## THE UNIVERSITY OF MANITOBA

The Effects of Exposure to Predation on Mean Vertebral and Fin Ray Counts in the Fathead Minnow (Pimephales promelas)
by

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

## MASTER OF SCIENCE

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Fathead minnows (Pimephales promelas) of varying length were exposed to predation by yellow perch (Perca flavescens) at several water temperatures. Body lengths and counts for seven meristic characters (dorsal and pectoral fin rays, total vertebrae, and four subdivisions of the vertebral column were compared between survivors of a predator exposed group and an unexposed control group. Meristic count distributions were also compared after correcting for the effect of length on count.

Predation affected the distribution of counts for all characters studied with the possible exception of total vertebrae. The effects on count distribution are not totally explained by an observed singificant effect of predation on length distribution of the data, although counts for the characters are length correlated. The effect on the count distributions for total, caudal, thoracic, caudm, and thorm vertebrae (subdivisions of the vertebral column defined by the author) and for pectoral fin rays appears to depend on prey body length. The effect on count distribution for total, caudm, and thorm vertebrae appears to depend on temperature. A dorsal fin ray count of 10 appears most favourable for survival at all body lengths and temperatures studied.

Possible mechanisms by which meristic count may effect survival under predation and possible optimum counts are discussed. The observed effects of predation on count
distribution provide a possible explanation for the degree of meristic variation present in fish populations and the existence of pleomerism and the latitudinal cline in vertebral number usually referred to as Jordan's Rule.

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Page
ABSTRACT ..... i
ACKNOWLEDGEMENTS ..... iii
LIST OF TABLES ..... vi
LIST OF FIGURES ..... vii
LIST OF APPENDICES ..... viii
INTRODUCTION ..... 1
MATERIALS AND METHODS ..... 4
a) Collection of Specimens ..... 4
b) Experimental Design ..... 6
c) Counts and Measurements ..... 11
d) Analytical Methods ..... 12
RESULTS ..... 20
a) Results of $t$ and F-tests ..... 20
b) Analysis of Covariance ..... 21
c) Correlation of Measured Variables ..... 25
DISCUSSION ..... 44
a) Test Statistics ..... 43
b) Changes in Length Conditioned Count Distribution ..... 44
c) Mechanisms by which Predation may act to Alter Count Distributions: Correlation Effects and Directness of Action ..... 57
d) Possible Mechanical Effects of Change in Parts Number. ..... 60
e) Pleomerism, Jordan's Rule, and a meristic Variability ..... 63

TABLE OF CONTENTS cont'd

Page

CONCLUSIONS ................................................................. 65
LITERATURE CITED . . ........................................ 67

Table Page
1 Experimental parameters ..... 9
2 Results of $t$ tests for differences in group meansand $F$-tests for differences in variance27
3 Statistics for total vertebrae ..... 29
4 Statistics for caudal vertebrae ..... 31
5 Statistics for thoracic vertebrae ..... 33
6 Statistics for caudm vertebrae ..... 35
7 Statistics for thorm vertebrae ..... 37
8 Statistics for dorsal fin rays ..... 39
9 Statistics for pectoral fin rays ..... 41
10 Correlation matrices all measured characters,control and experimental groups, 4, 5, 6:20 ${ }^{\circ} \mathrm{C} . . . . .442$

1 Divisions between caudm and thorm and caudal and thoracic vertebrae................................................ 13
$2 a, b$, and $c$ - Average total vertebrae within small length ranges against length28

3 a, b - Average caudal vertebrae within small length ranges against length30
$4 \mathrm{a}, \mathrm{b}$ - Average thoracic vertebrae within small length ranges against length........................................... 32

5 a, b - Average caudm vertebrae within small length ranges against length.34
$6 \mathrm{a}, \mathrm{b}$ - Average thorm vertebrae within small length ranges against length.36

7 a, b - Average dorsal fin ray count within small length ranges against length.38

8 Average pectoral fin ray count within small length ranges against length, 4, 5, 6:20 ${ }^{\circ}$ C.............. 40

9 a, b - Log caudm vertebrae against log length....... 62

## LIST OF APPENDICES

Appendix PageA Table i. Frequency distributions ofcounts of all meristic characters,experiment 6:20 ${ }^{\circ} \mathrm{C}$................................ 69B Table ii. Differences between treatmentgroups in mean length ......................... 71
B Figure ia, b, c, d - approximate percentsurvival against length ....................... 72

## INTRODUCTION

Meristic variation is variation in the number of units of serially arranged structural elements, such as vertebrae. Meristic variation is very pronounced in fish (Ali and Lindsay, 1974). The question arises: why does variation persist if selection is normalizing (removes random deviations arising from mutation or unusual allele combinations), and why is it greater among fish?

In addition to genetic effects the number of parts in a meristic series is affected by environmental influences (such as salinity or temperature) on the developing embryo (Ali and Lindsey, 1974). One possibility is that meristic variation is merely tolerated. The most efficient method of producing young which develop in an uncontrolled aquatic environment may involve a certain latitude in meristic part numbers. Selection against fish with non-modal counts may be nonexistent.

A second possibility is that meristic variation is maintained by balancedselection. This could occur if the optimal number of parts for survival and reproduction were different under different conditions and if the environmental conditions were variable.

Lindsey (1975) discovered a widespread tendency for the number of meristic parts of closely-related species to be correlated with their maximum body size. He named the phenomenon pleomerism. A correlation also occurs between
meristic part number and latitude ("Jordan's Rule"), (Jordan, 1892), which might be related to water temperature. These correlations suggest that the optimal parts number may be dependant on body size or water temperature.

Meristic variation would be maintained in a population if the optimum number of parts were correlated with length or water temperature, and the temperature or age (length) at which selection was most stringent were to fluctuate. The same results would occur if selection pressure were constant, and the time of exposure to selection at a given length or temperature were to fluctuate.

The meristic characters in question are divisions of the vertebral column and fin rays. Since they are involved in locomotion any direct effect their variation has on survival may be related to locomotion. Study of the effect of variation in skeletal part numbers on survival may therefore lead to greater understanding of the relationship between body form and swimming efficiency.

This study investigates the possibility that predation can affect the distribution in a population of counts for several meristic characters and that the effect is dependant on body length and water temperature. Fathead minnows (Pimephales promelas) of various sizes were exposed to predation by yellow perch (Perca flavescens) at several temperatures. The distribution of meristic counts for several characters were
then compared between samples taken before and after exposure to the predator. Comparisions between these two treatment groups were made without correction for length and with length removed as a covariate or with data which had otherwise been corrected for the effect of length on count. The resulting differences between treatment groups are discussed with regard to the mechanisms by which they were generated, identification of possible optimum counts for survival and possible associations between such optima and length or temperature. The possibilities of such differential survival providing a reason for the trends known as pleomerism and Jordan's Rule (through correlation of water temperature with latitude) and for the maintenance of meristic variation in fish population are discussed.
a) Collection of Specimens

Fathead minnows (Pimephales promelas) were the prey in all experiments. They are hardy, tolerate temperature variation, and display variation in several meristic series. All minnows were collected from a l-km stretch of a tributary of the Riviere La Salle, 12 km south of the town of Elie, Manitoba. Adult fish were seined in April, 1977. Dip net collections of young of the year were made periodically from June to October, 1976 and 1977. Water temperatures varied from $6{ }^{\circ} \mathrm{C}$ for the spring collections, to between 17 and $23^{\circ} \mathrm{C}$ for the summer collections. Since the minnows breed repeatedly throughout the spring, the size range in any one collection also represents some variation in age and probably incubation temperature.

Yellow Perch (Perca flavescens) were the predators in all experiments. They are hardy and available in a range of sizes throughout the summer. In 1976 all perch were seined from Lake Manitoba at the University of Manitoba Field Station, Delta Marsh. Collecting was repeated throughout the summer to provide larger perch and to replace holding losses. The perch used in 1976 ranged from 3 to 17 cm in length. A collection of 10 to 20 cm long perch was seined in May of 1977 from the Rennie River in the Whiteshell Provincial Park, Manitoba. These perch were used as predators on the
adult minnows collected that spring (experiment $6: 20^{\circ} \mathrm{C}$ ). Perch for the remaining 1977 experiment, ranging from 2 to 8 cm in length, were collected from Lake Manitoba as in 1976.

Perch and minnows were held in 228 litre glass or 205 litre fibreglass aquaria supplied with air and running dechlorinated water. Water temperature was established by mixing the inflows from $6^{\circ} \mathrm{C}$ and $25^{\circ} \mathrm{C}$ water supplies. Recently collected fish were held at approximately stream temperature and were then adjusted over two days to the experimental temperature. Fish were held at the experimental temperature for one day before use. Long-term holding was at $10^{\circ} \mathrm{C}$. All fish were on a ll L: 13 D light cycle during holding and experimenting. All fish were fed daily; the minnows were fed "tetramin", dried fish food, and the perch were fed frozen ocean perch fillets supplemented with live minnows. Perch were starved for 24 hours before beginning each experiment, but were not starved between trials within an experiment.

The stream from which the minnows were collected did not contain perch, but did contain mudminnows (Umbra limi) and young cat fish (Ictalurus sp). Catfish are known fish predators. Various minnow species, including Pimephales occurred in the creeks where perch were collected and minnows are known to be a common prey item for yellow perch. The same perch were used in several trials within each experiment, and in some
cases, in several experiments. Some experiments utilized both experienced and experimentally naive perch, recruited to replace losses.
b) Experimental Design

Predation experiments were conducted in open borrow pits, under semi-natural conditions, and in the laboratory. Experiments were numbered chronologically. The water temperature at which the experiment was conducted appears after the experimental number.

1. Borrow pit experiment: A major goal of the study was to ascertain the effects of predation in the wild on a population's meristic count distributions. Such effects may be dependent upon the nature of the physical environment (e.g., availability of cover). An attempt was therefore made to carry out experiments in borrow pits containing natural vegetation. Six $5-\mathrm{m} \times 8-\mathrm{m} \times 0.6-\mathrm{m}$ deep borrow pits at the University of Manitoba Field Station, Delta Marsh, were each stocked with approximately 1,000 minnows ranging in length from 1.22 to 2.76 cm . Twelve perch were introduced into each of three of these, the other three forming the controls. After three days the fish were recovered by seine. This formed experiment $1: 28^{\circ} \mathrm{C}$, the temperature being an approximate mean
of the diel range of 24 to $33^{\circ} \mathrm{C}$. Data from pits exposed to like treatment were pooled.
2. Laboratory experiments: Predation experiments were also performed in a laboratory where more rigid control could be maintained over environmental factors, particularly temperature. Experiments were conducted in four $150-\mathrm{cm} \mathrm{x}$ $32-\mathrm{cm} \times 30-\mathrm{cm}$ deep tanks in the Duff Roblin Building, University of Manitoba. The tanks were provided with aeration and a constant flow of dechlorinated, temperaturecontrolled water. Each tank contained a $25-\mathrm{cm}$ x $60-\mathrm{cm}$ panel of shredded green plastic which hung like a curtain and served as cover for the fish. The tanks were exposed to an llL:l3D light cycle. Placement of the experimental trials within the cycle was uncontrolled. The tanks were in an undisturbed location and were covered with translucent fibreglass tops.

Experiments were performed at several temperature. The size ranges of predators and prey and the time period of collection of the prey were changed between experiments. Experiments were replicated between and within tanks. The exposure of a number of minnows to predation at one time in one tank forms a trial. Each trial yields a control (cont.) group, consisting of fish removed from a subsample of the minnows in a holding tank immediately prior to the exposure of the rest of the subsample to predation, and an experimental (exp.) group, consisting of the survivors after exposure to
predation. The control and experimental groups will be referred to as the treatment groups for a trial or experiment. A series of trials run under the same experimental conditions, with subsamples of a single collection of minnows, constitutes an experiment. Table l lists the experiments and the conditions under which they were performed.

