

THE OCCURRENCE OF PLEROCERCOIDS OF SCHISTOCEPHALUS SOLIDUS
IN THE FRASER VALLEY AND THEIR EFFECT ON THE
INTERMEDIATE HOST GASTEROSTEUS ACULEATUS

by

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ABSTRACT

Samples of Gasterosteus aculeatus from 16 areas in the Fraser Valley and environs were examined for plerocercoids of Schistocephalus solidus. Fish at Coal Harbour and Alouette Lake were sampled several times over a twelve month period. The number and sizes of worms present in the Alouette Lake fish samples were recorded, and it was found that infected fish less than 45 mm. total length carried on average more worms than those over 45 mm., and that uninfected adult fish were caught only during the breeding season. In another lake, infected fish were found in a different area from the uninfected ones.

The fish intermediate host was shown to be affected by the infection in four ways:

- (i) Infected fish died sooner than uninfected fish.
- (ii) Heavily infected fish were lighter in weight of fish tissue than controls of the same length.
- (iii) The total standard respiration rate of infected fish was higher than that calculated by combining values obtained from uninfected fish and published values for in vitro plerocercoids.
- (iv) Heavily infected fish required up to twice as much oxygen per gram fish weight per hour when swimming at the same speed as control fish.

Other aspects were examined but the results were inconclusive or negative.

The observations on natural populations are discussed in the light of the experimental findings.

Errata

- p. 9 Line 7 Add 'samples' after 6th word
- p.10 Line 9 Add 'However' before first word
- p.47 Fig. 9 In caption for
open circles - parasitised
read open circles - unparasitised

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INTRODUCTION

The pseudophyllidian tapeworm Schistocephalus solidus (Muller, 1776) is widespread and locally common in the Northern Hemisphere over Lat. 45°N. Its life history follows the pattern; egg, free-swimming coracidium, proceroid in copepod, plerocercoid in fish, adult in piscivorous bird. Plerocercoids are commonly found in Gasterosteus aculeatus L., and the weight of plerocercoids carried by a fish sometimes exceeds the weight of the fish. This exceptional parasite burden, and its effect on the stickleback, has attracted, and continues to attract, much attention from parasitologists and other research workers, although up to the present no serious detrimental effect on the fish has been demonstrated.

The present study was initiated to establish the course of natural local infections, and to examine aspects not yet studied in which the parasite may effect the stickleback. It was felt that the results would form part of a theory on how a parasitic infection could influence the number of individuals in, or the structure of, a fish population.

First, a survey was made of local populations of Gasterosteus to locate infections of Schistocephalus that could be sampled regularly. The survey was restricted to Gasterosteus although plerocercoids of Schistocephalus solidus were also taken from two Cottus asper from Cranberry Lake near Powell River. The two natural infections that were chosen were at Coal Harbour and Alouette Lake, and these were visited several times over a twelve month period.

These areas also provided the infected fish and controls that were used in laboratory experiments. Assessment was made of the effect of the infection on the mortality of sticklebacks, the fish weight, the standard respiration rate and the swimming respiration rate of fish. Other aspects were examined but gave negative or inconclusive results. These included the number of eggs produced by female fish, and time to exhaustion of exercised fish.

LITERATURE REVIEW

There are several reports in the literature on the seasonal incidence of infected sticklebacks. Hynes (1950) found a 30% infection in fresh-water fish in a brook draining into the Mersey and observed no seasonal maximum. Clark (1954) sampled from a freshwater pond near Leeds, Yorkshire, and found that in the autumn of 1948 almost every fish was infected, though subsequently the percentage of infected fish dropped considerably. Similarly, Hopkins (1950) took fish from a reservoir near Dublin and found that parasitised fish were common from March to October, rare (1%) during the winter and increased in numbers again the following spring.

Seasonal changes in the size and number of plerocercoids in infected fish have been noticed by some people. Smyth (1946) found large numbers of small worms in fish during the summer months, and Clark (1954), at the same pond in a different year, found only a few worms per fish in the autumn and winter. Hopkins and Smyth (1951), sampling from an isolated lake in Yorkshire, found that during May and June, of the parasites of 33 fish examined (between 1 and 6 per fish) the greater proportion were over two centimetres long, whereas in August thirteen fish yielded over 400 larvae less than one centimetre long. If this infection is normal, they suggest, it would appear that there is an elimination of a large number of initial larvae. Arme and Owen (1967) present data on the mean number of worms per infected fish for various times over a four year period. In June 1962, 47 worms per fish were found; in April-

May-June 1963 only 12. In January-February-March 1963, 11, compared with 1 for the same period in 1964. Hence annual variation appears to be considerable. However, their data for the four quarters of 1963 (11, 12, 4 and 3) suggest a spring and summer increase in number of small worms in agreement with the three previous papers.

The most complete account of the effect of the parasite on the stickleback has been given by Arme and Owen (1967). They were able to demonstrate a correlation between low liver weight (expressed as a proportion of the fish weight) and high parasite burden (worm weight/total weight). They found some evidence of anaemia in heavily infected fish and were able to correlate it with parasite burden for the first and third quarters of 1963, though not in the other two quarters. Using histological techniques, they showed that male gonads were unaffected by the parasite but ovaries were delayed in maturation and at the end of the spawning season many corpora atretica were present, showing some inability on the part of the parasitised female to shed eggs. This, they propose, may be mechanical as a distended female was observed to destroy a nest in an attempt to spawn. They also found that whilst the male gonads were unaffected, greatly distended males were unable to construct nests. Examination of the pituitary revealed no histological change associated with infection.

Kerr (1948) had earlier found similar results. He found no evidence of effect on the pituitary. Males taken in May had testes that still contained relatively more germ cells than unparasitised fish but nevertheless, there were many spermatozoa

present. The males, he observed, developed full breeding colouration. The ovaries were in the secondary growth phase of the oocytes but among the largest eggs he found a marked degree of atresia.

Vik (1954) noticed that parasitised fish had less fatty tissue around the gut than unparasitised fish.

These effects are remarkably slight for so heavy a parasite burden. However, there is a possibility that Schistocephalus hastens the death of the fish. Threlfall (1968) recorded a mass die-off of sticklebacks in a lake near St. Johns, Newfoundland, in August 1966, and he attributed it to a combination of Schistocephalus (almost 100% infection) and Argulus canadensis, the fish louse, an external parasite. Mass die-offs of sticklebacks have been seen in the Wood River Lakes of Alaska where Schistocephalus could be seen crawling out of the fish (H. Smith, pers. comm.). Vik (1954) noticed that great masses of sticklebacks died in August, "due to plerocercoids crawling out through the wall of the abdomen". He examined fish trapped in a sunken boat and found that the live fish were "ready to burst on account of the plerocercoids" while those lying dead had no worms but perforations in the abdominal wall just in front of the anus. Some living fish had plerocercoids hanging out of the openings, and plerocercoids, both dead and alive, were found on the bottom in many parts of the lake. The temperature of the water was about 25°C., and he was working in lakes near Trondheim, Norway. Wardle (1933) records the finding of Schistocephalus plerocercoids lying free on the shore of Nanaimo Lake, B.C.

Clark (1954) noted that occasionally a worm was expressed when he was handling a stickleback, apparently through the rectum. These fish continued to live with no evident signs of distress.

Several people have noticed a change in the behaviour of heavily infected fish. They tend to be nearer the surface and more easily caught (Arme and Owen, 1967, and Clark, 1954). Smyth (1946) observed that infected fish had a characteristic swelling of the abdomen that produced unnatural swimming movements, though Clark (1954) thought that when aroused they could move as quickly as the unparasitised ones.

I. Survey of the distribution and abundance of *Schistocephalus plerocercoids* in Gasterosteus in the Lower Fraser Valley and environs

MATERIALS AND METHODS

Gasterosteus aculeatus were collected during 1968 from streams and lakes in the Fraser Valley to locate a suitable source for regular sampling. Dip nets and a pole seine of less than 3/16ths inch internal diameter stretched mesh were used in conjunction with a 30' beach seine of nylon bobbinet of 1/4 inch internal diameter stretched mesh.

The fish were opened using fine scissors by a ventral cut running posteriorly from in front of the pelvic girdle. Large worms were removed using a blunt seeker and small ones by flushing with distilled water from a bulb pipette. Fish were sometimes examined further under a binocular microscope, particularly when Diphyllobothrium plerocercoids were encountered.

Fish were measured to the nearest 5 mm. group below the total length and were separated into three races by running a needle over the side of the fish to feel for lateral plates; those with less than four plates were termed leiurus, those with a complete set trachurus, and the intermediates semi-armatus. This approximation was inaccurate for fish less than 25 mm.

Worms were relaxed in Petri dishes of distilled water in a refrigerator at 4°C for one week to allow for complete relaxation. The worm length was then measured to the nearest 5 mm. and the maximum width to the nearest 0.5 mm. From these figures, 'volume units' for the worms were calculated by cubing

the square root of 'length x 10 x width'. The width/length ratio was close to 1:10. This procedure overcame errors due to unequal relaxation and the more slender shape of smaller worms. As the worms relaxed an outer tegument was cast off, and measurements were all made on the underlying surface. This technique was used so that a relatively accurate estimate of the biomass of both small and large worms could be obtained. Net weights were inaccurate because of the varying amounts of coelomic fluid present on small worms, and dry weight was considered unsatisfactory because of the difficulty of obtaining relative weights of a range of worms less than one milligram. A similar technique has since been published (Orr et al, 1969).

RESULTS

The fish samples collected, together with percent infection, are listed in Table I. It can be seen that Schistocephalus is a frequent but not common parasite in many bodies of water in the Lower Fraser Valley.

Figure 1 shows the relative abundance of the different sub-species of sticklebacks in Coal Harbour for different quarters of the year, and also gives their length frequency and the occurrence of parasitised fish. The fish were caught with the help of a seine net and, because of the seine mesh size, some fish less than 30 mm. long were able to escape through the meshes. The histograms, therefore, do not give the number of small fish present relative to the numbers of the larger sizes. Fish less than 30 mm. long were difficult to separate into subspecies.

It can be seen that all sizes of fish over 25 mm. were present for most of the year, and that infected fish were scattered throughout all length groups and subspecies. Data on fish catch-rate is not presented as it was affected by many factors, however, the poorest catches were taken in early spring. The best catches of adult fish were in June-July-August when there appeared to be a massive influx of adult trachurus into Coal Harbour.

During hot weather in late August, 1969, many thousand dead adult trachurus littered the bottom in a shallow corner of Coal Harbour. Many of the dead fish were gravid females, no fish examined contained Schistocephalus.

Gasterosteus samples from Alouette Lake (Fig. 2) showed 100% infection throughout the winter, uninfected fish appeared in the late spring. Many of the uninfected fish caught were males in breeding colouration. It is possible that the uninfected fish were unsampled during most of the year because they were not present in the lake at that time. They may have migrated into the lake in the same manner that normal trachurus leave the sea and migrate up stream to breed during the summer. The only known outlets to the lake are over a high dam, or through the power turbine that operates in a tunnel between Alouette and Stave Lakes. Through neither outlet could fish enter the lakes.

Numerous creeks flow into the lake and uninfected fish may have remained in these creeks for most of the year and only moved down to the lake at the breeding season. The two creeks flowing into areas regularly visited were too small for most of the year to support fish, though infected sticklebacks were sometimes taken in about two inches of water at the creek mouth. A larger creek, Gold Creek, yielded a few infected and no uninfected fish on the two occasions it was visited. It is highly unlikely, then, that uninfected fish moved into the lake from another body of water.

