THE GENETIC AND ENVIRONMENTAL BASIS FOR EXTERNAL COLOURATION IN LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS* (MITCHILL)) FROM SOUTHERN INDIAN LAKE, MANITOBA

by

Christine Helga Johnston

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

FACULTY OF GRADUATE STUDIES
Zoology

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLOMBIA
June, 1984

86

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 or her 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
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date 1 AUGUST 1984.

ABSTRACT

The purpose of this study was to investigate the nature of the colour difference between light and dark-coloured whitefish from Southern Indian Lake, Manitoba and to examine related differences between them. Subjective assessment of whitefish colour is corroborated by quantifiable differences in melanophore numbers between the two forms. Spatial distribution of lights and darks differs both between and within regions. Lights occur throughout the lake, are slightly more abundant offshore than onshore and are primarily benthic in habit. Darks are restricted to certain areas of the lake, are more numerous onshore than offshore and are somewhat more pelagic than lights. The two forms showed significant differences in several morphometric characters and lower gill raker number, but not in hemoglobin or glycerol-3-phosphate dehydrogenase allele frequencies. Hatchery-reared offspring of dark parents had higher mean dorsal melanophore counts than offspring of light parents. The heritability estimate derived from the regression of offspring (age 111 days post-fertilization) on male parent melanophore count was 0.10. Short and long-term experiments showed that colour of larval whitefish is subject to environmental alteration in response to light conditions and background colour. Short-term change is effected through redistribution of melanin granules in the melanophores, long-term change through changes in numbers of melanophores. Level of infection with *Triaenophorus crassus* cysts is, on average, higher in darks than in lights. However, the mode for both forms is 0 indicating no direct causal connection between cyst count and pigmentation. Higher mean counts of darks may be related to diet and distribution. Morphometric and meristic characters are subject to

environmental modification, as shown by other studies. This plus the lack of difference between lights and darks in biochemical characteristics suggests no clear-cut separation between the two into non-interbreeding stocks. Whitefish colour is correlated with water colour and clarity and may be an adaptation for concealment.

TABLE OF CONTENTS

Page

ABSTRACT..... ii

LIST OF TABLES..... viii

LIST OF FIGURES..... x

ACKNOWLEDGEMENTS..... xiii

INTRODUCTION..... 1

STUDY AREA..... 4

COLLECTION OF SPECIMENS..... 9

COLOUR CLASSIFICATION OF ADULT WHITEFISH

Introduction..... 14

Methods

Subjective Method..... 14

Quantitative Method..... 15

Comparison of Subjective and Quantitative Methods..... 15

Results

Scale Melanophore Counts of Study Specimens..... 16

Variability in Colour Classification Between Observers... 16

Misclassification of Fish 26

Conclusion..... 26

SPATIAL DISTRIBUTION OF COLOUR CLASSES OF WHITEFISH IN SIL

Introduction..... 29

Methods..... 29

Results

Lake-wide Distribution Patterns of Lights and Darks..... 33

Areal Distribution of Lights and Darks in Region 5..... 33

Vertical Distribution of Lights and Darks in Region 5.... 33

Temporal Changes in Distribution of Lights and Darks in Region 5 40

Colour of Young-of-the-Year Whitefish from Different Regions 40

Conclusion 46

MORPHOLOGY AND BIOCHEMISTRY OF ADULT LIGHT AND DARK WHITEFISH

Introduction 47

Methods

Morphological Analyses 47

Age and Growth 50

Biochemical Analyses

Glycerol-3-Phosphate Dehydrogenase (G-3-PDH) Electrophoresis 50

Hemoglobin Electrophoresis 52

Results

Morphology

Differences in Morphological Characters Between Lights and Darks 53

Gill Raker Number 53

Age and Growth 53

Biochemical Genetics

Glycerol-3-Phosphate Dehydrogenase 59

Hemoglobin 59

Conclusion 59

INHERITANCE OF COLOUR

Introduction 62

Methods

Rearing of Fish..... 62

Sampling Procedure..... 67

Results

Mean Dorsal Melanophore Counts from Different Cross Types 70

Heritability Estimates..... 70

Conclusion..... 78

ENVIRONMENTAL ALTERATION OF COLOUR

Introduction..... 79

Long-term Colour Change Experiment

Methods

Experimental Design..... 79

Statistical Analysis of Data..... 80

Results..... 81

Conclusion..... 85

Short-term Colour Change Experiment

Methods

Experimental Design..... 85

Observations..... 86

Results

Length of Time to Adjust Colour..... 86

Maximum Colour Change Achieved..... 86

Conclusion..... 87

Response of Young Whitefish to Zero Incident Light

Observations..... 87

Conclusion..... 87

Short-term Colour Change in Adult Whitefish..... 88

TRIAENOPHORUS CRASSUS CYST LEVELS OF SIL WHITEFISH

Introduction..... 89

Methods..... 89

Results

Regional Differences in Mean Cyst Counts..... 91

Differences in Mean Cyst Counts Between Light and Dark Whitefish..... 91

Regional Differences in Mean Cyst Count Among Light Whitefish..... 96

Conclusion..... 96

DISCUSSION

Colour Classification of Adult Whitefish..... 98

Distribution of Colour Classes of Whitefish in SIL..... 100

Morphology and Biochemistry of Adult and Dark Whitefish..... 102

Inheritance of Colour..... 104

Environmental Alteration of Colour..... 108

Triaenophorus crassus Cyst Levels of SIL Whitefish..... 115

Functionnal Significance and Adaptive Value of Colour in Fish.....119

CONCLUSION..... 121

LITERATURE CITED..... 123

LIST OF TABLES

Table		Page
1	Scale melanophore counts of light, intermediate and dark lake whitefish colour classified by 4 different groups of observers.	25
2	Numbers of light and dark lake whitefish misclassified by different groups of observers.	27
3	Analysis of covariance on head and dorsal melanophore counts of young-of-the-year lake whitefish from regions 4, 5 and 6, Southern Indian Lake.	45
4	Morphometric measurements and meristic counts made on light and dark lake whitefish from region 5, Southern Indian Lake. * : measurements and counts selected for detailed examination in 1982 sample.	48
5	Age distributions, numbers of males and females and dates of capture of light and dark lake whitefish used for morphological analyses.	49
6	Analysis of covariance of morphometric characters of light and dark lake whitefish from region 5, Southern Indian Lake.	54
7	Observed and expected (Castle-Hardy-Weinberg) BB glycerol-3-phosphate dehydrogenase phenotype distributions for light and dark lake whitefish from region 5, Southern Indian Lake.	60
8	Observed and expected (Castle-Hardy-Weinberg) hemoglobin phenotype distributions for light and dark lake whitefish from region 5, Southern Indian Lake.	61

9	Ranges and means of scale melanophore counts of lake whitefish used as parents in breeding experiment.	63
10	Mean dorsal melanophore counts and variances for 111 day larval lake whitefish of each cross type.	71
11	Results of t-tests (using the formula for unequal variance) between mean dorsal melanophore counts of 111 day larval lake whitefish or different cross types.	72
12	Heritability estimates from 4 pre-hatch lake whitefish samples.	77
13	Long-term colour change experiment: Results of analysis of covariance of regressions of larval lake whitefish melanophore counts on length at 12 days.	82
14	Mesh sizes of gillnets used by different authors for collecting lake whitefish in Southern Indian Lake.	90
15	*Triaenophorus crassus* cyst counts of lake whitefish from different regions of Southern Indian Lake.	92
16	Mean *Triaenophorus crassus* cyst counts of light and dark lake whitefish in experimental catches, 1963, 1978, 1979, 1982, Southern Indian Lake.	93
17	Mean *Triaenophorus crassus* cyst counts of light lake whitefish from regions 4, 5 and 6, Southern Indian Lake, Bodaly et al. 1983).	97
18	Approximate values of the heritability of various characters in some mammals, birds and fishes.	106
19	*Triaenophorus crassus* cyst counts in experimental catches of lake whitefish, regions 4 and 5, Southern Indian Lake, 1978-1983.	118

LIST OF FIGURES

Figure		Page
1.	Map of Southern Indian Lake, Manitoba, showing limnological regions, relationship to the Churchill River diversion and adjacent water bodies (Bodaly et al. 1984).	6
2.	A. Map of region 5, Southern Indian Lake, B. Sites sampled in July 1982.	11
3.	Map of region 5, Southern Indian Lake showing sites sampled in September-October 1982.	13
4.	Scale melanophore counts of lake whitefish from region 5 Southern Indian Lake by colour class as subjectively classified by author. A. Lights, B. Intermediates, C. darks. Arrows show modes, triangles show means	18
5.	Scale melanophore counts of total sample of lake whitefish from region 5, Southern Indian Lake.	20
6.	Plot of scale melanophore count versus age for total sample of lake whitefish from region 5, Southern Indian Lake	22
7.	Plot of scale melanophore count versus fork length for total sample of lake whitefish from region 5, Southern Indian Lake.	24
8.	Dorsal view of lake whitefish larva showing head and dorsal melanophore count areas (for counts on wild-caught young-of-the-year lake whitefish from Southern Indian Lake)	32
9.	Proportion of light and dark lake whitefish in experimental and commercial catches, Southern Indian	35

Lake, 1963-1982. A. Sites sampled by Sunde (1963), B. Commercial catches, regions 4 and 5, 1979, 1980, 1981 (Bodaly et al. 1984), C. Experimental catches, regions 4, 5 and 6, 1982 (Bodaly et al. 1983).

Fig. 10. Areal distribution of light and dark lake whitefish in region 5 ,Southern Indian Lake, 1982. A. Scale melanophore counts of lake whitefish in onshore sets, B. Scale melanophore counts of lake whitefish in offshore sets. 39

Fig. 11. Vertical distribution of light and dark lake whitefish in region 5, Southern Indian Lake, 1982. A. Scale melanophore counts of lake whitefish in top 1/3 of net, B. Scale melanophore counts of lake whitefish in middle 1/2 of net, C. Scale melanophore counts of lake whitefish in bottom 1/3 of net. 42

Fig. 12. Scale melanophore counts of light and dark lake whitefish captured in region 5, Southern Indian Lake, in July 1982. 44

Fig. 13. Gill raker count distributions of light and dark lake whitefish from region 5, Southern Indian Lake. A. Upper gill rakers, B. Lower gill rakers, C. Total gill rakers. 56

Fig. 14. Plots of age versus fork length for light and dark lake whitefish from region 5, Southern Indian Lake. Open symbols represent means of samples with less than three fish. Closed symbols represent means of samples with three or more fish. Vertical bars show ranges. 58

Fig. 15. Experimental design utilized in crosses of light and dark lake whitefish. 65

Fig. 16. Dorsal view of lake whitefish larva showing head and dorsal mealanophore count areas (for counts on hatchery-reared larvae). 69

Fig. 17. Regressions of dorsal melanophore counts of 111 day lake whitefish larvae on parent scale melanophore counts. A. Offspring on mid-parent value, B. Offspring on female parent value, C. Offspring on male parent value. 74

Fig. 18. Long-term colour change experiment: Regressions of larval lake whitefish melanophore counts on total length before and after 12 day exposure to different light and background conditions. Group 1 - Pale tank, full light. Group 2 - Dark tank, full light. Group 3 - Dark tank, half light. Group 4 - Dark tank, low light. 84

Fig. 19. Triaenophorus crassus cyst count distributions of lake whitefish from region 5, Southern Indian Lake, 1982 (Bodaly et al. 1983). A. Lights, B. Darks. 95

ACKNOWLEDGMENTS

I would like to thank my thesis supervisor Dr. C.C. Lindsey for his patience, support and stimulation. I am also indebted to Drs. R.A. Bodaly and J.W. Clayton for their help. My advisory committee, Drs. D. Brooks, J.D. McPhail and J. Myers provided helpful advice and comments on thesis and proposal drafts.

My field crew humoured their inexperienced boss (most of the time) and worked very hard. For their help in this capacity I thank M. Dumas, C. Hrenchuk, R. Fudge and S. Witte. My venture into fish culturing was ably guided by L. Allard, R. Fudge and D. Tretiak. Drs. G.B. Ayles and C. Wehrhahn gave suggestions concerning interpretation of the breeding experiment data. D. Hayward introduced me to HP-9836 and thus helped facilitate data analysis. Thanks to E.J. Hrenchuk who translated two publications from the German for me.

I am very grateful to L. Wilson, D. Laroque and S. Ryland who cheerfully gave of their time and energy to put the manuscript through the word processor.

I would particularly like to thank Dr. R.A. Bodaly, with whom the idea for the study originated, for his input and encouragement throughout. Thanks also to the SIL project staff and to Dr. J.H. Gee who helped me get started in the first place.

My husband, Carl Hrenchuk, assisted in many capacities and was an unfailing and steady source of encouragement, enthusiasm, patience and humour. For all of that, I thank him.

Financial support to the author was provided by a National Science and Engineering Research Council of Canada Graduate Scholarship and by

NSERC grants to Dr. C.C. Lindsey. Field and laboratory work were supported by the Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Manitoba.

INTRODUCTION

Colour variation is quite common within fish species. This study concerns two distinctively coloured forms of lake whitefish (*Coregonus clupeaformis* (Mitchill)) which occur in Southern Indian Lake, Manitoba. So-called "lights" are silvery overall and light green on the dorsal surface; so-called "darks" are darker overall, especially above the lateral line, and dark brown to black dorsally. Darks are most abundant in the relatively shallow northern basin of the lake; where they occur in other basins they are confined to near-shore areas. Darks also tend to be more heavily infected with cysts of the cestode parasite *Triaenophorus crassus* than do lights.

The occurrence of the two forms is of economic as well as scientific interest. Southern Indian Lake (SIL), which is located in north-central Manitoba on the Churchill River, was subjected in 1974-1978 to flooding and major changes in flow regime as part of hydroelectric development of the Nelson River System. Before then, SIL supported northern Manitoba's largest commercial fishery, and lake whitefish made up about 85% of the total commercial catch. Because dark whitefish have less commercial value than light whitefish (due to their less attractive colouration and higher *T. crassus* cyst levels), fishermen traditionally avoided those areas of the lake where darks were known to occur. However, since impoundment, catch per unit of effort on traditional fishing grounds has declined to about one-half of pre-flooding levels (Bodaly et al. 1984). In response, the geographic distribution of effort has shifted into areas formerly avoided, and consequently darks have made up an increasing proportion of the catch. In 1975, prior to impoundment, dark whitefish were not present in the

summer commercial catch; in 1981, they made up 81% of it (Bodaly et al. 1984).

Dark lake whitefish have been noted in other lakes. Rawson (1947a) caught whitefish which he described as being darker coloured, longer and more compressed, and softer-fleshed than normal ones in the Gros Cap area of Great Slave Lake. They were relatively few in number and were confined to shallow near-shore areas. Rawson (1947b) also reported that a small proportion of the commercial lake whitefish catch from Lake Athabaska were dark, with small eyes, long shallow bodies, and elongate heads. The darks were of inferior quality with softer flesh, slower growth rates and heavier infection with *T. crassus* cysts than typical lake whitefish. Most were caught in shallow water along the north shore of the lake (Rawson 1947b). Imhof (1977) referred to two lake whitefish colour variants in Lake Michigan - "green backs", which were commonly caught in open waters, and "brown backs", which were found in central and lower Green Bay.

The basis of the colour difference between light and dark whitefish has not been investigated previously. The main questions addressed by this study were whether light and dark whitefish comprise separate subpopulations and whether the nature of the colour difference between them is genetic or environmental or both. The research tested the following six hypotheses, for which the methods and results are described separately:

1. There is no quantifiable difference in melanophore numbers to support the subjective classification of SIL whitefish into "lights" and "darks".

2. There is no difference in spatial distribution of lights and darks within the lake.
3. There are no morphological or biochemical differences between lights and darks.
4. There is no hereditary basis to colour differences between lights and darks.
5. Colour of larval whitefish is not subject to environmental alteration.
6. Colour differences are not correlated with infection by cysts of *T. crassus*.

STUDY AREA

Southern Indian Lake (SIL) is located in north-central Manitoba (57°N; 99°W) on the Churchill River (Fig. 1). For experimental purposes the lake was divided into numbered regions following natural divisions into irregular basins (Fig. 1).

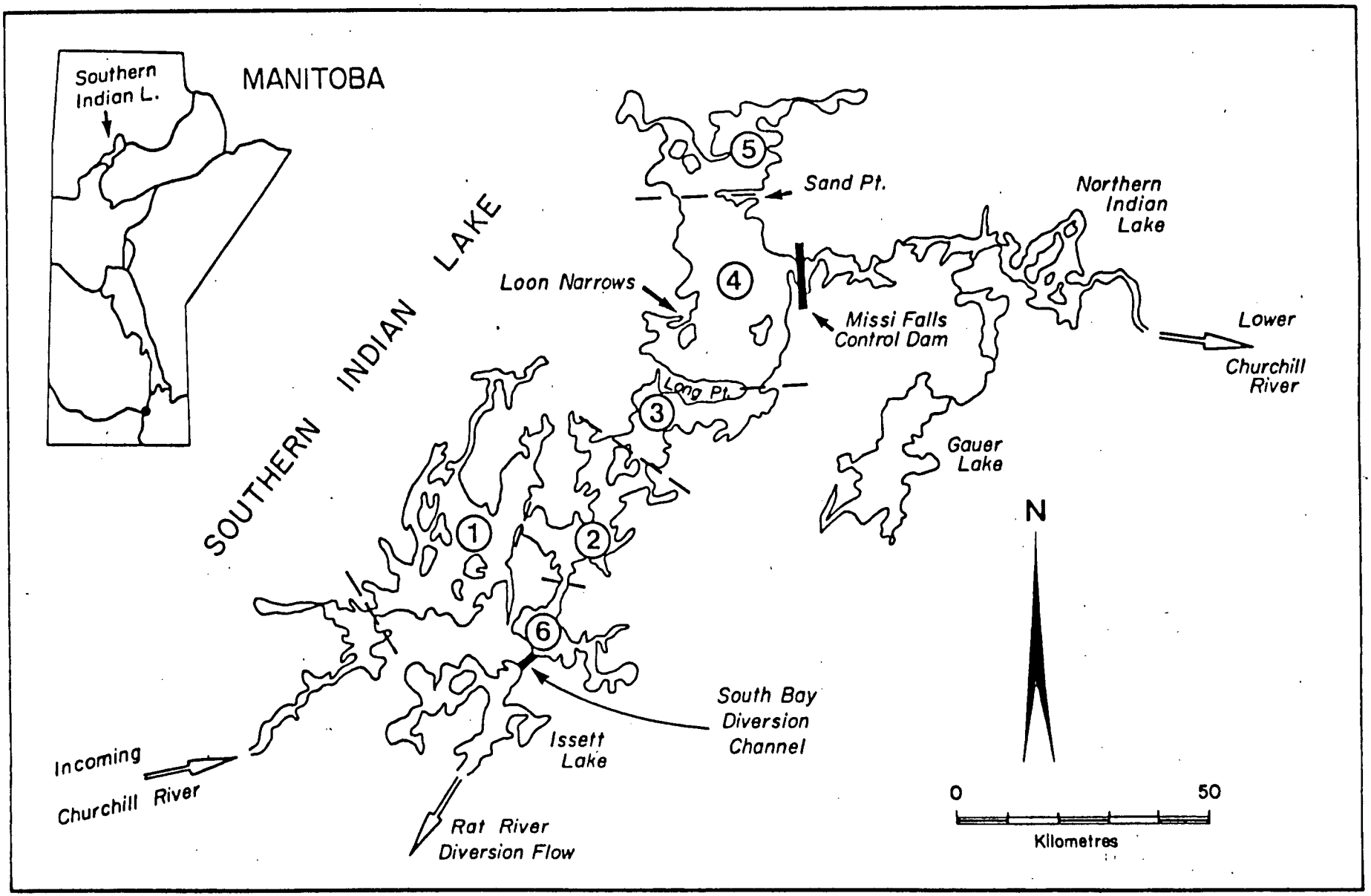
In the Southern Indian Lake area the Precambrian Shield bedrock is overlain with glacial deposits. Sands and gravels cover the uplands surrounding region 5 and the northern half of region 4, varved silty clays cover the land surrounding the southern 2/3 of the lake. Permafrost is widespread except in the glaciofluvial deposits of regions 4 and 5.

The Southern Indian Lake region lies in the boreal forest zone. The climate is continental with short, cool summers and long, cold winters. The mean annual temperature at the settlement of Southern Indian Lake is -5°C with average monthly temperatures ranging from -26°C in January to +16°C in July. Mean annual precipitation is 430 mm, of which about 1/3 falls as snow. The lake is ice-free for about 5 months from early June to late October (Newbury et al. 1984).

The lake has a surface area of 2391 km^2 and a mean depth of 9.8 m. Mean depths of regions 4, 5 and 6 are 13.0 m, 5.9 m and 5.8 m, respectively (McCullough 1981). The water exchange rate for the whole lake is 0.72 year and for individual basins ranges from 0.031 (region 6) to 2.8 years (region 5). Exchange time depends on the volume of the basin and whether or not it is in the direct flow of the Churchill River (Newbury et al. 1984).

There is no persistent thermal stratification, though during the warm season surface waters may be 1-2°C warmer than deeper waters. A

Fig. 1. Map of Southern Indian Lake, Manitoba, showing limnological regions, relationship to the Churchill River diversion and adjacent water bodies (Bodaly et al. 1984).


Southern Indian L.
MANITOBA
SOUTHERN INDIAN LAKE
Sand Pt.
Northern Indian Lake
Loon Narrows
Missi Falls Control Dam
Lower Churchill River
Long Pt.
Gauer Lake
N
South Bay Diversion Channel
Issett Lake
Incoming Churchill River
Rat River Diversion Flow
0
50
Kilometres
1
2
3
4
5
6

south to north negative thermal gradient during the open water season, involving regions 1 to 5, is imposed by the ice-out pattern and reinforced by river diversion so that temperatures in the northern regions are 1-2°C lower than those in the southern regions. Water mass temperatures at maximum heat content for regions 1, 2, 6, 4 and 5 in 1978 were 14.8°, 14.2°, 14.1°, 12.0° and 13.0° C, respectively (Hecky 1984).

Before impoundment less than 5% of the total shoreline length was actively eroding. The water in regions 4 and 5 was quite clear while that in region 6 was turbid. Immediately after impoundment over 80% of the shoreline was subject to erosion. An average of 4 x 10^6 tonnes of mineral sediment were added annually to the lake from surrounding shorelines during the first three years after flooding (Newbury and McCullough 1984). Suspended sediment concentrations in regions 1, 2, 4 and 6 increased markedly making the water much more turbid. Region 5 did not change significantly and the water remained relatively clear. Concentrations of filterable suspended solids (that is, those having a diameter of $\geq$1 micrometre) for regions 1, 2, 4, 6 and 5 in September 1978 were approximately 12.5, 11.9, 8.8, 16.6 and 1.2 $g \cdot m^3$, respectively (Hecky and McCullough 1984).

Hecky (1984) described the light regime of SIL. Average vertical extinction coefficients (k) for regions 4, 5 and 6 in 1978 were 1.11, 0.88 and 1.47-1.96, respectively. Average Secchi disc depths for regions 4, 5 and 6 were 1.4, 3.0 and 1.0 m. In regions 4 and 6 light scattering by suspended sediments is responsible for high values of k (Hecky 1984).

The water in poorly flushed areas, region 5 and some protected bays, is rich in dissolved humic substances which give it a dark brown or orange colour. The water in other areas is blue/green in colour.

Detailed descriptions of the geography of the SIL region and the hydraulic regime of the Churchill River and SIL are found in Newbury et al. (1984). Hecky (1984) and Hecky and McCullough (1984) discussed aspects of the physical limnology of SIL. Primary productivity, crustacean plankton and profundal macrobenthos of SIL are described in Hecky and Guildford (1984), Patalas and Salki (1984) and Wiens and Rosenberg (1984), respectively.

Common fish species in SIL include lake whitefish (*Coregonus clupeaformis*), white sucker (*Catostomus commersoni*) and longnose sucker (*C. catostomus*) as the most abundant benthivores, ciscoes (*Coregonus artedii* and related species) as the main open-water planktivores, and northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*) and burbot (*Lota lota*) as the dominant piscivores. The main forage fish are yellow perch (*Perca flavescens*), trout perch (*Percopsis omiscomaycus*), spottail shiners (*Notropis hudsonis*) and emerald shiners (*Notropis atherinoides*) (Bodaly et al. In press).

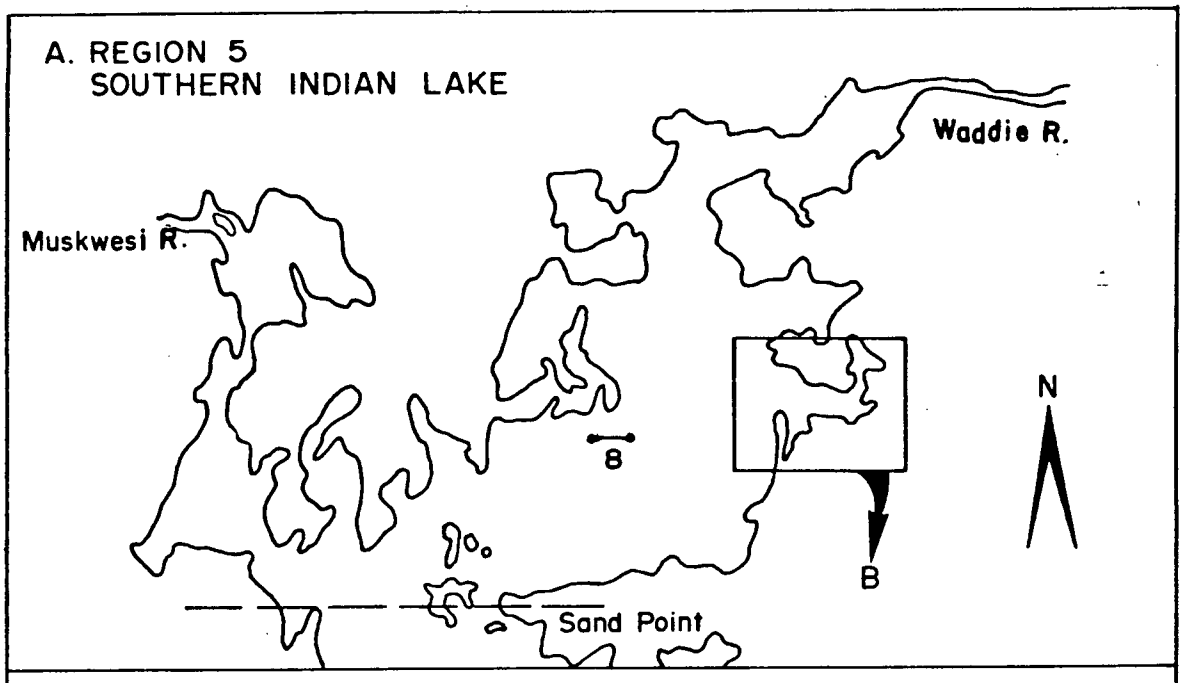
COLLECTION OF SPECIMENS

Adult lake whitefish were collected from region 5 of SIL during the periods 12-15 July and 20 September to 13 October, 1982.

