

VARIATION AND NATURAL SELECTION IN A  
POPULATION OF STICKLEBACKS (Gasterosteus).

by

James Alexander MacLean

B.Sc., University of Manitoba, 1966

M.Sc., University of Manitoba, 1969

A thesis submitted in partial fulfilment of  
the requirements for the degree of  
Doctor of Philosophy  
In the Department  
of  
Zoology

We accept this thesis as conforming to the  
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

July 1974

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of

ZOOLOGY

The University of British Columbia  
Vancouver 8, Canada

Date

SEPT 9, 1974

## ABSTRACT

Threespine sticklebacks are genetically polymorphic for the number and arrangement of bony plates on the sides of the body. The adaptive significance and maintenance of plate variation was investigated in Heisholt Lake, a small British Columbia lake with two separate basins. The population contains the low plated, partially plated, and completely plated freshwater morphs of threespine sticklebacks, and plate number varies considerably within morphs.

Frequencies of the plate phenotypes changed in space and time. Morph frequencies change spatially both between depths within an area, owing to segregation of breeding females, and between areas at the same depth. Phenotypic frequencies changed temporally both within and between generations. Phenotypes favored within a generation also increased in frequency from that generation to the next. At most stations in basin 1, low and completely plated sticklebacks increased, and partially plated sticklebacks decreased in frequency both within and between generations. In basin 2, partially plated sticklebacks were favored at many stations both within and between generations. Extreme phenotypes within all morphs increased in frequency both within and between generations, and asymmetrical disruptive selection acted during at least one generation within all morphs.

Interactions between genetic variation and structure of the stickleback population appear to explain changes in the frequency of phenotypes in both space and time. Experiments to investigate the movement pattern of sticklebacks in Heisholt Lake show that the population is composed of

resident individuals, which remain in a restricted area and maintain either a feeding or breeding territory, and non-residents, which move from area to area and do not breed. The phenotype of an individual influences its chances to become a resident. Low and completely plated sticklebacks were favored in competition for territories in basin 1, but partially plated sticklebacks were often favored in basin 2.) Females with extreme phenotypes had the greatest chance of breeding, and asymmetrical disruptive selection acted within all morphs.

The phenotype of a stickleback also influences its chances of being infected with Schistocephalus solidus, a cestode parasite that reduces the chances of infected sticklebacks to survive and reproduce. Partially plated sticklebacks had the highest rate of infection in basin 1, but had the lowest rate of infection in basin 2. Differential infection of phenotypes was at least part of the explanation for the observed temporal changes in phenotypic frequencies.

Spatial changes in phenotypic frequencies are caused by changes in space in the results of competition for territories. Temporal changes in phenotypic frequencies are explained by differential survival and reproduction of phenotypes as a result of differences between phenotypes in chances to obtain a territory.

## TABLE OF CONTENTS

	Page
ABSTRACT .....	ii
TABLE OF CONTENTS.....	iv
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
ACKNOWLEDGEMENTS.....	viii
INTRODUCTION.....	1
MATERIALS AND METHODS.....	7
A. Study Area .....	7
B. Variation in Sticklebacks.....	7
C. Collecting Sticklebacks.....	9
DISTRIBUTION OF STICKLEBACKS.....	10
A. Combining Samples from Successive Days.....	11
B. Morph Frequency and Depth.....	12
C. Morph Frequency and Area .....	17
D. Summary.....	19
ABUNDANCE OF STICKLEBACKS.....	19
VARIATION OF STICKLEBACKS.....	21
A. Between Morph Comparisons.....	21
(1) Changes in Morph Frequency from May to September .....	21
(2) Changes in Morph Frequency from Year to Year .....	27
B. Within Morph Comparisons .....	34
(1) Changes in Frequencies of Plate Number Phenotypes from May to September .....	34
(2) Changes in Frequencies of Plate Number Phenotypes from Year to Year .....	34
C. Summary .....	43

	Page
STICKLEBACKS AND <u>SCHISTOCEPHALUS SOLIDUS</u> .....	45
MOVEMENTS OF STICKLEBACKS.....	49
A. Movement Patterns .....	49
B. Relative Numbers of Residents and Non-residents.....	53
C. Summary .....	57
VARIATION OF RESIDENT AND NON-RESIDENT STICKLEBACKS.....	57
A. Nesting Males .....	59
B. Breeding Females .....	60
C. Residents and Non-residents in September .....	70
D. Summary .....	70
SUMMARY OF RESULTS.....	73
A. Changes in the Frequency of Phenotypes .....	73
B. Explanation of Observed Changes .....	74
DISCUSSION.....	75
A. Behavior and Movement of Sticklebacks.....	75
B. Physiological Variation in <u>Gasterosteus aculeatus</u> .....	81
C. Variation in Resident and Non-resident Sticklebacks.....	83
BIBLIOGRAPHY.....	88
APPENDICES.....	97

TABLE	LIST OF TABLES	Page
I	Morph frequencies of sticklebacks caught in an area of basin 2 on successive days in May 1970.....	13
II	Morph frequencies of sticklebacks at different depths in one area, 1970.....	14
III	Morph frequencies of sticklebacks at 10 stations in basin 2 in Heisholt Lake in May 1970.....	18
IV	Summary of Chi-squared tests of association between morph frequencies and station in Heisholt Lake 1971-1973.....	19 a
V	Summary of tests of homogeneity and morph frequencies of sticklebacks at a station in May and September 1971 and 1972.....	24
VI	Relative fitness of plate morphs of sticklebacks from May to September at stations in Basin 1 in 1971 and 1972.....	26
VII	Relative fitness of plate morphs of sticklebacks from May to September at stations in basin 2 in 1971-1972.....	29
VIII	Summary of tests of homogeneity of frequencies of plate morphs in May of 1971, 1972 and 1973.....	31
IX	Summary of tests of homogeneity of plate number frequencies within morphs in May and September of 1971 and 1972.....	35
X	Summary of tests of homogeneity of frequencies of plate number phenotypes within morphs from May of one year to May of the following year.....	41
XI	Proportion of sticklebacks with different plate morphs infected with <u>Schistocephalus solidus</u> in Heisholt Lake, June 1971.....	48
XII	Frequencies of marked and non-marked sticklebacks in an area in basin 2 in May 1972.....	56
XIII	Relative fitness of marks with different plate morphs breeding in basin 1 .....	61
XIV	Relative fitness of males with different plate morphs breeding in basin 2 , 1973.....	62
XV	Summary of tests of homogeneity of morph frequencies of nesting males at different stations.....	63
XVI	Summary of tests of association between the plate morph of female sticklebacks and breeding condition.....	64
XVII	Morph frequencies of breeding and non-breeding female sticklebacks and relative fitness of morphs in early May in Heisholt Lake 1971-1973	65
XVIII	Morph frequencies of resident and non-resident sticklebacks in basin 1 in August 1972.....	71

## LIST OF FIGURES

FIGURE		Page
1	Plate morphs of sticklebacks in Heisholt Lake.....	3 a
2	Heisholt Lake on Texada Island, British Columbia, showing location of sampling stations.....	8
3	Depth distribution of sticklebacks in basin 2 of Heisholt Lake, 1970.....	15
4	Depth distribution of breeding female sticklebacks with differing plate phenotypes in Heisholt Lake in June 1970.....	16
5	Average catch per unit effort (average of sticklebacks/trap) in basins of Heisholt Lake in May and September, 1970-1973.....	22
6	Comparison of frequencies of plate morphs of sticklebacks at stations in basin 1 in May and September of 1971 and 1972.....	25
7	Comparison of frequencies of plate morphs of sticklebacks at stations in basin 2 in May and September of 1971 and 1972.....	28
8	Comparison of frequencies of plate morphs of sticklebacks at stations in basin 1 in May of one year and May of the following year.....	32
9	Comparison of frequencies of plate morphs of sticklebacks at stations in basin 2 in May of one year and May of the following year.....	33
10	Relative fitness and plate number phenotypes within morphs: from May to September 1971 (0) and 1972 (●) in basin 1.....	36
11	Relative fitness of plate number phenotypes within morphs from May to September 1971 (0) and 1972 (●) in basin 2.....	38
12	Relative change of frequency of plate number phenotypes within morphs from May in one year to May in the following year in basin 1.....	40
13	Relative change of frequency of plate number phenotypes within morphs from May in one year to May in the following year in basin 2.....	44
14	Rate of infection of sticklebacks with <u>Schistocephalus solidus</u> in basin 2 during 1970.....	46
15	Sketch of U-shaped bay (Station 26) in basin 2 used for experiment on movement patterns of sticklebacks showing sites at which traps were set.....	51
16	Frequency of marked sticklebacks at different distances from release area in May and September 1971.....	52
17	Movement of resident and non-resident sticklebacks from release area in May, 1972.....	54
18	Relationship between density of sticklebacks (catch/unit effort) in release area on day one and the proportion of sticklebacks with territories (frequency of marked sticklebacks in release area) in release area on day one.....	58
19	Relative fitness of plate phenotypes of female sticklebacks in basin 1...	66
20	Relative fitness of plate phenotypes of female sticklebacks in basin 2...	68
21	The relationship between density of sticklebacks in a trap and the relative frequency of the partially plated morph in the breeding females caught in the trap - 1972.....	69



## ACKNOWLEDGEMENTS

Numerous people on Texada Island contributed to this research through their hospitality and assistance with the field work, but I would particularly like to thank Mr. M. Pero, Ron and Darlene Arnold, John and Jacqueline Sellinten, and Don Wise. I am also grateful to many members of the Institute of Animal Resource Ecology, who listened patiently to various ramblings about sticklebacks in Heisholt Lake. I thank Steven Stearns, and Drs. D. Chitty, J. Myers, and A. Birdsall for reading the manuscript and making many useful suggestions. I am indebted to Dr. Douglas Hay for the numerous stimulating discussions we had about sticklebacks, research, and where he/I was mistaken. I am particularly grateful to Dr. J.D. McPhail, my thesis supervisor, for his constant enthusiasm for discussion and research and his interest in my work.

FROM THE NORTHERN WHIG AND BELFAST POST: MAY 30, 1928.

'Dozens of tiny red fish were found on the roof of a bungalow on the farm of Mr. James McMaster, Drumhirk, near Comber, and on the ground in the vicinity yesterday morning, and the extraordinary occurrence caused considerable speculation. In the course of enquiries it was ascertained that just before the discovery of the fish there had been an exceptionally violent thunderstorm with heavy rain. There is no river in the neighbourhood, the nearest sheet of water being Strangford-hough, two miles distant, and the theory advanced by an expert was.....'

Adapted from Norman, J.R. and P. H. Greenwood.  
1963.

A History of Fishes. Ernest Benn Ltd. London  
398p.

## INTRODUCTION

Population biologists are currently interested in interactions between genetic variation and ecology, and particularly in questions about the adaptive significance and maintenance of variation in natural populations. While population geneticists and ecologists agree that a union between their disciplines is necessary to answer these questions, few actual attempts at such a union are made (Sheppard, 1969). This thesis investigates the adaptive significance and maintenance of variation in lateral plate number in threespine sticklebacks (Gasterosteus aculeatus L.).

Sticklebacks are ideal animals for the study of selection and evolution in natural populations. They are abundant, easy to catch, and small enough to be observed and experimented with in the field and laboratory. The biology of sticklebacks is well studied, although their ecology is relatively unknown. Marine and freshwater populations of threespine sticklebacks occur in Europe, Asia, and North America. Marine populations appear to be pelagic and feed on plankton. Freshwater populations occur in streams and lakes, and may be either pelagic or benthic feeders (Larson, 1972). Freshwater individuals mature in their first or second year, and live for a maximum of three years; marine individuals mature in one year, and seldom breed a second year (McPhail and Lindsey, 1970). Breeding behavior is described by Tinbergen (1951) and van den Assem (1967). Sticklebacks are extremely variable, showing polymorphic and polygenic morphological variation that can be scored or measured easily. Their short generation time in the laboratory facilitates

analysis of the inheritance of this variation.

This study is one of a series on the adaptive significance and maintenance of variation in populations of sticklebacks. The polymorphism for number and arrangement of bony plates on the sides of the body has attracted considerable attention (Bertin, 1925; Heuts, 1947a; Lindsey, 1962; Munzing, 1963; Hagen, 1967). Unfortunately, this attention has produced a state of advanced confusion, so I will briefly describe the variation in lateral plates, and summarize previous results of studies on inheritance and maintenance of this variation.

Bertin (1925) and Heuts (1947a) described two morphs of threespine stickleback:

- (1) a large, silvery, marine morph, with relatively high numbers of plates and gill rakers;
- (2) a small, drab green, freshwater morph, with fewer plates and gill rakers.

The marine morph is anadromous and breeds in freshwater, and hybrids between the morphs are found in areas of sympatry. Munzing (1963) shows that this model does not adequately account for observed differences between European populations, and proposed three morphs of stickleback:

- (1) a completely plated morph, trachurus;
- (2) a morph with few plates, leiurus;
- (3) a morph with intermediate plate numbers, semiarmatus.

He found anadromous populations with all three morphs; freshwater populations of trachurus; populations with either leiurus and semiarmatus or

trachurus and semiarmatus which lack the third morph to explain the presence of intermediates; and pure populations of semiarmatus. Hagen and Gilbertson (1973a) argue that variation in freshwater and marine populations should be considered separately, and use the terms low plated, partially plated, and completely plated for the freshwater morphs (Fig. 1). Plate numbers vary considerably within morphs. Hay (1974) suggests that the pattern of plate variation is as important as number of plates.

Heuts (1947a) and Munzing (1963) proposed a genetic model with two major genes to explain segregation in crosses between leiurus (low-plated) and trachurus. Hagen and Gilbertson (1973a) also found that freshwater morphs are determined by segregation of major genes, but that the simplest model to explain results of crosses involves two autosomal loci, each with two alleles. Lindsey (1962) and Hagen (1972) report high heritabilities for plate numbers within a morph (0.50 to 0.84). Hagen and Gilbertson (1973a) suggest that variation within morphs results from segregation of polygenes.

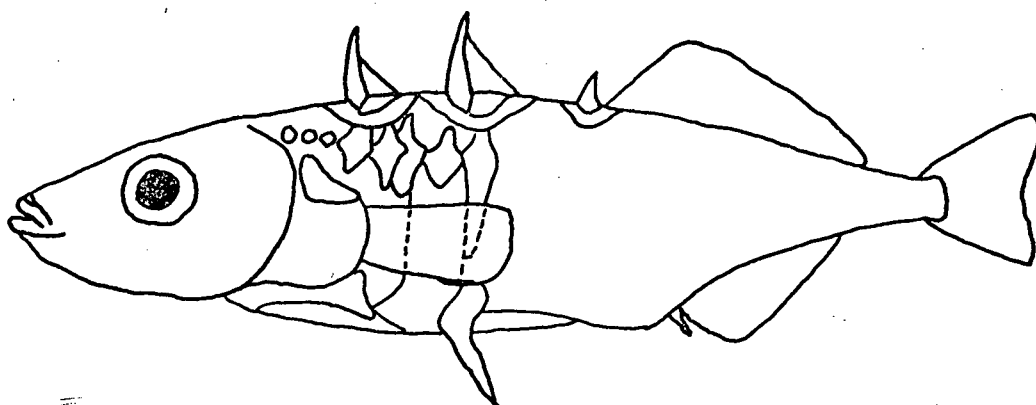
The central problem of ecological genetics of sticklebacks is to explain the variation in plate number within and between populations (Penczak, 1965, 1966; Miller and Hubbs, 1969; Hagen and Gilbertson, 1972). Munzing (1963) proposed two hypotheses to explain the observed pattern of variation:

(1) that leiurus and trachurus are morphs of a polymorphic species, implying that selection maintains variation;

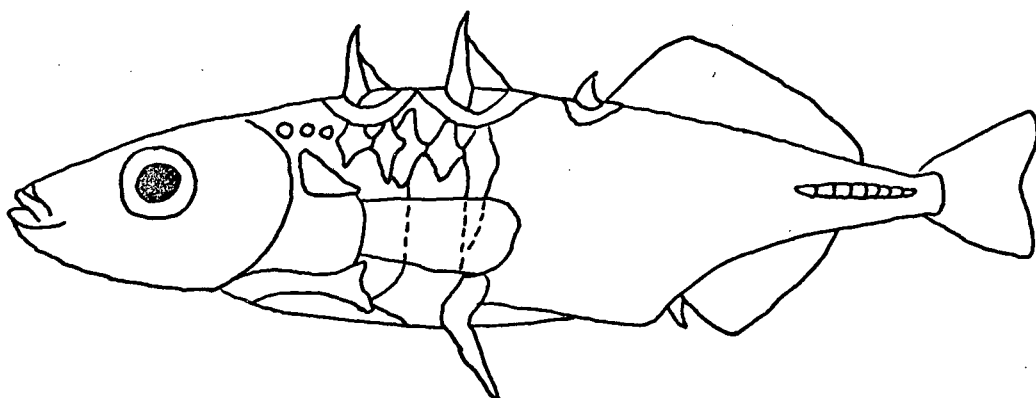
(2) that leiurus and trachurus were geographically isolated during the Pleistocene, so that the present pattern of variation is due to dispersal and subsequent introgression between these morphs.

FIG. 1: Plate Morphs of sticklebacks in Heisholt Lake

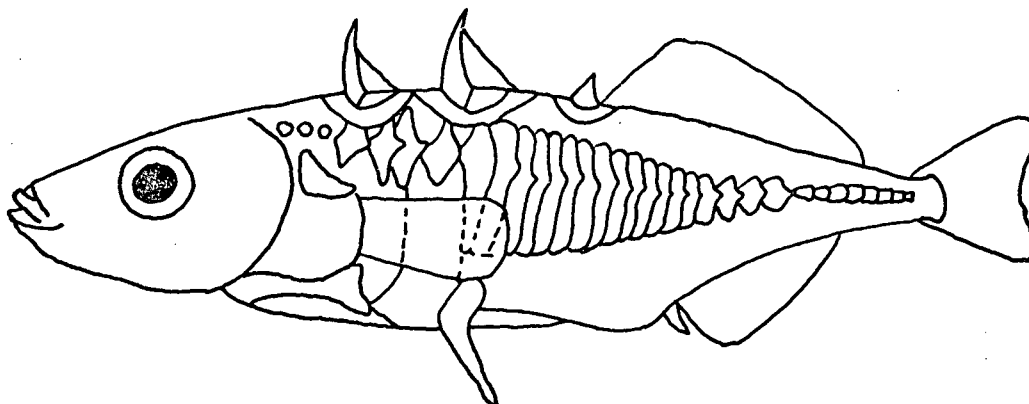
(From Hagen and Gilbertson, 1973a)



LOW PLATED MORPH



PARTIALLY PLATED MORPH



COMPLETELY PLATED MORPH

Numerous studies show that selection acts on variation in plate number. Heuts (1947b) shows that leiurus and trachurus are physiologically different, and suggests that these differences reduce gene flow through habitat selection. Plate number phenotypes within morphs are also associated with physiological differences (Heuts, 1947b; Lindsey, 1962). Hagen (1967) studied isolating mechanisms between marine anadromous trachurus and freshwater leiurus. Hybrids were confined to a narrow zone between the morphs. He found no behavioral or genetic barriers to hybridization, but that ecological isolation, involving numerous adaptations to different microhabitats, reduced gene flow between morphs. Hay (1969) found partial ethological isolation between morphs, as Ford (1971) anticipated. Several studies demonstrate selective predation on sticklebacks favoring certain plate numbers (Moodie, 1972a; Hagen and Gilbertson, 1972, 1973b; Hay, 1974; Lea, 1969). Laboratory experiments designed to examine predation suggest that differential survival of phenotypes within morphs is due to behavioral differences (McPhail, 1969; Moodie, McPhail and Hagen, 1973). Males with a particular plate count build nests in micro-habitats that differ from those chosen by other phenotypes (Moodie, 1972b; Hay, 1974; McPhail, pers. comm.). Plate phenotypes differ in fecundity of females (Hagen, 1967; Moodie, 1972b; Hay, 1974; McPhail, unpub. data). Although the adaptive significance of variation in plates is unknown, selection clearly acts on a variety of characters linked to plate number.

Hybridization occurs between leiurus and trachurus, and no selective mechanism acting against semiarmatus is known (Hay, 1974). Miller and Hubbs (1969) argue that introgression between leiurus and trachurus explains the observed geographical pattern of variation. While introgression occurs in some areas, permanent sympatric populations of all three plate morphs



also occur (Hagen and Gilbertson, 1972), suggesting that introgression does not necessarily lead to elimination of differences between morphs. Clearly, selection can maintain the morphs despite gene flow.

Other morphological characters of sticklebacks also vary within and between populations. Variation in gill raker numbers is related to feeding strategies of a population (Larson, 1972; Hagen and Gilbertson, 1972), and heritability of gill raker number is high (0.58) (Hagen, 1972). Male sticklebacks vary in breeding coloration, which is genetically inherited, and differential predation of color morphs is a selective force maintaining variation (McPhail, 1969; Semler, 1972; Moodie, 1972b). McPhail (1969) showed that hybrid inferiority is also involved in maintenance of variation in breeding color. Other characters known to show adaptive patterns of variation include pelvic spine length (Hagen, 1967; Moodie, 1972a), body size (Moodie, 1972b; Larson, 1972), and dorsal spine number (McPhail, pers. comm.) Until recently, biochemical variation in sticklebacks has been ignored, but preliminary studies (Jones, pers. comm.; Kusa, 1966; Callegarini and Cucchi, 1969a, b) suggest that morphological and biochemical analyses could be profitably combined in the future.

I was interested in the adaptive significance of variation in plate number, and in how that variation is maintained in populations of sticklebacks. I followed the guidelines suggested by Ford (1964) to choose a suitable population for the study. He identifies four situations where evolution occurs fast enough to be studied:

- (1) when marked numerical fluctuations affect isolated populations;

- (2) when polygenic characters are studied, either
  - (a) in populations inhabiting ecologically distinct and isolated areas; or
  - (b) even in the absence of isolation if subject to strong selective pressures;
- (3) in all types of genetic polymorphism;
- (4) when a species spreads into a new area. Ford suggests that most changes in this situation would be physiological, and difficult to study

The stickleback population in Heisholt Lake appeared to fulfill several of the suggested criteria. The lake was formed during the fall of 1966, and sticklebacks had been introduced in May 1967. When the population was sampled in May 1970, density was still very low, suggesting that population size would increase in subsequent years. Also, the three freshwater morphs (low plated, partially plated, and completely plated) were present in the population. This situation offered a unique opportunity to study selection and evolution in a natural population, and to investigate the adaptive significance and maintenance of plate variation of sticklebacks. My approach in this study was:

- (1) to describe spatial and temporal changes in frequencies of plate phenotypes;
- (2) to attempt to explain observed changes.

## MATERIALS AND METHODS

### A. Study Area

Heisholt Lake is a small lake (0.5 km in length) on Texada Island in Georgia Strait, British Columbia (Fig. 2). The lake formed when a limestone mine closed in 1966, and the pit filled with water. The two basins of the lake are connected for one to two months each winter by a small, shallow stream flowing from basin 1 to basin 2. Shallow riffles and a rock dam prevent sticklebacks from moving between basins. No streams enter or leave the lake, but a spring flows into basin 1, and water seeps through sand and gravel into a marsh at the south end of basin 2.

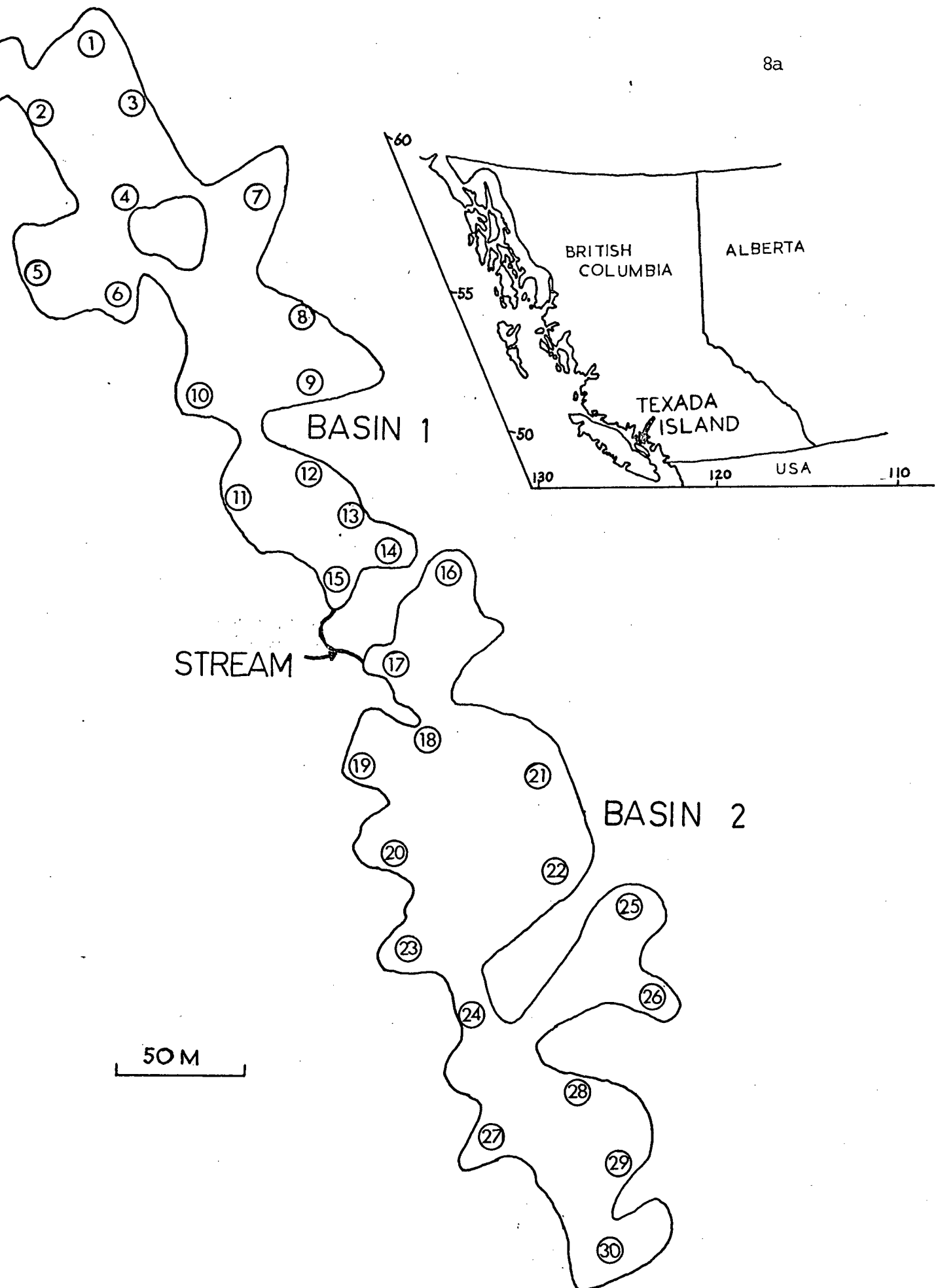
The limestone was removed in flat shelves, and the bottom of the lake is very flat (maximum depth 11 m). The rock is covered with 1-2 cm of marl, and Chara sp. grows abundantly in some areas.