Fish may have matured in the lake, uninfected, and then, when they became a certain size, became catchable and subsequently developed parasites. Alternatively, they may have been present in the lake throughout the year, and only became catchable in the breeding season. We may note in passing that it appears that these land-locked trachurus have retained their later spawning period compared to leiurus.

Fish less than 45 mm. long were poorly represented in the samples, indicating either that there were few small fish for most of the year, or that all fish sizes were not being equally sampled.

The worm size frequency charts in Fig. 2 suggest that there was an increase during May of the proportion of small worms found, however this apparent seasonal peak is due to the numbers of small worms found in the samples of fish less than 45 mm. long.

Table II shows the average number of worms taken from fish of different length frequencies using data from all samples, and also gives the maximum numbers of worms found in one fish. It can be seen that fish start picking up the infection when about 20 mm. in length, and continue to accumulate more worms until they were 35-40 mm. long. Larger fish contained fewer worms. As the samples of different fish lengths were unequal, the samples are divided by month in Table III. This confirms the view that smaller fish were carrying more worms than the larger fish.

In Fig. 3, the worm sizes are plotted against fish lengths. Solid symbols represent worms taken from a fish carrying only one worm. As the fish became larger their worms became larger and from the distribution of symbols it seems that worms from multiple infections are slightly smaller than those from single infections.

To further examine the relation between worm size and worm number in any one infected fish, Fig. 4 was constructed. It includes only data from fish in the 50 and 55 mm. length

groups to avoid complications of fish size affecting worm growth. Fig. 4b includes only those fish having worms over 325 vol. units, to ensure that if there is any effect it will be exaggerated by considering only large worms. The means and standard deviations from Fig. 4b are plotted in Fig. 4c. It is evident from this that, of the fish caught, worms from a quadruple infection are approximately 20% smaller than those from a single infection. This difference may be due to several factors such as the effect of intra-specific competition between the worms or an earlier mortality of the fish containing larger numbers of worms. However, the maximum effect each factor can have is the total observed difference. Therefore, we can conclude that the effect of the worms on each other's growth is small.

In Fig. 5a, the total worm burden is plotted against fish length group. Again solid circles represent single infections, and it can be seen that a fish in the 55 mm. length group, for example, can support up to three times the average burden imposed by a single worm. It is also noticeable that not many fish over 45 mm. were caught that were without a worm burden of at least 300 vol. units, except for the unparasitised fish that were caught during the breeding season. There was an absence of lightly infected fish even during the breeding season. If we go back to an earlier point about the absence of uninfected fish from the catches we concluded that it was possible that these fish became catchable and then developed an infection. This does not appear to be the case; mature fish

were either uninfected or heavily infected (over 300 volume units of worm). The alternative conclusion, that uninfected fish were present in the lake and only became catchable at the breeding season, may be closer to the truth. It appears then that there were two conditions that would enable large Alouette Lake fish to be caught in a beach seine, either they carried a worm burden of over 300 volume units, or they were breeding fish.

(Fig. 5b is included in order to relate volume units to dry weight. The data were taken from experimental fish that had been originally selected for carrying either a heavy parasite burden or no burden, the latter group being used as controls. The fish were taken from the same source as those in Fig. 5a. A comparison of the maximum burden carried in Figures 5a and 5b may be used as a crude estimate of the relation of volume units to milligrams).

The proposed increased catchability of breeding fish may have been due in part to the territorial behaviour of the male. Causes of the increase in parasitised fish are more obscure. Uninfected fish may have been lying beneath rocks when the seine swept the area during winter sampling, or these fish may not have been present in the shallow stream outlets visited. Evidence for the second possibility was gathered at Cortes Island. Samples of fish were taken from two small lakes joined by a short canal about 8' wide and 4' deep. The first sample (see Fig. 6) was taken from around some logs on a gently sloping shore in Haig Lake. Most of these fish were infected with Schistocephalus and some also with Glugea. Dead fish were found on the bottom but

no free plerocercoids were seen. The second sample was from the canal and here one third had Schistocephalus. The last sample came from several large shoals of fish that were milling over and around submerged exposed rock, well away from shore in Gun Flint Lake. Only a few of these fish were infected. In essentially one body of water then, two groups of sticklebacks were found, one heavily infected, the other relatively free of infection. It is possible that they were separate populations.

Some of the fish caught had abnormally short pelvic spines, and using these as a possible population characteristic, the samples were divided into two groups. The results are shown in Fig. 6. It is clear that the infected and uninfected fish were not separated by the spine character, and it remained possible that uninfected and infected fish were derived from the same population but were caught in different areas.

II. Collection and holding of fish used in the following experiments

Most laboratory experiments required the use of infected fish and uninfected controls from the same population of sticklebacks. They were matched by taking pairs of approximately the same total length.

Three methods for obtaining these were tried. To produce controlled laboratory infections of Schistocephalus in Gasterosteus, plerocercoids were cultured, eggs collected, embryonated and the hatched coracidia fed to copepods. Cyclops bicuspidatus and Macrocyclus fuscus containing developing proceroids died before fish could be infected.

The second method involved the removal of plerocercoids from parasitised fish. Two Alouette Lake fish were opened and the plerocercoids removed. The slit in one fish was not sewn up and it died in the next twelve hours, while the other fish was sewn up with a small surgical needle and suture and recovered well enough to feed. It developed a fungal infection around the stitches and eventually died on the fourth day.

In May, uninfected fish were first taken from Alouette Lake and so pairs for most of the following experiments were taken from this natural source, though this often meant that fish provisionally assumed to be unparasitised were found to contain worms after the experiment, and vice versa.

Fish that were caught in the field were brought back to the laboratory in two and three gallon jars aerated from an oxygen cylinder. During the summer this method exposed the fish to temperatures in excess of 20°C and losses frequently occurred

the following night, so if this was likely, the fish were transported in an aerated polythene bag in an ice chest with a few blocks of ice.

Large holding tanks in the basement were continually aerated and had a small flow of water. They fluctuated between 6-15°C during the year, and for all of the following experiments except where indicated were at 10-13°C. Fish were fed about three times per week with frozen brine shrimp occasionally varied with small meal pellets or Tubifex worms.

For the majority of experiments, fish were taken from Alouette Lake, and losses of these fish were attributed to heavy infection of Trichodina sp. and Bacterial Gill Disease (Davis, 1961). Other parasites that were commonly found in Alouette Lake included immature Proteocephalus sp., and the genera Gyrodactylus, Dactylogyrus, and plerocercoids of Diphyllobothrium. The Trichodina, Gyrodactylus and Dactylogyrus were removed by placing the fish in a 1:4000 solution of commercial formalin for one hour. The Bacterial Gill Disease was encountered by immersing the fish for one minute in a 1:2000 solution of copper sulphate, to which had been added three percent sodium chloride. However, it was found that by the time the disease was diagnosed, many fish died from the treatment, either from the effect of the heavy metal ion on the gill mucus or through shock.

III. Experiments designed to assess ways in which Schistocephalus may affect the survival of Gasterosteus individuals

1. Increased mortality due to the direct effect of Schistocephalus

(a) With no determination of cause

Methods

A sample of fish from Coal Harbour was provisionally separated into infected and controls by external examination, and equal numbers were placed in an aquarium at 12-15°C. During the following weeks all deaths were noted and at the end of the experiment all fish were dissected to determine the actual numbers of parasitised fish present. This experiment was duplicated.

A plan to hold fish in large underwater cages in their natural habitat was cancelled because of the lack of infected fish.

Results

The two batches of infected fish and controls that were held in tanks gave the data in Table IV. Using the Fisher Exact Probability Test, the probability values for the results and the next two more extreme results are 0.0007, 0.00005 and 0.000002 giving a total of 0.000752 which indicated that it is highly unlikely that parasitised fish and controls died at the same rate. It is concluded that parasitised fish were more liable to die from causes excluding predation than unparasitised fish.

(b) Death caused by the emergence of the worm from the fish

From Vik's vivid description (1954), the emergence of the plerocercoid may increase the host mortality rate. Fish were stressed by starvation and by high temperatures in an attempt to reproduce the phenomenon in the laboratory.

Methods

Two heavily infected Alouette fish were starved in the laboratory at 20-23°C and three fish at 10-12°C until death.

Three parasitised fish were slowly raised to their upper lethal temperature over several days.

Results

Both fish at 20 to 23°C died on the ninth day, those at 10 to 12°C died after 17, 21 and 24 days. In no instance did the worm show signs of emergence.

Three fish were raised to 33°C in two days and died with no emergence of the worms.

The only worm that emerged during this study was from a gravid female from Queen Elizabeth Park which was in a small tank in which a male had a nest. One morning (3.4.68), the female was found dead on the surface still containing many mature eggs and the worm was stretched out in front of the nest. The worm presumably emerged during egg laying attempts.

2. Possible indirect effects of the plerocercoid infection on the stickleback

(a) Assessment of the effect of the infection on the number of eggs produced by breeding female fish

Method

Counts of eggs were made on 14 Alouette Lake fish that were brought back alive to the laboratory. They were between 54 and 65 mm. in total length. The fish were killed by pithing and the gonads lifted into a water-filled Petri dish. The eggs were separated using forceps and a blunt seeker. Errors and variability in egg counts were due to the difficulty of counting eggs in unripe gonads, and the tendency of gravid females to spontaneously drop eggs.

Results

In 10 infected mature females egg number ranged from 26 to 78 with a mean near 55, and four unparasitised egg counts ranged from 41 to 53. With the small numbers of fish there was no demonstrable difference between the infected and uninfected fish.

The egg number was low when compared to the numbers of eggs found in Coal Harbour trachurus. Ten similar sized fish were carrying between 56 and 287 eggs with a mean near 130.

(b) Standard respiration rate of infected fish compared to controls

Method

The standard respiration rate of twenty four sticklebacks was found by sealing individual fish in jars for a known time

interval and measuring the decrease in oxygen content of the water.

The fish were paired, one infected and one control, on the basis of their length. All lengths were measured to the nearest mm. below the total length. The fish were not fed for the twenty four hours previous to the start of the experiment. Those fish whose oxygen consumption was measured at temperatures above their acclimation temperatures (i.e. 17, 18, 20 and 21°C, see Table V), were raised to those temperatures from their holding temperatures during the morning preceding sealing in the evening.

At the start of the experiment, the tank to be used as the water bath was at the appropriate temperature and contained the fish. The fish were caught with as little disturbance as possible and put into jars with a small amount of water. The tank was then aerated vigorously to ensure homogeneity of oxygen and the jars gently filled. A water sample from one of the jars, chosen at random, was then siphoned off, using a moistened tube, into a water sample bottle of about 280 ml. This sample was considered representative of the oxygen concentration in all the jars at the start of the experiment. The jar providing the initial sample was then refilled and all the jars sealed under water to avoid bubbles. They were surrounded by black plastic to minimise any disturbance, and left overnight in the tank. Air stones were left in the water to ensure mixing, and a maximum/minimum thermometer was placed in the water to record the temperature.

The jars were kept sealed until there had been an estimated drop of a half to two thirds of the original oxygen content. Immediately before unsealing the jars were inverted once to avoid any stratification, and the second sample siphoned out in the manner already described.

All oxygen determinations were made using the Winkler method as described in Ellis et al., 1948, and also in Hoar, 1956, Hoar and Hickman, 1967, and Jolly, 1963.