In July, 18 overnight sets were carried out at 8 different sites (Fig. 2) using gangs of gillnets with 6 panels of length 46 m (50 yd) and stretched mesh sizes of 3.8 cm (1 1/2 in), 5.1 cm (2 in), 7.0 cm (2 3/4 in), 8.9 cm (3 1/2 in), 10.8 cm (4 1/4 in) and 13.3 cm (5 1/4 in). Sixteen sets were on the lake bottom, 2 were floating surface sets. On removal from the net whitefish were recorded on the basis of external colouration as light-coloured, dark-coloured or intermediate-coloured. Position of each whitefish in the top, middle or bottom thirds of the net was recorded. Blood samples were taken from 90 fish for hemoglobin electrophoresis. Each whitefish captured was given a numbered tag, placed in a plastic bag, iced immediately, frozen within 4 days and transferred to -40°C storage until examination.

In September and October, 70 sets were carried out at 35 different sites (Fig. 3) using gangs of gillnets with 3 panels of length 46 m (50 yd) and stretched mesh sizes of 8.9 cm (3 1/2 in), 10.8 cm (4 1/4 in) and 13.3 cm (5 1/4 in). On removal from the net, colour of fish, position in net (sets 1-21) and, in most cases, sex and spawning condition (immature, ripe, running, spent) were recorded for each whitefish. Of 354 whitefish captured, 93 were kept. Of these, 12 lights and 11 darks were used in a breeding experiment (described below). All fish kept were tagged and frozen as above.

Fig. 2. A. Map of region 5, Southern Indian Lake, B. sites sampled in July 1982.


A. REGION 5
SOUTHERN INDIAN LAKE
Waddie R.
Muskwesi R.
8
N
B
Sand Point

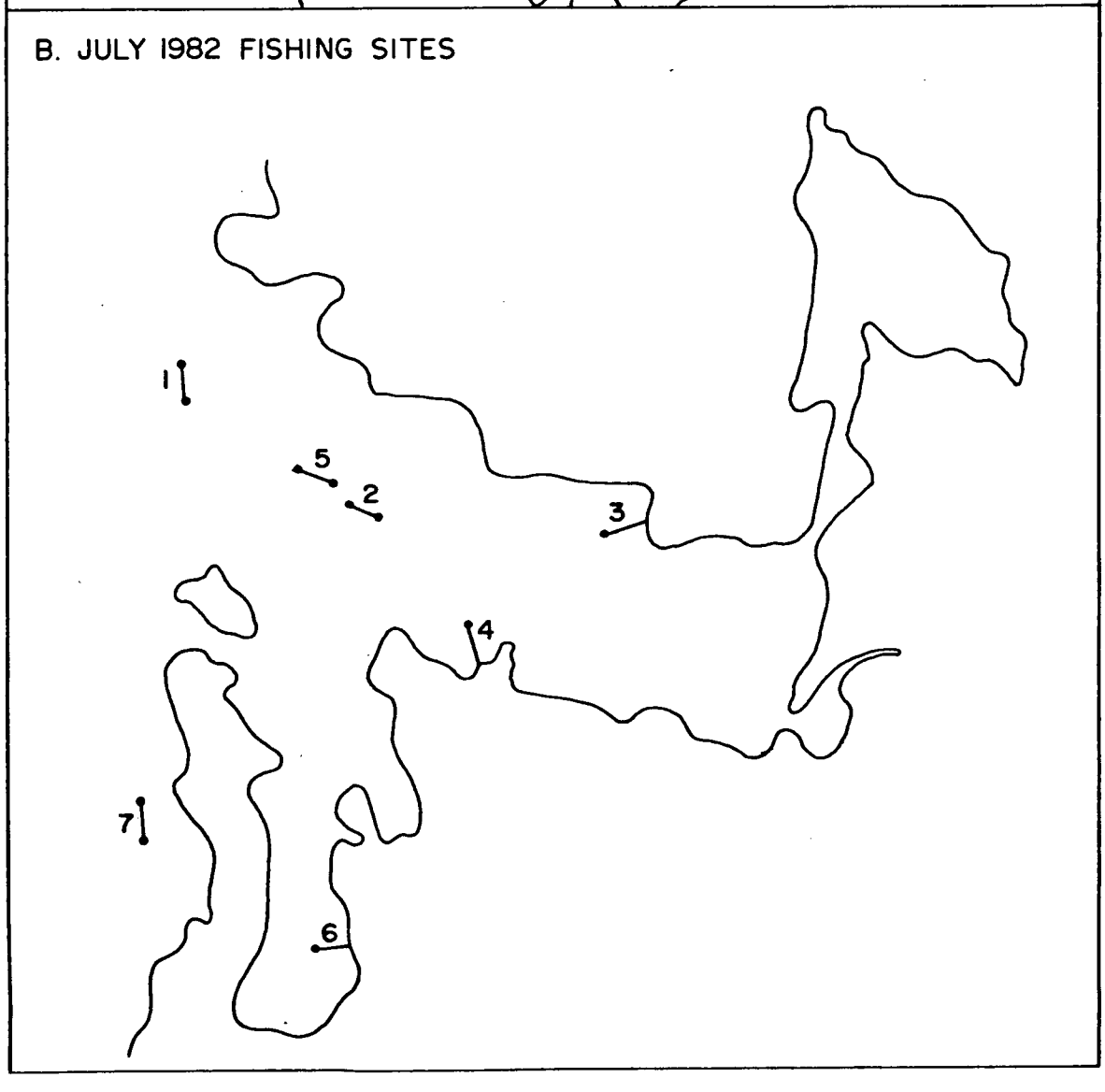
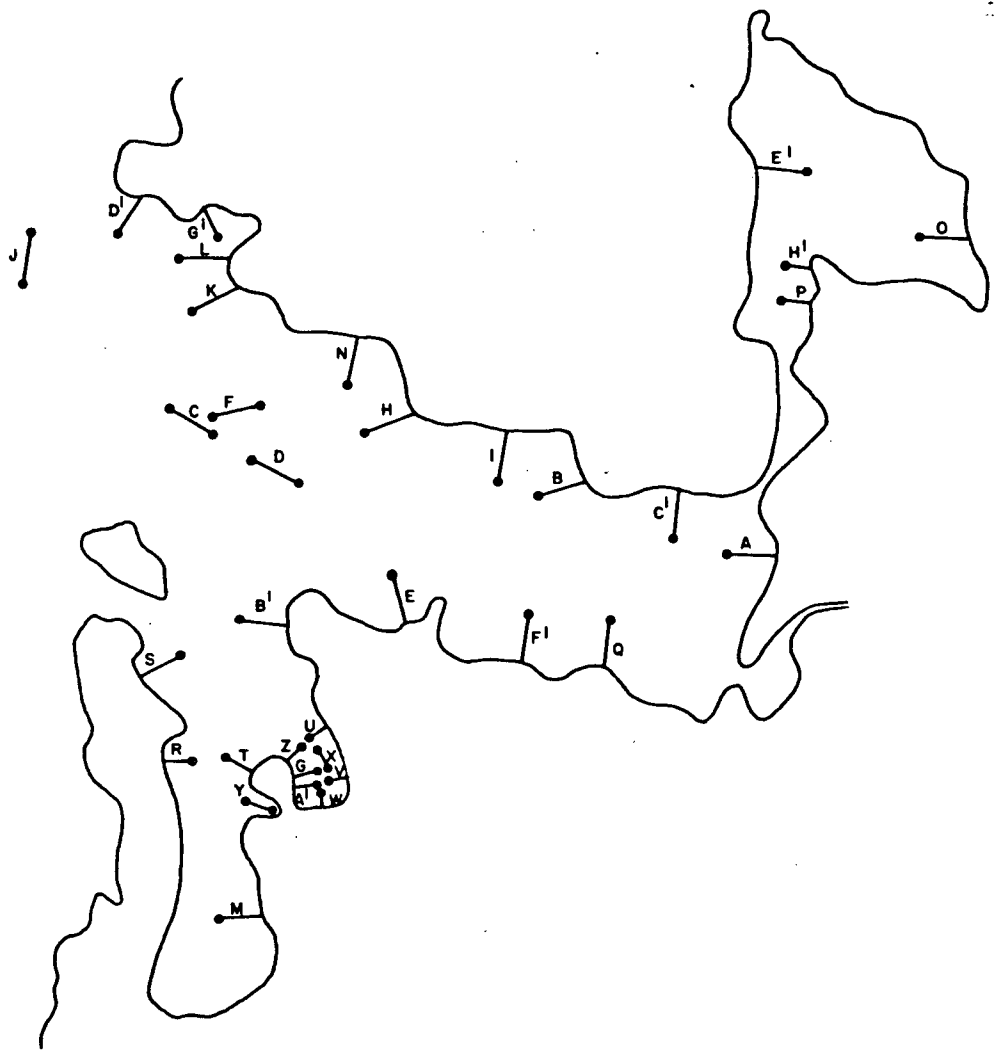

B. JULY 1982 FISHING SITES
1
5
2
3
4
7
6

Fig. 3. Map of region 5, Southern Indian Lake showing sites sampled in September-October 1982.

REGION 5, SOUTHERN INDIAN LAKE
SEPTEMBER - OCTOBER 1982 FISHING SITES



COLOUR CLASSIFICATION OF ADULT WHITEFISH

Introduction

Adult whitefish taken both in commercial and experimental catches at SIL have traditionally been classified subjectively according to the overall lightness or darkness of their external colouration. In order to determine whether subjective classification corresponds to an objective measure of pigment, the number of melanophores was counted on a standard patch of skin. Melanophore counts were compared between fish classified subjectively by the author, and also between fish classified subjectively by different observers.

Methods

Subjective Method

This method is used by the Freshwater Fish Marketing Corporation (FFMC) to classify commercial whitefish catches and by Fisheries and Oceans personnel to classify whitefish caught for experimental purposes.

The observer assesses the lightness or darkness of external colouration of the whitefish, noting especially colour of the top of the head, dorsal and lateral body surfaces, and fins. Whitefish classified as lights are typically silvery overall and light green dorsally. Those classified as darks are typically darker overall, particularly above the lateral line, and dark brown to black on the dorsal surface. A third class, intermediate-coloured, includes fish with grades of colour between the two extremes. This class is not recognized by the FFMC which generally calls intermediate-coloured whitefish darks.

Quantitative Method

Dark colouration in whitefish is due to the presence of melanophores (specialized colour cells which contain melanin granules) in the skin. Darkness of a fish may be quantified by counting the number of melanophores per unit area of skin (Odiorne 1933; Summer 1939; Ahmad 1972). The exposed part of a scale is covered by a patch of skin in which melanophores are visible. Because of the ease with which scales can be removed, stored, and handled and because virtually the same scale can be taken from each fish, melanophore counts were done on scales.

One scale was removed from the dorso-lateral surface of each whitefish (left side, 3 rows ventral and posterior to the dorsal insertion). Counts were done using a Bausch and Lomb projector-type scale reader which projected the scale image, magnified 45x, onto a grid. Melanophores, clearly visible as dark spots, were counted within what on the scale would be a 2 mm x 1 mm area. A melanophore on a grid line was included in the count only if more than half of it was within the count area. Counts were done in the centre of the patch or in an area representative of melanophore size and density over the whole patch.

Scale melanophore count distributions were determined for each colour class as well as for the total sample. Fish age and size were compared with scale melanophore count to see if linear relationships exist between them.

Comparison of Subjective and Quantitative Methods

Scale melanophore counts were done on 3 different samples of whitefish from region 5 caught at different times and subjectively

colour classed by different groups of observers (each group included 2 or more people, with some overlap between groups). Means and ranges for each colour class were compared between observer groups to determine variability between observers. Subjective colour classifications and scale melanophore counts of individual fish were compared to determine the number of fish misclassified by the different observer groups.

Results

Scale Melanophore Counts of Study Specimens

Mean scale melanophore counts for whitefish subjectively classified by the author as light, intermediate and dark-coloured are significantly different (light vs. intermediate, $t = 3.254$, $p < 0.005$; light vs. dark, $t = 16.175$, $p < 0.001$; intermediate vs. dark, $t = 11.785$, $p < 0.001$), but ranges are broad and overlapping, indicating error in the subjective classification (Fig. 4).

The distribution of scale melanophore counts for the total sample is positively skewed ($\chi^2 = 66.147$, 23 d.f., $p < 0.005$) and does not fit a normal distribution (Fig. 5).

There was no linear relationship between fish age and melanophore count or between fish size and melanophore count (Figs. 6 and 7). Young and small fish tended to have low scale melanophore counts, but larger and older fish showed a wide range of counts from low to high.

Variability in Colour Classification Between Observers

Ranges of scale melanophore counts of lights, intermediates, and darks are roughly similar for the 4 different samples of whitefish (study specimens plus the 3 other samples) (Table 1). Mean melanophore

Fig. 4. Scale melanophore counts of lake whitefish from region 5, Southern Indian Lake by colour class as subjectively classified by author. A. Lights, B. Intermediates, C. Darks. Arrows show modes, triangles show means.

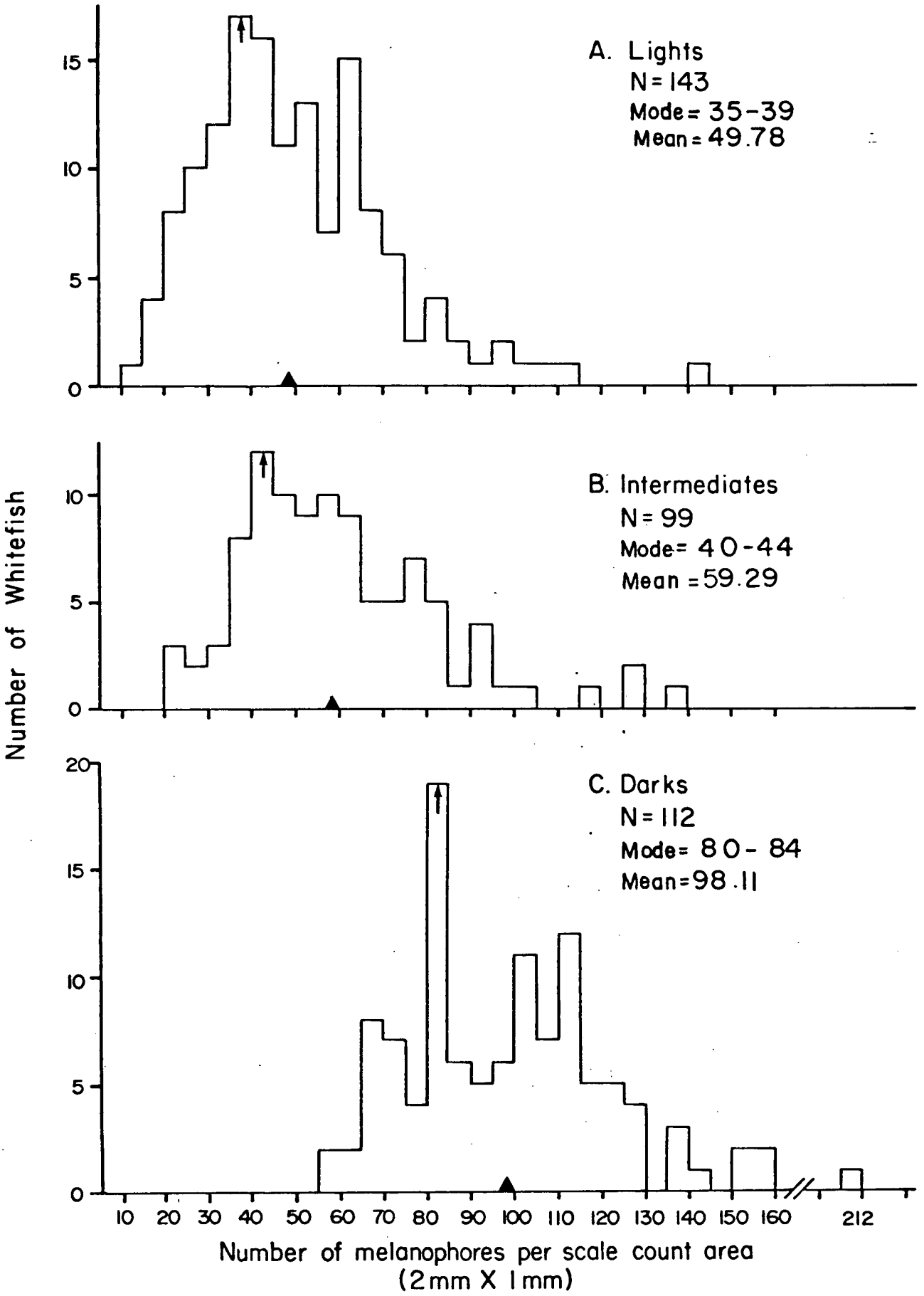

A. Lights
N = 143
Mode = 35-39
Mean = 49.78
B. Intermediates
N = 99
Mode = 40-44
Mean = 59.29
C. Darks
N = 112
Mode = 80-84
Mean = 98.11
Number of Whitefish
0
5
10
15
20
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 212
Number of melanophores per scale count area
(2mm X 1mm)

Fig. 5 Scale melanophore counts of total sample of lake whitefish from region 5, Southern Indian Lake.

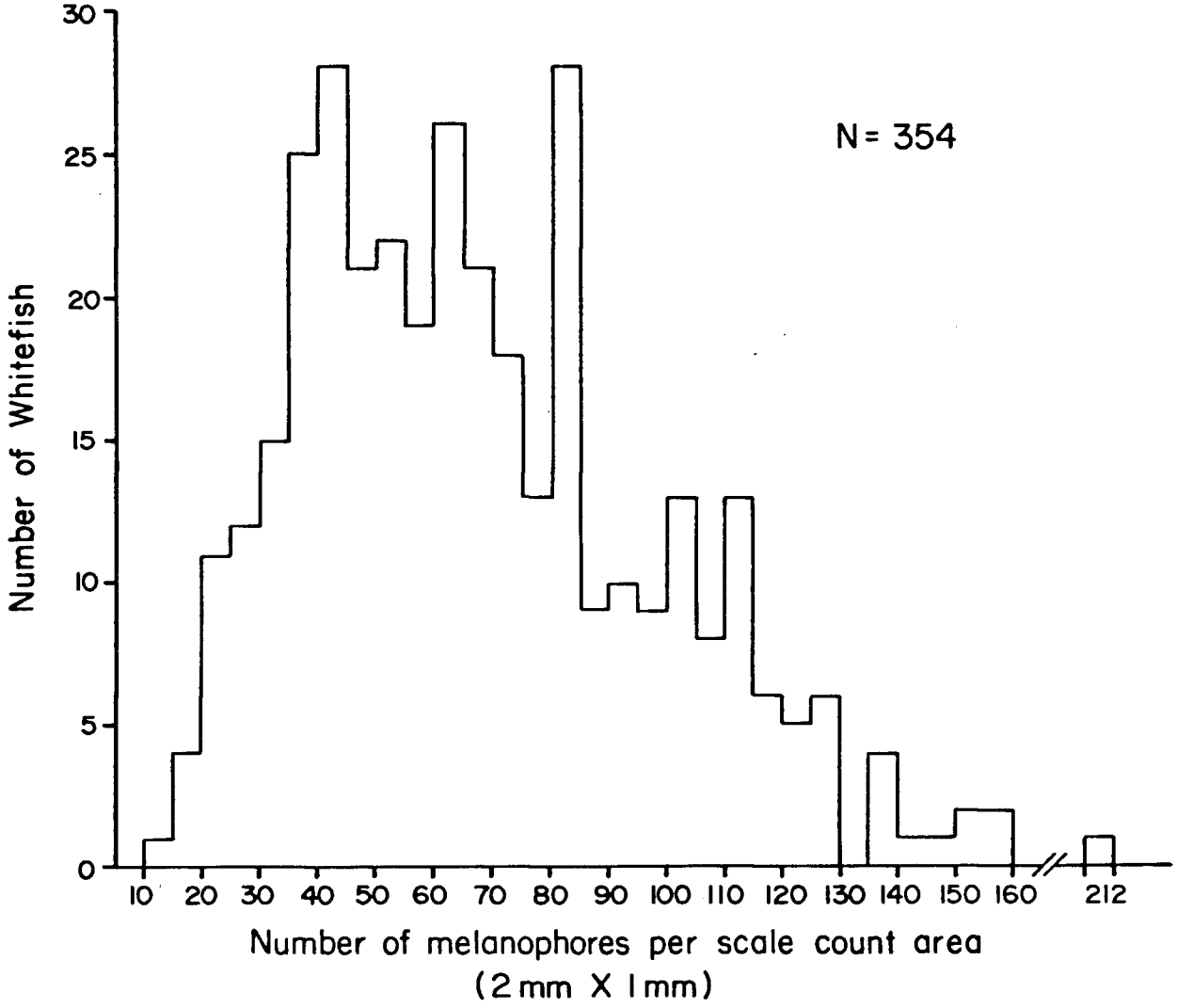

N = 354
Number of Whitefish
0
5
10
15
20
25
30
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 212
Number of melanophores per scale count area
(2 mm X 1 mm)

Fig. 6. Plot of scale melanophore count versus age for total sample of lake whitefish from region 5, Southern Indian Lake.

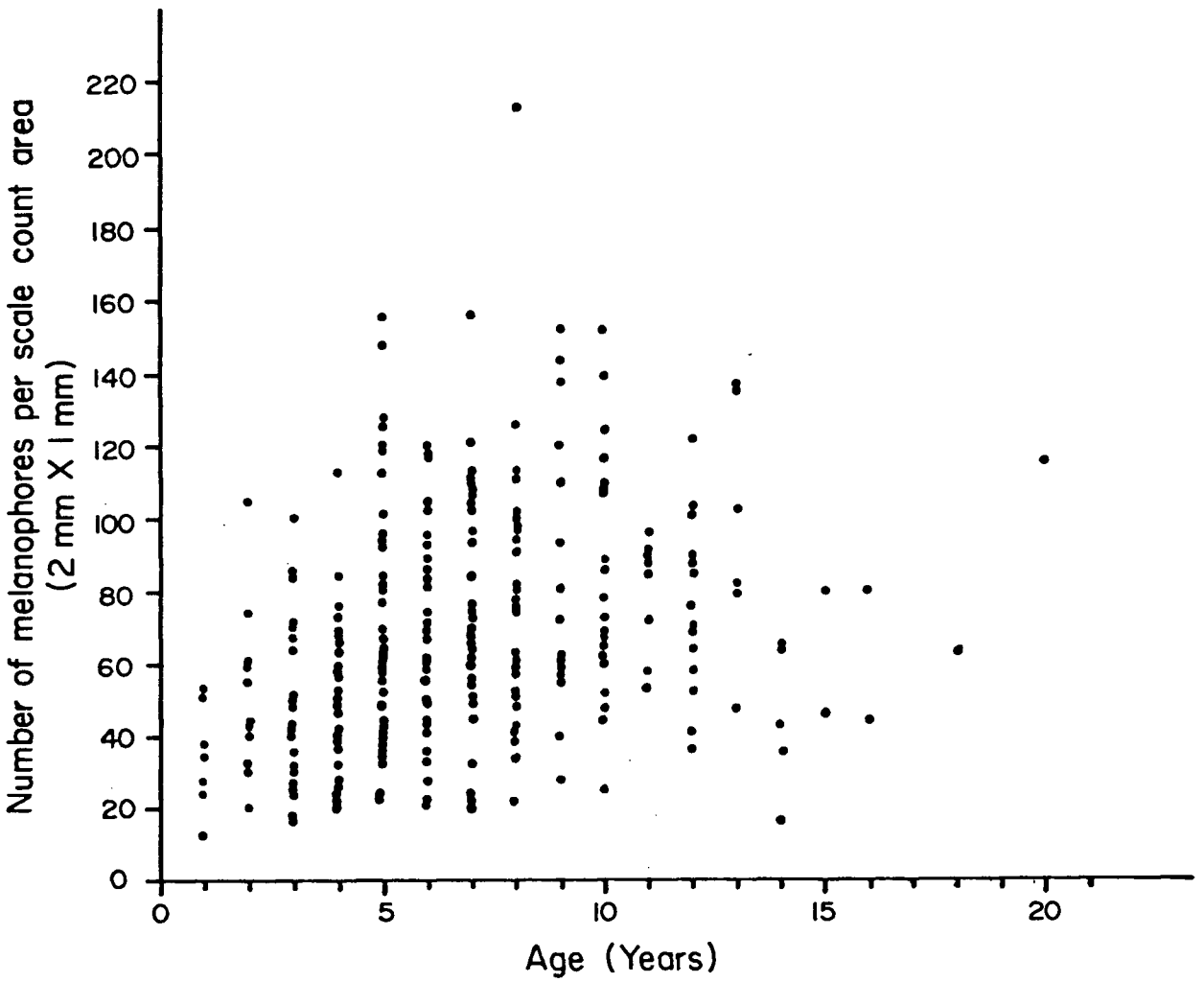

Number of melanophores per scale count area
(2 mm X 1 mm)
0
20
40
60
80
100
120
140
160
180
200
220
0
5
10
15
20
Age (Years)

Fig. 7. Plot of scale melanophore count versus forklength for total sample of lake whitefish from region 5, Southern Indian Lake.