The local Fish and Game club introduced approximately 1000 threespine sticklebacks and several hundred coho salmon (Oncorhynchus keta) and rainbow trout (Salmo gairdneri) into each basin in May, 1967. The fish were collected from Gilles Bay Creek, a small coastal stream on the island. Salmon are no longer found in the lake, but the trout have bred successfully and are still present in small numbers. Salamanders (Taricha granulosa) are abundant in the lake, particularly during spring, when they are breeding.

### B. Variation in Sticklebacks

Preliminary sampling in May, 1970, showed that three plate morphs

FIG. 2: Heisholt Lake on Texada Island, British Columbia,  
showing location of sampling stations.



are present in Heisholt Lake. These morphs differ in plate number and pattern, but not in body size, color, and gill raker number. Hagen and Gilbertson (1973a) propose the following definitions of the freshwater plate morphs:

- (1) the low plated morph includes all individuals with only anterior plates (Fig. 1). Plate numbers of sticklebacks of this morph vary from 3 to 17 in Heisholt Lake;
- (2) the partially plated morph includes individuals with a gap between anterior plates and a caudal keel of plates. Plate numbers of sticklebacks of this morph vary from 7 to 29;
- (3) the completely plated morph includes all individuals with a continuous series of plates along the sides of the body. Plate numbers of sticklebacks of this morph vary from 28 to 36.

Hagen and Gilbertson's terminology is used throughout this thesis. All three plate morphs are present in Gilles Bay Creek.

#### C. Collecting Sticklebacks

Sticklebacks were collected with wire mesh minnow traps (No. 12562, Canada Fishing Tackle and Sports Ltd.). Stott (1970) discussed several problems associated with the use of unbaited fish traps, but the most serious criticism is that the number of fish caught is dependent on the influence of environmental factors on activity levels.

Sticklebacks were collected from 30 stations in the lake (Fig. 1) during the first two weeks of both May and September from 1971 to 1973. During each

sampling period, two traps were placed on the bottom at exactly the same sites at each station, and sticklebacks were removed at the same time every day. I tried to take equal numbers of trap collections at each station during a sampling period, but some traps were moved or opened. Nesting male sticklebacks were collected with a dipnet.

Sticklebacks were preserved in 10% formalin, and later were counted and measured in the laboratory. Plate number and morph, standard length, sex, and gill raker number were recorded for each individual according to criteria discussed by Hagen and Gilbertson (1972). Numbers of eggs in ripe females (those with yellow eggs separated from white, undeveloped eggs in the ovary) and the number of Schistocephalus solidus plerocercoids were also counted.

#### DISTRIBUTION OF STICKLEBACKS

When I began this study, I was particularly interested in interactions between numbers of sticklebacks and genetic variation in the population; I intended to follow changes in population size and in the frequencies of phenotypes. I wanted to estimate plate number frequencies by collecting large samples from several areas, and to estimate population size with mark-recapture techniques. These procedures assume that all individuals in the population are mixing randomly. During 1970, I examined distribution of plate phenotypes in space to test this assumption in Heisholt Lake.

Space in a lake has both a horizontal and a vertical component (area and depth). To test the assumption of random mixing, I asked two questions about the distribution of phenotypes:

(1) do relative frequencies of morphs change with depth within an area? Heuts (1947a) found that stickleback morphs have different temperatures for optimal survival of eggs to hatching, suggesting that adults are physiologically different. Since temperature varies with depth during a year, I predicted that physiological differences between morphs would be reflected in differences in distribution of phenotypes with depth;

(2) do morph frequencies at the same depth change from area to area? Frequencies of phenotypes in stickleback populations are usually estimated from large numbers of individuals collected in a single area. This assumes that frequencies do not change between areas. When this assumption has been tested, no differences between areas were found (Moodie, 1972b; Hagen and Gilbertson, 1972; Hay, 1974), and I expected to find no differences in Heisholt Lake.

This section of the thesis presents results of tests of the assumption that sticklebacks assort randomly throughout a basin.

#### A. Combining Samples from Successive Days

A problem with answering questions about the distribution of phenotypes during 1970 was that few sticklebacks were caught in a 24 hr trap set. Samples were taken on several successive days and had to be combined for accurate estimates of morph frequencies. Sticklebacks were collected from a site in basin 2 for six successive days during May 1970 to test the assumption that morph frequencies at a site do not change from day to day



(Table I). Morph frequencies did not change significantly from day to day (chi-square test,  $\chi^2 = 6.77$ , 10 d.f.,  $p > 0.7$ ), so samples taken on successive days were combined in estimating morph frequencies.

#### B. Morph Frequency and Depth

Traps were set at 2 m intervals from 0 to 10 m in one area of basin 2 (near station 18) at four different times during 1970 to determine if morph frequencies changed with depth (Table II). Equal numbers of samples were taken at all depths during each sampling period.

The numbers of individuals caught at each depth shows that the depth distribution of sticklebacks changes during a year (Fig. 3). Sticklebacks are found in shallow areas during early spring, but they move deeper in the lake during June and July. No preference for a particular depth is apparent in August. Larson (1972) describes a similar seasonal pattern of distribution of sticklebacks in Paxton Lake on Texada island.

Morph frequencies changed with depth during June (chi-square test,  $\chi^2 = 25.98$ , 8 d.f.,  $p < 0.01$ ), but in May, July, and September, differences between depths were not significant.

Differences between depths in June appeared to be due to differences between morphs in the distribution of breeding females (Fig. 4). Females produce eggs from late April to mid-July in Heisholt Lake. Ripe females of

TABLE I: Morph frequencies of Sticklebacks caught in an area of Basin 2 on successive days in May, 1970. Chi-square is the result of a test of association between morph frequencies and days.

NUMBERS OF STICKLEBACKS			
DAY	LOW PLATED	PARTIALLY PLATED	COMPLETELY PLATED
1	17	11	18
2	12	9	14
3	10	5	9
4	10	15	16
5	11	13	9
6	11	15	17

$$\chi^2 = 6.77, 10df., p > 0.70$$

TABLE II: Morph frequencies of sticklebacks at different depths in one area, 1970. Chi-squares are results of tests of association between morph frequencies and depth for each sampling period. Samples from 0 and 2 m in June were combined in calculation of Chi-square.

NUMBERS OF STICKLEBACKS

Depth (m.)	May 15-18			June 15-18			July 15-19			August 23-25		
	Low Plated	Partially Plated	Completely Plated	Low Plated	Partially Plated	Completely Plated	Low Plated	Partially Plated	Completely Plated	Low Plated	Partially Plated	Completely Plated
0	25	55	34	4 } 3 }	2 } 1 }	5 }	4	9	6	7	12	9
2	5	5	7				11	21	16	12	24	14
4	9	12	11	5	4	11	1	4	7	7	9	4
6	9	14	16	11	10	10	5	9	5	3	17	9
8	3	10	14	17	29	12	8	36	28	11	20	18
10	2	15	13	5	14	12	8	39	29	13	16	8
$\chi^2 = 12.35, 10df, p>0.25.$				$\chi^2 = 25.98, 8df, p<0.01.$			$\chi^2 = 9.61, 10 df, p>0.25.$			$\chi^2 = 8.85, 10 df, p>0.5.$		

FIG. 3: Depth distribution of sticklebacks  
in Basin 2 of Heisholt Lake, 1970.  
Numbers in brackets are the total  
number of sticklebacks caught at  
all depths.

# FREQUENCY OF STICKLEBACKS (%)

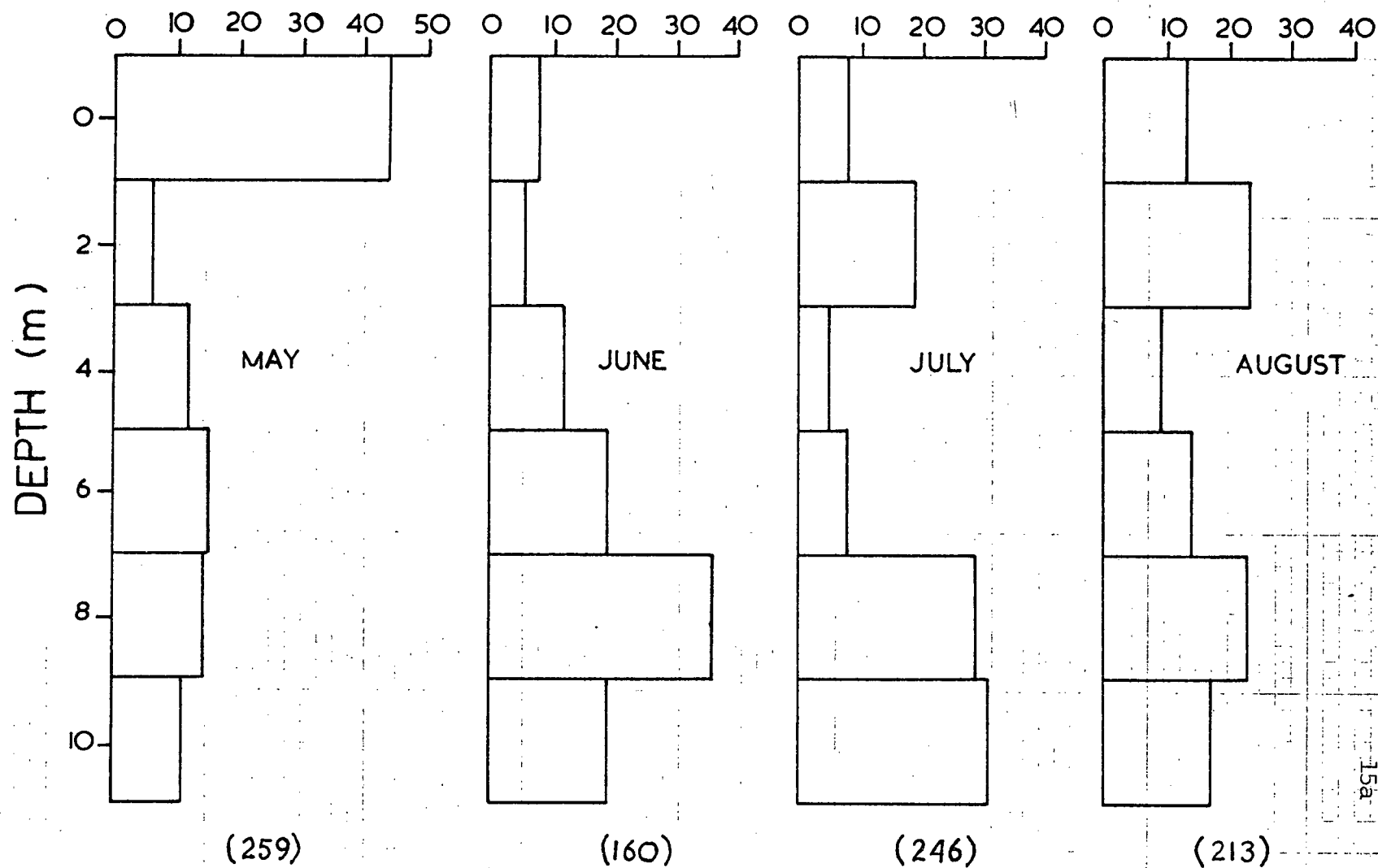
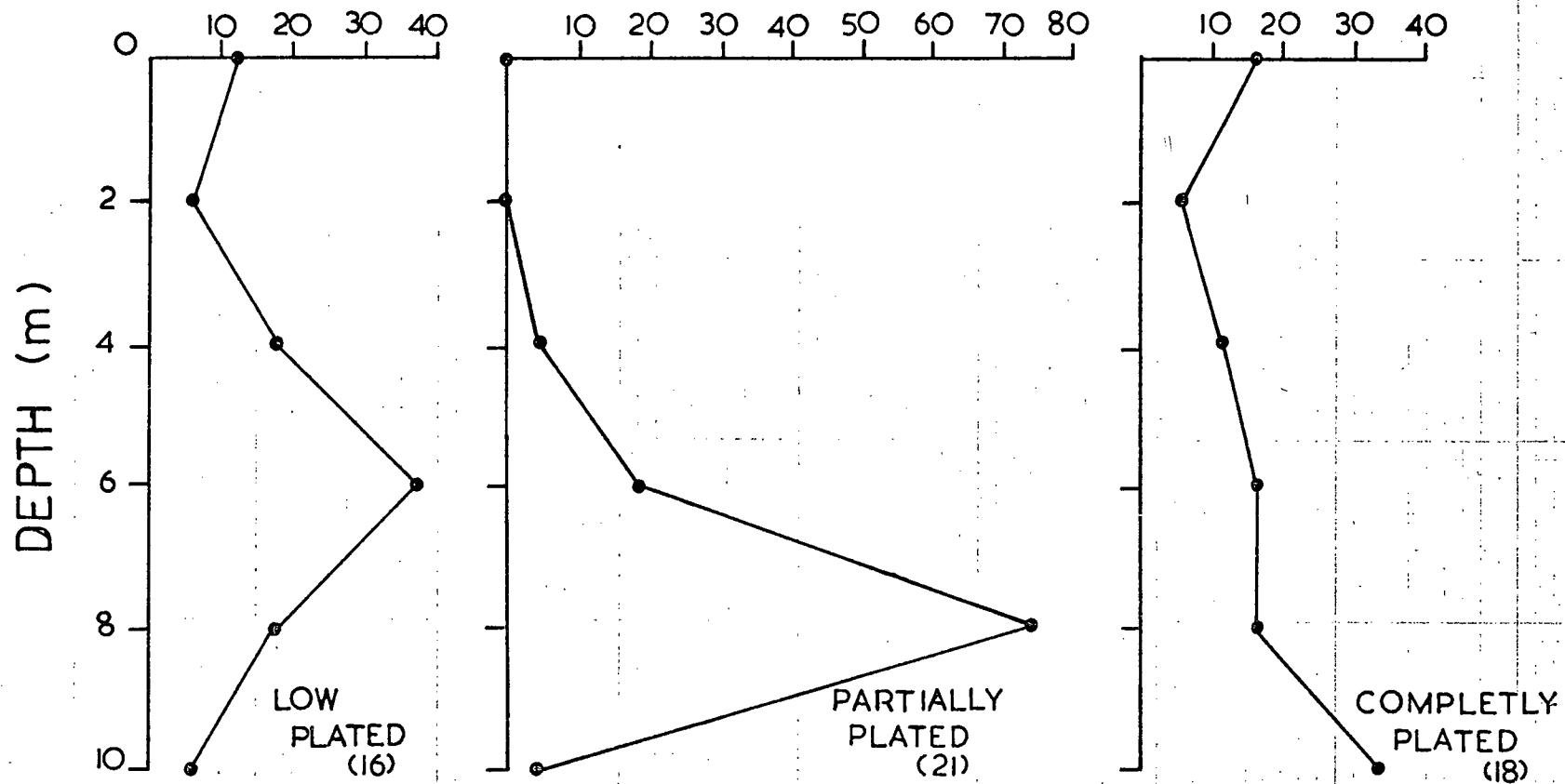


FIG. 4: Depth distribution of breeding  
female sticklebacks with  
differing plate phenotypes in  
Heisholt Lake in June, 1970.  
Numbers in brackets are the total  
number of females of each morph.

# FREQUENCY OF STICKLEBACKS (%)



all morphs were found at only 0 and 2 m depths in early May, but they move into deeper areas as the breeding season continues. In June, low plated females are found in shallow areas and completely plated females in deep areas, while partially plated females are caught at a narrow range of depths between the other morphs. This seasonal distribution pattern suggests that breeding females are not cueing on depth, but on an environmental factor, perhaps temperature, that changes seasonally at a given depth. Male sticklebacks were breeding at depths from 0 to 8 m in late June, 1971, so the depth at which a female lays her eggs may be influenced by her phenotype.

The prediction that morph frequencies would change with depth was true only in June, when segregation of breeding females occurs. Differences in the depth distribution of morphs does not occur at other times of the year. This result means that morph frequencies can only be estimated accurately either in early spring or after breeding ceases.

#### C. Morph Frequency and Area

Sticklebacks were collected at a depth of 3 m at 10 stations in basin 2 during May, to determine if morph frequencies of sticklebacks change between areas (Table III). Two traps were set at each station and sticklebacks were removed for five days.

Morph frequencies differed between stations (chi-square test,  $\chi^2 = 113.34$ , 18 d.f.,  $p \times 0.001$ ), indicating that sticklebacks do not move randomly throughout a basin in Heisholt Lake. Clearly, my original conception of the structure of stickleback populations was wrong, and I



TABLE III: Morph frequencies of sticklebacks  
at 10 stations in Basin 2 of Heisholt  
Lake in May, 1970. Chi-squared is  
result of a test of association between  
morph frequencies and sampling areas.

NUMBERS OF STICKLEBACKS

AREA	LOW PLATED	PARTIALLY PLATED	COMPLETELY PLATED
1	70	66	86
2	60	112	81
3	44	103	51
4	23	22	18
5	70	60	75
6	43	21	32
7	12	47	30
8	32	43	17
9	38	45	33
10	55	11	30

$$\chi^2 = 113.84, 18 \text{ d.f.}, p > 0.01$$

could not estimate either morph frequencies with large samples from one area or population size with mark-recapture techniques.

From 1971 to 1973, sticklebacks were collected at 15 stations in each basin in both May and September. Morph frequencies (Appendix A) did not differ between stations in all sampling periods (Table IV). Also, differences between stations were not significant at the same time in both basins. These results will be discussed again later, but they do not alter the conclusion that sticklebacks do not mix randomly within a basin.

#### D. Summary

The plate phenotype of a stickleback influences its distribution in space. Morph frequencies change with depth owing to segregation of breeding females. Morph frequencies also change from area to area within a basin, although differences between areas are not always significant.

### ABUNDANCE OF STICKLEBACKS

Low stickleback densities during May, 1970, suggested that population size would continue to increase during this study. I was interested in following changes in the numbers of sticklebacks because density might be important in explaining observed changes in frequencies of phenotypes with time. However, sticklebacks do not mix randomly in a basin, and therefore mark-recapture techniques could not be used to estimate numbers of sticklebacks.

TABLE IV: Summary of Chi-squared tests of  
association between morph frequencies  
and station in Heisholt Lake, 1971-1973  
(See Appendix A).

DATE	BASIN	$\chi^2$	d.f.	p
May 1971	1	30.28	28	> 0.25
	2	32.96	28	> 0.10
Sept 1971	1	29.83	28	> 0.25
	2	37.11	28	> 0.10
May 1972	1	42.83	28	< 0.05
	2	30.83	28	> 0.25
Sept 1972	1	47.86	28	< 0.025
	2	28.39	24	> 0.25
May 1973	1	36.40	28	> 0.10
	2	38.67	28	> 0.10

Instead, catch per unit effort was used to follow changes in population size. The number of sticklebacks in each trap was recorded during May and September from 1971 to 1973, and average number of sticklebacks per trap was calculated for each basin (Appendix B). Catch per unit effort was also estimated for 1970 from all samples collected in both basins in May and September.

Sticklebacks breed from May to mid-July in Heisholt Lake, and small numbers of young sticklebacks are first caught in traps during September. The young continue to grow in size throughout the winter, and almost all can be caught in traps during May.

The average number of sticklebacks per trap increased each May from 1970 to 1973 (Fig. 5), which suggests that population size increased each year throughout the study. The rate of increase appears slightly higher in basin 2, but the numbers of sticklebacks per trap varied considerably from station to station because of the clumped distribution of sticklebacks, so that differences between basins probably reflect the stations chosen rather than real differences in population size.

Large numbers of sticklebacks die each year between May and September. Length frequency analysis in May shows that only 1-2% of the breeding population survives for more than one year. Number of sticklebacks per trap in September did not increase from year to year, so a larger proportion of the population died between May and September each year from 1971 to 1973.

## Summary

The number of sticklebacks in Heisholt Lake increased <sup>in May</sup> each year during the study. Most individuals live less than one year, so that the proportion of the population that died between May and September increased each year.

## VARIATION OF STICKLEBACKS

I asked two questions about changes in frequencies of plate phenotypes with time:

(1) do phenotypic frequencies change from May to September (within generations)? Large numbers of sticklebacks die each year between May and September, and I was interested in determining if differential mortality of phenotypes occurs;

(2) do phenotypic frequencies change from year to year (generation to generation)? I was particularly interested in interactions between genetic variation and population size.

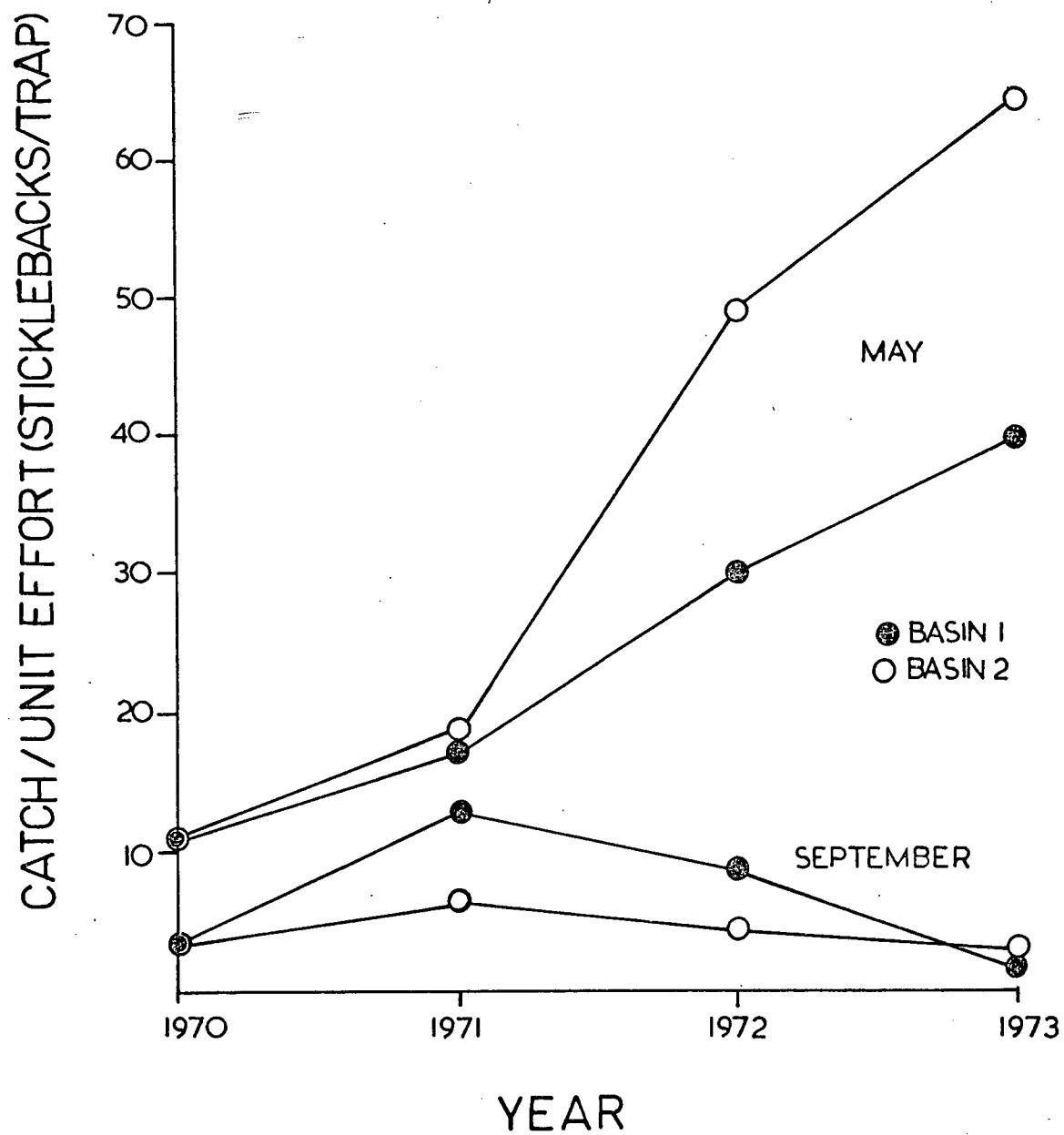
Sticklebacks were collected from 30 stations in both May and September each year. Frequencies of morphs and plate numbers were compared within and between years to determine if temporal changes occurred. This section of the thesis presents results of these comparisons.