Laboratory experiments were conducted over as large a temperature range as possible in order to detect any temperature effects.

Two problems with extreme temperatures were low levels of predation at low temperatures and low survival of both prey and predators at high temperatures. In 1976 the limited availability of perch required the use of higher temperatures in order to obtain a sufficient level of predation in the low temperature experiment. In 1977 more perch were obtained, providing greater predation pressure and allowing the lowering of the low temperature experiments to $6^{\circ} \mathrm{C}$. The high temperature experiments were lowered to $20^{\circ} \mathrm{C}$ to decrease losses from causes other than predation.

For each trial minnows were dip-netted from holding tanks into a 30 cm diameter pail. Approximately one quarter of this sample was removed with a $15 \mathrm{~cm} x 10 \mathrm{~cm}$ dip net passed through tightly packed mass of fish and preserved in formalin, these formed the control group. The remaining fish were placed in the tanks with the perch. Since the fish which were removed
from the pail always formed the control group it is possible that any differences observed between the treatment groups are due to differences between individuals in probability of removal by the dip net. It was impossible to randomize the assignment of removed and remaining fish between the two treatments without dividing the fish to be used in each trial into four equal subsamples and randomly selecting the control from among these. It was felt that this would require too much handling of the fish. It seems highly unlikely that differences between individuals would effect their probability of being removed from a tightly packed mass by a quickly moving dip net.

In 1977 all perch were approximately 1.5 x the length of the largest prey present. This was an attempt to maximize the probablity of prey escape through using the smallest predators able to consume the largest prey. The size ratio was chosen after observation of the fish in the 1976 experiments. Between 20 and 100 minnows and 8 and 20 perch were used per tank per trial. The minnows formed a loose school in open water while the perch hid in the plastic. Perch sortied from the cover and pursued particular minnows. Length of pursuit varied from a few cm to the length of the tank. Most successful pursuits were of a few cm. The trial was terminated when $2 / 3$ of the prey had been consumed. The survivors, after preserving in formalin, constitute the experimental group.
c) Counts and Measurements

Minnows were preserved in formalin, cleared in 10\% KOH , stained with $.05 \%$ alizarin, and transferred to full strength glycerin. Counts were made through a binocular microscope with cross hair. Fork length was measured with a rule bearing mm graduations. Meristic counting conventions were not strictly followed, variations in criteria being introduced in an attempt to define functionally significant characters. The terms "caudm" and "thorm" vertebrae were coined by the experimenter to designate two such characters. All counts were taken from the left side. The characters defined were:

1) Total vertebrae: The total number of freely articulating centra, including the urostyle, and counting each Weberian vertebra as a freely articulating centrum;
2) Caudal Vertebrae: All vertebrae lacking a rib or having an attached or floating rib less than 1.5 x the length of the associated centrum;
3) Thoracic Vertebrae: All vertebrae having a rib greater than or equal to 1.5 x the length of the centrum. Total, caudal, and thoracic vertebrae were counted separately. If the total of caudal and thoracic vertebrae did not equal the count obtained for total vertebrae the counts were retaken until agreement was obtained;
4) Caudm Vertebrae: All vertebrae, posterior to and including the most anterior vertebra bearing a transverse process in the
position of the diapophysis (see Figure 1). This variable was recorded in the 1977 experiments only;
5) Thorm Vertebrae: All vertebrae anterior to the first vertebra bearing a transverse process. Total, caudm, and thorm vertebrae were counted independently. Thorm vertebrae were counted only in 1977 experiments;
6) Dorsal Fin Rays: All dorsal fin rays whose length was greater than $.2 x$ the length of the immediately antecedent ray, thus excluding the anterior rudimentary rays. The two most posterior rays in Pimephales share a common base but were treated as separate rays;
7) Pectoral Fin Rays: All visible left side pectoral fin rays.

The experimental identity of all 1977 samples was concealed during counting.
d) Analytical Methods.

1) Detection of differential survival related to meristic count

The effect of meristic count on the survival of individuals in a population which is subject to predation could be directly measured by comparison of percentage survivals for fish having different numbers of parts. Percentage survivals could not be obtained due to the impossibility of obtaining counts from fish which had been consumed. The study therefore infers

Figure l. Divisions between caudm and thorm and caudal and thoracic vertebrae.

Figure la. Fish longer than 2.0 cm .
Figure lb. Fish shorter than 2.0 cm . "A" indicates most anterior caudal vertebra, "B" indicates most anterior caudm vertebra.

differential survival of fish having different parts numbers from differences between the control and experimental groups in count mean and variance. Differential survival of fish having different numbers of parts will cause a change in the population mean for the meristic series as selection proceeds under almost all conditions. It is possible that no change will occur if the initial population mean equals the count which confers the highest percentage survival. The variance of the count distribution for a character will also be affected by selection. It may display an initial increase if the initial modal count is not the most favoured but it will eventually decrease as selection proceeds, presuming the percentage survival: parts number relationship in unimodal.
i) $t$ and F-tests

The count distributions for each meristic character, before and after removal of individuals by predators, were initially compared by use of tand F-tests for differences in mean and variance respectively. A significant difference between control and experimental groups in mean or variance indicates that predation has affected the count distribution of that meristic character. It does not, however, prove that selection is operating on that character rather than on some factor with which the character is correlated.

## ii) Analysis of Co-variance

Preliminary analysis indicated that most characters were length correlated and that significant differences
in length distribution existed between the treatment groups (see Appendix B and Table 10). It was therefore necessary to adjust for any effect of length on mean count by use of analysis of covariance in order to ascertain if the observed changes in count distributions were solely due to changes in length distributions. Effects apparent in the covariate adjusted treatment means indicate an effect of parts number over and above effects due to length. Analysis of covariance requires that the relationship between the variable being analysed and the covariate be linear. Due to the amount of data and the discreet nature of the meristic characters, scatter plots of the counts against length were inadequate for testing linearity. The data were therefore condensed for plotting by division into length classes. The width of the classes was varied between .05 to 2.0 mm in order roughly to equalize the number of observations in each class. The number of observations still varied widely among classes, complicating interpretation of the graphs. The mean counts within these length classes were then plotted against length for each meristic character for each treatment group in each experiment.

The graphs indicated that, for several characters, the relationship between the character and length was not linear over the entire range of lengths represented. Nonlinearity appeared either as sharp changes (inflections) in the relationship or as a curvilinear relationship.

Inflections were accounted for by stratifying the data into length ranges over which the character:length relationship appeared to be linear and analyzing the resulting data subsets separately. For several characters the best stratification level appeared to be different for different treatment groups or experiments. When this occurred the best stratification level from each experiment and treatment group was applied to the data from all groups in all experiments. This was done both to obtain the stratification point giving the best linear fit within strata and to provide equal strata for all experiments to facilitate comparisions between experiments. Each set of data was therefore reanalyzed several times. The results for all strata are reported. This retesting must be taken into account when considering the $P$ values of the statistical tests. Test results based on unstratified data are also reported. Table 3 through 9 therefore contain entries for which there are indications that the assumption of linearity of effect of length on count has been violated. The violation may or may not invalidate the test. The analyses which best satisfy this assumption are indicated by an asterisk beside their entry number. Significant test probabilities resulting from these analyses are double underlined.

Logarithmic transformations were performed on data which exhibited a curved relationship between mean count and length. The data for thorm vertebrae, fish shorter than 2.0 cm , were analyzed using $\log _{e}$ of length. Analysis
of the pectoral fin ray data was done using $\log _{10}$ of both length and pectoral fin ray count. Choice of transformation was based on the shape of the graph of count means against length. The base of the logarithm used has no significance and choice of base was arbitrary.

Simple analysis of covariance also assumes equality of treatment group slopes. Both equality of treatment group slope and equality of length adjusted means were tested. A significant difference in slope invalidates the test for adjusted group mean. However, it in itself indicates an effect of the treatment on the meristic count distribution.
2) Detection of dependancy of count specific survival rate on body length and temperature.

The effects of predation on the count distribution for fish of specific lengths or of small ranges of lengths were compared for indications of changes in survival rate for fish having specific meristic counts, with body length and water temperature. Control and experimental means and variances for narrow length classes were compared both graphically and by use of $t$ tests and $F$ tests on the means and variances of selected length classes. Graphic comparison was facilitated by linking the control and experimental means with an arrow indicating the direction of movement of the mean. $t$ tests were applied to differences between control and experimental
means of length classes which appeared to display divergent movement of the mean at different temperatures or when the movement of the means at different lengths indicated changes in optimum count with length. Two problems with this approach were the drastic reduction in sample size caused by individual consideration of small length classes and the lack of a common control group mean or count distribution between length classes. The latter made comparison of the movements of means for different temperatures and length classes difficult. Changes in the count distribution for all lengths within length strata were therefore considered jointly by comparing the meristic character:length regressions performed on the control and experimental groups.

Under certain conditions which are discussed later differences between the regressions obtained from the control and experimental data can be taken as indication of the length dependance of the survival rate's for fish having different counts. If these conditions are met an increased slope in the experimental group together with increased regression goodness of fit indicates length dependance of the survival rates. The slopes of the regression lines are therefore reported.

Two measures of regression goodness of fit were used: 1) comparison of control and experimental group zero-slope probabilities, (l-the probability of obtaining a slope equal to or greater than that observed under the null hypothesis $\beta=0), 2$ ) an $F$ test of the Ho that control and experimental
group regression residual variance are equal.
One condition which must be met before the changes in the regression parameters which have been outlined can be taken as indications of the degree of length dependancy of count specific survival rates is that the count conferring the highest survival at each length must be within the observed range of values for fish of that length. To test this condition the standard deviation about the control mean for each length class has been added to the mean count against length graphs.
3) Correlation of meristic characters

A correlation matrix for the meristic characters was generated to investigate the possibility that changes in the count distribution for one character might be due to correlation with other measured characters.

## 4) Computation

The $t$ and F-tests were computed by use of the biomedical statistical programme BMDP3D (Brown, 1977). BMDPIR was used to generate meristic character-length regressions. Analysis of covariance was done using BMDPIV. The Statistical Programs for the Social Sciences (SPSS) package (Nie, et al., 1975) was used to determine count means and variances within small size classes.

RESULTS

Tables and graphs referred to in this section are grouped together, in the order they are referenced in the text, at the end of this section.
a) Results of $t$ and $F$-tests

Significant differences between control and predationexposed treatment groups in mean count and in variance were observed repeatedly for all meristic characters except total vertebrae (Table 2). The only significant difference noted for total vertebrae was a significant increase in variance in experiment $7: 6^{\circ} \mathrm{C}$.

Caudal and thoracic vertebrae display a bewildering array of significant increases and decreases in both mean count and variance. A significant increase in mean count was recorded for caudm vertebrae in two experiments and both significant increases and decreases in variance were recorded. Thorm vertebrae displayed a significant increase in mean count in two experiments and when the data from all $20^{\circ} \mathrm{C}$ experiments was pooled. Again the variance displayed both significant increases and decreases. Two significant increases in mean count were recorded for dorsal fin rays and three significant increases were recorded for pectoral fin rays.
b) Analysis of Covariance

## i) Total Vertebrae

The vertebrae means against length graph for the combined $20^{\circ} \mathrm{C}$ data suggested that stratification at 2.1 cm would yield strata over which the effect of length on count was linear (Figure 2a). The graph for the combined 1977 warm water data ( $1: 28^{\circ} \mathrm{C}$ and $2: 26^{\circ} \mathrm{C}$ ) suggested stratification at 1.75 cm (Figure 2c). The 1.75 cm stratification point is illustrated in figures $2 \mathrm{a}, \mathrm{b}, \mathrm{c}$. The zero slope probability was extremely low in some cases, particularly in the experimental groups after stratification, indicating a significant linear relationship between total vertebrae and length (Table 3). Only two significant changes in regression line slope and one significant decrease in adjusted mean were observed (Table 3, entries $4,18,20)$. These differences must be viewed with suspicion given the multiple tests run on the data.