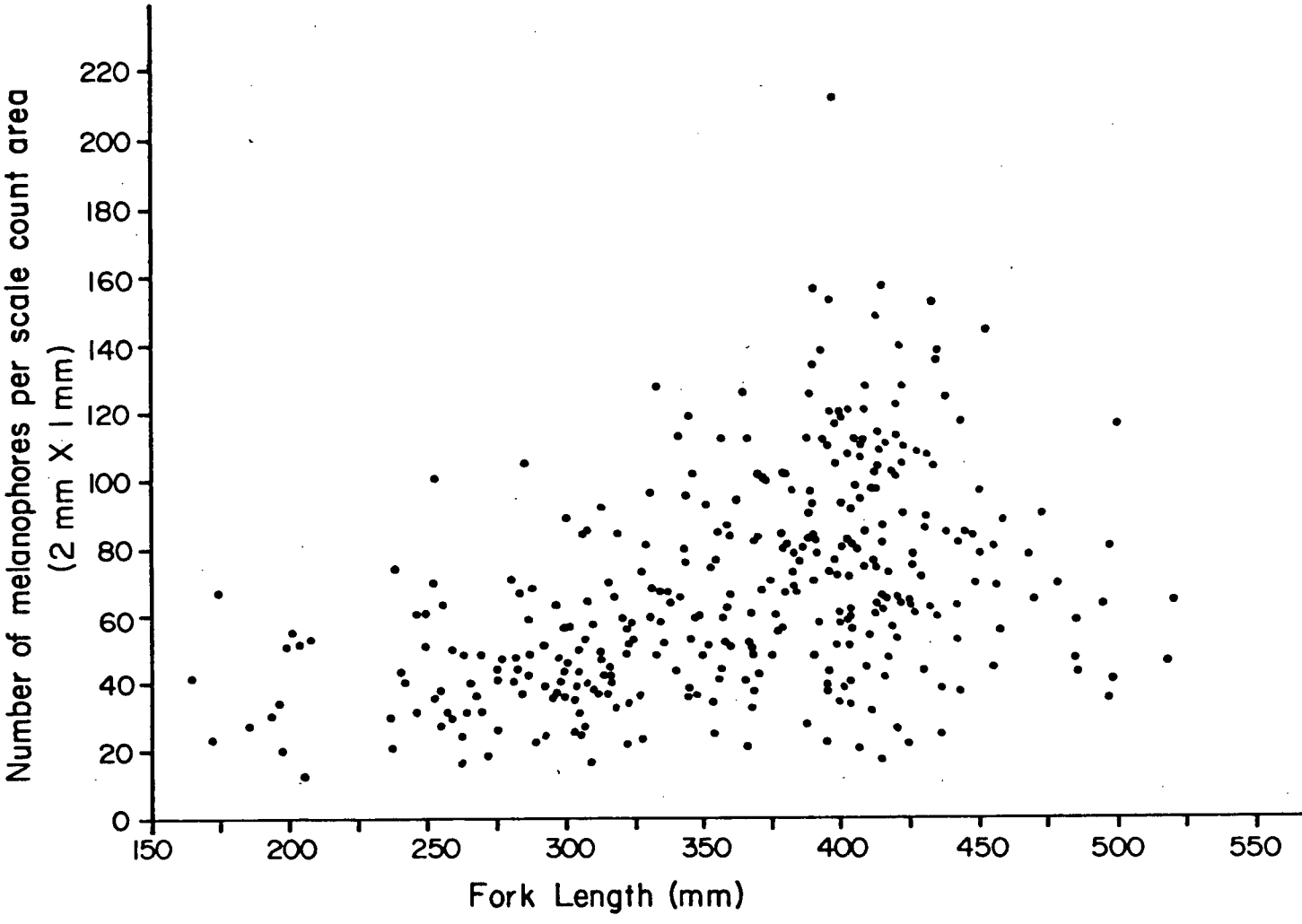

Number of melanophores per scale count area
(2 mm X 1 mm)
0
20
40
60
80
100
120
140
160
180
200
220
150
200
250
300
350
400
450
500
550
Fork Length (mm)

Table 1. Scale melanophore counts of light, intermediate and dark lake whitefish colour classified by 4 different groups of observers.

	Scale melanophore counts					
	Lights		Intermediates		Darks	
Observer group	Mean	Range	Mean	Range	Mean	Range
1	60.15	25-136	67.85	28-120	89.57	52-157
2	42.91	13-74	49.81	24-88	82.42	36-140
3	57.62	17-148	67.73	40-117	102.86	66-157
4	53.58	13-101	58.24	20-135	95.26	57-152

counts for each colour class differ between groups but each group had mean melanophore counts below 70 for their lights and intermediates and above 80 for their darks.

Misclassification of Fish

If only 2 classes of fish are considered, lights and darks, and if the dividing line between the 2 groups is considered to be 80 melanophores•2 mm^2 (re. Fig. 5), then the number of fish misclassified by the various observers can be determined.

For each of the 4 samples shown in Table 2 numbers of "lights" with counts above 80 and "darks" with counts below 80 were tallied. The percentage of fish which were called lights but had more than 80 melanophores•2 mm^2 ranged from 0 to 21%. The percentage of fish which were called darks but had less than 80 melanophores•2 mm^2 ranged from 12 to 50% (Table 2).

Sources of error in colour classification by subjective assessment of external colouration are discussed below (see Environmental Alteration of Colour - Adult Whitefish; and Discussion).

Conclusion

Fish classified subjectively by colour were found to have on average a corresponding difference in melanophore counts. This was true of subjective classification by the author, and by 3 other sets of observers. However, agreement was imperfect between the subjective and objective methods of classification.

Because most melanophore counts of whitefish classified subjectively as intermediates fall within the range of melanophore

Table 2. Numbers of light and dark lake whitefish misclassified by different groups of observers.

Observer group	Total fish classed as lights	Lights with counts above 80	Total fish classed as darks	Darks with counts below 80
1	27	5	23	9
2	32	0	38	19
3	39	8	42	5
4	104	5	70	18

counts of those classified as lights, the rest of this paper will recognize only light and dark whitefish. A light whitefish is quantitatively defined as one having a scale melanophore count of <80 melanophores$\cdot 2\ mm^2$, a dark is one with a count ≥ 80 melanophores$\cdot 2\ mm^2$.

SPATIAL DISTRIBUTION OF COLOUR CLASSES OF WHITEFISH IN SIL

Introduction

The purpose of this section is to describe the distribution of light and dark whitefish in SIL. Of interest are whether there is temporal consistency in their lake-wide distribution patterns, whether lights and darks show spatial or temporal segregation when they occur together, and whether young-of-the-year whitefish show the same colour and distribution differences as the adults.

Methods

Data from Sunde (1963), Bodaly et al. (1983), and Bodaly et al. (1984) were utilized to examine distribution of adult lights and darks between areas over several years. Sunde (1963) classified whitefish as lights or darks according to scale colour. The colour classification of Bodaly et al. (1983) was intended to follow that used by the Freshwater Fish Marketing Corporation. Data given in Bodaly et al. (1984) are from commercial catches which were colour classified subjectively by FFMC personnel.

Areal distribution of light and dark whitefish was examined by comparing scale melanophore counts of fish in 7 onshore and 9 offshore gillnet sets carried out in region 5 in July 1982 under this study (see Collection of Samples).

These 16 were bottom sets, an additional 2 were floating surface sets. Position in the net (top, middle or bottom thirds) was recorded for each whitefish captured in the bottom sets. Vertical distribution of lights and darks was examined by comparing scale melanophore counts

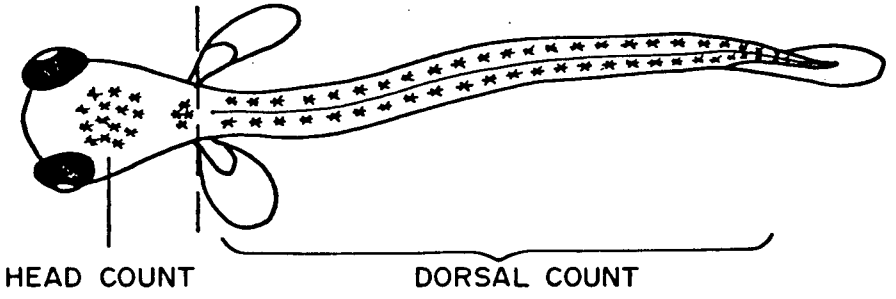
of whitefish caught in the top, middle and bottom thirds of the net. (Seventeen fish from the fall sample for which position in net was recorded are included. The 8 fish captured in floating sets are not included. Thus values of N (total fish) for areal and vertical distribution differ.)

Two x k contingency tables were used to compare areal and vertical distribution of lights and darks.

To determine whether there were temporal or seasonal changes in proportions of light and dark whitefish in a given area, July and September/October, 1982 catches of lights and darks in region 5 were compared. Scale melanophore counts were done on whitefish captured in July. As most fish captured in September/October were subsequently released their scale melanophore counts were not known. For these fish the comparison is based on the subjective colour classification. Whitefish subjectively classified as intermediates in both July and September/October catches were not included in these comparisons.

Young-of-the-year (YOY) whitefish were collected by Fisheries and Oceans personnel in regions 4, 5 and 6 in July and August of 1982. The fish were captured in a 1/2-metre net towed at the water surface for 3 minutes at a time by a boat at slow speed. Samples sizes were 9 fish from region 4, 29 from region 5 and 18 from region 6. YOY colour was quantified by counting dorsal and head melanophores under a binocular microscope. Dorsal counts included all dorsal melanophores between an imaginary line connecting the pectoral fin insertions and the caudal peduncle. Head counts were restricted to the cluster of melanophores on the top of the head (between the occiput and the lines joining the posterior thirds of the eyes) (Fig. 8). Analysis of covariance was used

Fig. 8. Dorsal view of lake whitefish larva showing head and dorsal melanophore count areas (for counts on wild caught young-of-the-year lake whitefish from Southern Indian Lake).


HEAD COUNT
DORSAL COUNT

to compare head and dorsal melanophore counts of YOY from the 3 regions, with length (measured from the tip of the snout to the urostyle, excluding the caudal fin) as the independent variable.

Results

Lake-wide Distribution Patterns of Lights and Darks

Distribution of light and dark whitefish throughout SIL is not homogeneous. Light-coloured whitefish are found in all regions and predominate in regions 3, 4 and 6. Dark-coloured whitefish occur mainly in region 5 but are also found in region 4 in small concentrations, generally near shore, and in regions 1 and 2 (Fig. 9).

These regional patterns are consistent between years (Fig. 9).

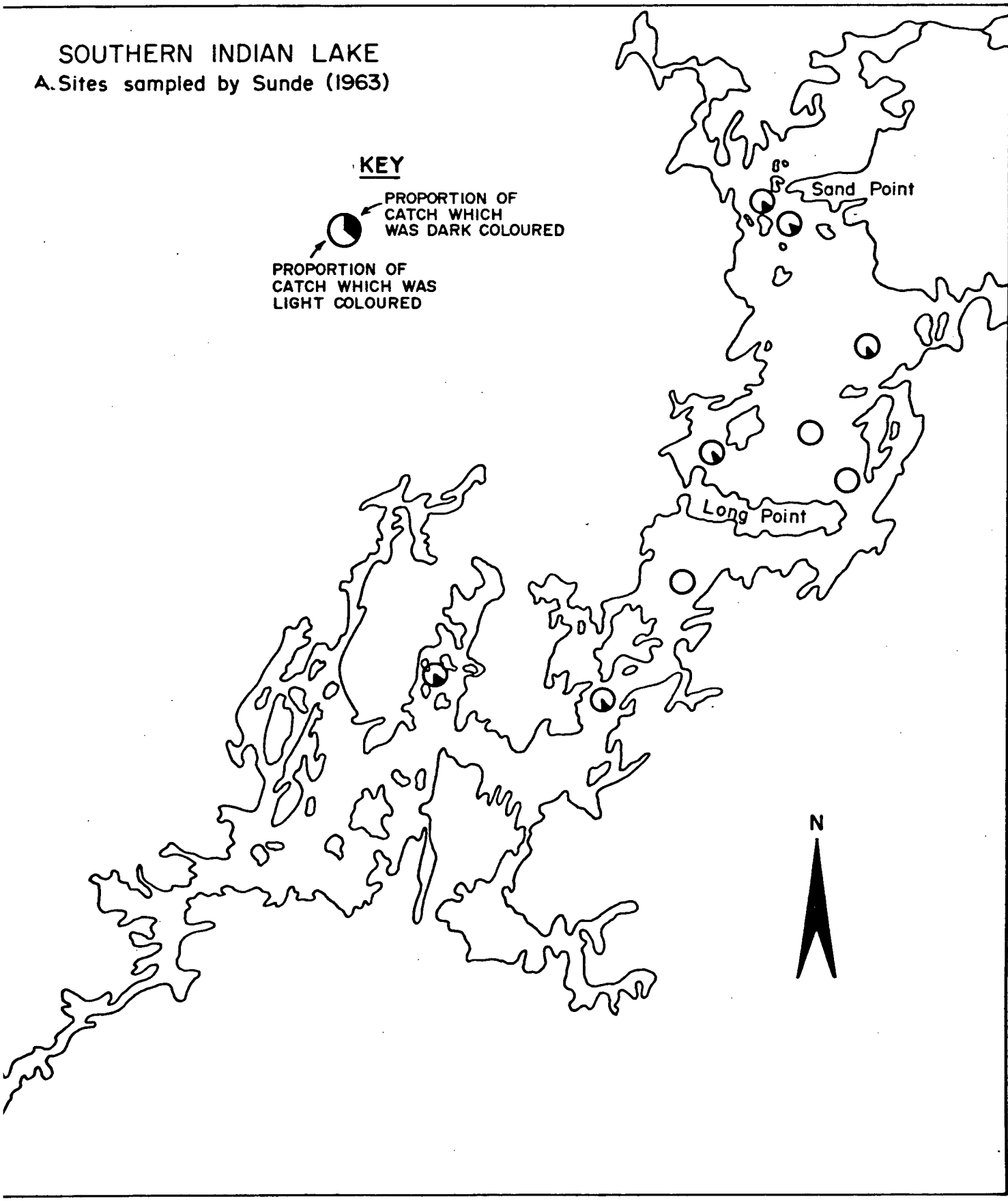
Areal Distribution of Lights and Darks in Region 5, 1982

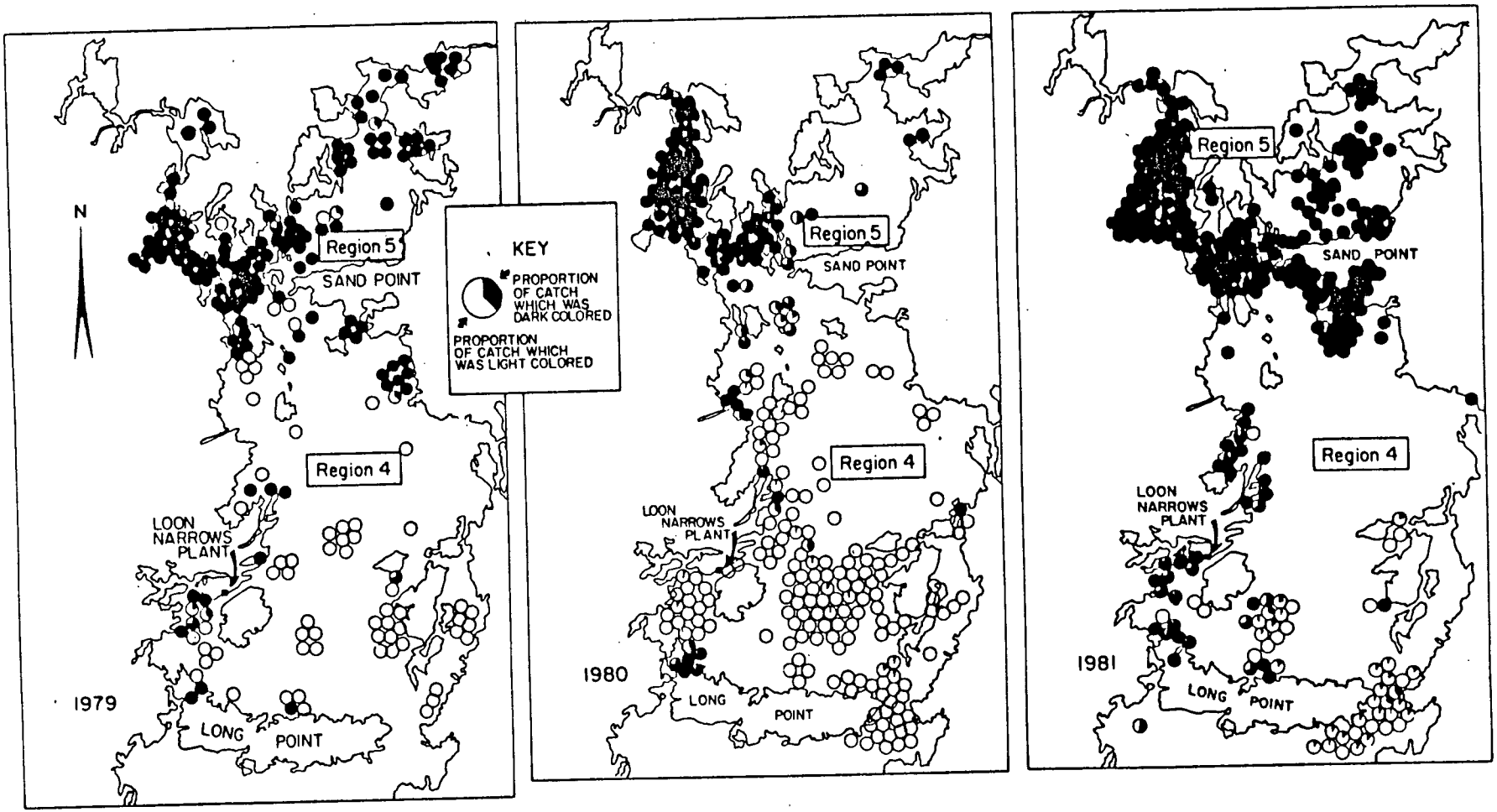
Of 117 whitefish captured in onshore sets, 76 (65%) were lights and 41 (35%) were darks (Fig. 10). Of 144 whitefish captured in offshore sets, 115 (80%) were lights and 29 (20%) were darks (Fig. 10). Slightly more lights were taken offshore than onshore (12.8 and 10.9 fish per set, respectively). Many more darks were taken onshore than offshore (5.9 and 3.2 fish per set, respectively). The distributions of lights and darks in onshore and offshore sets differed significantly ($\chi^2 = 7.9$, 1 d.f., $p < 0.005$).

Vertical Distribution of Lights and Darks in Region 5, 1982

Vertical distribution of lights in the nets was 16% in the top third, 28% in the middle, and 56% in the bottom (N = 187). Of 83 darks,

Fig. 9. Proportion of light and dark lake whitefish in experimental and commercial catches, Southern Indian Lake, 1963-1982. A. Sites sampled by Sunde (1963), B. Commercial catches, regions 4 and 5, 1979, 1980, 1981 (Bodaly et al. 1984), C. Experimental catches, regions 4, 5 and 6, 1982 (Bodaly et al. 1983).


SOUTHERN INDIAN LAKE
A. Sites sampled by Sunde (1963)
KEY
PROPORTION OF CATCH WHICH WAS DARK COLOURED
PROPORTION OF CATCH WHICH WAS LIGHT COLOURED
Sand Point
Long Point
N


N
Region 5
SAND POINT
Region 4
LOON NARROWS PLANT
LONG POINT
1979
KEY
PROPORTION OF CATCH WHICH WAS DARK COLORED
PROPORTION OF CATCH WHICH WAS LIGHT COLORED
Region 5
SAND POINT
Region 4
LOON NARROWS PLANT
LONG POINT
1980
Region 5
SAND POINT
Region 4
LOON NARROWS PLANT
LONG POINT
1981

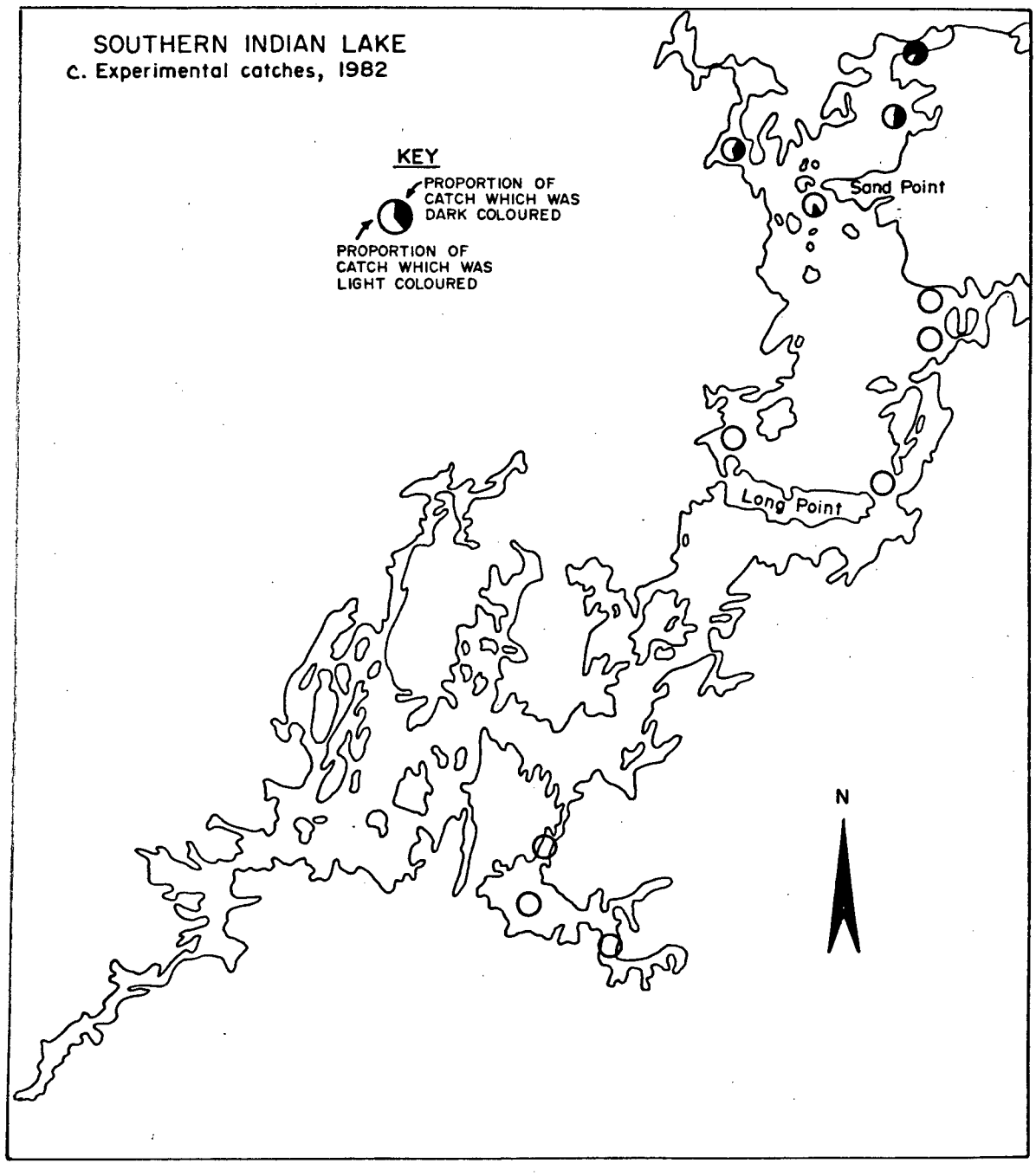
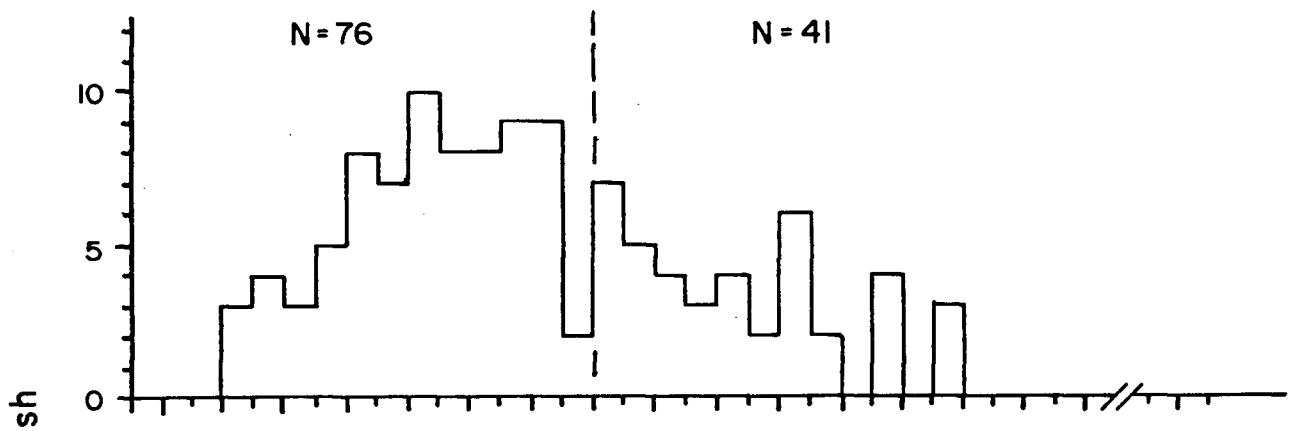
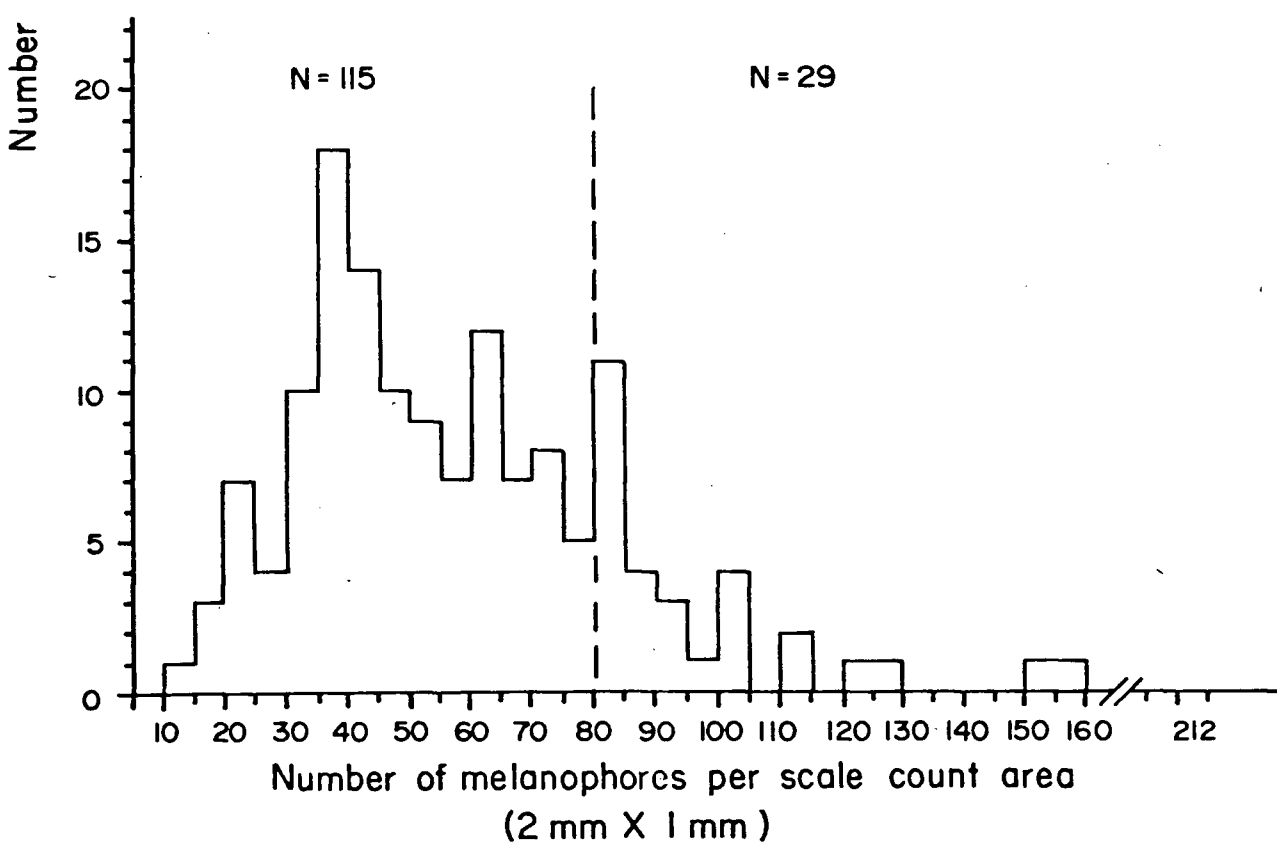

SOUTHERN INDIAN LAKE
c. Experimental catches, 1982
KEY
PROPORTION OF CATCH WHICH WAS DARK COLOURED
PROPORTION OF CATCH WHICH WAS LIGHT COLOURED
Sand Point
Long Point
N

Fig. 10. Areal distribution of light and dark lake whitefish in region 5, Southern Indian Lake, 1982. A. Scale melanophore counts of lake whitefish in onshore sets, B. Scale melanophore counts of lake whitefish in offshore sets.

