THE UNIVERSITY OF MANITOBA

THE APPLICATION OF CERTAIN TECHNIQUES OF FISHERIES

STATISTICS TO AN ISOLATED POPULATION OF BROOK

STICKLEBACKS, (<u>CULAEA</u> <u>INCONSTANS</u>) AT DELTA MARSH, MANITOBA
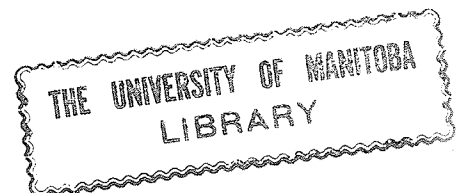
by

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ABSTRACT

The field study was done during the summers of 1969
and 1970. Assumptions and several methods used for mark-
recapture population estimates are discussed. Estimates of
population size were computed by the modification of the
Petersen method (Bailey, 1951) and by the stochastic model
of Jolly (1965). Results from the two methods were compared
and neither gave consistently higher estimates. Confidence
limits and standard errors for the estimates are provided.

Survival rates, total mortality rates and instan-
taneous rates of natural mortality are computed, all of which
are found to vary from one interval to the next. The
largest biomass, based on estimated population size was
found in September 1-5, 1969, when there was the greatest
surge of yearlings into the estimable population size.

Culaea inconstans in Delta Area, Lake Manitoba
matures in the second summer of life, when between 29 and
65 mm in total length and one year of age. Spawning starts
at the end of May after migration into the creeks and channels
in the marsh. By June 11-12 the yearlings are under 20 mm
in total length. The greatest part of growth is completed
in the first summer of life. Fish set the first ring, a
false check, in otoliths within the first month of life and
the annual ring is set by adults on June 1 of the second
summer of life. Aging of fish was done by reading otoliths

and plotting length frequency histograms. Condition factor
was found to be variable.

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INTRODUCTION

Knowledge of the vital statistics of fish species is an essential tool in the management of a fishery. Many models based on the Petersen type have been and are being developed for estimating population sizes of mobile animals. The literature on this subject is replete with ever increasing ingenious innovations ranging from deterministic, regression to completely stochastic models. Marking or tagging techniques too have advanced from fin clipping, tagging with nylon or metal wires to which are attached discs, to the use of either inert radio-active or fluorescent elements whose detection requires complicated equipment.

The present study was designed as an exercise in the use of mark and recapture techniques to obtain various vital statistics of an isolated fish population. Fish were marked by clipping dorsal, anal and pelvic spines. From the subsequent recapture samples were computed statistics such as estimates of population size, growth, mortality, survival rates and biomass. Estimates of population size were computed using the modified Petersen method and the completely stochastic model of Jolly (1965), as the only two methods which met the basic assumptions for mark-recapture experiments.

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Culaea inconstans was chosen for its abundance in Lake Manitoba and the adjacent marsh areas. This fish has also the added advantage of being short lived, the life span being two years at most.

DESCRIPTION OF THE STUDY AREA

The study was carried out in a channel located at
the University of Manitoba Field Station, Delta Marsh, on
the southern shore of Lake Manitoba, West of the Assiniboine
River Diversion. The channel, (Fig. 1), is connected to
Lake Manitoba only by one chain of channels linked with Cram
Creek to the west, which drains the southern farm land and
enters the lake about 2.5 km west of the Field Station. The
channel is 195.2 m long and ranges from 3.0 m at two narrow
points AB and BC, to 7.6 m wide at the middle of section B.
It was screened off from the rest of the chain of channels
using three sheets of fine wire gauze netting firmly fixed
against the mouth of the culvert at point C_3 (Fig. 1).

The northern and eastern shore of the channel along
the road is vertical; the opposite shore is shallow and flat.
The water depth throughout the summers ranged from about
30 cm at section C to 135 cm in the greater part of section B.
From May to June the water had a pale dark coloration due to
humic acid. From July to September it was clear only in
section C. The bottom was soft mud. From mid-July to the
autumn there was a thick overgrowth of aquatic vegetation.
In the summer of 1970 duck weed (Lemma) covered sections A
and B only from mid-July onwards, but was absent in the

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FIG. 1. Location of study area.

LAKE MANITOBA

U F S

A2   AB   B2

A1   H

BC

C2

CHANNEL

STUDY   CHANNEL

A,B,C, TEMPERATURE   POINTS

H   WATER   ANALYSIS

⊏ ⊐   CULVERT

— —   ROADS

24·4m

U F S   UNIVERSITY   FIELD   STATION

C3

N
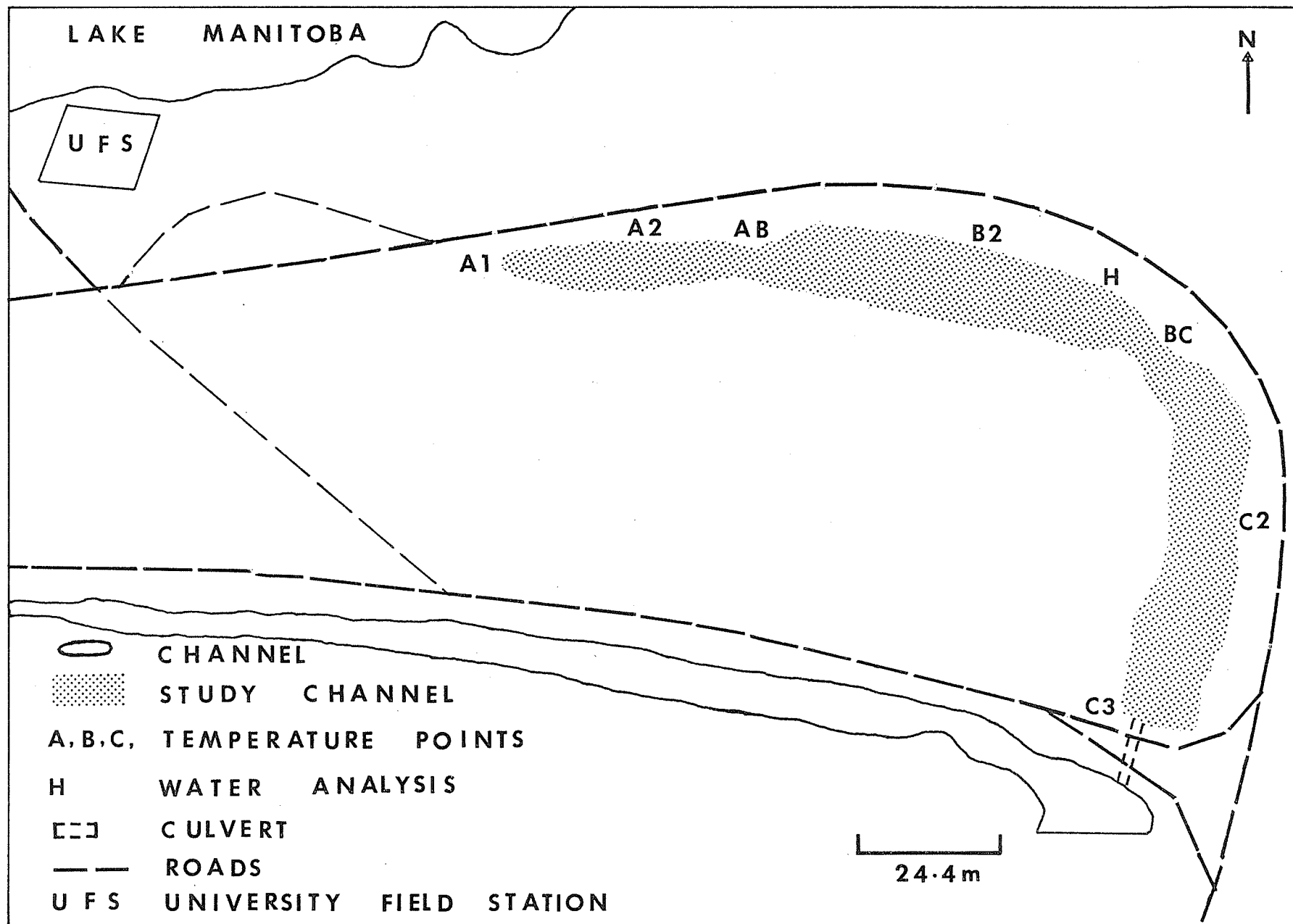
whole summer of 1969. Section C was free of duck weeds during the two summers.

Mean surface water temperature from May to August for the summers of 1969 and 1970 varied from 9° C to 25° C. The months of June and July in 1970 were warmer than in 1969; the mean temperature stayed in the range of 17° C to 25° C (Fig. 2). The bottom temperature was not measured. As the wind direction changed from day to day affecting the water level in the marsh and depth was slight, temperature stratification was probably never pronounced. The temperature at points A, B and C are shown in Fig. 2, and oxygen, pH, carbon dioxide and hardness at point H are given in Appendix I.

By the beginning of May ice had cleared from the marsh including the study channel. During the winter of 1969-70, snow and ice depth was 100 cm and there was about 15 cm of water on February 25, 1970. The oxygen was undetectable using a Hach Kit. Carbon dioxide was 24 parts per million, the pH was 8.5 and there was a strong smell of hydrogen sulphide.

The fish fauna consisted of the brook stickleback (Culaea inconstans), the ninespine stickleback (Pungitius pungitius), fathead minnow (Pimephales promelas), carp (Cyprinus carpio), common white sucker (Catostomus C. commersonnii), Iowa darter (Etheostoma exile), young yellow perch (Perca flavescens) and spottail shiner (Notropis

FIG. 2. Mean surface water temperature
         fluctuation during the summers
         of 1969 and 1970.
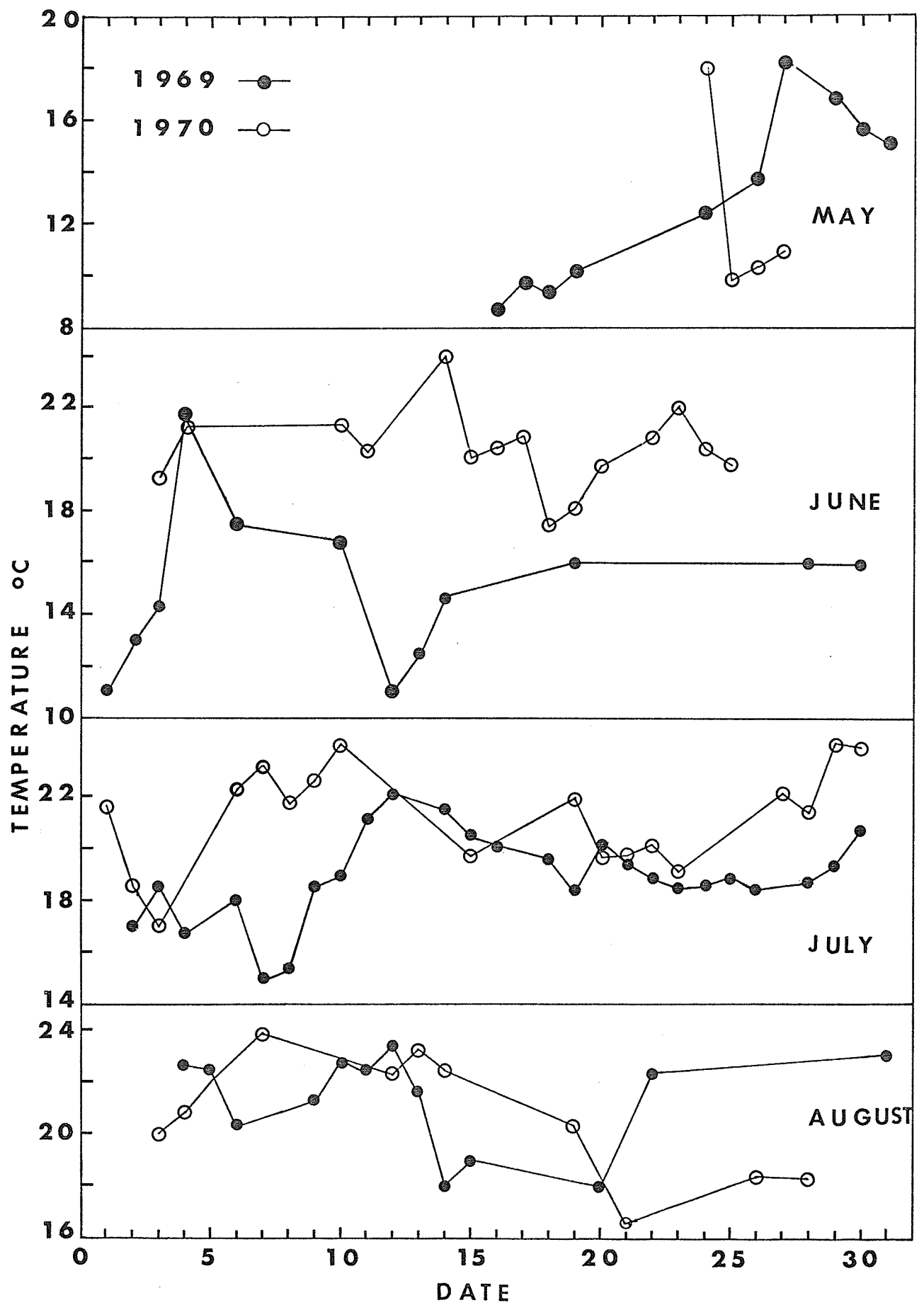
hudsonius).

       The predators in the study area were accounted for by the sticklebacks themselves, the Belted Kingfisher (Megaceryle alcyon alcyon), the giant waterbug (Belostomatidae) (Guthrie and Iverson, 1970), the water boatman (Corixidae) and backswimmers (Notonectidae).

METHODS AND MATERIALS

Stocking

The channel was seined on 9 May 1969, mostly in the middle areas excluding the shores, using a bag seine-net 5.0 mm stretch mesh, measuring 10.68 m long and 1.22 m deep with 91.5 cm wide central bag. The sample yielded 23 Culaea inconstans. The original population was augmented with wild Culaea inconstans caught with fish traps and dipnets at the mouth of the Assiniboine River Diversion on Lake Manitoba. Catching a large number of fish was facilitated by the mass spring spawning migration of sticklebacks and cyprinids from the lake to the creeks and channels in the marsh. An undetermined number of Culaea inconstans were caught in this manner in May 11-16, 1969; all were then placed in the study channel, including 265 which had the first dorsal spine clipped. In the second year of the study seining in the channel on May 5, 1970 resulted in the catch of only one C. inconstans. On May 18-22, 1970, 2,060 wild fish from the diversion mouth were stocked, 1,020 of which had the left pelvic spine clipped.

Sampling

In 1969 six samples were seined in different periods from May to October, of which four were returned to

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the water after clipping the 1st, 2nd, 3rd, 4th or 5th dorsal spines in successive batches. The other two samples were used for aging. In the summer of 1970 nine samples were seined, of which all but the last one were returned. In each case the sticklebacks seined were taken to the laboratory. They were anaesthetised in M.S. 222 (Tricaine methanesulfonate) in an aqueous solution of 1:10000 concentration for periods of two minutes, as recommended by Bell (1964). The total length of the immobilised sticklebacks was measured (Ricker and Merriman, 1945; Carlander and Smith, 1945) to the nearest 0.1 mm using "Helios" dial callipers. The dorsal spines were counted, checks for previous marks made and the appropriate spine was clipped using a fine pair of scissors. Surface water on the sticklebacks was blotted on paper towels, and fish were individually weighed on an electric "Sartorius" balance to the nearest 0.01 g. Fish were then transferred to fresh water from the study area held in pails. The time duration for measuring total length, clipping dorsal spines, removing body surface water and weighing lasted at most one minute for each fish. The clipped sticklebacks were observed for aberrant behaviour resulting from handling for at least one hour. The ones that apparently recovered fully were returned to areas where they were seined. The few sticklebacks that exhibited distress were retained in aquaria where they all died within three to five hours. In the summer of 1969,

recaptures of previous batches were retained for aging. However in 1970 all fish including recaptures with the exception of distressed ones were returned.

In July 1969, after the young sticklebacks and fathead minnows had hatched, batch staining using 'Bismarck Brown Y' in different concentrations was tried for varying times as recommended for young Salmonid fishes by Ward and Verhoeven (1963) and Lawler and Fitz-Earle (1968). Three experiments using 'Bismarck Brown Y' in aqueous solution of 1:30,000 for three hours, 1:60,000 for three hours and 1:90,000 for three hours were done on 21, 23 and 25 July 1969 respectively. Other concentrations combined with short dyeing periods were tried. Mortality was higher with stronger concentrations, and the brown-orange dye on the fish lasted only four days.

