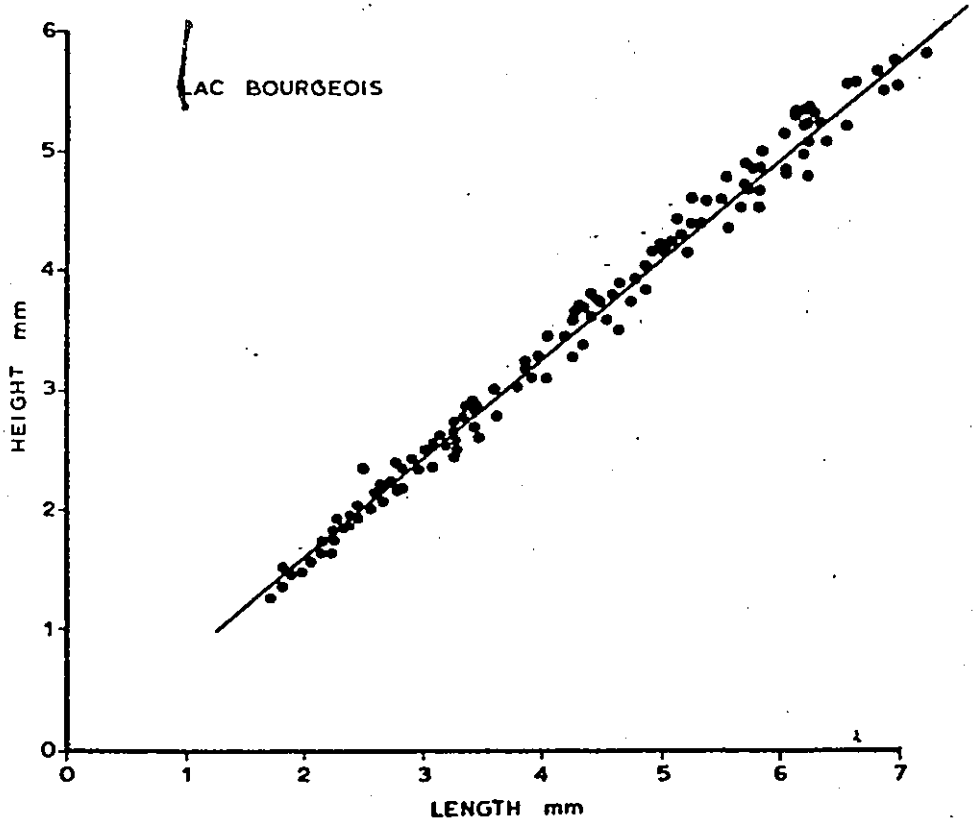
Individuals from each of the four populations studied have basic morphological differences. Usually clams from the Carp and Greely Pond populations have calyculate (capped) beaks where the nepionic valves are

Fig. 5 The length-height relationship of Musculium securis in Carp Pond ($Y = -0.22 + 0.90X$, $N = 158$, $r = 0.98$), Greely Pond ($Y = -0.18 + 0.88X$, $N = 130$, $r = 0.98$), Britannia Bay ($Y = -0.09 + 0.84X$, $N = 175$, $r = 0.98$), and Lac Bourgeois ($Y = -0.13 + 0.86X$, $N = 150$, $r = 0.99$).


CARP POND
HEIGHT mm
LENGTH mm
0
1
2
3
4
5
6
7


GREELY POND
HEIGHT mm
LENGTH mm
0
1
2
3
4
5
6
7


BRITANNIA BAY
HEIGHT mm
LENGTH mm
0
1
2
3
4
5
6
7


LAC BOURGEOIS
HEIGHT mm
LENGTH mm
0
1
2
3
4
5
6
7

separated from the adult valves by a distinct sulcus (Fig. 6). The Britannia Bay and Lac Bourgeois populations are represented by both calyculate and uncalyculate forms (Fig. 6). An annulated form is also present in the Lac Bourgeois population.

Experiments were carried out in the laboratory to determine the factors involved in calyculus formation. Several extra-marsupial larvae were excised from parents. In addition, several newly born clams were obtained from parents and kept in a 5°C cold room for 30 min. and 1, 2, 3, or 4 weeks. Newborn clams (i.e. had not grown since birth) from Carp Pond were also used. Groups of each of the extra-marsupial larvae and of the newborns of different ages were grown in dishes containing soil, water, and leaf litter. Calyculae formation for each group of clams was recorded.

Table 1 shows the age groups that develop into calyculate adults. Evidently the sulcus represents a rest period since clams which had not grown since birth (i.e. newborns older than 1 week, Table 1) form calyculae. Of the extra-marsupial larvae that survive, none forms a calyculus. Thus it appears that the rest periods occur sometime between the extra-marsupial larvae and newborn stages.

Experiments were also done in the field to confirm the results obtained in the laboratory. Newborns that had estivated and/or hibernated were isolated and maintained in growth tubes (described on p. 37) in Carp Pond, Britannia Bay, and Lac Bourgeois. Without exception, newborns developed into calyculate adults. Some adults in Britannia Bay growth tubes produced newborns early in the growing season. These newborns developed into uncalyculate adults. Other newborns that were produced later in the summer (early August) did not continue growing after birth but, apparently, began

Fig. 6 The shells of Musculium securis adults (including newborns) that occur in the Carp Pond, Greely Pond, Britannia Bay, and Lac Bourgeois populations.

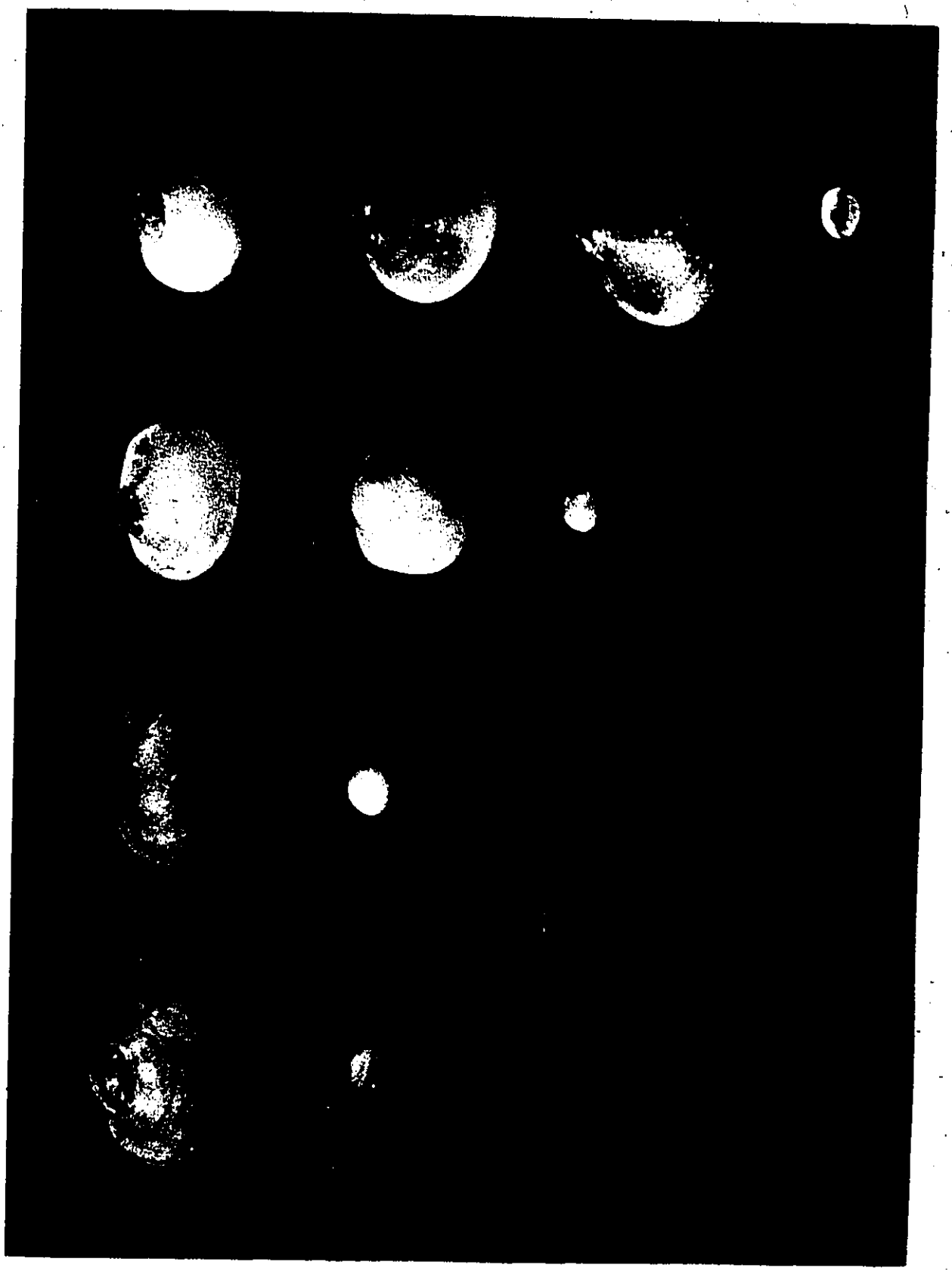


Table 1. Calyculus formation from extra-marsupial larvae and newborns of different ages in Musculium securis.

Ages of Musculium securis	Number Examined	Calyculus Formed	Calyculus Not Formed
Extra-marsupial larvae	10*	0	7
Newborns 30 min. old	6	5	1
Newborns 1 week old	6	6	0
Newborns 2 weeks old	6	6	0
Newborns 3 weeks old	5	5	0
Newborns 4 weeks old	5	5	0
Newborns 5 months old	15	15	0

* Three specimens died.

hibernating.

These results are of significance in life history studies, particularly since M. securis has a one year life span. Since the birth of newborns usually coincides with estivation periods (i.e. mid-summer in temporary ponds) or hibernation periods (i.e. autumn), calyculae are an important tool in identifying the approximate age of adults. Moreover, since the early summer and autumn generations can be distinguished by the absence and presence of calyculae, respectively, the calyculate character can be used to identify different generations in a population. Thus, adults with calyculae are of the first generation and adults without calyculae are of the second generation.

The sulcus is caused by a rest period but the factors that cause the rest periods are somewhat obscure. In the Britannia Bay growth tubes young were produced in late July but they did not grow despite the apparently favorable conditions in August and September. Thus, rest periods, hence calyculism, do not appear to be exclusively an ecophenotypic character. Nor does calyculism appear to have Mendelian ratios since Chi-squared tests failed to show the existence of either homozygous calyculism or heterozygous calyculism. At present, it can only be concluded that M. securis has some ability to either inhibit or induce growth upon birth.

Unlike a sulcus, an annulus appears to form as a direct result of environmental growth inhibiting factors (e.g. temperature). An annulus occurs anywhere on the shell; all adults that overwinter in Lac Bourgeois have an annulus on the shell but the annulus is located on different parts of the shell depending on the individual's length when growth was inhibited.

Conversely, a sulcus always demarks the nepionic valves from the adults valves. Thus, the sulcus is associated only with nepionic shells and the annulus only with adult shells.

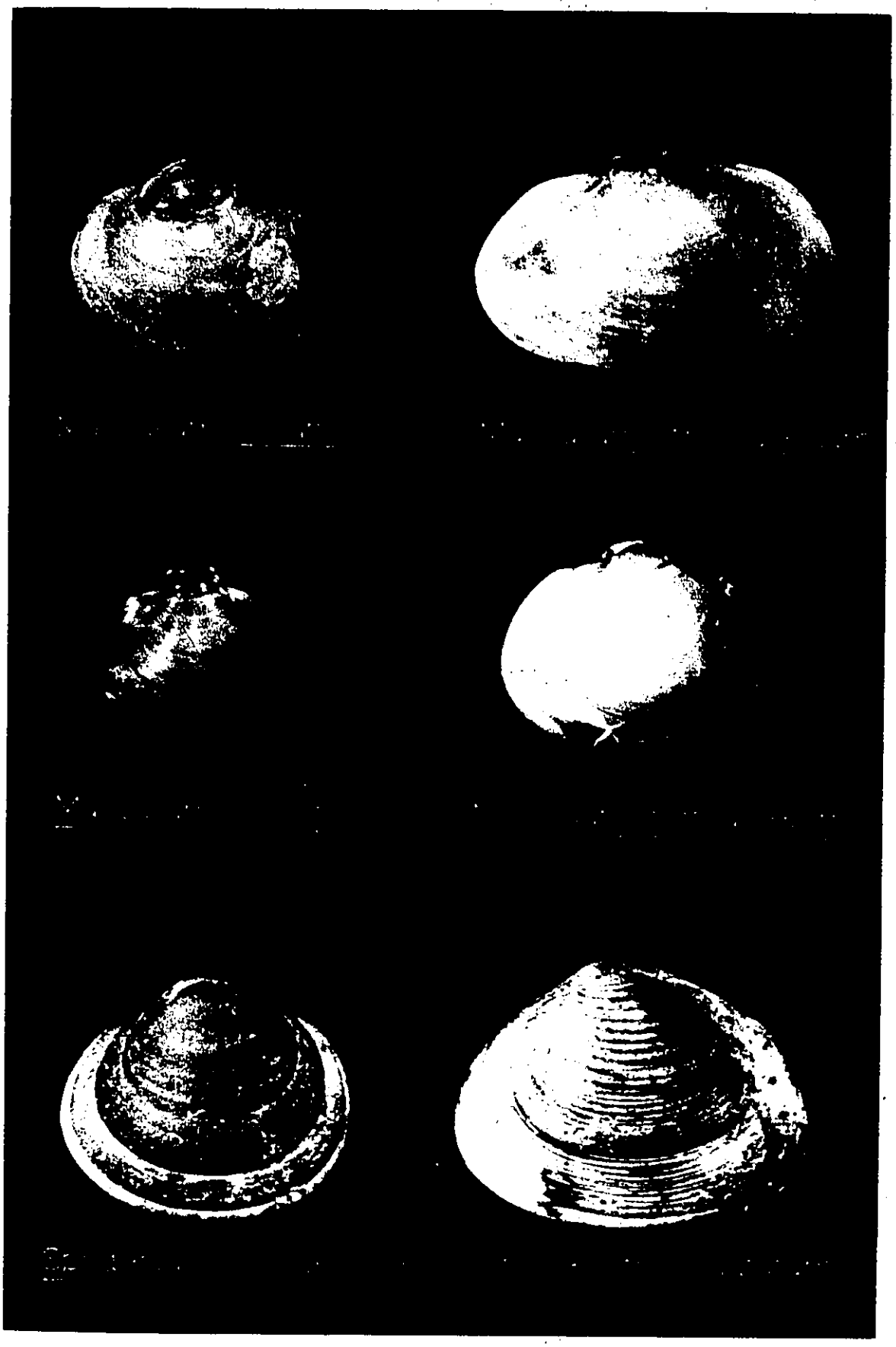
The distinction between a sulcus and an annulus also seems to apply to other species of Musculium and Sphaerium. Gale (1969) studied calyculus formation in Musculium transversum and also found that calyculism is associated with season of birth. Examinations of the shells of Sphaerium striatinum from Britannia Bay and of Sphaerium occidentale from Greely Pond show that several annuli may occur but they are associated with the adult valves and, therefore, not necessarily with the season of birth. Only occasionally is an annulus present at the base of the umbones in Sphaerium species and hence coincides with the season of birth. Therefore, in Musculium species the sulcus forms the calyculus but in Sphaerium species the annulus forms a pseudocalyculus . This pseudocalyculus apparently forms only when a growth inhibiting factor of the environment coincides with the birth of newborns. Therefore, on the basis of the distinction between sulci and annuli, the presence of calyculae, or caps, appears to be a valid characteristic of the genus Musculium.

Comparison With Other Musculium and Sphaerium Species

Only species with which M. securis commonly occurs or are easily confused are considered here. The following features can usually be used to distinguish M. securis from other species.

The ventral anterior margin of M. transversum is less steeply sloped and the shell is much longer in outline than that of M. securis (Fig. 7). The dorsal margin of M. transversum is long and straight and joins both the anterior and posterior ends at distinct angles; in M. securis the

Fig. 7 Typical shells of Musculium securis and of species with which it is often confused (Musculium transversum, Musculium lacustre, Musculium partumeium) or often occurs (Sphaerium occidentale, Sphaerium striatinum).



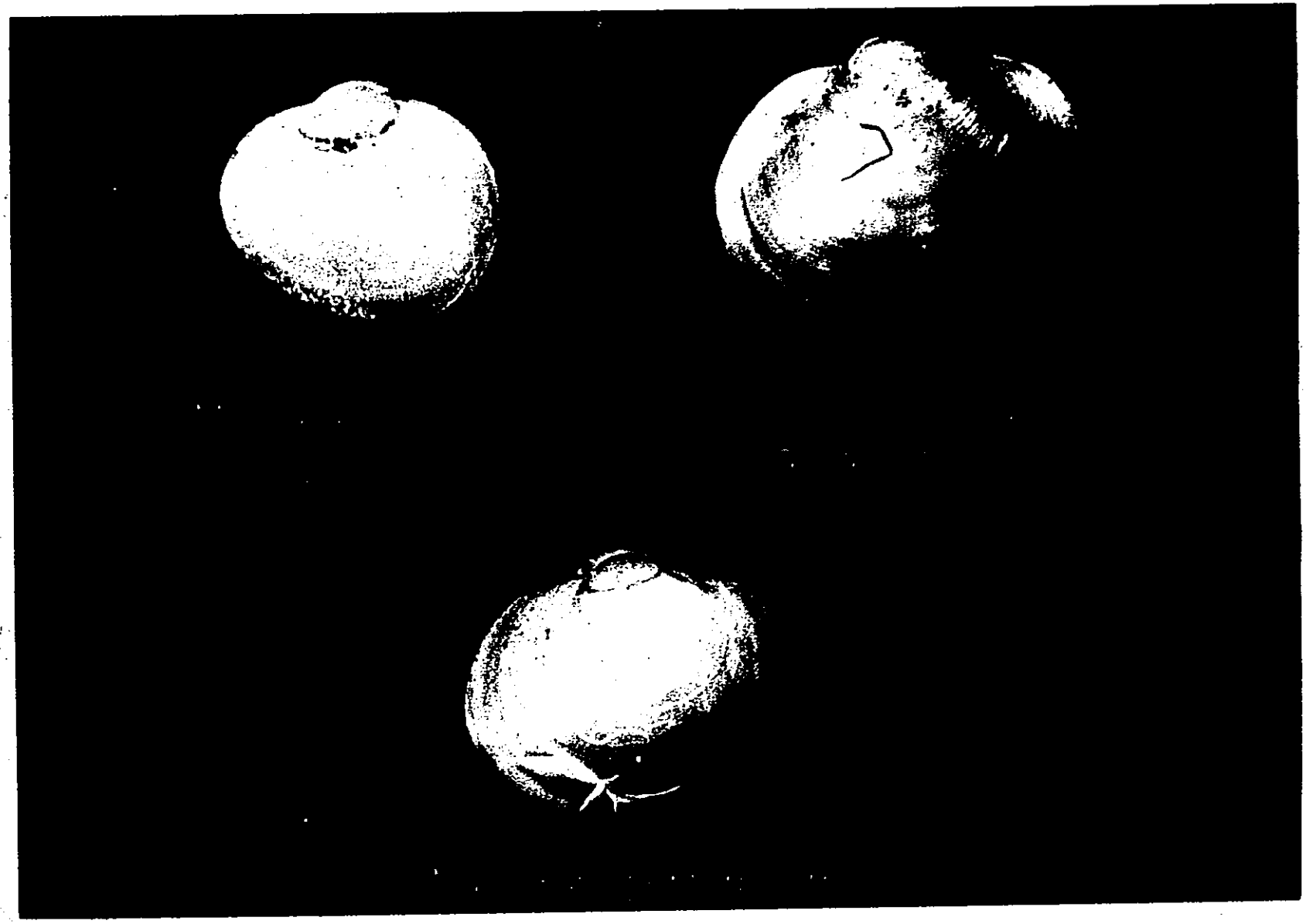
anterior end is rounded. The two species may occur together but one usually greatly outnumbers the other (cf Fig. 54, p. 153).

Musculium partumeium has a less sloped ventral anterior margin and its shell outline is more truncated in appearance than is M. securis. The umbones of M. securis tend to lean away from one another and appear to sit on the side of the shell; in M. partumeium the umbones lean forward and slightly towards one another so that they appear to sit more dorsally on the shell (Fig. 7). The dorsal margin of M. partumeium usually forms a sharper angle with and is more often at right angles to the posterior end than is the dorsal margin of M. securis. The striae of M. partumeium are less distinct than of M. securis so that the shell of the former usually has a higher gloss than the shell of the latter. The two species are very seldom found together.

When M. securis is grown in high concentrations of calcium chloride, the shell assumes many of the characters attributed to M. partumeium (Fig. 8). That is, the position of the umbone and the relationship of the dorsal margin to the anterior and posterior ends are very similar to those described for M. partumeium. However, the ventral anterior margin is sloped and the striae of the shell are distinct in the "calcium chloride specimens" as is typical of M. securis specimens.

Musculium lacustre is the smallest of the four Musculium species (Fig. 7). In M. lacustre the umbones tend to lean towards one another and sit high on the shell while in M. securis the umbones tend to lean away from each other and sit low on the shell. The dorsal margin of M. lacustre joins the anterior and posterior ends at distinct angles; in M. securis the dorsal margin either forms no angles or more rounded angles with the anterior and posterior ends. Very seldom are the two species found together.

Fig. 8 A comparison of the shell of Musculium securis when grown in a calcium chloride ($CaCl_2$) solution to a typical M. securis shell and a typical Musculium partumeium shell.



Sphaerium occidentale has been found, to the best of my knowledge, only in ponds that usually dry up every year. The species can be identified by the presence of a ridge extending down from the dorsal margin and about midway on the inside of the shell. The shell is rounded in outline so that the long dorsal margin is difficult to delimit (Fig. 7). True caps are absent on this species. Sphaerium occidentale and M. securis often occur together in large numbers (e.g. in Greely Pond).

The most common species of lakes, rivers, and creeks is S. striatinum. Compared to M. securis the shell of S. striatinum is much larger (10-16 mm) and has coarser, more irregularly spaced striae. The ventral margin of S. striatinum is gently curved and much longer than the sloped dorsal margin. True calyculae are absent on this species. In the larger lakes and rivers S. striatinum is often found in large numbers with M. securis (e.g. in Britannia Bay).

Anatomy

The anatomy of M. securis was studied in detail. Since the anatomy appears to be similar to that of other species described in the literature only a brief description of the organs and systems is given here. The development of brood sacs in M. securis is much different from that described for other species and is discussed in detail. The structure of byssal stalks is also given because there are no descriptions in the literature.

General anatomy - The gills of M. securis are of the eulamellibranch type (Hickman, 1967) with filaments fused laterally and the lamellae joined by cellular partitions. There are two pairs of gills, a pair of inner demibranchs and a pair of outer demibranchs. The outer pair

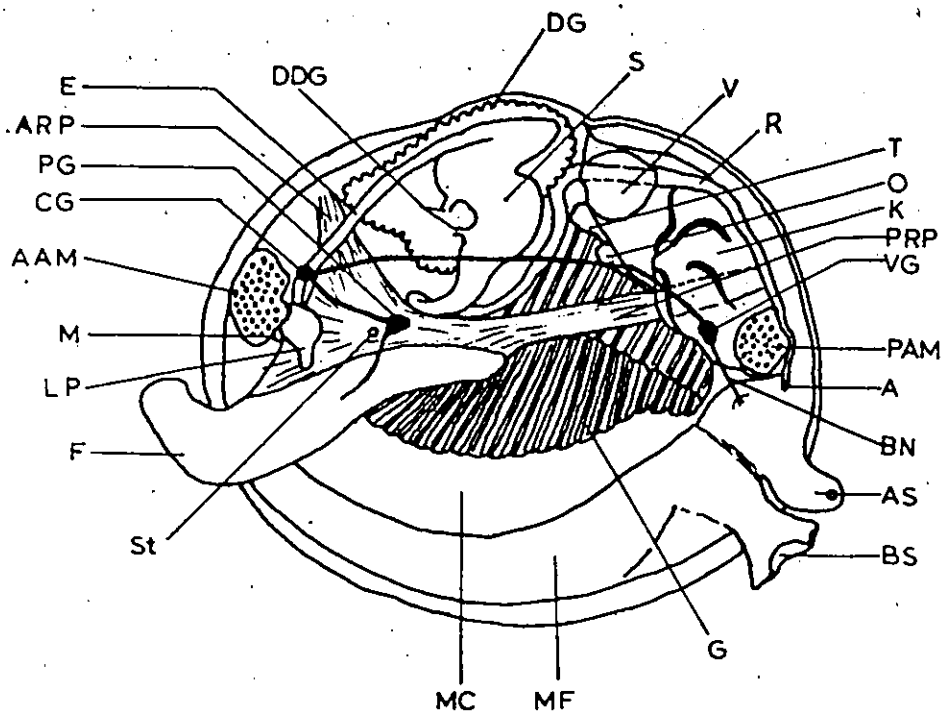
is smaller and occupies a dorso-posterior position. The inner lamella of the outer demibranch attaches to the outer lamella of the inner demibranch. Brood sacs are supported medially on the inner demibranch. Details of gill structure are identical with those described for other sphaeriids by Monk (1928) and Gilmore (1917).

The digestive system (Fig. 9) is of the basic pelecypod type. The mouth is at the base of the labial palps which are situated behind the anterior adductor muscle. Food passes through the esophagus to a large stomach that is perforated with ducts from the large, dorsal digestive gland. Near the end of the stomach and extending down into the intestine is a style sac with its crystalline style, the structure of which has been described by Nelson (1918) and Monk (1928). The intestine loops around the base of the stomach and ascends to near the posterior edge of the umbones where it bends and courses posteriorly along the interior margin of the shell as the rectum. An anus opens into the anal siphon immediately behind the posterior adductor muscle.

A muscular ventricle surrounds the rectum a short distance behind the stomach (Fig. 9). The ventricle and two auricles are enclosed in a pericardial sac. Blood circulation was not studied but is probably of the Anodonta type described by Monk (1928) and Hickman (1967).

The excretory system consists of a pair of coiled, thin walled tubules which constitute the kidneys or organs of Bojanus (Fig. 9). The kidneys lie against the dorso-posterior wall of the mantle and between the heart and the posterior adductor muscle. A pair of short ducts join the pericardium to the kidneys. Waste products are carried to the cloacal chamber by a urogenital duct. Monk (1928) and Ohdner (1929) have

Fig. 9 Camera lucida drawing showing anatomy of Musculium securis. A anus, AAM anterior adductor muscle, ARP anterior retractor pedis muscle, AS anal siphon, BN branchial nerve, BS branchial siphon, CG cerebral ganglion, DDG ducts of digestive gland, DG digestive gland, E esophagus, F foot, G gill (inner), K kidney (Bojanus' organ), LP labial palp, M mouth, MC mantle cavity, MF mantle fold, O ovary, PAM posterior adductor muscle, PG pedal ganglion, PRP posterior retractor pedis muscle, R rectum, S stomach, St statocyst, T testis, V ventricle of heart, VG visceral ganglion.


DG
S
V
R
T
O
K
PRP
VG
PAM
A
BN
AS
BS
G
MC
MF
St
F
LP
M
AAM
PG
CG
ARP
E
DDG

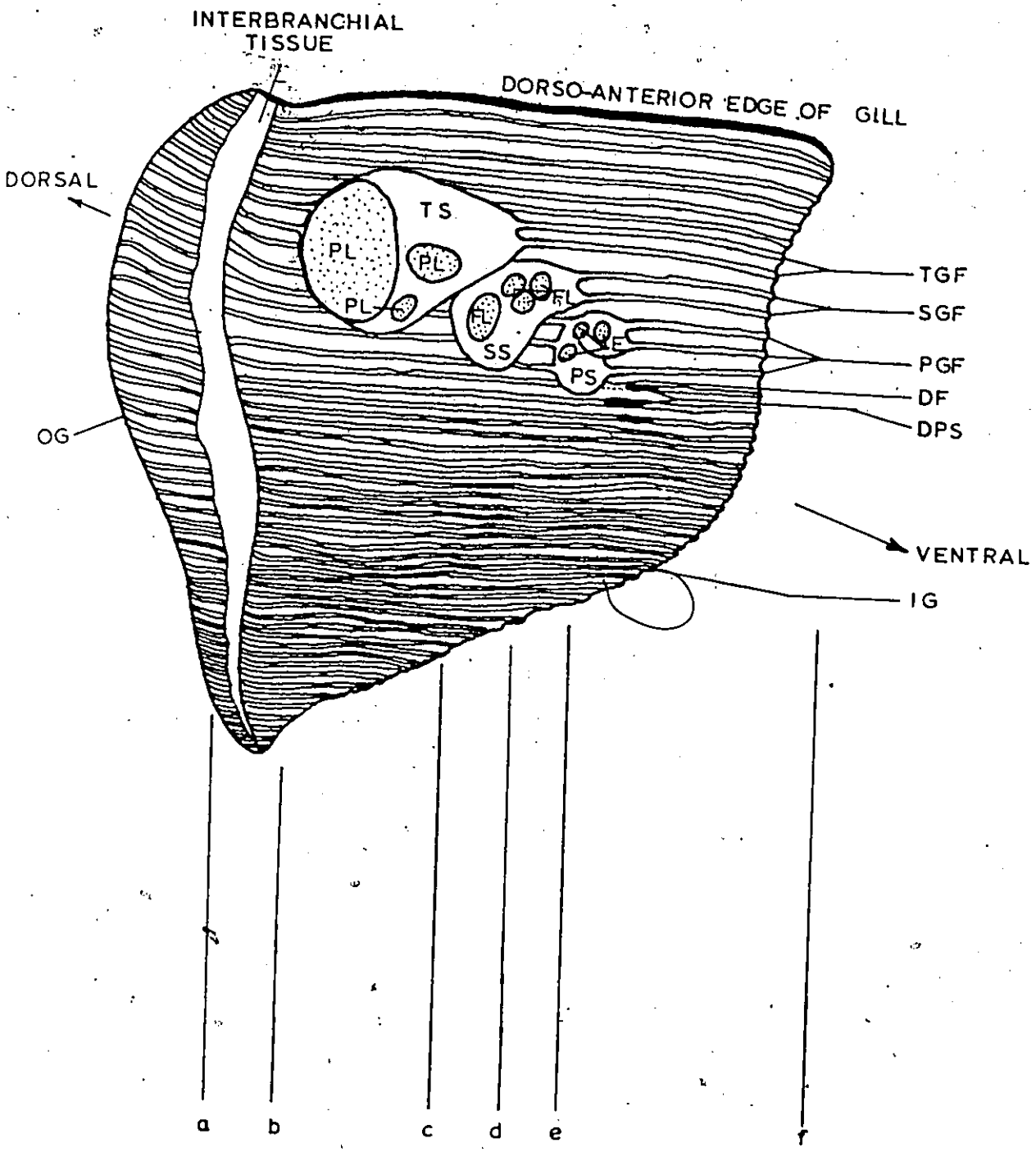
described the excretory process.

The nervous system consists of three pairs of large ganglia with their nerve fibers, two pairs of commissures, and two pairs of special sense organs (Fig. 9). A pair of cerebral ganglia lie dorsad the esophagus immediately behind the anterior adductor muscle. Two cerebro-visceral commissures connect the cerebral ganglia to the visceral ganglia which lie against the posterior adductor muscle. A pair of cerebro-pedal commissures connect the cerebral ganglia to the pedal ganglia which lie dorsal to the foot muscles. Two spherical, bead-like statocysts organs are situated immediately anterior to the pedal ganglia. Osphradia lie in the roof of the cloacal chamber and against the branchial nerve. Detailed descriptions of the statocysts and osphradia are given by Monk (1928).

The reproductive system consists of a pair of gonads and their reproductive ducts (Fig. 9). The gonads lie anterior to and against the outer wall of the pericardial sac. During early development the testis and ovary are indistinctly separated but eventually the testis comes to lie dorsal and anterior to the ovary. A gonoduct carries both sperm and ova to a short urogenital duct that opens into the cloacal chamber. Fertilization is internal and occurs near the urogenital orifice (Okada, 1935a). The reproductive system and process has been described in detail by Okada (1935a, 1935b, 1935c).

Brood sac development - The structure of brood sacs in M. securis is similar to that described for M. heterodon by Okada (1935b). However, the development of brood sacs appears to be different in the two species. In M. securis the brood sacs are associated with certain filaments of the inner gill (Fig. 10). Of an estimated 10,000 brood sacs examined, all develop from either two or three gill filaments. Counting down from the

Fig. 10 Position of the brood sacs and their relation to the gill filaments of the inner gill. DF degenerating filament, DPS developing primary sac, E embryo, FL fetal larvae, IG inner gill, OG outer gill, PGF gill filaments supporting primary sac, PL prodissoconch larvae, PS primary sac, SGF gill filaments supporting secondary sac, SS secondary sac, TGF gill filaments supporting tertiary sac. See text for explanation of a, b, c, d, e, and f.

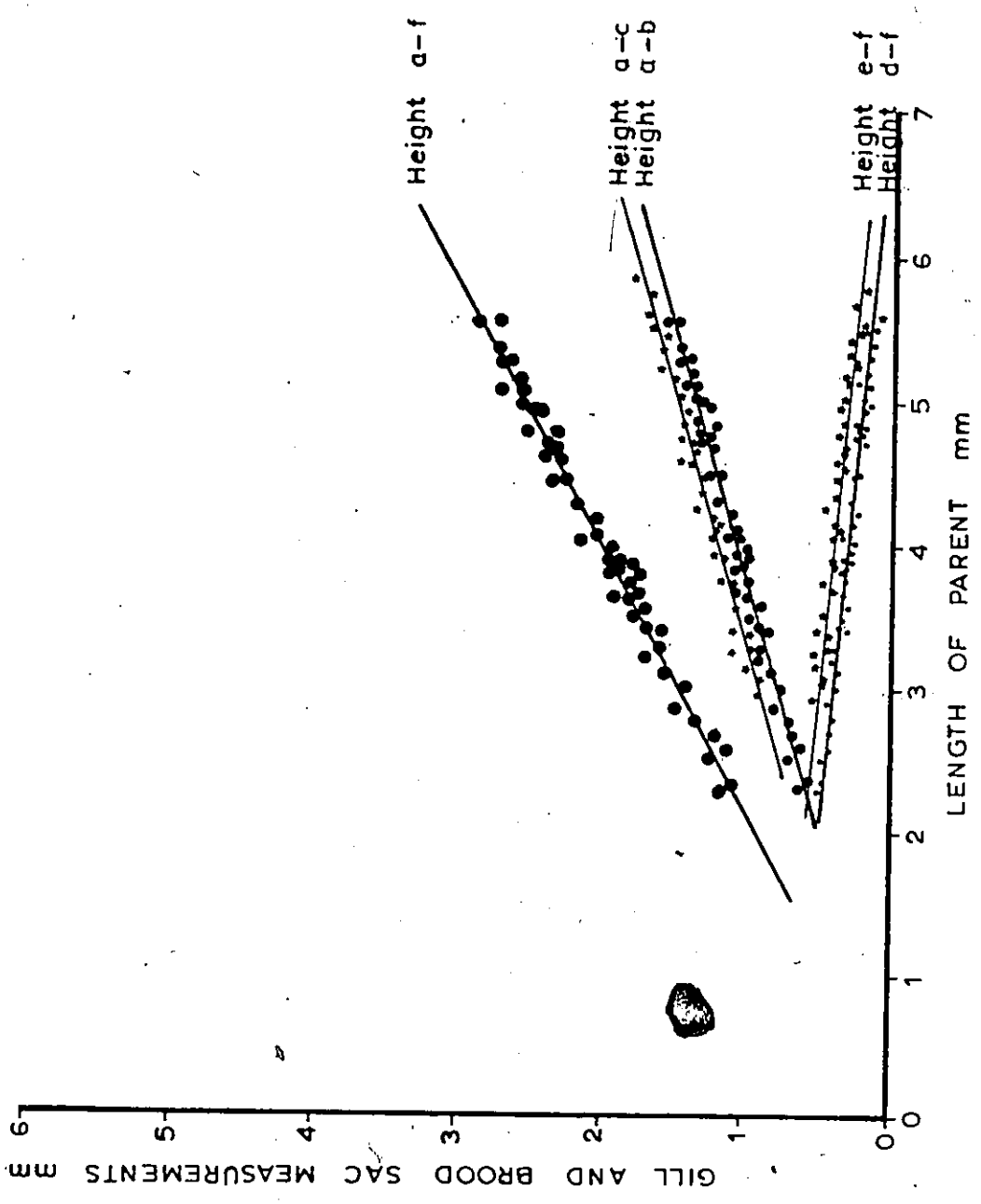

INTERBRANCHIAL TISSUE
DORSO-ANTERIOR EDGE OF GILL
DORSAL
TS
PL
PL
PL
FL
FL
SS
E
PS
TGF
SGF
PGF
DF
DPS
OG
VENTRAL
IG
a
b
c
d
e
f

dorso-anterior edge of the gill (Fig. 10), the first sac usually develops on the 7th and 8th gill filaments, the second on the 9th and 10th, the third on the 11th and 12th, and the fourth on the 13th and 14th gill filaments. Each sac remains associated with the filaments from which it arises until the sac ruptures, releasing the enclosed prodissoconch larvae. Occasionally brood sacs develop from three filaments so that the first sac is on filaments 7, 8, 9, the second on 10, 11, the third on 12, 13, and the fourth on 14, 15, 16 or the first is on 7, 8, and the second on 9, 10, 11, the third on 12, 13, and the fourth on 14, 15, 16. Nearly all combinations of gill filaments occur except two adjacent sacs each occupying three filaments.

Several measurements were taken to determine the relationship between the growth of gills and brood sacs and the growth of the parents. Referring to Fig. 10, the total length of the gill (a-f) and the lengths of brood sacs (b-d) and (c-e) were measured in parents of several ages. The lengths a-b, a-c and d-f, e-f (Fig. 10, 11) are measures of the brood sacs in the dorsal and ventral directions, respectively.

Measurements of 150 parents showed that the growth of brood sacs and gills are directly related to the growth of parents (Fig. 11). Also the growth of brood sacs is linearly related to the growth of gills (Fig. 11). The distance between the dorsal edge of the gill (a, Fig. 10) and the dorsal edge of the first sac (b, Fig. 10) decreases with increasing age of the parent, indicating that the sac advances dorsally (Fig. 11). However, the distance between the ventral edge of the first sac (d, Fig. 10) and the ventral edge of the gill (f, Fig. 10) remain constant and is exactly one half the length of the gill in all parents (Fig. 11). Since the gill

Fig. 11 Growth of the inner gill and various aspects of the first and second brood sacs in relation to growth in shell length of parents of Musculium securis. See text and Fig. 10 for explanation of a-f, a-c, a-b, e-f, and d-f.


Height a–f
Height a–c
Height a–b
Height e–f
Height d–f
GILL AND BROOD SAC MEASUREMENTS mm
LENGTH OF PARENT mm
0
1
2
3
4
5
6
7

grows in a ventral direction (Raven, 1958), the brood sacs must advance in the ventral direction at an identical rate.

Okada (1935b) did not associate the brood sacs with gill filaments in M. heterodon but maintains that "the sac moves upwards along the descending lamella" by formation and reformation of new sac stalks. This does not occur in M. securis since the ventral edge of the sacs advances ventrally (i.e. downwards) at an identical rate to the gills. Moreover, there is no evidence of the sac stalks forming and reforming since the sacs are always attached dorsally and ventrally to the gill filaments. Okada (1935b) also maintains that the sacs move from "the lower part to the upper part of the branchial chamber". This can not occur in M. securis because the sacs remain attached to the filaments from which they arose. Rather, the sacs merely enlarge with the growth of the enclosed larvae.

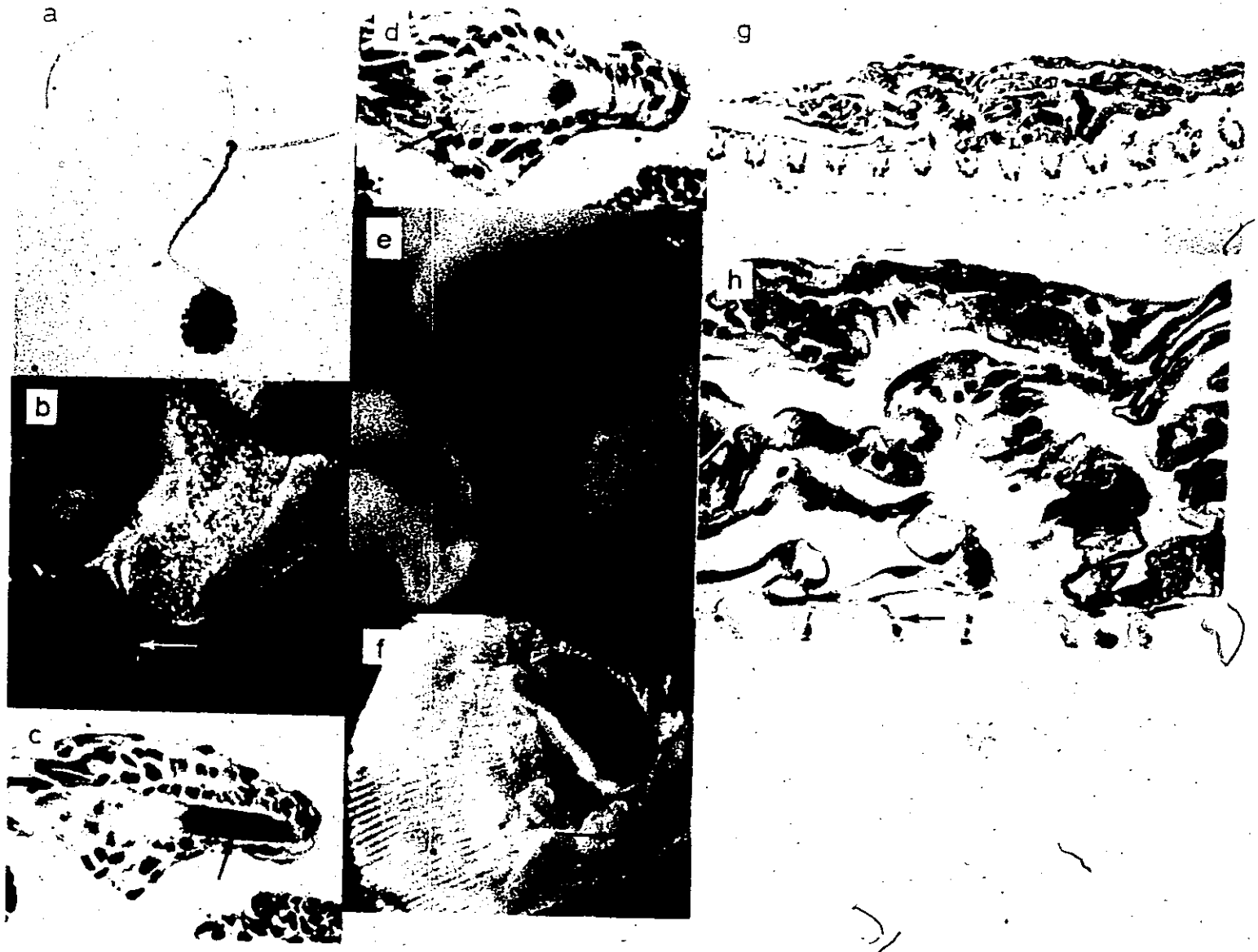
Since brood sacs are associated with certain gill filaments, the numbers of litters produced by a parent can be determined by back-calculation of brood sacs. Thus, parents that have produced one litter will not have brood sacs on filament numbers 7 and 8. Similarly, parents that have produced two litters will not have brood sacs on filament numbers 7 and 8 nor on 9 and 10. This technique can be applied to parents in which brood sacs develop from two filaments. For parents in which brood sacs develop from three filaments, one litter was produced if filament numbers 7, 8, 9 have no brood sacs, two litters if filament numbers 7, 8, 9, 10, 11 have no brood sacs (I have never seen the 12th filament used in the formation of the second brood sac), three litters if filament numbers 7-13 inclusive (or 7-14 inclusive) have no brood sacs. Usually sac remnants remain to determine whether a sac has developed from two or three filaments.

If no sac remnants are present, one only needs to refer to filament numbers 8, 10, and 12, since they are always present in the formation of the first, second, and third brood sacs, respectively, regardless of the number of filaments used in sac development. If indeed the 12th filament is used in the development of the second brood sac, errors would be introduced into the estimation of the third and fourth litters. This is particularly true if sac remnants are not present to determine the number of filaments used in sac development.

Byssus structure - Byssal stalks (Fig. 12a) are found in S. occidentale and S. corneum as well as in all North American Musculium species. They appear to be solid in cross section and are approximately 10μ in diameter and 0.5 mm long, the length increasing with age of the larvae. The byssus consists of a byssal stalk and a bulbous portion or byssal bulb at the insertion end (Fig. 12a). Several stalks, depending on the number of larvae in a brood sac, insert on one byssal bulb. The byssus has no apparent cellular structure. It originates in the byssal gland in the posterior base of the larva's foot (Fig. 12b). Serial sections of the foot in the region of the byssal gland show that the stalk is produced from cells at the base of the gland (Fig. 12c). The base of the stalk appears to be fibrous (Fig. 12d). The byssus first appears in prodissoconch larvae and only one stalk per larva is produced.

The byssal bulb with its stalk(s), insert(s) on the parent's gill on the same filaments from which the respective brood sac(s) arose (Fig. 12e). Usually the cells of the gill filaments below the byssal bulb proliferate and form a large saccular mass (Fig. 12f). Serial sections show the highly sacculated structure of this mass (Fig. 12g) and its origin from gill filaments (Fig. 12h). The function (if any) of

Fig. 12 Structure of byssus in Musculium securis. (a) Two byssal stalks twisted at the distal half and inserting on a common byssal bulb (50X). (b) Early stage in the development of the byssal stalk (indicated by arrow) from the byssal gland in the foot of a prodissoconch larva (50X). (c) Section through foot of extra-marsupial larva showing the basal portion of the byssal stalk (indicated by arrow) in the byssal gland (500X). (d) Same as (c) but section is 8 microns deeper to show fibrous nature of the base of the byssal stalk and its origin from cells (indicated by arrow) at base of gland (500X). (e) Insertion of the byssal bulb on gill of parent (50X). (f) Insertion of the byssal bulb on proliferated cells (indicated by arrow) of gill filaments (50X). (g) Section through proliferation showing sacculated structure (125X). (h) Same as (g) but 500X magnification to show origin of the sacculated mass from gill filaments (indicated by arrow).


a
b
c
d
e
f
g
h

this sacculated structure is not known but the increased surface area may be of respiratory significance to the larvae.