### A. Between Morph Comparisons

(1) Changes in morph frequency from May to September.

Morph frequencies in May and September at each station were compared to determine if natural selection acts on morph frequencies during a generation. The number of sticklebacks trapped during September, 1973, was too small to estimate morph frequencies.

FIG. 5: Average catch per unit effort  
(average number of sticklebacks/trap)  
in basins of Heisholt Lake in May and  
September, 1970-1973.



Differential mortality of morphs occurred at most stations in basin 1 during 1971 and 1972, but in both years changes were significant at only a few stations in basin 2 (Table V).

Two techniques were used to examine patterns of selection:

(1) For each morph I plotted frequency in May against frequency in September at each station, to examine the direction of change in frequencies of a morph within a basin;

(2) I calculated relative fitness of morphs from frequencies in May and September at each station to compare the chances of morphs to survive in different areas of the lake. Relative fitness, defined as the probability of survival from May to September, was calculated as suggested by O'Donald (1968, 1970). Hagen and Gilbertson (1973b) discuss some problems in interpreting relative fitnesses of sticklebacks.

The pattern of selection was similar at most stations in basin 1 during both 1971 and 1972 (Fig. 6). The frequency of low plated sticklebacks increased and decreased at an equal number of stations in 1971, and increased at most stations in 1972. The frequency of partially plated individuals decreased, and completely plated sticklebacks increased in frequency at most stations in both years. Relative fitnesses of morphs show that completely plated sticklebacks were favored at 14 of the 15 stations in basin 1 during 1971 (Table VI). Partially plated individuals had the lowest fitness at most stations and the fitness of low plated sticklebacks was generally intermediate. Partially plated sticklebacks were again selected against at all stations in 1972, but the favored morph changed from station to station. Low plated sticklebacks were favored at stations 4, 5, 6, 7, and 9 in adjacent areas of

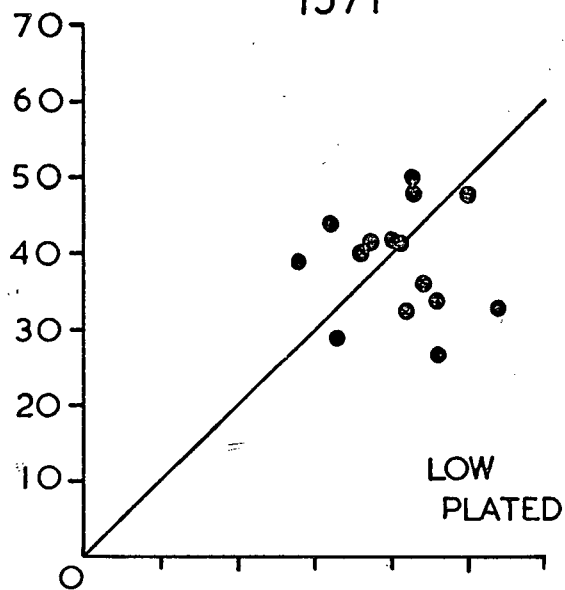


TABLE V: Summary of tests of homogeneity of morph frequencies of sticklebacks at a station in May and September, 1971 and 1972.

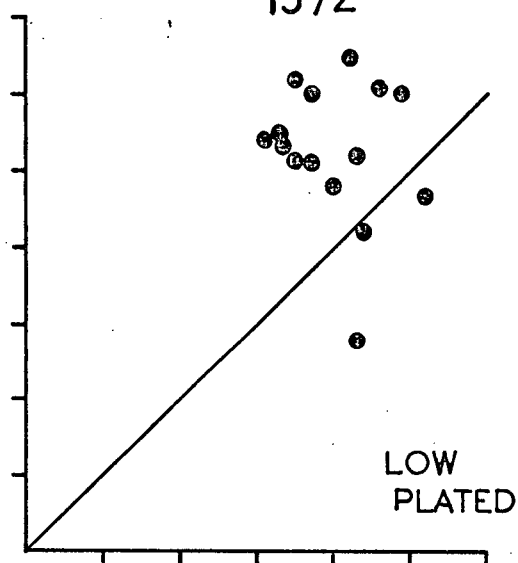
BASIN 1					BASIN 2				
Station	1971		1972		Station	1971		1972	
	$\chi^2$	P	$\chi^2$	P		$\chi^2$	P	$\chi^2$	P
1	4.43	> 0.10	5.10	> 0.05	16	7.42	< 0.025	1.99	> 0.25
2	4.02	> 0.10	6.35	< 0.05	17	0.58	> 0.50	8.01	< 0.025
3	7.03	< 0.05	4.43	> 0.10	18	4.02	> 0.10	0.54	> 0.75
4	8.54	< 0.025	5.15	> 0.05	19	2.31	> 0.25	1.52	> 0.25
5	8.62	< 0.025	13.43	< 0.005	20	0.91	> 0.50	0.41	> 0.75
6	3.04	> 0.10	6.74	< 0.05	21	3.06	> 0.10	-	
7	31.14	< 0.005	20.45	< 0.005	22	2.37	> 0.25	7.19	< 0.05
8	5.52	> 0.05	17.00	< 0.005	23	5.58	> 0.05	-	
9	15.49	< 0.005	9.60	< 0.01	24	2.10	> 0.25	0.91	> 0.50
10	6.17	< 0.05	18.28	< 0.005	25	0.27	> 0.75	2.98	> 0.10
11	10.80	< 0.005	13.69	< 0.005	26	2.60	> 0.25	2.53	> 0.25
12	1.87	> 0.25	7.73	< 0.025	27	4.83	> 0.05	0.83	> 0.50
13	2.46	> 0.25	4.04	> 0.10	28	3.14	> 0.10	2.21	> 0.25
14	8.15	< 0.025	24.63	< 0.005	29	1.09	> 0.50	1.41	> 0.25
15	3.36	> 0.10	4.39	> 0.10	30	1.44	> 0.25	7.73	< 0.025

FIG. 6: Comparison of frequencies of  
plate morphs of sticklebacks  
at stations in Basin 1 in May  
and September of 1971 and 1972.

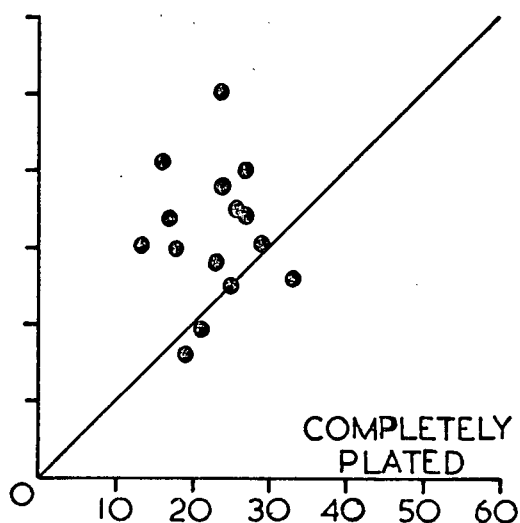
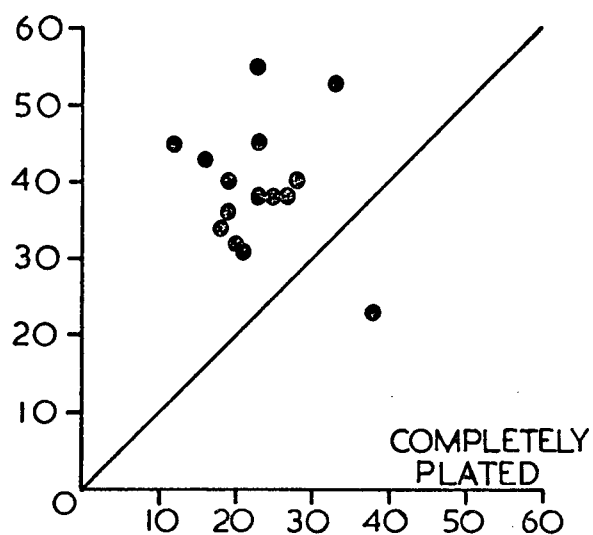
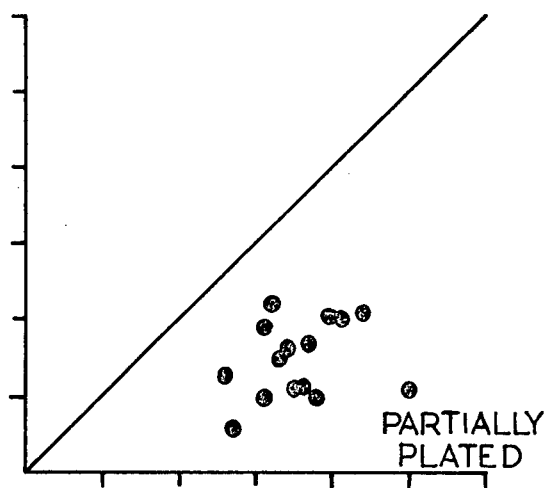
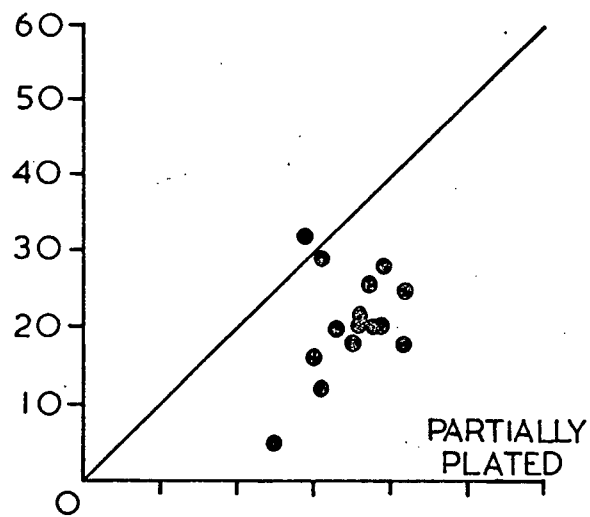
1971



1972



FREQUENCY IN SEPTEMBER (%)



FREQUENCY IN MAY (%)

TABLE VI: Relative fitness of plate morphs of sticklebacks from May to September at stations in Basin 1 in 1971 and 1972.

STATION	RELATIVE FITNESS					
	1971			1972		
	LOW PLATED	PARTIALLY PLATED	COMPLETELY PLATED	LOW PLATED	PARTIALLY PLATED	COMPLETELY PLATED
1	0.76	0.31	1	0.89	0.34	1
2	0.59	0.46	1	0.59	0.39	1
3	0.38	0.33	1	0.30	0.33	1
4	0.72	0.27	1	1	0.36	0.73
5	0.46	0.31	1	1	0.24	0.99
6	0.80	0.40	1	1	0.14	0.68
7	0.16	0.16	1	1	0.15	0.75
8	0.45	0.58	1	0.35	0.13	1
9	0.30	0.20	1	1	0.34	0.82
10	0.93	0.54	1	0.87	0.11	1
11	0.68	0.32	1	0.74	0.29	1
12	1	0.81	0.44	1	0.27	0.46
13	0.50	0.31	1	1	0.37	0.50
14	0.62	0.23	1	0.54	0.14	1
15	0.25	0.14	1	1	0.31	0.58

basin 1, and at stations 12, 13 and 15, which are also adjacent. Similarly, completely plated sticklebacks had the highest fitness in large adjacent areas of the basin. The favored morph changed at 7 of the 15 stations from 1971 to 1972. Average relative fitness of partially plated sticklebacks decreased from 0.35 in 1971 to 0.26 in 1972, suggesting that selection against this morph increased.

No general pattern of selection occurred throughout basin 2 in 1971 and 1972, as the direction and degree of changes in relative frequency varied from station to station (Fig. 7). In contrast to basin 1, partially plated sticklebacks increased in frequency at a majority of stations in basin 2 in both years. This suggests that partially plated sticklebacks are not always selected against, as observations in basin 1 would suggest. Relative fitnesses of morphs varied greatly from station to station (Table VII), suggesting that chances for sticklebacks of a particular morph to survive vary in space. Spatial patterns of fitnesses, similar to those observed in basin 1, are also apparent in basin 2. Fitness of partially plated sticklebacks was high at stations 16, 17, 18, 19, and 24, and lower at stations 20, 21, 22, and 23 in both 1971 and 1972, suggesting that in both years chances for a morph to survive were similar in large adjacent areas of the basin. The favored morph changed from 1971 to 1972 at 8 of 13 stations, suggesting that the selective environment for plate morphs of sticklebacks changes in both space and time in basin 2.

(2) Changes in morph frequency from year to year.

Morph frequencies in May of 1971, 1972, and 1973 were compared to

FIG. 7: Comparison of frequencies of plate morphs of sticklebacks at stations in basin 2 in May and September of 1971 and 1972.

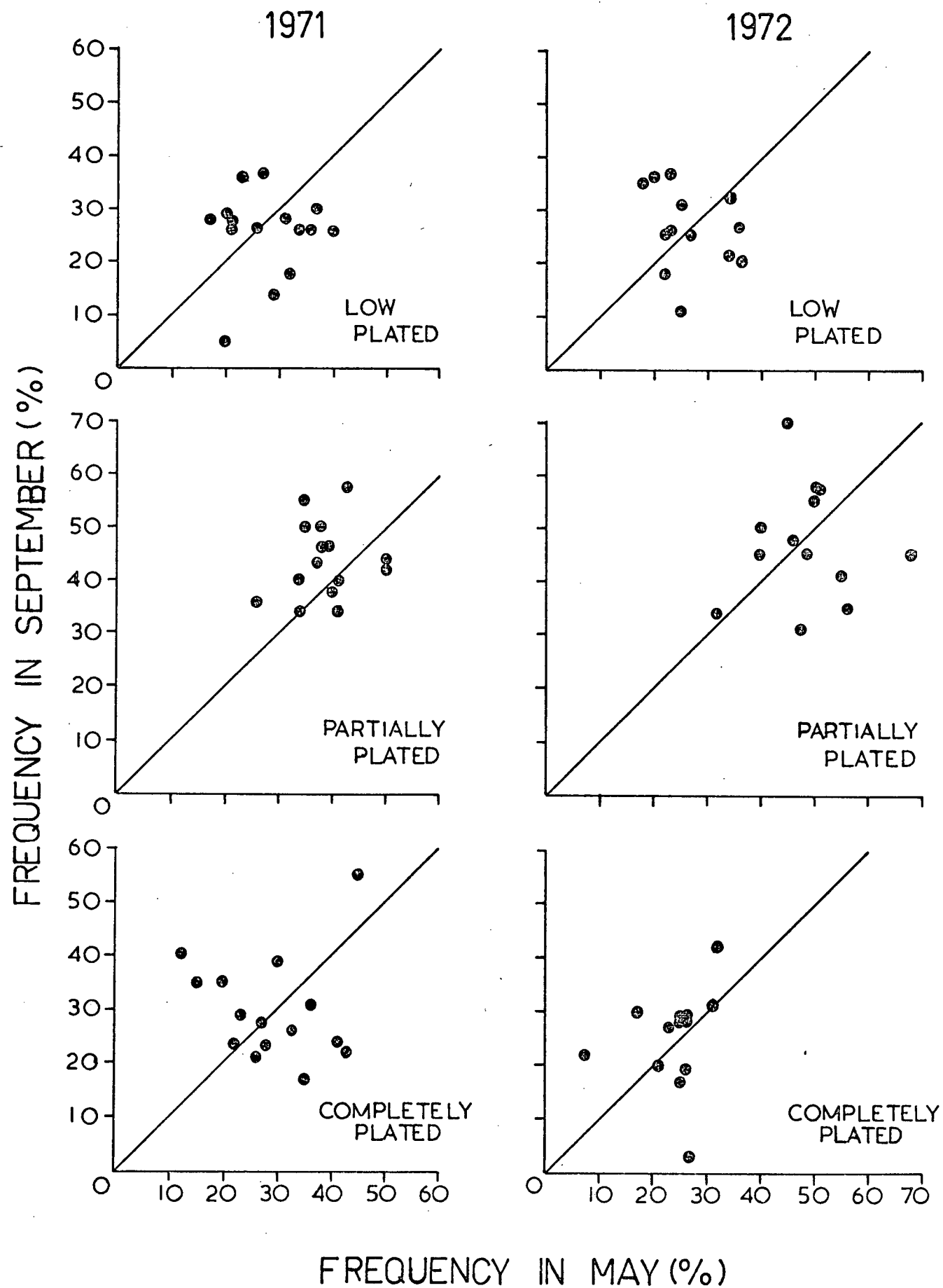


TABLE VII: Relative fitness of plate morphs of sticklebacks  
from May to September at stations in basin 2 in  
1971 and 1972.

STATION	RELATIVE FITNESS					
	1971			1972		
	LOW PLATED	PARTIALLY PLATED	COMPLETELY PLATED	LOW PLATED	PARTIALLY PLATED	COMPLETELY PLATED
16	0.35	1	0.72	1	0.98	0.64
17	0.70	1	0.86	0.61	1	0.08
18	0.37	1	0.50	0.74	1	0.82
19	0.20	0.96	1	0.75	1	0.57
20	0.78	0.68	1	1	0.81	0.95
21	1	0.86	0.41	-	-	-
22	0.40	0.62	1	0.40	0.20	1
23	0.36	0.25	1	-	-	-
24	0.48	1	0.56	0.40	1	1
25	1	0.79	0.70	1	0.37	0.56
26	1	0.81	0.38	1	0.32	0.57
27	1	0.83	0.32	0.65	0.96	1
28	0.37	0.54	1	1	0.22	0.59
29	1	0.54	0.51	0.47	0.80	1
30	0.60	0.78	1	0.29	0.58	1



determine if relative frequencies of morphs change from year to year.

Morph frequencies changed between years at 9 of the 30 stations (Table VIII).

Frequency of a morph in May was plotted against its frequency the following May to examine patterns of change in morph frequencies from year to year. At most stations in basin 1, low and completely plated sticklebacks increased in frequency from 1971 to 1972 and from 1972 to 1973, while partially plated individuals decreased. (Fig. 8) This pattern of change in morph frequency from year to year is similar to the pattern of change from May to September. Low and completely plated sticklebacks increased in frequency and partially plated individuals decreased both within and between years in basin 1 throughout the study.

Frequency of partially plated sticklebacks increased and low and completely plated sticklebacks decreased in frequency from 1971 to 1972 at most stations in basin 2. (Fig. 9) This pattern of change was reversed from 1972 to 1973, as low and partially plated individuals increased and partially plated individuals decreased in frequency at most stations, although changes in frequency of the completely plated morph were small. In both basins, the direction of change in the frequency of low and completely plated sticklebacks was identical and inversely related to the direction of change in frequency of partially plated sticklebacks. Changes in frequencies within and between years again appeared to be related in basin 2. Partially plated sticklebacks increased in frequency at most stations during 1971 and from 1971 to 1972.

TABLE VIII: Summary of tests of homogeneity  
of frequencies of plate morphs  
in May of 1971, 1972, and 1973.

BASIN 1			BASIN 2		
STATION	$\chi^2$	P	STATION	$\chi^2$	P
1	2.45	> 0.50	16	16.60	< 0.005
2	4.99	> 0.25	17	4.06	> 0.25
3	4.81	> 0.25	18	8.13	> 0.05
4	3.50	> 0.25	19	5.85	> 0.10
5	3.10	> 0.50	20	4.21	> 0.25
6	2.81	> 0.50	21	2.15	> 0.50
7	13.74	< 0.01	22	18.04	< 0.005
8	3.77	> 0.25	23	3.25	> 0.50
9	17.28	< 0.005	24	3.71	> 0.25
10	11.45	< 0.025	25	0.88	> 0.90
11	12.56	< 0.025	26	7.84	> 0.05
12	10.24	< 0.05	27	7.45	> 0.05
13	5.43	> 0.10	28	5.58	> 0.10
14	15.35	< 0.005	29	3.36	> 0.50
15	22.76	< 0.005	30	6.87	> 0.10

FIG. 8: Comparison of frequencies of plate morphs of sticklebacks at stations in basin 1 in May of one year and May of the following year.

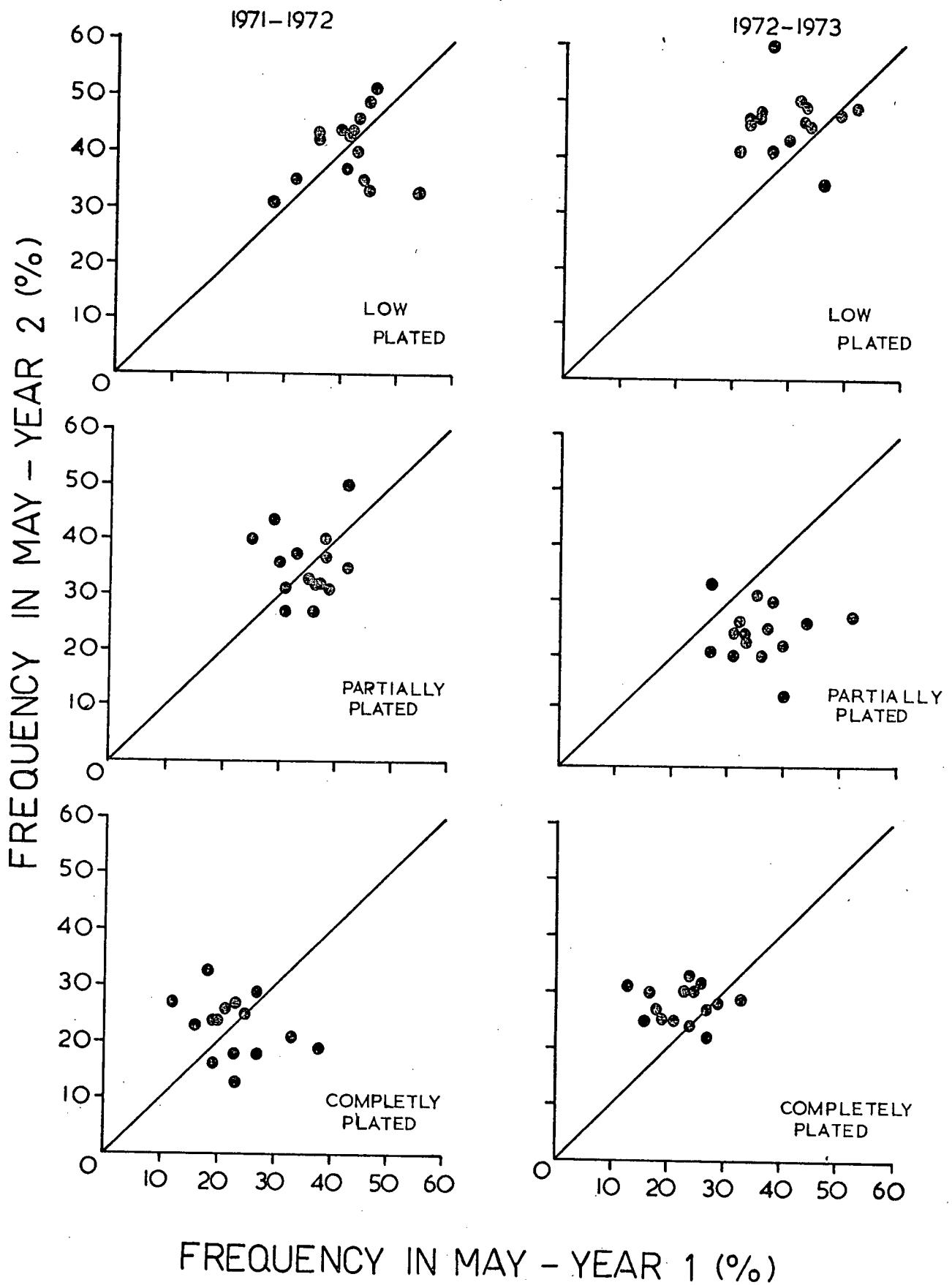
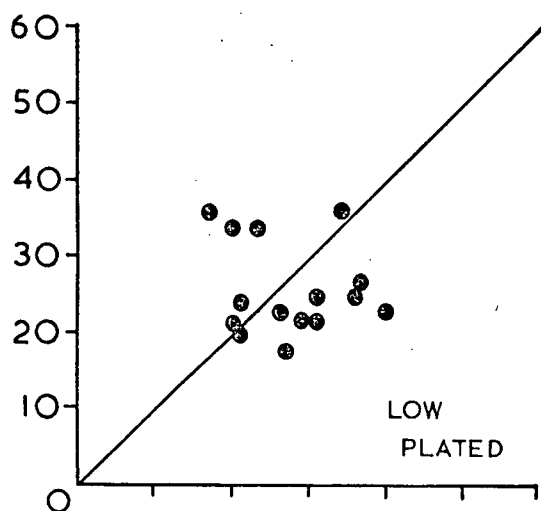
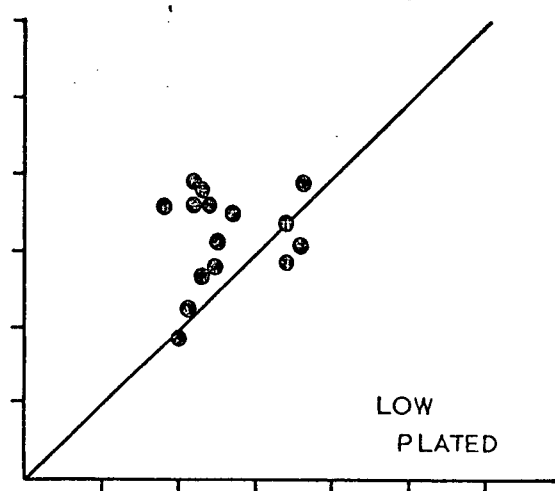


FIG. 9: Comparison of frequencies of plate morphs of sticklebacks at stations in basin 2 in May of one year and May of the following year.