Age Determination

Sticklebacks which died as a result of marking treatment were preserved by freezing. Otoliths were removed by making a triangular cut just behind the eye under dissecting binocular microscope. The largest of the three ear-stones, the sagitta, was used for aging as described by Jones and Hynes (1950). The sagitta was placed on a glass slide, a drop of water added and the enclosing membranes removed under the dissecting binocular microscope. It was dried with a piece of blotting paper and examined under the low power with either reflected or

direct light to determine the number of rings and opaque zones. In the summer of 1969 all sagittae were examined unmounted and discarded thereafter. In 1970 all sagittae were mounted in permount on glass slides under the cover-slips for later examination.

On July 4, 1969 the sagittae were stained with "methyl violet B" solution in 30 ml distilled water and one ml of 38% concentrated hydrochloric acid for one minute after the method of Albrechtsen (1968). However there was no differential staining of rings from the opaque zones. This method was abandoned. Some of the fairly thick sagittae were polished against the frosted sides of the glass slides which exposed distinct clear and opaque zones (Tesch, 1968 and De Bont, 1967), without staining.

The sagittae used for aging sticklebacks were measured along their longitudinal 'V' notched axis to determine the diameters of the transparent rings, according to the method of Hile (1936) used on scales of ciscos, and Smoker and Pearcy (1970) used on lantern fish. Total lengths of the sagittae were also measured to the nearest 0.1 mm. These measurements were obtained using an ocular micrometer inserted in the eye tube of the low power binocular and a micrometer mounted on the stage of the binocular.

Outermost diameters of the sagittae were plotted against total body length of fish. The resulting equation of this relationship is of the form,

$$Y = C + bx$$

where   x is the length of the otolith in mm,

         Y is the total length of the fish in mm,

         C is the Y intercept

and   b is the slope of the regression line.

From the above plot it is possible to read off directly the average total fish lengths at which the rings were set in the sagittae.

Length frequency distributions at one millimetre class intervals were plotted for age determination after the Petersen method described by Tesch (1968). Samples seined from August and onwards showed overlapping age distributions using length frequency polygons, and otolith readings were used for discrete separation of the age groups (Richards, 1967).

Growth Rates

Absolute average lengths for samples caught were plotted against time for three separate year classes. Growth rates for 1969 year class based on average lengths was plotted. These then are year class growth rates rather than individual stickleback growth rates. The measure of average length increments, ΔL in 1969 year class between times t_o and t_1 was

$$\Delta L = \bar{L}_{t_1} - \bar{L}_{t_o}.$$

The instantaneous rate of growth in length, h,

between times t_o and t_1 was

$$h = \ln (\bar{L}_{t_1}/\bar{L}_{t_o}).$$

Similarly the coefficient of growth in weight, the instantaneous growth rate g, was determined from means rather than from the individual sticklebacks using the expression of Ricker (1958), Chapman (1967, 1968) and Rounsfell and Everhart (1953):

$$g = \ln (\bar{W}_{t_1}/\bar{W}_{t_o})$$

where $\bar{W}_{t_o}$ and $\bar{W}_{t_1}$ are the average weight of one age group of sticklebacks in the population at times t_o and t_1 respectively.

Length-Weight Relationship

     The length weight relationship was calculated for individual age groups in each sample caught. The logarithmic expression of the relationship of length to weight results in the equation:

$$\ln \bar{W} = a + b \ln \bar{L}$$

where $\bar{W}$ is the average weight in mg for each one mm class interval,

        $\bar{L}$ is the average length for each class interval,

        a is the intercept

and   b is the slope of the regression line.

Because of large sample sizes seined, class lengths and weights were averaged as recommended by Ricker (1958),

Kitchen and Forrester (1966), Meehan and Siniff (1962), Le Cren (1951), Beckman (1948) and Hile (1936). The regression slopes were compared after testing for homogeneity of variance (Snedecor and Cochran, 1967 and Steel and Torrie, 1960).

Condition Factor

Condition factors or coefficients of condition for adults and yearlings were separately computed for each sample by applying the method of Le Cren (1951), Beckman (1948) and Hile (1936). This was done by comparing an ideal fish, whose length-weight regression slope is 3, with the empirical regression slopes of different age groups in each sample, according to the following formulae:

$$W = CL^b$$

or $\log W = a + b \log L$

$$K = \frac{100000\ W}{L^3} \quad \text{for ideal fish}$$

$\log K = 5 + a + (b - 3) \log L,$

where   W is the weight (mg),

L is the length of the fish (mm)

a is the intercept of the regression line,

b is the slope of the regression line

and   K is the coefficient of condition.

Test for Random Distribution of Marks

This was tested by dyeing two batches each of 32 sticklebacks in "Bismarck Brown Y" aqueous solution of 1:60,000 concentration for two hours and 1:30,000 concentration for one hour on June 24, 1970. The dyed sticklebacks

were replaced in the channel at section C_{3-2} (Fig. 1).
Seining samples were then taken at intervals of about 10-20
minutes for durations of about 20 minutes, at stations
progressively farther from the point of release. After six
hours from the time of release of the first stained batch,
one stickleback was recaptured at a distance between 84 and
102 m away, and other recaptures were made at intermediate
distances between the point of replacement and 84 m away
from it. From this it may be concluded that marked fish
did not all remain at the site of their release, but
dispersed widely in the channel.

Survival and Mortality Rates

Survival rates, S_t, were calculated according to
the method of Ricker (1945a, 1948), using recaptures of
marked sticklebacks at three consecutive periods of
sampling, as the ratio of one sampling recaptures to the
preceding ones:

$$\hat{S}_1 = \frac{R_{12}M_2}{M_1 R_{22}} \qquad \text{(Formula 5.1 in Ricker, 1958)}$$

where M_1 is the number marked at first sample,

         M_2 is the number marked at the second sample,

         R_{12} are recaptures of M_1 in the third sample,

and R_{22} are recaptures of M_2 in the third sample.

         The variance of survival estimated above was
calculated using formula 5.3 in Ricker (1958):

$$V(\hat{S}_1) = S_1^2 - \frac{M_2^2 \, R_{12} \, (R_{12} - 1)}{M_1^2 \, (R_{22} + 1)(R_{22} + 2)}$$

where $\hat{S}_1$ is the estimated survival rate during the

interval between the first and second samples,

$V(\hat{S}_1)$ is the variance for survival rate

and M_1, M_2, R_{12} and R_{22} are as above.

Survival rates, ϕ, and their variances were also obtained

using the method of Jolly (1965) whose details are given in

Appendix II.

Mortality rates, a_t, at the intervals between

sampling periods were calculated as the fraction of stickle-

backs dead between any consecutive samples, using the

survival rate as follows

$$\hat{a}_t = 1 - \hat{S}_t$$

Instantaneous mortality rates, Z_t, were calculated

from the expression:

$$S = e^{-Z}$$

where S is the survival rate as before

Z is the instantaneous rate of total mortality

and e is the natural logarithm.

Population Estimates

Sampling was done by a series of seine hauls

covering the whole study channel. The catch was taken to

the laboratory and sample size, n_i, number of recaptures

R_i, from the previous spine clippings and the number of

marks released M_i or S_i were recorded in tabular form. Each recapture was recorded under the period in which it was previously clipped. Sticklebacks with more than one type of spine clipping were recorded as many times as the marks they each bore as recommended by Ricker (1958) and Ford (1943). In a different table are shown recaptures of the most recent previous marks as described by Jolly (1963, 1965), Leslie (1952) and Seber (1963, 1965).

Population estimates were calculated using the Bailey (1951) modification of the Petersen method.

$$\hat{N} = \frac{M\ (n + 1)}{(R + 1)}$$

where $\hat{N}$ is the estimate of total population,

        M is the number of marked animals in the population,

        n is the sample size caught subsequently

and   R is the number of recaptures out of the M marks, caught in the sample size n.

The population estimates for different sampling periods using the modified Petersen method and Jolly (1965) method are given in Table 7. The population sizes estimated for 1969 and 1970 summer periods include sticklebacks above 25 mm and 35 mm respectively. Confidence intervals for the Petersen type estimates were computed using the Clopper and Pearson graphs for Poisson and Binomial distributions at 95 per cent level for recaptures and the proportion of recaptures in the samples caught respectively as exemplified

by Adams (1951), Ricker (1958) and Davis (1964). The
standard errors for the population estimates based on the
Jolly (1965) stochastic model are also provided. The
details of this stochastic model are given in Appendix II.

Estimate of Biomass

Biomass is the total weight of all living matter in
a system (Rounsfell and Everhart, 1953). This definition
can not be attained in practice, and in the present context
biomass means the total weight of all estimated population
sizes of sticklebacks above 25 mm and 35 mm for 1969 and
1970 summers respectively. This restriction of the
definition fits in with that adopted by Chapman (1967, 1968)
when calculating production for a year class. Production is
defined as the total elaboration of fish tissue during any
time interval Δt, including what is formed by individuals
that do not survive to the end of Δt. It may be measured
in terms of wet weight.

RESULTS

Marking with Bismarck Brown Y

Culaea inconstans stained in a 1:30,000 aqueous solution of Bismarck Brown Y incurred considerable mortality, out of 326, 307 had died by the end of the fourth day of Experiment I, and the dye was no longer distinct on the fish (Fig. 3A). Sticklebacks stained for three hours in 1:60,000 aqueous solution of Bismarck Brown Y also suffered heavy mortality and by the end of the fourth day of Experiment II, out of 21 sticklebacks, 18 had died and the dye on them had disappeared completely (Fig. 3B). In the third and final experiment, using a concentration of 1:90,000 aqueous solution for four hours, by the end of the third day of Experiment III, the dye had disappeared and out of 115 fish, 81 had died (Fig. 3C). In all these three experiments by the end of the third day the orange brown coloration had turned to a faint yellow which was difficult to distinguish from the cryptic colour which the fish assume from time to time.

This technique for marking was therefore abandoned except for its short term application to test for random distribution of marked fish in the population under study.

FIG. 3.   The duration of 'Bismarck Brown Y' dye
          on fish stained in different concentra-
          tions of 1:30,000 for 3 hours (Curve A),
          1:60,000 for 3 hours (Curve B) and
          1:90,000 for 4 hours (Curve C) and
          subsequent cumulative mortality percent.
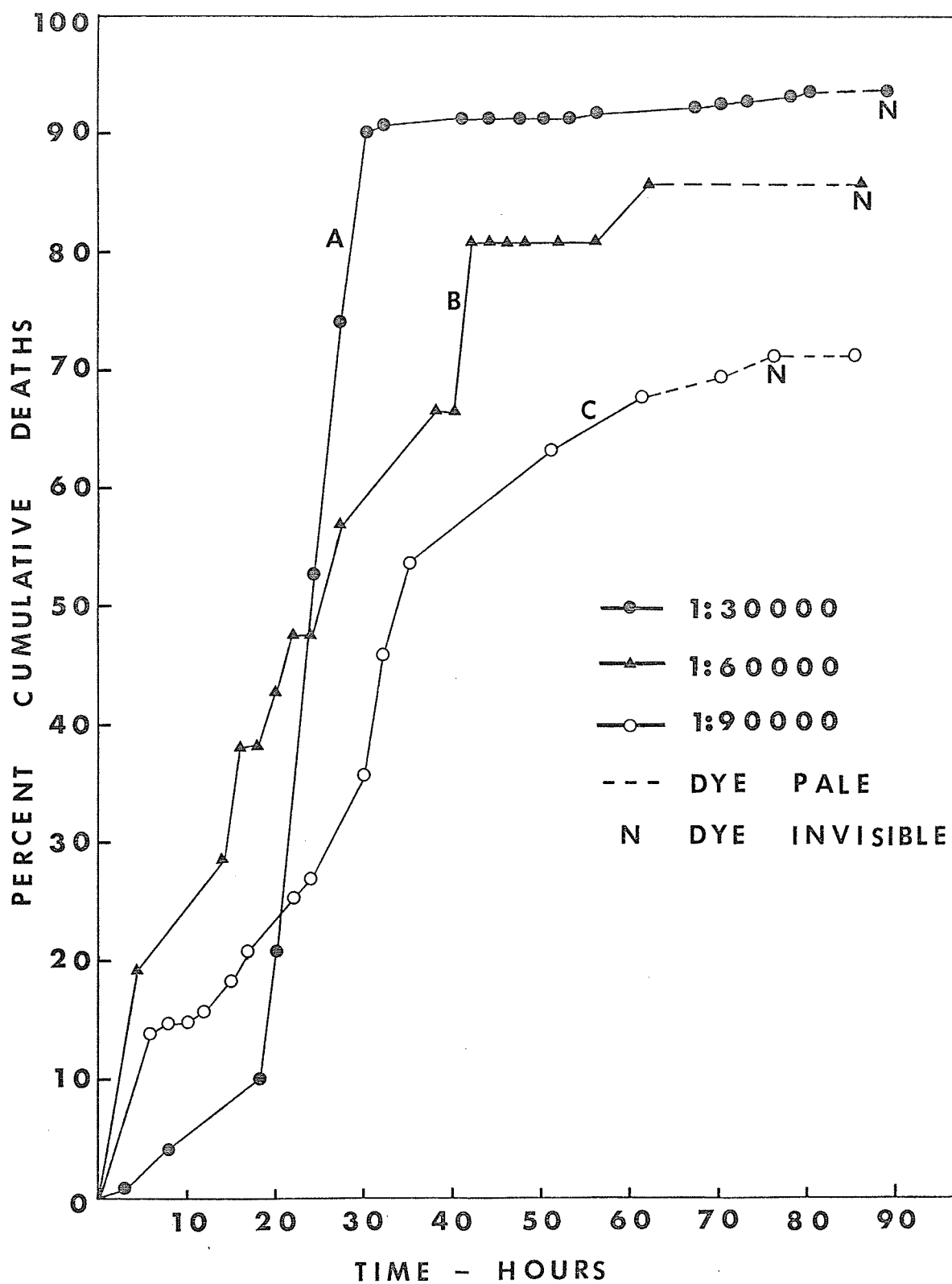
Random Distribution of Marked Fish

Some sampling periods extended over two days. When barrier nets were not used to block off the sampled sections of the channel, recaptures of marks released in the previous two days were obtained in areas of considerable distance from the sites of release.

The results of the staining experiment to test for random distribution, as previously described are given in Table 1.

Age and Growth

Length frequency distributions (Fig. 4) and otolith readings indicate that Culaea inconstans in Lake Manitoba area is an annual fish, which dies after spawning in the second summer of life. Spawning takes place from early June to mid-August and hardly any second summer spawners survive to live a third summer.

By the end of the summer of 1969 the young of the year average 38.48 mm and the post-spawners average 56.9 mm. At the end of the summer of 1970, the yearlings averaged 41.9 mm and the post-spawners averaged 59.75 mm in total length (Figs. 5 and 6 and Table 2). The longest Culaea inconstans caught in this area measured 69.1 mm total length on July 16, 1970, bearing a right pelvic spine mark of July 2, 1970. This also seems to indicate that the growth of Culaea inconstans was not hampered by the clipping of the spines. From Figs. 5 and 6, it is clear that the

TABLE 1A. Number of recaptures, out of 32 fish stained in
           1:60,000 solution of Bismarck Brown Y for 2 hours
           and released at least one hour before seining.

Released at 1.50 pm	Sample size		Distance from point of release in metres
Seining time	Stained	Unstained	
2.45-3.07 pm	10	17	10.7 - 29.0
3.30-3.50 pm	5	17	29.0 - 47.0
4.00-4.25 pm	6	17	47.0 - 65.6
4.40-5.00 pm	0	5	65.6 - 84.0
5.10-5.25 pm	0	11	84.0 -102.0

TABLE 1B. Number of recaptures, out of 32 fish stained in
           1:30,000 aqueous solution of Bismarck Brown Y
           for one hour and released one hour before seining.

Released at 5.35 pm	Sample size		Distance from point of release in metres
Seining time	Stained	Unstained	
7.15-7.45 pm	10	7	10.7 - 29.0
7.53-8.07 pm	10	3	47.0 - 65.6
9.27-9.45 pm	1	7	46.25- 94.6

FIG. 4.   Per cent length frequency distributions in
samples captured on different sampling
periods; arrows ↓ separate one-year-olds
and over from yearlings.