To find the fish and worm weights, the fish were killed by pithing, the worms removed by a ventral slit, fish and worms lightly blotted, weighed separately and then placed in a drying cabinet at 110°C for over forty hours. They were then removed from the oven, allowed to cool for about a minute while covered with 'Parafilm', and re-weighed. The wet weights were recorded as a check on the dry weights. Worm dry weights were usually close to 30% of the wet weight, and fish dry weights around 20% of the wet weight, though fish values tended to fluctuate more widely.

The volumes of the jars (approx. 920 ml.) were found by weighing the jars dry and again when filled with water.

Result

The results of the measurements of the standard respiration rate of infected fish and controls are given in Table V. Infected and uninfected fish of similar total length consume about the same amount of oxygen per hour.

However, it can be seen that the infected fish tend to have a lower dry weight of fish tissue compared with controls of the same length. Assuming that the parasitised fish tissue

respires at the same rate as that of the controls, an estimate of the amount of oxygen it would consume is given in the second column of Table VI. One would expect this to be an over-estimate as the parasitised fish were thinner than the controls and hence had a higher proportion of slowly metabolising tissue such as bone. While aware of the assumption that we have made above, it is possible to calculate the oxygen consumption of the worm alone by subtracting the second column from the first, and these results are tabulated in the third column. If the assumption is valid, then the worm is consuming up to one third of the total consumption of the infected fish.

The oxygen consumption of plerocercoids in vitro, in buffered saline solution, has been measured by Davies and Wälkey (1966) using a Warburg apparatus. The oxygen consumption of the plerocercoids used in Table V has been calculated from their findings and is listed in column 4 of Table VI. These values are relatively small, only about one tenth of the total consumption listed in column 1, and at the lower temperatures are lower than the values in column 3, thus casting doubt upon the validity of the earlier assumption. Measurement of the standard respiration rate at the higher temperatures was more exposed to error. The fish were sealed for a shorter time period and hence any disturbance at the start or finish produced a relatively greater effect. Also gonads were stimulated by the temperature rise and in one case a male fish changed into full breeding colours while sealed.

The oxygen uptake of worms in vitro, while open to errors resulting from the abnormal environment, does indicate that the

uptake when they are within the fish is probably very small compared to the total uptake of a parasitised fish, and hence, contrary to the earlier assumption, it would appear that most of the oxygen uptake is due to fish tissue alone. Assuming that the worm uptake is zero, the consumption of parasitised fish tissue per gram is given in Table VII, alongside values for unparasitised fish. The parasitised fish are seen to consume more oxygen per gram of fish tissue than the controls.

(c) A comparison of the swimming respiration rate of infected and uninfected fish

Method

A swimming tube was constructed for individual sticklebacks similar to that built by Brett (1965) for salmon. It consisted of a 36 cm. swimming tube of 3.1 cm. internal diameter (see Fig. 7); a 'Little Giant' 3-12N pump capable of lifting 5 metres of water and giving the apparatus a maximum flow of about 18 litres (four gallons) a minute; a 'Trident' household water meter calibrated in tenths of a gallon; a thermometer and devices for introducing water and fish into the system and for releasing air bubbles.

After the introduction of the fish, a water sample was taken at the start of the experiment and again at the end, and the two oxygen concentrations found by the Winkler method as already described. The interval between the first and second water samples was a maximum of three hours and was shortened if the fish was exhausted earlier. The fish was stimulated to swim by the electrified grid (see diagram) which carried two separate

spirals of copper wire. The grid was live for ten milliseconds once per second, and carried a maximum current flow of half an amp and an adjustable potential difference of up to 100 volts, 20 to 40 volts being adequate in most cases. The high voltages were found to be occasionally necessary because of mucus and algae that adhered to the grid. Fish were considered exhausted if they were seen to flinch but remain on the grid for twelve pulses, either consecutively or in two groups of six. The equilibrium temperature of the circulating water was one degree \pm 0.5 above the acclimation temperature of the fish.

The procedure of using the apparatus was as follows. First the apparatus was filled with water from a briskly aerated aquarium at 15-20°C and close to saturation point in oxygen. The flow through the apparatus was then adjusted using the tap, meter and stopwatch, the stimulator activated and the fish added. For the following twenty minutes the water was circulated and at the same time water was drawn in from the aquarium in one place and allowed to flow out slowly into a sample bottle in another. During this time about six litres drained through the system and the sample bottle was taken as being representative of the water content of the apparatus. This time also enabled the fish in its darkened tube to become used to the location of the grid. The water sample was then removed, inflow and outflow clamped closed, the stopwatch started and the meter read.

After three hours, or sooner if the fish was exhausted, the pump was stopped, 500 mls. drained from the apparatus and Winkler reagents immediately added to the sample. The number of gallons that had flowed through the meter divided by the time

gave the flow per minute, and from this and the diameter of the tube, the number of fish lengths per second was calculated. Errors due to laminar flow were reduced by the presence of grids in the swimming tube. The water meter error was 3-5% lower than the true flow. The total volume of the closed apparatus was constant at 950 mls.

Result

Fig. 8 shows the oxygen consumption for twenty seven fish, of 50-63 mm. in total length, for different swimming speeds expressed as lengths per second. The consumption per gram refers to fish weight only and therefore, from the standard respiration results, one would expect infected fish to have a slightly higher consumption regardless of flow. All fish are from Alouette Lake except for the square symbol which represents a leiurus from Mike Lake. The area within each symbol is shaded in proportion to the ratio: worm weight/fish weight, and it can be seen that heavily infected fish are using twice as much oxygen as the controls to swim at the same speed.

(d) Comparison between exhaustion times of infected and control fish

Method

The apparatus described in section 'c' was used without any water samples being taken and without the precautions necessary to remove air bubbles. Measurements of exhaustion times less than ten minutes were inaccurate because of the time taken for the fish to become accustomed to the tube and grid. Data was therefore collected on fish from ten minutes to three hours.

Result

The variability in the results obscured any difference between the two test groups, and the factors most important in determining exhaustion time appeared to be directly related to the extent of gill infections and the general health of the fish.

(e) Effect of infection on fish weight

Method

The dry weights of infected and uninfected fish used in various experiments were plotted against fish length (Fig. 9) and an analysis of covariance completed on fish whose lengths were 51 to 61 mms.

Result

The dry weights of 54 fish used in different experiments are plotted on Fig. 9. Those fish having a worm/fish ratio equal to or greater than 0.46 are indicated by solid circles, unparasitised by open circles. The ratio 0.46 was taken so that equal numbers of parasitised and control fish from 51 to 61 millimetres long could be analysed by covariance analysis. The regression coefficients did not differ in the two groups at the 95% level of probability, though through comparison of the variances of the adjusted means, it appeared probable that parasitism affected the fish weight. It was concluded that infected fish were generally lighter in weight of fish tissue than controls of the same length.

DISCUSSION

Several aspects of the possible effect of Schistocephalus plerocercoids on the stickleback were examined and three revealed demonstrable changes.

Infected sticklebacks were more likely to die than uninfected fish. This was not an unexpected result but had nevertheless not been previously confirmed. This mortality was unrelated to the emergence of the worm. In only one instance did the worm emerge spontaneously and in this case the fish died. Its death may not have been due to the emerging worm but to the opened coelomic cavity since in the instances where worms were removed surgically, the fish that was sewn up lived for four days while the other died within a few hours.

Considering the amount of tissue present in infected fish, the total standard respiration rate was higher than that found for normal fish tissue and in vitro worm tissue. The low worm respiration rates found by Davies and Walkey (1966) are supported by Smyth (1946). He found that plerocercoids exposed to air gradually turned brown and he recommended that all culture work with these worms be carried out in semi-anaerobic conditions. Assuming then that the worm was responsible for only a very small part of the total respiration of an infected fish, the infected fish tissue was respiring at a greater rate than uninfected fish tissue. This may have been due to many factors. Movements of the worm may have disturbed the fish, keeping it more active during the experiments, metabolic waste products of the worm may have been oxidised by the host or the host's cytological defence responses may have been using up extra energy.

During the observations on swimming fish, it was found that parasitisation had little effect on the swimming ability of fish. Any difference was obscured by factors unrelated to Schistocephalus. Both infected and uninfected fish were able to maintain a speed of 1 L/sec. (fish length per sec.) for several hours. At over 2 L/sec. the fish became greatly agitated and sought to escape from the tube. Bainbridge (1960) found that dace, trout and goldfish could sustain flows of 10 L/sec. for one second and about 4 L/sec. for twenty seconds. Brett, Hollands and Alderdice (1958) swam salmon fry at 0°C and 20°C for one hour and found that the maximum speed sustained for a 5.4 cm. coho was 1.1 L/sec. at 0°C and 5.5 L/sec. at 20°C. For sockeye at 6.9 cm. the values were 1.7 and 5.1 L/sec.

The stickleback cruising speed at 12-15°C (up to 1.8 L/sec.) is low compared with that of the salmonids and this may be related to the method of swimming. At 1 L/sec. the salmonids swim by movements of the body and tail whereas the stickleback uses its pectoral fins to scull through the water and the body and tail are kept stiff and straight. At flows of about 1.5 L/sec. sculling movements are not adequate and the stickleback drops back only to regain its position with a flick of the body and tail. Contrary to Smyth's observation (1946) that the swollen abdomen of infected fish produced unnatural swimming movements, the worms did not appear to physically affect sculling movements or the smooth passage of the fish through the water.

The amount of oxygen used by an unparasitised stickleback swimming at 1 L/sec. at 12-15°C is about 1 ml/hr./gm. dry wt. (Fig. 8). From data in Table IV on standard respiration, a

half to two thirds of this may be used in standard respiration (0.5-0.7 ml./hr./gm. dry wt.). The fish dry weights are approximately 20% of the wet weight so the total consumption at 1 L/sec. for 50 to 60 mm. fish can be expressed as 280 mgm. O_2 /hr./kgm. wet weight, of which a third to a half (90-180 mgm. O_2 /hr./kg.) may be used for swimming at 1 L/sec. This compares favourably with data presented by Brett (1963) for 180 mm. sockeye salmon which were using 63 mgm./hr./kgm. to swim 1 L/sec. at 15°C, though it appears that the stickleback is having to work a little harder. Above a speed of 1 L/sec. (Fig. 8), the graph rises sharply, the total consumption doubling by 1.7 L/sec., whereas the sockeye salmon doubled in total consumption at speeds above 2 L/sec. This reflects the jerky, more excited swimming of the stickleback at the high flows.

The heavily infected fish have a standard respiration rate of about 0.8-0.9 ml./hr./gm. and so the amount used for swimming at 1 L/sec. exceeds 1.0 ml./hr./gm. Compared with the 0.3-0.5 used by uninfected fish it appears that the parasite is having a marked effect on the stickleback.

In applying these experimental findings to the observations on natural infections, let us first consider the mass die-offs of sticklebacks recorded by many people.

The heavy mortality of mature Gasterosteus aculeatus seen in Coal Harbour was not due to the presence of Schistocephalus. The possibility of very local pollution cannot be ruled out but because of the widespread reports of mass deaths another explanation may be sought. On a hot calm day in August, the temperature of the water in this corner of Coal Harbour is over

22°C and hence its dissolved oxygen capacity is greatly reduced. It is conceivable that several large shoals passing to and fro could deplete the oxygen content to below a level necessary to support the fish and anoxia would result. Very few of the Coal Harbour fish were carrying Schistocephalus. However, it is clear from the results that the fish that are burdened with this parasite have an oxygen demand higher than normal and thus would be more susceptible to death through anoxia. The relation between the mass die-offs of fish and the emergence of plerocercoids remains unknown.