The differences between treatment groups, fish shorter than 1.75 cm , (in slope in the pooled $20^{\circ} \mathrm{C}$ data and in adjusted mean in $3: 10^{\circ} \mathrm{C}$ ) are, however, highly significant and obtained from analysis of data over which the effect of length on vertebral count appears linear.

Figure $2 b$ is a plot of vertebrae mean against length for $6: 7^{\circ} \mathrm{C}$.
ii) Caudal Vertebrae

The plots of mean caudal vertebrae count against length (Figures 3 a and b ) suggested the division of the caudal vertebrae data into length strata at about 2.25 cm . The graphs also suggested that the count:length relationship for short fish followed a curve of a type which could be corrected by taking the logarithm of length. Results of tests run on these transformed data are. reported in Table 4, entries 13-16. The caudal vertebrae regressions had low zero slope probabilities. There were significant differences between the control and experimental treatment groups in regression line slope in two experiments and when the $20^{\circ} \mathrm{C}$ data were pooled (data not stratified, Table 4 , entries $3,6,8$ ). In $2: 26^{\circ} \mathrm{C}$ (Table 4, entry 2) the group slopes were not significantly different, but the experimental group had a significantly higher adjusted mean count. Significant differences in slope also were recorded when the data were stratified, occurring in the lower stratum pooled $20^{\circ} \mathrm{C}$ data (transformed and untransformed, Table 4, entries 9 and 15) and in the lower strata of $4: 20^{\circ} \mathrm{C}$ and $7: 6^{\circ} \mathrm{C}$ (transformed data, Table 4, entries 13 and 16).

## iii) Thoracic Vertebrae

Graphs of thoracic vertebrae counts against length (Figures 4 a and b) suggested stratification of the data at a length of 1.85 cm . Significant differences between
control and experimental treatment groups in regression line slope were recorded in analysis of the unstratified data from experiments $1: 28^{\circ} \mathrm{C}, 4: 20^{\circ} \mathrm{C}, 7: 6^{\circ} \mathrm{C}$, and the pooled $20^{\circ} \mathrm{C}$ data (Table 5 , entries $1,3,6$, and 8 ). Significantly lower experimental group means were recorded in the unstratified data for $2: 26^{\circ} \mathrm{C}$ and the lower stratum (fish shorter than 1.85 cm ) of $7: 6^{\circ} \mathrm{C}$ (Table 5, entries 2 and 10). Regression zero slope probability was very low for most experiments.
iv) Caudm Vertebrae

The graph of caudm vertebraeagainst length for $7: 6^{\circ} \mathrm{C}$ (Figure 5b) suggested stratification at a length of 1.5 cm . The only significant change observed for this character was a significantly lower adjusted mean count in the experimental group of $7: 6^{\circ} \mathrm{C}$, which was detected in analysis of the data without stratification and for fish longer than 1.5 cm after stratification. The mean in the lower stratum also dropped. The unstratified data gave the best regression line fit, suggesting that stratification was unnecessary (Table 6, entries 5, 7, and 9). Non-linearity was not apparent in the graph for the pooled $20^{\circ} \mathrm{C}$ data.
v) Thorm Vertebrae

Graphs of thorm vertebrae counts against length suggested a curved relationship between the two variables
up to a length of about 2.0 cm . The data were stratified and analysis of covariance performed on both strata. Data in the lower stratum were reanalyzed using the logarithm of length. The results for the transformed data are not reported, since the transformation did not noticeably alter the results or improve the regression goodness of fit. A significant difference in slope between groups occurred in the unstratified $4: 20^{\circ} \mathrm{C}$ data (Table 7, entry 1). Significant increases in adjusted mean count were recorded in the unstratified pooled $20^{\circ} \mathrm{C}$ data and in the lower stratum of these data when stratification was applied (Table 7, entries 4 and 6).
vi) Dorsal Fin Rays

No significant differences between treatment groups in eitherslope or adjusted mean count were observed for dorsal fin rays (Table 8). The slope was; however, consistently lower in the experimental group. Figures 7 a and b are plots of dorsal rays against length for the pooled $20^{\circ} \mathrm{C}$ data and $7: 6^{\circ} \mathrm{C}$, respectively.
vii) Pectoral Fin Rays

The plots of mean pectoral fin ray count against length for the pooled $20^{\circ} \mathrm{C}$ data and $7: 6^{\circ} \mathrm{C}$ (Figure 8) suggested that the relationship followed a curve which
could be corrected by taking the logarithm of both variables. Statistics for the transformed data are reported in Table 9, entries 9 to 13. Significant differences in regression line slope between treatment groups were found in $1: 28^{\circ} \mathrm{C}$ and $5: 20^{\circ} \mathrm{C}$ (untransformed data for 7:6 ${ }^{\circ} \mathrm{C}$ (Table 9, entry 8). The significant difference in slope in $1: 28^{\circ} \mathrm{C}$ and in adjusted mean in 7: $6^{\circ} \mathrm{C}$ persists after transformation of the data (Table 9, entries 9 and 13). Transformation appears to have little effect on regression goodness of fit or the results of the analysis.
c) Correlation of Measured Variables

Correlation matrices for all experimental variables, pooled $20^{\circ} \mathrm{C}$ data, control and experimental groups, are contained in Tables l0a and b. Caudal and thoracic verebrae and pectoral fin rays are all strongly correlated with length caudal vertebrae being negatively correlated and the other two variables being positively correlated. Caudal, caudm, and thorm vertebrae are all strongly positively correlated with total vertebrae. The correlations with total vertebrae are slightly stronger in the experimental groups, in all experiments. Caudal and thoracic vertebrae display a strong
negative correlation. Caudm and thorm vertebrae also display a negative correlation which is stronger in the experimental group than in the control.
Table 2.
Results of $t$ tests for differences in group means and $F$ tests for differences in statistics are underlined. other abbreviations as for Table l. Significant Total Vertebrae

| Experiment | Cont. | Exp. | Cont. | Exp. | $t \underset{P}{t}$ test | Stnd. Cont. | Deviation Exp. | $\begin{gathered} \text { F test } \\ \mathrm{P} \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1:28 ${ }^{\circ} \mathrm{C}$ | 265 | 290 | 37.876 | 37.889 | . 819 | . 695 | - 730 | - 395 |
| 2:26 ${ }^{\circ} \mathrm{C}$ | 442 | 207 | 37.919 | 37.936 | . 792 | . 697 | . 624 | - 395 |
| $4: 20^{\circ} \mathrm{C}$ | 1340 | 1348 | 37.788 | 37.821 | . 241 | . 728 | . .701 | . 402 |
| $5: 20^{\circ} \mathrm{C}$ | 1089 | 980 | 37.750 | 37.714 | . 227 | . 664 | . 695 | . 147 |
| $6: 20^{\circ} \mathrm{C}$ | 502 | 579 | 37.835 | 37.853 | . 684 | . 710 | . 732 | . 482 |
| 7: $6{ }^{\circ} \mathrm{C}$ | 1473 | 1244 | 37.795 | 37.741 | . 052 | . 701 | $\begin{array}{r}.794 \\ \hline .79\end{array}$ | .482 .000 |
| $3: 10^{\circ} \mathrm{C}$ | 501 | 255 | 37.906 | 37.893 | . 791 | . 632 | . 670 | . 271 |
| 4,5,6:20 ${ }^{\circ} \mathrm{C}$ | 2096 | 2401 | 37.767 | 37.761 | . 777 | . 682 | . 695 | . 385 |
| Caudal Vertebrae |  |  |  |  |  |  |  |  |
| $1: 28{ }^{\circ} \mathrm{C}$ |  |  | 18.682 | 18.569 | . 072 | . 820 | . 717 |  |
| 2:26 ${ }^{\circ} \mathrm{C}$ |  |  | 18.465 | 18.627 | . 004 |  |  |  |
| 4:20 ${ }^{\circ} \mathrm{C}$ |  |  | 21.062 | $\underline{20.298}$ | . .000 | -.722 | . 640 | $\underline{.048}$ |
| $5: 20^{\circ} \mathrm{C}$ |  |  | 18.751 | $\underline{18.673}$ | . .011 | $\underline{1.861}$ | $\underline{1.428}$ | . 000 |
| 6:20 ${ }^{\circ} \mathrm{C}$ |  |  | 18.912 | 18.894 |  |  | . 695 | . 626 |
| 7: $6{ }^{\circ} \mathrm{C}$ |  |  | 20.114 | 19.530 |  | $\underline{.691}$ | -819 | . 000 |
| 3: $10^{\circ} \mathrm{C}$ |  |  | $\frac{20.114}{18.665}$ | $\frac{19.530}{18.698}$ | . 000 | 1.447 | 1.194 | . 0000 |
| 4,5,6:20 ${ }^{\circ} \mathrm{C}$ |  |  | 19.031 | 18.698 |  | .641 | . 863 | . 000 |
|  |  |  | 19.031 | 19.081 | . 080 | . 986 | . 938 | . 019 |

Thoracic Vertebrae

| Experiment | Cont. | Exp. | Cont. | Exp. | $\begin{gathered} t \text { test } \\ \mathrm{P} \\ \hline \end{gathered}$ | Stnd. Cont | ation Exp. | $\underset{\mathrm{P}}{\mathrm{~F}} \mathrm{test}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1: $28^{\circ} \mathrm{C}$ |  |  | 19.186 | 19.326 | . 057 | . 731 | . 695 | . 057 |
| 2:26 ${ }^{\circ} \mathrm{C}$ |  |  | 19.460 | 19.309 | . 003 | . 606 | . 567 |  |
| $4: 20{ }^{\circ} \mathrm{C}$ |  |  | 16.706 | $\underline{19.537}$ | . .000 | $\begin{array}{r}.606 \\ \hline\end{array}$ | $\begin{array}{r}.567 \\ \hline\end{array}$ | . 277 |
| $5: 20^{\circ} \mathrm{C}$ |  |  | 19.013 | 19.024 | $\underline{.000}$ | 1.728 | 1.392 | . 000 |
| $6: 20{ }^{\circ} \mathrm{C}$ |  |  | 18.922 | 18 |  | . 732 | . 604 | $\underline{.000}$ |
| 7: $6^{\circ} \mathrm{C}$ |  |  | 17.691 | 19.167 | 033 | . 630 | . 919 | . 000 |
| 3:10 ${ }^{\circ} \mathrm{C}$ |  |  | 19.234 | 19.167 | . 000 | 1.414 | 1.117 | . 000 |
| 4,5,6:20 ${ }^{\circ} \mathrm{C}$ |  |  | 18.724 | 18.697 | . 584 | . 590 | . 587 | . 942 |
|  |  |  |  |  | . 336 | . 893 | . 963 | . 000 |
| Caudm Vertebrae |  |  |  |  |  |  |  |  |
| 1:28 ${ }^{\circ} \mathrm{C}$ |  |  |  |  |  |  |  |  |
| 2:26 ${ }^{\circ} \mathrm{C}$ |  |  |  |  |  |  |  |  |
| 4:20 ${ }^{\circ} \mathrm{C}$ |  |  |  |  | 19.659 | 19.644 | . 556 |  | 782 | 333 |
| $5: 20{ }^{\circ} \mathrm{C}$ |  |  | 19.687 | 19.614 | . 027 |  | . 782 | . 333 |
| 6:20 ${ }^{\circ} \mathrm{C}$ |  |  | 19.701 |  | . 027 | . 694 | . 793 | . 000 |
| 7: $6^{\circ} \mathrm{C}$ |  |  |  | 19.687 | . 800 | . 847 | . 751 | . 005 |
| 3:10 ${ }^{\circ} \mathrm{C}$ |  |  | $\underline{19.673}$ | 19.510 | . 000 | . 757 | . 846 | . 000 |
| 4,5,6:20 ${ }^{\circ} \mathrm{C}$ | 2091 | 2399 | 19.645 | 19.622 | . 386 | . 961 | 773 | 000 |