PERCENT FREQUENCY
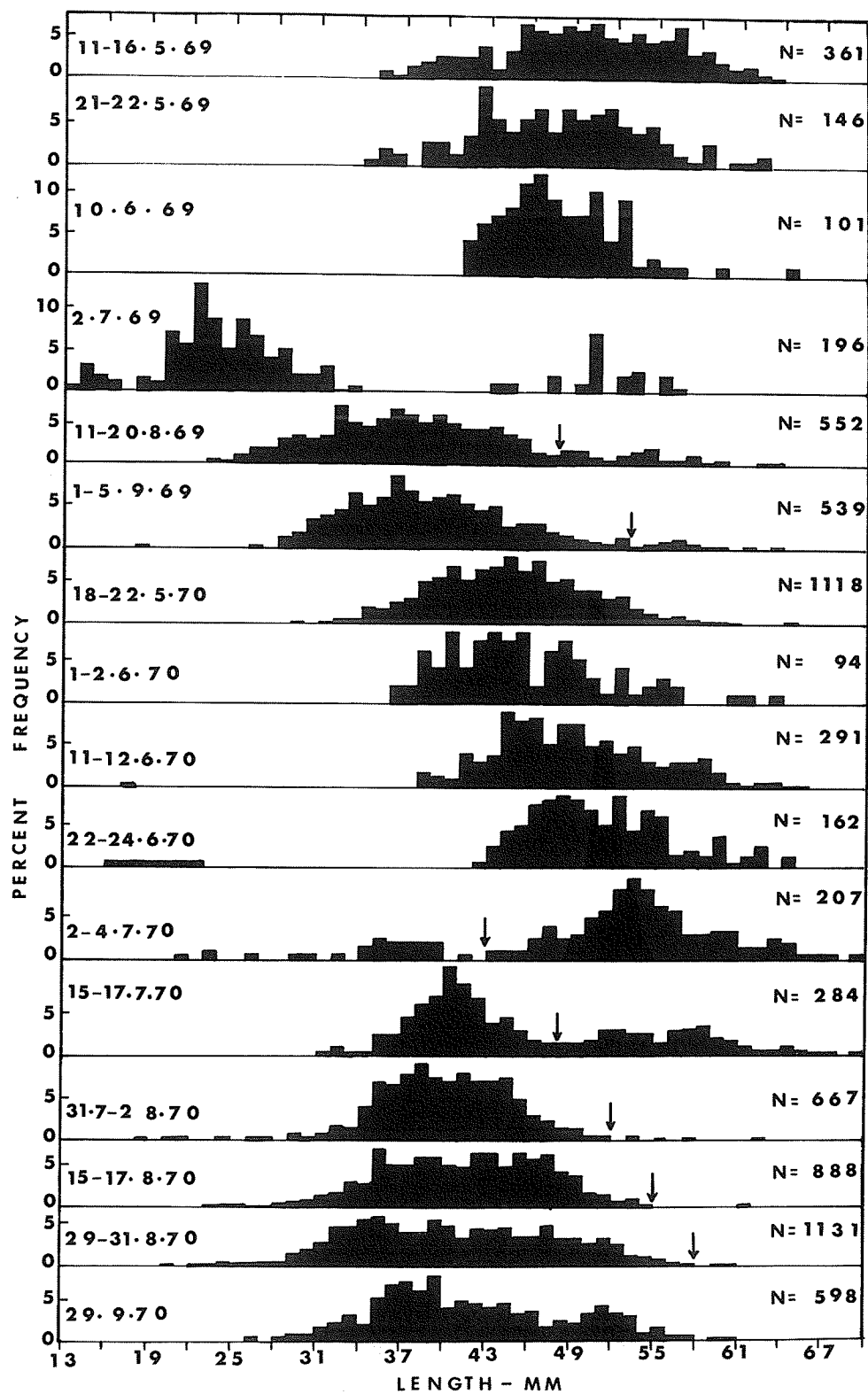
LENGTH – MM

FIG. 5. Growth in total length of different
         year classes of _Culaea inconstans_
         during the summers of 1969 and 1970.
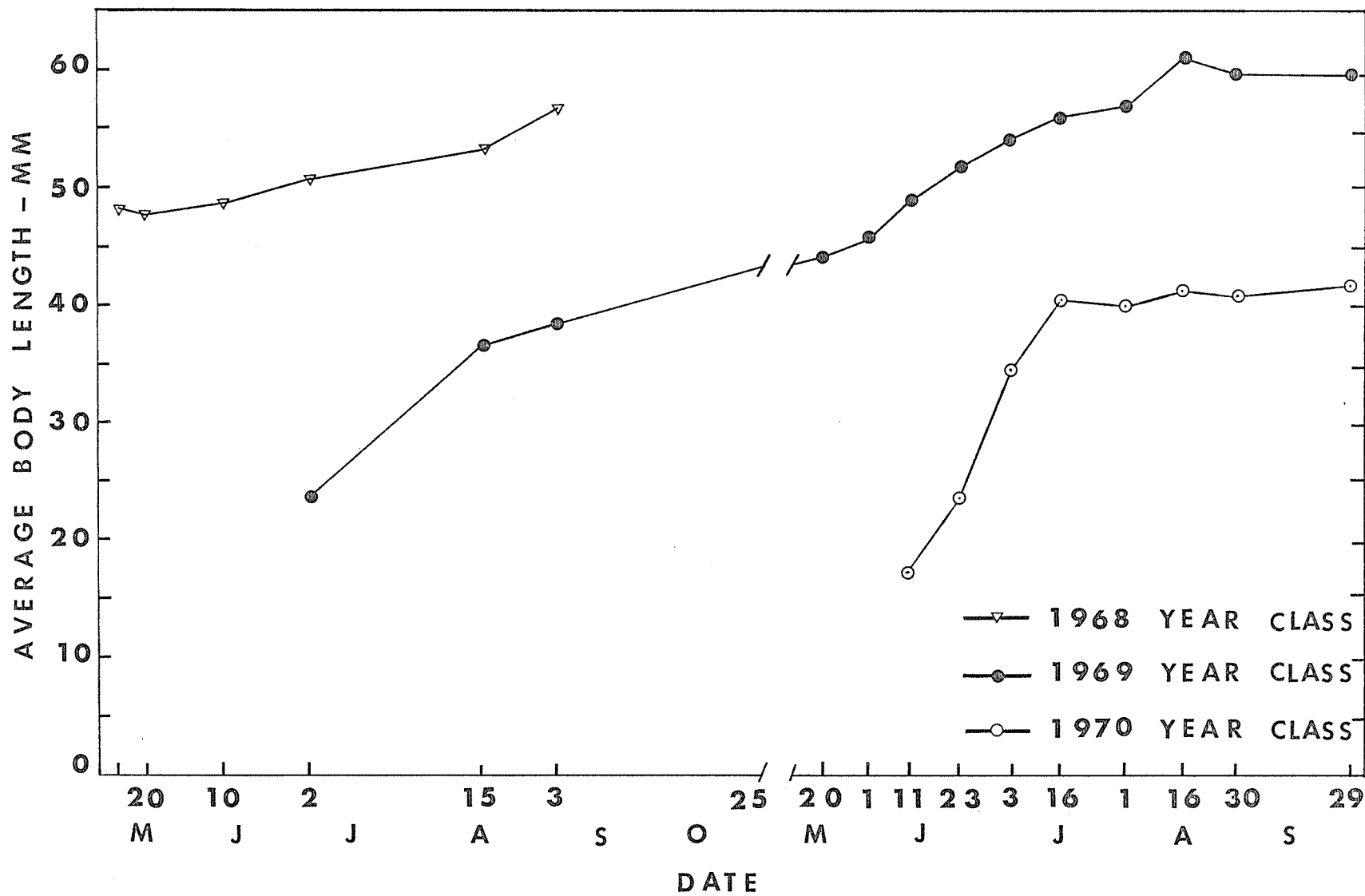
FIG. 6. Growth in total length of _Culaea inconstans_
         1969 year class: average length Curve A
         and relative growth Curve B, assuming that
         there was no increase in length during
         freeze up period.
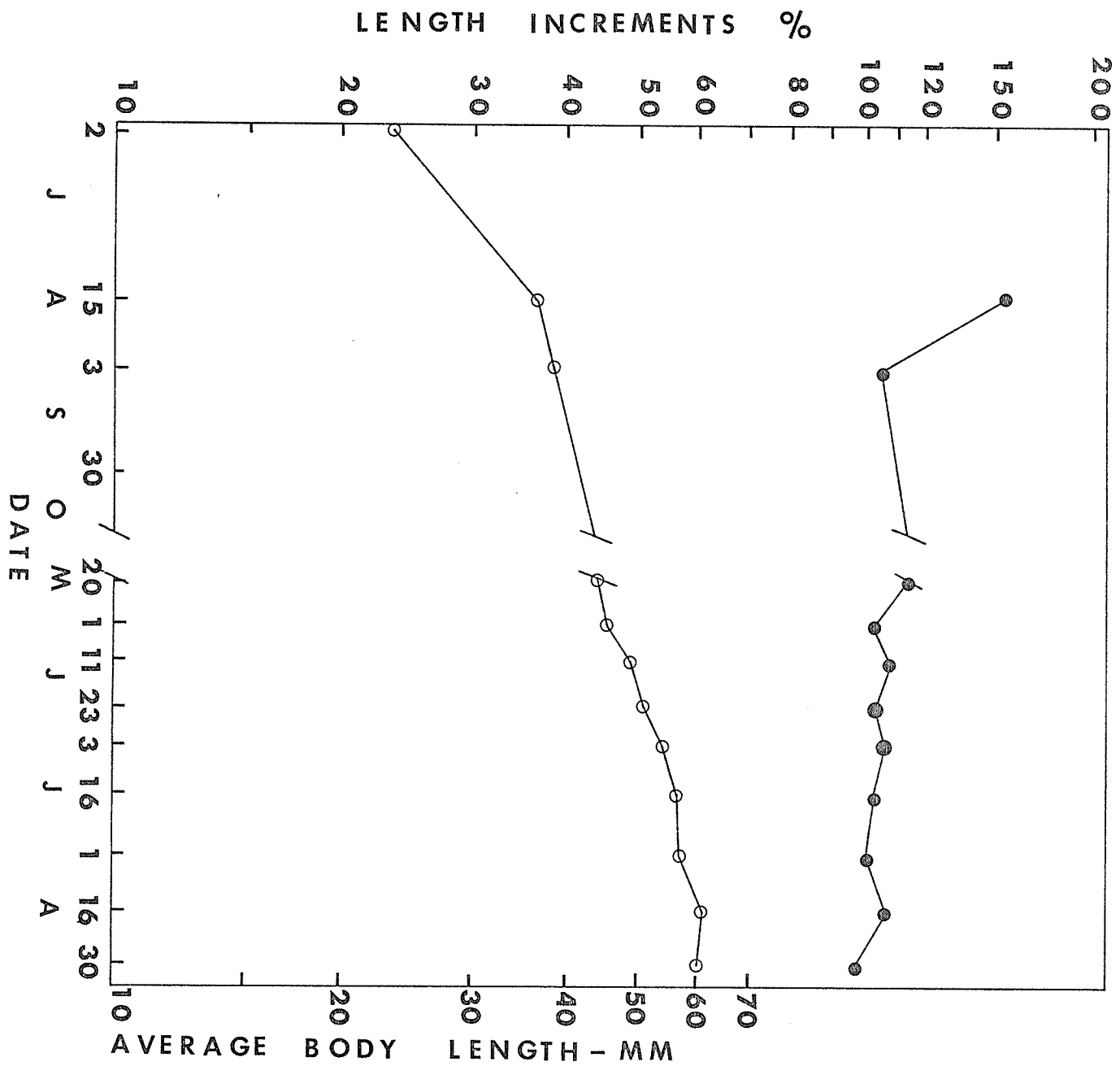
TABLE 2. Average lengths $\bar{L}$, average weight $\bar{W}$, instantaneous rate of growth in length h, and instantaneous rate of growth in weight g, for 1969 year class of <u>Culaea</u> <u>inconstans</u> during the summers of 1969 and 1970.

Date	Average length $\bar{L}$	Instantaneous growth rate h	Average weight $\bar{W}$	Instantaneous growth rate g
2.7.69	23.78		136.09	
		0.4324		1.2375
11-20.8.69	36.66		469.16	
		0.0478		0.1177
1-5 .9.69	38.48		527.70	
		0.1433		0.0593
18-22.5.70	44.44		559.94	
		0.0274		0.4892
1-2 .6.70	45.70		913.30	
		0.0725		0.2295
11-12.6.70	49.13		1148.79	
		0.0411		0.1766
22-24.6.70	51.17		1370.96	
		0.0593		0.1855
2-4 .7.70	54.29		1651.25	
		0.0344		-0.0135
15-17.7.70	56.19		1629.19	
		0.0137		-0.0580
31.7-2.8.70	56.95		1537.50	
		0.0706		0.0459
15-17.8.70	61.10		1610.00	
		-0.0224		-0.0944
29-30.8.70	59.75		1465.00	

sticklebacks scarcely increase in length during winter as shown by the almost flat curve.

The 1969 year class exhibited rapid growth in the first month of life. After August 15, 1969, there was a decline in length increments till September when it again increased. In the summer of 1970, there was constant increment in growth in length (Fig. 6B).

The instantaneous rate of growth in length, h, followed the same pattern (Table 2). The instantaneous rate of growth in weight, g, for 1969 year class portrays an increase in weight even through the winter! This is because there is no record for weight just before the onset of 1969/70 winter freeze up. After July 2-4, 1970, there was loss of weight in the 1969 year class, resulting in negative instantaneous growth rates.

Body-otolith Relationship

A least-square line was computed for the body-otolith relationship for Culaea inconstans (Fig. 7). The resulting equation for this relationship is

$$L = -6.531 + 68.1 D$$

where   L is the total body length of the fish

and   D is the longest diameter of the otolith.

A high positive correlation coefficient (r = 0.953), was found for the body length and otolith longest diameter.

From the otolith zonations, it was found from Fig. 7

FIG. 7. Fish body length: otolith longest
         diameter relationship of <u>Culaea</u>
         <u>inconstans</u>.
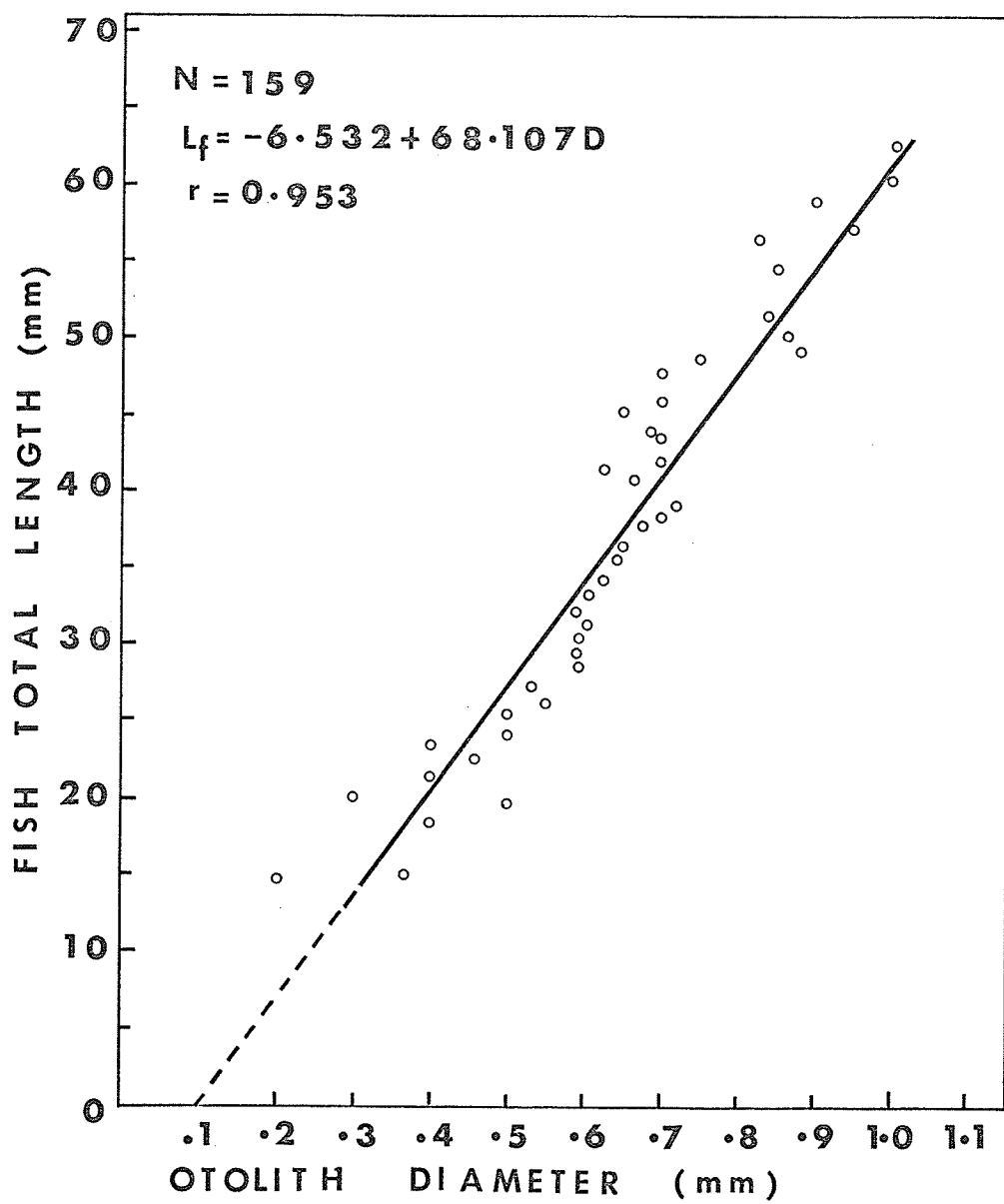
that the first ring, a false check, was set when the longest diameter of the otolith was between 0.4 and 0.5 mm. At this stage the total length is between 20.5 mm and 27.5 mm in the first month of life. The second ring, which is the true age check mark, is set on about June 1, in the second summer of life, when the otolith longest diameter is 0.6 mm and the total fish length is a minimum of 34.25 mm.