It is not known how the byssal stalks from several larvae eventually insert on a common byssal bulb. However, it is suggested that this process occurs very early in the development of prodissoconch larvae when they are in close proximity to each other. The byssal bulb has not been recorded in the literature but Heard (1973) states ".....larvae..... are anchored by a byssal thread to a common stalk which arises from their respective tertiary brood sacs". An examination of Fig. 12a shows that the "common stalk" which Heard (op. cit.) refers to is merely the twisting of several stalks; this twisting probably occurs as a result of the activity of extra-marsupial larvae.

The function of the byssus has only been speculated upon. Heard (1973) suggests that the byssus prevents "precocious birth until the larval gonads can develop to such an extent that they can participate in the next fertilization period following birth". The present study tends to support this interpretation.

MATERIALS AND METHODS

Most of the materials and methods are given below; others are given in more appropriate places throughout the text.

Physics and Chemistry of Water

Collection of water samples were made at the same time as samples of M. securis to enable a study of the relationship between seasonal differences in physical and chemical characters of the water and various

growth parameters of M. securis. The dates of collections may be found in Fig. 25, 27, 28, 30. No physical nor chemical vertical gradients existed in any of the habitats (except perhaps at the mud-water interface). All water samples were collected approximately 30 cm below the surface.

Three physical and eight chemical characters were analyzed on each water sample. Temperature was determined with a mercury thermometer. A Beckman conductivity meter was used to measure the conductivity in μmhos/cm. Color was determined in platinum-cobalt units on a D.R.E.L. Hach Water Chemistry Kit according to instructions in the fourth edition instruction manual (Hach Chemicals Co., Amea, Iowa).

Calcium hardness, total hardness, alkalinity, orthophosphate, sulfate, iron, and dissolved oxygen were measured in ppm (parts per million) on the D.R.E.L. Hach Water Chemistry Kit. The pH was determined with a color disc and wide range (4-14) pH indicator obtained from Hach Chemicals Co.

Temperature, dissolved oxygen content, pH, and conductivity were measured in the field. All other water parameters were analyzed in the laboratory usually on the same day of collection. When the water could not be analyzed on the same day, water samples were stored in a 5°C cold room for up to two days.

To assess the accuracy of the D.R.E.L. Hach Chemistry Kit, analytical results of each chemical character examined were compared to those derived from methods described in "Standard Methods for the Examination of Water and Waste Water" (1965). The closest agreement occurred with calcium hardness, total hardness, and iron with average differences of 5.6%, 6.2%, and 6.5%, respectively, between the two methods. Less than

5% difference occurred with sulfate at concentrations of less than 30 ppm and differences of up to 22% at concentrations greater than 30 ppm. A difference of 9% occurred between the two methods for dissolved oxygen and orthophosphate. Differences of 0 to 1 pH units occurred between the color disc and pH meter (Corning Scientific Instruments, Model 10) methods.

Coefficients of variability were determined for each parameter measured on the D.R.E.L. Hach Chemistry Kit. The following results were obtained: color - 6.3, pH - 0.3, dissolved oxygen - 0.2, calcium hardness - 3.6, total hardness - 3.7, alkalinity - 3.6, orthophosphate - 7.1, sulfate - 0.7, and iron - 1.5. The results indicated sufficient reproducibility to warrant use of the D.R.E.L. Hach Chemistry Kit.

Life History Studies

The life history of M. securis was studied on (a) seasonal (i.e. every two weeks to monthly) field collections, (b) adults maintained in the field and in the laboratory, and (c) adults cultured in the laboratory. Seven life history aspects were studied: (1) growth, (2) seasonal gonad activity, (3) number of brood sacs and larvae per brood sac, (4) sizes of litters produced, (5) number of litters produced, (6) birth period, and (7) longevity.

(a) Seasonal field collections - Seasonal field collections were made in each habitat at either two week or one month intervals. For the life history studies, random quantitative samples were taken from Britannia Bay with a standard Ekman grab (15 x 15 cm, with screen on top) and qualitative samples from the remaining habitats with an ordinary domestic sieve. Seasonal quantitative estimates of the Carp Pond

population were taken with the Ekman grab. The sizes of the samples needed to show differences between means of various life history aspects at $P \leq 0.05$ were determined from the sample size formula of Simpson et al. (1960, p 196). The specific dates of collections and the sample sizes may be found in Fig. 25, 27, 28, 30.

All clams used for life history studies were preserved immediately in 70% absolute ethanol. Since some clams prematurely released their young, individuals greater than approximately 3 mm were isolated and put into vials containing 70% ethanol. Clams to be used for histological examination were first narcotized in 10% sodium nembutal (cf van der Schalie, 1953), fixed in Bouin's fluid, and then preserved in 70% ethanol. For each clam in the seasonal field collections, lengths and heights were measured to two decimal places in millimeters with a Precision Tools and Instruments Co. Ltd., microscope micrometer, model 14.

The seasonal size-frequency distributions of M. securis in each habitat were determined by plotting the numbers of individuals of different size classes on size-frequency histograms. Thirteen size classes of 0.49 mm increments were used (i.e. size class 1 = 0 - 0.49 mm, 2 = 0.50 - 0.99 mm, 3 = 1.00 - 1.49 mm, ... 12 = 5.50 - 5.99 mm, and 13 = greater than 6.50 mm).

Seasonal gonad activities were determined from stained sections of gonads from 4 or 5 individuals of most field collections. Only specimens prepared for histological examination were used. The shells of parents and the extra-marsupial larvae were removed by hand. After dehydrating, clearing and embedding in paraffin, the soft parts were sectioned to a thickness of 8 microns. Sections were stained with Harris' haemato-

xylin and counterstained in alcoholic eosin.

The numbers of brood sacs and their litter sizes were determined for both the left and right demibranchs. Usually the embryos were so small that their numbers could not be determined accurately. Therefore, data were recorded for only fetal, prodissoconch, and extra-marsupial larvae. The lengths of all shelled larvae were also recorded. Since 99% of the extra-marsupial larvae were viable (as shown from growth studies), their numbers were taken as a valid measure of litter sizes produced by M. securis. Note that the litter size is the number of larvae per brood sac while the litter size produced is only the number of extra-marsupial larvae per litter.

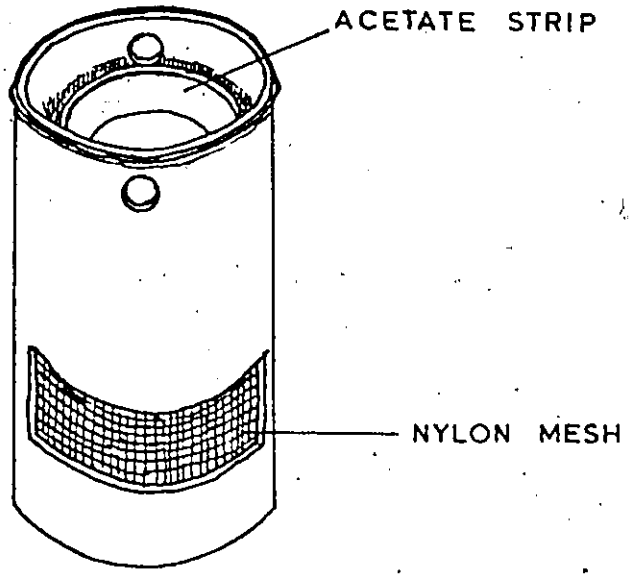
The numbers of litters produced by parents were determined by back-calculation of brood sacs; this technique was described earlier. Only parents which had completed growth were used to determine the numbers of litters produced. Parents that had completed growth could usually be identified by the formation of a black deposit on the margin of their shells.

The birth periods and longevities of M. securis for each population were determined from size-frequency histograms. These were confirmed by maintaining clams in the field.

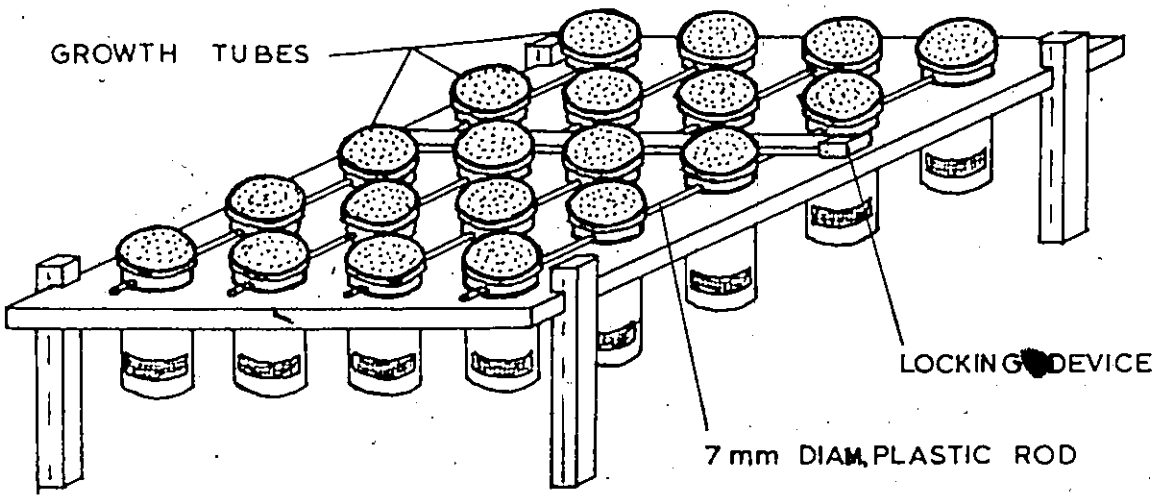
(b) Maintenance of M. securis in the lab and field - In the maintenance of adults, young are born but they are not kept alive to investigate their life cycles (Heard, 1973). Adults were maintained in the field and laboratory to complement the life history studies of seasonal field collections.

Growth tubes (Fig. 13) were used to maintain adults in the field. The growth tubes were prepared from 45 mm diam. x 70 mm ht. plastic vials

Fig. 13 Rearing apparatus used in maintaining Musculium securis in the field. (a) Enlarged view of a growth tube without the cap. (b) Assembly of 20 growth tubes.



GROWTH TUBE



RACK OF 20 GROWTH TUBES

with snap-on plastic caps. Two rectangular holes, 1 x 5 cm each, were cut out of the vial, 1 cm above the bottom (Fig. 13a). Nylon mesh with 0.30 mm openings was cut to fit the inner area of the vial. Strips of acetate, approximately 7 mm wide, were cut to fit the bottom and top inside circumferences. By softening in hot water, the acetate strips were fitted into the vial to hold the nylon mesh in place. Two, 7 mm diam. holes were drilled into the top walls of the vial and small air holes were punched into the cap.

Racks, made from 1 cm thick plexiglass sheet, were cut and drilled to hold twenty growth tubes (Fig. 13b). The legs and the locking device (Fig. 13b) were glued to the platform of the rack with glue made by dissolving plexiglass shavings in chloroform. The growth tubes were held in the rack by 7 mm plastic rods and the locking device.

For life history studies, a rack of twenty chambers was put into each of Carp Pond, Britannia Bay, and Lac Bourgeois on May 9, 1972. (Greely Pond was not investigated because it was first examined on June 6, 1972). Each growth tube contained one newborn M. securis and substrate (1 cm deep) from the habitat in which the chamber was placed. The lengths of adults were measured at approximately two week intervals until their deaths. Newborns were counted and removed as they appeared in each chamber. The numbers of litters produced by each parent were also noted.

Interpopulation transplants were performed to determine if the growth rates, sizes and numbers of litters produced, and longevity of M. securis had environmental or genetic bases. Newborn M. securis from each habitat were isolated and maintained in growth tubes in each of the other habitats (except Greely Pond) as well as its own. Lengths

of clams were measured at approximately two week intervals until their deaths. The litter sizes and the numbers of litters produced were also recorded.

Adults from Carp Pond, Britannia Bay, and Lac Bourgeois were also maintained in the laboratory. Since M. securis would grow only in the presence of tree foliage, only substrate and leaves from Carp Pond were used. "Pyrex" dishes 100 mm diam. x 50 mm ht. were used as growth dishes. Five M. securis newborns from each habitat were put into each of three dishes. Three replicates were made of each dish containing 5 M. securis, 50 g of air dry Carp Pond soil, 2 g of air-dried white elm leaves, and chlorine-free tap water. The lengths of adults were recorded at frequent intervals and the total number of young produced in each dish was recorded.

(c) Culturing of M. securis in the laboratory - Culturing involves keeping successive groups of newborns alive in order to study their life cycles (Heard, 1973). Only M. securis from Carp Pond were cultured. Culturing was also done to maintain a supply of newborns for various ecological studies.

Four generations of M. securis were studied. The first generation consisted of newborns from Carp Pond that were maintained in growth dishes for "substrate studies" (pp. 84-88). The newborns produced by clams grown on 40 g of soil were the second generation and were used in the "tree foliage experiment" (pp. 88-93). Newborns produced in dishes containing white elm leaves (of the tree foliage experiment) represented the third generation and were used in the "soils experiment" (pp. 88-95). The fourth generation consisted of newborns produced in the dishes with Carp Pond soil and black willow leaves and were used in the "road salt

experiment". By referring to each of these experiments, the life cycles of four generations of clams were determined.

Ecological Studies

Standard procedures - After trying several methods, I found that the combination of soil, leaves, and water was the best medium for maintaining M. securis in the laboratory. To standardize my technique, I followed the procedures outlined below.

With few exceptions, adults were grown in 100 mm diam. x 50 mm ht. "Pyrex" dishes containing air-dried soil, air-dried leaves, and either distilled or deionized water.

Soils were taken from the upper 15 cm of forest floors. They were then divided into "lots" according to the location and time taken. After removing the macroinvertebrates, each lot was air-dried, sieved through a 2 mm mesh sieve, tabled and the moisture content, pH, and calcium contents determined on subsamples. Moisture contents were determined to calculate the weight of air-dried soil which was equivalent to 50 g (the weight of soil used in the Pyrex dishes) of oven-dried (105°C) soil. Only air-dried soils were used in the growth experiments. A Fisher "Acumet" pH meter was used to determine the pH of a water; soil paste. Exchangeable calcium was extracted from 15 g of soil by washing the soil into Buchner funnels with 50 ml of 1N ammonium acetate at pH 7, followed by three additional aliquots of 25 ml each added successively after the previous one passed through the soil. Calcium concentration of the extracted soil solution was determined on a Jarrell-Ash Atomic Absorption Spectrophotometer, using standards prepared with the extracting solution and 1200 mg/l La as an interference inhibitor (Pawluk, 1967). A low

coefficient of variation of 2.2 for five replicate samples of Carp Pond soil indicated exceptional reproducibility.

The calcium content of leaf material was determined on preweighed samples of leaves that were ashed overnight in a muffle furnace at 580°C. Ashed samples were moistened with distilled water, dissolved in 2N HCl, diluted to known volume, and then filtered. Calcium concentration of the filtrate was determined on a Jarrell-Ash Atomic Absorption Spectrophotometer, using standards prepared with 0.25N HCl and 1200 mg/l of La as an interference inhibitor. A low coefficient of variation of 0.98 for five replicate samples of white elm leaves indicated exceptional reproducibility.

As a standard procedure for maintaining M. securis in ecological studies, "Pyrex" dishes were prepared with 50 g (oven-dry basis) of air-dried soil, 2 g of air-dried black willow or white elm leaves, and distilled or deionized water to capacity of each dish. After allowing one day for equilibration, pH and calcium hardness were determined and five, premeasured newborn M. securis were then added. The pH was determined with a pH color disc and wide range indicator and the calcium hardness with the D.R.E.L. Hach Water Chemistry Kit. At approximately two week intervals, the lengths of all adults were measured with a microscope micrometer. The number of newborn produced in each dish was recorded at the end of the experiment. An experiment ended when at least 75% (usually 100%) of the adults were dead.

Temperature - To determine the TLm (median tolerance limit) of M. securis to temperature, several size classes of adults were subjected to 26°C, 30°C, and 35°C for various intervals of time. Adults were taken from Carp Pond at 18°C and divided into size classes of lengths 1.50 - 1.99 mm, 2.00 - 2.99mm,

3.00 - 3.99 mm, 4.00 - 4.99 mm, and 5.00 - 6.00 mm. Three to five adults of each size class were put into a dish containing soil, leaves, and water from Carp Pond. Each dish was replicated six times and then floated in a water bath heated with an aquarium heater. Two other replicates were used as controls and kept at 18°C. The temperature of the water bath was slowly raised to 26°C, 30°C, and 35°C. Two dishes were removed after 60 min. at each temperature.

Adults were also grown in constant temperature rooms at 5°C, 10°C, 18°C, and 25°C. Other conditions, such as light intensity, appeared to be similar in each room but were not measured. Replicates of three dishes at each temperature were made and growth data on M. securis were recorded according to standard procedures.

Volume of soil - To determine if different amounts of soil affected the growth and natality of M. securis, newborns were grown on 20, 40, 60, 80, 100, and 120 g of Carp Pond soil and 200 ml of distilled water. Three replicates of each volume of soil were made. The growth and natalities of M. securis in each volume of soil were determined according to standard procedures.

Soil texture - To determine if soil texture was affecting the growth of M. securis in Britannia Bay, adults were grown on four size fractions of sediments. The sediment was taken from the 2 m depth of Britannia Bay where the soil particle size ranged from 0.050 mm to > 2.00 mm. After air drying, the sediment was sieved into size fractions of < 0.050 mm (silt and clay), 0.050 - 0.125 mm (fine sand), 0.125 - 0.50 mm (medium to fine sand), and 0.50 - 2.00 mm (coarse to very coarse sand). Macroinvertebrates were removed and then each size fraction was prepared according to standard procedures in replicates of three but without

the addition of leaves. After one month the newborns had not grown in any of the dishes so 2 g of elm leaves were added to each dish. Another three dishes were prepared containing only leaves, water, and newborn M. securis from Britannia Bay. Soil analyses and growth studies were performed according to standard procedures.

Tree foliage - To determine if the tree foliage in ponds of the deciduous and coniferous forest regions were affecting the growth and natality of M. securis, adults were grown on eight species of leaves characteristic of each forest region. Only freshly fallen leaves were used. The leaves tested were white elm (Ulmus americana), black willow (Salix nigra), trembling aspen (Populus tremuloides), white birch (Betula papyrifera), red maple (Acer rubrum), red oak (Quercus borealis), white spruce (Picea glauca), and white cedar (Thuja occidentalis). The taxonomic keys in White (1957) were used to identify the leaves and trees. Using soil from Carp Pond, three replicates of each leaf species were tested according to standard procedures.

Different soils - The effects of different soils were tested to complement the tree foliage studies above. Five soil samples from forest stands of willow-elm, birch-aspen, oak-maple, white spruce, and white cedar were prepared in replicates of three according to standard procedures. Leaves in the litter of each soil were used. Soils with two forest species were tested with each species of leaf litter. In addition, birch-aspen soil was tested with leaf litter from white spruce trees. The growth and natality of M. securis on each soil was determined according to standard procedures.

Sulfate - The effect of sulfate on the growth and natality of M. securis

was determined by maintaining adults in sulfate concentrations of 0, 20, 40, 60, 80, 100, 200, 300, 400, and 500 mg/l. Growth and natality of M. securis in each concentration was determined according to standard procedures.

The sulfate content of Carp Pond soil, used as a substrate in this experiment was determined by a modified turbidimetric technique of Toennies and Bakay (1953). Two solutions were required. (1) A 40% ethanol-glycol mixture was prepared by mixing 450 ml of absolute ethanol with 550 ml of dipropylene glycol. A 400 ml aliquot of this mixture was added to 500 ml of sulfate-free water. After adding 9.5 ml of HNO_3 (sp. gr. = 1.42), the mixture was cooled and diluted to 1000 ml with sulfate-free water. (2) A barium chloride solution was prepared by filtering a 1.34 M barium chloride solution through a fine sintered glass filter. A 6 ml aliquot of filtrate was diluted to 120 ml with sulfate-free water and made up to 200 ml with 40% ethanol-glycol.

A calibration curve for sulfate was prepared from standards containing 0, 10, 20, 30, 40, and 50 mg/l of sulfate. Six prestandards of 0, 20, 40, 60, 80, and 100 mg/l of sulfate were prepared using 98% sulphuric acid and sulfate-free water. A 5 ml aliquot of each was put into test tubes containing 0.2 ml of 6N HCl and 4.8 ml of $BaCl_2$ solution, thus reducing the prestandard concentrations of sulfate in half. The contents were mixed and allowed to stand for 15 minutes. The O.D. (optical density) was measured at 420 mμ in an automatic Coleman Model 10 Spectrophotometer using the 0 mg/l standard as a blank.

Five, 500 mg samples of dried soil were added to 25 ml test tubes containing 2.5 ml of sulfate-free water and 2.5 ml of 40% ethanol-glycol.

The mixture was stirred, allowed to stand overnight, decolorized with activated charcoal, allowed to stand again for at least 12 hours, and then filtered. The filtrate was diluted to 5 ml with 40% ethanol-glycol and tested for sulfate by the procedure described for obtaining the calibration curve. Sulfate concentration was expressed in mg/l.

Road salts - To determine the effect of road salts on the growth and natality of M. securis, newborns were grown in various concentrations of rock salt, calcium chloride ($CaCl_2$), and sodium chloride (NaCl). The rock salt was obtained from the storage sheds of the Ontario Department of Highways. The chemical composition (by weight) of the rock salt as specified by the Ministry of Transportation and Communications of Ontario (pers. comm.) had a moisture content of less than 0.5%, a sodium chloride content of more than 96.0%, and insoluble matter of less than 4.0%. Concentrations of 200, 400, 600, 800, and 1000 mg/l of each salt were made using deionized water. Growth dishes were prepared with each salt concentration according to standard procedures. Three control dishes (i.e. soil, leaves, and deionized water) were also prepared. Standard procedures were used to determine the growth and natality of M. securis in each salt concentration.

Pollution studies - Growth tubes were used to maintain M. securis below industrial and municipal sewage outfalls. Twenty growth chambers, each containing one newborn M. securis from Britannia Bay, were placed at each distance of 50 m, 330 m, 700 m, and 1000 m below the outfalls (Mackie, 1971) of a pulp and paper plant. Another twenty chambers were placed immediately upstream of the outfalls as controls. Twenty tubes were also placed 1.6 km below a slaughter house and several raw sewage outfalls; growth tubes

placed in Britannia Bay were used as controls. All growth tubes were placed in less than one meter of water. The growth in length of M. securis was measured at approximately two week intervals. The number of young produced by parents in each tube was recorded at the end of the experiment.

Population densities - To show the effects of different densities on the growth and natality of M. securis and to determine the holding capacity of the growth dishes, newborns were maintained at densities of 5, 10, 20, 30, and 40 per dish. Dishes were prepared in replicates of three for each density according to standard procedures. It was beyond the scope of this study to isolate the factors for which M. securis individuals were competing. Growth and natality data were recorded according to standard procedures.

Interspecific competition - Field experiments were carried out to determine if interspecific competition was occurring between M. securis and M. transversum in the shore and deep water zones of Britannia Bay. Growth tubes were used to maintain the species. The density of adults used in the tubes was chosen on the basis that M. transversum occurred in densities of up to $1500/m^2$ in the shore zones of Britannia Bay. Since clams were frequently found on the inside walls of the growth tubes, the surface of a tube was taken to be the total inside area (i.e. 123.5 cm^2). Therefore, a total of 20 clams was added to each growth chamber to make the density of clams approximately equal to that in the natural habitat. The ratios of M. transversum to M. securis used were 19:1, 18:2, 16:4, 10:10, 4:16, 2:18, and 1:19. Two additional tubes were prepared as controls with 20 M. transversum in one and 20 M. securis in the other. To determine the effect of smaller densities, ratios of 9:1, and 1:9 were prepared

with their controls of 10 M. transversum and 10 M. securis in four separate tubes. Replicates of six were made of each combination of clams, three of which were placed in the 0.3 m depth and the other three in the 3 m depth. In addition, five newborns of each species were isolated into growth chambers at each depth. The growth in length of each individual and the number of young produced in each growth tube was recorded at approximately two week intervals.

Estivation of Musculium securis - Fifty core samples were taken from Carp Pond in September, 1971 to determine the correlation between the distribution of M. securis and the magnitudes of various edaphic factors. Since M. securis estivated in the top 1 to 8 cm of soil, only cores of 8 cm in depth were taken. The number of M. securis, the pH, and the moisture content were determined for each core sample. To obtain a sufficient sample size, some cores were pooled for determinations of C.E.C. (cation exchange capacity) and organic matter content. The pH of soil paste, moisture content, C.E.C., and organic matter content of soil were analyzed according to procedures in Moodie and Koehler (1973).

Food Habits

The food habits of several size classes of adults were determined for the four populations of M. securis. Adults from the life history studies were used. Usually the intestinal contents were examined because the stomachs were often empty. The division of adults into size classes was based on the differences in the quality of food in the intestines. The genera of algae in the intestines were identified by Dr. R.K.S. Lee of the National Museums of Canada, Ottawa, Ontario.

The food habits of M. securis in the laboratory growth dishes

were also studied. Foliar leachate was prepared by allowing 12 g of white elm leaves to decompose for two months in each of four beakers containing 900 ml of distilled water. Two months was chosen as the time interval because it took M. securis this period of time to grow and reproduce. After two months had elapsed, the volume in each beaker was brought up to 1200 ml with distilled water. The leachate was then either filtered through No. 1 Watman Filter Paper, autoclaved, or left unaltered. Aliquots of 300 ml of the treated leachates were added to 50 g of either autoclaved or untreated Carp Pond soil in the following manner: (A) autoclaved soil with (1) unaltered leachate and leaves, (2) unaltered leachate less leaves, (3) filtered leachate, and (4) filtered and autoclaved leachate; (B) untreated soil with (1) unaltered leachate and leaves, (2) unaltered leachate less leaves, (3) filtered leachate, and (4) filtered and autoclaved leachate. Three replicates of each combination of leachate and soil were made. Five M. securis were added to each dish and their growth was measured at approximately two week intervals. Water samples from each dish were examined periodically for microorganisms. Some adults were sacrificed near the end of the experiment for analyses of intestinal contents.

Statistical Procedures

Dr. S. Walters of the University of Ottawa, was consulted for the statistical treatment of data. Since all growth curves of M. securis reached an asymptotic value on approximately the 70th day, asymptotic regression formulae were fitted to the growth data. The modified exponential, $Y = A + BR^X$, gave the best fit to hyperbolic growth curves but transgeneration of this regression to the logistic equation, $1/Y = A + BR^X$, gave the best fit to sigmoid growth curves. The coefficient, A,

is the asymptotic value or the maximum length (mm) attained, B is the distance between the asymptotic value and the value of Y when X = 0, and R is the ratio of successive differences along the curve.

The logistic regression is merely a modified exponential in terms of the reciprocals of the Y values. That is, A in the logistic expression equals 1/A of the modified exponential (when X = 0 and B = 0). Also, B of the logistic equation equals 1/Y - 1/A of the modified exponential (when X = 0). Therefore, to compare coefficients between the two curves it is necessary to make the appropriate conversions. A Fortran computer program was used to calculate the asymptotic regressions of M. securis in all growth experiments. The program is called "BMD 06R" and is described by Dixon (1971, pp. 297-311).

Results of the ecological experiments are reported in figures and tables. There were no significant differences ($P > 0.05$) in the growth of M. securis between replicates, as determined by the Student's t test (Simpson et al, 1960, p. 176) on A and B of the regressions. Therefore, the growth curves of M. securis are plotted as average observed growth in length within replicated dishes. Significant differences between mean asymptotic values (A) and between growth increments since birth (B) of different growth curves are presented in tables. However, as indicated above, it was necessary to make the appropriate inversions of the coefficients of the logistic expression to allow a comparison of these values with those in the modified exponential. Therefore, the A and B values of the logistic expression $1/Y = A + BR^X$, were re-inverted so that $A' = 1/A$ (X = 0, B = 0) and $B' = 1/(1/Y - A)$. The inversions are indicated in the tables with the expression $\hat{1/Y'} = A' + B'R^X$.

Also appearing in the tables are the mean natalities of M. securis

in replicated growth dishes (and growth tubes). All means side-scored by the same line are not significantly different at P = 0.05.

RESULTS

Physics and Chemistry of Water

The four habitats differ widely with respect to water quality. Generally the magnitudes of the different physical and chemical parameters are larger and show greater seasonal fluctuations in the temporary and permanent ponds than in the river habitat. Some of these fluctuations can be attributed to differences in the average yearly rainfall. The Weather Bureau of Ottawa recorded 23.45 in. (59.6 cm) in 1970, 21.28 in. (54.1 cm) in 1971, and 33.61 in. (85.4 cm) of rainfall in 1972. In 1970 and 1971 Carp Pond dried up by the end of July but in 1972 water remained in the pond all year as a result of the large amount of rainfall.

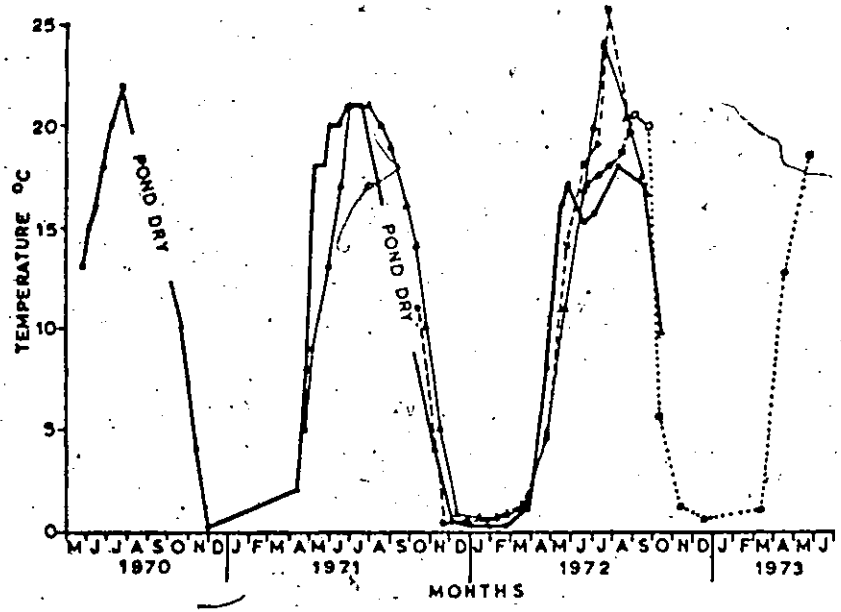
Ice had melted from the temporary ponds by early May in all three years of study, from Lac Bourgeois by mid-May in 1971 and 1972, and from Britannia Bay by late May in all three years of study. This resulted in approximately a two week lag in the rate of temperature increase in Lac Bourgeois and a four week lag in Britannia Bay compared to Carp Pond and Greely Pond (Fig. 14). Also, the large amount of rainfall in 1972 probably accounts for the lower maximum temperatures in Carp Pond than in previous years of study.

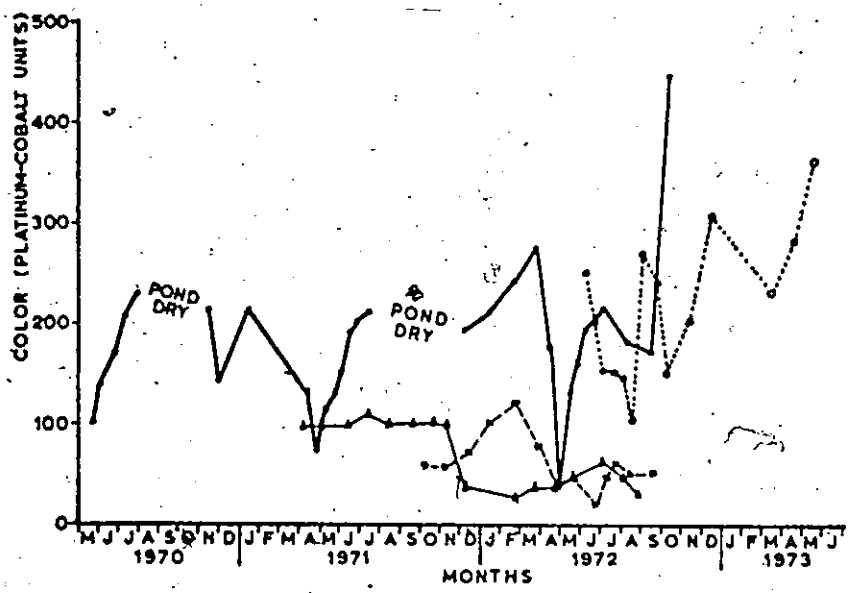
Large amounts of organic debris, mainly leaf litter, cause highly colored waters in the temporary ponds (Fig. 15). Increasing color of the water in Carp Pond and Greely Pond coincides with decreasing dilution as the evaporation of water progresses through the summer months and with leaf-fall in the autumn (October 1972, Carp Pond, Fig. 16). Conversely,

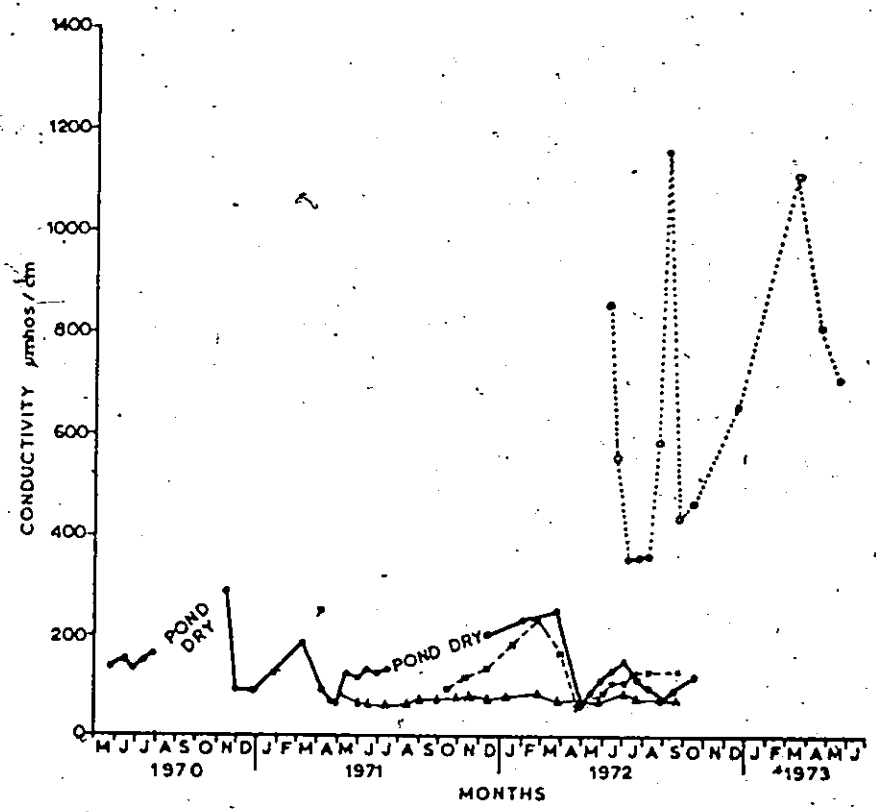
Fig. 14 Seasonal fluctuations in temperature in Carp Pond (—— ●), Greely Pond (..... o), Britannia Bay (——▲), and Lac Bourgeois (—— *).

Fig. 15 Seasonal fluctuations in color of water in Carp Pond (—— ●), Greely Pond (····· o), Britannia Bay (——▲), and Lac Bourgeois (—— *).

Fig. 16 Seasonal fluctuations in conductivity in Carp Pond (—— ●), Greely Pond (····· o), Britannia Bay (——▲), and Lac Bourgeois (—— *).


TEMPERATURE °C
25
20
15
10
5
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


COLOR (PLATINUM-COBALT UNITS)
500
400
300
200
100
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


CONDUCTIVITY µmhos/cm
1400
1200
1000
800
600
400
200
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS

decreasing color of the water is correlated with increasing dilution from snow-melt and from rainfall.

Unusually large conductivities occur in Greely Pond (Fig. 16). This can probably be attributed to road salts which are either washed into the pond from the road after a heavy rainfall or are distributed into the pond during salting operations. Calcium chloride is used on the roads during the summer months (to keep dust down) and probably sodium chloride during the winter months.

Using the technique described on page 33, it was found that the total alkalinity in each habitat is due mostly to bicarbonates. The seasonal fluctuations in total alkalinity (Fig. 17) are, therefore, related to fluctuations in bicarbonate ions and hence fluctuations in the concentrations of carbon dioxide. At high concentrations of carbon dioxide there is a corresponding rise in the hydrogen ion concentration and in the concentrations of carbonate and bicarbonate ions (Hutchinson, 1957). Since the concentration of carbon dioxide is probably inversely related to that of dissolved oxygen (Fig. 18), the total alkalinity is also inversely related to oxygen (cf. Fig. 17 and 18). The concentration of carbonate and bicarbonate ions is a measure of hardness so that both calcium hardness (Fig. 19) and total hardness (Fig. 20) are directly related to the total alkalinity in each habitat. High concentrations of of calcium chloride from road salts probably account for the high total alkalinity (Fig. 17), calcium hardness (Fig. 19), and total hardness (Fig. 20) values in Greely Pond. Greene (1971) has shown that pond soils absorb calcium from pond water until the requirement for calcium carbonate in the soil is "satisfied". This may explain the lower calcium hardness

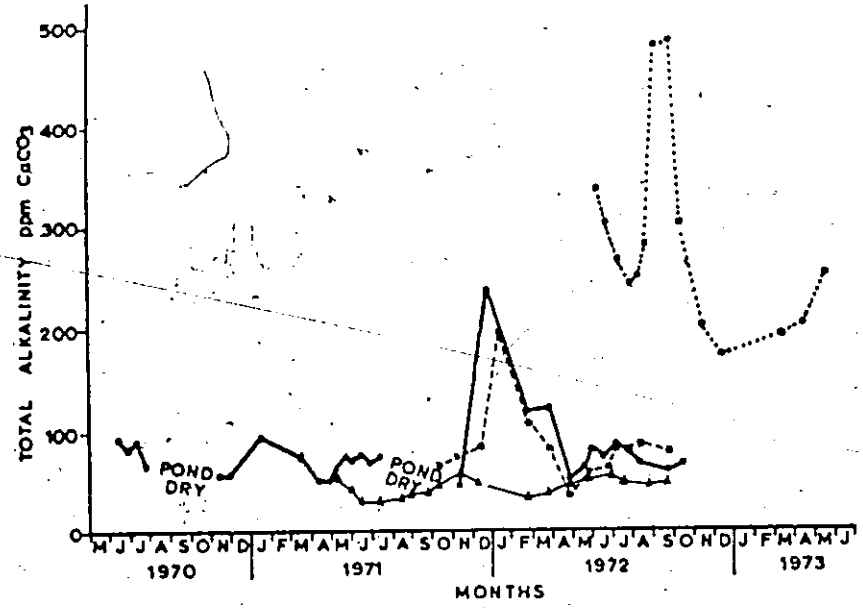
Fig. 17 Seasonal fluctuations in total alkalinity in Carp Pond (——●), Greely Pond (···· o), Britannia Bay (——▲), and Lac Bourgeois (—— *).

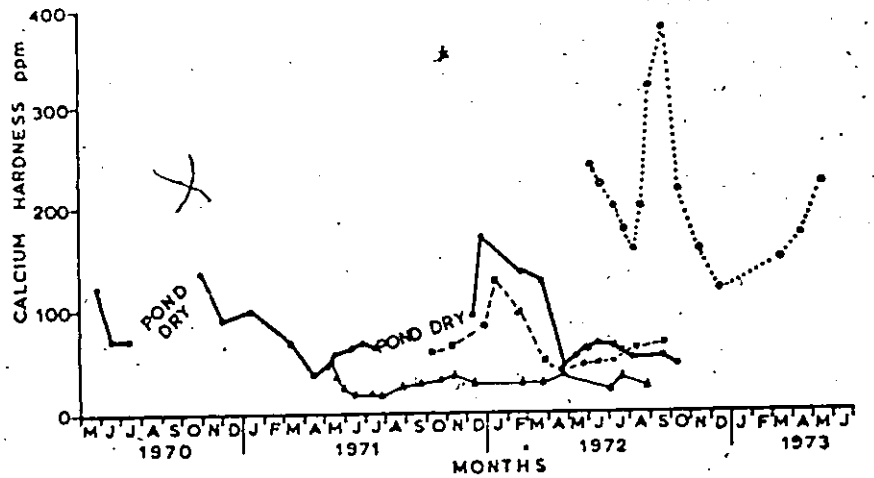
Fig. 19 Seasonal fluctuations in calcium hardness in Carp Pond (——●), Greely Pond (···· o), Britannia Bay (——▲), and Lac Bourgeois (—— *).

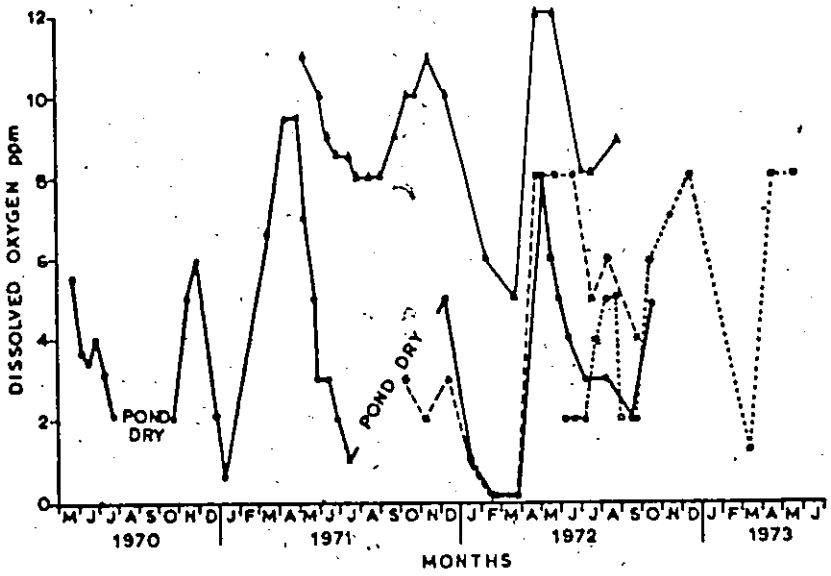
53i

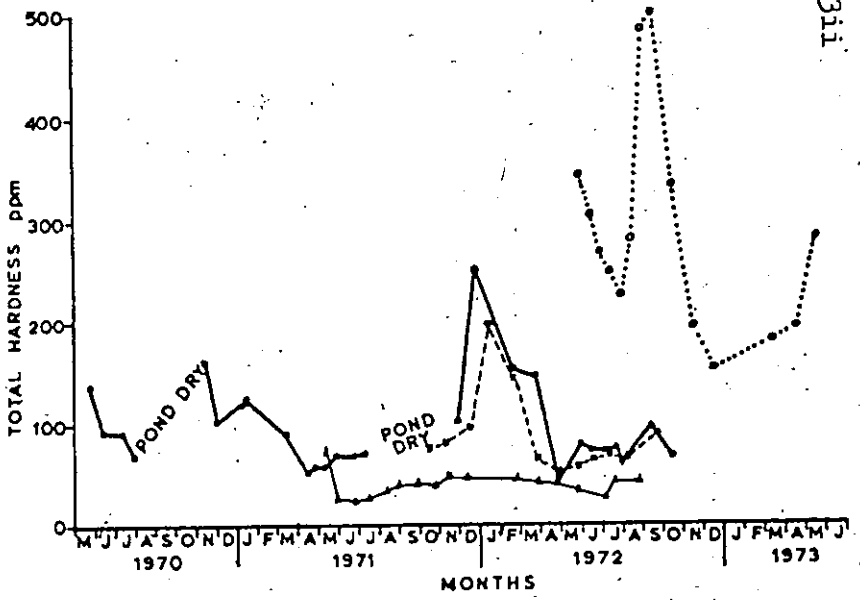
Fig. 18 Seasonal fluctuations in dissolved oxygen in Carp Pond (——●), Greely Pond (···· o), Britannia Bay (——▲), and Lac Bourgeois (—— *).

Fig. 20 Seasonal fluctuations in total hardness in Carp Pond (——●), Greely Pond (···· o), Britannia Bay (——▲), and Lac Bourgeois (—— *).


TOTAL ALKALINITY ppm CaCO3
500
400
300
200
100
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


CALCIUM HARDNESS ppm
400
300
200
100
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


DISSOLVED OXYGEN ppm
12
10
8
6
4
2
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


TOTAL HARDNESS ppm
500
400
300
200
100
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS

values (and hence total hardness) during the summer months in the temporary ponds.

The solubility of oxygen increases with decreasing temperatures until the winter months when biological and chemical processes under ice-cover deplete or lower the dissolved oxygen levels (cf. Fig. 14 and 18). Britannia Bay is at least 80% saturated with oxygen during all seasons except the winter when oxygen saturation falls to approximately 35%. The remaining habitats are 55-70% saturated with oxygen in the spring but usually have less than 33% in the summer months.

