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EFFECTS OF INFECTION BY DIGENETIC TREMATODES ON THE GASTROPOD, LITTORINA SAXATILIS (OLIVI), IN NOVA SCOTIA

by

Derek S. Davis

Submitted in partial fulfillment of the
requirements for the Degree of Doctor of Philosophy
at Dalhousie University, March 1972.

Approved 

DALHOUSIE UNIVERSITY

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ABSTRACT

A population of Littorina saxatilis at Blue Rocks, Nova Scotia was investigated. Snails in this population grow to a shell length of 10.0 mm in 14 to 18 months and breed twice during this period. Infections with larval trematodes, particularly Microphallus similis and Cryptocotyle lingua occur in reproductively spent snails. Castration of the host by the parasite has little effect on reproduction in the population. There was some evidence for increased rate of growth and longevity in snails infected by C. lingua. Snails infected with M. similis die within a few months.

An investigation of feeding in nature revealed a crude rhythm of feeding and digestion regulated by the tidal cycle.

Studies of feeding in the laboratory showed that the rate of ingestion and efficiency of assimilation were not affected by infection with larval trematodes. A rate of assimilation of 0.22 to 0.60 mg/6-hour, dry weight and an efficiency of growth of 1.8 to 11.1 per cent were calculated for L. saxatilis.

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INTRODUCTION

The relationships that exist between the parasitic larvae of digenetic trematodes and their molluscan hosts have stimulated considerable interest among biologists. Gastropod or bivalve molluscs are always involved in the complex life cycles of these parasites as first intermediate hosts. Of the many aspects studied in the past, the ecological relationships (including those factors influencing levels of infection), physiological relationships and relationships at the tissue level are particularly prominent. These findings have been comprehensively reviewed (Cheng and Snyder, 1962; Fretter and Graham, 1962; James, 1965; Wright, 1966; Cheng, 1967).

The molluscan species involved in these studies have included a wide range of freshwater and marine gastropods and bivalves. Among the marine gastropods studied, the prosobranch family Littorinidae features prominently.

The effects of parasitism on the tissues of Littorina littorea (Linné) were studied by Rees (1936) and more recently by Robson and Williams (1971 a and b). James (1965) studied the effects of five species of larval digeneans on the digestive tissues of Littorina saxatilis (Olivi). Both

physical and metabolic effects were detected. These included physical blocking by the parasites of the digestive tubules causing autolysis in the cells similar to that which results from prolonged periods of starvation. The degree of the effect was found to depend upon the nature of the parasite and the duration of the infection.

At the population level, James (1963, 1965, 1968 a and b and 1969) covered many aspects of the relationships between the parasites and the subspecies and varieties of L. saxatilis. These detailed studies of a single host species revealed the diversity of such relationships. For example: some parasites infect the juvenile snails, while others infect only reproductively spent adults; this results respectively in a progressive decrease or increase of the infection levels within any age group of the population.

Digenean larvae may be very abundant in the snail host and live in close association with the digestive tubules, often causing them to be damaged. Quantitative studies which compare digestion and assimilation in infected and uninfected snails would be of fundamental importance in the understanding of host-parasite relationships. To date only one such study has been made (Platt, MS1968); all other quantitative studies on digestion in molluscs have involved only uninfected animals. Such studies have been fairly numerous upon filter and detritus-feeding bivalves (Owen,

1967) but similar studies on herbivorous gastropods are limited (North, 1954; Carefoot, 1967).

Studies of the histology of the digestive tubules of bivalves have demonstrated that there are cyclic phases of ingestion and excretion (Owen, 1966; Purchon, 1968). Morton (1956), studying the intertidal bivalve, Lasaea rubra (Montagu), showed that this cyclic activity could be related to an imposed tidal rhythm of feeding. The phenomenon, a diphasic digestive cycle, was studied in detail by McQuiston (1969) using the electron microscope. A similar cycle has been shown by Morton (1969), in the freshwater bivalve, Dreissena polymorpha (Pallas) and also in the marine intertidal bivalve, Cerastoderma edule (Linné). Though the tissue structures associated with a diphasic digestive cycle have been identified in some gastropods (Morton, 1955 a and b) only one attempt has been made to relate them to feeding rhythms of intertidal species. Merdsoy (MS 1971) identified phasic activity in the digestive cells of L. littorea but could not relate this to the tidal cycle. Such phasic digestive activity would be of significance in quantitative studies of digestion and assimilation in these animals.

The present study of L. saxatilis takes advantage of the quantity of information already available on this species and its digenean parasites. It forms part of a wider investigation of host-parasite relationships in Nova Scotian

Littorinidae. Other parts of this investigation have already been reported: Lambert (MS 1967), Lambert and Farley (1968), Platt (MS 1968) and Merdsoy (MS 1971). The variation in form of L. saxatilis and the diversity of its trematode parasite fauna were investigated on a limited scale on the Atlantic Coast of Nova Scotia. The results were used as a basis for selecting a suitable population for more detailed study. This study of host-parasite relationships examined the growth and reproduction of the host and incidences of trematode infection. In addition the effects of the parasites on digestion and assimilation were investigated. As a preliminary to this, the feeding and digestive cycles of the snails were examined, both in nature and in the laboratory. Attempts were made to apply radioactive tracer techniques to these studies.

MATERIALS AND METHODS

Studies of a population of L. saxatilis.

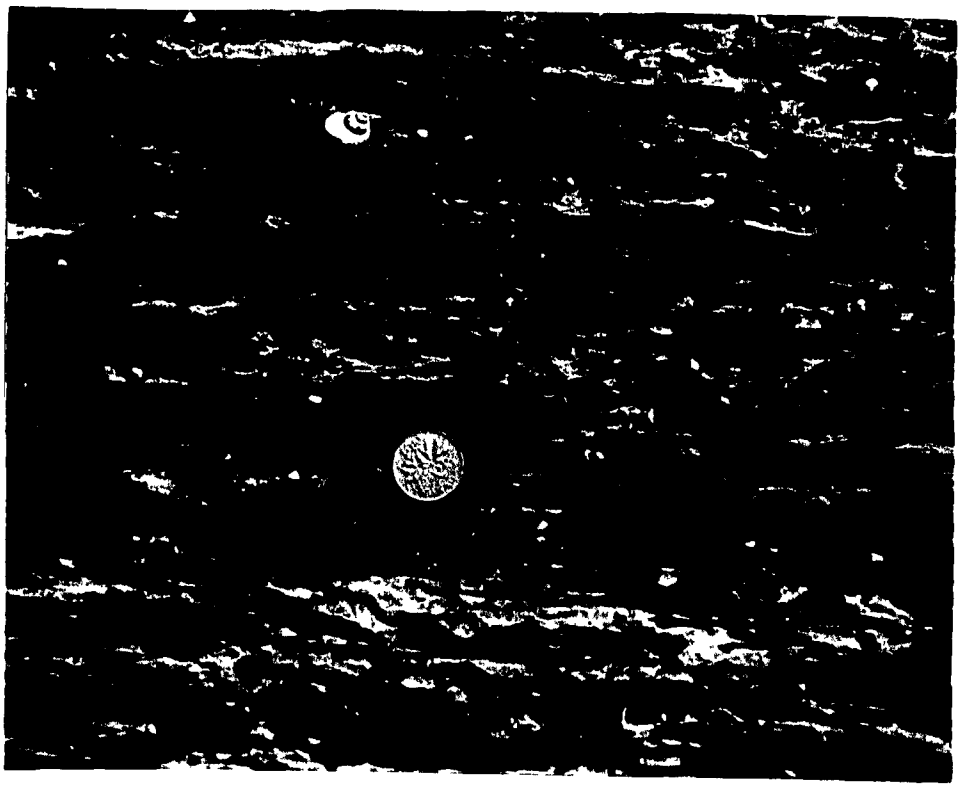
During the period 23 March 1967 to 15 September 1968 samples of L. saxatilis were collected from a sheltered rocky shore at Blue Rocks, Lunenburg County, Nova Scotia. The sampling station was a sloping outcrop of Meguma Slate, surrounded by mud and stones, and growths of Spartina alterniflora Loisel (Fig. 1). In the summer the snails were distributed over the rock surface (Fig. 2) and attained a population density of about 1,200 individuals in a square meter. In the winter, the snails were found in cracks in the rock and under stones at the foot of the outcrop.

On each visit to Blue Rocks the temperatures of air, rock surface and water surface, and surface salinity were measured. The temperatures were measured with a hand therometer. Salinity was determined from specific gravity measurements made with a hydrometer, and corrected from the tables of Zerbe and Taylor (1953). The temperature and salinity values obtained are shown in Table 1.

Samples of L. saxatilis were taken at about monthly intervals in the summer and less frequently during the autumn and spring. Each sample was made up of about 250 individuals all collected from the same area. On one occasion, 24 July 1968, a sample of 424 individuals was taken.

Fig. 1. Blue Rocks, Lunenburg County, Nova Scotia. The locality from which the population samples of L. saxatilis were taken, 23 March 1967 to 14 September 1968. The sampling station was the flat rock in centre, foreground.

Fig. 2. L. saxatilis on the grooved surface of Meguma Slate at Blue Rocks, 15 September 1968. The scale is indicated by the coin which is 19 mm in diameter.



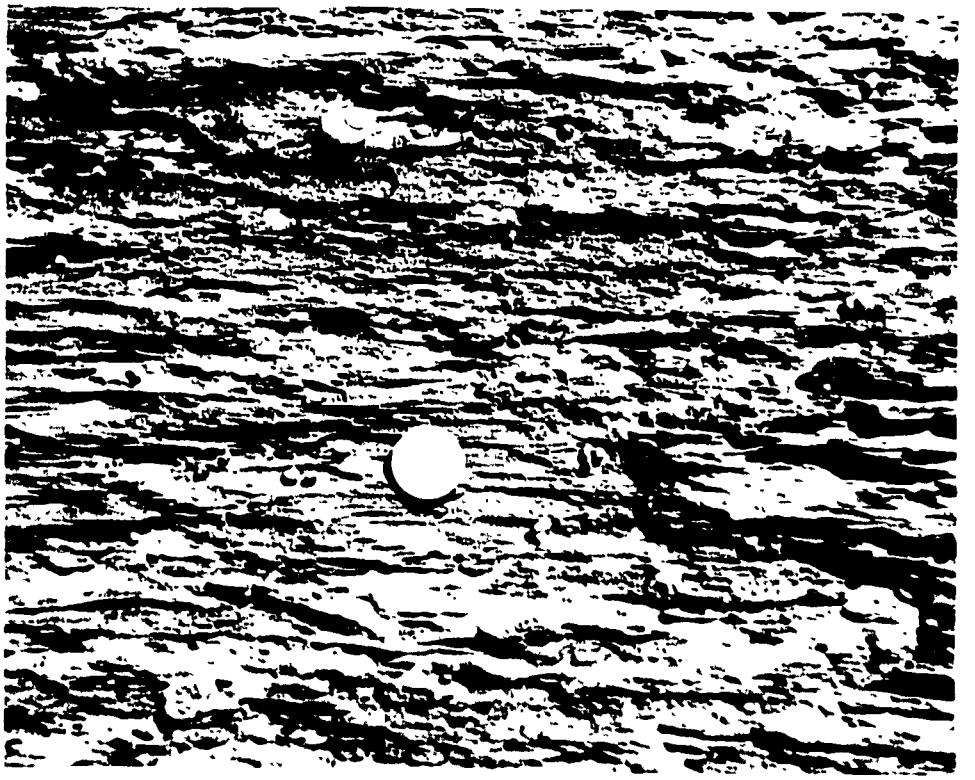


Table I. A summary of the visits made to Blue Rocks, Lunenburg County, showing the samples of L. saxatilis taken and associated temperature and salinity data. The two dates when ice was present on the shore are indicated (ice).

Date	Sample No.	Temperature °C			Surface salinity %	Remarks
		Air	Rock Surface	Sea Surface		
23 Mar. 1967	1	6.5	-	0.5	30.1	Ice
10 May 1967	2	12.0	-	11.0	31.1	
14 June 1967	3	14.0	21.5	7.0	31.4	
18 July 1967	4	21.0	26.0	17.0	30.3	
30 Aug. 1967	5	13.0	16.0	11.0	29.8	
3 Oct. 1967	6	16.0	17.5	11.0	32.7	
15 Nov. 1967	-	4.0	4.0	6.5	32.8	
29 Nov. 1967	7	0.3	0.0	5.0	33.1	
20 Jan. 1968	-	6.0	-	-1.0	28.5	Ice
29 Mar. 1968	8	6.5	6.5	4.5	31.8	
31 May 1968	9	15.5	21.0	10.5	33.5	
24 July 1968	10	23.5	26.0	-	33.5	
15 Sept.1968	11	19.0	23.0	18.0	32.8	

Littorina saxatilis is a species with wide diversity in shell form and habitat preference. The specimens from Blue Rocks were examined as part of a wider study of variation of characters of L. saxatilis on the Atlantic coast of Nova Scotia. This study is described in Appendix II. The specimens from Blue Rocks were identified as L. saxatilis tenebrosa tenebrosa (Montagu).

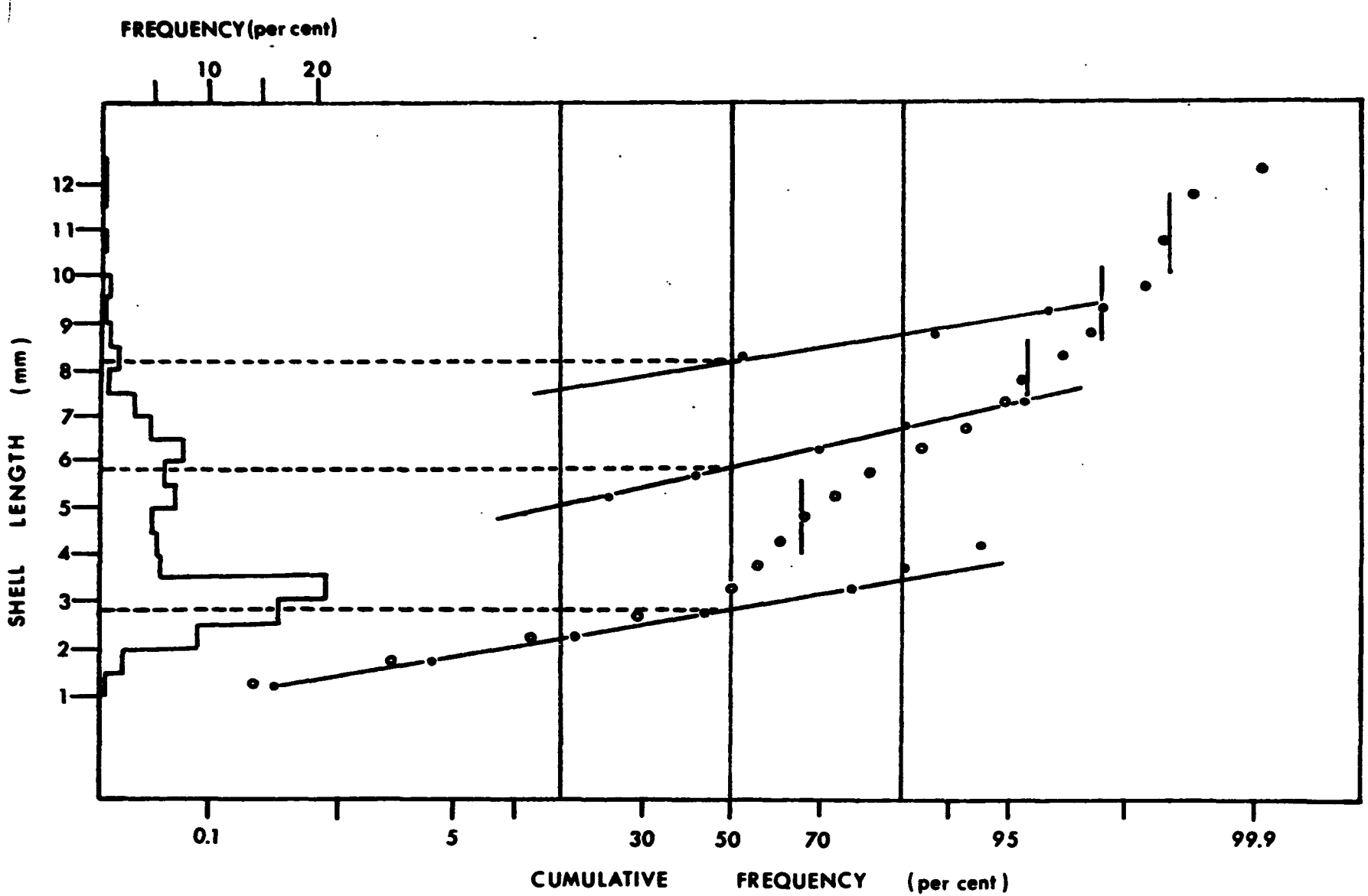
The larvae of digenetic trematodes infecting L. saxatilis were identified in a survey of 23 stations along the Atlantic and Bay of Fundy shores of Nova Scotia. The records obtained from this survey are given in Appendix II. The seven species of Digenea identified in the survey were all present in the L. saxatilis population at Blue Rocks. They were: Parvatrema homeotecnum James, 1964; Himasthla littorinae Stunkard, 1966; Microphallus pygmaeus (Levinsen, 1881); Microphallus similis (Jägerskiöld, 1900); cercaria roscovita Stunkard, 1932; Podocotyle atomon Rudolphi, 1809; and Cryptocotyle lingua (Creplin, 1725).

The samples taken at Blue Rocks were analysed as follows: each snail was measured for shell length; the sex and number in brood, if any, were recorded; and the presence of parasites was recorded. Shell length was used as a parameter for growth and a measure of age. The numbers of gravid females and the level of parasite infection were correlated with the age of the snail through shell length measurements. The

snails were measured for shell length to the nearest 0.25 mm and these measurements arranged into 0.5 mm size groups. The percentage size-frequency distributions obtained showed that the population was polymodal but components were not easy to distinguish visually. The samples were analysed by arithmetic probability analysis using the method of Harding (1949) as modified by Cassie (1954). This method may be used to analyse populations with polymodal frequency distributions, because such populations are generally made up of components with normal distributions. When the cumulative percentage frequencies of the polymodal population are plotted on probability paper, a curve is produced which is the resultant of two or more straight lines. These straight lines, which are used to locate the means and standard deviations of age components in the population, are calculated from points of inflexion in the curve. The polymodal population of L. saxatilis was comprised of various age/size groups. An example of the curve is shown in Fig. 3.

The relationship between shell length and weight was determined to allow conversion of increment in length to increment in weight, which was required for determination of efficiency of growth. Whole live snails were weighed to the nearest 0.01 g. Shells and bodies were separated and dried overnight in an oven at 65°C. Shells were then weighed to the nearest 0.01 g using a "Sartorius" balance, and bodies

Fig. 3. Arithmetic probability analysis and size frequency distribution for the sample of L. saxatilis collected at Blue Rocks, 24 July 1968. N = 424. Short, vertical solid lines indicate points of inflextion in the curve at 66.0 per cent, 96.0 per cent and 98.6 per cent. The horizontal, broken lines indicated the mean shell lengths of component groups as determined from the intersection of each straight line and the 50 per cent level.


FREQUENCY (per cent)
10
20
SHELL LENGTH (mm)
12
11
10
9
8
7
6
5
4
3
2
1
0.1
5
30
50
70
95
99.9
CUMULATIVE FREQUENCY (per cent)

were weighed to the nearest 0.1 mg using a "Cahn Gram" electrobalance.

Studies of the feeding and digestive rhythm of L. saxatilis in nature.

Rhythmic feeding and digestion related to the tidal cycle has been demonstrated in the intertidal bivalve Lasaea rubra (Montagu) by Morton (1956). It was considered possible that L. saxatilis, occupying a similar level in the intertidal zone, would also possess a feeding and digestive rhythm. Such a phenomenon would be of importance when evaluating the rate of assimilation for this species. Three experiments were carried out in the field over a 12-hour period from one high tide to the next. Snails were sampled at intervals during this period. The first two studies were made at Purcell's Cove, Halifax County, and the third at Black Rock, Point Pleasant Park, Halifax. Both localities are fairly sheltered boulder beaches and have populations of L. s. tenebrosa tenebrosa with low levels of parasite infection.

Samples of 20 snails each were taken at hourly intervals in the first study, 28 May 1968. The specimens were immediately fixed in Bouin's solution and later transferred to 70 percent ethanol. Each specimen was subsequently examined for the distribution of food and faeces in the digestive tract. This was accomplished either by dissection or by

dehydrating the specimen and then clearing it in xylene. The food or faeces were recorded as being either present or absent in parts of the digestive tract identified as oesophagus, proximal stomach, distal stomach, intestine and rectum. Only the material in the oesophagus proved difficult to observe.

In the second study, 12 July 1968, six samples of six snails each were taken at intervals of two hours. The shells were crushed and the snails' bodies immediately fixed in Bouin's solution. They were later transfered to 70 percent ethanol. The digestive gland was removed from each of the preserved specimens, dehydrated, and embedded in paraffin. Sections were cut at 8μ and stained in hematoxylin and eosin. The sections were examined to determine whether these tissues showed any evidence of cyclic activity which could be related to the tidal rhythm.

In the third study, 21 September 1968, samples of six snails each were taken at intervals of two hours. Shells were crushed and the snail bodies dissected while fresh to determine the distribution of food and faeces in the digestive tract.

Laboratory studies.

Samples of L. saxatilis for use in laboratory experiments

were obtained from Blue Rocks, Lunenburg County, and Purcell's Cove, Halifax County. The habitat at both localities was a sheltered rocky shore. The snails were kept in aerated sea water aquaria at the required temperature, for the shortest practical period of time before experiments.

In the laboratory, snails were put separately into dishes of seawater and kept for varying periods of time to observe any shedding of cercariae. In this way, the infected and uninfected snails were initially separated. However, the infected snails did not always shed cercariae, especially during the winter, or at low temperatures in the laboratory. In addition to this, two of the trematode species, Microphallus pygmaeus and Parvatrema homeotecnum do not shed cercariae. For these reasons, the absence of parasites from any snail, inferred by lack of shedding-cercariae, was always confirmed by crushing it and examining the tissues at the end of the experiment.

Blue Rocks was a good source of infected snails, but uninfected specimens were often difficult to obtain. In these cases the stock of snails was supplemented from Purcell's Cove, where the level of infection was apparently near zero.

Laboratory experiments, involving both infected and uninfected L. saxatilis, were designed to obtain information on the time taken for food to pass through the digestive tract,

the rate of ingestion and the efficiency of assimilation. The conditions of each experiment are summarised in Table II.

Preparation and use of food in the feeding experiments.

A variety of food types was used in the feeding experiments. These were: living Chlorophycean algae (Urospora spp. and Enteromorpha spp.); powdered detritus prepared from these algae; and the detritus forms labelled with ^{14}C. The food types used in the experiments are listed in Table III. Details of the methods for the preparation of food are given below.

Live Urospora spp. and Enteromorpha spp. were collected from the upper shore where L. saxatilis is most common. Urospora spp. were available in the winter and spring but became less common and eventually absent from the shore in summer. At this time Enteromorpha spp. were used in the experiments requiring live algal food.

A laboratory culture of Urospora spp. was maintained during the early summer to provide a continuous source of live food. Seawater was pumped through a rotating lawn sprinkler which sprayed onto the inside of a clear plastic cylinder. The cylinder was approximately five feet high and two feet in diameter and supported by a wooden frame. Waste water drained away at the bottom. Constant illumination was provided by four, four-foot long fluorescent tubes.

Table II. A summary of the conditions in experiments to obtain information on feeding and digestion in L. saxatilis. Experiments in the A-group using ^{14}C were to determine the rate of passage of food through the digestive tract. Autoradiography was used in experiment B to follow the passage of food in the digestive tissues during a single feeding/digesting period (12 hours). The C-group experiments evaluated the rate of ingestion and the efficiency of assimilation for carbon and nitrogen.

Experiment No.	Temperature °C	Salinity °/oo	Imposed feeding cycle hr.
A.1 - A.3 ^{14}C	6	35.1	6
B. Auto-radiography	10-15	?	6
C. Total Carbon and Nitrogen			
1.	6	33.8	6
2.	10-15	34.0	6
3.	10-15	33.8	24
4.	10-15	34.0	6
5.	10-15	34.0	6

This apparatus is illustrated in Fig. 4. The inner surface of the plastic cylinder was roughened and scored to encourage settlement of the algae. Freshly collected Urospora spp. were liberally smeared over the roughened surface and allowed to dry for a few minutes. The water supply was then turned on and the system left in continuous operation. Good growths of Urospora spp., developed in the initial phase, but later in the summer the culture was lost due to a power failure. The culture could not be re-established as the Urospora spp. had by this time disappeared from the shore.

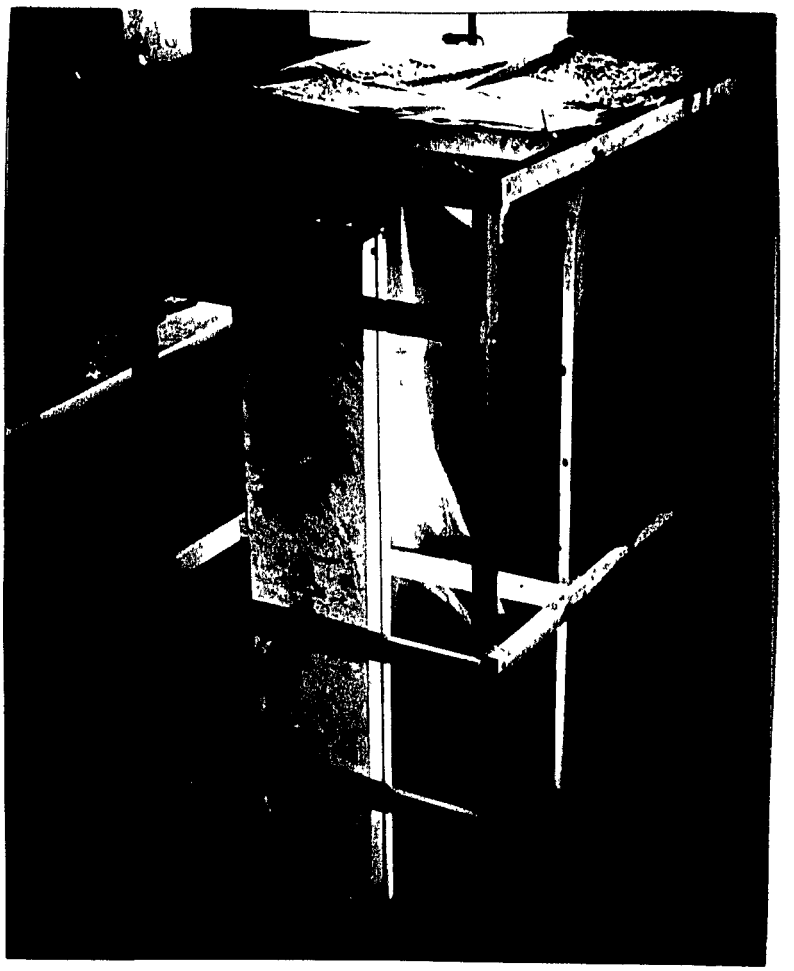
Dry powdered foods were prepared from living Urospora spp. and Enteromorpha spp. in the same way. Living plants were macerated in a Waring blender and the resulting material filtered, washed with distilled water, then rewashed and dried in an oven at 65° for 24 hours. The dry residue was ground to a powder and passed through a sieve to give a maximum particle size of 1 mm. Tests with the food showed that there were great changes in weight and in carbon and nitrogen content when the powder was re-hydrated in the feeding dishes. Since these values needed to be accurately known to determine the rate of ingestion and efficiency of assimilation, the food was refined in the following manner. The powdered algae were washed again with distilled water and then dried. This refined food was more stable when re-hydrated in the feeding dishes. However, there was still an apparent mean gain in weight of 3.9 ± 12.03 percent for Urospora spp. Carbon

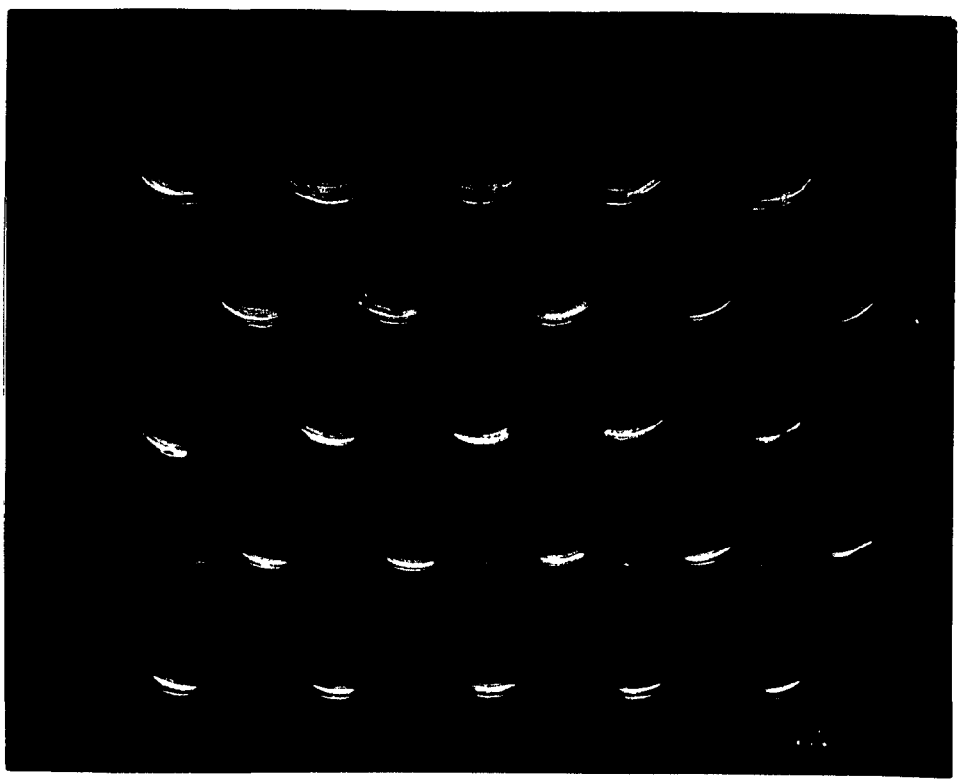
Table III. A summary of the types of food used in the experiments to obtain information on feeding and digestion in L. saxatilis. Specific activities of ^{14}C-labelled foods are given for experiments in groups A and B. The carbon and nitrogen values in the C-group experiments are those used for the calculation of efficiency of assimilation. The values are means ± standard deviation.

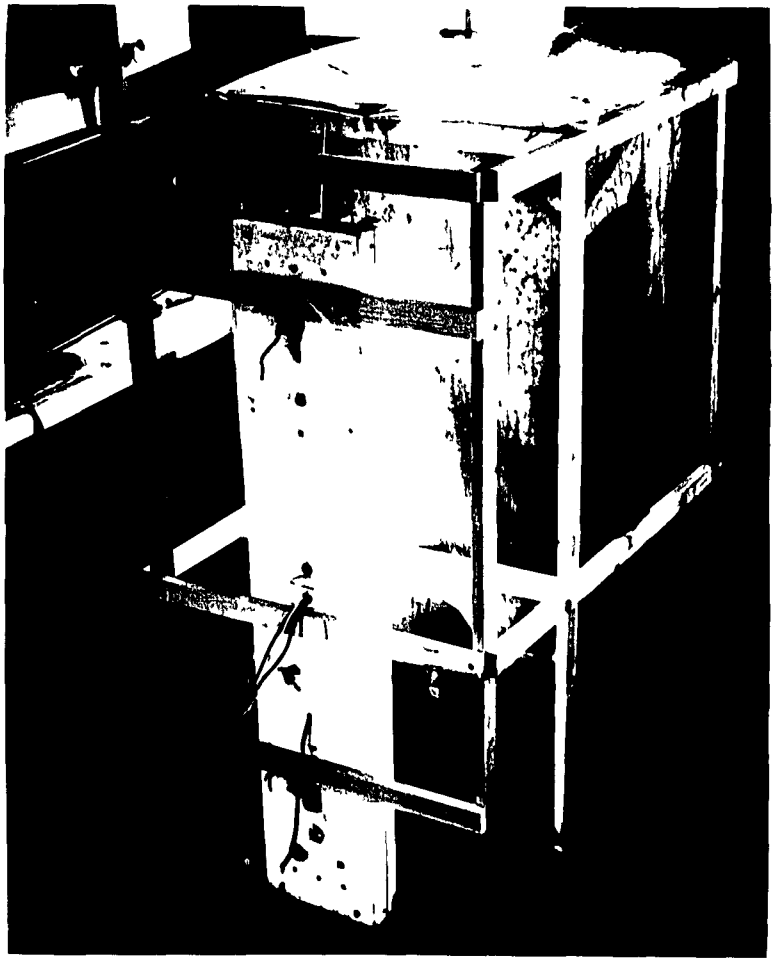
Exp. No.	Food used	Specific activity cm/0.1mg	Carbon in food (%)	Nitrogen in food (%)
A.1	Urospora spp. detritus	c. 576	-	-
A.2		c. 351	-	-
A.3		c. 351	-	-
B	Enteromorpha spp. detritus	c. 10,000	-	-
C.1	Urospora spp. detritus	-	29.99±3.60	4.09±0.56
C.2	Urospora spp. detritus	-	41.24±2.44	6.46±0.95
C.3	Urospora spp. detritus	-	41.24±2.44	6.46±0.95
C.4	Enteromorpha spp. detritus	-	35.73±2.08	1.82±0.22
C.5	living Enteromorpha spp.	-	43.34±3.38	2.15±0.62

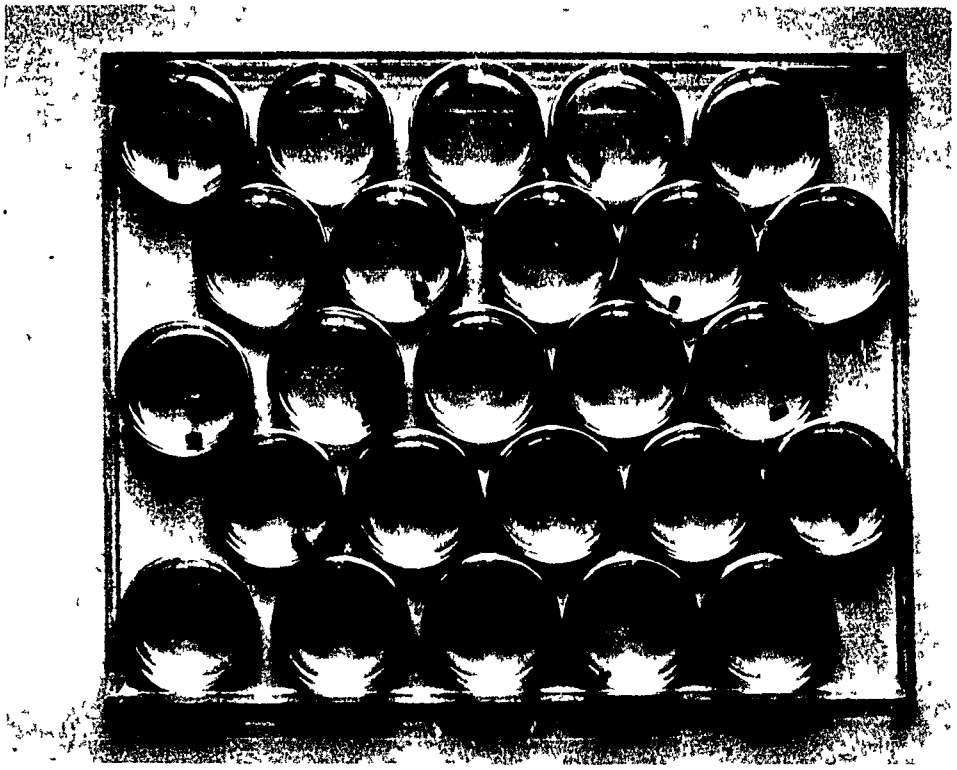
Fig. 4. The apparatus used for the spray-culture of the algae Urospora spp., required as food in the experiments to obtain information on feeding and digestion in L. saxatilis. The plastic cylinder is about five feet in height.

Fig. 5. The apparatus used in experiments to obtain information on feeding and digestion in L. saxatilis. The snails were kept individually in 50 mm petri dishes.









content showed a mean loss of 4.7 ± 7.11 percent for Urospora spp., and a mean gain of 0.3 ± 15.25 percent for Enteromorpha spp. The nitrogen content was decreased by a mean of 14.3 ± 16.75 percent for Urospora spp., and increased by a mean of 11.2 ± 17.02 percent for Enteromorpha spp.

The percentage carbon and nitrogen values for both live and detritus Urospora spp. and Enteromorpha spp. foods are listed in Table III. These values were used in the calculation of efficiency of assimilation.

Analysis for carbon and nitrogen.

The samples of food and the faeces produced by L. saxatilis during the feeding experiments were analysed for carbon and nitrogen using a Hewlett Packard Model 185 Carbon, Hydrogen and Nitrogen Analyser. In this apparatus, the samples were burned in the presence of an oxidising catalyst and the products measured in a gas chromatograph. Calibrations were obtained using a standard of known composition, Cyclohexanone - 2.4 Ditrophenyl-hydrazone ($C_6 H_{10} N.NH.C_6.H_3(NO_2)_2$), wich contained 51.79 percent carbon, 20.4 percent nitrogen and 5.07 percent hydrogen.

The regressions used for calculation of the carbon and nitrogen values are given below. Two regressions are given in each case because the apparatus was repaired

during the course of the experiments.

Carbon 1.

$y = x\ (0.18) - 4.3$ $\quad t = 65.85$ (7 d.f.)

Carbon 2.

$y = x\ (0.14) + 4.61$ $\quad t = 12.95$ (8 d.f.)

Nitrogen 1.

$y = x\ (0.4) - 4.7$ $\quad t = 157.47$ (8 d.f.)

Nitrogen 2.

$y = x\ (0.3) - 0.18$ $\quad t = 27.96$ (12 d.f.)

Where y is the quantity of carbon or nitrogen in μg and x is the peak height in mm measured from the analyser chart.

The food and faecal samples to be analysed for carbon and nitrogen content were washed in ammonium formate solution (isotonic with seawater at 3 percent) and transferred with a micropipette into pre-weighed aluminum boats. They were dried overnight in an oven at 65°C and re-weighed. Weights were measured on a Cahn "Gram" electrobalance, to the nearest 0.001 μg. Each sample was burned in the aluminum boat with the oxidising catalyst. Carbon and nitrogen correction values for each set of analyses were obtained by burning blanks, that is, aluminum boats with only the catalyst. The peak heights were taken from the recorder chart, corrected for the blank values and converted to weights using the appropriate calibration. The final values were given as μg (carbon or nitrogen) for each 100 μg of sample weight, that is, as

the percentage.

Preparation of algal detritus labelled with ^{14}Carbon.

Radioactive ^{14}C was used to label samples of Urospora spp. and Enteromorpha spp. Sodium bicarbonate ($NaHC^{14}O_3$) in aqueous solution, with a specific activity of 54.5 mc/mM was obtained from the Radiochemical Centre at Amersham, England. The 1 ml of solution was diluted to 20 ml with distilled water and divided into twenty, 1 ml portions each containing 50 µc of ^{14}C. These portions were sealed in vials and refrigerated.

The live algae were kept in stoppered glass flasks with 100 ml of seawater. One vial of sodium bicarbonate labelled with ^{14}C as above was added to each flask. The flasks were maintained at 10°-$15^{\circ}C$ in a 12-hour cycle of illumination. It was found that under these conditions the highest specific activity values for the algae were reached after about three hours. After this time the specific activity decreased as the ^{14}C was apparently recycled from the plant back to the water.

Detritus food was prepared from ^{14}C-labelled Urospora spp. and Enteromorpha spp. by the procedure previously described for unlabelled detritus. The specific activities of the detritus foods used in the experiments are given in Table III.