Length-Weight Relationship

Length-weight regression lines gave slopes, b, which ranged from a very low value of 1.257 for the sample of May 11-16, 1969 to the high value of 3.4446 for the yearlings in the sample caught on July 2, 1969 (Table 3). The samples for the summer of 1970 ranged from b values of 2.3141 to 3.2624 for the yearlings captured on June 22-24, 1970 and July 2-4, 1970 respectively (Table 3). There was a correlation coefficient $r > 0.7$ for all the samples. The slopes were significantly different from zero, the F-value being significant at 1% level except for the adults in the sample of July 2, 1969 for which significance was at 5% level (Appendix IV).

The analysis of covariance for the homogeneity of 23 regression slopes given in Appendix IV showed that they were significantly different at 1% level. These regression slopes resulting from within age groups indicate growth is sometimes isometric and sometimes allometric. These results strongly show the dependency of the regression slopes on the

TABLE 3.   The relationship of length weight,
           Log $\overline{W}$ = a + b log $\overline{L}$, the intercept a, the
           slope of the regression line, b and the
           condition factor (relative) K, for different
           periods and age.S = whole sample, A = adults
           and Y = yearlings.

Date	No. of fish	Intercept a	Slope b	Log K
16-18.5.69 S	190	1.0236	1.2570	3.0901
21.5.69 S	146	-1.1328	2.4624	2.9643
10.6.69 S	101	0.4983	1.5524	3.0540
2.7.69 AS	39	0.4418	1.6027	3.0589
2.7.69 Y	157	-2.6497	3.4446	2.9622
11-20.8.69 A	66	-1.2331	2.5098	2.9211
11-20.8.69 Y	486	-2.2993	3.1552	2.9435
1-5 .9.69 A	21	-1.0729	2.4094	2.8905
1-5 .9.69 Y	518	-1.0101	2.3510	2.9611
18-22.5.70 S	1118	-2.5421	3.1958	2.7805
1-2 .6.70 S	94	-2.0414	3.0017	2.9614
11-12.6.70 S	290	-1.4513	2.6610	2.9753
22-24.6.70 A	155	-1.2429	2.5631	3.0104
22-24.6.70 Y	7	-1.0702	2.3141	2.9868
2-4 .7.70 A	176	-1.9715	2.9875	3.0068
2-4 .7.70 Y	31	-2.4949	3.2624	2.9092
15-17.7.70 A	100	-2.1881	3.0813	2.9542
15-17.7.70 Y	184	-1.7877	2.8221	2.9261
31.7-2.8.70A	4	-2.1000	3.0092	2.9162
31.7-2.8.70Y	663	-2.1802	3.0575	2.9120
15-17.8.70 S	886	-2.3994	3.1824	2.8956
29-30.8.70 S	1131	-2.4117	3.1669	2.8274
29.9.70 S	598	-2.2099	3.0600	2.8875

range of lengths and weights plotted as well as the condition
of the fish.

Condition Factor

The condition factor, K, for each age group in the
sample, relative to an ideal fish, are shown in Table 3,
together with the intercepts, a, and slopes, b, for length-
weight regression lines. The relative condition factor
within an age group is dependent on the intercept, slope
and range of lengths and weights that are utilised for the
length-weight relationship. The lowest relative condition
factor, log K = 2.7805, was obtained for the sample of
May 18-22, 1970 when the ice was melting, and gave a value
of -2.5421 for the intercept and 3.1958 for the regression
slope. There is usually a low condition factor during the
winter months.

Survival Rates

Survival rates for intervals between sampling
periods ranging from 5 to 30 days during the summer and for
the winter of 1969/70, are given in Table 4. Survival
rates, S_R, derived by Ricker's method, have confidence
limits which include the survival rates, ϕ_i, derived by the
Jolly estimator, except for the 2.6823 value which falls
far beyond. Neither of these methods gives a consistently
higher estimate. There is a very low survival rate in the
winter. There is a great decline in survival rate from

TABLE 4. Survival rates--S_R by the method of Ricker and ϕ by the method of Jolly and their respective standard errors; total mortality rate a, and instantaneous mortality rates between consecutive sampling periods.

Sampling Date	t	Ricker's survival rate S_R	Standard error of survival	Jolly(1965) survival rate ϕ	Standard error for ϕ	Total mortality rate a	Instantan. mortality rate Z
14-18.5.69	1						
		0.7528	0.3673	0.8019	0.3340	0.2472	0.2839
21-22.5.69	2						
		0.3421	0.2240	0.4862	0.2633	0.6579	1.0729
10.6.69	3						
		0.1987	0.1987	0.3577	0.1860	0.8014	1.6164
11-20.8.69	4						
		0.3397	0.3397	2.6823	1.7560	0.6603	1.0797
1-5 .9.69	5						
		0.1331	0.1331	0.0908	0.0564	0.8669	2.0167
16-22.5.70	6						
		0.2127	0.0680	0.1745	0.0421	0.7873	1.5479
1-2 .6.70	7						
		0.8347	0.3513	0.6156	0.1609	0.1653	0.1807
11-12.6.70	8						
		0.3015	0.0923	0.3508	0.0734	0.6985	1.1991
22-24.6.70	9						
		0.6425	0.2466	0.6171	0.1580	0.3575	0.4424
2-4 .7.70	10						
		0.4387	0.3290	0.1569	0.0464	0.5614	0.8240
15-17.7.70	11						
		0.3969	0.1434	0.4734	0.1105	0.6031	0.9241
31.7-2.8.70	12						
		0.5951	0.5657	0.5608	0.0841	0.4049	0.5190
15-17.8.70	13						
		0.8205	0.2196	0.8710	0.1938	0.1795	0.1979
29-30.8.70	14						

June to July, which is also the spawning period. The
survival rates computed from both methods indicate lack of
constancy in survival from interval to interval and also
show discrepancies in the two methods used.

Mortality Rates

The total mortality rates between sampling periods
is contributed by only natural mortality, as fishing
mortality is negligible. There was a significant fluctuation
of total mortality rates between the sampling periods.
Natural mortality was more pronounced in the summer of 1969
and the winter of 1969/70 than in the summer of 1970 as
shown in Table 4.

Similarly instantaneous total natural mortality
rates, Z, also varied between the different sampling
periods; the largest value (Z = 2.0167) was attained in the
interval between September 1-5, 1969 and May 18-22, 1970.

Population Size Estimates

Tables 5 and 6 display the tabulation of sample
sizes seined (n_i), releases (s_i) and recaptures (R) from
previously released marks for Petersen and Jolly estimates
respectively. The total population sizes of Culaea
inconstans estimated by the two methods for different
sampling periods are given in Table 7. The estimates for
the summers of 1969 and 1970 exclude fish below 25 mm and
35 mm respectively except for May 18-22, 1970 which includes

TABLE 5. Sample sizes caught n_i, marked released M_i, recaptures from previously released marks, R..., including multiple recaptures for Petersen method.

Date	t	Sample caught n_i	Marks released M_i	R_1	R_2	R_3	R_4	R_5	R_{Lps}	R_{23}	R_{24}	R_{AS}	R_{rps}	R_{25}	R_{21}	R_{13}	R_{14}
16-18.5.69	1	265	265														
21.5.69	2	146	133	13													
10.6.69	3	101	91	5	5												
2.7.69	4	132	0	3	0	3											
11-20.8.69	5	561	470	0	3	2											
1-5 .9.69	6	530	479	2	0	0	25										
25.10.69	7	320	0	0	0	1	1	2									
18-22.5.70	8	1020	1020	0	0	0	0	0									
1-2 .6.70	9	94	94	0	0	0	0	0	15								
11-12.6.70	10	290	269	0	0	0	4	0	30	12							
22-24.6.70	11	156	147	0	0	0	1	0	9	7	23						
2-4 .7.70	12	177	170	2	0	0	0	1	8	4	16	28					
15-17.7.70	13	276	261	0	0	0	0	0	7	3	7	10	17				
31.7-2.8.70	14	611	518	0	0	0	0	0	0	0	0	1	2	6			
15-18.8.70	15	786	722	0	0	0	0	0	0	0	0	0	0	9	44		
29-30.8.70	16	876	850	0	0	0	0	0	0	0	0	0	0	10	38	88	
29.9.70	17	462	0	0	0	0	0	0	0	0	0	0	0	3	11	23	32
Totals				25	8	6	31	3	69	26	46	39	19	28	93	111	32

TABLE 6. Sample size caught n_i, number marked and released s_i, recaptures of previous marks R..., and total recaptures of different sample marks released, R_i, according to Jolly (1965) method.

Date	i	Sample n_i	Released s_i	Previously released marks recovered in subsequent samples to be marked													
				R_1	R_2	R_3	R_4	R_5	R_{Lps}	R_{23}	R_{24}	R_{As}	R_{rps}	R_{25}	R_{21}	R_{13}	R_{14}
16-18.5.69	1	265	265														
21-22.5.69	2	146	133	13													
10.6.69	3	101	91	5	5												
11-20.8.69	4	693	470	3	3	5											
1-5 .9.69	5	530	479	2	0	0	25										
18-22.5.70	6	1020	1020	0	0	1	1	2									
1-2 .6.70	7	94	94	0	0	0	0	0	15								
11-12.6.70	8	290	269	0	0	0	4	0	25	12							
22-24.6.70	9	156	147	0	0	0	1	0	3	5	23						
2-4 .7.70	10	177	170	2	0	0	0	1	2	2	10	28					
15-17.7.70	11	276	261	0	0	0	0	0	2	1	5	5	17				
31.7-2.8.70	12	611	518	0	0	0	0	0	0	0	0	0	1	6			
15-17.8.70	13	786	722	0	0	0	0	0	0	0	0	0	0	9	44		
29-30.8.70	14	875	850	0	0	0	0	0	0	0	0	0	0	8	27	88	
29.9.70	15	462	0	0	0	0	0	0	0	0	0	0	0	2	8	19	32
Total recaptures, R_t				25	8	6	31	3	47	20	38	33	18	25	79	107	32

TABLE 7. Population size estimates, and confidence limits for Petersen type method and standard errors of estimation for Jolly (1965) estimator. A indicates when adults were last distinguishable.

Sampling Date	Petersen type estimates of			Jolly type estimates of	
	L. conf. limit of $\hat{N}_i$	Population size $\hat{N}_i$	U. conf. limit of $\hat{N}_i$	Population size $\hat{N}_i$	Stand. error of $\hat{N}_i$
11-16.5.69	1767	2783	5300	--	--
21-22.5.69	1209	2261	6650	2387	1165.4
10.6.69	404	933	4550	1633	900.4
11-20.8.69	6714	310A 8592	15667	5470	2699.7
1-5 .9.69	11975	28261	95800	28740	19493.0
18-22.5.70	4250	6056	12750	--	--
1-2 .6.70	940	2104	3760	1302	417.3
11-12.6.70	1196	1760	3165	1219	285.6
22-24.6.70	639	902	1470	690	156.0
2-4 .7.70	586	859	1545	623	159.2
15-17.7.70	144 4350	270A 9582	1500A 17400	372	140.8
31.7-2.8.70	4504	8336	10360	11478	5004.4
15-17.8.70	5157	6117	9025	5126	939.5
29-30.8.70	6071	9855	13077	6355	1463.9

all fish above 29 mm. Confidence intervals for the Petersen
type estimates were provided using the Pearson and Clopper
Charts. The standard errors for the population estimates
based on the Jolly estimator are given. Neither the
Petersen type estimates nor the Jolly ones are consistently
higher. There is a decline of the population size from
June to the end of July of each summer. This declining
trend is very distinct in the summer of 1970 in which the
population size estimates were made at average intervals of
15 days. This period of decline of the spawning age group
coincides with the peak period of spawning.

Biomass

The biomass for the markable age groups are shown
in Tables 8 and 9 for the Petersen type and Jolly estimates
of the population sizes respectively. The mean biomass, $\bar{B}$,
between any two consecutive population size estimates are
provided. The biggest estimated biomass was obtained for
September 1-5, 1969, which also corresponds with the largest
population size estimates by both methods of Petersen and
Jolly. This however does not correspond with the largest
average weight, but with the lowest average weight as shown
in Fig. 8A and Tables 8 and 9.

FIG. 8. Average weight (mg) Curve A, and estimates
of population size (Curves in B) by
Petersen and Jolly methods used in
computing biomass.

TABLE 8. Computation of Biomass and mean Biomass at different sampling periods and intervals in between for Petersen type population size estimates.

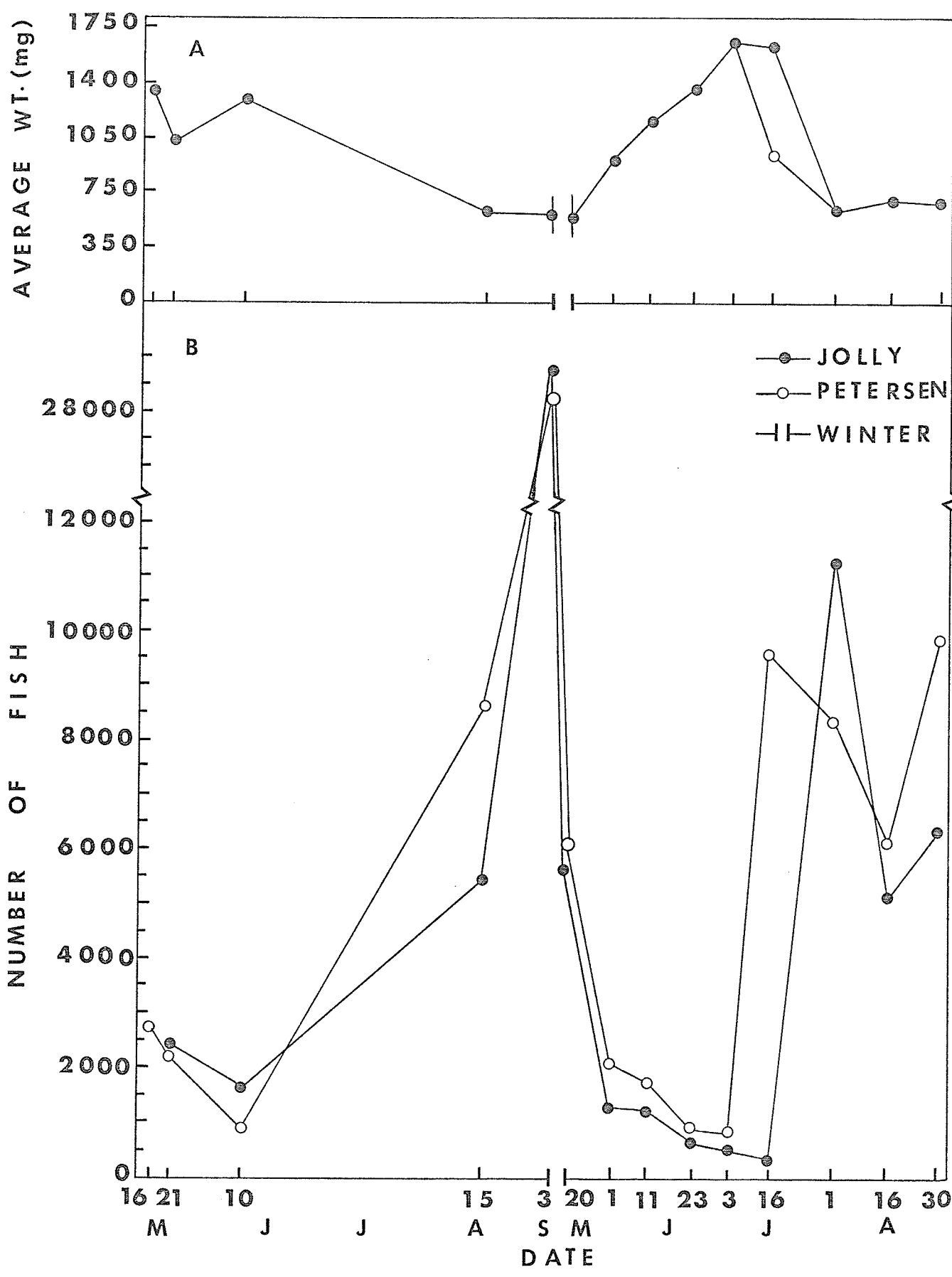| Date	Mean weight $\overline{W}$	Stock numbers $\hat{N}$	Stock biomass B	Mean biomass $\overline{\overline{B}}$
	gm		Kg	Kg
16-18.5.69	1.3404	2783	3.7303	
21-22.5.69	1.0334	2261	2.3365	3.0334
10.6.69	1.2896	933	1.2032	1.7699
11-20.8.69	0.5744	8592	4.9352	3.0692
1-5 .9.69	0.5640	28261	15.9392	10.4372
18-22.5.70	0.5599	6056	3.3908	9.6650
1-2 .6.70	0.9133	2104	1.9216	2.6562
11-12.6.70	1.1488	1760	2.0219	1.9718
22-24.6.70	1.3710	902	1.2366	1.6293
2-4 .7.70	1.6513	859	1.4185	1.3276
15-17.7.70	0.9454	9582	9.0588	5.2387
31.7-2.8.70	0.5875	8336	4.8974	6.9781
15-17.8.70	0.6563	6117	4.0146	4.4560
29-30.8.70	0.6429	9855	6.3358	5.1752

TABLE 9. Computation of Biomass and mean Biomass at different sampling periods and intervals in between respectively for population sizes estimated by the Jolly method.

