30677

NATIONAL LIBRARY
OTTAWA

CANADA

BIBLIOTHÈQUE NATIONALE
OTTAWA

NAME OF AUTHOR........TODD FOLSOM........

TITLE OF THESIS. An Ecological Study of *Dugesia tigrina* (Turbellaria: Tricladida) in Lake Wabamun, Alberta, a thermally enriched lake.

UNIVERSITY..University of Alberta........

DEGREE FOR WHICH THESIS WAS PRESENTED...M.Sc.........

YEAR THIS DEGREE GRANTED.....1976........

Permission is hereby granted to THE NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(Signed)..Todd Folsom........

PERMANENT ADDRESS:

11102 78 Ave
Edmonton Alberta

DATED...2 June........1976

NL-91 (10-68)

THE UNIVERSITY OF ALBERTA

AN ECOLOGICAL STUDY OF *DUGESIA TIGRINA* (TURBELLARIA: TRICLADIDA) IN LAKE WABAMUN, ALBERTA, A THERMALLY ENRICHED LAKE.

by

TODD C. FOLSOM ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE.

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL, 1976

UNIVERSITY OF ALBERTA

FACULTY OF GRADUTE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance a thesis entitled

AN ECOLOGICAL STUDY OF DUGESIA TIGRINA
(TURBELLARIA: TRICLADIDA) IN LAKE WABAMUN,
ALBERTA, A THERMALLY ENRICHED LAKE.

submitted by Todd C. Folsom
in partial fulfilment of the requirements for the degree of
Master of Science

Hugh F. Clifford
Supervisor

W. C. Mackay

J. L. Mohr

Michael Hickman

Date 2 June 1976

ABSTRACT

The triclad flatworm Dugesia tigrina (Girard) is abundant in Lake Wabamun, a west central Alberta lake enriched with thermal effluent. A year's study was carried out at Lake Wabamun to investigate D. tigrina's population ecology and the effect a thermally altered environment might have on Dugesia. Data on reproductive parameters, growth and shrinkage rates, temperature relations, size structure, and biomass were collected.

Two hypotheses were tested. The first stated that triclads are characteristically limited by food during and after breeding. Food shortage causes shrinkage of adults and mortality of young and small triclads, and this re-adjusts the population size to the pre-breeding level. This hypothesis is supported for populations in the thermally altered and the normal lake habitats.

Through measurements of growth, righting reaction time, and temperature preferences, D. tigrina was found to prefer warm water above about 15°. Triclads from both populations grew rapidly in spring and began to produce cocoons. Breeding intensified food competition, causing shrinkage and mortality. The spring gain in length and biomass was lost through shrinkage, and autumn numbers of triclads were similar to pre-breeding numbers.

The second hypothesis proposed a difference in

reproductive strategy for populations in the two environments. The thermally enriched region of the lake was thought to be more stable and constant, thereby reducing density independent mortality. The K- selection pressure should then cause changes in the reproductive strategy to cope with the observed high numbers of <u>Dugesia</u>. The thermally affected triclads were, contrary to theory, found to be twice as fertile as normal lake triclads. This is interpreted as a population dynamic effect due to mortality caused by mechanical weed harvesting and other factors. No differences in reproductive strategy between populations could be detected, hence the hypothesis is not supported.

ACKNOWLEDGMENTS

I would like to thank Dr. H.F. Clifford for his supervision of this study and critical review of the manuscript. Dr. T.B. Reynoldson generously imparted his knowledge of triclad biology. Dr. J.F. Addicott provided helpful discussion and reviewed the manuscript. Drs. W.C. MacKay and M. Hickman also reviewed the manuscript.

Doug Currie gave invaluable assistance in the field and laboratory and performed all SCUBA diving. H. Hamilton, T. Lee, and C. Wilcox also assisted in the field. C. Wilcox worked on many of the figures. Other advice and assistance came from R. Baker, G. Bergstrom, H. Boerger, H. Hamilton, G. Hutchinson, J. Rassmussen, and R. Seward. Land owners at Point Alison and Fallis Point gave permission to cross their property.

Financial support came from graduate teaching assistantships and research grants to Dr. H.F. Clifford from the National Research Council.

TABLE OF CONTENTS

ABSTRACT iv

ACKNOWLEDGMENTS vi

LIST OF TABLES ix

LIST OF FIGURES x

INTRODUCTION 1

DESCRIPTION OF STUDY SITES 7

    The Heated Water Site 7

    The Normal Lake Site 11

METHODS 13

RESULTS 18

    Water Chemistry 18

    Temperature 21

    Macrophyte Harvesting 23

    Food Habits 25

    Temperature Relations 28

        Righting Reactions 28

        Temperature Preference 31

        Growth and Shrinkage of Adults 40

        Growth of Young 41

    Cocoon Production 44

    Young 47

    Adults 51

    The Total Population 53

The PA Population 53
The FP Population 58
Mean Length and Biomass 62
DISCUSSION 68
COMPARATIVE SYNOPSIS 76
LITERATURE CITED 78
APPENDIX 1: Percentage composition of samples 82
APPENDIX 2: Sampling data 85
APPENDIX 3: Mean number/brick, mean length, standard error, and biomass 87
APPENDIX 4: Mean length of young grown at two temperatures 89

LIST OF TABLES

Table	Description	Page
1.	Number and number per dry weight gram of triclads and cocoons found on harvested and harvestable macrophytes.	26
2.	Summary of reproductive data for PA and FP showing the seasonal production of young and cocoons.	48

LIST OF FIGURES

Figure	Description	Page
1.	Morphometric map of Lake Wabamun showing study sites, power stations, and canals.	8
2.	Map of Kapasiwin Bay with study site and macrophyte harvesting sector.	9
3.	Seasonal variation in water chemistry parameters from March 1975 (month 1) to March 1976 (month 13).	19-20
4.	Surface water temperature.	22
5.	Righting reaction times over the range of 5° to 26°.	30
6.	Diagram of temperature preference apparatus.	32
7.	Temperature preference of PA <u>Dugesia</u> as shown by number of triclads (histograms) in each region of the temperature tube.	34-35
8.	Temperature preference of FP <u>Dugesia</u>.	38-39
9.	Growth of FP and PA young at two temperatures.	43
10.	The percentage of young and adults present in each population from mid June to mid September.	50
11.	Size structure histograms of the percentage of PA <u>Dugesia</u> in each size class.	54-55
12.	The cumulative percentage in each size class for the PA population throughout the year.	57
13.	Size structure histograms of the percentage of FP <u>Dugesia</u> in each size class.	59
14.	The cumulative percentage in each size class for the FP population throughout the year.	61
15.	Seasonal variation in mean length of each population.	63
16.	Regression lines of the length-biomass	

relationship. 65

17. Seasonal variation in total biomass as mg-percent or mg per 100 individuals. 66

INTRODUCTION

Most ecological studies of free-living flatworms have dealt with descriptive natural history of the organisms, e.g. distributional records, descriptions of new species and their habitats, studies of vertical stream zonation, substrate, current, and temperature preferences (see Boddington and Mettrick 1971; Riser and Morse 1974). There are few triclad studies, especially in North America, that were designed to test hypotheses about patterns of distribution and abundance.

In contrast, the British triclad fauna has been studied extensively by T.B. Reynoldson and his students. Breeding, fecundity, recruitment, distribution, and population size structure have been examined for most British species (Reynoldson 1960-1961, Taylor and Reynoldson 1962, Young and Reynoldson 1965, Reynoldson and Sefton 1972). Reynoldson found that triclad numbers are regulated by intraspecific competition for food and do not flucuate greatly over the year because of almost continual food shortage. Triclads shrink when starved and this delays mortality and contributes to the numerical stability. Breeding increases numbers and the competition for food. Consequently, many young and shrunken adults die and this re-adjusts population size. Also, interspecific competition for food is thought to restrict the distribution and abundance of lake-dwelling triclads (Reynoldson 1966a). Additional studies on food refuges (Reynoldson and Davies 1970), food overlap

(Reynoldson 1975), recruitment (Reynoldson 1966b), and competition (Reynoldson 1964, Reynoldson and Bellamy 1971 1973) support these hypotheses.

Pickavance (1968 1971a 1971b) studied an asexual race of D. tigrina in Britian, where it is an immigrant, with special attention to D. tigrina's life cycle, food habits, and interaction with other species. Pickavance found that population size structure at the start of spring showed a preponderance of large individuals, but as asexual reproduction occurred, the number of small individuals increased until intraspecific competition for food halted reproduction and caused shrinkage. Predation on the asexual race was believed to cause over-winter mortality, and this reduced numbers to pre-breeding levels. This is in contrast to sexually reproducing species where mortality by starvation of young and small triclads is the important factor in population regulation (Reynoldson 1960 1961 1966b, Taylor and Reynoldson 1962).

Seasonal changes in chemical composition and food reserves of D. tigrina were studied by Boddington and Mettrick (1971) for a Toronto, Canada, population. The amount of lyo-glycogen, a food reserve, was found to decrease rapidly, as did triclad size, when numbers were increasing in the breeding season. The food reserves and worm length increased again in autumn, presumably after mortality reduced competition. They interpret this as support of Reynoldson's (1966a) hypothesis that population size is regulated by food shortage.

Dugesia tigrina occurs from coast to coast in North America and into South America (Ball 1969), and it has emigrated to Europe (Dahm 1955). The northen limit of its range is not known, but it is found in southern Maine (pers. obs.), New Brunswick, Quebec, Ontario, Alberta, and British Columbia (Ball 1969). Because of low summer temperature and a short ice-free season, I suspect that _Dugesia_ probably does not extend far into the boreal forest zone. My study, therefore, is on a population close to the northern limit of its distribution.

Dugesia species are warm-water species. They generally require higher water temperatures for successful breeding than other triclads (Russier-Delolme 1965, Reynoldson, Young, and Taylor 1965). _Dugesia_ has a greater acclimation capacity for higher temperatures and a longer righting reaction time at cold temperature than other triclads (Chandler 1966). Consequently, _D. tigrina_ is usually excluded from cold headwaters of streams (Chandler 1966; Pennak 1953) and is mainly found in lakes and slow streams.

Triclads are predaceous upon damaged or dying invertebrates, which cannot escape from the slow-moving triclads. The flatworms are attracted by body juices or "struggling" behavior of damaged prey. Triclads may rest in sheltered areas, such as under rocks, for long periods until attracted to potential prey, or they may begin a cruising activity in order to encounter their prey. Feeding is communal and results in a large number of triclads covering the prey. If a triclad is starved, it will shrink. The process is easily reversed when the animal can again consume adequate food. Shrinkage or, conversely, growth of triclads over time, provides a means of gauging intraspecific competition for food (Reynoldson 1964, Reynoldson and Bellamy 1967).

Little is known about the population ecology of native North American triclads. This study represents one of the first attempts to gain such knowledge. The study site is Lake Wabamun, a thermally enriched lake in west central Alberta. Since D. tigrina is very abundant in the lake, I felt that this would be an excellent site for the study of Dugesia's basic ecology and its responses to a thermally altered environment.

The broad objectives of the study are twofold. The first is to gain basic knowledge of the reproductive ecology and the effect of intraspecific competition on populations of D. tigrina. The second is to compare reproductive parameters and population characteristics between a normal lake site population and a population influenced by heated water discharge.

A year's study was carried out to follow changes in population numbers, size structure, and biomass. Reproductive parameters measured were fecundity, number and size of young, length of adults at maturity, length and timing of the breeding season, and recruitment. Basic biological information was obtained on temperature preferences, righting reaction times, growth rate of young and adults at different temperatures, and shrinkage rates at different temperatures.

Two hypotheses were tested. The first states that triclads compete for food and that this competition causes mortality of small individuals and shrinkage of large ones. The mortality reduces competition, allowing shrunken individuals to grow and reach adult size before they start to breed the next spring. The appearance of young increases competition until mortality re-adjusts the population to its food supply. The hypothesis can be supported if 1) shrinkage is observed after breeding; 2) the percentage of adults increases in spring and then goes down; 3) numbers increase through breeding and then decline to pre-breeding levels.

The second hypothesis concerns differences in reproductive biology between the two populations in the context of r- and K- selection. This theory states that certain predictable changes will occur in the reproductive strategy of a species according to the degree of density-dependence of mortality factors (Pianka 1970, Gadgil and Solbrig 1972). Species or populations existing near their carrying capacity (K) for long periods usually experience high density-dependent mortality. They are often found in stable, constant environments. Competitive ability, rather than a high rate of increase, is selected for. Species or populations occurring in environments imposing high density-independent mortality will often be below carrying capacity. Selection will favor a high rate of increase (r). Organisms under r- selection should allocate a greater proportion of their energy or resources to reproduction than K- selected organisms (Gadgil and Solbrig 1972).

The thermally affected regions of Lake Wabamun were thought to be more stable and constant than the normal part of the lake, which freezes over. These regions should be protected from harsh environmental conditions that may create density-independent mortality in the normal lake. A warm-water species, such as Dugesia tigrina, should be able to function all year and breed for longer periods in the heated region. This should increase competitive pressures and K- selection. At low winter temperatures in the normal lake, D. tigrina does not move or feed very much. They also have a shorter summer breeding season. This population should be more r- selected if density-independent mortality is greater in the normal lake.

The degree of r- or K- selection can be evaluated through several population characteristics. The K- selected Dugesia are hypothesized to have a low fecundity and recruitment, larger, more competitive young, fewer young per cocoon, and a greater length at maturity (delayed maturity). Dugesia that are r- selected should have high fecundity and recruitment, smaller young, more young per cocoon, and a shorter length at maturity (Pianka 1970).

DESCRIPTION OF THE STUDY SITE

The Heated Water Site

The site chosen for studying the ecology of D. tigrina is Lake Wabamun, a large moderately eutrophic lake (Figs. 1 and 2). It is 64km west of Edmonton in the boreal-parkland transition zone. The length is 19.2km; the mean width is 4.3km; the mean depth is 5.4m. Due to the proximity of strippable coal, two thermal electric generating stations, which use lake water for cooling purposes, have been built on the lake. The Wabamun station is on the north shore near the hamlet of Wabamun; it began operations in 1956. Discharge of heated water from the station keeps a large area of Kapasiwin Bay ice-free in winter and elevates the water temperature throughout the year. This has caused substantial changes in the macrophyte community composition (Allen 1973) and in the abundance of animals and plants. The greater primary production caused by longer periods of high light levels and the elevated temperatures creates a large increase in biomass over unaffected areas of the lake. Nuisance growths of Elodea canadensis and other macrophytes forced the Calgary Power Company to initiate a weed harvesting program in 1972 (Gallup, Hickman, and Rasmussen 1975). A number of recent studies have examined the effects of the lake's thermal effluent on macrophytes (Allen 1973), phytoplankton (Wheelock 1969, Noton 1974), epiphytes (Klarer 1973), rotifers (Horkan 1971), and whitefish (Ash 1974).

The Wabamun power plant draws its cooling water from

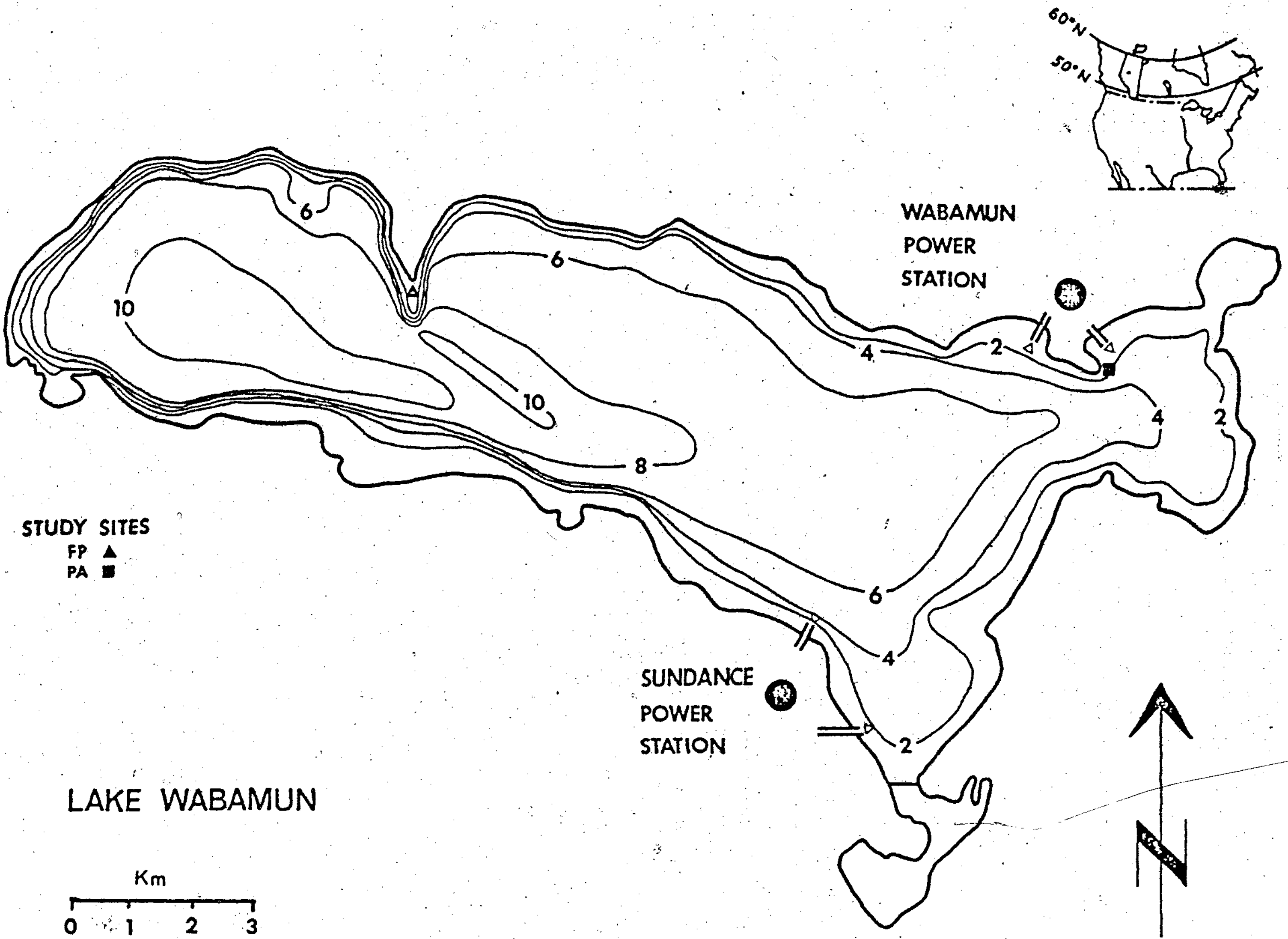


Figure 1. Morphometric map of Lake Wabamun showing study sites, power stations, and canals. Depth is in meters.