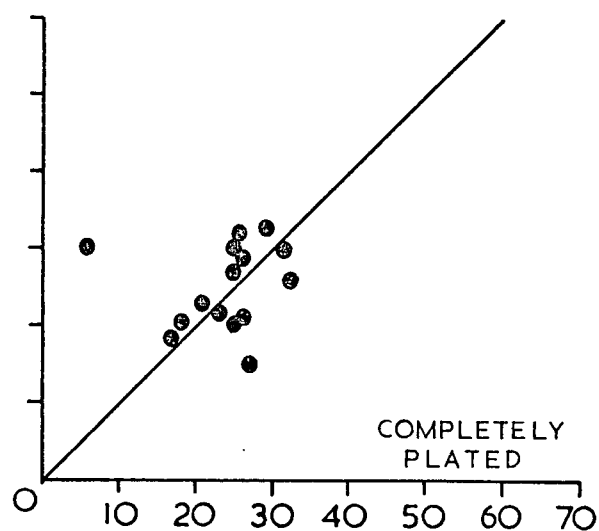
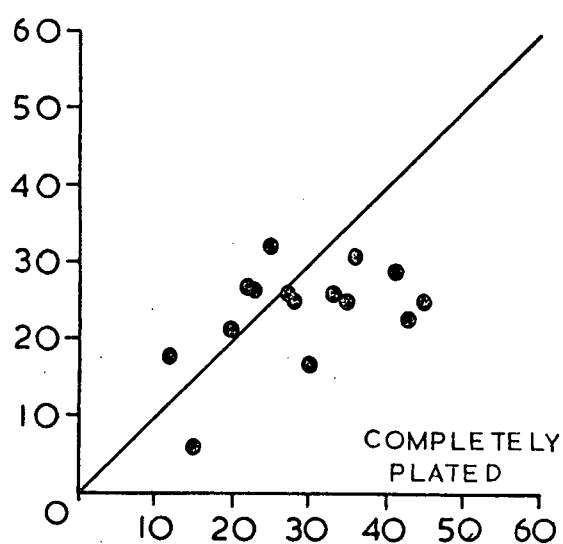
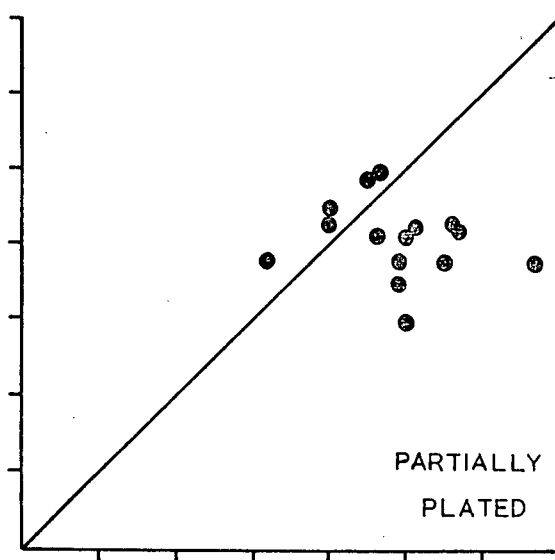
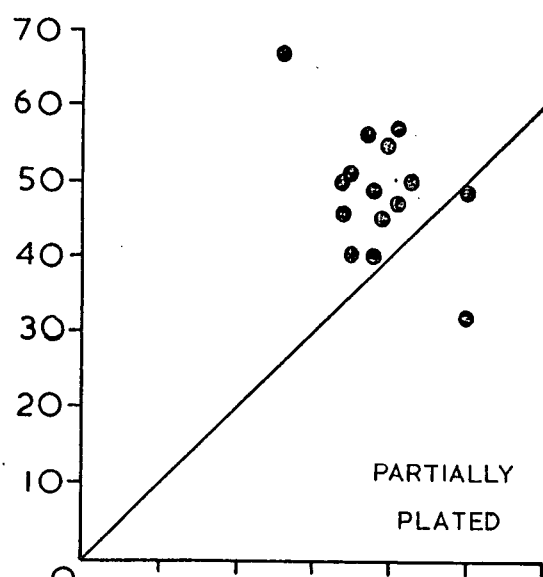
1971-1972



1972-1973



FREQUENCY IN MAY - YEAR 2



FREQUENCY IN MAY - YEAR 1

## B. Within Morph Comparisons

- (1) Changes in frequencies of plate number phenotypes from May to September.

Frequencies of plate number phenotypes within a morph were estimated for each basin in May and September from 1971 to 1973. Samples from all stations in a basin were combined to reduce sampling errors in estimating frequencies. This assumes that plate number frequencies do not change from area to area in a basin. Interpretation of changes in frequencies within and between years must recognize the possibility that observed changes are due to differences between areas.

Frequencies of plate number phenotypes in May and September were compared to determine if natural selection acts within generations on variation in plate number within morphs (Appendix C). Differential mortality of plate number phenotypes occurred within the low and partially plated morphs in basin 1 in both 1971 and 1972, and within the low and completely plated morphs in basin 2 during 1971 (Table IX). Other changes in relative frequency of plate number frequencies within morphs were not significant.

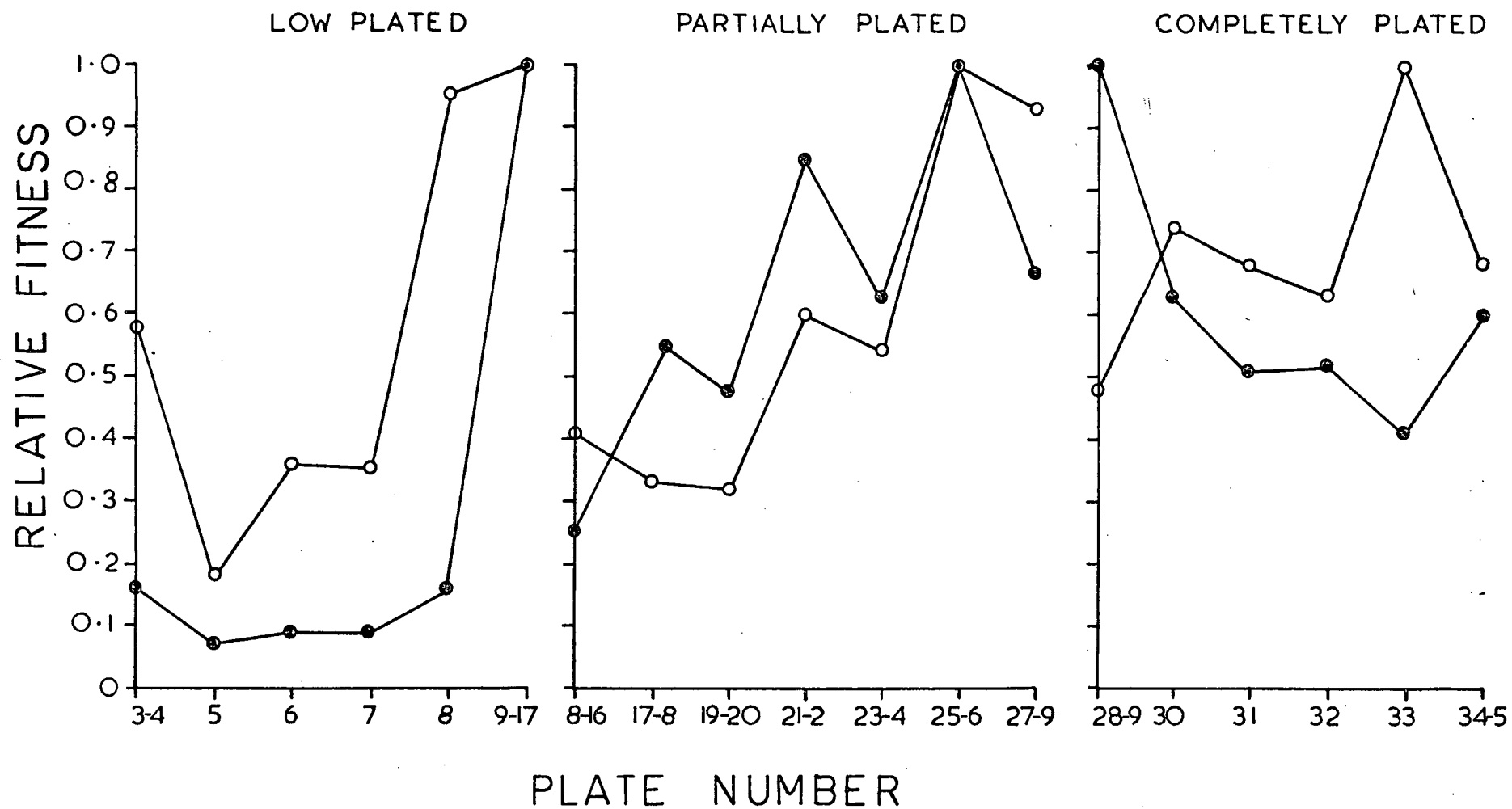
Relative fitnesses of plate number phenotypes within morphs were calculated to examine patterns of selection. In basin 1, disruptive selection favored individuals within the low plated morph with extreme plate numbers in both 1971 and 1972 (Fig. 10). This disruptive selection also had a directional component, as 9 - to 17 - plated individuals had a selective advantage over 3-to 4-plated sticklebacks in both years.

TABLE IX: Summary of tests of homogeneity  
of plate number frequencies within  
morphs in May and September of  
1971 and 1972.

BASIN	YEAR	PLATE MORPH	$\chi^2$	df	P
1	1971	Low plated	34.72	5	< 0.005
		Partially plated	26.37	6	< 0.005
		Completely plated	3.84	5	> 0.50
	1972	Low plated	95.23	5	< 0.005
		Partially plated	16.84	6	< 0.01
		Completely plated	2.94	5	> 0.50
2	1971	Low plated	17.18	5	< 0.005
		Partially plated	8.49	6	> 0.10
		Completely plated	23.57	5	< 0.005
	1972	Low plated	2.94	5	> 0.50
		Partially plated	7.62	6	> 0.25
		Completely plated	4.71	5	> 0.25



FIG. 10: Relative fitness of plate number  
phenotypes within morphs from  
May to September, 1971 (O) and  
1972 (●) in Basin 1.



Thoday (1972) uses the term asymmetrical disruptive selection for this pattern of fitnesses. Asymmetrical disruptive selection also occurred within the completely plated morph during both years. The favored phenotype had 33 plates in 1971 and 28 to 29 plates in 1972. No specific pattern of selection occurred within the partially plated morph in either 1971 or 1972, although fitnesses of phenotypes were similar in both years.

In basin 2, directional selection favored 3-to 4-plated sticklebacks within the low plated morph during 1971 (Fig. 11). The favored phenotype in 1972 was again 3-to 4-plated, but selection was disruptive, as 7-plated sticklebacks had a higher fitness than 5-, 6-, and 8-plated individuals. Disruptive selection favored extreme plate numbers within the completely plated morph in both years. The favored phenotype within the completely plated morph was similar in both basins, as 33- and 34-plated sticklebacks were favored during 1971 in basin 1 and basin 2, respectively, and 28-to 29-plated individuals were favored in both basins in 1972. Asymmetrical disruptive selection favored individuals with extreme phenotypes within the partially plated morph in 1971. In 1972, the pattern of fitnesses of phenotypes within this morph were similar to that in basin 1 in both 1971 and 1972.

Disruptive selection favoring individuals with extreme phenotypes acted within all morphs. This suggests a relationship between the frequency of a phenotype in the population and the chances for an individual with that phenotype to survive from May to September. The most frequent

FIG. 11: Relative fitness of plate number  
phenotypes within morphs from  
May to September, 1971 (○) and  
1972 (●) in basin 2.

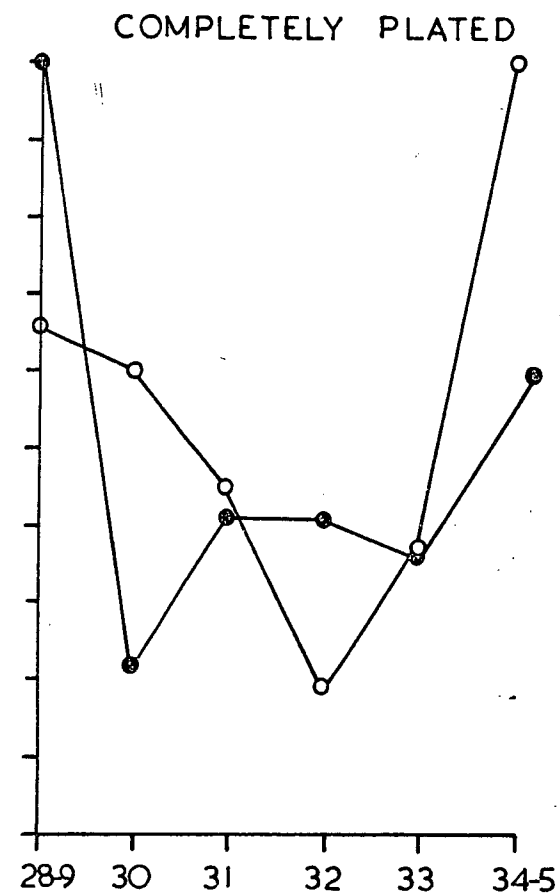
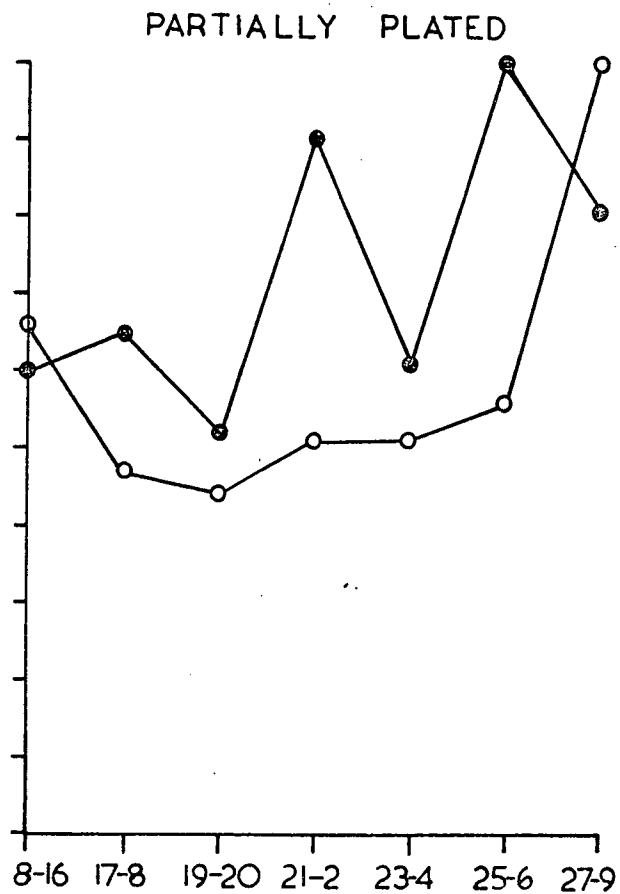
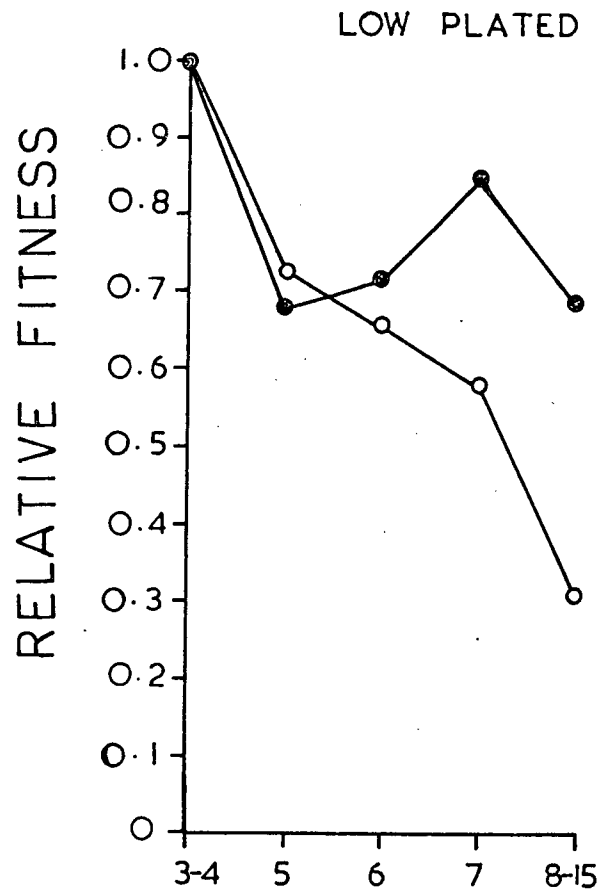


PLATE NUMBER

phenotypes within a morph were never the optimum phenotype, and often had the lowest fitness. Disruptive selection could be due to environmental heterogeneity in either space (differences between areas) or time (changes from May to September).

(2) Changes in frequencies of plate number phenotypes from year to year.

Frequencies of plate number phenotypes within morphs in May of 1971, 1972, and 1973 were compared to determine if frequencies change from year to year. Frequencies of phenotypes within the low and completely plated morphs changed from year to year in both basins (Table X). Relative frequencies of partially plated phenotypes changed from year to year in basin 2, but did not change significantly between years in basin 1.

Relative change in frequency was calculated for each phenotype to examine patterns of change in frequencies of plate phenotypes between years. The phenotype within a morph with the greatest increase in frequency from one year to the next was given a value of 1, and other phenotypes were compared to this "optimum" phenotype. Relative change in frequency from year to year is not relative fitness.

Extreme plate numbers within the low plated morph decreased in frequency in basin 1 from 1971 to 1972 (Fig. 12), and 8-plated sticklebacks were the optimum morph. Extreme phenotypes within this morph increased in frequency from 1972 to 1973, while central phenotypes

FIG. 12: Relative change of frequency of  
plate number phenotypes within  
morphs from May in one year to  
May in the following year in  
basin 1.

(O—O 1971-1972, ●—● 1972-1973).

RELATIVE CHANGE OF FREQUENCY

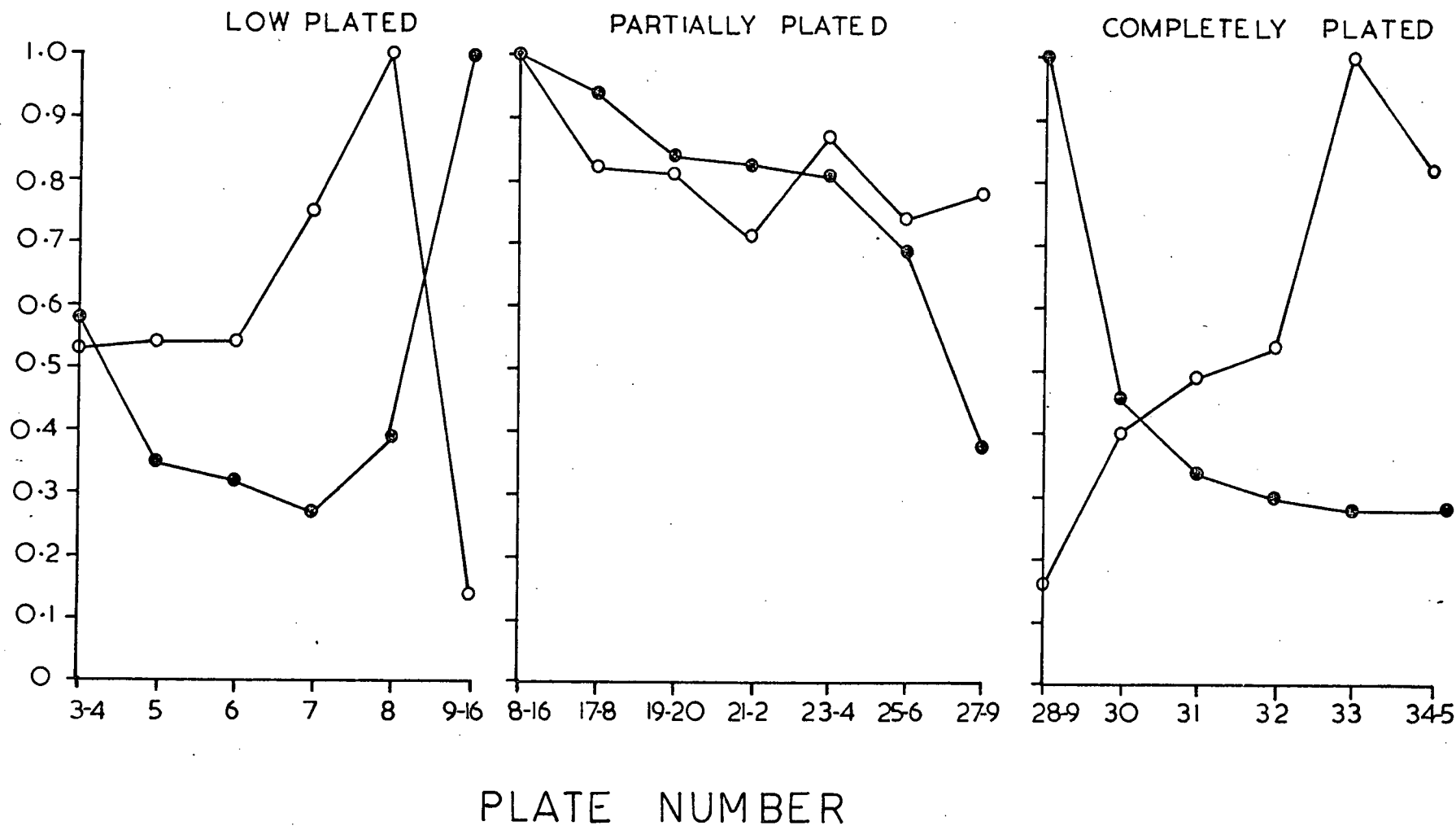




TABLE X: Summary of tests of homogeneity of  
frequencies of plate number phenotypes  
within morphs from May of one year to  
May in the following year.

BASIN	YEARS	PLATE MORPH	$\chi^2$	df.	P
1	1971-1972	Low plated	37.31	5	< 0.005
		Partially plated	2.96	6	> 0.75
		Completely plated	19.74	5	< 0.005
	1972-1973	Low plated	23.10	5	< 0.005
		Partially plated	12.26	6	> 0.05
		Completely plated	16.32	5	< 0.005
2	1971-1972	Low plated	37.42	5	< 0.005
		Partially plated	30.41	6	< 0.005
		Completely plated	31.96	5	< 0.005
	1972-1973	Low plated	29.03	5	< 0.005
		Partially plated	32.76	6	< 0.005
		Completely plated	32.15	5	< 0.005

decreased. An extreme phenotype within the completely plated morph was favored from both 1971 to 1972 and 1972 to 1973. The optimum phenotype from 1971 to 1972 had 33 plates and 28-to 29-plated individuals showed the greatest decrease in frequency, but this pattern was reversed from 1972 to 1973, with 28-to 29-plated sticklebacks being favored and 33-to 35-plated individuals decreasing in frequency. Patterns of change in frequency of phenotypes within the partially plated morph were similar from 1971 to 1972 and 1972 to 1973, favoring 8-to 16-plated individuals while higher plate numbers decreased in frequency.

In basin 2, extreme phenotypes were favored between years within all morphs (Fig. 13). Within the low and completely plated morphs the extreme phenotype that was favored from 1971 to 1972 showed the greatest decrease in frequency from 1972 to 1973, and the other extreme phenotype showed the inverse pattern. Both extreme phenotypes within the partially plated morph were favored from 1971 to 1972, and showed the greatest decrease in frequency from 1972 to 1973, when central phenotypes were favored.

The favored phenotype between years within the low and completely plated morph were similar in both basins. From 1971 to 1972, 33-to 35-plated individuals were favored within the completely plated morph in both basins. From 1972 to 1973, 9-to 16-plated individuals were favored within the low plated morph in both basins. This suggests that factors causing changes in the frequency of plate number phenotypes from year to year were similar in both basins.

Sticklebacks with extreme phenotypes within the low and completely plated morphs were favored both within and between years in both basins. The optimum phenotype within these morphs from May to September of a year was also often favored from that year to the next, although the optimum phenotype switched from one extreme to the other in time.