Date	Mean weight $\overline{W}$ gm	Stock numbers $\hat{N}$	Stock biomass B Kg	Mean biomass $\overline{B}$ Kg
16-18.5.69	1.3404	2409	3.2290	
				2.8476
21-22.5.69	1.0334	2387	2.4667	
				2.2863
10.6.69	1.2896	1633	2.1059	
				2.6240
11-20.8.69	0.5744	5470	3.1420	
				9.6757
1-5 .9.69	0.5640	28740	16.2094	
				9.6867
18-22.5.70	0.5599	5651	3.1640	
				2.1766
1-2 .6.70	0.9133	1302	1.1891	
				1.2948
11-12.6.70	1.1488	1219	1.4004	
				1.1732
22-24.6.70	1.3710	690	0.9460	
				0.9874
2-4 .7.70	1.6513	623	1.0288	
				0.8085
15-17.7.70	1.6292	361	0.5881	
				3.5879
31.7-2.8.70	0.5875	11213	6.5876	
				4.9759
15-17.8.70	0.6563	5126	3.3642	
				3.7249
29-30.8.70	0.6429	6355	4.0856	

DISCUSSION

The assumptions and methods pertinent to mark-recapture studies are to be discussed with reference to the results obtained.

Age, Growth and Survival

The validity of age analysis is based on the formation of an annual ring during mid-summer and length-weight frequency distributions for separating the age groups without an apparent overlap of either length or weight (Richards, 1967).

In the threespine stickleback (Gasterosteus aculeatus) in Birket, England, Jones and Hynes (1950) reported that the otoliths without a ring (S-) occurred only during and just after the spawning season, and the first ring (S) appeared only from June or July to September. Rings in the order of 2S, 3S and 4S occurred only in July to September. Rings with outer opaque zones (S+, 2S+ and 3S+) occurred in almost all months, although 2S+ and 3S+ were relatively scarce in summer. This indicates that the transparent S ring begins to be laid down in June or July and that the opaque zone, (+), was laid down in July and is present in all fish by October. These authors offerred no physiological explanation for the appearance of transparent

rings and false rings often present in the centre and outer opaque zones. Jones and Hynes (1950) report that Bertin (1925) in his statistical study of size distribution in samples of Gasterosteus aculeatus taken at various seasons in many places in France and the Netherlands obtained a unimodal size distribution of nearly all his samples, with some samples showing more than one peak. Bertin then concluded that the sticklebacks in those regions lived for only two summers and died after breeding, though in some localities they lived for more than two summers. Bertin is also reported to quote Warington (1855), who was unable to keep sticklebacks alive in the aquarium after breeding. Jones and Hynes (1950) found that both Gasterosteus aculeatus and Pygosteus pungitius have a high growth rate in the first year of life and after only about 3 months of life the largest fish are at least as large as the smallest second-year fish. It seemed to them that possibly towards the end of life at about the third breeding season, the larger fish die off before the smaller ones, some of the smaller fish surviving until the following September. Lindsey (personal communication) among others, holds the view that fast growing fish mature early and also die earlier than their slow growing counterparts. Jones and Hynes concluded the G. aculeatus and P. pungitius have a maximum life span of 3 1/2 years and that differences in growth rate alone account for the differences in mean and

maximum size of fish in different populations.

Swarup (1959) demonstrated that Gasterosteus aculeatus at Raddley, Oxford, hatched in the summer and continued to grow up to March of the following year without showing any external sexual differences, though they spawned in the next two months of April and May. In October of their second year, the catch showed that the parent stock had almost disappeared from the pond which was full of young fish. He concluded that the parent stock of Gasterosteus aculeatus is replaced every year by the young.

Mullen and van der Vlugt (1964) observed a decline of the adult Gastosteus aculeatus in the samples, the presence of dead adult fish in the ditches, and absence of sticklebacks in oyster ponds and along the Dutch Sea Coast. They also report other authors to have found many dead sticklebacks, mostly on the bottom of ditches at the end of June. They cite Leiner (1931) mentioning an 'epidemic dicease' in the end of June, and Münzing is also reported by the same authors to have found fish 'with weak life at the end of June and July'. Mullen and van der Vlugt there-fore concluded that the absence of sticklebacks in the sea and reports of dead fish seemed to indicate a disease of the adults. They seemed to die in the period of June 16 to September 22, but mostly in July and some remained alive until the end of August after living for one year only.

Winn (1960) observed the size categories of Culaea

inconstans in Sylvan Ponds in Michigan to be made up mostly

of one-year-olds, some two-year-olds and possibly a few

three-year-olds. After the ponds were poisoned in the fall

of 1952 a small population survived, but by the spawning

season of 1954, the population had attained its original

size. Winn then concluded that maturity was attained in

one year, a conclusion identical with the one he reports

for Jacobs (1948). Mac Lean (1969) found that the length

frequency graphs suggested that the population of Culaea

inconstans in the Roseau River, S. Manitoba, consisted

mainly of one-year-old individuals born in the previous

spring and a smaller percentage of age two plus. He found

a few males later in deep areas of the temporary pools,

but the majority were never found. MacLean speculated that

the adult sticklebacks may have moved downstream into

permanent ponds after spawning.

In the present study it was found that Culaea

inconstans set the first ring (S) in the otolith within the

first month of life in the very summer of hatching. There

was no winter ring or check mark set. The second ring (2S)

was set in the sagittae at the beginning of June of the

second summer of existence which approximates to one year of

life. By June 11, 1970 all fish hatched in the summer of

1969 had set a second ring, and an opaque zone was being

laid around the second ring. Growth was observed to be very

rapid in the first summer of existence, attaining an average

total length of 38.48 mm and 41.9 mm for those hatched in 1969 and 1970 respectively. There was little growth during the ice cover (Figures 5 and 6).

There was a decline in adults throughout the spawning period, June to July; there were more adults still alive by the end of the summer study in 1969 than in 1970 (Fig. 4). The presence of 1969 summer spawners was indicated by the recapture of two sticklebacks in the sample of July 2-4, 1970 previously marked on May 11-16, 1969. This tends to agree with the findings of Bertin on Gasterosteus reported by Jones and Hynes (1950), and those of MacLean (1969) on Culaea inconstans. There were many spent dead adult sticklebacks floating on the surface and some were retrieved from the bottom of the channel by the seine-net. There was also a decline of adults in the length frequency histograms (Fig. 4) in the subsequent samples. The above strongly suggest that Culaea inconstans, like Gasterosteus aculeatus, is an annual fish. The adults die after spawning in the second summer, though a few may survive to live a third summer to complete two full years of life. All the spring samples from Lake Manitoba utilized in this study exhibited a unimodal length-frequency distribution. In the sample of May 18-22, 1970 from the lake, there was one fish that was completely separated from the rest indicating that possibly it was in the third summer completing two years of age. This tends to agree

with the abundance of fish over one year old in the sample
of September 1-5, 1969.

The use of otoliths alone for aging was found to be
satisfactory, provided it had been realised that the first
ring was a false check mark, especially after July 15, when
it became difficult to separate the yearlings from the
one-year olds by length frequency distributions alone. For
fish that set several false checks on their otoliths or
scales, it becomes imperative to apply more than two methods
which may include the use of probability paper in the
analysis of size frequency distributions (Cassie, 1954) for
assessing age.

Length-Weight Relationship and Condition Factor

Growth in length-weight is not strictly isometric.
Cleaver (1949) found values for length-weight regression
slopes of 3.214 and 3.577 for petrole sole less than and
greater than 40 cm respectively. Beckman (1948), Ricker
(1958) and Meeham and Siniff (1962) demonstrated that the
exponents for the slopes of length-weight relationship vary
from species to species, area to area, time to time and
age to age for the same species. Hile (1936) found values
of 1.3771 for ciscos between 145-179 mm in Trout Lake and
3.68489 for ciscos between 150-389 mm in Clear Lake. This
pattern was found to occur in Culaea inconstans in the
present study. This variation in slopes of length-weight
regression lines was found to be very significant, a

situation which could not be attributed to purely random errors of sampling, nor to systematic errors.

Hile (1936) observed that the variation in the values of a, the intercept, were dependent on the values taken by the slope b. When b is high, a is small and vice versa. Thus the values of a do not depend on the relative heaviness but on the rate of change in relative heaviness as measured by the exponents b - 3 and b. The values taken by b show further that this quantity is not fixed either for a species or a population. The values of the exponent not only vary tremendously from population to population but also vary considerably from time to time in samples of single populations. The values of b determined for samples apply only to the length intervals for which the equations were fitted and do not hold for fish whose lengths lie outside these length ranges. This variation makes length-weight equations and condition factors derived from them of little practical use in fisheries management.

Assumptions for Estimates of Population Size

There are basic and fundamental conditions to be satisfied for valid estimates of population size which are based on mark and recapture techniques. There are five principal kinds of information which can be obtained from marking studies (Ricker, 1958):

1. the rate of exploitation of the population;

2. the size of the population;

3. the survival rate of the population from one time interval to the next;

4. the rate of recruitment to the population;

5. the rate of dispersal of the animals.

Not all the above information can be obtained from every mark-and-recapture experiment. However in the present study all five types of informations were obtained.

The underlying assumptions for mark-and-recapture experiments are:

1. Sampling must be done at discrete time intervals and the actual time involved in capturing animals must be small in relation to the total time for the experiment.

2. Marked animals suffer the same natural mortality as the unmarked ones.

3. Marked and unmarked animals are equally vulnerable to capture irrespective of past history.

4. Marked and unmarked fish are randomly mixed in the population.

5. Marked animals do not lose marks.

6. Marked animals are recognized and reported on recovery (Ricker, 1958; Kelly and Barker, 1963 and Cormack, 1968).

7. There is a single population available and recruitment to this population is negligible. If any animals leave the population they do so permanently (Jolly, 1963, 1965).

Assumption 1, of sampling at discrete time intervals which are small in relation to the total time, was satisfied in the present study. The periods ranged from 2 to 6 days and the time between any two successive sampling periods ranged from 5 to 50 days in the summer of 1969 and 10 to 30 days in the summer of 1970. The distribution of marks in the subsequent three samples suggest that the first interval between release and recapture of marks was long enough, as the ratio of marks remained more or less constant.

The assumption 2, of equal mortality between marked and unmarked animals, is difficult to determine in a population of unknown size. A frequent effect of marking is extra mortality among marked animals either as a direct result of the marks or tags, or indirectly from the exertion and handling incidental to these operations. In either event the recoveries are too few to be representative, hence population estimates obtained from them will be too great and the rates of exploitation will be too small (Ricker, 1958). Immediate marking mortality can be controlled by holding the marked animals for observation until they are fully recovered to be released. The animals that show weakness are recorded individually and are not used even if they are released and some of them recaptured subsequently. Delayed marking mortality may be detected by change in the proportion of a group of marks in the subsequent samples over the period of the experiment, in the

case of experiments where many recapture samples are obtained.
If there is recruitment this sampling fraction will be
diluted, and this effect can be removed by the method to be
discussed later under assumption 7.

Ricker (1949) found no significant difference in the
survival and growth between three groups each consisting of
large-mouth bass and yellow perch fingerlings: with left
pectoral fin clipped, with left ventral fin missing and
with all the fins intact, after two months in a pond with
predators such as gar, bowfin, channel catfish and bullheads.

Shetter (1952) obtained similar results from
removal of either pectoral fin or right pelvic fin of lake
trout fingerlings held in a pond for a year in the presence
of predators such as brook, brown, rainbow and lake trout.
Shetter (1966) however, found difference in growth between
mouth tagged and untagged trout, and a slight difference
between clipped and unclipped trout. Churchill (1963)
concluded that removal of left pectoral or left pelvic fin
from three inch Walleye fingerlings had no significant
effect on their survival or growth during the following
four years after release into a hundred acre lake with
mixed fish populations including largemouth bass and
northern pike.

Nielson, Reimers and Kennedy (1957) could not detect
any difference in survival of stocked brown trout with a
ventral fin removed and control brown trout that were

unmarked, after one year in an experimental section of
Convict Creek. Brynildson and Brynildson (1966) reached
the same conclusion for wild brown trout in Wisconsin Stream;
moreover there was no difference in summer growth between
marked and unmarked fingerlings of trout.

Hagen (1967) found that marking the first dorsal
spine of Gasterosteus did not cause any mortality to the
fish held in the stream in live boxes. In the present
study there was some indication of delayed marking mortality
setting in after about one month, as shown by change in
sampling fraction in the fourth and subsequent samples of
recaptures (Tables 5 and 6). Since only the first
recapture of each batch mark was utilized in the Petersen
type estimates, the delayed mortality after the first
recapture should not affect the results considerably.
However the estimates based on the Schnabel (1938) and
Schumacher and Eschmeyer (1943) methods would be highly
biased towards overestimation. This delayed mortality would
also affect the survival estimates based on Jolly (1965) as
these would be unrepresentative of the whole population and
would apply only to the marked population.

Assumption 3, of equal vulnerability between marked
and unmarked animals is the most crucial one. If estimates
only of mortality, and not of population size, are required,
this assumption is relaxed only for marked animals. The
failure of this assumption may be due to either or both of

two causes:

      i.   the probability that a particular animal is caught in any sample is a property of the individual, this catchability having some distribution over the population,

      ii. the probability that any individual is caught in any sample depends upon its previous history (Cormack, 1968).

It has been found that marked or tagged fish tend to be either more, or less, vulnerable to fishing than are unmarked wild fish (Ricker, 1958). If the fish used were not originally part of the population being estimated, they may behave differently whether or not they are marked or tagged. The process of capturing and marking a fish may often exert a certain physical or psychological hardship upon it. The effects of these sorts will in general be hard to detect and hard to distinguish from actual mortality due to tagging. The rate of recapture in successive weeks or months after tagging may provide suggestive information (Ricker, 1958).

Buck and Thoits (1965) used three different marks for three estimates of fish in one-acre ponds by seining. The period between marking and recapture samples was between 12 and 72 hours. The three different estimates obtained were comparable, suggesting that marking does not influence vulnerability. After the recapture sample had been seined, the ponds were drained and a complete census

of the fish obtained. The restrictions advocated by Robson and Regier (1964), that the marking sample, M, times the recapture sample, n, should exceed 4 times the guessed population estimates for precision with any specified degree of confidence, were supposedly adhered to. However the Petersen estimates were found to be considerably biased with errors, which in many cases, were much larger than might reasonably be due to chance. Buck and Thoits concluded that conditions for a valid Petersen estimate do not hold, in spite of normally accepted indications to the contrary; they ruled out recruitment and mortality, the errors being apparently due to unequal vulnerability amongst the fish. However the evidence of their experiments would suggest that the time of between 12 and 72 hours might not have been sufficiently long for completely random distribution of marked fish in the pond population. If this was the case then assumption 4 was violated, though the others may have been fulfilled.