Radioactivity counts were made with either of two gas-flow detectors using helium-butane. One was a Nuclear-Chicago model D.47 gas-flow detector with model T-3 time delay, model C-110 B automatic sample changer, model 181 A decade scaler and model C-111 B time interval printer. When operated at 1,150 volts and 7 lb/sq. in gas pressure, the counter gave 3.28 percent efficiency, as tested with a 0.1 μg ^{14}C standard from Nuclear-Chicago. The other counter was a Nuclear-Chicago Model 470 gas-flow detector with model 1120 lead shield, model 1042 automatic sample changer, model 8703 scaler decade-timer and model 8437 lister. When operated at 1,150 volts and 7.5 lb/sq. in gas pressure, an efficiency of 4.5 percent was obtained with the same ^{14}C standard.

The ^{14}C-labelled food was used in trial experiments to evaluate efficiency of assimilation. However, due to the very poor results obtained when comparing specific activities of food and faeces this method was not used in the main series of experiments.

In all feeding experiments, the L. saxatilis were kept individually in 10 mm x 50 mm petri dishes arranged in series in perspex trays (Fig. 5). Complete sets of dishes, sufficient to meet the needs of the 6-hour or 24-hour changing cycle were set up at the beginning of each experiment. This facilitated rapid change of each snail to a new dish without change of temperature.

Size of L. saxatilis specimens used in the experiments.

The snails were selected to be approximately the same size. The mean live weights for uninfected and infected groups are given with the data for each experiment (Appendix I, Data Sheets 24 to 33). There was no significant difference in size between the snails in either infected or uninfected groups in any experiment ($P < 0.3$).

Experimental Details.

Experiments to evaluate the time taken for food to pass through the digestive tract of L. saxatilis.

In these experiments radioactivity counts were made on faeces produced by the snails during successive six-hour periods. Thus it was possible to measure the time taken for a ^{14}C-labelled meal to pass through the digestive tract. Three experiments, A1, A2 and A3, were carried out, as summarised in Tables II and III.

Twenty snails were used in each experiment, and food was offered on a six-hour cycle, that is to say, food and water were alternately present and absent for six-hour periods. Unlabelled food was offered to the snails initially, followed by ^{14}C-labelled food for a single six-hour period, and then more unlabelled food. The dishes were changed and the faeces collected with a micropipette at the end of each

six-hour period. Five or seven samples were taken in each experiment. Faeces were briefly washed in 3 percent ammonium formate solution and then transferred to small aluminum foils of known weight. The samples were dried in an oven at 65°C overnight and then weighed. They were then put onto aluminum counting planchettes, covered with Parafilm M* and radioactivity counts made. The specific activity (counts per minute per unit weight) was obtained for each sample.

An experiment to observe the passage of ^{14}C-labelled food in the digestive tract of L. saxatilis, using auto-radiography technique.

The technique of autoradiography involves the exposure of photographic emulsion by radioactive emissions in total darkness. Liquid emulsion can be applied to thin sections of tissue to determine the location of radioactive material in the cells. By this method it was possible to trace the movement of ^{14}C-labelled food in the digestive gland of L. saxatilis.

Eight uninfected snails from Purcell's Cove and eight snails from Blue Rocks infected with C. lingua, were used in experiment B. These snails were maintained in the petri dishes for some days to obtain regular feeding, and were

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* Parafilm M is a multipurpose laboratory film manufactured by the American Can Company.

then offered ^{14}C-labelled Enteromorpha spp. detritus for a single six-hour period. Two uninfected and two infected snails were sampled before the ^{14}C-labelled food was offered and two more of each at 6, 12 and 18 hours after commencement of feeding. These snails were removed from their shells and immediately fixed in Bouin's solution. After about 12 hours they were transferred to 70 percent ethanol and subsequently dehydrated, cleared and embedded in paraffin. Sections of 8 μ thickness were cut from the visceral region of each specimen. Strips of sections were mounted on glass slides and dried. Some series of sections were stained with hematoxylin and eosin while others were used for autoradiography.

The autoradiography technique closely followed that described by Gude (1968). The paraffin was removed from one series of sections from each specimen. The sections were then dehydrated and dried. Kodak NTB_2 liquid emulsion was applied with a small metal roller in light dimmed by a series 2 Wratten filter. The time allowed for exposure was 12 days. During this period the slides were stored in a dry, light-tight box at room temperature. The exposed emulsion was developed with Kodak Dektol at 15°C under light dimmed with a series 2 Wratten filter. The slides were then washed with distilled water and dried. Later the sections were dehydrated and mounted in Canada balsam. The tissues were examined and photographed using phase-contrast microscopy.

Experiments to evaluate the rate of ingestion in *L. saxatilis*.

The rate of ingestion is the amount of food eaten by an animal in any given time. This amount is readily evaluated by comparing the weight of food offered to the animal with the weight of food residue left at the end of the feeding period.

Measurements of the rate of ingestion were made in experiments C.1 and C.4 using detritus foods prepared from *Urospora* spp. and *Enteromorpha* spp. respectively. Weighed portions of food were offered to each snail for a six-hour period. At the end of this period the faeces were collected with a micropipette and the food residues filtered with 25 mm plain 5 µ Millipore membrane filters of known weight. The residues were washed with distilled water and dried on the filters at 65°C for from 36 to 48 hours. The samples were weighed directly after removal from the oven.

The rate of ingestion was evaluated as the loss in weight of the food offered, in a given time.

$$I = \frac{w_1 - w_2}{t}$$

Where I is the rate of ingestion, w_1 is the weight of food offered, w_2 is the weight of food residue and t is the time.

Experiments to evaluate the efficiency of assimilation in L. saxatilis.

The efficiency of assimilation was measured by comparing the carbon or nitrogen contents of the food offered and of the faeces produced by the snails. The experiments, C.1 to C.5, used different foods, temperatures and lengths of feeding cycle as shown in Table II. The carbon and nitrogen values of food are shown in Table III. The snails were kept separately in petri dishes and were subjected to the selected 6-hour or 24-hour feeding cycle at least 24 hours before sampling commenced. Faecal pellets were removed from the dishes with a micropipette at the end of each period, washed with distilled water, and put into aluminum boats of known weight. The boats and samples were dried at 65°C for 24 hours and then weighed immediately after being removed from the oven. The samples were analysed for total carbon and total nitrogen content in the carbon, hydrogen, nitrogen analyser previously described.

Platt (MS 1968) evaluated efficiency of assimilation for L. littorea on a 24-hour feeding cycle. One parallel experiment was carried out in the present study on L. saxatilis, but in the others a six-hour feeding cycle was used. This most closely resembled the normal tidal, feeding cycle in nature.

Twenty snails were used in each experiment and in most cases these were sampled on more than one occasion. The number of samples taken varied between experiments because some snails did not produce faeces regularly.

The efficiency of assimilation was calculated as

$$U = \frac{O_1 - O_2}{O_1} \times 100$$

Where U is the efficiency of assimilation, O_1 is the percentage carbon or nitrogen content of the food and O_2 is the percentage carbon or nitrogen content of the faeces.

Calculation of rate of assimilation for L. saxatilis.

The rate of assimilation was calculated from the values for rate of ingestion and efficiency of assimilation for carbon obtained in experiments C.1 and C.4. The calculation follows the method used by Platt (MS 1968). The rate is given by:

$$A = I \times O_1 \times U$$

Where A is the rate of assimilation, I is the rate of ingestion, O_1 is the proportion of carbon in the food and U is the efficiency of assimilation for carbon.

Calculation of efficiency of growth for L. saxatilis.

Efficiency of growth has been defined by Smith (1966)

as the relationship between assimilated energy and energy used in growth. The same relationship has been termed "gross efficiency" by North (1954).

In the present study an estimation of the efficiency of growth has been made for L. saxatilis using the summer rate of growth, expressed as increment of dry body weight, and the rate of assimilation for a comparable period.

$$\text{Efficiency of growth} = \frac{\text{increment of dry body weight}}{\text{rate of assimilation}}$$

Statistical methods.

The means calculated for age components in the population samples and for values obtained in the feeding experiments are given, together with the standard deviation.

Tests of significance were made using Student's t-test and analysis of variance. Differences where $P = <0.01$ were considered to be significant.

RESULTS

Relations between some parameters of growth in L. saxatilis.

Because shell length was chosen as the parameter of growth in the population of L. saxatilis at Blue Rocks, the relations between this and the total live weight, total dry weight, and dry body weight were determined.

The relations between shell length and total live weight in 26 specimens collected on either 14 June 1967 or 22 January 1968, are shown in Fig. 6. The relationship is a straight line, $\log w \sim \log a + 3 \log l$. Similar results were found in the relations between shell length and total dry weight, shell length and dry body weight for the same 26 specimens (Fig. 7).

Individual juvenile L. saxatilis, while still in the brood pouch of the parent, had a total dry weight of about 0.04 µg (Table IV). The early stages (egg to early veliger) and later stages (late veliger to juvenile) did not appear to differ significantly in weight, $t = 0.465$ (8 d.f.). The juveniles had a range of shell length from 0.50 to 0.75 mm when they escaped from the parent.

These relations between shell length and total and body weights show that shell length is a useful parameter for growth in L. saxatilis.

Fig. 6. The relations between total live weight and shell length of 26 specimens of L. saxatilis collected at Blue Rocks on either 14 June 1967 or 22 January 1968. The line is fitted by eye.

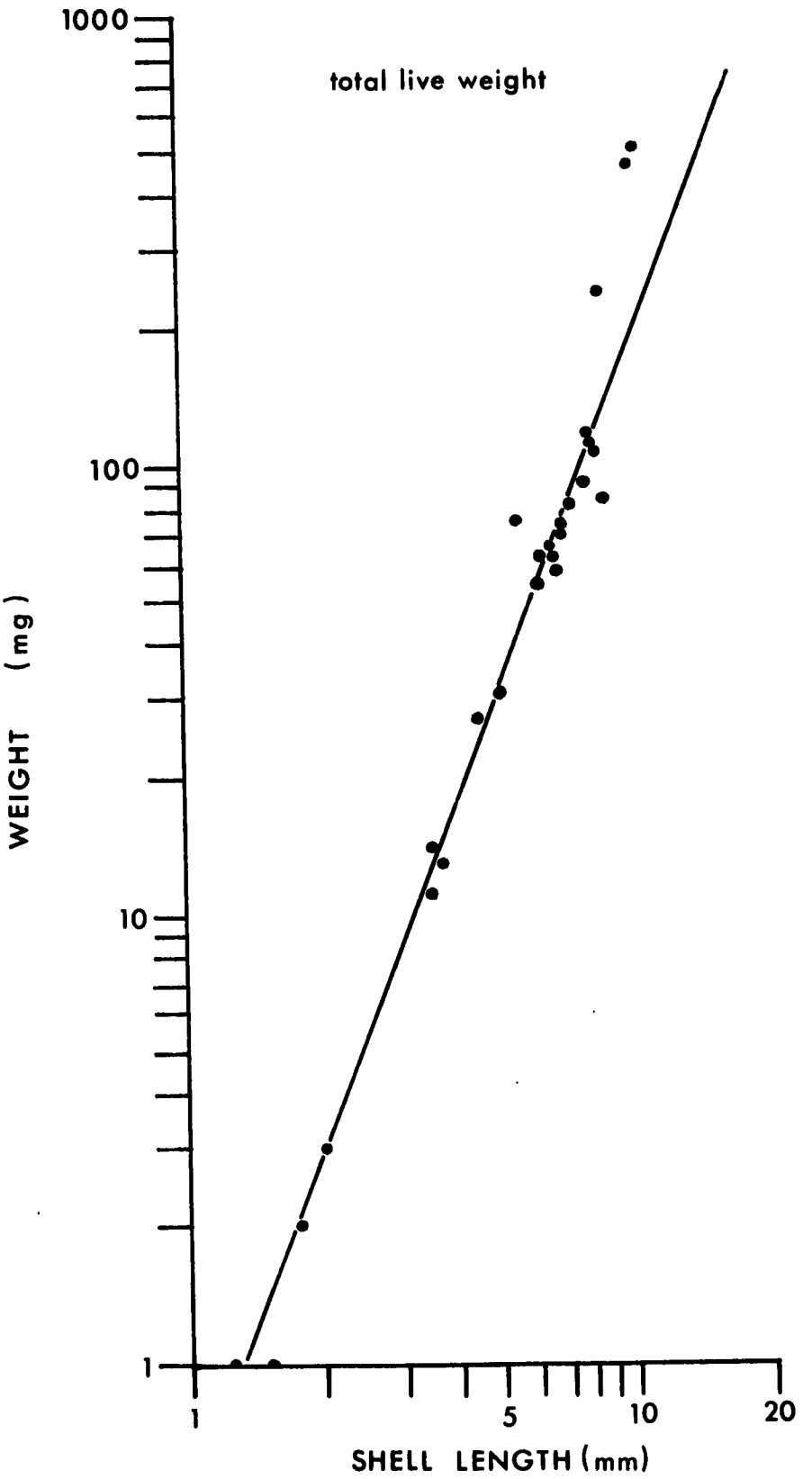

total live weight
1000
100
10
1
WEIGHT (mg)
1
5
10
20
SHELL LENGTH (mm)

Fig. 7. The relations between total dry weight and shell length, and dry body weight and shell length of 26 specimens of L. saxatilis collected at Blue Rocks on either 14 June 1967 or 22 January 1968. The lines are fitted by eye.

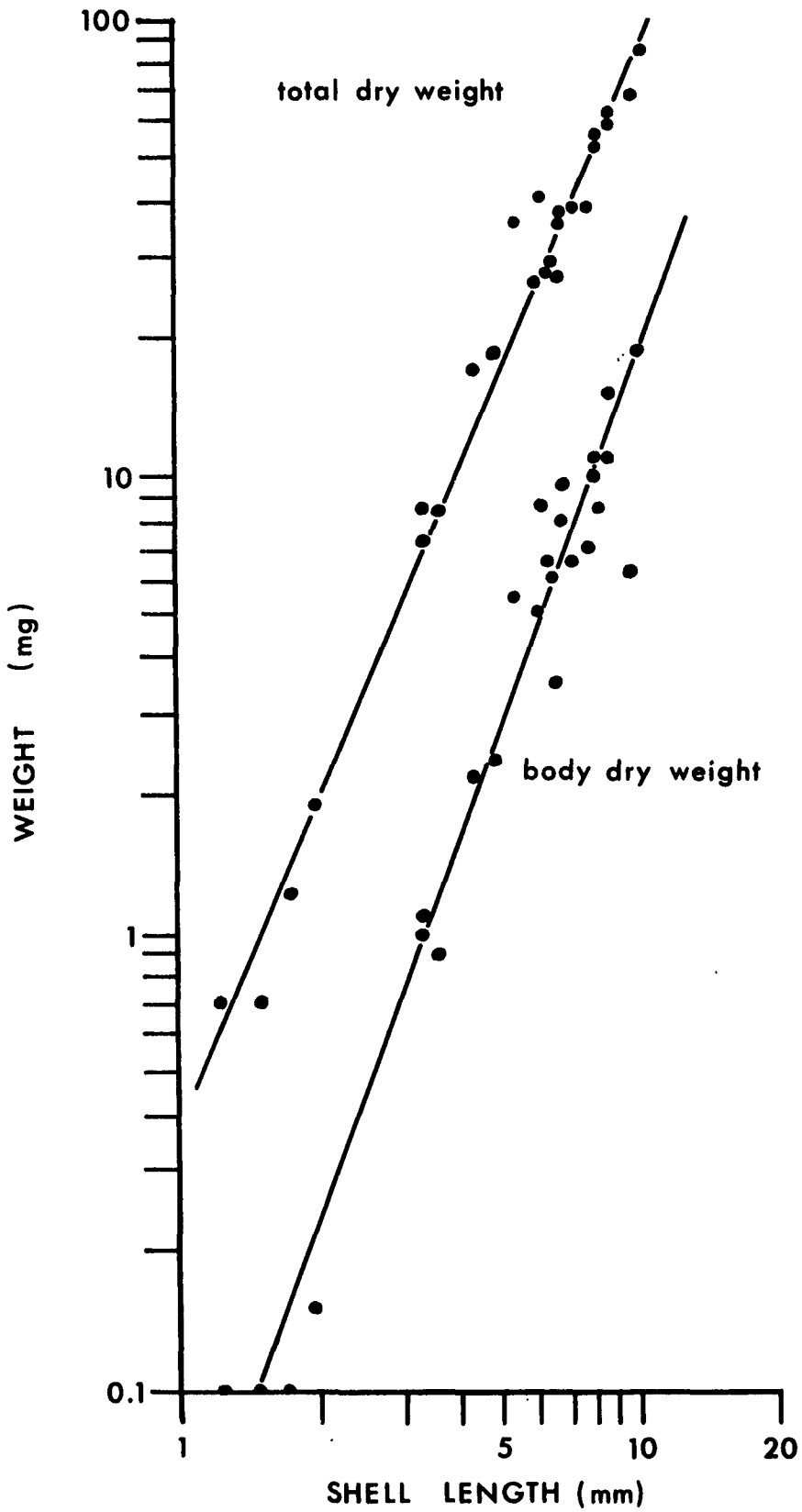

100
10
1
0.1
total dry weight
body dry weight
WEIGHT (mg)
1
5
10
20
SHELL LENGTH (mm)

Table IV. Total dry weights of individual early and late stage juveniles taken from the brood pouches of female L. saxatilis collected at Blue Rocks, summer 1968. The early and late stages do not differ significantly in weight. $t = 0.465$ (8 d.f.)

Stage	Individual Weight (µg)
early	0.045
early	0.022
early	0.035
early	0.053
early	0.021
$\bar{x}$ ± S.D.	0.035 ± 0.014
late	0.024
late	0.070
late	0.027
late	0.034
late	0.046
$\bar{x}$ ± S.D.	0.040 ± 0.018

Studies of a population of L. saxatilis at Blue Rocks.

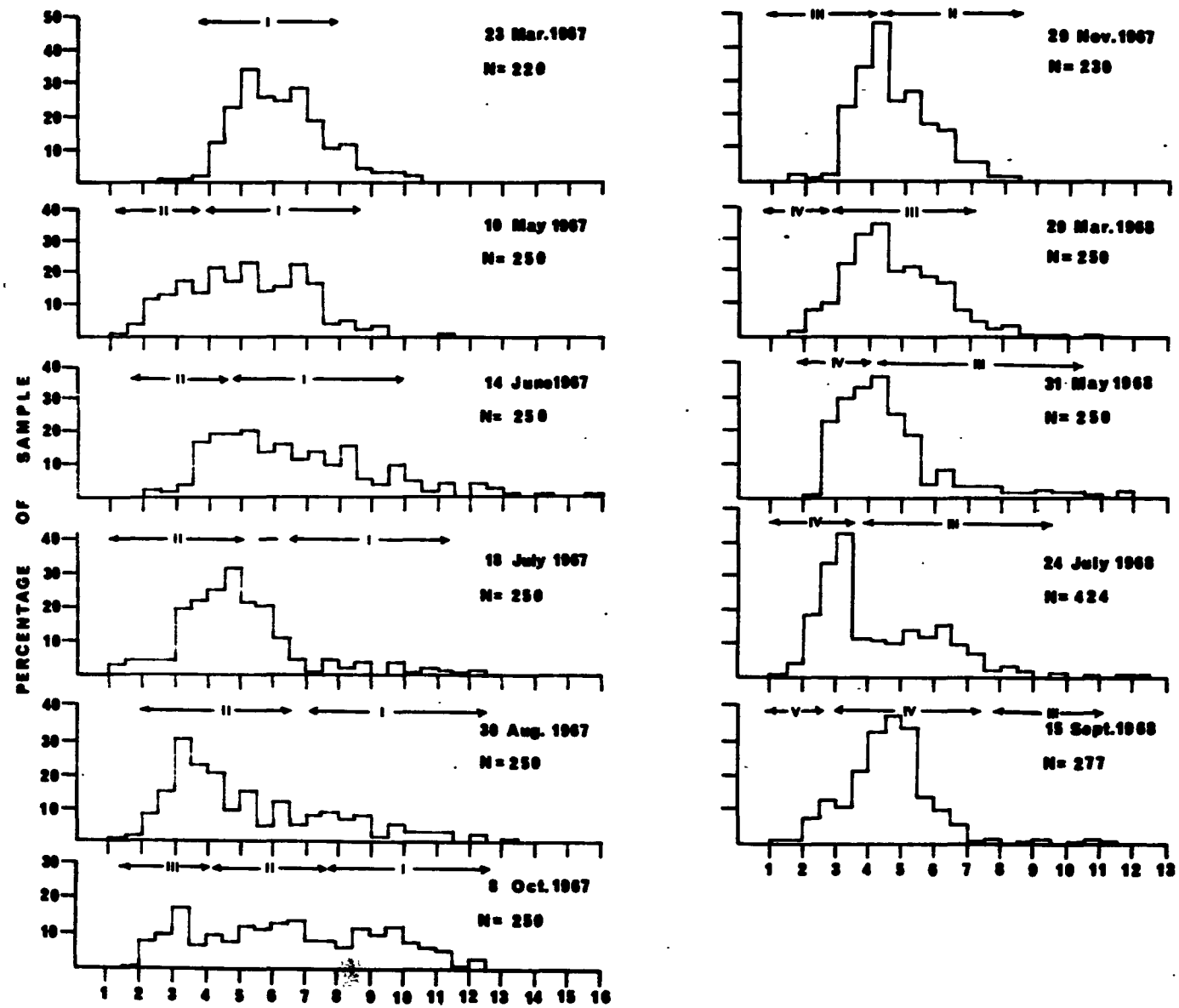
The results of size-frequency analysis and arithmetic probability analysis are given in detail in Appendix I, Data sheets 1 to 11. An example of the relations between the size-frequency distribution and the arithmetic probability analysis is shown in Fig. 3 for the sample collected on 24 July 1968. The size frequency distribution histograms are shown in Fig. 8.

Growth rate and longevity.

The analysis showed that snails of small size, 1.0 to 3.0 mm, were always present in the population indicating a continuous addition of juveniles. The proportion of juveniles increased in the early spring and early fall. Components with mean shell lengths of 2.25 mm were detected in May 1967, October 1967 and March 1968. The component with mean shell length 2.85 mm in the sample of 24 July 1968 may have been associated with the release of juveniles in the spring of that year.

Growth rates for L. saxatilis were not easily calculated from the sample data. Components of the population were obscured by the long period over which juveniles were being released. Juvenile components detected in the spring and autumn of any year could not be distinguished from each other

Fig. 8. Size-frequency distributions of samples of L. saxatilis collected at Blue Rocks from March 1967 to September 1968. The arrows indicate the approximate size-ranges of the age groups, I to V, identified in Fig. 9.


PERCENTAGE OF SAMPLE
23 Mar.1967
N= 220
16 May 1967
N= 250
14 June1967
N= 250
18 July 1967
N= 250
30 Aug. 1967
N=250
8 Oct.1967
N= 250
29 Nov.1967
N= 230
29 Mar.1968
N= 250
31 May 1968
N= 250
24 July 1968
N= 424
15 Sept.1968
N= 277
SHELL LENGTH (mm)

by the following spring. The mean shell lengths for components identified by arithmetic probability analysis were grouped together by eye, and linear regressions for growth (length against time) were calculated for each group. The four groups separated in this way were numbered in chronological order, I to IV and are shown in Fig. 9. They represent age classes of the population.

The regressions for each of the groups or age classes, are given below with estimated summer growth increment in terms of shell length (Y) per 30-day month (X).

Group I (1966 spring and autumn juveniles)

Increment was 0.85 mm in 30 days.

$Y = X\ (0.0298) + 3.41$ (correlation coefficient 0.89 percent).

Group II (1967 spring juveniles)

Increment was 0.75 mm in 30 days.

$Y = X\ (0.248) - 0.0626$ (correlation coefficient 0.72 percent).

Group III (1967 spring and autumn juveniles)

Increment was 0.90 mm in 30 days.

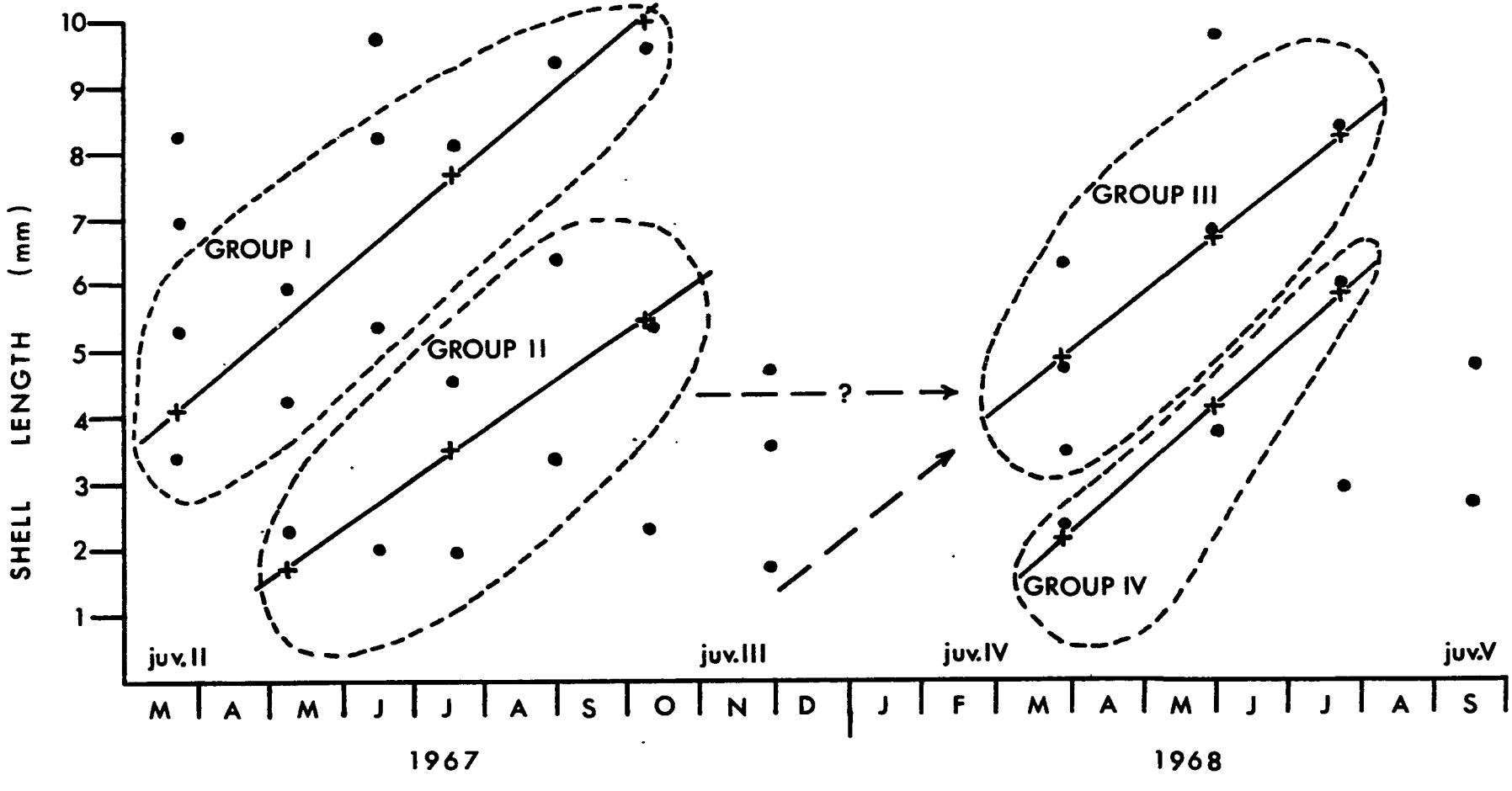
$Y = X\ (0.0289) - 6.665$ (correlation coefficient 0.84 percent).

Group IV (1968 spring juveniles)

Increment was 0.95 mm in 30 days.

$Y = X\ (0.0310) - 10.142$ (correlation coefficient 0.99 percent).

Fig. 9. Regressions for summer growth rates in L. saxatilis at Blue Rocks during 1967 and 1968. The mean values of components separated by arithmetic probability analysis have been associated into age Groups (I to V). The positions of spring and summer release of juveniles are also indicated. The dots are mean shell lengths of size components separated for each sample by arithmetic probability analysis. Juv. II, etc., refer to approximate peak periods of release of juveniles from females, and thus indicate the origins of each age-group.


SHELL LENGTH (mm)
10
9
8
7
6
5
4
3
2
1
GROUP I
GROUP II
GROUP III
GROUP IV
?
juv.II
juv.III
juv.IV
juv.V
M A M J J A S O N D J F M A M J J A S
1967
1968

These groups are also indicated on Figs. 8, 10 and 11. Groups II and III are basically the same population component except that group III also includes the juveniles released in autumn, 1967. An additional age-group V was detected as juveniles in September 1968. Regression analysis cannot be used to determine the winter growth rate, but continuity between the groups allows for very little growth increment.

The difficulty of distinguishing distinct components in the population results from the relatively long period over which juveniles emerge, and also from the high incidence of parasite infections. The effect of these infections will be shown in a later section.

Longevity of L. saxatilis at Blue Rocks can be determined from these data. Although individuals may attain a length of 15 mm, the largest mean shell length of any well-defined population component was 9.7 mm. This length, in groups II and III was attained by about fourteen months after release from the parent.

Reproduction.

Female L. saxatilis became mature at a shell length of about 3.5 to 4.0 mm. The level of reproduction in the population at various sampling times was determined by

examination of the females. Since L. saxatilis is ovoviviparous, the number of young being produced at any instant is obtained by counting the contents of the brood pouches.

In the first five samples, 23 March 1967 to 30 August 1967, only the number of gravid females was noted, but in the remaining samples the number of ova or veligers was also obtained (Appendix I, data sheets 12). The occurrences of gravid females in each sample are summarised in Table V. The gravid females in each 0.5 mm size group, expressed as a percentage of the total gravid females in the sample, are shown for each sample in Fig. 10.

There were no significant differences between the samples of gravid females or mean numbers of brood (Table V), although peak values for gravid females were indicated in June and July 1967, and March and May 1968, and for numbers in brood in October 1967 and May 1968.

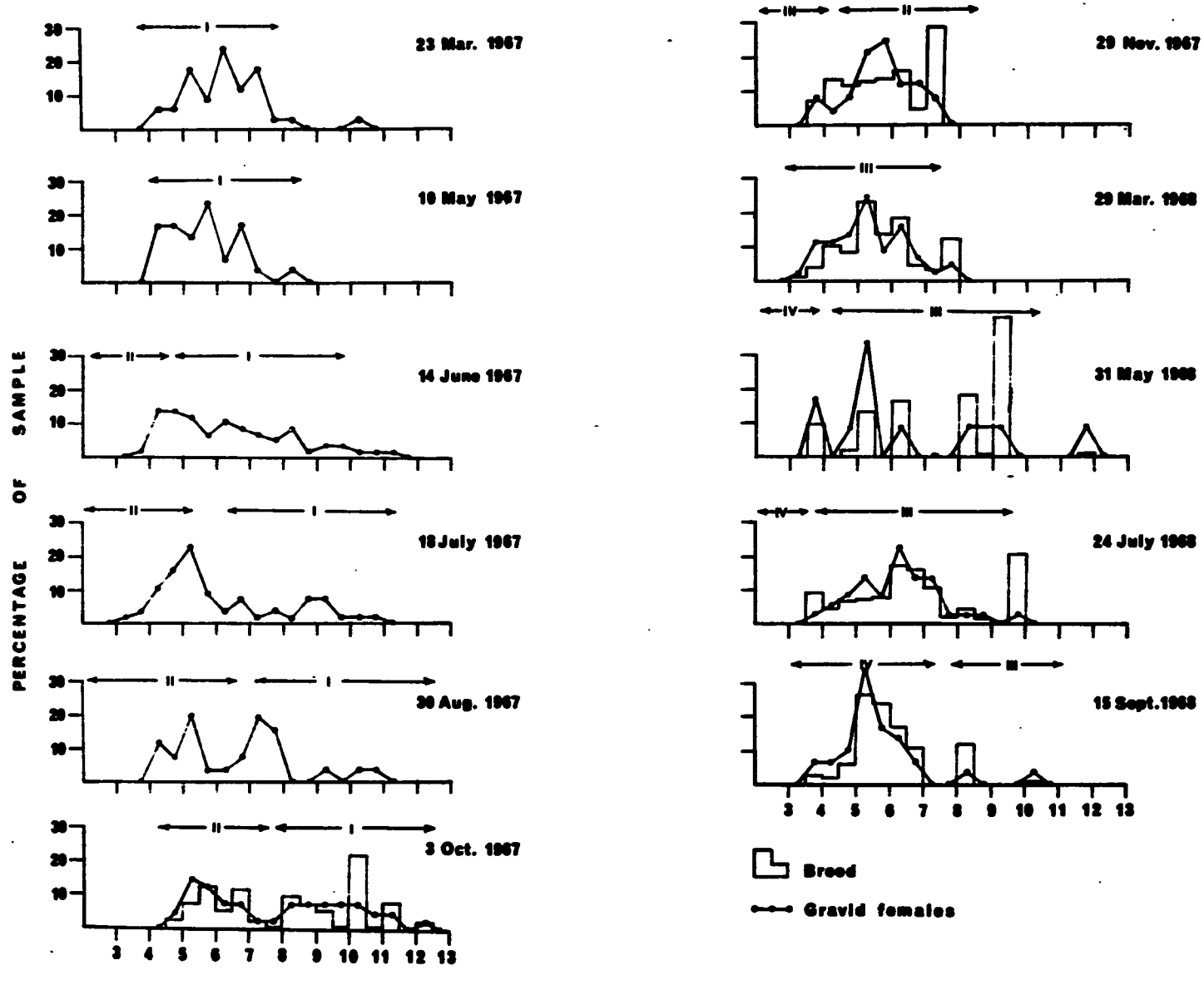
In Fig. 10 the percentage gravid females in the 0.5 mm size groups show seasonal variations in relation to the age groups I to IV, as defined in Fig. 9. In 1967 the samples of 23 March, 10 May and 14 June, show that the reproductive function was largely within Group I (autumn 1966 juveniles). During the summer, however, Group I became less important compared to Group II (spring 1967 juveniles). In the sample of 3 October 1967, snails from both Groups I and II were

Table V. The gravid females in each sample of *L. saxatilis* collected at Blue Rocks, 1967 to 1968. The mean number of ova and veligers in the broods in each sample are also given. Details of the broods in each sample will be found in Appendix I, data sheet 12.

Sample date	Total n	Gravid n	Gravid %	Mean number in brood.
23 Mar. 1967	118*	34	28.81	-
10 May 1967	119	30	25.21	-
14 June 1967	161	59	36.65	-
18 July 1967	134	57	42.54	-
30 Aug. 1967	106	26	24.53	-
3 Oct. 1967	131	41	31.30	46.61
29 Nov. 1967	145	24	16.55	12.00
29 Mar. 1968	139	45	32.37	19.67
31 May 1968	117	12	10.26	43.91
24 July 1968	160	36	22.50	30.33
15 Sept.1968	108	30	27.78	17.30

* Note: Sex was not determined for 13 of the 220 snails in sample, 23 March 1967 and so they have been omitted from this analysis.

Fig. 10. Reproduction in the population of L. saxatilis at Blue Rocks, 1967 to 1968. The frequency polygon represents the total number of gravid females in each 0.5 mm size group as a percentage of the total gravid females in the sample. The solid histogram represents the number of ova and veligers in females of each 0.5 mm size group as a percentage of total ova and veligers in the sample. The arrows indicate the approximate size-ranges of the age groups, I to IV, identified in Fig. 9.


23 Mar. 1967
10 May 1967
14 June 1967
18 July 1967
30 Aug. 1967
3 Oct. 1967
29 Nov. 1967
29 Mar. 1968
31 May 1968
24 July 1968
15 Sept. 1968
PERCENTAGE OF SAMPLE
SHELL LENGTH (mm)
Brood
Gravid females

breeding. From November 1967, to March 1968, Group II was breeding. Group III (autumn 1967 juveniles) was breeding in March, May, June and September 1968, but by the end of this period the most important contribution to reproduction was being made by Group IV (spring 1968 juveniles). These results obtained from the analysis of gravid females were supported, in the samples from 7 October 1967 to 15 September 1968, by similar results shown by the percentage brood values.

Although a seasonal variation in the level of breeding could not be shown for the whole population, it could be demonstrated for individual age groups within the population. Group I was seen to be functioning mainly in March to May 1967, and again in October 1967; Group II was functioning mainly in July 1967, to March 1968; Group III became functional in May 1968, and again in July to September 1968. In general, the females in any age group reproduce twice during their life.

Infections by larval trematodes.

Seven species of larval trematodes were recorded from L. saxatilis at Blue Rocks, from March 1967 to September 1968. The records for each sample are given in Appendix I, data sheets 13 to 23. The occurrences of the parasites are summarised in Table VI. The most frequently occurring species was Cryptocotyle lingua which infected 13.36 percent of the 3,100 L. saxatilis examined. The microphallids, Microphallus

Table VI. The single and double infections of L. saxatilis by seven species of digenetic trematodes, in samples collected at Blue Rocks, March 1967 to September 1968.