### C. Summary

I expected to find general trends in the changes in frequencies of phenotypes with time, perhaps similar to those observed in changes in morph frequencies in basin 1. Clearly, such trends did not occur. The expectation resulted from an over-simplified view of the population structure, and arguments, based on that view, about the effect of increasing population size on genetic variation in populations.

The observed changes in phenotype frequencies lead to several conclusions:

- (1) natural selection acts on variation in plate numbers, producing changes in relative frequency of phenotypes within generations.
- (2) frequencies of phenotypes also change from generation to generation, and changes within and between generations are related;
- (3) chances for an individual to survive and for its phenotype to increase in relative frequency in the next generation depend on interactions between its phenotype and the environment in space and time;
- (4) the selective environment for a stickleback is clearly variable in both space and time.

FIG. 13: Relative change of frequency of  
plate number phenotypes within  
morphs from May in one year to  
May in the following year in  
basin 2.

(0—0 1971-1972, ●—● 1972-1973)

RELATIVE CHANGE OF FREQUENCY

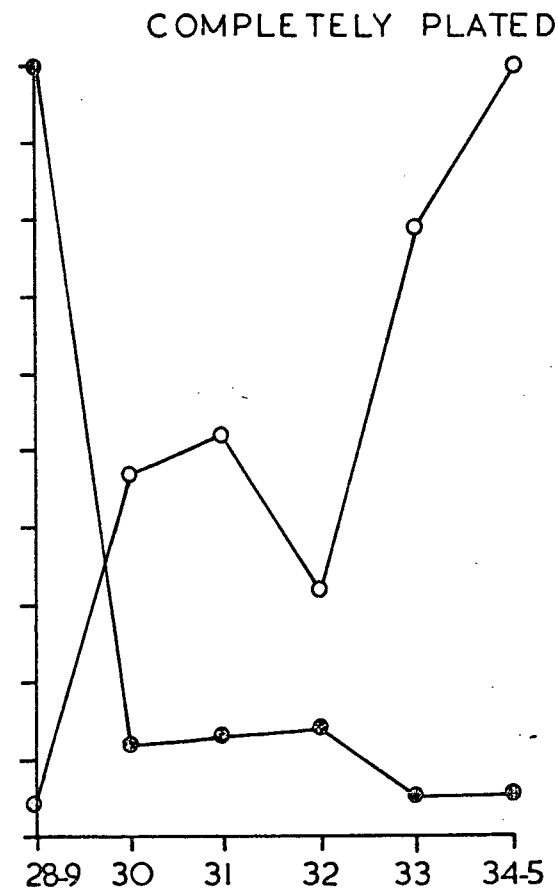
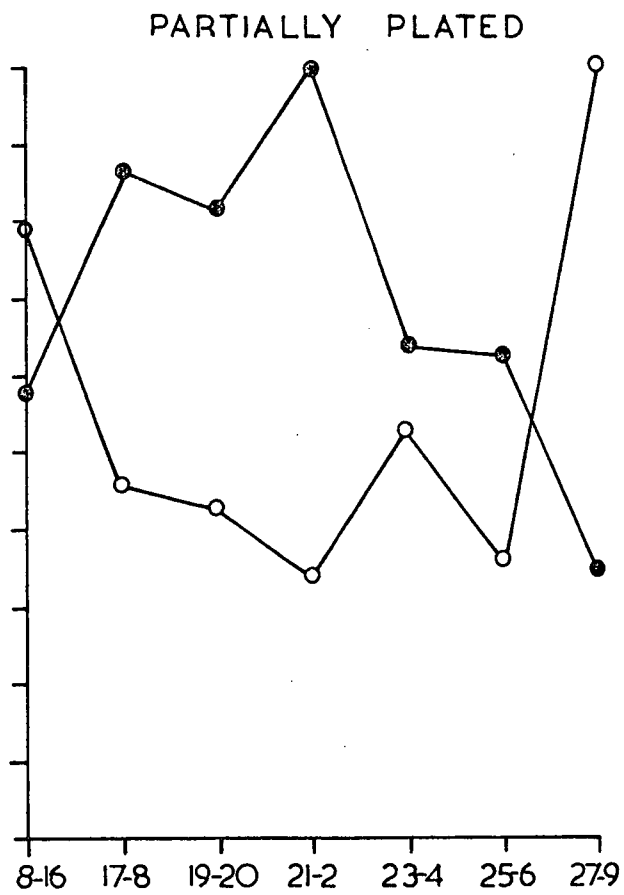
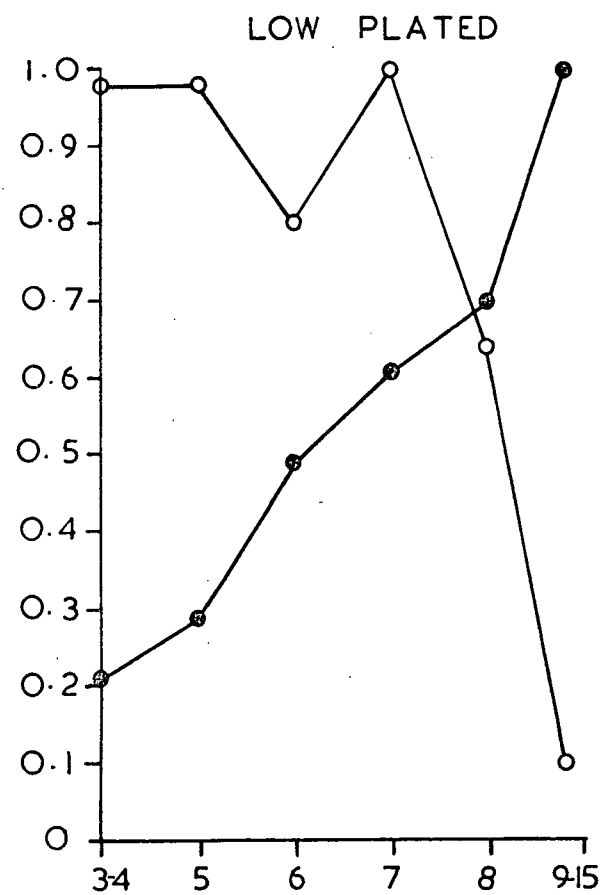


PLATE NUMBER

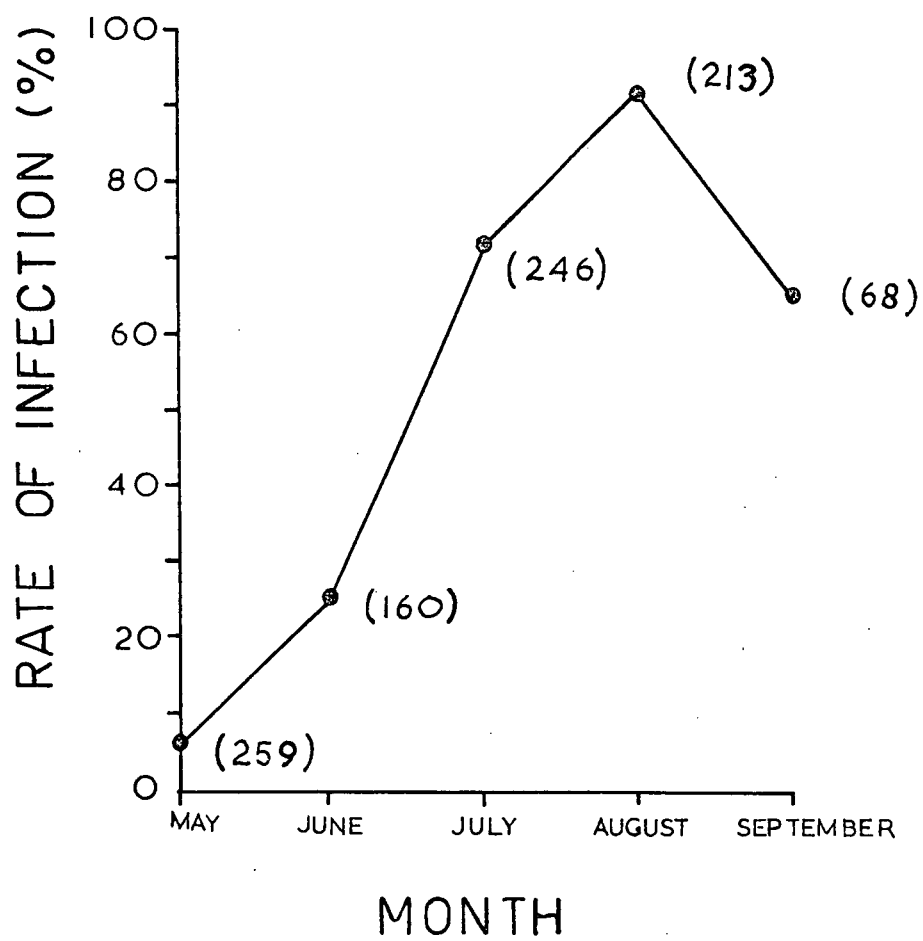
STICKLEBACKS AND SCHISTOCEPHALUS SOLIDUS

Schistocephalus solidus is a tapeworm found as a plerocercoid in Gasterosteus aculeatus. The life history of Schistocephalus follows the pattern; egg, free-swimming coracidium, proceroid in copepod, plerocercoid in fish, adult in piscivorous bird. Infection prevents normal egg maturation of female sticklebacks (Arme and Owen, 1967), reduces the chances of a male to build a nest (McPhail, pers. comm.), and increases the probability that an individual will be eaten by birds, as infected sticklebacks are sluggish and found in shallow water (Lester, 1971). Since infection with Schistocephalus affects the chances for an individual to survive and reproduce, I was interested in determining if differential infection of plate phenotypes might explain observed changes in frequencies of phenotypes with time.

The proportion of infected sticklebacks changes within a year (Fig. 14). The rate of infection increased from May to August, and decreased from August to September in basin 2 during 1970.

Samples of sticklebacks from basin 2 in June, 1970, suggested that differential infection of morphs occurred, even though differences between morphs were not significant. Large samples of sticklebacks were collected from a station in each basin (stations 11 and 18) during June, 1971, to test the hypothesis that morphs have different probabilities of becoming infected. Proportions of infected and uninfected sticklebacks of each morph were compared to determine if morphs were differentially infected.

FIG. 14: Rate of infection of sticklebacks  
with Schistocephalus solidus in basin  
2 during 1970. Numbers in brackets  
are the total number of sticklebacks  
caught.





The morphs were differentially infected in both basins (Table XI). In basin 1, the proportion of infected individuals was higher for the partially plated morph than for the low and completely plated morphs. In basin 2, the proportion of infected sticklebacks was lower for the partially plated morph than for the other morphs. Partially plated sticklebacks decreased and low and completely plated individuals increased in relative frequency both within and between years in basin 1. At station 18 in basin 2, partially plated individuals increased in relative frequency during 1971 and from 1971 to 1972. This suggests that the selective environment for a stickleback varies in space, and that differential infection of morphs is at least part of the explanation for changes in the relative frequencies of phenotypes with time.

Two hypotheses could explain the observed differences between morphs in rate of infection:

(1) All morphs have the same probability of becoming infected, and differences between morphs in level of infection are due to differential survival of infected sticklebacks on the basis of phenotype. Two observations argue against this hypothesis:

- (a) few plerocercoids are mature during June, and therefore unlikely to cause mortality;
- (b) differential survival during the summer favors the morphs with the lowest infection rates rather than those with the highest infection rate, as this hypothesis requires.

(2) the morphs have different probabilities of becoming infected.

Sticklebacks become infected by eating copepods carrying a proceroid, and this hypothesis argues that the phenotype of an individual influences its

TABLE XI: Proportion of sticklebacks with different plate morphs infected with Schistocephalus solidus in Heisholt Lake, June 1971. Chi-squares are from test of association between infection rate and morphs in each basin.

BASIN	PLATE MORPH	INFECTED		NON-INFECTED	
		NUMBER	%	NUMBER	%
1	Low plated	15	17	75	83
	Partially plated	27	27	74	73
	Completely plated	6	10	53	90
$\chi^2 = 7.17, 2df, p < 0.05$					
2	Low plated	16	31	36	69
	Partially plated	14	14	87	86
	Completely plated	29	28	73	72
$\chi^2 = 8.20, 2df, p < 0.025$					

chances to eat an infected copepod.

#### Summary

Morphs were differentially infected with Schistocephalus in both basins during June: partially plated sticklebacks had the highest infection rate in basin 1 and the lowest infection rate in basin 2. Increased mortality of infected individuals would account for at least part of the change in relative frequencies of morphs.

#### MOVEMENTS OF STICKLEBACKS

The observation that morph frequencies change from area to area within a basin led to a series of experiments on movements of sticklebacks in Heisholt Lake. These experiments involved releasing marked sticklebacks in the area where they were collected and following their movements for short periods. This section of the thesis presents results of these experiments.

##### A. Movement Patterns

In May and August, 1971, experiments were conducted to determine the pattern of movement of sticklebacks. Traps were set in an area at the base of a U-shaped bay (Fig. 15) for 24 hrs (Day 0). All sticklebacks in the traps were then marked with a clipped spine, and released at the exact site they had been caught. Equal numbers of traps were set in the release area and at distances of 5, 10, 15, and 20 m from this area. Traps were checked every 24 hrs for three days (Days 1-3), and the numbers of marked and unmarked sticklebacks in each trap were recorded. Sticklebacks were always released where they had been caught, and the traps were replaced at the same sites each day.

In May, 299 marked sticklebacks were released in a bay in basin 2. The frequency of marked sticklebacks on Day 1 was highest in traps in the release area, and declined as the distance from the release area increased (Fig. 16). The frequency of marked sticklebacks did not change from day to day in the release area, but it decreased from Day 1 to Day 3 at 5, 10, and 15 m, and from Day 2 to Day 3 at 20 m from the release area.

In August, 238 marked sticklebacks were released in a bay in basin 1. The pattern of change in frequency of marked sticklebacks from day to day was similar to that in May. Frequency of marked individuals did not change from day to day in the release area, and declined during the experiment at all distances outside the release area.

Results of these experiments suggest that the population is composed of two groups of sticklebacks with very different patterns of movement:

- (1) a resident group that remains within a restricted area;
- (2) a non-resident group that moves from area to area.

An experiment was conducted to examine patterns of movement of these two groups. In May, 1972, 332 sticklebacks were caught in a U-shaped bay in basin 2, marked, and released at the site where they had been caught. Equal numbers of traps were set in the release area and at 5, 10, 15 and 20 m from this area. A second spine was clipped on all marked sticklebacks caught in traps on Day 1, but those caught in the release area (residents) were marked so that they could be distinguished from those caught outside the release area (non-residents). All double-marked sticklebacks were released at the same site in the release area.

FIG. 15: Sketch of U-shaped bay  
(Station 26) in basin 2 used  
for experiment on movement patterns  
of sticklebacks, showing sites at  
which traps were set.

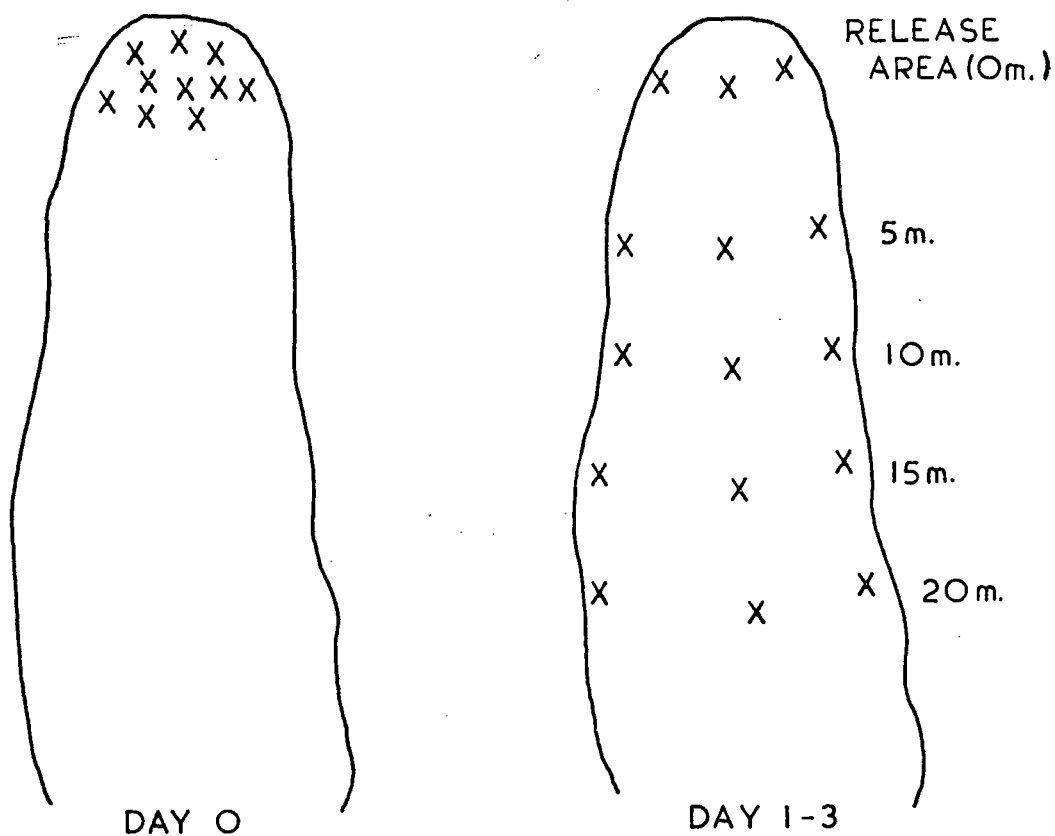
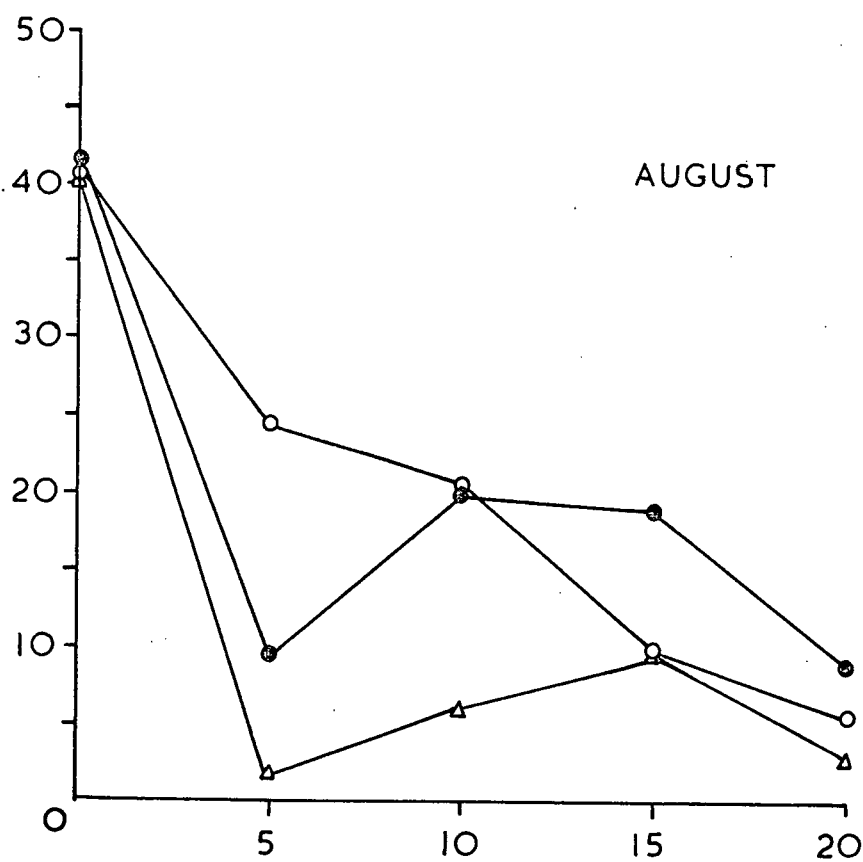
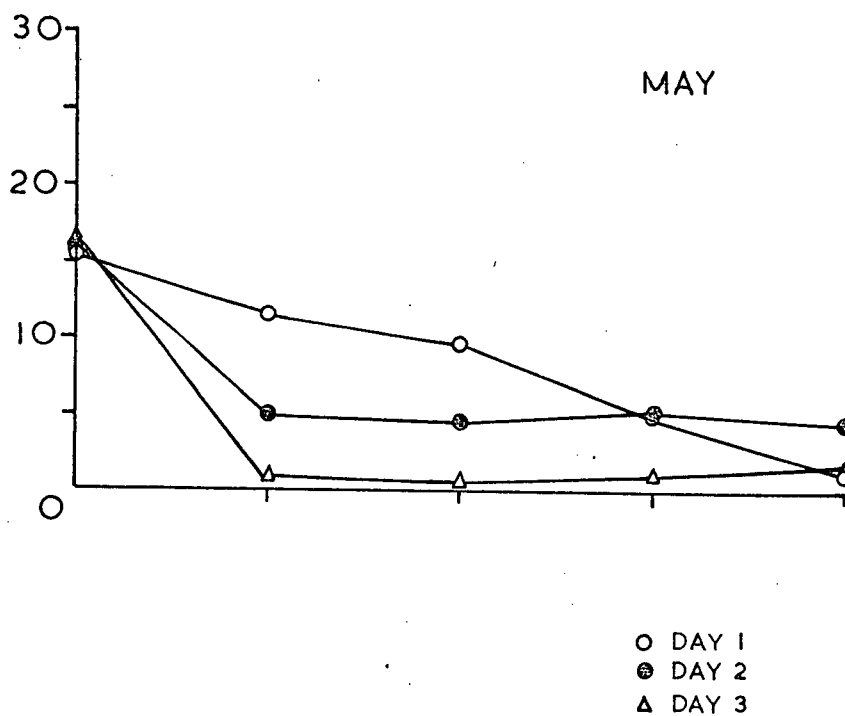


FIG. 16: Frequency of marked sticklebacks  
at different distances from release  
area in May and September, 1971.

FREQUENCY OF MARKED STICKLEBACKS (%)



DISTANCE FROM RELEASE AREA (m.)



Movement patterns of resident and non-resident sticklebacks were very different (Fig. 17). Most residents (86%) stayed in the release area, while most non-residents (83%) moved. While this result supports the hypothesis that the population is composed of two groups with different movement patterns, it also raises questions about why the frequency of marked individuals did not decline from day to day in the release area during previous experiments, since this experiment suggests that some of the marked individuals caught in the release area on Day 1 were actually non-residents.

Several hypotheses would explain differences between individuals in movement patterns. Breeding sticklebacks do not leave the release area, suggesting that they are residents. Territoriality of breeding sticklebacks would explain differences in movement patterns in May, but not in September. Larson (1972) showed that sticklebacks maintain feeding territories, and territorial behavior was observed throughout the summer in Heisholt Lake. A combination of breeding and feeding territories would explain behavioral differences between residents and non-residents.

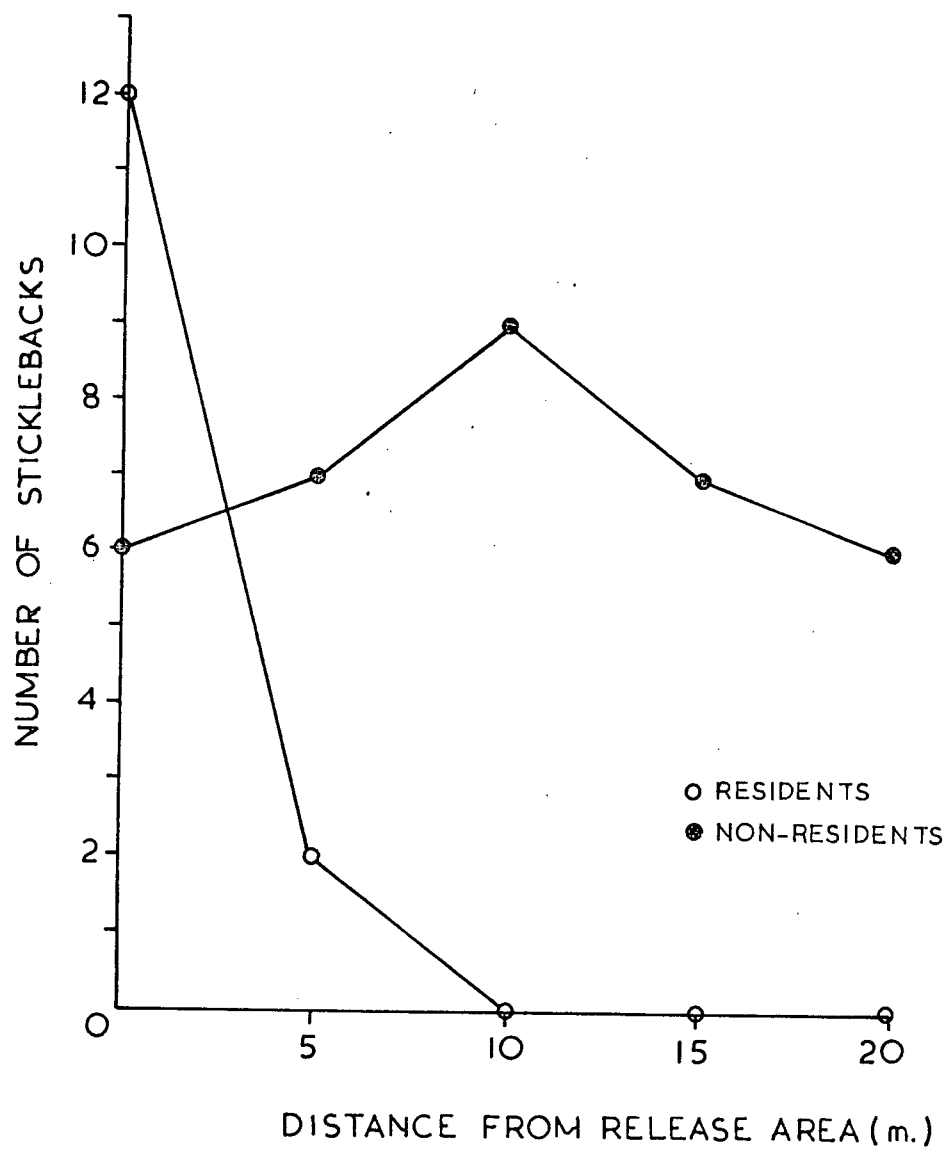
#### B. Relative Numbers of Residents and Non-Residents

Frequency of marked sticklebacks in the release area was higher in May than in August. This difference can be explained by two alternative hypotheses:

- (1) relative numbers of residents and non-residents did not change from May to August, but a lower proportion of residents in the release area were marked in May, when density of sticklebacks was higher;

- (2) relative numbers of residents and non-residents change, so that more sticklebacks are residents during August.