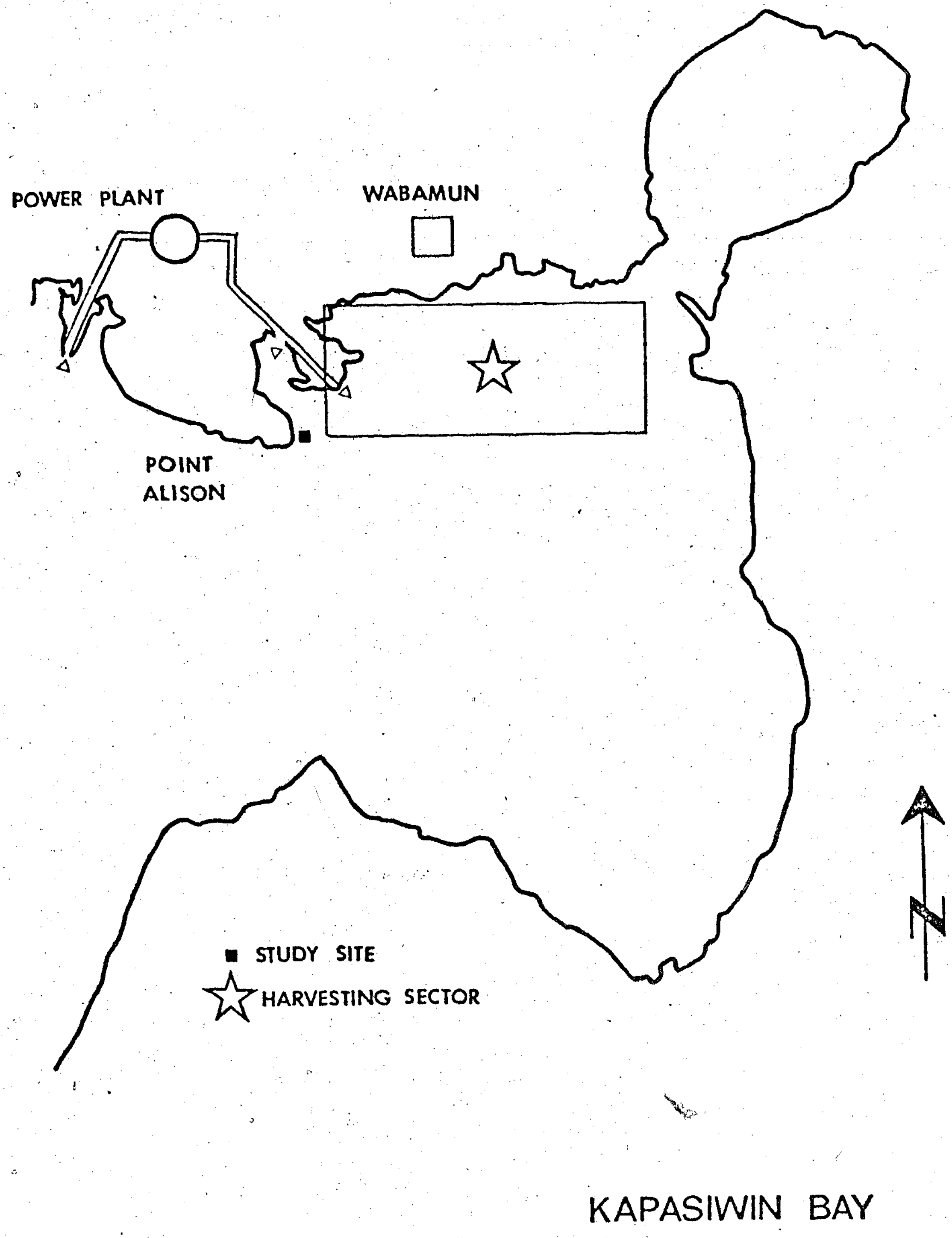


Figure 2. Map of Kapasiwin Bay with study site and macrophyte harvesting sector.

the lake through an inlet canal and discharges the thermal effluent through an outlet canal into Kapasiwin Bay. The two canals are separated by Point Alison, a jutting, hooked moraine. The point forms the western end of the bay and tends to shelter some of the bay from prevailing westerly winds. My sampling site was chosen at the extreme end of the point, at the only place offering a hard substrate and shelter from wave action. The Point Alison heated water site and its triclad population will hereafter be designated PA.

The littoral substrate is of sand and rocks, but rapidly changes to ooze farther from shore. The emergent macrophytes Phragmites and Scirpus validus grow nearby and the submersed macrophytes Potamogeton richardsonii and P. zosteriformis grow from the ooze substrate. P. pectinatus, Elodea canadensis, Chara globularis, and Myriophyllum exalbescans are other important bay plants. All of the rooted plants provide substrates for D. tigrina.

The mouth of the outlet canal is about 250m to the east. The heated water that flows out can be 8° above ambient water temperature in the summer and 19° above ambient in the winter. This water forms a plume that rests on colder water below, resulting in a sharp drop in temperature below the first meter. The heated water is often supersaturated with oxygen, while the normal lake waters rarely exceed 100% saturation (Gallup and Hickman 1975).

Wind exerts a great influence on the shape and position of the thermal plume and consequently the ice free area

(Horkan 1971, Nursall and Gallup 1971). Westerly winds prevail and usually blow the plume into Kapasiwin Bay. Easterly winds are common, and these tend to blow the plume toward Point Alison and the inlet canal. The PA study site has not been observed to freeze over.

The shoreline area is subject to blanketing by stagnant masses of dead plant matter. In summer and especially autumn, at the time of macrophyte die-off, partially decomposed plants are washed against the shoreline where they pile up on the bottom and cause the emigration or death of triclads. Young triclads in cocoons might be asphyxiated when the bottom is covered with these decaying weeds. On January 17, dissolved oxygen was 3.9 ppm within the mass of plants and a distinct sulfer dioxide odor was detected. The absence of triclads from the site under such conditions forced me to use alternate means of sampling on several occasions.

The Normal Lake Site

The normal lake site is located about 11km from PA at another jutting moraine known as Fallis Point. The sampling site is located about 100m off the end of the point, in shallow water (1.3m). The area is unsheltered from waves. The substrate is sand, rocks, and small pieces of coal. Common plants are <u>Scirpus</u>, <u>Potamogeton</u>, <u>Hippuris</u> <u>vulgaris</u>, and <u>Chara</u>. The blue-green alga <u>Nostoc</u> often covers the rocks.

This site is fairly inaccessible. There is about 1km of private land between the site and a public boat launching site. The landowner kindly gave permission for access during autumn and winter sampling trips, but most summer visits were by boat. It was necessary to use SCUBA gear extensively at this site. However, after the water level had receded in autumn it was possible, when the water was calm, to reach the site by wading out in chest waders. Heavy waves often severely hampered or prevented sampling.

This site was chosen when, after a search of the Fallis area, a single _Dugesia_ was found near the shore in May. Repeated searches of the shoreline during the summer never revealed any more triclads. Wave action may be responsible for their absence, although it was the lee side of the point being searched. Interactions with the abundant leeches may inhibit _Dugesia_'s presence along the shoreline. _Dugesia_ was never observed on plant substrates. The main concentration of triclads was underneath rocks in deeper water away from the shore. The normal lake site at Fallis Point and its triclad population is hereafter referred to as FP.

METHODS

Field samples were taken from March 1975 to March 1976. Temperature data and water chemistry samples were collected over the whole span. Biological samples were taken at PA from March to March and at FP from May to November 1975. Temperature was measured with a hand thermometer and a Ryan model D-30 recording thermograph. Dissolved oxygen samples were analysed by the Alsterberg modification of the Winkler Method (A.P.H.A. 1971). Water samples were either frozen or analysed within 24 hours. Parameters measured were conductivity, calcium and total hardness, phenolphthalein and total alkalintiy, pH, and turbidity. These were analysed according to Standard Methods (A.P.H.A. 1971) in the water laboratory of the Department of Zoology, University of Alberta.

Quantitative sampling of triclads is difficult because these soft-bodied organisms are easily damaged or destroyed. Consequently, the brick sampling method of Young and Reynoldson (1965) was employed. Artificial substrates of building bricks, each 20x10x6cm, were placed in the water, and these were colonized by triclads and other aquatic organisms. Bricks were generally placed in rows, with about a meter between bricks. Properly conditioned bricks should differ little from the natural rock substrate found at each site, and they will give a semi-quantitative measure of abundance.

To test whether all sizes of *Dugesia* were equally attracted to the bricks, rocks were marked with paint and returned to the lake. Marked rocks were sampled at the same time as the bricks. Student's t-test (Sokal and Rolph 1969) was used to compare mean length between the triclad population on bricks and rocks. Two tests of PA data yielded t=1.347 (p<0.2) and t=0.718 (p<0.5). Two tests of FP data gave t=1.347 (p<0.2) and t=0.995 (p<0.4). Hence, there seems to be no size difference between populations on bricks and natural rocks.

The sampling procedure consisted of retrieving a brick from the bottom and carefully bringing it out of water. Since triclads generally adhere firmly to substrates via mucus and cocoons are cemented to substrates, few, if any, triclads were lost when the bricks were retreived. Losses may be larger at FP because of the deeper water and retrieval by SCUBA, but the loss should be consistent each time. Triclads were transferred from the bricks to a jar with an artist paint brush. Cocoons were cut off at their stalk with a penknife and placed in the same jar as the adults. A sample size of between 100 to 200 Dugesia will approximate a normal distribution of size class frequencies according to Kolmogorov-Smirnov tests for normality.

Macrophyte samples were taken at PA. The plants were broken off and transferred to plastic bags or jars. Triclads were picked from the sample in the lab; the macrophytes were identified, dried, and weighed. Triclad numbers are per gram dry weight of plant.

Samples were taken monthly, except in summer months, when an approximate two-week schedule was followed. As many triclads, cocoons, and young as possible were returned to the lake to avoid over-sampling and altering the population.

The recolonization of the bricks into a representative sample of the population was tested to determine whether recolonization would occur in the 2 week minimum span between samplings. Several experiments were run at both sites. Bricks were retrieved, the animals on them were counted, and then the animals were released into the water. The bricks were returned to water at least 20m or more away from their original position. After a varying number of days, the bricks were again retrieved and the numbers of triclads counted. Data from a 5 day test at PA were tested for difference in numbers per brick by the Mann-Whitney U test (Sokal and Rolph 1969). There was no difference in numbers after 5 days ($U=16$; $p>0.05$). A 1 week test at FP showed no difference ($U=9$; $p>0.05$) and a 2 week test showed that there was a difference ($U=16$; $p=0.05$). However, these bricks were more densely populated after being moved 20 m away to a previously undisturbed site. I conclude that 2 weeks is an adequate period to provide for full recolonization.

The macrophytes and filamentous algae die off in autumn at PA. This mass of plant debris covered the bricks from November until March. Some bricks were moved to a clear site during the November sample, but they were covered again in

December. In January, some bricks were moved around the end of the point to where wave action kept the substrate cleaner. These were colonized by February. An increase in numbers per brick seen in March is attributed to moving the bricks from the sandy substrate to a rockier substrate which increased the brick surface available. In October, the bricks were found embedded in sand and partially weed covered. Probably wind action and human activity are responsible for the embedding. When brick samples could not be obtained, triclads were collected from macrophytes, rocks, and sweep-net samples of bottom material.

I experimented with a winter sampling technique to retrieve bricks through the ice at FP. Groups of three bricks were tied with string to stakes acting as floats with their ends out of the water. The stakes should have been visible above the ice and snow. Unfortunately, heavy waves, boat motor failure, and no underwater visibility hampered work. The long strings allowed the stakes to lean in the water and only about 20cm of the stake was visible. Further declines in lake water level may have aggravated the situation. Neither stakes nor a buoy could be located after freeze-up and snowfall in December. Sampling at FP was terminated in January 1976 after another futile attempt to find triclads.

Triclads were measured to the nearest 0.5mm while gliding normally in a petri dish placed over 1mm graph paper. Cocoon diameters and young triclads hatched in the laboratory were measured under a dissecting microscope to the nearest 1 unit of an ocular micrometer for cocoons and to the nearest 5 units for young triclads. This corresponds to an accuracy of roughly 0.05mm and 0.4mm respectively. Dry weight biomass was determined after drying individual animals on preweighed circles of aluminum foil for 24 hours. Weight was measured to the nearest 0.01mg on a Cahn electrobalance.

The state of sexual maturity was determined in three ways. 1) Triclads were measured, fixed, and cut into 7 micron sections. The sections were stained with Erhlich's haematoxylin and eosin. The slides were then examined for the presence of sexual structures such as the bursa or the penis papilla. 2) I examined the posterior part of a triclad, which was gently squashed on a microscope slide, for the presence of sperm, bursa, and penis papilla. 3) Live Dugesia were visually examined from their ventral side. Sperm, if present, shows up as white lines flanking the pharynx and joining at the penis. An animal was judged to be mature if sperm or sexual organs were present. Specific methods relevant to other experiments will be be described when the results of the experiments are presented.

RESULTS

Water Chemistry

Water chemistry data are plotted on a monthly basis to show seasonal trends. Dissolved oxygen showed little seasonal trend (Fig. 3). FP values were always above 6 ppm and generally were somewhat higher than PA values. An exception was the April PA value, which was much higher than FP. PA values flucuated markedly with a nadir of 3.7 ppm, occurring in November after a period of macrophyte die-off and decay. A more prominent seasonal trend is apparent when percent saturation data are considered (Fig. 3). FP values were lowest during late winter before ice break-up. Percent saturation rises to a summer maximum and then declines again under the ice. PA value flucuations were due to movement of the thermal plume. The lowest saturation, 31%, occurred in November during weed decay.

The lake water was alkaline and pH ranged from 7.6 to 8.8. The pH values were similar at the two sites throughout the year (Fig. 3). An exception was the difference in April, when the lowest pH value for FP occurred. After ice break-up in early May, pH increased as it already had at PA. Maximum pH occurred in June and then it declined slightly. The June maxima may be correlated with high primary productivity which increases pH through the liberation of carbon dioxide into the water.

Except for April, conductivity values were similar at

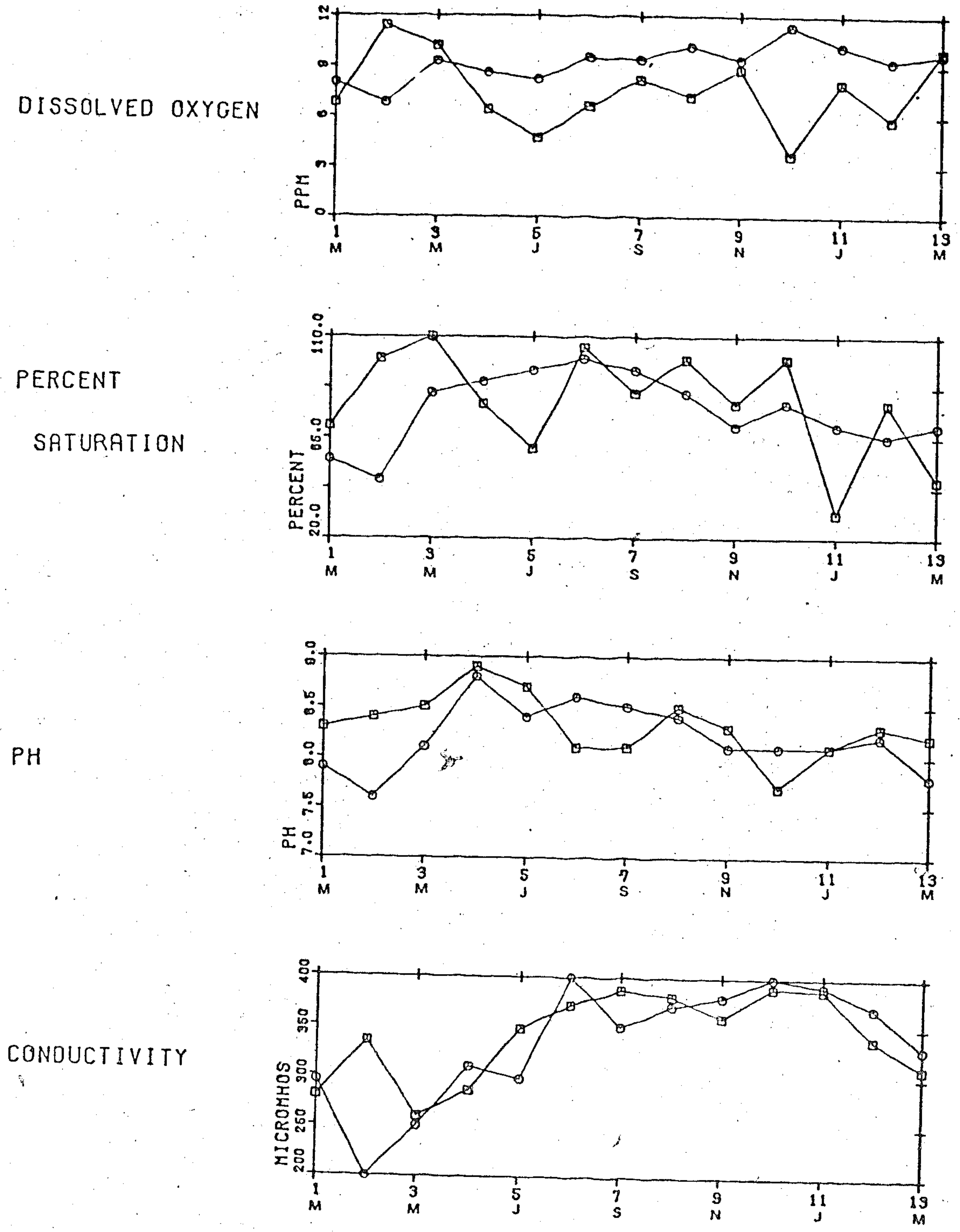


Figure 3. Seasonal variation in water chemistry parameters from March 1975 (month 1) to March 1976 (month 13). Abscissa numbers on this and similar figures indicate months as a serial progression. □ PA; ○ FP.

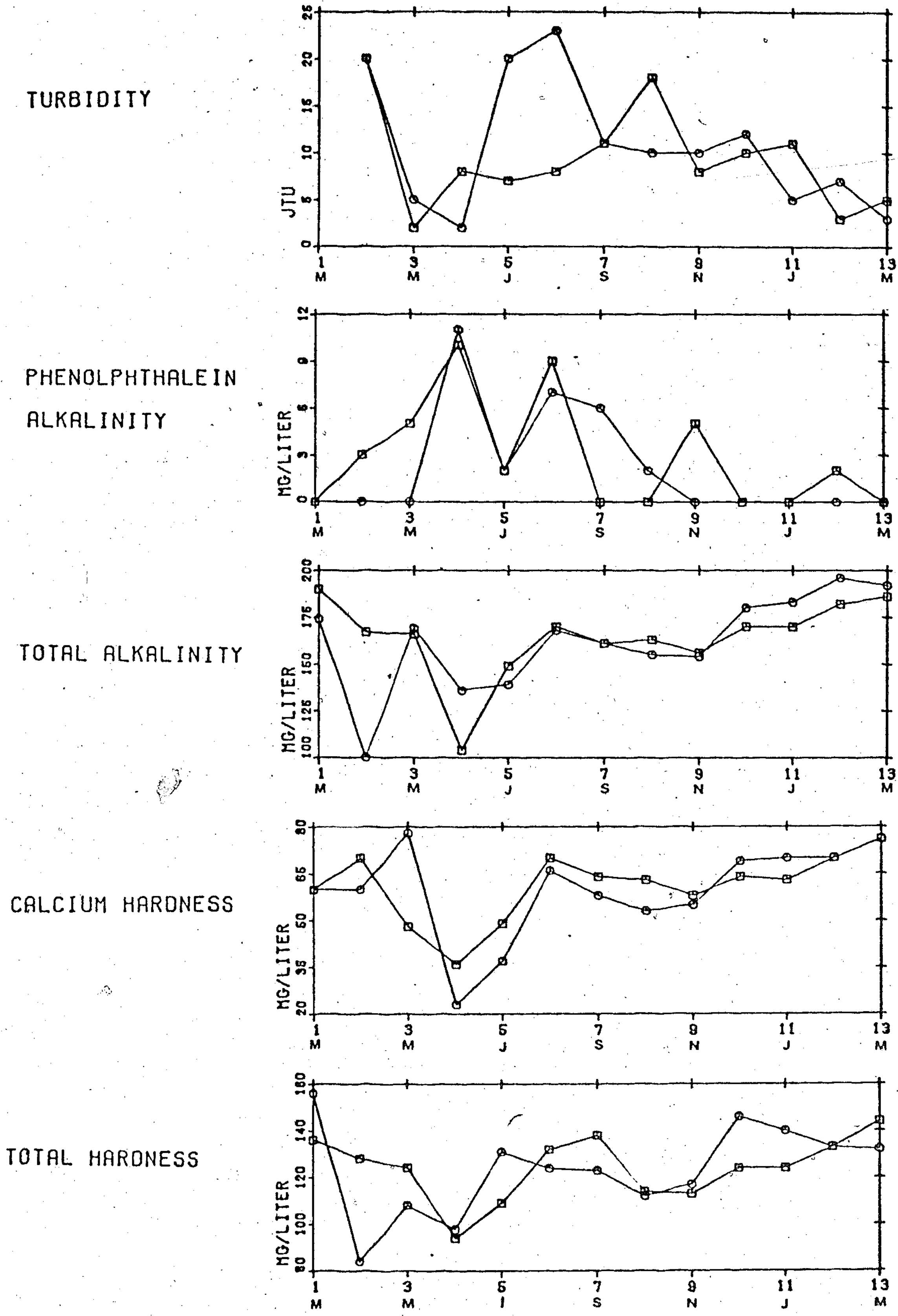


Figure 3. Continued.

both sites. Conductivity was maximal from August to January and then declined in spring and early summer. Turbidity was not determined in March, 1975; succeeding values show that turbidity can vary widely. Highest values occurred in April and summer, while there seemed to be a decline in autumn and winter. Phenolphthalein alkalinity is zero whenever the pH is below 8.3; hence there were many zero values throughout the year. FP and PA values for total alkalinity were similar, except for April and June. Alkalinity was lowest in spring and summer and highest during winter. Calcium hardness was generally lowest in spring and highest from August on through winter.