A. Scale melanophore counts of lake whitefish in onshore sets



B. Scale melanophore counts of lake whitefish in offshore sets



19% were in the top third, 47% in the middle and 34% in the bottom (Fig. 11). These distributions differ significantly (χ^2 = 12.6, 4 d.f., p <0.025). Eight whitefish were captured in the 2 floating sets. Two of these were lights (scale melanophore counts of 60 and 74), 6 were darks (scale melanophore counts of 81-152).

Temporal Changes in Distribution of Lights and Darks in Region 5, 1982

Of 174 whitefish captured in region 5 in July and classified on capture as light or dark, 117 (67%) were lights and 57 (33%) were darks (Fig. 12). Of 164 whitefish caught in the same area in September/October, 54 (33%) were lights and 110 (67%) were darks.

Colour of Young-of-the-year Whitefish from Different Regions

Region 5 YOY whitefish had significantly higher mean head and dorsal melanophore counts than YOY from regions 4 and 6 (Table 3). Slopes of the regression lines for the various samples were not significantly different.

Because both dark and light adults occur there one might expect the colour distribution of region 5 YOY to be bimodal. Sample size was insufficient to test this.

The contrast in appearance between YOY from regions 5 and 6 was striking. Region 5 YOY were dark-looking; large melanophores covered the entire dorsal surface, extending down the sides, and on the ventral surface followed the gut to the tail. There were small melanophores along and below the lateral line. On region 6 YOY of similar size melanophores were small, did not cover the whole head and were few ventrally.

Fig. 11. Vertical distribution of light and dark lake whitefish in region 5, Southern Indian Lake, 1982. A. Scale melanophore counts of lake whitefish in top 1/3 of net, B. Scale melanophore counts of lake whitefish in middle 1/3 of net, C. Scale melanophore counts of lake whitefish in bottom 1/3 of net.

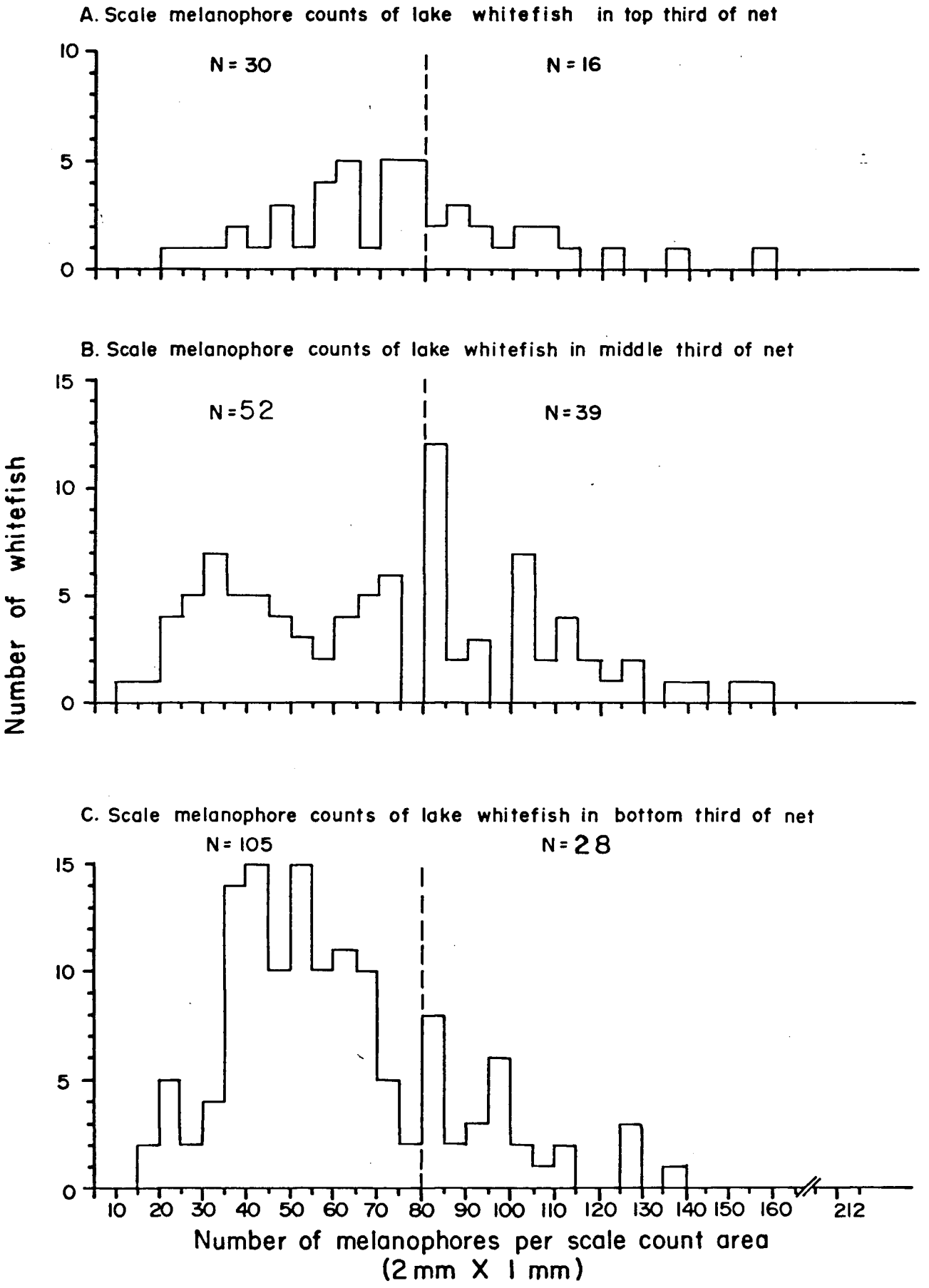

A. Scale melanophore counts of lake whitefish in top third of net
N = 30
N = 16
B. Scale melanophore counts of lake whitefish in middle third of net
N = 52
N = 39
C. Scale melanophore counts of lake whitefish in bottom third of net
N = 105
N = 28
Number of whitefish
0
5
10
15
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 212
Number of melanophores per scale count area
(2 mm X 1 mm)

Fig. 12. Scale melanophore counts of light and dark lake whitefish captured in region 5, Southern Indian Lake, in July 1982.

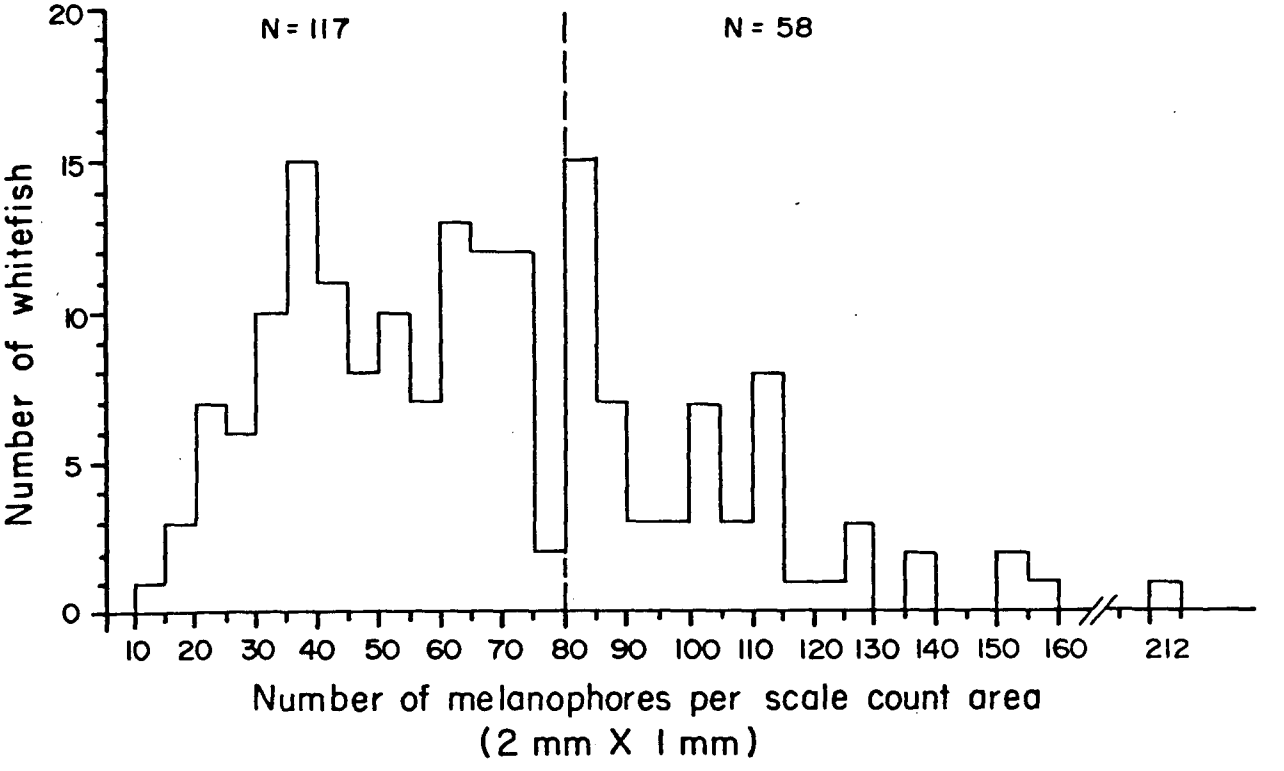

N = 117
N = 58
Number of whitefish
0
5
10
15
20
10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 212
Number of melanophores per scale count area
(2 mm X 1 mm)

Table 3. Analysis of covariance on head and dorsal melanophore counts of young-of-the-year lake whitefish from regions 4, 5 and 6, Southern Indian Lake.

Type of count	Comparison	Adjusted group means	F (adjusted group means)	d.f.	p
Head	Region 6, Region 4	367.3, 350.9	0.244	1,24	0.626
	Region 6, Region 5	324.9, 549.8	107.635	1,37	0.000
	Region 4, Region 5	326.6, 584.5	47.492	1,28	0.000
Dorsal	Region 6, Region 4	55.7, 58.1	0.083	1,23	0.775
	Region 6, Region 5	56.9, 80.5	13.676	1,43	0.001
	Region 4, Region 5	60.8, 86.6	7.598	1,33	0.009

Conclusion

Distribution of light and dark-colourd whitefish (both adults and young-of-the-year) in SIL is not homogeneous. Dark whitefish are restricted to particular areas of the lake. Where they occur together, lights and darks appear to segregate to some degree both areally and vertically. Lights were more abundant offshore than onshore and were most often found on the lake bottom. Darks were more numerous onshore than offshore and were more often caught off the bottom. Relative numbers of lights and darks in region 5 changed over time in 1982 with lights predominating in the summer catch and darks predominating in the fall catch. Region 5, where dark adults were most numerous, also had young-of-the-year with higher melanophore counts.

MORPHOLOGY AND BIOCHEMISTRY OF ADULT LIGHT AND DARK WHITEFISH

Introduction

The purpose of this work was to investigate whether light and dark colouration is correlated with morphometric measurements, meristic counts or biochemical characters.

Methods

Morphological Analyses

Fifty-two morphometric measurements and 16 meristic counts were taken on a preliminary sample of 24 light and 24 dark whitefish caught in region 5, SIL in 1979 (Table 4). Girth is the circumference of the body immediately anterior to the dorsal fin origin. Pectoral and pelvic fin ray counts included all principal rays.

Regression lines of morphometric measurements on fork length and frequency distributions of meristic counts were compared between lights and darks. Measurements and counts thought most likely to show differences between lights and darks were chosen for further study.

Subsamples of 45 fish of each colour were taken from the 1982 summer and fall samples. Fish were selected on the basis of scale melanophore count, age and sex. Only lights with scale melanophore counts $\leq$60 and darks with counts $\geq$80 were included. All age classes from 2 years to 16 years were represented as equally as possible and roughly equal numbers of females and males were chosen (Table 5).

Twenty-two morphometric measurements, as chosen from the preliminary set (above) were taken for each fish (Table 4). Before examination the fish were thawed overnight at 1°C. All measurements were taken on the left side of the fish. Measurements were straight

Table 4. Morphometric measurements and meristic counts made on light and dark lake whitefish from region 5, Southern Indian Lake. *: measurements and counts selected for detailed examination in 1982 sample.

Measurement or count	Reference
Fork length	Lindsey 1963
Standard length	Lindsey 1962
Body contour	Loch 1974
Head length*	Lindsey 1963
Head depth*	Ibid
Head width	Hubbs and Lagler 1958
Body length*	Lindsey 1963
Body width*	Loch 1974
Predorsal depth	Ibid
Postdorsal depth	Ibid
Occipital to dorsal distance	Ibid
Dorsal to adipose distance	Kristofferson 1978
Ventral to anal distance	Ibid
Anal to caudal distance	Loch 1974
Anal depth	Ibid
Peduncle depth	Lindsey 1962
Peduncle length	Hubbs and Lagler 1958
Snout length*	Ibid
Premaxilla height*	Bodaly 1979
Maxilla length*	Lindsey 1962
Maxilla width	Ibid
Width of gape*	Hubbs and Lagler 1958
Prepostorbital distance	Lindsey 1963
Postorbital length of head	Hubbs and Lagler 1958
Suborbital width	Ibid
Interorbital width*	Lindsey 1962
Orbit length*	Hubbs and Lagler 1958
Eye length	Ibid
Eye diameter*	Bodaly 1979
Vertical pupil diameter*	Ibid
Horizontal pupil diameter	Ibid
Height of cheek	Hubbs and Lagler 1958
Length of cheek	Ibid
Orbit to angle of preopercle	Ibid
Dorsal fin origin	Kristofferson 1978
Length of dorsal base	Hubbs and Lagler 1958
Length of depressed dorsal fin*	Ibid
Length of longest dorsal ray	Ibid
Pectoral fin origin	Lindsey 1963
Length of pectoral fin*	Ibid
Pelvic fin origin	Ibid
Length of pelvic fin*	Kristofferson 1978
Adipose fin origin	Ibid
Length of adipose fin*	Lindsey 1963
Anal fin origin	Kristofferson 1978
Length of anal base	Hubbs and Lagler 1958
Length of depressed anal fin*	Ibid
Gill raker length*	Kliewer 1970
Gill raker space*	Ibid
Length of lower arch*	Bodaly 1979
Average gill raker space*	Ibid
Girth*	See text
Branchiostegal rays	Hubbs and Lagler 1958
Standard lateral line scales	Ibid
Total lateral line scales	Lindsey 1962
Scales above lateral line	Hubbs and Lagler 1958
Scales below lateral line	Ibid
Scales before dorsal fin	Ibid
Suprapelvic scales	Lindsey 1962
Caudal peduncle scales	Ibid
Circumference scale count	Hubbs and Lagler 1958
Dorsal fin rays	Lindsey 1962
Pectoral fin rays	See text
Pelvic fin rays	See text
Anal fin rays	Kristofferson 1978
Upper gill rakers*	See text
Lower gill rakers*	See text
Total gill rakers*	See text

Table 5. Age distributions, numbers of males and females and dates of capture of light and dark lake whitefish used for morphological analyses.

Colour	Number of fish and age												Sex			Date of capture	
	2	3	4	5	6	7	8	9	10	11	12	13+	F	M	Imm	July	October
Light	4	4	4	4	4	4	4	4	4	2	1	6	21	22	2	26	19
Dark	1	3	1	5	5	5	5	4	4	4	4	4	19	25	1	27	18

line and did not follow body contour. Analysis of covariance was used to discern morphometic differences between light and dark whitefish. Body length (fork length minus head length) was used as the independent variable.

Three meristic counts (upper, lower and total gill rakers) were made on the whitefish samples using a dissecting microscope. Gill raker number was counted on the entire first left gill arch after it was removed in its entirety from the fish, including every bony rudiment. Lower gill raker number includes the middle gill raker. Differences in the distributions of meristic counts between lights and darks were tested by 2 x k contingency tables. Where necessary counts were combined so that no expected value was less than 4.5. Mean gill raker number of lights and darks was compared using a t-test.

Age and Growth

Scales were taken from each fish on the left side just below the dorsal fin origin. Scale ages were determined by L. Patterson, Manitoba Department of Natural Resources, Winnipeg. Scale age was plotted against fork length to provide an estimate of growth rates of light and dark whitefish from region 5.

Biochemical Analysis

Glycerol-3-Phosphate Dehydrogenase (G-3-PDH) Electrophoresis

G-3-PDH was selected for study because Bodaly et al. (1984) showed that there were regional differences in G-3-PDH allele frequencies among whitefish in SIL before flooding.

Subsamples of 36 fish of each colour were taken from the original sample. All fish used as parents in the breeding experiment, lights with scale melanophore counts <50 and darks with counts >95 were chosen. Not all fish used for morphological analysis were included.

A white muscle sample was excised from the epaxial muscle bundle just below the dorsal fin on the right side of the fish. Tissue samples were placed in plastic bags and frozen for later analysis.

Tissue extracts were prepared by macerating approximately 1 g of white muscle tissue in a solution of 0.25 M sucrose, 300 mg•L nicotinamide adenine dinucleotide (NAD) at a 1:3 ratio of muscle tissue to solution. The extracts were centrifuged at 18 000 RPM and 1°C for 20 minutes. The clear fraction was removed by pipette and frozen until needed.

Starch gel electrophoresis of tissue extracts was done following Tsuyuki et al. (1966). The buffers were citric acid adjusted to pH 8.0 with tris (hydroxymethyl) amino methane. The gel buffer concentration was 0.002 M, the electrode buffer was 0.04 M. NAD was added to the buffers to a concentration of 100 mg•L. The samples were run at 160 V for 2 hours at a temperature of 1°C.

G-3-PDH phenotypes were visualized by the methods of Clayton et al. (1973). Genotypes of individual fish were inferred from electrophoretic phenotypes according to an established genetic model for G-3-PDH (Clayton et al. 1973).

Hemoglobin Electrophoresis

Blood was collected from 63 light whitefish (scale melanophore counts <80) and 27 dark whitefish (scale melanophore counts ≥80) on capture. Blood was taken from the caudal artery (immediately behind the anal fin) of live fish by vacutainer. Samples were kept in ice water and used within 6 days.

The whole blood was centrigued to separate the plasma and erythrocytes. The erythrocytes were washed 3 times with a 1% NaCl solution, then lysed with 3 volumes of distilled water and centrifuged. The clear fraction was pipetted off and used immediately.

Starch gel electrophoresis of hemoglobin extracts was done following Tsuyuki et al. (1966). The buffers were boric acid adjusted to pH 8.5 with NaOH. The gel buffer concentration was 0.023 M, the electrode buffer was 0.3 M. EDTA was added to the gel buffer to a concentration of 0.025%. The samples were run at 160V for 2 hours at a temperature of 1°C.

Hemoglobin phenotypes were visualized using amido black stain (2.2 g amido black, 1000 ml distilled water, 200 ml acetic acid, 1 000 ml methanol). Genotypes of individual fish were inferred from electrophoretic phenotypes according to an established genetic model for hemoglobin (J.W. Clayton, pers. comm.).

G-3-PDH and hemoglobin allele frequencies were calculated for light and dark samples. The Castle-Hardy-Weinberg expected distributions of phenotypes were compared with observed phenotypic distributions to test for any lack of homogeneity within samples. Allele numbers were compared between lights and darks using 2 x k contingency tables.

Results

Morphology

Differences in Morphological Characters Between Lights and Darks

Seven of the 21 morphometric characters, all head measurements, showed statistically significant differences between dark and light whitefish (Table 6). Where the difference was between adjusted group means (head depth, interorbital width, snout length and lower arch length), values were larger for lights than for darks. Where the difference was in the slopes (snout length, eye diameter, maxilla length and orbit length), those for darks were steeper than those for lights. For snout length and eye diameter, values for lights were greater than those for darks at all sizes included in the sample. For maxilla length and orbit length, values for lights were greater than those for darks in fish <316 mm body length, and less than those for darks in larger fish.

Gill Raker Number

Mean lower gill raker numbers for light and dark whitefish were 17.71 and 17.33, respectively. These values are significantly different ($t = 2.197$, 88 d.f., $p < 0.05$). Gill raker count distributions and mean upper and total counts of lights and darks were not significantly different, though modes were consistently lower in darks than in lights for all 3 types of counts (Fig. 13)

Age and Growth

Growth rates of lights and darks were similar up to age 10. At that point growth of darks appears to level off, while lights continue to increase in size (Fig. 14).

Table 6. Analysis of covariance of morphometric characters of light and dark lake whitefish from region 5, Southern Indian Lake. Standard length is the independent variable. F values (and degrees of freedom) are given for tests of homogeneity of slopes and for adjusted group means. *: significant at $p \leq 0.05$ level. Blank: not significant

Morphometric character	F(d.f.) slopes	F(d.f.) adjusted group means
Girth	.162 (1,86)	.966 (1,87)
Body width	.233 (1,86)	.438 (1,87)
Head length	2.493 (1,86)	.788 (1,87)
Head depth	.840 (1,86)	*4.776 (1,87)
Interorbital width	.805 (1,86)	*4.427 (1,87)
Snout length	*5.462 (1,86)	*8.108 (1,87)
Premaxilla height	.511 (1,86)	1.016 (1,87)
Maxilla length	*7.799 (1,86)	.005 (1,87)
Gape width	2.480 (1,86)	.572 (1,87)
Orbit length	*4.570 (1,86)	.267 (1,87)
Vertical pupil diameter	.838 (1,86)	.000 (1,87)
Eye diameter	*5.675 (1,86)	.365 (1,87)
Dorsal fin length	2.076 (1,86)	2.594 (1,87)
Adipose fin length	.000 (1,86)	.294 (1,87)
Pectoral fin length	1.373 (1,86)	.906 (1,87)
Pelvic fin length	2.027 (1,86)	.044 (1,87)
Anal fin length	2.230 (1,86)	.001 (1,87)
Gill raker length	.256 (1,86)	.196 (1,87)
Gill raker space	.378 (1,86)	.143 (1,87)
Lower arch length	.844 (1,86)	*3.962 (1,87)
Average gill raker space	1.376 (1,86)	.193 (1,87)

Fig. 13. Gill raker count distributions of light and dark lake whitefish from region 5, Southern Indian Lake. A. Upper gill rakers, B. Lower gill rakers, C. Total gill rakers.