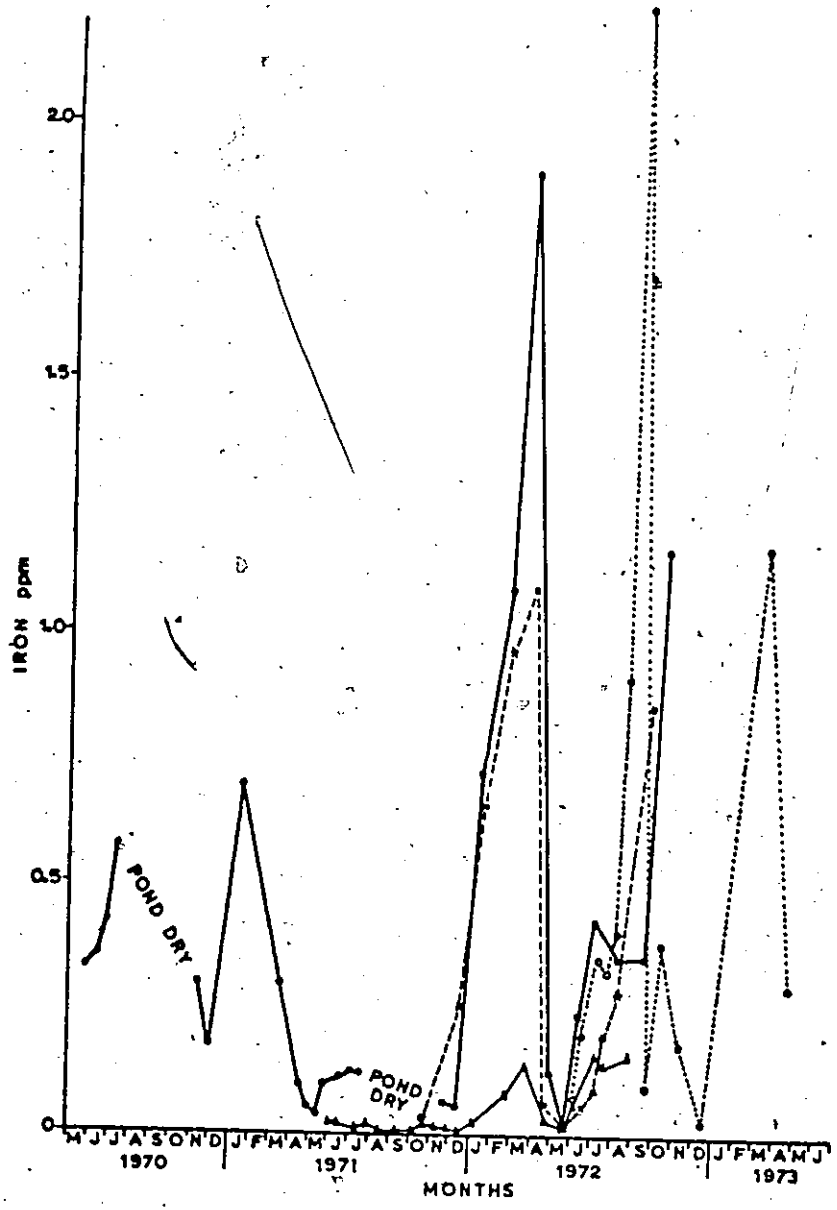
Iron (Fig. 21) and orthophosphate (Fig. 22) become increasingly soluble with decreasing oxygen tensions (cf. Fig. 21, 22, and 18). The high concentrations of iron probably also contribute to the total hardness values in the pond habitats. Concentrations of both iron and orthophosphate are lowest in Britannia Bay.

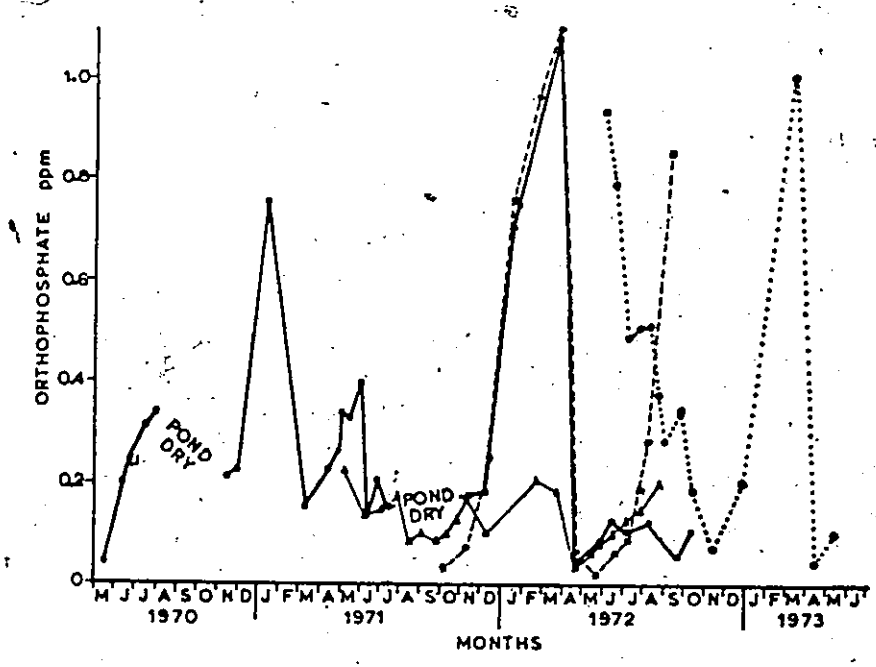
Sulfate becomes increasingly more soluble with increasing oxygen tensions in all habitats (cf. Fig. 23 and 18). There is an inverse correlation with total alkalinity. Sulfate concentrations are high in the spring and fall and low in summer and winter while total alkalinity is low in the spring and fall and high in the summer and winter (cf. Fig. 23 and 17). Mann (1958) and Tucker (1958) in studies of British ponds found the same phenomena; they attribute decreasing sulfate content to the reduction of sulfate to sulfide as ferrous sulfide. Decreasing alkalinity is attributed partly to the action of sulfuric acid when sulfide is reoxidized, converting a portion of the calcium bicarbonate to calcium sulfate.

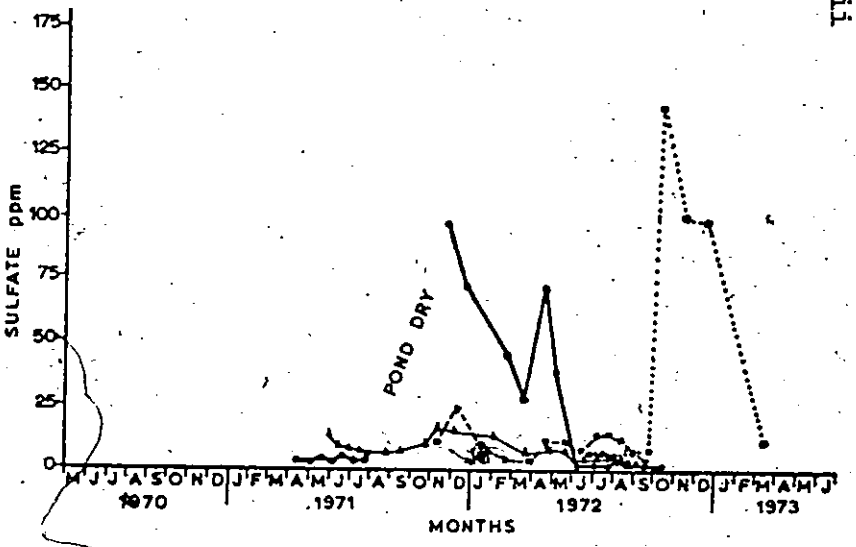
Fig. 21 Seasonal fluctuations in iron content in Carp Pond (———●), Greely Pond (····· o), Britannia Bay (———▲), and Lac Bourgeois (—— *).

Fig. 22 Seasonal fluctuations in orthophosphate content in Carp Pond (———●), Greely Pond (····· o), Britannia Bay (———▲), and Lac Bourgeois (—— *).

Fig. 23 Seasonal fluctuations in sulfate content in Carp Pond (———●), Greely Pond (····· o), Britannia Bay (———▲), and Lac Bourgeois (—— *).


IRON ppm
2.0
1.5
1.0
0.5
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


ORTHOPHOSPHATE ppm
1.0
0.8
0.6
0.4
0.2
0
POND DRY
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS


SULFATE ppm
175
150
125
100
75
50
25
0
POND DRY
M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1970
1971
1972
1973
MONTHS

Life History

Growth

The relationship between growth in length (of shell) and dry weight of M. securis is shown in Fig. 24. Shell weight accounts for over 90% of the total weight.

The seasonal size-frequency distributions of M. securis in Carp Pond for the three years of study are shown in Fig. 25. Parents in the first collection (May 25, 1970) were arbitrarily designated the P1 (first parental) generation. Larvae contained within these parents were called the F1 (first fetal) generation. The sample of May 25 was unimodal and the shift of this mode was easy to follow in the frequency plots throughout the year. Parents of size class 9 were present in late May but were not gravid until mid-June indicating that gravidity was a function of both incubation time and size of parent.

A P2 generation (size class 4, Fig. 25) appeared in early July giving the sample a bimodal distribution. Bimodality occurred only in the month of July with the P1 generation dying in late July or early August when the pond was drying up. Only newborns (i.e. size classes 3, 4, and 5) estivated during the summer months. Water appeared in the pond again by November 15 and the newborns hibernated until early May, 1971 when growth ensued. Similar events occurred in 1971 as in 1970 with a P3 generation appearing in late June. The spring and summer growth of M. securis is exemplified by plotting modes of the frequency plots in 1971 (Fig. 26).

In 1972 a P4 generation appeared in mid-July as in previous years but the pond did not dry up and the bimodal distribution persisted until

Fig. 24 Relation between total weight and shell length ($Y = 1.86 - 1.63X + 0.47X^2$, $N = 80$, $r = 0.91$) and shell weight only and shell length ($Y = 1.96 - 1.57X + 0.42X^2$, $N = 80$, $r = 0.97$) of Musculium securis.

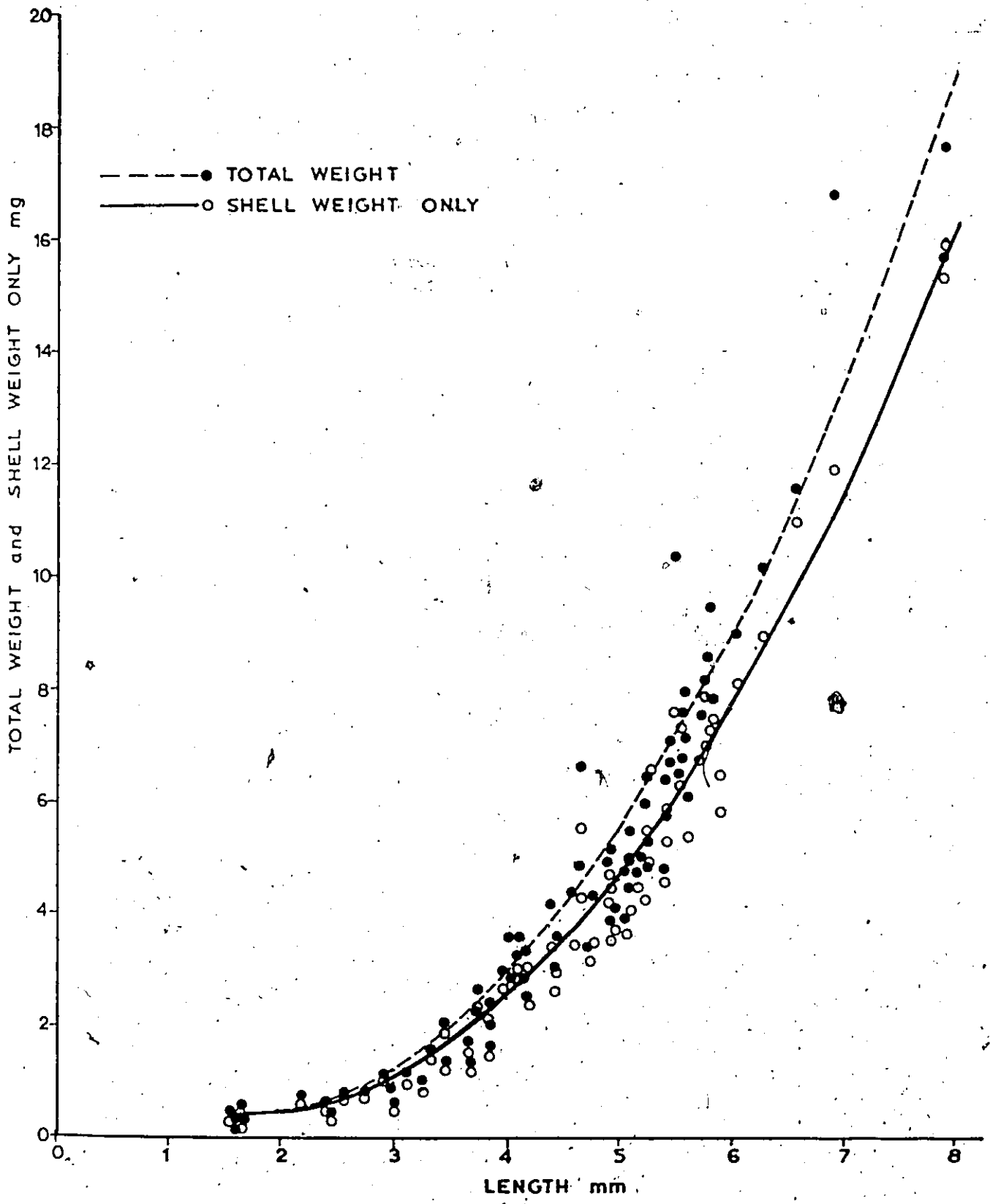
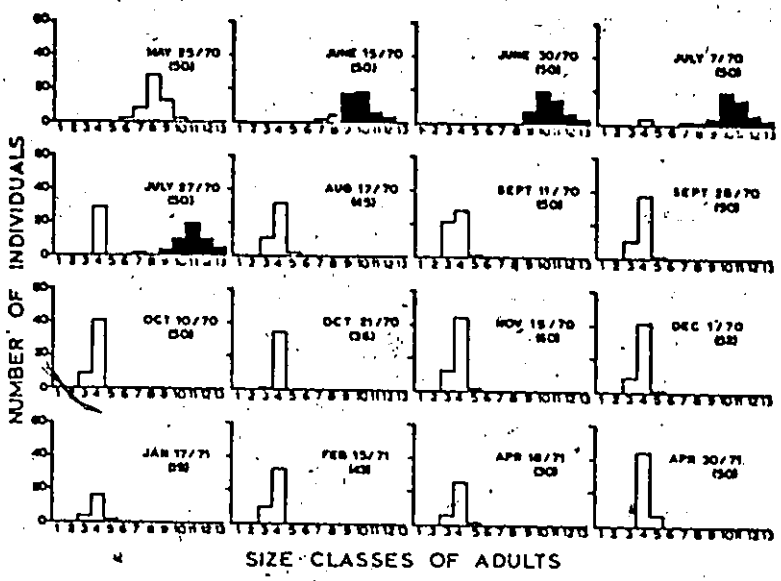
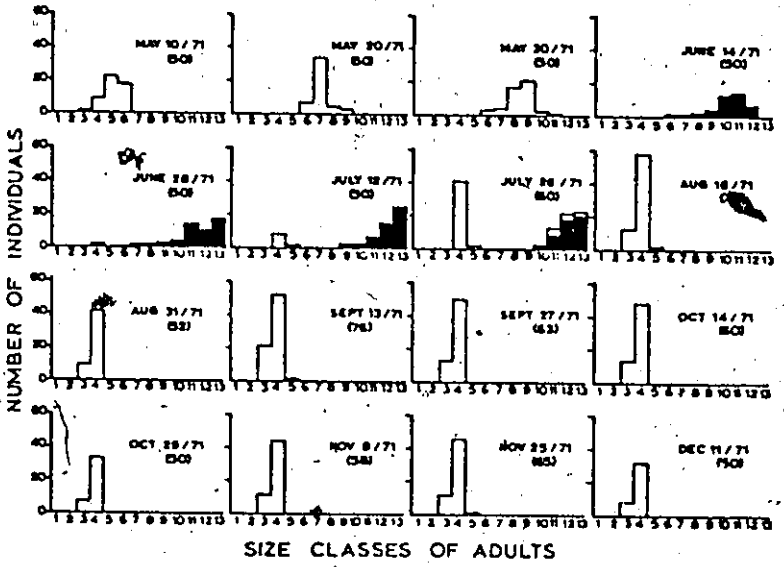

TOTAL WEIGHT
SHELL WEIGHT ONLY
TOTAL WEIGHT and SHELL WEIGHT ONLY mg
LENGTH mm
0
2
4
6
8
10
12
14
16
18
20
1
3
5
7

Fig. 25 Seasonal size-frequency distribution of Musculium securis in Carp Pond for three years of study. Size classes 1-12 represent length increments of 0.50 mm; size class 13 is lengths greater than 6.50 mm. Shaded areas indicate gravid adults.


NUMBER OF INDIVIDUALS
SIZE CLASSES OF ADULTS


NUMBER OF INDIVIDUALS
SIZE CLASSES OF ADULTS

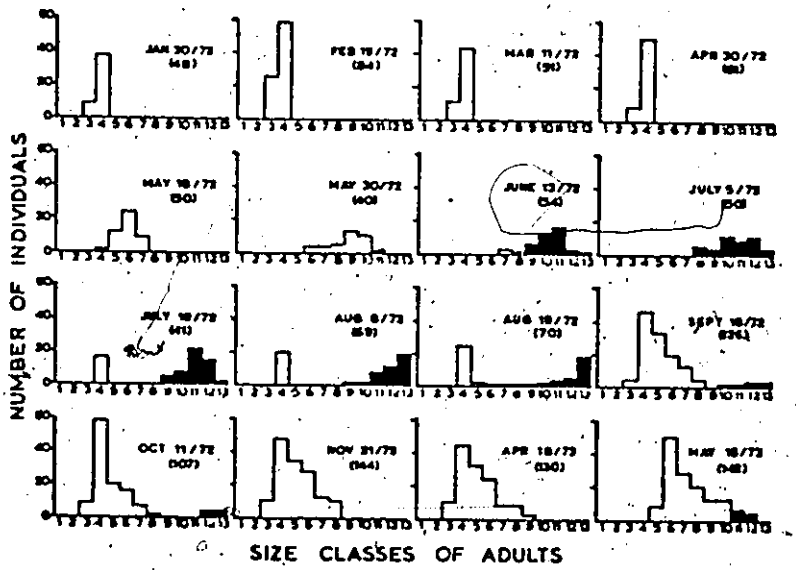
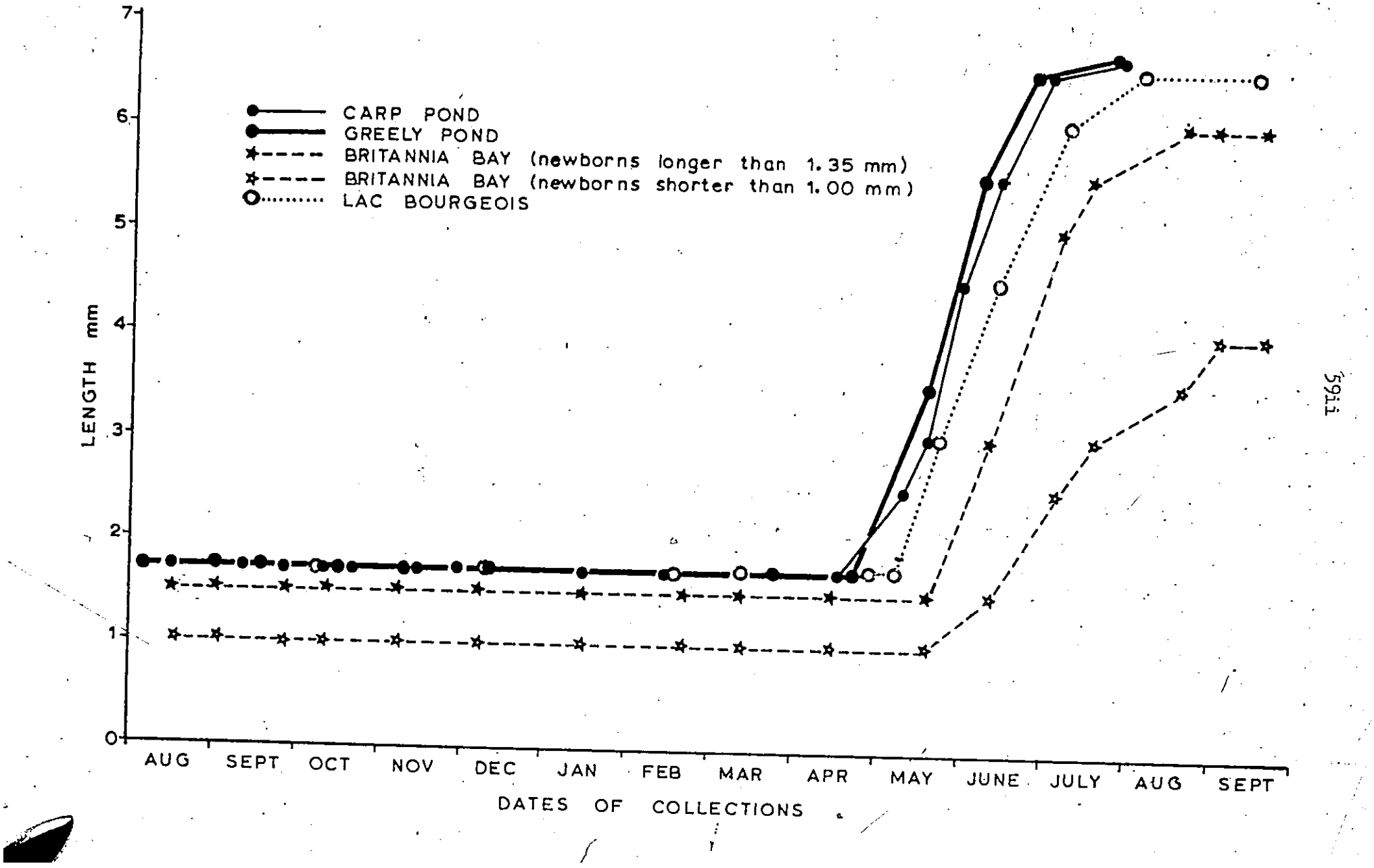

NUMBER OF INDIVIDUALS
SIZE CLASSES OF ADULTS

Fig. 26 Frequency plots of modes showing growth of Musculium securis for one year in Carp Pond (1971-72), Greely Pond (1972-73), Britannia Bay (1971-72), and Lac Bourgeois (1971-72).


CARP POND
GREELY POND
BRITANNIA BAY (newborns longer than 1.35 mm)
BRITANNIA BAY (newborns shorter than 1.00 mm)
LAC BOURGEOIS
LENGTH mm
0
1
2
3
4
5
6
7
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
DATES OF COLLECTIONS

mid-October. Moreover, growth of the P4 generation began in late August so that the hibernating generation consisted of several size classes of adults.

The seasonal size-frequency distribution of M. securis in Greely Pond (Fig. 27) is similar to that in Carp Pond in 1972-1973. Newborns dominate the hibernating generation but several other size classes are also present. The spring and summer growth of M. securis in Greely Pond appears to be almost identical to that in Carp Pond (Fig. 27).

Samples collected from Britannia Bay in 1970 exhibited a bimodal distribution of size classes for the P1 generation. This bimodal character is more clearly seen in the P2 generation of 1971 samples (Fig. 28) and indicates the presence of two generations. However, on the basis of calyculism, only one generation was present until June 24 but the population consisted of slow-growing (mode a) and fast-growing (mode A) individuals. Measurements of the lengths of calyculae showed that the newborns born at lengths greater than 1.35 mm had growth rates similar to those of other populations while those born at less than 1.00 mm appeared to have much slower growth rates. This is more clearly revealed by plotting modes (Fig. 26) of the seasonal size-frequency distributions. The four week lag in growth of M. securis in Britannia Bay can probably be attributed to the lag in temperature increase (Fig. 13).

A trimodal distribution with modes a, A, and B occurred in samples collected on July 15, July 29, and August 17 (Fig. 28). The third mode (B) represents the P3 generation. Mode B was also composed of slow-growing (mode b) and fast-growing (mode B) individuals which are clearly seen in the sample of July 5, 1972. The fast-growing adults were not

Fig. 27 Seasonal size-frequency distribution of Musculium securis in Greely Pond for one year of study. Size classes 1-12 represent length increments of 0.50 mm; size class 13 is lengths greater than 6.50 mm. Shaded areas indicate gravid adults.

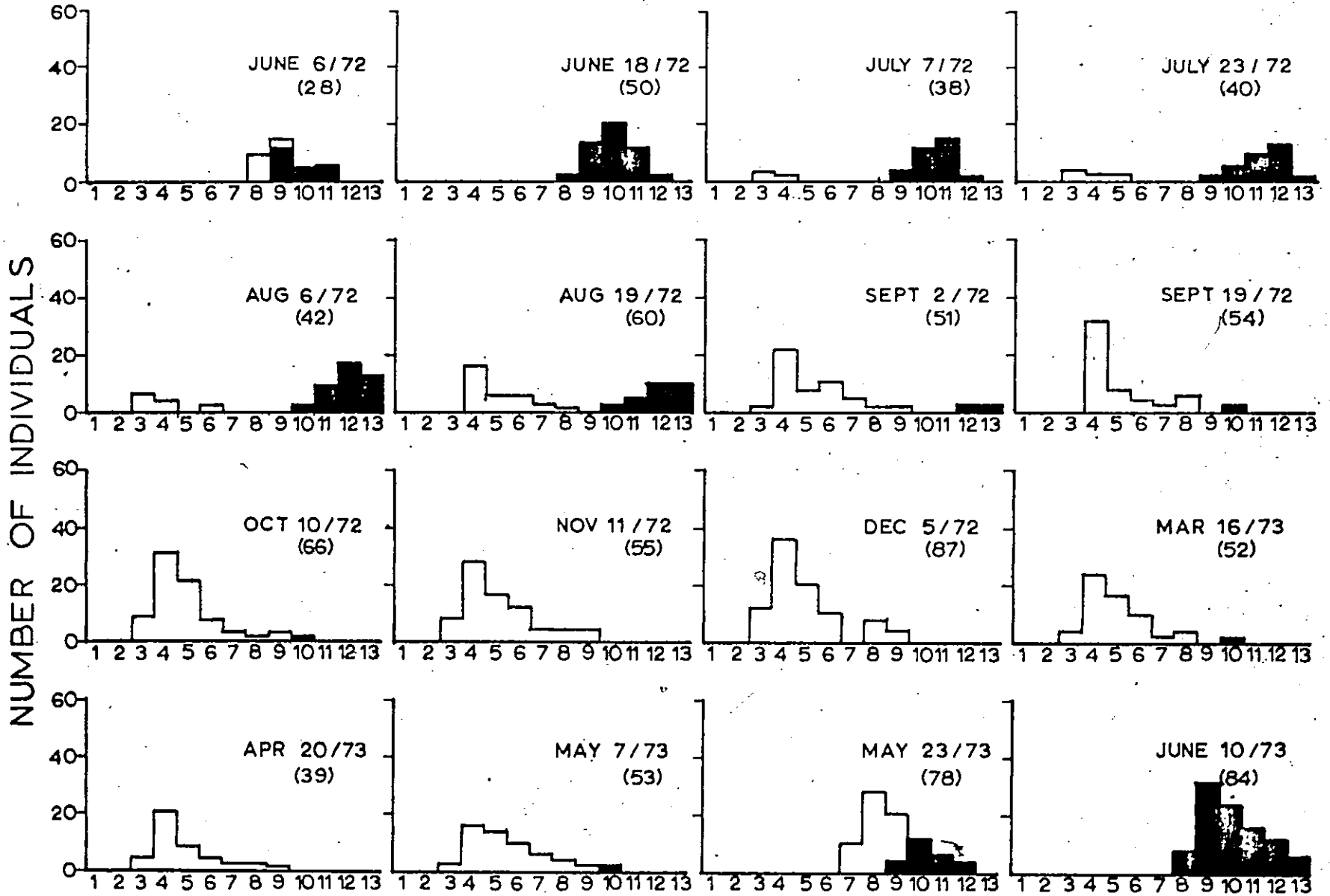
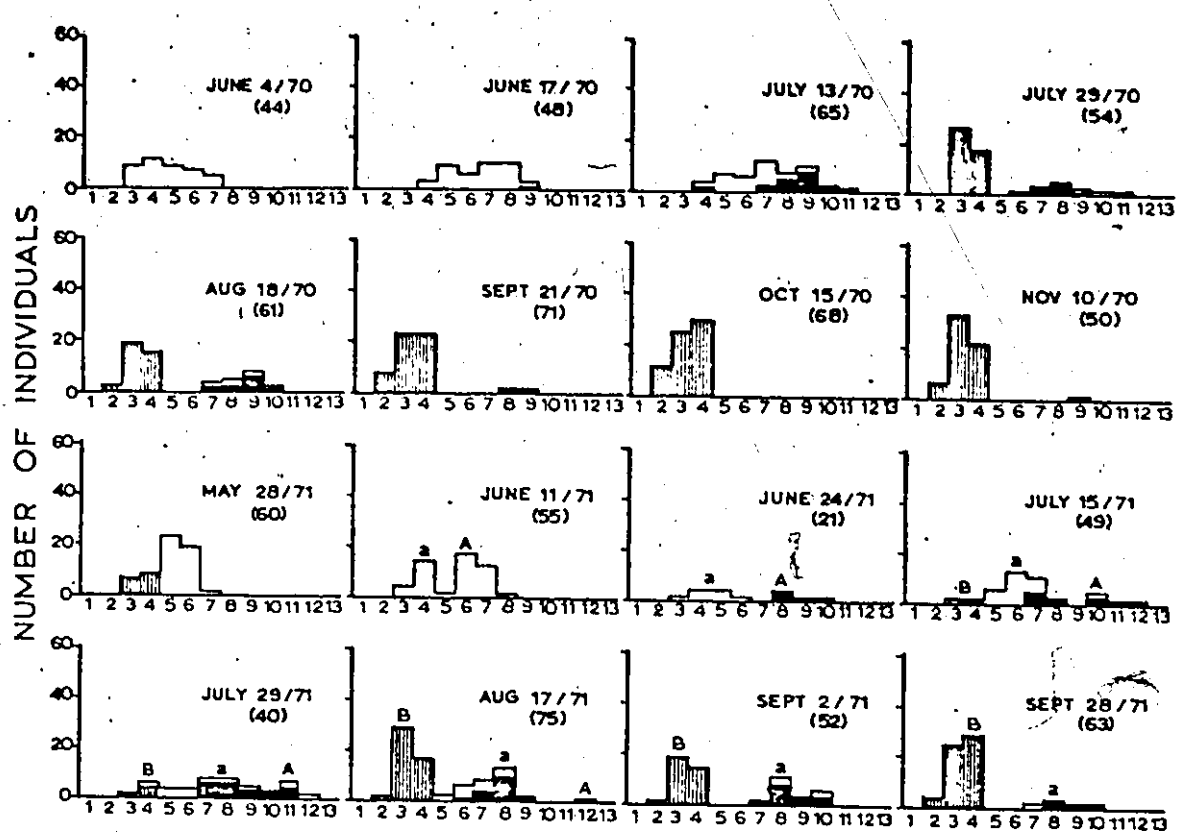
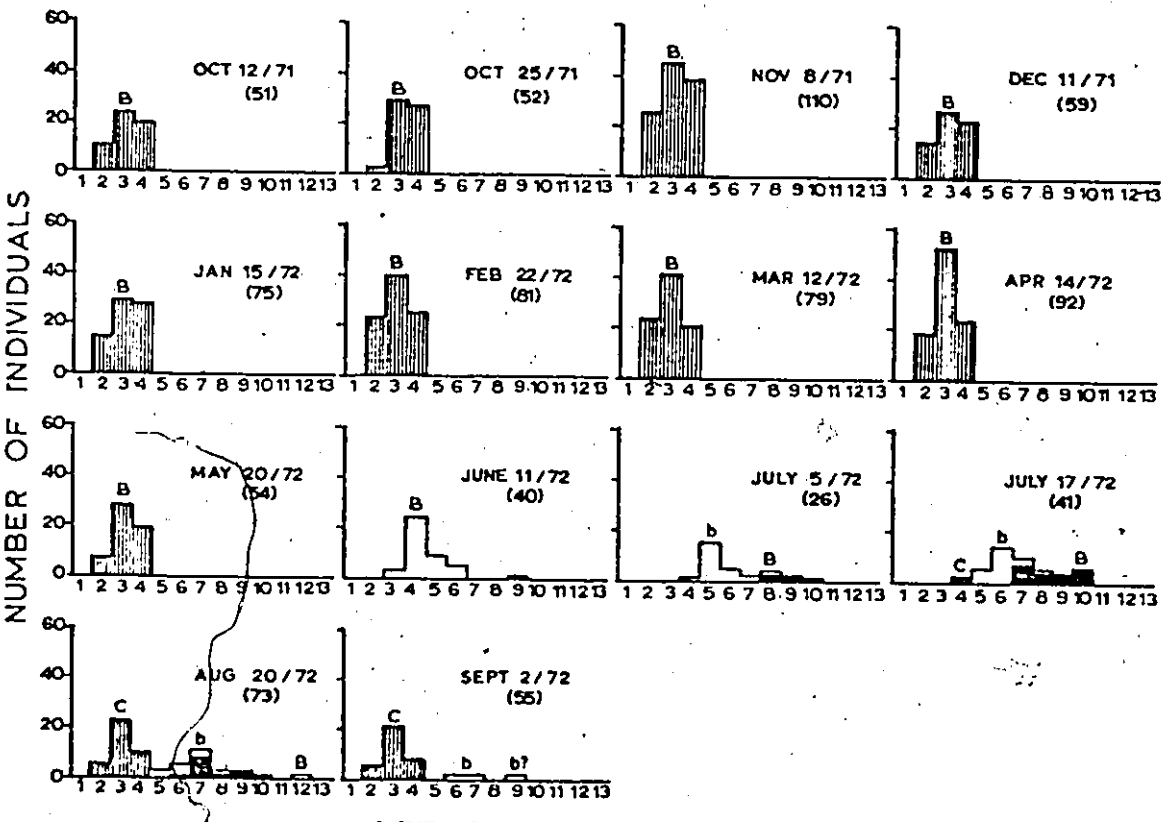

JUNE 6/72 (28)
JUNE 18/72 (50)
JULY 7/72 (38)
JULY 23/72 (40)
AUG 6/72 (42)
AUG 19/72 (60)
SEPT 2/72 (51)
SEPT 19/72 (54)
OCT 10/72 (66)
NOV 11/72 (55)
DEC 5/72 (87)
MAR 16/73 (52)
APR 20/73 (39)
MAY 7/73 (53)
MAY 23/73 (78)
JUNE 10/73 (84)
NUMBER OF INDIVIDUALS
SIZE CLASSES OF ADULTS

Fig. 28 Seasonal size-frequency distribution of Musculium securis in Britannia Bay for three years of study. Size classes 1-12 represent length increments of 0.50 mm; size class 13 is lengths greater than 6.50 mm. Bars with vertical lines indicate newborns. Shaded areas indicate gravid adults.


JUNE 4/70 (44)
JUNE 17/70 (48)
JULY 13/70 (65)
JULY 29/70 (54)
AUG 18/70 (61)
SEPT 21/70 (71)
OCT 15/70 (68)
NOV 10/70 (50)
MAY 28/71 (60)
JUNE 11/71 (55)
JUNE 24/71 (21)
JULY 15/71 (49)
JULY 29/71 (40)
AUG 17/71 (75)
SEPT 2/71 (52)
SEPT 28/71 (63)
NUMBER OF INDIVIDUALS
SIZE CLASSES OF ADULTS


OCT 12/71 (51)
OCT 25/71 (52)
NOV 8/71 (110)
DEC 11/71 (59)
JAN 15/72 (75)
FEB 22/72 (81)
MAR 12/72 (79)
APR 14/72 (92)
MAY 20/72 (54)
JUNE 11/72 (40)
JULY 5/72 (26)
JULY 17/72 (41)
AUG 20/72 (73)
SEPT 2/72 (55)
NUMBER OF INDIVIDUALS
SIZE CLASSES OF ADULTS

gravid until they attained lengths of 3.50-4.00 mm while slow-growing adults were gravid at lengths of 2.50-3.00 mm. Mode A had disappeared by September so that only slow-growing individuals of the P2 generation and newborns of the P3 generation were present. However, some members of the P3 generation had grown to maturity by late September, as indicated by the absence of calyculae. The hibernating generation thus consisted of newborns of the P3 generation and also of a P4 generation.

These results were confirmed by the maintenance of adults in growth tubes in Britannia Bay. Newborns from the P2 generation with calyculae longer than 1.35 mm had grown rapidly (Fig. 29) but some had produced young precociously early in July. These precocious young had grown to maturity by September to produce another generation. The newborns of this new generation were significantly smaller ($P < 0.05$) in lengths than those of the original (P2) generation. It, therefore, appears that newborns of lengths less than 1.00 mm were from uncalyculate parents. The growth rates of adults with calyculae of lengths less than 1.25 mm in the growth tubes were significantly slower ($P < 0.05$) than those of lengths greater than 1.35 mm and did not produce young.

A bimodal size-frequency distribution (modes A and B, Fig. 30) was characteristic of the fall and winter populations in Lac Bourgeois. The relative proportions of newborns, calyculate, uncalyculate, and annulated adults in the samples are shown in Fig. 31. The fall and winter populations must have been born in the summer months of 1971 since calyculae were absent on the adults. Spring and summer populations of 1972 consisted of calyculate adults that were born in the fall and/or winter of 1971, and of uncalyculate and uncalyculate-annulated adults that were born in the

Fig. 29 Growth of Musculium securis from Carp Pond, Britannia Bay, and Lac Bourgeois in growth tubes placed in respective habitats. Day 0 = May 9, 1972.

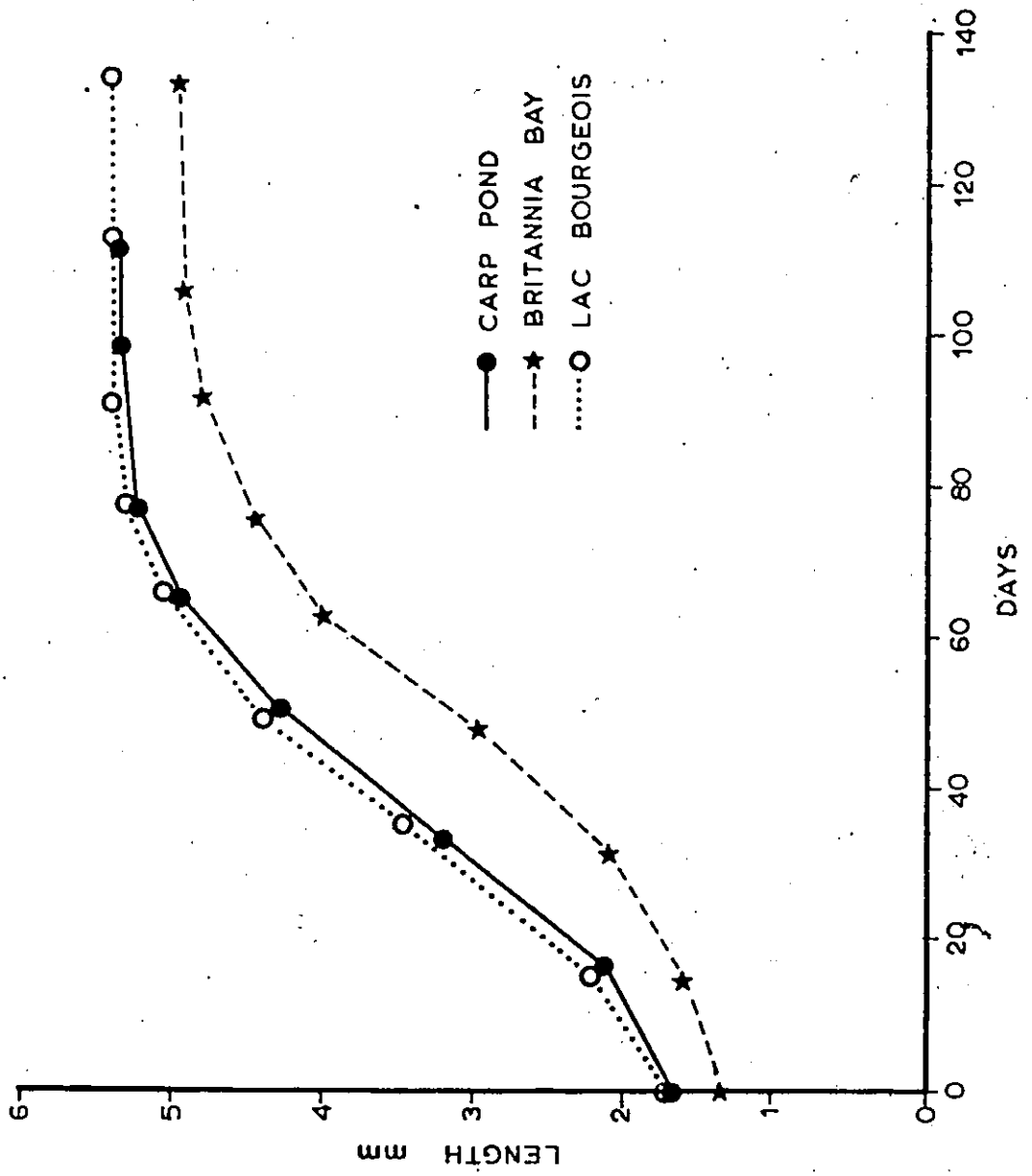
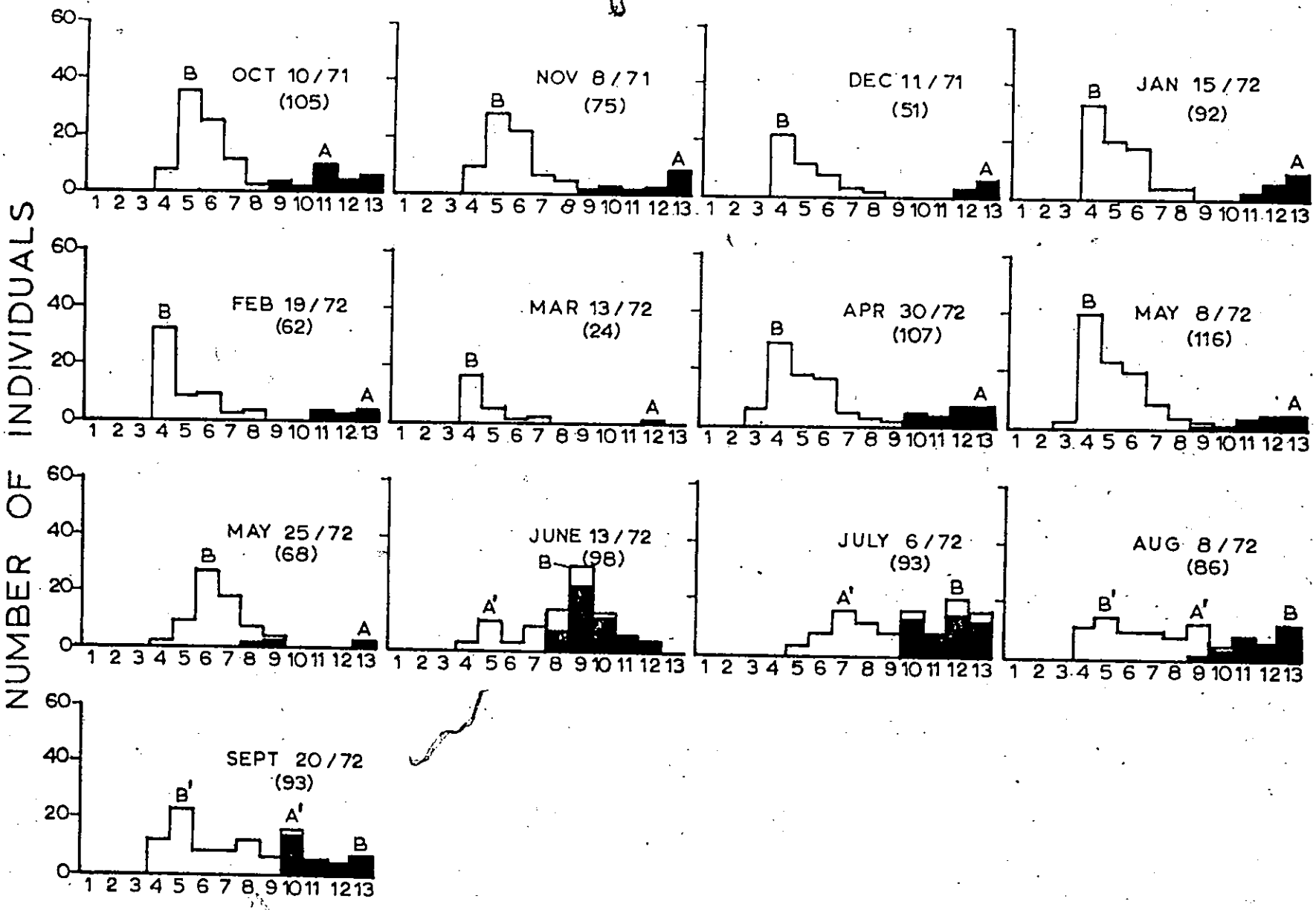
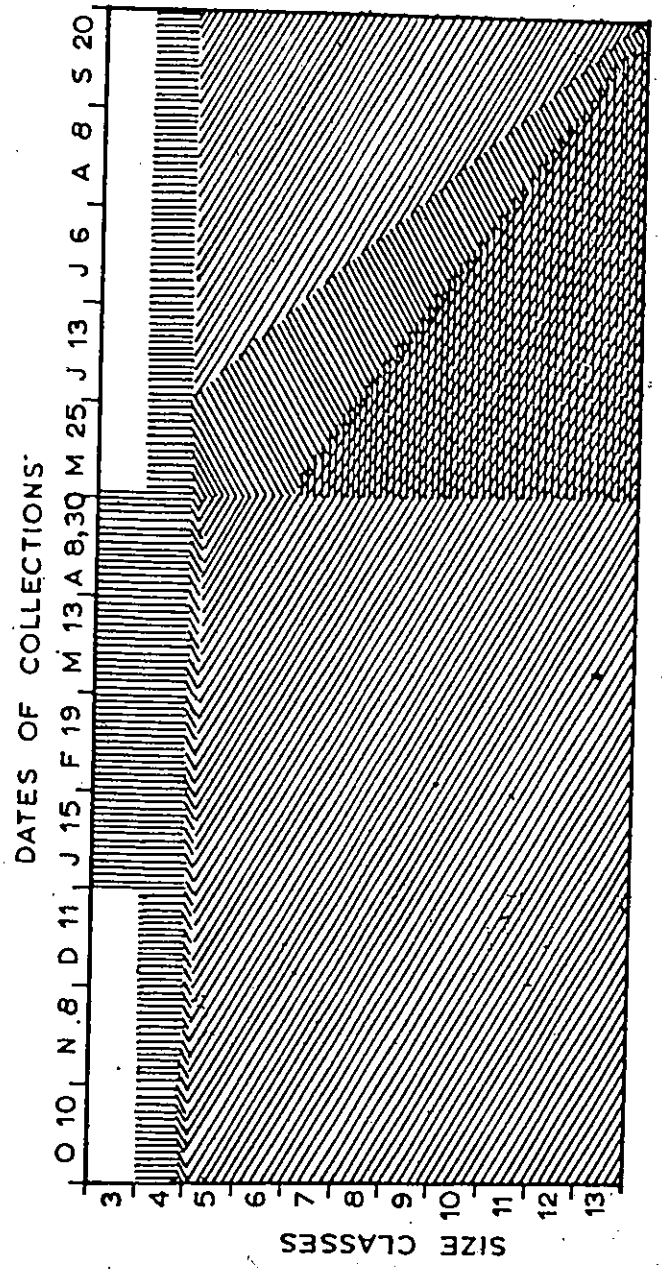

CARP POND
BRITANNIA BAY
LAC BOURGEOIS
LENGTH mm
DAYS
0
1
2
3
4
5
6
0
20
40
60
80
100
120
140

Fig. 30 Seasonal size-frequency distribution of Musculium securis in Lac Bourgeois for one year of study. Size classes 1-12 represent length increments of 0.50 mm; size class 13 is lengths greater than 6.50 mm. Shaded areas indicate gravid adults.