The most detailed information on a natural local infection was obtained from Alouette Lake. The fish caught were close to 100% infected throughout the year and this obscured any seasonal fluctuations in the proportion of total population infected. Infected fish between 20 and 45 mm., total length, carried more worms than those fish over 45 mm., and since more of the smaller fish were caught in the summer, larger numbers of small worms were found in the summer. This agrees with the summer increase in numbers of small worms found by other authors (Smyth, 1946; Arme and Owen, 1967; etc.), though they do not indicate whether the increase is also related to the average size of fish sampled.

The results have shown that large plerocercoids have little effect on each other's growth (Fig. 5). This has already been shown to be true for very small plerocercoids by Clark (1954). He experimentally infected eight sticklebacks with one proceroid each, and three with two. During the first 50 days there was no difference in worm growth between the single and double infections. Orr, Hopkins and Charles (1969) exposed fish

to infected copepods three times over a period of a month and found that within the sticklebacks there were three sizes of young plerocercoids, indicating that immunity was not developed by infected fish. In Alouette Lake, fish less than 45 mm. carried on average more worms than large fish, so, from the foregoing, it is concluded that small fish were more exposed to infection than the larger fish. This agrees to some extent with Hynes' (1950) data on the food of Gasterosteus aculeatus leiurus. He found that fish up to 25 mm. long ate three times as many copepods as those fish at 55 mm.

A worm burden decreases the weight of the fish (Fig. 9), it affects the liver weight and blood cell count (from Arme and Owen, 1967), abundance of fat tissue (Vik, 1954), and infected fish are more liable to die (Table III). It is concluded then, in opposition to Smyth's (1946) suggestion that the worms are eliminated, that the heavily infected fish die sooner than those containing only one or two worms, in other words, as the total worm burden increases, so the mortality rate increases.

Though it is inevitably risky to build up a theory on data derived from natural populations, so far the facts have provided reasonable grounds for conclusions. The results of section I have already suggested that a Schistocephalus infection increased the catchability of the fish at Alouette Lake so the conclusions can be summarised as follows. At Alouette Lake, the fish start accumulating worms when the fish are 20 mm. long. As the fish grow, the weight of worms grows, each worm growing more or less independently of its neighbour, and the more heavily infected fish die. At the same time the fish become less

exposed to infection and also become less catchable by beach seine. The worms continue to grow and when the total worm burden reaches a certain size, the fish again become catchable.

The increased catchability of adult fish once the worm has attained a certain size may also reflect a change in the type and rate of natural predation. There is little information on predators at Alouette Lake. The lake has been stocked with lake trout. No large trout were ever seen in the shallow stream outlets and it is possible that predation by fish is lower in the outlets than in the deeper waters of the lake. The only bird predator seen at the lake was a kingfisher but, from the occurrence of infected fish in very shallow water one could conclude that the possibility of predation by shore birds is high at the outlets. It is possible then that after infection fish become less susceptible to fish predation and more susceptible to bird predation, an example of a host/parasite interaction which increases the chances of a parasite reaching the next stage in its life cycle.

Incidentally, the apparent shortage of bird predators at Alouette Lake may account for the abundance of catchable infected fish compared with neighboring bodies of water such as Cultus or Pitt Lakes.

A non-random distribution of infected fish in a fish population has been reported by Orr (1966). He found that rudd, Scardinius erythrophthalmus, infected with Ligula intestinalis, a closely related cestode that also reaches a large size relative to its host, did not gather into spawning shoals with other individuals. This he attributed to the inhibiting effect of

Ligula on the gonads, thereby preventing secretion of, or response to, sterohormones, important in the behaviour of spawning fish. This cannot be the case in Schistocephalus as segregation appeared to occur outside the breeding season. Fish schools usually consist of fish of the same size (Marshall, 1965) and it may well be that the physical distortion, and the extra physiological stresses that this imposes, prevent infected fish from schooling with the uninfected ones. For example, the respiration measurements have shown a marked change with infection, especially in active fish. This is more dramatic than other effects previously noted, and would be expected to affect fish behaviour in several ways. Infected fish may seek well oxygenated water, for example at the surface or in a creek, and these fish may also avoid excessive activity and would therefore seek a sheltered habitat. This corresponds well with the observed distribution. The infected fish in Alouette Lake were found in shallow water around stream outlets.

This study was initiated to examine the effect of the worm on the fish with a view to predict the effect on the fish population. However, time scales are obscure because of the lack of information on the rate of growth of the worm and the rate of growth of the stickleback. The best data on the growth of the worm is given by Orr and Hopkins (1969), who show that after three months at 19°C worms weighed 20 mgm. dry weight. The Alouette Lake worms from 45-65 mm. fish weighed 50-150 mgm. dry weight, and over the year the surface temperature of the lake varied from 6°C to 22°C, while creek water running into the lake never rose above 13°C.

The literature abounds with papers on the growth rate of sticklebacks. Some propose a four year growth period (Wunder, 1928 and 1930; Bock, 1928; Jones and Hynes, 1950), others a single year (van Mullem and van der Vlugt, 1964), and others through laboratory experiments find that fish can be reared to maturity in six to eight months (Wunder, 1930; Baggarman, 1958; Craig-Bennet, 1931). The presence of immature 30-35 mm. fish in the May-June sample, i.e. immediately prior to the spawning season, may indicate that fish take two years to reach maturity in Alouette Lake. However, the population was probably not randomly sampled, as has been suggested in the results, and so little information can be gleaned about growth from the length frequencies presented. Without some idea of the growth rate of the fish and of the plerocercoids, it is difficult to assess the course of the infection in Alouette Lake.

However, this study has given an indication of the nature of the parameters important for an analysis of the effect of the infection on a population. First, possibility of infection is high in fish from 15 to 35 mm., and then decreases in larger fish. Secondly, as the total weight of worms increases, so mortality increases. Thirdly, in fish over 40 mm., when the worm weight/fish weight ratio is about 0.3 the fish probably become more exposed to bird predation and less to fish predation.

Many authors have shown that individual fish harbouring this large parasitic growth do not exhibit the effects normally associated with parasites, and Schistocephalus in Gasterosteus is generally considered a 'well-adapted' parasite. This study

has shown that the standard respiration rate of the parasitised fish is higher than normal considering the amount of fish tissue present. However, it may well be that the main result of the infection is to increase the energy requirement of the fish to enable it to carry its burden through the water.

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Fig. 1. Length frequencies of Gasterosteus aculeatus
from Coal Harbour.

shaded - infected with Schistocephalus

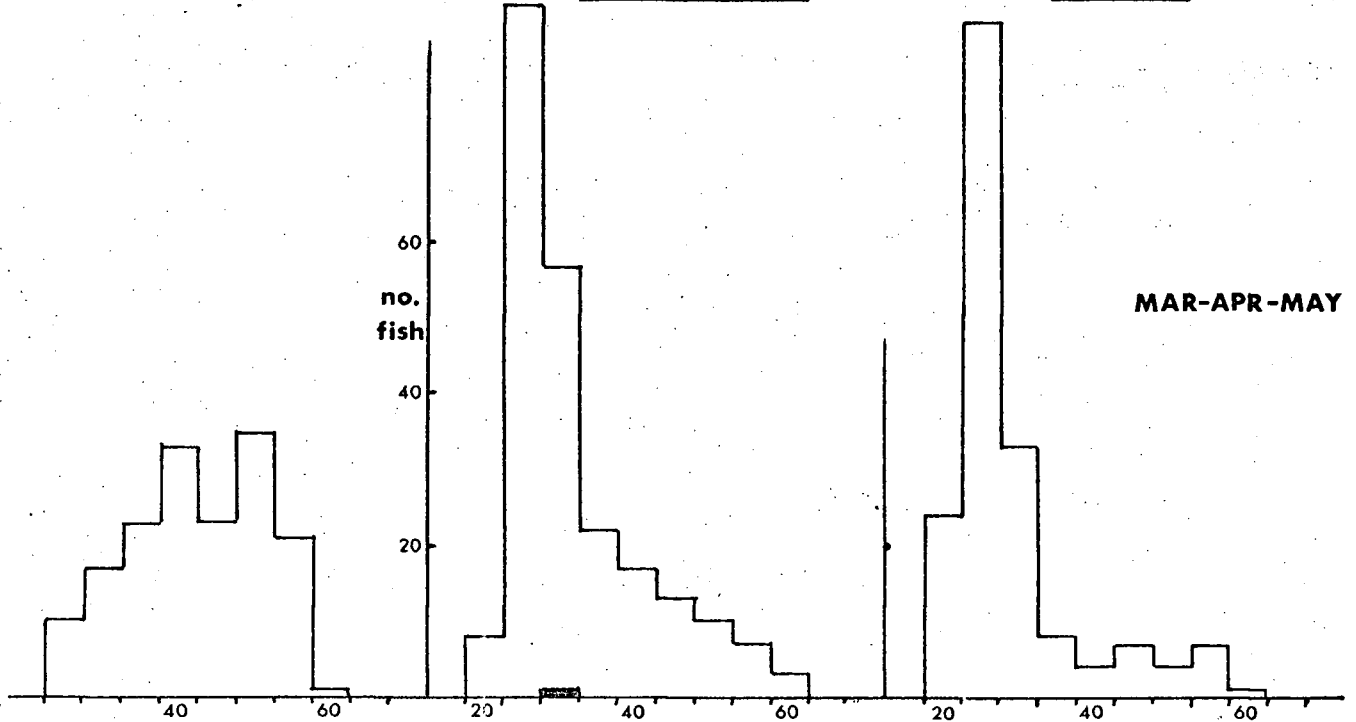
v. trachurus

v. semi-armatus

v. leiurus

no.
fish

MAR-APR-MAY

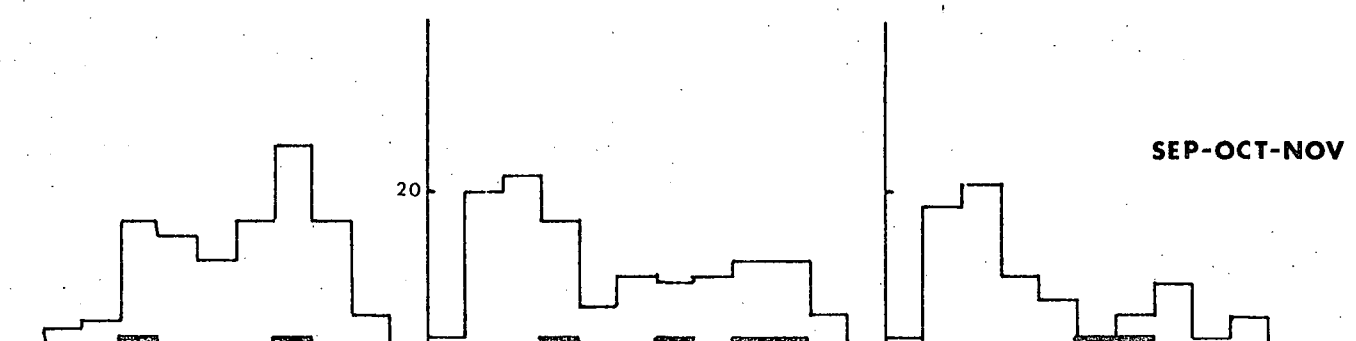


length mm.