Thorm Vertebrae

| Experiment | Cont. | Exp. | $\begin{array}{r} \mathrm{m} \\ \text { Cont. } \\ \hline \end{array}$ | $\operatorname{Exp} .$ | $\underset{\mathrm{P}}{\mathrm{t}} \mathrm{t}$ | Stnd Cont | Deviation Exp. | $F$ test |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $4: 20^{\circ} \mathrm{C}$ |  |  | 18.124 |  |  |  |  |  |
| $5: 20^{\circ} \mathrm{C}$ |  |  | $\frac{18.124}{18.030}$ | $\frac{18.182}{18.067}$ | $\underline{.015}$ | . 634 | . 603 | . 071 |
| 6:20 ${ }^{\circ} \mathrm{C}$ |  |  | 18.030 | 18.067 | . 085 | . 791 | . 717 | . 007 |
| 7: $6{ }^{\circ} \mathrm{C}$ |  |  | 18.116 | 18.166 | . 210 | . 660 | . 640 | . 482 |
| 4,5,6:20 ${ }^{\circ} \mathrm{C}$ |  |  | 18.110 | 18.217 | . 000 | . 690 | . 753 | . 001 |
|  | 2089 | 2399 | 18.069 | 18.133 | . 004 | . 810 | . 657 | . 000 |
| Dorsal Fin Rays |  |  |  |  |  |  |  |  |
| 1:28 ${ }^{\circ} \mathrm{C}$ | 295 | 294 | 9.959 | 9.973 |  |  |  |  |
| $2: 26{ }^{\circ} \mathrm{C}$ | 441 | 207 | 9.986 |  |  | .230 | . 260 | . 035 |
| $4: 20{ }^{\circ} \mathrm{C}$ | 1265 | 1298 | 9.986 | 9.971 | . 563 | . 316 | . 310 | . 772 |
| $5: 20^{\circ} \mathrm{C}$ | 1085 | 978 |  | $\underline{9.987}$ | . 000 | 1.659 | 1.468 | . 000 |
| $6: 20{ }^{\circ} \mathrm{C}$ | 501 | 574 | 9.984 | 9.964 | . 070 | . 248 | . 255 | . 350 |
| 7: $6^{\circ} \mathrm{C}$ | 1465 | 1440 | 9.982 | 9.983 | . 925 | . 236 | . 219 | . 089 |
| $3: 10^{\circ} \mathrm{C}$ | 500 | 184 284 | $\underline{9.959}$ | $\underline{9.982}$ | . 015 | . 269 | . 238 | . 000 |
| 4,5,6 |  |  | 9.981 | 9.976 | . 751 | . 172 | . 250 | . 000 |
|  | 2084 | 379 |  | 9.984 | . 676 | . 241 | . 247 | . 249 |

Pectoral Fin Rays

| $\frac{\text { Experiment }}{\text { l } 28^{\circ} \mathrm{C}}$ | Cont. | Exp. | mean |  | $\begin{gathered} t \text { test } \\ \mathrm{P} \\ \hline \end{gathered}$ | Stnd. Deviation |  | $\begin{gathered} \mathrm{F} \text { test } \\ \mathrm{P} \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $1: 28{ }^{\circ} \mathrm{C}$ | 273 | 237 | 14.051 | 14.152 | . 385 | 1.277 |  |  |
| 2:26 ${ }^{\circ} \mathrm{C}$ | 428 | 200 | 14.661 | 14.265 | . 250 | 1.277 | 1.335 | . 476 |
| $4: 20^{\circ} \mathrm{C}$ | 964 | 1143 | 10.720 | 11.138 | . 250 | . 965 | 1.089 | . 043 |
| $5: 20^{\circ} \mathrm{C}$ | 876 | 926 | 13.262 |  | . 000 | 1.699 | 1.468 | . 000 |
| 6:20 ${ }^{\circ} \mathrm{C}$ | 485 | 572 | $\frac{13.262}{15.132}$ | $\frac{14.072}{15.260}$ | . 000 | 1.311 | 1.209 | . 015 |
| 7: $6{ }^{\circ} \mathrm{C}$ | 11.86 | 1112 |  | 15. | . 055 | 1.048 | 1.112 | . 176 |
| $3: 10^{\circ} \mathrm{C}$ | 491 | 250 | $\frac{12.843}{14.662}$ | 13.143 | . 000 | 1.344 | 1.329 | . 714 |
| 4,5,6:20 ${ }^{\circ} \mathrm{C}$ | 1749 | 2196 | 14.662 | 14.732 | . 379 | 1.016 | 1.043 | . 621 |
|  |  | 2196 | 13.646 | 13.621 | . 662 | 1.737 | 1.845 | . 008 |

Figure 2a, b, c. Average total vertebrae within small length ranges against length.
2a: $4,5,6: 20^{\circ} \mathrm{C}$
2b: $7: 6^{\circ} \mathrm{C}$
2c: $1: 28^{\circ} \mathrm{C}$ and $2: 26^{\circ} \mathrm{C}$
O control group mean.
$\triangle$ experimental group mean.
$\uparrow$ arrow linking control and
experimental group means
for the same length range, indicating direction of change.

-     + or - one standard deviation above and below of control group mean.
—4, 5, 6:20 ${ }^{\circ} \mathrm{C}$ experimental group regression lines.
- 7: $6^{\circ} \mathrm{C}$ (unstratified data). experimental group regression line.
: stratification point, 4, 5, 6:20 ${ }^{\circ} \mathrm{C}$ analysis.



Table 3. linearity of effect of length are marked with an asterisk(*) and significant statistics from such analyses are
double underlined.
Table 3. cont'd.


Figure 3a, b. Average caudal vertebrae within small length ranges against length.

3a: 4, 5, 6:20 ${ }^{\circ} \mathrm{C}$
3b: $\quad 7: 6^{\circ} \mathrm{C}$

Symbols as for Figure 2.


Abbreviations and symbols as for Table 3.


Figure 4a, b. Average thoracic vertebrae within small length ranges against length.
$4 \mathrm{a}: \quad 4,5,6: 20^{\circ} \mathrm{C}$
$4 \mathrm{~b}: \quad 7: 6^{\circ} \mathrm{C}$

Symbols as for Figure 2.


Abbreviations and symbols as for Table 3.

|  |  |  |  |  |  | R | E G | R E | S | S I | 0 |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Entry | Treat <br> -ment | $t$ Experiment | Size Range | n | Intercept | Coefficient | P Equal Slopes | Adj. <br> Mean |  | P Equal Means | P | res. mean square | $\begin{aligned} & \quad \mathrm{P} \\ & \mathrm{~F} \text { test } \\ & \mathrm{r} \mathrm{~ms} \end{aligned}$ |
| 1 | $\begin{aligned} & \overline{\mathrm{C}} \\ & \mathrm{E} \end{aligned}$ | 1:280 |  | $\begin{aligned} & 300 \\ & 300 \end{aligned}$ | $\begin{aligned} & 18.320 \\ & 19.159 \end{aligned}$ | $\begin{array}{r} .505 \\ .098 \end{array}$ | $\underline{.018}$ | $\begin{aligned} & 19.248 \\ & 19.322 \end{aligned}$ |  | . 232 | $\begin{aligned} & .000 \\ & .401 \end{aligned}$ | $\begin{aligned} & .455 \\ & .387 \end{aligned}$ |  |
| 2 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | $2: 26{ }^{\circ} \mathrm{C}$ | $\begin{aligned} & 1.32-3.4 \\ & 1.7-3.5 \end{aligned}$ | $\begin{aligned} & 442 \\ & 207 \end{aligned}$ | $\begin{aligned} & 19.194 \\ & 19.354 \end{aligned}$ | $\begin{array}{r} .128 \\ -.017 \end{array}$ | . 403 | $\begin{aligned} & 19.463 \\ & 19.308 \end{aligned}$ |  | . 003 | $\begin{array}{r} .190 \\ .901 \end{array}$ | $\begin{array}{r} .361 \\ .320 \end{array}$ |  |
| 3 | $\underset{\mathrm{E}}{\mathrm{C}}$ | 4:20 ${ }^{\circ} \mathrm{C}$ | $\begin{array}{r} .82-1.71 \\ .99-1.82 \end{array}$ | $\begin{array}{r} 942 \\ 1109 \end{array}$ | $\begin{aligned} & 6.320 \\ & 9.917 \end{aligned}$ | $\begin{aligned} & 8.246 \\ & 5.645 \end{aligned}$ | . 000 | $\begin{aligned} & 17.255 \\ & 17.404 \end{aligned}$ |  | . 002 | $\begin{aligned} & .000 \\ & .000 \end{aligned}$ | $\begin{aligned} & 1.138 \\ & 1.066 \end{aligned}$ |  |
| 4 | $\underset{\mathrm{E}^{\prime}}{\mathrm{C}}$ | $5: 20{ }^{\circ} \mathrm{C}$ | $\begin{aligned} & 1.12-3.27 \\ & 1.02-3.36 \end{aligned}$ | $\begin{array}{r} 1089 \\ 979 \end{array}$ | $\begin{aligned} & 18.589 \\ & 18.525 \end{aligned}$ | $\begin{aligned} & .212 \\ & .238 \end{aligned}$ |  |  |  |  | $\begin{aligned} & .005 \\ & .008 \end{aligned}$ | $\begin{aligned} & .460 \\ & .361 \end{aligned}$ | . 01 |
| 5 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | 6:20 ${ }^{\circ} \mathrm{C}$ | $\begin{aligned} & 1.38-6.72 \\ & 1.87-7.6 \end{aligned}$ | $\begin{aligned} & 502 \\ & 579 \end{aligned}$ | $\begin{aligned} & 18.841 \\ & 18.947 \end{aligned}$ | $\begin{array}{r} .023 \\ .014 \end{array}$ |  |  |  |  | $\begin{aligned} & .478 \\ & .733 \end{aligned}$ | $\begin{array}{r} .401 \\ .714 \end{array}$ | . 01 |
| 6 | $\begin{array}{ll} \mathrm{C} & 4 \\ \mathrm{E} \end{array}$ | $4,5,6: 20^{\circ} \mathrm{C}$ | $\begin{aligned} & .82-6.72 \\ & .99-7.6 \end{aligned}$ | $\begin{aligned} & 2293 \\ & 2603 \end{aligned}$ | $\begin{aligned} & 16.880 \\ & 17.395 \end{aligned}$ | $\begin{array}{r} .611 \\ .456 \end{array}$ | . 000 | $\begin{aligned} & 18.206 \\ & 18.386 \end{aligned}$ |  | . 000 | $\begin{aligned} & .000 \\ & .000 \end{aligned}$ | $\begin{aligned} & 1.713 \\ & 1.301 \end{aligned}$ | . 01 |
| 7 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | 3:10 ${ }^{\circ} \mathrm{C}$ | $\begin{aligned} & 1.4-3.6 \\ & 1.62-3.23 \end{aligned}$ | $\begin{array}{r} 488 \\ 249 \end{array}$ | $\begin{aligned} & 19.576 \\ & 19.066 \end{aligned}$ | $\begin{array}{r} -.161 \\ .039 \end{array}$ | . 168 | $\begin{aligned} & 19.230 \\ & 19.168 \end{aligned}$ |  | . 201 | $\begin{array}{r} .057 \\ .739 \end{array}$ | $\begin{array}{r} .352 \\ .344 \end{array}$ |  |
| 8 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | 7: $6^{\circ} \mathrm{C}$ | $\begin{array}{r} .83-2.58 \\ .92-2.72 \end{array}$ | $\begin{aligned} & 1473 \\ & 1444 \end{aligned}$ | $\begin{aligned} & 13.932 \\ & 15.019 \end{aligned}$ | $\begin{aligned} & 2.69 \\ & 2.028 \end{aligned}$ | . 000 | $\begin{aligned} & 18.082 \\ & 18.137 \end{aligned}$ |  | . 220 | $\begin{aligned} & .000 \\ & .000 \end{aligned}$ | $\begin{array}{r} .804 \\ .757 \end{array}$ |  |
| *9 | $\begin{array}{ll} \mathrm{C} & 4 \\ \mathrm{E} \end{array}$ | 4,5,6:20 ${ }^{\circ} \mathrm{C}$ | $\begin{aligned} & \mathrm{GT1.2} \\ & \mathrm{LTI} .85 \end{aligned}$ | $\begin{aligned} & 1053 \\ & 1061 \end{aligned}$ | $\begin{aligned} & 12.112 \\ & 12.655 \end{aligned}$ | $\begin{aligned} & 4.047 \\ & 3.718 \end{aligned}$ |  |  |  |  | $\begin{aligned} & .000 \\ & .000 \end{aligned}$ | . |  |
| *10 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | 7: $6^{\circ} \mathrm{C}$ | $\begin{aligned} & \text { GT1.2 } \\ & \text { LT1. } 85 \end{aligned}$ | $\begin{aligned} & 933 \\ & 838 \end{aligned}$ | $\begin{aligned} & 13.076 \\ & 13.565 \end{aligned}$ | $\begin{aligned} & 3.401 \\ & 3.016 \end{aligned}$ | . 118 | $\begin{aligned} & 18.126 \\ & 18.042 \end{aligned}$ |  | $\frac{050}{0}$ | $\begin{array}{r} .000 \\ .000 \end{array}$ | $\begin{array}{r} .755 \\ .740 \end{array}$ |  |
| *11 | $\begin{array}{ll} \mathrm{C} & 4 \\ \mathrm{E} \end{array}$ | $4.5,6: 20^{\circ} \mathrm{C}$ | GT1. 85 | $\begin{aligned} & 1001 \\ & 1424 \end{aligned}$ | $\begin{aligned} & 19.071 \\ & 19.063 \end{aligned}$ | $\begin{array}{r} -.028 \\ -.003 \end{array}$ |  |  |  |  | $\begin{array}{r} .165 \\ .661 \end{array}$ | $\begin{array}{r} .482 \\ .569 \end{array}$ | . 01 |