NUMBER OF INDIVIDUALS
OCT 10/71 (105)
NOV 8/71 (75)
DEC 11/71 (51)
JAN 15/72 (92)
FEB 19/72 (62)
MAR 13/72 (24)
APR 30/72 (107)
MAY 8/72 (116)
MAY 25/72 (68)
JUNE 13/72 (98)
JULY 6/72 (93)
AUG 8/72 (86)
SEPT 20/72 (93)
SIZE CLASSES OF ADULTS

65ii

Fig. 31 Diagram showing the seasonal occurrence of newborns, uncalyculate adults, calyculate adults, and annulated adults of Musculium securis in Lac Bourgeois. First collection was made on October 10, 1971.


DATES OF COLLECTIONS
O 10 N 8 D 11 J 15 F 19 M 13 A 8,30 M 25 J 13 J 6 A 8 S 20
SIZE CLASSES
3 4 5 6 7 8 9 10 11 12 13
LEGEND
NEWBORNS
UNCALYCULATE ADULTS
CALYCULATE ADULTS
ANNULATED ADULTS

summers of 1972 and 1971, respectively. The modes therefore represent adults born in the summer months (mode A) and adults born in the fall and winter months (mode B). By February 19, all parents had released their extra-marsupial larvae so that mode A' probably represents the birth of second (and third) litters of extra-marsupial larvae. Mode B' represents adults that were probably born in late July. Presumably, mode B disappeared and the size-frequency distribution in October, 1972 would have been similar to that of October, 1971.

Plots of the mode B (Fig. 30) show that the growth of M. securis during the spring and summer in Lac Bourgeois was rapid and did not appear to differ from the growth of clams in other populations except the slow-growing adults of Britannia Bay.

Birth periods

The Carp Pond population displays only one birth period. In 1970 and 1971, birth of extra-marsupial larvae occurred immediately before the disappearance of water (i.e. late July) from the pond. Upon birth, the newborns burrow 1-8 cm below the soil where they estivate until November. In 1972 the birth period extended from late July to mid-October when most parents died in both Carp Pond and Greely Pond (Fig. 25 and 27).

There are two birth periods in Britannia Bay. Some young are born in July-August. Those born in early July grow rapidly to produce a litter in September.

Births occur throughout the year in Lac Bourgeois although newborns dominate the winter population suggesting that many births occur in late fall or early winter. Another birth period probably

occurs in July since the August 8 collection (Fig. 30) was dominated by size class 5.

Maintenance of adults in all habitats, except Greely Pond, supports the above results. Births occur in the growth tubes during late July in Carp Pond, early July and mid-September in Britannia Bay, and late July in Lac Bourgeois. The newborns born early in Britannia Bay growth tubes, grow rapidly to produce a mid-September litter. Similar results are obtained when adults from Carp Pond and Lac Bourgeois are transplanted into Britannia Bay and when newborns from each of these populations are maintained in the laboratory. Therefore, the birth period usually occurs 60-70 days after the onset of growth of the newborns.

The earliest newborns are usually born with a smaller size than those born later in the temporary habitats and with a larger size than those born later in the permanent aquatic habitats. Newborns born in early July in Carp Pond and Greely Pond are of size classes 3 and 4 while those born later are of size class 5. Conversely, newborns born in early July in Britannia Bay are of size classes 3 and 4 while those born in late summer are of size class 2.

The births of 28 extra-marsupial larvae were observed for seven parents. It took one parent approximately 18 minutes to release four young. All parents had released their young within 45 minutes. During the birth of young, the parent usually lies on its side with the valves slightly gaping and the siphons either fully extended or relaxed. Prior to birth, the extra-marsupial larvae move almost continuously within the parent. This action may sever the attachment of the byssal stalk from the foot of the larvae. The extra-marsupial larvae are always released

via the anal siphon and usually "head-first". In this manner the foot of the larvae usually precedes the body proper and grasps either the parent's shell or the substrate to pull itself out. If the larvae are released with the posterior end first, the parent appears to "spit" them out by first extending its siphon and then suddenly retracting it. It is not known what factors are responsible for inducing birth of extra-marsupial larvae.

Seasonal gonad activity

The gonads of newborns are small and often difficult to locate. Primary oocytes are often seen in newborns that have estivated and/or hibernated in Carp Pond and Greely Pond but neither oogenesis nor spermatogenesis is strongly apparent (Fig. 32-1). Gametogenesis does not appear to begin until growth of adults ensues in the spring. At this time the ovary appears to be in further stages of development than the testis. (Fig. 32-2). Throughout May, June, and early July, both fully developed ova and sperms are present but there is no evidence of increasing gonad activity with time (Fig. 32-3, -4, -5, -6). Spermatogonia and spermatocytes are readily visible and usually fill the entire follicular cavity. It is not until late July that spermatogenic activity is maximum (Fig. 32-7). In late-July specimens the spermatozoa are usually found in the central lumen of the testicular follicles (Fig. 32-7) where the tails of the sperms are clearly visible (Fig. 32-8). Frequently the testis is so large in these late July specimens that the ovary cannot be located.

There appear to be no major differences in seasonal gonad activity between the four habitats. However, the smaller size classes of slow-growing adults in Britannia Bay are usually in the same stage of gameto-

Fig. 32 Photomicrographs of seasonal gonad activity in Musculium securis in Carp Pond. DO developing oogonia, I intestine, PO primary oocytes, ST spermatozoa, STT tails of spermatozoa, SY spermatocytes.

1. October 10, 1970. Length of parent 1.70 mm. 500X.
2. May 20, 1971. Length of parent 3.35 mm. 500X.
3. May 30, 1971. Length of parent 3.76 mm. 500X.
4. June 14, 1971. Length of parent 4.65 mm. 500X.
5. June 28, 1971. Length of parent 5.22 mm. 500X.
6. July 12, 1971. Length of parent 5.68 mm. 500X.
7. July 26, 1971. Length of parent 5.75 mm. 125X.
8. Same as no. 7 but 500X.


1
DO
2
SY
3
4
PO
5
ST
6
PO
ST
7
8
STT

genesis as larger size classes of fast-growing adults of the same age. This indicates that gametogenesis is more a function of time than of size of parent. In specimens over 4 mm in length collected between November and April from Lac Bourgeois, the testicular follicles show evidence of a decided reduction in spermatogenesis and primary oocytes are usually absent in the ovaries. The central lumens of the ovaries and testis are devoid of gametes so that gametogenesis probably does not occur during the winter months.

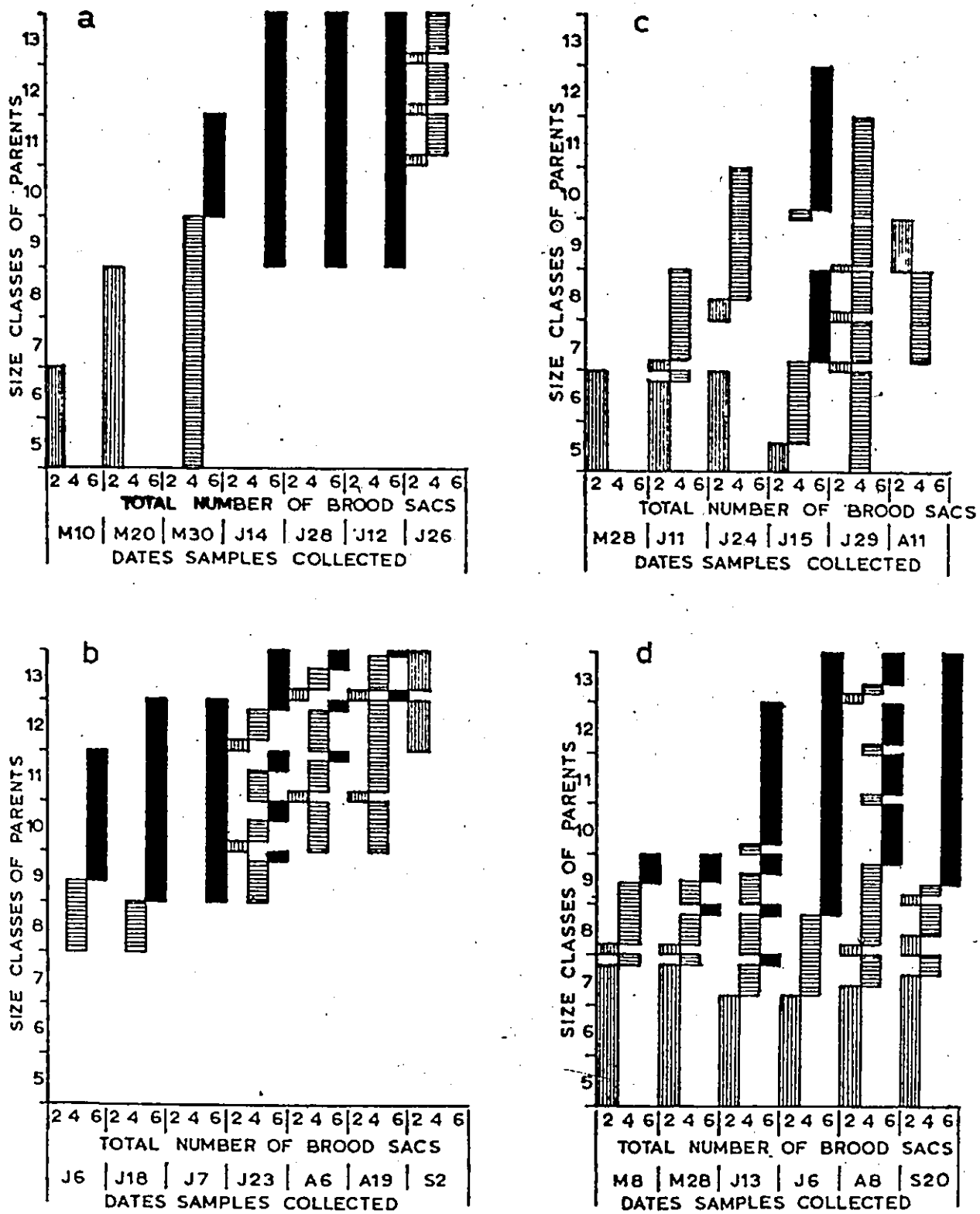
Although there are variations, gametogenesis is first apparent in adults of size class 5. The testis greatly dwarfs the ovary in adults larger than size class 11. On the basis of the earliest appearance of primary sacs, eggs are first fertilized in adults of size class 5.

Number of brood sacs and larvae per sac

Demibranchs within a parent usually contain the same number of brood sacs. A maximum of three brood sacs per demibranch (i.e. six brood sacs per gill) is usually found but four brood sacs also occur, although very rarely. The total number of brood sacs per gill varies with the size class and age of the parent (Fig. 33).

During the summers of 1970 and 1971, only parents larger than size class 9 of the Carp Pond population contained 6 brood sacs (Fig. 33a). By late June extra-marsupial larvae are present but 6 brood sacs also occur indicating that a total of 8 brood sacs (i.e. 2 primary, 2 secondary, and 4 tertiary) are produced. This is probably the average maximum number since only four brood sacs per gill (i.e. 2 secondary and 2 tertiary) are found in parents taken at the end of July. In 1972 when the pond did not dry up, the same phenomena occurred (as exemplified

Fig. 33 Total number of brood sacs per gill in parents collected between (a) May 10 and July 26, 1971 from Carp Pond, (b) June 6 and September 2, 1972 from Greely Pond, (c) May 28 and August 11, 1971 from Britannia Bay, and (d) May 8 and September 20, 1972 from Lac Bourgeois. Each size class interval also represents 100%.


a
SIZE CLASSES OF PARENTS
5 6 7 8 9 10 11 12 13
2 4 6 2 4 6 2 4 6 2 4 6 2 4 6 2 4 6 2 4 6
TOTAL NUMBER OF BROOD SACS
M10 M20 M30 J14 J28 J12 J26
DATES SAMPLES COLLECTED
c
SIZE CLASSES OF PARENTS
5 6 7 8 9 10 11 12 13
2 4 6 2 4 6 2 4 6 2 4 6 2 4 6 2 4 6
TOTAL NUMBER OF BROOD SACS
M28 J11 J24 J15 J29 A11
DATES SAMPLES COLLECTED
b
SIZE CLASSES OF PARENTS
5 6 7 8 9 10 11 12 13
2 4 6 2 4 6 2 4 6 2 4 6 2 4 6 2 4 6 2 4 6
TOTAL NUMBER OF BROOD SACS
J6 J18 J7 J23 A6 A19 S2
DATES SAMPLES COLLECTED
d
SIZE CLASSES OF PARENTS
5 6 7 8 9 10 11 12 13
2 4 6 2 4 6 2 4 6 2 4 6 2 4 6 2 4 6
TOTAL NUMBER OF BROOD SACS
M8 M28 J13 J6 A8 S20
DATES SAMPLES COLLECTED

by results from Greely Pond, Fig. 33b) and new sacs were not produced in late summer. Therefore, the extended aquatic season has little effect on the total number of brood sacs produced although more brood sacs mature (i.e. 4 brood sacs per gill remained in 1970 and 1971 adults but 2 remained in the 1972 adults).

Six brood sacs are uncommon in the Britannia Bay population and are found only in July (Fig. 33c). There appear to be no major differences in the total number of brood sacs between 1970, 1971, and 1972 populations of Britannia Bay. A total of six brood sacs are usually produced but only two brood sacs mature since four remain at the end of the summer. Size classes 5, 6, and 7 represent slow-growing adults which usually produce a total of only four brood sacs (Fig. 33c).

Six brood sacs per gill are most common in adults of size classes larger than 9 in Lac Bourgeois (Fig. 33d). At least 8 brood sacs are produced by many parents since one litter of extra-marsupial larvae is released and 6 brood sacs still remain by mid-September. Some parents release another litter of extra-marsupial larvae in the fall and many still have 6 brood sacs per gill. Therefore, some parents of Lac Bourgeois produce as many as 10 brood sacs per gill.

The numbers of larvae in brood sacs of parents from each population are given in Table 2. Primary sacs are not included because the embryos are too small to be counted accurately. The total number of larvae increases with age of the parent indicating that the generative performance increases with age.

A significantly larger number ($P < 0.05$) of extra-marsupial larvae occurred in 1971 than in 1970 or 1972 in Carp Pond, Britannia Bay, and

Table 2. Sizes of litters in marsupial chamber and brood sacs of Musculium securis in four habitats for each year of collection. Only parents in which all larvae were present and from which no extra-marsupial larvae had been released were examined.

LARVAL STAGES AND BROOD SACS	CARP POND			GREELY POND	BRITANNIA BAY			LAC BOURGEOIS	
	1970	1971	1972	1972	1970	1971	1972	1971	1972
	X (N) SD[a]	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD
Extra-marsupial larvae in branchial chamber	3.0 (25) 1.10	4.0 (40) 1.61	2.6 (28) 0.90	2.7 (28) 0.84	2.4 (18) 0.83	3.1 (15) 1.44	2.4 (16) 0.90	3.8 (14) 1.48	4.8 (20) 1.56
Prodissoconch larvae in tertiary sacs	4.8 (25) 1.35	5.5 (40) 1.57	5.0 (28) 2.01	5.4 (28) 1.70	3.9 (18) 1.39	4.1 (15) 1.36	3.4 (16) 0.77	5.1 (14) 1.92	6.0 (20) 2.13
Fetal larvae in secondary sacs	6.8 (25) 1.64	7.4 (40) 1.12	7.3 (28) 2.07	6.8 (28) 1.29	5.6 (18) 1.23	6.1 (15) 1.23	5.6 (16) 1.02	7.4 (14) 1.18	7.8 (20) 2.20

[a] X = mean, (N) = number of specimens examined, SD = standard deviation.

Lac Bourgeois. There are no significant differences ($P > 0.05$) in the numbers of prodissoconch larvae nor of fetal larvae between the 1970, 1971 and 1972 populations of Carp Pond and Britannia Bay nor between the 1971 and 1972 populations of Lac Bourgeois. The numbers of each larval stage in Greely Pond adults are similar to those in Carp Pond adults in 1972. Smaller numbers ($P < 0.05$) of prodissoconch larvae and of fetal larvae are produced in the Britannia Bay populations than in other populations. Lac Bourgeois parents produced larger ($P < 0.05$) numbers of extra-marsupial larvae in 1972 than did other populations in the same year and similar numbers ($P > 0.05$) of prodissoconch and of fetal larvae as Carp Pond and Greely Pond in the last two years of study.

Number of litters produced

Table 3 gives the percentages of adults that produced one, two, or three litters in each population and for each year of study. There are no significant differences ($P > 0.25$) in the proportion of parents in Carp Pond producing one and two litters in 1970 and 1971. Significantly more ($P < 0.005$) parents produced two litters in 1972 than in previous years of study in Carp Pond. The 1972 increase is attributable to the extended aquatic season since the data were obtained from parents sampled in August and September when the pond was usually dry. The data for 1970 and 1971 were obtained from parents collected at the end of July, just prior to the disappearance of water from the pond. Parents of Carp and Greely Ponds produced the same proportions of one and two litters in 1972. A larger proportion ($P < 0.005$) of parents produce one litter in Britannia Bay than in other habitats. No differences are observed in the proportion of parents producing one and two litters in Lac Bourgeois,

Table 3. Percentage of Musculium securis parents producing one, two, and three litters in each of four habitats for each year of collection. The percentages are based on back-calculation of brood sacs in parents that had completed growth.

YEAR OF COLLECTION	CARP POND			GREELY POND			BRITANNIA BAY			LAC BOURGEOIS			
	No. of litters			No. of litters			No. of litters			No. of litters			
		One	Two		One	Two		One	Two		One	Two	Three
	(N)[a]	%	%	(N)	%	%	(N)	%	%	(N)	%	%	%
1970	(25)	64.0	36.0	No collections			(19)	84.2	15.8	No collections			
1971	(40)	45.0	55.0	No collections			(17)	88.4	11.6	(30)	38.5	53.2	8.3
1972	(30)	6.8	93.2	(31)	13.0	87.0	(16)	81.1	18.9	No collections			

[a] (N) = Number of specimens examined.

Carp Pond, and Greely Pond although a small percentage of parents produces three litters in Lac Bourgeois.

One litter was most commonly produced in the growth tubes placed in Carp Pond, Britannia Bay, and Lac Bourgeois and in the laboratory growth dishes. A maximum of three litters was produced in all these maintenance studies. The results were obtained by noting the presence or absence of newborns in the growth containers in approximately two week intervals. Analyses of parents from seasonal field collections show that in a few instances two litters of extra-marsupial larvae occur together, particularly when the litter sizes are small. Therefore, it is possible that two litters may have been produced within two weeks in the maintenance containers. If this occurred then a maximum of six litters were produced. However, studies on the numbers of brood sacs produced show that usually four sacs, and rarely five, are formed in each demibranch. Therefore, the maximum number of litters most likely produced in the maintenance containers was four.

Sizes of litters produced

Since only extra-marsupial larvae are released, their numbers represent the sizes of litters produced. Table 4 gives the sizes of the first litters in all populations for each year of study and of second litters in populations of which at least 35% of the parents produced two litters. The sizes of the first and second litters of prodissoconch and fetal larvae in sequential parents are also included in Table 4. Sequential parents are those parents that represent a stage in the sequential development of each litter of extra-marsupial larvae. That is, the sizes of the first and second litters of prodissoconch and fetal larvae that

Table 4. Sizes of first and second litters per gill and the percent viability of larvae in sequential parents of Musculium securis in four habitats for each year of collection.

TYPES OF LITTERS	CARP POND			GREELY POND	BRITANNIA BAY			LAC BOURGEOIS	
	1970	1971	1972	1972	1970	1971	1972	1971	1972
First larval litters in sequential parents	X (N) SD[a]	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD	X (N) SD
Extra-marsupial larvae	3.0 (25) 1.10	4.0 (40) 1.61	2.6 (28) 0.91	2.7 (28) 0.84	2.4 (18) 0.83	3.1 (15) 1.44	2.4 (16) 0.90	3.8 (14) 1.48	4.8 (20) 1.56
Prodissoconch larvae	4.7 (31) 1.26	5.3 (38) 1.54	5.5 (36) 1.70	5.4 (20) 1.30	4.0 (23) 0.93	3.9 (22) 1.72	3.8 (16) 1.29	4.8 (30) 1.84	6.0 (34) 1.78
Fetal larvae	7.0 (37) 1.67	6.9 (38) 1.77	7.4 (37) 2.27	7.0 (22) 1.91	5.9 (28) 0.99	5.8 (12) 1.56	6.1 (25) 1.20	6.7 (23) 1.29	7.6 (34) 2.02
% viability[b]	45	58	37	39	41	58	39	57	63
Second larval litters in sequential parents°									
Extra-marsupial larvae	2.1 (9) 0.11	3.1 (14) 0.88	2.4 (35) 0.77	2.4 (34) 0.74	Insufficient			4.2 (15) 1.27	No
Prodissoconch larvae	4.6 (25) 1.30	5.0 (55) 1.44	4.8 (50) 1.93	6.1 (42) 1.95	size			6.6 (31) 1.99	Data
Fetal larvae	6.1 (34) 1.51	6.6 (50) 1.67	7.4 (50) 2.11	7.8 (45) 2.16	of			8.0 (32) 2.30	
% viability	34	47	32	31	Sample			52	

[a] X = mean, (N) = number of specimens examined.

[b] % viability = (no. of extra-marsupial larvae/ no. of fetal larvae) X 100.

represent the first and second litters of extra-marsupial larvae were counted in parents from three successive field collections.

The results (Table 4) show that the sizes of the first and second litters of each larval stage are similar ($P > 0.05$) but there are always significantly larger numbers ($P < 0.01$) of fetal larvae than of prodissoconch larvae which in turn are numerically larger ($P < 0.01$) than extra-marsupial larvae. Clearly, the results indicate that not all larvae are viable. Some fetal and prodissoconch larvae die before reaching the extra-marsupial stage. The percent viability of larvae fluctuates within habitats from one year to the next but tends to remain relatively constant between habitats for each year of study (except Lac Bourgeois in 1972).

The numbers of extra-marsupial larvae were significantly larger ($P < 0.05$) in 1971 in Carp Pond and Britannia Bay than in other years of study. Parents of the Lac Bourgeois population produced larger litters of extra-marsupial larvae in 1972 than in 1971. The sizes of the first and second litters of fetal and prodissoconch larvae are smaller ($P < 0.05$) in Britannia Bay than in other habitats; the litter sizes of fetal and prodissoconch larvae tend to remain constant within and between the remaining habitats.

Table 5 shows that parents maintained in growth chambers in Carp Pond, Britannia Bay, and Lac Bourgeois produce similar ($P > 0.05$) litter sizes as parents in the natural habitats. Parents maintained in the laboratory produce larger ($P < 0.01$) litters than both parents in the natural habitat (except Lac Bourgeois) and parents maintained in the field.

Longevity

Analyses of the size-frequency histograms (Fig. 25, 27, 28, 30)

Table 5. Sizes of litters produced by parents maintained in growth containers in three habitats and in the lab.

Adults Maintained In: Growth tubes in:	Number Of Parents Producing: One litter	Two litters	Sizes Of Litters First litter	Second litter	Total Litter Size Per Parent
Carp Pond	17	12	3.0	3.0	6.0
Britannia Bay	18	8	2.8	1.7	4.5
Lac Bourgeois	18	16	2.8	4.3	7.1
Laboratory growth dishes:					
Carp Pond adults	15	15	3.8	4.2	8.0
Britannia Bay adults	15	9	3.5	2.0	5.5
Lac Bourgeois adults	15	15	4.0	5.1	9.1

show that M. securis lives for approximately one year in each habitat. The life span was extended for only three months with the persistence of an aquatic environment in Carp Pond in 1972. The longevity of M. securis in the maintenance and culture studies is 80-100 days when newborns were permitted to grow immediately after birth. The life span increases significantly by maintaining newborns in a cold room at 5°C for four months and then growing at 18°C for 80-100 days.

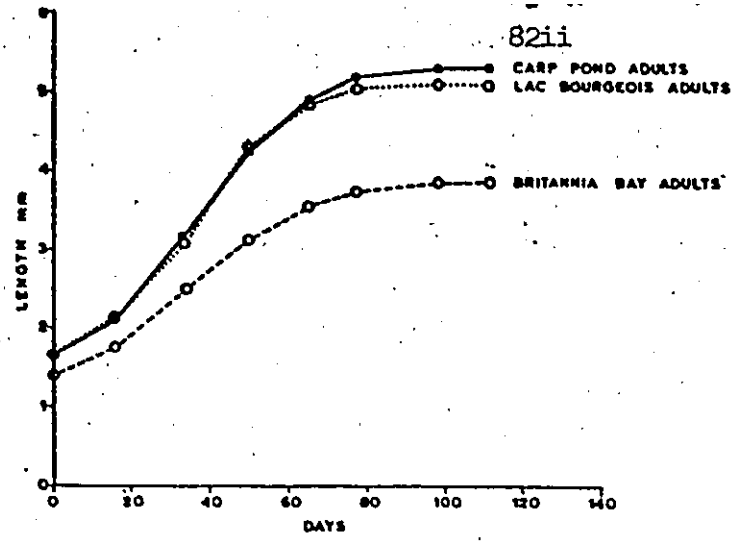
Interpopulation transplants

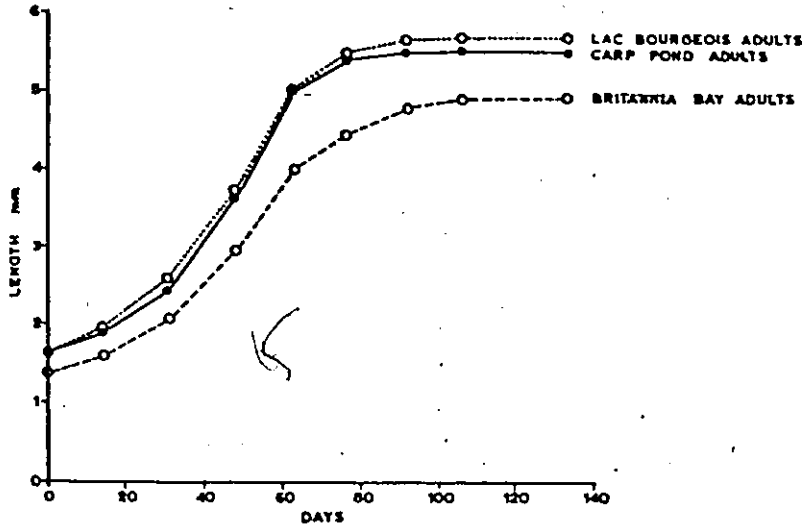
The results (Fig. 34, Table 6) show that the growths of Carp Pond and Lac Bourgeois adults in their own habitats do not differ significantly from those transplanted into other habitats. The growth of Britannia Bay adults in Britannia Bay differs ($P < 0.05$) from those transplanted into Carp Pond and Lac Bourgeois.

The natalities of M. securis in the interpopulation transplants are shown in Table 6. Approximately 25% of the Britannia Bay adults, as well as adults from Carp Pond and Lac Bourgeois transplanted into Britannia Bay, produce young in early July. These mature into calyculate adults that produce a litter in September. Newborns that appear near the end of July and early August do not continue growth in the fall in any of the habitats.

Most of the first generation adults die by early August and those that are still alive in August do not grow substantially in September (Fig. 34). Dissection of the adults that are alive in September (mainly uncalyculate adults) show that all extra-marsupial larvae have been released and that the other larval stages appear to be too immature to be born before the onset of cold weather.

Fig. 34 Growth of Musculium securis from Carp Pond, Britannia Bay, and Lac Bourgeois transplanted into (a) Carp Pond, (b) Britannia Bay, and (c) Lac Bourgeois. Day 0 = May 9, 1972.


CARP POND ADULTS
LAC BOURGEOIS ADULTS
BRITANNIA BAY ADULTS
LENGTH mm
DAYS
0
20
40
60
80
100
120
140


LAC BOURGEOIS ADULTS
CARP POND ADULTS
BRITANNIA BAY ADULTS
LENGTH mm
DAYS
0
20
40
60
80
100
120
140

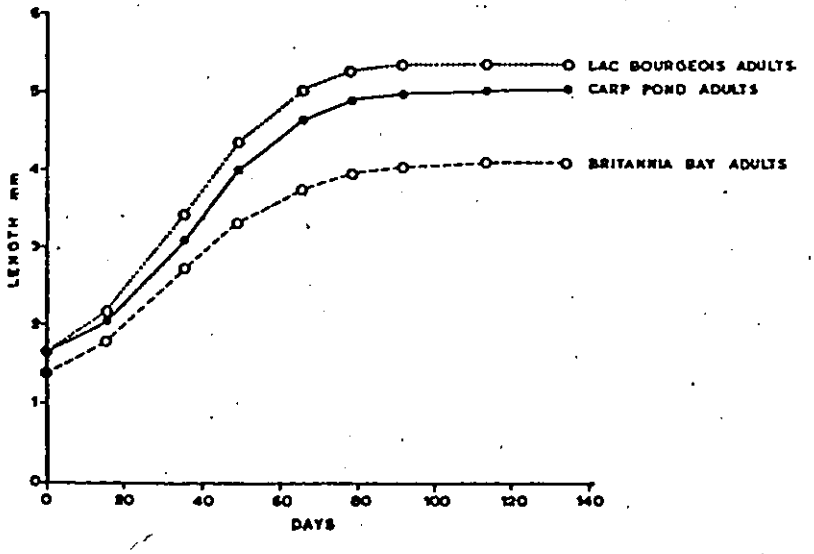

LAC BOURGEOIS ADULTS
CARP POND ADULTS
BRITANNIA BAY ADULTS
LENGTH mm
DAYS
0
20
40
60
80
100
120
140

Table 6. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the litter size per average adult of Musculium securis transplanted into Carp Pond, Britannia Bay, and Lac Bourgeois. The A and B values of the logistic equation are transformed to permit tests of significant differences among all groups. Means side-scored by the same line are not significantly different at $P = 0.05$. Twenty specimens were put into each habitat but only N number matured.

Populations transplanted from:	Growth form	Mean and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Total litter size per average parent and standard deviations ( )	
		A mm		B mm		R			
Lac Bourgeois into:									
Britannia Bay (N = 16)	1/Y	0.151	(0.033)	0.477	(0.033)	0.980	(0.0044)	8.2	(1.7)
	1/Y'	6.42	(0.72)	-5.94	(0.68)				
Lac Bourgeois (Control) (N = 18)	1/Y	0.161	(0.015)	0.469	(0.015)	0.989	(0.0036)	7.1	(1.8)
	1/Y'	6.21	(0.62)	-4.68	(0.60)				
Carp Pond (N = 16)	1/Y	0.166	(0.009)	0.465	(0.010)	0.986	(0.0028)	6.5	(2.0)
	1/Y'	6.02	(0.34)	-4.50	(0.33)				
Carp Pond into:									
Britannia Bay (N = 17)	1/Y	0.162	(0.021)	0.464	(0.020)	0.985	(0.0038)	6.8	(2.5)
	1/Y'	6.18	(0.80)	-4.65	(0.76)				
Carp Pond (Control) (N = 17)	1/Y	0.164	(0.010)	0.463	(0.010)	0.985	(0.0021)	6.0	(2.2)
	1/Y'	6.09	(0.34)	-4.58	(0.33)				
Lac Bourgeois (N = 16)	1/Y	0.172	(0.030)	0.457	(0.030)	0.978	(0.0051)	4.3	(2.5)
	1/Y'	5.82	(0.94)	-4.37	(0.90)				
Britannia Bay into:									
Britannia Bay (Control) (N = 18)	1/Y	0.188	(0.014)	0.439	(0.012)	0.983	(0.0051)	4.5	(1.2)
	1/Y'	5.32	(0.38)	-3.81	(0.32)				
Lac Bourgeois (N = 15)	Y	4.63	(0.73)	-2.19	(0.68)	0.989	(0.0035)	0.2	(0.4)
Carp Pond (N = 14)	Y	4.44	(0.58)	-2.00	(0.54)	0.985	(0.0023)	0.1	(0.1)

Ecology of Musculium Securis

Effect of temperature

When M. securis is exposed to high temperatures, the clams relax and the shells gape. Without acclimating, 50% of the adults die after 10 minutes exposure to 26°C. Only adults of lengths 1.50 to 2.50 mm recover when returned to 18°C pond water. Adults longer than 2.00 mm die after 5 minutes exposure to 30°C and only adults of lengths 1.50 to 2.00 mm (i.e. newborns) recover when returned to 18°C pond water.

When M. securis is slowly acclimated to 26°C all adults survive with no evidence of gaping shells. After one hour at 30°C the shells of most adults gape but only adults of lengths 5.00 to 6.00 mm do not recover when returned to 18°C pond water. Exposure of adults to 30°C for longer intervals of time show that only newborns survive after two hours and all clams are dead after three hours.

Fig. 35 shows the growth of M. securis at 5°C, 10°C, 18°C, and 25°C. Differences in the growth parameters and the natalities of M. securis at each temperature are given in Table 7. Growth apparently begins between 5°C and 10°C. The optimum temperature for growth and reproduction is probably between 18°C and 25°C. A temperature of 25°C has a greater adverse effect on the natalities than on the growth of M. securis (Table 7).

Effect of substrates

(1) Quantity of soil - The growth curves of M. securis are more sigmoid on 20 and 40 g of soil than on 60, 80, 100, and 120 g of soil (Fig. 36). Faster growth rates and greater lengths are attained by M. securis on 40 g than on most other quantities of soil but few differences are observed

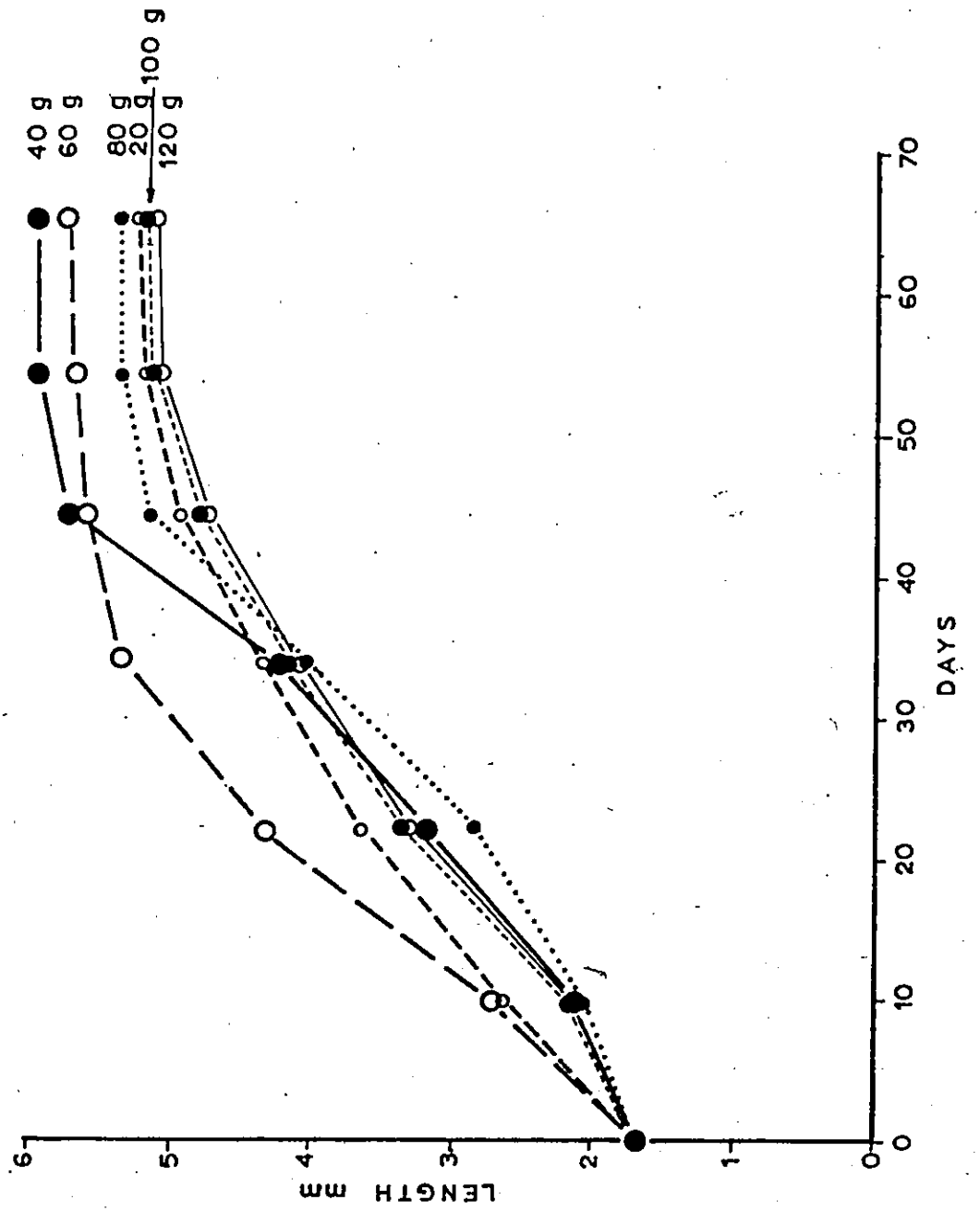
Fig. 35 Observed average growth in shell length of 15 Musculium securis adults at each of four temperatures in the laboratory.

25 °C
18 °C
10 °C
5 °C
LENGTH mm
DAYS
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70

Table 7. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown at four different temperatures. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all groups. Each temperature was replicated three times with five clams in each replicate. Means side-scored by the same line are not significantly different at P = 0.05.

Temperature °C	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
25	1/Y	0.157	(0.009)	0.472	(0.010)	0.988	(0.0048)	14.7	(3.1)
	1/Y'	6.37	(0.40)	-4.88	(0.40)				
18	1/Y	0.167	(0.009)	0.465	(0.009)	0.987	(0.0030)	49.7	(4.2)
	1/Y'	5.98	(0.32)	-4.51	(0.30)				
10	Y	3.83	(0.96)	-2.37	(0.94)	0.922	(0.0085)	0	
5	Little or no growth							0	

Fig. 36 Observed average growth in shell length of 15 Musculium securis adults on each of five quantities of Carp Pond soil in the Laboratory.


40 g
60 g
80 g
100 g
120 g
20 g
LENGTH mm
DAYS
0
1
2
3
4
5
6
10
20
30
40
50
60
70

in natalities (Table 8). All adults died by the 65th day of growth from the newborn stage.

(2) Soil texture - Fig. 37 shows the growth of M. securis on soils of different textures from Britannia Bay. Since little or no growth occurred in control dishes containing only water and soil of different textures, the results are combined and shown in Fig. 37 as "sediment only". Little growth also occurs in control dishes containing only leaves and water. The fastest growth rates and largest natalities occur in dishes containing fine sand and silt-clay (Table 9). However, growth rates and natalities of M. securis in all dishes are significantly different ($P < 0.05$) from those observed on 40 g of Carp Pond soil in the previous experiment. This may indicate that M. securis grows better (i.e. attains greater lengths) on substrates that have high organic contents and nutrient supplies. All adults grown on Britannia Bay sediments in the laboratory died by the 64th day of growth from the newborn stage.

(3)Tree foliage - Of the eight leaf species tested, growth rates of M. securis are fastest and similar on white elm, white cedar, and black willow (Fig. 38, Table 10). Adults with the fastest growth rates usually produce more young than adults with slower growth rates (Table 10). Growth of M. securis on all foliage species is essentially completed after 56 days but all adults were not dead until the 78th day.

(4) Different soils - The growth of M. securis on different soils is shown in Fig. 39. Growth rates are fastest and similar on willow-elm soil with black willow litter, birch-aspen soil with white spruce litter, and oak-maple soil with red oak litter (Table 11). Growth was essentially completed after 64 days and all clams were dead by the 80th day.

Table 8. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown on different quantities of soil. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all groups. Three replicates were made for each quantity of soil and five clams were added to each replicate. Means side-scored by the same line are not significantly different at P = 0.05.

Quantity of soil	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
grams									
40	1/Y	0.156	(0.020)	0.476	(0.023)	0.988	(0.0037)	52.0	(6.2)
	1/Y'	6.31	(0.99)	-4.80	(0.95)				
60	Y	6.02	(0.45)	-4.57	(0.42)	0.979	(0.0031)	47.3	(10.2)
80	Y	5.88	(0.25)	-4.41	(0.26)	0.957	(0.0042)	40.7	(5.5)
20	1/Y	0.172	(0.020)	0.456	(0.020)	0.988	(0.0037)	51.3	(9.3)
	1/Y'	5.83	(0.64)	-4.35	(0.61)				
100	Y	5.35	(0.28)	-3.75	(0.26)	0.974	(0.0031)	38.7	(7.2)
120	Y	5.30	(0.30)	-3.72	(0.30)	0.968	(0.0043)	33.3	(6.5)

Fig. 37 Observed average growth in shell length of 15 Musculium securis adults on each of four different soil textures (taken from Britannia Bay) in the laboratory.

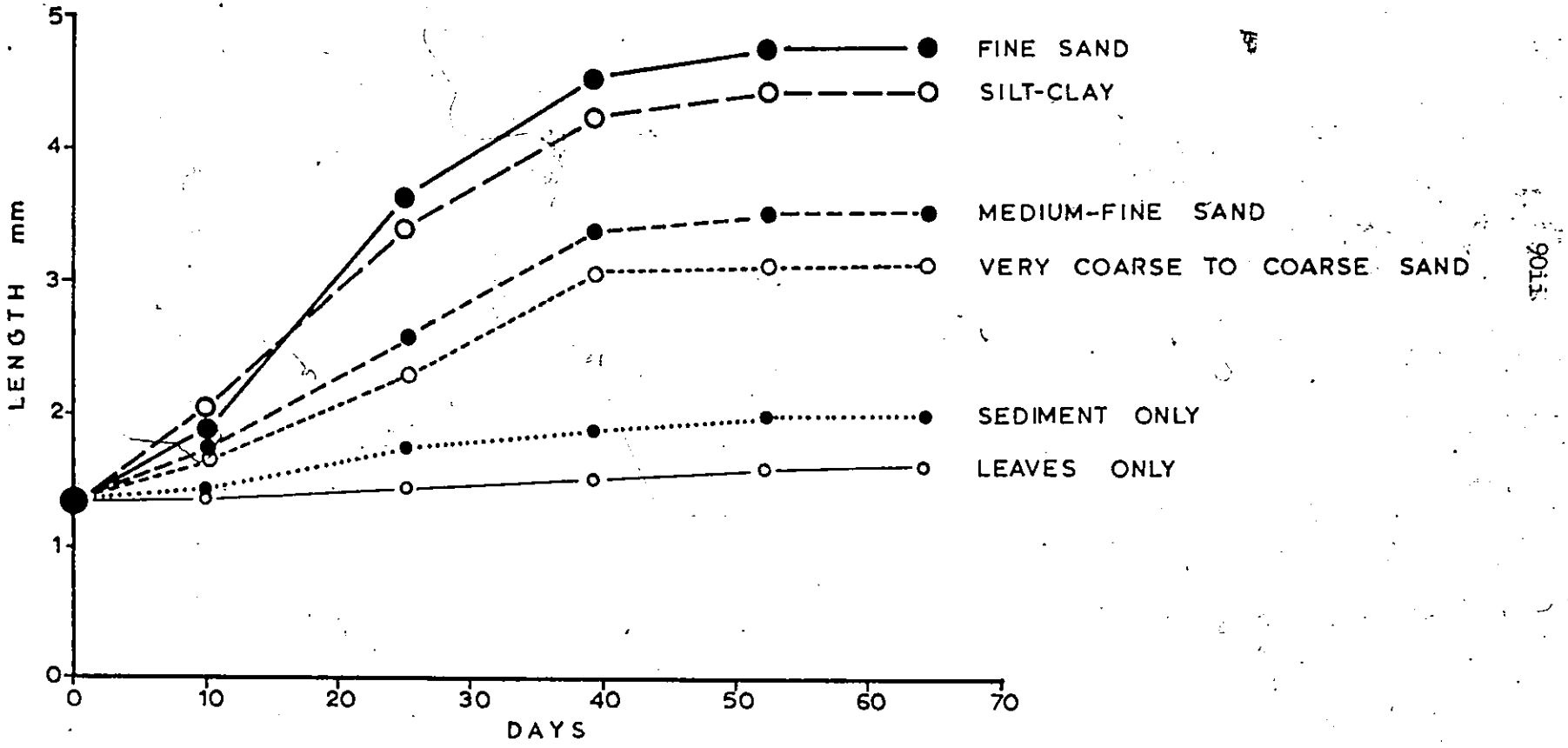

LENGTH mm
0
1
2
3
4
5
0
10
20
30
40
50
60
70
DAYS
FINE SAND
SILT-CLAY
MEDIUM-FINE SAND
VERY COARSE TO COARSE SAND
SEDIMENT ONLY
LEAVES ONLY

Table 9. Asymptotic growth data for the regression $Y = A + BR^X$ and the natalities of Musculium securis adults grown on four different soil textures. Three replicates were made for each soil texture with five clams in each replicate. Means side-scored by the same line are not significantly different at $P = 0.05$.