The water chemistry study indicates that Lake Wabamun is an alkaline, fairly productive, lake and supports the classification of Lake Wabamun as a moderately eutrophic lake (Gallup and Hickman 1975). Although the lake is moderately eutrophic, oxygen content is generally quite high, except perhaps locally and temporarily at Point Alison.

Temperature

Seasonal changes in surface water temperatures followed the same pattern at both sites (Fig. 4). Yearly temperature change was 25° at PA and 20° at FP. Winter temperatures were low and constant under the ice at FP. Ice generally covers the non-thermal areas from December to April. After ice break-up in early May, the temperature at first rose rapidly

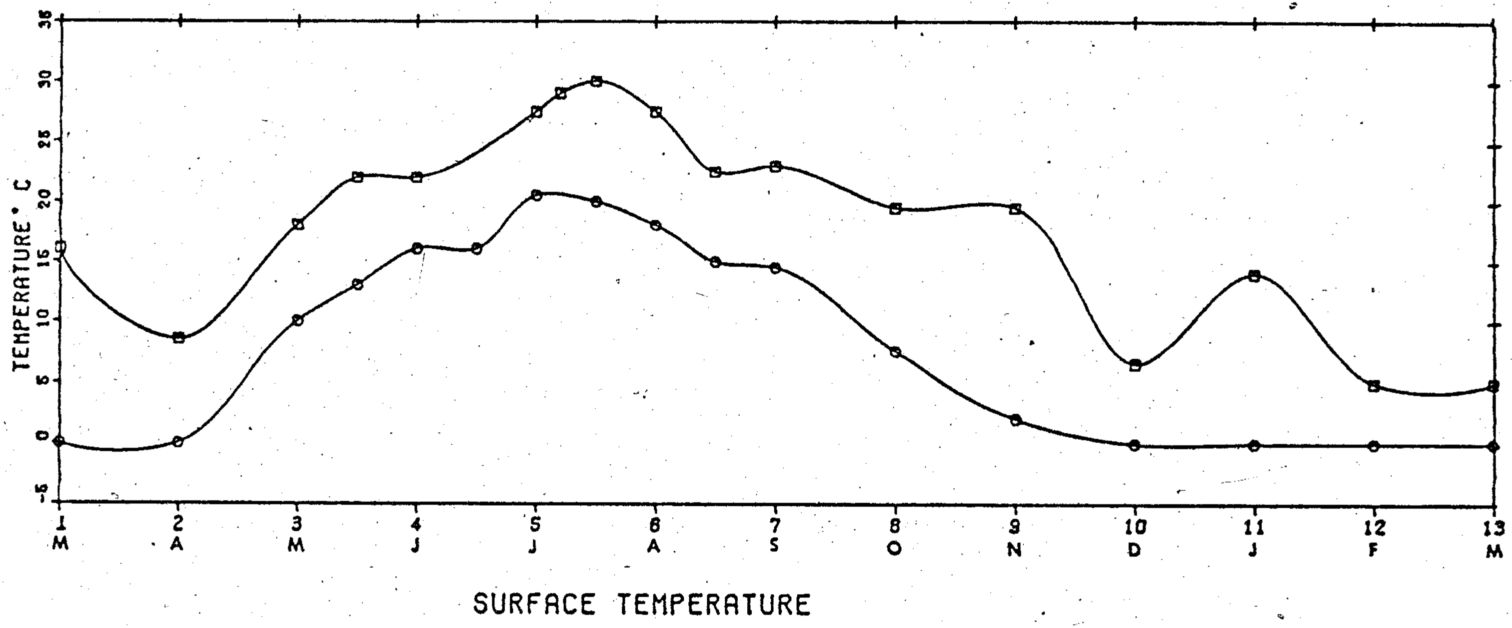


Figure 4. Surface water temperature. □PA; ○FP.

and then more slowly, to a maximum of 20° C in July. Temperatures start declining in August and again reach a minimum in late November when ice starts to form.

Seasonal change occurred in the thermal area at PA, but winter temperatures are more variable than at FP. Early spring temperatures were quite high and slowly rose to a maximum of 30°, recorded in July. Temperature slowly declined in autumn, but remained relatively high when compared with FP. At PA, winter temperatures flucuate according to the position of the thermal plume; the lowest winter temperature observed being 5°.

Macrophyte Harvesting

The discharge of heated water into Kapasiwin Bay has resulted in changes in the aquatic macrophyte communities (Nursall and Gallup 1971, Allen and Gorham 1973). Many macrophytes develop large standing crops during the summer and can impede navigability of boats. Elodea canadensis often breaks off from its roots and forms large floating mats, which can be blown ashore creating a nuisance for cottage owners. In 1972, a management program was initiated in an effort to control these nuisance growths by mechanical harvesting and removal from the lake. The number of metric tons removed from the sect [illegible] 2) and the total tonnage removed from the lake[1] were as follows:

Year	Harvest in Grid (Metric Tons)	Total Weeds Removed (Metric Tons)
1972	1,406	1,543
1973	3,264	4,660
1974	1,148	2,064
1975	302	316

Large numbers of Dugesia live on the weeds that are subject to harvesting and removal. If large numbers of the population are being removed, the population may be below the equilibrium size and subject to r- selection pressures instead of K- selection (Pianka 1970). Data were collected to determine whether Dugesia was, in fact, being removed by harvesting activities.

Hand grabs of macrophytes were taken from regions around the outlet canal and within the harvesting sectors, which were marked by buoys. Harvesting machines were also observed to work near the shoreline, outside the sectors, where they remove plants growing quite close to the PA sampling site. I also collected the harvested weeds from the unloading site on shore to determine whether triclads were being removed rather than shaken off during weed cutting. Triclads and cocoons were counted and the macrophytes were

---

[1] Courtesy Calgary Power Ltd. (unpublished data).

dried and then weighed.

Numbers of Dugesia and cocoons obtained from the samples are shown in Table 1. Numbers per dry weight gram are given to allow comparison between samples. Number of Dugesia per gram of plant before harvesting ranged from 3.7 to 47 (mean=19.9). Number of Dugesia per gram from harvested plants ranged from 3.1 to 11.8 (mean=6.8). Mean number of cocoons per gram before harvesting was 13.8 and after harvesting 4.8 cocoons/gm. The means from harvested weeds were both approximately one-third of the preharvesting means, but there is a 10% chance that this difference is due to chance effects ($t=2.1$; $0.05<p<0.1$). There was no significant difference in numbers of Dugesia or cocoons on the plants before and after harvesting ($t=0.2$, 0.08; not significant). The possible reduction in numbers per gram of plant may be due to inclusion of filamentous algae or macrophytes from sectors where Dugesia is less abundant in the harvested samples. Most of the triclads and cocoons on a plant being harvested appear to be removed from the lake along with the plant. My data indicate that substantial numbers of triclads are harvested with these tons of weeds, and this must be a potent mortality factor for the D. tigrina population in the thermal area.

Food Habits

Food of triclads in the field can be determined through a serological technique (Davies 1969), and this was used by

Table 1. Number and number per dry weight gram of triclads and cocoons found on harvested and harvestable macrophytes. Four harvested and eight harvestable samples were analyzed. N=number; x=mean; s=standard deviation.

	N	N/gm
HARVESTED		
Triclads		
N	229	
x	57.2	6.8
s	49.9	11.6
Cocoons		
N	122	
x	30.5	4.8
s	11.6	2.8
HARVESTABLE		
Triclads		
N	408	
x	51	19.9
s	43.8	16.8
Cocoons		
N	252	
x	31.5	13.8
s	30.6	11.6

Pickavance (1971b) to determine the diet of British D. tigrina. Since knowledge of D. tigrina's diet was not central to my study, this costly technique was not used. Two other methods of investigating Dugesia tigrina's diet were utilized. Setal remains of oligochaetes can be detected in squashed triclads when scanned under a microscope. Potential prey can be offered to Dugesia in the laboratory to see which prey are consumed.

Thirty six PA Dugesia from July and August collections were squashed on microscope slides and each squash was examined for the presence of oligochaete setae. Twelve positive squashes were found indicating that 33.3% of the Dugesia had recently fed on oligochaetes. Although setae could not be assigned to oligochaete genera, Stylaria is a common oligochaete found among the macrophytes, and Lumbriculus is a common bottom-dweller at this site.

Twenty two squashes were made of July FP samples, but only two (9.1%) were found to contain setae. Oligochaetes are less abundant at FP and are represented by Lumbriculus and Nais. Gallup et al (1975) report summer averages of 729.6 oligochaetes /m² from the thermal bay and 68.3/m² at Fallis Point. They were collecting tubificids, and the data show that oligochaetes are more abundant there than at Fallis. Dugesia seem to have responded to this abundance by feeding more on oligochaetes at PA.

Various undamaged potential prey items were offered to groups of Dugesia to determine which items could be consumed. Recently hatched Physa (Gastropoda), which are about 2mm in length, were eaten. Larger Physa were not so easily taken unless damaged. Several Stylaria were captured and consumed, but Lumbriculus often avoided capture; a 1cm long leech, Helobdella stagnalis, was eaten. Prey that can be captured after entanglement in triclad mucus or weakened by other factors include ephemeropterans, Daphnia, Gammarus, and Hyalella. These results support the more extensive work of Pickavance (1971a), who concludes that "D. tigrina has a very catholic, opportunistic diet, full advantage being taken of the young, the old, and the weakened."

Temperature Relations

Knowledge of Dugesia's reaction to temperature is useful in understanding its geographic distribution, seasonal movements in the littoral zone, feeding, breeding season, and reaction to thermal effluent. Several experiments were conducted to investigate D. tigrina's righting reaction, temperature preferences, and rates of growth and shrinkage. A further objective was to look for differing reactions to temperature between the normal lake population and the heated water population.

Righting Reaction Times

The time taken for a triclad to right itself after being turned over onto its dorsum is known as the righting reaction time (Chandler 1966). This time is affected by temperature and reflects the animal's ability to function in its environment. A triclad that is adversely affected will react slowly. My experiment was conducted on June 2 using large Dugesia reserved 10 days earlier for a fecundity experiment. Four beakers containing five triclads each and two beakers with four triclads each were maintained at each of the following temperatures: 5°, 10°, 15°, 20°, and 26°. Preliminary data on unacclimated animals revealed high variablity; hence an acclimation period of ten days was allowed. This is consistent with Chandler's (1966) use of a 14 day acclimation period. Each individual was turned over with a metal spatula and timed to the nearest 0.1 second, except 1 second at 5°. The righting was judged to be complete when the tail again touched the substrate.

Righting time (Fig. 5) was fairly constant at about 7 seconds over the range 15° to 26°. Below 15° there was a sharp increase in righting time to about 50 seconds at 5°. No difference in response was apparent between the two populations.

Chandler (1966) found that the righting time of Indiana D. tigrina was quite constant at 4 seconds from 11° to 31°. Below 11°, the righting time increased sharply, to over a minute at 1°. The results of these investigations show that Dugesia's movement is not inhibited by temperatures above 11° and that lower temperature strongly inhibits movement. Pickavance (1971a) reports that feeding was inhibited at temperatures less than 6° and this appears to be due to the

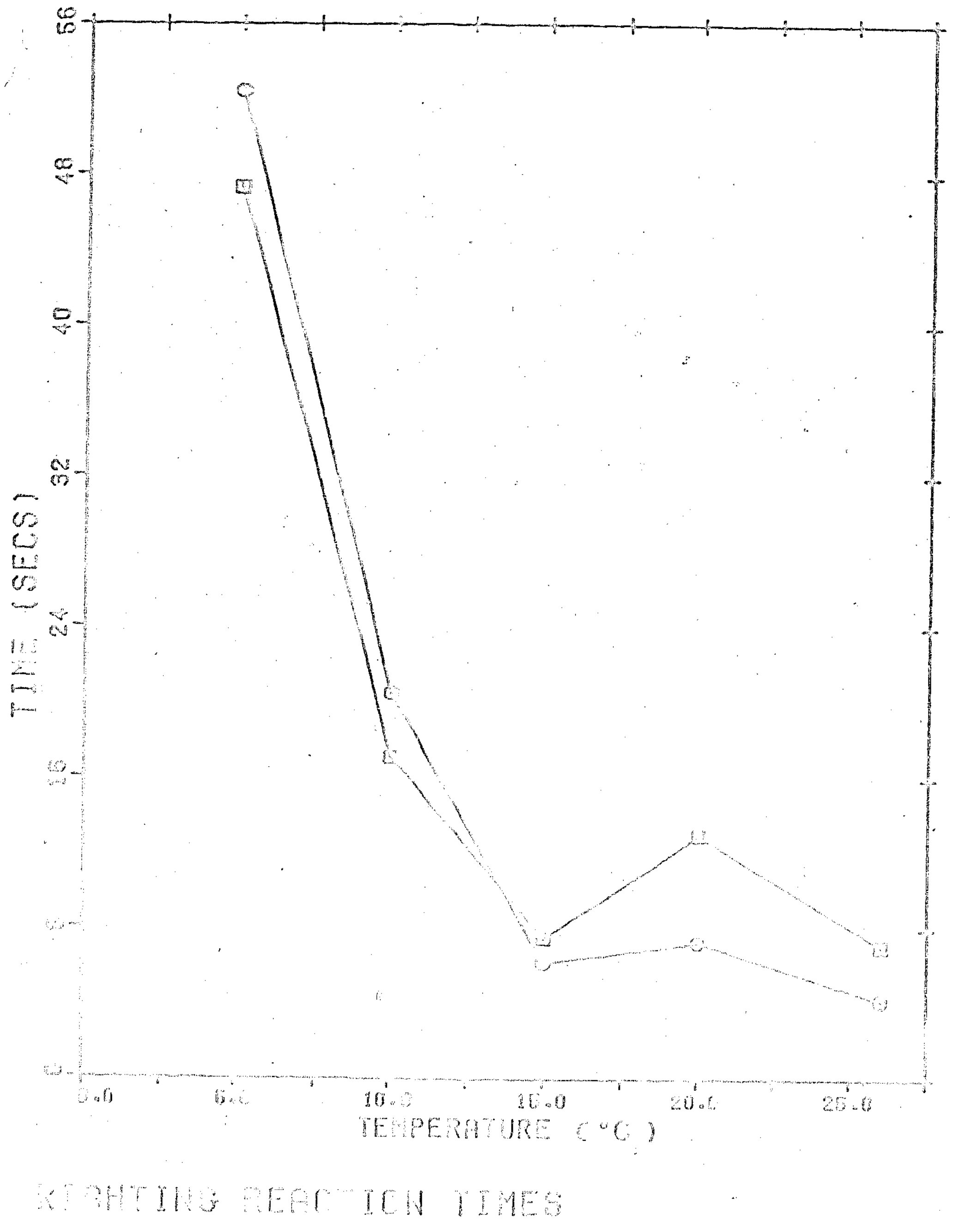
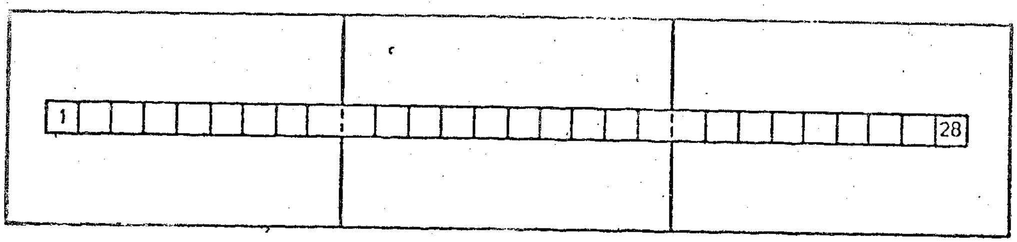


Figure 5. Righting reaction times over the range of 5° to 26°. □PA; ○FR.

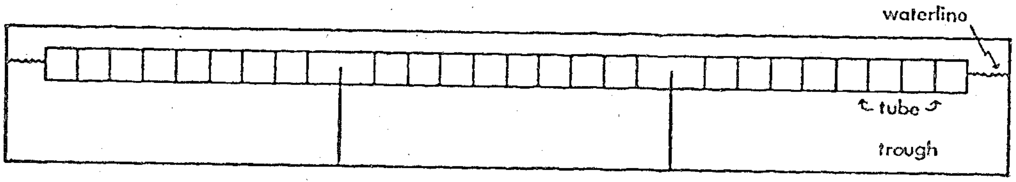
reduced mobility at low temperatures.

Temperature Preference

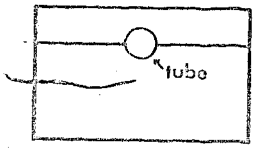
To determine Dugesia's temperature preferences, I used a plexiglass temperature gradient tube, which was 140cm long, 4.5cm diameter, and marked off in 5cm sections (Fig. 6). The ends were sealed with rubber stoppers. Holes were drilled at intervals along the top to allow insertion of a thermometer. The 5cm regions were numbered from 1-28, left to right, hot to cold. The tube was filled to half its diameter with water; and when set in a trough, the trough water reached the same level as the tube water. The trough was made of plexiglass and divided into three compartments by two partitions. The tube was set into semicircle cutouts in the partitions. Hot water from a water bath was circulated through the left trough compartment. A refrigerating coil cooled the water in the right hand compartment. The middle compartment was untreated. A temperature difference of at least 25° between the two ends of the tube could be obtained. There were two main difficulties with this apparatus. Firstly, it was often difficult to count the triclads when vision was obscured by condensed vapor in the tube or refracted by the water and plexiglass. Secondly, the tube did not present a uniform habitat for Dugesia. Triclads characteristically seek sheltered places. The tube's rubber stoppers provided a shelter spot because they were opaque and at right angle to



TOP VIEW



SIDE VIEW



END VIEW

Figure 6. Diagram of temperature preference apparatus. The left compartment was heated and the right was cooled. Regions 1-28 are indicated on the tube. Scale is 1:10cm.

the tube. Two additional shelters were caused by the clear plexiglass partitions that support the tube. The partitions created a shelter effect at the boundary of regions 9 and 10 and at 19 and 20. Triclads tend to congregate at these shelters and this is apparent in some of the histograms that follow.