Figure 5a, b. Average caudm vertebrae within small length ranges against length.

5a: 4, 5, 6:20 ${ }^{\circ} \mathrm{C}$
5b: $\quad 7: 6^{\circ} \mathrm{C}$

Symbols as for Figure 2.


Table 6. Statistics for caudm vertebrae. Abbreviations and symbols as for Table 3.

|  |  |  |  |  |  | R | E G | R E | $\mathrm{S} \quad \mathrm{I}$ | 0 |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Entry | Treat -ment | $t$ Experiment | Size Range | n | Intercept | Coefficient | P Equal Slopes | Adj. <br> Mean | P Equal Means | P | $\begin{gathered} \text { res. } \\ \text { mean } \\ \text { square } \end{gathered}$ |  |
| *1 | c | $4: 20^{\circ} \mathrm{C}$ |  | 942 | 20.376 | -. 541 | . 373 | 19.659 | . 714 | . 003 | . 567 |  |
|  | E |  |  | 1109 | 20.033 | -. 322 |  | 19.646 |  | . 053 | . 611 |  |
| *2 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | $5: 20{ }^{\circ} \mathrm{C}$ |  | $\begin{array}{r} 1089 \\ 980 \end{array}$ | $\begin{aligned} & 19.792 \\ & 19.877 \end{aligned}$ | $\begin{aligned} & -.054 \\ & -.115 \end{aligned}$ |  |  |  | $\begin{array}{r} .494 \\ .267 \end{array}$ | $.494$ | $\underline{.01}$ |
| * 3 | c | 6:20 ${ }^{\circ} \mathrm{C}$ |  | $\begin{array}{r} 502 \\ 579 \end{array}$ | $\begin{aligned} & 19.734 \\ & 20.087 \end{aligned}$ | $\begin{aligned} & -.011 \\ & -.097 \end{aligned}$ |  |  |  | $\begin{aligned} & .793 \\ & .006 \end{aligned}$ | $\begin{aligned} & .689 \\ & .558 \end{aligned}$ | $\stackrel{.01}{ }$ |
| * 4 |  | 4,5,6:20 ${ }^{\circ} \mathrm{C}$ |  | $\begin{aligned} & 2604 \\ & 2293 \end{aligned}$ | $\begin{aligned} & 19.661 \\ & 19.625 \end{aligned}$ | $\begin{array}{r} .003 \\ .004 \end{array}$ |  |  |  | $\begin{aligned} & .844 \\ & .771 \end{aligned}$ | $\begin{array}{r} .735 \\ .614 \end{array}$ | $\bigcirc 01$ |
| *5 | $\mathrm{C}$ | 7:6 ${ }^{\circ} \mathrm{C}$ |  | $\begin{aligned} & 1473 \\ & 1444 \end{aligned}$ | $\begin{aligned} & 20.139 \\ & 20.147 \end{aligned}$ | $\begin{aligned} & -.324 \\ & -.391 \end{aligned}$ | . 558 | $\begin{aligned} & 19.631 \\ & 19.538 \end{aligned}$ | . 008 | $\begin{aligned} & .001 \\ & .000 \end{aligned}$ | $\begin{aligned} & .515 \\ & .662 \end{aligned}$ | . 05 |
| *6 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | 4,5,6:20 ${ }^{\circ} \mathrm{C}$ | LT1.5 | $\begin{aligned} & 879 \\ & 898 \end{aligned}$ | $\begin{aligned} & 20.212 \\ & 20.151 \end{aligned}$ | $\begin{aligned} & -.405 \\ & -.379 \end{aligned}$ |  |  |  | $\begin{aligned} & .058 \\ & .131 \end{aligned}$ | $\begin{array}{r} .560 \\ .651 \end{array}$ | $\underline{.05}$ |
| * 7 | $\begin{gathered} \mathrm{C} \\ \mathrm{E} \end{gathered}$ | 7:6 ${ }^{\circ} \mathrm{C}$ | LT1. 5 | $\begin{aligned} & 753 \\ & 385 \end{aligned}$ | $\begin{aligned} & 19.736 \\ & 20.984 \end{aligned}$ | $\begin{array}{r} -.006 \\ -1.003 \end{array}$ | . 143 | $\begin{aligned} & 19.719 \\ & 19.624 \end{aligned}$ | . 068 | $\begin{aligned} & .982 \\ & .052 \end{aligned}$ | $\begin{array}{r} .591 \\ .785 \end{array}$ | $\bigcirc$ |
| *8 | $\begin{aligned} & C \\ & \mathrm{E} \end{aligned}$ | 4,5,6:20 ${ }^{\circ} \mathrm{C}$ | GT1. 5 | $\begin{aligned} & 1396 \\ & 1682 \end{aligned}$ | $\begin{aligned} & 19.605 \\ & 19.605 \end{aligned}$ | $\begin{aligned} & .020 \\ & .010 \end{aligned}$ |  |  |  | $\begin{array}{r} .370 \\ .556 \end{array}$ | $\begin{array}{r} .846 \\ .592 \end{array}$ | $\stackrel{.01}{ }$ |
| *9 | $\underset{\text { E }}{\substack{c}}$ | 7: $6^{\circ} \mathrm{C}$ | GT1. 5 | $\begin{aligned} & 40 \\ & 69 \end{aligned}$ | $\begin{aligned} & 20.115 \\ & 19.72 \end{aligned}$ | $\begin{aligned} & -.319 \\ & -.171 \end{aligned}$ | . 748 | $\begin{aligned} & 19.546 \\ & 19.425 \end{aligned}$ | $\underline{.040}$ | $\begin{aligned} & .067 \\ & .345 \end{aligned}$ | $\begin{aligned} & .593 \\ & 1.134 \end{aligned}$ | $\stackrel{.01}{ }$ |

Figure 6a, b. Average thorm vertebrae within small length ranges against length.

6a: 4, 5, 6:20 ${ }^{\circ} \mathrm{C}$
6b: $\quad 7: 6^{\circ} \mathrm{C}$

Symbols as for Figure 2.


Table 7. Statistics for thorm vertebrae. Abbreviations and symbols as for Table 3.