For a population subject to death and immigration (or recruitment), no procedure has been proposed for testing for equal vulnerability between marked and unmarked animals. Seber (1962, 1965) and Darroch (1958, 1959) have proposed methods for testing this assumption in populations where there is either death or immigration but not both.

In attempts to reduce the bias introduced by differential vulnerability several authors (Junge, 1963;

Ricker, 1958 and Lawrence, 1952) have suggested that recapture sampling be carried out by a different technique from that used in capturing for marking. In the present study the sampling method was such that every area was seined. Since this was a moving gear it is assumed that, barring the anomalies created by marked foreign fish introduced into the population twice, this assumption was satisfied as the estimates show a seemingly reliable trend. Any gear that is stationary would not be appropriate for random capture of fish that are territorial in behaviour, especially during the prespawning and spawning period.

Assumption 4, that marked and unmarked fish are randomly mixed is testable. If the population is not subject to dilution the proportion of the population at time t, which were first marked in the ith sample, should be the same for all t > i, that is the number of marks in the samples should be constant. The results of (a) staining experiment, (b) recaptures of previous days marks in the same sampling period and (c) seining the whole area, all suggest that there was random mixing of marked and unmarked sticklebacks during the time intervals between successive samples.

Assumption 5, that marked animals do not lose their marks applies only to situations where tags are used or where fins are clipped and regenerated while the experiment is still in progress. Hagen (1967) found that Gasterosteus

<u>aculeatus</u> with the first dorsal spine clipped showed no sign of regenerating spines even though the fish had grown. In the present study marking was done by clipping spines, and at no time was any stickleback found to have regenerated clipped spines.

Assumption 6, that marked fish are recognized and reported on recovery was satisfied in the present study in which every fish captured was closely examined under anaesthesia for the number of dorsal spines born and for marks, if any, that were clipped in the previous samples.

Assumption 7, that there is a single population available and recruitment to this population is negligible applies only to the Petersen method, and can be tested by several methods. Robson and Flick (1965) provide a non-parametric test for removing the effects of recruitment of the juveniles in the intervening period. Parker (1955) published the arcsin sign method for removing the effects of recruits from the population estimates. Leslie (1952) gives a method for detecting dilution in the samples by calculating the expected number of marks in the sample size n_i corresponding to $m_{i.t}$ marks as

$$\left(n_i \sum_{t=i+1}^{k} m_{i.t} \right) \Big/ \left(\sum_{t=i+1}^{k} n_t \right) .$$

The expected number of unmarked fish in each sample captured on each occasion is obtained by subtraction. A χ^2 with $(k - 1)k/2$ degrees of freedom then tests for the absence of

dilution. Dilution will be shown by this test if catchability is a function of capture history. Ricker (1958) suggested that a minimum size of fish to be marked be established and all recapture samples should include fish beyond the original marking size by the amount of growth in length gained in the intervening time interval. This method could be considered as the basis of the non-parametric method propounded by Robson and Flick (1965). In the present study screening the culvert at point C_3 prevented fish entering or leaving the study channel. The recruits from the summer hatching were eliminated by use of the above procedure for the Petersen type estimates. However there was no need for doing so in the case of the Jolly estimates.

Mark-and-Recapture Methods

The mark-and-recapture methods are basically the same. Petersen (1896) first suggested the use of records of the proportion of marked individuals in the study of fish population: 'when we spread the labelled fish over the whole fishing-ground, we may with some reason suppose that, proportionally, as many of the unlabelled fish which are living there will be caught as of those that are labelled.' The first use of this idea was by Dahl (1919). Without knowing of this work, Lincoln (1930) used band returns from sportsmen to estimate the size of wildfowl population in North America. Jackson (1933) independently applied the same method on insect population. Cormack (1968) and

Southwood (1966) give complete reviews of the literature on
the development and refinement of the technique up to the
completely stochastic model by Seber (1965) and Jolly
(1965). Cormack (1968) discusses the advantages and dis-
advantages of both deterministic and stochastic models so
far advanced.

Petersen Method

This method is named after Petersen who first
suggested it, or after Lincoln (1930). The method consists
of marking animals in one occasion and sampling for
recaptures on a single occasion or over a period of time.
Thus out of a population of N individuals, M are marked and
returned to the population. The probability of subsequently
capturing one of these marked animals depends on all the
preceding conditions or assumptions. Assuming that there
is randomness, the probability that a sampled animal is
marked in M/N. Out of a sample of n animals one would
expect to get exactly nM/N marked ones, which may be denoted
by r, to give,

$$r = nM/N$$

and rearranging terms gives

$$N = nM/r.$$

Bailey (1951) and Chapman (1951) suggested that the above
formula overestimated the population. A better approxima-
tion is obtained from a model in which the number of marked
animals per sample is treated as a random variate. This

can be done by considering the probability distribution of numbers of marked animals out of a sample size n (Jones, 1963). This is the very approach used by Bailey (1951), Chapman (1951) and Schaefer (1951).

Bailey (1951) contended that although the ratio r/nM gives an unbiased estimate of 1/N, its reciprocal is not an unbiased estimate of N. To counter this bias, various modifications of the basic Petersen type equation, N = nM/r, were proposed as more suitable for estimating N. The modified estimators of N and their variances are summarised in Table 10. Equations (A) to (D) are appropriate for direct sampling, that is sampling until a predetermined sample size, n, has been obtained, and equation (E) is for the alternative procedure known as the inverse sampling in which sampling is continued until a predetermined number of marked animals r, have been captured. Bailey (1951) and Chapman (1952) assume that the inverse sampling procedure is simpler than direct sampling. However an intermediate procedure is sometimes more practical in field conditions.

Bailey (1951) argued that the modification, N = (n + 1) M/(r + 1) gives a slightly lower estimate of the population size, on account of the fact that the inflation of the number of recaptures r, is proportionally greater than the increase in the product of the number marked, M, and the sample size in the census n. For very large samples the addition of one to n, and r, do not make a very

TABLE 10. Formulae for estimating population size (N) by the modified Petersen method.

Reference	Type of Sampling	Estimates of Population size (N)	Variance of (N)
A. Bailey, 1951	Direct	Mn/r	$M^2 n(n - r)/r^3$
B. Bailey, 1951	Direct	$M(n + 1)/(r + 1)$	$\dfrac{M^2(n + 1)(n - r)}{(r + 1)^2(r + 2)}$
C. Chapman, 1951	Direct	$\dfrac{(M + 1)(n + 1)}{r + 1}$	$N^2\left[\dfrac{N}{nM} + 2\left(\dfrac{N}{nM}\right)^2 + 6\left(\dfrac{N}{nM}\right)^3\right]$
D. Schaefer, 1951	Direct	$\dfrac{(n + 1)(M + 1)}{r + 1} - 1$	none given
E. Bailey, 1951 Chapman, 1952	Inverse	$\dfrac{n(M + 1)}{r} - 1$	$\dfrac{(M - r + 1)(N + 1)(N - M)}{r(M + 2)}$

significant difference (Ricker, 1958).

In the present study both the sample size and the number of recaptures were governed by sampling the whole channel within a discrete time without fixing the size to be caught. This procedure was thus intermediate between direct and indirect sampling though the estimates were computed from the formula fitted for direct sampling.

Schnabel (1938) Method

Schnabel (1938) assumed that the total number of marked animals M_i, in the population immediately before the ith sample is taken are known. The situation then is identical with a series of Petersen type estimates which have to be combined and averaged to yield a single estimate of the population size. However the fundamental difference is that whereas in the Petersen method, the proportion of marked individuals, (M/N), in the population is assumed constant, in the Schnabel method it is the population size N, that is assumed constant. The number of marked individuals, M, is not constant, but increases as the experiment continues. Schnabel considered practical situations in which the number of marked individuals is negligible compared with the population size, and gave a simplified equation for direct estimation of N, as

$$N = \Sigma \; n_i \; M_i / \Sigma \; r_i.$$

Chapman (1952) suggested that a better estimate would be $N = \Sigma \; n_i \; M_i / \Sigma \; (r_i + 1)$. Schumacher and Eschmeyer

(1943) suggested that the population size N, could be estimated by,

$$N = \Sigma \; n_i \; M_i^2 / \Sigma \; r_i \; M_i .$$

Mortality causes the population to decline and thus the Schnabel estimate of the population size would not apply to any definite time period, and would be less than the Petersen estimate from the first sampling. De Lury (1951) used this fact to measure mortality. Within the models of closed populations where there is no recruitment and mortality, a Petersen type study with a single release of marked animals is less affected by the failure of the assumptions than is a Schnabel type study (Cormack 1968). Recapture over a period allows most of the assumptions to be tested, but does not test for immediate additional mortality due to marking.

In the present study no immediate additional mortality was detected, and there were no dead marked fish found immediately after release. If any fish did die as a result of marking, they must have sunk to the bottom. This possibility cannot be ruled out for during recapture sampling dead fish both marked and unmarked were retrieved by the seine-net from the bottom, particularly during the spawning period in the months of June and July. Because of the fairly long interval between recapture samples any marked fish dying immediately would decompose at the bottom before the next recapture was obtained. The assumption of

a constant population was violated as the adult population declined steadily to a negligible size.

In conditions in which this study was carried out, the Schnabel method was inappropriate. All other methods requiring summation of sample sizes and recaptures over extended time periods, such as Schumacher and Eschmeyer (1943) method, and Triple Trellis by Dowdeswell, Fisher and Ford (1940, 1949) were equally unsuitable for the prevailing situation.

All the above methods are based on deterministic models that assume that the survival rate over an interval is an exact value, whereas it would be more correct to state that in nature an animal has a probability of surviving over the interval (Jolly, 1965). This probability is well expressed by a stochastic model, but initially it was thought that computations arising from a stochastic model would be too complex (Southwood, 1966). Darroch (1958, 1959) showed that for a closed population with either death or immigration but not both occurring a fully stochastic model, giving explicit solutions for the estimation of population parameters, was possible. Seber (1965) and Jolly (1965) have independently extended this method to cover situations in which there is both loss (death and emigration) and dilution (births and immigration).

Jolly (1965) Stochastic Model

The methods of Seber (1965) and Jolly (1965) give

similar solutions, except that Jolly's makes allowance for any animals killed after capture and hence are not released again. Seber's method on the other hand has one advantage for testing for equi-catchability in a closed population, an asset which is not given by Jolly (1965) except for reference to the work of Darroch (1958, 1959) and Seber (1962, 1965).

Jolly's method, being based on an efficient method of grouping the data and on a fully stochastic model, appears to be the most appropriate for studies involving three or more successive samples where both dilution and loss are occurring, especially in commercially exploited fish populations. In Jolly's method, like other data-grouping methods, no significance is attached to any mark other than the last, and hence the term multiple recapture should not be applied in connection with these methods. The only relevant information is the occasion on which an individual was last seen. Its history of capture prior to that last previous sighting contains no information about its chance of death or recapture after that sighting. The information provided by a single individual caught at times t_i, t_j, t_k, is precisely the same as if one individual released at t_i were recaptured and removed at t_j, a second individual released at t_j and recaptured at t_k Cormack (1968). Thus a commercial fishery with single recaptures yields the same estimates as a research project with multiple recaptures, as

far as the estimation of population parameters are concerned. However multiple recaptures can still be recorded in a separate table for testing the assumption of equal catchability between marked and unmarked animals. The results obtained by Jolly (1963) based on a deterministic model are similar to those obtained using the stochastic model. In both methods the number of marked animals M_i, in the population at time of capturing sample size n_i, is estimated. However the deterministic model involves complicated weighted sums of various recapture frequencies amounting to iterative solutions, whereas in the stochastic model $\hat{M}_i$ is estimated by terms of unweighted sums r_i--the number of releases s_i subsequently recaptured and Z_i--the number of individuals marked before t_i, not caught at t_i, but which are recaptured subsequently.

The Jolly (1965) method facilitates determination of the number of new animals B_i, joining the population in the interval between the t and t + 1th samples and alive at time t + 1. Jolly defines $B_o = N_1$. By allowing for both death or permanent emigration from and immigration into or recruitment from the young groups into the population under study, assumption 7 of no recruitment is no longer needed.

For the asymptotic variances to apply the s_i, Z_i and R_i should be assumed large, but there is no need, as in the deterministic model, for the sampling fraction α_i to be small; the present theory would apply even if the whole

population were caught on each occasion Jolly (1965). Each sample is taken to be a random sample from the population, and the s_i animals are assumed to have so distributed themselves after release that they have the same probability as any other animal of being caught in the t + 1th sample. Apart from this restriction, there is no condition on the length of time between successive samples, nor are the time intervals necessarily equal.

Although sampling should be random, Jolly (1965) states that in respect of samples used for obtaining the proportion of marked animals m_i in the sample n_i ($\alpha_i = m_i/n_i$), or the ratio Z_i/R_i of future recaptures, complete randomness may not be necessary in particular instances. What is necessary is that for estimation of $\alpha_i = m_i/n_i$ the probability of capturing an animal of M_i must be the same as that of capturing one of N_i, and similarly for the ratio Z_i/R_i, which implies that n_i should be selected at random from the population. These particular instances could be due to spawning in two or more areas where one group may not be accessible for capture. The selection of breeding area is assumed not to be influenced by past history.

It is further propounded that should circumstances be such that random selection of a sample is impracticable, then the s_i might either be a non-random sample or possibly even introductions from outside the population. Since M_i is estimated solely from counts of marked animals, there is a

sub-population of which the s_i are random sample. Jolly (1965) asserts that estimates of M_i and consequently of ϕ, the probability of survival, can be estimated as in Cormack (1964), and he recognizes the drawbacks in this procedure of introducing foreign marked animals into the population because of the questions posed and left unanswered, while emphasizing the point of equal catchability for the sub-populations.

However, Jolly (1965) estimator, despite the above advantages, has some drawbacks similar to those of the preceding methods. Its estimate of population size, N_t, is very sensitive to the failure of assumption of equal catchability for marked and unmarked animals, to which the probability of survival is insensitive. The precision of the estimates of N_i are related to m_i the recaptures at t for when m_i is small N_i is large and when m_i is large N_i is small.

The estimates of the new individuals joining the population between t and t+1 and alive at t + 1 are difficult to interpret as the signs are not indicative of dilution or death.

The reference to Cormack (1964) is rather unwarranted as the available data is on marked individuals only, random sampling of the whole population being impossible. The estimates obtained are for the mortality of the marked population. For these estimates to be

applicable to the whole population some assumption of the representative character of the marked animals is required. In general no estimate of population size is possible from such data, and if sampling of marked and unmarked individuals are totally separate the proviso in Jolly's statement will be impossible to fulfill (Cormack, 1968). For the data obtained in commercial studies, n_i not being recorded although m_i is, N_i cannot be estimated and the survival estimates of ϕ_i apply strictly only to the marked sub-population. However, Jolly claims that this situation fits the framework of his model within which s_i and n_i need not be composed of the same individuals, and rightly points out that such estimates and their variances as given by Cormack are a special case of the general formulae. It should be noted that in most commercial fisheries, catch data are recorded, although often not satisfactorily.

The Jolly (1965) estimators have the most unfortunate disadvantage of providing estimates of variance which are disastrously high. This tends to make the confidence limits for the estimates less reliable at 95% confidence level.

Estimates of Population Size

In Tables 5 and 6 are tabulated the catch size n_i, number marked and released s_i or M_i and recaptures of previous marks released into the population. The discrepancy between the two tables is that in Table 5 all recaptures including individuals with multiple marks were recorded

accordingly, whereas in Table 6 only the most recent mark was considered. In Table 6 the sample caught on July 2, 1969 was combined with that of August 11-20, 1969, and the sample caught on October 25, 1969 was tabulated under May 18-22, 1970 according to Jolly (1965).

The estimate of more than 2060 fish for May 18-22, 1970 by both the Jolly and Petersen methods is inconceivably high because of the fact that only one fish was recovered on May 10, 1970, after seining the whole channel except the shores. There are four possible explanations.

1. The above seems to imply that besides the 2060 fish introduced, some fish had access into the study area between May 10, 1970 and June 2, 1970. Since the screen against the culvert was at no time passable to fish, this possibility can be dismissed.