FIG. 17: Movement of resident and non-resident  
sticklebacks from release area in  
May, 1972.



The first hypothesis argues that, if I continue to mark sticklebacks in the release area in May, the frequency of marked individuals would increase from day to day as more residents became marked. To test this prediction, I set ten traps in a bay in basin 2 in May, 1972, and all sticklebacks in the traps were marked the next day, and released. The traps were replaced at the same sites and checked each day for three days. The numbers of marked and unmarked sticklebacks were recorded each day and all unmarked sticklebacks were marked. Frequency of marked individuals did not increase from day to day (Table XII) suggesting that most residents in the area had been caught and marked on the first day. This result supports the hypothesis that changes in the relative numbers of resident and non-resident sticklebacks explain differences between experiments in May and September.

Changes in the relative frequency of resident and non-resident sticklebacks from May to September suggest a relationship between density of sticklebacks and the proportion of sticklebacks in the population that obtains a territory and becomes resident. Several mark-recapture experiments were conducted during 1972 and 1973 to examine this relationship (Appendix D). Fig. 18 summarizes all observations on the relationship between density (number of sticklebacks per trap) in the release area and the frequency of marked sticklebacks in the release area on Day. 1. The proportion of the population that obtains a territory and becomes resident appears to decrease as stickleback density increases. However, the relationship is confounded by seasonal changes in behavior, as breeding and feeding territories are not the same. This hypothesis requires further testing before a conclusion can be made.

TABLE XII: Frequencies of marked and unmarked  
sticklebacks in an area in basin 2  
in May, 1972.

DAY	NUMBER OF STICKLEBACKS		FREQUENCY OF MARKED STICKLEBACKS (%)
	MARKED	UNMARKED	
0	0	403	
1	65	287	18.5
2	77	349	18.1
3	78	303	20.5

### C. Summary

The stickleback population in Heisholt Lake is composed of resident individuals, which maintain either a feeding or a breeding territory, and non-resident individuals, which move rapidly from area to area. The proportion of sticklebacks that obtain territories appears to decrease as population density increased.

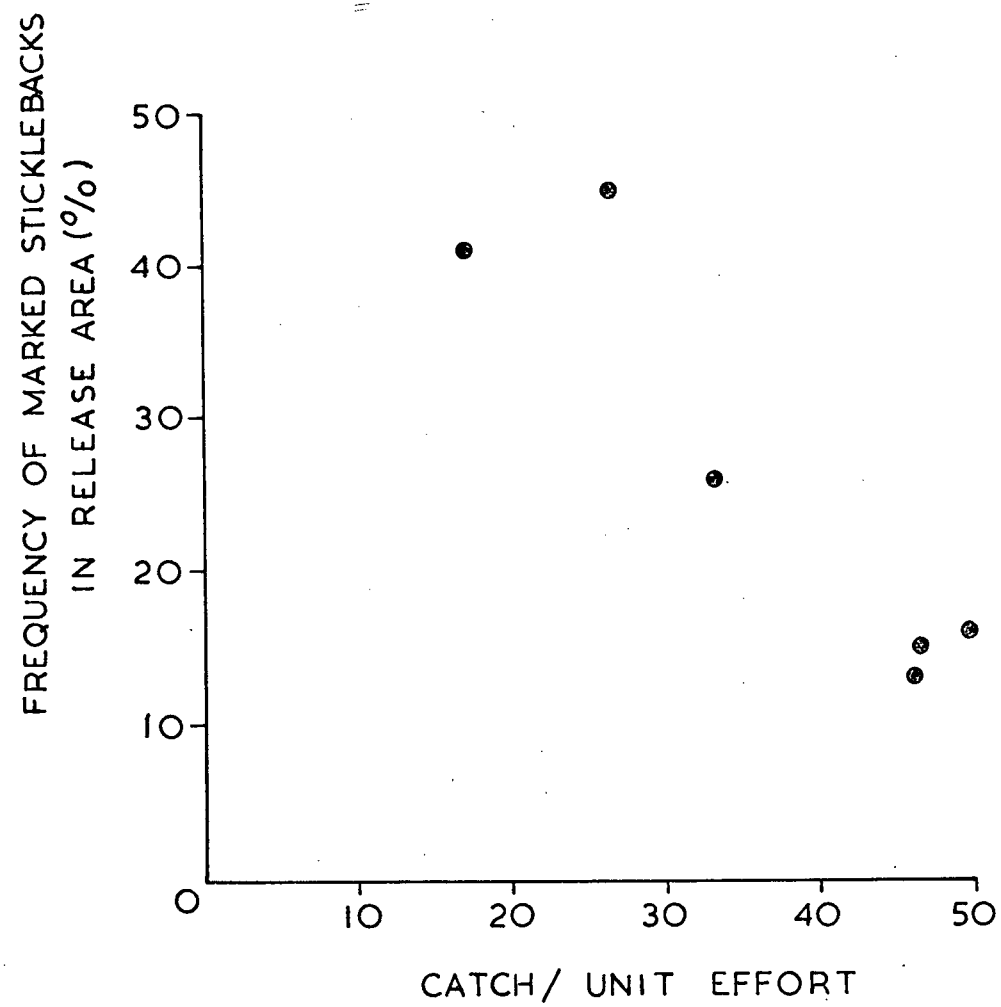
#### VARIATION OF RESIDENT AND NON- RESIDENT STICKLEBACKS

Experiments on movement patterns of sticklebacks in Heisholt Lake show that the population is composed of residents, which remain in a restricted area, and non-residents, which move from area to area. Only resident sticklebacks breed, and the proportion of sticklebacks with territories appears to decrease with population density. These observations argue that sticklebacks compete for territories, and the change in frequencies of phenotypes from area to area suggest that the plate phenotype of an individual influences its chance of becoming a resident in an area. Plate phenotypes of resident and non-resident sticklebacks were compared to determine if all phenotypes had equal probabilities of becoming a resident.

I asked three questions:

- (1) does the plate phenotype of a male affect his chances of obtaining a breeding territory?
- (2) does the plate phenotype of a female affect her chances of breeding?
- (3) does the plate phenotype of an individual affect its chances of obtaining a feeding territory, and thus becoming a resident outside

FIG. 18: The relationship between density of sticklebacks (catch/unit effort) in release area on day 1 and the proportion of sticklebacks with territories (frequency of marked sticklebacks in release area) in release area on day 1.





the breeding season?

This section of the thesis presents results of comparisons of the phenotypes of resident and non-resident sticklebacks.

#### A. Nesting Males

Nesting males were collected at five stations in basin 1 each year from 1971 to 1973, and at five stations in basin 2 in 1973. All nests at a station were collected within 36 hours during mid-May. Territories vacated by removal of a male were usually reoccupied within 24 hr. Morph frequencies of males collected at a station during early May and morph frequencies of males nesting at the same station were used to calculate relative fitnesses of morphs. Relative fitnesses of morphs were compared to determine if the phenotype of a male affects his chances of obtaining a breeding territory (Table XIII).

In basin 1, partially plated males had the lowest chances of obtaining a territory at all stations in all years. The favored phenotype varied from station to station in 1971 and 1972, but completely plated males had the highest fitness at all stations in 1973.

In basin 2, the favored morph varied greatly between stations (Table XIV). Partially plated males had a selective advantage at station 30, but they also had the lowest fitness at three of the five stations.

Morph frequencies of nesting males at all stations in a basin were compared to determine if the phenotypes of nesting males varied in space. Differences between stations in basin 1 were not significant in either 1971, 1972, or 1973 (Table XV), but morph frequencies of nesting males varied between stations in basin 2 in 1973.

TABLE XIII: Relative fitness of marks with different  
plate morphs breeding in basin 1.

STATION	MORPH	1971			1972			1973		
		SAMPLE MALES	NESTING MALES	RELATIVE FITNESS	SAMPLE MALES	NESTING MALES	RELATIVE FITNESS	SAMPLE MALES	NESTING MALES	RELATIVE FITNESS
2	Low plated	23	12	1	46	10	1	33	9	0.57
	Partially plated	20	3	0.29	42	7	0.77	24	3	0.26
	Completely plated	16	4	0.48	36	7	0.89	29	14	1
5	Low plated	6	7	0.58	32	22	0.90	28	7	0.31
	Partially plated	14	9	0.32	31	10	0.42	29	7	0.30
	Completely plated	6	12	1	21	16	1	21	17	1
7	Low plated	14	8	0.57	15	11	0.73	24	10	0.46
	Partially plated	5	0	0	20	5	0.25	19	5	0.29
	Completely plated	4	4	1	9	9	1	11	10	1
9	Low plated	15	14	0.39	20	6	0.21	42	11	1
	Partially plated	9	6	0.36	28	5	0.13	26	4	0.58
	Completely plated	5	12	1	10	14	1	38	10	1
11	Low plated	27	14	1	43	12	0.50	47	9	0.65
	Partially plated	31	4	0.25	25	4	0.28	33	6	0.62
	Completely plated	26	13	0.96	32	18	1	34	10	1

TABLE XIV: Relative fitness of males with  
different plate morphs breeding  
in basin 2, 1973.

STATION	PLATE MORPH	SAMPLE MALES	NESTING MALES	RELATIVE FITNESS
19	Low plated	5	7	1
	Partially plated	13	11	0.60
	Completely plated	9	8	0.63
23	Low plated	10	11	0.49
	Partially plated	18	6	0.15
	Completely plated	8	18	1
25	Low plated	11	13	1
	Partially plated	12	11	0.78
	Completely plated	8	7	0.74
27	Low plated	12	12	1
	Partially plated	15	11	0.73
	Completely plated	6	5	0.83
30	Low plated	31	11	0.83
	Partially plated	28	12	1
	Completely plated	18	3	0.39

TABLE XV: Summary of tests of homogeneity of  
morph frequencies of nesting males at  
different stations.

BASIN	YEAR	$\chi^2$	d.f.	P
1	1971	8.76	6	$\gg 0.25$
	1972	8.74	8	$\gg 0.25$
	1973	5.03	8	$\gg 0.75$
2	1973	17.11	8	$\lt 0.05$

These results show that the plate phenotype of a male influences his chances of obtaining a breeding territory in a particular area, and that the selective environment for males varies in space.

#### B. Breeding Females

The breeding condition of female sticklebacks collected during May from 1971 to 1973 was recorded. Plate phenotypes of breeding and non-breeding females were compared to determine if all phenotypes have an equal chance of breeding. I assumed that, if a female had ripe eggs, she would breed. Numbers of females breeding at a station were small, so all collections from a basin were combined.

Differential breeding of morphs occurred within both basins in 1971 and 1972, but differences between morphs were not significant in 1973 in either basin 1 or basin 2 (Table XVI). Partially plated females were selected against in all years in basin 1 (Table XVII). Low plated females were favored in 1971 and 1972, and completely plated females were favored in 1973. In basin 2, partially plated females were favored in 1971 and 1973, and completely plated females had the highest relative fitness in 1972. Low plated females were selected against in basin 2 in all years.

Relative fitnesses of plate number phenotypes within morphs were calculated to determine if plate number affects the chances for females of a particular morph to breed (Appendix E). Disruptive selection favored extreme phenotypes of the completely plated morph in 1972 and 1973 (Fig. 19). Directional selection favored an extreme phenotype of the completely plated morph in 1971. The type of selection changed from year to year within the partially plated morph, as selection was stabilizing in 1971, and disruptive,

TABLE XVI: Summary of tests of association  
between the plate morph of female  
sticklebacks and breeding condition.

DATE	BASIN	$\chi^2$	p
1971	1	7.30	< 0.025
	2	13.86	< 0.005
1972	1	6.26	< 0.05
	2	20.12	< 0.005
1973	1	3.03	> 0.10
	2	0.91	> 0.50

TABLE XVII: Morph frequencies of breeding and non-breeding  
female sticklebacks and relative fitness of  
morphs in early May in Heisholt Lake, 1971-1973.

BASIN	PLATE MORPH	1971			1972			1973		
		NUMBER OF FEMALES		RF	NUMBER OF FEMALES		RF	NUMBER OF FEMALES		RF
		BREEDING	NON-BREEDING		BREEDING	NON-BREEDING		BREEDING	NON-BREEDING	
1	Low plated	146	175	1	183	128	1	378	161	0.93
	Partially plated	105	176	0.79	150	151	0.85	185	80	0.93
	Completely plated	54	99	0.78	77	79	0.84	226	74	1
2	Low plated	61	66	0.95	66	121	0.62	95	146	0.91
	Partially plated	97	95	1	136	250	0.62	118	153	1
	Completely plated	55	116	0.64	73	56	1	73	100	0.97

FIG. 19: Relative fitness of plate  
phenotypes of female sticklebacks  
in basin 1. Fitness is defined  
in terms of chances to breed (Appendix E).



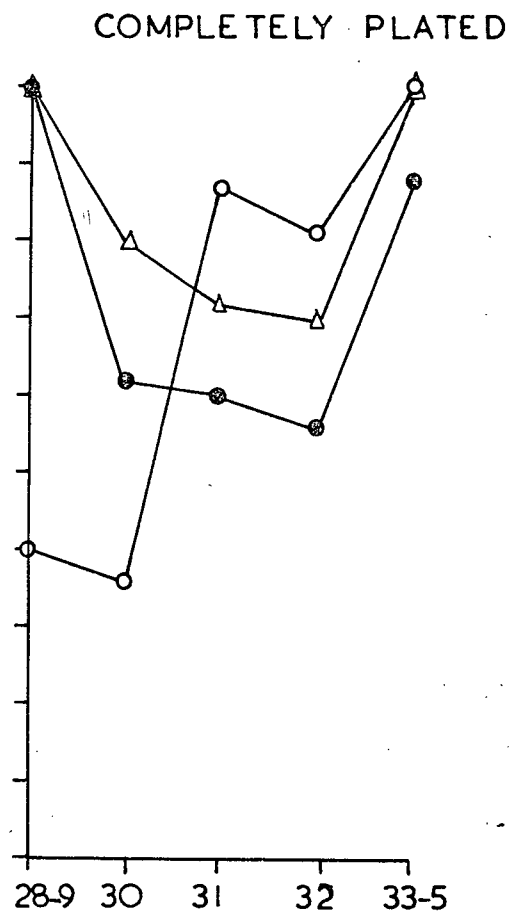
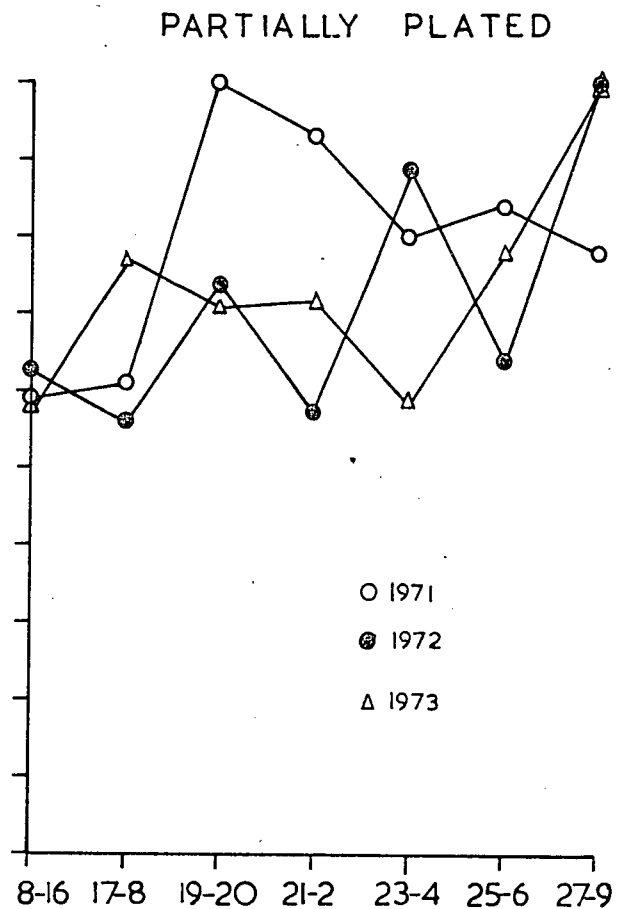
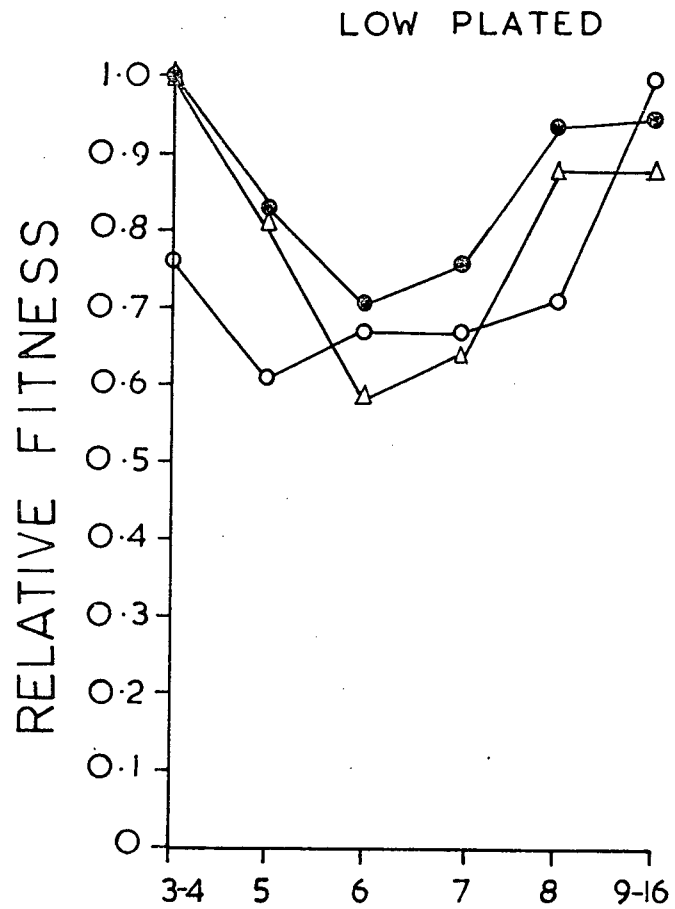


PLATE NUMBER

favoring an extreme phenotype, in 1973.

In basin 2, disruptive selection favored extreme phenotypes within the low plated morph in 1972 and 1973, and within the completely plated morph in all years (Fig. 20). Selection was also of the disruptive type in all years within the partially plated morph, but extreme phenotypes were not always favored.

The disruptive pattern of selection within all morphs in both basins suggests that the chances for a female to breed are influenced by the relative frequency of her plate phenotype in the population. Phenotypes within a morph with relatively low frequencies have a greater chance of breeding.

Density also appears to influence the relative chances for females of a particular phenotype to breed. The relative frequency of partially plated females in the breeding group at each site in basin 1 during 1972 appeared to decrease as density of sticklebacks at the site increased (Fig. 21). This result suggests that partially plated females had a lower probability of breeding as density increased, but this conclusion must be considered tentative, as this relationship was not observed in either 1971 or 1973.

The plate phenotype of a female stickleback influences her chances of breeding. The selective environment for females varies in space (differences between basins) and time (differences between years).

FIG. 20: Relative fitness of plate phenotypes  
of female sticklebacks in basin 2.  
Fitness is defined in terms of chances  
to breed (Appendix E).

# RELATIVE FITNESS

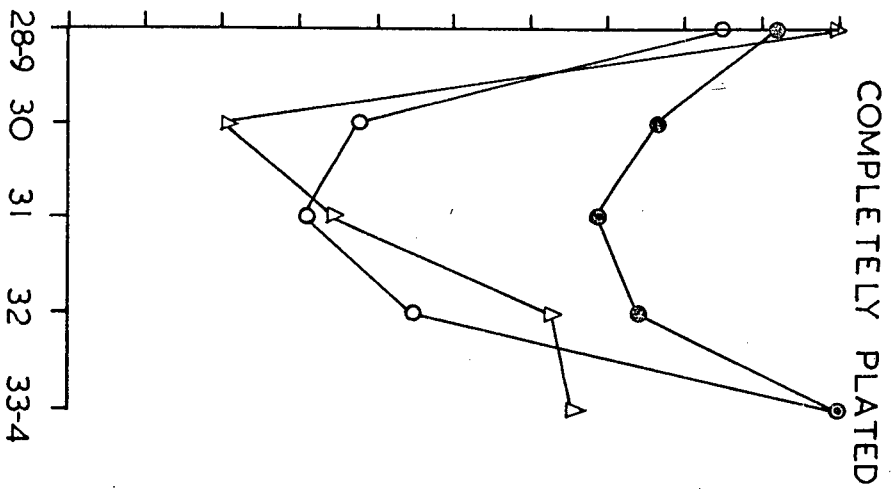
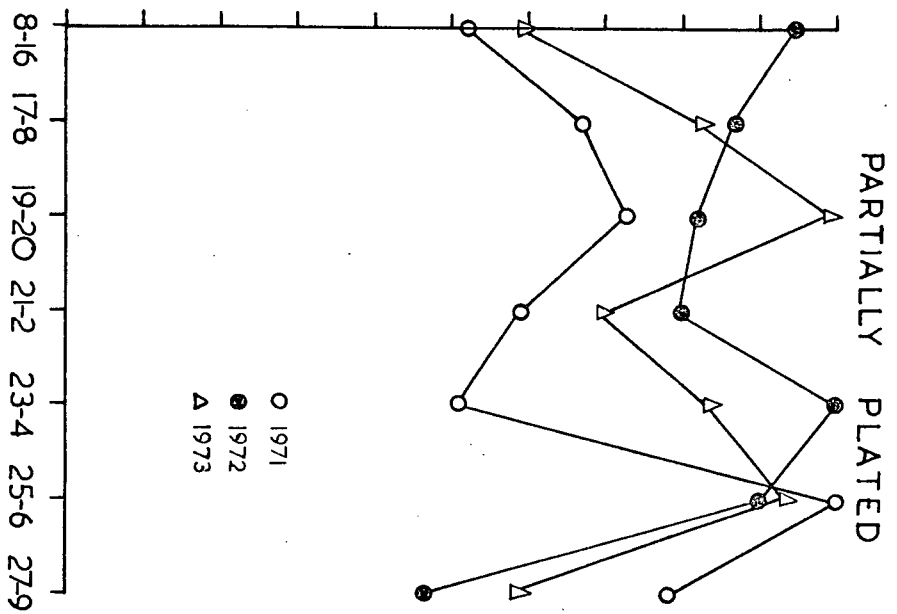
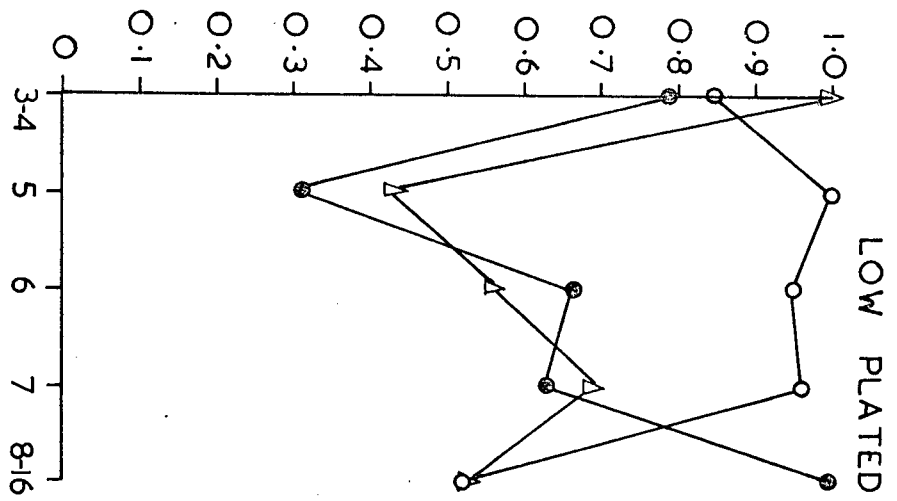
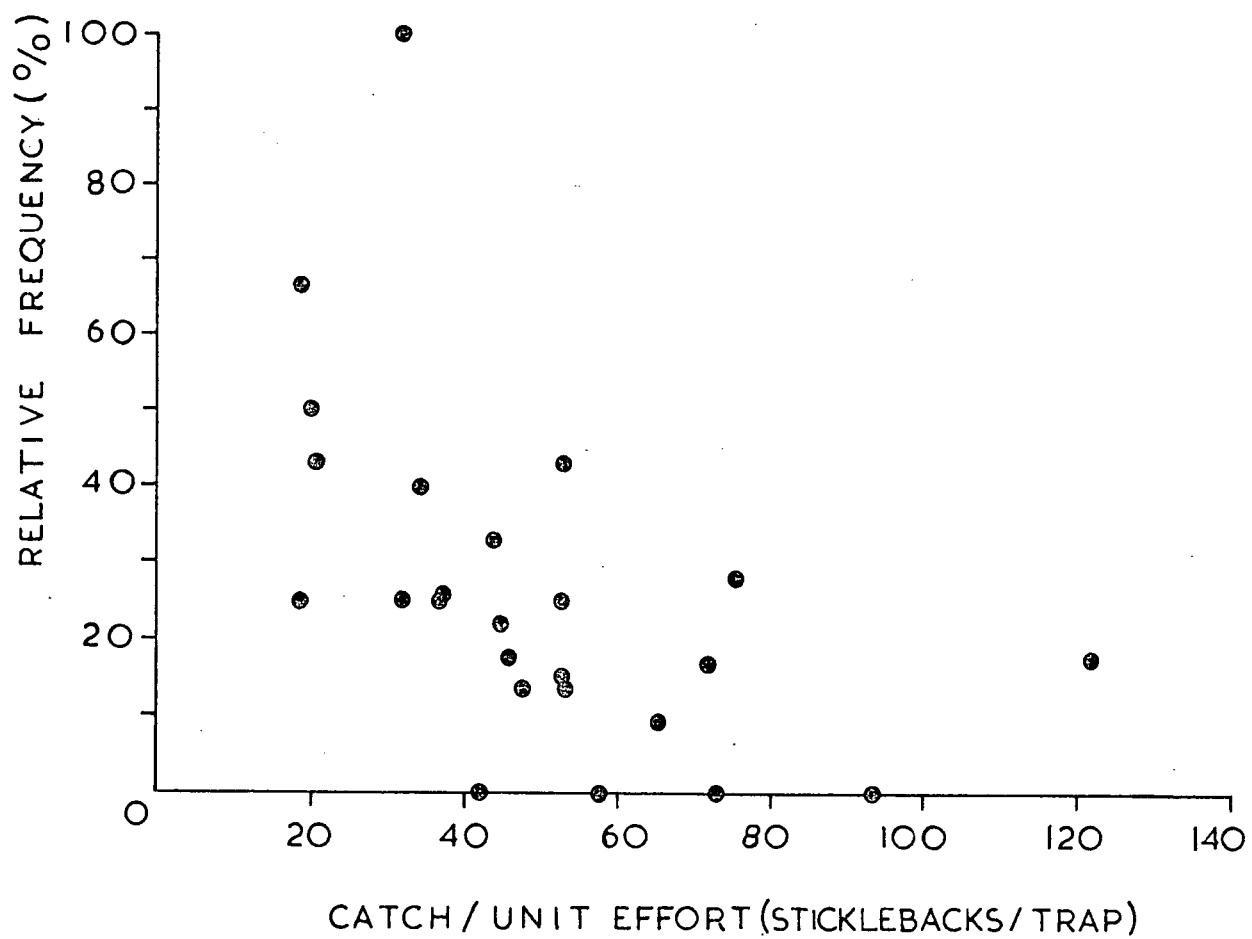