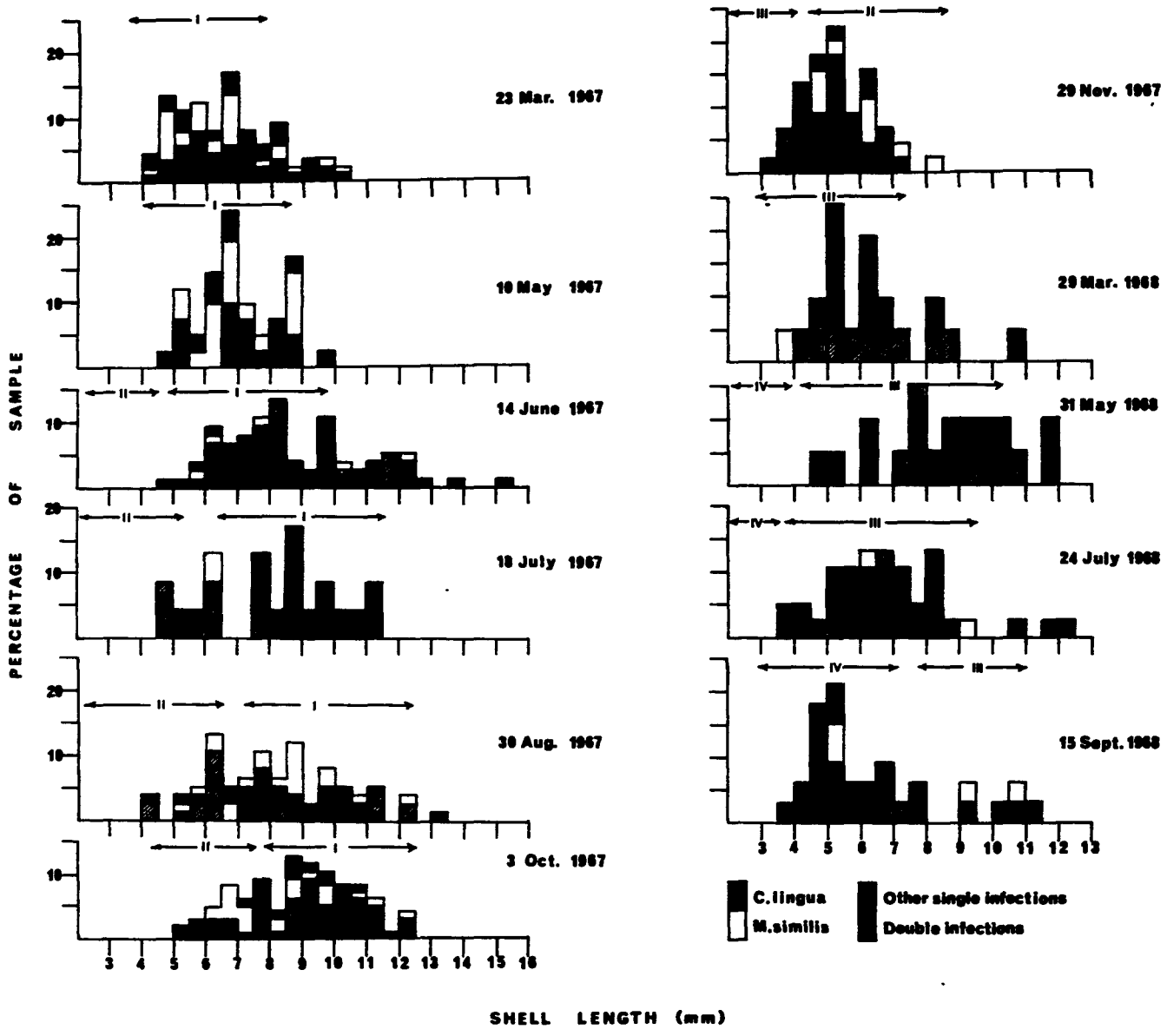
Sample Date	Total	Ph	Hl	Mp	Ms	cr	Pa	Cl	Ms and Mp	Ms and Cl	Ms and cr	Ms and Pa	Cl and cr	Cl and Mp	Cl and Hl	Neg.
23 Mar. 1967	220	-	1	2	29	7	-	41	1	3	3	-	2	-	-	131
10 May 1967	250	-	-	3	18	3	-	16	-	-	-	-	-	1	-	209
14 June 1967	250	-	2	2	5	1	-	62	-	-	-	-	1	-	-	177
18 July 1967	250	-	-	-	2	-	-	21	-	-	-	-	-	-	-	227
30 Aug. 1967	250	-	1	2	20	2	-	48	-	1	-	-	-	-	-	176
3 Oct. 1967	250	-	1	3	22	-	-	63	-	1	-	1	-	3	2	154
29 Nov. 1967	230	-	-	4	9	4	-	27	-	1	-	-	-	-	-	185
29 Mar. 1968	250	-	-	4	1	2	-	14	-	-	-	-	-	-	-	229
31 May 1968	250	-	-	3	-	-	2	15	-	-	-	-	-	-	-	230
24 July 1968	424	1	-	5	2	-	-	29	-	1	-	-	-	-	-	386
15 Sept. 1968	277	1	3	3	4	-	1	21	-	-	-	-	-	-	-	244
Total	2901	2	8	31	112	19	3	357	1	7	3	1	3	4	2	2348
%		.07	.28	1.07	3.86	0.65	0.10	12.31	0.03	0.24	0.10	0.03	0.10	0.14	0.07	80.94

Note: Ph = Parvatrema homeotecnum
Hl = Himasthla littorinae
Mp = Microphallus pygmaeus
Ms = Microphallus similis
cr = cercaria roscovita
Pa = Podocotyle atomon
Cl = Cryptocotyle lingua

pygmaeus and Microphallus similis infected 1.10 percent and 4.13 percent of the 3.100 snails respectively. Four other species; Parvatrema homeotecnum, Himasthla littorinae, cercaria roscovita and Podocotyle atomon, were less important, each infecting less than 1.0 percent of the snails examined. Twenty-one cases of double infection were noted; seven involving the two common parasites C. lingua and M. similis. The records of the two most common species, C. lingua and M. similis were studied in more detail in relation to the L. saxatilis population. The occurrence of these two species, other single infections and double infections in 0.5 mm size-groups of each sample are shown in Fig. 11. The number of each type of infection is expressed as a percentage of the total infected snails in the sample.

Cryptocotyle lingua was found infecting snails as small as 3.5 mm shell-length. There was a general increase in the level of infection in larger snails. The general pattern of infection can be seen in Fig. 11. The snails of age-group I (autumn 1966 juveniles) were infected in March 1967 and the progressive growth of this group, as marked by the infection, can be followed until October, 1967. Age-group II (spring 1967 juveniles) became infected in late summer 1967 and its growth can be followed until March 1968. Age-group III (autumn 1967 juveniles) became infected in the spring of 1968 and the progress of this group can be followed in the

Fig. 11. The larval digenetic trematode infections of L. saxatilis in samples collected at Blue Rocks, March 1967 to September 1968. The values given in each 0.5 mm size group are the infections by C. lingua and M. similis, other single infections, and double infections expressed as percentages of the total infection in each sample. The arrows indicate the approximate size-ranges of the age groups I to IV, identified in Fig. 9.


PERCENTAGE OF SAMPLE
SHELL LENGTH (mm)
23 Mar. 1967
10 May 1967
14 June 1967
18 July 1967
30 Aug. 1967
3 Oct. 1967
29 Nov. 1967
29 Mar. 1968
31 May 1968
24 July 1968
15 Sept. 1968
C. lingua
M. similis
Other single infections
Double infections

samples of July and September, 1968. Snails of age-group IV (spring 1968 juveniles) became infected in July and the infection was very prominent in September, 1968.

When these results (Fig. 11) were compared with the results of the study of reproduction (Fig. 10) there was evidence to suggest that C. lingua infected reproductively spent snails. The lower level of infection found in the sample of March, 1968 compared with the infection of the previous autumn, could have been due to mortality among infected individuals of age-group II.

The second most common parasite, M. similis occurred in all samples except that of 31 May, 1968. The species was most frequent in the spring and autumn. In Fig. 11, the growth of the infected age-groups can be followed through the series of samples. Age-group I (autumn 1966 juveniles) was heavily infected with M. similis in March, 1967 and the association continued until the level of infection reached its lowest, in July. In the August and October, 1967 samples, age-group I became infected again. This infection disappeared when the age-group died during the winter. A similar sequence can be demonstrated for age-group III (autumn 1967 juveniles). Some members of this age-group became infected by November, 1967, but the infection had disappeared by May, 1968. The results thus indicate that M. similis infected reproductively spent snails and also that infected snails

died prematurely. Some previously uninfected snails in the age-group became infected following the second reproductive period.

Some gravid female L. saxatilis were found to be infected with parasites. These occurrences are listed in Table VII. It will be seen from the table that the gravid females infected were mostly large (shell length > 5.25 mm), that the number in the brood was generally low and that the majority of parasite germinal sacs (rediae or sporocysts) did not contain mature cercariae. These observations support the view that parasite infection, particularly with C. lingua and M. similis, took place as soon as the snail released the final batch of eggs into its brood pouch, and that they multiplied while the young snails were developing.

The feeding and digestive rhythm of L. saxatilis in nature.

Food.

Casual observations of the types of food eaten by L. saxatilis in nature were made at Purcell's Cove, Black Rock and Blue Rocks. On exposed rock surfaces in the spring the snails were seen feeding on blue-green algae, and faecal pellets examined contained algae, mineral particles and other material. In the summer, faeces contained mostly mineral particles compacted in mucus. The snails were also observed feeding on Urospora spp. and Enteromorpha spp. Filaments of

Table VII. Records of the infection of gravid L. saxatilis by larval trematodes in samples collected at Blue Rocks, March 1967 to September 1968.

Sample date	Shell length (mm)	Number in brood	Parasites	
			species	cercariae present
23 Mar. 1967	10.25	70	Ms	+
	6.50	7	Ms	
14 June 1967	10.75	4	Cl	
	5.50	?	Cl	
	6.00	?	Cl	
	7.00	?	Cl	
18 July 1967	9.50	40	Cl	
	12.00	25	Cl	+
	9.50	11	Cl	
	8.50	?	Cl	
30 Aug. 1967	5.25	?	Cl	
	7.50	?	Cl	
	11.00	?	Cl	
	7.75	?	Ms	
	8.25	?	Cl	
	5.25	?	Mp	
3 Oct. 1967	9.50	2	Cl	
	7.50	4	Cl	
	10.00	4	Cl	
	10.50	?	Cl	
	9.00	29	Cl	
	10.75	4	Cl	
	9.25	27	Cl	
	11.25	6	Cl	+
	8.75	2	Cl and Mp	+
	9.75	6	Ms	
	12.25	45	Ms	
29 Nov. 1967	6.75	1	Cl	
31 May 1968	8.75	1	Cl	
	11.75	4	Cl	
29 July 1968	6.25	13	Cl	
	7.25	2	Mp	
15 Sept. 1968	5.25	14	Hl	
	5.25	2	Cl	

Note: Ms = Microphallus similis, Mp = Microphallus pygmaeus, Cl = Cryptocotyle lingua, Hl = Himasthla littorinae.

Urospora spp. and diatoms were found undigested, in the faeces.

Feeding cycle in nature.

Three tide-cycle studies resulted in the detection of a crude rhythm of feeding activity for L. saxatilis. The snails grazed at high tide and remained active until the rock surfaces became dry as the tide ebbed. They were inactive during the dry period and did not feed again until they were submerged by the next flood tide. These observations are summarized in Table VIII.

Evidence for cyclic feeding activity in relation to these alternating wet and dry conditions was obtained from observations of the sequence of movement of food and faeces in the digestive tracts of dissected snails. The snails were feeding at high tide and faeces were being voided. By four hours after high tide, when the snails were dry and inactive, food in the stomach was being processed by a rotary action around a mucus rod. This mucus rod became more prominent as food was processed during the low tide period. At about four hours after low tide, just before the snails became submerged, faeces were packed tightly into the intestine and rectum. The faeces were shed as feeding activity was resumed. The stages in this sequence are described more precisely in Fig. 12. These observations are only of summer

Table VIII. A summary of three series of field observations of the feeding activity of L. saxatilis, during a single tidal cycle. These observations were made at Purcell's Cove, (1) 28 May 1968, (2) 12 July 1968 and at Black Rock, (3) 21 September 1968.

Sample series	Time (AST)	Tide level (ft.)	Air temp. °C	Water temp. °C	Observations
1	8.30	5.70 (ht)	9.4	7.8	Snails submerged and active
	9.30	5.50	7.8	8.3	Snails exposed and active
	10.40	4.95	9.4	8.3	Snails exposed and active
	11.40	4.20	10.0	7.8	Snails exposed, active in sheltered places
	14.00	2.70	9.4	8.3	Snails exposed, dry and inactive
	15.00	2.70 (lt)	12.8	8.9	Snails exposed, dry and inactive
	16.00	2.70	10.0	7.8	Snails exposed, dry and inactive
	17.00	3.20	12.8	8.3	Snails exposed, dry and inactive
	18.00	3.95	11.7	7.8	Snails becoming submerged and active
2	8.30	5.70	-	15.5	Snails submerged and active
	9.30	6.45 (ht)	18.9	-	Snails submerged and active
	10.30	6.20	22.8	15.5	Snails submerged and active
	12.30	4.45	17.2	16.0	Snails exposed and active
	13.30	3.45	16.7	17.0	Snails exposed and inactive
	14.30	2.70	15.6	16.5	Snails exposed and inactive
	16.30	1.70 (lt)	16.1	16.5	Snails exposed and inactive
	17.30	2.20	15.6	-	Snails exposed and inactive
	18.30	3.20	15.6	16.0	Snails exposed and inactive
3	7.00	- (ht)	-	-	Snails submerged and active
	9.00	-	24.0	18.0	Snails exposed and active
	11.00	-	31.0	19.0	Snails exposed
	13.00	- (lt)	34.0	19.0	Snails exposed, dry and inactive
	15.00	-	32.5	20.5	Snails exposed, dry and inactive
	17.00	-	26.0	20.5	Snails becoming submerged and active

Note: lt = Low tide
ht = High tide

conditions; winter feeding activity was not studied.

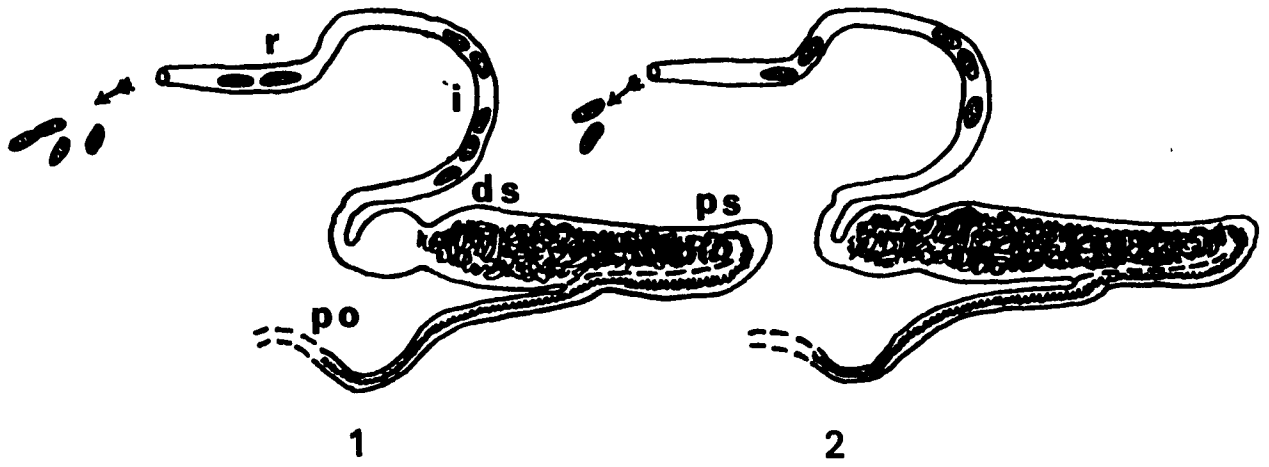
Since L. saxatilis occupies a narrow band in the supralittoral fringe, on spring tides they would be completely submerged for two or three hours at each high tide. On some neap tides, the snails would be submerged for a shorter period. Allowing for a period of four hours after high tide for the rocks to dry, it is reasonable to assume that six hours is available in each tidal cycle for feeding by L. saxatilis. This represents a summer daytime situation. It is possible that at night, with lower temperatures and high humidity, the feeding period would be extended.

Snails of the second series of collections at Purcell's Cove, 13 July 1968, were fixed and prepared for microscopic examination. The digestive tissues were examined from snails sampled at two-hour intervals during the tidal cycle. Some changes in the structure of the digestive cells were noted during this period. The general structures of the tissues are shown for each sampling period in Figs. 13 to 18. At high tide, Figs. 13 and 14, the cells of the digestive tubules were distinct and contained numerous and often large food vacuoles (diameter 5 to 10 μ). The sample collected at four hours after high tide showed numerous dark spherules, up to 10 μ in diameter, in the digestive cells (Fig. 15). Each digestive cell contained one of the spherules in a vacoule. The distribution of these spherules throughout a wide area of

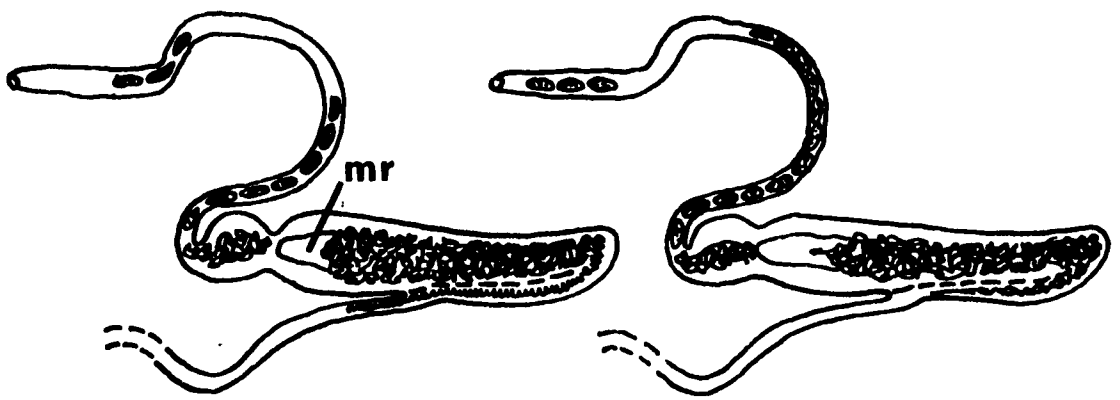
Fig. 12. A diagram of the digestive tract of L. saxatilis to show the passage of food. The six stages were recorded at two-hour intervals from one high tide to the next high tide. The stages were as follows:

1. High tide. The snails were submerged, active and feeding. Faecal pellets were being voided.
2. High tide plus two hours. The snails were exposed, active and feeding. Faeces were still being shed but fewer were in the rectum, at this time.
3. High tide plus four hours. The snails were exposed and inactive. In the stomach the first stages were seen in the development of a mucus rod at the posterior end of the rotating food mass.
4. Low tide. The snails were exposed and inactive. There was no food in the oespohagus and the mucus rod was more developed.
5. Low tide plus two hours. The snails were exposed and inactive. The rectum was being filled with faeces as the stomach contents were processed.
6. Low tide plus four hours. The snails were soon to be submerged by the flood tide. There was almost no food in the stomach and the mucus rod was well developed. Faeces were packed into the intestine and rectum.

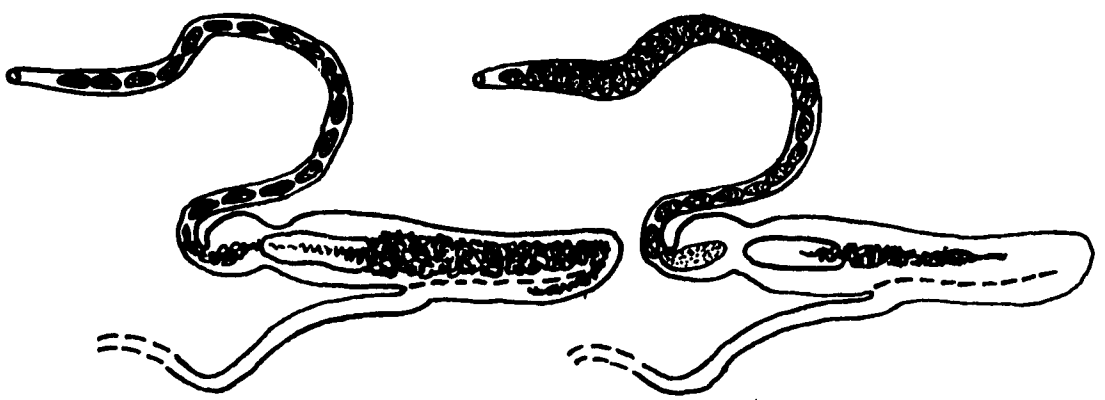
Key to symbols: r. = rectum, i. = intestine, d.st, = distal stomach, p.st. = proximal stomach, m.r. = mucus rod, p.o. = posterior oesophagus.



1 2



3 4



5 6

the digestive tissue is shown in Fig. 16. Most of the spherules had disappeared by eight hours after high tide (Fig. 17). At ten hours after high tide, immediately before the snails were due to start feeding again, some digestive cells showed signs of fragmentation, but no very extensive fragmentation was observed (Fig. 18).

This study was carried out only to establish a time sequence for feeding and digestion. A more detailed examination would be required to obtain information on the functioning of the digestive system of L. saxatilis.

Passage of food through the digestive tract of L. saxatilis in the laboratory.

The time taken for passage of food through the digestive tract.

Snails were fed Urospora spp. labelled with ^{14}C and the passage of this food through the digestive tract was timed by sampling the faeces at six-hour intervals. The results obtained from experiments A.1, A.2 and A.3 are shown in Tables IX and X. In each experiment the faeces with highest specific activity had been voided by 18 hours after the commencement of feeding. Residual material appeared in the faeces during the following twelve hours, indicating that the snails voided remnants of digestion as well as excretory

products, with undigested food of the next feeding period.

In Table X, the amounts of radioactivity of the faeces for each sampling period have been given as cumulative percentages of the total radioactivity for each uninfected and infected group of snails in the experiment. There were consistent differences between the uninfected and infected groups in that values for infected snails were higher. These differences were found to be not significant ($P < 0.6$).

Passage of food labelled with ^{14}Carbon in the digestive gland.

Autoradiography technique was used in experiment B to follow the passage of food, labelled with ^{14}C, in the digestive glands of infected and uninfected L. saxatilis. Poor resolution, resulting from the different focal planes of the exposed emulsion and tissue section, prevented examination and photography at high magnification. The low magnification autoradiographs show the gross relationships.

One section of an infected snail and one section of a snail infected with C. lingua are shown in Figs. 19 and 20, respectively. These sections were stained with eosin and hematoxylin to show the general arrangement of the digestive gland tissues, as a basis for interpreting the unstained autoradiographs. The stomach wall consisted of a single layer of columnar epithelial cells each with numerous small granules near the outer membrane. Tubules of the digestive

Table IX. Passage of ^{14}C-labelled food through the digestive tract of L. saxatilis as shown by the specific activities of faeces collected in experiments A.1 to A.3. Food offered between 0 and 6 hours. Specific activities are given as c/m per 0.1 mg dry weight. Each value is the mean ± standard deviation.

		Time after commencement of feeding (hr.)					
		0	6	12	18	24	30
A.1	uninfected n = 6	0	0	24.53±39.80	47.80±86.72	12.28±14.17	0.18± 0.49
A.1	infected n = 10	0	0.25±0.82	35.24±30.13	72.81±94.54	6.99±7.62	0.86± 0.98
A.2	uninfected n = 8	0	0.29±0.57	6.21±5.12	7.63±5.79	7.24±7.69	-
A.2	infected n = 9	0	0.89±1.71	7.73±7.95	9.15±7.62	7.93±6.48	-
A.3	uninfected n = 4	0	0	1.20±0.98	0.63±0.98	0.40±0.82	-
A.3	infected n = 9	0	0	7.20±14.01	1.92±2.73	1.03±1.26	-

Table X. Passage of ^{14}C-labelled food through the digestive tract of *L. saxatilis* as shown by the specific activities of faeces collected in experiments A.1 to A.3. Food was offered between 0 and 6 hours. The amount of radio-activity passed by each sampling period is expressed as a cumulative percentage of the total radio-activity passed.

		Time after commencement of feeding (hr.)					
		0	6	12	18	24	30
A.1	uninfected (n = 6)	0	0	29.93	85.31	99.79	100.00
A.1	infected (n = 10)	0	0.22	30.56	93.25	99.27	100.00
A.2	uninfected (n = 8)	0	1.36	30.44	66.13	100.00	-
A.2	infected (n = 11)	0	3.47	33.53	69.25	99.99	-
A.3	uninfected (n = 4)	0	0	53.93	82.02	99.99	-
A.3	infected (n = 9)	0	0	75.69	88.86	100.00	-

gland were about 200 to 300 μ in diameter and were closely packed. In transverse section the lumena of the tubules were rounded in outline. The epithelial digestive cells measured about 50 μ in length and often had large numbers of vacuoles. Interspaced amongst the digestive cells were small groups of darkly staining cells with granular contents. These features have also been shown in Figs. 13 and 14. Connective tissue and vascular sinuses were seen between the digestive tubules. Gonads were not seen in any of the sections. The section of L. saxatilis infected with C. lingua (Fig. 20) illustrates the position of the rediae between the digestive tubules with compression of the tubule lumena in some places.

The autoradiographs of uninfected snails are shown in Figs. 21 to 24. At the end of the six-hour feeding period (Fig. 22) food labelled with ^{14}C was observed in the stomach and also along the sides of the lumena of the digestive tubules. At 12 hours after the commencement of feeding (Fig. 23) food was present in the stomach, lumena of the digestive cells. At 18 hours after commencement of feeding (Fig. 24) food labelled with ^{14}C was distributed throughout the digestive cells.

The autoradiographs of snails infected with C. lingua are shown in Figs. 25 to 28. At the end of the six-hour period of feeding, food labelled with ^{14}C was present in the

stomach and in the lumena of the tubules of the digestive gland. It was observed that the labelled food had also penetrated those tubules constricted by outside pressure from the rediae. The stages at 12 hours (Fig. 27) and 18 hours (Fig. 28) are essentially similar to the stages shown for uninfected L. saxatilis. At the final stage food labelled with ^{14}C was distributed throughout the lengths of the digestive cells. There was no indication of any uptake of ^{14}C by the rediae.

The rate of ingestion by L. saxatilis in laboratory conditions.

The rate of ingestion of food by individuals was studied in laboratory conditions as part of experiments C.1 and C.4. The results are given in data sheets 24 and 25, and summarized in Table XI. Details of experimental conditions are given in Tables II and III.

Individuals varied considerably in their rates of ingestion. Mean values for uninfected and infected snails, in experiments with both Urospora spp. detritus and Enteromorpha spp. detritus, did not differ significantly, (P=0. 30 and P=0. 60 respectively). The combination of values from both experiments gave mean rates of ingestion of 0.43 mg per 0.1 g live weight for uninfected snails and 0.33 mg per 0.1 g live weight for infected snails.

Efficiency of assimilation by L. saxatilis in laboratory conditions.

Efficiency of assimilation was assessed through determination of nitrogen and carbon in food and faeces. The conditions in experiments C.1 to C.5 are described in Tables II and III.

Analyses for nitrogen were made in experiments C.2, C.3 and C.5. Complete results are given in data sheets 26, 27 and 28, and are summarized in Table XII. The percentage nitrogen in the food was low (under 6.5 per cent) and there were correspondingly low nitrogen values for faeces. The values for efficiency of assimilation covered a wide range and some negative values, which appear in the data sheets as percentages in excess of 100, were obtained. In all three experiments the mean values for efficiency of assimilation were lower in infected snails than in uninfected snails, but these differences were not significant ($P < 0.20$).

The efficiencies of assimilation obtained with different foods were compared in experiments C.2 (Urospora spp. detritus) and C.5 (living Enteromorpha spp.). The efficiency appeared to be greater in C.5 for both infected and uninfected snails, but the differences were not significant ($P = 0.02$ and $P = 0.03$ respectively).

Table XI. Rates of ingestion of detritus foods by L. saxatilis in laboratory conditions. The snails in experiment C.1 were offered Urospora spp. detritus for 6 hours at 6°C, those in C.4 were offered Enteromorpha spp. detritus for 6 hours at 10°-15°C. Each value is the mean with standard deviation.

	Live weight of snail (g)	Dry weight of food ingested (mg)	Ingestion per 0.1g live weight (mg)/6-hr.
C.1			
Uninfected (N = 9)	0.09 ± 0.05	0.53 ± 0.25	0.53 ± 0.28
Infected (N = 8)	0.14 ± 0.05	0.37 ± 0.28	0.26 ± 0.19
C.4			
Uninfected (N = 10)	0.14 ± 0.04	0.49 ± 0.32	0.35 ± 0.20
Infected (N = 8)	0.16 ± 0.08	0.59 ± 0.40	0.39 ± 0.34
Combined values C.1 and C.4			
Uninfected (N = 19)	0.12 ± 0.05	0.51 ± 0.29	0.43 ± 0.25
Infected (N = 16)	0.15 ± 0.06	0.48 ± 0.36	0.33 ± 0.27

The values for efficiency of assimilation obtained with Urospora spp. detritus in experiments C.2 and C.3, were compared in respect to the 6-hour and 24-hour feeding cycles. Efficiency of assimilation was significatly greater with the 6-hour cycle for both uninfected and infected snails ($P = 0.01$ and $P = 0.001$ respectively).

The foods used in experiments to determine efficiency of assimilation contained approximately 10 times as much carbon as nitrogen. The values obtained from carbon analyses were considered to be more reliable than those obtained from nitrogen analyses, and so the former have been used in the calculation of values for efficiency of assimilation. Carbon analyses were made of samples of faeces, taken in experiments C.1, C.2, C.3, C.4, and C.5. Details of experimental conditions are given in Tables II and III. The results are shown in data sheets 29 to 33 and are summarized in Table XIII. The combinations of conditions used in the series of experiments allowed evaluation of the effects of temperature, quality of food, length of feeding cycle and parasite infection, on the efficiency of assimilation.

In experiment C.2, faeces of 10 uninfected snails were sampled and analyzed from three successive 6-hour feeding periods. There were no significant differences, either between individuals sampled on successive occasions or

Table XII. Efficiency of assimilation using nitrogen in uninfected and infected L. saxatilis in laboratory conditions. The conditions of these experiments were as follows: in C.2 Urospora spp. detritus food was used at 10°-15°C for 6-hours; in C.3 Urospora spp. detritus food was used at 10°-15°C for 24-hours and in C.5 living Enteromorpha spp. food was used at 10°-15°C for 6-hours. Each value is the mean with standard deviation.

Experiment number	Efficiency of Assimilation (nitrogen)	
	Uninfected snails	Infected snails
C.2	76.08 ± 24.72 (n = 40)	75.00 ± 36.47 (n = 33)
C.3	58.89 ± 26.55 (n = 59)	50.14 ± 22.67 (n = 43)
C.5	90.11 ± 10.72 (n = 20)	85.26 ± 11.47 (n = 19)

between 10 snails sampled on the same occasion, at the 95% level ($F = 0.78$). From this is was assumed that efficiency of assimilation did not vary significantly among the snails, or from one 6-hour sampling period to the next, within any one experiment. All values were used to calculate mean efficiencies of assimilation.

Effects of parasite infection.

The mean values for efficiency of assimilation of carbon in infected snails were consistently lower than those in uninfected snails. These differences were not significant ($P = 0.02$ to 0.90).

Effects of types of foods.

Three types of food were offered to the snails, namely Urospora spp. detritus, Enteromorpha spp. detritus and live Enteromorpha spp. On the 6-hour feeding cycle Urospora spp. detritus gave a higher efficiency than Enteromorpha spp. detritus (experiments C.2 and C.4 respectively). The difference was significant for infected snails ($P = 0.01$) but not significant for uninfected snails ($P= 0.05$).

Effects of temperature.

A comparison was made between the results of experiments

Table XIII. Efficiency of assimilation using carbon in uninfected and infected L. saxatilis in laboratory conditions. The conditions of these experiments were as follows: in C.1 Urospora spp. detritus food was used at 6°C for 6-hours, in C.2 using Urospora spp. detritus food was used at 10°-15°C for 6-hours, in C.3 using Urospora spp. detritus food was used at 10°-15°C for 24-hours, in C.4 using Enteromorpha spp. detritus food was used at 10°-15°C for 6-hours and in C.5 using live Enteromorpha spp. food was used at 10°-15°C for 6-hours. Each value is the mean with standard deviation.

Experiment number	Efficiency of assimilation (carbon) (%)	
	Uninfected snails	Infected snails
C.1	41.35 ± 21.45 (n = 14)	18.78 ± 26.15 (n = 18)
C.2	64.23 ± 16.48 (n = 40)	57.49 ± 18.13 (n = 33)
C.3	57.29 ± 17.40 (n = 58)	55.08 ± 14.83 (n = 44)
C.4	53.63 ± 23.88 (n = 30)	44.56 ± 18.22 (n = 25)
C.5	78.74 ± 14.76 (n = 20)	78.63 ± 11.38 (n = 19)

C.1 and C.2 with respect to temperature (60°C and 10°-15°C respectively). A higher efficiency of assimilation was obtained at 10°-15°C and this was significant for both uninfected and infected snails (P = 0.001).

Effects of length of feeding cycles.

Efficiencies of assimilation for carbon were compared on 6-hour and 24-hour feeding cycles, using Urospora spp. detritus food (experiments C.2 and C.3). Higher values were obtained with the 6-hour cycle, but the differences were not significant for either uninfected snails (P = 0.10) or infected snails (P = 0.60).

Calculation of rate of assimilation.

The rate of ingestion and the efficiency of assimilation (as per cent carbon) were evaluated for the same snails in experiments C.1 and C.4. The rate of assimilation was then calculated from these results. The values are given in data sheets 34 and 35 and summarized in Table XIV. The rates of assimilation; 0.22 mg dry weight/6-hours for uninfected snails and 0.60 mg dry weight/6-hours for infected snails, feeding on Urospora spp. detritus were not significantly different (P = 0.5).

Table XIV. Rates of ingestion, efficiencies of assimilation, and rates of assimilation calculated for uninfected and infected L. saxatilis in laboratory conditions. The snails in C.1 were offered Urospora spp. detritus food at 6°C for 6-hours, those in C.4 were offered Enteromorpha spp. detritus food at 10°-15°C for 6-hours. Each value is the mean with standard deviation.

	Uninfected snails	Infected snails
C.1 Rate of ingestion (mg/6-hr.) dry weight.	0.53 ± 0.25 (n = 9)	0.37 ± 0.28 (n = 8)
Efficiency of assimilation (%)	41.35 ± 21.45	18.78 ± 26.15
Rate of assimilation (mg/6-hr.) dry weight.	0.22 ± 0.18	0.60 ± 0.08
C.4 Rate of ingestion (mg/6-hr.) dry weight.	0.49 ± 0.32 (n = 10)	0.59 ± 0.40 (n = 8)
Efficiency of assimilation (%)	53.63 ± 23.88	44.56 ± 18.22
Rate of assimilation (mg/6-hr.) dry weight.	0.32 ± 0.19	0.38 ± 0.12

Calculation of efficiency of growth in L. saxatilis.

Since values for growth in terms of increment of shell length may be converted to increments in dry body weight or dry total weight, and since values have been obtained for rate of assimilation, it is possible to calculate efficiency of growth. This calculation applies to summer efficiency of growth for snails in the range of 5.0 mm to 8.0 mm shell length.

The value for summer rate of growth at Blue Rocks, taken as the mean for age groups I to IV, was an increment of 0.86 mm/30 days in shell length. This may be converted into an increment of 0.38 mg/30 days in dry body weight or an increment of 2.4 mg/30 days in total dry weight (Fig. 6).

The comparable value for rate of assimilation at 10°-15°C is 0.36 mg (0.32 to 0.38 mg) in six hours. Assuming that the snail has two, 6-hour feeding periods in each 24 hours, in 30 days the total organic matter, measured as total carbon, assimilated will be 30 x 0.72 mg or 21.6 mg dry weight.

Using the value for increment in dry body weight,

$$\text{efficiency of growth} = \frac{0.38}{21.6} \times 100$$ or 1.78 percent.

Using the value for increment in dry total weight,

efficiency of growth = $\frac{2.4}{21.6} \times 100$ or 11.1 percent.

Since uninfected and infected snails did not differ significantly in their rates of growth or rates of assimilation, no differences in efficiency of growth were expected.

DISCUSSION

Littorina saxatilis is a common intertidal species in Nova Scotia. Populations occur in the supralittoral fringe of exposed and rocky shores and also in the areas of marsh grass and eel grass. There is variation in body and shell form of L. saxatilis in some Nova Scotia populations but the diversity observed is not as extensive or as complex as in some European populations described by Fischer-Piette et al. (1963) and James (1968c). (See Appendix II).

The population of L. saxatilis tenebrosa at Blue Rocks is typical for sheltered rocky shores on the Atlantic coast of Nova Scotia. It was selected for study because of the relatively high (19.0 per cent) total infection by seven species of Digenea, of which only two, Microphallus similis and Cryptocotyle lingua were common. The study of this population has provided information on reproduction and growth of the host, and seasonal variations in the levels of parasite infections. These observations can be compared to studies made by Berry (1961 and 1962) at Whitstable, England and by James (1969) at Aberystwyth, Wales.

At Blue Rocks the juvenile L. saxatilis are released from the females at any time of the year; although from any particular age group of the population maximum releases occur in spring and autumn. These results are similar to those

obtained at Aberystwyth, where main releases of juveniles were recorded in spring (April and May) and autumn (September and November), and at Whitstable where main releases occurred in January and February and again in July and August. James 1969 recorded a vertical migration of L. saxatilis to lower tide levels during the breeding season, however, Berry (1961) although noting reproductive differences between the upper and middle shore populations at Whitstable, observed no seasonal migration. No vertical migration in relation to the breeding season was recorded in the population at Blue Rocks; the only movement observed was a limited horizontal or vertical movement of the snails into sheltered locations during the winter. The presence or absence of migratory behaviour in any population could be related to different climatic conditions and tidal ranges. Aberystwyth has a milder climate and more than double the tide range at Blue Rocks. James (1968a) attributed differences in migratory behaviour to differences in subspecific identity; namely that migration was characteristic of L. s. tenebrosa. However, the Blue Rocks population may also be referred to this subspecies and so climatic and tidal range factors are probably more important to such behavioural differences than taxonomic differences.

The seven species of Digenea recorded from L. saxatilis at Blue Rocks were all previously known from this host (See Appendix III). Microphallus similis and Cryptocotyle

lingua were the only two species which occurred in sufficient numbers of snails to allow examination in relation to the lifecycle of the host. These species present two different situations for comparison with previous studies (Berry 1962, James (1969) and Robson and Williams (1971a)). Microphallus similis is well-known from populations of L. saxatilis, whereas C. lingua is uncommon in L. saxatilis in Europe and has only been studied in populations of L. littorea. Cryptocotyle lingua is normally associated with L. littorea and studies of this host/parasite relationship have been made at the population level by Sindermann and Farrin (1962), Lambert and Farley (1968) and Robson and Williams (1971a). The study at Blue Rocks is the first on a population of L. saxatilis infected with C. lingua. The origin of this unusual relationship is discussed in Appendix III.

Microphallus similis has a seasonal cycle of infection at Blue Rocks, and is most numerous in the spring and autumn. The study of levels of infection in the different age-groups of the host population shows that the autumn release of snails becomes infected immediately after breeding the following spring. The infected snails die after four or five months. The parasite population is again established in the same snail age-group after the autumn breeding and all of these snails are dead by the following spring.

Berry (1962) noted that infection of L. saxatilis by

M. similis at Whitstable reached a maximum in the summer after reproduction ceased but no mention was made of subsequent mortality. James (1969) found that juvenile L. saxatilis were relatively resistant to infection but that their susceptibility to infection increased with age. The level of infection reached its peak after the spring breeding season of the host but declined markedly during the ensuing three months. There was a second infection of the population after the breeding season and then a decline of infection level within three or four months. James' observations are supported by the present study of the population at Blue Rocks.

A relatively distinct seasonal cycle of infection by C. lingua occurs in the population of L. saxatilis at Blue Rocks. The largest numbers of infected snails were found in the spring and autumn. The snails from the autumn generation become infected in the following spring, after the main breeding period. These snails do not die prematurely as do those infected with M. similis, and the age-group becomes more infected following the autumn breeding period. Susceptibility to infection thus increases with age and a high level of infection (70 to 100 per cent) occurs in the larger snails of this population.

The seasonal variations in levels of infection by C. lingua of a population of L. littorea in Yorkshire, England, have been reported by Robson and Williams (1971a). They

found highest infection levels in autumn and early winter, and lowest levels in summer. It would seem that the difference in seasonal levels of infection by C. lingua between L. saxatilis and L. littorea populations is due to differences in the breeding seasons. Littorina saxatilis has two main breeding periods, in spring and autumn, whereas L. littorea has one in the autumn and early winter. Thus there are two peak periods of infection in L. saxatilis, and only one in L. littorea. Since some L. saxatilis are breeding at any time of the year it is likely that some infection also takes place throughout the year.

Studies of the bivalve molluscs Lasaea rubra (Morton, 1956 and McQuiston, 1969), Cardium edule (Morton, 1969) and Dreissena polymorpha (Morton 1969) have shown the importance of cyclic changes in the digestive gland epithelium. The phases of these cycles - regeneration, absorption, intracellular digestion and fragmentation, are related to rhythms of feeding activity which are, in the first two species, induced by tides. Purchon (1971) has suggested that such changes are organized in distinct phases in some genera but may be conducted at random in others. This author stresses that digestion cannot be considered a simple process involving only the digestive tract, but must take account of the animal's bodily activities as they are controlled by tidal or other rhythms.