2. The next possibility to be considered is that there was mortality among the 1020 marked fish stocked in the channel between May 18 and 22, 1970. Since all marked fish stocked had been held overnight in aquaria and only normally behaving ones were stocked, extensive death among marked fish is not suspected. Hagen (1967) reported that clipping dorsal spines of Gasterosteus did not affect the survival of the fish in live boxes kept in the stream. There is no evidence that spines are used in locomotion and their absence should not hinder mobility. This may not be true for pelvic spines. If pelvic spines are used for

offence and defence, there were no predatory fish in the
present study area that could have selectively attacked the
sticklebacks with left pelvic spine clipped.

3. The third alternative for this apparently
anomalous high estimate could be that there was a large
number of survivors of the winter, which were not detected
on May 10, 1970. Although only one Culaea inconstans, two
Pungitius pungitius and 18 fathead minnows were seined on
May 10, 1970, the seining for the whole area was only for
one hour and covered only the middle parts of the channel.
The shore areas of the channel were not searched. Possibly
at this period of the month the fish were still inactive.
Reisman and Cade (1967) report that the sticklebacks in
Thorndon pond seemed quiescent throughout the month of May,
remaining hidden in recesses under rocks, along the
periphery, under dead leaves on the bottom or burried in
light vegetative detritus. The amount of effort and its
distribution over the study channel on May 10, 1970 would
tend to support the likelihood that fish had overwintered
but were not caught.

4. The strongest suspicion concerns the behaviour
of marked fish themselves, especially as they were wild
foreign fish. This aspect has already been dealt with in
connection with assumption 3 of equal catchability or
vulnerability for marked and unmarked animals. The skittish
behaviour of these sticklebacks during most of the month of

May and the use of marked fish of completely foreign origin
are suspected to be responsible for the apparently high
estimate of population size for May 18-22, 1970.

There is no way of defining the real source of the
error, if any. It may be noted that the survival rate
calculated using the Petersen type estimates for May 18-22,
1970 and June 1-2, 1970 is 0.3474 which is equivalent to the
upper confidence limit for survival rate for the same period
using the method of Ricker (1945a). The additional fact
that there was random distribution between marked and
unmarked sticklebacks would tend to make the estimate less
suspect than otherwise.

Neither the Petersen type method nor the Jolly
estimator gives a consistently higher estimates of popula-
tion size and survival rates in progressive sampling periods
(Tables 4 and 7). The estimates for survival rates for
both methods are quite similar throughout the period of
study except for the very high value of 2.6823 for the
period between August 11-20, 1969 and September 1-5, 1969,
given by the Jolly estimator. A value greater than 1.0
for the probability of survival seems unstatistical. Jolly
·(1965) obtained a value of 1.015 for the probability of
survival, when the estimates of population size were
increasing. Jolly does not provide an explanation for such
a value in his experiment. This may be an artifact intro-
duced by a large surge of recruits, although it does not

reccur in 1970. The estimates of population size obtained in this study using the Petersen and Jolly methods show both disagreements and agreements in different time periods, indicating the need for using more than one method in the absence of a way of ascertaining the validity of the estimates provided by one method. The Jolly method has also given high variances for the estimates of population size, whose lower confidence limits are almost zero using 2 standard errors. In practice the lower limit can be taken to be the larger of n_i and $\hat{N}_i$ - 2 S.E. The population estimates based on the Jolly estimator in this study suffer from delayed failure of assumption 2, of equal natural mortality between marked and unmarked sticklebacks, since all subsequent recaptures belonging to any batch of marks released are used in the computations, together with the subsequent sample sizes as shown in Appendix III. However, the failure of the assumption on equal vulnerability and/or mortality for marked and unmarked fish does not affect the estimates on the probability of survival.

The estimates of new individuals B_i, joining the population between times t and t + 1 are mostly positive and yet the population size may be declining and no new animals are entering until the time of recruitment of yearlings.

Biomass

The classical definition of biomass to include the

weight of all living matter in the system under study is difficult to estimate. Chapman (1967, 1968) provided a more realistic definition which is managable. In the present study the largest estimate of biomass corresponds to the peak of recruitment of yearlings, when the population estimates became highest, although the average weight of the fish was second lowest (Figure 8 and Tables 8, 9). This is explained by the fact that the stickleback population was composed mostly of one year class except during the spawning periods when there are yearlings, one-year-olds and scarcely any two-year-olds. The yearlings were many and their low average weight was compensated by their numbers. However, as the one-year-and over-old fish disappeared from the population, there was an increase in weight of the yearlings, but their abundance was declining.

Life History in Delta Area

The spawning migration from Lake Manitoba to the channels and creeks in the marsh took place between 10-20 May in the spring of 1969 and 1970. The migration involves *Culaea inconstans*, *Pungitius pungitius*, *Pimephales promelas*, *Cyprinus carpio* and *Esox lucius*.

In the marsh, *Culaea inconstans* builds a spherical grass nest, which is attached to the stem of an aquatic plant, in the last half of May. By June 11-12, the first batch of yearlings is already hatched and grown to just under 20 mm in total length (Fig. 5). The yearlings set

the first ring, a false check, in their otoliths in the first month of life while the adults set an annual ring on June 1, of the second summer. Spawning period extends to mid-August as indicated by the presence of still gravid females and an abundance of very small fish.

Sexual maturity is attained in one year, that is in the second summer of life, when the fish range between 29 mm and 65 mm in total length (Fig. 4). There are scarcely any two-year-olds in the spawning population. The post-spawners die off as was shown by the number of spent dead fish floating on the surface along the shores of the study channel, and also retrieved from the bottom by seining. The number of adults diminishes in the subsequent samples and by July 15, there is a merger in lengths of the fast growing yearlings and small slow growing one-year-olds. In August 15-17, 1970, there were very few reminants of the adults, although in the summer of 1969, the adults were still abundant in the sample caught on September 1-5 (Fig. 4). The recaptures of fish in 1970 which were marked in 1969 indicates that some sticklebacks had overwintered in the study channel which did not freeze over completely, though there was very low oxygen and high hydrogen sulphide concentrations.

Predators

Culaea inconstans was preyed upon in the study area by the Giant Waterbug, the Belted Kingfisher, the common

terns, laughing gulls and leeches all of which were found

there. In the aquaria, corixids and notonectids were

observed to attach themselves on the fish which resulted in

fish mortalities if the former were not removed from the

aquaria. In the field, notonectids were found to inflict

very irritating bites on the hands of the experimenter while

sorting out the fish from the seine-bag. The bites used to

swell up and at night they inflamed.

Food

The food of the brook stickleback was found to con-

sist of fish eggs, possibly including their own, young of

their own and of Pungitius pungitius, Chironomid larvae,

Diptera larva, ostracods, copepods, cladocerans, amphipods,

snails, blue algae and seeds of aquatic plants.

Conclusion

Conflicting evidence has been obtained regarding

the efficiency of such methods as poisoning or draining in

providing an accurate account of the fish population sizes

in ponds, as checks on the estimates based on mark-recapture

methods. These methods have the disadvantage of providing

a count of a population size which is different from the

initial one, and are also limited to small drainable water

bodies. There is therefore no direct way of checking the

accuracy of the estimates based on mark-recapture methods.

It is difficult to put reliability on one method. It is

imperative that recapture experiments be planned in such a way that the catch in samples can be subjected to more than one type of computation. However, in a real fisheries study for management aspect, it would not really be philosophically valid to try several statistical analyses on the same data. One should instead pick the best for the situation in advance and stick to it, so long as it meets the basic assumptions (Green, personal communication).

For such a design to be successful, a priori knowledge of the biology of the species must be available. Spawning and post-spawning behaviour of the fish should be investigated first, including the life span and other aspects of social behaviour. This knowledge would help in ensuring that the assumptions are not violated during the sampling periods and at the intervals in between while the experiment is in progress.

The investigator should collect the data in such a fashion that the assumptions about the form of the sampling distributions are tested. The use of empirical variance estimates should be provided if there is any doubt about the validity of the underlying assumptions. Cormack (1968) rightly asserts that fine adjustments of the statistical theory—the removal of purely statistical bias, improved approximation, exact probability levels are futile in the presence of gross errors in the assumptions. The obstacles associated with mark-recapture studies are those of random

sampling, proper mixing, equal vulnerability and other

behavioural factors.

LITERATURE CITED

LITERATURE CITED

Adams, L. 1951. Confidence limits for the Petersen or Lincoln index used in animal population studies. J. Wildl. Mgmt. 15(1):12-19.

Albrechtsen, A. 1968. A dyeing technique for otolith age reading. J. du Conseil 32(2):278-280.

Bailey, N. T. J. 1951. On estimating the size of mobile populations from recapture data. Biometrika 38:293-306.

Beckman, W. C. 1945. The length-weight relationship, factors for conversions between standard and total lengths and coefficients of condition for seven Michigan fishes. Trans. Amer. Fish. Soc. 75(1945) 1948:237-256.

Bell, G. R. 1964. A guide to the properties, characteristics and uses of some general anaesthetics for fish. Fish. Res. Bd. Canada Bull. No. 148, 4 p.

Bertin, L. 1925. Recherches bionomiques, biometrique et systematiques sur les épinoches. Ann. Inst. Océanogr. Monaco 2:1-208. (Cited by Jones, J. W. and H. B. N. Hynes, 1950. The age and growth of Gasterosteus aculeatus, Pygosteus pungitius and Spinachia vulgaris as shown by their otoliths. J. Anim. Ecol. 18(2):59-73).

Brynildson, O. M. and C. L. Brynildson. 1967. The effect of pectoral and ventral fin removal on survival and growth of wild brown trout in a Wisconsin stream. Trans. Amer. Fish. Soc. 96(3):353-355.

Buck, D. H. and C. F. Thoits. 1965. An evaluation of Petersen estimation procedures employing seines in one-acre ponds. J. Wildl. Mgmt. 29:598-621.

Carlander, K. D. and L. L. Smith. 1945. Some factors to consider in the choice between standard, fork and total lengths in fishery investigations. Copeia 1945(1): 7-12.

Cassie, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. Australian J. Mar. and Freshwater Res. 5:513-522.

Chapman, D. G. 1952. Inverse, multiple and sequential sample census Biometrics 8:286-306.

_____. 1954. The estimation of biological populations. Ann. Math. Statist. 25:1-15.

Chapman, D. W. 1967. Production in Fish populations. (In Gerking, S. D. 1967 edition). The biological basis of Fresh water fish production. Blackwell Scientific Publications, Oxford and Edinburgh, 495 p.

_____. 1968. Production. (In Ricker, W. E. 1968 edition). Methods for assessment of fish production in fresh waters. I. B. P. Handbook No. 3. Blackwell Scientific Publications, Oxford and Edinburgh, 313 p.

Chapman, G. C. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. Univ. Calif. Publ. Statist. 1:131-160.

Churchill, W. S. 1963. The effect of fin removal on survival, growth and vulnerability to capture of stocked Walleye fingerlings. Trans. Amer. Fish. Soc. 92(3): 298-300.

Cleaver, F. C. 1949. The Washington otter trawl fishery with reference to the petrale sole (Eopsetta jordani). Washington Dept. of Fisheries, Biol. Rept. 49A:1-45.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429-438.

_____. 1968. The statistics of capture-recapture methods. Oceanogr. Mar. Biol. Ann. Rev. 6:455-506.

Crawford, R. N. 1958. Behaviour, growth and mortality in the bluegill (Lepomis michrochirus Rafinesque) following fin clipping. Copeia 1958(4):330-331.

Dahl, K. 1919. Studies of trout and trout-waters in Norway· Salmon and Trout Magazine 18:16-33 (cited by Cormack, R. M., 1968). The statistics of capture recapture methods. Oceanogr. Mar. Biol. Ann. Rev. 1968 (6):455-506.

Darroch, J. N. 1958. The multi-recapture census. 1. Estimation of a closed population. Biometrika 45: 343-359.

_____. 1959. The multi-recapture census. 2. Estimation when there is immigration or death. Biometrika 46:336-351.

Davis, W. S. 1964. Graphic representation of confidence intervals for Petersen population estimates. Trans. Amer. Fish. Soc. 93(3):227-232.

De Bout, A. F. 1967. Some aspects of age and growth of fish in temperate and tropical waters. (In Gerking, S. D., 1967 edition). The biological basis of fresh-water fish production. Blackwell Scientific Publications, Oxford and Edinburgh, 495 p.

Dowdeswell, W. H., R. A. Fisher and E. B. Ford. 1940. The quantitative study of populations in Lepidoptera. 1. Polyommatus icarus Rott. Ann. Eugen. London 10:123-136.

_____, _____ and _____. 1949. The quantitative study of populations in Lepidoptera. 2. Maniola jurtina L. Heredity 3:67-84.

Guthrie, J. E. and S. L. Iverson. 1970. Some observations of captive giant waterbugs (Lethocerus americanus (Leidy)) Hemiptera, Belostomidae. The Blue Jay XXVIII(1):47-49.

Hagen, D. W. 1967. Isolating mechanisms in the threespine sticklebacks (Gasterosteus). J. Fish. Res. Bd. Canada 24(8):1637-1692.

Hile, R. 1936. Age and growth of the Cisco Leicichthys artedi (Le Sueur) in lakes of the northeastern highlands Wisconsin. U. S. Bur. Fish. Bull. 48:211-217.

_____. 1970. Body-scale relations and calculation of growth in fishes. Trans. Amer. Fish. Soc. 99(3):468-474.

Jackson, C. H. N. 1939. The analysis of animal populations. J. Anim. Ecol. 8:238-246.

Jacobs, D. L. 1948. Nesting of the brook stickleback. Proc. Minn. Acad. Sci. Abstract 16:33-34.

Jolly, G. M. 1963. Estimates of population parameters from multiple recapture data with both death and dilution--a deterministic model. Biometrika 50:113-128.

_____. 1965. Explicit estimates from capture-recapture data with both death and immigration - Stochastic model. Biometrika 52:225-247.

Jones, J. W. and H. B. N. Hynes. 1950. The age and growth of Gasterosteus aculeatus, Pygosteus pungitius and Spinachia vulgaris as shown by their otoliths. J. Anim. Ecol. 18(2):59-79.

Jones, R. 1963. A review of methods of estimating population size from marking experiments. Rapp. P.-V. Réun. Cons. perm. int. Explor. Mer. 155:202-209.

Junge, C. O. 1963. A quantitative evaluation of the bias in population estimates based on selective samples. I.C.N.A.F. Spec. Publ. 4:26-28.

Kelly, G. F. and A. M. Barker. 1963. Estimation of population size and mortality rates from tagged Redfish (Sebastes marinus L.) at Eastport, Maine. I.C.N.A.F. Spec. Publ. 4:204-209.

Ketchen, K. S. and Forrester. 1966. Population dynamics of the petrale sole (Eopsetta jordani) in waters of Western Canada. Fish. Res. Bd. Canada Bull. 153, 195 p.

Lawler, G. H. and M. Fitz-Earle. 1968. Marking small fish with stains for estimating populations in Heming Lake, Manitoba. J. Fish. Res. Bd. Canada 25(2):255-266.

Lawrence, J. M. 1952. A trapping experiment to estimate the bluegill population in a farm pond. Proc. Iowa Acad. Sci. 59:475-479.

Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch, (Perca fluvatilis). J. Anim. Ecol. 20(1):201-219.

Leiner, M. 1931. Okologisches von Gasterosteus aculeatus L. Zool. Anz. 93:317-333. (Cited by P. J. van Mullein et al. 1964. On the age, growth and migration of the anadromous sticklebacks Gasterosteus aculeatus L. investigated in mixed populations. Archiv. Neerl. Zool. 16(1), 1964:111-139).

Leslie, P. H. 1952. The estimation of population parameters from data obtained by means of capture-recapture method. II. The estimation of total numbers. Biometrika 39: 363-388.

MacLean, J. A. 1969. Movement, size, age, sex-ratio and lengevity of Culaea inconstans in Roseau River near Dominion City, S. Manitoba. Unpublished M. Sc. Thesis, University of Manitoba.

Meehan, W. R. and D. B. Siniff. 1962. A study of the downstream migration of anadromous fishes in the Taku River, Alaska. Trans. Amer. Fish. Soc. 91(3):399-407.

Mullem, P. J. van and J. C. van der Vlugt. 1964. On the age, growth and migration of the anadromous sticklebacks (Gasterosteus aculeatus L.), investigated in mixed populations. Archiv. Neerl. Zool. 16(1), 1964:111-139.