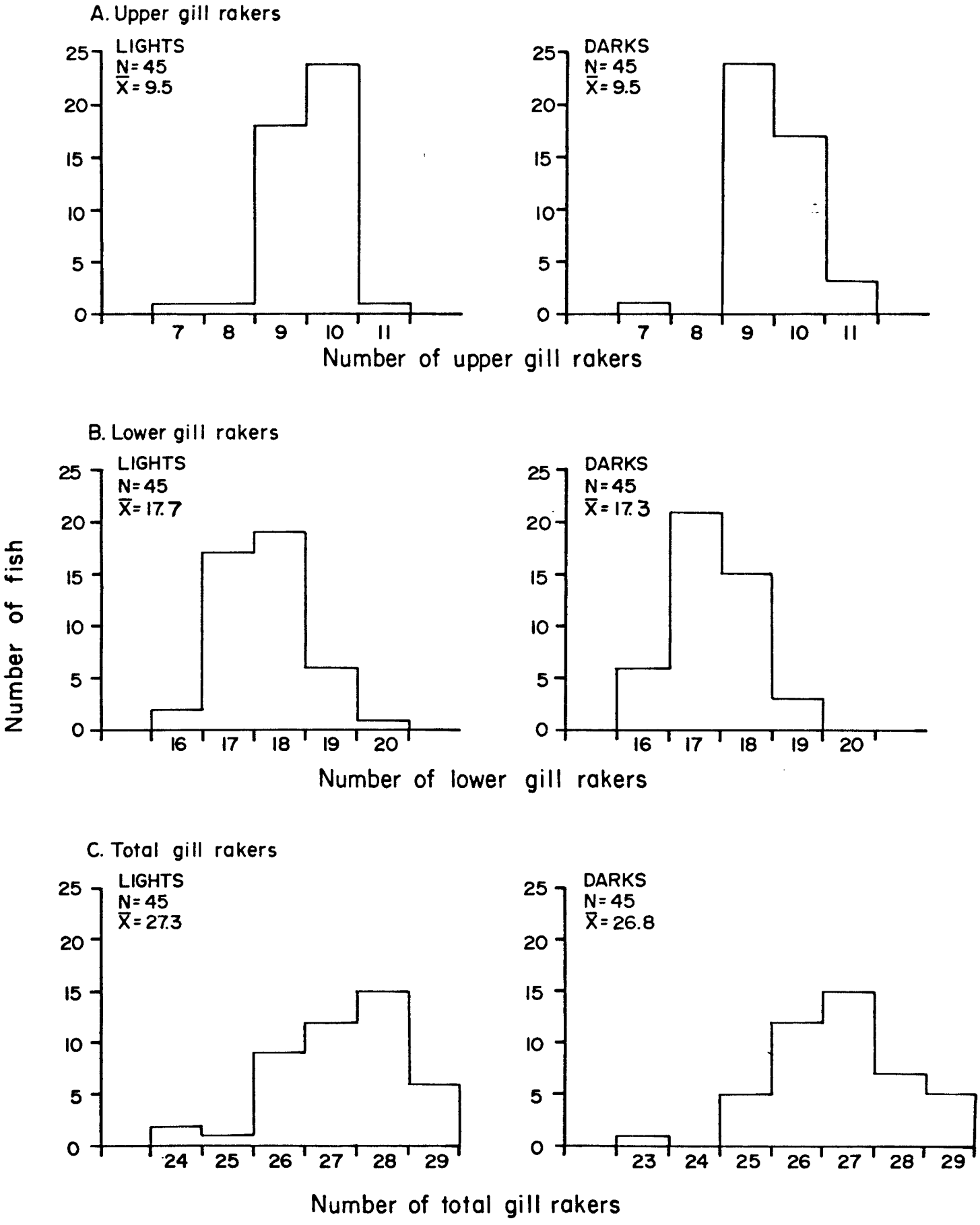
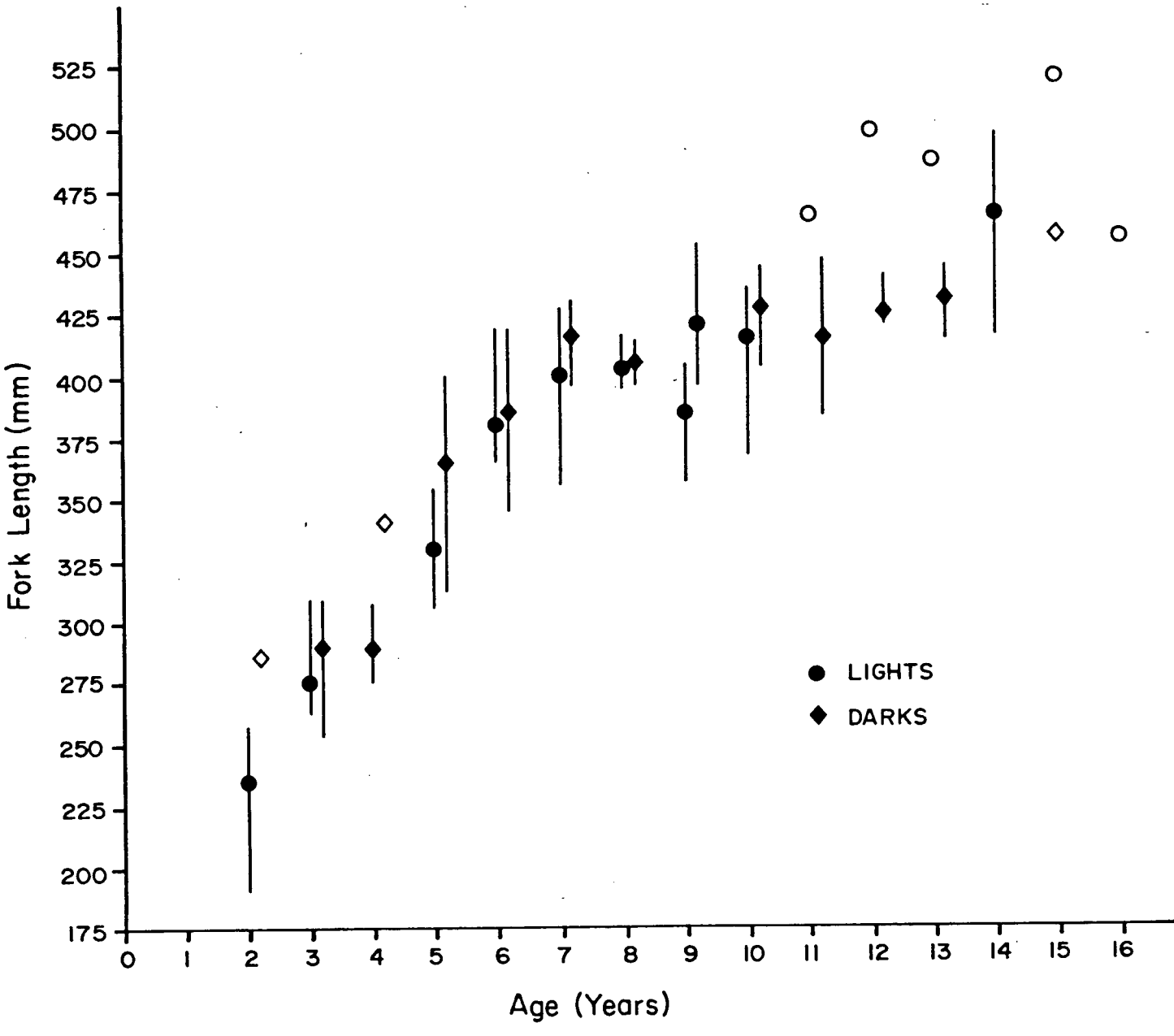

A. Upper gill rakers
LIGHTS
N=45
X̄=9.5
DARKS
N=45
X̄=9.5
Number of upper gill rakers
B. Lower gill rakers
LIGHTS
N=45
X̄=17.7
DARKS
N=45
X̄=17.3
Number of lower gill rakers
C. Total gill rakers
LIGHTS
N=45
X̄=27.3
DARKS
N=45
X̄=26.8
Number of total gill rakers
Number of fish

Fig. 14. Plots of age versus forklength for light and dark lake whitefish from region 5, Southern Indian Lake. Open symbols represent means of samples with less than three fish. Closed symbols represent means of samples with three or more fish. Vertical bars show ranges.


525
500
475
450
425
400
375
350
325
300
275
250
225
200
175
Fork Length (mm)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Age (Years)
LIGHTS
DARKS

Biochemical Analyses

Glycerol-3-Phosphate Dehydrogenase

The $\underline{a}^2$ allele had a frequency of 1.0 in both light and dark whitefish samples. Observed BB G-3-PDH phenotype distributions agreed with expected distributions for both light and dark samples (Table 7). A 2 x 3 contingency table comparing numbers of alleles at $\underline{b}$ loci for lights and darks showed no significant difference between the two groups (χ^2 = 1.05, 2 d.f., p >0.50).

Hemoglobin

Observed and expected hemoglobin phenotype distributions were in agreement for both light and dark samples (Table 8). A 2 x 2 contingency table comparing numbers of alleles for lights and darks showed no significant difference between the 2 groups (χ^2 = 0.973, 1 d.f., p >0.25).

Conclusion

The presence of significant differences between lights and darks in several morphometric characters and in lower gill raker numbers demonstrates that more is involved than simply variation in degrees of pigmentation. However, the broad overlap in characters between the two groups, and absence of significant differences in the two biochemical characters examined suggest no clear-cut separation into non-interbreeding stocks.

Table 7. Observed and expected (Castle-Hardy-Weinberg) BB glycerol-3-phosphate dehydrogenase phenotype distributions for light and dark lake whitefish from region 5, Southern Indian Lake. Expected numbers in brackets.

Colour	No. of fish and BB G-3PDH phenotypes							
	1,1	1,2	1,3	2,2	2,3	3,3	x^2 (4d.f.)	p
Light	3(3.36)	7(6.72)	9(8.56)	4(3.36)	7(8.56)	6(5.44)	0.54	p>.95
Dark	1(2.07)	8(5.36)	7(7.95)	2(3.46)	10(10.27)	8(7.62)	2.61	p>.50

Table 8. Observed and expected (Castle-Hardy-Weinberg) hemoglobin phenotype distributions for light and dark lake whitefish from region 5, Southern Indian Lake. Expected numbers in brackets.

Colour	No. of fish and hemoglobin phenotypes SS	SF	FF	x^2 (1d.f.)	p
Light	32(31.40)	25(26.15)	6(5.45)	0.118	p>.50
Dark	15(16.34)	12(9.33)	0(1.33)	2.204	p>.10

INHERITANCE OF COLOUR

Introduction

To determine whether or not there is a genetic basis for observed colour differences between light and dark whitefish a breeding experiment was performed.

Methods

Rearing of Fish

Adult whitefish were captured by gill netting in Area 5 in October, 1982. (See Collection of Samples). Twelve light and 11 dark parents were chosen on the basis of their external colouration as assessed by the subjective method. These classifications were later verified by the quantitative method. Ranges and means of scale melanophore counts of parents are given in Table 9. While the ranges do not fall above and below 80 melanophores per count area (the dividing line between lights and darks, re. Colour Classification of Adults) they are non-overlapping and the mean counts are significantly different ($t = 8.22$, 21 d.f., $p < 0.001$).

Four sets of crosses were done, 3 3 x 3 crosses and 1 3 x 2 cross. Experimental design is illustrated in Fig. 15.

The crosses were made in the field using the dry fertilization method. The eggs were held in screened plastic containers in the lake (surface temperature 5.5°-4.5°C) before being transferred to the Freshwater Institute. The eggs were transported by truck on Oct. 20, 1982. The egg containers were carried in plastic coolers filled with ice water at 1°C. Of a possible 33 batches (families), 7 were not completed or were lost and 26 were installed in the hatchery (6 light x

Table 9. Ranges and means of scale melanophore counts of parents used in breeding experiment.

Colour	N	Range of scale melanophore counts	Mean scale melanophore count
Light	11	17-69	45.58
Dark	12	76-126	105.64

Fig. 15. Experimental design utilized in crosses of light and dark lake whitefish.

Set 1

		Sex	♂		
		Tag no.	15333	15337	15334
		Colour	D(121)	L(20)	D(126)
Sex	Tag no.	Colour	Family number		
♀	15335	D(97)	1	2	3
	15338	L(17)	4	5	6
	15336	D(102)	7	8	9

Set 2

		Sex	♂		
		Tag no.	15340	15341	15342
		Colour	L(63)	D(105)	L(65)
Sex	Tag no.	Colour	Family number		
♀	15343	L(44)	10	11	12
	15344	D(117)	13	14	15
	15345	L(64)	16	17	18

Set 3

		Sex	♀		
		Tag no.	15346	15347	15348
		Colour	L(54)	D(110)	L(47)
Sex	Tag no.	Colour	Family number		
♂	15349	L(69)	19	20	21
	15350	D(110)	22	23	24
	15351	L(27)	25	26	27

Set 4

		Sex	♀	
		Tag no.	15352	15353
		Colour	L(22)	L(55)
Sex	Tag no.	Colour	Family number	
♂	15354	D(116)	28	29
	15355	D(82)	31	32
	15356	D(76)	34	35

Tag no. - that of individual fish.
Colour - L = light; D = dark. Number in brackets is scale melanophore count.

light, 15 light x dark, 5 dark x dark). Initial losses were due to inability to strip sufficient eggs from some females and to egg mortality. The number of extant families diminished somewhat over the incubation period, primarily due to sampling, so that at hatching 20 families remained (4 light x light, 11 light x dark, 5 dark x dark).

The eggs were incubated in screen-covered clear plastic jars. Cooled dechlorinated water was supplied to the jars from a head tank. A constant flow was maintained through each jar at a rate just high enough to tumble the eggs very slowly.

The jars stood in a cool water bath which also had a flowthrough water supply. Temperature in the head tank was 1° - 1.5°C, in the water bath was 2.5° - 2.75°C, and in the egg jars was 1.5° - 4°C at different times during incubation.

Dead eggs were removed from the jars regularly. Malachite green treatments were given over the incubation period to retard growth of fungus on the eggs.

Before hatching began the egg jars were transferred to fish tanks where they were clamped above the water surface in the tanks. Flowthrough water was supplied to both jars and tanks; the latter were also provided with airstones. Hatching began in early February and continued until the end of March. During this period jar temperatures were gradually allowed to rise to 6° - 7°C. Hatched fish were carried out of the jars into the tanks by the flow of water. Tank temperatures were 9° - 10°C. The lights in the hatchery were on a 12-hour daily cycle, on at 0800 hours and off at 2000 hours.

The fry were initially fed brine shrimp (*Artemia*) nauplii and ground Tetra Min, and were later switched to wild-caught *Daphnia*

supplemented with a mixture of ground Tetra Min and rainbow trout starter. The fry were fed 2 or 3 times daily. The tanks were siphoned daily to remove waste and scrubbed weekly.

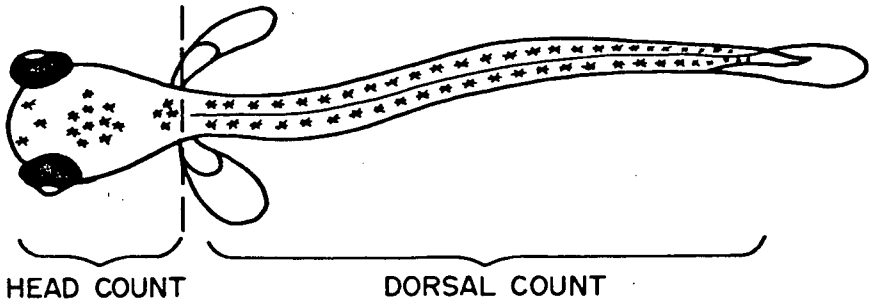
Sampling Procedure

As early as 35 days after fertilization some larvae had visible melanophores, including a double dorsal line, a ventral line, and scattered melanophores on the yolk sac. Somewhat later melanophores became visible on the top of the head.

Melanophore counts were used as a means of quantifying and comparing the colour (lightness or darkness) of progeny of different crosses. Four pre-hatch samples were taken from most families (at 85-86, 92, 111, and 119-126 days after fertilization). Not all families were sampled at each age because some egg batches were too small to allow it. For the 111 day sample subsample size was 12 fish from each family; for other samples smaller subsamples were sometimes used. Larvae were removed from the eggs, preserved in 5% formalin, and stored in amber-coloured jars in the dark.

In initial samples melanophore counts were done on the head, dorsal surface, yolk sac and ventral surface of a larva. The latter 2 counts proved difficult to do and of questionable accuracy, thus were discontinued. Dorsal and head melanophore counts were done on subsequent samples. Head counts included all melanophores visible on the dorsal surface of the head and the occiput. Dorsal counts included the double dorsal row of melanophores which extends from behind the occiput to the caudal peduncle (Fig. 16). Because dorsal counts were easier to do and more reliable than head counts, they alone were used in most analyses.

Fig. 16. Dorsal view of lake whitefish larva showing head and dorsal melanophore count areas (for counts on hatchery-reared larvae).


HEAD COUNT
DORSAL COUNT

Results

The 111 day samples comprise the most complete set of counts (24 of 26 families represented) and therefore were chosen for the following analyses.

Dorsal Melanophore Counts from Different Cross Types

Mean dorsal melanophore counts and variances for each cross type at 111 days post-fertilization are given in Table 10. The number of families and total number of fish included in the calculations for each cross type are also given. Mean dorsal melanophore counts differ in the direction expected if colour is inherited and all differences, except between the means for DD and D♀L♂ crosses, are statistically significant (Table 11). That is, progeny of DD and D♀L♂ crosses have significantly more dorsal melanophores than those of L♀D♂ crosses; the latter have counts significantly higher than offspring of LL crosses.

Heritability Estimates

The heritability (h^2) of a trait expresses the proportion of the phenotypic variance which is due to gene effects. Heritability of a trait can be estimated from the regression coefficient of offspring value on mid-parent value (h^2 = slope) or offspring on 1 parent ($1/2\ h^2$ = slope) (Falconer, 1960). Figure 17 shows the regressions of 111 day larval dorsal melanophore counts on parent scale melanophore counts. The correlation between larval and mid-parent values is significant ($r = 0.411$, 22 d.f., $p < 0.05$).

Estimates of h^2 from all 4 pre-hatch samples are given in Table 12. Estimates of h^2 from offspring on mid-parent regressions are

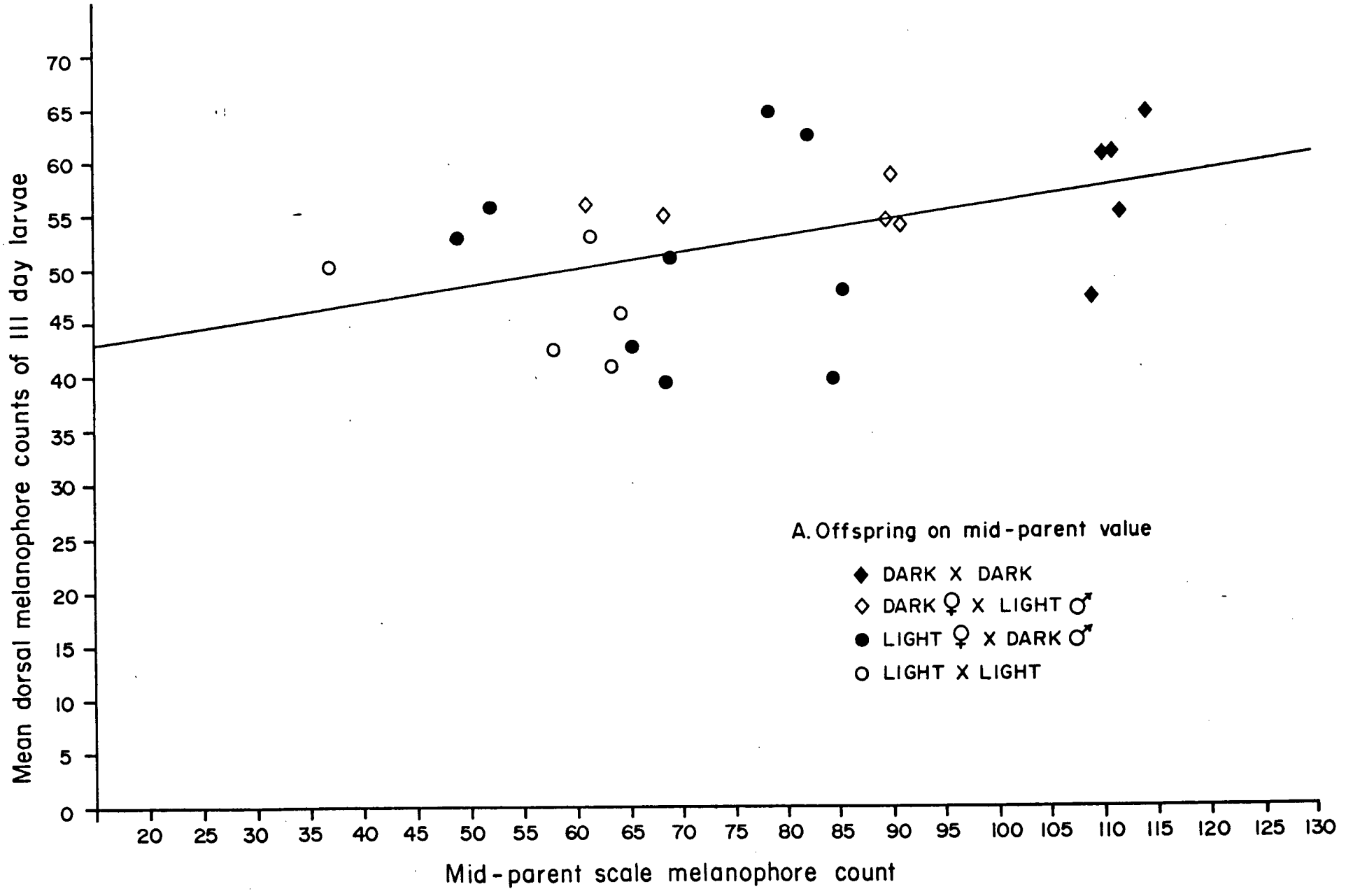
Table 10. Mean dorsal melanophore counts and variances for 111 day larval whitefish of each cross type.

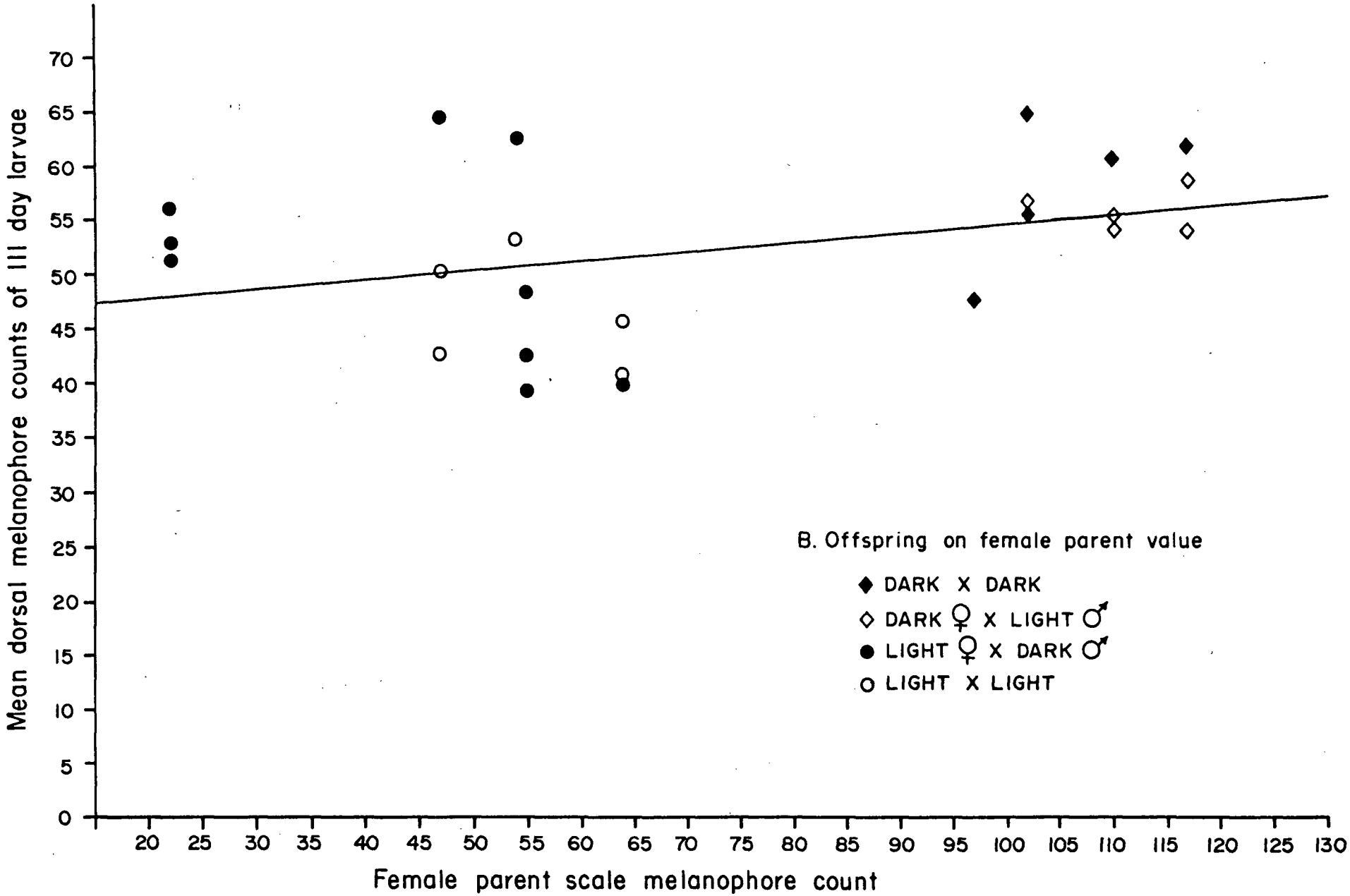
Cross type	Number of families	Number of larvae	Mean dorsal melanophore count	Variance
L x L	5	60	46.58	161.41
L♀ x D♂	9	108	50.87	177.85
D♀ x L♂	5	60	55.72	88.27
D x D	5	60	58.12	142.54

Table 11. Results of t-tests (using the formula for unequal variances) between mean dorsal melanophore counts of different cross types at 111 days post-fertilization.

Comparison	Value of t	Degrees of freedom	Level of significance
DD vs D♀ L♂	1.213	118	not significant
DD vs L♀ D♂	3.591	166	$p<.001$
DD vs LL	5.086	118	$p<.001$
D♀ L♂ vs L♀ D♂	2.729	166	$p<.01$
D♀ L♂ vs LL	4.443	118	$p<.001$
L♀ D♂ vs LL	2.046	166	$p<.05$

Fig. 17. Regressions of dorsal melanophore counts of 111 day lake whitefish larvae on parent scale melanophore counts. A. Offspring on mid-parent value, B. Offspring on female parent value, C. Offspring on male parent value.