Texture of soil	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$						Mean natality and standard deviation ( ) per growth dish	
	A mm		B mm		R			
Fine sand	5.60	(0.22)	-4.38	(0.21)	0.970	(0.0034)	21.3	(3.1)
Silt-clay	4.30	(0.08)	-2.92	(0.09)	0.959	(0.0033)	19.7	(3.5)
Medium-fine sand	4.20	(0.12)	-2.86	(0.11)	0.965	(0.0037)	4.7	(1.5)
Very coarse sand	3.60	(0.13)	-2.22	(0.14)	0.959	(0.0068)	1.0	(1.7)
Sediment only (control)	Little or no growth						0	
Leaves only (control)	Little or no growth						0	

Fig. 38 Observed average growth in shell length of 15 Musculium securis adults on each of eight species of tree foliage in the laboratory.

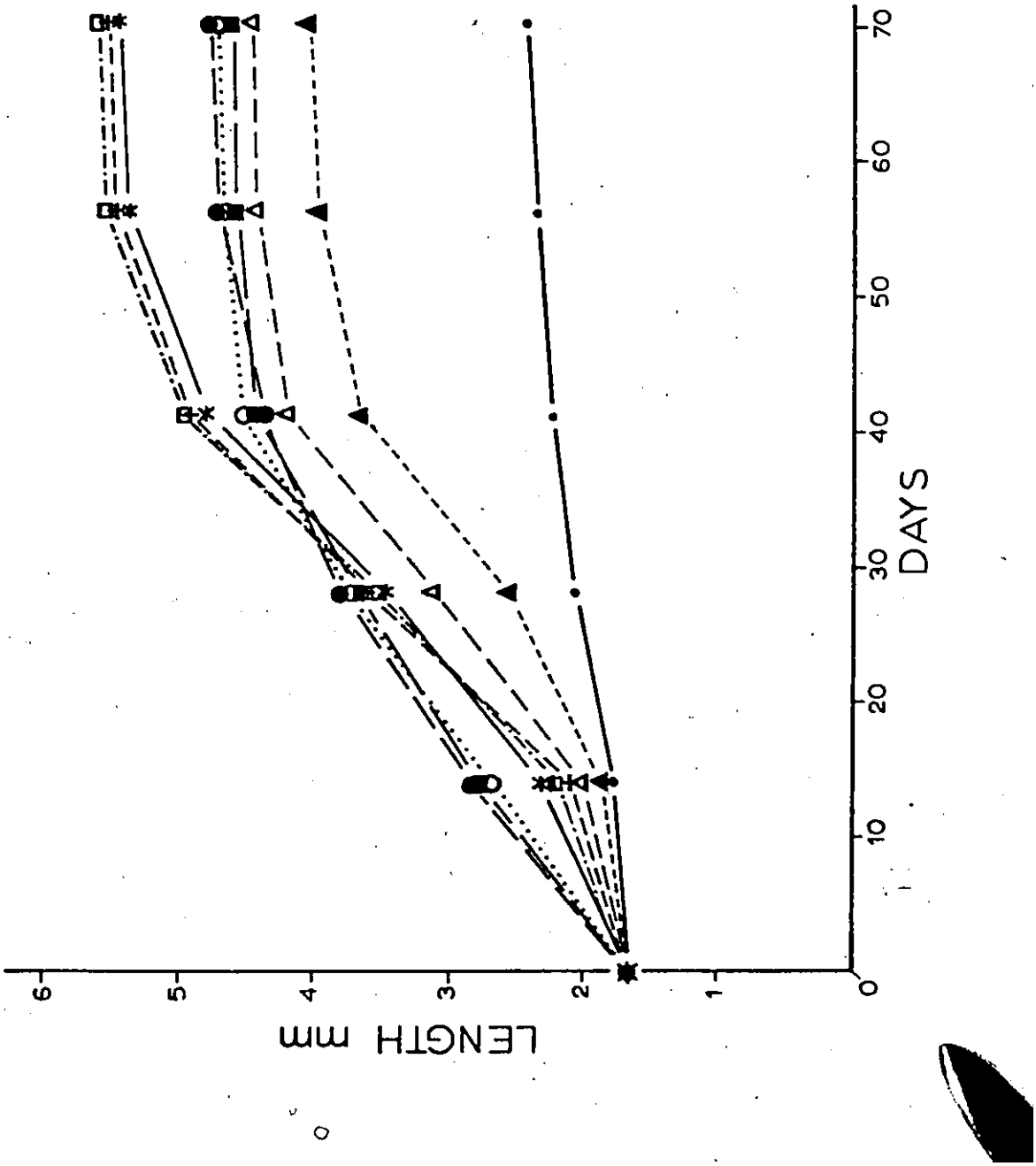

WHITE ELM
WHITE CEDAR
BLACK WILLOW
TREMBLING ASPEN
WHITE BIRCH
WHITE SPRUCE
RED OAK
RED MAPLE
CONTROL (NO LEAVES)
LENGTH mm
DAYS
0
1
2
3
4
5
6
10
20
30
40
50
60
70

Table 10. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown on three replicates of eight species of freshly fallen leaf litter. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all groups. Means side-scored by the same line are not significantly different at P = 0.05.

Leaf species	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
White elm	1/Y	0.159	(0.010)	0.469	(0.010)	0.961	(0.0022)	40.3	(6.8)
	1/Y'	6.29	(0.38)	-4.77	(0.36)				
White cedar	1/Y	0.162	(0.027)	0.477	(0.025)	0.971	(0.0028)	40.7	(5.0)
	1/Y'	6.18	(0.99)	-4.63	(0.96)				
Black willow	1/Y	0.165	(0.013)	0.416	(0.013)	0.963	(0.0023)	38.3	(4.2)
	1/Y'	6.06	(0.50)	-4.51	(0.49)				
Red oak	1/Y	0.195	(0.059)	0.434	(0.055)	0.975	(0.0048)	34.0	(1.7)
	1/Y'	5.13	(1.58)	-3.64	(1.52)				
White birch	Y	5.20	(0.11)	-3.63	(0.11)	0.969	(0.0024)	31.3	(8.3)
White spruce	Y	5.10	(0.47)	-3.54	(0.45)	0.980	(0.0030)	29.0	(4.4)
Trembling aspen	Y	5.25	(0.13)	-3.64	(0.13)	0.969	(0.0026)	27.3	(4.0)
Red maple	1/Y	0.241	(0.008)	0.388	(0.008)	0.933	(0.0030)	5.3	(2.3)
	1/Y'	4.15	(0.24)	-2.68	(0.23)				
No leaves (control)	Not described by asymptotic regressions, maximum length attained = 2.38 (0.14)							0	

Fig. 39 Observed average growth in shell length of 15 Musculium securis adults on each of five different soils containing different species of leaf litter in the laboratory.

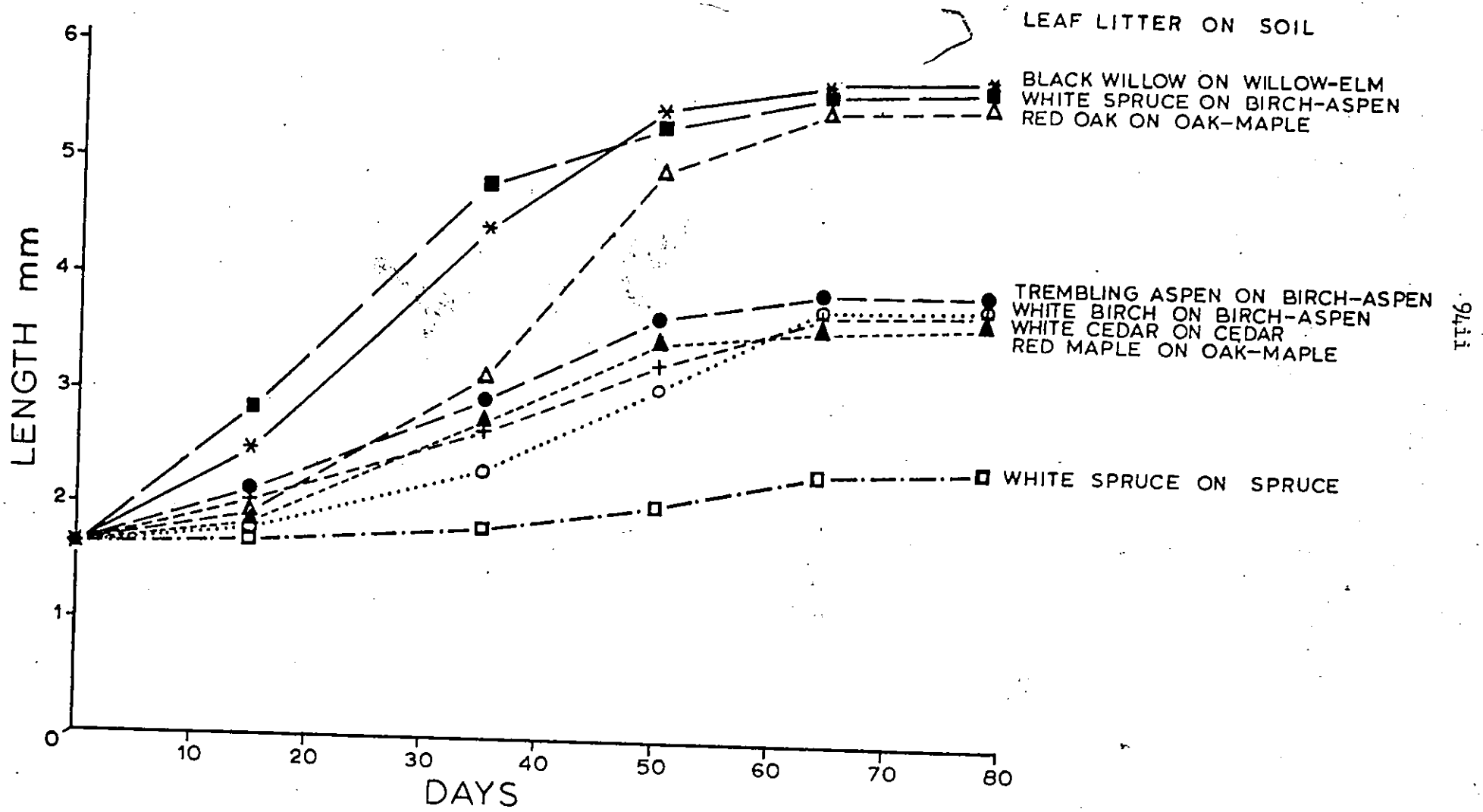

LEAF LITTER ON SOIL
BLACK WILLOW ON WILLOW-ELM
WHITE SPRUCE ON BIRCH-ASPEN
RED OAK ON OAK-MAPLE
TREMBLING ASPEN ON BIRCH-ASPEN
WHITE BIRCH ON BIRCH-ASPEN
WHITE CEDAR ON CEDAR
RED MAPLE ON OAK-MAPLE
WHITE SPRUCE ON SPRUCE
LENGTH mm
DAYS
0
1
2
3
4
5
6
10
20
30
40
50
60
70
80

Table 11. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown on three replicates of five different soils with seven species of leaf litter. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all groups. Means side-scored by the same line are not significantly different at $P = 0.05$.

Leaf litter on soil	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
Black willow on Willow-Elm	1/Y	0.161	(0.018)	0.468	(0.015)	0.985	(0.0021)	42.0	(5.3)
	1/Y'	6.21	(0.68)	-4.73	(0.64)				
White spruce on Birch-Aspen	Y	6.08	(0.20)	-4.54	(0.20)	0.969	(0.0036)	44.0	(2.7)
Red oak on Oak-Maple	1/Y	0.167	(0.028)	0.462	(0.030)	0.967	(0.0038)	35.3	(5.7)
	1/Y'	5.98	(0.92)	-4.51	(0.90)				
Trembling aspen on Birch-Aspen	Y	4.23	(0.88)	-2.80	(0.76)	0.972	(0.0040)	11.0	(3.6)
White cedar on cedar	1/Y	0.243	(0.033)	0.387	(0.031)	0.970	(0.0033)	5.7	(1.5)
	1/Y'	4.12	(0.74)	-2.60	(0.72)				
White birch on Birch-Aspen	1/Y	0.268	(0.013)	0.360	(0.013)	0.994	(0.0032)	7.0	(4.6)
	1/Y'	3.73	(0.20)	-2.27	(0.18)				
Red maple on Oak-Maple	Y	3.62	(0.80)	-2.17	(0.81)	0.958	(0.0066)	7.3	(1.2)
White spruce on spruce	Not described by asymptotic regressions, maximum length attained = 2.41 (0.16)							0	

Effect of pollutants

(1) Sulfate - The mean sulfate content of Carp Pond soil is 216 mg/100g of soil. Therefore, the total sulfate content in the growth dishes was the concentration of sulfate added plus a portion of 108 mg that went into solution from the soil. Table 12 gives the pH and sulfate contents of the test solutions before and two weeks after adding soil. The results show that the pH decreases with increasing concentration of sulfate. Also, the increase in pH after adding soil indicates the buffering capacity of Carp Pond soil. The amount of sulfate that goes into solution from the soil tends to decrease with increasing concentration of sulfate.

Increased concentrations of sulfate, either directly or indirectly, affect the growth of M. securis (Fig. 40). Growth is slightly better in sulfate contents of 92 and 108 mg/l than in control dishes with 80 mg/l. Significant reductions in the magnitudes of the growth parameters and natalities of M. securis occur in concentrations of sulfate exceeding 230 mg/l (Table 13); most clams in these concentrations form blackish shells. Growth was completed in 54 days with death occurring between the 54th and 75th day.

(2) Road salts - Increased concentrations of rock salt and pure sodium chloride have greater effects on the growth and natality of M. securis (Fig. 41, 42 and Tables 14, 15) than does calcium chloride (Fig. 43, Table 16). Growth rates are faster and the natalities higher in control dishes than in experimental dishes containing rock salt and sodium chloride. Growth of M. securis is similar in the control dishes and dishes containing 1000 and 800 mg/l of calcium chloride but the natalities

Table 12. Changes in the pH and sulfate concentrations after adding Carp Pond soil to growth dishes.

Before adding soil		Two weeks after adding soil	
pH	sulfate mg/l	pH	sulfate mg/l
7.00	0	6.80	80
3.90	20	6.60	92
3.10	40	6.40	108
2.75	60	6.30	118
2.60	80	6.16	128
2.45	100	6.10	144
2.25	200	5.65	230
2.15	300	5.45	333
2.00	400	5.15	427
1.90	500	4.70	515

Fig. 40 Observed average growth in shell length of 15 Musculium securis adults in each of nine different sulfate concentrations (mg/l) in the laboratory.

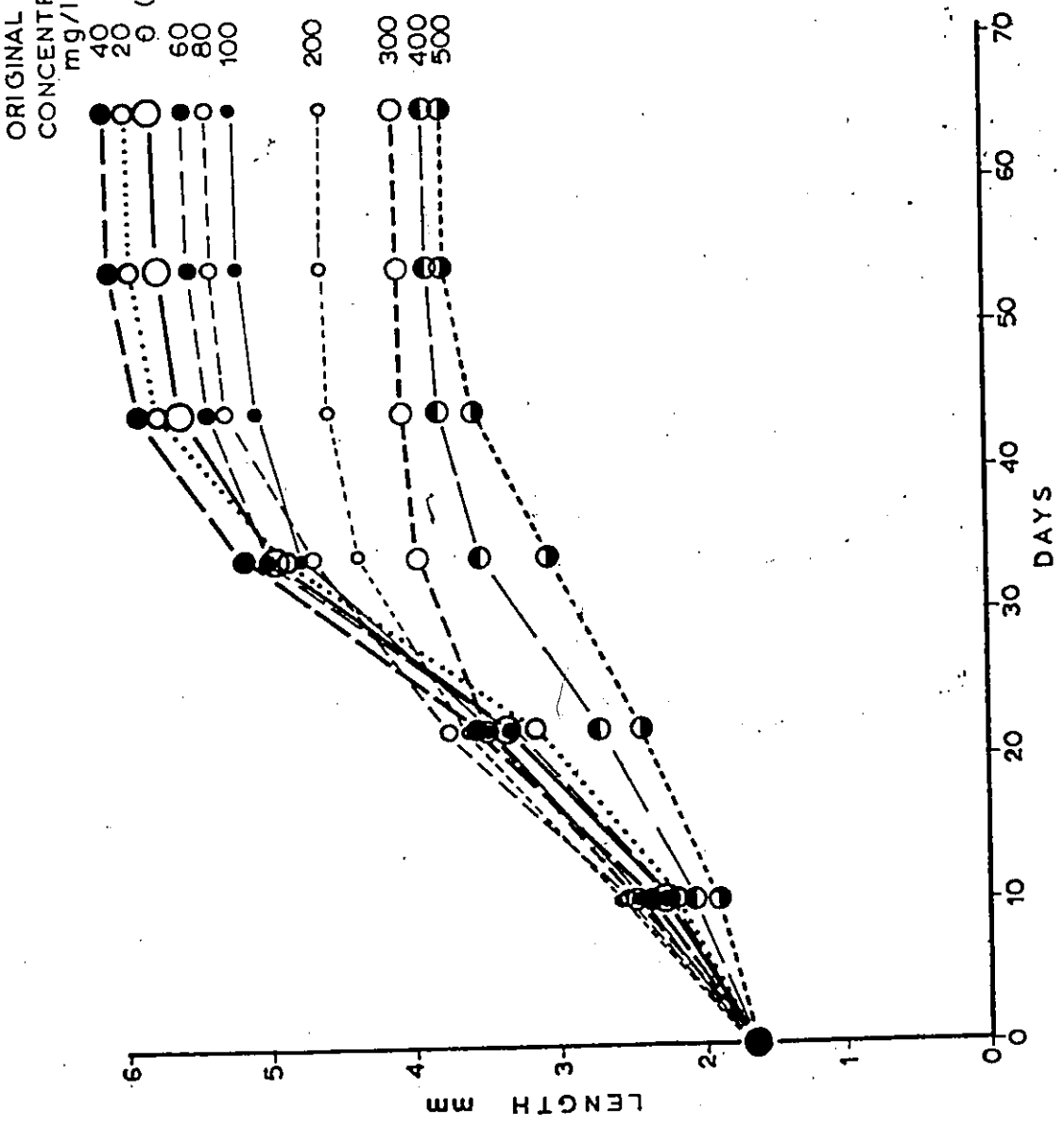

ORIGINAL SULFATE CONCENTRATION mg/l
40
20
0 (CONTROL)
60
80
100
200
300
400
500
LENGTH mm
DAYS
0
10
20
30
40
50
60
70
1
2
3
4
5
6

Table 13. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown in nine concentrations of sulfate. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all concentrations. Each concentration was replicated three times with five clams in each replicate. Means side-scored by the same line are not significantly different at P = 0.05.

Original sulfate concentration mg/l	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
40	1/Y	0.146	(0.012)	0.487	(0.010)	0.987	(0.0031)	52.0	(9.2)
	1/Y'	6.85	(0.56)	-5.39	(0.52)				
20	1/Y	0.157	(0.013)	0.475	(0.010)	0.937	(0.0031)	43.1	(7.5)
	1/Y'	6.36	(0.52)	-4.92	(0.49)				
0	1/Y	0.164	(0.011)	0.469	(0.009)	0.922	(0.0021)	43.6	(5.6)
	1/Y'	6.10	(0.35)	-4.55	(0.32)				
60	1/Y	0.168	(0.018)	0.463	(0.014)	0.968	(0.0030)	43.3	(9.2)
	1/Y'	5.85	(0.40)	-4.31	(0.38)				
80	Y	6.00	(0.35)	-4.62	(0.33)	0.978	(0.0026)	40.7	(1.2)
100	Y	5.61	(0.15)	-4.16	(0.15)	0.967	(0.0028)	39.7	(0.6)
200	Y	4.95	(0.11)	-3.40	(0.11)	0.961	(0.0035)	21.0	(15.6)
300	Y	4.33	(0.08)	-2.78	(0.09)	0.954	(0.0043)	10.7	(2.9)
400	Y	4.27	(0.46)	-2.65	(0.43)	0.994	(0.0043)	10.3	(5.7)
500	Y	4.09	(0.21)	-2.50	(0.20)	0.972	(0.0048)	0	

Fig. 41 Observed average growth in shell length of 15 Musculium securis adults in each of five different concentrations (mg/l) of sodium chloride in the laboratory. Control concentration = 0 mg/l.

CONTROL
200 mg/l
400 mg/l
600 mg/l
800 mg/l
1000 mg/l
LENGTH mm
DAYS
0
1
2
3
4
5
6
10
20
30
40
50
60
70
80

Table 14. Asymptotic growth data for the regression $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown in five concentrations of sodium chloride. Three replicates were made for each concentration with five clams in each replicate. Means side-scored by the same line are not significantly different at P = 0.05.

Sodium chloride concentration	Growth form	Means and standard deviations ( ) of asymptotic regression data for $1/Y = A + BR^X$						Mean natality and standard deviation ( ) per growth dish	
mg/l		A mm		B mm		R			
0 - Control	1/Y	0.144	(0.015)	0.485	(0.015)	0.982	(0.0021)	54.3	(5.1)
200	1/Y	0.185	(0.018)	0.444	(0.018)	0.985	(0.0044)	28.7	(2.1)
400	1/Y	0.208	(0.019)	0.419	(0.014)	0.983	(0.0026)	22.0	(7.6)
600	1/Y	0.222	(0.046)	0.406	(0.042)	0.978	(0.0038)	8.7	(4.1)
800	1/Y	0.244	(0.038)	0.385	(0.031)	0.958	(0.0042)	5.0	(5.6)
1000	1/Y	0.251	(0.040)	0.377	(0.036)	0.956	(0.0058)	0	

Fig. 42 Observed average growth in shell length of 15 Musculium securis adults in each of five different concentrations (mg/l) of rock salt in the laboratory. Control concentration = 0 mg/l.

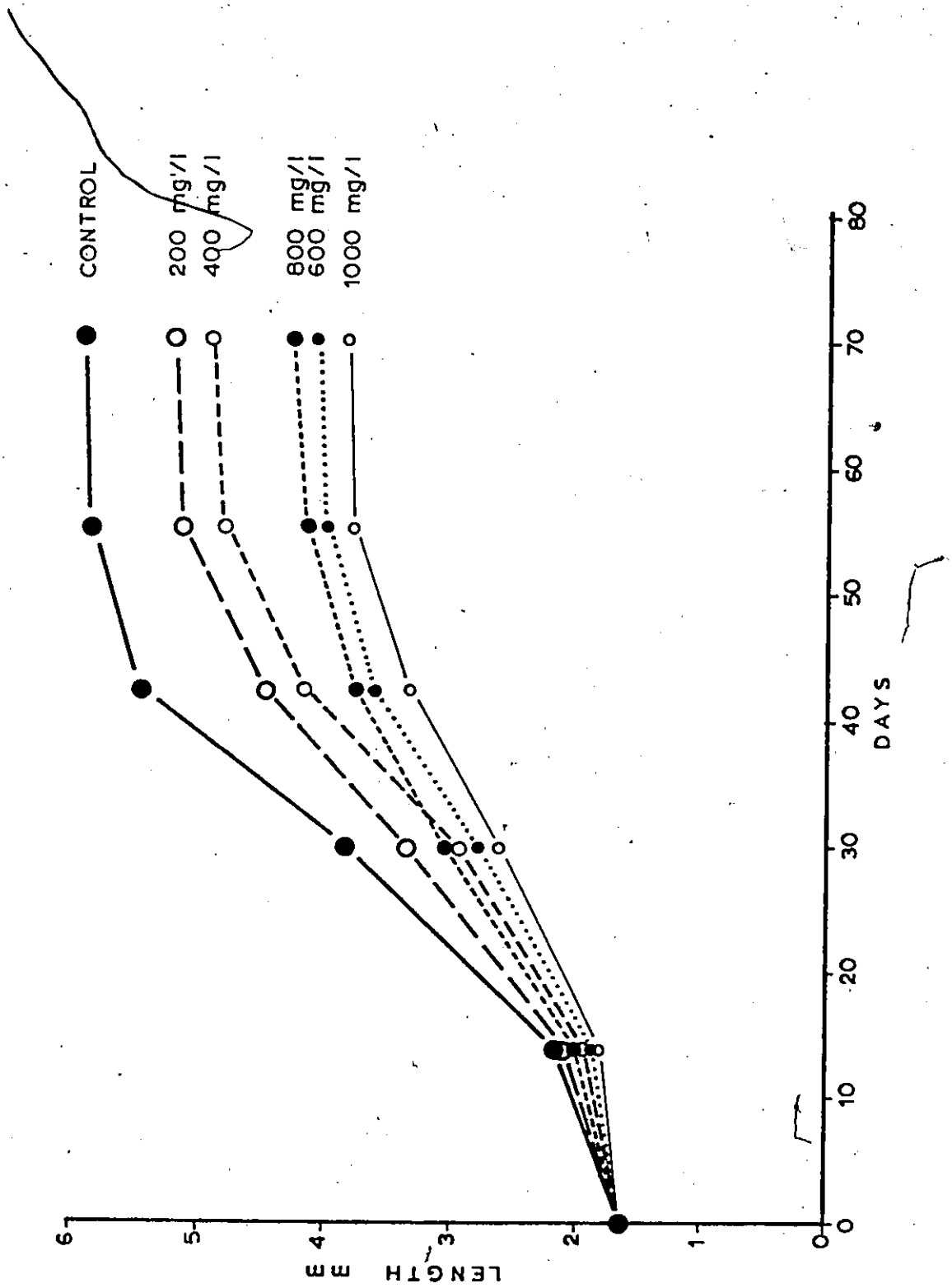

CONTROL
200 mg/l
400 mg/l
800 mg/l
600 mg/l
1000 mg/l
LENGTH mm
DAYS
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80

Table 15. Asymptotic growth data for the regression $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown in five concentrations of rock salt. Three replicates were made for each concentration with five clams in each replicate. Means side-scored by the same line are not significantly different at P = 0.05.

Rock salt concentration	Growth form	Means and standard deviations ( ) of asymptotic regression data for $1/Y = A + BR^X$						Mean natality and standard deviation ( ) per growth dish	
mg/l		A mm		B mm		R			
0 - Control	1/Y	0.144	(0.015)	0.485	(0.015)	0.982	(0.0021)	54.3	(5.1)
200	1/Y	0.180	(0.011)	0.450	(0.011)	0.983	(0.0043)	33.7	(2.5)
400	1/Y	0.192	(0.012)	0.434	(0.012)	0.978	(0.0041)	19.3	(3.2)
800	1/Y	0.228	(0.030)	0.400	(0.030)	0.965	(0.0038)	8.3	(2.7)
600	1/Y	0.230	(0.024)	0.398	(0.023)	0.977	(0.0028)	3.0	(1.5)
1000	1/Y	0.260	(0.048)	0.368	(0.049)	0.953	(0.0049)	0	

Fig. 43 Observed average growth in shell length of 15 Musculium securis adults in each of five different concentrations (mg/l) of calcium chloride. Control concentration = 0 mg/l.

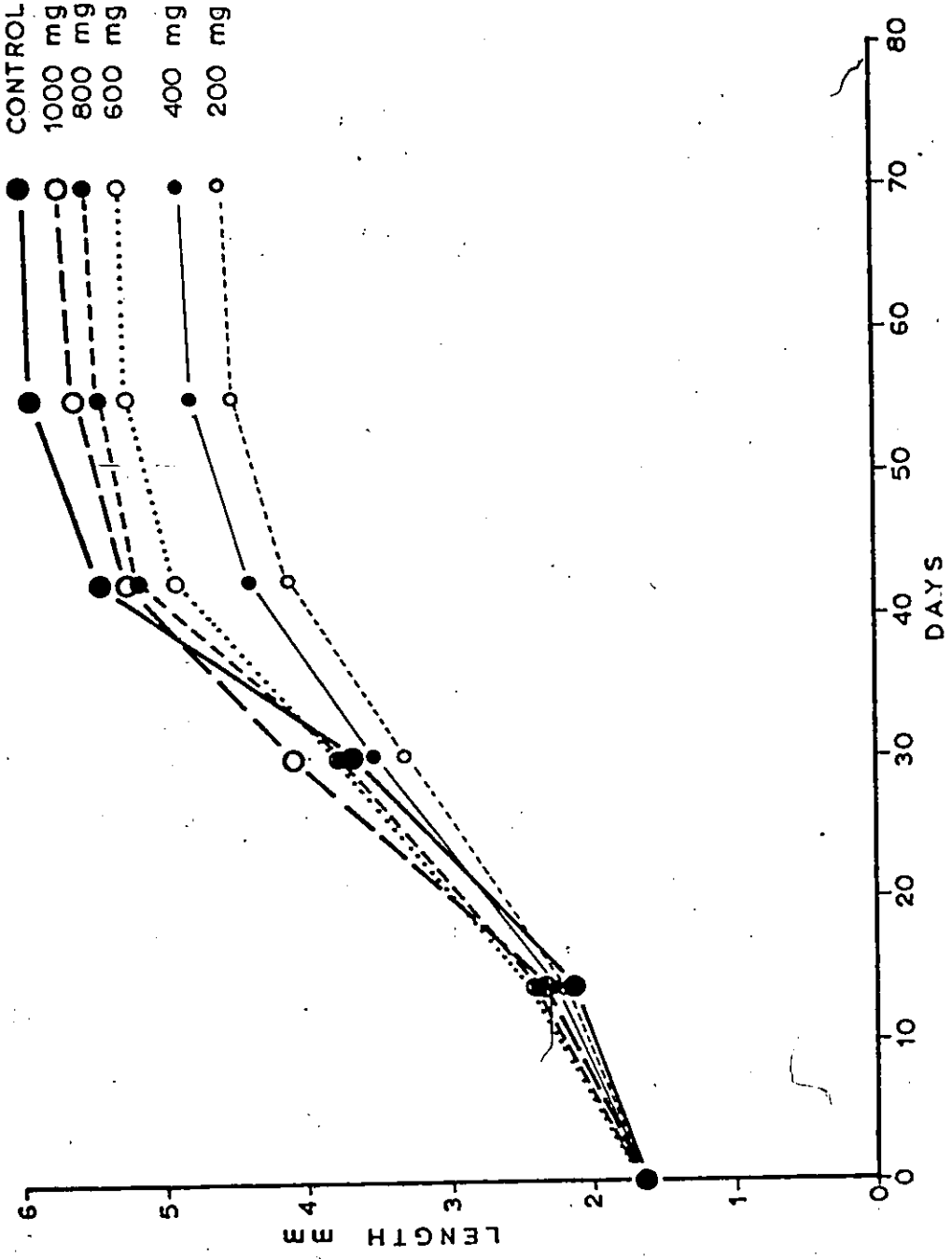

CONTROL
1000 mg/l
800 mg/l
600 mg/l
400 mg/l
200 mg/l
LENGTH mm
DAYS
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80

Table 16. Asymptotic growth data for the regression $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown in five concentrations of calcium chloride. Three replicates were made for each concentration with five clams in each replicate. Means side-scored by the same line are not significantly different at P = 0.05.

Calcium chloride concentration mg/l	Growth form	Means and standard deviations ( ) of asymptotic regression data for $1/Y = A + BR^X$						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
0 - Control	1/Y	0.144	(0.015)	0.485	(0.015)	0.982	(0.0021)	54.3	(5.1)
1000	1/Y	0.158	(0.035)	0.475	(0.038)	0.985	(0.0036)	30.3	(7.5)
800	1/Y	0.172	(0.028)	0.460	(0.031)	0.994	(0.0037)	40.7	(8.1)
600	1/Y	0.181	(0.018)	0.451	(0.020)	0.989	(0.0030)	31.3	(5.1)
400	1/Y	0.193	(0.025)	0.433	(0.022)	0.988	(0.0036)	22.0	(8.5)
200	1/Y	0.206	(0.031)	0.420	(0.030)	0.981	(0.0040)	28.7	(2.1)

differ in these dishes. Increased concentrations of road salt have little effect on the longevity since adults in all dishes died on or before the 70th day of growth.

The effects of calcium chloride on shell morphology of M. securis were mentioned earlier (p. 20, Fig. 8). These effects appear to be similar in all concentrations of calcium chloride tested.

(3) Pulp and paper wastes - The growth of M. securis at various distances above and below pulp and paper outfalls are shown in Fig. 44. Growth rates and natalities are larger above the outfalls than below the outfalls (Table 17). In general, faster growth rates and higher natalities occur with increased distance below the outfalls.

As many as eight leeches of the species, Helobdella stagnalis, were present in the growth chambers above the outfalls. The mortalities of M. securis in the chambers were low and most produced young so that the leeches had little effect on the production of first litters of young. Most M. securis adults died by the end of August in the control tubes but it is not known whether they died of natural causes or leech predation.

High mortalities of M. securis occur in growth tubes below the outfalls. No leeches occur in the growth tubes below the outfalls. Premature deaths of adults are probably attributable to chemicals or other properties of the effluents. Table 18 gives some physical and chemical properties of the water at various distances from the outfalls during the study period.

(4) Raw sewage and slaughter house wastes - There is very little growth and reproduction of M. securis in a creek carrying raw sewage and slaughter house wastes (Fig. 45, Table 19). The quality of water in the creek is

Fig. 44 Observed average growth in shell length of Musculium securis adults isolated in growth tubes placed above and several locations below a pulp and paper outfalls. Numbers of specimens used are given in Table 17.

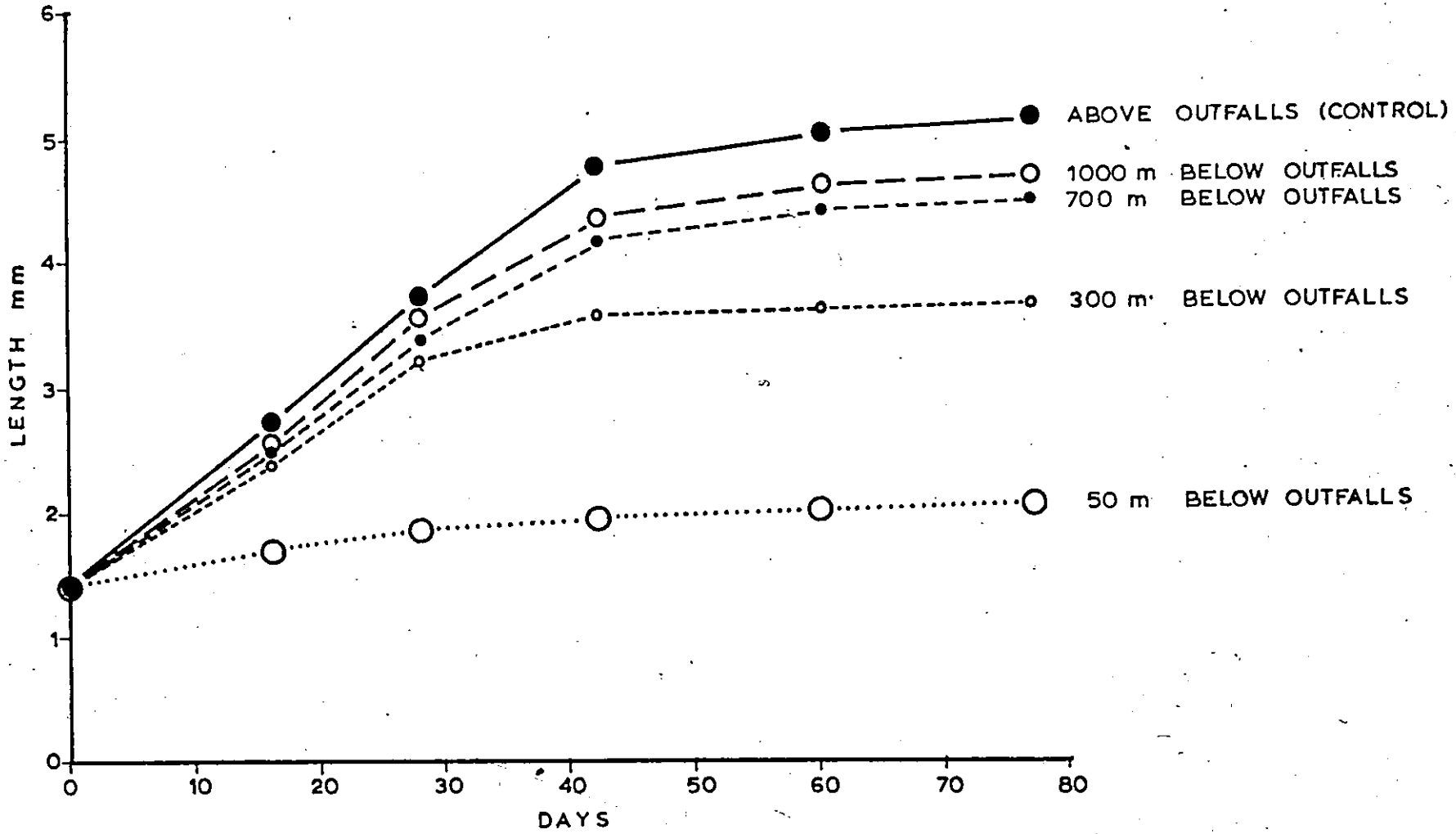

LENGTH mm
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
DAYS
ABOVE OUTFALLS (CONTROL)
1000 m BELOW OUTFALLS
700 m BELOW OUTFALLS
300 m BELOW OUTFALLS
50 m BELOW OUTFALLS

Table 17. Asymptotic growth data for the regression $Y = A + BR^X$ and the natalities of Musculium securis adults maintained in growth tubes and placed at various distances above and below a pulp and paper outfalls. Means side-scored by the same line are not significantly different at $P = 0.05$.

Distance from outfalls	Number of clams that survived[a]	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$						Mean natality and standard deviation ( ) per growth tube	
		A mm		B mm		R			
ABOVE OUTFALLS	16	5.60	(0.56)	-4.21	(0.53)	0.991	(0.0034)	3.8	(1.6)
BELOW OUTFALLS									
1000 m	14	5.28	(0.67)	-3.91	(0.65)	0.982	(0.0027)	2.1	(0.6)
700 m	12	4.91	(0.58)	-3.60	(0.54)	0.978	(0.0038)	1.8	(1.1)
300 m	14	4.27	(0.81)	-2.94	(0.76)	0.972	(0.0074)	0.8	(1.3)
50 m	4	Little or no growth						0	

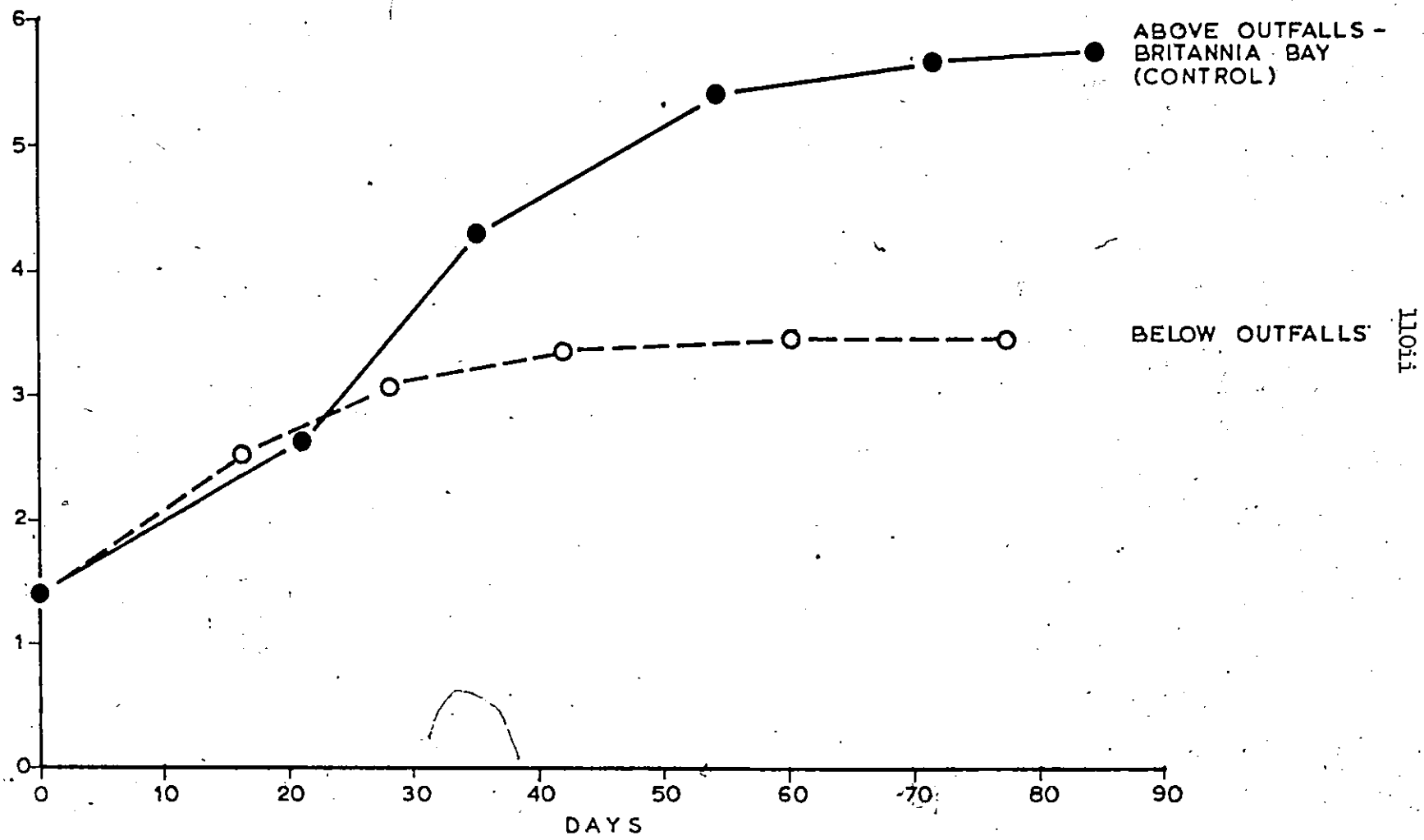
[a] A total of twenty clams was placed at each distance from the outfalls but only the numbers indicated survived.

Table 18. The means and ranges ( ) of several factors of the water at various distances above and below pulp and paper outfalls. The values are based on five water samples taken at approximately two week intervals. All values are in mg/l unless indicated otherwise.

Parameters	Above outfalls	Below outfalls			
		50 m	300 m	700 m	1000 m
Temperature °C	17.6 (8.0-22.5)	18.6 (9.0-24.5)	17.8 (8.0-22.5)	17.6 (8.0-22.5)	17.6 (8.0-22.5)
Alkalinity	25.0 (18.0-30.3)	22.2 (18.0-26.0)	24.7 (18.0-28.0)	24.5 (18.0-29.0)	24.4 (18.0-29.6)
Conductivity µm/cm	62.2 (48.2-80.0)	60.4 (43.2-72.1)	64.7 (46.7-75.0)	67.3 (50.0-78.5)	65.1 (48.5-78.2)
Dissolved oxygen	8.5 (7.0-12.0)	6.5 (5.0-9.0)	7.5 (6.0-11.0)	7.5 (7.0-12.0)	7.5 (7.0-12.0)
Hardness (calcium)	32.0 (25.2-36.3)	43.6 (35.3-64.4)	30.1 (27.3-34.4)	38.6 (27.1-45.5)	39.5 (23.1-46.0)
Hardness (total)	49.7 (42.4-54.7)	61.3 (53.0-83.2)	47.8 (44.0-54.8)	53.4 (42.1-60.0)	55.3 (41.7-60.0)
pH	6.9 (6.5-7.5)	6.7 (6.5-7.0)	6.7 (6.5-7.0)	6.7 (6.5-7.0)	6.7 (6.5-7.0)
Sulfate	17.8 (10.0-23.0)	30.4 (10.0-62.0)	32.3 (10.0-55.0)	18.6 (10.0-20.0)	15.6 (10.0-20.0)
Biochemical oxygen demand (5 days, 20°C)[a]	1.6 (0.5-4.0)			6.8 (0.4-29.4)	
Total coliform bacteria (Most probable number per 100 cc)[a]	(2300-21000)			(9300-2400000)	

[a] Values taken from Mackie (1971)

Fig. 45 Observed average growth in shell length of Musculium securis adults isolated in growth tubes placed above (number of specimens, N = 5) and below (N = 13) slaughter house and raw sewage outfalls.


6
5
4
3
2
1
0
0
10
20
30
40
50
60
70
80
90
DAYS
ABOVE OUTFALLS - BRITANNIA BAY (CONTROL)
BELOW OUTFALLS

1110i1

Table 19. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults maintained in growth tubes and placed above and below slaughter house and raw sewage outfalls. All differences are significant at the 5% level.

Location	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality & standard deviation ( ) per growth tube	
		A mm		B mm		R			
Above outfalls[a]	1/Y	0.151	(0.010)	0.477	(0.010)	0.985	(0.0023)	9.8	(2.4)
	1/Y'	6.63	(0.42)	-5.14	(0.40)				
Below outfalls	Y	4.00	(0.76)	-2.65	(0.72)	0.980	(0.0066)	0	

[a] Data is taken from the isolate controls of the interspecific competition experiment (Table 22).

Table 20. The means and ranges of several factors of the water below a slaughter house and several raw sewage outfalls. The values are based on five water samples taken at approximately two week intervals. Values are in mg/l unless indicated otherwise.