Test #1-- Dugesia from the PA warm water site were tested for high and low temperature preferences. Fifty triclads were placed in the middle of the tube in 22° water and cooling power was supplied. The shelter effect of the rubber stoppers is obvious here as there were 15 Dugesia in region 1 and 10 Dugesia in region 28 (Fig 7A). After 10 hours of cooling, the temperature in #1 was 25° and 6.6° in #28. Those Dugesia in the cold end remained there as the temperature dropped, and they appeared paralyzed. Many were lying on their sides or dorsum. This arrangement was the initial condition for the next test, which attempted to measure heat intolerance.

Test #2-- Refrigeration was turned off and the heat input turned on. After 12.5 hours, all the triclads had left the heated end and many animals are at the right hand stopper in 22° water (Fig. 7B). There was a large number of Dugesia at the partition shelter of region 9-10 in 33° water. The warmest available water was 36°. The shelter "response" apparently is stronger than any undesirable effects of 33° water, so I conclude that Dugesia can tolerate 33° water. Possibly even higher temperatures may be

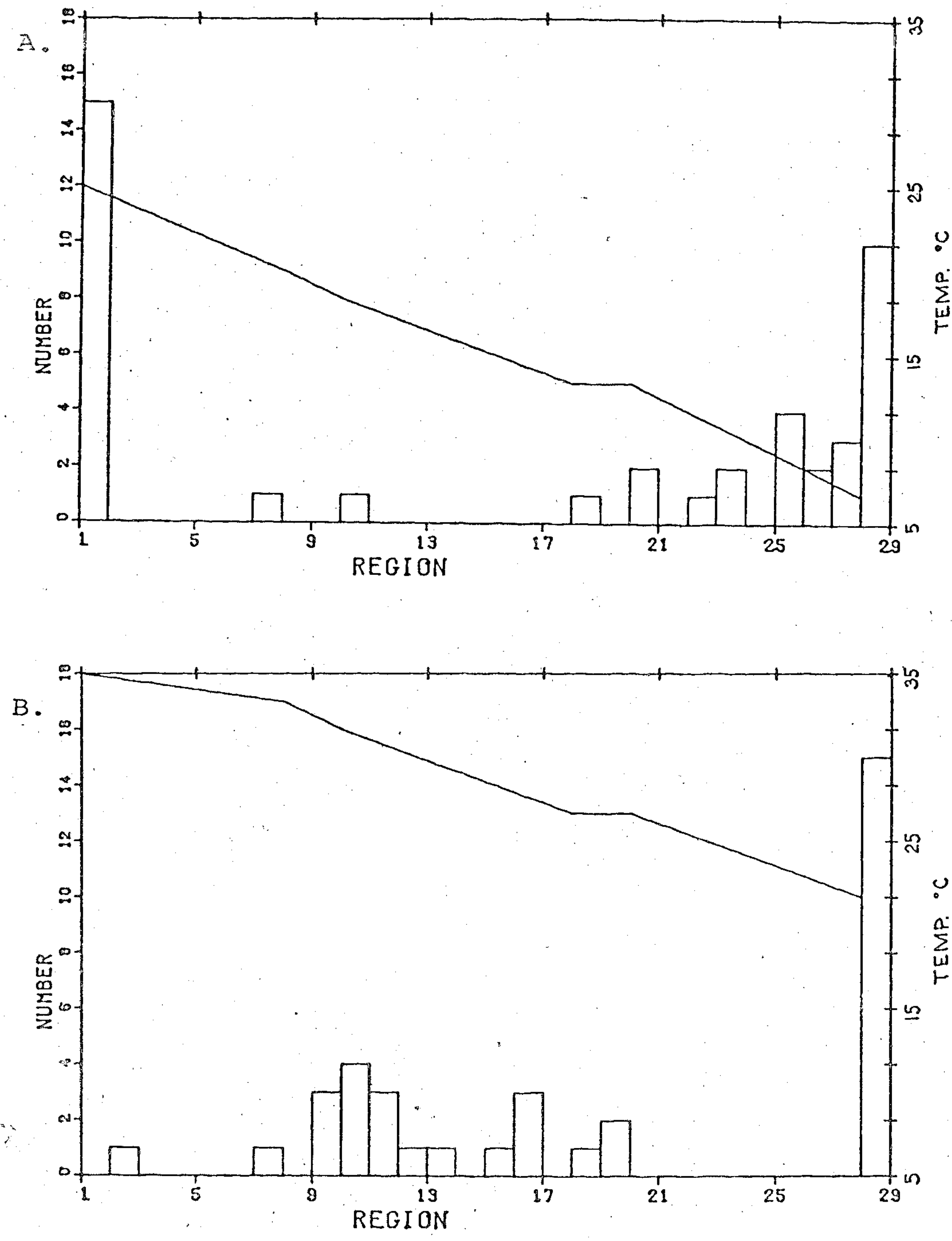


Figure 7. Temperature preference of PA _Dugesia_ as shown by number of triclads (histograms) in each region of the temperature tube. The temperature of the regions is indicated by the line. A., Test #1. B., Test #2.

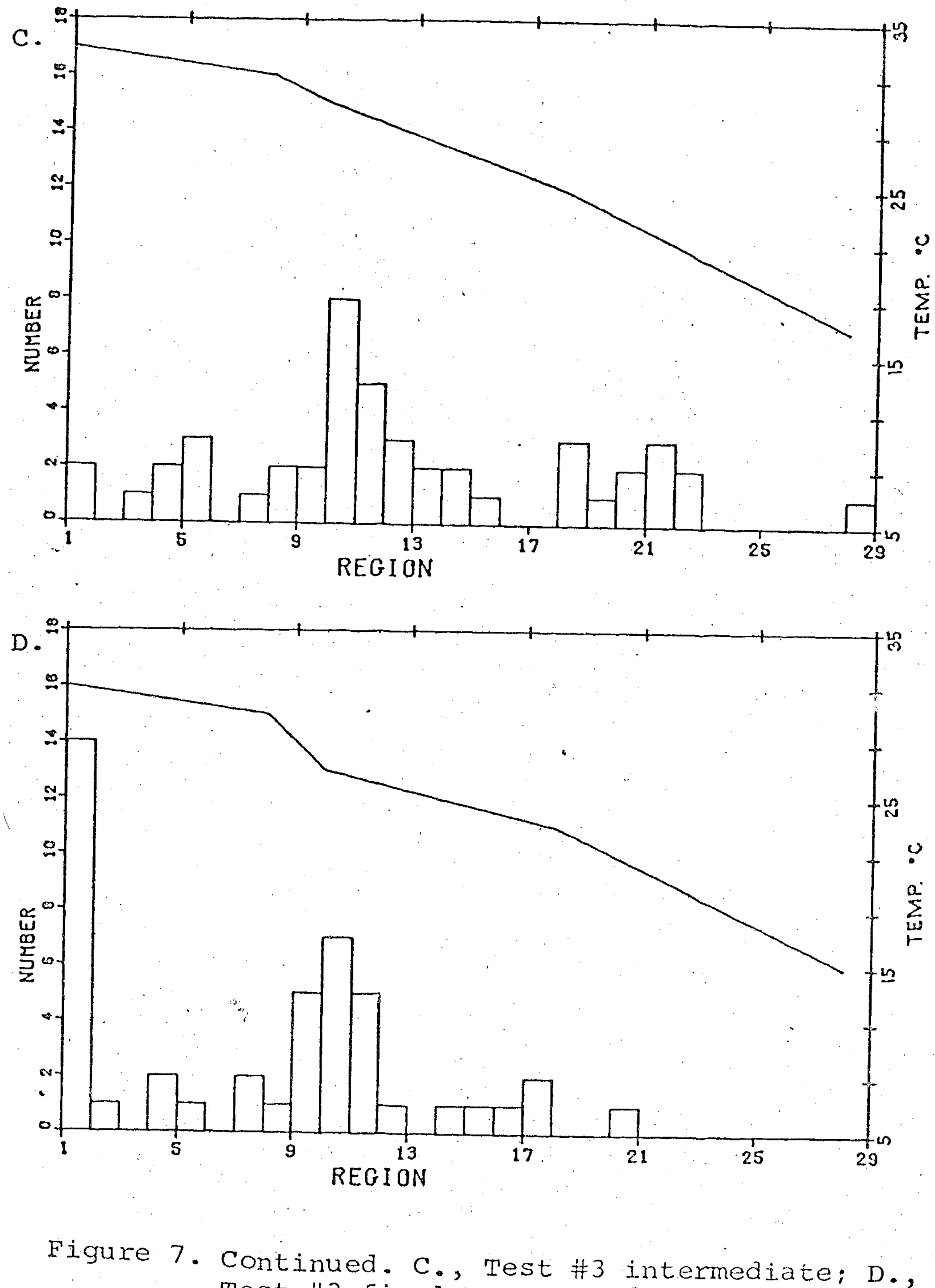


Figure 7. Continued. C., Test #3 intermediate; D., Test #3 final.

tolerated, since there were two triclads in warmer water below region 9.

Test #3-- A test of low temperature tolerance was carried out next. Heat was decreased and refrigeration was turned on in an attempt to drive the Dugesia from the cold end. The initial distribution is shown in Fig. 7B. After 4.5 hours the intermediate distribution was observed (Fig. 7C). Most animals had left the cooling end and there was some clumping at the partition shelters. The coolest water in which Dugesia remained was 21.5°. Several animals had followed the 33° temperature to region 1. The final distribution after 7 hours is shown in Fig. 7D. Most Dugesia were at the stopper in 32° water, and there were several at the warm partition shelter in 28° water. There were no triclads in water colder than 21°.

Dugesia from PA tolerated water temperatures between about 35° and 17° (Figs. 7B and C). When given a choice, they seem to prefer water of 25°-33°. Further testing could perhaps give more precise values; but these data do indicate that D. tigrina is a warm-water species, can be incapacitated by short term exposure to low temperatures, and are not affected by short term exposure to high temperatures associated with thermal effluent.

Test #4-- Dugesia from FP, the normal lake site, were tested in the same way. Fifty animals were put into the middle of the tube. The tube water varied from 19°-31° and was 24° in the middle of the tube. After further heating and cooling for 12 hours, the distribution of triclads was determined (Fig. 8A). Many had clumped in the region 9-16, in water temperature of 22°-29°. Two Dugesia were in warmer water, up to 32°. Many were in the cold region at 8.4°. Rather than a preference for very cold water, this is probably a result of several Dugesia going to the sheltered end when it was initially at 19°. Dugesia frequently failed to move out of slowly cooling water.

Test #5-- The inactive triclads from above region 19 in the previous experiment were moved by pushing them with a small spatula into region 19, which was at 20°. In this region, they again became active. After 1 hour, the distribution and temperature were recorded (Fig. 8B). Dugesia was still clumped at the warm partition shelter (28°), but none in warmer water. Many triclads that were moved to region 19 stayed there in water at 20°. Some triclads moved back to cooler water, probably immediately. This water continued to cool over the hour to 10° at region 24. There were only three animals in water colder than 10°. FP triclads seem to prefer a low temperature of 15°-20°, but will tolerate temperatures as low as about 10°.

Test #6 A final test was made on 50 FP Dugesia put into 25° water, in a tube having a steep temperature gradient in it. After 1 hour, the distribution was observed (Fig. 8C). Most Dugesia clustered in the temperature range of 21°-29° although several were at 32° and some at 9°-12°. I conclude that FP Dugesia prefer water at 20°-30°, but will tolerate

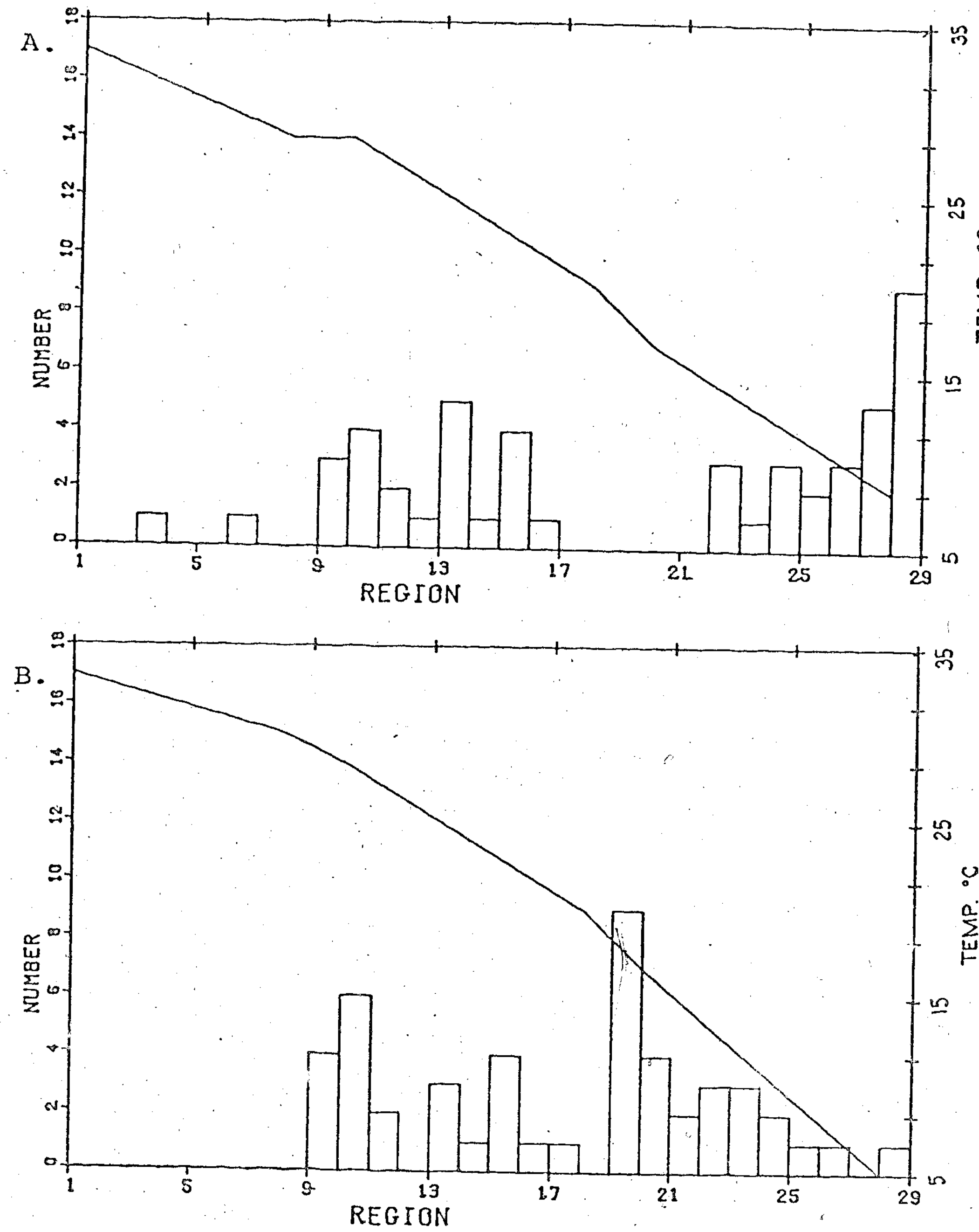


Figure 8. Temperature preference of FP <u>Dugesia</u>. See Fig. 7 for explanation. A., Test #4; B., Test #5.

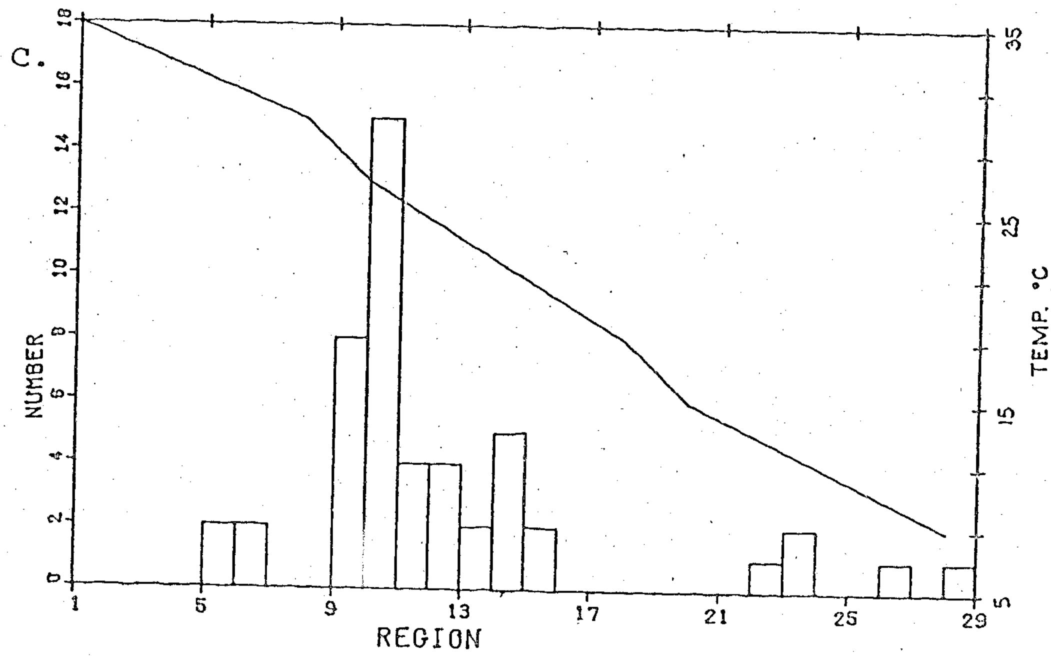


Figure 8. Continued. C., Test #6.

water temperatures down to 10° and up to about 32°.

In summary, Dugesia from the warm habitat prefer water about 5° warmer than those from the normal lake habitat. Both populations will not leave a shelter spot in 33° water nor will they often stay in warmer water. When given a choice of several temperatures, the lower limit of tolerance is about 17° for PA and 10° for FP. Of course in the lake, both populations must tolerate much lower temperatures in winter.

Growth and Shrinkage of Adults

Rates of shrinkage and growth at 20° and 30° were measured for laboratory populations collected at PA. Animals were kept in beakers or bowls, which were cleaned weekly. The 20° populations were kept on a lab bench and the 30° populations were maintained in a water bath. Some populations were fed equal portions of earthworm weekly and others were starved.

For three populations, the shrinkage rate for starving triclads at 20° was 1.0, 2.0, and 2.6 mm per month. Shrinkage proceeds at 4.8 to 5.6 mm/month for triclads living at 30°.

When a 20° population was fed weekly, the animals grew at a rate of 1.3 mm/month. However, animals fed at 30° did not grow; instead they exhibited net shrinkage of 1.4 to 1.7 mm/month. The 30° animals may not receive enough food energy to counteract the energy lost through increased respiratory rate at the high temperature. Even if each triclad filled its gut entirely at each feeding, one meal a week may not be sufficient to supply the needed nutrition.

In the lake, the elevated PA temperatures will contribute to the effect of food shortage by accelerating shrinkage, which in time will lead to greater mortality. Growth will be slowed if food energy is lost to increased respiration. Water of 30° or more does not occur for long periods at PA, but water is above 20° for much of the summer.