The possibility of feeding or digestive rhythms controlled by tides were not considered by James (1965) in his study of the effects of starvation and digenetic trematode infection on the digestive gland of L. saxatilis. Although no cyclic phases of the digestive gland cells could have been related to tidal cycles in the long period that these animals were in the laboratory, the random sequence of cell fragmentation should have been considered. Platt (MS 1968) used a 24-hour feeding cycle for experiments on L. littorea but did not examine the possible importance of such a cycle to efficiency of assimilation. In the present study, L. saxatilis feeding in nature was found to have a crude rhythm of activity induced by the tides. Microscopic examination of digestive tissues of snails sampled over a tidal cycle showed that there were also structural changes indicating diphasic cycles of digestion and excretion in the digestive cells. These structural changes were not studied in detail, but they are similar to changes reported in the bivalve species mentioned previously and also to those reported in the high tide-level pulmonates Otina otis (Turton) and Leucophytia bidentata (Montagu). (Morton, 1955a and b). This preliminary investigation of diphasic digestive activity in L. saxatilis is the first report of such a rhythm induced by tides in a littoral snail. Merdsoy (MS 1971) observed structural changes in the digestive tissues of L. littorea but was unable to relate them to any tidal rhythm.

The discovery in L. saxatilis of a tidal feeding and digestion rhythm in nature was applied to studies of feeding and digestion in the laboratory. The 6-hour active, feeding period and the 6-hour inactive, digesting period in each tidal cycle were translated into 6-hour periods with food and water which alternated with 6-hour periods without food and water. In these conditions, food labelled with ^{14}C was used to trace the passage of food through the digestive tract. It was shown that most of the food ingested during a 6-hour period passed through the digestive tract in 12 hours. The autoradiographic study however, gave visual indication that some food was retained in the digestive cells from one feeding period to the next.

The results obtained from the feeding experiments with L. saxatilis in the laboratory did not generally show significant differences in the rates of ingestion or the efficiency of assimilation, with different foods, temperatures or feeding cycle periods. There were no differences between the efficiencies of assimilation of nitrogen or carbon when compared on 6-hour and 24-hour feeding cycles at 10° to $15^{\circ}C$. The values obtained for nitrogen were 59 per cent for uninfected snails and 50 per cent for infected snails and for carbon were 57 per cent for uninfected snails and 55 per cent for infected snails. These values are slightly higher than the range of 35 to 45 per cent obtained for L. littorea on a 24-hour

feeding cycle by Platt (MS 1968).

Some published information on efficiency of assimilation and rate of assimilation in herbivorous marine gastropods is reviewed in Table XV. The efficiencies of assimilation are all similar, indicating that such values are reasonable for these animals. The rates of assimilation are undoubtedly related to the size of the animal. Littorina littorea is largest of the littorinids mentioned and would assimilate more than the others.

Efficiency of growth has been calculated for L. saxatilis in the present study, based upon the rates of assimilation and increment of dry body weight for the same period. The results obtained were 1.78 per cent using dry body weight and 11.1 per cent using dry total weight. North (1954) obtained 7.9 per cent as a gross value of efficiency of growth for Littorina planaxis Philippi, which has a similar diet and habitat to L. saxatilis. Some difference in the values might be expected since the climate at La Jolla, California, where L. planaxis was studied is warmer than that of Nova Scotia.

Mann (1970) noted the difficulty of obtaining values for the energetics of natural populations of benthic organisms and also emphasised the need for gross values of efficiency at the level of the population rather than at the level of the individual. The value obtained for L. saxatilis represents the overall efficiency of growth for an individual in one age-group, and it can give an indication of the efficiencies of

Table XV. A summary of some published values for efficiency of assimilation and rate of assimilation in marine herbivorous gastropods.

Species	Food	Efficiency of assimilation (%)	Rate of Assimilation mg/day	Source
Littorina planaxis Philippi	organic matter + minerals	36	0.06 to 0.10	North (1954)
Littorina irrorata Say	organic matter	45	-	Odum and Smalley (1960)
Littorina littorea (L.)	organic matter	35 to 45	2.27	Platt (MS 1968)
Littorina saxatilis (Olivi)	carbon in organic matter	41.35 to 53.63	0.44 to 1.20	present study
Aplysia punctata (Cuvier)	algae	45 to 71	-	Carefoot (1967)

growth in the whole population.

Platt (MS 1968), in a discussion of the effects of trematodes on digestion and nutrition in hosts, considered the various terms in an energy flow through an animal (after MacFadyen, 1963).

Energy ingested	=	Energy assimilated + Energy in faeces
Energy assimilated	=	Energy stored (reproduction, growth and residual) + Metabolised energy
Energy metabolised	=	Energy liberated + Energy in breakdown products (secretion and excretion)

North (1954) has proposed that 80 per cent of the energy assimilated by L. planaxis is lost as energy metabolised. This same figure can be taken as a general indication of the energy lost in metabolism by L. saxatilis and, as such, would be the same for both infected and uninfected individuals since von Brand and Files (1947) have shown that parasite infection does not drastically alter the metabolic rate of the host.

From the equation given above, if 80 per cent of assimilated energy is lost in metabolism, 20 per cent must remain as energy "stored" for use in reproduction, growth and nutrition. It is this 20 per cent of the energy that could be utilised by the parasites.

Littorina saxatilis is ovoviviparous and the energy

contribution made to reproduction by an individual female can be estimated from the dry weight of juveniles produced and retained, during development, in the brood pouch. Berry (1961) has shown that eggs are released into the brood pouch in several batches of 60 - 90 individuals, up to a total of about 300 eggs. This would indicate that about four batches were released during the breeding season. The batches of eggs observed in female L. saxatilis at Blue Rocks contained on the average 25 individuals. With four batches released this would indicate a total of 100 eggs produced in the breeding season. The average dry weight of an individual egg was calculated as 0.04 mg. Thus the total contribution of organic matter by an individual female is approximately 4.0 mg. dry weight.

It was shown that individual L. saxatilis assimilated 21.6 mg dry weight of food in 30 days, and, ignoring possible differences between summer and winter rates, a value of 259.2 mg per year is obtained. The 4.0 mg dry weight used in reproduction represents only 1.5 per cent of this figure. In addition, it has been shown above that 1.8 per cent is used in growth.

Thus by subtracting, the residual energy available is

$$100 - (1.5 + 1.81 + 80.0)$$

$$= 16.7 \text{ per cent of assimilated energy.}$$

This figure is very general; no consideration has been given to seasonal variations in rates of assimilation and growth.

The parasites infecting a snail would therefore be able to utilize this 17 per cent of assimilated energy, and also the 1.5 per cent energy that would have been directed to the needs of reproduction, without altering the matabolism or the rate of assimilation of the host.

The L. saxatilis at Blue Rocks breed twice during their life unless they become infected with trematode larvae following the first breeding season. Each age-group in the population makes its greatest contribution to reproduction in the first breeding season. For example, in the sample of September 1968, shown in Fig. 10, the individuals of group IV include 93 per cent of the gravid females whereas the older group III included only 7 per cent. Also group IV contained 88 per cent of the brood and group III only 12 per cent. Castration of some individuals by trematode infection after the first breeding season would be of little significance to the population as a whole.

In the Blue Rocks population there are indications of either increased longevity or accelerated growth in infected snails. Of the 95 snails recorded with shell lengths of over 10.0 mm, 83 were infected with larval trematodes, and 71 of these were infections by C. lingua. An example of increased rate of growth of L. saxatilis when infected with M. similis after the first breeding period has been reported by James (1965) and the much quoted captive L. littorea of Meyerhof

and Rothschild (1940) may again be cited as an example of longevity in an infected snail. Although infection by M. similis may cause an increase in rate of growth of the host, it causes the host to die prematurely. The increases in rates of growth and longevity of Lymnaea stagnalis (L.) when infected by Trichobilharzia ocellata McMullen and Beaver, have been demonstrated by McClelland and Bourns (1969). It is reasonable to expect that a similar effect would be seen in Littorina spp. infected with C. lingua.

The observations of the present study are related to the differing life styles and requirements of M. similis and C. lingua in the same host species. The cercariae of M. similis develop in sporocysts which rupture to release the mature cercariae. The infection develops rapidly and will kill the host in as little as four months. The cercariae of C. lingua develop in rediae which have birthpores. The maturation and release of cercariae is a steady process and all stages of development occur in a mature redia . The host can live with the infection and its life may in fact be prolonged. Two different types of infection are thus indicated, one with rapid development to utilize the host's energy in a short period and the other with slower development and slower utilization of the host's energy.

Robson and Williams (1971a) showed that C. lingua infects spent L. littorea after the first breeding and that castration

of the individual had little significance to the snail population. The same authors (1971b) also found that glycogen level of L. littorea infected with C. lingua was lower and that seasonal changes in this level were smaller than in uninfected specimens. They found C. lingua less damaging to the host than another parasite, Renicola roscovita although seasonal changes in glycogen level were less affected in snails infected with the latter species.

With this type of "life-time" association between C. lingua and L. saxatilis it is not surprising that no significant differences were found when comparing the efficiencies of assimilation of infected and uninfected hosts. However, some significant differences in efficiencies of assimilation for infected and uninfected snails were noted when comparisons were made for temperature and food type between experiments. When comparing results from 10° to 15°C and 6 °C there were reductions from 55 per cent to 19 per cent assimilation of carbon for infected snails compared to 57 per cent to 41 per cent for uninfected snails. The greater effect of decreased temperature on the infected snails may indicate some form of stress, perhaps rendering the snail less active. Enteromorpha spp. detritus food gave a significantly higher efficiency of assimilation than did Urospora spp. detritus food, in infected snails, but not in uninfected snails. No explanation can be offered for this difference. Platt (MS 1968) was unable to

find any significant differences in efficiency of assimilation between uninfected L. littorea and those infected with C. lingua.

From the several aspects of the present study there is evidence to support the views of Kendall and Ollerenshaw (1963) and Platt (MS 1968), that trematode parasites can develop in the host without any significant effects upon reproduction, growth and nutrition of the population.

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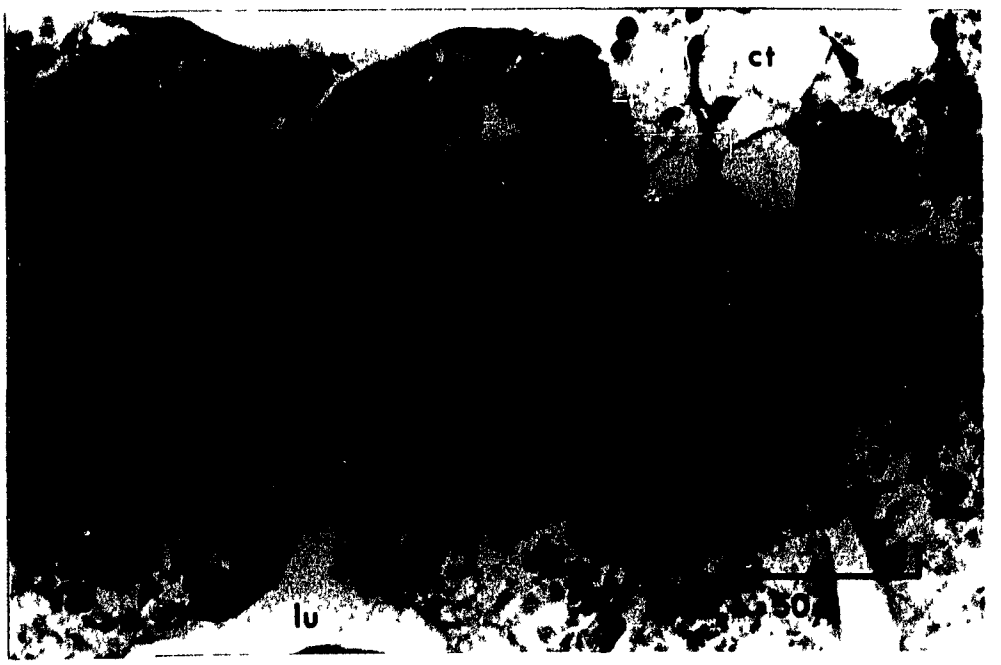
KEY TO SUMBOLS USED IN FIGURES 14 to 29.

c.t.	Connective tissue.
dt.	Digestive gland tubules.
dt.c.	Digestive gland cells.
lu.	Lumina of digestive gland tubules.
s.c.	Dark-staining cells with possible secretory function.
ex.sp.	Dark-staining spherules with possible excretory function.
f.m.	Food mass.
r.	Rediae of C. lingua.
st.ep.	Stomach epithelium.

Fig. 13. A section of the digestive gland of L. saxatilis. The specimen was collected at high tide during the investigation of feeding activity at Purcell's Cove, 12 July, 1968. The section was stained with eosin and hematoxylin. The cells of the digestive tubules are well formed and contain numerous food vacuoles.

Fig. 14. A section of the digestive gland of L. saxatilis. The specimen was collected at high tide during the investigation of feeding activity at Purcell's Cove, 12 July, 1968. The section was stained with eosin and hematoxylin. The groups of dark staining cells with possible secretory function are clearly seen.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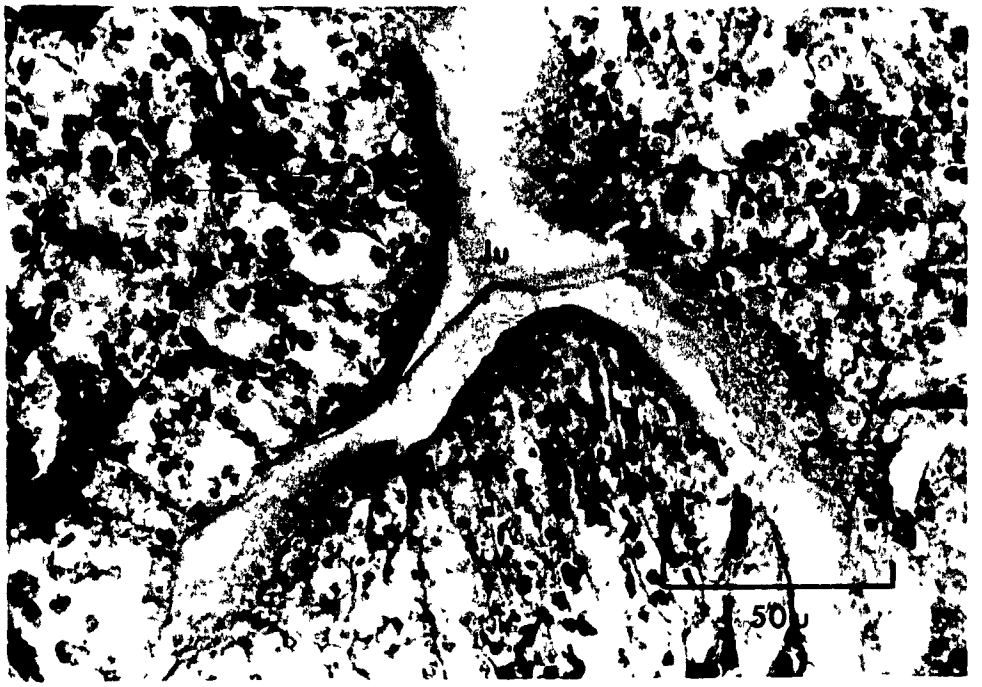
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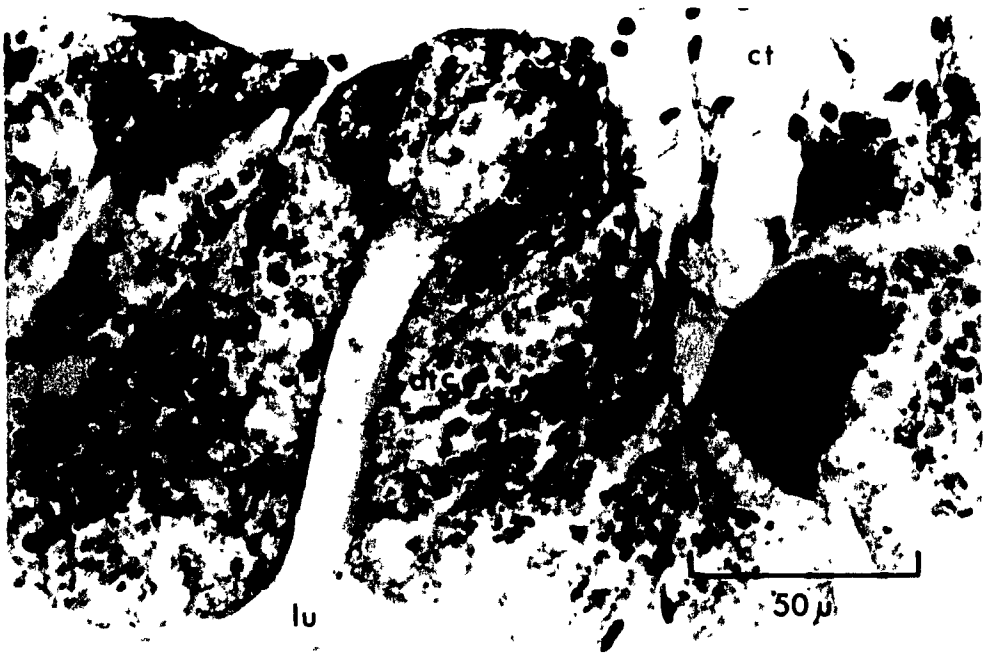
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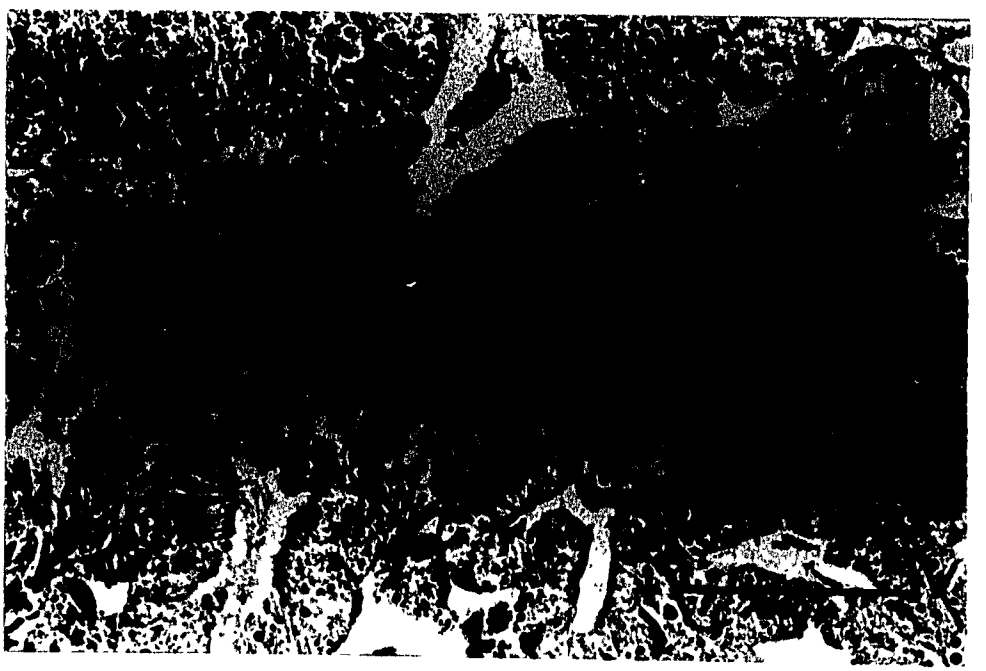
Fig. 15. A section of the digestive gland of L. saxatilis. The specimen was collected at four hours after high tide during the investigation of feeding activity at Purcell's Cove, 12 July, 1968. The section was stained with eosin and hematoxylin. Dark staining spherules with possible excretory function are seen throughout the digestive cells.

Fig. 16. A section of the digestive gland of L. saxatilis. The specimen was collected at four hours after high water during the investigation of feeding activity at Purcell's Cove, 12 July, 1968. The section was stained with eosin and hematoxylin. This low magnification micrograph shows the wide distribution of the spherules at that time.



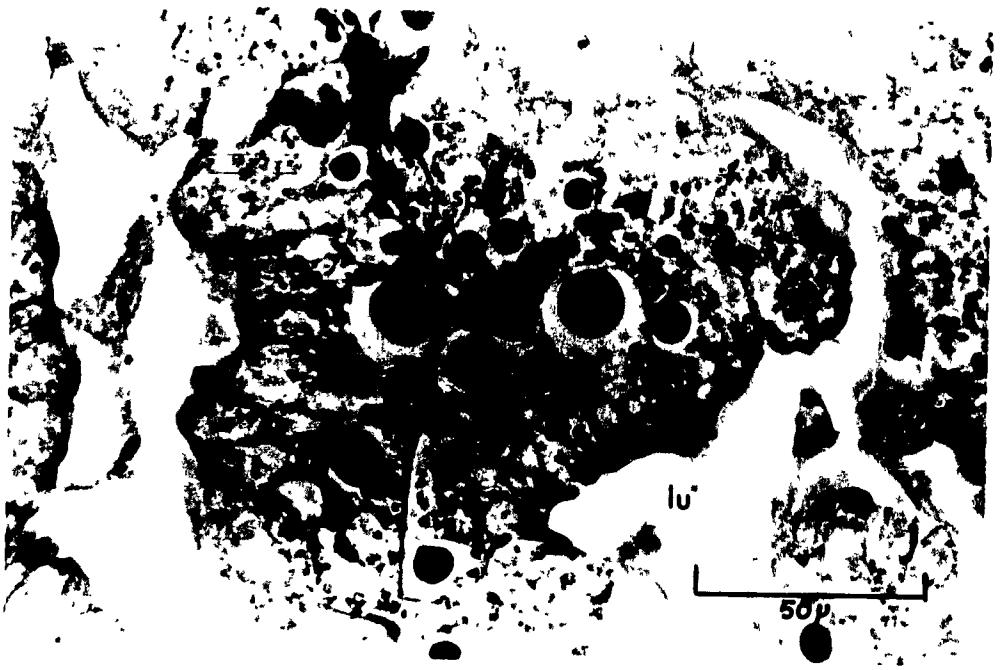

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Fig. 17. A section of the digestive gland of L. saxatilis. The specimen was collected at eight hours after high tide during the investigation of feeding activity at Purcell's Cove, 12 July, 1968. The section was stained with eosin and hematoxylin. The digestive cells are still distinct but most of the spherules have disappeared.

Fig. 18. A section of the digestive gland of L. saxatilis. The specimen was collected at ten hours after high tide during the investigation of feeding activity at Purcell's Cove, 12 July, 1968. The section was stained with eosin and hematoxylin. Some digestive cells appear to be in a stage of fragmentation.

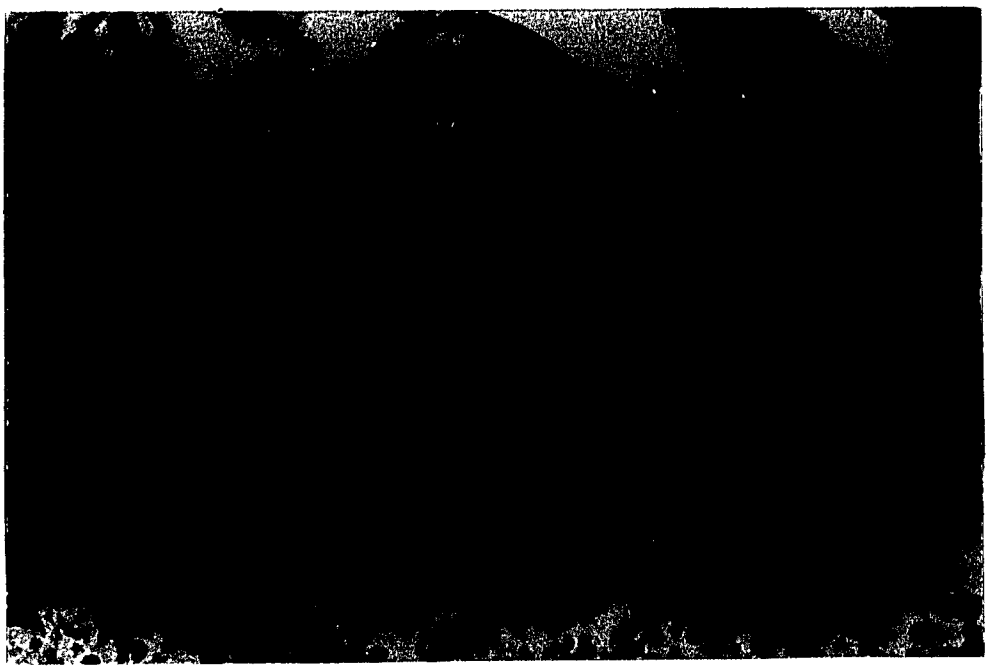


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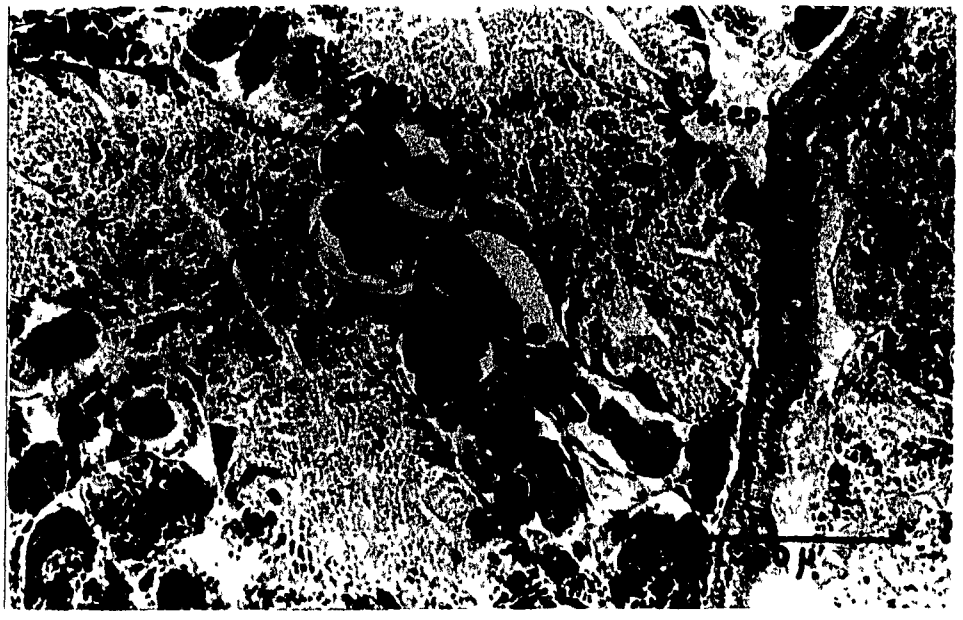
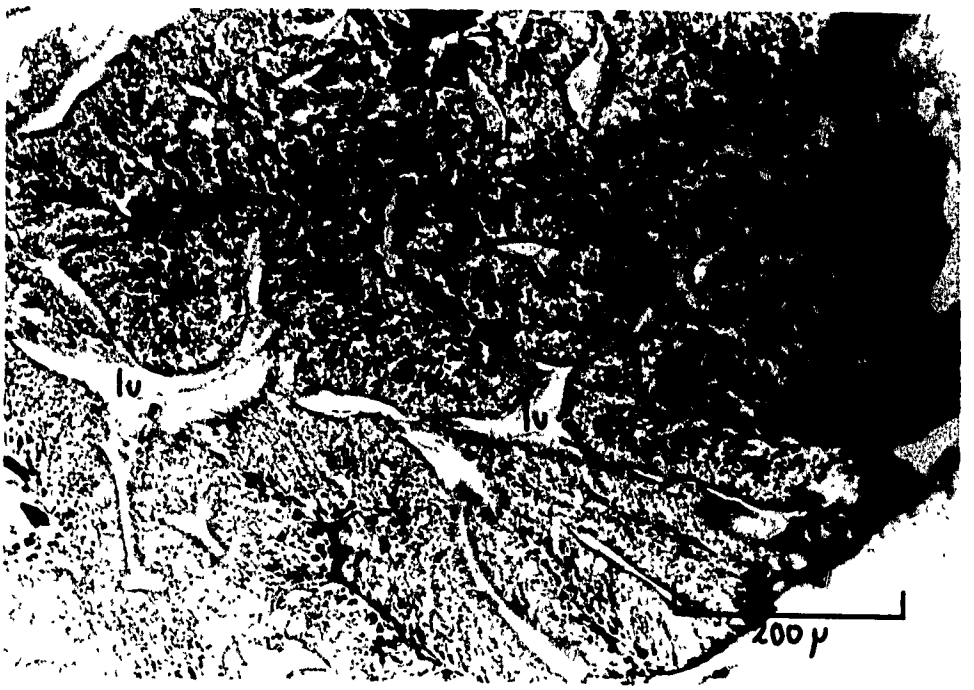
Fig. 19. A section of the digestive gland of an uninfected L. saxatilis. The section was stained with eosin and hematoxylin and shows the gross structure of the tissues.

Fig. 20. A section of the digestive gland of L. saxatilis infected with C. lingua. The section was stained with eosin and hematoxylin. The rediae of the parasite are seen in the spaces between the digestive tubules. The reduction of the lumina of the tubules as a result of outside pressure from the parasites is well shown.

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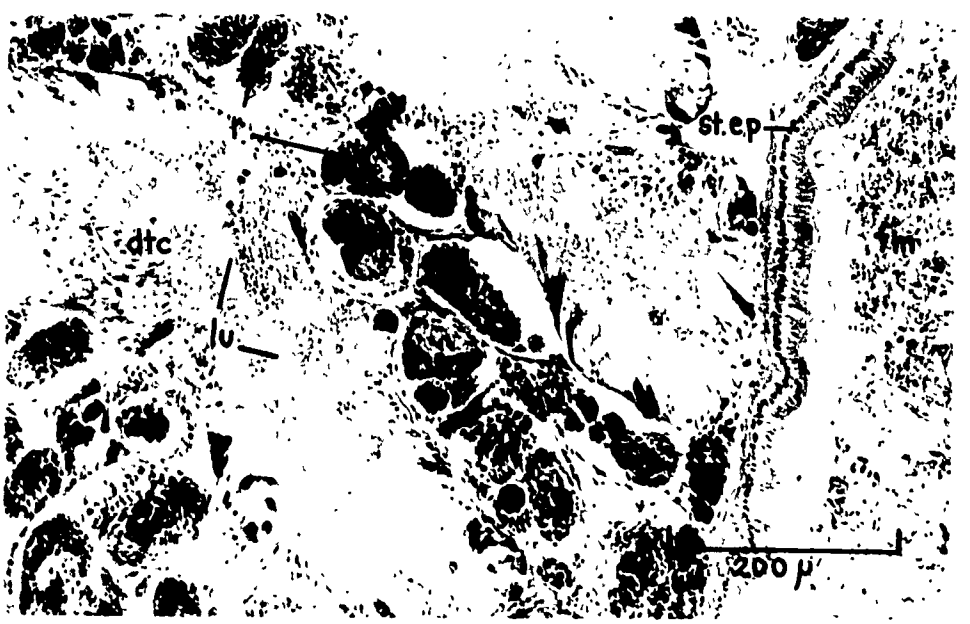
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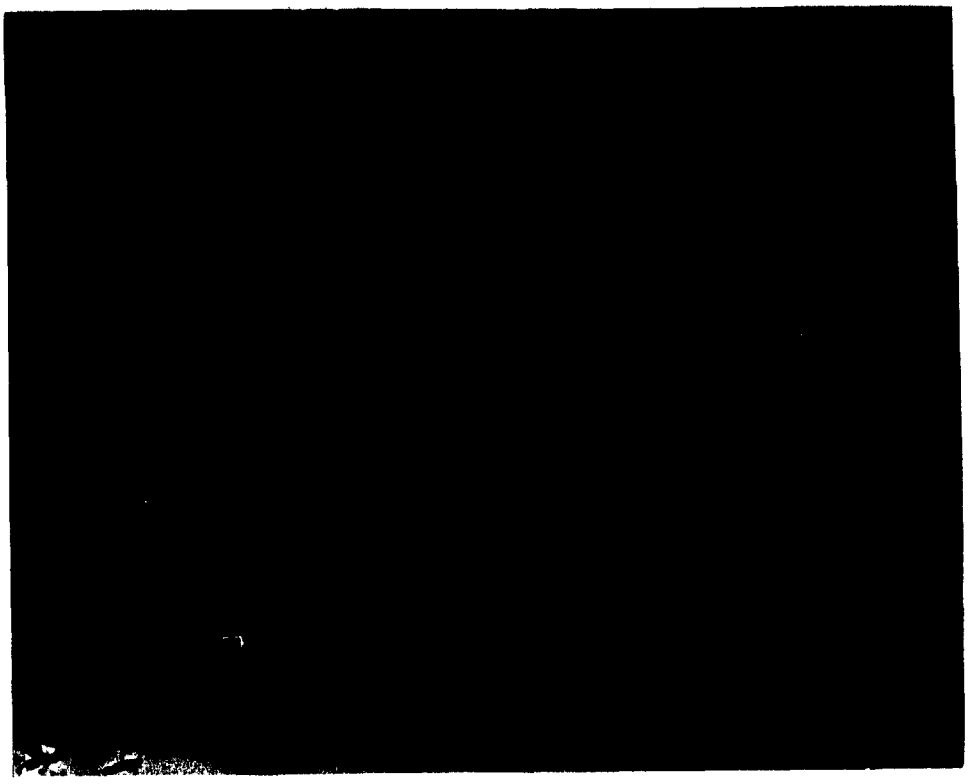
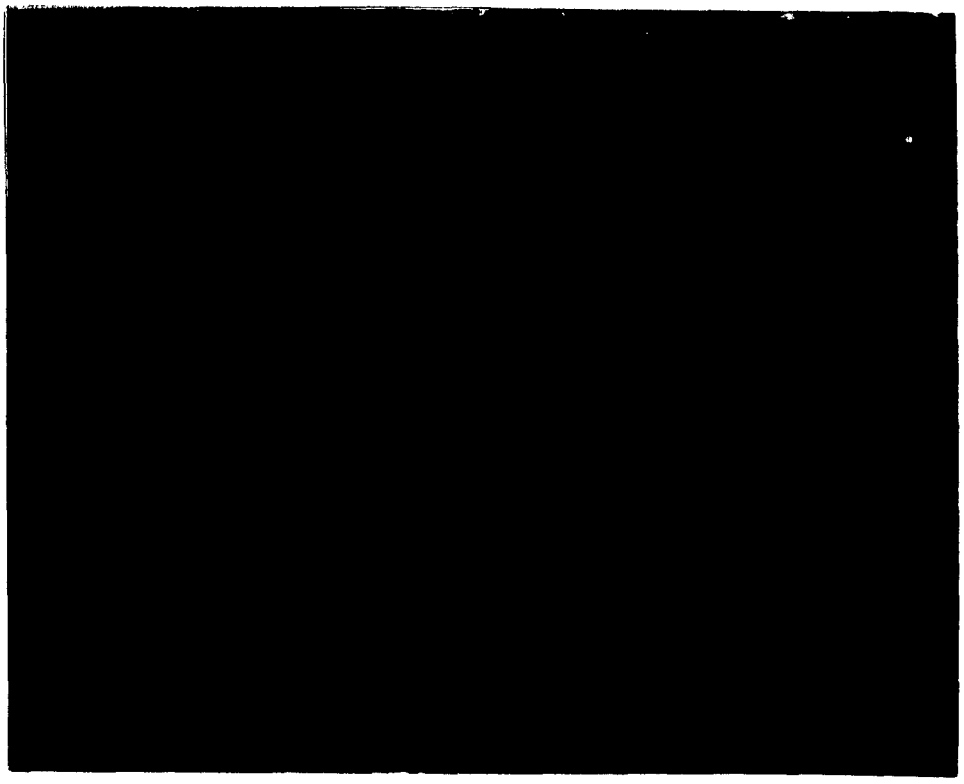
Fig. 21. Phase-contrast photograph of an unstained section of the digestive gland of an uninfected L. saxatilis. The specimen was sampled at the end of a short period of starvation and before feeding with ^{14}C-labelled food.

Fig. 22. Phase-contrast autoradiograph of an unstained section of the digestive gland of an uninfected L. saxatilis. The specimen was sampled at the end of a 6-hour period of feeding on ^{14}C-labelled food. The food is clearly seen where the emulsion is exposed, in the stomach and along the margins of the lumina of the digestive tubules.





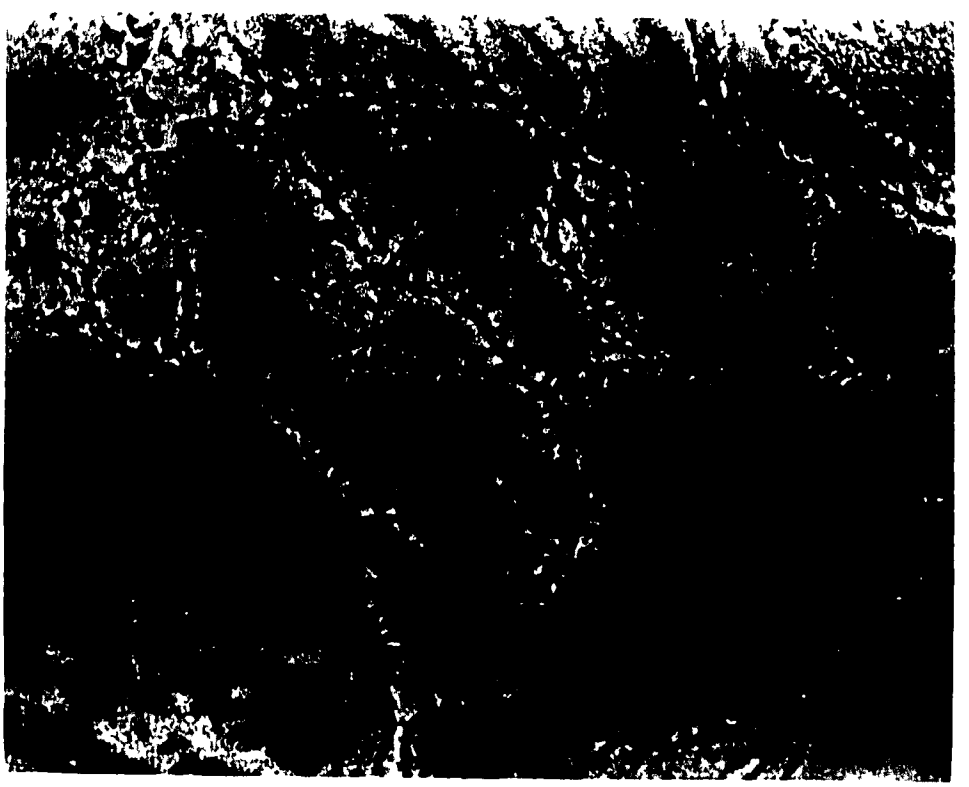
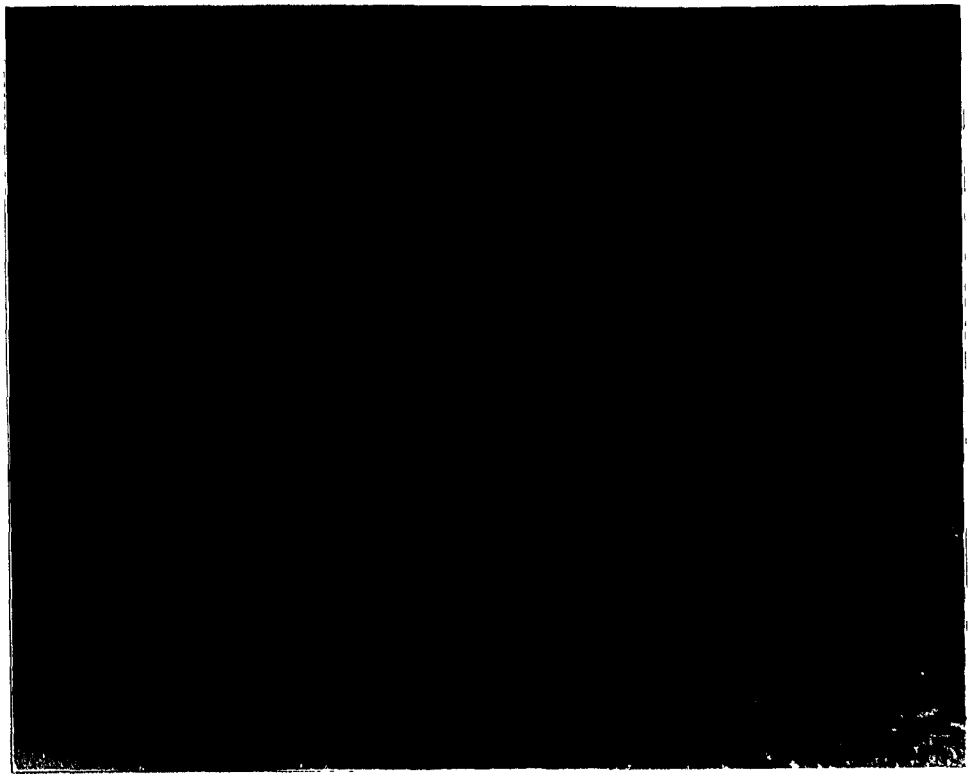
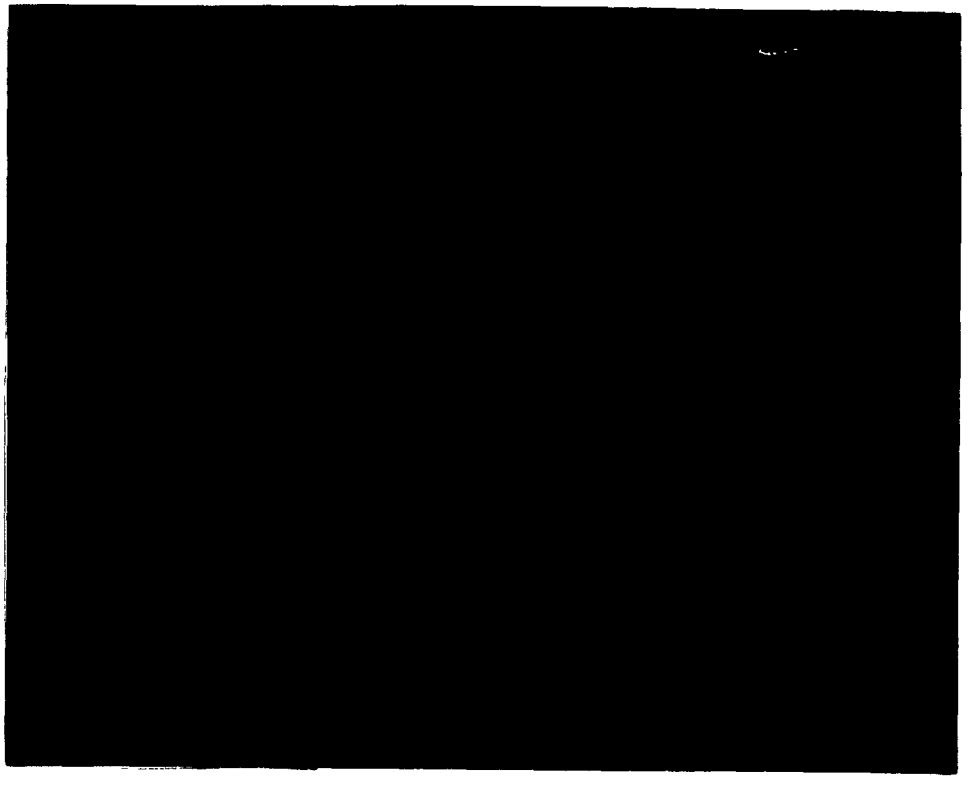


Fig. 23. Phase-contrast autoradiograph of an unstained section of the digestive gland of an uninfected L. saxatilis. The specimen was sampled 12 hours after commencement of feeding on ^{14}C-labelled food. The food is still seen where the emulsion is exposed, in the stomach and lumina of the digestive tubules.