JUN-JUL-AUG



SEP-OCT-NOV



DEC-JAN-FEB

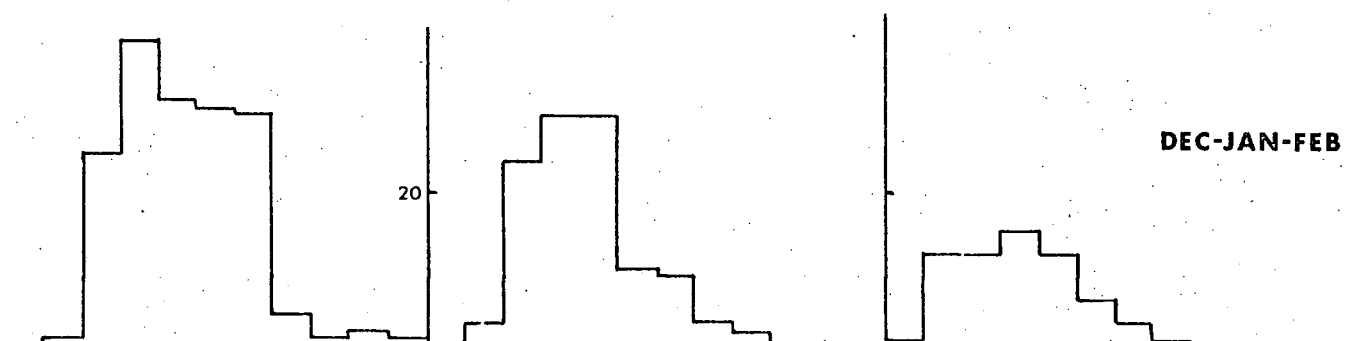


Fig. 2. Size frequencies of Schistocephalus and length frequencies of Gasterosteus aculeatus trachurus from Alouette Lake.

shaded - infected with Schistocephalus

stippled - not infected with Schistocephalus

Schistocephalus

Gasterosteus

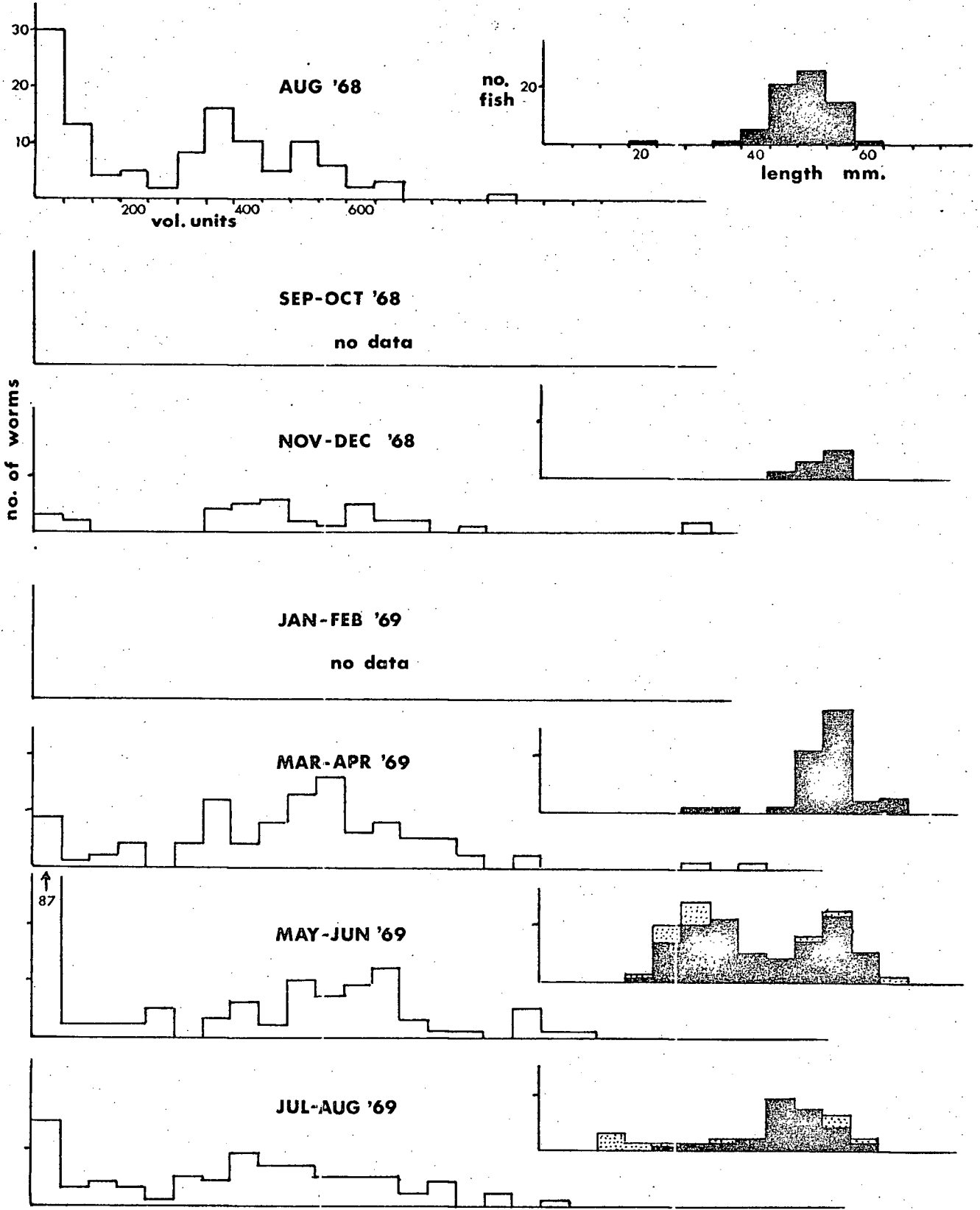


Fig. 3. Size of plerocercoids plotted against host length (from Alouette Lake, 1968-69).

open circle - multiple infection

solid circle - single infection

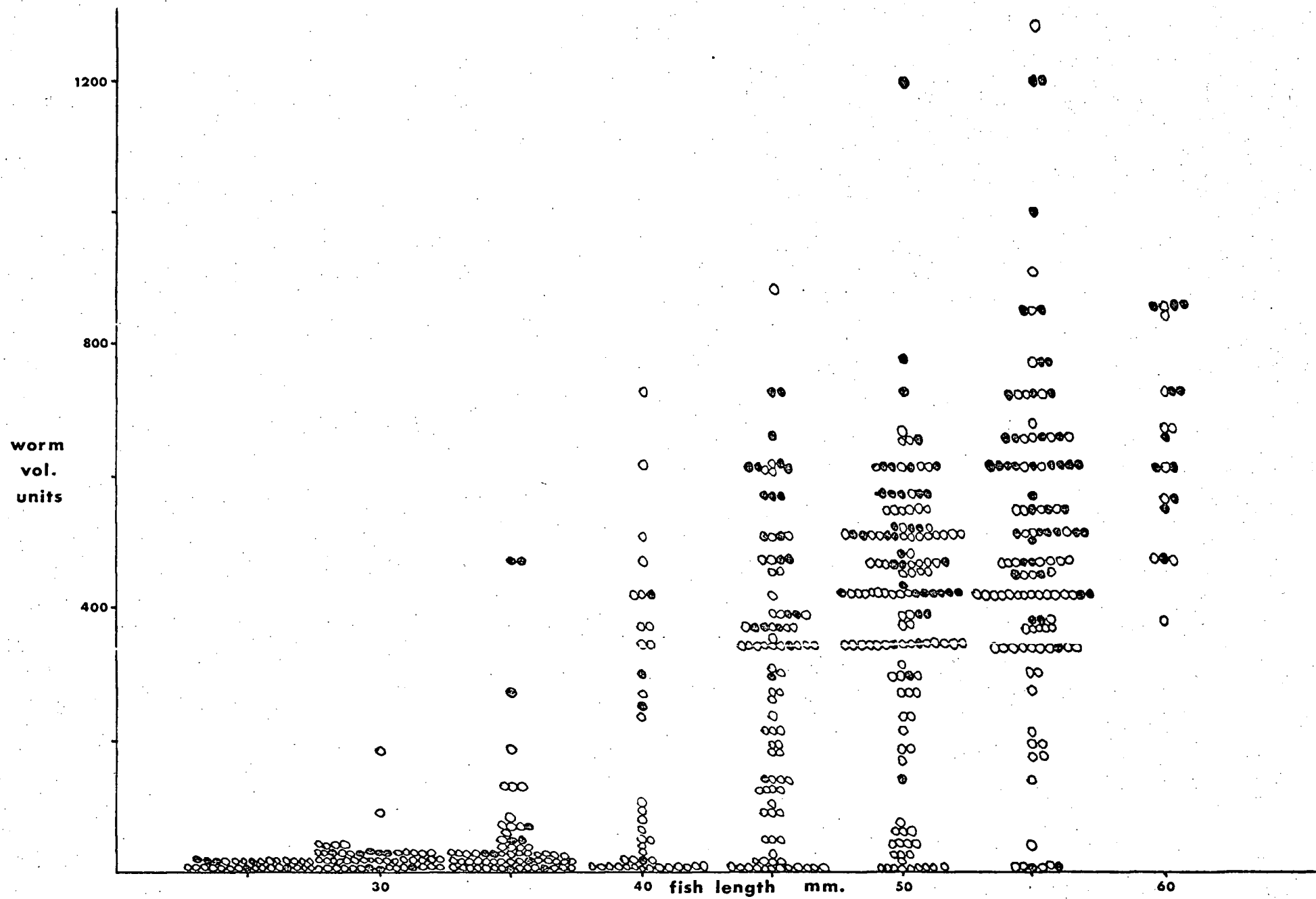


Fig. 4. Size of plerocercoids plotted against number present in host (from Alouette Lake, 1968-69).

- (a) From all fish in 50 and 55 mm. length groups.
- (b) From the 50 and 55 mm. fish in (a) omitting those with worms less than 325 volume units.
- (c) Means and standard deviations from (b). One standard deviation shown on either side of mean.