Parameters	Mean	Range
Temperature	17.6	8.0-22.5
Alkalinity	28.8	24.0-36.0
Conductivity um/cm	70.2	62.0-80.0
Dissolved oxygen	5.5	3.0-8.0
Hardness (calcium)	35.6	28.6-53.2
Hardness (total)	56.4	48.7-72.3
pH	6.7	6.5-7.0
Sulfate	11.8	7.0-25.0
Biochemical oxygen demand (5 days, 20°C)[a]	3.8	0.6-16.5
Total coliform bacteria (MPN/100 cc)[b]		43000-2400000

[a] Taken from Mackie (1971)

[b] MPN = Most Probable Number, taken from Mackie (1971)

given in Table 20; the physics and chemistry of the water in Britannia Bay has already been described (see Fig. 14 - 23).

Effect of population density

The effects of five different densities on the growth and reproduction of M. securis are shown in Fig. 46 and Table 21. The results show that (a) there is less length variation in populations with small densities, (b) this variation tends to be constant with time in populations with small densities and increases with time to an asymptotic value in populations with large densities, (c) some individuals in each density grow at maximum rates, (d) growth curves tend to be sigmoid for the average individual in small densities and hyperbolic for the average individual in large densities, and (e) the litter size per reproductive individual and the total number of young in each dish approaches an asymptotic value as the density increases.

All adults in densities of 5 and 10 individuals per dish mature to produce young. Only 13 to 19 adults mature to produce young in dishes with densities of 20, 30, and 40 individuals. Therefore, on the basis of the number of reproductive individuals, the carrying capacity of each dish is approximately 16 parents. Since as many as 40 to 86 newborns are produced in the growth dishes, the reproductive adults produce a surplus of 24 to 70 young. Fig. 47 shows that the average number of young released per reproductive parent decreases with increased densities until the carrying capacity is reached; then the litter size per reproductive parent remains constant.

The mortality increases with increased density. No adults die prematurely in dishes with densities of 5 individuals. The number of

Fig. 46 Observed average growth in shell length of Musculium securis in laboratory growth dishes containing densities of 5, 10, 20, 30, or 40 clams. Vertical lines represent observed range in length.

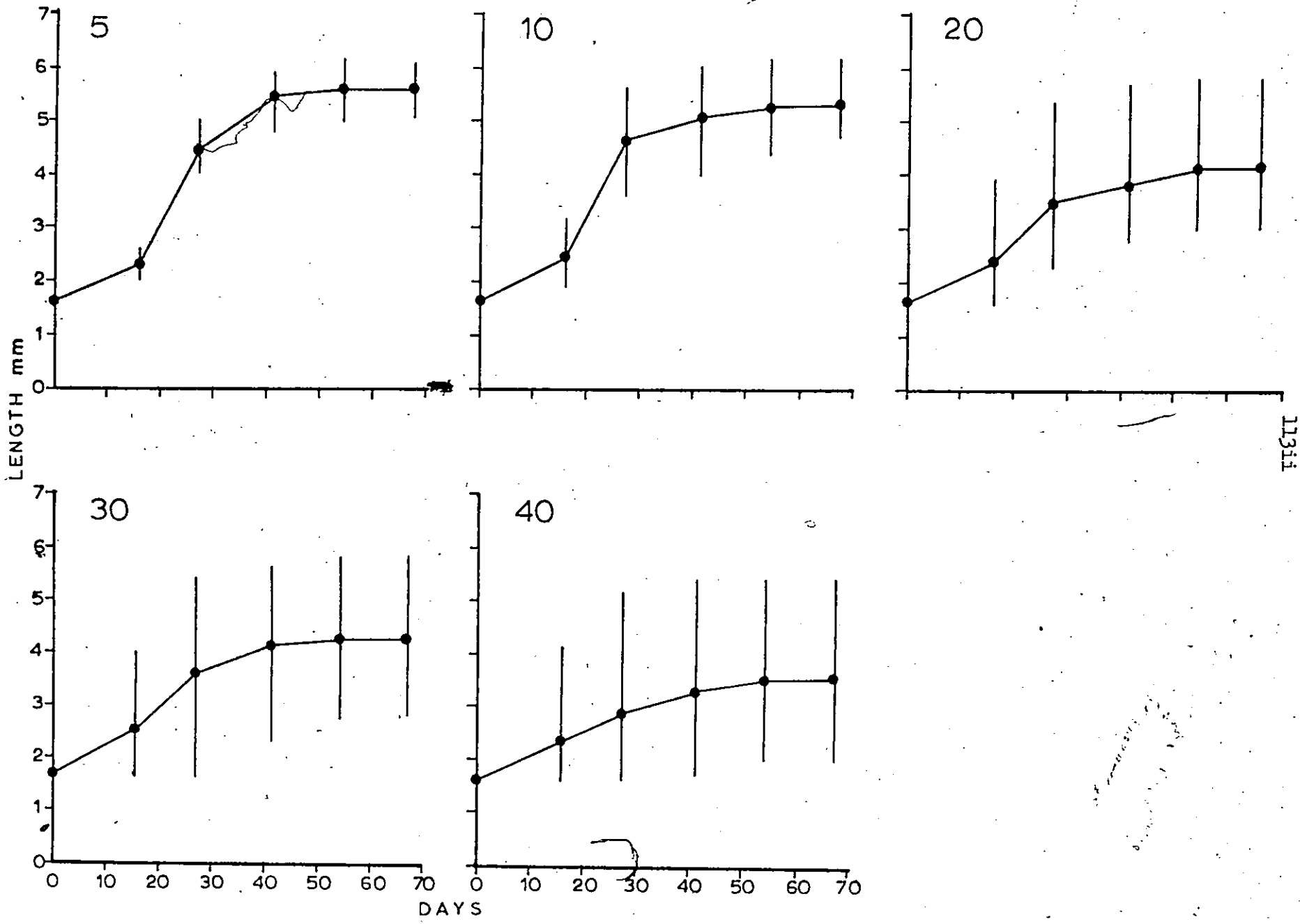
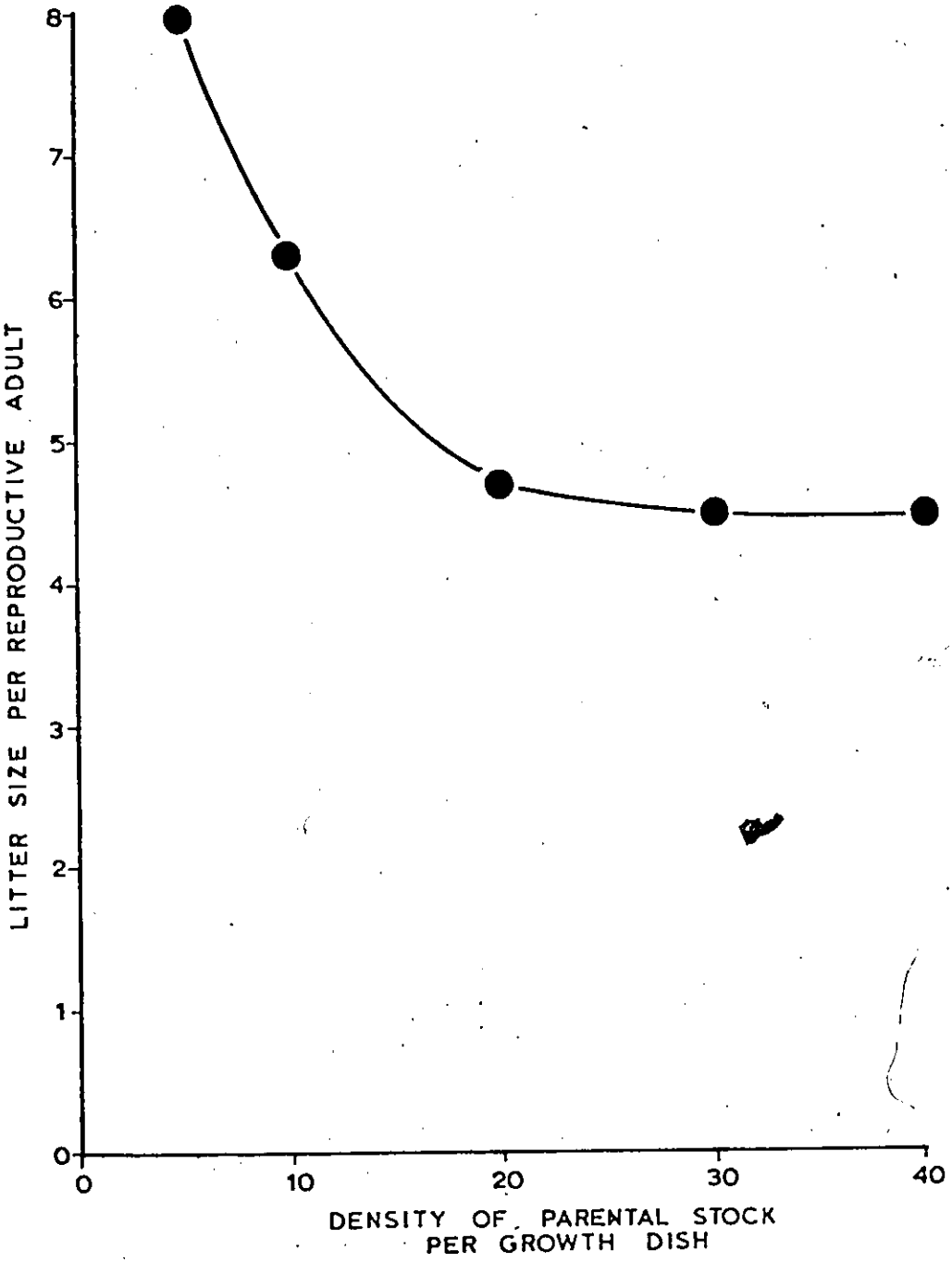

5
10
20
30
40
LENGTH mm
DAYS
0
1
2
3
4
5
6
7
0 10 20 30 40 50 60 70

Table 21. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown in five different densities. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all densities. Three replicates were made for each density. Means side-scored by the same line are not significantly different at P = 0.05.

Number of clams per dish	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean natality and standard deviation ( ) per growth dish	
		A mm		B mm		R			
5	1/Y	0.139	(0.008)	0.490	(0.008)	0.986	(0.0022)	47.0	(3.6)
	1/Y'	7.19	(0.35)	-5.70	(0.34)				
10	Y	6.59	(0.33)	-5.12	(0.31)	0.974	(0.0034)	63.0	(2.5)
20	Y	5.16	(0.62)	-3.61	(0.58)	0.978	(0.0073)	66.3	(3.0)
30	Y	4.99	(0.72)	-3.43	(0.70)	0.973	(0.0082)	71.3	(2.7)
40	Y	4.73	(0.80)	-3.18	(0.76)	0.983	(0.0077)	73.7	(3.7)

Fig. 47 Relation between the average litter size per reproductive adult and the density of parental stock in laboratory growth dishes. Curve was fitted by eye.


LITTER SIZE PER REPRODUCTIVE ADULT
0
1
2
3
4
5
6
7
8
0
10
20
30
40
DENSITY OF PARENTAL STOCK
PER GROWTH DISH

premature mortalities range from 1-2, 2-3, 3-4, and 4-8 in dishes with densities of 10, 20, 30, and 40 adults, respectively. Most of the adults that die prematurely are less than 3.00 mm in length. The remaining adults essentially complete growth after 67 days when many of the reproductive adults die. The remaining reproductive individuals and most of the non-reproductive ones die between 67 and 81 days of growth.

Effect of interspecific competition

The growth curves of M. securis and M. transversum as they compete between and amongst themselves in different densities in the shore zone of Britannia Bay are shown in Fig. 48. In the absence of competition, the growth curves tend to be sigmoid for both species (Fig. 48a); M. securis essentially completes growth in 54 days and M. transversum in 71 days. In the other controls, (Fig. 48b, c) intraspecific competition occurs and the growth per average individual is significantly different from those in the isolate-controls (Table 22). During intraspecific competition, some adults of both species grow at maximum rates and complete growth very quickly but do not produce young until growth is completed. On the basis of the number of reproductive individuals, the carrying capacity of the growth chambers is approximately 6 adults.

Various degrees of interspecific competition between M. securis and M. transversum under overcrowded conditions are shown in Fig. 48d - j. When M. securis greatly outnumbers M. transversum, the form of growth of the former species resembles that in the intraspecific-controls (cf. Fig. 48d and 48b); the form of growth of the latter species resembles that in isolate-controls (cf. Fig. 48d and 48a), but the magnitudes of the growth parameters and natalities differ significantly. As the numbers of

Fig. 48 Observed average growth in shell length of Musculium securis (———•) and Musculium transversum (------o) in growth tubes placed in the shore zone of Britannia Bay and containing:

a. Isolated M. securis or M. transversum

b. 20 M. securis or 20 M. transversum

c. 10 M. securis or 10 M. transversum

d. 19 M. securis and 1 M. transversum

e. 18 " " 2 "

f. 16 " " 4 "

g. 10 " " 10 "

h. 4 " " 16 "

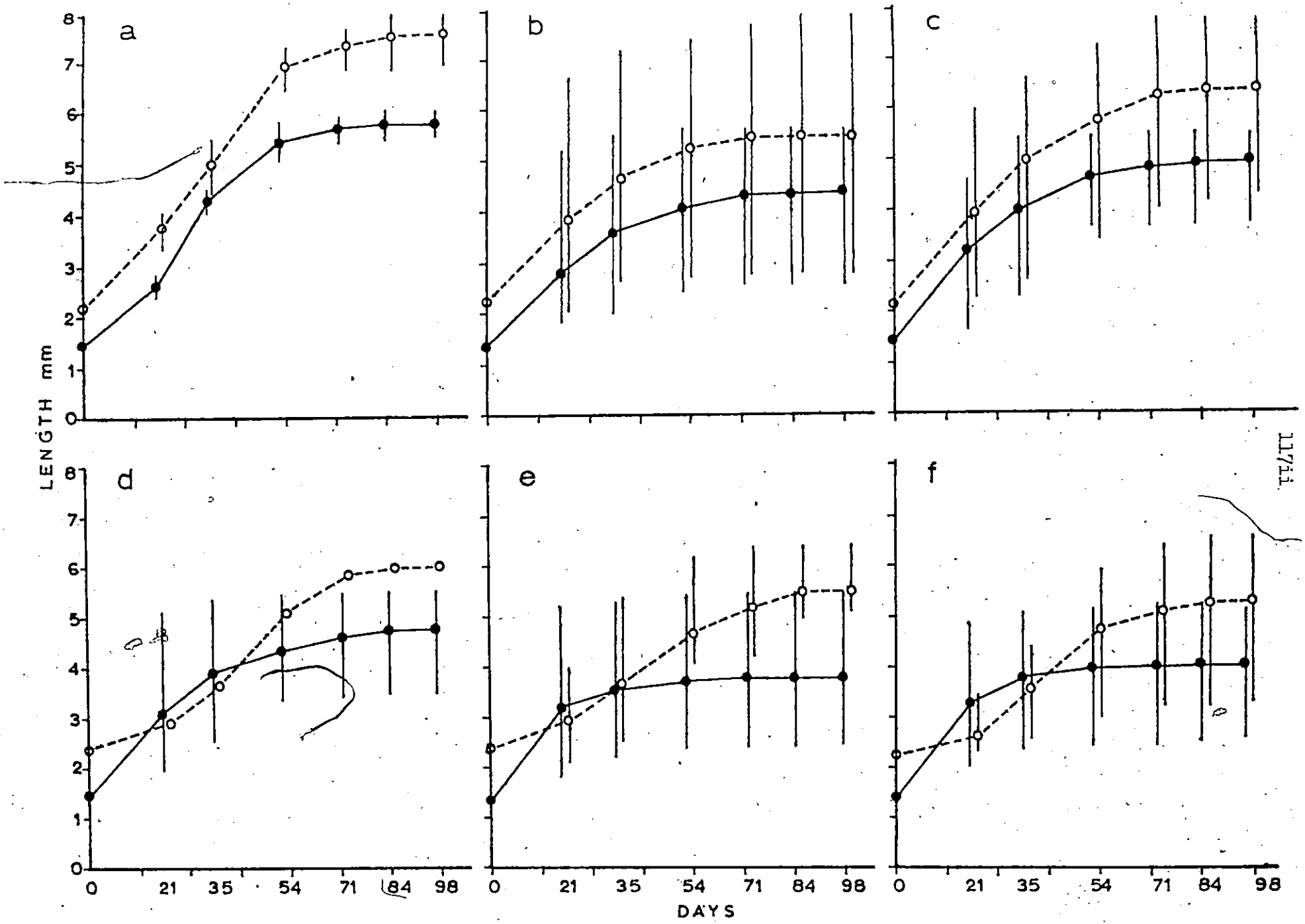
i. 2 " " 18 "

j. 1 " " 19 "

k. 9 " " 1 "

l. 1 " " 9 "

Vertical lines represent observed range in length.



117ii

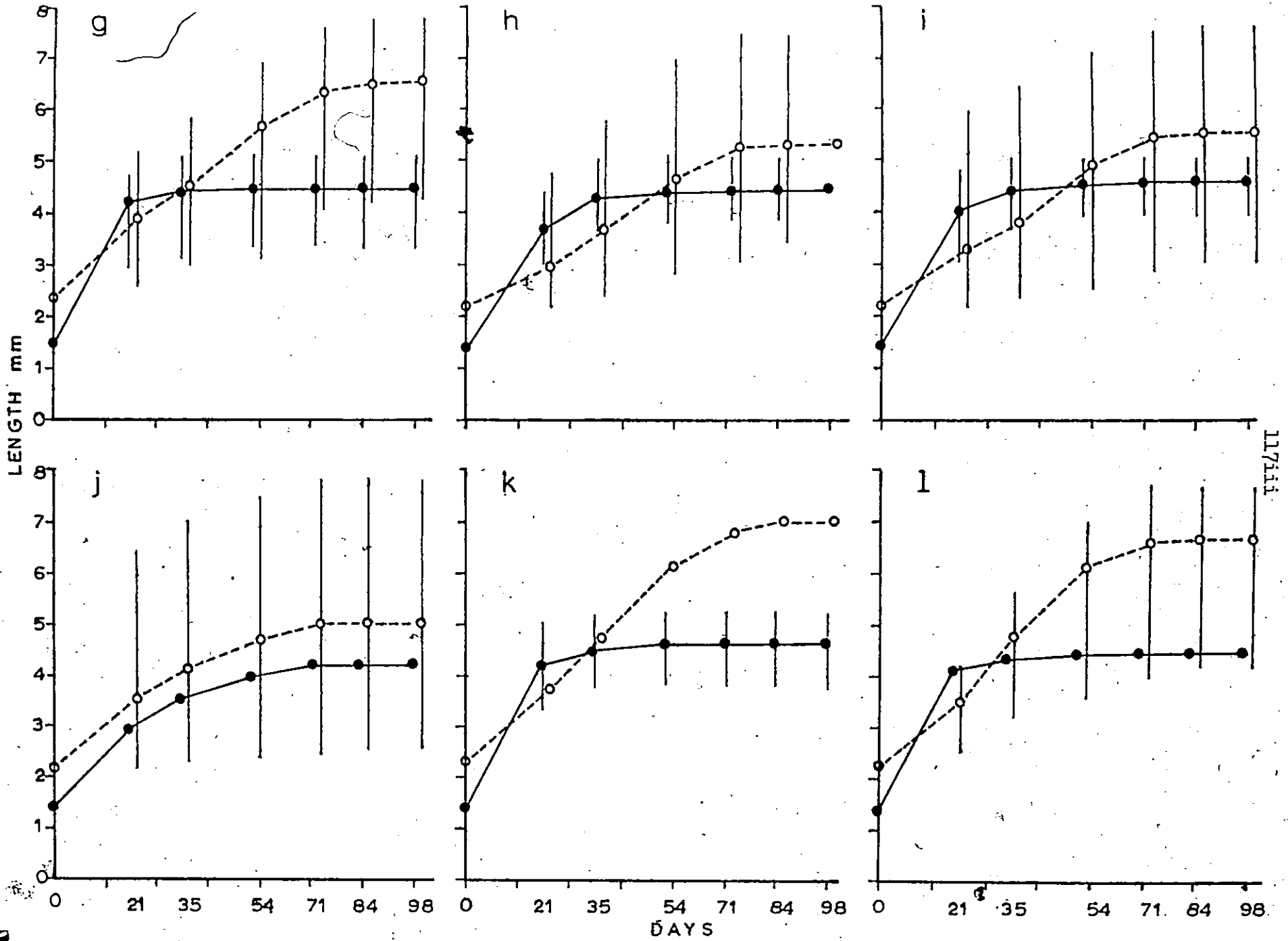

g
h
i
j
k
l
LENGTH mm
0
1
2
3
4
5
6
7
8
0
21
35
54
71
84
98
DAYS

Table 22. Asymptotic growth data for the regressions $Y = A + BR^X$ and $1/Y = A + BR^X$ and the average litter size per reproductive adult of Musculium securis and M. transversum during interspecific competition in Britannia Bay growth tubes in the shore zone. The A and B values of the logistic equation are also transformed to permit tests of significant differences among all groups within a species. Means side-scored by the same line are not significantly different at P = 0.05.

Fig. 48:	Initial number of adults in growth tubes	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^X$ and $1/Y = A + BR^X$ (or $1/Y' = A' + B'R^X$)						Mean litter size and standard deviation ( ) per reproductive parent	
	Musculium securis		A mm		B mm		R			
a	Isolates (Control)	1/Y	0.151	(0.010)	0.477	(0.010)	0.984	(0.0023)	9.8	(2.4)
		1/Y'	6.63	(0.42)	-5.14	(0.40)				
c	10 (Control)	Y	5.37	(0.75)	-3.91	(0.72)	0.973	(0.0095)	7.0	(0.3)
k	9	Y	5.10	(0.85)	-3.70	(0.83)	0.981	(0.0048)	7.2	(0.6)
a	19	Y	5.27	(0.81)	-3.87	(0.79)	0.974	(0.0100)	4.5	(0.8)
b	20 (Control)	Y	4.86	(0.85)	-4.40	(0.83)	0.965	(0.0141)	4.5	(0.4)
f	16	Y	4.71	(0.73)	-3.25	(0.68)	0.969	(0.0112)	4.7	(1.0)
e	18	Y	4.63	(0.94)	-3.20	(0.92)	0.976	(0.0130)	4.4	(0.5)
g	10	Y	4.96	(0.93)	-3.50	(0.90)	0.962	(0.0097)	3.4	(0.8)
i	2	Y	5.01	(0.63)	-3.52	(0.58)	0.987	(0.0042)	2.3	(2.1)
h	4	Y	4.93	(0.65)	-3.50	(0.62)	0.983	(0.0083)	2.2	(0.5)
l	1	Y	4.98	(0.45)	-3.53	(0.41)	0.987	(0.0043)	1.7	(1.5)
j	1	Y	4.51	(0.51)	-3.04	(0.50)	0.982	(0.0013)	2.3	(0.6)

continued next page

Table 22 (continued)

Fig. 48:	Initial number of adults in growth tubes	Growth form	Means and standard deviations ( ) of asymptotic regression data for $Y = A + BR^x$ and $1/Y = A + BR^x$ (or $1/Y' = A' + B'R^x$)						Mean litter size and standard deviation ( ) per reproductive parent	
			A mm		B mm		R			
	Musculium transversum									
a	Isolates (Control)	1/Y	0.111	(0.018)	0.534	(0.018)	0.985	(0.0031)	11.8	(3.2)
		1/Y'	9.02	(0.42)	-7.00	(0.40)				
c.	10 (Control)	Y	8.75	(1.00)	-6.72	(0.98)	0.970	(0.0103)	9.5	(0.3)
l	9	1/Y	0.124	(0.013)	0.524	(0.012)	0.985	(0.0055)	9.3	(0.7)
		1/Y'	8.07	(0.88)	-6.00	(0.85)				
k	1	1/Y	0.121	(0.014)	0.520	(0.015)	0.988	(0.0037)	6.3	(0.6)
		1/Y'	8.27	(0.92)	-6.25	(0.88)				
h	16	Y	6.14	(1.01)	-4.08	(0.98)	0.983	(0.0104)	6.0	(0.8)
i	18	Y	6.32	(0.96)	-4.30	(0.94)	0.972	(0.0130)	6.0	(0.4)
j	19	Y	6.11	(1.28)	-4.05	(1.24)	0.979	(0.0123)	6.1	(0.9)
b	20 (Control)	Y	6.08	(1.23)	-4.03	(1.20)	0.964	(0.0151)	6.4	(0.4)
g	10	Y	7.44	(0.91)	-5.43	(0.87)	0.971	(0.0122)	4.4	(0.3)
e	2	1/Y	0.146	(0.011)	0.502	(0.011)	0.990	(0.0037)	0.7	(1.2)
		1/Y'	6.85	(0.62)	-4.86	(0.60)				
f	4	1/Y	0.146	(0.010)	0.502	(0.010)	0.977	(0.0047)	0	
		1/Y'	6.85	(0.62)	-4.83	(0.60)				
d	1	1/Y	0.143	(0.012)	0.505	(0.011)	0.987	(0.0039)	0	
		1/Y'	6.98	(0.54)	-4.93	(0.51)				

M. securis decrease and M. transversum increase. greater proportions of M. securis adults complete 90% of their growth in the first 21 days (Fig. 48e, f). Acceleration in growth of M. transversum does not begin until after most M. securis adults have completed growth. Also, M. securis produces more young per reproductive adult than does M. transversum when the former species is more numerous than the latter.

When the numbers of the two species are equal, interspecific competition apparently favors the growth of M. transversum (Fig. 48g). Many M. securis adults complete growth in the first 21 days but there is a significant reduction in the average litter size (Table 22). Conversely, M. transversum responds with a significantly faster average growth rate, a larger average asymptotic value, and a larger average natality per reproductive adult than it does as a subdominant species.

As the numbers of M. transversum increase, the growth curves tend to undergo a transformation from a sigmoid shape (Fig. 48h, i) to a hyperbolic shape (Fig. 48j) and competition is primarily intraspecific.

When less crowded conditions prevail, interspecific competition is more apparent than intraspecific competition (Fig. 48k, l). There is no significant difference in the growth of M. transversum (nor of M. securis) when grown as a dominant (i.e. more numerous) and subdominant species. Under less crowded conditions, M. transversum produces as many or more young per reproductive individual, regardless of its relative abundance, than does M. securis (Table 22).

Evidently, interspecific competition between M. securis and M. transversum is not prevalent in the deeper waters of Britannia Bay.

Even as isolate-controls, M. transversum does not grow to sufficient size to produce young (Fig. 49) and M. securis attains smaller average lengths (4.85 mm, standard deviation = 0.34) and has smaller litter sizes (3.2, standard deviation = 0.8) in the 3 m depth than in the shore zone. Since there is no interspecific competition between the two species in the 3 m depth, further discussion is not necessary.

Effect of parasitism

Parasitism of M. securis is prevalent only in Britannia Bay. Dr. G. Gibson of Canadian Wildlife Services, Environment Canada, Ottawa, identified the parasites as rediae of the digenetic trematode, Crepidostomum cooperi Hopkins, 1931. The larval stages of the trematode develop in the digestive gland of M. securis. Infected digestive glands usually contain part or fully developed cercariae which apparently escape into the water and encyst in mayfly nymphs (Gibson, pers. comm.). Hexagenia sp. probably serves as the intermediate host since the nymphs are abundant (approx. 400/m^2) and usually accompany M. securis in samples taken from the 3 to 4 m depths of Britannia Bay. "The cercariae are known as ophthalmoxiphidiocercariae, because they have eyespots and a stylet; adults are common in many local fish including walleye, bass, and catfish, where they occur as intestinal parasites" (Gibson, pers. comm.). Only one species of parasite was found.

There is a seasonal occurrence of parasitism (Table 23) and only M. securis adults larger than 3.50 mm appear to be infected. Parasitism occurs with maximum intensity in late July and early August. The percentages given in Table 23 are based on infected adults that were alive at the time of sampling. Empty M. securis shells often appeared in samples

Fig. 49 Observed average growth in shell length of Musculium securis and Musculium transversum isolated in growth tubes and placed in the 3 m depth of Britannia Bay.

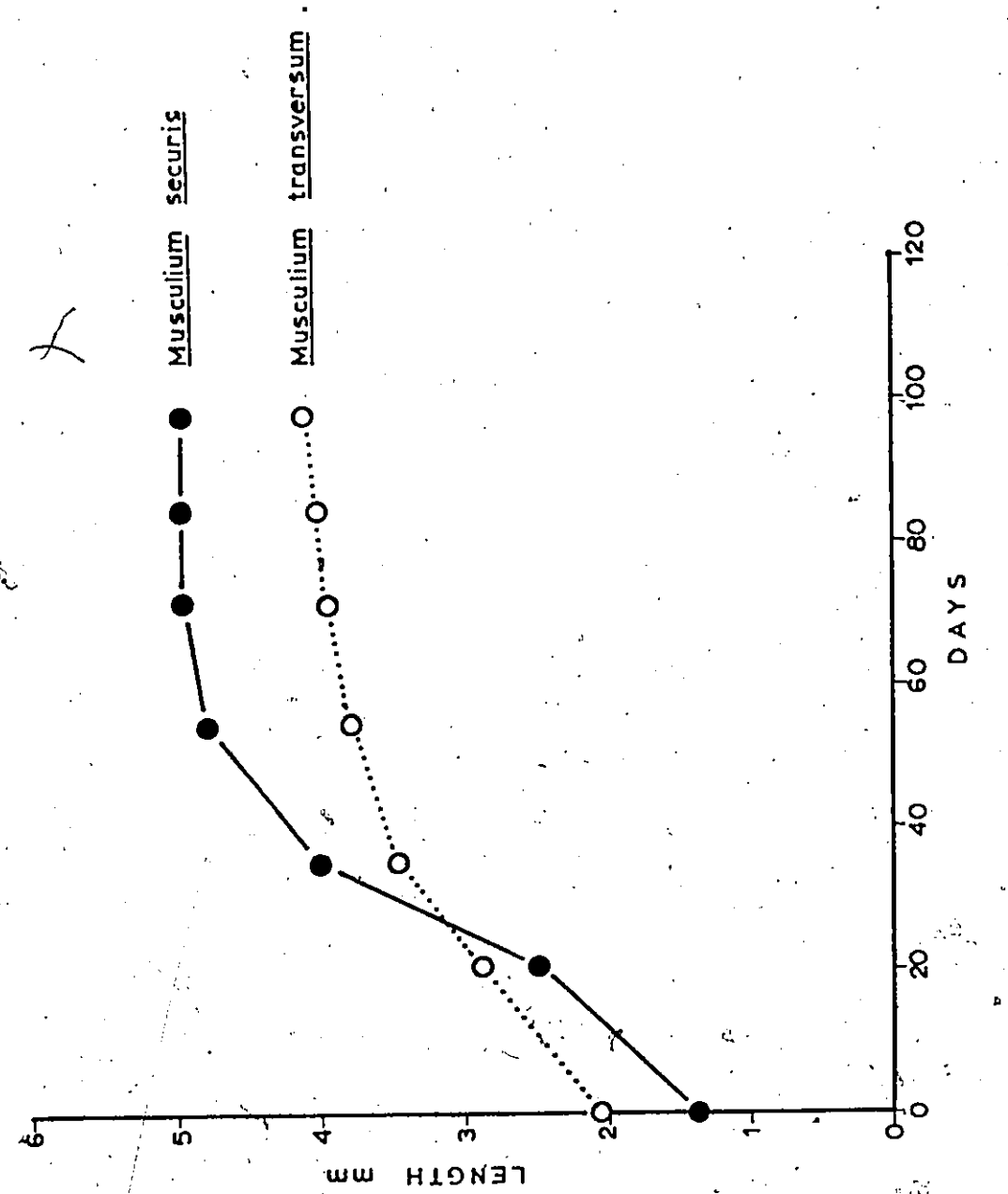

Musculium securis
Musculium transversum
LENGTH mm
DAYS
0
1
2
3
4
5
6
0
20
40
60
80
100
120

Table 23. Percentage of parents in the Britannia Bay population of Musculium securis that were parasitized in the summer months of 1970, 1971, and 1972. Only clams collected in July, August, and early September were parasitized.

1970			1971				1972			
July 13	July 29	Aug. 18	July 15	July 29	Aug. 3	Sept. 2	July 5	July 17	Aug. 20	Sept. 2
22.8%	27.8%	5.0%	2.0%	13.3%	25.0%	4.0%	4.0%	20.0%	21.8%	2.0%

Table 24. Some physical and chemical properties of Carp Pond soil and the correlation (r) between the number of Musculium securis newborns and the values of various soil factors in core samples.

Parameters	Number of core samples examined	Mean	Range	Standard deviations	Correlation (r) between number of newborns and soil factor values
Number of newborns per core	50	2.3	0-13	10.47	———
pH	20	5.43	5.02-6.10	0.32	0
Moisture content (%)	50	3.94	2.78-5.16	0.86	0.01
Organic matter content (as % volatile matter)	13	13.04	9.89-13.72	0.93	0
Exchangeable calcium (% by weight)	10	3.04	1.18-4.05	0.83	0
Cation exchange capacity (meq./g)	5	32.48	30.27-35.28	1.89	0

collected in July and August and it is possible that parasites caused the death of these clams. It is therefore conceivable that the percentages in Table 23 are under-estimates of the total M. securis population that is parasitized in Britannia Bay.

Adult M. securis as large as 6.05 mm in length were parasitized suggesting that parasitism does not affect the growth of clams. However, it is possible that such individuals had been parasitized only recently. Parasitism appears to have a greater effect on the reproductive capacity of M. securis. Of the parasitized adults, approximately 96% are devoid of brood sacs; the remaining 4% contain brood sacs but larvae are either absent or poorly developed.

Effect of predation

Evidently, predation of M. securis by the dominant fish species in Britannia Bay is negligible. Smith (MS 1973) examined the stomachs of 254 channel catfish and found only two M. securis specimens. Mr. Peter Rubec (pers. comm.) did not find any M. securis specimens in 50 stomachs of the brown bullhead, although many stomachs were empty. Walleyes and saugers have a piscivorous habit and only incidentally ingest mollusks (Osterberg, pers. comm.). Only the larger length classes of perch ingest a very small percentage of clams (Stobo, 1971).

No fish are present in Carp Pond, Greely Pond or Lac Bourgeois. Ducks are probably the most important predators of M. securis in these habitats but no data were collected to confirm this.

Estivation of Musculium securis

A contagious distribution of estivating newborns in Carp Pond was suspected since the variance ($s^2 = 10.42$) was larger than the mean

number of newborns (X = 2.3) per core sample. Using the X^2 test for goodness-of-fit to test for agreement with a negative binomial distribution (Elliot, 1971, p. 53), it was shown that the estivating newborns are indeed distributed contagiously. That is, the X^2 value of 14.02 is less than the 5% point of 18.3 with 10 degrees of freedom.

Correlation coefficients (r, Simpson et al, 1960, p. 240) were calculated to determine if there was any relationship between the abundance of M. securis and the magnitudes of certain factors in the soil. The results (Table 24) show that in no instance do the correlation coefficients exceed 0.01.

Only 3.4% of the total number of newborns found in the core samples taken in September, 1971 were dead. If all newborns experience birth at the same time (i.e. late July) and if monthly mortality rates are the same, only about 10% of the estivating population die during the estivation period (3 months).

Food Habits

The presence and absence of food organisms in the intestine of M. securis for a complete year of study in each habitat are given in Table 25. Usually the filamentous algae were fragmented beyond generic recognition and are often recorded at the phylum level. Clams less than 2.50 mm in length were not examined due to difficulty in separating out the intestinal contents. The gut analyses indicate that all length classes above 2.50 mm had similar intestinal contents on any one sampling date. This suggests that food ingestion is similar among all size classes. The intestinal contents of all length classes during the twelve months are

Table 25. The presence (P) and absence (A) of organisms in the intestines of Musculium securis during twelve months of the year in four habitats. "E" indicates that more than 75% of the intestines examined were empty. "N" denotes that newborns dominated the population and that the intestines were not examined.

INTESTINAL ORGANISMS	CARP POND												GREELY POND											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
	"N"	"N"	"N"	"N"				"N"	"N"	"N"	"N"	"N"	"E"	"E"	"E"	"E"								
Chrysophyta																								
Vaucheria?[a]				A	A	A							A	A	A	A	A	A	A	A				
Diatoms																								
Achnanthes				P	P	P							P	P	P	P	A	A	A	A				
Amphiprora				A	A	A							A	A	A	A	A	A	A	A				
Ampora				P	P	P							A	A	A	A	A	A	A	A				
Cocconeis				P	P	P							A	A	A	A	A	A	A	A				
Cymbella				P	P	P							A	A	A	A	A	A	A	A				
Fragilaria				P	P	P							P	P	P	P	P	P	P	P				
Gomphonema				A	P	P							P	P	P	P	P	A	A	A				
Navicula				P	P	P							P	P	P	P	P	P	P	P				
Nitzschia				A	A	A							P	P	P	P	P	P	P	P				
Rhoicosphenia[b]				P	P	P							A	A	A	A	A	A	A	A				
Synedra[b]				A	A	A							A	A	A	A	A	A	A	A				
Chlorophyta				P	P	P							P	P	P	P	P	P	P	P				
Gloeocystis				A	A	A							A	P	P	P	A	A	A	A				
Sphaerocystis				P	P	P							P	P	P	P	P	P	P	A				
Stigeoclonium				P	P	A							A	A	A	A	A	A	A	A				
Tetraedron				A	A	A							P	P	P	P	A	A	A	A				
Cyanophyta																								
Lyngbya?[a]				A	A	A							A	A	A	A	A	A	A	A				

INTESTINAL ORGANISMS	BRITANNIA BAY												LAC BOURGEOIS											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
	"N"	"N"	"N"	"N"	"N"			"N"	"N"	"N"	"N"		"E"	"E"	"E"	"E"								
Chrysophyta																								
Vaucheria?[a]				P	P	P							A	A	A	A	A	A	A	A				
Diatoms																								
Achnanthes				A	A	A							A	A	A	A	A	A	A	A				
Amphiprora				A	A	A							P	P	P	P	P	A	A	A				
Ampora				A	A	A							A	A	A	A	A	A	A	A				
Cocconeis				A	A	A							A	P	P	P	A	A	A	A				
Cymbella				A	A	A							A	A	A	A	A	A	A	A				
Fragilaria				P	P	P							P	P	P	P	P	P	P	P				
Gomphonema				A	A	A							A	A	A	A	A	A	A	A				
Navicula				P	P	P							P	P	P	P	P	P	P	P				
Nitzschia				A	A	A							A	A	A	A	A	A	A	A				
Rhoicosphenia[b]				A	A	A							A	A	A	A	A	A	A	A				
Synedra[b]				P	P	P							A	A	A	A	A	A	A	A				
Chlorophyta				P	P	P							P	P	P	P	P	P	P	P				
Gloeocystis				A	A	A							A	A	A	A	A	A	A	A				
Sphaerocystis				A	A	A							A	P	P	P	P	P	P	A				
Stigeoclonium				A	A	A							A	A	A	A	A	A	A	A				
Tetraedron				A	A	A							A	A	A	A	A	A	A	A				
Cyanophyta																								
Lyngbya?[a]				P	P	P							A	A	A	A	A	A	A	A				

[a] The phylum is probably represented by the genus indicated. [b] Identified by the author but not by Dr. R. K. S. Lee.

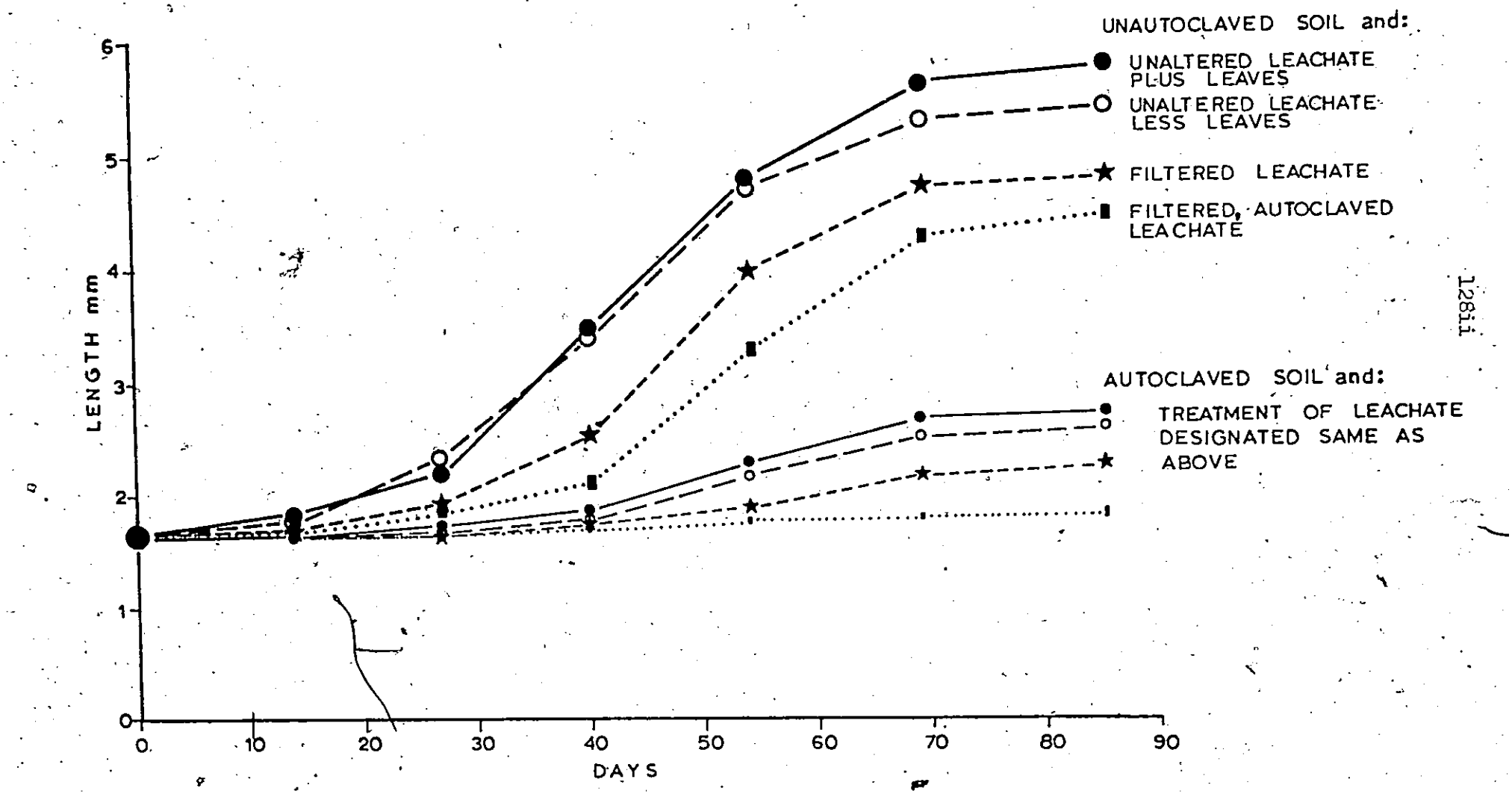
summarized in Table 25. Diatoms appear to be the most common organisms ingested by M. securis. The esophagus and stomach were usually empty and did not permit a study of which organisms were digested. Empty stomachs may also indicate diurnal feeding habits (i.e. do not feed during the day when specimens were collected, but rather during the evening), however, this aspect was not investigated.

Ingestion of food organisms appears to be heaviest in early summer in Carp Pond and Greely Pond, but early to late summer in the other habitats. Many of the food organisms in the rectum appear to be viable. Adults in Carp Pond have empty intestines during and after releasing their young in late July (immediately prior to the drying up of the pond). Approximately 86% of the adults have empty intestines during the hibernating period in Lac Bourgeois.

Fig. 50 and Table 26 show the growth and natalities of M. securis in dishes containing autoclaved and unautoclaved soil and leaf leachate. Little or no growth of M. securis occurs on autoclaved soils, regardless of the type of treatment given to the leachate. Clams attain greater lengths on unautoclaved soils but filtering and/or autoclaving the leaf leachate significantly reduces the growth and natality.

One or two clams were removed from each dish at the end of the experiment for analyses of intestinal contents. However, the intestines were empty, probably because the clams were not removed early enough. The growth dishes, in which living organisms were present (i.e. soils were not autoclaved), contained Navicula, Fragilaria, Sphaerocystis, Oscillatoria, Lyngbya, Bozia, and fungal spores. Adults that were analyzed for intestinal contents, often contained extra-marsupial larvae and were considered mature

Fig. 50 Observed average growth in shell length of 15 Musculium securis adults on each of eight different combinations of autoclaved and unautoclaved soil and leaf-leachate in the laboratory.


UNAUTOCLAVED SOIL and:
UNALTERED LEACHATE PLUS LEAVES
UNALTERED LEACHATE LESS LEAVES
FILTERED LEACHATE
FILTERED, AUTOCLAVED LEACHATE
AUTOCLAVED SOIL and:
TREATMENT OF LEACHATE DESIGNATED SAME AS ABOVE
LENGTH mm
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
80
90
DAYS

12811

Table 26. Asymptotic growth data for the regression $1/Y = A + BR^X$ and the natalities of Musculium securis adults grown on autoclaved and unautoclaved soil and leaf-leachate. Each combination of soil and leaf-leachate shown in the table was replicated three times with five clams in each replicate. Means side-scored by the same line are not significantly different at $P = 0.05$.

Combinations of soil and leaf-leachate	Means and standard deviations ( ) of asymptotic regression data for $1/Y = A + BR^X$						Mean natality and standard deviation ( ) per growth dish	
	A mm		B mm		R			
UNAUTOCLAVED SOIL and:								
unaltered leachate plus leaves	0.160	(0.021)	0.469	(0.019)	0.987	(0.0024)	38.4	(3.7)
unaltered leachate less leaves	0.168	(0.015)	0.458	(0.015)	0.980	(0.0025)	33.7	(9.2)
filtered leachate	0.183	(0.018)	0.445	(0.016)	0.976	(0.0051)	27.2	(4.1)
filtered and autoclaved leachate	0.195	(0.024)	0.433	(0.022)	0.970	(0.0060)	21.5	(3.8)
AUTOCLAVED SOIL and:								
unaltered leachate plus leaves	No fit obtained with asymptotic regressions						0	
unaltered leachate less leaves	No fit obtained with asymptotic regressions						0	
filtered leachate	No fit obtained with asymptotic regressions						0	
filtered and autoclaved leachate	No fit obtained with asymptotic regressions						0	

enough to be born and included in the natality data of Table 26.