Fig. 24. Phase-contrast autoradiograph of an unstained section of the digestive gland of an uninfected L. saxatilis. The specimen was sampled 18 hours after commencement of feeding on ^{14}C-labelled food. The food is located where the emulsion is exposed, throughout the digestive cells.

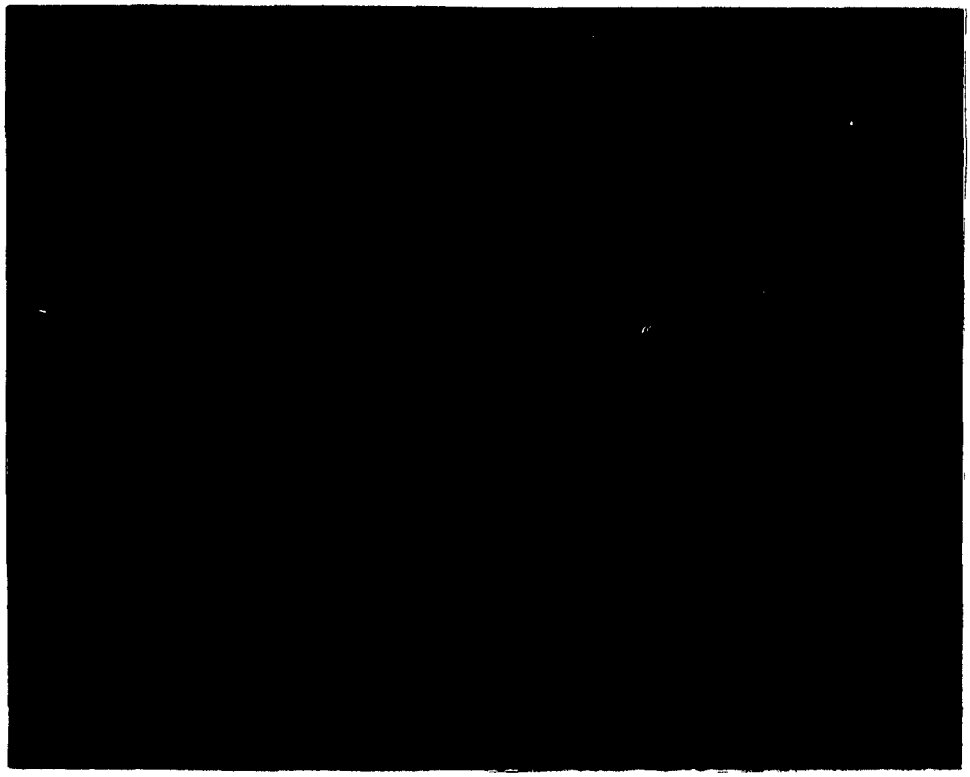


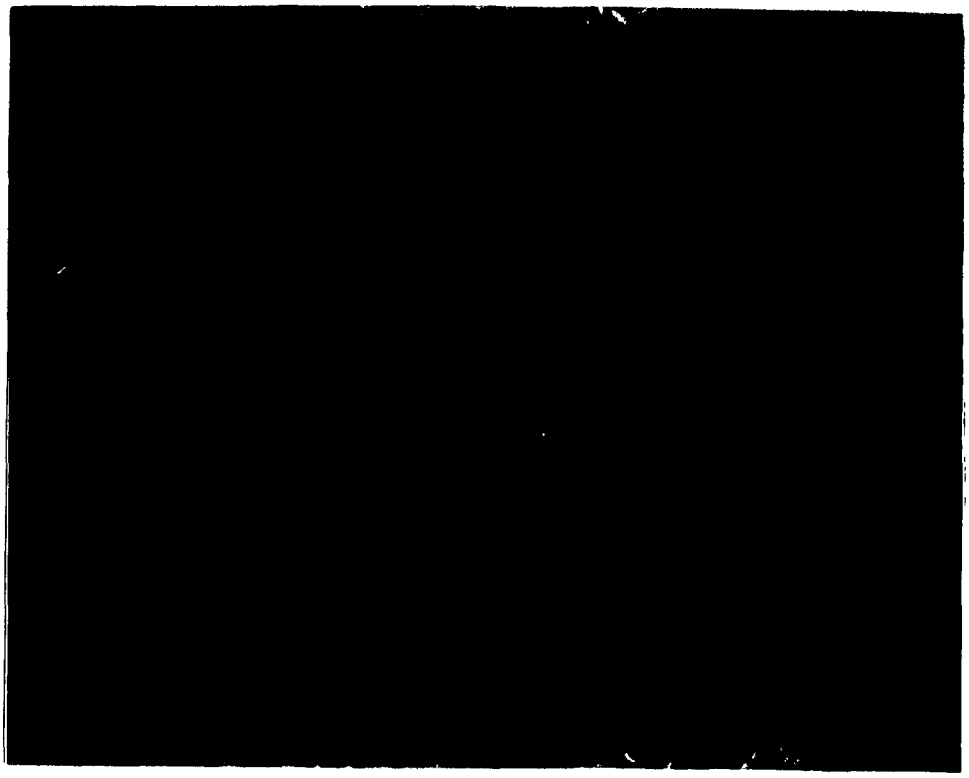



200μ

Fig. 25. Phase-contrast autoradiograph of an unstained section of the digestive gland of L. saxatilis infected with C. lingua. The specimen was sampled at the end of a short period of starvation and before feeding with ^{14}C-labelled food.

Fig. 26. Phase-contrast autoradiograph of an unstained section of the digestive gland of L. saxatilis infected with C. lingua. The specimen was sampled at the end of a 6-hour period of feeding on ^{14}C-labelled food. The food is seen where the emulsion is exposed, in the stomach and in the lumina of the digestive tubules.



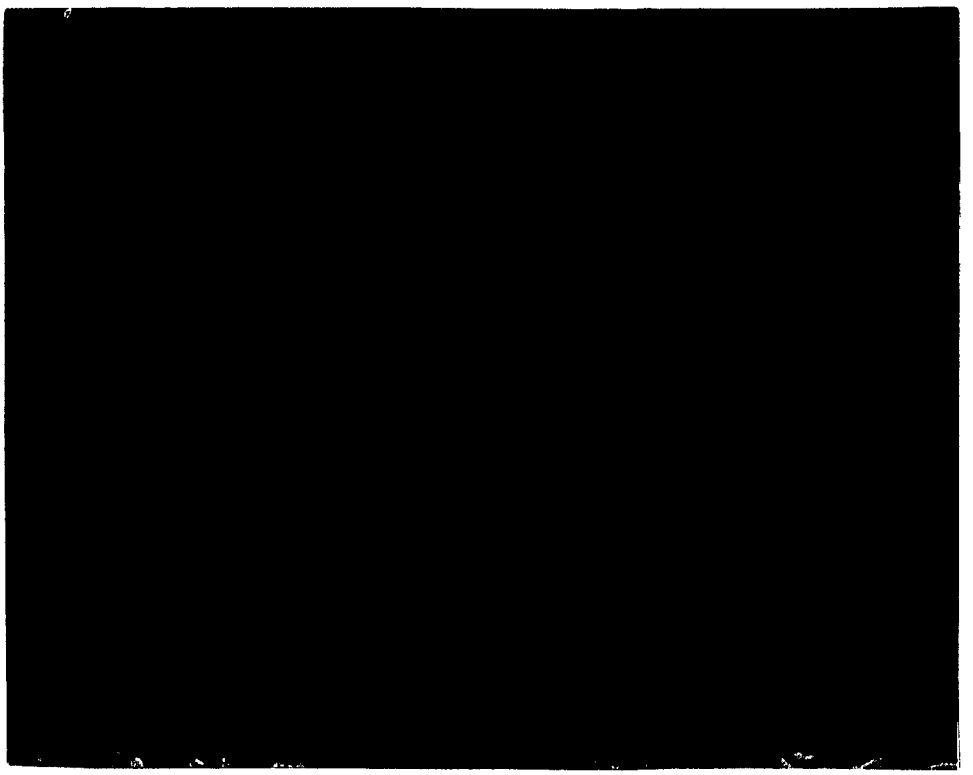


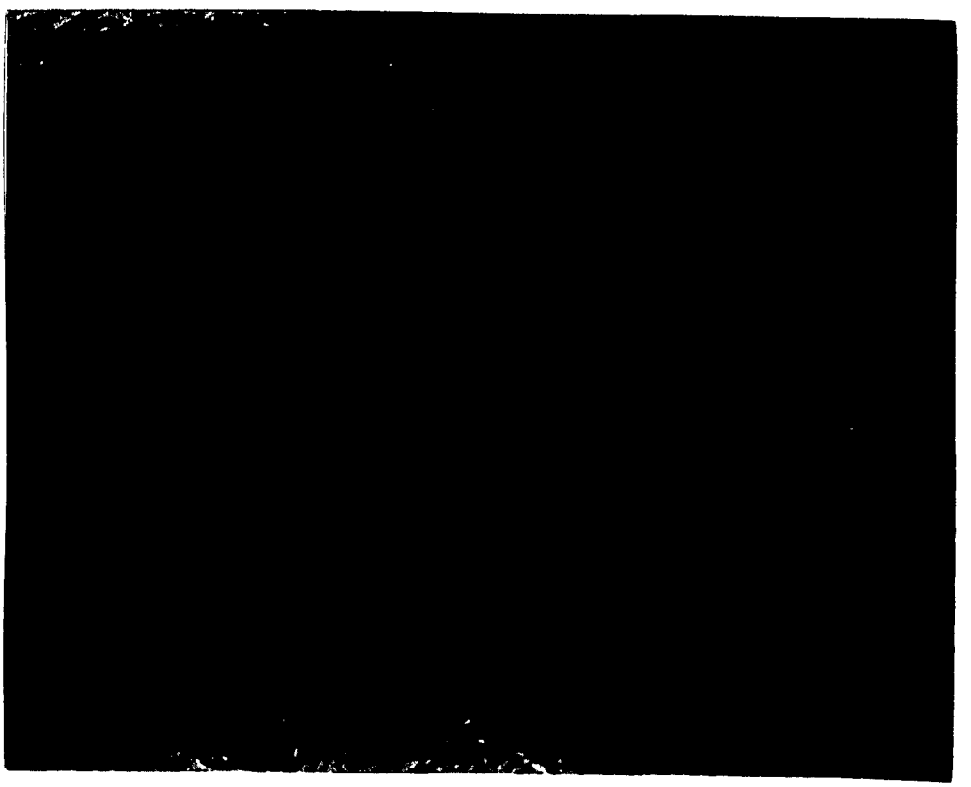

400 μ

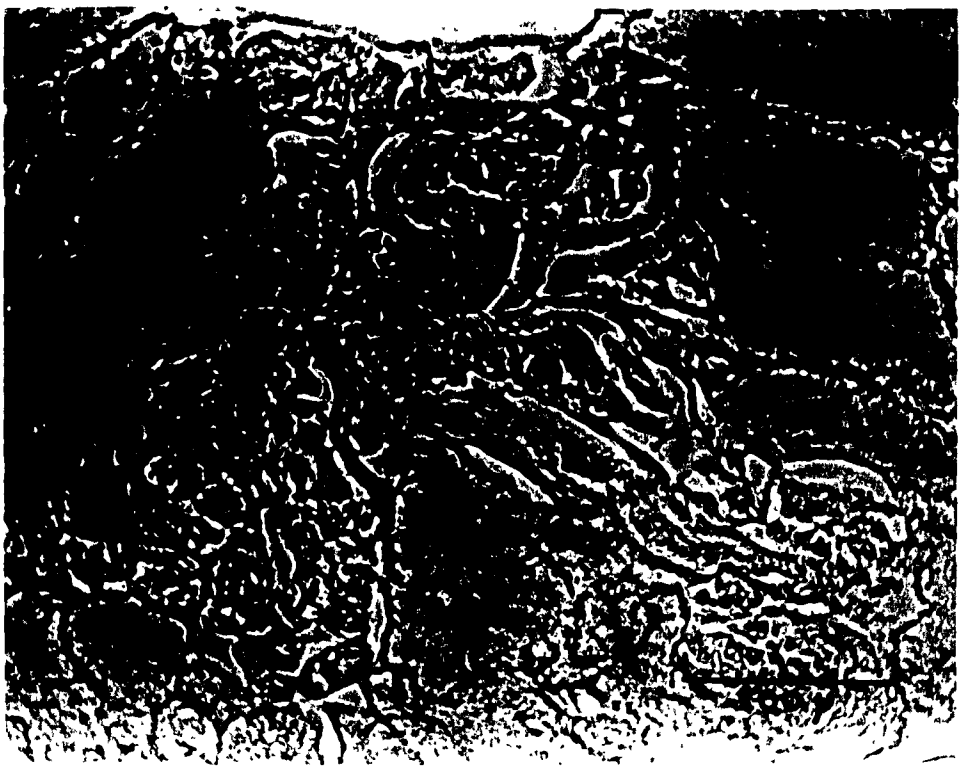

P
dtc
200 μ

Fig. 27. Phase-contrast autoradiograph of an unstained section of the digestive gland of L. saxatilis infected with C. lingua. The specimen was sampled 12 hours after commencement of feeding on ^{14}C-labelled food. The food is located where the emulsion is exposed, in the digestive cells and lumina of the digestive tubules.

Fig. 28. Phase-contrast autoradiograph of an unstained section of the digestive gland of L. saxatilis infected with C. lingua. The specimen was sampled 18 hours after commencement of feeding on ^{14}C-labelled food. The food is located where the emulsion is exposed, in the digestive cells and lumina of the digestive tubules.







APPENDIX 1

Data sheets 1 to 11. Size frequency distributions of *L. saxatilis* in samples taken at Blue Rocks.

Data sheet 12. Mean numbers of brood in gravid female *L. saxatilis* in population samples taken at Blue Rocks.

Data sheets 13 to 23. Numbers of larval trematode parasites in samples of *L. saxatilis* taken at Blue Rocks.

Data sheets 24 and 25. Rates of ingestion in *L. saxatilis* in the laboratory.

Data sheets 26 to 33. Estimates of efficiency of assimilation in *L. saxatilis* in the laboratory.

Data sheets 34 and 35. Estimates of rate of assimilation in *L. saxatilis* in the laboratory.

Data sheet 1. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 23 March 1967. The arithmetic probability analysis showed inflexions in the curve at the 2.2%, 65.0%, 90.0% and 98.0% levels. The components above the 98% inflexion are represented by only five snails (all infected with larval trematodes), and constitute 2.16% of the sample.

0.5 mm length groups	frequency n	frequency %	cumulative percentage	component length x ± S.D.
2.50 - 2.99	1	.45	.45	
3.00 - 3.49	1	.45	.90	3.35 ± 0.45
3.50 - 3.99	2	.90	1.80	
4.00 - 4.49	13	5.90	7.70	
4.50 - 4.99	25	11.36	19.06	
5.00 - 5.49	37	16.81	35.87	5.25 ± 0.80
5.50 - 5.99	28	12.72	48.59	
6.00 - 6.49	27	12.27	60.86	
6.50 - 6.99	31	14.09	74.95	
7.00 - 7.49	20	9.09	84.04	6.90 ± 0.55
7.50 - 7.99	11	5.00	89.04	
8.00 - 8.49	12	5.45	94.49	
8.50 - 8.99	4	1.81	96.30	8.20 ± 0.60
9.00 - 9.49	3	1.36	97.66	
9.50 - 9.99	2	.90	99.92	
Total	220	99.92	99.92	

Data sheet 2. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 10 May 1967. The arithmetic probability analysis showed inflexions in the curve at the 15.0%, 50.0% and 74.0% levels. The components above the 74.0% inflexion are represented by 66 individuals or 26.4% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.00 - 1.49	1	.40	.40	
1.50 - 1.99	5	2.00	2.40	
2.00 - 2.49	14	5.60	8.00	2.25 ± 0.50
2.50 - 2.99	15	6.00	14.00	
3.00 - 3.49	21	8.40	22.40	
3.50 - 3.99	17	6.80	29.20	
4.00 - 4.49	26	10.40	39.60	4.15 ± 0.90
4.50 - 4.99	21	8.40	48.00	
5.00 - 5.49	28	11.20	59.20	
5.50 - 5.99	17	6.80	66.00	5.85 ± 0.60
6.00 - 6.49	19	7.60	73.60	
6.50 - 6.99	27	10.80	84.40	
7.00 - 7.49	20	8.00	92.40	
7.50 - 7.99	5	2.00	94.40	
8.00 - 8.49	6	2.40	96.80	
8.50 - 8.99	3	1.20	98.00	
9.00 - 9.49	4	1.60	99.60	
9.50 - 9.99	0	.00	99.60	
10.00 - 10.49	0	.00	99.60	
10.50 - 10.99	1	.40	100.00	
Total	250	100.00	100.00	

Data sheet 3. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 14 June 1967. The arithmetic probability analysis showed inflexions in the curve at the 2.0%, 74.0%, 86.0% and 93.5% levels. The components above the 93.5% inflexion are represented by 18 individuals or 7.2% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
2.00 - 2.49	3	1.20	1.20	
2.50 - 2.99	2	.80	2.00	1.95 ± 0.20
3.00 - 3.49	5	2.00	4.00	
3.50 - 3.99	21	8.40	12.40	
4.00 - 4.49	24	9.60	22.00	
4.50 - 4.99	24	9.60	31.60	
5.00 - 5.49	25	10.00	41.60	5.25 ± 1.50
5.50 - 5.99	17	6.80	48.40	
6.00 - 6.49	20	8.00	56.40	
6.50 - 6.99	14	5.60	62.00	
7.00 - 7.49	17	6.80	68.80	
7.50 - 7.99	12	4.80	73.60	
8.00 - 8.49	19	7.60	81.20	
8.50 - 8.99	7	2.80	84.00	8.15 ± 0.55
9.00 - 9.49	4	1.60	85.60	
9.50 - 9.99	12	4.80	90.40	
10.00 - 10.49	6	2.40	92.80	9.65 ± 0.40
10.50 - 10.99	2	.80	93.60	
11.00 - 11.49	5	2.00	95.60	
11.50 - 11.99	0	.00	95.60	
12.00 - 12.49	5	2.00	97.60	
12.50 - 12.99	3	1.20	98.80	
13.00 - 13.49	1	.40	99.20	
13.50 - 13.99	0	.00	99.20	
14.00 - 14.49	1	.40	99.60	
14.50 - 14.99	0	.00	99.60	
15.00 - 15.49	0	.00	99.60	
15.50 - 15.99	1	.40	100.00	
Total	250	100.00	100.00	

Data sheet 4. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 18 July 1967. The arithmetic probabilty analysis showed inflexions in the curve at the 8.8%, 89.0% and 94.0% levels. The components above the 94.0% inflexion are represented by 20 individuals or 8.0% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.00 - 1.49	4	1.60	1.60	
1.50 - 1.99	6	2.40	4.00	1.35 ± 0.60
2.00 - 2.49	6	2.40	6.40	
2.50 - 2.99	6	2.40	8.80	
3.00 - 3.49	25	10.00	18.80	
3.50 - 3.99	28	11.20	30.00	
4.00 - 4.49	32	12.80	42.80	
4.50 - 4.99	40	16.00	58.80	4.45 ± 1.00
5.00 - 5.49	27	10.80	69.60	
5.50 - 5.99	26	10.40	80.00	
6.00 - 6.49	14	5.60	85.60	
6.50 - 6.99	6	2.40	88.00	
7.00 - 7.49	1	.40	88.40	
7.50 - 7.99	6	2.40	90.80	8.00 ± 0.80
8.00 - 8.49	3	1.20	92.00	
8.50 - 8.99	5	2.00	94.00	
9.00 - 9.49	0	.00	94.00	
9.50 - 9.99	6	2.40	96.40	
10.00 - 10.49	1	.40	96.80	
10.50 - 10.99	3	1.20	98.00	
11.00 - 11.49	2	.80	98.80	
11.50 - 11.99	1	.40	99.20	
12.00 - 12.49	2	.80	100.00	
Total	250	100.00	100.00	

Data sheet 5. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 30 August 1967. The arithmetic probability analysis showed inflexions in the curve at the 56.0%, 86.0% and 97.0% levels. The components above the 97.0% inflexion are represented by eight individuals or 3.2% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.00 - 1.49	1	.40	1.40	
1.50 - 1.99	3	1.20	1.60	
2.00 - 2.49	11	4.40	6.00	
2.50 - 2.99	19	7.60	13.60	3.25 ± 0.80
3.00 - 3.49	39	15.60	29.20	
3.50 - 3.99	29	11.60	40.80	
4.00 - 4.49	26	10.40	51.20	
4.50 - 4.99	12	4.80	56.00	
5.00 - 5.49	19	7.60	63.60	
5.50 - 5.99	6	2.50	66.00	
6.00 - 6.49	15	6.00	72.00	
6.50 - 6.99	6	2.40	74.40	6.25 ± 1.30
7.00 - 7.49	10	4.00	78.40	
7.50 - 7.99	11	4.40	82.80	
8.00 - 8.49	8	3.20	86.00	
8.50 - 8.99	10	4.00	90.00	
9.00 - 9.49	2	.80	90.80	
9.50 - 9.99	7	2.80	93.60	9.25 ± 0.95
10.00 - 10.49	4	1.60	95.20	
10.50 - 10.99	4	1.60	96.80	
11.00 - 11.49	4	1.60	98.40	
11.50 - 11.99	0	.00	98.40	
12.00 - 12.49	3	1.20	99.60	
12.50 - 12.99	0	.00	99.60	
13.00 - 13.49	1	.40	100.00	
Total	250	100.00	100.00	

Data sheet 6. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 3 October 1967. The arithmetic probability analysis showed inflexions in the curve at the 10.0%, 70.0% and 95.5% levels. The components above the 95.5% inflexion are represented by 20 individuals or 8.0% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.50 - 1.99	1	.40	.40	
2.00 - 2.49	11	4.40	4.80	2.25 ± 0.35
2.50 - 2.99	13	5.20	10.00	
3.00 - 3.49	23	9.20	19.20	
3.50 - 3.99	9	3.60	22.80	
4.00 - 4.49	13	5.20	28.00	
4.50 - 4.99	10	4.00	32.00	
5.00 - 5.49	16	6.40	38.40	5.25 ± 1.60
5.50 - 5.99	15	6.00	44.40	
6.00 - 6.49	17	6.80	51.20	
6.50 - 6.99	18	7.20	58.40	
7.00 - 7.49	11	4.40	62.80	
7.50 - 7.99	11	4.40	67.20	
8.00 - 8.49	8	3.20	70.40	
8.50 - 8.99	15	6.00	76.40	
9.00 - 9.49	13	5.20	81.60	9.45 ± 0.60
9.50 - 9.99	16	6.40	88.00	
10.00 - 10.49	10	4.00	92.00	
10.50 - 10.99	8	3.20	95.20	
11.00 - 11.49	7	2.80	98.00	
11.50 - 11.99	1	.40	98.40	
12.00 - 12.49	4	1.60	100.00	
Total	250	100.00	100.00	

Data sheet 7. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 29 November 1967. The arithmetic probability analysis showed inflexions in the curve at the 1.6%, 30.0% and 96.5% levels. The components above the 96.5% inflexion are represented by eight individuals or 3.55% of the sample.

0.5 mm length groups	frequency n	frequency %	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.50 - 1.99	2	.86	.86	
2.00 - 2.49	1	.43	1.29	1.65 ± 0.7
2.50 - 2.99	2	.86	2.15	
3.00 - 3.49	25	10.86	13.01	3.35 ± 0.30
3.50 - 3.99	39	16.95	29.96	
4.00 - 4.49	54	23.47	53.43	
4.50 - 4.99	27	11.73	65.16	
5.00 - 5.49	30	13.04	78.20	4.65 ± 1.05
5.50 - 5.99	19	8.26	86.46	
6.00 - 6.49	17	7.39	93.85	
6.50 - 6.99	6	2.60	96.45	
7.00 - 7.49	6	2.60	99.05	
7.50 - 7.99	1	.43	99.48	
8.00 - 8.49	1	.43	99.91	
Total	230	99.91	99.91	

Data sheet 8. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 29 March 1968. The arithmetic probability analysis showed inflexions in the curve at 10.0%, 40.0%, 82.0% and 96.8% levels. The components above the 96.8% inflexion are represented by 11 individuals or 4.4% of the sample.

0.5 mm length groupe	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.50 - 1.99	2	.80	.80	
2.00 - 2.49	10	4.00	4.80	2.25 ± 0.35
2.50 - 2.99	12	4.80	9.60	
3.00 - 3.49	27	10.80	20.40	
3.50 - 3.99	38	15.20	35.60	3.40 ± 0.35
4.00 - 4.49	42	16.80	52.40	
4.50 - 4.99	24	9.60	62.00	
5.00 - 5.49	26	10.40	72.40	4.65 ± 0.8
5.50 - 5.99	22	8.80	81.20	
6.00 - 6.49	20	8.00	89.20	
6.50 - 6.99	10	4.00	93.20	6.25 ± 0.7
7.00 - 7.49	6	2.40	95.60	
7.50 - 7.99	3	1.20	96.80	
8.00 - 8.49	4	1.60	98.40	
8.50 - 8.99	1	.40	98.80	
9.00 - 9.49	1	.40	99.20	
9.50 - 9.99	1	.40	99.60	
10.00 - 10.49	0	.00	99.60	
10.50 - 10.99	1	.40	100.00	
Total	250	100.00	100.00	

Data sheet 9. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 31 May 1968. The arithmetic probability analysis showed inflexions in the curve at the 86.0%, 96.0% and 98.8% levels. The components above the 98.8% inflexion are represented by three individuals or 1.2% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length $\bar{x} \pm$ S. D.
2.00 - 2.49	4	1.60	1.60	
2.50 - 2.99	28	11.20	12.80	
3.00 - 3.49	37	14.80	27.60	
3.50 - 3.99	41	16.40	44.00	3.70 ± 0.95
4.00 - 4.49	45	18.00	62.00	
4.50 - 4.99	31	12.40	74.40	
5.00 - 5.49	23	9.20	83.60	
5.50 - 5.99	5	2.00	85.60	
6.00 - 6.49	10	4.00	89.60	
6.50 - 6.99	4	1.60	91.20	
7.00 - 7.49	4	1.60	92.80	6.60 ± 1.15
7.50 - 7.99	4	1.60	94.40	
8.00 - 8.49	2	.80	95.20	
8.50 - 8.99	2	.80	96.00	
9.00 - 9.49	3	1.20	97.20	
9.50 - 9.99	2	.80	98.00	9.70 ± 0.9
10.00 - 10.49	2	.80	98.80	
10.50 - 10.99	1	.40	99.20	
11.00 - 11.49	0	.00	99.20	
11.50 - 11.99	2	.80	100.00	
Total	250	100.00	100.00	

Data sheet 10. Size frequency distribution of a sample of L. saxatilis collected at Blue Rocks on 24 July 1968. The arithmetic probability analysis showed inflexions in the curve at the 66.0%, 96.0% and 98.6% levels. The components above the 98.6% inflexion are represented by six individuals or 1.39% of the sample.

0.5 mm length groups	frequency n	%	cumulative percentage	component length x ± S. D.
1.00 - 1.49	1	.23	.23	
1.50 - 1.99	9	2.12	2.35	
2.00 - 2.49	39	9.19	11.54	
2.50 - 2.99	72	16.98	28.52	2.85 ± 0.6
3.00 - 3.49	91	21.46	49.98	
3.50 - 3.99	24	5.66	55.64	
4.00 - 4.49	23	5.42	61.06	
4.50 - 4.99	21	4.95	66.01	
5.00 - 5.49	30	7.07	73.08	
5.50 - 5.99	25	5.89	78.97	
6.00 - 6.49	33	7.78	86.75	5.90 ± 0.85
6.50 - 6.99	20	4.71	91.46	
7.00 - 7.49	14	3.30	94.76	
7.50 - 7.99	4	.94	95.70	
8.00 - 8.49	7	1.65	97.35	
8.50 - 8.99	4	.94	98.29	8.15 ± 0.55
9.00 - 9.49	1	.23	98.52	
9.50 - 9.99	3	.70	99.22	
10.00 - 10.49	0	.00	99.22	
10.50 - 10.99	1	.23	99.45	
11.00 - 11.49	0	.00	99.45	
11.50 - 11.99	1	.23	99.68	
12.00 - 12.49	1	.23	99.91	
Total	424	99.91	99.91	

Data sheet 11. Size frequency distribution of a sample of L. saxatilis taken at Blue Rocks on 15 September 1968. The arithmetic probability analysis showed inflexions in the curve at the 19.0% and 96.5% levels. The components above the 96.5% inflexion are represented by ten individuals or 3.61% of the sample.

0.5 mm length groups	frequency n	frequency %	cumulative percentage	component length $\bar{x} \pm$ S. D.
1.00 - 1.49	2	.72	.72	
1.50 - 1.99	2	.72	1.44	
2.00 - 2.49	11	3.97	5.41	2.60 ± 0.55
2.50 - 2.99	18	6.50	11.91	
3.00 - 3.49	15	5.42	17.33	
3.50 - 3.99	30	10.83	28.16	
4.00 - 4.49	47	16.97	45.13	
4.50 - 4.99	53	19.13	64.26	
5.00 - 5.49	48	17.33	81.59	4.65 ± 0.8
5.50 - 5.99	19	6.86	88.45	
6.00 - 6.49	14	5.05	93.50	
6.50 - 6.99	8	2.89	96.39	
7.00 - 7.49	1	.36	96.75	
7.50 - 7.99	2	.72	97.47	
8.00 - 8.49	1	.36	97.83	
8.50 - 8.99	0	.00	97.83	
9.00 - 9.49	2	.72	98.55	
9.50 - 9.99	0	.00	98.55	
10.00 - 10.49	1	.36	98.91	
10.50 - 10.99	2	.72	99.63	
11.00 - 11.49	1	.36	99.99	
Total	277	99.99	99.99	

Data sheet 12. The mean number of brood found in gravid female L. saxatilis in each 0.5 mm length group of samples taken at Blue Rocks from 3 Oct. 1967 to 15 Sept. 1968. The size frequency distributions of these samples are shown in data sheets 6 to 11.

0.5 mm length groups	3 Oct. 1967	29 Nov. 1967	29 Mar. 1968	31 May 1963	24 July 1968	15 Sept. 1968
3.00- 3.49	-	-	9.00	-	-	-
3.50- 3.99	-	6.50	8.60	24.00	10.00	7.00
4.00- 4.49	-	13.00	19.40	-	23.00	5.00
4.50- 4.99	26.50	11.50	13.00	10.00	25.30	10.33
5.00- 5.49	23.17	12.60	19.09	18.50	15.80	13.70
5.50- 5.99	48.40	12.80	29.75	-	27.60	24.60
6.00- 6.49	35.33	15.30	23.00	85.00	26.80	21.95
6.50- 6.99	74.67	4.00	13.30	-	34.80	27.00
7.00- 7.49	41.00	28.50	25.00	-	22.80	-
7.50- 7.99	4.00	-	51.50	-	20.00	-
8.00- 8.49	63.00	-	-	94.00	46.00	60.00
8.50- 8.99	49.67	-	-	1.00	18.00	-
9.00- 9.49	35.33	-	-	216.00	-	-
9.50- 9.99	6.00	-	-	-	225.00	-
10.00-10.49	144.33	-	-	-	-	3.00
10.50-10.99	3.00	-	-	-	-	-
11.00-11.49	78.00	-	-	-	-	-
11.50-11.99	-	-	-	4.00	-	-
12.00-12.49	45.00	-	-	-	-	-
Total gravid females	41	25	45	12	36	30
Total brood	1911	300	885	527	1092	519
mean brood per individual	46.61	12.00	19.67	43.91	30.33	17.30

Data sheet 13. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 23 March 1967.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
2.50 - 2.99	1	-	-	-	-	-	-	-	-
3.00 - 3.49	1	-	-	-	-	-	-	-	-
3.50 - 3.99	2	-	-	-	-	-	-	-	-
4.00 - 4.49	13	-	-	-	1	-	-	1	2
4.50 - 4.99	25	-	-	-	7	1	-	3	1
5.00 - 5.49	37	-	-	1	2	1	-	5	1
5.50 - 5.99	28	-	-	-	4	-	-	7	-
6.00 - 6.49	27	-	-	-	2	1	-	4	-
6.50 - 6.99	31	-	-	1	7	1	-	5	1
7.00 - 7.49	20	-	-	-	-	-	-	6	1
7.50 - 7.99	11	-	1	-	1	1	-	2	-
8.00 - 8.49	12	-	-	-	2	1	-	3	2
8.50 - 8.99	4	-	-	-	1	-	-	1	-
9.00 - 9.49	3	-	-	-	-	1	-	1	1
9.50 - 9.99	3	-	-	-	1	-	-	2	-
10.00 - 10.49	2	-	-	-	1	-	-	1	-
Total	220	-	1	2	29	7	-	41	9
Percentage infection of the total		-	0.5	0.9	13.2	3.2	-	18.6	4.1

Data sheet 14. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 10 May 1967.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
1.00 - 1.49	1	-	-	-	-	-	-	-	-
1.50 - 1.99	5	-	-	-	-	-	-	-	-
2.00 - 2.49	14	-	-	-	-	-	-	-	-
2.50 - 2.99	15	-	-	-	-	-	-	-	-
3.00 - 3.49	21	-	-	-	1	-	-	-	-
3.50 - 3.99	17	-	-	-	-	-	-	-	-
4.00 - 4.49	26	-	-	-	-	-	-	-	-
4.50 - 4.99	21	-	-	1	-	-	-	-	-
5.00 - 5.49	28	-	-	-	-	-	-	3	-
5.50 - 5.99	17	-	-	1	2	-	-	-	-
6.00 - 6.49	19	-	-	1	1	-	-	-	-
6.50 - 6.99	27	-	-	-	4	2	-	4	-
7.00 - 7.49	20	-	-	-	4	-	-	3	1
7.50 - 7.99	5	-	-	-	1	-	-	1	-
8.00 - 8.49	6	-	-	-	1	-	-	3	-
8.50 - 8.99	3	-	-	-	-	1	-	2	-
9.00 - 9.49	4	-	-	-	4	-	-	-	-
9.50 - 9.99	0	-	-	-	-	-	-	-	-
10.00 - 10.49	0	-	-	-	-	-	-	-	-
10.50 - 10.99	0	-	-	-	-	-	-	-	-
11.00 - 11.49	1	-	-	-	-	-	-	-	-
Total	250	-	-	3	18	3	-	16	1
Percentage infection of the total		-	-	1.2	7.2	1.2	-	6.4	0.4

Data sheet 15. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 14 June 1967.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
2.00 - 2.49	3	-	-	-	-	-	-	-	-
2.50 - 2.99	2	-	-	-	-	-	-	-	-
3.00 - 3.49	5	-	-	-	-	-	-	-	-
3.50 - 3.99	21	-	-	-	-	-	-	-	-
4.00 - 4.49	24	-	-	-	-	-	-	-	-
4.50 - 4.99	24	-	-	1	-	-	-	-	-
5.00 - 5.49	25	-	-	-	-	-	-	1	-
5.50 - 5.99	17	-	-	-	1	1	-	1	-
6.00 - 6.49	20	-	1	-	1	-	-	5	-
6.50 - 6.99	14	-	-	-	-	-	-	5	-
7.00 - 7.49	17	-	1	-	-	-	-	5	-
7.50 - 7.99	12	-	-	-	1	-	-	7	-
8.00 - 8.49	19	-	-	1	-	-	-	9	-
8.50 - 8.99	7	-	-	-	-	-	-	3	-
9.00 - 9.49	4	-	-	-	-	-	-	1	1
9.50 - 9.99	12	-	-	-	-	-	-	8	-
10.00 - 10.49	6	-	-	-	1	-	-	2	-
10.50 - 10.99	2	-	-	-	-	-	-	2	-
11.00 - 11.49	5	-	-	-	-	-	-	3	-
11.50 - 11.99	0	-	-	-	-	-	-	-	-
12.00 - 12.49	5	-	-	-	1	-	-	4	-
12.50 - 12.99	3	-	-	-	-	-	-	3	-
13.00 - 13.49	1	-	-	-	-	-	-	1	-
13.50 - 13.99	0	-	-	-	-	-	-	-	-
14.00 - 14.49	1	-	-	-	-	-	-	1	-
14.50 - 14.99	0	-	-	-	-	-	-	-	-
15.00 - 15.49	0	-	-	-	-	-	-	-	-
15.50 - 15.99	1	-	-	-	-	-	-	1	-
Total	250	-	2	2	5	1	-	62	1
Percentage infection of the total		-	0.8	0.8	2.0	0.4	-	24.8	0.4

Data sheet 16. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 18 July 1967.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
1.00 - 1.49	4	-	-	-	-	-	-	-	-
1.50 - 1.99	6	-	-	-	-	-	-	-	-
2.00 - 2.49	6	-	-	-	-	-	-	-	-
2.50 - 2.99	6	-	-	-	-	-	-	-	-
3.00 - 3.49	25	-	-	-	-	-	-	-	-
3.50 - 3.99	28	-	-	-	-	-	-	-	-
4.00 - 4.49	32	-	-	-	-	-	-	-	-
4.50 - 4.99	40	-	-	-	-	-	-	2	-
5.00 - 5.49	27	-	-	-	-	-	-	1	-
5.50 - 5.99	26	-	-	-	2	-	-	1	-
6.00 - 6.49	14	-	-	-	-	-	-	2	-
6.50 - 6.99	6	-	-	-	-	-	-	-	-
7.00 - 7.49	1	-	-	-	-	-	-	-	-
7.50 - 7.99	6	-	-	-	-	-	-	3	-
8.00 - 8.49	3	-	-	-	-	-	-	-	-
8.50 - 8.99	5	-	-	-	-	-	-	1	-
9.00 - 9.49	0	-	-	-	-	-	-	-	-
9.50 - 9.99	6	-	-	-	-	-	-	4	-
10.00 - 10.49	1	-	-	-	-	-	-	1	-
10.50 - 10.99	3	-	-	-	-	-	-	2	-
11.00 - 11.49	2	-	-	-	-	-	-	1	-
11.50 - 11.99	1	-	-	-	-	-	-	1	-
12.00 - 12.49	2	-	-	-	-	-	-	2	-
Total	250	-	-	-	2	-	-	21	-
Percentage infections of the total		-	-	-	0.8	-	-	8.4	-

Data sheet 17. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of *L. saxatilis* collected at Blue Rocks on 30 August 1967.