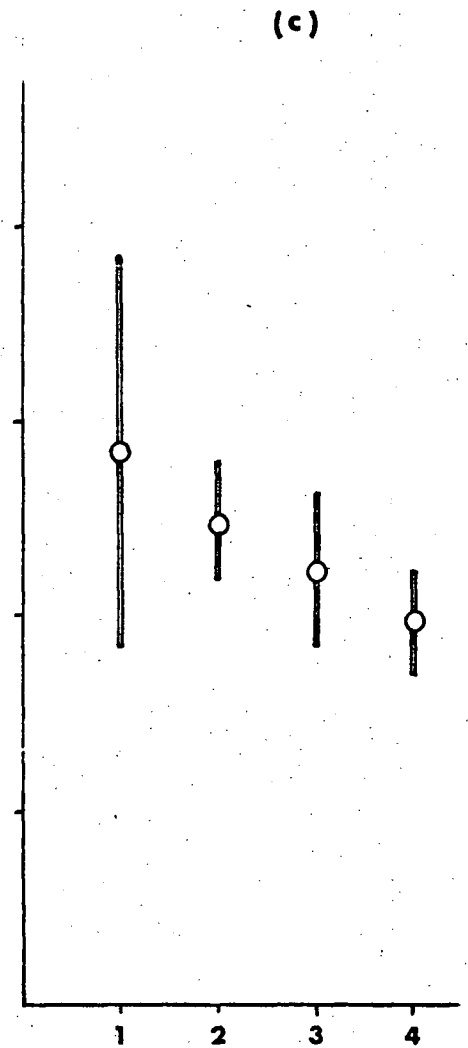
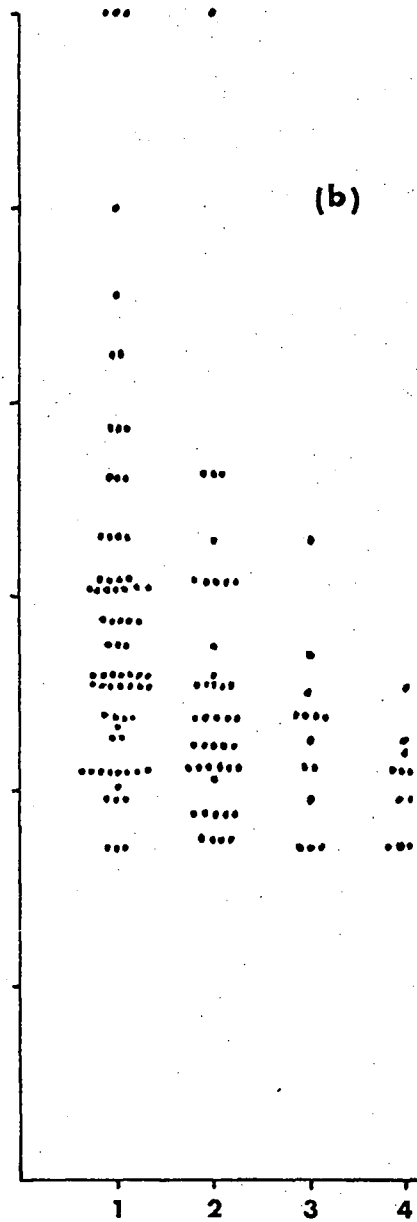
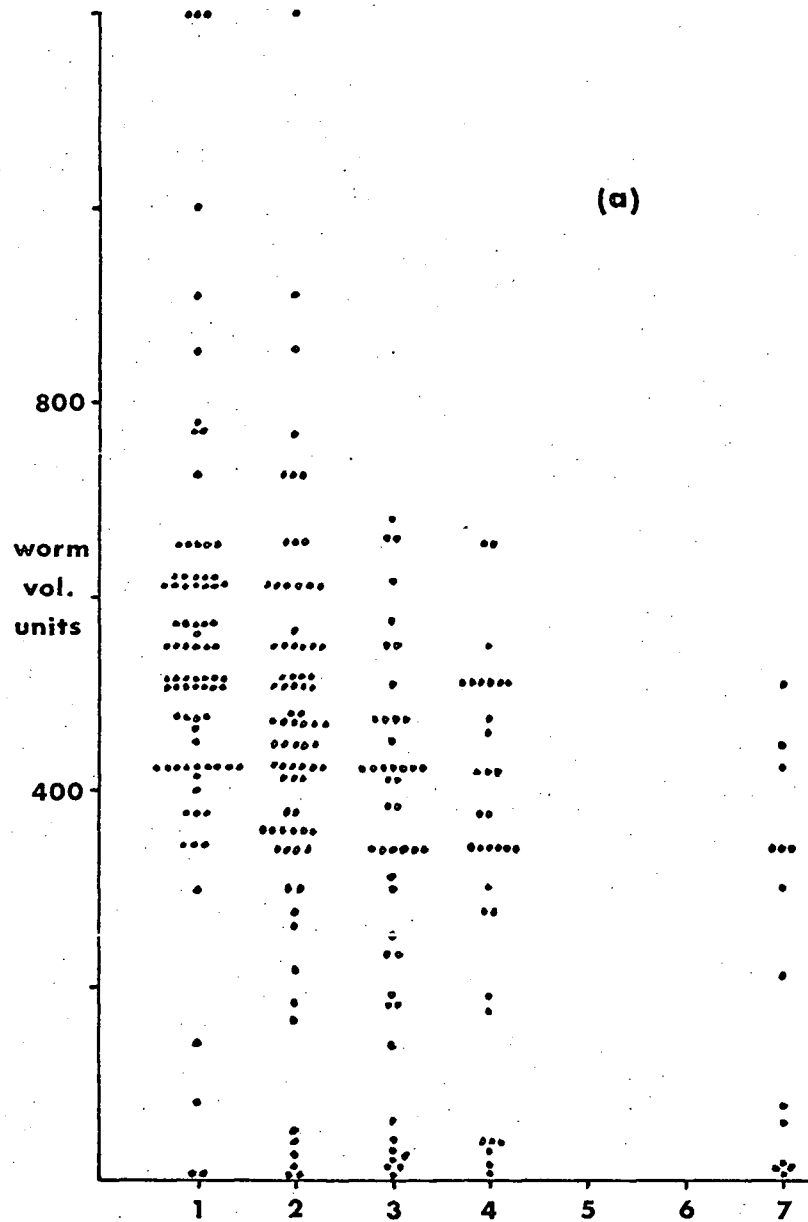


Fig. 5. Total worm burden plotted against fish length
(Alouette Lake fish, 1968-69).

(a) Random samples.

(b) Fish selected for use in experiments.

open circle - multiple infection

closed circle - single infection

cross - unparasitised fish

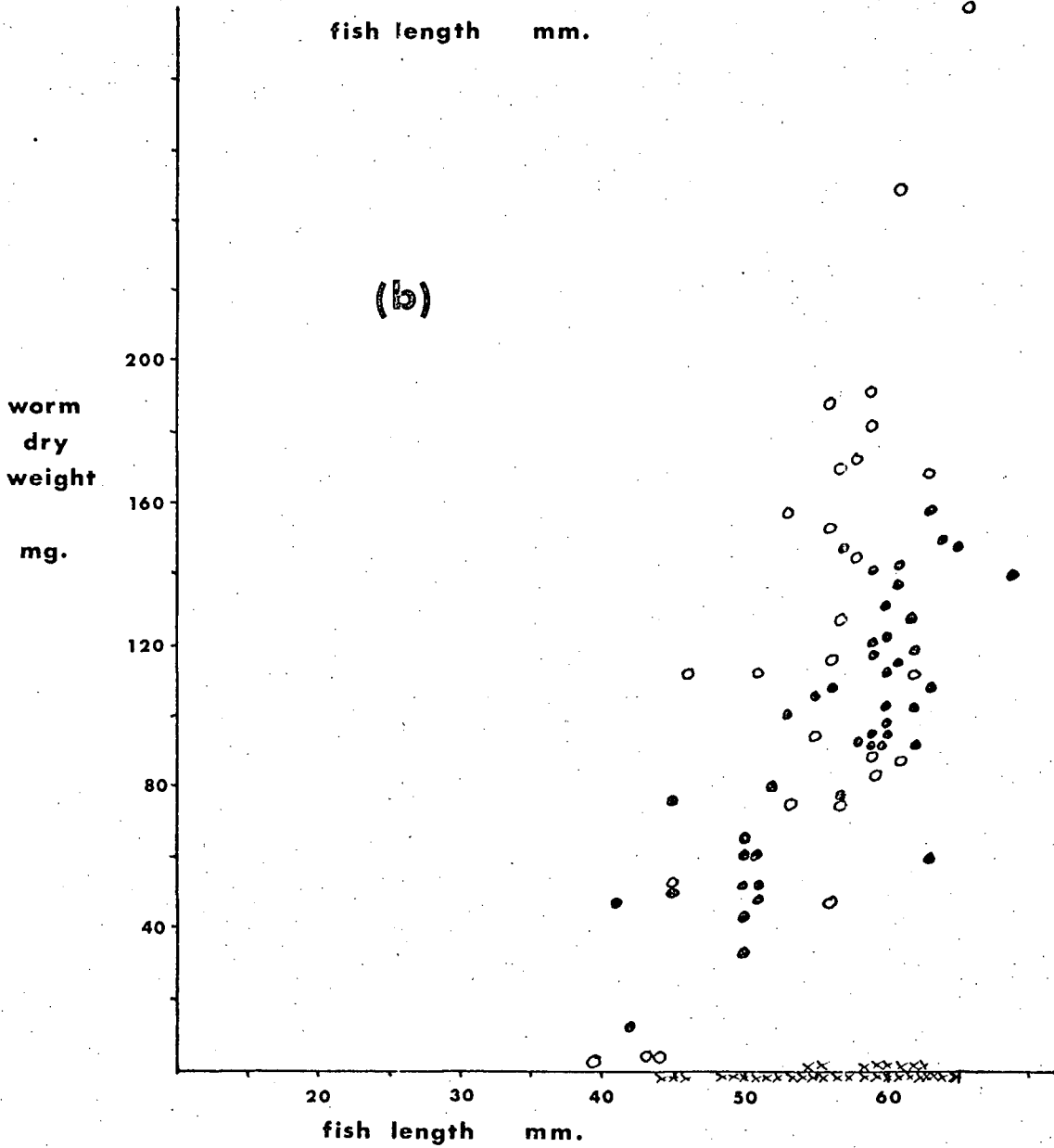
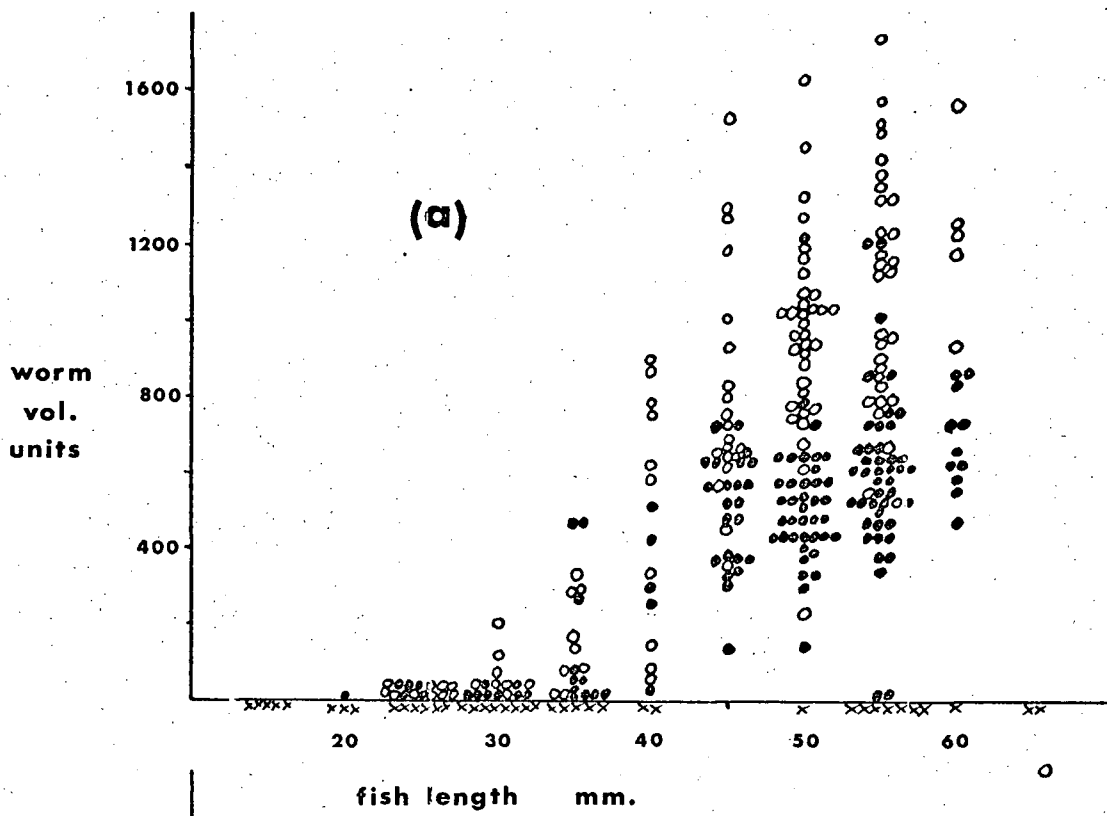
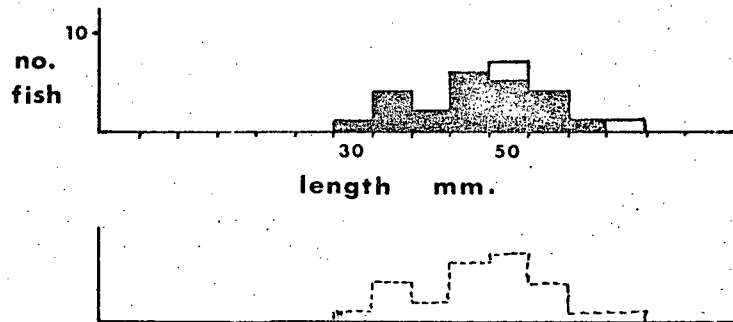


Fig. 6. Length frequencies of 3 fish samples for Haig Lake, Cortes Island.