DISCUSSION AND CONCLUSIONS

Intraspecific Variations in the Life History of Musculium securis

The data indicate variations in growth, birth periods, number of brood sacs and larvae per sac, and number and sizes of litters produced. These variations are present at the intrapopulation level (i.e. within populations) and/or at the interpopulation level (i.e. among populations).

Fig. 26 shows the growth of M. securis in Carp Pond in 1971 but plots of frequency modes in 1970 and 1972 will show that the growth curves were similar in all three years of study. However, the large amounts of rainfall in the summer of 1972 had a significant effect on the growth and hence the size-frequency distribution of the summer-born individuals. In 1970 and 1971 the newborns lay dormant and estivated from August to November, but in 1972 water remained in the pond during this period and the newborns started growing immediately after birth (late July). In the permanent habitats there is no estivation period and the large amount of rainfall in 1972 had no apparent effect on the growth and seasonal size-frequency distributions of M. securis. Consequently, rainfall has a greater effect on the growth of M. securis in the temporary habitats than in the permanent habitats.

The temporary habitats have unimodal size-frequency distributions while the permanent habitats have bimodal, and often trimodal size-frequency distributions. Bimodality results from two different phenomena. In Britannia Bay the bimodal character is the result of differences in growth rates of slow- and fast-growing adults. The fast-growing adults

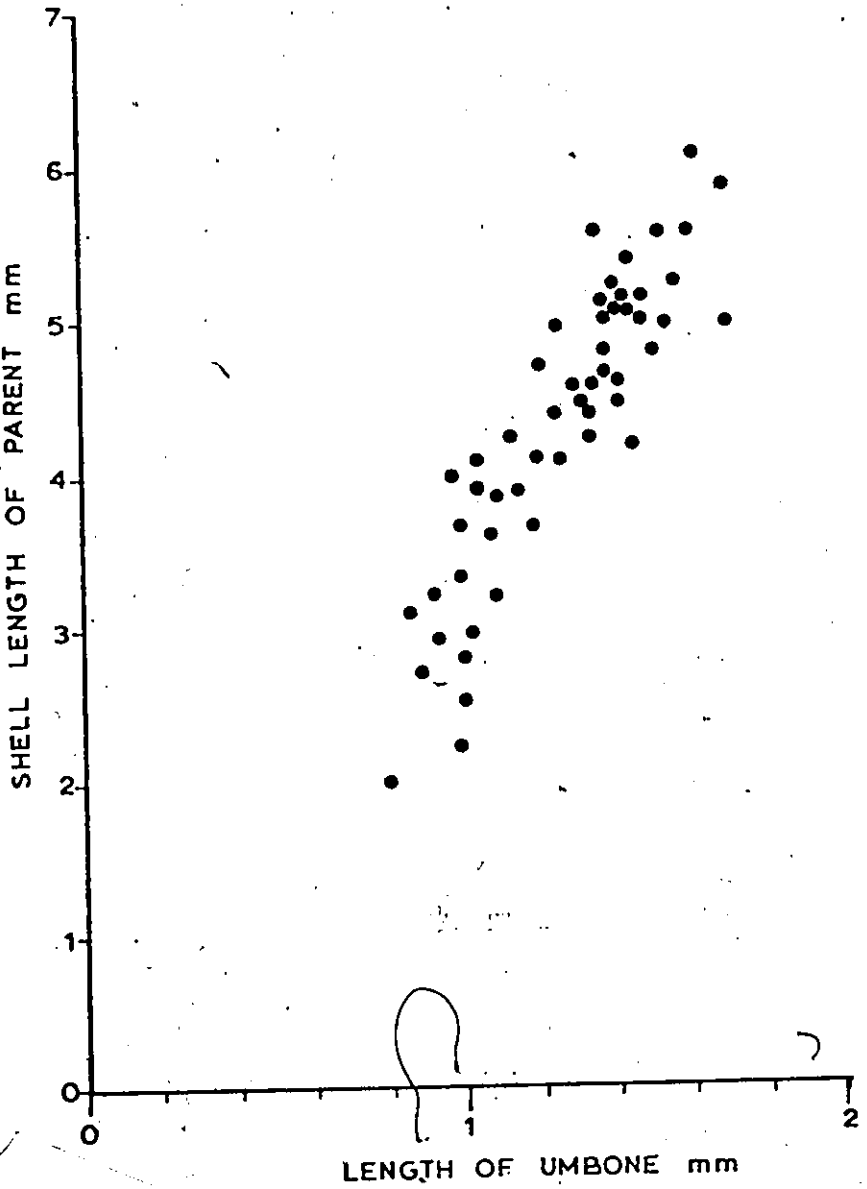
produce young in mid-July so that the remainder of the summer is represented by three modes (C, b, B, Fig. 28). Lac Bourgeois has two overlapping generations, one represented by adults born in early summer and the other by adults born in late fall or early winter.

The transplant studies indicate that the growth of individuals in the Britannia Bay population is slower than those of other populations. By correlating the lengths of calyculae (i.e. length of newborns at birth) with maximum length attained, a correlation coefficient (r) of 0.87 is obtained (Fig. 51). Thus larger newborns usually attain greater maximum lengths than smaller newborns. The average length of newborns at birth in Britannia Bay is 1.36 mm; this would explain the smaller average maximum length attained in Britannia Bay than in other habitats where newborns are usually larger than 1.65 mm.

Temperature may also be an important factor in the growth of Britannia Bay clams. Growth of M. securis apparently begins at approximately 10°C and probably occurs at optimum rates near 18°C. Examination of Fig. 13 shows that these temperatures are reached approximately four weeks later in Britannia Bay than in other habitats. Therefore, the slow-rate of temperature increase may be a factor in the reduced growth of Britannia Bay clams. Also, since the Britannia Bay population has four weeks less time in which to produce young, it would be to the advantage of the population if the production of smaller newborns was selected for. In this context the growth of Britannia Bay clams may be adaptively modified to temperature.

The growth and seasonal size-frequency distribution has been described for several sphaeriids but only a few have demonstrated intra-

Fig. 51 Relation between length of umbone (calyculus) and shell length of parent. Correlation coefficient (r) = 0.87.


SHELL LENGTH OF PARENT mm
0
1
2
3
4
5
6
7
0
1
2
LENGTH OF UMBONE mm

specific variation within and/or among habitats. Thomas (1963, 1965) studied a population of M. partumeium in a temporary habitat and also found that summer growth varies with the amount of rainfall; adults attained larger lengths and the newborns, which usually estivated upon birth and lay dormant, showed more growth in a summer of high rainfall than in summers of low rainfall. The present study indicates that the estivating populations of M. securis consist only of newborns. Thomas (1963) showed that the estivating populations of M. partumeium consist of adults of lengths 1-5 mm, although newborns were the most numerous. Intraspecific variations were also noted by Avolizi (1971) but he concludes that interspecific differences in life-cycle and growth between S. striatinum and S. simile are greater than intraspecific differences.

There is only one birth period per generation of M. securis adults. The birth period is usually of 2-4 weeks duration. Only one generation and hence one birth period is present in the temporary aquatic habitats while two generations and two birth periods are present in the permanent aquatic habitats.

The birth period of the Carp Pond population extended throughout July in all three years of study but both the number of birth periods and the birth period would probably change in 1973. By May 15, 1973 (Fig. 25) some adults were already gravid and probably would produce young in June of 1973. If young were produced early in June, there would probably be sufficient time for these young to grow and reproduce before the pond dries up in August, 1973. The probability of two overlapping generations occurring in 1973 would increase if the pond does not dry up or if the summer aquatic season is longer than usual.

The birth periods of the fast-growing adults in the Britannia Bay population are during July and September and of the slow-growing adults, during August. Young born in late July and early August do not grow until the following spring, as is typical of newborns in temporary aquatic habitats. Since only newborns estivate in the temporary ponds it is reasonable to assume that only individuals of this size class are capable of (or adapted to) estivation. If only newborns can survive estivation there would be greater survival value if a genetic determinant for "cessation of growth at birth" was selected for during evolution of the species. Conversely, there would be greater survival value in a permanent aquatic habitat if a genetic determinant for "cessation of growth at birth" was not selected for. Speculating on this basis, M. securis may have evolved in a temporary aquatic habitat since the newborns in Britannia Bay and Lac Bourgeois do not continue growth when born in late July, as shown in the interpopulation transplant studies.

Intraspecific variations in the birth periods of other sphaeriid species are also common. Foster (1932) cites the birth period of S. striatinum as occurring in December but Avolizi (1971) reported June and July as the months of greatest "spat-fall" for the same species. The birth rate of S. simile is highest during the winter and summer months as reported by Zumoff (1973) but during late June- early July and late fall according to Avolizi (1971). Sphaerium corneum produces two generations but Thiel (1926a, b) reports the birth periods as early summer and autumn and Mitropolskii (1966) as no distinct boundaries between the two birth periods.

Heard (1973) describes five types of reproductive cycles in

Sphaerium and Musculium. The Type I cycle includes such species as M. lacustre and S. corneum in which semelparous individuals (production of only one litter in its life span) display one period of fertilization, although two periods of fertilization (and births) are represented in the population. The Type II cycle is similar, except the population shows 3 separate fertilization and birth periods in a year (e.g. M. transversum). The Type III cycle is one of iteroparous reproduction (production of more than one litter in a species life span) with each individual in the population undergoing two fertilizations and two birth periods per year (e.g. M. partumeium, S. striatinum). The Type IV cycle includes M. japonicum in which individuals experience two fertilizations and one or two births per year but the population exhibits two periods of fertilization and births per year. The Type V cycle is more complex and is described in detail by Heard (1973).

The Type II cycle describes reproduction of M. securis in the Britannia Bay and Lac Bourgeois populations. However, neither of the five cycles defined by Heard (1973) describe reproduction of M. securis in the Carp Pond and Greely Pond populations. In conformity with Heard's (1973, Table 41) criteria, the reproductive cycle of the latter two populations can be described as having a life span of approximately one year, semelparous reproduction with one litter (or two litters in one birth period) per year, rarely a fall and winter incubation period, and only one birth period (summer).

There is very little intrapopulation variation in the total number of brood sacs produced per parent from one year to the next. However, interpopulation variations in brood sac production are present. Indi-

viduals in Britannia Bay usually produce a total of six brood sacs while those in other populations usually produce eight, and occasionally ten (Lac Bourgeois), brood sacs. Of these totals, only two to four (occasionally six) brood sacs mature. Therefore, the potential total number of litters (i.e. six to ten) is rarely if ever achieved.

Heard (1973) proposes that M. securis can "produce several litters over a life span of several years". The results from this study indicate that the total maximum number of litters that M. securis can potentially produce, is ten. This conclusion is drawn from data on Lac Bourgeois parents that produce ten brood sacs; in these parents four or six brood sacs mature and only secondary and/or tertiary sacs remain. That is, new primary sacs, hence additional sacs, are not produced after two litters are released. However, it is possible that brood sac production also is a function of environmental stress (e.g. intraspecific competition).

Environmental factors appear to be responsible for differences in the numbers of litters produced within and among habitats. With the extended aquatic season, a greater proportion of parents in the Carp Pond population produced two litters in 1972 than in 1970 and 1971. The large amount of rainfall had no significant effect on the numbers of litters produced in the Britannia Bay population in 1972. As indicated in the life history and transplant studies, a significantly smaller proportion of parents produce two litters in Britannia Bay than in other habitats (Tables 5,6). The results from the transplant studies also suggest that the Britannia Bay population may be adaptively modified with respect to number of litters produced; that is with four weeks less time in which to grow and reproduce, it would be to the advantage of

the population to select for one litter than for several litters.

Van Cleave et al. (1947) have given data to indicate that Musculium species might have larger brood sizes than Sphaerium species and suggested that differences in fecundity might support the retention of the genus, Musculium. Herrington (1962) indicated a need for data on more species before evaluating the significance of differential fecundities.

Gale (1969) proposes that more discretion is needed in comparing the numbers of embryos in various species since differences may reflect seasonal or parental size class variations; also purported differences between species may be due to differences in the procedures of various investigators. The present study indicates that brood sizes of M. securis vary greatly within and among habitats, primarily because of differences in larval mortalities. There is less variation in the brood sizes of secondary and tertiary sacs within and among similar habitats. Therefore, the numbers of fetal and/or prodissoconch larvae appear to be valid measurements for determining differential fecundities among species within similar habitats.

The data also indicate that both intrapopulation and interpopulation variations in litter sizes are present. Within the Carp Pond, Britannia Bay, and Lac Bourgeois populations, the sizes of litters released are significantly larger in the second year of study than in the first. These higher values may represent the response of M. securis to replace those individuals that had been removed for life history analyses by the author in the previous year of study. The removal of samples by the author is interpreted here as representing a mortality factor that is not normally present in the populations. In this context, M. securis

compensated for the high mortality by producing large litters in the following year. This appears to be achieved not by producing more larvae (since the total number of larvae per parent remained relatively constant, but by maintaining a greater survival rate (reflected in % viability, Table 4) of larvae already produced. Evidently, the sampling efforts of the author ultimately had little effect on the litter sizes produced since the litter sizes in the third year of study are not significantly different from those in the first year (Table 4). This is a valid interpretation if the large amount of rainfall in 1972 did not cause reductions in the litter sizes produced. In fact there is little evidence to suggest that high rainfall does affect the sizes of litters. For example, if high rainfall causes a reduction in litter sizes then the results (Table 4) from Carp Pond and Britannia Bay are inconsistent with those in Lac Bourgeois where an increase in the litter size occurred in 1972.

The viability of M. securis larvae from the fetal stage of development ranges from 37% to 58% in the first litter and from 31% to 52% in the second litter, depending on the year of study and the habitat. Since the number of embryos probably exceeds the number of fetal larvae, the percent viability of larvae from point of fertilization of the egg is probably smaller. The data (Table 4) also indicate that M. securis produces a certain number of eggs, this number being genetically fixed. This is suggested from the similar numbers of fetal larvae (approx. 7.0) per first litter in Carp Pond, Greely Pond and Lac Bourgeois. The Britannia Bay population produces significantly smaller numbers ($P < 0.01$) of fetal larvae per secondary brood sac than other populations. This implies that either a high mortality of embryos occurs in the Britannia Bay.

population or that the Britannia Bay population is genetically distinct with respect to egg production. If indeed egg production is genetically controlled, the percent larval viability also may be a valuable species (or generic) index in calculating egg production from the litter sizes of fetal larvae. This remains to be shown for M. securis as well as for other sphaeriid species.

Avolizi (1971) has also studied larval viabilities but presented his data in terms of "embryonic mortality"; the maximum embryonic mortalities of S. striatinum and S. simile are 90% and 77-65%, respectively (i.e. larval viabilities of 10% and 23-35%, respectively). Avolizi (op. cit.) suggests that "the dying off of younger stages contributes to the nutrition of.....embryos which survived". The litter sizes of S. striatinum and S. simile at birth range from 1-2 for both species.

The annual ratio of selection of M. securis (i.e. number of young born annually per average adult) varies widely within and among populations. For example, the Carp Pond population in 1970 and 1972 and the Greely Pond population in 1972 had an annual ratio of selection of about 5:1; this ratio increased to about 7:1 in the 1971 Carp Pond population. With only one litter, the Britannia Bay population has a low annual ratio of selection of about 2-3:1 while parents in Lac Bourgeois have the highest annual ratio of selection (8:1).

Analyses of results obtained from seasonal field collection and the maintenance of adults in the field and laboratory (Table 5) indicate that the annual ratio of selection is a function of density dependent and independent factors. This is also suggested in the results obtained from ecological studies (e.g. intraspecific and interspecific competition,

temperature, pollution, etc.). Similar conclusions are reported by Avolizi (1971) for S. simile and S. striatinum. Burky (1968) has demonstrated that the annual ratio of selection for Ferrissia rivularis varies from 35:1 in an eutrophic habitat to 8:1 in an oligotrophic stream.

The life span of M. securis is typically 12 months in all habitats. However, the life span can be increased to 15-16 months in the temporary aquatic habitats after a summer of high rainfall. As discussed previously, this increase in longevity has a significant effect on other life history aspects such as the seasonal size-frequency distribution and the numbers of litters produced.

On the basis of the number of annuli on the valves, Heard (1973) suggests that the maximum life span of M. securis is three years. Using this technique, Lac Bourgeois adults which have one annulus, would be in their second year of life. However, results from field and laboratory studies clearly show that these annulated adults were in their first year of life and lived for only approximately 12 months. Moreover, annuli may not always represent annual rest periods, as suggested by Baker (1927). This is particularly true of clams that live in temporary habitats where water levels fluctuate from one month to the next. Heard (1973) gives the life spans of several other sphaeriids and his predicted values (on the basis of the number of annuli) are invariably higher than those observed by other investigators using other techniques. For example, Avolizi (1971) and Foster (1932) on the basis of length class distributions report an 18-24 and 12 month life span, respectively for S. striatinum but Heard predicts a 5 year life span; by marking and recapture, Herrington (1948) has shown that the life span of S. occidentale is 3

years but Heard predicts six years.

There is some variation in the seasonal gonad activities between slow- and fast-growing adults in Britannia Bay. In slow-growing adults gametogenesis is first apparent in length classes 2.00-2.49 mm and length classes 3.00-3.49 mm in fast-growing adults (and of adults in other populations).

Gametogenesis and fertilization appear to continue until the death of the individual in all populations but is most active in the summer months. Similar observations have been reported by Okada (1935 a) for M. japonicum; spermatozoa and oogonia are found almost throughout the year but the periods of greatest gonad activity occur in the spring and autumn. Okada (op. cit.) also noted that spermatogenesis is most active in clams measuring 3-7 mm in length and oogenesis in those measuring more than 8 mm; protandrous maturation of M. japonicum is therefore suggested. The results of the present study indicate that ova and sperm mature at approximately the same time although primary oocytes (ova lying free in the ovarian cavity) are often present before spermatids; therefore, protogyny may occur in some individuals. Zumoff (1973) does not state what type of maturation occurs in S. simile but her results indicate that sperms and ova mature simultaneously and gametogenesis is most active in June and July. Although Thomas (1959) did not do a detailed study of gonad activity, her general observations on serial sections of M. partumeium also indicate simultaneous maturation of gametes. Thomas (1959) also demonstrated self fertilization in M. partumeium by the production of as many as six generation in isolation cultures.

Heard (1963) concludes that intraspecific variation in pill clams

(i.e. Pisidium spp) "is primarily ecological in nature and is reflected in differences in times of gonad activity (caused by abiotic factors) and average litter size (due to both abiotic and biotic forces)". Foster (1932) suggests that maximum-size adults of S. striatinum are sterile and reproduction occurs in the winter months; Avolizi's (1971) data indicate that reproduction in this species occurs until the death of the animal with peak reproduction in spring and fall. Finally, Monk (1928) found that reproduction of S. striatinum is at a peak during the summer months.

Factors Affecting the Life History and Distribution of Musculium securis

In the design of the ecological experiments an attempt was made to simulate, as closely as possible, the conditions in the natural environment, particularly those in Carp Pond. However, because of the heterogencity of the natural habitat and the multiplicity of factors which operate through factor interaction, the simulation was not precise. For example, such factors as predation, parasitism, and competition were not usually present in the laboratory growth dishes.

Although the simulation was not exact, it is believed that close to optimum conditions for the growth and reproduction of M. securis prevailed in the laboratory growth dishes. This is apparent when it is realized that growth and reproduction of M. securis in the laboratory control dishes equal or exceed those in the natural habitat. For example, growth of M. securis in the laboratory is completed in 50 to 60 days but 70 to 80 days in the natural habitat; the average parent produced approximately eight newborns in the laboratory but only two to four in the natural habitat. Therefore, conditions in the natural habitat appear

to be more limiting on the growth and reproduction of M. securis than conditions in the laboratory. In this context, the author is reasonably certain that if a factor limits the growth and reproduction of M. securis in the laboratory, it would almost certainly be limiting in the natural habitat.

(1) Abiotic factors

Temperature is a limiting factor; laboratory experiments show that growth begins at approximately 10°C and clams reared in the field show some growth between 8°C and 10°C. Similar results were obtained by other investigators studying the sphaeriids, M. partumeium (Thomas, 1965) and S. corneum (Thiel, 1928; Mitropolskii, 1966) and several freshwater gastropods (van der Schalie and Berry, 1973).

It was mentioned earlier that a slow rate of temperature increase probably affects the growth and reproduction of M. securis in Britannia Bay. Also, high temperatures may limit the distribution of M. securis in Britannia Bay. Fig. 52 shows the abundance of M. securis in relation to the maximum water temperatures observed during July. Musculium securis was absent in the shore zone where water temperatures often reached at least 32°C. Laboratory experiments show that M. securis can tolerate 30°C for only a short period of time. Therefore, the absence (or extremely small densities) of the species in the shore zone may reflect its low tolerance to high temperatures, although interspecific competition and food supply may also be limiting dispersal factors (pp. 152 and 160). Thomas (1959) suggested that "21°C is close to the threshold" for M. partumeium.

Apparently some growth factor is present in sufficient magnitude

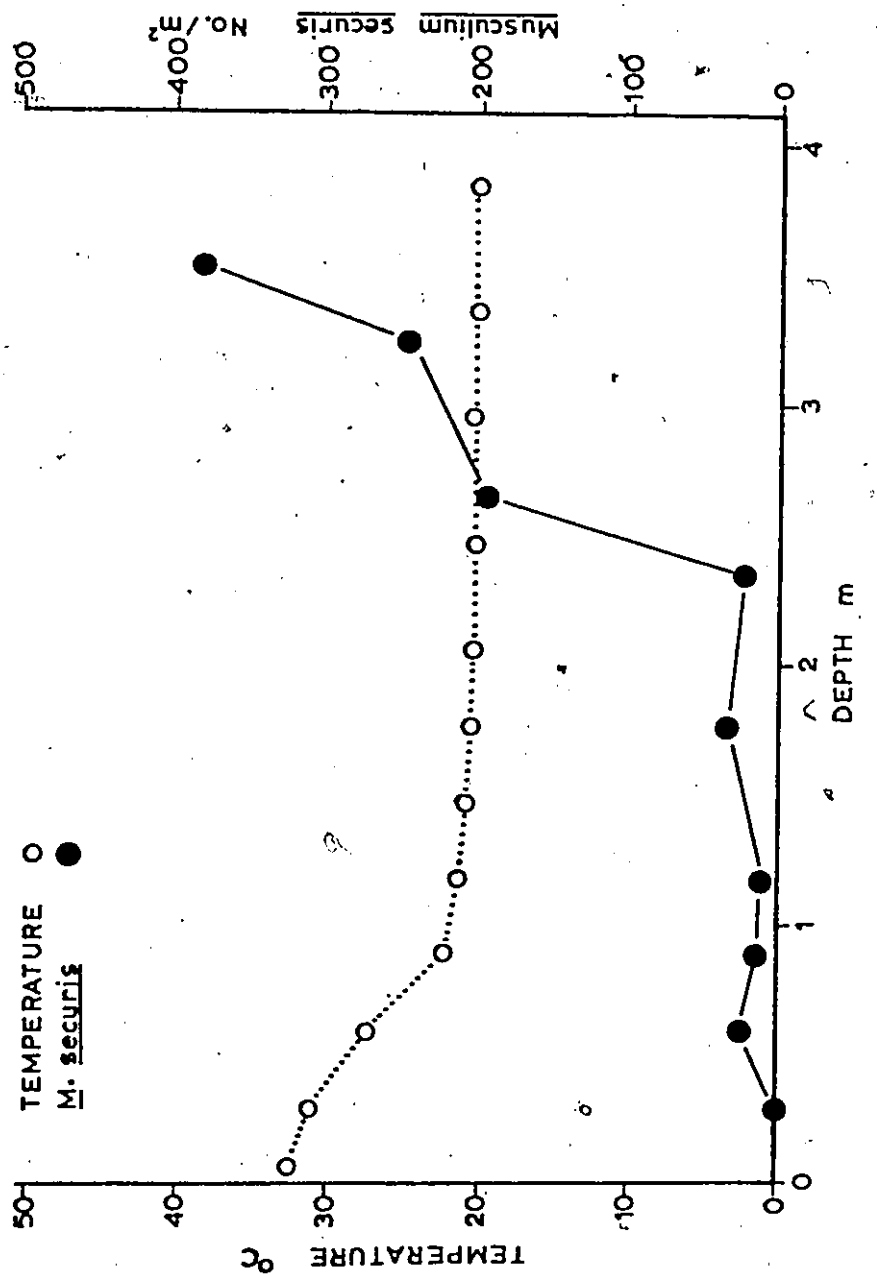
to initiate the immediate growth of M. securis on large quantities of soil (60 - 120 g) but in insufficient quantity to suppress the immediate growth on small quantities of soil (20 - 40 g, Fig. 36). Therefore, the quantity of soil appears to be more important during early stages of growth than during the latter stages. Although there are some significant differences in growth and natalities, the differences are not in proportion to the differences in quantities of soils used. This may indicate that growth and reproduction, especially during the latter stages, is a function of the surface-exchange area rather than the quantity of substrate.

The growth and reproduction of M. securis are also affected by soil texture (Fig. 37, Table 9). Soil texture is related to several other variables (Buckman and Brady, 1969) all of which may act independently or synergistically in the natural habitat. Such variables include the soil particle size and soil porosity, both of which affect the movement of clams through the soil and the supplies of nutrients to the clams.

The results show that M. securis attains greater lengths and natalities on fine sand and silt-clay than on coarser sediments, and suggests that the species should be distributed according to soil particle size in Britannia Bay. This is not generally observed; very small densities occur in fine sand but larger densities are present in silt-clay. However, it is possible that other factors limit the distribution of M. securis on fine sand. It was suggested earlier that temperature may be a limiting dispersal factor and it is shown later that interspecific competition and food supply may also be limiting.

Gale (1969) showed that M. transversum prefers mud over sandy-mud and sand in a circular substrate apparatus. Meier-Brook (1969) found that

Fig. 52 The relation between the distribution of Musculium securis and the maximum temperature observed at various depths of water in Britannia Bay.

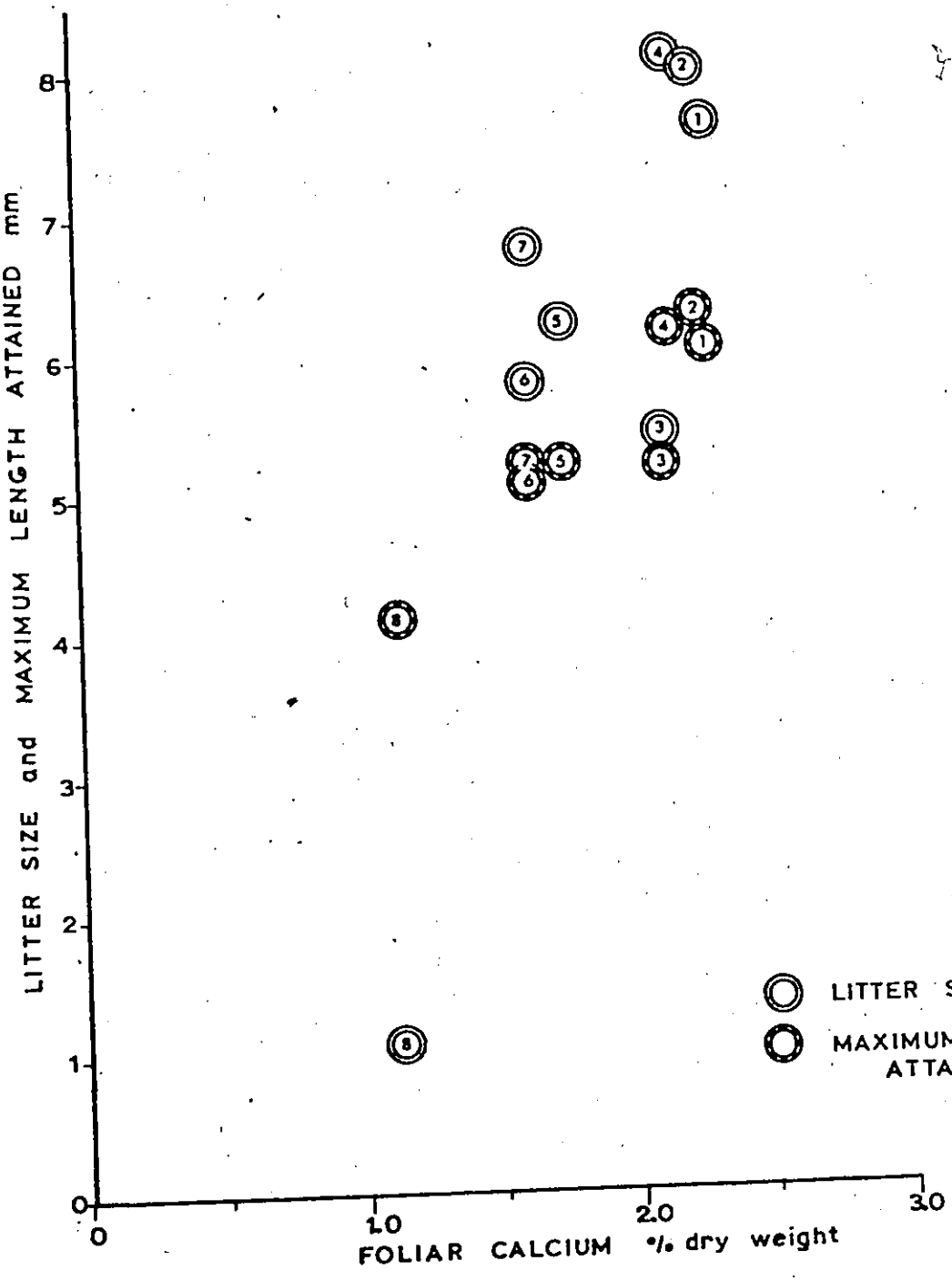

TEMPERATURE °C
50
40
30
20
10
0
TEMPERATURE ○
M. securis ●
Musculium securis No./m²
500
400
300
200
100
0
DEPTH m
0
1
2
3
4

Pisidium lilljeborgi prefers fine-grained organic sediment and that P. nitidum and P. hibernicum prefer coarse organic substrates with large-pored interstitial spaces.

Of the several factors in leaves and soil that could affect the growth and reproduction of M. securis, calcium would be among the most important since it is used in shell formation. The importance of calcium is indicated in Fig. 53 which shows a strong correlation between the calcium content of leaves and the growth and natality of M. securis; no correlation occurs with the calcium content of soils. The significance of soils and leaves to the growth and reproduction of M. securis is discussed later in the section "Food habits". Comparable calcium contents were found for the same leaf species by Chandler (1939, 1941), Bard (1945), Lutz and Chandler (1946), Scott (1955), Coile (1937). Slack (1964) has discussed the effects of tree leaves on water quality.

In one mole of calcium carbonate (i.e. 100.08 g) there are approximately 40.08 g Ca/100.08 = 0.4 parts of calcium. Since the shell is composed primarily of calcium carbonate, the dry weight of the shell multiplied by 0.4 gives an approximate estimate of the calcium in the shell. The estimate is only approximate because it does not consider the weight of the periostracum and conchiolin of the shell. The average maximum length attained by M. securis in Carp Pond and Greely Pond is 5.80 mm and from Fig. 24 this length corresponds to an average dry shell weight of 6.70 mg. Therefore, the approximate calcium content per adult shell (i.e. not considering requirements of developing larvae) is 6.70 x 0.4 = 2.68 mg. Since the calcium content of leaves varies from approximately 10 to 30 mg/g, one adult M. securis requires appro-

Fig. 53 The average litter sizes and maximum shell lengths attained by Musculium securis in relation to the calcium content (% of dry weight) of eight species of tree foliage: (1) black willow, (2) white elm, (3) trembling aspen, (4) white cedar, (5) white birch, (6) white spruce, (7) red oak, and (8) red maple. Correlation coefficient (r) for litter size = 0.79 and for maximum length attained = 0.90.


LITTER SIZE and MAXIMUM LENGTH ATTAINED mm
0
1
2
3
4
5
6
7
8
0
1.0
2.0
3.0
FOLIAR CALCIUM % dry weight
LITTER SIZE
MAXIMUM LENGTH ATTAINED

ximately 7.5% to 37.5% of calcium in each gram of leaf litter. This percentage may be higher if adults also store calcium in the soft tissues, as in some gastropods (Kapur and Gibson, 1968: Haley and Gibson, 1971).

Several factors have to be considered before assessing the importance of tree foliage and different soils as limiting factors in the distribution of M. securis. First, a high water table must be present and the soil should have properties which are conducive to the formation of a body of water for at least a part of the year (the life history studies indicate the necessity of water from November to July). Second, only certain forest tree species can tolerate wet environments e.g. white elm, some willows, red maple, cedars, and some oaks (Hosie, 1969). Third, leaves of some tree species are more conducive to the growth and reproduction of M. securis than are others; therefore, the abundance of one tree species relative to another may often be important. Fourth, the importance of tree foliage and different soils as limiting factors probably decreases with increasing size (volume) of the body of water.

Some investigators (Shimek, 1930) have related the distribution of land mollusks to the distribution of certain tree species but none has studied this relation with freshwater mollusks. However, Krull (1936) has found that leaves (oak) are also important in raising M. partumeium in the laboratory. Boycott (1936) has discussed several other factors that limit the distribution of mollusks, including sphaeriids, in Britain.

The present study indicates that sulfate concentration in excess of 100 mg/l are harmful to the growth of M. securis but natalities are not significantly affected until exposed to concentrations exceeding 200 mg/l. However, as the sulfate concentration is increased, the pH

decreases. Therefore, it is difficult to determine whether pH or sulfate is the limiting factor. Since the same inverse relationship usually exists between pH and sulfate in the natural habitat, it can only be concluded that high sulfate concentrations have either a direct or indirect effect on the growth and reproduction of M. securis.

High concentrations of sulfate may also limit the distribution of M. securis although specimens have been collected near Sudbury, Ontario (see collection in National Museums of Canada, #NMC 28610) where sulfur dioxide apparently is a serious atmospheric pollutant (Rao and Leblanc, 1967). In the presence of moisture, sulfur dioxide forms sulfurous acid which is slowly oxidized to sulfuric acid; the acid in turn is converted to sulfates such as ammonium and calcium sulfate (Johnstone and Coughanowr, 1958). The effects of sulfate on the distribution (as well as on growth and reproduction) of sphaeriids, and indeed on other mollusks, have not been reported in the literature.

High concentrations of rock salt and sodium chloride have a greater adverse effect on the growth and reproduction of M. securis than do high concentrations of calcium chloride. Less growth and smaller natalities occur with increased concentrations of rock salt and sodium chloride, particularly in concentrations greater than 200 mg/l. The results obtained using calcium chloride are more difficult to explain. Clams show more growth with increased concentration of calcium chloride but growth in all concentrations studied are less than those observed in the control dishes (Fig. 43). To explain this phenomenon, the author can only speculate that chloride has an adverse effect while calcium has a stimulating effect on the growth and reproduction of M. securis. If this interpretation is correct then the adverse effects of chloride are

more pronounced at low calcium chloride concentrations and the stimulating effects of calcium are more pronounced at high concentrations. As Table 16 indicates, calcium chloride has a greater effect on the growth than on the natalities of M. securis.

The results also indicate that road salts could be a major factor in limiting the distribution of M. securis. This is particularly true in northern latitudes where sodium chloride is used in the winter months to remove ice from roads. The effects of road salts on growth, reproduction and distribution of other sphaeriids have not been reported in the literature.

It is apparent that M. securis cannot tolerate gross chemical and/or organic pollution of pulp and paper, slaughter house, and raw sewage effluents. It is not possible to identify those factors in the effluents that affect the growth and reproduction of M. securis although the water quality data indicate that large B.O.D.'s and coliform bacteria counts may be major factors. Since M. securis often is exposed to very low oxygen levels (less than 1 ppm) in the temporary aquatic habitats, it is doubtful that oxygen is a limiting factor in the growth of M. securis below the outfalls. Thomas (1965) also concludes that oxygen is not a limiting factor in the growth of M. partumeium.

The effluent below the pulp and paper mill carries large quantities of wood fibers but very little entered the chambers in which M. securis adults were maintained. Therefore, growth of M. securis below the pulp and paper outfalls may not represent the added effects of wood fibers.

The increase in growth and reproduction of M. securis with increased distance from the pulp and paper outfalls indicates that the species can survive in recovery zones. However, as indicated above,

the environment in the growth chambers may not have been representative of the environment in the "natural" habitat below the outfalls. Wurtz (1956) suggested that M. securis, as well as several other sphaeriids, "can survive, at least to some degree, in the zones of degradation and recovery". Ingram et al. (1953) concluded that S. solidulum could not tolerate intensive pollution from domestic sewage but that it may respond to a slight fertilization effect from domestic sewage by increased productivity. Kehr et al. (1941) and Purdy (1930) consider the Sphaeriidae as a group of sewage-tolerant organisms while many others (Morgan, 1930; Carpenter, 1928; Baker, 1922) associate them with clean waters.

(2) Biotic factors

The effects of population density on the life history of M. securis are discussed in the section "Significance of litter size".

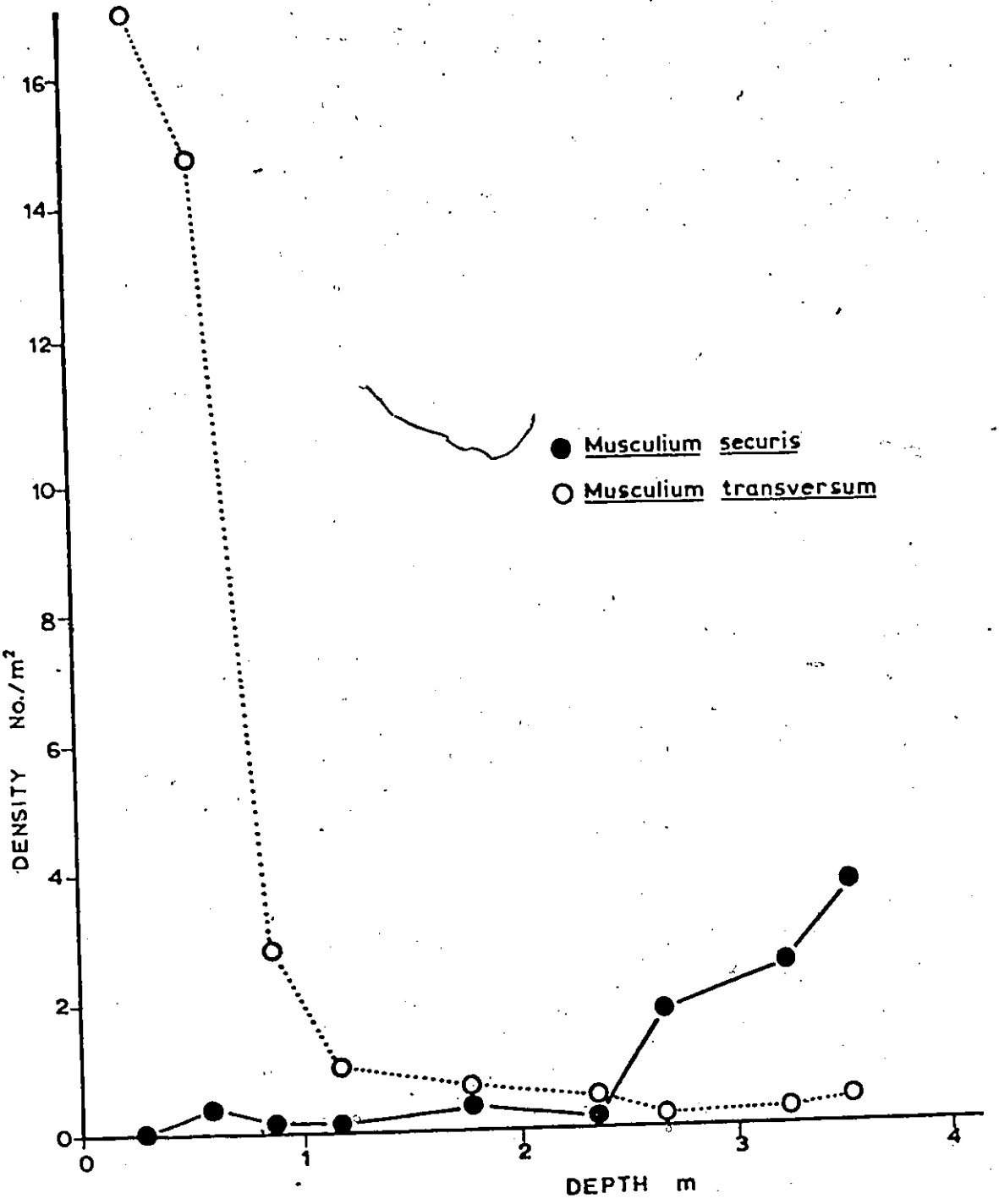
Although the author cannot define the factors for which M. securis and M. transversum were competing, he is reasonably certain that space was one of the most important; the "open-nature" of growth tubes, presumably permitted a constant supply of food organisms. The results indicate that under overcrowded conditions and where one species predominates (i.e. greatly outnumbers the other) (1) competition among individuals of the predominant species is primarily intraspecific, and the presence of the subdominant species has little effect on their growth and reproductive capacity, (2) interspecific competition results in reduced growth and reproductive capacity of individuals of the subdominant species, and (3) M. securis is usually more prolific and therefore a better competitor as a subdominant species than is M. transversum. When the numbers of individuals in each species are equal under overcrowded

conditions, competition is primarily interspecific, particularly during early stages of growth; M. transversum is more prolific and therefore a better competitor than M. securis. Where less crowded conditions prevail, competition is primarily interspecific and M. transversum is the better competitor since individuals produce more young per parent than do M. securis.

The competitive exclusion principle (Hardin, 1960) states that complete competitors cannot coexist. Although there is no definitive evidence that M. securis and M. transversum are complete competitors, the present study indicates that coexistence in nominal numbers is possible under overcrowded conditions and when one species greatly outnumbers the other. However, in the natural habitat, overcrowded conditions usually do not prevail. Also, the sequence of events that occurs in the colonization of a suitable habitat where M. securis and M. transversum have just been introduced, would probably favour establishment of the latter. For example, M. transversum has a higher reproductive capacity than M. securis and population growth of the former species would be proportionately faster. Theoretically, as the densities of the two species increase, interspecific competition would also increase and the reproductive capacity of M. securis would be depressed. Without mortality, eventually the carrying capacity of the habitat would be filled at which point the population of M. securis either becomes extinct or is present in nominal numbers.

Support for the competitive exclusion principle is seen in the distribution patterns of M. securis and M. transversum in Britannia Bay (Fig. 54). The two species may be found together but one usually greatly outnumbers the other in the deeper waters. However, experiments showed

Fig. 54 Relation between the distribution of Musculium securis and Musculium transversum in Britannia Bay.


16
14
12
10
8
6
4
2
0
DENSITY No./m²
0
1
2
3
4
DEPTH m
Musculium securis
Musculium transversum

that M. securis grows much faster than M. transversum in the 3-4 m depth of Britannia Bay, even in the absence of interspecific competition. Therefore some factor is apparently present in these depths that favours growth of M. securis but not M. transversum; hence they are not complete competitors in the 3-4 m depth.

Apparently parasitism has little effect on the growth of M. securis, although this needs to be studied further. The main effect of parasitism is on the reproductive cycle since no developing larvae are present in parasitized adults. Similar results have been reported for M. transversum (Wenke, 1965; Gale, 1969) and S. striatinum (Cheng and James, 1960).

Evidently, predation on M. securis by fish is of little significance as a mortality factor. Although there are no data, several observations indicate that the primary predators of M. securis are probably waterfowl. Black ducks usually breed and feed in Carp Pond, Greely Pond and Lac Bourgeois during the early summer months; several diving ducks are commonly seen in Britannia Bay. Gale (1969) attributed predation by ducks, fish and leeches as important factors in reducing densities of M. transversum.

The contagious distribution of estivating newborns in Carp Pond suggests the influence of factors in the soil which are themselves contagiously distributed. Only a few soil factors were analyzed but their values show no influence on the newborn dispersal. One suggestion is that the parents release their extra-marsupial larvae in "bunches" and thus produce a contagious distribution.