PLATE NUMBER

FIG. 21: The relationship between density of sticklebacks in a trap and the relative frequency of the partially plated morph in the breeding females caught in the trap, 1972.



### C. Residents and Non-residents in September

A mark-recapture experiment was conducted during September, 1972, to compare the plate phenotypes of resident and non-resident sticklebacks outside the breeding periods. Traps were set for 24 hours in a bay of basin 1, and 423 sticklebacks were caught and released. Equal numbers of traps were set in the release area and at 5, 10, 15, and 20 m from the release area. The traps were checked for the next three days, and all marked individuals caught in the release area (residents) and outside the release area (non-residents) were compared to determine if the phenotype of an individual influenced its chances of obtaining a feeding territory (Table XVIII).

Morph frequencies of resident and non-resident sticklebacks were significantly different (chi-square test,  $\chi^2 = 10.78$ ; 2 d.f.,  $p > 0.01$ ). Partially plated sticklebacks were more frequent in the non-resident group than in the resident group, completely plated sticklebacks were more frequent in the resident group, and the frequency of low plated individuals was similar in both groups. This shows that the plate phenotype of a stickleback influenced its chances of obtaining a feeding territory, and that low and completely plated sticklebacks had an advantage over partially plated sticklebacks in obtaining a feeding territory in an area of basin 1.

### D. Summary

Clearly, the plate phenotype of a stickleback influences its chances of

TABLE XVIII: Morph frequencies of resident and non-resident sticklebacks in basin 1, in August, 1972. Chi-square is from test of association between morph and movement pattern.

	LOW PLATED		PARTIALLY PLATED		COMPLETELY PLATED	
	NUMBER	%	NUMBER	%	NUMBER	%
Residents	27	47	6	10	25	43
Non-residents	40	50	23	29	17	21

$$\chi^2 = 10.78, 2df, p > 0.01.$$



obtaining a territory both during and after the breeding season. In basin 1, low and completely plated sticklebacks had a selective advantage over partially plated sticklebacks in obtaining a breeding territory in all years. Low and completely plated sticklebacks were also favored over partially plated individuals in obtaining a feeding territory. In basin 2, the favored morph varied from area to area and from year to year. Partially plated males were favored in certain areas and partially plated females had a selective advantage in 1971 and 1973. In both basins, disruptive selection favored extreme female phenotypes with all morphs during the breeding season.

## SUMMARY OF RESULTS

I was interested in the adaptive significance and maintenance of variation in plate number in threespine sticklebacks. My approach in the study was:

(1) to describe spatial and temporal changes in the frequencies of plate phenotypes in Heisholt Lake;

(2) to attempt to explain observed changes.

This section of the thesis presents a summary of the results of the study.

A. Changes in the Frequency of Phenotypes

Spatial and temporal changes in phenotypic frequencies were observed in Heisholt Lake. Morph frequencies changed with depth during June owing to segregation of breeding females, which suggests that the morphs differ physiologically. Morph frequencies also changed from area to area within a basin. Changes in phenotypic frequencies occurred both within generations (from May to September) and between generations (from year to year). In basin 1, low and completely plated sticklebacks increased and partially plated sticklebacks decreased in frequency both within and between generations at most stations. In basin 2, partially plated sticklebacks increased and low and completely plated sticklebacks decreased in frequency at many stations in both 1971 and 1972, and at most stations from 1971 to 1972. However, from 1972 to 1973 this pattern was reversed. Extreme phenotypes within all morphs increased in frequency both within and between generations in both basins. Disruptive selection favoring both extreme phenotypes within generations occurred within all morphs.

## B. Explanation of Observed Changes

The observed changes in phenotypic frequencies in space and time in Heisholt Lake result from interactions between genetic variation and structure of the stickleback population. A series of experiments designed to determine the pattern of movement of sticklebacks in the lake show that the population is composed of resident individuals, which appear to maintain either a feeding or a breeding territory and remain in a restricted area, and non-residents, which move rapidly from area to area. Non-resident sticklebacks do not breed.

The phenotype of an individual influences its chances of becoming a resident (i.e. to obtain a territory). In basin 1, low and completely plated sticklebacks had a selective advantage over partially plated sticklebacks in becoming a resident both during and after the breeding season. In basin 2, partially plated males were favored at some stations during the breeding season, and partially plated females had the greatest chance of breeding in both 1971 and 1973. Females with extreme phenotypes within morphs had the highest chances of breeding in both basins, and disruptive selection often favored both extreme phenotypes within a morph.

The phenotype of a stickleback also influences its chances of being infected with Schistocephalus solidus during June. Partially plated sticklebacks had the highest infection rate in basin 2. A hypothesis to explain the observed differences in infection rate is that the morphs differ in their probability of becoming infected because of differences in feeding behavior.

Although population size increased each year during the study, density of sticklebacks was not a major factor influencing the observed spatial and temporal changes in phenotypic frequencies.

Spatial changes in phenotypic <sup>frequencies</sup> are a result of variation in space of the outcome of competition among phenotypes for territories. Physiological differences between phenotypes may be a factor in this competition. Temporal changes in phenotypic frequencies are also explained by interactions between genetic variation and population structure, as phenotypes that are favored in competition for territories have the lowest rate of infection with Schistocephalus, and increase in frequency both within and between generations. Differences in survival rates of resident and non-resident individuals, owing partially to differences in infection rate, would explain the observed changes in phenotypic frequencies within generations. Changes in the phenotypic frequencies between generations are explained by observed differences between phenotypes in chances of breeding.

## DISCUSSION

### A. Behavior and Movements of Sticklebacks

Experiments on the movement patterns of sticklebacks in Heisholt Lake show that the adult population is composed of a territorial resident group and a non-resident group that moves from area to area. Residents maintain either a feeding or a breeding territory.

Differences between individuals in a population in patterns of movement are documented with other species of fish, particularly juvenile salmonids (Chapman and Bjornn, 1969; Jenkins, 1969; Symons, 1972), and with a variety of other vertebrates (Myers and Krebs, 1971; Watson and Moss, 1972). Complex social groupings within juvenile salmonid populations include dominant and subordinate territorial individuals; 'station-fish', who remain in an area but do not defend it; and wanderers, who move from place to place (Symons, 1972). Van den Assem (1967) shows that complex social hierarchies exist between male sticklebacks with adjacent breeding territories, and that courtship success is influenced by social rank. The non-residents in Heisholt Lake may be individuals at the bottom of a complex social hierarchy. Rank in this hierarchy may determine the chances for an individual to survive and reproduce.

Possession of a territory confers numerous selective advantages:

- (1) growth rates of territorial fish are higher (Mason, 1969; Symons, 1970, 1972);
- (2) territorial fish have a lower probability of being eaten by a predator because of familiarity with an area (Jenkins, 1969; Symons, 1972);
- (3) territorial behavior of males reduces interference during breeding (van den Assem, 1967; Bartnik, 1973);
- (4) territorial fish have an advantage in feeding in a familiar area (Bartnik, 1973).

Larson (1972) studied feeding behavior of two forms of sticklebacks that occur in Paxton lake on Texada Island. Pairs of sticklebacks were placed in tanks, and in every case one fish became dominant and the other became subordinate and moved away from the bottom of the tank. Preliminary

laboratory observations show that dominant-subordinate relationships occur within other stickleback populations, and that dominant individuals grow faster than subordinates (McPhail, per. comm.). This argues that growth rates are higher for resident individuals than for non-residents in Heisholt Lake.

Observations of nesting males in Heisholt Lake suggest that behavior changes during a breeding cycle. Males are almost colorless and hide in a crevice or in vegetation during the early stages of the cycle, but later they become highly colored and are more active. Kynard (1972) shows that the response of breeding males to predators changes during the cycle. Males flee from a predator early in the cycle, but later they approach the predator. A hiding place will reduce chances of being eaten by a predator, and rate of predation will be lower for resident sticklebacks than for non-residents.

The resident group during the breeding season includes breeding males and females, and perhaps non-reproductive individuals with feeding territories. Long-term movement patterns of reproductive males and females probably differ. Breeding males establish territories in late April, build nests, court females, and guard eggs and young until their progeny are free-swimming. Males can go through this sequence at least twice, and may move their nest site between sequences (Black, 1972; Kynard, 1972). Both solitary and synchronous groups of nesting males were observed in Heisholt Lake. Females establish residence in an area, and may have several clutches of eggs before moving. Groups of synchronous males may be more attractive to females than solitary males (van den Assem, 1967; Bartnik, 1974).

During this study I observed that breeding females do not move from area to area. Laboratory observations suggest that females maintain 'feeding territories', or at least will become dominant over another stickleback. Morris (1958) described territoriality of breeding females in nine-spined sticklebacks, Pungitius pungitius, but such behavior has not been recorded for three-spined sticklebacks. This apparent contradiction may be resolved by comparisons of pelagic feeding populations, which tend to breed in the open, and benthic feeding populations, which tend to breed in vegetation (Larson, 1972). Females in the former case may not be territorial in both Pungitius and Gasterosteus. Behavioral observations must not be made without an awareness of the ecological setting and genetic variation of the populations from which experimental individuals are collected.

Non-resident sticklebacks are not solitary, but move rapidly in schools from area to area in Heisholt Lake. Keenleyside and Yamamoto (1962) reported that non-territorial salmon parr form schools at high densities and avoid territory holders, thereby reducing the number of agonistic encounters. When a male stickleback is removed from his territory, another male, presumably a non-resident, usually occupies the territory within 24 hours. Territories become vacant in an area owing to movement of males and females that have either finished breeding or abandoned territories after failing to breed, and, if we assume that non-residents are searching for a vacant territory, the best strategy for non-residents is to move rapidly from area to area.

Hagen (1967) transferred marked sticklebacks from area to area in the Little Campbell River, and followed the movement of marked individuals. When low plated sticklebacks were transferred from a pond to a nearby section of the river in March, numbers of marked fish at the release site decreased slowly, but upstream or downstream movement of marked sticklebacks was not apparent. Sticklebacks in Heisholt Lake do not move during March, but remain closely associated with the lake bottom. Hagen transferred low plated sticklebacks to a trachurus habitat and trachurus to a low plated habitat in June. In both experiments, sticklebacks moved away from the release area. Marked sticklebacks which are transferred between areas in Heisholt Lake move rapidly from the release area (Maclean, unpubl data).

During summer and early fall, young-of-the-year sticklebacks move in large schools in shallow areas of Heisholt Lake. Young in laboratory tanks show no aggressive behavior during the same time period. In late fall, the young begin to fight, both in the lake and in the laboratory. The schools break up and the young sticklebacks settle in vegetation and crevices on the lake bottom. This fighting may determine social rank and subsequent chances to survive and reproduce.

Watson and Moss (1970) suggest that four conditions must hold in a population before we can conclude that behavior can limit breeding populations of sticklebacks.

(1) a substantial part of the population does not breed. This study and van den Assem's (1967) laboratory *studies* indicate that only a certain number of sticklebacks can breed in a particular area. Also, a minimum territory size exists, and the number of non-territorial individuals appears to increase with density;



(2) such non-breeders are physiologically capable of breeding if dominant or territorial animals are removed. When male sticklebacks are removed from their nests in the field, they are usually replaced within 24 hours;

(3) breeding animals are not completely using up some resource, such as food, space, or nest sites. The area defended by a male stickleback is much larger than the nest site. The number of males breeding in an area is greatly affected by settling pattern (van den Assem, 1967);

(4) mortality or depressed recruitment due to the limiting factor changes in an opposite sense to, and at the same rate as, other causes of mortality or depressed recruitment. Changes in the numbers of sticklebacks in Heisholt Lake affect the relative numbers of resident and non-resident sticklebacks. Once territories are filled, additional individuals become non-residents. Vacant territories are filled by non-residents.

Behavior clearly limits the density of breeding sticklebacks in a particular area at a particular time, but may not limit the total number of sticklebacks breeding in the lake during a year, as several breeding cycles can occur within an area during a year.

The population structure outlined in this discussion does not apply to all stickleback populations. In some populations, adults form large schools, feed pelagically (Moodie, 1972b), and hold territories only during the breeding season. A comparative study of population structure would be most interesting.

B. Physiological Variation in Gasterosteus aculeatus.

During June, the phenotype of a breeding female influences her distribution with depth in Heisholt Lake. Low and completely plated females are found at the shallowest and deepest depths respectively, while partially plated females occur at a narrow, intermediate range of depths. Seasonal changes in depth distribution of breeding females suggests that they cue on an environmental parameter, perhaps temperature, that changes seasonally at a given depth.

Heuts (1947a) showed that temperatures for optimal survival of eggs are higher for eggs from crosses between low plated males and females than for eggs from crosses between trachurus individuals. Females will attempt to lay their eggs at optimal temperatures for survival, and differences in the preferred temperatures of females might explain differences between morphs in depth distribution. MacLean (1970) showed that preferred temperatures of five-spined sticklebacks (Culaea inconstans) are narrower during breeding than at other times of the year, and that normal breeding behavior occurs only within this narrow temperature range. Heuts (1947b) showed that the geographical distribution of low plated and trachurus sticklebacks is consistent with their physiological differences.

Heuts (1945) found that optimal temperatures for survival of eggs from crosses between low-plated and trachurus sticklebacks are determined by the phenotype of the mother. Lindsey (1962) describes maternal effects on inheritance of vertebral number, a meristic character influenced by developmental temperature. However, the distribution of partially plated females in Heisholt Lake suggests that they are physiologically intermediate. Hitzeroth,

et al. (1968) show that maternal genes in trout hybrids are activated 40 days prior to activation of paternal genes at the same locus. Apparent maternal inheritance in sticklebacks might reflect differences in the temperature-dependent activities of products of maternal and paternal genes. Partially plated adults appear physiologically intermediate.

The range of depths at which females are found is narrower for partially plated females than females of the other morphs. Bachmann (1969) reported that the temperature range for survival is narrower for hybrids between races of Rana pipiens than for parental populations. Temperatures for optimal survival of eggs may be narrower for eggs from partially plated females than for eggs from females of the other morphs, and this hypothesis should be tested in the laboratory.

Heuts (1947a) and Lindsey (1961) found physiological differences between plate number phenotypes within a morph. When low plated adults are placed in warm water, 3-4-plated individuals survive longer than those with seven plates. Temperatures for optimal survival of eggs are higher for 2-4-plated females than for females with seven plates. These results suggest that stickleback populations are composed of a series of physiologically, and therefore ecologically, specialized phenotypes. Water temperatures in lakes and streams are extremely heterogeneous in space and time, and physiological variation in sticklebacks permits them to survive and reproduce in a wide variety of habitats. Recent studies show differences between plate phenotypes within morphs in nesting site (Moodie, 1972b; Kynard, 1972; Hay, 1974), in predator escape behavior (Moodie, McPhail and Hagen, 1973), and fecundity

(Kynard, 1972; Hay, 1974). Hagen (1972) suggests that plate numbers within morphs are inherited polygenically, but the pleiotropic interactions between plate number and a variety of characters influencing fitness of the individual suggest that inheritance of a plate number variation will not be simple (see also Hay, 1974). The selective value of gene interactions, the degree of linkage, and the genes involved in the interacting complexes will probably vary from population to population (Jones, 1973).

#### C. Variation in Resident and Non-resident Sticklebacks

Not all sticklebacks have equal chances of obtaining a territory in a particular area. The phenotype of an individual influences its chances to obtain a territory, and thereby its chances to survive and reproduce. In basin 1, low and completely plated sticklebacks had a selective advantage in acquiring a territory both during and after the breeding season. The low and completely plated morphs increased in relative frequency during the summer and from year to year. In basin 2, the morph favored in breeding varied from area to area and from year to year. In certain areas the partially plated morph was favored, while it was selected against throughout basin 1. The chances for an individual of a particular morph to survive from May to September also varied from area to area and from year to year in most areas. From 1971-1972, the partially plated morph increased in frequency and the other morphs decreased, but this pattern was reversed from 1972-1973.

Females with extreme plate numbers within the low and completely plated morphs had the greatest chance of acquiring a breeding territory. Low and completely plated sticklebacks with extreme plate counts increased in frequency from May to September and from year to year in both basins.

These results show that a relationship exists between the relative ability of individuals with a particular phenotype to successfully compete for a territory and the chances for individuals with that phenotype to survive and reproduce (i.e., increase in relative frequency within and between years). The selective environment influencing the fitness of phenotypes competing for territories varies in space and time.

Phenotype frequencies varied between areas at certain times in both basins. Movement of non-resident sticklebacks obscures differences in frequencies of phenotypes of residents from area to area, so significant differences are observed only when population density is low and the selective environment influencing the phenotypes of individuals that acquire territories differs considerably between areas.

Plate phenotypes were differentially infected with Schistocephalus in both basins. Partially plated sticklebacks had the highest infection rate in basin 1, and the lowest infection rate in basin 2. Partially plated sticklebacks were selected against in competition for territories throughout basin 1, but in some areas of basin 2, including the area where infection rate was examined, they were selected for. Differential infection of phenotypes can be explained by differences in the feeding behavior of resident and non-resident sticklebacks. Territorial sticklebacks feed predominantly on benthic organisms, while non-residents move away from the bottom and feed largely on plankton (Larson, 1972). Infection with Schistocephalus reduces the probability of survival and reproduction, and may be a selective force causing changes in the frequencies of phenotypes with time.

Disruptive selection favored females with extreme plate numbers within

morphs in both basins. Disruptive selection also favored extreme phenotypes in the low and completely plated morphs within years, and extreme phenotypes showed the greatest increase in frequency between years. These results suggest a relationship between frequency of a phenotype in the population and the ability of individuals with that phenotype to compete successfully for territories, which determines chances to survive and reproduce. Thoday (1972) concludes that disruptive selection occurs:

(1) where heterogeneity of selection is intrinsic to the biology of the population (sex dimorphism, etc.);

(2) where heterogeneity of selection arises from environmental heterogeneity in space.

Thoday suggests that maintenance of two or more optima may be dependent upon relative fitness being frequency-dependent.

Roughgarden (1972) develops a model for evolution in populations in which individuals specialize on a specific region of a resource axis (where resources are arranged from small to large or from low to high along a single axis) present in the environment. The model predicts that there is an optimum number of individuals of each phenotype for a given set of resources, and that if a population has this optimum distribution, then fitnesses of all phenotypes are equal. If a sexual population is to attain the optimum population distribution, the distribution of phenotypes in offspring from a given cross must have a certain shape, which will be molded by natural selection. This molding takes time, and the model predicts that when a population emigrates from a source with complex fauna, the variance of the offspring distribution will result in an overcrowding of the center phenotypes, which would result in

disruptive selection.

This model has intriguing parallels with observations on the population of sticklebacks in Heisholt Lake. Plate phenotypes of sticklebacks appear to be specializing on a specific range of temperatures. Fitnesses of extreme plate numbers within morphs are higher than those of center phenotypes. The population is the result of a recent introduction of sticklebacks into an unoccupied lake. A continuing study of plate variation in this population may reveal further parallels and since the source population is known, may lead to further understanding of the adaptive significance and maintenance of plate variation. Also, the introduction of a predator, such as trout, into one of the basins would be an interesting experiment.

Selander (1970) also finds differences between areas in restricted populations of mice, but he invokes genetic drift in small subdivided groups to explain changes from area to area. Numerous studies show that isoenzyme variation is responsive to local conditions (Koehn and Rasmussen, 1967; O'Gower and Nicol, 1968; Johnson et al., 1969; Koehn, 1970; Prakash et al., 1969; Richmond, 1970; Marshall and Allard, 1970; Koehn et al., 1971; Smith and Koehn, 1971; Koehn and Mitton, 1972; Merritt, 1972; Williams et al., 1973). Myers and Krebs (1971) show that frequencies of certain genotypes are more common in dispersing Microtus pennsylvanicus than in residents.

In summary, spatial and temporal changes in the frequencies of plate phenotypes were observed in Heisholt Lake. Changes in both space and time result from selection acting on individuals competing for territories. Differences between areas are caused by environmental heterogeneity in parameters affecting the chances for an individual with a particular phenotype of obtaining a territory. Changes of the frequency of a phenotype in time

are a result of the selective advantages of territorial sticklebacks in terms of survival and reproduction.



## BIBLIOGRAPHY

- Arne, C., and R.W. Owen. 1967. Infections of the three-spined stickleback, Gasterosteus aculeatus L., with the plerocercoid larvae of Schistocephalus solidus (Muller, 1776), with special reference to pathological effects. *Parasitology* 57:301-314.
- Bachmann, K. 1969. Temperature adaptations of amphibian embryos. *Amer. Natur.* 103:115-130.
- Bartnik, V.G. 1973. Behavioral ecology of the longnose dace, Rhinichthys cataractae (Pisces, Cyprinidae): Significance of dace social organization. Ph.D. Thesis. University of British Columbia.
- Bertin, L. 1925. Recherches bionomiques, biometriques et systematiques sur les Epinoches (Gasterosteides). *Ann. Inst. Oceanograph, Monaco*, N.S., 2, fasc. 1.
- Callegarini, C., and C. Cucchi. 1968. Polimorfismo emoglobinico in varie popolazioni di Gasterosteus aculeatus di bacini idrografici diversi. *Annali. Univ. Ferrara (Ser. 13)* 2:31-35.
- \_\_\_\_\_. 1969. Le emoglobine di Gasterosteus aculeatus e di Gasterosteus pungitius (Teleostea Gasterosteidae). *Annali Univ. Ferrara (Ser. 13)* 2: 145-150.
- Chapman, D.W., and T.C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. *In*: H.R. MacMillan Lectures in Fisheries, Symposium on Salmon and Trout in Streams, 1968. Univ. British Columbia, Institute of Fisheries. Pp: 153-176.