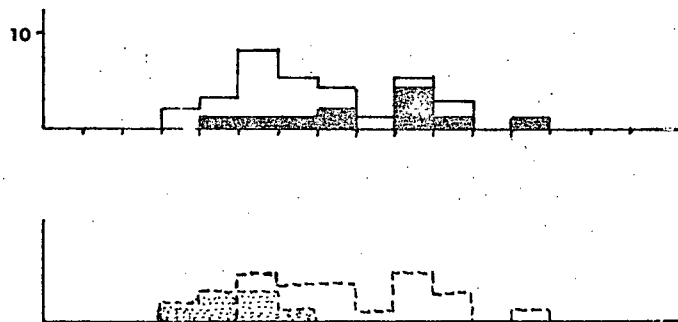
Upper histogram: shaded - parasitised

Lower histogram: stippled - reduced pelvic spines

Shore



Canal



Open water

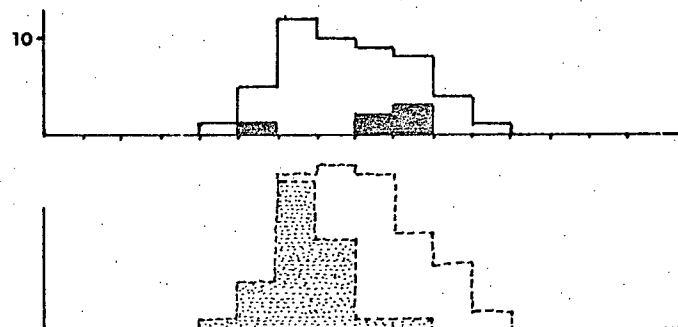


Fig. 7. Apparatus for measuring the oxygen consumption of swimming sticklebacks.

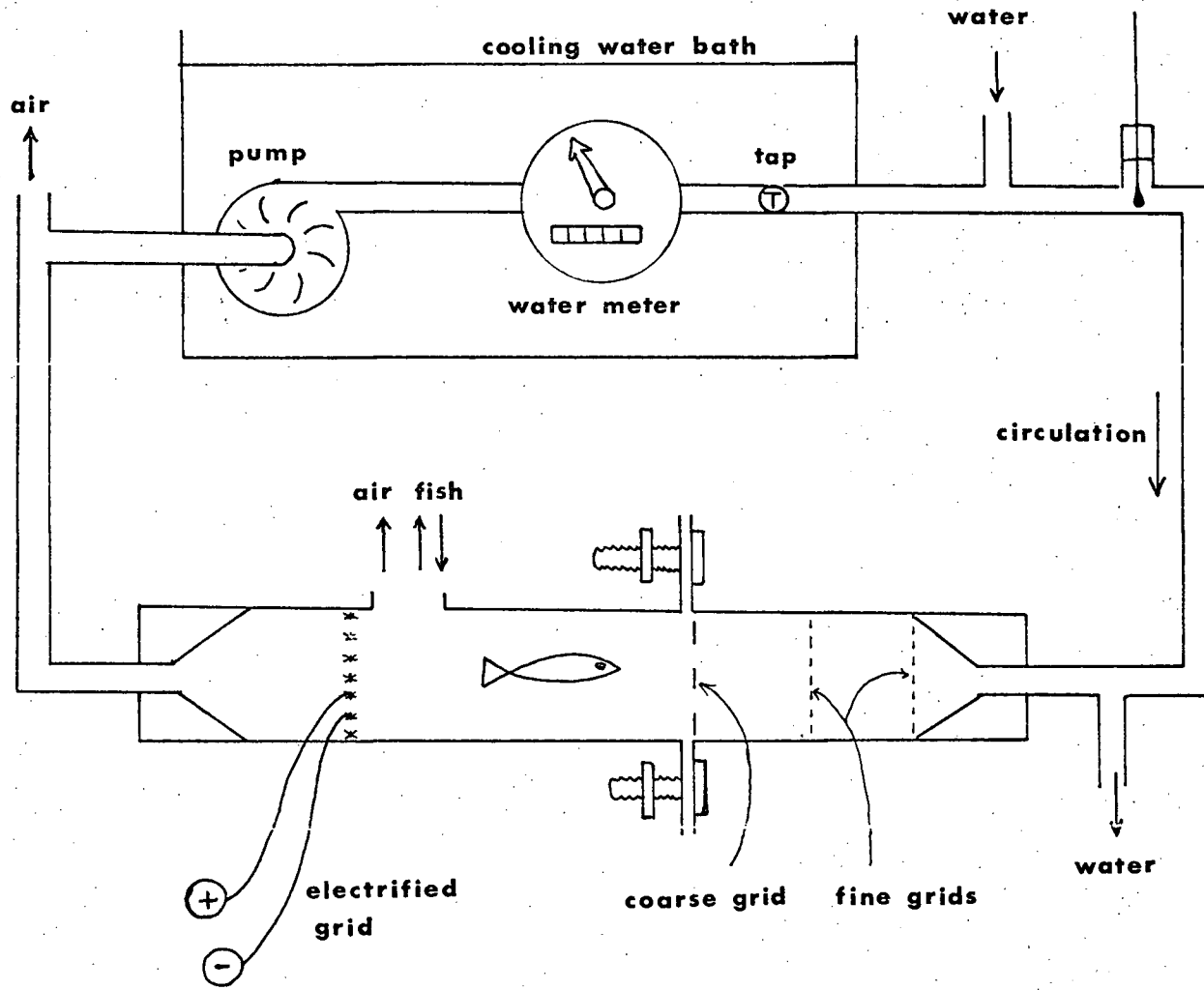


Fig. 8. Oxygen consumption of sticklebacks at different swimming speeds.

circles - Alouette Lake fish

square - Mike Lake fish

Amount of shading in proportion to $\frac{\text{worm wt.}}{\text{fish wt.}}$ ratio

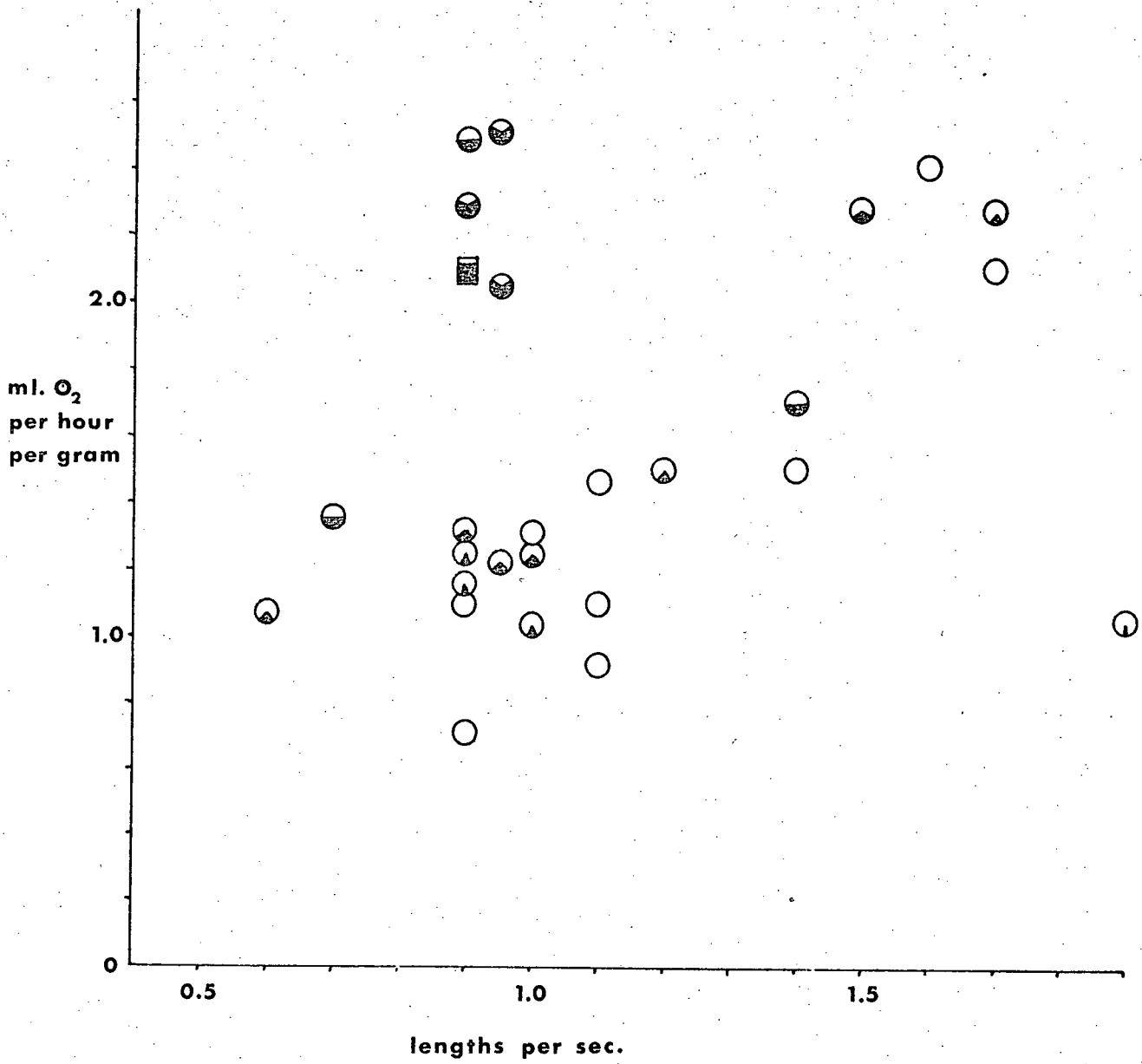


Fig. 9. Length/weight relationship for Gasterosteus aculeatus trachurus.

open circles - parasitised

closed circles - $\frac{\text{worm wt.}}{\text{fish wt.}}$ ratio greater than 0.46