Several species of sphaeriids including M. partumeium (Thomas,

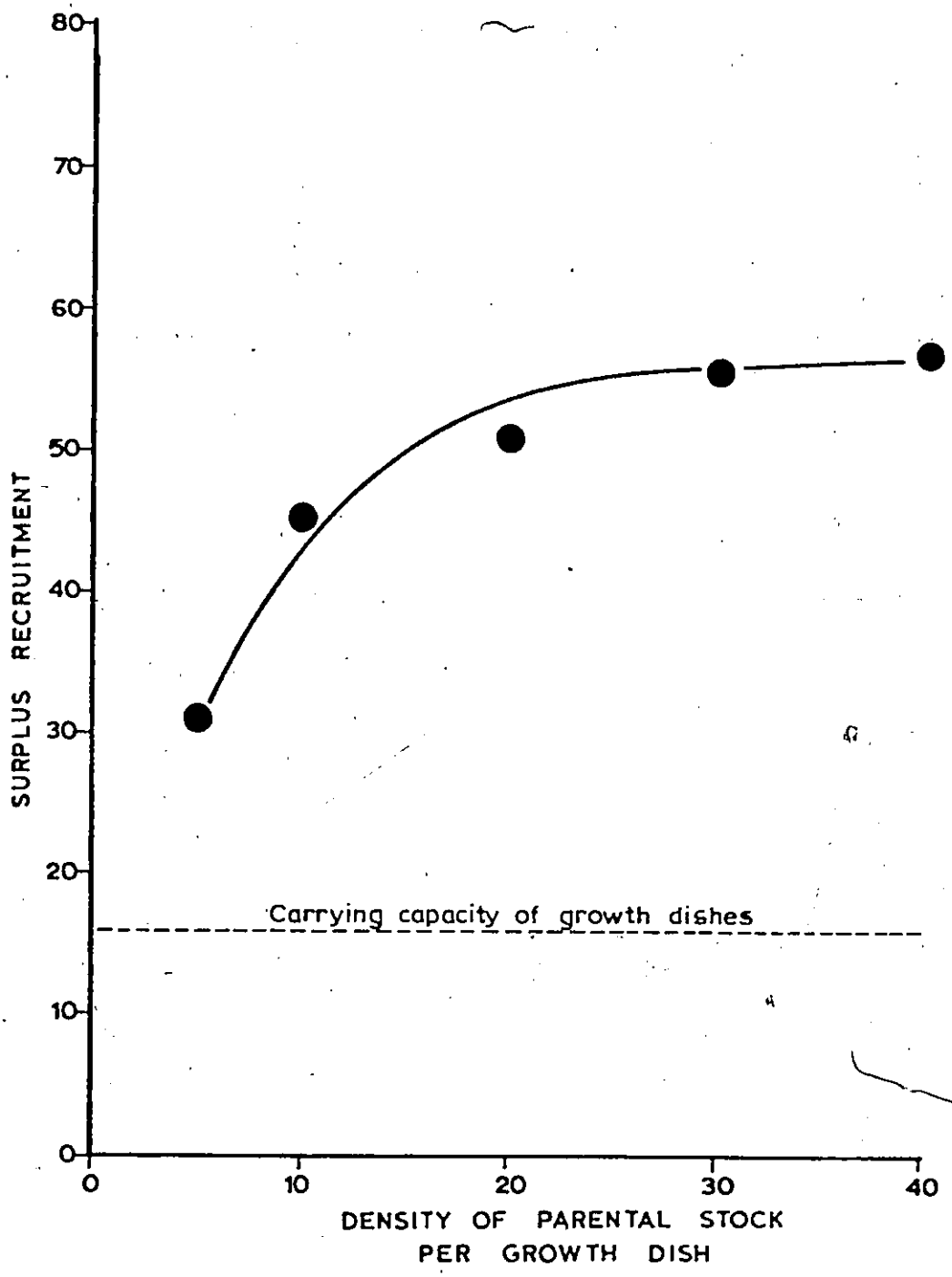
1959, 1963), M. lacustre (Mitropolskii, 1965), M. transversum (Gale, 1969), S. occidentale (Herrington, 1948), and S. corneum (Mitropolskii, 1965), are capable of estivating. Very little is known about the estivating habits and associated physiological processes of sphaeriids, although Mitropolskii, (1965) has studied the tolerance of drying in M. lacustre.

Significance of Litter Size

The data in Table 21 and Fig. 47 show clearly that (1) the total recruitment per growth dish increases with increasing densities of the parental stocks, to an asymptotic value (approx. 72), (2) recruitment is greater than the carrying capacity (approx. 16 reproductive parents) of the growth dishes, (3) the total litter size per average reproductive parent decreases with increasing densities of the parental stock, to an asymptotic value (4.5). These results support Lack's (1948) hypothesis that "litter-size is selected per se, and that the genotypes selected are those which result in the maximum number of descendants".

Since recruitment exceeds the carrying capacity, it can be inferred that reproductive parents produce a surplus of young. This surplus represents mortality above the carrying capacity in a balanced population and is a function of population densities (Fig. 55). Therefore, mortality increases with increased densities to an asymptotic value. Figs. 47 and 55 indicate that mortality increases as the litter size per parent decreases, to an asymptotic value. This is in direct contrast to Lack's (1948) proposal that as "litter-size increases, the proportionate mortality among the young increases, and that eventually an optimum

Fig. 55 Relation between surplus recruitment and density of parental stock of Musculium securis in laboratory growth dishes. Curve was fitted by eye.


80
70
60
50
40
30
20
10
0
SURPLUS RECRUITMENT
Carrying capacity of growth dishes
0
10
20
30
40
DENSITY OF PARENTAL STOCK
PER GROWTH DISH

litter-size is reached beyond which the initial advantage of an extra youngster is more than offset by the rise in proportionate mortality". While it is true that in a balanced population, birth rate and mortality must be equal, Lack (1948) maintains that this balance is primarily brought about by variations in the mortality and the birth rate (litter-size). The present study indicates that this is a valid hypothesis only for surplus recruitment. That is, surplus recruitment acts as a buffer in maintaining the carrying capacity. However, if mortality exceeds this surplus, the balanced population can only be restored by increased reproductive activity. Lack (1943) further contends that litter size does not vary sufficiently to achieve population balance; it is suggested here that marked variations in litter size may not be common due to the buffer effect of the surplus recruitment. Although largely speculative, the buffer effect of surplus recruitment may be an important mechanism in population control. It is possible, although it remains to be shown, that the wide fluctuations in population densities that normally occur in nature (Nicholson, 1933; Ehrlich and Birch, 1967) are partly the fluctuations in densities of surplus individuals.

The life history studies tend to support the above conclusions. The total litter size per average reproductive parent in each habitat is given in Table 27, and was calculated from data in Tables 3 and 4. That is, the total litter size per average parent = (average number of extra-marsupial larvae in first litter x proportion of parents producing one litter) + (total number of extra-marsupial larvae in two litters x proportion of parents producing two litters). For example, the average parent in the 1970 Carp Pond population produced a total litter size of

$(3.0 \times 0.36) + (5.1 \times 0.64) = 4.34$. The data from the Carp Pond population are particularly important because clams from this population were used in the growth experiments to obtain the results in Table 21 and Fig. 47. As explained earlier, the increase in total litter size per average parent in 1971 probably reflects the effects of the author's sampling efforts in 1970. In this context, the 1971 data support the contention that the total litter size per average reproductive parent increases with decreasing densities. Although the increase in 1971 was not substantial (and may indicate the buffering effect of surplus recruitment), an increase of one extra newborn per parent becomes more important in dense populations.

The total litter sizes per average parent in Britannia Bay (Tables 4,5,6, 27) are much smaller than those in other habitats. This supports Lack's (1948) contention that litter size can be modified adaptively; the transplant studies indicate that the Britannia Bay population has adapted to conditions in Britannia Bay and adults show little reproductive capacity in other habitats (Table 6).

Table 27. Total litter sizes per average parent in four populations.

	CARP POND			GREELY POND	BRITANNIA BAY			LAC BOURGEOIS
	1970	1971	1972	1972	1970	1971	1972	1971
Total litter size per average parent	4.32	5.70	4.83	4.79	2.43	3.12	2.44	5.62

A comparison of Tables 5, 6, and 27 shows that larger total litter sizes are achieved primarily by an increase in the number of litters produced.

However, the data also show that there may be an increase in the average litter size as well. As discussed previously, this appears to be achieved by an increase in the viability of developing larvae rather than by an increase in egg production. Therefore, increased recruitment in M. securis is a function of both larval viability and of number of litters produced.

The results also support Wright and Eaton (1929) who suggest that small litter sizes to some extent indicate unfavourable conditions. Britannia Bay is a more stable environment (at least with respect to fluctuation of water levels and water quality) than the other habitats and favour reduced litter sizes; instability of conditions in the ponds favours increased litter sizes. Cody (1966) on the basis of environmental stability and utilization of food resources, predicted that birds favor reduced clutches in stable environments (e.g. the tropics, islands, and coasts) and increased clutch sizes in unstable environments (e.g. inland temperate regions). Cole (1954) postulated several mechanisms by which semelparous and iteroparous animals could increase their biotic potential through an increase in the total litter size. Heard (1973) considered these postulates with regard to sphaeriids.

The significance of litter size in interpreting the results of the ecological experiments is also important. It has just been shown that M. securis produces a surplus of newborns. This surplus must be sufficient to compensate for mortality due to environmental resistance factors that occur in nature but not in the laboratory growth dishes. Therefore, if mortality due to predation, parasitism, competition, etc. (i.e. factors not usually present in growth dishes) exceeds surplus recruit-

ment, the population will not be maintained at carrying capacity, especially if reproduction is already occurring at maximum rates.

Food Habits

The food habits of sphaeriids have received little attention. The present study indicates that there is no selectivity in the ingestion of food items among different size classes. No plankton samples of the water from the four habitats were taken to determine the selectivity in ingestion of food items by M. securis, but Gale (1971) has shown that M. transversum feeds non-selectively on phytoplankton; his studies also indicate that diatoms are important organisms in clam guts.

Laboratory studies show that there are factors in both soil and leaves that are important to the growth and reproduction of M. securis. Autoclaving of soils and leaf-leachate kills all organisms. Therefore, the lack of growth in dishes containing autoclaved soils and autoclaved, filtered leachate indicates that living organisms are necessary for growth and that nutrients in elemental or detritus form are not sufficient to sustain M. securis. Since more growth occurs in dishes containing unaltered soil and autoclaved, filtered leachate, than in dishes containing autoclaved soil and autoclaved, filtered leaf-leachate, most of the food organisms must be in the soil. Also, M. securis must derive some nourishment (although apparently little) from leaf tissue since more growth occurs in dishes containing leaves (and unautoclaved soil; unaltered leachate). Several unsuccessful attempts have been made to grow M. securis in dishes with only soil and distilled water. The fact that M. securis can grow in dishes with unautoclaved soil and autoclaved, filtered leachate but not in dishes with unautoclaved soil and only

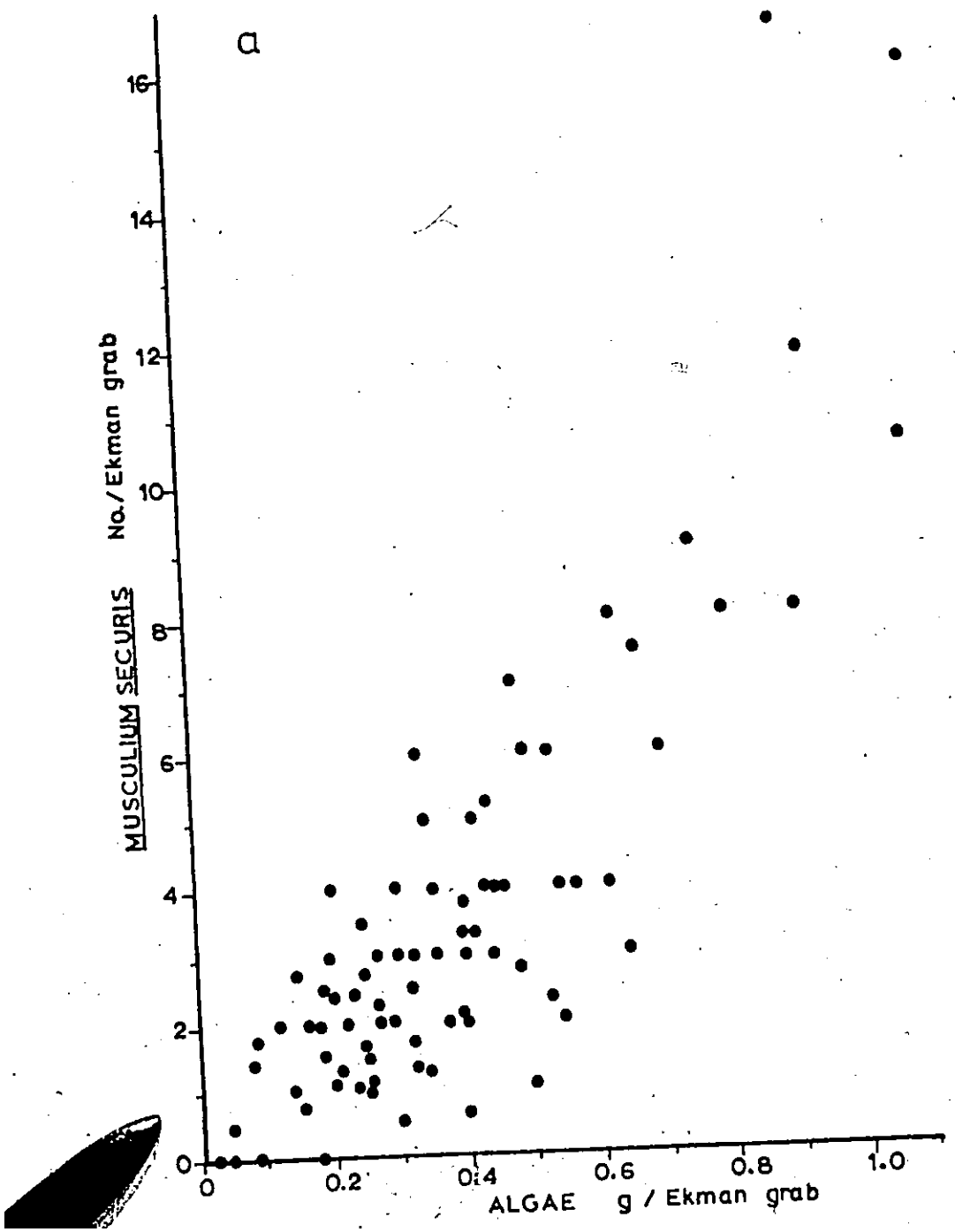
distilled water indicates that leaves contribute nutrients in elemental form. However, it was shown above that living organisms are necessary for growth of M. securis. Therefore, it is implied that the nutrients in elemental form are taken up by microorganisms which in turn are devoured by M. securis.

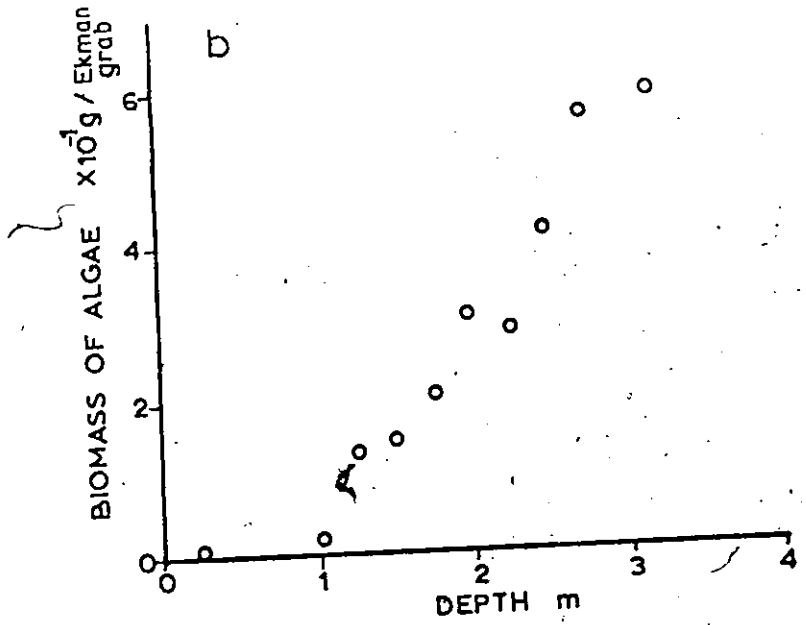
Apparently, tree foliage is not pertinent to the growth of M. securis because the species occurs in Britannia Bay where tree foliage is absent. However, there is a large biomass of algae (primarily Vaucheria and Lyngbya) in the sediments of Britannia Bay. Analyses of the intestinal contents of M. securis from Britannia Bay shows that they feed on cyanophytes and chrysophytes (as well as diatoms) which are probably Lyngbya and Vaucheria, respectively. Further support is seen in the strong correlation ($r = 0.79$) between the biomass of Lyngbya-Vaucheria (the two genera occur together in entangled masses) in the sediment and the densities of M. securis in various depths of Britannia Bay (Fig. 56 a, b); each plot in the figure represents the average dry weight of algae and the respective densities of M. securis in four samples, each sample being composed of four pooled Ekman grab samples (i.e. total of 16 samples per plot). Fig. 56 c shows a strong correlation between the calcium content of the algae and the abundance of M. securis in various depths of Britannia Bay. The calcium contents were determined in the same manner as for the tree foliage (see Materials and Methods).

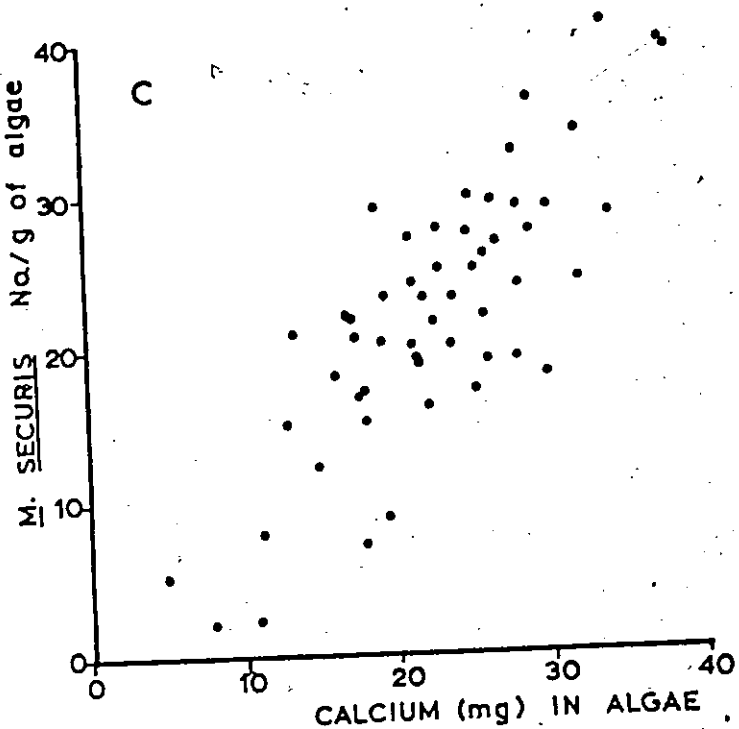
Distribution of Musculium securis

Being restricted to the North American continent, M. securis has a nearctic distribution (Fig. 57 a). It occurs in a variety of habitats such as temporary and permanent ponds, lakes, rivers, and creeks. Herring-

Fig. 56 Relation between the abundance of Musculium securis and the biomass of Lyngbya-Vaucheria algae. (a) The abundance of M. securis per gram of Lyngbya-Vaucheria algae in several Ekman grab samples of Britannia Bay sediments. Correlation coefficient (r) = 0.79. (b) The biomass (g/Ekman grab) of Lyngbya-Vaucheria algae in various depths of water in Britannia Bay. (c) Relation between the abundance of M. securis (no./g of algae) and the calcium content (mg) of Lyngbya-Vaucheria algae. Correlation coefficient (r) = 0.81.


a
MUSCULIUM SECURIS No./Ekman grab
ALGAE g / Ekman grab
0
0.2
0.4
0.6
0.8
1.0
2
4
6
8
10
12
14
16


b
BIOMASS OF ALGAE x10⁻¹g / Ekman grab
DEPTH m
0
1
2
3
4
6


c
M. SECURIS No./g of algae
CALCIUM (mg) IN ALGAE
0
10
20
30
40

ton (1962) has recorded the species from Newfoundland, Nova Scotia, New Brunswick, Quebec, southern Ontario, and British Columbia. It has since been found by Clarke (1973) in northern Ontario, Manitoba, Saskatchewan, and Alberta in the Hudson Bay drainage systems. In the United States M. securis has been reported from the states of Washington, Montana, and most states east of, but not including North Dakota, South Dakota, western Nebraska, Kansas, Oklahoma, and western Texas (Herrington, 1962; Heard, 1962a,b, 1963). The species has not been recorded from but probably does occur in the eastern states of West Virginia and Kentucky.

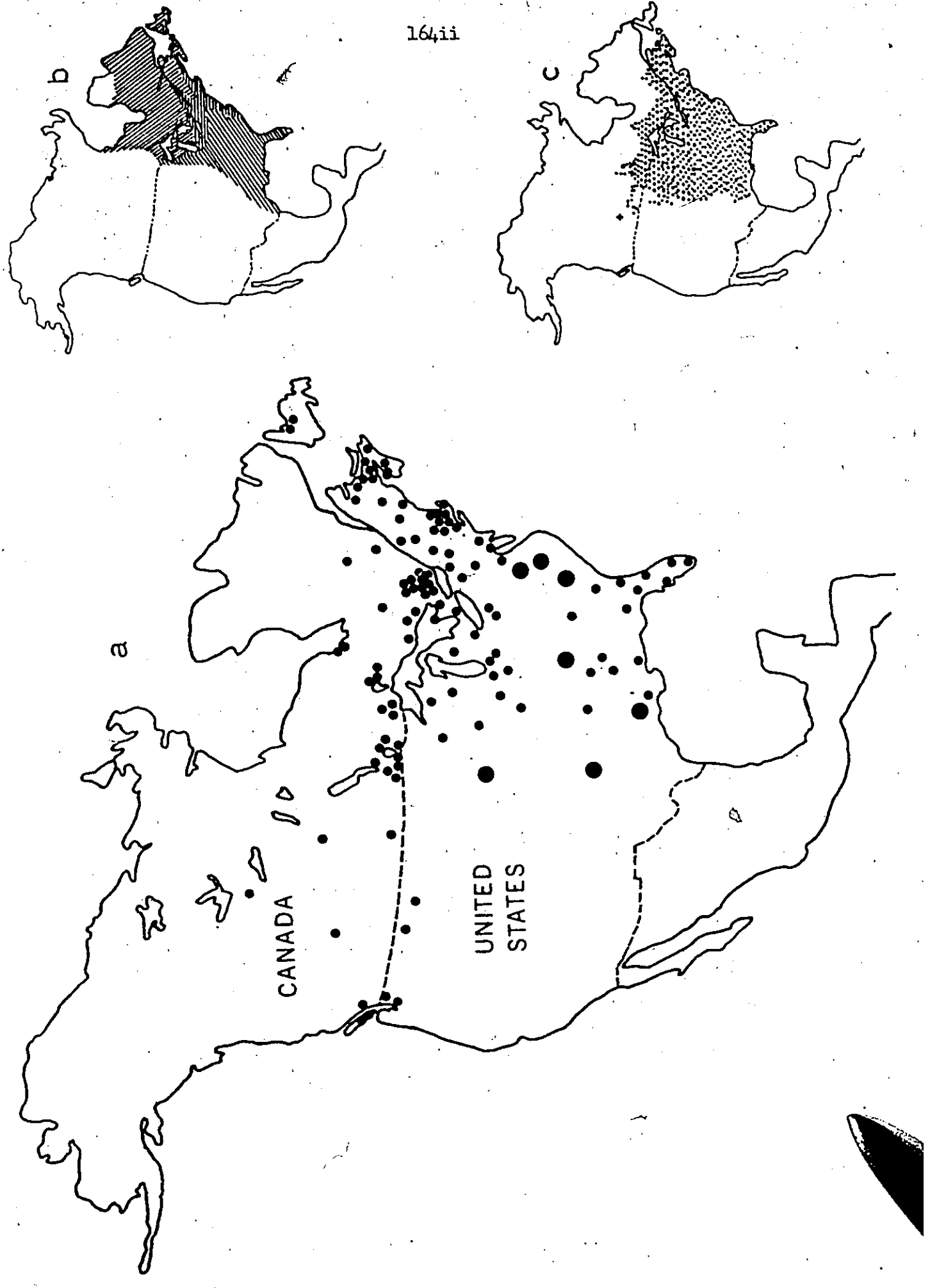
The original range of M. securis is difficult to determine because the species not only occurs in several drainage systems but also in isolated aquatic habitats such as temporary forest ponds. Since it is a common inhabitant of isolated ponds and has no apparent ability to actively emigrate overland, the primary means of dispersal are probably passive in nature.

Of the several animals that may serve as agents of transport overland, the black duck, Anas rubripes, may be among the most important. Black ducks breed and/or feed in Carp Pond, Greely Pond, and Lac Bourgeois, all of which have no connection with any drainage systems. Perhaps of greater significance is the similar distribution patterns of the black duck (Fig. 57 b) and M. securis (Fig. 57 a). The distribution of M. securis in the western parts of Canada and the northwestern parts of the United States can probably be explained by the migration of other migratory birds such as mallards (Anas platyrhynchos) and greater scaups (Aythya marila), both of which frequent Britannia Bay. If M. securis is dispersed to a body of water within a drainage system, it is possible that

Fig. 57 (a) Distribution of Musculium securis in North America. The small black dots represent locations of M. securis that were identified by H. B. Herrington or reported in the literature (Heard, 1962b, 1963; Clarke, 1973) or found by the author. The large dots refer to states in which M. securis has been found but the specific localities were not reported.

(b) Distribution of the black duck, Anas rubripes, as reported by Stewart (1958). \\\\ summer range, //// winter range, ≡ yearly occurrence.

(c) General distribution of the deciduous forests in North America (adapted from Hosie, 1969 and Fowells, 1965).


b
c
a
CANADA
UNITED
STATES

the species may be further distributed by agents (i.e. fish) of that drainage system. The ecological requirements, discussed in previous chapters, are of course pertinent to the occurrence of M. securis.

To determine if M. securis could survive aerial transport, several size classes of adults were suspended from strings (held between the shells) for 10, 20, and 30 minutes. All clams survived after 10 min., 50% died after 20 min., and all adults were dead after 30 min. when returned to water. Their death was attributed to the formation of an air bubble between the shells. Other adults were then kept between a damp cloth and all survived after 30 min. when returned to water. Evidently a thin film of water was necessary to prevent the formation of air bubbles. If the clams did not die from the direct effects of the air bubbles, they probably eventually succumbed to the buoyancy effect where the air bubble kept the clams afloat.

It is also possible that M. securis could survive transport in the intestines of animals. The species is viviparous so that the larvae are protected by the parent's shell and gills. It follows that a greater percentage of extra-marsupial larvae would probably pass through the intestine than would adults since the latter would be more vulnerable to the digestive juices of the transport agent. Another adaptation to internal (and external) transport may be the appearance of extra-marsupial larvae in parents during the feeding season of migratory birds such as black ducks. However, it still remains to be shown if M. securis can survive intestinal transport.

Several authors have suggested that the dispersal of mollusks may be passive, effected by attachment to aquatic insects, crayfishes,

frogs, salamanders, and aquatic birds (Kew, 1893; Rees, 1965) or by passing unharmed through the intestinal tract of fish (Ohdner, 1951). Other authors (Boycott, 1936; Baker, 1945) have suggested and Malone (1965a) has shown that snails are capable of attaching themselves to the feet of birds and of retaining their viability for sufficient lengths of time to effect passive overland dispersal. In a study of internal transport, Malone (1965b) thought it unlikely that the dispersal of snails "via the intestinal tract is of much significance" since a very small percentage of snail's eggs remain viable in feces; he concluded that internal transport would be more effective if snails and egg masses were carried in the bird's crop and later regurgitated. Although a very small percentage of eggs passed unharmed through the intestines of birds in Malone's study (1965b), it is only necessary for one egg to develop in order to start a population. This is particularly true for hermaphroditic species.

The ecological studies showed that, in general, leaves from deciduous trees, especially willows and white elms, are more conducive to the growth and reproduction of M. securis than are leaves from conifers, although the soil is also a major factor. Fig. 57 c shows the striking similarity in the distribution patterns of M. securis and deciduous forests in North America and supports the results of laboratory growth studies. White birch and trembling aspen are common deciduous trees in the coniferous forest region (Hosie, 1969) and may explain the occurrence of M. securis in western Canada and United States. Also, some localities are large bodies of water and forest tree foliage has relatively little effect on the water quality (compared to small isolated forest ponds).

SUMMARY

The taxonomy, anatomy, life history, ecology, food habits, and distribution of M. securis have been discussed. This study shows that (1) the presence of calyculae on shells is probably a reliable diagnostic character of the genus Musculium. (2) Brood sacs develop on certain filaments of the inner gill, this brood sac-filament relationship being a reliable tool in determining the number of litters produced. (3) The byssus consists of a byssal stalk that is secreted from cells in the base of the byssal gland of the prodissoconch larva's foot, and a byssal bulb that inserts on the parent's gill filaments; the probable function of the byssus is to prevent precocious birth of extra-marsupial larvae. (4) The life history of M. securis typically consists of a one year life span with growth and reproduction limited to the spring and/or summer months, a birth period occurring in mid-summer or late fall, semelparous reproduction with one litter (or two litters in one birth period) per year, and a fall and winter dormancy period. (5) Intraspecific variations in the life history exist at both the intrapopulation and interpopulation level. Intrapopulation variations are primarily caused by abiotic and biotic factors. Adaptive modification in growth and litter sizes may cause interpopulation variations in life history. (6) Reproduction in M. securis does not occur at maximum potential rates but is of sufficient magnitude to cause surplus recruitment. (7) M. securis ingests phytoplankton with diatoms being the most important intestinal organism. Food organisms come primarily from the soil. Tree foliage contributes considerable amounts of calcium which is probably taken up by M. securis through the food chain. (8) The geographic and local distribution of M. securis is a function of the distribution of dispersal agents and of abiotic and biotic factors.

LITERATURE CITED

Anderson, H. G. 1959. Food habits of migratory ducks in Illinois. Ill. Nat. Hist. Surv. Bull. 27: 289-344.

Avolizi, R. J. 1971. Biomass turnover in natural populations of viviparous sphaeriid clams. PhD dissertation, Syracuse Univ., Syracuse, New York 150 p.

Baker, F. C. 1922. The molluscan fauna of the Big Vermillion River, Illinois. Ill. Biol. Monogr. 7: 1-26.

_____ 1927. Molluscan associations of White Lake, Michigan: A study of a small inland lake from an ecological and systematic viewpoint. Ecology 8: 353-370.

_____ 1945. The molluscan family Planorbidae. The University of Illinois Press, Urbana 530 p.

Bard, G. E. 1945. The mineral nutrient content of the foliage of forest trees on three soil types of varying limestone content. Soil Soc. Am. 10: 419-422.

Boycott, A. E. 1936. The habitats of fresh-water Mollusca in Britain. J. Anim. Ecol. 5: 116-186.

Buckman, H. O. and N. C. Brady. 1969. The nature and properties of soils. Macmillan Co., London 653 p.

Burch, J. B. 1972. Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America. In Identification Manual No. 3, Biota of freshwater ecosystems, Environmental Protection Agency, Washington D. C. pp 1-31.

Burky, A. J. 1968. Biomass turnover, energy balance and interpopulation variation in the stream limpet, Ferrissia rivularis (Say), with special reference to respiration, growth, and fecundity. PhD dissertation, Syracuse Univ.

Carpenter, K. E. 1928. Life in inland water. Sedgwick and Jackson, Ltd., London 627 p.

Chandler, R. F. 1939. The calcium content of the foliage of forest trees. Cornell Univ. Agr. Exp. Stat., Memoire 228, 15 p.

_____ 1941. The amount and mineral nutrient content of freshly fallen leaf litter in the hardwood forests of central New York. J. Am. Soc. Agron. 33: 859-871.

Cheng, C. C. and H. A. James. 1960. The histopathology of Crepidostomum sp. infection in the second intermediate host, Sphaerium striatinum. Helminth. Soc. Proc. 27: 67-68.

Clarke, A. H. 1973. The freshwater molluscs of the Canadian Interior Basin. Malacologia 13: 1-509.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.

Coile, T.S. 1937. Composition of the leaf litter of forest trees. Soil Sci. 43: 349-355.

Cole, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103-137.

Dixon, W. J. 1971. Biomedical computer programs, University of California. Published in Automatic Computation No. 2, Univ. California Press, Berkley, Los Angeles 600 p.

Ehrlich, P. R. and L. C. Birch. 1967. The "Balance of Nature" and " Population Control". Am. Nat. 101: 97-107.

Elliot, J. M. 1971. Statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Sci. Publ. No. 25, 144 p.

Ellis, M. M. 1937. Detection and measurement of stream pollution. Bur. Fish. Bull., No. 22: 365-437.

Foster, T. D. 1932. Observations on the life history of a fingernail shell of the genus Sphaerium. J. Morph. 53: 473-497.

Fowells, H. A. 1965. Agriculture Handbook No. 271. Silvics of forest trees of the United States. U. S. Dept. Agr., Washington, D. C. Compiled and revised by H. A. Fowells 762 p.

Gale, W. F. 1969. Bottom fauna of Pool 19, Mississippi River with emphasis on the life history of the fingernail clam, Sphaerium transversum. PhD dissertation, Iowa State Univ., Ames, Iowa. 233 p.

_____ 1971. Phytoplankton ingestion by the fingernail clam, Sphaerium transversum (Say), in Pool 19, Mississippi River. Ecology 52: 507-513.

Gaufin, A. R. and C. M. Tarzwell. 1952. Aquatic invertebrates as indicators of stream pollution. Public Health Rpt. 67: 57-64.

Gilmore, R. J. 1917. Notes on reproduction and growth in certain viviparous mussels of the family Sphaeriidae. Nautilus 31: 16-30.

Greene, G. N. 1971. An experiment on the effect of pond soil on calcium in pond water. Trans. Am. Fish. Soc. 100: 580-582.

Haley, G. F. and M. A. Gibson. 1971. Calcium storage in the soft tissues of freshwater gastropods. The influence of environmental calcium concentrations. Can. J. Zool. 49: 1001-1004.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

Heard, W. H. 1962 a. The Sphaeriidae (Mollusca: Pelecypoda) of the North American Great Lakes. Am. Midl. Nat. 67: 194-198.

_____ 1962 b. Distribution of Sphaeriidae (Pelecypoda) in Michigan, U. S. A. Malacologia 1: 139-161.

_____ 1963. Survey of the Sphaeriidae (Mollusca: Pelecypoda) of the Southern United States. Proc. Louisiana Acad. Sci. 26: 102-120.

_____ 1965. Comparative life histories of North American pill clams (Sphaeriidae: Pisidium). Malacologia 2: 381-411.

_____ 1973. Manuscript of "Comparative life histories of fingernail clams (Sphaeriidae: Sphaerium and Musculium)". Malacologia (in press).

Herrington, H. B. 1948. Further proof that Sphaerium occidentale does not attain full growth in one year. Can. Field Nat. 62: 74-75.

_____ 1962. A revision of the Sphaeriidae of North America (Mollusca: Pelecypoda). Misc. Publ. Mus. Zool. Univ. Mich., No. 118, 74p.

Hickman, C. P. 1967. Biology of the invertebrates. C. V. Mosby Co., Saint Louis 673 p.

Hosie, R. C. 1969. Native trees of Canada. Can. Forestry Serv., Dept. Fish. Forestry. Obtainable at Queen's Printer, Ottawa 380 p.

Hutchinson, G. E. 1957. A treatise in limnology, geography, physics, and chemistry. Vol. I. John Wiley & Sons, New York 1015 p.

Ingram, W. M., D. G. Ballinger, and A. R. Gaufin. 1953. Relationship of Sphaerium solidulum Prime to organic pollution. Ohio J. Sci. 53: 230-235.

Johnstone, H. F. and D. R. Coughanowr. 1958. Absorption of sulfur dioxide from air. Indust. Eng. Chem. 50: 1169-1172.

Judd, W. W. 1966. Studies of the Byron Bog in southwestern Ontario XXIV. Distribution of fingernail and pill clams (Pelecypoda: Sphaeriidae). Nat. Mus. Canada, Nat. Hist. Pap. No. 33, 3 p.

Kapur, S. P. and M. A. Gibson. 1968. A histochemical study of calcium storage in the foot of the freshwater gastropod, Helisoma duryi eudiscus (Pilsbry). Can. J. Zool. 46: 987-990.

Kehr, R. W., W. C. Purdy, et al. 1941. A study of the pollution and natural purification of the Scioto River. Public Health Bull. 276: 1-153.

Kew, H. W. 1893. The dispersal of shells. Kegan Paul, Trench, and Trübner, London 291 p.

Krull, W. H. 1936. Raising Musculium partumeium Say under laboratory conditions. Papers Mich. Acad. Sci. Arts and Letters 21: 635-637.

Lack, D. 1948. The significance of litter-size. J. Anim. Ecol. 17: 45-50.

Ladle, M. and F. Baron. 1969. Studies on three species of Pisidium (Mollusca: Bivalvia) from a chalk stream. J. Anim. Ecol. 407-413.

Link, H. F. 1807. Beschreibung der Naturalien—Sammlung der Universität zu Rostock, Rostock, 2/3: 82-160 (as cited by Herrington, 1962).

Lutz, H. J. and R. F. Chandler. 1946. Forest soils. John Wiley & Sons, Inc., New York 514 p.

Mackie, G. L. 1971. Some aspects of the distribution and ecology of macrobenthos in an industrialized portion of the Ottawa River near Ottawa and Hull, Canada. MSc thesis, Univ. Ottawa, Ottawa, Ontario 161 p.

_____ and S. U. Qadri. 1973. Abundance and distribution of Mollusca in an industrialized portion of the Ottawa River near Ottawa-Hull, Canada. J. Fish. Res. Bd. Canada 30: 167-172.

Malone, C. R. 1965 a. Dispersal of aquatic gastropods via the intestinal tract of water birds. Nautilus 78: 135-139.

_____ 1965 b. Killdeer (Charadrius vociferus Linnaeus) as a means of dispersal for aquatic gastropods. Ecology 46: 551-552.

Mann, K. H. 1958. Annual fluctuations in sulfate and bicarbonate hardness in ponds. Limnol. Oceanogr. 3: 418-422.

Meier-Brook, C. 1969. Substrate relations in some Pisidium species (Eulamellibranchiata: Sphaeriidae). Malacologia 9: 121-125.

Mitropolskji, W. I. 1965. Observations on the life cycle, growth rate and tolerance of drying in Musculium lacustre (Muller) (Lamellibranchiata). Trudy Inst. Biol. Vnutrennikh Vod, 8: 118-124. (as cited by Heard, 1973).

_____ 1966. "Observations of the life cycle of Sphaerium corneum L. (Mollusca: Lamellibranchia)" and "On the mechanism of filtration and the feeding habits of Sphaeriidae (Mollusca: Lamellibranchia)". English translation of pp 125-134 in "Plankton i benthos vnutrennikh vodoemov", Akademiya Nauk SSSR, Institut Biologii Vnutrennikh Vod, Trudy, vypusk 12 (15), 1966.

Monk, G. R. 1928. The anatomy and life-history of a freshwater mollusk of the genus Sphaerium. J. Morph. 45: 473-503.

Moodie, C. D. and F. E. Koehler. 1973. Laboratory manual for soil fertility. Washington State Univ., Dept. Agron. and Soils, Pullman, Washington 206 p.

Morgan, A. H. 1930. Fieldbook of ponds and streams. G. P. Putnam's Sons, New York 448 p.

Neave, S. A. 1940. Volume III. Nomenclator Zoologicus. Ed M. A. Edwards and A. T. Hopewood. The Zoological Soc. London, London, England 1065 p.

Nelson, T. C. 1918. On the origin, nature, and function of the crystalline style of lamellibranchs. J. Morph. 31: 53-112.

Nicholson, A. J. 1933. The balance of animal populations. J. Anim. Ecol. 2: 132-178.

Odhner, N. H. 1929. English translation of, Die molluskenfauna des Takern. Sjon Takerns Fauna och Flora, 8, Almquist und Boktryckeri - A. -B., Stockholm 129 p.

_____ 1951. The mountain fauna of the Virihaure Area in Swedish Lapland. Lunds Univ., Arsskrift. N. F. Aud. 2, 46: 26-50.

Okada, K. 1935 a. Some notes on Musculium heterodon (Pilsbry), a freshwater bivalve. I. The genital system and gametogenesis. Sci. Rpt. Tohoku Imp. Univ., Ser. 4, Biol. 9: 315-328.

_____ 1935 b. Some notes on Musculium heterodon (Pilsbry), a freshwater bivalve. II. The gill, breeding habits and marsupial sac. Ibid. 9: 375-391.

_____ 1935 c. Some notes on Musculium heterodon (Pilsbry), a freshwater bivalve. III. Fertilization and segmentation. Ibid. 10: 467-483.

_____ 1936. Some notes on Sphaerium japonicum biwaense Mori, a freshwater bivalve. IV. Gastrula and fetal larva, Ibid. 11: 49-68.

_____ 1938. Some notes on Sphaerium japonicum biwaense Mori, a freshwater bivalve. V. Prodissoconch-larva. Ibid. 12: 425-466.

O'Malley, H. 1924. Food and feeding in freshwater mussels. Bull. U. S. Bur. Fish. 39: 439-471.

Pawluk, S. 1967. Soil analyses by atomic absorption spectrophotometry. Atomic Absorption Newsletter 6: 53-56.

Poyarkoff, E. 1910. Incubation des embryon et regeneration des branchies chez Cyclas. Arch. Zool. Exp. 5 (Ser 5): CXXV-CXXVIII.

Prime, T. 1851. Descriptions of Cycladidae. Proc. Boston Soc. Nat. Hist. 4: 155-165.

_____ 1853. Notes on the species of Cycladidae in the United States. Ibid. 4: 271-286.

_____ 1865. Monograph of American Corbiculadae. (Recent and fossil). Smiths. Misc. Coll. No. 145, 80 p.

Purdy, W. C. 1930. A study of the pollution and natural purification of the Illinois River. II. The plankton and related organisms. Public Health Bull. 198: 1-212.

Rao, D. N. and F. Leblanc. 1967. Influence of an iron-sintering plant on corticolous epiphytes in Wawa, Ontario. Bryologist 70: 141-157.

Raven, C. P. 1958. Morphogenesis: the analysis of molluscan development. Pergamon Press, New York 311 p.

Rees, W. J. 1965. The aerial dispersal of Mollusca. Proc. Malac. Soc. London 36: 269-282.

Richardson, R. E. 1928. The bottom fauna of the middle Illinois River, 1913-1925: its distribution, abundance, valuation and index value in the study of stream pollution. Bull. Ill. Nat. Hist. Surv. 17: 387-475.

Rogers, J. P. and L. J. Korschgen. 1966. Foods of lesser scaup on breeding, migration and wintering areas. J. Wildl. Mgmt. 30: 258-264.

Scott, D. R. M. 1955. Amount and chemical composition of the organic matter contributed by overstory and understory vegetations to forest soil. Yale Univ., Scool of Forestry, Bull. No. 62, 73 p.

Shimek, B. 1930. Land snails as indicators of ecological conditions. Ecology 11: 674-686.

Simpson, G. G., A. Roe, and R. C. Lewonton. Quantitative zoology. Harcourt, Brace and Co., New York 440 p.

Slack, K. V. 1964. Effect of tree leaves on water quality in the Cacapon River, West Virginia. U. S. Geol. Surv., Prof. Papers 475 D, Article 161, pages D181-D185.

Smith, N. 1973. Study of age, growth, and distribution of channel catfish in the Ottawa River near Ottawa and Hull, Canada. MSc thesis, Univ. Ottawa, Ottawa

Standard Methods for the Examination of Water and Wastewater. 1965. 12th Edition. American Public Health Assoc., New York 769 p.

Sterki, V. 1909. Descriptions of two new species of Musculium. Nautilus 23: 66-67.

_____ 1916. A preliminary catalog of North American Sphaeriidae. Ann. Carnegie Mus. 10: 429-474.

Stewart, R. E. 1958. Distribution of the black duck. Fish and Wildl. Serv., U. S. Dept. Interior, Circular 51, 8 p.

Stobo, W. 1971. Distribution and growth of yellow perch in the polluted and unpolluted waters of the Ottawa River. MSc thesis, Univ. Ottawa, Ottawa 124 p.

Thiel, M. E. 1924. Versuch, die Verbeitung der Arten der Gattung Sphaerium in der Elbe bei Hamburg aus ihrer Lebensweise zu erklären. Arch. Hydrobiol., Suppl. 4: 1-70. (as cited by Mitropolskji, 1966).

_____ 1926 a. Vorlaufige Mitteilung über das Wachstum und die Fortpflanzung von Sphaerium corneum L. im Hamburg Hafen. Mitteil. aus d. Zool. Staatsinst. u. Zool. Mus., Hamburg. (as cited by Mitropolskji, 1966).

_____ 1926 b. Die Vermehrung von Sphaerium corneum im Hamburger Hafen. Mitteil. aus d. Zool. Staatsinst. u. Zool. Mus., Hamburg. (as cited by Mitropolskji, 1966).

Thomas, G. J. 1959. Self-fertilization and production of young in a sphaeriid clam. Nautilus 72: 131-140.

_____ 1963. Study of a population of sphaeriid clams in a temporary pond. Nautilus 77: 37-43.

_____ 1965. Growth in one species of sphaeriid clam. Nautilus 79: 47-54.

Toennies, G. and B. Bakay. 1953. Photonephelometric microdetermination of sulfate and organic sulfur. Anal. Chem. 25: 160-165.

Tucker, D. S. 1958. The distribution of some fresh-water invertebrates in ponds in relation to annual fluctuations in the chemical composition of the water. J. Anim. Ecol. 27: 105-123.

Van Cleave, H. J., A. G. Wright, and C. William Nixon. 1947. Preliminary observations on reproduction in the molluscan genus Musculium. Nautilus 61: 6-11.

van der Schalie, H. 1953. Nembutal as a relaxing agent for mollusks. Am. Midl. Nat. 50: 511-512.

_____ and E. G. Berry. 1973. Abstract: The effects of temperature on growth and reproduction in aquatic snails. Malacol. Rev. 6: 60.

Wenke, T. L. 1965. Some ecological relationships of mayflies, caddis flies, and fish in the Mississippi River near Keokuk, Iowa. Unpubl. PhD dissertation, Iowa State Univ., Sci. Technol., Ames, Iowa, 181 p. (as cited by Gale, 1969).

White, J. H. 1957. Revised by Hosie. The forest trees of Ontario and the more commonly planted foreign trees. Dept. Lands Forests, Ontario 81 p.

Wilson, A. E. 1956. A guide to the geology of the Ottawa district. Can. Field-Nat. 70: 1-68.

Wurtz, C. B. 1956. Fresh-water mollusks and stream pollution. Nautilus 69: 96-100.

Wright, S. and O. N. Eaton. 1929. The persistence of differentiation among inbred families of guinea pigs. U.S. Dept. Agr. Tech. Bull. 103: 1-45.

Zumoff, C. H. 1973. The reproductive cycle of Sphaerium simile. Biol. Bull. 144: 212-228.

UNIVERSITÉ D'OTTAWA
UNIVERSITY OF OTTAWA