Mean dorsal melanophore counts of III day larvae
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
Mid-parent scale melanophore count
A. Offspring on mid-parent value
DARK X DARK
DARK ♀ X LIGHT ♂
LIGHT ♀ X DARK ♂
LIGHT X LIGHT


Mean dorsal melanophore counts of III day larvae
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
Female parent scale melanophore count
B. Offspring on female parent value
DARK X DARK
DARK ♀ X LIGHT ♂
LIGHT ♀ X DARK ♂
LIGHT X LIGHT

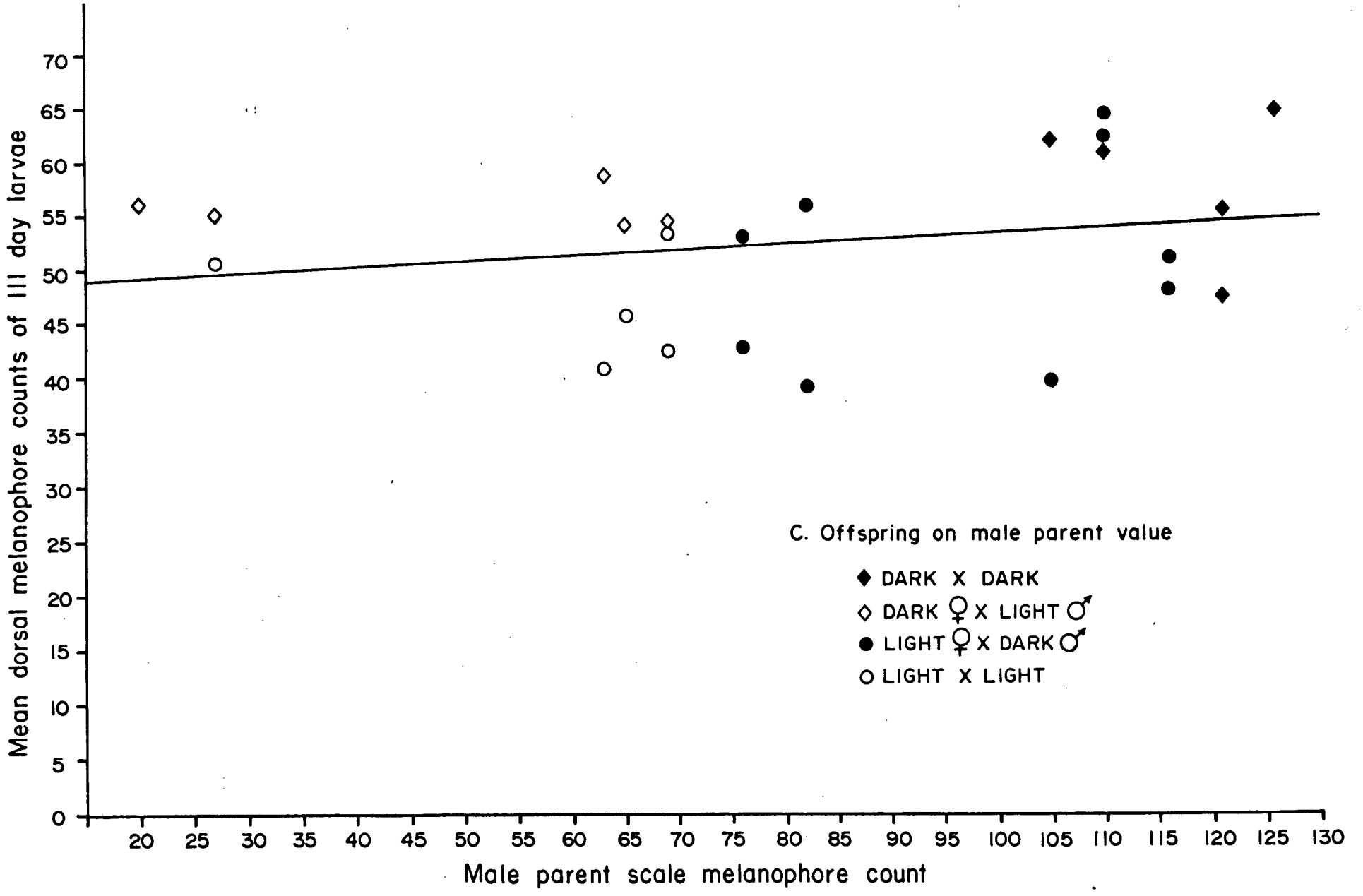

Mean dorsal melanophore counts of III day larvae
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
Male parent scale melanophore count
C. Offspring on male parent value
DARK X DARK
DARK ♀ X LIGHT ♂
LIGHT ♀ X DARK ♂
LIGHT X LIGHT

Table 12. Heritability estimates from 4 pre-hatch lake whitefish samples.

Sample	Estimate of h^2 from regression of offspring on - Mid-parent	Female parent	Male parent
85-86 days	0.10	0.12	0.06
92 days	0.15	0.14	0.14
111 days	0.15	0.16	0.10
119-126 days	0.12	0.16	0.0008

similar for the 4 samples, but those from offspring on female and male parents are quite different over the 4 samples. If the estimated h^2 from the regression of offspring on female parent is greater than that of offspring on male parent a maternal effect is indicated (Falconer 1960). In 3 of 4 cases the h^2 estimated by the regression of offspring on mother is higher than that estimated by the regression of offspring on father, indicating some maternal effect (Table 12). Possible reasons for the very low value of h^2 estimated by offspring on father regression at 119-126 days are discussed below (See Discussion).

Conclusion

There are significant differences in colour (as measured by dorsal melanophore counts) between larval whitefish from different colour crosses. These differences are in the direction expected if colour is at least partly inherited. Heritability estimates show that maternal effects account for part but not all of the observed colour differences. That is, there is a measurable genetic component to the colour differences between dark and light whitefish which is independent of environmental or maternal effects.

ENVIRONMENTAL ALTERATION OF COLOUR

Introduction

Experiments were performed to test the effects both of long- and short-term exposure to different light and background conditions on colour of young whitefish. Some observations were made on short-term colour change in adult whitefish.

Long-term Colour Change Experiment

Methods

Experimental Design

Four plastic 12 litre dishpans (3 dark brown, 1 cream-coloured) were used as experimental tanks. Each tank had an airstone and flow-through water supply (water replacement time was 20 minutes).

Fish from 1 family (X - 24 L♀ D♂) were divided into 4 groups. Age of the fish was 245 days (since fertilization) at the outset and 257 days at the end of the experiment. Eight fish from each group were preserved immediately in 5% formalin and stored in amber-coloured jars (these comprise 0 day samples 1 - 4). The remaining fish (about 32 in each group) were put in the 4 tanks. There was a control group and 3 experimental conditions.

1. cream-coloured tank, uncovered, exposed to full light. Since this was very similar to the conditions under which other experimental fish were reared (in light-coloured, uncovered tanks exposed to light), it was considered the control.
2. dark brown tank, uncovered, full light.
3. dark brown tank covered with screen which excluded half the incident light (as measured with an incident light meter).

4. dark brown tank covered with light-proof black plastic. Even though they were covered with baffles, a low level of light entered the tank through the drain and airstone holes.

The fish were fed daily on live Daphnia and dried food (ground Tetra Min and rainbow trout starter). The tanks were cleaned daily. Water temperature throughout the experiment was 10° - 11°C. The tanks were lit by a bank of ceiling fluorescent lights which were left on for the duration of the experiment except when the covers were removed from the light exclusion tanks for cleaning and feeding.

After 12 days 12 - 14 fish remained in each group and the experiment was terminated. One or 2 fish from each group were preserved directly from the experimental tanks to use for comparing melanophore configuration of fish from the 4 treatments. The remaining fish in each group were put in a white bucket for about 5 minutes (so that the melanin granules would aggregate thus facilitating counting of melanophores), then preserved.

Larvae were 15.0 to 18.5 mm in length at the beginning of the experiment and 15.5 to 24.5 mm at the end of it.

Head and dorsal melanophore counts were done on the 0 day and 12 day samples. Head counts included just the melanophores on the top of the head; dorsal counts included dorsal melanophores from a line even with the pectoral insertion to the caudal peduncle.

Statistical Analysis of Data

Analysis of covariance was used to discern differences in melanophore counts between the 4 12 day samples with length (measured

from the tip of the snout to the urostyle, excluding the caudal fin) as the independent variable.

Since samples 1 to 4 at 0 days were random subsamples of the same population they were combined. The 0 day sample was compared with the 12 day sample from group 1 (the control), using ANCOVA, to determine whether any significant gain or loss of melanophores occurred in the control group over the experimental period.

Results

Comparison of melanophore configuration of fish from the 4 groups showed that in bright surroundings the melanophores appeared small and discrete, with their pigment aggregated. With increasing environmental darkness (tubs 2 - 4), melanophore pigment was increasingly dispersed.

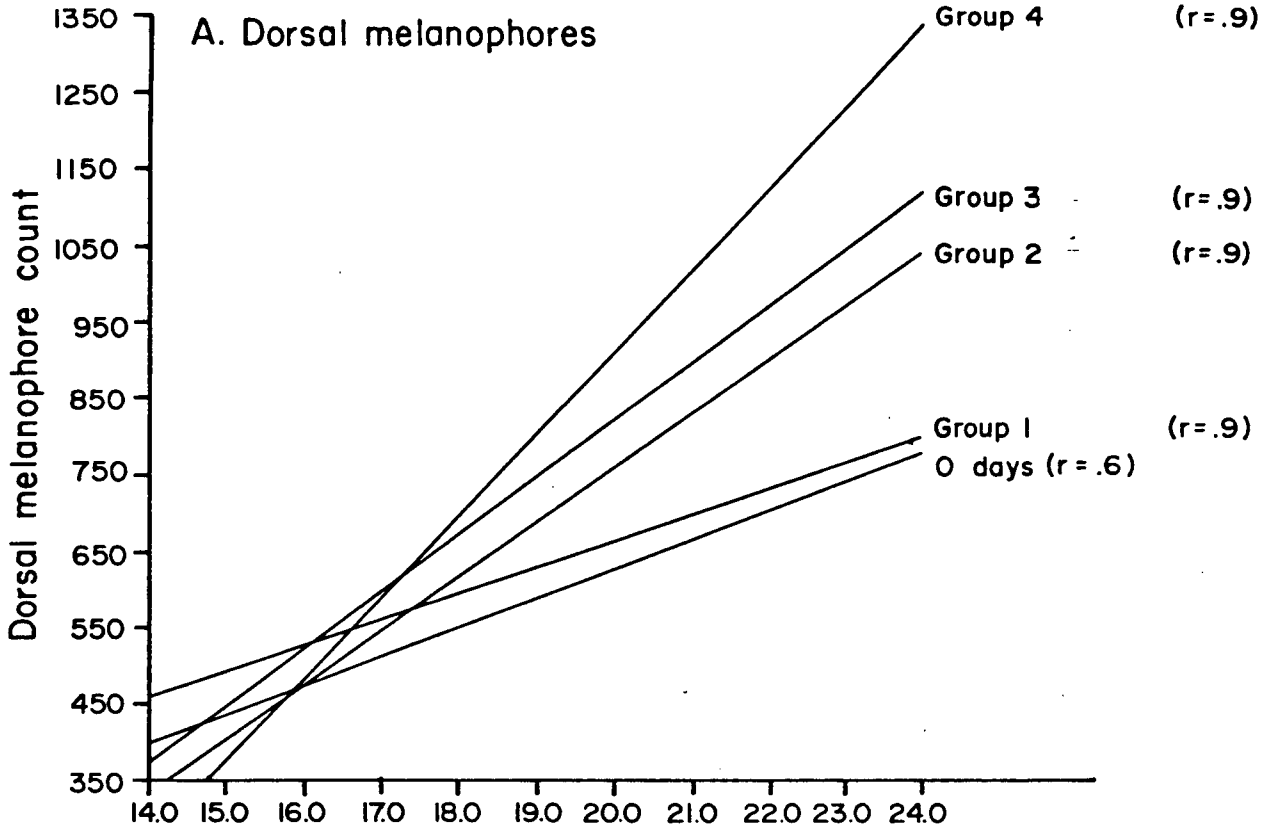
At 12 days there were significant differences between mean melanophore counts and slopes of regression lines of the 4 groups (Table 13). With increasing environmental darkness the fish became darker by producing more melanophores (Fig. 18). The adjusted group mean dorsal melanophore counts at 12 days were 659, 726, 779 and 865 for groups 1 to 4 respectively. The adjusted group mean head melanophore counts at 12 days were 159, 164, 179 and 222 for groups 1 to 4 respectively.

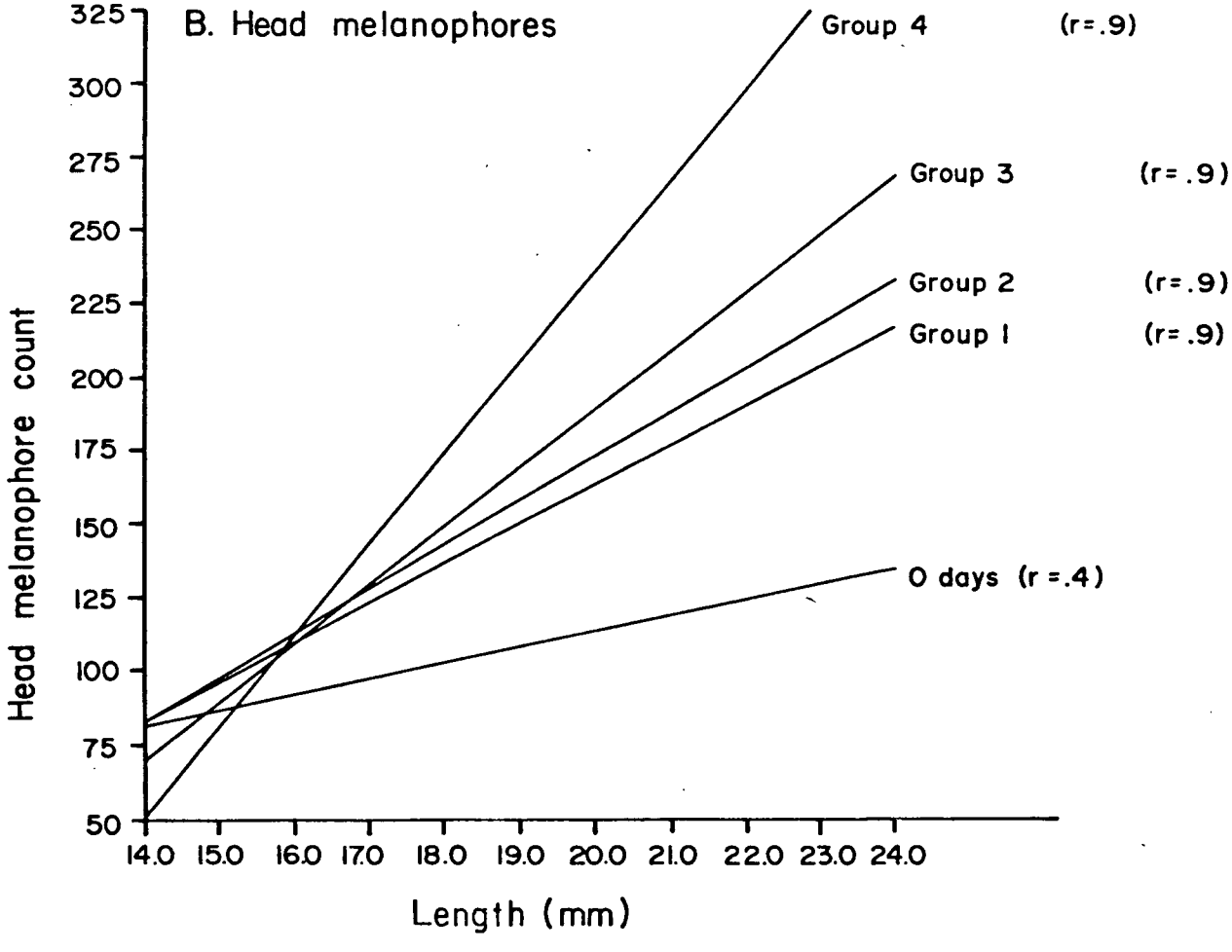
There were significant gains in numbers of both dorsal and head melanophores in group 1 over the experimental period, as evidenced by comparison of 0 day and group 1 12 day samples (dorsal melanophores - F (adjusted group means) = 5.524, 1,41 d.f., $p = 0.024$; head melanophores - F (adjusted group means) = 23.292, 1,4 d.f., $p = 0.00002$). Such gains would be expected with increased size (the fish grew about 2.5 mm in length over the 12 days). There was no evidence of decreased melanophore number in any group.

Table 13. Long-term colour change experiment: Results of analysis of covariance of regressions of larval lake whitefish melanophore counts on length at 12 days.

Type of count	F_1 (adjusted group means)	d.f (for F_1)	F_2 (slopes)	d.f. (for F_2)	Level of significance (F_1 and F_2)
Dorsal	10.431	3,41	8.175	3,38	$p<.001$
Head	16.972	3,41	9.777	3,38	$p<.001$

Fig. 18. Long-term colour change experiment: Regressions of larval lake whitefish melanophore counts on total length before and after 12 day exposure to different light and background conditions. Group 1 - Pale tank, full light. Group 2 - Dark tank, full light. Group 3 - Dark tank, half light. Group 4 - Dark tank, low light.


A. Dorsal melanophores
Dorsal melanophore count
1350
1250
1150
1050
950
850
750
650
550
450
350
14.0 15.0 16.0 17.0 18.0 19.0 20.0 21.0 22.0 23.0 24.0
Group 4 (r=.9)
Group 3 (r=.9)
Group 2 (r=.9)
Group 1 (r=.9)
0 days (r=.6)


B. Head melanophores
Head melanophore count
325
300
275
250
225
200
175
150
125
100
75
50
14.0 15.0 16.0 17.0 18.0 19.0 20.0 21.0 22.0 23.0 24.0
Length (mm)
Group 4 (r=.9)
Group 3 (r=.9)
Group 2 (r=.9)
Group 1 (r=.9)
0 days (r=.4)

Conclusion

Young whitefish modify their colour to correspond with external conditions. Fish exposed to a light environment stay light while those in darker surroundings become more pigmented. Apparently colour can be altered both through changes in melanophore number and in melanophore configuration (the state of dispersion of melanin granules in the melanophores). In this experiment there was no evidence of loss of melanophores in fish in any tank.

Short-term Colour Change Experiment

Of particular interest in this experiment was the length of time for young fish to adjust their colour in response to background colour and the maximum degree of lightness or darkness achieved over a short period.

Methods

Experimental Design

Two experimental tanks, 1 light and 1 dark, were used. The tanks were aerated throughout the experiment. Water temperature in the tanks went from 12.5° to 14.0°C over the experimental period (about 3 1/2 hours).

A sample of fish was put in the light tank for 10 minutes (to standardize colour at the outset), 1 of these was preserved (Sample 1). The rest were transferred to the dark tank and sampled at short intervals (15 sec, 30 sec, 1 min, 5 min, 30 min, 60 min), then switched to the light tank and sampled at the same intervals. Samples (1 fish in each) were preserved in 5% formalin and stored in amber-coloured jars in the dark.

The experiment was done 3 times using fish from a different family each time (X-7 DD, X-13 D♀L♂; X-21 LL). Fish ranged in length from 24.5 to 35.0 mm.

Observations

For each fish the state of dispersion of melanin granules in the melanophores (particularly whether aggregated, partly dispersed, or very dispersed), degree of overlap between melanophores, and overall shade was described. Shade was assessed by comparing fish from dark-tank samples with Sample 1 and fish from light-tank samples with Sample 7 (dark-tank, 60 min).

Results

Length of Time to Adjust Colour

Melanophores began to change configuration (that is, show pigment dispersion in the dark tank and pigment aggregation in the light tank) within 15 seconds. They changed most markedly during the first minute of exposure to the light or dark background and little thereafter. Overall colour likewise changed most during the first minute and little thereafter.

Maximum Colour Change Achieved

Overall colour differences between fish from the light and dark treatments were not dramatic, but were apparent to the naked eye. Fish from the light treatment were paler overall, sometimes greenish or yellowish dorsally; those from the dark treatment were darker overall, quite grey dorsally.

Conclusion

Young whitefish are capable of rapid colour change (within one minute), pale to dark and vice versa, which they effect through redistribution of pigment granules in the melanophores.

Response of Young Whitefish to Zero Incident Light

Observations

The above experiments show that against a dark background and under reduced levels of incident light young whitefish get darker (in the short-term by dispersing melanin granules in the melanophores, in the long-term by producing more melanophores).

No experiment was performed to test the effect of zero incident light on melanophore configuration, but the following observation was made. At night all lights in the hatchery in which these whitefish were reared are extinguished and the room becomes totally dark. It was observed on several occasions that in total darkness all fish in all tanks stayed on or close to the bottom and all were extremely pale. Examination showed that pigment in the dorsal melanophores was aggregated so that the cells appeared as small dots. Pigment in the melanaphores on the top of the head was slightly dispersed.

The fish responded when light was switched on by swimming actively and gradually darkening in colour.

Conclusion

Young whitefish respond to light conditions in a direct fashion, that is, become light in light surroundings and dark in dark surroundings, except in total darkness. There may be a threshold light

intensity below which the usual response to dark surroundings is reversed.

Short-term Colour Change in Adult Whitefish

Although no experiment was done on short- or long-term colour change in adults two points can be made.

1. When capturing and holding whitefish for spawn-taking purposes it was noted that a very dark-coloured whitefish placed in a light-coloured open fish tub would blanch to an intermediate colour within seconds. On two occasions fish which were light-coloured when removed from the net became dark-coloured within seconds.
2. To determine sources of error in colour classification of adults, configurations of melanophores on the scales of "misidentified" lights and darks was described. It was found that most fish which were called lights but which had high melanophore counts had their melanophores aggregated; most fish which were called darks but which had low counts had their melanophores dispersed. This indicates that adult whitefish can control their colouration to a marked degree. Aggregation of pigment can make a whitefish with a high melanophore count appear quite pale; dispersion of pigment can make a fish with a low melanophore count appear quite dark.

TRIAENOPHORUS CRASSUS CYST LEVELS OF SIL WHITEFISH

Introduction

Coregonids are the second intermediate host of the cestode parasite *Triaenophorus crassus*. A copepod (*Cyclops bicuspidatus* in North America) is the first intermediate host, the northern pike (*Esox lucius*) is the adult host. If an infected copepod is eaten by a coregonid the *T. crassus* plerocercoid stage can develop and encyst in the fish's musculature (Lawler, 1970). The parasite, though harmless to man, is objectionable in appearance and commercial catches of lake whitefish with high levels of muscle cysts are downgraded.

In Southern Indian Lake levels of *T. crassus* infection in whitefish differ between regions and between colours of fish. Data both from experimental and commercial catches show that dark whitefish have higher average cyst levels than light whitefish (Bodaly et al. 1980). Cyst count data gathered by different observers over many years were used to examine whole lake patterns (that is, consistent differences or similarities in mean counts between regions over time) and the relation of cyst count to colour of whitefish.

Methods

Data were taken from McTavish (1952), Sunde (1963), Watson (1977), and Bodaly et al. (1983).

Sunde (1963) took fish from commercial sets which used only nets of stretched mesh size about 13.3 cm (5 1/4 in). The other authors did experimental fishing using a range of mesh sizes (Table 14). The experimental catches thus represent a wider range of size and age classes of fish than do the commercial catches. From these data mean

Table 14. Mesh sizes of nets used by different authors for collecting lake whitefish in Southern Indian Lake.

Author	Stretched mesh sizes (cm; size in inches in brackets)
McTavish (1952)	7.3(2 7/8); 10.8(4 1/4); 12.1(4 3/4); 13.3(5 1/4)
Sunde (1963)	12.8(5 1/16) - 13.6(5 3/8)
Watson (1977)	1.3(1/2); 3.8(1 1/2); 5.1(2); 7.0(2 3/4); 8.9(3 1/2); 10.8(4 1/4); 13.3(5 1/4)
Bodaly et al. (1983)	3.8(1 1/2); 5.1(2); 7.0(2 3/4); 8.9(3 1/2) 10.8(4 1/4); 13.3 (5 1/4)

cyst counts and mean weights of catches were determined for regions of SIL.

Sunde (1963) and Bodaly et al. (1983) provided data on colour of whitefish. Mean cyst counts of light and dark fish in these samples were calculated. Cyst count distributions of lights and darks captured in region 5 in 1982 were compared using a 2 x k contingency table. Counts of 6 or more cysts were combined in the analysis.

Finally, mean cyst counts of lights captured in regions 4, 5 and 6 in 1982 were compared to determine whether there are significant differences in cyst counts among fish of the same colour.

Results

Regional Differences in Mean Cyst Counts

Region 5 consistently had the highest mean counts in a given year while region 4 had the lowest counts except in 1963. Region 6 had levels between those of regions 4 and 5 in a given year. Counts for regions 1, 2 and 3 were variable (Table 15).

Regions 4, 5 and 6 showed trends of increasing cyst levels in the years following impoundment (1978-1982).

Differences in Mean Cyst Counts Between Light and Dark Whitefish

Sunde's (1963) data showed no difference between cyst counts of lights and darks. Data from Bodaly et al. (1983) for region 5 showed that in 1979 the mean count for darks was significantly lower than that for lights. However, this represents only 22 darks compared to 222 lights. The 1978 and 1982 means for darks were significantly higher than those for lights (though again in 1978 the sample of darks was very small) (Table 16).

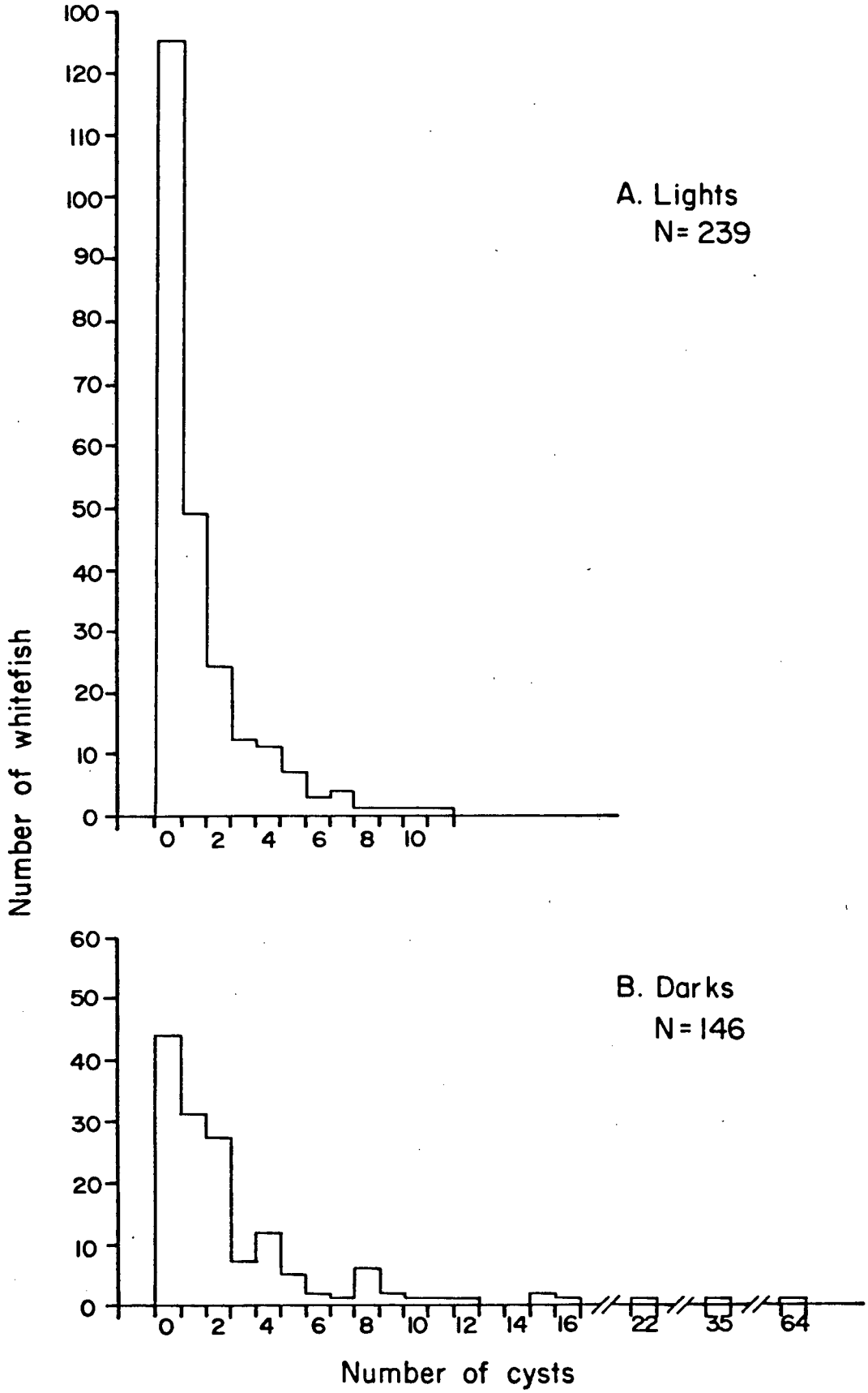
Table 15. *Triaenophorus crassus* cyst counts of lake whitefish from various regions of Southern Indian Lake. (Number of individuals examined in brackets).