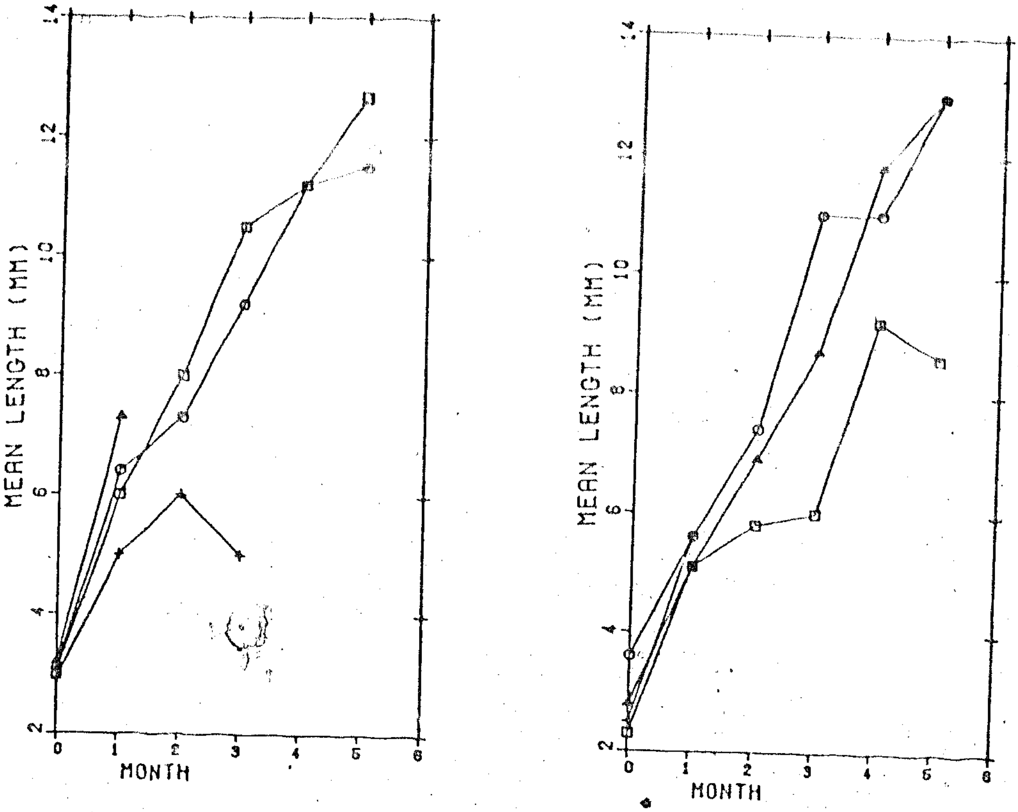
Growth of Young

Growth of newly hatched young was examined for differences in rate of growth between young from the two sites. If differences in growth rates could be detected, this would indicate some inherited adaptation for more efficient functioning at the temperatures likely to be encountered at each site. Young were grown for 5 months at 10° or 20°. Although no young in the field would necessarily begin growing in 10° water, those at FP would encounter 10° by early October, perhaps 2 months after hatching for some young.

All young from each cocoon were placed in a beaker filled with lake water. There were four beakers for each site and each treatment. The 10° beakers were kept in a refrigerated incubator through which air circulated at 1 liter per minute. The 20° beakers were kept on a lab bench and directly aerated. All triclads were fed chopped earthworm weekly and measured monthly. Two beakers of FP young succumbed, probably due to parasitic infections during the first month. They were restarted with newly hatched young. No other dead triclads were replaced.

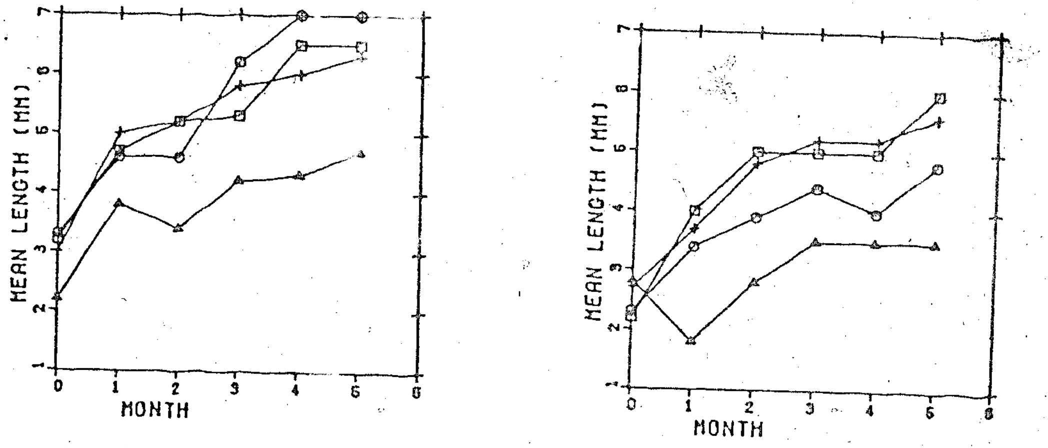
No obvious difference between sites is apparent, although there is a striking difference between temperature treatments (Fig. 9). Regression lines were calculated for the mean monthly lengths to determine the rate of growth and whether there was a difference between sites. The slope of the 10° line for FP was 0.61 and 0.48 for PA, so at 10° growth was about 0.54 mm a month. The regression coefficients were not significantly different ($t=0.98$; $p>0.05$). The slope of the 20° line for FP was 1.66 and 1.76 for PA, so at 20° growth was about 1.7mm a month. The regression coefficients were not significantly different ($t=0.42$; $p>0.05$). The growth rate at 20° was three times greater than that at 10°. The difference is probably due to the reduced metabolic rate and the reduced mobility for feeding caused by the low temperature.

Newly hatched FP triclads were larger than PA young (Fig. 9). If FP and PA growth rates are similar, the FP size advantage should be maintained. The final size of the remaining 20° PA young was not significantly greater than the final size of FP young ($t=1.95$; $p>0.05$), but the 10° FP young were, with one exception, larger than PA young grown at that temperature. The length advantage of FP young seems



GROWTH OF YOUNG FP 20°C

GROWTH OF YOUNG PA 20°C



GROWTH OF YOUNG FP 10°C

GROWTH OF YOUNG PA 10°C

Figure 9. Growth of FP and PA young at two temperatures. Each line represents the mean length of young from one cocoon.

to be maintained throughout early growth.

I draw several conclusions about Dugesia's response to temperature. 1) D. tigrina maintains a fairly constant righting reaction time over the temperature range 15°-26°, and there are no apparent differences in this response due to site of origin of the triclads. 2) D. tigrina generally prefers warm water (as high as 33° if shelter is available). 3) The FP triclads will stay in water that is 5° cooler than the water in which [illegible] will stay. 4) The lower limit of preference for [illegible] Wabamun is about 10°. 5) The growth of [illegible] is about three times slower at 10° than [illegible] growth rate is similar for both populations [illegible] be no adaptations to the local thermal regime [illegible] site with respect to the parameters tested. [illegible] Dugesia may be acclimated to higher temperatures [illegible] so prefer them when given a choice.

Cocoon Production

Dugesia tigrina produces a spherical cocoon that is cemented to a substrate by means of a short stalk. When first laid, the cocoons are a light tan color, which gradually darkens to brown. Cocoons laid on bricks and plants were used to assess fecundity and the time of the breeding season. Some cocoons were hatched out in the lab to provide data on size and numbers of young.

Very few cocoons were collected off of the bricks at [illegible] because the bricks were often covered by dead plant debris and benthic algae during the summer. Triclads cannot inhabit bricks at these times, so cocoons are not continually being deposited on the bricks at PA. The first coverage occurred sometime before June 24. The debris was removed by a wind storm in early July and the bricks were recolonized. Since number of cocoons on the bricks was never large, most data on production and fecundity are from macrophyte samples. FP data are from the brick and marked rock samples.

Cocoon diameters were measured for 100 cocoons from each site. PA cocoons were 1.22mm (sd=0.159) in diameter and FP cocoons were 1.30mm (sd=0.144) in diameter. A t-test on the means gives t=4.00, ($p< 0.001$), so FP cocoons are significantly larger. The mean number of young hatching per cocoon was 3.9 at both sites with a range of 1 to 7 young.

The time span from cocoon deposition to hatching was estimated from the number of days between deposition and hatching of cocoons in the laboratory. The range was 15-21 days at a room temperature of about 20°. Mean hatching time was 17 days for FP and 18 days for PA cocoons. The longest periods from date of field collection to date of laboratory hatching were similar to the range for laboratory deposited cocoons.

Cocoons that failed to hatch for some time were examined for signs of sterility or development. Fifteen of 82 PA cocoons failed to hatch and showed no signs of developing young. Therefore, I assumed that 18% of PA cocoons were sterile. Four of 93 FP cocoons did not hatch. On examination, three of these had breaks in the cocoon shell, which were probably caused by handling, since most sterile cocoons remain intact until decomposition sets in. The one positively sterile cocoon (no break in shell) represents a 1% sterility factor in the FP population.

Cocoon production for certain dates was calculated as number of cocoons per adult. To account for the sterile cocoons on macrophytes at PA, I reduced by 18% (the sterility factor) the total number of cocoons collected on July 2 and thereafter. I did not apply the sterility factor to the May 29 and June 10 samples because there was no build-up of sterile cocoons at these times. No correction was necessary for FP samples because all cocoons were removed from sampled bricks and no sterile cocoon build-up occur

Cocoon production started in late May-early June at the heated site, but started in late June at FP (Table 2 and Appendix). Water temperature is above 18° at this time at PA and is 16° in late June at FP. Production increased during July and then dropped off rapidly in August at both sites. PA *Dugesia* breed for about 11 weeks and FP *Dugesia* for 8 weeks.

Cocoon fecundity can be calculated as the average number of cocoons per adult for each date or as the total number of cocoons divided by the total number of adults sampled. Both methods give equivalent results. Cocoon fecundity of PA Dugesia was 1.4 cocoons per adult, and these cocoons will hatch out an average of 5.5 young, or 4.5 young if 18% of the cocoons are sterile. FP Dugesia produced 0.7 cocoons per adult or 2.7 young. Dugesia from the heated site are twice as fecund as those from the normal site.

Young

Recently hatched young are usually 2.0-4.5mm in length. They are lightly pigmented and semi-transparent at birth. The yolk cells that fill the gut are golden colored. As the young triclad develops, the yolk is used up and the dorsal pigment spots become larger and darker. Based on these characteristics, triclads that were ≤4.5mm long were classified as either truly young or small; small triclads being either shrunken adults or older young that have failed to grow. The recognition period for young is about 2 weeks. Numbers of young or small triclads in field samples provide information on recruitment and the effects of food shortage.

The mean length of PA young hatching from cocoons in the laboratory was 2.92mm (sd=0.693). The mean length of FP young was 3.06mm long (sd=0.627). PA young were significantly smaller ($t=2.7$; $p<0.01$). This corresponds with the observation that PA cocoons were smaller in diameter than FP cocoons.

Young triclads were not well represented in the brick samples from either site. At PA, this probably reflects the lack of cocoon deposition on bricks. For most summer field

Table 2. Summary of reproductive data for PA and FP showing the seasonal production of young and cocoons.

Date	% Adults	% Young	Cocoons per Adult
PA			
May 29	77.0	0.0	0.03
Jun 3	56.0	0.0	0.92
Jun 10	67.8	1.6	1.57
Jul 2	25.4	21.0	1.33
Jul 8	22.3	12.4	1.76
Jul 24	16.6	14.6	3.97
Aug 7	34.0	3.5	0.20
Aug 19	19.1	5.2	0.00
FP			
Jun 30	99.4	0.0	0.13
Jul 16	86.5	12.8	1.25
Jul 29	93.6	3.5	1.14
Aug 12	98.0	0.0	0.38
Aug 27	91.3	3.5	0.00

samples, I combined brick and macrophyte data. However, the August 7 PA sample is omitted from consideration as the triclads on the macrophytes were not measured. The lack of young in FP brick samples may be attributed to factors such as continually removing cocoons from the bricks and not always being able to return these samples to the lake water directly over the bricks. Also, keeping 46 cocoons from marked rocks in the laboratory for hatching may contribute to the lack of young. Of course, since I hypothesize that young triclads suffer heavy mortality from competition, I did not expect a large number of young.

The percentage young of the total PA population reached a peak of 17% in early July (Fig. 10 and Table 2). By the end of breeding, the percentage had declined to 5.1%. Fecundity was measured as the total percentage of young divided by the total percentage of adults from June 10 to August 19. The fecundity value was 0.36 young per adult.

Young were first collected at FP on July 16 and made up 12.8% of the population (Fig. 10 and Table 2). The percentage declined rapidly to 3.5%. Fecundity expressed as young per adult was 0.07. (The August 12 sample was omitted as no young were collected.) This fecundity value is 10% of cocoon fecundity; hence cocoon fecundity may be more accurate in describing the reproductive effort of FP Dugesia.

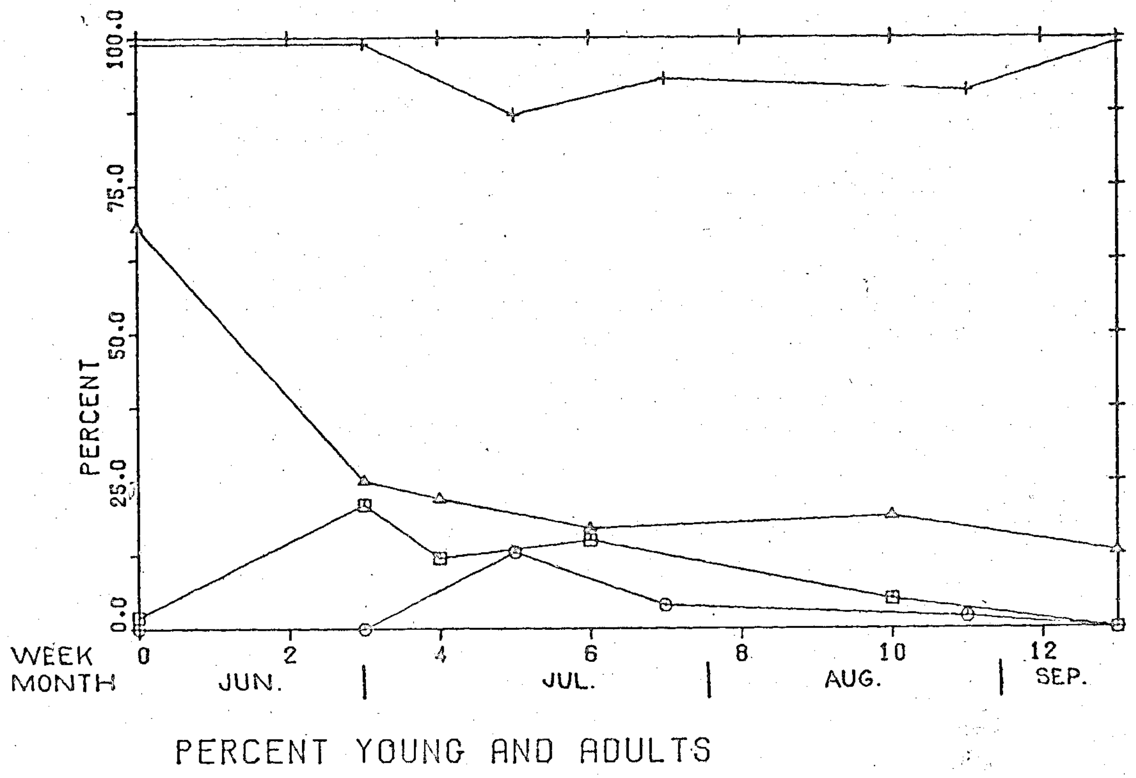


Figure 10. The percentage of young and adults present in each population from mid June to mid September. □ PA young; ○ FP young; △ PA adults; + FP adults.

Adults

Dugesia become sexually mature after reaching a certain length, and triclads equalling or exceeding that length are adults. Maturity can be judged by the presence of genital structures and sperm in the vas deferens. When sperm is present in the animal, as determined by the sectioning or squash methods, then the male and female systems (since Dugesia is not known to be protandrous) are assumed to be mature and the animal is considered an adult.

Ten FP triclads collected on May 29 were sectioned, and the June 30 triclad sample was visually examined for sperm. These observations indicate that triclads ≥8mm in length were mature. PA triclads from late May and mid-July were sectioned. Others were squashed and visually examined. Some of the 10mm triclads were found to be mature while others were immature. No 9mm or less PA triclads were mature. PA triclads ≥10mm in length were considered adults as they were either mature or maturing. These results are consistent with the finding that length at maturity decreases as temperature increases for Dugesia polychroa (Reynoldson, Young, and Taylor 1965).

The proportion of adults changed throughout the year, but was highest in the spring before breeding. The FP population was composed entirely of adults in June, but the PA population at this time was only 77% adults. When the percentage of adults and young are plotted together, there are trends in the breeding season (Fig. 10). The proportion of adults decreased markedly over summer at PA, but only slightly at FP. This decreasing proportion could be due to shrinkage, dilution by young, mortality, or emigration from the bricks.

By correlating increases in young with changes in the adult percentage, the dilution effect of young can be estimated. There was a 43% decrease in PA adults between June 10 and July 2, but young only increased by 20% in that period. The remaining summer reduction in adult percentages cannot entirely be accounted for by dilution with young, because the decline in young parallels the adult decline. For the FP population, the July 16 reduction in adults is due to dilution by young. There is little further change in adult percentage at FP because a tremendous amount of shrinkage would be necessary to reduce the large adults (up to 17mm) to less than the adult length of 8mm.

Mortality is discounted as a factor because adults breeding in the laboratory exhibited no mortality. Similarly, when starved, Dugesia shrinks but does not die. The relatively small decrease in adult percentage at FP is not consistent with the post-breeding mortality idea.

Emigration from the bricks is not a possibility at PA because the bricks usually contained more adults than do the macrophytes, at least in summer. No difference in preference between bricks and rocks has been demonstrated for FP triclads, but if they migrate to deeper waters in autumn, there may be differential emigration. The best explanation for the loss of adults is shrinkage due to food shortage.

The Total Population

The PA Population

Both triclad populations show well defined cycles of growth, breeding, and shrinkage, with consequent changes in the biomass present. It was not possible to study the FP population for a full cycle because of sampling problems previously mentioned. However, there is evidence from changes in autumn numbers per brick that FP <u>Dugesia</u> moves into deeper water to overwinter, and regardless of sampling problems, they would be unavailable for sampling by the brick method. Such movement out of the littoral zone by <u>Dugesia</u> has been observed in a Toronto pond (Boddington and Mettrick 1971).