|  |  |  |  |  |  | R | E G | R E | S | $\mathrm{S} \quad \mathrm{I}$ | 0 | N |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Entry | Treat -ment | Experiment | Size Range | n | Intercept | Coefficient | P Equal Slopes | Adj. Mean |  | P Equal Means | P | res. mean square | $\quad \mathrm{P}$ F test r ms |
| 1 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | $4: 20^{\circ} \mathrm{C}$ | $\begin{aligned} & .82-1.71 \\ & .99-1.82 \end{aligned}$ | $\begin{array}{r} 942 \\ 1109 \end{array}$ | $\begin{aligned} & 13.769 \\ & 18.463 \end{aligned}$ | $\begin{array}{r} .253 \\ -.204 \end{array}$ | . 029 | $\begin{aligned} & 18.092 \\ & 18.185 \end{aligned}$ |  | . 002 | $\begin{array}{r} .139 \\ .109 \end{array}$ | $\begin{array}{r} .515 \\ .355 \end{array}$ | . 05 |
| 2 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | $5: 20{ }^{\circ} \mathrm{C}$ | $\begin{aligned} & 1.12-3.27 \\ & 1.02-3.36 \end{aligned}$ | $\begin{array}{r} 1089 \\ 980 \end{array}$ | $\begin{aligned} & 17.748 \\ & 17.347 \end{aligned}$ | $\begin{array}{r} .138 \\ .335 \end{array}$ |  |  |  |  | $\begin{aligned} & .106 \\ & .003 \end{aligned}$ | $\begin{aligned} & .583 \\ & .526 \end{aligned}$ | . 05 |
| 3 | C | $6: 20^{\circ} \mathrm{C}$ |  | $\begin{aligned} & 502 \\ & 579 \end{aligned}$ | $\begin{aligned} & 18.123 \\ & 17.872 \end{aligned}$ | $\begin{aligned} & .001 \\ & .071 \end{aligned}$ |  |  |  |  | $\begin{array}{r} .964 \\ .019 \end{array}$ | $.418$ <br> .408 |  |
| 4 | $\underset{\mathrm{F}}{\mathrm{C}} 4$ | $4,5,6: 20^{\circ} \mathrm{C}$ |  | $\begin{aligned} & 2604 \\ & 2293 \end{aligned}$ | $\begin{aligned} & 18.032 \\ & 18.106 \end{aligned}$ | $\begin{aligned} & .019 \\ & .013 \end{aligned}$ | . 484 | $\begin{aligned} & 18.064 \\ & 18.136 \end{aligned}$ |  | . 001 | $\begin{array}{r} .149 \\ .245 \end{array}$ | $\begin{aligned} & .664 \\ & .436 \end{aligned}$ | .01 |
| * 5 | $\begin{aligned} & \mathrm{C} \\ & \mathrm{E} \end{aligned}$ | $7: 6^{\circ} \mathrm{C}$ | $\begin{array}{r} .83-2.58 \\ .92-2.72 \end{array}$ | $\begin{aligned} & 1473 \\ & 1444 \end{aligned}$ | $\begin{aligned} & 17.657 \\ & 17.496 \end{aligned}$ | $\begin{aligned} & .322 \\ & .454 \end{aligned}$ | . 202 | $\begin{aligned} & 18.163 \\ & 18.190 \end{aligned}$ |  | . 453 | $\begin{aligned} & .000 \\ & .000 \end{aligned}$ | $\begin{aligned} & .483 \\ & .506 \end{aligned}$ |  |
| * 6 | $\underset{\mathrm{E}}{\mathrm{C}} 4$ | $4,5,6: 20^{\circ} \mathrm{C}$ | LT2.0 | $\begin{aligned} & 1465 \\ & 1332 \end{aligned}$ | $\begin{aligned} & 18.258 \\ & 18.570 \end{aligned}$ | $\begin{array}{r} -.146 \\ -.287 \end{array}$ | . 22 | $\begin{aligned} & 18.044 \\ & 18.153 \end{aligned}$ |  | . 000 | $\begin{array}{r} .087 \\ .000 \end{array}$ | .506 .767 .342 | . 01 |
| * 7 | C | 5:20 ${ }^{\circ} \mathrm{C}$ | LT2.0 | $\begin{aligned} & 520 \\ & 223 \end{aligned}$ | $\begin{aligned} & 17.848 \\ & 17.783 \end{aligned}$ | $\begin{aligned} & .063 \\ & .113 \end{aligned}$ | .947 | $\begin{aligned} & 17.90 \\ & 17.994 \end{aligned}$ |  | . 706 | $\begin{aligned} & .845 \\ & .766 \end{aligned}$ | $\begin{array}{r} 1.222 \\ .281 \end{array}$ | . 01 |
| * 8 | C | $7: 6^{\circ} \mathrm{C}$ | LT2. 0 | 1122 971 | $\begin{aligned} & 17.673 \\ & 17.604 \end{aligned}$ | $\begin{array}{r} .310 \\ .370 \end{array}$ |  | 17.99 |  |  | .001 <br> .009 | $\begin{array}{r} .486 \\ .855 \end{array}$ | .01 |
| * 9 | $\begin{array}{ll} \mathrm{C} \\ \mathrm{E} \end{array}$ | $4,5,6: 20^{\circ} \mathrm{C}$ | GT2.0 | $\begin{array}{r} 843 \\ 1292 \end{array}$ | $\begin{aligned} & 18.020 \\ & 17.964 \end{aligned}$ | $\begin{aligned} & .026 \\ & .053 \end{aligned}$ | . 356 | $\begin{aligned} & 18.099 \\ & 18.128 \end{aligned}$ |  | . 356 | $\begin{array}{r} .250 \\ .005 \end{array}$ | $\begin{aligned} & .476 \\ & .525 \end{aligned}$ |  |
| *10 | C | $5: 20^{\circ} \mathrm{C}$ | GT2.0 | $\begin{aligned} & 364 \\ & 724 \end{aligned}$ | $\begin{aligned} & 17.858 \\ & 19.257 \end{aligned}$ | $\begin{array}{r} .094 \\ .370 \end{array}$ | . 234 | $\begin{aligned} & 18.077 \\ & 18.101 \end{aligned}$ |  | . 629 | $.603$ $.007$ |  |  |
| *11 | $\begin{aligned} & \text { C } \\ & \text { E } \end{aligned}$ | $7: 6^{\circ} \mathrm{C}$ | GT2. 0 | $\begin{array}{r} 64 \\ 145 \end{array}$ | $\begin{aligned} & 16.685 \\ & 16.249 \end{aligned}$ | $\begin{array}{r} .768 \\ 1.015 \end{array}$ | . 693 | $\begin{aligned} & 18.342 \\ & 18.497 \end{aligned}$ |  | .123 | $\begin{array}{r} .179 \\ .010 \end{array}$ | .445 <br> .442 |  |

Figure 7a, b. Average dorsal fin ray counts within small length ranges against length.

7a: $4,5,6: 20^{\circ} \mathrm{C}$
$7 \mathrm{~b}: \quad 7: 6^{\circ} \mathrm{C}$

PR = regression zero slope probability.
control group regression line.
--- experimental group regression
line.
All other symbols as for Figure 2.


Table 8. Statistics for dorsal fin rays. Abbreviations and symbols as for Table 3.


Figure 8. Average pectoral fin ray count within small
length ranges against length $4,5,6: 20^{\circ} \mathrm{C}$. Symbols as for Figure 2.

Table 9. Statistics for pectoral fin rays. Abbreviations and symbols as for Table 3.

Table 10. Correlation matrices 4, 5, 6:20 ${ }^{\circ} \mathrm{C}$; all measured characters; control and Control Group. $\quad \mathrm{df}=2291$

|  | Vertebrae | Caudal | Thoracic | Dorsal | Pectoral | Size | Caudm | Thorm |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| vertebrae | 1.000 |  |  |  |  |  |  |  |
| caudal | -.397 | 1.000 |  |  |  |  |  |  |
| thoracic | -0.090 | -.877 | 1.000 |  |  |  |  |  |
| dorsal | 0.038 | -.086 | .095 | 1.000 |  |  |  |  |
| pectoral | .007 | -.460 | .491 | .055 | 1.000 |  |  |  |
| size | .200 | -.417 | .452 | .069 | .620 | 1.000 |  |  |
| caudm | .484 | .238 | -.051 | .024 | .029 | .013 | 1.000 |  |
| thorm | .316 | -.012 | .117 | -.038 | .009 | .011 | -.136 | 1.000 |

Experimental Group. $\mathrm{df}=2601$

|  | Vertebrae | Caudal | Thoracic | Dorsal | Pectoral | Size | Caudm | Thorm |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| vertebrae | 1.000 |  |  |  |  |  |  |  |
| caudal | .392 | 1.000 |  |  |  |  |  |  |
| thoracic | .118 | -.776 | 1.000 |  |  |  |  |  |
| dorsal | .014 | -.040 | .060 | 1.000 |  |  |  |  |
| pectoral | -.030 | -.478 | .508 | .005 | 1.000 |  |  |  |
| size | .017 | -.398 | .431 | .008 | .664 | 1.000 |  |  |
| caudm | .590 | -.376 | -.068 | .005 | -.010 | .001 | 1.000 |  |
| thorm | .357 | -.021 | .205 | .016 | -.023 | .020 | -.415 | 1.000 |

## DISCUSSION

a)

## Test Statistics

The large number of highly significant changes in mean count and variance which was observed for all measured meristic characters except total vertebrae (Table 2) strongly suggests that predation can alter the distribution of meristic counts in a population. This may occur because meristic variation has a direct effect on survival, possibly by affecting the ability of a fish to swim and hence avoid a predator, or alternatively, because parts number is correlated with some non-meristic factor which is important in determining survival. Since the length distribution of the fish differed significantly between control and experimental treatment groups (Appendix B) length was a possible correlated non-meristic factor.

The analysis of covariance results contained in Tables 3 through 9 include enough significant differences between control and experimental treatment groups to justify the conclusion that predation has caused changes in the frequency distribution of the meristic characters, with the possible exception of total vertebrae, that are not merely attributable to predation effects on the size distribution. Information on the dependance of count specificsurvival rates on length and temperature can be obtained by examination of changes in the count distribution for fish of equal size for
experiments done at different temperatures.
b) Changes in Length Conditioned Count Distribtuion

If one count under a given set of experimental conditions, confers a higher probability of survival than all other counts the population mean will move towards this optimum count as selection proceeds and less favoured individuals are removed. If two or more counts equally confer the highest probability of survival the population mean will proceed to a value between these most favoured counts, the exact value being dependent upon the proportions of the counts in the original population. This, quite possibly fractional count will be referred to as the optimum count for that population under the experimental condtions.

In this study the "optimum count" therefore means the mean count which will be observed when all the remaining fish in the population (or all the remaining fish of a given length if count specific survival rate depends on length) within a population have an equal probability of survival. This optimum count may be dependent upon the original distribution of counts within the population as well as characteristics of the individual fish and the experimental conditions. It is also unlikely that it will be directly observed, and it is certainly difficult to determine how well an observed experimental mean approximates this optimum.

Except where there are clear indications that an experimental mean is a good approximation of an optimum count discussion will be concerned with indications of movement of the means towards an optimum count, as indicated by changes in regression parameters, rather than attempting to identify optimum counts.

If the optimum count for a character changes with length a correlation would develop between mean count and length as less fit individuals were removed. If the optimum counts for a range of sizes lie on a straight line (the "optimum line") the movement of the means of the count distributions for each length towards the optimum count for each length as selection proceeds will be reflected in the parameters of regressions done on the data as selection proceeds. The expected result, if the optimum line has a non-zero slope, would be a decrease in zero slope probability and regression residual variance, possibly accompanied by an increase in regression slope. Comparison of control and experimental group regression lines therefore provides a possible method for simultaneously using all of the data for a stratum over which the effect of length on count appears to be linear to detect length dependence of the optimum count.

Length dependence of the optimum count will cause the development of a length:count correlation as selection proceeds only when the optimum count for each length present in the experiment is within the range of counts observed at
that length. The standard deviation about the control mean for each length class has been added to the mean count against length graphs. This is intended to provide a rough indication of the control group count distribution. Increases in count:length correlation are considered to be indications of length dependence of the optimum count if the experimental group regression line (estimator of the optimum line) falls within these standard error bars. The test is flawed by circularity since it assumes that the experimental regression line is an estimator of the optimum line in order to establish the conditions under which it can be predicted to be an estimator of the optimum line.

If a mean count:length regression differing from the optimum count:length correlation exists in the control sample then removal of less fit individuals would cause an initial drop in correlation and regression goodness of fit. The best indication of this situation will be a difference in slope between control and experimental group regression lines. If the slope in the experimental group is the steeper of the two, this is an indication that the optimum count line has a non-zero slope (the optimum is length dependent).

Increases in regression line slope and increases in regression goodness of fit can be predicted to occur as individuals are removed in the absence of length dependence of the optimum count. Such increases could be caused by changes in the length distribution of the data if the relationship between mean count and length at any stage of
selection is best represented by a curve. The increases will be caused by weighting of the regression on different segments of the curve rather than by concentration of the data at all lengths on the experimental regression line. Since the existence of non-linearity cannot be conclusively disproved, and since the length distribution of the data does change, increases in slope and regression goodness of fit, even if significant, do not prove length dependence of the optimum count. However, if the mean count for most length classes over the entire range of lengths being considered moves towards the experimental regression line this is a direct indication that the development of a mean count:length relationship is attributable to length dependence of the optimum count rather than to changes in length distribution of the data. Changes in regression parameters therefore provide useful information as to the nature of the optimum count:length relationship if they are considered in conjunction with direct information about changes in count distribution for specific lengths or small length classes. We will now consider changes in mean for individual length classes and the combined changes in mean and variance for fish of all lengths as estimated by the differences in slope, residual variance, and regression zero slope probability observed between control and experimental regressions.
i) Total Vertebrae

The graph of the data for total vertebrae, pooled $20^{\circ} \mathrm{C}$ data (Figure 2a), strongly suggest an inflection point in the count:length association between 1.75 and 2.10 cm . The average total vertebrae count appears to be negatively correlated with length up to this range of lengths and positively correlated thereafter. Although only one significant difference between treatment groups in adjusted mean or regression line slope was observed (significant change in regression slope in $5: 20^{\circ} \mathrm{C}$, Table 3 , entry 4) closer examination of the length-conditioned data reveals evidence for the interpretation of this association as an optimum count:length correlation.