Ford, E.B. 1971. Ecological Genetics. Chapman and Hall Ltd., London.

3rd ed., 410 p.

Hagen, D.W. 1967. Isolating mechanisms in threespine sticklebacks

(Gasterosteus). J. Fish. Res. Bd. Canada 24:1637-1692.

\_\_\_\_\_. 1972. Inheritance of numbers of lateral plates and gill rakers

in Gasterosteus aculeatus. Heredity 30:301-312.

Hagen, D.W., and L.G. Gilbertson. 1972. Geographic variation and

environmental selection in Gasterosteus aculeatus L. in the Pacific

Northwest, America.. Evolution 26:32-51.

\_\_\_\_\_. 1973a. The genetics of plate morphs in freshwater threespine

sticklebacks. Heredity 31:75-84.

\_\_\_\_\_. 1973b. Selective predation and the intensity of selection acting

upon the lateral plates of threespine sticklebacks. Heredity 30:

273-287.

Hay, D.E. MS 1969. Mate selection in threespine sticklebacks (Gasterosteus).

M.Sc. Thesis, Department of Zoology, University of British Columbia.

\_\_\_\_\_. MS 1974. Ecological genetics of threespine sticklebacks

(Gasterosteus). Ph.D. Thesis, Department of Zoology, University of

British Columbia.

Heuts, M.J. 1947a. Experimental studies on adaptive evolution in

Gasterosteus aculeatus L. Evolution 1:89-102.

- Heuts, M.J. 1947b. The phenotypical variability of Gasterosteus aculeatus L. populations in Belgium. *Klarse der Wetenschappen*, Jaargang IX, No. 25.
- Hitzeroth, H., J. Klose, S. Ohno, and U. Wolf. 1968. Asynchronous activation of parental alleles at the tissue-specific gene loci observed on hybrid trout during early development. *Biochem. Genet.* 1: 287-300.
- Jenkins, T.M. 1969. Social structure, position choice and microdistribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. *Anim. Behav. Monog.* 2:57-123.
- Johnson, F.M., H.E. Schaeffer, J.E. Gillaspay, and E.S. Rochwood. 1969. Isoenzyme genotype-environment relationships in natural populations of the harvester ant, Pogonomyrmex barbatus from Texas. *Biochem. Genet.* 5:211-222.
- Jones, J.S. 1973. Ecological genetics and natural selection in molluscs. *Science* 182:546-552.
- Keenleyside, M.H.A., and F.T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (Salmo salar L.). *Behaviour* 19:139-169.
- Koehn, R.K. 1970. Functional and evolutionary dynamics of polymorphic esterases in catostomid fishes. *Trans. Amer. Fish. Soc.* 99:219-228.

- Koehn, R.K., and J.B. Milton. 1972. Population genetics of marine pelycypods. I. Ecological heterogeneity and evolutionary strategy at an enzyme locus. *Amer. Natur.* 106:47-56.
- Koehn, R.K., J.E. Perez, and R.B. Merritt. 1971. Esterase enzyme function and genetical structure of populations of the fish Notropis stramineus. *Amer. Natur.* 105:51-69.
- Koehn, R.K., and D.I. Rasmussen. 1967. Polymorphic and monomorphic serum esterase heterogeneity in Catastomid fish populations. *Biochem. Genet.* 1:131-144.
- Kusa, M. 1966. Lactate dehydrogenase isoenzyme patterns of the stickleback (Pungitius pungitius). *Proc. Jap. Acad.* 42:146-150.
- Kynard, B.E. 1972. Male breeding behavior and lateral plate phenotype in the threespine stickleback (Gasterosteus aculeatus). Ph.D. Thesis. Univ. of Washington.
- Larson, G. 1972. Social behavior and feeding ability of two phenotypes of Gasterosteus aculeatus in relation to their spatial and trophic segregation in a temperate lake. Ph.D. Thesis. University of British Columbia.
- Lea, G.R. 1968. Lateral plates in the threespine stickleback (Gasterosteus aculeatus Linnaeus) as a defence against predators. B.Sc. Thesis. University of British Columbia.
- Lester, R.J.G. 1971. The influence of Schistocephalus plerocercoids on the respiration of Gasterosteus and a possible resulting effect on the behavior of the fish. *Can. J. Zool.* 49:361-366.

- Lindsey, C.C. 1962. Experimental study of meristic variation in a population of threespine sticklebacks, Gasterosteus aculeatus. Can. J. Zool. 40:271-312.
- MacLean, J.A., and J.H. Gee. 1971. Effects of temperature on movements of prespawning brook sticklebacks, Culaea inconstans, in the Roseau River, Manitoba. J. Fish. Res. Bd. Canada 28:919-923.
- Marshall, D.R., and R.W. Allard. 1970. Maintenance of isoenzyme polymorphisms in natural populations of Avena barbata. Genetics 66:393-399.
- Mason, J.C., and D.W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Bd. Canada 22:173-190.
- Merritt, R.B. 1972. Geographic distribution and enzymatic properties of Lactate dehydrogenase allozymes in the fat-head minnow, Pimephales promelas. Amer. Natur. 106:173-184.
- McPhail, J.D. 1969. Predation and evolution in a stickleback (Gasterosteus). J. Fish. Res. Bd. Canada 26:3183-3208.
- McPhail, J.D., and C.C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Bull. Fish. Res. Bd. Canada 173. 381p.
- Miller, R.R., and C.L. Hubbs. 1969. Systematics of Gasterosteus aculeatus, with particular reference to intergradation and introgression along the Pacific coast of North America: a commentary on a recent contribution. Copeia 1969: 52-69.

- Moodie, G.E.E. 1972a. Prédation, natural selection and adaptation in an unusual threespine stickleback. *Heredity* 28:155-168.
- \_\_\_\_\_. 1972 b. Morphology, life history, and ecology of an unusual stickleback (Gasterosteus aculeatus) in the Queen Charlotte Islands, Canada. *Can. J. Zool.* 50:721-732.
- Moodie, G.E.E., J.D. McPhail, and D.W. Hagen. 1973. Experimental demonstration of selective predation on Gasterosteus aculeatus. *Behaviour* XLVII: 95-105.
- Morris, D. 1958. The reproductive behaviour of the ten-spined stickleback (Pygosteus pungitius L). *Behaviour* Suppl. 6. 154p.
- Munzing, J. 1963. The evolution of variation and distribution patterns in European populations of the three spined stickleback, Gasterosteus aculeatus. *Evolution* 17: 320-332.
- Myers, J.H., and C.J. Krebs. 1971 Genetic, behavioral, and reproductive attributes of dispersing field voles Microtus pennsylvanicus and Microtus ochrogaster. *Ecol. Monog.* 41: 53-78.
- O'Donald, P. 1968. Measuring the intensity of natural selection. *Nature* 220: 197-198.
- \_\_\_\_\_. 1970. Change of fitness by selection for a quantitative character. *Theor. Pop. Biol.* 1:219-232.
- O'Gower, A.K., and P.I. Nicol. 1968. A latitudinal cline of haemoglobins in a bi-valve mollusc. *Heredity* 23: 485-492.

- Penczak, T. 1965. Morphological variation of the stickleback (Gasterosteus aculeatus L.) in Poland. Zool. Pol., Wroclaw 15:3-49.
- \_\_\_\_\_. 1966. Comments on the taxonomy of the three-spined stickleback, Gasterosteus aculeatus Linnaeus. Ohio J. Sci. 66:81-87.
- Prakash, S., R.C. Lewontin, and J.L. Hubby. 1969. A molecular approach to the study of genic heterozygosity in natural populations. IV. Patterns of genic variation in central, marginal, and isolated populations of Drosophila pseudoobscura. Genetics 61:858.
- Richmond, R.C. 1970. Non-Darwinian evolution: A critique. Nature 225:1025-1028.
- Roughgarden, J. 1972. Evolution of niche width. Amer. Natur. 106:683-718.
- Selander, R.K. 1970. Behavior and genetic variation in natural populations. Amer. Zoologist 10:53-66.
- Semler, D.E. 1971. Some aspects of adaptation in a polymorphism for breeding colours in the threespine stickleback (Gasterosteus aculeatus). J. Zool., Lond. 165:291-302.
- Sheppard, P.M. 1969. Evolutionary genetics of animal populations: The study of natural populations. Proc. XII Intern. Congr. Genetics 3:261-279.
- Smith, G.R., and R.K. Koehn. 1971. Phenetic and cladistic studies of biochemical and morphological characteristics of Catostomus. Syst. Zool. 20:282-297.

- Stott, B. 1967. The movements and population densities of roach (Rutilus rutilus(L)) and gudgeon (Gobio gobio(L)) in the River Mole. J. Anim. Ecol. 36:407-423.
- \_\_\_\_\_. 1970. Some factors affecting the catching power of unbaited fish traps. J. Fish Biol. 2:15-22.
- Symons, R.E.K. 1969. The possible role of social and territorial behaviour of Atlantic salmon parr in the production of smolts. Tech. Rep. Fish. Res. Bd. Canada 206. 25p.
- Symons, P.E.K. 1972. Behavioural adjustment of population density to available food by juvenile Atlantic salmon. J. Anim. Ecol. 41:569-587.
- Thoday, J.M. 1972. Disruptive selection: A review. Proc. R. Soc. Lond. B. 182:109-143.
- Tinbergen, N. 1951. The study of instinct. Clarendon Press, Oxford.
- Van den Assem, J. 1967. Territory in the three-spined stickleback Gasterosteus aculeatus L. Behaviour, Suppl 16: 164p.
- Watson, A. and R. Moss. 1970. Dominance, spacing behavior and aggression in relation to population regulation in vertebrates. In: Animal Populations in Relation to Their Food Resources. A. Watson (ed). British Ecol. Soc. Symp. 10. Pp:167-220.



Williams, G.C., R.K. Koehn, and J.B. Milton. 1973. Genetic differentiation without isolation in the American eel, Anguilla rostrata. Evolution 27: 192-204.

Wootton, R.J. 1972. The behaviour of the male three-spined stickleback in a natural situation: a quantitative description. Behaviour 41:232-241.

APPENDIX A: MORPH FREQUENCIES OF STICKLEBACKS  
IN HEISHOLT LAKE, 1971 - 1973.

TABLE A - I: Morph frequencies of sticklebacks caught  
at 15 stations in basin 1 in May and  
September from 1971-1973.

Station	MAY 1971			SEPTEMBER 1971			MAY 1972			SEPTEMBER 1972			MAY 1973		
	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated
1	33	27	16	22	8	14	46	38	30	22	7	16	18	10	13
2	35	34	18	37	28	32	89	63	48	30	14	27	19	9	14
3	49	44	23	14	11	17	27	20	15	5	4	9	111	60	54
4	39	28	23	37	10	30	47	28	26	37	8	15	49	47	41
5	21	27	15	30	26	46	74	69	53	35	8	25	73	54	47
6	13	13	10	24	12	23	23	15	16	21	2	10	32	14	14
7	58	36	13	45	28	61	42	48	34	44	8	27	83	53	44
8	58	39	28	30	26	32	42	25	13	39	9	34	65	32	31
9	38	33	14	31	18	37	38	43	25	46	18	25	112	54	71
10	8	12	8	33	16	34	22	35	12	24	5	15	54	36	31
11	82	83	51	35	17	32	84	72	36	54	18	31	116	65	71
12	10	9	12	15	11	8	27	34	15	23	8	6	54	30	21
13	15	12	6	10	5	8	16	16	16	24	9	12	58	29	31
14	56	36	28	5	3	10	88	66	25	60	12	31	50	21	31
15	15	9	12	7	1	9	30	32	17	15	5	5	82	18	31

TABLE A - II: Morph frequencies of sticklebacks caught  
at fifteen stations in basin 2 in May and  
September from 1971 - 1973.

NUMBERS OF STICKLEBACKS

	MAY 1971			SEPTEMBER 1971			MAY 1972			SEPTEMBER 1972			MAY 1973		
Station	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated	Low Plated	Partially Plated	Com- pletely Plated
16	30	44	28	13	54	25	47	103	55	25	54	19	62	48	46
17	18	19	11	16	24	12	30	50	30	7	19	1	20	28	9
18	18	20	19	7	21	10	23	53	27	10	31	13	44	52	26
19	7	12	16	1	8	11	29	34	21	18	28	10	15	22	14
20	17	33	15	23	39	26	40	83	44	20	34	21	41	60	49
21	7	13	14	18	29	15	26	61	36	-	-	-	16	31	24
22	12	10	6	17	22	21	16	42	4	14	21	10	20	24	19
23	9	17	5	13	17	20	12	28	9	-	-	-	27	31	15
24	14	13	11	11	21	10	26	52	26	2	10	5	21	31	23
25	9	17	15	6	9	7	22	51	34	8	7	7	20	51	31
26	10	14	13	14	16	7	10	31	14	5	5	4	27	32	15
27	7	15	17	14	25	11	20	22	13	11	18	11	21	30	15
28	24	24	12	9	13	12	12	29	11	11	12	6	32	32	20
29	9	19	10	7	8	4	19	18	18	5	8	10	31	34	24
30	28	28	25	17	22	25	51	64	24	14	33	21	50	53	24

APPENDIX B: NUMBER OF STICKLEBACKS/TRAP  
IN HEISHOLT LAKE, 1970-1973.

YEAR	MONTH	BASIN	NUMBER OF STICKLEBACKS	NUMBER OF TRAPS	CATCH/ UNIT EFFORT	STANDARD DEVIATION
1970	May	1,2	364	34	10.7	11.1
	September	1,2	289	82	3.5	6.4
1971	May	1	1249	73	17.1	22.2
		2	734	39	18.8	12.5
	September	1	999	77	13.0	15.9
		2	732	113	6.5	4.9
1972	May	1	1680	56	30.0	23.2
		2	1470	30	49.0	27.6
	September	1	902	105	8.6	7.7
		2	568	130	4.4	6.6
1973	May	1	2070	52	39.8	26.8
		2	2506	39	64.3	27.1
	September	1	187	113	1.7	3.5
		2	344	115	3.0	4.9

APPENDIX C: FREQUENCIES OF PLATE NUMBER  
PHENOTYPES WITHIN MORPHS IN  
HEISHOLT LAKE, 1971-1973.

TABLE C - I: Frequencies of plate number phenotypes  
within the low plated morph in basin 1.

PLATE NUMBER	MAY 1971		SEPTEMBER 1971		MAY 1972		SEPTEMBER 1972		MAY 1973	
	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%
3	0	0	0	0	0	0	1	0	0	0
4	7	1	7	2	8	1	7	2	20	2
5	75	14	23	6	88	13	38	8	132	13
6	190	36	115	31	224	32	126	26	311	32
7	186	35	110	29	299	43	167	35	352	36
8	29	5	47	13	63	9	61	13	105	11
9	8	1	15	4	5	1	30	6	23	2
10	4	1	17	5	3	0	12	3	12	1
11	4	1	5	1	1	0	13	4	8	1
12	6	1	0	0	1	0	7	1	1	0
13	7	1	7	2	1	0	3	1	4	0
14	4	1	4	1	2	0	5	1	5	1
15	7	1	0	0	0	0	4	1	3	0
16	3	1	0	0	0	0	4	1	0	0
17	0	0	0	0	0	0	1	0	0	0



TABLE C - II: .Frequencies of plate number phenotypes  
within the partially plated morph in basin 1.

PLATE NUMBER	MAY 1971		SEPTEMBER 1971		MAY 1972		SEPTEMBER 1972		MAY 1973	
	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%
8	0	0	0	0	2	0	0	0	2	0
9	1	0	0	0	6	1	0	0	1	0
10	0	0	0	0	9	1	0	0	4	1
11	0	0	3	1	8	1	0	0	5	1
12	2	0	0	0	4	1	1	1	6	1
13	13	3	2	1	8	1	0	0	20	4
14	12	3	6	3	16	3	0	0	17	3
15	18	4	10	4	27	4	3	2	28	5
16	25	6	6	3	37	6	7	5	38	7
17	29	7	8	3	48	8	8	6	48	9
18	39	9	13	6	45	7	11	8	42	8
19	33	7	10	4	56	9	10	7	49	9
20	45	10	13	6	50	8	9	7	44	8
21	34	8	16	7	53	9	16	12	38	7
22	48	11	30	13	44	7	15	11	45	9
23	28	6	16	7	39	6	9	7	37	7
24	24	5	16	7	37	6	9	7	27	5
25	28	6	26	11	36	6	16	12	27	5
26	26	6	24	10	31	5	9	7	21	4
27	24	5	20	9	21	4	6	4	11	2
28	9	2	8	3	19	3	6	4	4	1
29	4	1	4	2	8	1	0	0	4	1

TABLE C - III: Frequencies of plate number phenotypes  
within the completely plated morph  
in basin 1.

PLATE NUMBER	MAY 1971		SEPTEMBER 1971		MAY 1972		SEPTEMBER 1972		MAY 1973	
	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%
28	0	0	0	0	0	0	0	0	3	1
29	19	7	19	5	8	2	11	4	31	5
30	69	25	104	26	75	20	65	23	148	26
31	81	29	113	29	108	28	75	26	158	27
32	80	29	103	26	117	31	84	29	148	26
33	23	8	47	12	62	16	44	15	75	13
34	4	1	6	2	11	3	7	3	10	2
35	1	0	1	0	0	0	2	1	3	1

TABLE C - IV: Frequencies of plate number phenotypes  
within the low plated morph in basin 2.

PLATE NUMBER	MAY 1971		SEPTEMBER 1971		MAY 1972		SEPTEMBER 1972		MAY 1973	
	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%
3	0	0	1	1	2	1	2	1	2	0
4	17	8	22	12	35	9	17	11	19	4
5	53	24	52	28	115	30	40	27	89	20
6	74	34	66	30	132	34	49	33	177	39
7	37	17	29	16	82	21	36	24	136	30
8	7	3	10	5	10	3	5	3	19	4
9	5	2	1	1	4	1	1	0	8	2
10	2	1	0	0	0	0	0	0	5	1
11	6	3	1	1	2	1	0	0	3	1
12	4	2	1	1	1	0	0	0	2	0
13	3	1	3	2	0	0	0	0	1	0
14	5	2	0	0	0	0	0	0	0	0
15	6	3	0	0	0	0	0	0	0	0

TABLE C - V: Frequencies of plate number phenotypes  
within the partially plated morph in basin 2.

PLATE NUMBER	MAY 1971		SEPTEMBER 1971		MAY 1972		SEPTEMBER 1972		MAY 1973	
	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%
7	0	0	0	0	1	0	0	0	0	0
8	0	0	1	0	5	1	3	1	1	0
9	0	0	2	1	6	1	6	2	1	0
10	1	0	4	1	21	3	7	3	10	2
11	3	1	5	2	22	3	9	3	10	2
12	10	3	8	2	26	4	9	3	23	4
13	16	5	16	5	38	5	10	4	29	5
14	8	3	17	5	41	6	9	3	34	6
15	8	3	20	6	47	7	19	7	31	6
16	28	9	22	7	51	7	17	6	36	6
17	22	7	24	7	47	7	20	7	52	9
18	26	9	20	6	51	7	16	6	48	9
19	27	9	20	6	43	6	12	4	44	8
20	20	7	20	6	47	7	15	5	38	7
21	29	10	18	5	39	5	17	6	42	8
22	17	6	18	5	31	4	19	7	40	7
23	17	6	15	5	42	6	11	4	28	5
24	17	6	19	6	38	5	17	6	24	4
25	16	5	18	5	30	4	17	6	23	4
26	17	6	18	5	24	3	14	5	17	3
27	10	3	21	6	35	5	10	4	12	2
28	6	2	10	3	23	3	13	5	9	2
29	0	0	0	0	13	2	10	4	8	1

TABLE C - VI: Frequencies of plate number  
phenotypes within the completely  
plated morph in basin 2.

PLATE NUMBER	MAY 1971		SEPTEMBER 1971		MAY 1972		SEPTEMBER 1972		MAY 1973	
	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%	NUMBER	%
28	1	0	0	0	0	0	0	0	0	0
29	13	6	23	11	2	1	2	1	17	5
30	41	19	61	28	72	20	16	12	72	20
31	51	24	58	27	99	27	42	30	108	31
32	79	36	38	17	95	26	39	28	111	31
33	28	13	26	12	83	23	30	28	38	11
34	3	1	7	3	12	3	9	7	8	2
35	1	0	3	1	3	1	0	0	0	0

APPENDIX D: SUMMARY OF OBSERVATIONS ON THE  
RELATIONSHIP BETWEEN DENSITY OF  
STICKLEBACKS IN THE RELEASE AREA  
(CATCH/UNIT EFFORT) AND RELATIVE  
FREQUENCY OF RESIDENT STICKLEBACKS.

DATE	CATCH/UNIT EFFORT (NUMBER STICKLEBACKS/TRAP) IN RELEASE AREA	FREQUENCY OF MARKED STICKLEBACKS IN RELEASE AREA ON DAY 1 (%)
May 1971	49.8	16
August 1971	17.0	41
May 1972	33.2	26
August 1972	26.5	45
May 1973	46.0	13
June 1973	46.5	15

APPENDIX E: PLATE NUMBERS OF BREEDING AND  
NON-BREEDING FEMALE STICKLEBACKS  
IN HEISHOLT LAKE IN MAY, 1971 - 1973.



TABLE E - I: Plate numbers of breeding and non-breeding  
female sticklebacks of the low plated morph  
in Basin 1.

PLATE NUMBER	NUMBER OF FEMALES					
	1971		1972		1973	
	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING
4	2	2	3	1	11	0
5	18	27	26	16	59	14
6	51	66	55	44	92	63
7	47	62	75	57	127	72
8	9	8	19	8	52	7
9	2	2	1	0	15	1
10	2	2	2	0	5	0
11	2	1	0	0	3	2
12	2	2	2	0	2	1
13	4	0	0	0	7	0
14	3	0	0	2	5	1
15	3	2	0	0	0	0
16	1	1	0	0	0	0

TABLE E - II: Plate numbers of breeding and non-breeding female sticklebacks of the partially plated morph in basin 1.

PLATE NUMBER	1971		1972		1973	
	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING
9	0	0	0	1	1	0
10	0	0	2	2	0	1
11	0	0	2	6	0	4
12	0	2	0	1	2	1
13	4	5	1	3	3	4
14	2	7	4	5	6	1
15	4	7	7	6	8	4
16	7	12	10	7	10	7
17	3	14	8	20	20	7
18	7	14	13	11	19	4
19	9	20	15	12	19	7
20	15	12	11	11	15	7
21	14	19	8	22	16	6
22	8	14	15	11	18	7
23	7	17	17	4	9	10
24	8	12	8	10	11	4
25	5	13	6	8	11	5
26	7	8	5	5	10	1
27	3	4	9	3	6	0
28	2	4	5	3	1	0
29	0	2	4	1	0	0

TABLE E - III: Plate numbers of breeding and  
non-breeding female sticklebacks  
of the completely plated morph in  
basin 1.

PLATE NUMBER	NUMBER OF FEMALES					
	1971		1972		1973	
	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING
28	0	0	0	0	1	0
29	2	8	3	1	15	1
30	7	32	14	16	58	19
31	20	26	19	23	54	25
32	17	25	20	28	51	26
33	7	7	19	10	40	3
34	1	1	2	1	7	0

TABLE E - IV: Plate numbers of breeding and non-breeding  
female sticklebacks of the low plated morph  
in basin 2.

PLATE NUMBER	NUMBER OF FEMALES					
	1971		1972		1973	
	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING
3	0	0	1	0	1	0
4	5	6	8	11	5	3
5	15	13	10	43	11	27
6	23	22	29	43	38	64
7	13	12	12	20	31	36
8	0	2	5	4	4	7
9	0	2	1	0	3	3
10	0	1	0	0	2	3
11	3	3	0	0	0	2
12	1	1	0	0	0	1
13	0	3	0	0	0	0
14	0	0	0	0	0	0
15	1	1	0	0	0	0

TABLE E - V: Plate numbers of breeding and non-breeding  
female sticklebacks of the partially plated  
morph in basin 2.

PLATE NUMBER	NUMBER OF FEMALES					
	1971		1972		1973	
	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING
8	0	0	0	1	0	0
9	0	0	1	1	0	0
10	0	1	5	7	1	5
11	0	0	5	7	2	4
12	1	4	3	11	5	8
13	3	8	7	11	4	8
14	5	0	8	12	9	6
15	6	8	9	8	4	9
16	7	9	9	18	2	12
17	9	6	13	16	11	13
18	5	11	8	23	12	12
19	9	7	11	22	12	13
20	8	5	8	16	13	6
21	9	11	8	14	12	16
22	6	6	5	13	8	14
23	5	5	12	19	7	8
24	2	5	7	9	4	4
25	6	3	5	8	4	4
26	6	0	3	6	4	3
27	7	6	6	16	1	4
28	3	0	2	10	3	2
29	0	0	1	2	0	2

TABLE E - VI: Plate numbers of breeding and  
non-breeding female sticklebacks  
of the completely plated morph in  
basin 2.

PLATE NUMBER	NUMBER OF FEMALES					
	1971		1972		1973	
	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING	BREEDING	NON-BREEDING
29	1	1	6	3	8	1
30	8	28	15	12	7	30
31	8	36	16	16	17	38
32	12	33	23	20	31	24
33	18	17	12	5	8	6
34	8	0	1	0	2	1
35	0	1	0	0	0	0