Changes in the PA population can be studied through size structure histograms (Fig. 11). Spring was a period of growth as small triclads increase in length and become sexually mature. The percentage of adults was maximal in late May-early June, when cocoons were first collected in the field. The number of triclads per brick was constant at about 30 for this period, and young triclads (≤4.5mm) appear in the July 2 and 8 samples. By July 24, there were many intermediate sized triclads and very few adults. The number of triclads per brick had more than doubled to about 70 (see Appendix and Fig. 15). By August 19, only a few cocoons could be found and there are many small, but not young,

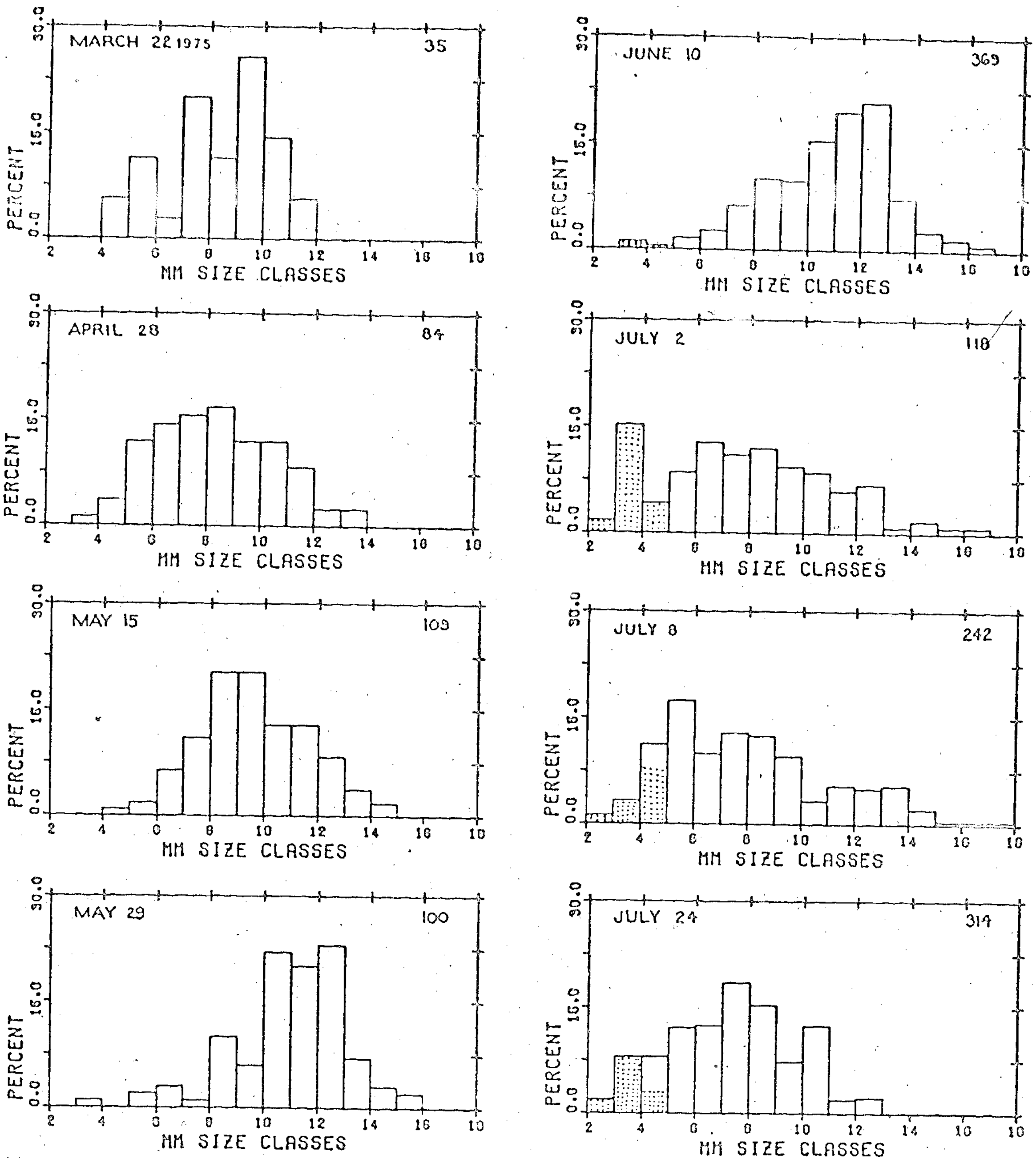


Figure 11. Size structure histograms of the percentage of PA <u>Dugesia</u> in each size class. Stippling represents the percentage of young. Inset figures are sample sizes.

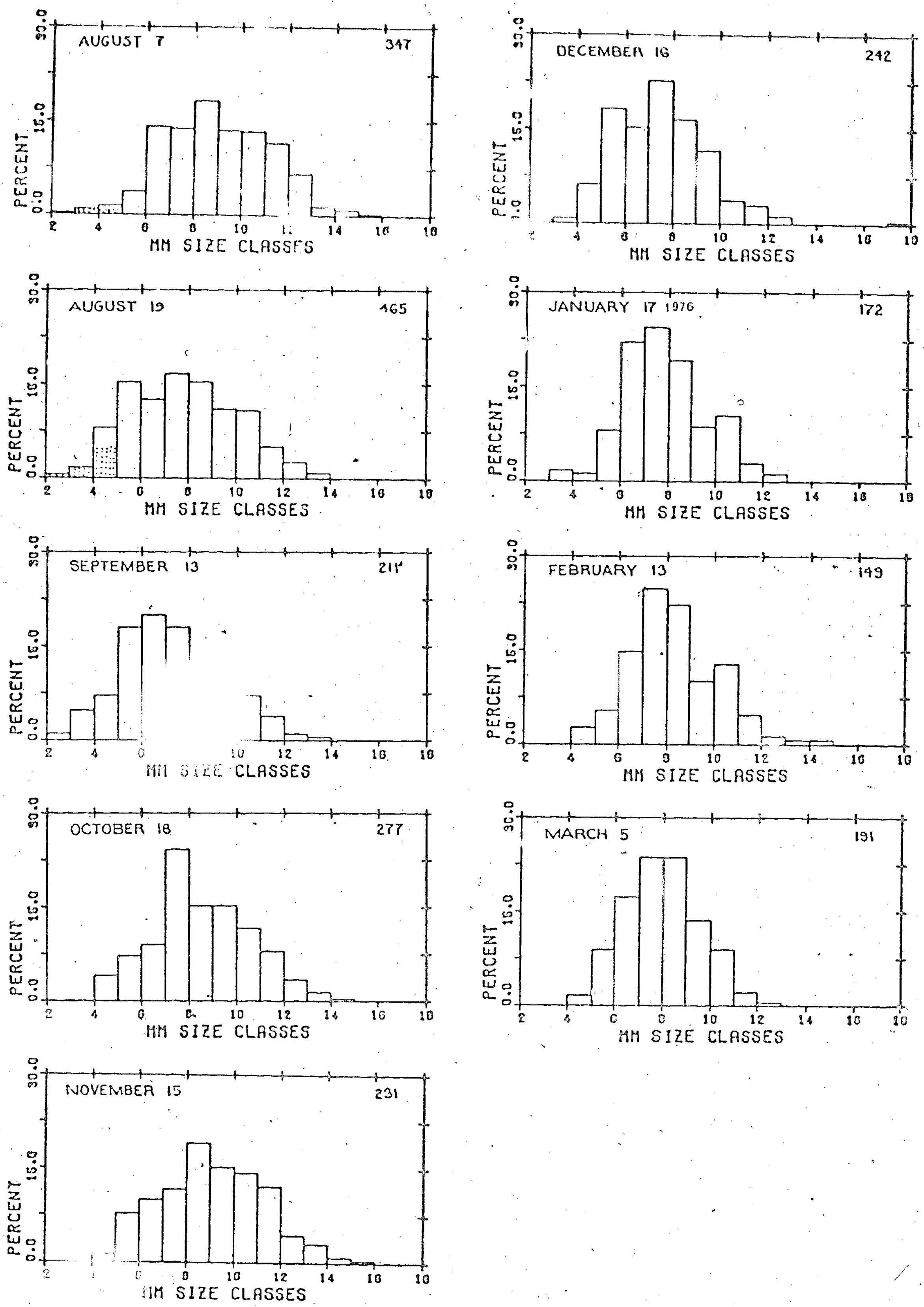


Figure 11. Continued.

triclads. These were recent young that have failed to grow or were shrunken adults. No cocoons were found in the field after August 19 and by September there were no young present. All triclads ≤4.5mm were shrunken adults, and by October there were no triclads smaller than 4mm (Fig. 11). The numbers per brick had been declining since August 7; by September there were only 38 Dugesia per brick. This indicates mortality in the population. From November until March, most triclads were from 6 to 9mm long. In February, there were 41 triclads per brick. This is comparable to the number present in September (38/brick), October (30/brick), and the number present in the previous spring (about 30/brick). Post-breeding mortality of young and shrunken adults had re-adjusted the population size to that which the environment can support.

The cumulative percentage of individuals in each size class shows PA population changes with time (Fig. 12). Adult percentages increase to over 50% in May and June. There was a sharp change in percentage composition between June 10 and July 2 when young appeared in the population. After July 2, adult percentages continued to decline, except for the August 7 sample. The majority of the population was in the intermediate size ranges by August and September. Triclads greater than 11mm, made up only a small fraction of the population from late August through winter. The larg individuals present in spring have shrunk.

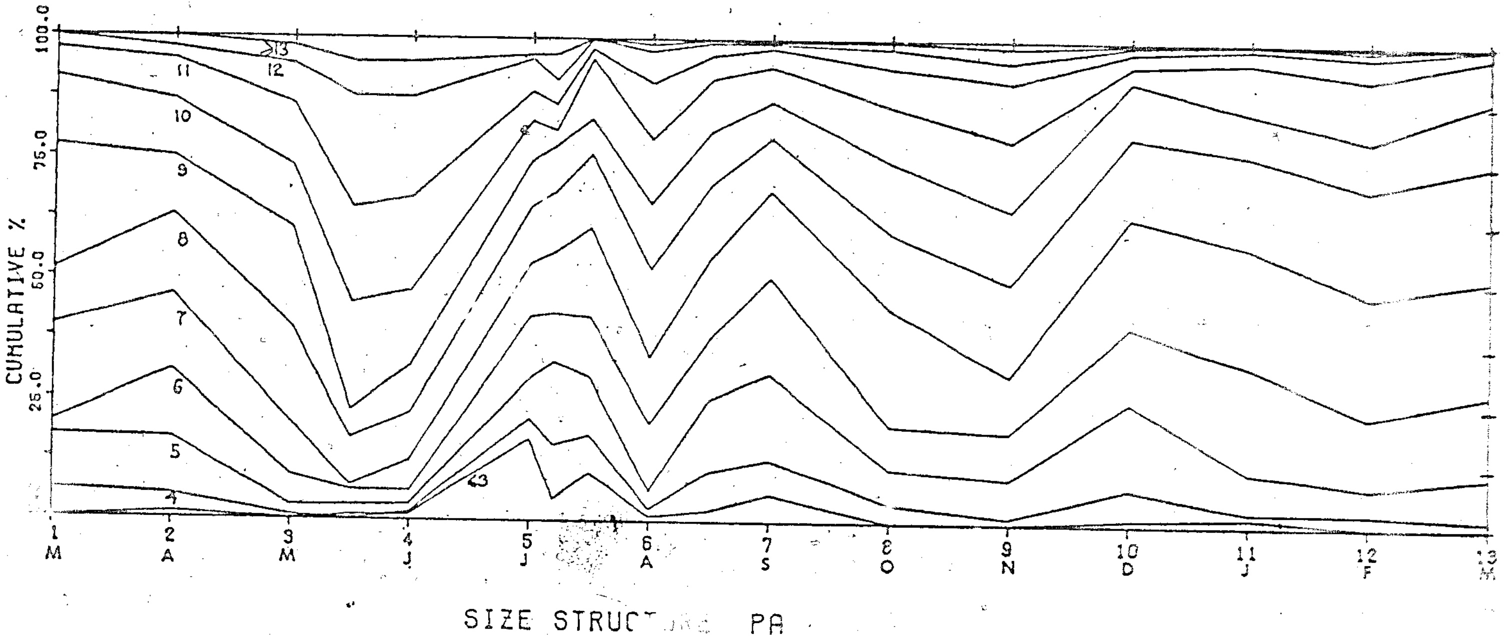


Figure 12. The cumulative percentage in each size class for the PA population throughout the year.

The FP Population

The Fallis population was studied during the ice free season. Histograms of size structure show that virtually all of the population was of adult size (≥8mm) in May (Fig. 13). Growth continues in June, and by late June cocoons appeared. Young were first taken in the July 16 sample. Fewer young were present by July 29 and none were present in the August 12 sample. Large triclads remained abundant throughout the summer.

There was a striking change in the FP population by August 27. Triclads were present in size classes from which they were absent two weeks ago, and the number per brick had increased to 49 from 16. This change cannot be explained by growth, shrinkage, or recruitment. The best explanation seems to be immigration of triclads to the brick area from shallower areas as part of a seasonal movement to deeper water. By August 27, the water temperature had fallen to 10°, and is close to the point where Dugesia's reaction time begins to increase. It seems likely that the triclads would begin moving before water temperatures inhibit a migration.

In September, there were no triclads smaller than 8mm, indicating no [illegible] in the small size classes. At this time, intermediate sized triclads were abundant, and [illegible] October and November, the number [illegible] size classes increased. Number per brick increased to 65 for September and 76 for October but dropped to 12 per brick in November, when most triclads had left the

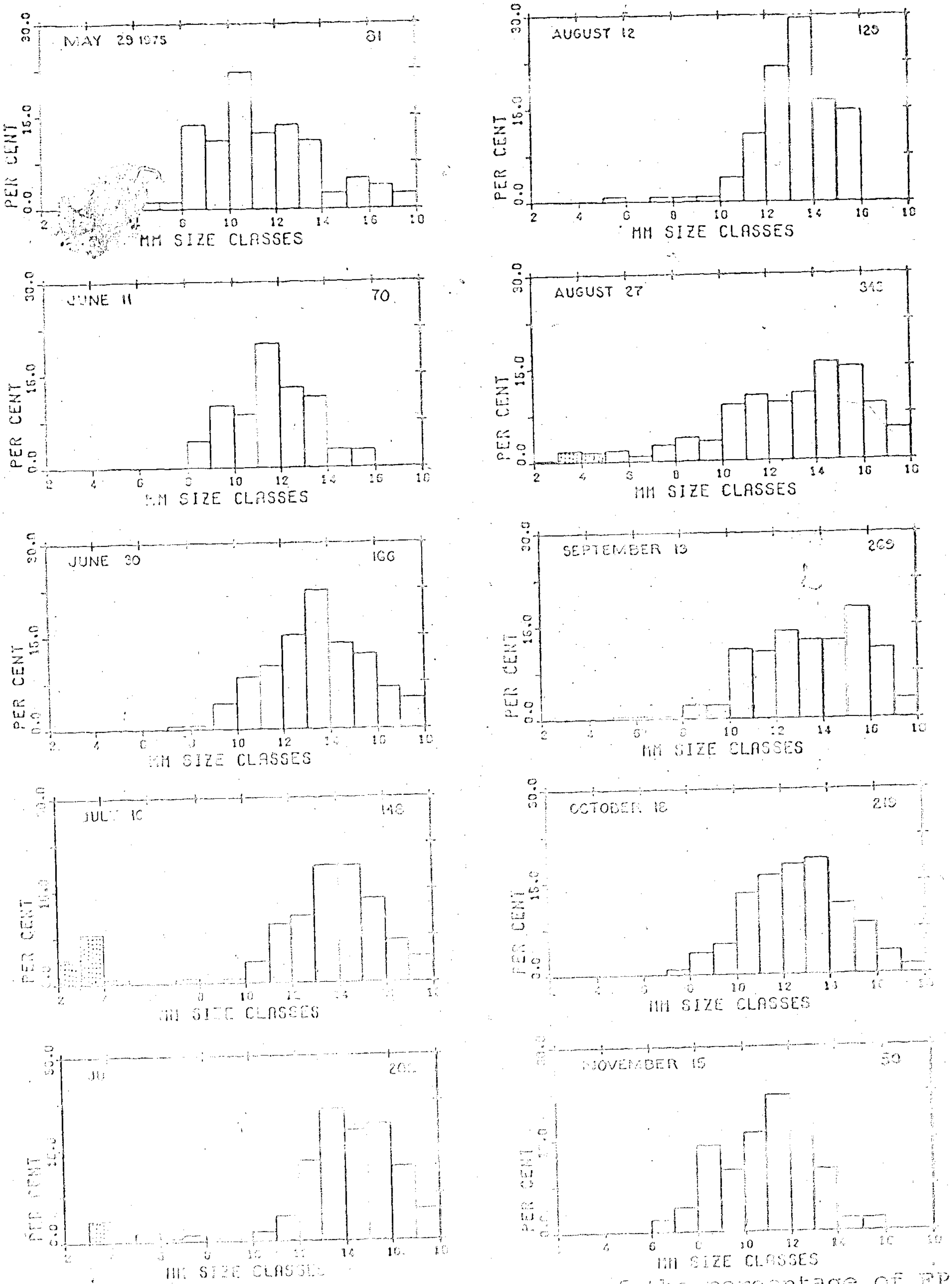


Figure 13. Size structure histograms of the percentage of FP *Dugesia* in each size class. Stippling represents the percentage of young. Insets are sample size.

area.

When size structure is examined on a cumulative percent basis, these seasonal changes are more apparent (Fig. 14). Adult triclads formed the entire FP population by late June. In July, young were produced, but their numbers rapidly decline, indicating that most fail to grow. Some young were again present in late August, but they have disappeared by September. The large triclads began shrinking in August and the smaller size classes made up most of the population by November.

The disappearance of large triclads was due to shrinkage of Dugesia. There are not enough young triclads to be recruited into the population in autumn and the few present could [illegible] grow into the 7 and 8mm size classes in the time available or at the water temperatures of this season. Mortality of large triclads cannot explain the abundance of smaller triclads because those ≤9mm were only a minor proportion of the September population, but made up about 30% of the November population. The slopes of the lines (Fig. 14) from September to November are similar and this would indicate gradual shrinkage rather than mortality of certain sizes.

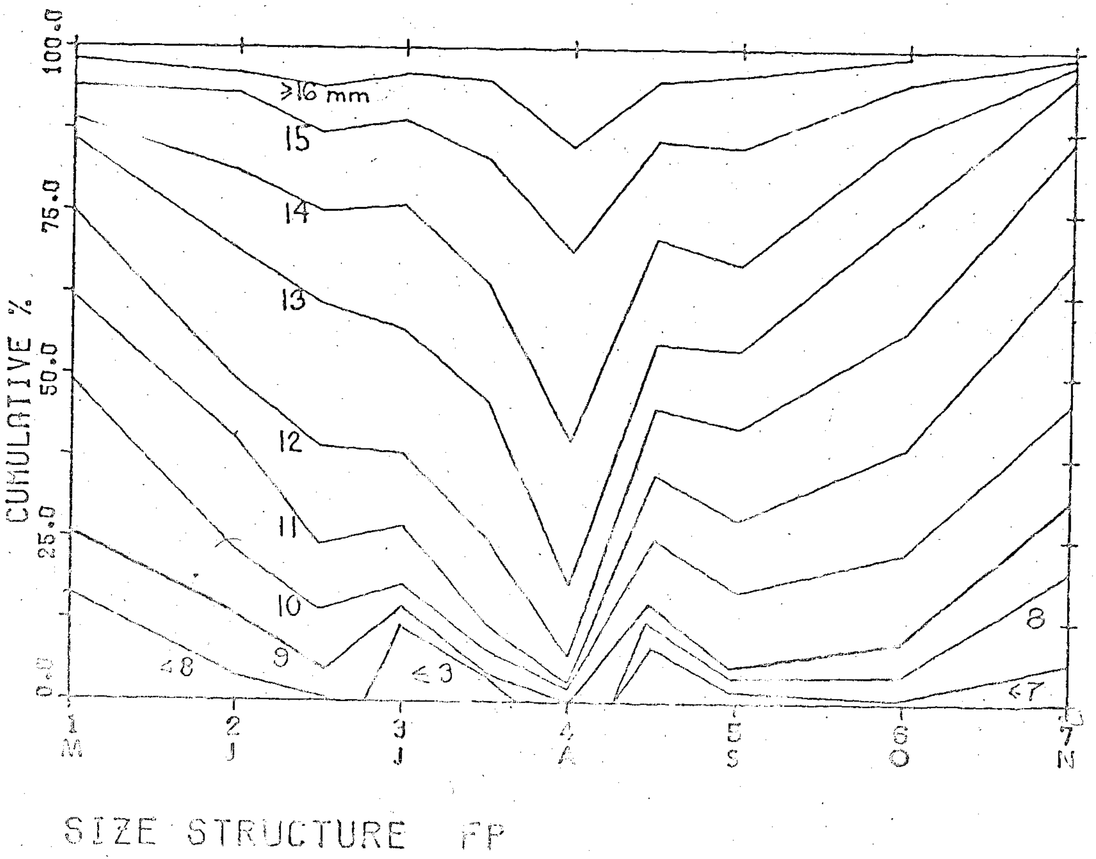


Figure 14. The cumulative percentage in each size class for the FP population throughout the year.

Mean Length and Biomass

Seasonal changes in mean length also illustrate size structure changes (Fig. 15). Length increased by 2mm during spring growth at PA. In part, the occurrence of young in July decreased the mean length. Mean length was smallest in September after post-breeding shrinkage. There was a slight increase in length during October and November, possibly caused by Dugesia feeding on animals that die before winter. Mean length was fairly constant at between 7 and 8mm throughout the winter. These data suggest that Dugesia can only find enough food to support growth during the spring and early summer, and possibly in late autumn.