Year	Source	Region	Mean cyst count	Mean weight (lbs)
1952	McTavish	1	1.15 (117)	3.4
		2 & 3	1.04 (92)	3.9
		4	0.75 (99)	3.5
		5	3.78 (14)	2.4
		6	0.82 (39)	2.2
1963	Sunde	1	0.27 (30)	3.3
		2	0.34 (30)	3.2
		3	0.53 (30)	3.0
		4 - south of Missi	0.36 (135)	2.5
		4 - north of Missi	0.52 (60)	2.8
1975-76	Watson (1977)	1 & 6	0.81 (486)	(weights not given)
1978	Bodaly et al. (1983)	4	0.54 (248)	1.23
		5	0.91 (99)	0.91
1979	Bodaly et al. (1983)	4	0.88 (495)	1.13
		5	1.22 (361)	1.37
1982	Bodaly et al. (1983)	4	1.13 (587)	1.72
		5	1.93 (520)	1.01
		6	1.46 (108)	0.78

Table 16. Mean *Triaenophorus crassus* cyst counts of light and dark lake whitefish in experimental catches, 1963, 1978, 1979, 1982, Southern Indian Lake.

Source	Year	Region	Colour	Sample size	Mean cyst count	Variance	Significance
Sunde (1963)	1963	1,2,4	lights	254	0.41	0.60	t = 0.375, 283 d.f.
			darks	31	0.35	0.68	n.s.
Bodaly et al. (1983)	1978	5	lights	90	0.87	1.52	t = 1.909, 95 d.f.
			darks	7	1.71	1.06	$p<.05$
	1979	5	lights	222	1.21	3.83	t = 1.692, 242 d.f.
			darks	22	0.77	1.08	$p<.05$
	1982	5	lights	239	1.24	3.80	t = 3.403, 383 d.f.
			darks	146	3.18	45.12	$p<.005$

Fig. 19. Triaenophorus crassus cyst count distributions of lake whitefish from region 5, Southern Indian Lake, 1982 (Bodaly et al. 1983). A. Lights, B. Darks.


A. Lights
N= 239
B. Darks
N= 146
Number of whitefish
Number of cysts
100
120
110
100
90
80
70
60
50
40
30
20
10
0
0 2 4 6 8 10
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 22 35 64

Cyst count frequency distributions for lights and darks captured in region 5 in 1982 are significantly different (χ^2 = 26.37, 6 d.f., $p<0.005$) (Fig. 19). However, in both cases the mode is 0 cysts.

Regional Differences in Mean Cyst Counts Among Light Whitefish

Mean cyst levels of light whitefish in regions 5 and 6 were higher than those of lights captured in region 4 in 1982 (Table 17). The difference between the mean counts for regions 4 and 6 is statistically significant.

Conclusion

There are consistent regional differences in whitefish cyst levels in SIL. Cyst count is correlated with colour in that dark fish tend to have higher average cyst levels than light fish, however for both darks and lights the modal count is 0 cysts. Light whitefish from different regions of the lake have different cyst levels. This indicates that there is not a direct causal connection between cyst count and pigmentation, and the observed overall regional differences in cyst counts are not entirely due to the presence or absence of darks.

Table 17. Mean *Triaenophorus crassus* cyst counts of light lake whitefish from regions 4, 5 and 6, Southern Indian Lake, 1982 (Bodaly et al. 1983). Means of samples from Regions 4 and 6 are significantly different ($t = 1.762$, 664 d.f.; $t_{.05} = 1.645$).

Region	Sample size	Mean cyst count	Variance
4	558	1.09	3.17
5	239	1.24	3.80
6	108	1.46	4.01

DISCUSSION

Colour Classification of Adult Whitefish

Observed colour differences between so-called light and dark whitefish are real and result from differences in the amount of pigment in the skin (as measured by melanophores per unit area).

The subjective method of colour classifying SIL whitefish, introduced by FFMC as a way of grading commercial catches and followed by F. and O. personnel in classifying experimental catches, is imperfect. For four different groups of observers the error rate in colour classifying experimental whitefish catches ranged from 0 to 50%. In most cases the error rate was higher for dark than for light whitefish (there were more fish with low melanophore counts classified as darks than there were fish with high melanophore counts classified as lights).

There are two main sources of error in subjective colour classification of whitefish. One is human. Colour assessment is relative in that fish are compared to one another not to a standard colour scale. An observer's judgement may be biased if s/he is accustomed to seeing only one type or if s/he desires to catch one particular colour of fish. Experience of the observer in colour classifying whitefish may also be a factor.

The second source of error is created by the ability of fish to effect short-term colour change through redistribution of melanin granules in the melanophores. These transitory colour changes (so named by Sumner (1940)) are rapid (in some species occurring within seconds or minutes) and are evoked by any one of several stimuli including light, background colour and a multitude of physical, chemical and pharmacological agents (Brown 1962; Fujii 1970).

Light, in conjunction with background colour, is the most important environmental factor influencing chromatophore systems of animals (Brown 1962). The shade of a fish when it is caught may depend on light and background conditions at that particular time. Badcock (1969) described light and dark pigment forms of the mesopelagic fish Valencienellus tripunctulatus and showed that the extent of pigmentation was related to light conditions prevailing at the time of capture. The light form was caught during the day, the dark form at night. Jenkins, Jr. (1969) observed that Salmo trutta and S. gairdneri in streams both showed lightening and darkening in response to bottom colour and light intensity.

In this study, examination of the scale melanophores of misclassified whitefish showed that classification errors were correlated with melanophore configuration. Pigment granules in fish which were classified as lights but which had high melanophore counts were generally aggregated, whereas pigment in fish which were classified as darks but which had low counts was generally dispersed. Melanophore counts of misclassified whitefish ranged from a low of 36 melanophores/2 mm^2 for a fish subjectively classified as a dark to a high of 148 melanophores•2 mm^2 for one classified as a light, indicating the high degree of control whitefish can have over their observed colour.

The choice of 80 melanophores•2 mm^2 as the division between lights and darks was based on the fact that there is a distinct peak at 80-84 melanophores•2 mm^2 in the melanophore count distribution for the total sample of whitefish (Fig. 5). Use of this criterion for classifying all

whitefish, regardless of size and age, may bias the numbers in favour of lights (for example, when comparing total numbers of each colour class, age distributions, etc.). Young and/or small darks may have fewer melanophores than this and thus be erroneously counted as lights. To avoid this error ideally one should compare melanophore counts of fish within narrow age/size classes. Because the number of young, small fish captured in this study was low compared to the total number of fish this kind of comparison was not made.

Distribution of Colour Classes of Whitefish In SIL

The lake-wide distribution of light and dark-coloured whitefish in SIL is not homogeneous and has been consistent over time. Impoundment of the lake appears not to have markedly affected the spatial distribution patterns of lights and darks in relation to one another.

Dark whitefish are most abundant in region 5, have a restricted occurrence in region 4 and are absent from region 6 (Fig. 9). Distribution of the two colour classes is correlated with limnological conditions. On a lake-wide scale, dark whitefish occur in shallow, clear, dark-coloured water; light whitefish occur in deep, clear or turbid, light-coloured water or shallow, turbid water.

The lake-wide distribution of light and dark-coloured young-of-the-year whitefish parallels that of adults. Young-of-the-year from region 5 are more pigmented than those from regions 4 and 6. The latter are not significantly different from one another.

Because both lights and darks occur in region 5 one might expect the colour distribution of region 5 young-of-the-year to be bimodal. This was not found, possibly because the kind of sample required (a

large sample of fish of similar size from different parts of the region) was not available.

Populations of dark coloured whitefish have been reported to occur in shallow, near-shore areas of several large North American lakes (Rawson 1947a, 1947b; Imhof 1977). In SIL where lights and darks occur together (region 5) their vertical and areal distribution patterns differ significantly. Lights are benthic in habit, concentrated at the bottom, while darks are apparently somewhat more pelagic. This finding is corroborated by the observation that darks have a higher percentage of pelagic food items in their diet than do lights (33% compared to 15%, respectively) (R.A. Bodaly, unpublished data). Lights were slightly more abundant offshore than onshore, but darks were almost twice as abundant onshore than offshore.

There were changes in the numbers of lights and darks captured in region 5 from summer to fall, 1982. In July, light whitefish predominated in the catch whereas in September and October darks did. There are several possible explanations for this change.

The first is that different sites were fished in the fall than in the summer. The same general area was fished both times and in some cases the same net sites were used (Figs. 2 and 3). Most of the fall sets were onshore and darks are more abundant onshore than offshore, but in July absolute numbers of lights captured onshore were greater than numbers of darks (Fig. 10). Use of different sites is thus not a likely explanation.

A second possibility is that when light whitefish move onshore to spawn (in region 5) they change colour. There were many intermediate-coloured whitefish in the fall catches whose melanophore

counts are not known and which could have been within either the light or dark range. Larval whitefish under appropriate conditions show significant darkening in less than two weeks (re. - Environmental Alteration of Colour). Therefore if an adult light spent sufficient time on the spawning grounds it might undergo significant colour change. Definitely light-coloured fish were captured onshore in both summer and fall indicating that such a change does not necessarily happen or does not happen very quickly. However, this possibility cannot be totally discounted.

A third explanation is that some lights left the area, perhaps to spawn elsewhere. Migration of whitefish to particular areas at spawning time has been noted by Budd (1956) in Lake Huron and by Qadri (1968) in Lac La Ronge. Ayles (1976) suggested that changes in whitefish distribution in SIL in early September might be due to migration to specific spawning locations, particularly in region 4. Possibly, by the time of the fall sampling, some region 5 lights had migrated to spawning locations outside of the area sampled, while darks remained in the area.

Morphology and Biochemistry of Adult Light and Dark Whitefish

Light whitefish tend to have larger heads and eyes, more gill rakers and slightly better growth than dark whitefish. Though these differences are not pronounced they are consistent with some of the findings in the literature.

The generally expected correlation between head and eye size and growth rate is that slower growing fish have larger heads and eyes than faster growing ones. This relationship was noted in whitefish by Kliewer (1970), Svardson (1970) and Loch (1974). In contrast, as in the

present study, Bodaly (1977) found that growth rates of two whitefish forms in Yukon lakes were similar initially, then diverged. The slower-growing form had smaller head and eye size than the other.

Eye size may also be correlated with water transparency and depth at which fish feed (Kozikowska 1961). Kliewer (1970) observed that within a group of seven Manitoba lakes, the whitefish with the largest eyes came from the two lakes with the lowest Secchi disc readings. In SIL, light whitefish, with larger eyes, are found at the lake bottom (in region 5) and in turbid water (throughout the lake). Presumably larger eyes are advantageous to fish living under conditions of reduced light.

Gill raker number, type of food eaten and growth rate often appear to be related such that fish with fewer gill rakers tend to eat primarily benthic in contrast to pelagic food types and exhibit better growth (Svardson 1952, 1965, 1970; Bodaly 1977). Kliewer (1970), however, found a correlation between more gill rakers, benthic food and better growth. This corresponds to findings for region 5 light whitefish which have higher modal gill raker counts, a higher proportion of benthic food types in their diets and somewhat better growth rates than dark whitefish.

Though there were significant differences between lights and darks in some morphological characteristics the separation between them was not enough to make these characters useful in discerning one from the other. There was scatter in the data and the 95% confidence intervals for the regression lines were generally wide.

There is historical evidence from biochemical data of genetically distinct whitefish stocks in SIL. Before impoundment and Churchill River diversion there were regional differences in G-3-PDH allele

frequencies among whitefish in the lake. However, after flooding there were no significant regional differences (Bodaly et al. 1984a). No differences in numbers of hemoglobin or G-3-PDH alleles were found between light and dark whitefish from region 5.

Neither the results of the morphological analysis nor those of the biochemical analysis give strong evidence for genetic isolation of light and dark whitefish or support for the idea that they are separate subpopulations. Morphological characteristics of whitefish are known to be highly influenced by environmental conditions (Svardson 1952, 1970). Even gill raker number, which has a high hereditary component, is subject to some direct phenotypic modification (Lindsey 1981). The observed morphological differences between light and dark whitefish may be phenotypic responses induced by inhabiting somewhat different environments.

Inheritance of Colour

There are numerous descriptions in the literature of colour differences in fish, some known to be genetic in origin, though none involving whitefish. There are at least five colour variants of the rainbow trout, Salmo gairdneri, and the mode of inheritance of colour is partly understood (Kincaid 1975; Klupp and Kaufmann 1979). In some variants colour is pleiotropically associated with other traits, for example, activity rate and sensitivity to light (Clark 1970) and growth rate (Kincaid 1975). Cichlasoma nigrofasciatum occurs as two colour phenotypes, dark grey and pink, the former due to a dominant allele, the latter recessive (Itzkovich et al. 1981). The guppy, Poecilia reticulata, exhibits various patterns of colouration. Three

melanic guppy colour patterns were genetically analysed by Nayudu (1979). He found that each of the three has single gene inheritance, is determined by a different locus, is sex-linked on both the x and the y chromosomes and is dominant in expression in both sexes. Two of the genes showed epistatic interactions with other traits.

Takeda et al. (1978) found four atypical colour patterns among specimens of char, Salvelinus leucomaenis. Electrophoretic and morphometric evidence indicated that these were colour variants as opposed to hybrids between S. leucomaenis and other salmonid species. Similarly, Graves and Rosenblatt (1981) concluded from electrophoretic evidence that ten colour morphs of the hamlet, Hypoplectrus unicolor, represent a single species polymorphic for colour, as opposed to separate species.

In this study melanic colouration in lake whitefish was found to be inherited to some degree. The mode of inheritance was not investigated. Heritability estimates for colour from the regressions of mean larval dorsal melanophore count on male parent scale melanophore count at 92 and 111 days were 0.14 and 0.10, respectively. Heritability estimates for various traits in other species are given in Table 18. The values for colour in whitefish are comparable to those for reproductive traits like growth rate and litter size.

Estimation of the genetic contribution to a particular trait may be confounded by environmental influences. In this study, variability in the external environment in which the eggs were incubated and the larvae reared was controlled as much as possible. Certain conditions did vary, for example, temperature in individual egg jars and position of egg jars in the water bath. However neither factor showed a relationship with larval melanophore count.

Table 18. Approximate values of the heritability of various characters in some mammals, birds and fishes.

Source	Species	Trait	Heritability
Falconer 1960	cattle	conception rate	.01
	poultry	viability	.10
	pigs	litter size	.15
	mice	litter size	.15
	rates	age at puberty in females	.15
Ayles 1974	splake	survival of eyed egg	.09 ± .11
		survival of alevin	.41 ± .18
		resistance to blue sac disease	.76 ± .28
Gjedrem 1975	rainbow trout fingerlings	growth rate	.09-.32
	salmonids	growth rate	.10-.20
	carp	growth rate	.10-.20
	salmon	vibrio disease resistance	.07-.10

Maternal effects, which are pre- and post-natal influences of the mother on her young, are environmental influences which could not be controlled. Maternal effects are especially important in mammals (Falconer 1960), but may be marked in fish as well. Ayles (1974) attributed 68-78% of the variance in survival of splake hybrids (Salvelinus fontinalis x S. namaycush) during the egg stages to maternal effects.

Heritability estimates given by the regression of offspring on female parent value were generally slightly higher than those given by offspring on midparent and substantially higher than those given by offspring on male parent, indicating a maternal effect on offspring colour. If the differences in melanophore counts between progeny of different crosses were strictly due to maternal effects one might expect the mean counts for offspring of homozygous and heterozygous crosses to be equal. At 111 days there was no statistically significant difference between mean dorsal melanophore counts for DD and D♀L♂ crosses ($\bar{x}$ = 58.12 and 55.72 melanophores), but the means for LL and L♀D♂ crosses were significantly different from each other ($\bar{x}$ = 46.58 and 5.87 melanophores, t = 2.046, 166 d.f., $p<0.05$). Also, if offspring colour were strictly due to maternal effects one might expect the heritability estimates given by the regression of offspring on father to be negligible. In two cases, the estimated heritability was in fact low, but at 111 days it was 0.10 and at 92 days it was 0.14, which is equal to that given by the regression of offspring on mother.

The heritability estimate from the regression of offspring melanophore count at 119-126 days on father's scale melanophore count

was very low (0.0008). The low value of this estimate may be due in part to poor sampling technique. The set 1 crosses (3 DD and 2 D♀L♂) were sampled at 119 days post-fertilization while the other sets were sampled at 126 days. A week is probably long enough for significant change in larval melanophore count to occur. Including the 119 day with the 126 day samples might decrease the slope of the regression line thus reducing the heritability estimate.

Environmental Alteration of Colour

The ability of fish to change colour through movement of pigments in specialized cells (chromatophores) in response to environmental changes or conditions has long been of interest to researchers (for example, Cunningham and MacMunn 1893).

Two general types of chromatophore response are recognized - physiological and morphological colour changes. The former are alterations in external colouration produced by changes in the distribution of pigment in the chromatophores. They are relatively rapid and are evoked by any one of many stimuli. The latter arise from quantitative changes in pigmentation, that is, increases or decreases in the number of chromatophores or the amount of pigment they contain. They are gradual and inconspicuous but may finally be more marked than changes due to pigment migration. Sumner (1940) argued that the terms "physiological" and "morphological" colour change, which were introduced by Sécérov (1909, in Sumner (1940)), were unclear as both processes are physiological. He suggested that the names "transitory" and "quantitative" were more appropriate. The nomenclature of Sumner will be adopted here.

There are several kinds of chromatophores and various chromatic pigments (Fujii 1970; Fox 1957). Melanophores, which are of primary interest in this study, are brown or black and contain melanins - oxidized, polymerized end-products of tyrosine metabolism. With carotenoids, which give erythrophores and xanthophores their red and yellow colour, melanins are primarily responsible for external colouration of fishes (Fox 1957). The colour responses of lake whitefish described above involve melanophores.

Early researchers noted that fish kept for extended periods under conditions which caused transitory colour change eventually underwent quantitative colour change (Odiorne 1933; Sumner and Wells 1933; Sumner 1940; Osborn 1941a). Initial theories postulated a causal relationship between the two. However, it is now believed that the conditions which bring about transitory change will, if maintained, cause quantitative change. Quantitative colour changes arise not from transitory changes themselves, but from the operation of the agents which produce the latter (Odiorne 1957; Ahmad 1972, and references therein).

Transitory colour change may be controlled by blood-borne hormones or nervous pathways or both. Hormonal control is phylogenetically older and is present in cyclostomes, elasmobranchs and chondrosteans (Krasnodemskaya 1978). In teleosts it is replaced or supplemented by direct nerve stimulation of the melanophores. Pituitary hormones, possibly melanophore stimulating hormone (MSH), are thought to control melanin dispersion in fish (Fujii 1973). A melanophore concentrating hormone (MCH) from the pituitary has been proposed, but its existence has not been substantiated (Fujii 1970). There is some evidence that pineal melatonin may function in melanin concentration (Hafeez 1970; Smith and Weber 1976).

The dominant control mechanism for colour change in teleosts is nervous (Scott 1965). In 1911, von Frisch (cited in Iwata and Fukuda (1973)) discovered that sympathetic neurones controlled pigment aggregation. Subsequent researchers have argued for (Parker 1943; Robertson 1951; Ahmad 1972, 1974) and against (Scott 1965) the presence of dispersing fibres. Iwata and Fukuda (1973) traced the nervous pathways from the retina to the melanophore in the crucian carp (Carassius carassius). They found that the systems controlling movement of melanophore pigment are mononeuronic in the peripheral system (aggregating fibres) and dineuronic in the central system, one set of nerves exciting the peripheral aggregating motor neurones (when the fish is on a light background), the other set inhibiting them, thus allowing pigment dispersion (when the fish is on a dark background).

There is evidence that the hormonal and neural pathways involved in transitory colour change also regulate quantitative colour change (Osborn 1941b; Fujii 1970; Ahmad 1974).

A multitude of physical, chemical and pharmacological agents have been found to affect the state of pigment dispersion in melanophores (see reviews by Fujii 1970, 1973). However, the most important single environmental factor influencing pigment systems of animals is light (Brown 1962). There are two types of chromatic response to light, primary and secondary. The former occur by direct action of light on the chromatophores or through an extraocular receptor, and predominate in embryos, larvae with underdeveloped eyes and blinded fish. Pigment disperses in light and concentrates in darkness. Secondary responses are controlled by way of the eyes and allow adaptation to the background. Pigment disperses on a dark background in light and

concentrates on a light background in light. In most adults the secondary response is dominant (Brown 1962).

Apparently a fish adjusts to the background colour by responding to the relative amounts of illumination received from above and below, that is, the ratio of incident to reflected light (Sumner and Keys 1929; Sumner and Doudoroff 1937; Sumner 1940). The retina is differentiated to a certain degree, the dorsal portion associated with the paling response, the ventral portion with darkening (Sumner 1933; DeGroot et al. 1969; Iwata and Fukuda 1973). At very low light intensities (<1.75 foot-candles) fish respond to illumination regardless of background colour (Brown 1936); in complete darkness they become pale (Sumner 1940).

The time required for transitory colour change is highly variable between species. For example, in Crenilabrus it takes a few seconds; in Fundulus, 1 to 2 minutes; in Ameiurus, 1 to 3.5 hours; and in Anguilla, more than 20 days (Odiorne 1957). Neill (1940) gave the general rule that if the total time for transitory colour change is less than 10 minutes control is nervous; if the time is more than 2 hours control is hormonal.

Transitory colour change in response to light or background colour is fully reversible (though paling and darkening responses may not occur in the same length of time (Neill 1940)), requiring only that the conditions which caused the change be reversed.

Noticeable quantitative colour change can occur within 7-15 days, though it may be 3-4 weeks before the change is complete (Odiorne 1933; Sumner and Wells 1933; Ahmad 1974).

There is some evidence that quantitative colour change may not always be entirely reversible, or at least that complete reversal may take a long time. Sumner and Wells (1933) found that guppies (Lebistes reticulatus) born and reared on a white background showed an extreme condition of depigmentation never attained by those which had been reared in a normal environment and then as adults subjected to a white background for 3 months (maximum exposure time in their experiment). Stickney and White (1975) observed that over a 3 month experimental period five of twenty moderately ambicolourate flounders (Paralichthys dentatus) entirely lost their ambicolouration; the rest retained it to a light or moderate degree. (Ambicolouration refers to the development of pigmentation on the underside of the fish.) Love (1974) held light and dark-coloured cod (Gadus morhua) from different grounds in the Atlantic together in an aquarium for 8 1/2 months. The fish maintained their colour differences. Love did not know whether the colour difference was genetic or environmental, but thought that it might be a response to background colour (light-coloured cod came from a bank where the substrate was brilliant white sand).

The results of this study of colour change in lake whitefish may be summarized as follows -

1. Larval and adult lake whitefish are capable of rapid transitory colour changes. As these occur within minutes they are probably under neural control.
2. When kept for an extended period under conditions which cause transitory darkening, larval whitefish undergo quantitative colour change (become more pigmented).
3. Larval whitefish respond to total darkness by blanching.

These results are all consistent with chromatic responses of other fish species reported in the literature, as described above.

There has been at least one other study on the chromatic behaviour of larval coregonids, that by Koller (1934). Duspiva (1931) reported that light intensity was the main stimulus for colour change for the larvae of Perca fluviatilus, Salmo salvelinus, Abramis brama and Leuciscus rutilus. This prompted Koller (1934) to test the chromatic responses of larval Coregonus lavaretus and C. holsatus. He found that, unlike those species investigated by Duspiva, both responded to background colour as opposed to light intensity.

The colour of lake whitefish in SIL is partly under genetic control, but appears to have a large environmental component as well. The physical limnology of regions 4, 5 and 6 of SIL has been described above (Study Area and Distribution of Colour Classes of Whitefish in SIL). Fish respond chromatically to ambient light conditions and to the colour of their surroundings. Thus, the important characteristics of the water in the three basins are clarity (measured by suspended sediment concentrations, vertical extinction coefficients and Secchi disc readings) and colour.

The water in region 5, where there are many dark-coloured whitefish (and dark-coloured fish of other species, for example, northern pike (Esox lucius) and walleye (Stizostedion vitreum)), is clearer and much darker in colour than the water in regions 4 and 6. A fish in region 5, at shallow depths and swimming off the bottom, is essentially in dark surroundings with light from above. Presumably, in order to match its background its colour darkens. At greater depths, where light is at very low intensity or extinct, the chromatic response of the fish would be to remain pale.

In regions 4 and 6, the water is turbid and light in colour. Fish blanch in response to light-coloured surroundings and under conditions of very reduced light, such as would be produced by high turbidity. Thus, one would expect the whitefish in these regions to be light in colour.

Brown (1936) reported that fish taken from the Illinois River are pale in colour when the water is silty and dark when the water is clear. He suggested that fish swimming off the bottom in clear water are on the equivalent of a black background since almost no light is reflected from below, and that the silt in turbid water both reduces incident light and augments the reflected light entering the eyes of the fishes, thus prompting the paling response.