The results for fish shorter than 2.10 cm point rather strongly to a negative correlation between optimum total vertebrae count and length. The regression slope is negative in both treatment groups but it is steeper in the experimental than the control group. The experimental group also has a lower zero slope probability and regression residual variance and higher correlation coefficient. The experimental regression line lies well within the area defined by the count mean standard error bars. The most striking observation is the movement of the means for the size classes between 1.0 and 1.7 cm to the experimental regression line. The difference between the treatment group means in the length class 1.2 to 1.3 cm (an increase from 37.77 to 37.89 ) is highly significant
( $Z=69.838, P^{>} .001$ ). However, the decrease in mean from 37.78 to 37.68 in the 1.7 to 1.8 cm size class is not significant and so fails to provide statistical proof of length dependence of the optimum. The regression for fish longer than 2.1 cm shows an increase in positive slope, an increase in regression residual variance and a great decrease in zero slope probability. The length class mean plots show some convergence on the line but suggest that the optimum relationship has a negative slope between 4.5 and 5.5 cm and that these data lowered the regression line slope.

The data from 7: $6^{\circ} \mathrm{C}$ suggest that the optimum relationship may be different in cold water. The length class means in Figure 2 b do not converge on the pooled $20^{\circ} \mathrm{C}$, shorter than 2.1 cm , experimental regression line. Both the regression parameters and the graph suggest that the optimum count in cold water increases with body length between .85 and 2.75 cm . One length class (l.15 to 1.25 cm ) displays divergent movement of the means at different temperatures (from comparable control group means to a higher mean at $20^{\circ} \mathrm{C}$ and to a lower mean at $6^{\circ} \mathrm{C}$ ). However, the decrease in mean for the class in $7: 6^{\circ} \mathrm{C}$ is not significant.

While no statistical evidence for an effect of predation on the distribution of counts for total vertebrae exists, examination of the movement of the means and the parameters of the treatment group regressions suggests that a complex
relationship exists. Specifically, at $20^{\circ} \mathrm{C}$, the optimum count decreases with increased length for lengths between 1.1 and 1.75 cm . There is also some evidence that this association does not apply at $6^{\circ} \mathrm{C}$.
ii) Caudal Vertebrae

Figures 3 a and b illustrate that the average caudal vertebrae count in both treatment groups decreases rapidly as length increases from 1.0 cm to about 2.25 cm , at both $6^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. The division between caudal and thoracic vertebrae was dependent upon rib length. Not all of the ribs in fish shorter than about 1.3 cm were sufficiently ossified to be seen. There was therefore a decrease in mean caudal vertebrae count with increasing length which was due to continued growth and hence detectability of the ribs. The treatment groups differed in length distribution. There appeared to be a curve in the mean caudal vertebrae count-length relationship. There was also a lack of a clear trend in the regression parameters and the failure of the error bars for some short fish length classes to overlap the regression line obtained using the data for fish larger than 2.25 cm . These factors precluded the conclusion, using only the regression parameters, that these downward sloping regression lines are optima. However, Figure 3a, the length class mean plot, pooled $20^{\circ} \mathrm{C}$ data, does suggest a negative correlation between
optimum caudal vertebra number and length from 1.2 to 2.1 cm . It also suggests a positive correlation from 2.1 to 3.5 cm . Except for the point of inflection, this closely parallels the results obtained for total vertebrae. The experimental means for two length classes, 1.4 to 1.5 cm and 1.5 to 1.6 cm are both significantly higher than the corresponding control means ( $P=.014$ and $P$ < .001, respectively). No length class containing larger fish and having a control mean equal or lower than the control means in these classes displays a significant decrease. However, it is fairly evident from the movement of the means in Figure 3 a that the optimum is lower for fish approximately 2.0 cm in length than it is for shorter fish. Optimum caudal vertebrae count therefore appears to be negatively correlated with length between 1.1 and 2.1 cm . It is also evident from Figure 3a and from the regression parameters contained in Table 4, entry ll, that the optimum count is most probably positively correlated with length for fish longer than 2.0 cm . The experimental group slope is slightly larger than that in the control regression and the experimental group has a much lower zero slope probability. Figure 3a suggests that the positive correlation may not persist beyond 3.5 cm . There is no evidence that the optima are correlated with water temperature.

## iii) Thoracic Vertebrae

The thoracic vertebrae against length graph (Figure 4a) suggest a positive correlation between optimum thoracic vertebrae count and length for lengths from 1.2 to 1.85 cm .

Both the experimental and control group regressions, using fish from 1.2 to 1.85 cm long are highly significant (P) .001, Table 5, entry 9), but there are no significant differences between groups. Although the experimental means in this size range appear to converge on a positively sloped line from both above and below (Figure 4a), none of the differences in mean between treatment groups are significant. The optimum count for fish between 1.85 and at least 6.0 cm long appears to be 19. Figure 4 a illustrates the convergence of the length class means on 19, a convergence which is reflected in the regression parameters (Table 5, entry Il). There is no evidence that the optima are different at $6{ }^{\circ} \mathrm{C}$. The 7:6 ${ }^{\circ} \mathrm{C}$ length adjusted experimental mean for fish between 1.2 and 1.85 cm long was significantly lower than the corresponding control mean. Both the regression parameters and the length class means plot (Table 5, entry l0, Figure 4b) are similar to those obtained for the pooled $20^{\circ} \mathrm{C}$ data).
iv) Caudm Vertebrae

The significantly lower length adjusted mean caudm vertebrae count in the $7: 6^{\circ} \mathrm{C}$ experimental group and the
large numbers of significant differences between treatment groups in regression residual mean square (Table 6) indicate that predation has an effect on the distribution of caudm vertebrae counts, beyond what is accounted for by its effect on the length distribution of the data. The regression parameters suggest the existence of a negative correlation between optimum caudm vertebrae count and length at $6^{\circ} \mathrm{C}$. However, this is not strongly supported by the movements of the length class means in Figure 5b. No conclusions can be reached as to the optimum count. While no significant differences between treatment groups were noted in the pooled $20^{\circ} \mathrm{C}$ data the count mean against length graph, Figure 5 a , is interesting because it indicates that the pre-exposure population did not conform to the negative correlation seen in the cold water experimental data and that there was no movement towards such a correlation after predation. The optima for, or the importance of, caudm vertebrae may therefore be temperature dependent. Figure 5a reveals convergence of the after predation data on a curve strikingly similar to that seen in Figure 2 a , the graph for total vertebrae, pooled $20^{\circ} \mathrm{C}$ data. Both lines appear to reach minima at 1.75 and 5.0 cm and a maximum at 3.0 cm .
v) Thorm Vertebrae

The experimental group for thorm vertebrae, pooled $20^{\circ} \mathrm{C}$ data (Figure 6a), displays the same minima and maximum
found in the graphs for total and caudm vertebrae, with which it is highly correlated - (Table lo). The analysis of covariance for fish shorter than 2.0 cm reveals a significant increase in adjusted mean ( $P>.001$ ) and the appearance in the experimental group of a highly significant correlation. The experimental group regression has a very low zero slope probability. The control group regression has a high zero slope probability. The experimental group also has a non-significantly greater negative slope and significantly ( $\mathrm{P}>.01$ ) smaller regression residual variance (Table 7, entry 6). The length class means (Figure 6a) converge on the experimental regression line from both above and below. The decrease in mean count observed in the 1.7 to 1.8 cm length class is not significant. However, the development of such strong convergence on a non-zero sloped line, lying well within the standard error bars on Figure 6a, strongly suggests that the optimum thorm vertebrae count decreases with increased length in this length range.

There is also strong evidence for the existence of a positive correlation between optimum thorm vertebrae count and length for fish longer than 2.0 cm . The experimental group, pooled $20^{\circ} \mathrm{C}$ data, has a low zero slope probability ( $\mathrm{P}=.05$, Table 7 , entry 9 ), not seen in the control group. Except for a possible dip at about 5.5 cm the length class
means again appear to converge on the experimental regression line (Figure 6a), which lies well within the region defined by the $\pm$ l standard deviation error bars. The results for $6^{\circ} \mathrm{C}$ resemble the results for total vertebrae at $6^{\circ} \mathrm{C}$ and therefore are dissimilar to those obtained at $20^{\circ} \mathrm{C}$. Both the length class mean plot, Figure 6b, and.the regression parameters in Table 7, entries 5, 8, and 11, suggest the existence at $6^{\circ} \mathrm{C}$ of a positive correlation between optimum thorm vertebrae count and length for fish shorter than 2.5 cm and possibly also for longer fish. While no proof of the correlation exists, Figure 6b shows that the length class mean in $7: 6^{\circ} \mathrm{C}$ moved away from rather than towards the experimental regression lines obtained from the pooled $20^{\circ} \mathrm{C}$ data. The optima therefore may be temperature dependent.
vi) Dorsal Fin Rays

Examination of the statistics for dorsal fin ray count in Table 8 and the movement of the length class means in Figures 7 a and b indicate that fish having 10 dorsal fin rays are favoured at all lengths tested and at both $6^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. The length class means for both temperatures show consistent movement to the zero slope line with intercept 10. The regression parameters for all experiments except $3: 10^{\circ} \mathrm{C}$ are consistent, with shallower slopes, and higher zero slope
probabilites being recorded in the experimental groups. In several experiments the zero slope probability climbs from significant low values to insignificance. These changes, combined with the significant increases in mean (not length adjusted) in $4: 20^{\circ} \mathrm{C}$ and $7: 6^{\circ} \mathrm{C}$ (Table 2), strongly indicate an optimum count of 10 independent of length and temperature.
vii) Pectoral Fin Rays

Figure 8 illustrates the strong association between pectoral fin ray count and length. The increase in mean count with length is probably largely due to continued development of the rays as the fish grow, making more rays visible in larger fish. The analysis of covariance (Table 9) indicates that predation had an effect on the distribution of pectoral fin ray counts, which cannot be accounted for by its effect on the length distribution of the data. Since the error bars for some length classes fail to overlap the experimental regression line no conclusions can be made concerning the nature of the optimum count or its association with length. However, the correlation in the experimental group is of approximately equal strength to that in the control group. This suggests that the optimum count is positively correlated with length. There is no indication that the optimum count is temperature dependent.
c) Mechanisms by Which Predation May Act to Alter Count Distribution: Correlation Effects and Directness of Action

The experiments indicate that the count distributions of all the meristic characters examined were affected by predation. The strength of the indication varies from character to character. There is no proof that the counts for all or any of the characters have a direct effect on survival by influencing locomotion. The changes in meristic count distribution observed for a character may be caused by its correlation with another meristic character or some other factor which in turn has a direct effect on survival. Even if the character does have a direct effect, the apparent optimum count at any length or temperature may be affected by simultaneous selection for a correlated factor.

The complexity of the apparent optimum count-length relationships for total, caudal, caudm, and thorm vertebrae suggests selection acting on several correlated factors. These variables display a fairly high degree of intercorrelation (Table l0) and the mean count within length classes plots for the pooled $20^{\circ} \mathrm{C}$ experimental data (Figures 2a, 3a, 5a, 6a) are strikingly similar. However, the first minimum in the count mean-length relationship may occur at a slightly
longer length for caudal vertebrae. The mean count plots for the control data are not as similar. Possibly all are moving towards a common relationship because of common correlation with an unmeasured factor.

If only one of this group of characters is subject to direct selection it is most likely to be thorm vertebrae, for which the clearest indications of selection for length dependent optima were obtained.