0.5 mm length groups	*L. saxatilis* (n)	Parasites (n)							
		P. homeotecnum	*H. littorinae*	*M. pygmaeus*	*M. similis*	*C. roscovita*	*P. atomon*	*C. lingua*	double infected
1.00 - 1.49	1	-	-	-	-	-	-	-	-
1.50 - 1.99	3	-	-	-	-	-	-	-	-
2.00 - 2.49	11	-	-	-	-	-	-	-	-
2.50 - 2.99	19	-	-	-	-	-	-	-	-
3.00 - 3.49	39	-	-	-	-	-	-	-	-
3.50 - 3.99	29	-	-	-	-	-	-	-	-
4.00 - 4.49	26	-	-	1	-	-	-	2	-
4.50 - 4.99	12	-	-	-	-	-	-	-	-
5.00 - 5.49	19	-	-	1	1	-	-	1	-
5.50 - 5.99	6	-	-	-	1	-	-	3	-
6.00 - 6.49	15	-	-	-	2	-	-	8	-
6.50 - 6.99	6	-	1	-	2	-	-	-	1
7.00 - 7.49	10	-	-	-	1	-	-	4	-
7.50 - 7.99	11	-	-	-	2	-	-	6	-
8.00 - 8.49	8	-	-	-	1	-	-	4	-
8.50 - 8.99	10	-	-	-	6	-	-	3	-
9.00 - 9.49	2	-	-	-	-	1	-	1	-
9.50 - 9.99	7	-	-	-	2	-	-	4	-
10.00 - 10.49	4	-	-	-	-	1	-	3	-
10.50 - 10.99	4	-	-	-	1	-	-	2	-
11.00 - 11.49	4	-	-	-	-	-	-	4	-
11.50 - 11.99	0	-	-	-	-	-	-	-	-
12.00 - 12.49	3	-	-	-	1	-	-	2	-
12.50 - 12.99	0	-	-	-	-	-	-	-	-
13.00 - 13.49	1	-	-	-	-	-	-	1	-
Total	250	-	1	2	20	2	-	48	1
Percentage infection of the total		-	0.4	0.8	8.0	0.8	-	19.2	0.4

Data sheet 18. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 3 October 1967.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
1.50 - 1.99	1	-	-	-	-	-	-	-	-
2.00 - 2.49	11	-	-	-	-	-	-	-	-
2.50 - 2.99	13	-	-	-	-	-	-	-	-
3.00 - 3.49	23	-	-	-	-	-	-	-	-
3.50 - 3.99	9	-	-	-	-	-	-	-	-
4.00 - 4.49	13	-	-	-	-	-	-	-	-
4.50 - 4.99	10	-	-	-	-	-	-	-	-
5.00 - 5.49	16	-	1	-	-	-	-	1	-
5.50 - 5.99	15	-	-	-	-	-	-	3	-
6.00 - 6.49	17	-	-	-	2	-	-	3	-
6.50 - 6.99	18	-	-	-	5	-	-	3	-
7.00 - 7.49	11	-	-	-	4	-	-	1	1
7.50 - 7.99	11	-	-	-	-	-	-	9	-
8.00 - 8.49	8	-	-	1	2	-	-	1	-
8.50 - 8.99	15	-	-	1	2	-	-	6	2
9.00 - 9.49	13	-	-	-	1	-	-	9	1
9.50 - 9.99	16	-	-	1	3	-	-	5	1
10.00 - 10.49	10	-	-	-	-	-	-	7	1
10.50 - 10.99	8	-	-	-	1	-	-	6	1
11.00 - 11.49	7	-	-	-	1	-	-	5	-
11.50 - 11.99	1	-	-	-	-	-	-	1	-
12.00 - 12.49	4	-	-	-	1	-	-	3	-
Total	250	-	1	3	22	-	-	63	7
Percentage infection of the total		-	0.4	1.2	8.8	-	-	25.2	2.8

Data sheet 19. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 29 November 1967.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
1.50 - 1.99	2	-	-	-	-	-	-	-	-
2.00 - 2.49	1	-	-	-	-	-	-	-	-
2.50 - 2.99	2	-	-	-	-	-	-	-	-
3.00 - 3.49	25	-	-	1	-	-	-	-	-
3.50 - 3.99	39	-	-	-	-	1	-	2	-
4.00 - 4.49	54	-	-	-	-	1	-	5	-
4.50 - 4.99	27	-	-	-	3	1	-	4	-
5.00 - 5.49	30	-	-	-	1	1	-	8	-
5.50 - 5.99	19	-	-	-	-	-	-	4	-
6.00 - 6.49	17	-	-	2	3	-	-	2	-
6.50 - 6.99	6	-	-	1	-	-	-	1	1
7.00 - 7.49	6	-	-	-	1	-	-	1	-
7.50 - 7.99	1	-	-	-	-	-	-	-	-
8.00 - 8.49	1	-	-	-	1	-	-	-	-
Total	230	-	-	4	9	4	-	27	1
Percentage infection of the total		-	-	1.7	3.9	1.7	-	11.7	0.4

Data sheet 20. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 29 March 1968.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
1.50 - 1.99	2	-	-	-	-	-	-	-	-
2.00 - 2.49	10	-	-	-	-	-	-	-	-
2.50 - 2.99	12	-	-	-	-	-	-	-	-
3.00 - 3.49	27	-	-	-	-	-	-	-	-
3.50 - 3.99	38	-	-	-	1	-	-	-	-
4.00 - 4.49	42	-	-	1	-	-	-	-	-
4.50 - 4.99	24	-	-	1	-	1	-	-	-
5.00 - 5.49	26	-	-	1	-	-	-	4	-
5.50 - 5.99	22	-	-	-	-	-	-	1	-
6.00 - 6.49	20	-	-	1	-	-	-	3	-
6.50 - 6.99	10	-	-	-	-	1	-	1	-
7.00 - 7.49	6	-	-	-	-	-	-	1	-
7.50 - 7.99	3	-	-	-	-	-	-	-	-
8.00 - 8.49	4	-	-	-	-	-	-	2	-
8.50 - 8.99	1	-	-	-	-	-	-	1	-
9.00 - 9.49	1	-	-	-	-	-	-	-	-
9.50 - 9.99	1	-	-	-	-	-	-	-	-
10.00 - 10.49	0	-	-	-	-	-	-	-	-
10.50 - 10.99	1	-	-	-	-	-	-	1	-
Total	250	-	-	4	1	2	-	14	-
Percentage infection of the total		-	-	1.6	0.4	0.8	-	5.6	-

Data sheet 21. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 31 May 1968.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
2.00 - 2.49	4	-	-	-	-	-	-	-	-
2.50 - 2.99	28	-	-	-	-	-	-	-	-
3.00 - 3.49	37	-	-	-	-	-	-	-	-
3.50 - 3.99	41	-	-	-	-	-	-	-	-
4.00 - 4.49	45	-	-	-	-	-	-	-	-
4.50 - 4.99	31	-	-	1	-	-	-	-	-
5.00 - 5.49	23	-	-	-	-	-	1	-	-
5.50 - 5.99	5	-	-	-	-	-	-	-	-
6.00 - 6.49	10	-	-	1	-	-	1	-	-
6.50 - 6.99	4	-	-	-	-	-	-	-	-
7.00 - 7.49	4	-	-	-	-	-	-	1	-
7.50 - 7.99	4	-	-	1	-	-	-	2	-
8.00 - 8.49	2	-	-	-	-	-	-	1	-
8.50 - 8.99	2	-	-	-	-	-	-	2	-
9.00 - 9.49	3	-	-	-	-	-	-	2	-
9.50 - 9.99	2	-	-	-	-	-	-	2	-
10.00 - 10.49	2	-	-	-	-	-	-	2	-
10.50 - 10.99	1	-	-	-	-	-	-	1	-
11.00 - 11.49	0	-	-	-	-	-	-	-	-
11.50 - 11.99	2	-	-	-	-	-	-	2	-
Total	250	-	-	3	-	-	2	15	-
Percentage infection of the total		-	-	1.2	-	-	0.8	6.0	-

Data sheet 22. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of *L. saxatilis* collected at Blue Rocks on 24 July 1968.

0.5 mm length groups	*L. saxatilis* (n)	Parasites (n)							
		P. homeotecnum	*H. littorinae*	*M. pygmaeus*	*M. similis*	*C. roscovita*	*P. atomon*	*C. lingua*	double infected
1.00 - 1.49	1	-	-	-	-	-	-	-	-
1.50 - 1.99	9	-	-	-	-	-	-	-	-
2.00 - 2.49	39	-	-	-	-	-	-	-	-
2.50 - 2.99	72	-	-	-	-	-	-	-	-
3.00 - 3.49	91	-	-	-	-	-	-	-	-
3.50 - 3.99	24	-	-	1	-	-	-	1	-
4.00 - 4.49	23	-	-	1	-	-	-	1	-
4.50 - 4.99	21	-	-	-	-	-	-	-	-
5.00 - 5.49	30	-	-	2	-	-	-	1	1
5.50 - 5.99	25	-	-	-	-	-	-	4	-
6.00 - 6.49	33	-	-	-	1	-	-	4	-
6.50 - 6.99	20	-	-	-	-	-	-	5	-
7.00 - 7.49	14	-	-	1	-	-	-	3	-
7.50 - 7.99	4	-	-	-	-	-	-	2	-
8.00 - 8.49	7	1	-	-	-	-	-	4	-
8.50 - 8.99	4	-	-	-	-	-	-	1	-
9.00 - 9.49	1	-	-	-	1	-	-	-	-
9.50 - 9.99	3	-	-	-	-	-	-	-	-
10.00 - 10.49	0	-	-	-	-	-	-	-	-
10.50 - 10.99	1	-	-	-	-	-	-	1	-
11.00 - 11.49	0	-	-	-	-	-	-	-	-
11.50 - 11.99	1	-	-	-	-	-	-	1	-
12.00 - 12.49	1	-	-	-	-	-	-	1	-
Total	424	1	-	5	2	-	-	29	1
Percentage infection of the total		0.2	-	1.2	0.5	-	-	6.8	0.2

Data sheet 23. The species and numbers of larval digenetic trematode infections found in each 0.5 mm length group in a sample of L. saxatilis collected at Blue Rocks on 15 September 1968.

0.5 mm length groups	L. saxatilis (n)	Parasites (n)							
		P. homeotecnum	H. littorinae	M. pygmaeus	M. similis	C. roscovita	P. atomon	C. lingua	double infected
1.00 - 1.49	2	-	-	-	-	-	-	-	-
1.50 - 1.99	2	-	-	-	-	-	-	-	-
2.00 - 2.49	11	-	-	-	-	-	-	-	-
2.50 - 2.99	18	-	-	-	-	-	-	-	-
3.00 - 3.49	15	-	-	-	-	-	-	-	-
3.50 - 3.99	30	1	-	-	-	-	1	-	-
4.00 - 4.49	47	-	2	-	-	-	-	-	-
4.50 - 4.99	53	-	-	1	-	-	-	5	-
5.00 - 5.49	48	-	1	1	2	-	-	3	-
5.50 - 5.99	19	-	-	1	-	-	-	1	-
6.00 - 6.49	14	-	-	-	-	-	-	2	-
6.50 - 6.99	8	-	-	-	-	-	-	3	-
7.00 - 7.49	1	-	-	-	-	-	-	1	-
7.50 - 7.99	2	-	-	-	-	-	-	2	-
8.00 - 8.49	1	-	-	-	-	-	-	-	-
8.50 - 8.99	0	-	-	-	-	-	-	-	-
9.00 - 9.49	2	-	-	-	1	-	-	1	-
9.50 - 9.99	0	-	-	-	-	-	-	-	-
10.00 - 10.49	1	-	-	-	-	-	-	1	-
10.50 - 10.99	2	-	-	-	1	-	-	1	-
11.00 - 11.49	1	-	-	-	-	-	-	1	-
Total	277	1	3	3	4	-	1	21	-
Percentage infection of the total		0.4	1.1	1.1	1.5	-	0.4	7.6	-

Data sheet 24. Experiment C 1. The quantity of Urospora spp. detritus food ingested by individual L. saxatilis during a six-hour period in the laboratory at 6°C. Because the snails were of varied live weights, the weight of food ingested has been standardized as per 0.1 g live weight of snail. Separate values are shown for unifected snails and those infected with digenetic trematode larvae.

	live snail weight g	food ingested mg dry wt	ingestion (mg dry wt) per 0.1g live wt of snail
Unifected	0.147	0.984	0.669
	0.081	0.318	0.393
	0.190	0.658	0.346
	0.122	0.712	0.584
	0.069	0.526	0.762
	0.055	0.538	0.978
	0.050	0.324	0.648
	0.040	0.154	0.385
	0.037	0.510	1.378
$\bar{x} \pm$ S. D.	0.088±0.053	0.525±0.246	0.530±0.284
Infected	0.072	0.858	1.192
	0.211	0.244	0.116
	0.206	1.062	0.516
	0.123	0.062	0.050
	0.137	0.408	0.298
	0.139	0.608	0.437
	0.102	0.300	0.294
	0.127	0.500	0.394
$\bar{x}$ + S. D.	0.139±0.048	0.372±0.284	0.263±0.189

Data sheet 25. Experiment C 4. The quantity of Enteromorpha spp. detritus food ingested by individual L. saxatilis during a six-hour period in the laboratory at 10°-15°C. Because the snails were of varied live weights, the weight of food ingested has been standardized as per 0.1 g live weight of snail. Separate values are shown for uninfected snails and those infected with digenetic trematode larvae.

	live snail weight g	food ingested mg dry wt	ingestion (mg dry wt) per 0.1 g live wt of snail
Uninfected	0.119	0.208	0.175
	0.190	0.276	0.145
	0.203	0.992	0.489
	0.104	0.388	0.373
	0.117	0.820	0.701
	0.144	0.080	0.056
	0.088	0.164	0.186
	0.104	0.512	0.492
	0.142	0.636	0.448
	0.201	0.820	0.408
$\bar{x} \pm$ S. D.	0.141±0.042	0.490±0.317	0.347±0.201
Infected	0.112	0.884	0.789
	0.253	0.388	0.153
	0.143	0.868	0.607
	0.173	0.708	0.409
	0.105	1.140	1.086
	0.303	0.970	0.320
	0.079	0.860	1.089
	0.119	1.024	0.861
$\bar{x} \pm$ S. D.	0.161±0.078	0.585±0.402	0.393±0.336

Data sheet 26. Experiment C 2. Estimates of efficiency of assimilation for nitrogen by uninfected L. saxatilis and those infected with larval digenetic trematodes. The snails, in individual dishes, were fed Urospora spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 10°-15° C. Each value is the efficiency of assimilation for a single snail, determined by comparison of the nitrogen content of food and faeces.

Efficiency of assimilation (nitrogen) %

Uninfected snails ($\bar{x}$ live weight 0.14 ± 0.042 g)			Infected snails ($\bar{x}$ live weight 0.16 ± 0.042 g)	
81.59	49.85	44.27	55.42	46.28
126.01	64.55	60.53	60.84	79.26
83.13	71.05	44.89	133.75	90.25
61.76	85.60	62.54	115.48	74.15
99.23	72.76		143.50	38.54
62.38	108.67		41.95	51.24
114.71	89.01		96.06	77.24
123.07	50.93		78.95	84.67
78.64	88.54		180.03	34.06
61.76	83.44		49.07	57.12
83.44	94.27		41.18	85.76
69.20	82.04		55.88	37.46
70.12	87.15		119.35	15.33
67.49	129.72		102.63	63.14
90.09	60.84		20.90	110.99
17.96	103.25		75.54	
56.97	78.64		70.90	
49.54	33.75		88.24	
$\bar{x}$ ± S. D. 76.08 ± 24.72			75.00 ± 36.47	

Data sheet 27. Experiment C 3. Estimates of efficiency of assimilation for nitrogen by uninfected L. saxatilis and those infected by larval digenetic trematodes. The snails, in individual dishes, were fed Urospora spp. detritus. Food was available for 24 hours. The temperature was 10-15 °C. Each value is the efficiency of assimilation for a single snail, determined by comparison of the nitrogen content of food and faeces.

Efficiency of assimilation (nitrogen) %

Uninfected snails ($\bar{x}$ live weight 0.08 ± 0.060)				Infected snails ($\bar{x}$ live weight 0.10 ± 0.058)		
57.12	61.61	39.16	93.96	39.78	52.79	26.78
57.28	64.87	24.46	48.45	27.24	60.53	65.33
48.61	65.17	11.46	55.26	40.87	37.62	87.46
174.92	55.88	69.97	71.67	67.80	67.34	53.87
71.21	40.25	28.12	36.22	20.90	87.62	69.35
19.66	80.65	80.03	69.50	65.02	34.21	56.66
141.80	57.43	38.08	58.67	35.29	62.38	37.07
71.98	61.76	34.83	57.43	58.98	37.62	56.35
35.45	78.17	34.52		11.76	87.93	36.22
25.23	66.25	27.55		27.24	48.92	
16.59	50.93	77.09		45.82	39.16	
62.23	72.45	60.68		56.19	38.08	
58.67	66.56	40.09		99.38	17.03	
52.32	52.32	43.50		43.34	57.28	
53.56	56.35	82.66		86.53	60.99	
87.15	88.24	65.17		41.64	13.78	
64.24	55.11	54.49		82.04	13.93	
$\bar{x}$ ± S. D. 58.89 ± 26.55				50.14 ± 22.07		

Data sheet 28. Experiment C 5. Estimates of efficiency of assimilation for nitrogen by uninfected L. saxatilis and those infected by larval digenetic trematodes. The snails, in individual dishes, were fed live Enteromorpha spp. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 10-15°C. Each value is the efficiency of assimilation for a single snail, determined by the comparison of the nitrogen content of food and faeces.

Efficiency of assimilation (nitrogen) %			
uninfected snails ($\bar{x}$ live weight 0.14 ± 0.041 g)		infected snails ($\bar{x}$ live weight 0.16 ± 0.055 g)	
91.63	100.00	78.14	78.14
97.67	100.00	93.95	94.42
100.00	100.00	82.79	96.24
80.47	65.12	53.02	92.09
94.42	89.30	96.74	86.51
94.42	100.00	92.09	79.53
100.00	86.51	77.67	81.40
96.74	96.28	100.00	74.42
74.42	82.79	74.42	93.49
78.14	74.42	94.88	
$\bar{x}$ ± S.D. 90.11 ± 10.72		85.26 ± 11.47	

Data sheet 29. Experiment C I. Estimates of efficiency of assimilation for carbon by uninfected L. saxatilis and those infected with larval digenetic trematodes. The snails, in individual dishes, were fed Urospora spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 6°C. Each value is the efficiency of assimilation for a single snail, determined by comparison of the carbon content of food and faeces.

Efficiency of assimilation (carbon) %	
uninfected snails ($\bar{x}$ live weight 0.11 ± 0.049 g)	infected snails ($\bar{x}$ live weight 0.14 ± 0.062 g)
43.81	10.94
27.54	- 4.37
10.00	22.34
83.79	- 2.03
42.51	- 6.00
56.29	21.17
52.52	20.24
36.98	24.21
13.20	4.47
14.47	24.98
25.11	20.91
53.62	56.72
54.92	- 8.37
64.15	5.54
	63.12
	4.13
	86.16
	- 6.04
$\bar{x} \pm$ S.D. 41.35 ± 21.45	18.78 ± 26.15

Data sheet 30. Experiment C 2. Estimates of efficiency of assimilation for carbon by uninfected L. saxatilis and those infected with larval digenetic trematodes. The snails, in individual dishes, were fed Urospora spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 10°-15°C. Each value is the efficiency of assimilation for a single snail determined by comparison of the carbon content of food and faeces.

Efficiency of assimilation (carbon) %			
uninfected snails ($\bar{x}$ live weight 0.14 ± 0.042 g)		infected snails ($\bar{x}$ live weight 0.16 ± 0.074 g)	
63.31	66.78	47.09	70.71
95.03	71.97	54.87	66.85
70.76	65.23	87.63	48.21
44.54	93.43	59.31	4.53
73.38	71.61	80.41	64.65
58.95	54.00	53.98	69.50
80.77	87.08	82.47	42.46
86.13	76.84	62.78	51.55
61.42	87.17	34.46	80.09
51.41	77.13	50.70	41.88
74.88	73.79	49.61	36.08
49.81	101.04	50.90	63.85
62.27	53.30	69.40	59.68
46.56	51.96	67.48	
71.05	61.54	38.22	
30.75	41.29	40.13	
46.17	47.36	66.44	
48.76	59.00	73.88	
51.89	45.90	45.81	
56.23	58.97	72.65	
$\bar{x}$ ± S. D. 64.23 ± 16.48		57.49 ± 18.13	

Data sheet 31. Experiment C 3. Estimates of efficiency of assimilation for carbon by uninfected L. saxatilis and those infected by larval digenetic trematodes. The snails, in individual dishes, were fed Urospora spp. detritus. Food was available for 24 hours. The temperature was 10°-15°C. Each value is the efficiency of assimilation for a single snail determined by comparison of the carbon content of food and faeces.

Efficiency of assimilation (carbon) %

uninfected snails ($\bar{x}$ live weight 0.08 ± 0.060 g)			infected snails ($\bar{x}$ live weight 0.10 ± 0.058 g)		
13.00	66.22	46.07	48.98	37.20	35.34
48.30	58.41	45.44	58.85	39.94	56.28
43.62	76.45	43.87	40.79	72.41	43.33
98.57	60.86	73.88	59.97	68.02	43.33
12.29	61.25	58.85	45.88	48.91	
37.83	71.73	56.94	36.52	68.79	
85.98	69.08	54.63	64.94	56.06	
45.42	50.46	74.25	77.50	68.21	
25.51	64.96	66.85	52.38	41.61	
44.03	66.03	69.30	81.86	55.82	
39.33	61.57	85.04	52.52	22.53	
59.92	72.04	60.43	61.08	39.11	
64.77	31.09	63.19	66.51	30.02	
53.64	51.53	78.66	73.13	45.37	
57.15	32.35	44.59	44.67	71.41	
81.87	20.42	68.84	67.60	87.49	
64.16	74.93	65.81	49.56	64.67	
62.15	44.57	61.28	75.73	59.26	
47.58	69.69		47.60	48.52	
65.59	50.68		62.80	39.38	
$\bar{x}$ + S. D.	57.29 ± 17.40		55.08 ± 14.83		

Data sheet 32. Experiment C 4. Estimates of efficiency of assimilation for carbon by uninfected L. saxatilis and those infected with larval digenetic trematodes. The snails, in individual dishes, were fed Entreomorpha spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 10°-15°C. Each value is the effieceny of assimilation for a single snail determined by comparison of the carbon content of food and faeces.

Efficiency of assimilation (carbon) %			
uninfected snails ($\bar{x}$ live weight 0.14 ± 0.043 g)		infected snails ($\bar{x}$ live weight 0.16 ± 0.071 g)	
89.00	55.44	94.21	28.44
61.66	88.30	62.08	41.66
53.48	18.89	41.81	60.26
80.24	21.89	34.84	30.20
75.90	21.38	51.02	38.46
78.62	37.92	32.05	25.69
85.22	27.62	49.17	58.44
76.74	55.86	40.44	41.25
68.12	59.31	89.17	29.83
39.24	30.59	54.91	44.47
67.20	21.63	53.74	
52.87	67.62	27.48	
67.70	58.52	30.70	
81.14	27.29	30.25	
12.06	27.40	23.31	
$\bar{X}$ + S. D.	53.63 ±23.88	44.56 ±	18.22

Data sheet 33. Experiment C 5. Estimates of efficiency of assimilation for carbon by uninfected L. saxatilis and those infected with larval digenetic trematodes. The snails, in individual dishes, were fed live Enteromorpha spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 10°-15°C. Each value is the efficiency of assimilation for a single snail, determined by comparison of the carbon content of food and faeces.

Effieiency of assimilation (carbon) %

uninfected snails ($\bar{x}$ live weight 0.14 ± 0.041 g)		infected snails ($\bar{x}$ live weight 0.16 ± 0.055 g)	
74.85	83.02	58.14	88.83
87.33	92.29	81.43	86.85
85.07	60.82	69.77	89.80
79.88	87.70	63.89	78.70
58.99	100.00	78.84	78.08
79.99	50.07	63.24	92.80
46.65	84.56	65.53	94.51
88.88	72.93	80.09	74.78
100.00	87.84	67.99	85.53
77.07	77.02	95.22	
$\bar{x}$ + S. D.	78.74 ± 14.76		78.63 ± 11.38

Data sheet 34. Experiment C 1. Rates of assimilation in L. saxatilis, calculated from the rates of ingestion and corresponding efficiencies of assimilation. The snails, in individual dishes, were fed Urospora spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 6°C. Each value is the rate of assimilation for a single snail.

	Rate of ingestion mg/6 hrs.	Efficiency of assimilation (carbon) %	Rate of assimilation mg/6 hrs.
uninfected	0.98	43.81	0.43
	0.32	27.54	0.09
	0.66	10.00	0.07
	0.71	83.79	0.59
	0.53	42.51	0.23
	0.54	56.29	0.30
	0.32	52.52	0.17
	0.15	36.98	0.06
	0.51	13.20	0.07
$\bar{x} \pm$ S. D.	0.53 ± 0.25	- - -	0.22 ± 0.18
infected	0.86	10.94	0.09
	0.24	-4.37	-0.01
	1.06	22.34	0.24
	0.06	-2.03	-0.01
	0.41	-6.00	-0.02
	0.61	20.24	0.12
	0.30	24.21	0.07
	0.50	4.47	0.02
$\bar{x} \pm$ S. D.	0.37 ± 0.28	- - -	0.06 ± 0.08

Data sheet 35. Experiment C 4. Rates of assimilation in L. saxatilis calculated from the rates of ingestion and corresponding efficiencies of assimilation. The snails, in individual dishes, were fed Enteromorpha spp. detritus. Food was alternately available for six-hours and withdrawn for six-hours. The temperature was 10^{o}-15^{o}C. Each value is the rate of assimilation for a single snail.

	Rate of ingestion mg/6 hrs.	Efficiency of assimilation (carbon) %	Rate of assimilation mg/6 hrs.
uninfected	0.21	89.00	0.19
	0.28	61.66	0.17
	0.99	53.48	0.53
	0.39	80.24	0.31
	0.82	75.90	0.62
	0.08	78.62	0.06
	0.16	85.22	0.14
	0.51	76.74	0.39
	0.64	68.12	0.44
	0.82	39.24	0.32
$\bar{x} \pm$ S. D.	0.49 ± 0.32	- - -	0.32 ± 0.18
infected	0.88	62.08	0.55
	0.39	41.81	0.16
	0.87	34.84	0.30
	0.71	51.02	0.36
	1.14	32.05	0.37
	0.97	49.17	0.48
	0.86	-	-
	1.02	40.44	0.41
$\bar{x} \pm$ S. D.	0.59 ± 0.32	- - -	0.38 ± 0.18

Appendix II

Variation in characters of the northern rough periwinkle, Littorina saxatilis (Olivi) in Nova Scotia (Gastropoda, Prosobranchia).

INTRODUCTION

The northern rough periwinkle, Littorina saxatilis (Olivi), occurs commonly on the shores of the North Atlantic and Arctic Oceans. It characteristically occupies the middle and upper tide levels on shores with a stable substratum.

In Europe, the species extends from the southern bays of Novaya Zemlya (Zenkevitch, 1963), south to Gibraltar, the Azores (Thorson, 1941) and the Mediterranean. It is present on all of the intermediate coast, including the British Isles, Faroes, Iceland and South Spitzbergen. In the Baltic Sea, the distribution is as far east as the west coast of Rugen (Stresemann, 1957).

In North America, Littorina saxatilis occurs in the Canadian Arctic, east of the MacKenzie Delta (Dall, 1919), West Greenland (Thorson, 1951) and Baffin Island (Ellis, 1955), and extends southward along the coast to New Jersey, U. S.A. (Becquaert, 1943). Stephenson and Stephenson (1952) give the most southerly record at Beaufort Inlet, North Carolina. Wells (1965), has shown that the extensive sand beaches and higher water temperatures south of New Jersey effectively prohibit the southerly extension of Littorina littorea (L.) populations. These barriers would similarly restrict Littorina saxatilis which has boreal-arctic distribution and lacks a planktonic laval stage for dispersal. Littorinids reported from the North American west coast as Littorina saxatilis

are considered to be forms of Littorina sitkana Philippi (Becquaert 1943, and Urban 1962).

Over its wide geographic and habitat range, Littorina saxatilis shows great variation in the morphology of the shell as well as in ecology and reproductive biology. As a result many subspecies and varieties have been described. The complex synonymy that appeared in the earlier literature was effectively clarified by Dautzenburg and Fischer (1912), who redescribed the various forms as subspecies and varieties of a single species, Littorina saxatilis. Despite this, such synonyms as Littorina rudis (Maton) have continued in use by many authors. In Europe, there has been renewed interest in the variation of Littorina saxatilis, particularly of populations on the shores of France, the Iberian Peninsula and the British Isles (Fischer-Piette and Gaillard, 1960, 1961, 1966 and 1968; Fischer-Piette et al. 1966; Fischer-Piette et al. 1963 and 1964, Fischer-Piette et al. 1961; and James 1968 a and b).

There are six subspecies of Littorina saxatilis described and, of these three have been further differentiated into varieties, largely on the basis of shape and sculpturing of the shell. These subspecies are listed in Table I. All other names referring to Littorina saxatilis are considered to be synonymous with the appropriate subspecies.

Table I. A list of the names and authors of subspecies and varieties of Littorina saxatilis (Olivi) currently in use. (After James, 1968).

SUB SPECIES	VARIETY
L. saxatilis saxatilis (Olivi, 1792).	
L. saxatilis rudis (Maton, 1797)	rudis, 1797. rudissima Bean, 1844 nigrolineata Grey, 1839 jugosoides James, 1968
L. saxatilis jugosa (Montagu,1803)	jugosa Montagy, 1803 rudissimoides James, 1968 tenuis James, 1968 attenuata Dautzenburg and Fischer, 1912
L. saxatilis tenebrosa (Montagu, 1803)	tenebrosa Montagu, 1803 similis Jeffreys, 1865 patula Thorpe, 1844 elata Dautzenburg and Fischer, 1912
L. saxatilis neglecta (Bean, 1844)	
L. saxatilis grönlandica (Menke, 1830)	

In addition to the subspecies and varieties listed in Table I, there are 21 names assigned to distinct colour-forms. These are listed in Table II. Several of these colour-forms occur throughout the subspecies and varieties. Some are illustrated in the figures given by Dautzenburg and Fischer (1912).

Colour is one of the most variable characters of Littorina saxatilis. Fischer-Piette et al. (1963) describe two populations with extreme colour diversity; one having 164 colour variations in 400 specimens and the other, 155 variations in 468. Specimens were frequently found to have the characteristics of more than one of the colour-forms listed in the Table.

Fischer-Piette et al (1964) and James (1968a) have described the characteristics of shell, radula, number of penial glands, head pigmentation and size of emerging juveniles, together with the habitat and larval trematode parasites of each subspecies and variety. The authors admit, and in fact describe, the wide variation that occurs within a defined subspecies or variety. These variations are particularly apparent when different populations are contrasted. In their 1964 paper, Fischer-Piette et al summarize as follows:

Table II. A summary of the names of colour-forms of *Littorina saxatilis* (Olivi), occurring in the literature. These colour-forms generally are found throughout the different subspecies and varieties.

Name	Colouration	Authority
L. s. albida	Uniform white	Dautzenburg, 1887
L. s. zonaria	White or yellow with brown bands	Bean, 1844
L. s. bi-zonaria		James, 1963
L. s. tessellata	White and grey tesselations	Daultzenburg, 1893
L. s. interupta	White with dark brown hyphens	Fischer-Piette *et al*, 1961
L. s. bi-interupta		Fischer-Piette and Gaillard, 1963
L. s. flammulata		Dautzenburg and Fischer, 1912
L. s. hieroglyphica	White background with brown or grey designs	Fischer-Piette *et al*, 1961
L. s. lineata	Pale yellow with brown lines	Dautzenburg and Fischer, 1912
L. s. fusca	Uniform brown	Dautzenburg and Fischer, 1912
L. s. sanguinea	Uniform red	Dautzenburg and Duronchoux, 1900
L. s. mineata	Uniform brick red	Dautzenburg and Fischer, 1912
L. s. aurantia	Uniform yellow-orange	Dautzenburg, 1887

Table II continued:

Name	Colouration	Authority
L. s. fulva	Uniform fawn	Monterosato, 1872
L. s. lutea	Uniform lemon	Dautzenburg and Duronchoux, 1900
L. s. tractibus	Light background with light brown hyphens	Fischer-Piette et al, 1961
L. s. maculata	Black with light-yellow or grey patches	Fischer-Piette and Gaillard, 1963
L. s. trifasciata	Two light and two dark bands	Dautzenburg and Fischer, 1912
L. s. nojensis	Uniform green-grey to green-yellow	Fischer-Piette and Gaillard, 1964
L. s. nigrolineata	Light background with fine dark spiral lines, only in L.s. rudis nigrolineata	Grey, 1839

Tessellations may be described as alternately arranged light and dark areas, in a spiral mosaic.

Hyphens may be described as elongate, narrow, broken light and dark lines

James (1968) has considered L. s. trifasciata and also a further colour form L. s. fasciata-Dautzenburg, as synonymous with L. s. zonaria.

"(a) some populations are homogeneous with respect to shell character and others in similar environmental conditions are heterogenous.

(b) some heterogeneous populations have intermediates between extremes but others, again in similar conditions, do not.

(c) stations with similar topography may have populations with widely different shell characters.

(d) populations of varieties occur discontinuously and randomly in regions with apparently different topography.

(e) some variations in shell characters, which are usually correlated with changes in the environment, may sometimes occur without, with apparent disregard for or even against, such changes.

These observations further illustrate the extreme variation of L. saxatilis and the difficulty in trying to understand the causes of this variation."

Fischer-Piette and Gaillard (1966) have further shown that a progressive colour change toward darker forms has taken place during a period of from one to 16 years in some populations on the coasts of France and Spain. They do not, however, speculate on the causes for this change.

There have been very few descriptions of the variation of L. saxatilis in North America. Becquaert (1943), in a review of the genus Littorina in the western Atlantic, examined diverse L. saxatilis specimens but found it difficult to distinguish the different subspecies and varieties. No consistent differences were found between the southern forms and those northern forms that had been identified as L. s. grönlandica. L. s. jugosa was considered to be a form with few, but well-defined spiral ridges on the shell, whereas L. s. vestita (Say) and L. s. obligatus (Say) had similar shells but with less well-defined ridges. L. s. tenbrosa was described by Becquaert as having a thinner and more elongate shell, and as living in brackish water creeks and marshes. Gould (1870) has listed L. s. obligatus as a synonym of L. s. rudis, and L. s. vestita as a synonym of L. s. tenebrosa. Coleman (1932) considered the synonymy of L. saxatilis but confined his statistical treatment to a comparison of European and North American Littorina obtusata (L.).

Littorina saxatilis has been frequently reported from

the shores of Nova Scotia. Published records are summarized by LaRocque (1953). Occurrences are also cited for the upper tidal zone of the Bay of Fundy, Minas Channel and Cobequid Bay by Bousfield and Leim (1959), and for southern and western shores as " very common along rocky shores at high water level, and in estuaries among eel grass", by Bousfield (1958). Gowanloch and Hayes (1926) give a brief description of L. saxatilis at Halifax, Nova Scotia and St. Andrews, New Brunswick. The wall of shells is described as thin, but thick in gross appearance due to the coarse texture and spiral ridges.

> "The shell is very variable in texture, ranging from a smooth appearance with no spiral ridges visible to the unaided eye, to a coarse looking shell with or without spiral ridges. The colour is extremely variable, and may be various shades of white, red or black, or a colour combination"

Stephenson and Stephenson (1954), during their studies of the intertidal zone in Nova Scotia and Prince Edward Island, recorded two distinct forms of L. saxatilis which they called "types A and B". "Type B" resembled L. obtusata in general shell form and was present at several localities including exposed rocks at Peggy's Cove, Nova Scotia. "Type A" had a more sharply pointed shell and was more widely distributed, though commonly occurring with type B.

The recent studies of variation in characters and ecology of L. saxatilis in Europe have provided a good basis for similar studies in North America. A study was made of some populations in Nova Scotia with the object of relating them to their European counterparts.

METHODS

Studies were made of L. saxatilis populations at nine localities on a variety of shores in Halifax and Lunenburg Counties, Nova Scotia. These localities are listed in Table III and indicated on the map, Figure I. Sample size varied from 50 to 250 individuals, with a total of 958 snails being examined. Collections were made at random, and without any special reference to tide level.

The individual snails in each sample were examined for anatomical characters and notes and measurements were made as follows:

(a) shell dimensions. Measurements of the length and breadth were made to the nearest 0.25 mm. Shell-length is the distance from the apex to the lower margin of the aperture, through the axis of the shell. Breadth is the greatest distance through the body whorl, at right angles to the shell axis.

Table III. The localities in Halifax and Lunenburg Counties, Nova Scotia where samples of *L. saxatilis* were collected for examination of variation in characters.