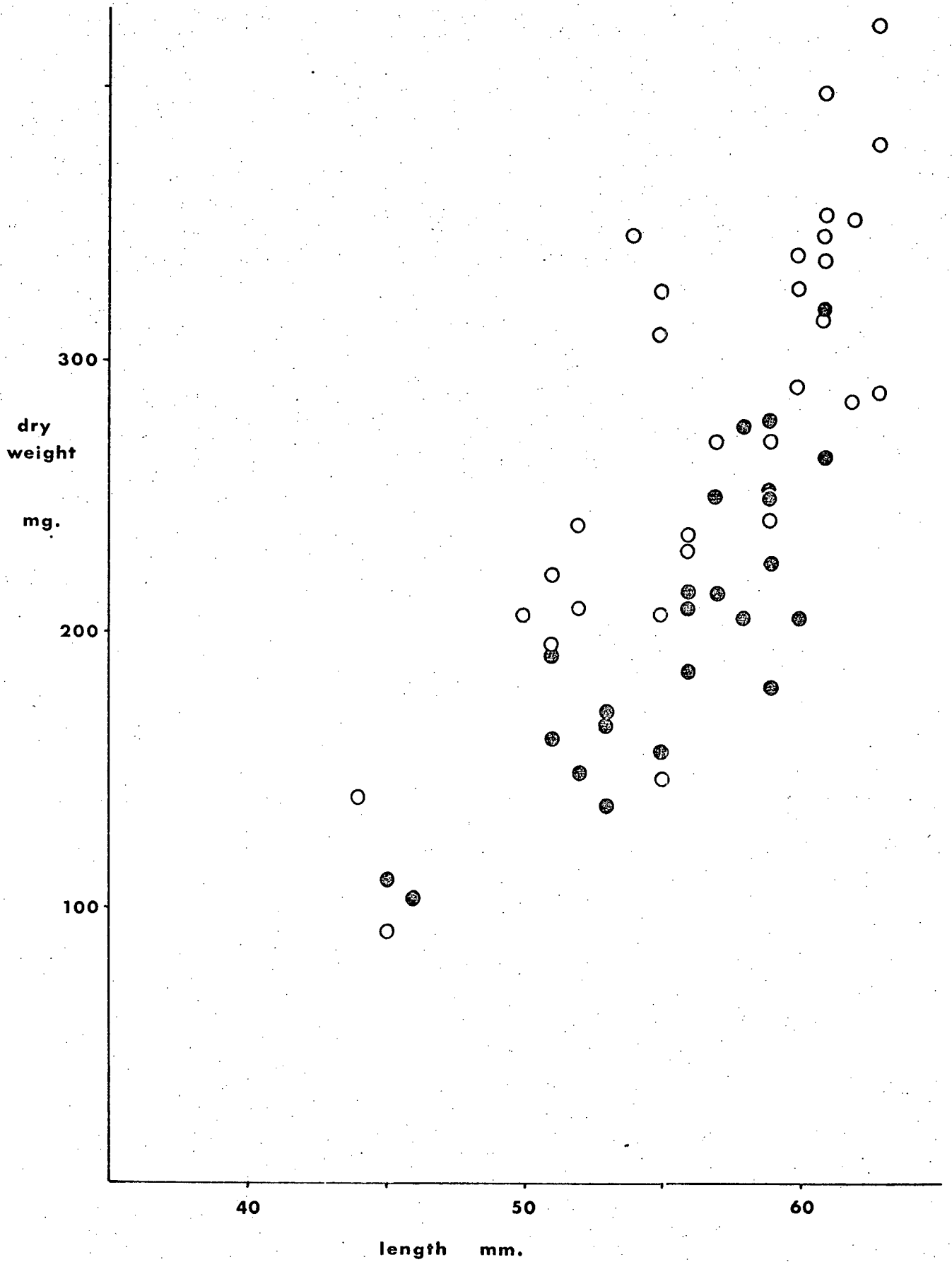


Table I. Schistocephalus infections in the Fraser Valley and environs

	Date	% infected to nearest 1%	Number in sample	Race	
Stave River	28.1.68	0	10	-	dip net
Little Campbell	15.8.68	0	69	mixed	pole seine
Q.E. Park	5.7.68	3	33	<u>leiurus</u>	dip net
	7.8.68	0	100	"	pole seine
	12.9.68	2	51	"	" "
Tin Can Creek (Musqueam Res.)	4.7.68	3	39	-	dip net
Pitt Lake	6.7.68	0	29	-	dip net
Horse Shoe Bay	9.7.68	0	105	<u>trachurus</u>	dip net
	9.8.68	0	32	"	" "
Burnaby Lake	3.10.68	0	11	<u>leiurus</u>	dip net
Cultus Lake	26.9.68	3	92	<u>trachurus</u>	trap
Haig Lake, Cortes Is.	6.9.68	88	26	<u>trachurus</u>	beach seine
Canal, Cortes Is.	6.9.68	34	32	<u>trachurus</u>	"
Gunflint Lake, Cortes Is.	6.9.68	12	50	<u>trachurus</u>	pelagic seine
Kendall Creek	13.3.69	1	50	<u>leiurus</u>	pole seine
Mike Lake	24.4.69	29	42	<u>leiurus</u>	dip net

... Cont.

Table I. (Cont.)

Coal Harbour	29.3.69	7	145	mixed	dip net from pier
	1.5.68	13	16	"	"
	31.5.68	36	33	"	"
	3.7.68	20	35	"	"
	15.8.68	3	86	"	beach seine
	3.9.68	4	54	"	" "
	10.10.68	6	108	"	" "
	20.10.68	0	46	"	seine from pier
	31.10.68	1	1000+	"	beach seine
	24.11.68	0	132	"	seine from pier
	16.12.68	0	75	"	" "
	7.1.69	0	68	"	" "
	12.2.69	0	146	"	beach seine
	26.3.69	0	27	"	" "
	3.4.69	0	154	"	seine from pier
	8.5.69	1	140	"	" "
	27.6.69	2	65	"	beach seine
	14.8.69	1	148	"	seine from pier
Alouette Lake	25.8.68	100	67	<u>trachurus</u>	beach seine
	6.10.68	100	18	"	" "
	24.12.68	100	18	"	" "
	8.3.69	100	27	"	" "
	20. 4.69	100	35	"	" "
	13.5.69	100	41	"	" "
	23.5.69	72	67	"	" "
	5.6.69	80	35	"	" "
	7.7.69	88	17	"	" "
	7.8.69	75	52	"	" "

Table II. Number of worms per fish. Alouette Lake 1968-69

Fish length group mms.	No. of fish sampled	No. fish infected	Total no. worms	Infected fish Average no. worms	Max. no. worms found
15	5	0	0	0	0
20	4	1	1	1.0	1
25	25	15	30	2.0	5
30	26	16	48	3.0	11
35	24	19	66	3.5	10
40	17	15	44	2.9	16
45	45	45	98	2.2	10
50	71	70	133	1.9	7
55	84	77	121	1.6	4
60	18	17	22	1.3	2
65	2	0	0	0	0

Table III. Numbers of fish with specific numbers of worms,
(All fish, Alouette Lake 1968-69)

No. of worms	Aug. '68	Dec.	Mar. '69	April	May	June	July	Aug.	Totals	
0	0	0	0	0	3 (18)	4 (1)	2	6 (9)	15 (28)	43
1	15 (3)	9	12	16 (1)	24 (22)	8 (2)	6 (1)	27 (3)	117 (32)	149
2	8 (2)	4	12	12	12 (10)	2	3 (1)	2 (1)	55 (14)	69
3	9	2	1	6	2 (5)	1 (1)			21 (6)	27
4	4 (1)	3	1	1			1	3 (1)	13 (2)	15
5	3				(2)		(2)		3 (4)	7
6					(2)				(2)	2
7	2				(1)				2 (1)	3
8							1		1	1
9					(1)			(1)	(2)	2
10	1		(1)		(1)				1 (2)	3
11					(1)				(1)	1
16	(1)								(1)	1
Total	42 (7)	18	26 (1)	35 (1)	41 (63)	15 (4)	13 (4)	38 (15)		

No brackets = fish 45 mm. and over
 Brackets = fish less than 45 mm.

Table IV. Mortality of infected and uninfected Gasterosteus

Fish kept in lab. aquaria at 12-15°C

Coal Harbour Fish

Expt. A 4th Aug.-12th Oct. 69 days (9 weeks)

	Died	Alive
Infected	5	3
Uninfected	1	16

Expt. B 20th Oct.-29th Jan. 100 days (14 weeks)

	Died	Alive
Infected	4	2
Uninfected	3	12

Combined A and B

	Died	Alive	Totals
Infected	9	5	14
Uninfected	4	28	32
Totals	13	33	46

Table V. Standard respiration rate of paired fish

Date	Control fish				Parasitised fish				Expt. Temp. °C	Acclim. Temp. °C
	Length mm.	Fish wt. gm.	Worm wt. gm.	O ₂ ml/hr.	Length mm.	Fish wt. gm.	Worm wt. gm.	O ₂ ml/hr.		
11/12 June	56	0.2291	-	0.117	58	0.2050	0.1717	0.164	10	10
16/17 June	56	0.2291	-	0.146	58	0.2050	0.1717	0.174	11	11
18/19 June		0.1571	-	0.113		0.1556 0.1365	0.0832 0.0086	0.131 0.101	12 12	11 11
29/30 June	62 60 55 61	0.3523 0.3265 0.2073 0.3466	- - - -	0.135 0.139 0.091 0.094	62 59 56 60	0.3327 0.2776 0.2146 0.3900	0.1121 0.1405 0.1541 0.1308	0.149 0.131 0.110 0.148	10 10 10 10	10 10 10 10
10/11 July	50 62	0.1628 0.2566	0.0444 0.0909	0.265 0.334	46 59	0.1037 0.2256	0.1105 0.1812	0.189 0.383	21 20	11 11
4/5 Aug.	51 60	0.2205 0.2916	- -	0.209 0.297	51 58	0.1620 0.2760	0.1127 0.1452	0.181 0.305	18 18	12 12
12/13 Aug.	59	0.2697	-	0.263	59	0.2106	0.0913	0.237	17	14

Table VI. Oxygen consumptions of parasitised fish as observed and as calculated

Total O ₂ ml/hr. observed	Fish tissue O ₂ ml/hr. estimated†	Difference ml/hr.	Worm tissue O ₂ ml/hr. estimated*
0.164	0.105	0.059	0.013
0.174	0.132	0.042	0.013
0.101	0.098	0.003	0.002
0.149	0.126	0.025	0.008
0.131	0.120	0.011	0.006
0.110	0.094	0.016	0.009
0.148	0.105	0.044	0.007
0.189	0.169	0.020	0.024
0.383	0.293	0.090	0.026
0.181	0.154	0.027	0.022
0.305	0.281	0.014	0.036
0.237	0.206	0.031	0.014

* Values calculated from in vitro experiments of Davies and Walkey, 1966

† Values calculated from respiration rate of control fish

Table VII. Total oxygen consumption as per gram fish tissue only

Control mls./hr./gm.	Parasitised mls./hr./gm.
0.51	0.80
0.64	0.85
0.72	0.84
	0.74
0.38	0.45
0.43	0.47
0.44	0.47
0.27	0.38
1.63	1.82
1.30	1.70
0.95	1.12
1.02	1.05
0.98	1.13