Dugesia from FP grew rapidly in the spring, up to 2mm per month (Fig. 15). The July mean length reduction was due to dilution by young. Growth continued in August, but length declined sharply during autumn. By November, the average size of Dugesia was 10.5mm, which is comparable to the initial spring length of 11mm. There was probably little change in mean length under the ice at FP, as was the case at ice-free PA.

Since shrinkage is an indication of intraspecific competition in triclads, it is instructive to compare FP shrinkage with that of PA. When the minimum length is subtracted from the maximum, the decrease is 3.8mm at PA and 4.2mm at FP. These values are quite close and indicate that shrinkage is comparable in each population. This is somewhat surprising since the FP triclads are consistently larger (in

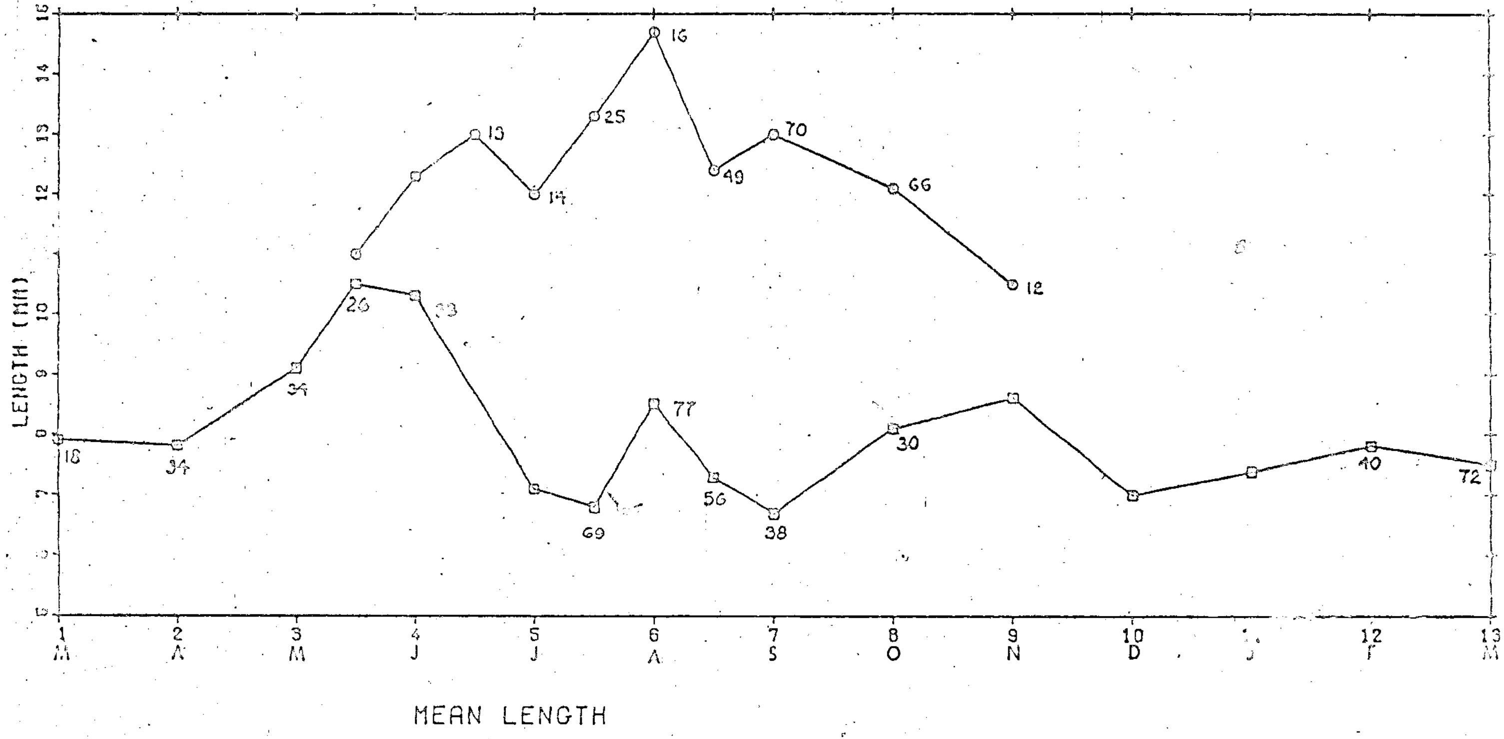


Figure 15 Seasonal variation in mean length of each population. Inset numbers are the numbers of triclads per brick when brick samples were possible. □ PA; ○ FP.

length) than PA triclads, and there were periods when the disparity in mean length was as high as 6mm. FP triclads are commonly 17 and 18mm long, while PA triclads usually do not exceed 16mm in length.

Regression lines for a length-biomass relationship were calculated for FP and PA populations (Fig. 16). A total of 224 triclads were measured and weighed. The equations were $\log Y = -1.71 + 2.55 \log X$ for FP, and $\log Y = -1.46 + 2.31 \log X$ for PA, where Y is dry weight in mg and X is length in mm. Although the regression coefficients were not significantly different, the biomass of each population was calculated using the predicted values generated by the equation for that population. Predicted values for each size class are multiplied by the percentage which that size class represents, giving values with the units of mg-percent (or mg per 100 individuals). Cumulative values of biomass for all size classes represents the total mg-percent biomass present on a sampling date (Fig. 17).

Biomass increased 400 mg-percent from March to May at PA. It then decreased 500 mg-percent by September and flucuated around the 400 mg-percent level through the winter. The FP population increased by 800 mg-percent from May to mid August and then the biomass decreases by 1100 mg-percent through November. In both populations, the spring biomass gain is lost through shrinkage and mortality in summer and autumn. These data illustrate the characteristic adjustment of triclad populations to their carrying capacity

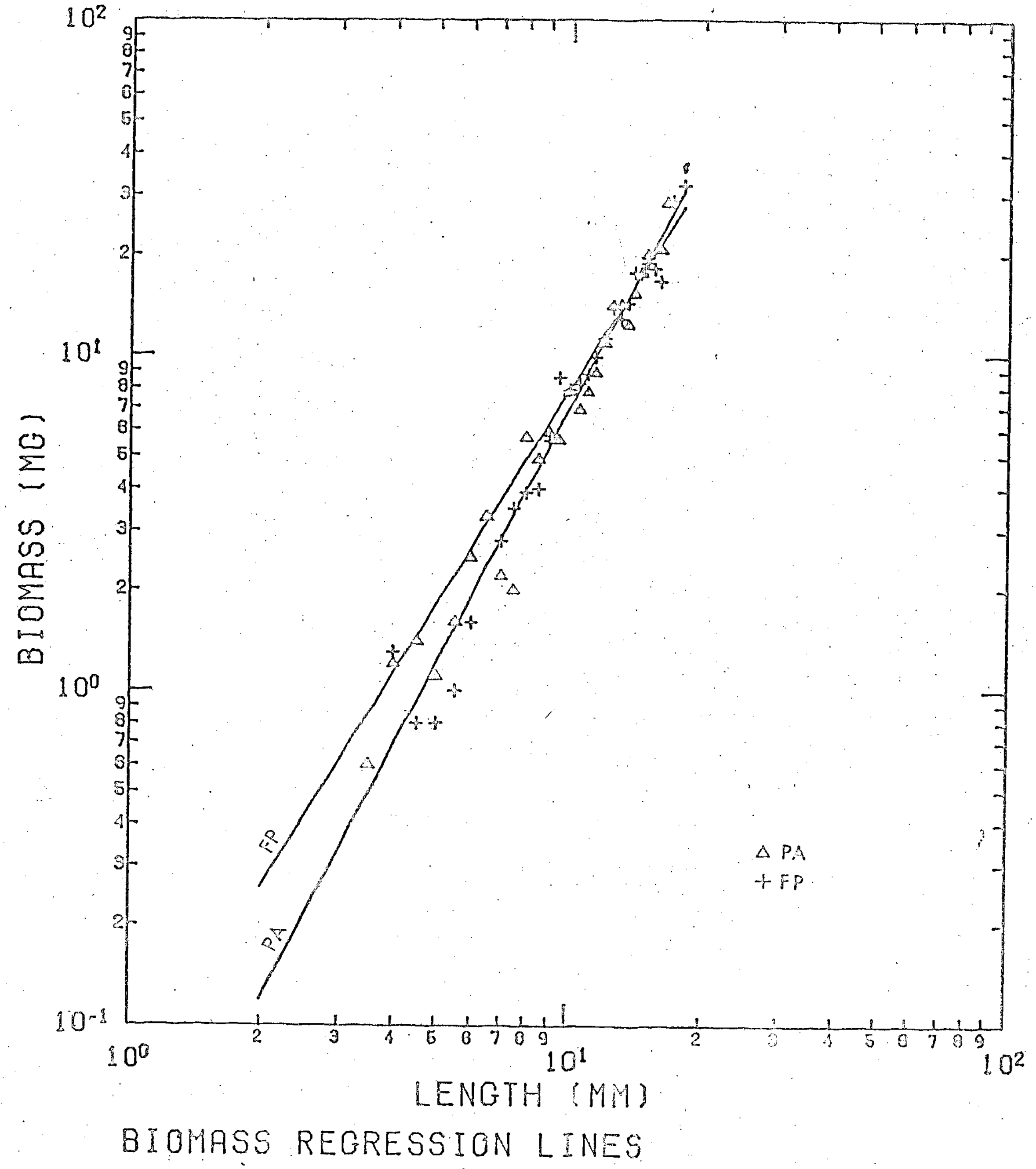


Figure 16. Regression lines of the length-biomass relationship. Symbols are means of all measurements for each size class.

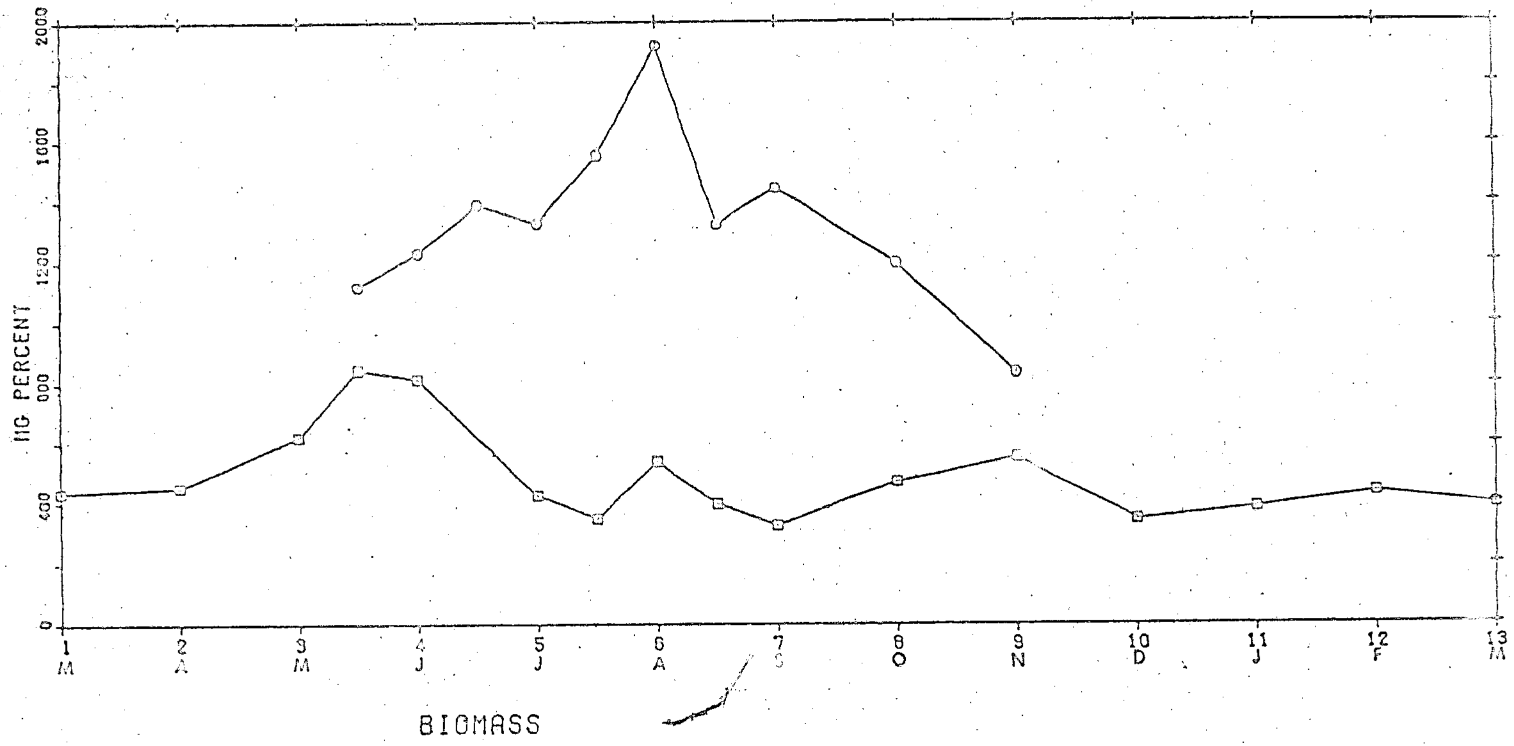


Figure 17. Seasonal variation in total biomass as mg-percent or mg per 100 individuals. □PA; OFP.

after the rapid growth and breeding in spring.

The large difference in biomass between the two populations may be attributed to the length-biomass relationship. Because of the exponential nature of the relationship, large triclads, especially those over 10mm, will weigh proportionally much more than triclads only a few millimeters shorter. The greater mean FP length, always above 10mm, produces the large difference in biomass. Shrinkage of large triclads will result in a greater biomass loss than shrinkage of shorter ones. Hence, FP triclads may seem more affected by intraspecific competition, because starvation has been severe enough to cause a greater loss of biomass than that experienced by PA triclads. However, competition has only reduced the FP biomass and mean length to levels somewhat below the springtime values in the same manner as at PA.

DISCUSSION

Biology of Dugesia-- The triclad Dugesia tigrina is a species that functions best in warm water. Its righting reaction time is quickest above 15°. It prefers water above 20° and young grow three times as fast at 20° than at 10°. Temperatures below 6° strongly inhibit feeding (Pickavance 1971a). These characteristics help explain my field observations.

The normal regions of Lake Wabamun, as represented by the Fallis Point study site, are ice-covered for 5 months of the year. Rapid warming proceeds in the spring, but a maximum of only 20° is reached by late July. FP Dugesia grow rapidly in the spring and become physiologically ready to breed. Cocoons are produced in late June, at a temperature of 16°. This corresponds to the temperature at which Dugesia become most active and also to the range that Pickavance (1968) found to be critical for the initiation and termination of asexual reproduction. Cessation of cocoon reproduction occurs before water temperatures fall to 16°, indicating causes other than temperature are important in terminating reproduction. The temperature goes down quickly in autumn and limits the mobility of the triclads. From the time of ice formation in December and throughout winter the triclads will rarely feed.

Winter temperatures at PA are higher, but often below Dugesia's optimum. Feeding may not be as strongly inhibited at PA; but this warmer water does not seem to benefit the population much, as there are no over-winter increases in length and biomass. Water temperature at PA reaches the optimum in May; so PA <u>Dugesia</u> have a 1 month start over FP <u>Dugesia</u> in their breeding activities, and the PA population breeds for about 3 weeks longer than at FP. Since triclads at both sites take 2 months for growth to maximum length and biomass and 3 months for consequent shrinkage, warmer water at PA seems to have little additional influence on <u>D. tigrina</u>'s life history.

Cooler water throughout the year at FP may be a factor in explaining the greater size achieved by FP triclads. An increase in ambient temperature will increase the metabolic rate of a poikilothermic animal. A triclad in warm water, such as at PA, will have a higher metabolic rate than a triclad in cooler water and thus, assuming equal amounts of food for each, will have less energy available for growth and maintenence. Laboratory data show that triclads maintained and fed at 30° will shrink while those at 20°, receiving the same food, will grow. Possibly FP <u>Dugesia</u> in cooler water can put more of their food energy into growth, thus maintaining greater lengths and biomass. The metabolic rate of FP <u>Dugesia</u> should be quite low in winter whereas PA triclads would probably have much higher metabolic demands in the warmer winter water.

It is instructive to compare the life cycle of the sexually reproducing Alberta <u>D. tigrina</u> to that of asexual, immigrant <u>D. tigrina</u> in Britian, which were studied by

Pickavance (1968). He found that Dugesia grew rapidly in spring and started to reproduce when the water temperature reached 16°. The population increased seven-fold. Fission ceased in mid-September and the population size structure stabilized for 3 months, which is a period of competition for food. In Britian, winter is a season of shrinkage and numerical decrease to early spring levels. Shrinkage did not cause direct mortality in this situation, because shrinkage was not prolonged enough to result in very small triclads that die. This is analogous to the FP situation of my study, where no small (former adult) triclads were produced through shrinkage. Since predators of Dugesia were abundant Pickavance's site, Pickavance feels that the numeri decrease is due to predation, rather than to compe

The major differences in life cycles between e British and Alberta population are in respect to reproduction and the mechanism of population regula British Dugesia can increase seven-fold, but the Lake Wabamun Dugesia only approximately double their population size. Wabamun triclads compete during and after the breeding season, causing mortality of young and shrunken adults. Although British D. tigrina compete for food and shrink after breeding, predation apparently is the major factor in reducing their population. Predation, if it is the cause of the reduction in the British population, reduces numbers to the level present in the previous spring.

The Competition Hypothesis-- The results of the breeding and populat [illegible] es can be interpreted with respect to the hypoth [illegible] at triclad populations are regulated by intraspecific competition for food. For both populations, spring is a period of rapid growth in which length, biomass, and proportion of adults increases. After copulation, cocoon deposition occurs and young start to hatch out 2-3 weeks later. The maximum proportion of young is 21% at PA and 13% at FP. During the breeding season the proportion of adults decreases at both sites. In July at FP, this can be accounted for as dilution by young, but such dilution does not fully account for the PA reduction and later FP reduction. Numbers of young present begin to decline and mean length also decreases after mid-summer. Small, non-young appear at PA, and I have interpreted these as shrunken adults or young that fail to grow. Since shrinkage of adults is not sufficient to produce the small triclads at FP, mortality at FP must occur mainly in the young of the year.

By autumn, the numbers of triclads per brick had declined to numbers that were similar to the spring population levels prior to breeding. This result is obscured at FP by an autumn littoral zone migration. At PA, this decrease is due to mortality of starved young and shrunken adults. The spring-summer gains in length and biomass have been lost because of the food shortage created by breeding. Autumn values of these parameters are equivalent to the early spring values. Thus, all results are consistent with the competition for food hypothesis. Both populat[illegible]st close to their environmental carrying capacities for much of the year; and as the abundant food in spring and summer gives way to shortages in autumn, there is a re-adjustment of population size.

The Life History Strategy Hypothesis-- My results can be considered with respect to the hypothesis that triclads inhabiting thermally different environments are under selection for differing life history strategies. The r-selection strategy requires a greater allocation of resources to reproductive activities by an organism, under all density-independent and dependent mortality conditions, than a [illegible]ated organism allocates (Gadgil and Solbrig 1972). This allocation is necessary to offset high density-independent mortality. High mortality resulting in an elevated death rate will result in a new and higher equilibrium birth rate. This is the population dynamic effect (Gadgil and Solbrig 1972), which is independent of any [illegible] derived through natural selection [illegible] differential [illegible] of resources [illegible] [illegible] [illegible] and [illegible]

[illegible] organisms [illegible] high [illegible], early [illegible] [illegible] small body size, and small [illegible] [illegible] [illegible] compet[illegible] are applied to triclads, the parameters of interest become fecundity, length of young, size of cocoons, number of young per cocoon, and length at maturity. A measure of mortality and competition is also useful in evaluating strategy.

When compared to FP triclads, the PA triclads exhibit greater fecundity, smaller young, and the same number of young per cocoon. These features might indicate an r-selection strategy at PA and K- selection at FP, but other explanations are possible.