Station No.	Locality	Date	Habitat	Number of snails examined
1	Lawrencetown Lake	3 May 1967	Salt marsh	50
2	Point Pleasant Park, Halifax	12 Aug. 1968	Exposed boulder beach	100
3	Sandy Cove	28 Feb. 1968	Exposed rocky shore	107
4	Prospect Cove	28 Feb. 1968	Sheltered boulder beach	100
5	Peggy Point	29 Mar. 1968	Exposed rocky shore	97
6	Indian Harbour	29 Mar. 1968	Sheltered rocky shore	107
7	Mason Cove	28 Apr. 1968	Sheltered boulder beach	97
8	Queensland	29 Nov. 1967	Exposed boulder beach	50
9	Blue Rocks	3 Oct. 1967	Sheltered rocky shore	250

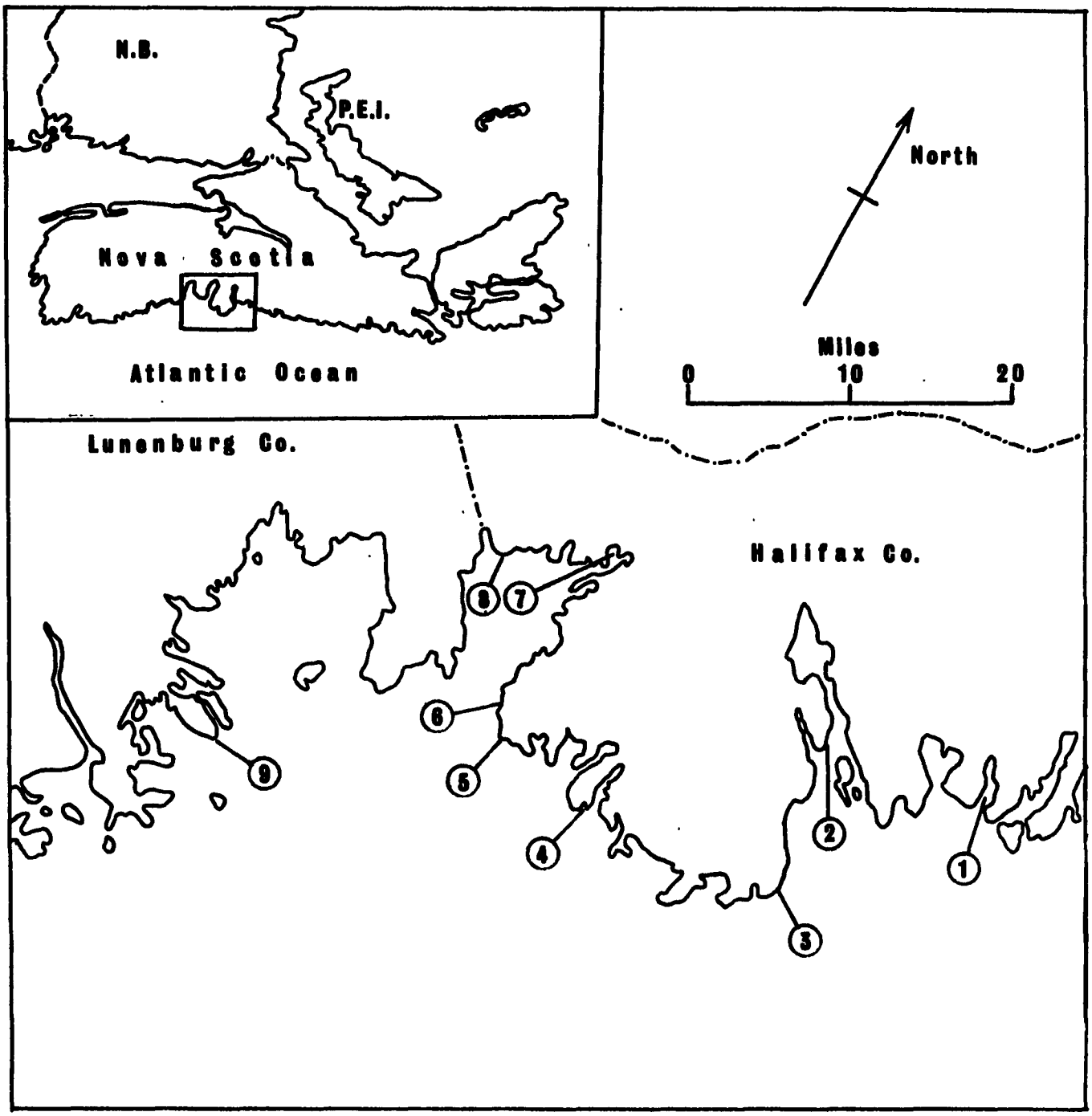


Fig. 1 A map of part of the shore line of Halifax and Lunenburg Counties, Nova Scotia. Single samples of L. saxatilis were collected at each of the stations, 1 to 9 between May 1967 and August 1968, for determination of variation in characters.

These dimensions are shown in Figure 2. The ratio of shell breadth to shell length is used to describe the general proportions of the shell.

(b) Shell whorls. The number of shell whorls was noted.

(c) Shell colour. The colour of each shell was described according to the list in Table 2, or by direct reference to the colour or colour-combination where no trivial name is given.

(d) Shell sculpture. Shell sculpture is described by use of an index; 0 (smooth) to 3 (coarse ribbed) which roughly correspond to the stages shown in Figure 2.

(e) Pigmentation of the head and tentacles. Indices have also been assigned to describe stages in the degree of pigmentation of the snail's head and tentacles. These stages, A to F, are shown in Figure 3. Intermediates occur

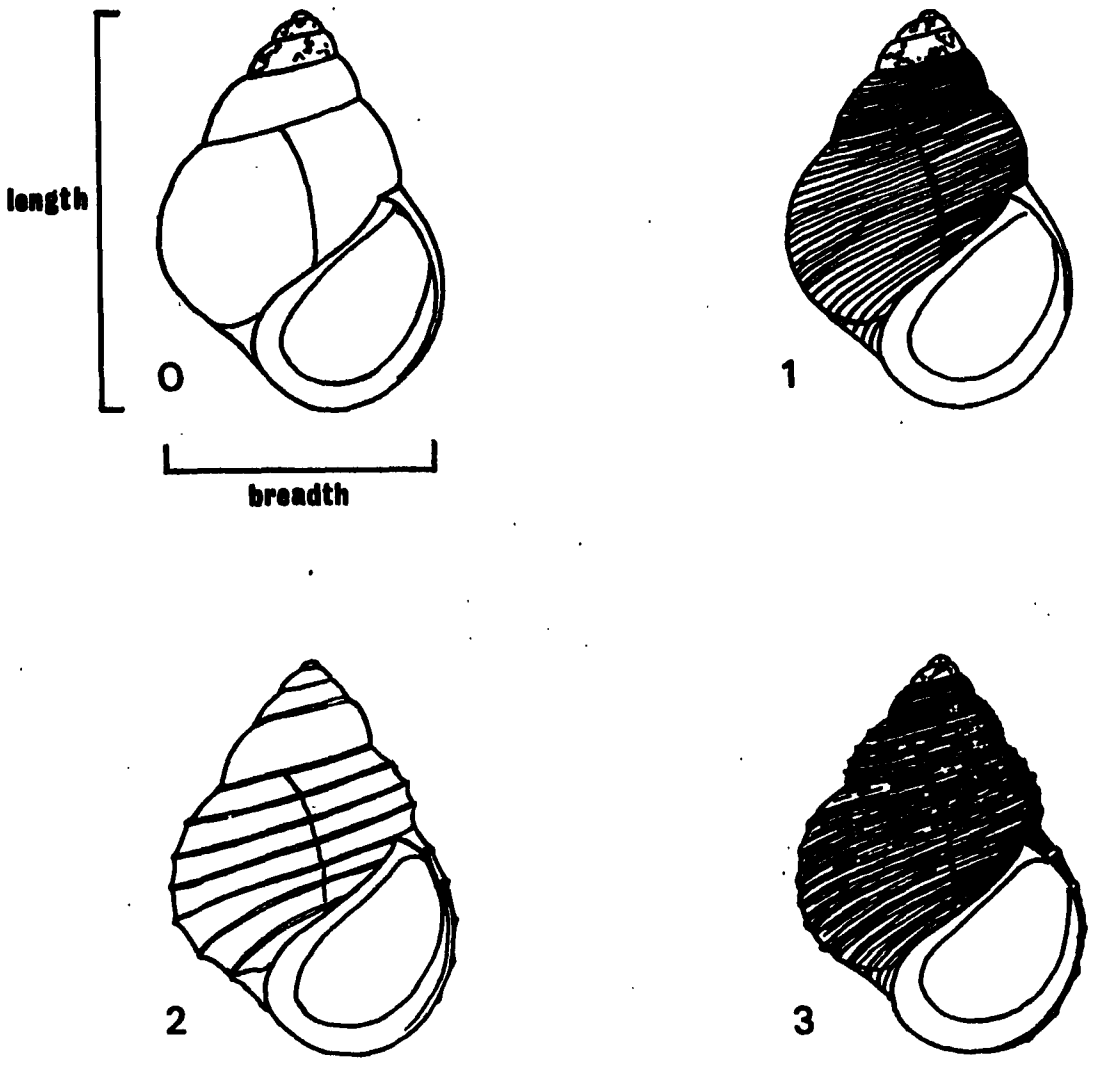


Fig. 2 Shell sculpture in L. saxatilis. The four stages in degree of development of shell sculpturing observed in Nova Scotia specimens are shown. The index numbers 0-3 are used to describe the sculpturing of individual specimens. The main shell dimensions, length and breadth, used to describe shell shape are shown.

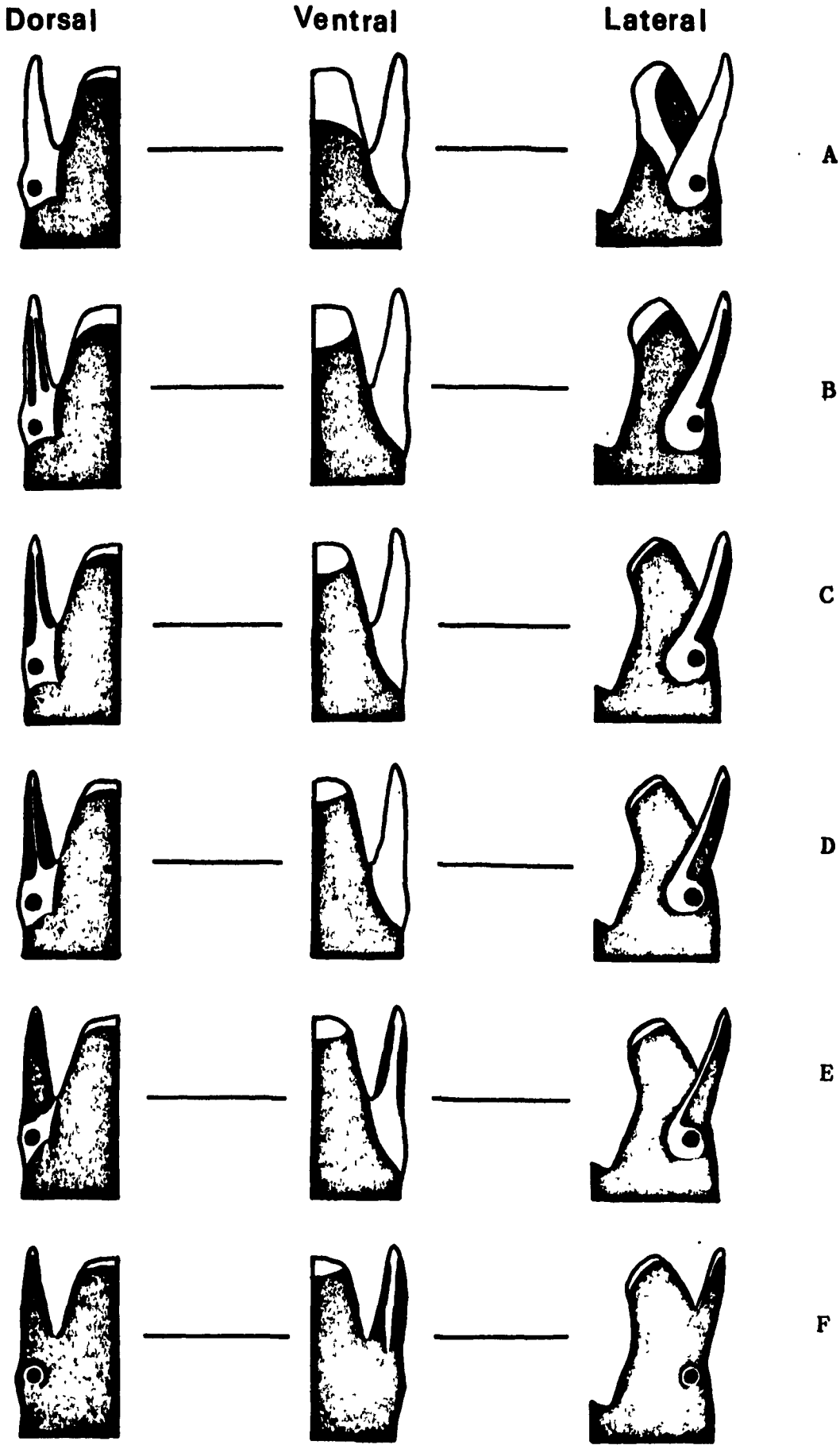


Fig.3 Pigmentation patterns on the head of L. saxatilis. The six stages shown occured throughout samples collected at nine stations in Nova Scotia. The index letters A-F are used to define the degree of pigmentation.

but these have been grouped with the closest stage illustrated. In some males the penis is pigmented as well as the head and tentacles. This system was defined for use in the present investigation before James (1968a) published a similar system for British L. saxatilis. The two systems are compared in Table IV.

(f) The number of penial glands. The number of mucus glands on the penis of each male was counted. These glands are arranged in one, two or rarely three rows.

(g) Brood pouch contents. Littorina saxatilis is ovoviviparous, and the eggs, embryos and larvae are retained during their development in a pouch-like expansion of the oviduct. The young were counted and any abnormalities such as sinistral and dentalioid shell forms, as described by Thorson (1946), were noted.

Table IV. The stages in development of pigmentation on the head and tentacles of Littorina saxatilis used by James (1968a) and the approximately equivalent stages used in the present investigation.

James (1968a) Index	Recent investigation Index
1	A
2	-
3	B
4	-
5	C
6	D
7	-
8	E
9	-
10	F
11	-

(h) Larval trematode infections. The infection of any individual snail by larval trematodes was noted. The parasites were named using the key and descriptions of James (1968b). Only specimens with a shell length greater than 3.0 mm were used in this study.

Parts of the nine samples taken for examination are now in the collection of the Nova Scotia Museum, under accession number 1968-Z-60.

RESULTS AND DISCUSSION

The nine samples of L. saxatilis collected along the Atlantic coast, in Halifax and Lunenburg Counties, Nova Scotia, were examined for anatomical characters as outlined on pages 11 to 19. Each title (a to h) will be considered separately. Examples of the specimens from these stations are shown in Figure 12. These illustrate some of the shell characters encountered in the samples.

a) Shell dimensions.

The maximum shell length and the ratio of shell breadth to shell length in each of the nine samples are shown in Table V.

The range in shell lengths is not great but at Station 1, a salt marsh, the snails are distinctly smaller than those at other stations. The maximum shell length was only 5.00 mm. The largest specimens, with a shell length of 14.00 mm were found at Station 5, a very exposed situation. The shells collected at the other stations, which were either sheltered or exposed, had maximum shell lengths of from 8.75 to 10.50 mm. The variation in maximum shell length between these stations is most probably related to environmental conditions.

Table V. The maximum shell length, average ratio of shell breadth to shell length and number of shell whorls of L. saxatilis collected at nine stations on the Atlantic coast of Nova Scotia.

Station no.	Maximum shell length (mm)	Average ratio of shell width to shell length (Range of ratios)	number of shell whorls
1	5.00	1: 1.27 (1.00 - 1.67)	4
2	8.75	1: 1.29 (1.12 - 1.48)	4 - 5
3	10.50	1: 1.37 (1.13 - 1.57)	4 - 6
4	9.00	1: 1.41 (1.18 - 1.63)	5 - 6
5	14.00	1: 1.28 (1.14 - 1.44)	4 - 5
6	10.50	1: 1.33 (1.13 - 1.71)	4 - 6
7	10.00	1: 1.44 (1.16 - 1.67)	4 - 6
8	9.25	1: 1.30 (1.11 - 1.45)	4 - 6
9	12.00	1: 1.35 (1.16 - 1.69)	4 - 6

Remane and Schlieper (1958) recorded a decrease in the maximum size attained by Buccinum undatum (L.) from marine to brackish waters, and noted that this was also true, but to lesser degree, for littorinids. Such observations would indicate that the conditions of salinity, temperature, etc., found in brackish waters either reduce longevity or stunt growth in these animals.

The values for average ratio of shell breadth to shell length show a difference in the proportion of the shells between each of the nine samples. The ratios at sheltered marine localities such as Stations 4 and 9 are larger than those from exposed locations such as Stations 2 and 5 and from the salt marsh, Station 1. That is, the shells from sheltered marine locations have relatively higher spires than do those from exposed localities and the salt marsh.

Stephenson and Stephenson (1954) used shell shape to distinguish two forms of L. saxatilis, which they called "type A" and "type B". The difference in shell shape is shown by comparing the shell breadth to shell length ratios of specimens of "type A" from Mason Cove (Station 7) and of "type B" from Peggy Point (Station 5). The "type A" has a ratio of 1: 1.44, whereas the "type B" has a ratio of 1: 1.28. The distinction of the two populations is clearly

seen in Figure 4, where the shell breadth to length ratios have been plotted against shell length. It may be seen from the illustrations of the "type B" shell in Figure 10/11 and 12, that the smaller shell breadth to length ratio results from an enlargement of the body whorl and aperture. This aperture can accommodate a larger foot and since this character would be an advantage in situations exposed to wave action, selection would increase the proportion of "type B" in the population. Becquaert (1943) has suggested that a difference in the ratio of breadth to length that he observed in L. saxatilis was associated with the sex of the individual. Females would require a larger body whorl to accommodate the brood pouch. This hypothesis was tested in the sample collected at Sandy Cove (Station 3), which was a mixture of high-spired and short-spired individuals. The ratios of shell breadth to shell length are shown in Figure 5. No difference between the dimensions of males and females can be seen, although there is a wide range of breadth to length ratios in the sample.

b) Number of shell whorls.

The results show no great variation in the number of shell whorls. The range from four to six whorls shown in Table V, is associated with the range in shell length. That is,the number of shell whorls increases with shell length.

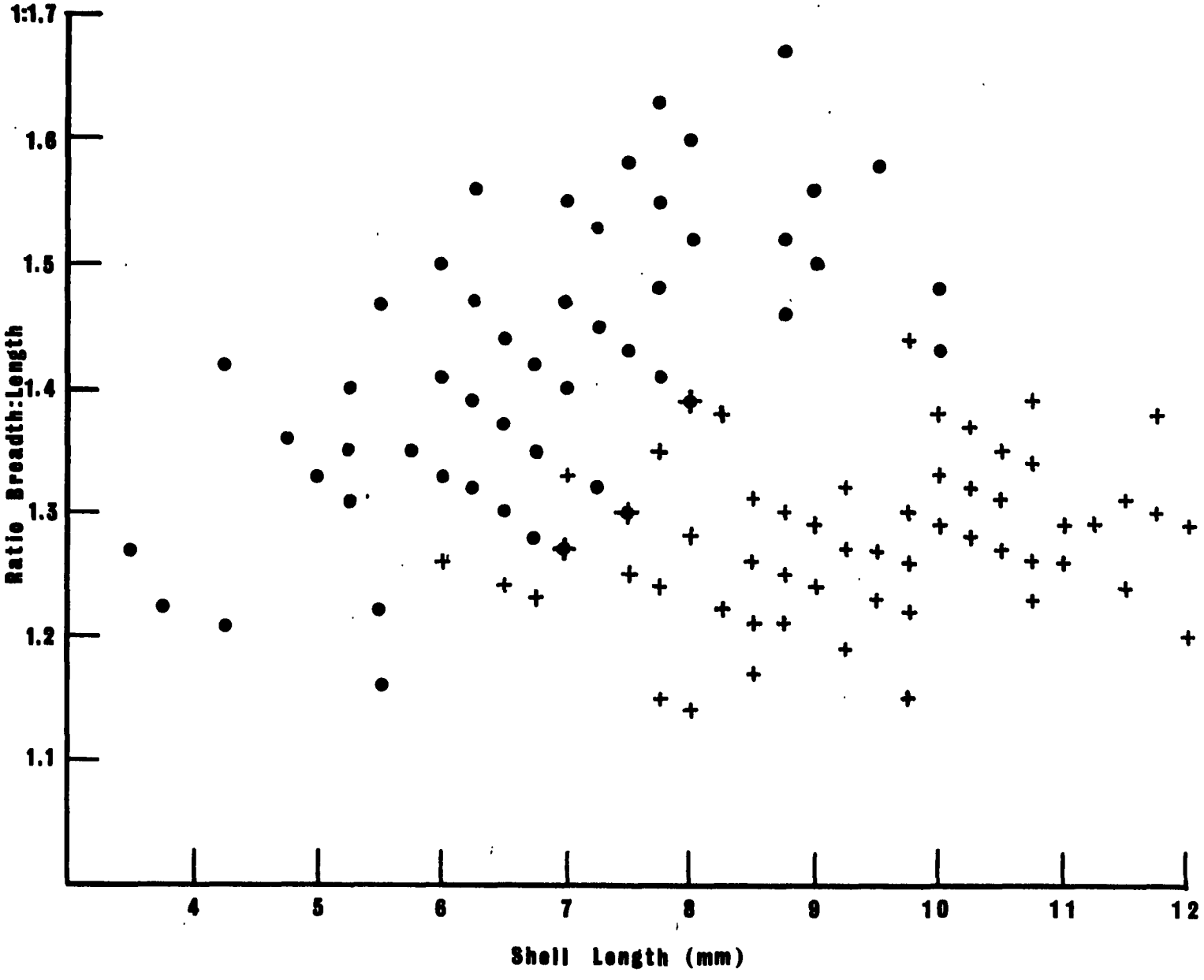


Fig. 4. The relationship between shell length and shell breadth to length ratio of L. saxatilis at two stations with different environmental conditions. Station 5, at Peggy Point, is a rocky shore exposed to wave action. Station 7, at Mason Cove, is a sheltered rocky shore. Both samples were taken in March 1968. Peggy Point data are plotted as crosses (+), Mason Cove data, as dots (•).

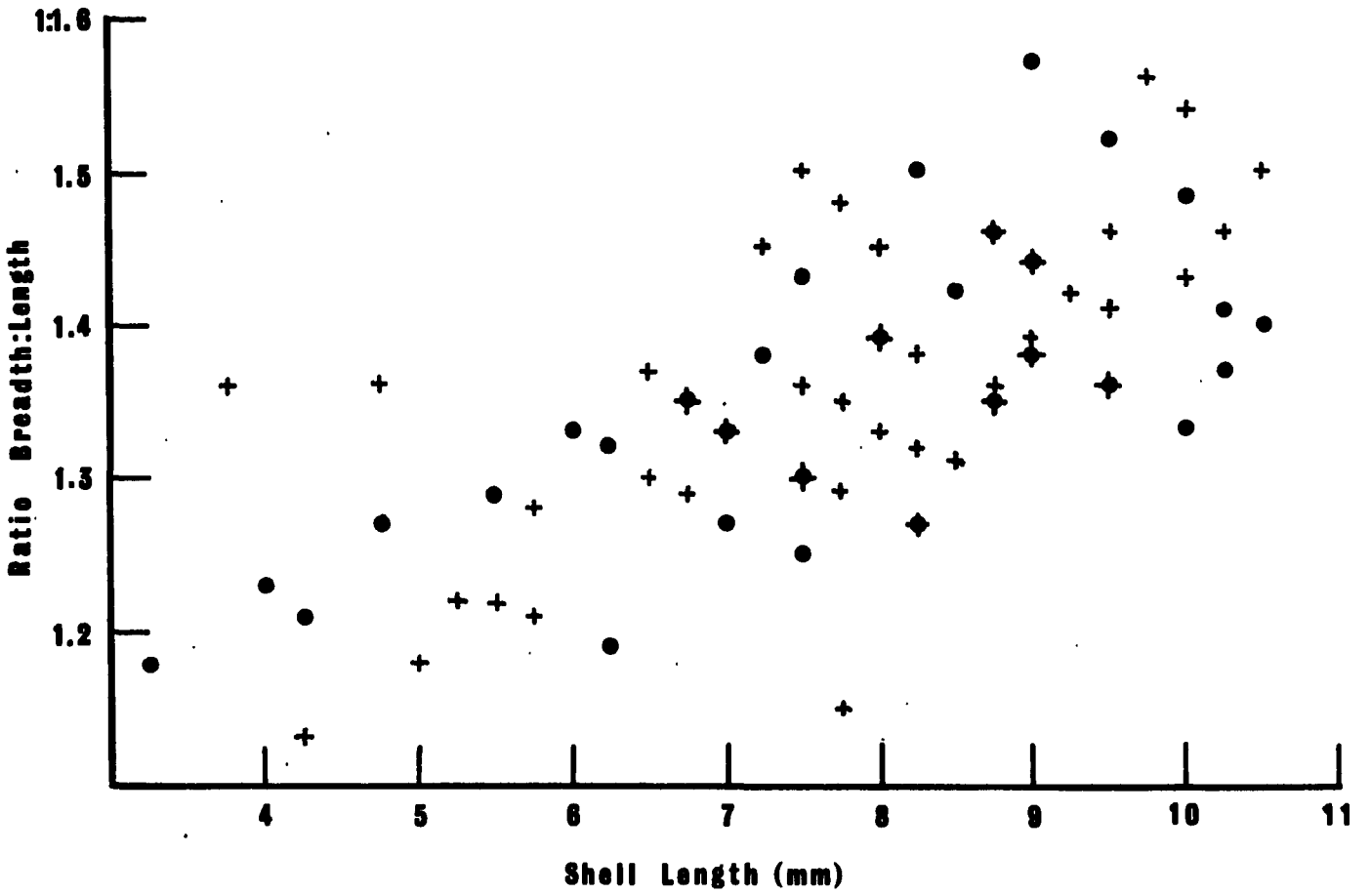


Fig. 5. The relationship between shell length and shell breadth to length ratio of male and female L. saxatilis. The values are all taken from the same sample, collected at Sandy Cove (Station 3) on 28 February 1968. Males are plotted as crosses (+), females as dots (•).

c) Shell colour.

The shell colour forms found in the nine samples are listed in Table VI, and some examples are illustrated in Figure 11. The majority of the forms distinguished could be associated with named forms which are included in Table II. A small proportion, however, are listed according to their colour because they could not be confidently associated with any of the named forms. One single example from Station 9, being white with a single brown spiral line apparently has not been previously described. (Figure 10/22). There was only little colour variation in most of the samples and in two cases this may have been a result of selection by predators. At Queensland (Station 8) and Mason Cove (Station 6) the only colour forms present were L. s. fusca, L. s. fulva and L. s. lutea all of which blend fairly well with the colour of the weathered granite. The more distinctly coloured forms would be more easily seen against this background. In direct contradiction to this situation, the greatest colour range was found at Blue Rocks (Station 9), where the snails are completely exposed and conspicuous against a dark slate background. Fischer-Piette et al (1963) found wide colour variation in some populations in Europe, both on exposed rock surfaces and in deep crevices. They attribute the wide range of colour in these populations to their isolation by

Table VI. The occurrence of various colour forms of L. saxatilis collected at nine stations on the Atlantic coast of Nova Scotia. The names forms are defined in Table II. The values are percentages of the total number of individuals in each sample.

Colour form	Station number								
	1	2	3	4	5	6	7	8	9
L. s. albida	-	12.0	0.9	10.0	-	0.9	-	-	10.5
L. s. zonaria	-	9.4	9.4	8.0	1.0	5.6	-	-	14.0
L. s. tessellata	+	25.0	-	11.0	24.8	33.6	-	-	9.5
L. s. interupta	-	-	-	2.0	-	-	-	-	18.5
L. s. fusca	-	27.0	0.9	18.0	-	24.3	78.4	-	23.5
L. s. sanguinea	-	-	-	-	-	-	-	-	1.0
L. s. aurantia	-	-	-	1.0	-	0.9	-	-	0.5
L. s. fulva	-	5.0	-	25.0	42.3	12.1	21.6	88.0	7.0
L. s. lutea	-	-	-	-	-	-	-	12.0	0.5
L. s. maculata	-	-	0.9	-	10.3	-	-	-	-
L. s. zonaria/tessellata	-	-	2.8	-	-	-	-	-	-
*L. s. zonaria/grey	-	-	-	-	-	-	-	-	0.5
Uniform grey	-	10.0	-	4.0	-	-	-	-	7.5
Uniform olive green	-	4.0	-	-	-	-	-	-	-
Red brown	-	-	-	6.0	-	-	-	-	1.0
Yellow brown	-	-	-	3.0	-	1.9	-	-	-
Fawn with a dark band	-	-	-	-	-	2.8	-	-	-
Brown with dark spiral lines	-	15.0	-	12.0	-	17.8	-	-	5.0
White with a single brown line	-	-	-	-	-	-	-	-	0.5
Corroded shells	+	-	85.1	-	11.6	-	-	-	-

* showing a distinct colour change during life

physical barriers. The mode of reproduction and development of L. saxatilis does not allow wide dispersal of the offspring and mixing of populations. In the population, the various genetic combinations are always present and they are manifested in situations where there is little selection by predators. This, however, does not explain why such selection should be more severe in one population compared with another.

The wide range of colour variation at Blue Rocks includes individuals with combinations of named forms. This may be a permanent combination with one pattern imposed upon another as in the example with L. s. zonaria and tessellata (Figure 10/28), or a distinct change of colour following a seasonal growth interruption. An example of the latter is the change from L. s. zonaria to uniform grey. Such combinations of colour were also encountered by Fischer-Piette et al (1963).

d) Shell sculpture.

Shell sculpturing ranged from completely smooth (0) to coarse ridged (3) as illustrated in Figure 2. The sample from Station 1 contained only smooth shells, but the others had various sculptural forms (Table VII). When a comparison is made between populations from extremes of environmental conditions there is an indication of some relationship

between ridged shells and exposure to wave action. The shells at Station 1 were all smooth (0), whereas at the exposed Station 5, 66% of the shells were ridged (2 and 3). It might be deduced that the shells are reinforced by the ridges and that this feature would be selected in very exposed habitats. However, a further comparison made with the shells from Station 7 does not support this. At this Station, in very sheltered conditions, 99% of the shells were ridged (2 and 3).

In the sample from Blue Rocks (Station 9) there were examples of change from ridged to smooth shell during the life of an individual. This change was always associated with a growth interruption, similar to the changes in shell colour observed in the same sample.

e) Pigmentation of the head and tentacles.

The extent of head pigmentation L. saxatilis collected at the nine sampling Stations is shown in Table VIII. The stages (A to F) are illustrated in Figure 3. In all but two cases the most commonly occurring stages were C or D, being represented by from 42.0 to 57.0% of the individuals in each sample. At Station 7, a sheltered rocky shore, 52.6% of the snails had pigmentation at stage F, and at Station 1, a salt marsh, 96.0% had pigmentation at stage E. In all samples,

Table VII. The shell sculpturing found in L. saxatilis collected at nine stations on the Atlantic coast of Nova Scotia. The extent of sculpturing is indicated by the reference numbers 0 to 3 (from no sculpturing to maximum sculpturing; see Fig. 2). The values are percentages of the total number of individuals in each sample.

Station No.	Thin Shells	Solid Shells	Occurrence of each type of sculpturing %				Shells showing change of sculpturing during life		
			0	1	2	3	1 to 0	2 to 0	3 to 0
1	+	-	100.0	-	-	-	-	-	-
2	+	-	84.0	11.0	4.0	1.0	-	-	-
3	-	+	94.4	2.8	2.8	-	-	-	-
4	+	-	-	8.0	41.0	51.0	-	-	-
5	+	-	34.0	-	57.7	8.2	-	-	-
6	+	-	61.7	2.8	15.9	17.8	-	-	-
7	+	-	1.0	-	3.1	95.9	-	-	-
8	-	+	78.0	22.0	-	-	-	-	-
9	+	-	24.5	9.5	7.5	49.5	1.5	1.0	6.5

Table VIII. The extent of head pigmentation found in L. saxatilis collected at nine stations on the Atlantic coast of Nova Scotia. The extent of pigmentation is indicated by the reference letters A to F (from minimum to maximum pigmentation, see Fig. 3). The values are percentages of the total individuals in each sample.

Extent of Pigmentation	Occurrence at each station, %								
	1	2	3	4	5	6	7	8	9
A	-	-	0.9	-	2.1	-	-	-	-
B	-	12.0	15.9	3.0	16.5	5.6	4.1	2.0	0.5
C	-	57.0	57.0	30.0	45.4	32.7	9.3	26.0	21.5
D	4.0	27.0	21.5	45.0	32.0	42.1	21.6	54.0	54.5
E	96.0	4.0	4.7	21.0	4.1	18.7	12.4	18.0	16.0
F	-	-	-	1.0	-	0.9	52.6	-	4.0
Undetermined	-	-	-	-	-	-	-	-	3.5

except that from Station 1, there was a wide variation in the extent of pigmentation.

James (1968a) found some differences in the extent of pigmentation which could be related to the different subspecies of L. saxatilis in Britain. In the nine samples taken in Nova Scotia, only those populations at Stations 1 and 7 show any marked differences from the others.

It was also noted by James (1968a) that pigmentation became darker with age. Table IX shows the occurrence of pigmentation stages B to F throughout the size range of the sample taken at Station 9. The stages C and D are best represented in the sample and occur at all intervals of shell length. Darker forms, to stage F, occur less commonly in individuals of intermediate shell length, and the lightest form B, occurs only in one of the largest individuals. This result does not support the view that pigmentation becomes darker with age, but would apparently support the idea that the extent of pigmentation on the head and tentacles was characteristic for subspecies or forms of L. saxatilis.

f) The number of penial glands.

In the samples of L. saxatilis taken in Nova Scotia, males were found to have one, two or rarely three rows of

Table IX. The occurrence of the stages B to F in extent of head pigmentation through the size range of a sample of L. saxatilis collected at Station 9 on 3rd October 1967. These stages are illustrated in Fig. 3.

Shell length 0.5 mm intervals	n	number in each size group				
		B	C	D	E	F
1.75	1	-	1	-	-	-
2.25	11	-	4	7	-	-
2.75	13	-	7	6	-	-
3.25	23	-	7	15	1	-
3.75	9	-	4	5	-	-
4.25	13	-	3	7	2	1
4.75	10	-	2	3	3	2
5.25	16	-	3	11	2	-
5.75	15	-	5	6	3	1
6.25	17	-	4	10	3	-
6.75	18	-	2	11	4	1
7.25	10	-	3	4	3	-
7.75	11	-	3	7	-	1
8.25	8	-	2	4	2	-
8.75	13	-	5	6	2	-
9.25	12	-	3	6	1	2
9.75	13	-	3	8	2	-
10.25	10	-	2	8	-	-
10.75	8	-	1	5	2	-
11.25	7	1	1	5	-	-
11.75	1	-	-	1	-	-
12.25	4	-	-	4	-	-

penial glands. These results are given in Table X. Examples from specimens with glands in a short, single row (from Station 1), a long, single row (from Station 7) and a double row (from Station 5) are shown in Fig. 6.

At Stations 1, 2, 6, 8 and 9 all individuals had glands in a single row, the number varying from 0 to 18. The mean number of penial glands for all males in each sample ranged from 5 to 11, these extremes being for Stations 1 and 8 respectively.

At the other Stations (3, 4, 5 and 7) there was a mixture of individuals with single or multiple rows of penial glands. At Stations 4 and 7 there were only one and two examples respectively, with a double row of glands. At Stations 3 and 5 about half of the males in each sample had glands in double or triple rows. There were between 5 and 19 glands in the first row and 1 to 18 glands in the second row. The single example with three rows of glands, had four glands in the third row.

Of the Stations sampled, 3 and 5 were the most exposed to wave action, and there may be an association between the L. saxatilis with multiple rows of penial glands and such habitats. The other distinct penial gland arrangement, a short, single row, found at Station 1, may also be associated with a form of L. saxatilis living in salt marshes. James (1968a) has shown that in L.s. rudis, the number of penial glands is

Table X. The penial gland arrangements in L. saxatilis collected at nine stations on the Atlantic coast of Nova Scotia. The mucus glands occur on the penis in either a single or multiple rows.

	Station number								
	1	2	3	4	5	6	7	8	9
With a single row of glands. (n)	26	33	24	38	21	43	42	27	87
$\bar{x}$ number of glands	5	8	8	11	11	10	13	11	9
range of numbers	4-9	0-17	0-15	0-17	0-20	0-15	4-19	6-18	2-17
With a double or triple row of glands (n)	-	-	25	1	18	-	2	-	-
row No.1 $\bar{x}$ number	-	-	11	11	12	-	8	-	-
range of numbers	-	-	5-19	11	5-19	-	7-9	-	-
row No.2 $\bar{x}$ number	-	-	4	2	4	-	6	-	-
range of numbers	-	-	1-8	2	1-8	-	5-6	-	-
row No.3 $\bar{x}$ number	-	-	4	-	-	-	-	-	-
range of numbers	-	-	4	-	-	-	-	-	-

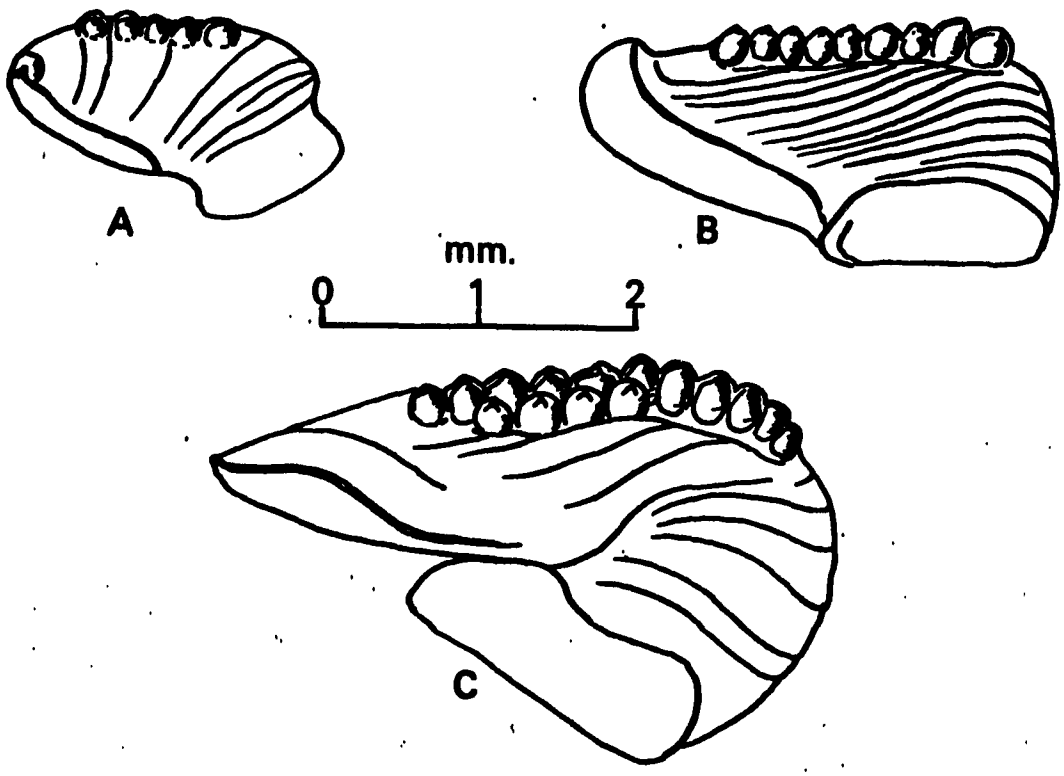


Fig. 6. The form of the penis in selected examples of L. saxatilis from three localities in Nova Scotia. A. A specimen from Lawrencetown (station 1) which has a single row of five glands. B. A specimen from Mason Cove (station 7) which has a single row of nine glands. C. A specimen from Peggy Point (station 5) which has a double row of glands; eleven in the long row and four in the short row.

reduced on sheltered shores as compared to exposed shores.

g) Brood pouch contents.