While it seems reasonable to assume that variation in the structure of the vertebral column has an effect on ability to swim it is not possible to conclude that the results obtained stem from such differences. For example, the selection for high lateral plate number morphs in the stickleback, Gasterosteus acculeatus, was attributed by Moodie, et al. (1973) to correlation of plate numbers with a behavioural. trait. The high plate count morph was less active and presumably was therefore less frequently exposed to predation. The changes in count distribution for total, caudal, caudm, and thorm vertebrae may be the result of such a correlation. The results obtained are probably the end product of a complex interaction of selection pressures acting on one or more of the correlated characters measured as well as other unmeasured correlated factors.

The apparent optima for thoracic vertebrae for fish between . 75 and 1.75 cm long may result from a strong negative correlation with caudal vertebrae. The apparent selection for a count of 19 at all greater lengths cannot be explained by correlation.

The results for caudal vertebrae, dorsal rays and pectoral rays may, of course, be due to correlation of the characters with unmeasured factors which are subjected to selective force.
d) Possible Mechanical Effects of Change in Parts Numbers

The possible effect of fin ray number on the mechanical support and possibly the size of a fin, and hence on its hydrodynamic characteristics is self evident. Possible effects of variation in the structure of the vertebral column on locomotion (and hence presumably on the ability to avoid a predator) and the dependence of such effects on length and water temperature are less obvious.

Spouge and Larkin (1979) have developed a mathematical model to explain the existence of pleomerism which predicts the effect of change in the number of propulsive vertebrae on locomotor ability. The model relates maximum thrust to the number of vertebrae present in a given length of propulsive musculature and predicts a nonlinear association between the logarithms of the optimum number of propulsive vertebrae and length. The model predicts that the optimum number should decrease with increasing length up to approximately 5 cm and then increase, the slope of the log propulsive vertebrae vs. log length graph reaching about . 43 for lengths greater than 50 cm . The propulsive vertebrae in the model (the more posterior vertebrae involved in generating propulsive undulations) bear a prominence for muscle insertion. They therefore correspond to caudm vertebrae. The predicted optimum count-length association in this model roughly corresponds to the mean count-length association observed
in the experimental data for total, caudal, caudm, and thorm vertebrae. The minimum optimum count in these associations is however reached at or below a length of 2.0 cm , considerably below the predicted 5.0 cm in the model. While no regressions were run on the common logarithms of the data, plots of $\log$ caudm vertebrae against log length were done for the experimental groups of the pooled $20^{\circ} \mathrm{C}$ data and $7: 6^{\circ} \mathrm{C}$ (Figures 9a and b). A vague indication of a $V$ shaped association appears to persist in the log transformed, pooled $20^{\circ} \mathrm{C}$ data. Spouge and Larkin (1979) also predict that the optimum line would be affected by water viscosity and therefore temperature. Temperature appears to affect the optima for several variables, including caudm vertebrae. The Spouge and Larkin (1979) model therefore provides a possible mechanism by which variation in caudm vertebrae count and possibly variation in other divisions of the vertebral column could affect swimming ability. Experiments involving longer fish would allow further testing of the predictions drawn from the model.

Lindsey (1975) suggested that change in vertebral numbers may change swimming ability by affecting the lengths of related structures, such as the myomeres, or by affecting flexibility. The second suggestion is most interesting, particularly since Blight's (1977) development of a fish

Figure 9a, b. $\log _{10}$ caudm vertebrae against log length.
9a: experimental group 4, 5, 6:20 ${ }^{\circ} \mathrm{C}$
9b: experimental group $7: 6^{\circ} \mathrm{C}$.


propulsion model in which the relative flexibility of different body regions is of critical importance. The model suggests that change in the structure of the vertebral column should affect locomotion, if it affects flexibility. Such a model would explain the apparent importance of changes in the number of parts in divisions of the vertebral column, including the number of anterior or thoracic vertebrae which are excluded from consideration in the Spouge and Larkin (1979) model. It also postulates that the movement of fish results from the interaction of the resistive force of the water and the flexibility of the fish. Since the resistive force of the water would be affected by its viscosity, which is in turn affected by temperature, the ideal vertebral structure should be dependent on temperature, as suggested by this study.

The results of this study are insufficient to test the predictions made under these theories.
e) Pleomerism, Jordan's Rule and Meristic Variability

Pleomerism is the tendency for the average vertebral numbers of species to be positively correlated with the maximum size attained by the species, (Lindsey, 1975). If the optimum count increases with length, as it appears to over the greater range of lengths tested for total, caudal, caudm, and thorm vertebrae, and for pectoral fin rays, and if the relative predation pressures for two species remains constant with changes in length, then the larger species will have a
higher average count. These optimum count length relationships therefore could lead to the development of pleomerism. In fact, if the timing of predation is manipulated, pleomerism can be generated wherever optimum count is length dependent. The assumption of approximately equal predation ratios for all lengths would seem reasonable for most species. Positively sloped optimum count:length lines are therefore most likely to lead to the development of pleomerism.

Jordan's Rule is a correlation between meristic parts numbers and latitude, (Pennak, 1964). The apparent dependence of the optimum counts for several divisions of the vertebral column on temperature opens the possibility that the cline might be caused by selection for optimum meristic counts.

With respect to meristic variation, the results of this study indicate for all characters except dorsal fin rays, that no one count confers a selective advantage at all body lengths and water temperatures. Meristic variation therefore may be maintained in fish population by balanced selection, fish with different counts having an advantage at different times so that selection does not operate to eliminate all but one count. Such balanced selection also provides a negative incentive for controlling phenotypic variation induced by environmental factors.

## CONCLUSIONS

1. Removal of individuals from a population by predators has a significant effect on the count distributions for four subdivisions of the vertebrae column; caudal, thoracic, caudm, and thorm vertebrae, and probably affects the count distribution for the total number of vertebrae in the column. Predation also has a significant effect on the count distributions for dorsal and pectoral fin rays. These effects are still significant even after significant effects of predation on the length distribution of fish in the population have been accounted for.
2. The optimum count for survival for total, caudal, caudm, and thorm vertebrae appears to be correlated with length. The optimum count-length relationships for these meristic characters appear to be similar, optimum count decreasing with length to a length of 1.75 to 2.1 cm and then increasing with length, at least to 5.0 cm . A second minimum may occur between 5.0 and 6.0 cm . The complexity of these apparently optimum relationships, their similarity, and the deqree of correlation between the characters suggests that the apparent optima are the result of selection acting on several correlated characters, possibly including factors which were not measured.
3. There is some indication that the optimum counts for total, caudm, and thorm vertebrae are temperature dependent.
4. The optimum thoracic vertebrae count appeared to increase rapidly with length up to a length of 1.85 cm possibly because of correlation with caudal vertebrae count. The optimum count for longer fish appeared to be 19, regardless of length. There was no indication that optimum count was affected by water temperature.
5. The optimum count for dorsal fin rays appeared to be 10 at all body lengths and temperatures examined.
6. The optimum count for pectoral fin rays probably increases with body length. There was no evidence that it is temperature dependent.
7. The existence of a predation effect on the distributions of counts for meristic characters which appears for some characters to be dependent upon body length and water temperature provides a possible explanation for the magnitude of meristic variation displayed by fish populations and also for the correlation of meristic parts numbers with maximum body length attained for a species (pleomerism) and latitude (Jordan's Rule).

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## APPENDICES

| Table i. <br> Meristic Character | ```Appendix A. Frequency distributions of counts of all meristic characters, experiment 6:20}\mp@subsup{}{}{\circ}\textrm{C}\mathrm{ . cont. = control group exp. = experimental group``` |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Number |  | Frequency (\%) |  |
|  | Count | Cont. | Exp. | Cont. | Exp. |
| vertebrae | 35 |  | 3 |  | . 5 |
|  | 36 | 14 | 12 | 2.8 | 2.1 |
|  | 37 | 128 | 146 | 25.5 | 25.2 |
|  | 38 | 287 | 325 | 57.2 | 56.1 |
|  | 39 | 69 | 88 | 13.7 | 15.2 |
|  | 40 | 3 | 3 | . 6 | . 5 |
| caudal | 16 |  | 4 |  | . 7 |
|  | 17 | 6 | 5 | 1.2 | . 9 |
|  | 18 | 119 | 140 | 23.7 | 24.2 |
|  | 19 | 291 | 338 | 58 | 58.4 |
|  | 20 | 79 | 86 | 15.7 | 14.9 |
|  | 21 | 5 | 3 | 1.0 | . 5 |
| thoracic | 17 | 8 | 1 | 1.8 | . 2 |
|  | 18 | 89 | 105 | 17.7 | 18.1 |
|  | 19 | 335 | 379 | 66.7 | 65.5 |
|  | 20 | 64 | 86 | 12.7 | 14.9 |
|  | 21 | 3 | 3 | . 6 | . 5 |
| caudm | 17 | 1 | 4 | . 2 | . 7 |
|  | 18 | 19 | 29 | 3.8 | 5.0 |
|  | 19 | 149 | 168 | 29.7 | 29.0 |
|  | 20 | 278 | 316 | 55.4 | 54.6 |
|  | 21 | 49 | 57 | 9.8 | 9.8 |
|  | 22 | 1 | 1 | . 2 | . 2 |
|  | 23 | 1 |  | . 2 |  |


| Meristic Character | Count | Number |  | Frequency ( $\%$ ) |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Cont. | Exp. | Cont. | Exp. |
| thorm | 16 | 5 |  | 1 |  |
|  | 17 | 60 | 66 | 12 | 11.4 |
|  | 18 | 313 | 358 | 62.4 | 61.8 |
|  | 19 | 115 | 141 | 22.9 | 24.4 |
|  | 20 | 6 | 9 | 1.2 | 1.6 |
|  | 21 |  | 1 |  | . 2 |
| dorsal | 9 | 18 | 17 | 3.6 | 2.9 |
|  | 10 | 471 | 552 | 94 | 95.3 |
|  | 11 | 10 | 6 | 2.0 | 1.0 |
|  | 12 |  | 1 |  | . 2 |
| pectoral | 11 | 1 | 4 | . 2 | . 7 |
|  | 12 | 4 | 6 | . 8 | 1.0 |
|  | 13 | 22 | 21 | 4.5 | 3.7 |
|  | 14 | 94 | 89 | 19.4 | 15.6 |
|  | 15 | 184 | 201 | 37.9 | 35.1 |
|  | 16 | 136 | 190 | 28.0 | 33.2 |
|  | 17 | 40 | 52 | 4.0 | 9.1 |
|  | 18 | 1 | 6 | 1.0 | 1.0 |
|  | 25 |  | 1 |  | . 2 |

APPENDIX B

Size Selection

The average length of survivors was greater than that of controls in every experiment (Table ii). The number of survivors (experimental data) in length intervals ranging from . 05 to .2 cm wide was divided by 3 X the corresponding number of controls to give an estimate of percent survival within each size interval. Graphs of the results for experiments $3: 10^{\circ} \mathrm{C}$ and $7: 6^{\circ} \mathrm{C}$ and $1: 28^{\circ} \mathrm{C}, 2: 26^{\circ} \mathrm{C}$ combined data (Fig. i) reveal that percent survival decreased with increased length to lengths of about 1.5 cm and then increased sharply. The same results, with greater scatter, were obtained with the combined $20^{\circ} \mathrm{C}$ data (Fig. ia). The small number of large fish in $7: 6^{\circ} \mathrm{C}$ and $1: 28^{\circ} \mathrm{C}, 2: 26^{\circ} \mathrm{C}$ combined data had the lowest percent survival (Figs. lc and d).

Figure ia, b, c, d. Approximate percent survival against length:
ia: $4,5,6: 20^{\circ} \mathrm{C}$
ib: $3: 10^{\circ} \mathrm{C}$
ic: $7: 6^{\circ} \mathrm{C}$
id: combined $1: 28^{\circ} \mathrm{C}$ and $2: 26^{\circ} \mathrm{C}$