Smaller young will have less resistance to mortality than larger ones because the small ones have fewer yolk cells and body tissues that can be lost through starvation before death occurs. Larger young would be more competitive. Smaller cocoons and young may allow diversion of resources into additional cocoon production, and this would be advantageous to an increasing population. Although one would expect smaller cocoons and young from the smaller PA Dugesia, the greater number of cocoons produced per PA adult might represent a greater reproductive allocation than would [illegible] by FP adults. There are no data on these problems.

Smaller body size and early maturity are advantageous [illegible] organisms, because [illegible] resources [illegible] time are spent on adult growth and young are produced at an earlier age. The small size of PA Dugesia may be explained by the thermal regime as already discussed rather than by r-selection. Delayed maturity is usual to a K-selected organism if it allows for increased competitive ability.

establishment of a supply of resources or both before reproducing. Triclads are not known for their learning ability or territoriality, so delayed maturity should be of little consequence to Dugesia. A greater length at maturity might indicate delayed maturity. However, the greater length at maturity of PA triclads is similar to the temperature dependent pattern found in Dugesia polychroa, i.e. D. polychroa raised at higher temperatures had a greater length at maturity (Reynoldson, Young, and Taylor 1965). The effect of the different thermal regimes is a simpler explanation for the observed difference in PA-FP maturation lengths.

The greater PA fecundity is almost certainly due to the mortality factors found only in the thermally affected region. The primary cause of mortality is macrophyte harvesting, which removes large numbers of triclads and cocoons from the lake. The blanketing of some littoral zone areas with decaying plant masses may asphyxiate developing young in cocoons as well as older triclads. My laboratory data suggest that mortality is greater for triclads cultured at 30° than at 20°. In the lake, a comparable mortality could occur in shallow regions depleted of oxygen. Outboard motor propellors [illegible] up macrophytes [illegible] to the water surface and probably kill [illegible] of triclads. Because Dugesia inhabit [illegible] they might be exposed to more predatory [illegible] of all cocoons are sterile and this is a mortality factor probably related to the elevated temperatures. This mortality must be compensated for by increased fecundity.

The reproductive parameters can be explained as either supporting r- and K- selection or as due to other factors. Competition seems equally intense at both sites, hence it does not support the hypothesis. The parsimonious explanation of the observed reproductive parameters is that the greater PA fecundity is a population dynamic effect in which the birth rate has increased to equal a death rate that is higher than that of FP triclads. Further study could perhaps support a difference in life history strategy, but such a difference can not be supported by the data of my study. In general, *Dugesia tigrina* seems to be very much a K- strategist which is limited by intense competition and lives under conditions of food shortage for much of the year.

COMPARATIVE SYNOPSIS

1) Macrophyte harvesting results in substantial triclad mortality at PA. Triclads do not inhabit macrophytes at FP, nor is there any harvesting there.

2) Thirty three percent of PA Dugesia and 10% of FP Dugesia had recently fed on oligochaetes. Dugesia will feed on many other small or weakened animals.

3) Dugesia's righting time is about 7 seconds at water temperatures above 15°, but the righting time increases sharply at temperatures below 15°. PA Dugesia prefer water temperatures from 20° to 33° and FP triclads prefer water from 15°-33°.

4) Adults grow 1.3mm a month at 20°, but shrink 1.5mm a month at 30° when fed. They shrink 2mm a month at 20° and 5mm a month at 30° when starved. Young from both populations grow at the same rate: 0.5mm a month at 10° and 1.7mm a month at 20°.

5) Cocoon production begins in late May at PA and late June at FP. The cocoon fecundity is 1.4 cocoons per adult (18% sterile) at PA and 0.7 (1% sterile) at FP.

6) At PA, adults, young, and cocoons are smaller than those at FP. The maximum percentage of young is 21% at PA and 13% at FP. Fecundity based on young is 0.36 and 0.07 young per adult for PA and FP respectively.

7) Adults make up [illegible]7% and 100% of the population at the spring maximum for the two sites. The percentage adults

declines to 17% at PA, but does not decline substantially at FP.

8) The loss in mean length and biomass is approximately equal in both populations and the post-breeding loss is equivalent to the spring gain. The shrinkage of the population and the decline in numbers of young and small triclads supports the hypothesis of food competition. The reduction in number per PA brick after breeding to pre-breeding levels also supports the hypothesis.

9) Although several reproductive parameters are consistent with the theory of r- and K- selection, there are other explanations for the observations. Since competition seems equally intense at both sites, there is no reason why one population should be more K- selected. I suggest that the increased fecundity of PA triclads is due to greater mortality at PA, primarily from macrophyte harvesting.

LITERATURE CITED

Allen, E.D., 1973. An ecophysiological study of the effects of thermal discharges on the submerged macrophytes of Lake Wabamun. M.Sc. thesis. Dept. of Botany, Univ. Alberta 88 p.

Allen, E.D., and P.R. Gorham. 1973 Changes in the submerged macrophyte communities of Lake Wabamun as a result of thermal discharges. in Proc. Symp. "Lakes of Western Canada", Univ. Alberta, Water Res. Center publication no. 2, Univ. Alberta Press: 313-324.

American Public Health Association. 1971. Standard Methods for the Examination of Water and Wastewater (13th ed.). Amer. Public Health Assoc., New York. 769 p.

Ash, G.R. 1974. The effects of heated water discharge upon the whitefish (*Coregonus clupeaformis* (Mitchell)) in Lake Wabamun, Alberta. M.Sc. thesis. Dept. of Zoology, Univ. Alberta 130 p.

Ball, I.R. 1969. An annotated checklist of the freshwater Tricladida of the Nearctic and Neotropical regions. Can. J. Zool. 47:59-64.

Boddington, M.J., and D.F. Mettrick. 1971. Seasonal changes in the chemical composition and food reserves of the freshwater triclad *Dugesia tigrina*. J. Fish. Res. Bd. Can. 28:7-14.

Chandler, C.M. 1966. Environmental factors affecting the local distribution and abundance of four species of stream dwelling triclads. Invest. Indiana Lakes and Streams 7:1-56.

Dahm, A.G. 1955. *Dugesia tigrina* (Girard), an American immigrant into European waters. Verh. Int. Verein. Limnol. 12:554-561.

Davies, R.W. 1969. The production of antisera for detecting specific triclad antigens in the gut contents of predators. Oikos 20:248-260.

Gadgil, M., and O.T. Solbrig. 1972. The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. Amer. Nat. 106:14-31.

Gallup, D.M., and M. Hickman. 1975. Effects of the discharge of thermal effluent from a power station on Lake Wabamun, Alberta, Canada -Limnological features. Hydrobiologia 46:45-69.

Gallup, D.M., M. Hickman, and J. Rasmussen. 1975. Effects of thermal effluent and macrophyte harvesting on the benthos of an Alberta lake. Ver. Int. Ver. Limnol. 19:552-561.

Horkan, J.P.K. 1971. Some ecological effects of thermal pollution on Lake Wabamun, Alberta, with special reference to the Rotifera. M.Sc. thesis. Dept. of Zoology, Univ. Alberta 168 p.

Klarer, D.M. 1973. The effect of thermal effluent upon an epiphytic algal community in Lake Wabamun, Alberta. M.Sc. thesis. Dept. of Botany, Univ. Alberta 193 p.

Noton, L.R. 1974. Phytoplankton productivity in Lake Wabamun, Alberta, and the effect of thermal effluent. M.Sc. thesis. Dept. of Zoology, Univ. Alberta 163 p.

Nursall, J.R., and D.M. Gallup. 1971. The responses of the biota of Lake Wabamun, Alberta, to thermal effluent. In Proc. of the Int. Symp. of Ident. Meas. Environ. Pollut., Ottawa:295-304.

Pennak, R.W. 1953. Freshwater Invertebrates of the United States. Ronald Press Co., New York. 769 p.

Pianka, E.R. 1970. On r- and K- selection. Amer. Nat. 104:592-597.

Pickavance, J.R. 1968. The ecology of <u>Dugesia tigrina</u> (Girard) -an American immigrant planarian. Ph.D. thesis. Univ. Liverpool 306 p.

Pickavance, J.R. 1971a. The diet of the immigrant planarian

Dugesia tigrina I. Feeding in the laboratory. J. Anim. Ecol. 40:623-636.

Pickavance, J.R. 1971b. The diet of the immigrant planarian *Dugesia tigrina* 2. Feeding in the wild and comparison with some British species. J. Anim. Ecol. 40:637-650.

Reynoldson, T.B. 1960. A quantitative study of the population biology of *Polycelis tenuis*. Oikos 11:125-141.

Reynoldson, T.B. 1961. A quantitative study of the population biology of *Dugesia lugubris*. Oikos 12:111-125.

Reynoldson, T.B. 1964 Evidence for intra-specific competition in field populations of triclads. Jubilee Symp. Suppl. J. Anim. Ecol. 33:187-201.

Reynoldson, T.B. 1966a. The distribution and abundance of lake-dwelling triclads -towards a hypothesis. Adv. Ecol. Res. 3:1-71.

Reynoldson, T.B. 1966b. Preliminary laboratory experiments on recruitment and mortality in triclad populations. Ver. Int. Ver. Limnol. 16:1621-1631.

Reynoldson, T.B. 1975. Food overlap of lake-dwelling triclads in the field. J. Anim. Ecol. 44:245-250.

Reynoldson, T.B., and L.S. Bellamy. 1971. Intra-specific competition in lake-dwelling triclads; a laboratory study. Oikos 22:315-328.

Reynoldson, T.B. [illegible] L.S. Bellamy. 1973. Interspecific competition [illegible] lake-dwelling triclads; a laboratory study. Oikos 24:301-313.

Reynoldson, T.B., and R.W. Davies. 1970. Food niche and coexistence in lake-dwelling triclads. J. Anim. Ecol. 39:599-617.

Reynoldson, T.B., and A.D. Sefton. 1972. The population biology of *Planaria torva*. Oecologia 10:1-16.

Reynoldson, T.B., J.O. Young, and M.C. Taylor. 1965. The efect of temperature on the four species of lake-dwelling triclads. J. Anim. Ecol. 34:23-43.

Riser, N.W., and M.R. Morse. 1974. The biology of the Turbellaria. McGraw-Hill, New York. 530 p.

Russier-Delolme, R. 1972. Coefficients thermiques et ecologie de quelque planaires d'eau douce 6. *Dugesia tigrina*. Ann. Limnol. 8:119-140.

Sokal, R.R., and F.J. Rolph. 1969. Biometry. W.H. Freeman and Co., San Francisco. 776 p.

Taylor, M.C., and T.B. Reynoldson. 1962. The population biology of lake-dwelling *Polycelis* species with special reference to *P. nigra* (Mull.) (Turbellaria, Tricladida). J. Anim. Ecol. 31: 273-291.

Wheelock, J.M. 1969. Phytoplankton ecology in Wabamun Lake and the effect of thermal pollution. M.Sc. thesis. Dept. of Botany, Univ. Alberta 178 p.

Young, J.O., and T.B. Reynoldson. 1965. A quantitative study of the population biology of *Dendrocoelum lacteum* (Turbellaria, Tricladida). Oikos 15:237-264.

Appendix 1: Percentage composition of FP samples.

Date	N	2	3	4	5	6	7	8	9
		% in each size class							
197[illegible]									
May 29	81					1.2	1.2	13.6	11.1
Jun 11	70							4.3	10.0
Jun 30	166						0.6	0.6	4.2
Jul 16	148	4.1	8.1	0.7			0.7		0.7
Jul 29	202		3.5		1.5	0.5	1.0	0.5	
Aug 12	129				0.8		0.8		
Aug 27	343	0.3	1.8	1.5	1.8	0.9	2.6	3.8	3.2
Sep 13	269				0.4	0.4	0.4	2.2	2.2
Oct 18	219						0.9	3.7	5.0
[illegible] 5	50					2.0	4.0	14.0	10.0

	10	11	12	13	14	15	16	≥17
May 29	22.2	12.3	13.6	11.1	2.5	4.9	3.7	2.4
Jun 11	8.6	17.1	8.6	20.0	12.9	11.4	2.9	2.8
Jun 30	8.4	10.2	15.1	22.3	13.8	12.0	6.6	4.9
Jul 16	3.4	9.5	10.3	18.9	18.9	13.5	6.8	4.1
Jul 29	1.5	4.0	12.9	21.3	17.8	18.8	11.8	5.0
Aug 12	0.8	0.8	3.9	10.9	21.7	29.5	16.3	14.7
Aug 27	9.0	10.5	9.3	10.3	15.7	14.9	9.0	5.0
Sep 13	11.2	10.8	14.1	12.5	12.6	17.8	11.2	4.[illegible]
Oct 18	13.2	16.0	17.8	18.7	11.4	8.2	3.7	1.4
Nov 15	16.0	22.0	18.0	10.0	2.0	2.0		

Appendix 1: Percentage composition of PA samples.

		% in each size class							
Date	N	2	3	4	5	6	7	8	9
1975									
Mar 22	35			5.7	11.4	2.9	20.0	11.4	25.7
Apr 28	84		1.2	3.6	11.9	14.3	15.5	16.7	11.9
May 15	109			0.9	1.8	6.4	11.0	20.2	20.2
May 29	100		1.0		2.0	3.0	1.0	10.0	6.0
Jun 10	369		1.1	0.5	1.6	2.7	6.2	10.0	9.7
Jul 2	118	1.7	15.2	4.2	8.5	12.7	11.0	11.9	9.3
Jul 8	242	1.2	3.3	11.2	17.[illegible]	9.9	12.8	12.4	9.5
Jul 24	314	1.9	8.0	8.0	12.1	12.4	18.5	15.3	7.3
Aug 7	347	0.3	0.9	1.4	3.7	14.1	13.8	18.2	13.5
Aug 19	465	0.6	1.7	8.0	15.3	12.5	16.6	15.3	11.0
Sep 13	211	1.0	4.7	7.1	18.0	19.0	18.0	10.9	7.6
Oct 18	277			4.0	7.2	9.0	24.2	15.2	15.2
Nov 15	231			1.3	7.7	9.9	11.7	19.0	15.2
Dec 16	242	0.4	0.8	5.2	18.2	15.3	22.7	16.5	11.6
1976									
Jan 17	172		1.7	1.2	8.1	22.1	24.4	19.2	8.[illegible]
Feb 13	149			2.7	5.4	14.8	24.8	22.2	10.1
Mar 5	191			1.6	8.9	17.3	23.6	23.6	13.6

Percentage composition of PA samples continued.

Date	% in each size class 10	11	12	13	14	15	16
1975							
Mar 22	[illegible]	5.7					
Apr 28	11.9	8[illegible]	[illegible]	2.4			
May 15	12.8	[illegible]	[illegible]	3.7	1.8		
May 29	22.0	2[illegible]	23.0	7.0	3.0	2.0	
Jun 10	15.4	1[illegible].5	20.8	7.3	2.7	1.6	0.8
Jul 2	8.5	5.9	6.8	0.8	1.7	0.8	0.8
Jul 24	12.4	1.9	2.2				
Aug 7	13.3	11.5	6.6	1.4	0.9	0.3	
Aug 19	10.8	5.0	2.6	0.9			
Sep 13	7.1	3.8	1.0	0.5			
Oct 18	11.6	7.9	3.4	1.4	0.4		
Nov 15	14.2	12.1	4.3	3.0	0.9	0.4	
Dec 16	3.7	2.9	1.2	0.4			
1976							
Jan 17	10.5	2.9	1.2				
Feb 13	12.8	4.[illegible]	1.3	0.7	0.7		
Mar 5	8.9	2.1	0.5				

Appendix 2: Sampling data for FP.

Date	% Adults	% Young	# Cocoons	Type of Sample
1975				
May 29	97.5	0	0	rocks
Jun 11	100	0	0	rocks
Jun 30	99.4	0	22	11 bricks
Jul 16	86.5	12.8	160	8 bricks
Jul 29	93.6	3.5	214	7 bricks
Aug 12	98.0	0	49	8 bricks
Aug 27	91.3	3.5	3	7 bricks
Sep 13	98.9	0	0	6 bricks
Oct 18	99.1	0	0	6 bricks
Nov 15	94.0	0	0	5 bricks

Appendix 2: Sampling data for PA.

Date	% Adults	% Young	# Cocoons	Type of Sample
1975				
Mar 22	22.9	0	0	2 bricks
Apr 28	25.0	0	0	3 bricks
May 15	39.5	0	0	4 bricks
May 29	77.0	0	2	4 bricks
Jun 10	67.8	1.6	158	9 bricks and plants
Jul 2	25.4	21.0	66	rocks and plants
Jul 8	22.3	12.4	84	plants
Jul 24	16.6	14.6	36	5 bricks and plants
Aug 7	34.0	3.5	6	5 bricks and plants
Aug 19	19.1	5.2	0	5 bricks and plants
Sep 13	12.8	0	0	5 bricks and plants
Oct 18	25.3	0	0	6 bricks and plants
Nov 15	35.1	0	0	plants
Dec 16	8.3	0	0	sweep-net
1976				
Jan 17	14.5	0	0	rocks
Feb 13	20.1	0	0	4 bricks
Mar 5	11.4	0	0	5 bricks

Appendix 3: Mean number/brick, mean length, standard error, and biomass for FP.

Date	Number /brick	Length mm	St. error	Biomass mg-percent
May 29	-	11.01	0.27	1121
Jun 11	-	12.01	0.28	1230
Jun 30	13	12.99	0.17	1391
Jul 16	14	12.05	0.33	1333
Jul 29	25	13.28	0.20	1555
Aug 12	16	14.72	0.16	1919
Aug 27	49	12.37	0.17	1329
Sep 13	70	13.03	0.15	1448
Oct 18	66	12.11	0.14	1197
Nov 15	12	10.48	0.28	836

Appendix 3: Mean number/brick, mean length, standard error, and biomass for PA.

Date	Number /brick	Length mm	St. error	Biomass mg-percent
Mar 22	18	7.88	0.33	433
Apr 28	34	7.82	0.24	453
May 15	34	9.14	0.20	620
May 29	26	10.51	0.21	846
Jun 10	33	10.31	0.12	816
Jul 2	-	7.10	0.30	425
Jul 8	-	7.48	0.20	456
Jul 24	69	6.84	0.13	348
Aug 7	77	8.50	0.12	538
Aug 19	56	7.30	0.10	395
Sep 13	38	6.71	0.15	325
Oct 18	30	8.06	0.12	472
Nov 15	-	8.61	0.14	552
Dec 16	-	6.97	0.13	345
Jan 17	-	7.38	0.14	383
Feb 13	40	7.81	0.15	436
Mar 5	72	7.49	0.11	391

Appendix 4: Mean length of young grown at two temperatures.

Culture number	Month 0	1	2	3	4	5
10° FP						
C1	3.2	4.7	5.2	5.3	6.5	6.5
C2	3.2	4.6	4.6	6.2	7.0	7.0
C3	2.2	3.8	3.4	4.2	4.3	4.7
C4	3.0	5.0	5.2	5.8	6.0	6.3
10° PA						
C5	2.2	4.0	5.0	5.0	5.0	5.9
C6	2.3	3.4	3.9	4.4	4.1	4.9
C7	2.8	1.8	2.8	3.5	3.5	3.5
C8	2.7	3.7	4.8	5.2	5.1	5.7
20° FP						
C9	3.0	6.0	8.0	10.5	11.2	12.3
C10	2.9	5.0	6.0	5.0		
C11	3.1	6.4	7.2	9.2	11.2	11.5
C12	3.2	7.2				
20° PA						
C13	2.3	5.1	5.8	6.0	9.2	8.7
C14	3.6	5.6	7.4	11.0	11.0	13.0
C15	2.8	5.1	6.9	8.7	11.8	13.0
C16	2.5	5.6				