Knowing that fish colour (lightness or darkness) is plastic, the question of colour stability of SIL whitefish arises. In comparing the characteristics and habits of light and dark-coloured whitefish one makes an assumption about their phenotypic history - that a light fish has always been light and a dark fish has always been dark.

Transitory colour change is completely reversible. Whitefish are capable of marked transitory colour change. Thus, for example, a light whitefish (one with a low scale melanaphore count) can appear either light or dark according to its surrounding at a given time. Theoretically, quantitative change should be reversible too, although in a much longer period of time. However evidence from studies cited above (Sumner and Wells 1933; Stickney and White 1975) suggest that it may not be. Love (1974) observed that the colour differences between light and dark cod (*Gadus morhua*) were very stable.

Loss of melanophores may be temperature dependent. Odiorne (1933) found that killifish (Fundulus heteroclitus) kept in light surroundings at 10°C showed only a slight reduction in melanophores over several weeks. At 20°C melanophore degeneration set in quickly. In SIL temperatures at 5 m depth in region 5 in July 1982 averaged about 12.5°C, which may be too cool for significant melanophore loss to occur. According to the results of the long-term colour change experiment significant increases in melanophore numbers can occur at temperatures of 10°-11°C.

If colour of whitefish in region 5 was totally unstable and if any fish could be a quantitative light or dark depending on conditions at the time, one might not expect to find any other differences between lights and darks. However, results of the comparison of morphological characteristics of adult light and dark whitefish showed that there are some morphometric and meristic differences between them. Also, the breeding experiment showed that colour is in part inherited. These results support the idea that colour of lights and darks has some stability.

Triaenophorus crassus Cyst Levels of SIL Whitefish

The regional differences observed in lake whitefish cyst counts are correlated with differences in water depth and abundance of northern pike (Esox lucius) and cisco (Coregonus artedii).

Rawson (1947a, 1947b) reported that lake whitefish taken from shallow, near-shore areas of Great Slave Lake and Lake Athabasca had much higher T. crassus levels than did fish from deeper, offshore waters. According to Lawler (1970) it is a general rule that whitefish

from shallow areas are more heavily infected than those from deeper water. In SIL, whitefish with the highest cyst levels came from region 5, which has a post-flooding mean depth of 5.9 m, while those with the lowest levels came from region 4, which has a post-flooding mean depth of 13.0 m. Region 6, where whitefish in experimental catches had intermediate mean cyst levels, has a post-flooding mean depth of 5.8 m (McCullough 1981).

The northern pike is the adult host and the cisco is the preferred intermediate host of T. crassus. Catch per unit of effort statistics from 1982 (Bodaly et al. 1983) show that pike are twice as abundant and cisco almost four times so in region 5 as in region 4. There are more pike but fewer cisco in region 6 than in region 4.

Data from experimental fishing show that dark whitefish generally have higher mean cyst counts than do light whitefish. There does not, however, appear to be a causal relationship between high cyst count and dark colouration, for several reasons. The modal cyst count is zero for both light and dark whitefish and approximately three-quarters of all whitefish have counts of 0, 1 or 2 cysts, regardless of colour (Fig. 19). According to MacLaren (1978), in 1969 SIL was zoned into three areas based on whitefish grade as determined by cyst levels. Fish from region 6 were classed as "cutters", the lowest grade. Fish from region 4 north of Missi Rapids and region 5 were classed as "continental" or second grade. Distribution data shows that region 6 whitefish are all light in colour, as are many of those from the northern half of region 4 (Fig. 9). Furthermore, the results of this study have shown that differences in external colouration between lights and darks from SIL are partly genetically determined and partly environmentally induced.

If individual level of infection is not causally related to colour the question concerning the basis of the average correlation remains.

The regional differences in cyst counts among lights suggest that mean cyst levels may be related to conditions in the particular region. Certain characteristics of region 5 are known correlates of higher cyst levels - shallow water and large pike and cisco populations. Limnological conditions in region 5 promote dark colouration of fish - shallow, clear, dark-coloured water. Finally, the habits of dark whitefish probably make them more susceptible to infection - they prefer onshore, shallower areas, they are slightly more pelagic in distribution than are lights, and they have substantially more pelagic-type food items in their diets than do lights.

Whitefish do not generally accumulate T. crassus cysts with increasing age (past 2-3 years) because of dietary changes from planktonic to benthic (Miller 1952, cited in Watson (1977)). Because of this, mean cyst count generally decreases in whitefish samples as mean size increases (MacLaren 1978). However, Petersson (1971) found that high raker whitefish (Coregonus peled and C. oxyrhynchus) with a high frequency of plankton in the diet did accumulate T. crassus plerocercoids with age and were more heavily infected than were low raker fish which fed mainly on the bottom. Bodaly et al. (1984) calculated mean cyst count per pound of whitefish of round weight >1.8 lb (commercial size) captured in experimental catches in regions 4 and 5, 1978-1982 (Table 19). Mean cyst count per pound is generally low, except for the fish captured in region 5 in 1982. All fish included in this subsample were classified as darks. The mean weight of fish in the subsample (2.28 lb, N = 62) is higher than that for the total catch of

Table 19. *Triaenophorus crassus* cyst counts in experimental catches of lake whitefish, regions 4 and 5, Southern Indian Lake, 1978-1982. Fish of round weight >1.8 lbs only sampled and catches of total round weight approximately 14.5 lbs only considered (Bodaly et al. 1984). Number of fish sampled in brackets

Year	Region	Mean cysts per lb	Mean weight (lb)
1978	4	0.07 (64)	2.15
	5	0.48 (20)	2.20
1979	4	0.32 (93)	2.11
	5	0.46 (92)	2.39
1982	4	0.36 (78)	2.31
	5	2.04 (62)	2.28

darks in region 5 in 1982 (1.47 lb, N = 146). However the mean cyst counts per lb of the subsample and the total catch are almost equal (2.04 vs 2.16, respectively).

Thus the inverse relationship between age/size and cyst count does not necessarily hold for dark whitefish. This could be because darks continue to be somewhat pelagic in habit as they get older and thus continue to accumulate *T. crassus* cysts.

Functional Significance and Adaptive Value of Colour

Chromatic responses in animals may serve in several capacities - protective colouration, thermoregulation, mating displays and parental care, protection of the body from harmful illumination (Fingerman 1965), communication of psychic state (for example, fright, aggression) to conspecifics (Lanzing and Bower 1974).

Probably the most widespread function of colour change in fish is that of concealment. There are numerous descriptions of crypsis in fish, but few test of the theory. A fish may conceal itself by mimicking substrate colour or pattern (Jenkins, Jr. 1969; Lanzing 1977), vegetation conspecifics (McFarland et al. 1979), prey (Kaufman 1976), or by adjusting to ambient light conditions in deep water (Badcock 1969). These examples involve transitory colour changes in which a fish may "select" from a number of available patterns that which is most appropriate to conditions at a given time.

Sumner (1935) presented experimental evidence for the protective value of changeable colouration in fish. He exposed black and white-adapted mosquito fish (*Gambusia patruelis*) in black or white tanks

to piscivorous birds, both diving and wading species. Those fish which matched the background were less vulnerable to predation than were those which contrasted with it.

Colouration of whitefish in SIL may be an adaptation for concealment. In shallow, clear, dark-coloured water (region 5) a dark-coloured fish would presumably be less visible, thus less vulnerable to predators.

CONCLUSION

There are quantifiable differences in melanophore numbers to support the subjective classification of SIL whitefish into lights and darks. Mean scale melanophore counts of fish subjectively classified as lights and darks were significantly different. Lights are quantitatively defined as having scale melanophore counts <80 melanophores•2 mm^2 while darks have counts $\geq$80 melanophores•2 mm^2.

There are differences in spatial distribution of lights and darks within SIL. Lights are found throughout the lake and predominate in regions 3, 4 and 6; darks occur mainly in region 5. Within region 5, lights were most abundant offshore and on the lake bottom, darks were more numerous onshore than offshore and were more often caught off the bottom. Young-of-the-year from region 5 were darker in colour than those from regions 4 and 6.

There were significant differences between lights and darks in several morphometric characters and in lower gill raker numbers. There were no significant differences between them in two biochemical characters (Hb and G-3-PDH) examined. The evidence does not suggest clear-cut separation into reproductively isolated stocks.

There is some hereditary basis to colour differences between lights and darks such that dark parents produce darker offspring than do light parents. Heritability estimates show that there is a genetic component to colour differences which is independent of environmental or maternal effects. At 111 days post-fertilization h^2 measured by the regression of offspring on male parent value was comparable to estimates for reproductive traits like growth rate and litter size.

Colour of larval lake whitefish is subject to environmental alteration. Rapid short-term colour changes are effected through redistribution of melanin granules in the melanophores. Over the long-term colour is altered through changes in melanophore number. Adult whitefish are also capable of rapid short-term colour change.

Colour differences between SIL whitefish are correlated with infection by *T. crassus* cysts in that darks tend to have higher average cyst levels than lights. However, as both lights and darks have modes of 0 cysts and as there are regional differences in cyst levels of lights, there does not appear to be a causal connection between cyst count and pigmentation. Darks, because of their distribution patterns and dietary preferences, may be more susceptible to infection than lights.

REFERENCES

Ahmad, R.U. 1972. Quantitative ("morphological") colour changes on prolonged black & white background adaptations of the minnow Phoxinus phoxinus (L.) & the effects of chromatic spinal section on these colour changes. J. Comp. Physiol. 77: 170-189.

Ahmad, R.U. 1974. Transitory colour changes in the new melanophores formed by quantitative colour change in the minnow Phoxinus phoxinus. J. Zool. Lond. 174: 285-313.

Ayles, G.B. 1974. Relative importance of additive genetic and maternal sources of variation in early survival of young splake hybrids (Salvelinus fontinalis x S. namaycush). J. Fish. Res. Board Can. 31: 1499-1502.

Ayles, H.A. 1976. Lake whitefish (Coregonus clupeaformis (Mitchill)) in Southern Indian Lake, Manitoba. Tech. Rep. Fish. Mar. Serv. Res. Dev. 640. 34 pp.

Badcock, J. 1969. Colour variation in two mesopelagic fishes and its correlation with ambient light conditions. Nature 221: 383-385.

Bodaly, R.A. 1977. Evolutionary divergence between currently sympatric lake whitefish, Coregonus clupeaformis, in the Yukon Territory. Ph.D. thesis, University of Manitoba. 119 pp.

Bodaly, R.A. 1979. Morphological and ecological divergence within the lake whitefish (Coregonus clupeaformis) species complex in Yukon Territory. J. Fish. Res. Board Can. 36: 1214-1222.

Bodaly, R.A., C.J.Hrenchuk, and R.J.P. Fudge. 1983. Post-impoundment experimental fishing, Southern Indian Lake, Manitoba: Catches (1982) and Triaenophorus crassus cyst counts in lake whitefish (1978, 1979, 1982). Can. Data Rep. Fish. Aquat. Sci. 401: vi + 75 pp.

Bodaly, R.A., T.W.D. Johnson, and R.J. Fudge. 1980. Post-impoundment changes in commercial fishing patterns and catch of lake whitefish (Coregonus clupeaformis) in Southern Indian Lake, Manitoba. Can. MS Rep. Fish. Aquat. Sci. 1555: iv + 14 p.

Bodaly, R.A., T.W.D. Johnson, R.J.P. Fudge, and J.W. Clayton. 1984. Collapse of the lake whitefish fishery in Southern Indian Lake, Manitoba, following lake impoundment and river diversion. Can. J. Fish. Aquat. Sci. 41: 692-700.

Bodaly, R.A., D.M. Rosenberg, M.N. Gaboury, R.E. Hecky, R.W. Newbury, and K. Patalas. In press. Ecological effects of hydroelectric development in northern Manitoba, Canada: The Churchill-Nelson River diversion. In Sheehan, P.J., D.R. Miller, G.C. Butler and Ph. Bourdeau (eds.) Effects of Pollutants at the Ecosystem Level, SCOPE 22. John Wiley & Sons, Chichester, New York, Brisbane, Toronto.

Brown, F.A., Jr. 1936. Light intensity and melanophore response in the minnow, Ericymba buccata Cope. Biol. Bull. Mar. Biol. Lab. 70: 8-15.

Brown, F.A., Jr. 1962. Chromatophores and color change, p. 502-537. In C.L. Prosser and F.A. Brown, Jr. Comparative Animal Physiology. W.B. Saunders Co., Philadelphia.

Budd, J. 1956. Movements of tagged whitefish in northern Lake Huron and Georgian Bay. Trans. Am. Fish. Soc. 86: 128-134.

Clark, F.H. 1970. Pleiotropic effects of the gene for golden color in rainbow trout. J. Hered. 61: 8-10.

Clayton, J.W., W.G. Franzin, and D.N. Tretiak. 1973. Genetics of glycerol-3-phosphate dehydrogenase isozymes in white muscle of lake whitefish (Coregonus clupeaformis). J. Fish. Res. Board Can. 30: 187-193.

Cunningham, J.T., and C.A. MacMunn. 1893. On the coloration of the skins of fishes, especially of Pleuronectidae. Phil. Trans. Royal Soc. Lond. Ser. B. Biol. Sci. 184: 765-812.

Duspiva, F. 1931. Beitrage sur Physilogie der Melanophoren von Fischembryonen. Akad. Wiss. Wien, Math.-naturw. kl, Sitzunber. Abt. 1, 140: 553.

Falconer, D.S. 1960. Introduction to Quantitative Genetics. The Ronald Press Co. New York. 365 pp.

Fingerman, M. 1965. Chromatophores. Physiol. Rev. 45: 296-339.

Fox, D.L. 1957. The pigments of fishes, p. 367-385. In M.E. Brown (ed.) The Physiology of Fishes, Vol. II Behavior Academic Press Inc., New York. 526 p.

von Frisch, K. 1911. Beitrage zur Physiologie der Pigmentzellen in der Fischhaut. Pflugers Arch Ges Physiol. 138: 319-387.

Fujii, R. 1970. Chromatophores and pigments, p. 307-353. In W.S. Hoar and D.J. Randall (ed.) Fish Physiology. Vol. III. Academic Press, New York.

Fujii, R. 1973. Responses of fish pigment cells to environmental changes. p. 342-362. In W. Chavin (ed.) Responses of fish to environmental changes. Proceedings of a United States-Japan seminar. Tokyo, Japan. Nov. 23-26, 1970. Charles C. Thomas, Springfield, ILL., U.S.A.

Gjedrem, T. 1975. Possibilities for genetic gain in salmonids. Aquaculture 6: 23-29.

Graves, J.E., and R.H. Rosenblatt. 1980. Genetic relationships of the color morphs of the serranid fish Hypoplectrus unicolor. Evol. 34(2): 240-245.

deGroot, S.J., R. Norde, and F.J. Verheijen. 1969. Retinal stimulation and pattern formation in the common sole Solea solea (L.) (Pisces: Soleidae). Neth. J. Sea Res. 4(3): 339-349.

Hafeez, M.A. 1970. Effect of melatonin on body coloration and spontaneous swimming activity in rainbow trout, Salmo gairneri. Comp. Biochem. Physiol. 36: 639-656.

Hecky, R.E. 1984. The thermal and optical characteristics of Southern Indian Lake before, during and after impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41: 579-590.

Hecky, R.E., and S.J. Guildford. 1980. The primary productivity of Southern Indian Lake before, during and after impoundment and river diversion. Can. J. Fish. Aquat. Sci. 41: 591-604.

Hecky, R.E., and G.K. McCullough. 1984. The effect of impoundment on the sediment budget and nearshore sedimentation of Southern Indian Lake. Can. J. Fish. Aquat. Sci. 41: 567-578.

Hubbs, C.L., and K.F. Lagler. 1958. Fishes of the Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan. 213 pp.

Imhof, M.A. 1977. Population genetic structure of lake whitefish, (Coregonus clupeaformis) in Green Bay and northern Lake Michigan, as assessed by electrophoresis of lactate, glycerol-3-phosphate, and malate dehydrogenase isoenzymes. M.Sc. thesis, University of Wisconsin, Stevens Point, WI. 44pp.

Itzkovich, J., S. Rothbard, and G. Hulata. 1981. Inheritance of pink body colouration in Cichlasoma nigrofasciatum Gunther (Pisces, Cichlidae). Genetica 55(1): 15-16. (Abstract only seen)

Iwata, K.S., and H. Fukuda. 1973. Central control of color changes in fish, p. 316-341. In W. Chavin (ed.) Responses of Fish to Environmental Changes. Proceedings of a United States-Japan seminar. Tokyo, Japan. Nov. 23-26, 1970. Charles C. Thomas, Springfield, ILL., U.S.A.

Jenkins, T.M., Jr. 1969. Observations of colour changes of brown and rainbow trout (Salma trutta and S. gairdneri) in stream habitats, with description of an unusual color pattern in brown trout. Trans. Am. Fish. Soc. 98: 517-519.

Kaufman, L. 1976. Feeding behaviour and functional coloration of the Atlantic trumpet fish, Aulostomus maculatus. Copeia 1976(2); 377-378.

Kincaid, H.L. 1975. Iridescent metallic blue color variant in rainbow trout. J. Hered. 66: 100-101.

Kliewer, E.V. 1970. Gill raker variation and diet in lake whitefish Coregonus clupeaformis in northern Manitoba, p. 147-165. In C.C. Lindsey and C.S. Woods (ed.). Biology of Coregonid Fishes. University of Manitoba Press, Winnipeg, Manitoba. 560 pp.

Klupp, R., and F. Kaufman. 1979. The heredity of colour in rainbow trout. Fisch. Teichwirt. 30(2): 19-20. (Abstract only seen).

Koller, G. 1934. Uber den Farbwechsel von Coregonenlarven. Biol. Zentralbl., 54: 419.

Kozikowska, Z. 1961. Influence of the habitat on the morphology and biology of fish. Small whitefish, perch, selected elements. Ekol. Polsk. A, 9(27): 541-678.

Krasnodembskaya, K.D. 1978. Formation of pigment reactions and their regulatory mechanism in chondrostean fishes. J. Ichthyol. 18(1): 120-131.

Kristofferson, A.H. 1978. Evidence for the existence of subpopulations of lake whitefish, Coregonus clupeaformis (Mitchill) in Lake Winnipeg. M.Sc. Thesis. University of Manitoba, Winnipeg, 94 pp.

Lanzing, W.J.R. 1977. Reassessment of chromatophore pattern regulation in two species of flatfish (Scophthalmus maximus; Pleuronectes platessa). Neth. J. Sea Res. 11(2): 213-222.

Lanzing, W.J.R., and C.C. Bower. 1974. Development of colour patterns in relation to behaviour in Tilapia mossambica (Peters). J. Fish. Biol. 6: 29-41.

Lawler, G.H. 1970. Parasites of coregonid fishes, p 279-309. In C.C. Lindsey and C.S. Woods (ed.). Biology of Coregonid Fishes. University of Manitoba Press, Winnipeg, Manitoba. 560 pp.

Lindsey, C.C. 1962. Distinctions between the broad whitefish, Coregonus nasus, and other North American whitefishes. J. Fish. Res. Board Can. 19: 687-714.

Lindsey, C.C. 1963. Sympatric occurrence of two species of humpback whitefish in Squanga Lake, Yukon Territory. J. Fish. Res. Board Can. 20: 749-767.

Lindsey, C.C. 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. Can. J. Fish. Aquat. Sci. 38: 1497-1506.

Loch, J.S. 1974. Phenotypic variation in the lake whitefish, Coregonus clupeaformis, induced by introduction into a new environment. J. Fish. Res. Board Can. 31: 55-62.

Love, R.M. 1974. Colour stability in cod (Gadus morhua L.) from different grounds. J. Cons. Int. Explor. Mer 35(2): 207-209.

McLaren, J.F., Ltd. 1978. Report to Manitoba Hydro on changes in quality of whitefish fishery on Southern Indian Lake. May 1978.

McCullough, G.K. 1981. Water budgets for Southern Indian Lake, before and after impoundment and Churchill River diversion, 1972-79. Can. MS. Rep. Fish. Aquat. Sci. 1620, Winnipeg, 22 p.

McFarland, W.N., J.C. Ogden and J.N. Lythgoe. 1979. The influence of light on the twilight migration of grunts. Env. Biol. Fish. 4(1): 9-22.

McTavish, W.B. 1952. A biological survey of Southern Indian Lake. Report for the Manitoba Department of Mines and Natural Resources.

Miller, R.B. 1952. A review of the Triaenophorus problem in Canadian lakes. Bull. Fish. Res. Board Can. No. 95.

Nayudu, P.L. 1979. Genetic studies of melanic color patterns and atypical sex determination in the guppy, Poecilia reticulata. Copeia 1979 (2): 225-231.

Neill, R.M. 1940. On the existence of two types of chromatic behaviour in teleostean fishes. J. Exp. Biol. 17: 74-98.

Newbury, R.W., and G.K. McCullough. 1984. Shoreline erosion and restabilization in Southern Indian Lake reservoir. Can. J. Fish. Aquat. Sci. 41: 558-565.

Newbury, R.W., G.K. McCullough, and R.E. Hecky. 1984. The Southern Indian Lake impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41: 548-557.

Odiorne, J.M. 1933. Degeneration of melanophores in Fundulus. Proc. Nat. Acad. Sci. Wash. 19: 329-332.

Odiorne, J.M. 1967. Color changes, p. 387-401. In M.E. Brown (ed.) The Physiology of Fishes, Vol. II Behavior. Academic Press Inc., New York. 526 pp.

Osborn, C.M. 1941a. Studies on the growth of integumentary pigment in the lower vertebrates. I. The origin of artificially developed melanophores on the normally unpigmented vertral surface of the summer flounder (Paralichthys dentatus). Biol. Bull. 81: 352-363.

Osborn, C.M. 1941b. Studies on the growth of integumentary pigment in the lower vertebrates. II. The role of the hypophysis in melanogenesis in the common catfish (Amieurus melas). Biol. Bull. 81: 352-363.

Parker, G.H. 1943. Animal color changes and their neurohumours. Quart. Rev. Biol. 18: 205-227.

Patalas, K., and A. Salki. 1984. Effect of impoundment and diversion on the crustacean plankton of Southern Indian Lake. Can. J. Fish. Aquat. Sci. 41: 613-637.

Petersson, A. 1971. The effects of lake regulation on populations of Cestodan parasites of Swedish whitefish Coregonus. Oikos 22: 74-83.

Qadri, S.U. 1968. Growth and reproduction of the lake whitefish, Coregonus clupeaformis, in Lac la Ronge, Saskatchewan. J. Fish. Res. Board Can. 25(10): 2091-2100.

Rawson, D.S. 1947a. Great Slave Lake, p. 45-68. In North West Canadian Fisheries Surveys in 1944-1945. Fish. Res. Board Can. Bull. No. 72.

Rawson, D.S. 1947b. Lake Athabasca, p. 69-85. In North West Canadian Fisheries in 1944-45. Fish. Res. Board Can. Bull. No. 72.

Robertson, O.H. 1951. Factors influencing the state of dispersion of the dermal melanophores in rainbow trout. Physiol. Zool. 24: 309-323.

Scott, G.T. 1965. Physiology and pharmacology of color change in the sand flounder Scopthalmus aquosus. Limnol. Oceanogr. 10: R230-R246.

Sécérov, S. 1909. Farbenwechselversuche an der Bartgrundel (Nemachilus barbatula L.). Arch. EntwMech. Org. 28: 629-660.

Smith, J.R., and L.J. Weber. 1976. Alterations in diurnal pineal hydroxyindole-o-methyltransferase (HIOMT) activity in steelhead trout (Salmo gairdneri) associated with changes in environmental background color. Comp. Biochem. Physiol. 53C:33-35.

Stickney, R.R., and D.B. White. 1975. Ambicoloration in tank cultured flounder, Paralichthys dentatus. Trans. Am. Fish. Soc. 104(1): 158-160.

Sumner, F.B. 1933. The differing effects of different parts of the visual field upon the chromatophore responses of fishes. Biol. Bull. 65: 266-282.

Sumner, F.B. 1935. Evidence for the protective value of changeable coloration in fishes. Am. Nat. 69: 245-266.

Sumner, F.B. 1939. Quantitative effects of visual stimuli upon pigmentation. Am. Nat. 73: 219-234.

Sumner, F.B. 1940. Quantitative changes in pigmentation, resulting from visual stimuli in fishes and Amphibia. Biol. Revs. Cambridge Phil. Soc. 15: 351-375.

Sumner, F.B., and P. Doudoroff. 1937. Some quantitative relations between visual stimuli and the production or destruction of melanin in fishes. Proc. Nat. Acad. Sci., Wash. 23: 211-219.

Sumner, F.B., and A.B. Keys. 1929. The effects of differences in the apparent source of illumination upon the shade assumed by a flatfish on a given background. Physiol. Zool. 2: 495-504.

Sumner, F.B., and N.A. Wells. 1933. The effects of optic stimuli upon the formation and destruction of melanin pigment in fishes. J. Exp. Zool. 64(3): 377-403.

Sunde, L.A. 1963. South Indian Lake whitefish infestation test, March 5 to 7, 1963. Manitoba Department of Mines and Natural Resources, Fisheries Branch MS Report.

Svardson, G. 1952. The coregonid problem. IV. The significance of scale and gill-rakers. Rep. Inst. Fw. Res. Drott. 33: 204-232.

Svardson, G. 1965. The coregonid problem. VII. The isolating mechanisms in sympatric species. Rep. Inst. Fw. Res. Drott. No. 46.

Svardson, G. 1970. Significance of introgression in coregonid evolution, p. 33-59. In C.C. Lindsey and C.S. Woods (ed.). Biology of Coregonid fishes. University of Manitoba Press, Winnipeg, Manitoba. 560 pp.

Takeda, K., S. Onodera, and K. Yoshiyasu. 1978. Salvelinus leucomaenis with atypical color patterns, collected in the Mogami and Nikko river systems, Yamagata Prefecture. Jap. J. Ichthyol. 25(1): 58-64. (Abstract only seen.)

Tsuyuki, H., E. Roberts, R.H. Kerr, and A.P. Ronald. 1966. Micro starch gel electrophoresis. J. Fish. Res. Board Can. 23: 929-933.

Watson, R.A. 1977. Metazoan parasites from whitefish, cisco and pike from Southern Indian Lake, Manitoba: a preimpoundment and diversion analysis. M.Sc. Thesis, University of Manitoba. xi + 197 pp.

Weins, A.P., and D.M. Rosenberg. 1984. The effect of impoundment and diversion of profundal macrobenthos of Southern Indian Lake, Canada. Can. J. Fish. Aquat. Sci. 41: 638-648.