Although females carrying embryonic snails or brood were found in all nine samples taken, examinations of the brood were only made at Stations 1, 3, 5, 6, 7 and 9.

The stages in the development of eggs and embryos of L. saxatilis were studied by Berry (1961). The periodic release of batches of eggs into the brood pouch and their retention during development results in there being a range of developmental stages within any individual female. The number of embryos present varies with the season of the year. The nine samples from Nova Scotia were not all taken at the same time of the year, but broods were always found.

All stages of development were observed, from eggs to juveniles about to be released. Various deformities were detected, including sinistral shell coiling and the open coiling (dentalioid) and plane spiral coiling (planorbioid) forms described by Thorson (1946). None of the abnormal forms was common however. Some examples are illustrated in Fig.7. The shell breadth of juveniles at the time of release from the parents brood pouch was from 0.5 mm to 0.75 mm.

The mean number of brood occurring at 0.5 mm intervals of shell length of females at each station is given in Table XI. For all the stations there was an overall increase in

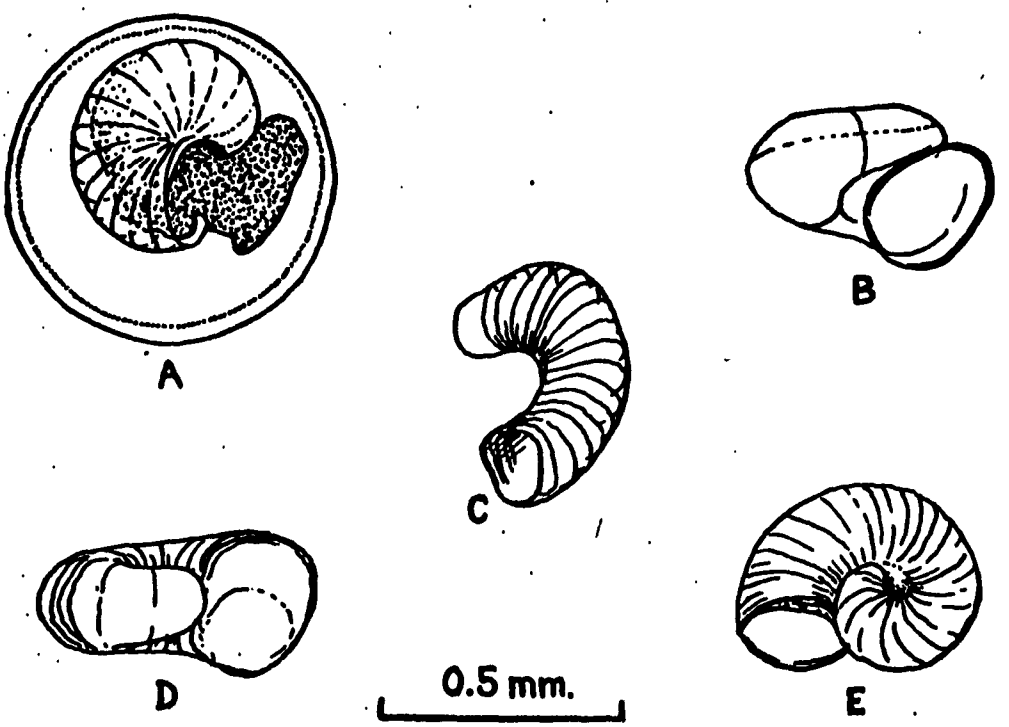


Fig. 7. Examples of juvenile L. saxatilis taken from the brood pouches of selected females collected from stations along the Atlantic coast of Nova Scotia. A. An embryo developing inside an egg capsule. B. A juvenile shell at the time of hatching. C. An embryonic shell with open coiling (named dentalioid by Thorson, 1946). D. An embryonic shell having a plane spiral (named planorbioid by Thorson, 1946). E. An embryonic shell having sinistral coiling.

Table XI. The mean number of embryonic snails in brood pouches of female L. saxatilis at six stations on the Atlantic coast of Nova Scotia. The mean number is given for all snails in each group at 0.5 mm intervals of shell length.

Shell length 0.5 mm intervals	station no.					
	1	3	5	6	7	9
3.50 - 3.99	11.3	-	-	3.0	-	-
4.00 - 4.49	12.1	-	-	20.5	-	-
4.50 - 4.99	13.5	-	-	7.0	-	26.5
5.00 - 5.49	25.5	-	-	23.3	-	23.2
5.50 - 5.99	-	-	-	27.7	9.0	48.4
6.00 - 6.49	-	22.0	-	37.2	13.7	35.3
6.50 - 6.99	-	26.0	-	31.6	4.0	74.7
7.00 - 7.49	-	12.3	-	79.5	26.0	41.0
7.50 - 7.99	-	39.3	-	-	21.0	4.0
8.00 - 8.49	-	25.8	23.0	113.0	34.0	63.0
8.50 - 8.99	-	33.0	42.8	79.0	60.5	49.7
9.00 - 9.49	-	31.6	55.0	52.0	48.5	35.3
9.50 - 9.99	-	22.0	46.6	-	7.0	6.0
10.00 - 10.49	-	29.3	60.1	-	-	144.3
10.50 - 10.99	-	18.0	61.7	-	-	3.0
11.00 - 11.49	-	-	76.0	-	-	78.0
11.50 - 11.99	-	-	102.7	-	-	-
12.00 - 12.49	-	-	206.0	-	-	45.0
12.50 - 12.99	-	-	55.0	-	-	-
13.00 - 13.49	-	-	-	-	-	-
13.50 - 13.99	-	-	-	-	-	-
14.00 - 14.49	-	-	179.0	-	-	-

the number of brood with increase in size (and age). The range extends from a minimum of three juveniles in adults of 3.50 - 3.99 mm shell length, to 206 in adults of 12.00 - 12.49 mm shell length. In Fig. 8 the mean numbers of brood have been plotted against shell length for the samples from Stations 1, 5 and 7. A relationship between the numbers of brood and the size of the female is clearly implied.

h) Larval trematode infections.

The larvae of seven species of digenetic trematodes were found in L. saxatilis at the nine stations sampled. These species were Parvatrema homeotecnum James, Himasthla littorinae Stunkard, Microphallus pygmaeus (Levinsen), Microphallus similis (Jägerskiöld), cercaria roscovita Stunkard, Podocotyle atomon (Rudolphi) and Cryptocotyle lingua (Creplin). All are previously known from L. saxatilis at other localities.

One or more of these species was found at Stations 1, 2, 5, 6, 7 and 9. No parasites were found at Stations 3, 4 and 8. The results are summarised in Table XII. The greatest diversity of parasite fauna occurred at the most sheltered localities, Stations 1, 7 and 9. The high infection level of 39.2% at Station 9 was due to the presence of large numbers of gulls attracted by discarded wastes of local fish processors.

Of the seven trematode species, three occurred at only one of the stations. Parvatrema homeotecnum occurred at Station

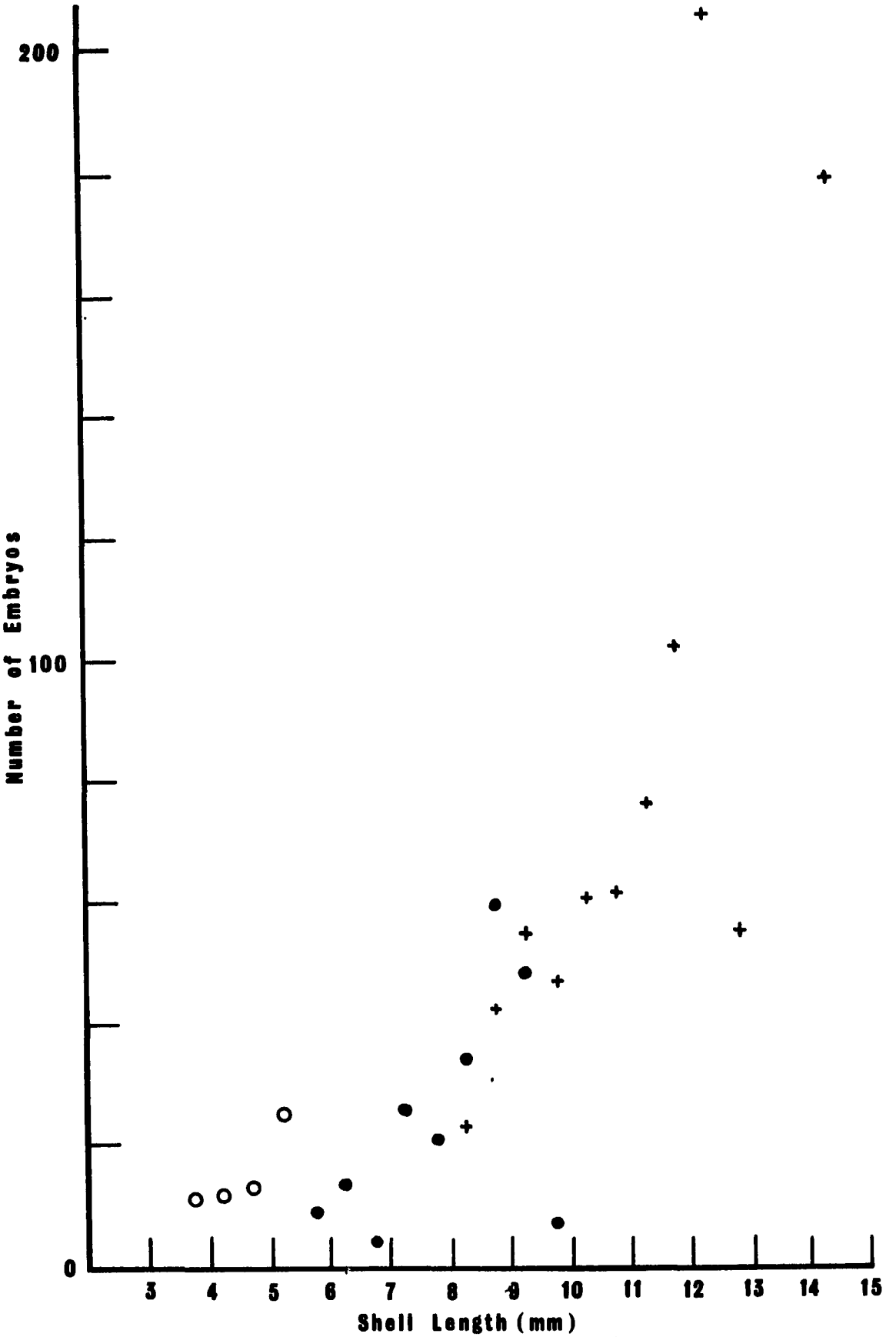


Fig. 8. The mean number of embryonic snails in brood pouches of female L. saxatilis at three Stations on the Atlantic coast of Nova Scotia. The mean number is given for all snails in each group at 0.5 mm intervals of shell length. Lawrencetown Lake (Station 1) data are plotted as circles (o), Peggy Point (Station 5) data as crosses(+) and Mason Cove (Station 7) data as dots (•).

Table XII. The occurrence of larvae of seven species of digenetic trematodes in L. saxatilis collected at nine stations along the Atlantic coast of Nova Scotia. The number of L. saxatilis infected with each species is given. Some specimens were double inflected with two species of parasite.

	Stations								
	1	2	3	4	5	6	7	8	9
Total snails in sample	50	100	107	100	97	107	97	50	250
Parvatrema homeotecnum	2	-	-	-	-	-	-	-	-
Himasthla littorinae	-	-	-	-	-	-	-	-	1
Microphallus pygmaeus	1	3	-	-	-	-	1	-	3
Microphallus similis	-	-	-	-	1	-	2	-	22
cercaria roscovita	-	-	-	-	-	4	2	-	-
Podocotyle atomon	2	-	-	-	-	-	1	-	1
Cryptocotyle lingua	-	-	-	-	-	-	-	-	63
double infections	-	-	-	-	-	-	1	-	7
Total snails infected	5	3	-	-	1	4	7	-	98
% infection (all species)	10.0	3.0	-	-	1.0	3.7	7.2	-	39.2

1, Himasthla littorinae and Cryptocolyle lingua at Station 9. The other four species were found in L. saxatilis from a variety of shores.

INTRASPECIFIC CLASSIFICATION OF L. SAXATILIS IN NOVA SCOTIA

Many of the descriptions of the subspecies and varieties of L. saxatilis in Europe have been based upon characters of the shell and habitats. The recent work of James (1968 a and b) has used many other characters for forms occurring in Britain, and this has been a most useful guide in the present study.

The examination of the nine samples for particular characters reveals the presence of three distinct forms of L. saxatilis in the Lunenburg-Halifax counties area of Nova Scotia. The size and shape of the shell, as used by Stephenson and Stephenson (1954) to distinguish their "Types A and B", were the most useful distinguishing characters. The distinction was made clearer, however, when shell proportions were related to the pigmentation of head and tentacles, the number of penial glands and the shell sculpturing. These features have been combined in Fig. 9 for Stations 1, 5 and 7. Stations 5 and 7 are the recorded localities for "Types A and B". It will be seen that the three populations can be clearly distinguished.

The possible synonyms, and the characters of the three forms of L. saxatilis may be summarized as follows:-

Form A. Synonyms: Type A (Stephenson and Stephenson, 1954), L. s. tenebrosa tenebrosa (Montagu, 1803). The shells

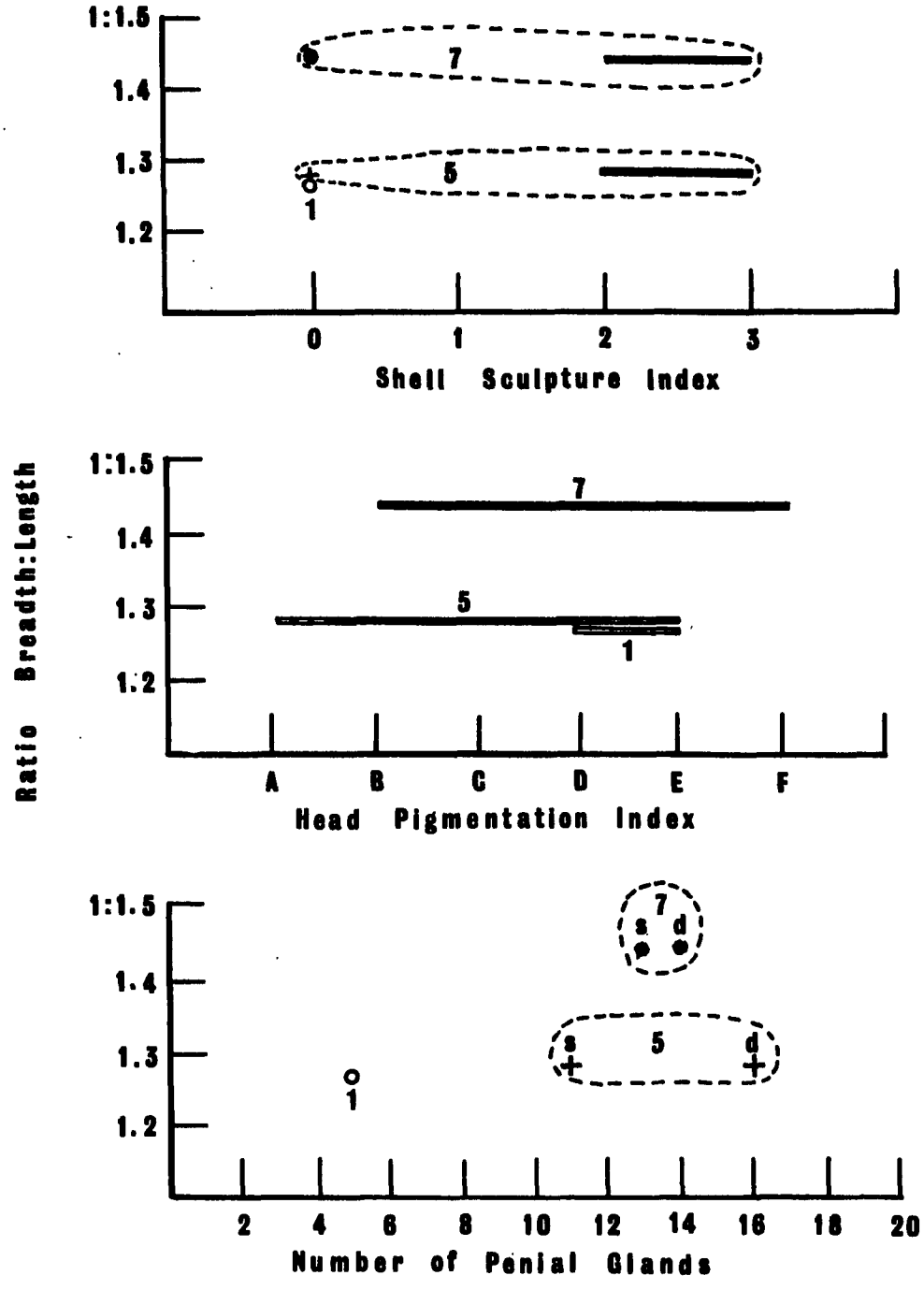


Fig. 9. Shell sculpturing, head pigmentation and number of penial glands shown in relation to shell breadth to length ratios for samples from Stations 1, 5 and 7. The mean numbers of penial glands in specimens with a single row(s) and those with a double row (d) are shown separately.

were thin and either smooth or ridged with maximum length of 14.0 mm and breadth to length ratio of 1: 1.44. The head pigmentation was mostly of stages D, E and F and males had a mean number of nine penial glands arranged in a single row. This form was abundant on fairly exposed to sheltered rocky shores.

Form B. Synonyms: Type B (Stephenson and Stephenson, 1954), L. s. tenebrosa similis (Jeffreys, 1865). The shells were generally thin and smooth or ridged. The maximum recorded shell length was 14.0 mm and shell breadth to length ratio was 1: 1.28. The head pigmentation was mainly of stages B, C and D. Males had penial glands arranged in two rows with 12 glands in the long row and 4 glands in the short row. The form occurred on very exposed rocky shores.

Form C. Synonyms: L. s. neglecta (Bean, 1844). The shells were thin and smooth, with maximum shell length of 5.0 mm and shell breadth to length ratio of 1: 1.27. The head pigmentation was mostly stage E and males had a mean number of five penial glands arranged in a single row. This form was extremely abundant in salt marshes and eel grass ponds.

From this preliminary examination and from the descriptions given by Becquaert (1943), L. saxatilis does

not appear to be as variable in North America as it is in Europe. There is no geographic continuity between the European and North American populations but L. s. grönlandica is known from both continents and L. s. gronlandica, L. s. rudis and L. s. tenebrosa are known from Iceland (Thorson, 1941). In Iceland, L. s. tenebrosa is recorded as a brackish water form which intergrades with the other two subspecies. L. s. tenebrosa is the name commonly given to forms living in eel grass beds on both sides of the Atlantic, particularly in Denmark (Thorson, 1946 and Muus, 1967) and New England (Dexter, 1947 and Hunninen and Cable, 1943). James (1968a) does not describe L. s. tenebrosa from this habitat in Britain but does record L. s. neglecta from salt marshes. The latter is the most common form in salt marshes and eel grass beds in Nova Scotia.

In Nova Scotia there seems to be a close relationship between the forms described. Certainly there is mixing of forms A and B at some localities (e.g Station 3) and possibly also between forms A and C in sheltered situations (e.g. Station 9). James (1968) has suggested lines of evolution of the subspecies and varieties of L. saxatilis in Britain. He indicates a gradation between L. s. tenebrosa similis and L. s. tenebrosa tenebrosa with different grades of exposure to wave action. Also, a main evolutionary line from L. s. tenebrosa tenebrosa to L. s. neglecta is indicated. Both of these ideas are supported by the forms and habitats of L. saxatilis in Nova Scotia.

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Fig. 10. Examples of the shells of L. saxatilis collected at nine stations along the Atlantic coast of Nova Scotia, from May 1967 to August 1968. These examples illustrate the range of shell proportions, sculpturing and colour encountered in the collections. Enlargement is 2.6 times life size.

1 and 2. Station 1, Lawrencetown Lake, Halifax Co. Form C.

3 and 4. Station 2, Black Rock, Point Pleasant Park, Halifax. Both are form A. Specimen 3 is L. s. albida.

5, 6 and 7. Station 3, Sandy Cove, Halifax Co. Specimens 5 and 6 are form B and 7 is form A.

8, 9 and 10. Station 4, Prospect, Halifax Co. All are form A. Specimen 9 is L. s. zonaria.

11 and 12. Station 5, Peggy Point, Halifax Co. Both are form B.

13 and 14. Station 6, Indian Harbour, Halifax Co. Both are form A.

15 and 16. Station 7, Mason Cove, Halifax Co. Both are form A.

17. Station 8, Queensland, Halifax Co.

18 to 29. Station 9, Blue Rocks, Lunenburg Co. All are form A. 18 is L. s. albida, 19 and 20 are L. s. fulva, 21 is a pale L. s. zonaria, 22 is unnamed (white with a thin brown line), 23 is L. s. interupta, 24 is L. s. maculata, 25 is L. s. tessellata, 26 and 27 are L. s. zonaria, 28 is a combination of L. s. zonaria and tessellata, and 29 is L. s. fusca.


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Appendix III

Digenetic trematode larvae from the northern rough periwinkle, Littorina saxatilis (Olivi) in Nova Scotia.

INTRODUCTION

The periwinkles, Littorinidae, which are conspicuous components of the marine intertidal fauna in many parts of the world, are commonly the hosts of larval digenetic trematodes. Lebour (1911) and Fretter and Graham (1962) discussed some of these host/parasite associations and listed the species of trematodes found in British Littorinidae. Stunkard (1932) described the parasite species from the Roscoff region of France. Recently, James (1960, 1964 and 1968d) studied the larval Digenea of the British Littorinidae, particularly Littorina saxatilis (Olivi). However, there have been no similar studies of these parasites in the Littorinidae of the Atlantic coast of Canada. Records and descriptions of species occurring in New England were given by Stunkard (1930, 1966), Hunninen and Cable (1943) and Sinderman and Farrin (1962). Lambert and Farley (1968) and Platt (1968) gave some Nova Scotia localities for Littorina littorea (L.) infected with Cryptocotyle lingua (Creplin).

Seven species of parasite were identified in the present study. Since the extent of the distribution of these parasites is not well known, details of their occurrence in Nova Scotia were recorded. Some incidental records of infections of Cryptocotyle lingua in Littorina littorea and Littorina obtusata (L.), syn: L. littoralis (L.), are also given. The relationships between the European and North American digenean parasites of L. saxatilis are discussed.

MATERIALS AND METHODS

Samples of Littorina saxatilis were collected from 23 stations along the Bay of Fundy and Atlantic shores of Nova Scotia during the period October, 1965 to August, 1968. These stations are listed in Table I. At each station one sample was taken. The size of these samples varied from 37 to 270 snails, depending upon the sampling time available and the abundance of the snail.

Generally these snails were examined while alive; others were preserved in 10 per cent formalin in seawater. The tissues of the Littorina were searched for the germinal sacs, cercariae and metacercariae of the parasites. The parasites were removed from the snail and examined while under minimum pressure of a No. 1 cover glass. 5 per cent Neutral Red in seawater was used as a vital stain. Identifications of parasites were made using the key published by James (1968d).

The systematic treatment and nomenclature used in this paper are those used by Holliman (1961) and James (1968c and 1969), based upon the scheme of LaRue (1957).

Table 1. Stations along the Atlantic and Bay of Fundy shores of Nova Scotia at which samples of L. saxatilis were collected and examined for digenetic trematode larvae. The samples shown for Stations 1 and 13 were taken as part of more detailed studies of L. saxatilis at these localities. The abbreviations used in the locality names are for counties as follows: Hfx.; Halifax Co., Lun.; Lunenburg Co., Yar.; Yarmouth Co., Dig.; Digby Co., King.; Kings Co., and Cumb.; Cumberland Co.

Station No.	Date	Locality	Coordinates	Habitat
1	3 May 1967	Lawrencetown, Hfx.	44°39'N. 63°21'W.	Sheltered lake
2	29 Sept. 1966	Lawrencetown, Hfx.	44°38'N. 63°21'W.	Exposed boulders
3	12 June 1966	MacNabs Is., Hfx.	44°37'N. 63°32'W.	Boulders
4	12 Aug. 1968	Point Pleasant, Hfx.	44°37'N. 63°34'W.	Boulders
5	28 May 1968	Purcell's Cove, Hfx.	44°37'N. 63°34'W.	Sheltered boulders
6	1 June 1966	Ketch Hbr., Hfx.	44°21'N. 63°37'W.	Sheltered boulders
7	28 Feb. 1968	Sandy Cove, Hfx.	44°27'N. 63°33'W.	Exposed rocks
8	29 March 1968	Prospect, Hfx.	44°27'N. 63°47'W.	Sheltered boulders
9	29 March 1968	Peggy Point, Hfx.	44°29'N. 63°55'W.	Exposed rocks
10	29 March 1968	Indian Hbr., Hfx.	44°31'N. 63°56'W.	Sheltered rocks
11	28 May 1968	Mason Cove, Hfx.	44°41'N. 63°54'W.	Sheltered boulders
12	29 Nov. 1967	Queensland, Hfx.	44°38'N. 64° 2'W.	Exposed boulders
13	3 Oct. 1967	Blue Rocks, Lun.	44°22'N. 64°14'W.	Sheltered rocks
14	10 May 1967	Blue Rocks, Lun.	44°22'N. 64°16'W.	Sheltered pool
15	7 May 1966	Tusket, Yar.	43°43'N. 65° 4'W.	Sheltered saltmarsh
16	7 May 1966	Tusket, Yar.	43°50'N. 65°56'W.	Sheltered boulders
17	23 July 1966	Waterford, Digby	44°34'N. 65°57'W.	Bound Shingle
18	22 July 1966	Tommy Beach, Dig.	44°27'N. 66°10'W.	Exposed rocks
19	21 July 1966	Gulliver Cove, Dig.	44°36'N. 66°55'W.	Exposed rocks
20	23 July 1966	Gulliver Cove, Dig.	44°36'N. 66°55'W.	Boat slipway
21	24 July 1966	Digby Hbr., Dig.	44°37'N. 65°46'W.	Sheltered wharf
22	20 March 1966	Scot's Bay, King.	45°18'N. 64°24'W.	Exposed wharf
23	6 Aug. 1966	Cap D'or,Cumb.	45°17'N. 64°47'W.	Exposed rocks

RESULTS AND DISCUSSION

The species and numbers of digenetic trematode larvae found in 23 samples of Littorina saxatilis are listed in Tables IIa and IIb. There was a wide variation in the results from different stations. At five of the stations no parasites were found; at Station 13, 91 out of 250 snails were infected.

The individual species recorded are as follows:

Order Strigeatoidea LaRue, 1957.

Family Gymnophallidae Morozov, 1955.

Parvatrema homeotecnum James, 1964.

Parvatrema homeotecnum has furcocercous cercariae which develop in germinal sacs in the digestive gland of L. saxatilis. These cercariae develop directly to the metacercariae and there is no free-swimming larval stage. (James, 1964).

This species was only found at Station 1, it was present in two of the 50 snails examined. It has not been previously recorded from North America. James (1964) states that the definitive host in Britain is the oyster catcher, Hematopus ostralegus occidentalis Neumann, but this bird does not occur in Nova Scotia. Of the birds observed at Station 1 it is possible that a saltmarsh species such as the willet, Catoptrophorus semipalmatus semipalmatus (Gmelin), or spotted sandpiper, Actitis macularia (Linnaeus), is the definitive

Table IIa. The number of infections by seven species of digenetic trematodes of *L. saxatilis* in samples taken along the Atlantic and Bay of Fundy shores of Nova Scotia. Stations 1 to 12 are in Halifax County.

	Stations											
	1	2	3	4	5	6	7	8	9	10	11	12
Parvatrema homeotecnum	2	-	-	-	-	-	-	-	-	-	-	-
Himasthla littorinae	-	1	-	-	-	-	-	-	-	-	-	-
Microphallus pygmaeus	1	-	-	3	-	-	-	-	-	-	1	-
Microphallus similis	-	2	1	-	-	-	-	-	1	-	2	-
cercaria roscovita	-	-	-	-	-	-	-	-	-	4	2	-
Podoctyle atomon	2	-	2	-	-	2	-	-	-	-	1	-
Cryptocotyle lingua	-	2	-	-	-	-	-	-	-	-	-	-
Total number for seven species	5	5	3	3	0	2	0	0	0	4	6*	0
Number of *L. saxatilis* examined	50	40	50	100	270	80	107	100	97	107	97	50

* one case of infection of a single snail with more than one parasite species has not been included here.

Table IIb. The number of infections by seven species of digenetic trematodes of *L. saxatilis* in samples taken along the Atlantic and Bay of Fundy shores of Nova Scotia. Stations 13 to 23 are in Lunenburg to Cumberland Counties.

	Stations										
	13	14	15	16	17	18	19	20	21	22	23
Parvatrema homeotecnum	-	-	-	-	-	-	-	-	-	-	-
Himasthla littorinae	1	-	-	-	-	-	-	-	-	-	-
Microphallus pygmaeus	3	-	1	1	-	5	2	6	1	-	18
Microphallus similis	22	3	-	-	-	-	-	1	3	-	1
cercaria roscovita	-	2	-	-	-	-	2	-	-	-	-
Podocotyle atomon	1	-	-	1	-	-	-	-	-	-	-
Cryptocotyle lingua	64	2	-	2	-	-	-	-	1	-	-
Total number for seven species	91*	7	1	4	0	5	4	7	5	0	19
Number of *L. saxatilis* examined	250	50	90	63	50	50	50	125	100	37	109

* seven cases of infections of single snails by more than one parasite species have not been included here.

host. The habitat of the host L. saxatilis at Station 1 is a sheltered brackish lake and eel-grass bed; James (1968c) recorded P. homeotecnum in Britain only from L. saxatilis in the supralittoral fringe of exposed rocky shores.

Order Echinostomida LaRue, 1957.

Family Echinostomatidae Looss, 1902.

Himasthla littorinae Stunkard, 1966.

Himasthla littorinae has echinostome cercariae developing in rediae in the hemal sinuses of L. saxatilis and L. obtusata. The cercariae encyst in the bivalves, Mya arenaria (L.) and Mytilus edulis L., and the life cycle is completed in the herring gull, Larus argentatus Pontoppidan. (Stunkard, 1966).

Single infections of L. saxatilis by H. littorinae were found at Stations 2 and 13.

Order Plagiorchida LaRue, 1957.

Family Microphallidae Travassos, 1921.

Microphallus pygmaeus (Levinsen, 1881).

Microphallus pygmaeus is a parasite of both L. saxatilis and L. obtusata. The cercariae develop in thin-walled sporocysts and the metacercariae remain within the snail host. These metacercariae are typically observed in a 'rolled-up' attitude in the sporocyst. There is no free living stage. (Lebour, 1911 and James, 1968b).

M. pygmaeus is a common parasite of L. saxatilis in

Nova Scotia. It was recorded at 11 of the collecting stations. The habitats ranged from exposed rocks, at Stations 18, 19 and 23, to a sheltered marsh and a pool at Stations 1 and 15 respectively.

James (1968b) found that M. pygmaeus occurred in two size forms in Britain, depending upon the species of the definitive host and whether adult or juvenile snails were infected. The average unrolled length of the metacercariae collected in Nova Scotia was 280 μ (200-330 μ), smaller than the small form of 380 μ average length, found in Britain. However, the only definitive host found commonly in Nova Scotia is the herring gull, L. argentatus, which James associated with the large (460 μ average length) form of the parasite. The rock or water pipit, Anthus spinoletta (L.), which is the definitive host of the small form of the parasite in Britain, is only a transient in Nova Scotia. (Tufts, 1961).

M. pygmaeus has also been reported as a parasite of Littorina scutulata Gould on the Pacific coast of Canada (Ching, 1962).

Microphallus similis (Jagerskiold, 1900)

(Synonyms: Cercaria ubiquita Lebour, 1907; Cercaria ubiquitoides Stunkard, 1932 and Spelotrema excellens Nicoll, 1907).

Microphallus similis has monostome xiphidocercariae which develop in sporocysts in the digestive gland of

L. littorea, L. saxatilis and L. obtusata. When mature the cercariae are shed and encyst in shore crabs such as Carcinas maenas L., which act as the second intermediate host. The definitive host is the herring gull, L. argentatus. (Stunkard, 1957).

This parasite is common in L. saxatilis in Nova Scotia. It was recorded at eight of the 23 stations. At Station 13 L. littorea and L. obtusata were examined as well as L. saxatilis. Although M. similis was common in L. saxatilis (22 of the 91 snails examined were infected), it was not found in the other two species.

Family unknown.

Cercaria roscovita Stunkard, 1932.

Cercaria roscovita is a plagiorchid, distome xiphidiocercaria which develops in sporocysts in the hemal spaces of the digestive gland of L. saxatilis. The cercariae are shed when mature and encyst in Littorina spp., or in Carcinas maenas. The definitive host is unknown.

This parasite was not common in Nova Scotia. It occurred at four of the 23 stations. Three of these were sheltered habitats. Since no detailed examination was made of the internal structure of the parasite, it was not always possible to make a clear distinction between c. roscovita and cercaria parvicaudata Stunkard and Shaw, 1931. The latter species occurs mainly in L. littorea, but is also known from L. saxatilis (Stunkard and Shaw, 1931).

Family Opecoelidae Ozaki, 1925.

Podocotyle atomon (Rudolphi, 1909).

Podocotyle atomon has cotylomicrocercous cercariae which develop in elongated sporocysts in the hemal spaces of the digestive gland of L. saxatilis. When mature, the cercariae are shed and encyst in an amphipod, which acts as the second intermediate host. The definitive host may be one of several species of marine fish, including the eel, Anguilla rostrata (LeSueur), and the four-spined stickleback, Apeltes quadracus (Mitchill). (Hunninen and Cable, 1943).

Podocotyle atomon occurred at six stations, generally in sheltered localities.

Order Opisthorchiida LaRue, 1957.

Family Heterophyidae Odhner, 1914.

Cryptocotyle lingua (Creplin, 1825).

(Synonym: cercaria lophocerca Lebour, 1911).

Cryptocotyle lingua is a common parasite of L. littorea, with pleurolophocercous cercariae developing in rediae in the hemal spaces of the hosts' gonads and digestive glands. Mature cercariae are shed into the water where they swim actively. Encystment takes place in the skin of pelagic fish such as the herring, Clupea harengus L., causing dark pigment spots to form. The definitive host is the Herring Gull, L. argentatus. The eggs of the parasite are released in the birds' droppings and are picked up by the snails as they feed. (Stunkard, 1930; Sinderman and Farrin, 1962).

C. lingua has been recorded from L. littorea in Nova Scotia by Lambert and Farley (1968) and Platt (1968). It is a common parasite of L. saxatilis in Nova Scotia and occurred at five of the stations sampled. The highest level of infection occurred at Station 13, where local fish processing attracts many gulls. At this locality 64 specimens of the 250 examined were infected with C. lingua. This high infection level was also found in L. littorea (three of five snails were infected) and in L. obtusata (12 of 24 snails were infected). James (1968d) noted that C. lingua had been recorded from unidentified subspecies of L. saxatilis, but the parasite was not previously known from L. obtusata before the present study.

The digenetic trematodes show varying forms and degrees of host specificity. One common form is phylogenetic specificity and within this there is a gradation from the stenobionts with a narrow range of host-specificity to the eurybionts with a wide range of host-specificity. The parasites may be host-specific at the species or subspecies level in L. saxatilis. In the following discussion the degree of host-specificity implied has been stated in parentheses.

James (1968d and 1969), listed 22 species of larval Digenea from British Littorinidae and of these 16 were recorded from L. saxatilis. This same author found that certain species of parasite tended to be host-specific (subspecies) to L. saxatilis, but added that the results

could be due to paucity of collecting.

Werding (1969), investigating L. littorea on the german coast, recorded two species of larval Digenea considered by James (loc. cit.) to be host-specific (species) to L. saxatilis These were Microphallus pygmaeus believed host-specific (subspecies) to L. saxatilis rudis (Maton) and L. saxatilis tenebrosa (Montagu), and Podocotyle atomon considered host-specific (subspecies) to L. saxatilis rudis. It would appear that even within a single geographic region some species of larval Digenea were not host-specific (species).

The results from the collections made in Nova Scotia supports the view that these parasites are not host-specific (species). Three forms of L. saxatilis were recorded in Nova Scotia (Davis, MS 1972). These were L. s. neglecta (Bean, 1844) from Station 1, L. s. tenebrosa tenebrosa (Montagu, 1803) from Station 4 and Station 13; and L. s. tenebrosa similis (Jeffreys, 1865) from Station 9. The digenean parasites found in association with these hosts are listed in Table III, with the definitive host where known.

The variety of parasites was greatest in L. s. tenebrosa tenebrosa; H. littorinae and c. roscovita were only found in this form. P. homeotecnum was only found in L. s. neglecta. The occurrences of P. homeotecnum, P. atomon and C. lingua in Nova Scotia do not conform to the pattern of host-specificity (species and subspecies) shown by James (loc. cit.).

The records of C. lingua infecting L. saxatilis and L. obtusata in Nova Scotia indicate some relationships between the European and North American digeneans infecting northern Littorinidae. C. lingua is a common parasite of L. littorea in Europe but it is rare or absent in L. saxatilis and L. obtusata (James, 1969d). In Nova Scotia the parasite occurs in all three Littorina spp.

The Pleistocene fossil record for eastern Canada shows that L. saxatilis and L. obtusata were part of the immediate post-glacial fauna (Wagner, 1968). L. littorea however is not recorded. It was originally thought that L. littorea was introduced to North America as a result of the immigration of European settlers (Becquaert, 1943), but Clarke and Erskine (1961) have established that it was part of the native fauna in pre-columbian times. Sindermann and Farrin (1962) suggested that C. lingua was introduced to North America with L. littorea. The Nova Scotia records of this parasite may be of significance if considered in relation to the wide distribution of the definitive host, the herring gull and the immediate post-glacial distribution of the Littorina spp.

In the Pleistocene, the Nova Scotia marine fauna was more arctic in nature, with L. littorea absent. Herring gulls which became infected with C. lingua in Europe could cross the Atlantic giving a potential source of infection of L. saxatilis and L. obtusata. The reason for the establishment of a C. lingua population in L. saxatilis and L. obtusata in North America

Table III. The species of larval Digenea found in three forms of L. saxatilis in Nova Scotia, and their definitive hosts. L. s. neglecta was found at Station 1; L. s. tenebrosa tenebrosa was found at Station 4 and Station 13; and L. s. tenebrosa similis was found at Station 9.

Parasite	snail host: L. saxatilis neglecta	L. saxatilis tenebrosa tenebrosa	L. saxatilis tenebrosa similis	Definitive host
Parvatrema homeotecnum	+			oyster catcher (James, 1964)
Himasthla littorinae		+		herring gull (Stunkard, 1966)
Microphallus pygmaeus	+	+		herring gull and water pipit (James, 1968b)
Microphallus similis		+	+	herring gull (Stunkard, 1957)
cercaria roscovita		+		unknown
Podocotyle atomon	+	+		marine fish (Hunninen and Cable, 1943)
Cryptocotyle lingua		+		herring gull (Stunkard, 1930)

rather than in Europe would be one of selection. Since L. littorea was absent from the North American fauna, the fish, which form the gulls food, would only carry encysted metacercariae of C. lingua with a capacity for infection of either L. saxatilis or L. obtusata. In this way the C. lingua infection would be perpetuated. Later, L. littorea was added naturally to the North American fauna, since its egg capsules are planktonic. Considering the wide range of the herring gulls, infection with C. lingua would have been concurrent.

The digenetic trematodes infecting L. saxatilis in Nova Scotia appeared to be less diverse than in Europe. In general, L. saxatilis from sheltered localities tended to be more heavily infected than those from exposed localities. It may be that further collecting will reveal the presence of additional species; but it is also possible that others will not be found due to the absence of definitive hosts.

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