Münzing, J. 1959. Biologie variabilitat und Genetik von Gasterosteus aculeatus L. (Pisces). Untersuchungen im Elbegebiet. Int. Rev. Ges. Hydrobiol. 44:317. (Cited by Mullem, P. J. van and J. C. van der Vlugt, 1964). On the age, growth and migration of the anadromous stickle-backs (Gasterosteus aculeatus L.), investigated in mixed populations. Archiv. Neerl. Zool. 16(1), 1964:111-139.

Nielsen, R. S., N. Reimer and H. D. Kennedy. 1957. A six year study of the survival and vitality of hatchery-reared trout of catchable size in Convict Creek, California. Calif. Fish and Game 43:5-42.

Parker, R. A. 1955. A method for removing the effect of recruitment on Petersen type population estimates. J. Fish. Res. Bd. Canada 12:447-450.

Reisman, H. M. and T. J. Cade. 1967. Physiological and behavioural aspects of reproduction in the brook stickleback Culaea inconstans. The Amer. Midl. Naturalist. 77(2):257-295.

Richards, C. E. 1967. Age, growth and fecundity of cobia, Rachycentron canadum from Chesapeake Bay and adjacent Mid-Atlantic waters. Trans. Amer. Fish. Soc. 96(3): 343-350.

Ricker, W. E. 1945a. Abundance, exploitation and mortality of fishes in two lakes. Investigations of Indiana Lakes and streams 2(17):345-448. In Ricker, 1958 (ed.) Handbook of Computation for Biological Statistics of Fish Populations. Fish. Res. Bd. Canada. Bull. 119, 300 p.

_____. 1947. Mortality rates in some little exploited populations of freshwater fishery. Trans. Amer. Fish. Soc. 77:114-128.

_____. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ., Sci. Serv. No. 15, 101 p. (Cited by Ricker, W. E., 1958). Hand-book of Computation for biological statistics of fish populations. Fish. Res. Bd. Canada. Bull. 119, 300 p.

_____. 1949. Effects of removal of fins upon the growth and survival of spiny-rayed fishes. J. Wildl. Mgt. 13(1):29-40.

_____. 1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Bd. Canada Bull. 119, 300 p.

_____, and D. Merriman. 1945. On the methods of measuring fish.Copeia 1945(4):184-191.

Robson, D. S. 1963. Maximum likelihood estimate of a sequence of annual survival rates from a capture-recapture series. I.C.N.A.F. Spec. Publ. 4:330-336.

_____ and H. A. Regier. 1964. Sample size in Petersen mark-recapture experiments. Trans. Amer. Fish. Soc. 93(3):215-226.

_____ and W. A. Flick. 1965. A non-parametric statistical method for culling recruits from a mark-recapture experiment. Biometrics 21:936-947.

Rounsfell, G. A. and W. H. Everhart. 1953. Fisheries Science, its methods and applications. John Wiley & Sons, Inc., New York, Chapman and Hall, Limited, London, 444 p.

Schaefer, M. B. 1951. Estimation of size of animal populations by marking experiments. Fish. Bull. U. S. 52:191-203.

Schnabel, Z. E. 1938. Estimation of total fish population of a lake. Amer. Math. Monthly 45(6):348-352.

Schumacher, F. X. and R. W. Eshmeyer. 1943. Estimate of fish population in lakes and ponds. J. Tennesee Acad. Sci. 18(3):228-249.

Seber, G. A. F. 1962. The multi-sample single recapture census. Biometrika 49:339-349.

_____. 1965. A note on multiple-recapture census. Biometrika 52:249-259.

Shetter, D. S. 1952. The mortality and growth of marked and unmarked lake trout fingerlings in the presence of predators. Trans. Amer. Fish. Soc. 81:17-34.

_____. 1967. Effects of jaw tags and fin excision upon the growth, survival and exploitation of hatchery rainbow trout fingerlings in Michigan. Trans. Amer. Fish. Soc. 96:394-399.

Smoker, W. and W. G. Pearcy. 1970. Growth and reproduction of the lantern fish Stenobrachius leucopsarus. J. Fish. Res. Bd. Canada 27(7):1265-1275.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods, 6th ed. The Iowa State University Press, Ames, Iowa, U. S. A., 593 p.

Southwood, T. R. E. 1966. Ecological methods with particular reference to the study of insect populations. Methuen.and Co. Ltd. London, 391 p.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of Statistics with special reference to the biological sciences. McGraw-Hill Book Co. Inc., New York, Toronto, London, 481 p.

Swarup, H. 1959. The reproductive cycle and development of gonads in Gasterosteus aculeatus. Zoological Soc. Calcutta Proceedings 1959:47-61.

Tesch, F. W. 1968. Age and growth, p. 93-123. In W. E. Ricker (ed.) Methods for assessment of fish population in freshwaters. I.B.P. Handbook No. 3, Blackwell Scientific Publications, Oxford and Edinburgh, 313 p.

Ward, F. J. and L. A. Verhoeven. 1963. Two biological stains as markers for sockeye salmon. Trans. Amer. Fish. Soc. 92(4):379-383.

Winn, H. E. 1960. Biology of Brook stickleback Eucalia inconstans (Kirtland). American Midland Naturalist, 63(2):424-437.

Warington, E. 1855. Observations on the habits of the stickleback (being a continuation of a previous paper). Ann. Mag. Nat. Hist. (2)16:330-332. (Cited by Jones, J. W. and H. B. N. Hynes, 1950). The age and growth of Gasterosteus aculeatus, Pygosteus pungitius and Spinachia vulgaris, as shown by their otoliths. J. Anim. Ecol. 19:59-73.

APPENDIXES

APPENDIX I. Physical and Chemical data for the study
channel for surface water recorded at
point H.

Date	Oxygen p.p.m.	Carbon dioxide p.p.m.	pH	Hardiness p.p.gallon
2.7.69	--	55.0	9.0	--
4.7.69	8.0	45.0	9.0	--
7.7.69	8.0	40.0	9.0	--
9.7.69	8.0	50.0	9.0	35.0
11.7.69	8.0	40.0	9.0	31.0
14.7.69	6.0	20.0	9.25	37.0
16.7.69	7.0	50.0	9.25	37.0
18.7.69	5.0	40.0	9.25	35.0
20.7.69	7.0	35.0	9.25	36.0
22.7.69	6.0	40.0	9.25	35.0
24.7.69	5.0	40.0	9.25	36.0
26.7.69	3.0	25.0	9.25	35.0
28.7.69	3.0	15.0	9.50	35.0
5.8.69	6.0	5.0	10.0	32.0
9.8.69	6.0	20.0	10.0	33.0
11.8.69	8.0	--	8.0	33.0
13.8.69	7.0	--	10.0	27.0
15.8.69	6.0	25.0	10.0	29.0
20.8.69	6.0	15.0	9.5	31.0
22.8.69	9.0	10.0	10.0	32.0

APPENDIX I (Continued)

Date	Oxygen p.p.m.	Carbon dioxide p.p.m.	pH	Hardiness p.p. gallon
23.8.69	12.0	0.0	10.0	30.0
24.8.69	12.0	0.0	10.0	30.0
31.8.69	12.0	0.0	10.0	32.0
25.2.70	Undetected	24.0	8.5	--
24.5.70	4.0	40.0	9.0	29.0
25.5.70	3.0	40.0	9.0	31.0
26.5.70	4.0	40.0	9.0	31.0
27.5.70	8.0	30.0	9.0	30.0
3.6.70	8.0	50.0	9.0	34.0
4.6.70	6.0	45.0	9.0	36.0
10.6.70	7.0	40.0	9.0	36.0
11.6.70	7.0	40.0	9.0	38.0
15.6.70	5.0	50.0	9.0	36.0
16.6.70	4.0	55.0	9.0	37.0
17.6.70	5.0	55.0	9.0	38.0
18.6.70	4.0	45.0	9.0	38.0
19.6.70	5.0	50.0	9.0	37.0
20.6.70	5.0	50.0	9.0	34.0
22.6.70	5.0	50.0	9.0	33.0
23.6.70	4.0	45.0	9.0	37.0
24.6.70	3.0	45.0	9.0	36.0
25.6.70	5.0	49.0	9.0	38.0

APPENDIX I (Continued)

Date	Oxygen p.p.m.	Carbon dioxide p.p.m.	pH	Hardiness p.p. gallon
1.7.70	4.0	20.0	9.50	--
2.7.70	5.0	25.0	9.25	--
3.7.70	6.0	20.0	9.25	--
6.7.70	10.0	20.0	9.25	--
7.7.70	9.0	20.0	9.25	--
8.7.70	6.0	20.0	9.25	--
9.7.70	4.0	25.0	9.25	--
10.7.70	4.0	25.0	9.25	--
15.7.70	2.0	40.0	9.25	31.0
19.7.70	4.0	30.0	9.0	33.0
20.7.70	4.0	30.0	9.0	28.0
21.7.70	3.0	35.0	9.0	30.0
22.7.70	3.0	30.0	9.0	31.0
23.7.70	3.0	35.0	9.25	30.0
27.7.70	6.0	25.0	9.25	31.0
28.7.70	4.0	30.0	9.0	31.0
29.7.70	5.0	20.0	9.25	33.0
30.7.70	5.0	20.0	9.25	34.0
3.8.70	4.0	25.0	9.25	32.0
4.8.70	5.0	20.0	9.25	33.0
5.8.70	7.0	15.0	9.25	33.0
6.8.70	7.0	15.0	9.25	34.0

APPENDIX I (Continued)

Date	Oxygen p.p.m.	Carbon dioxide p.p.m.	pH	Hardiness p.p. gallon
7.8.70	7.0	10.0	9.25	35.0
12.8.70	3.0	10.0	9.25	33.0
13.8.70	4.0	5.0	9.25	33.0
14.8.70	3.0	5.0	9.25	35.0
19.8.70	4.0	5.0	9.50	35.0
20.8.70	5.0	10.0	9.25	36.0
21.8.70	5.0	0.0	9.75	33.0
26.8.70	6.0	0.0	9.75	34.0
27.8.70	4.0	0.0	9.75	33.0
28.8.70	6.0	0.0	9.75	34.0

APPENDIX II

Definitions used in the Jolly (1965) estimator.

1 = Number of samples.

N_i = Total number in the population when the ith sample is captured in time i.

n_i = Number captured in the ith sample.

M_i = Total number of marked animals in the population at time i.

m_i = Number of marked animals in ith sample.

s_i = Number released from the ith sample after marking.

ϕ_i = Probability that an animal alive at the moment of release of the ith sample will survive till the time of capture of the i + 1th sampling (emigration and death being synomous). The period of captivity is assumed very short compared with the interval between successive samplings.

B_i = Number of new animals joining the population in the interval between the i and i + 1th samples and alive at time i + 1. B_o is defined equal to N_1.

p_i = Probability of an animal alive at time i being caught in the ith sample.

α_i = Sampling fraction that is, the fraction of marked in the sample captured.

n_{ij} = The number in the ith sample last captured in the

jth sample $(1 \leq j \leq i - 1)$.

N_{ij} = Total number in the population at time i last captured in the jth sample $(1 \leq j \leq i - 1)$.

a_{ij} = Number in the ith sample last caught in the jth sample or before which is equal $\sum\limits_{k=1}^{j} n_{ik}$.

Z_i = $\sum\limits_{k=i}^{L} a_{k,i-1}$ = The number marked before time i which are not caught in the ith sample but are caught subsequently.

R_i = $\sum\limits_{k=i+1}^{L} n_{ki}$ = The number of the s_i animals released from the ith sample that are caught subsequently.

The formulaes for the above used in the present study estimates.

$\hat{\alpha}_i$ = $\hat{M}_i/\hat{N}_i = m_i/n_i$ (i = 2,3,...,L) (Formula 17 in Jolly, 1965)

$\hat{M}_i$ = $\dfrac{s_i Z_i}{R_i} + m_i$ (i = 2,3,...L-1). (Formula 22).

$\hat{N}_i$ = $\hat{M}/\hat{\alpha}_i$ (i = 2,3,...L-1). (Formula 23).

$\hat{\phi}_i$ = $\dfrac{\hat{M}_{i+1}}{M_i - m_i + s_i}$ (i = 1,2,...L-2). (Formula 24).

$\hat{B}_i$ = $\hat{N}_{i+1} - \hat{\phi}(\hat{N}_i - n_i + s_i)$ (i = 2,3,...L-2) (Formula 25).

Variances equations used for present study estimates.

$$V(\hat{\phi}_i) = \hat{\phi}_i^{\,2} \quad \frac{(\hat{M}_{i+1} - m_{i+1})(\hat{M}_{i+1} - m_{i+1} + s_{i+1})}{\hat{M}_{i+1}^{\,2}} \quad (\frac{1}{R_{i+1}} - \frac{1}{s_{i+1}})$$

$$+ \frac{\hat{M}_i - m_i}{\hat{M}_i - m_i + s_i} \quad (\frac{1}{R_i} - \frac{1}{s_i}) + \frac{1 - \hat{\phi}_i}{\hat{M}_{i+1}} \qquad \text{(Formula 27)}.$$

$$V(\hat{N}_i/N_i) = \hat{N}_i(\hat{N}_i - n_i) \left\{ \frac{\hat{M}_i - m_i + s_i}{\hat{M}_i} \quad (\frac{1}{R_i} - \frac{1}{s_i}) + \frac{1 - \alpha_i}{m_i} \right\},$$

$$\text{(Formula 28)}.$$

APPENDIX III. The entries in each row are cumulative recaptures, resulting from the summation of rows in Table 6, to give m_i on the diagnal, and Z_{i+1} is total recaptures in samples subsequent to the one following marking.

	n_i	s_i	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
1	265	265	I													
2	146	133	13	II												
3	101	91	5	10	III											
4	693	470	3	6	11	IV										
5	530	479	2	2	2	27	V									
6	1340	1020	0	0	1	2	4	VI								
7	94	94	0	0	0	0	0	15	VII							
8	290	269	0	0	0	4	4	29	41	VIII						
9	156	147	0	0	0	1	1	4	9	32	IX					
10	177	170	2	2	2	2	3	5	7	17	45	X				
11	276	261	0	0	0	0	0	2	3	8	13	30	XI			
12	611	518	0	0	0	0	0	0	0	0	0	1	7	XII		
13	786	722	0	0	0	0	0	0	0	0	0	0	9	53	XIII	
14	875	850	0	0	0	0	0	0	0	0	0	0	8	35	123	XIV
15	462	0	0	0	0	0	0	0	0	0	0	0	2	10	29	61
Total recaptures subsequent to the one following marking, Z_{i+1}			12	10	5	9	8	40	19	25	13	1	19	45	29	--

APPENDIX IV. The F-test for regression line slopes and the
coefficients of correlation r, for length-
weight relationships for separate age groups
in each sample, * indicates significancy at
1% level and ** indicates significancy at 5%
level, S.S. is sums of square, d.f. is degrees
of freedom and M.S. is mean square.

Date		Error d.f.	Regression S.S. 1 d.f.	Residual M.S.	F-value	r
16-18.5.69	S	26	0.2397	0.0020	119.85**	0.9042**
21.5.69	S	26	0.9869	0.0025	397.93**	0.9688**
10.6.69	S	16	0.1153	0.0030	37.94**	0.8377**
2.7.69	A	7	0.0329	0.0044	7.76*	0.7193*
2.7.69	Y	17	3.1576	0.0025	1263.04**	0.9934**
11-20.8.69	A	12	0.1122	0.0019	58.12**	0.9104**
11-20.8.69	Y	23	2.0628	0.0008	2546.63**	0.9956**
1-5 .9.69	A	7	0.0285	0.0007	43.18**	0.9277**
1-5 .9.69	Y	25	1.6824	0.0007	2438.29**	0.9948**
18-22.5.70	S	30	2.7480	0.0016	1570.27**	0.7393**
1-2 .6.70	S	22	0.9853	0.0013	788.22**	0.9906**
11-12.6.70	S	26	0.9140	0.0002	4154.5 **	0.9859**
22-24.6.70	A	20	0.4109	0.0015	277.64**	0.9968**
22-24.6.70	Y	5	0.2902	0.0005	630.83**	0.9651**
2-4 .7.70	A	24	0.8026	0.0005	1744.72**	0.9960**
2-4 .7.70	Y	11	0.9629	0.0025	383.62**	0.9930**
15-17.7.70	A	19	0.4122	0.0006	675.66**	0.9860**
15-17.7.70	Y	15	0.0165	0.0011	15.01**	0.9867**
31.7-2.8.70	S	32	5.4315	0.0015	3745.83**	0.9809**

APPENDIX IV (Continued)

Date		Error d.f.	Regression S.S. 1 d.f.	Residual M.S.	F-value	r
31.7-2.8.70	A	2	0.0197	0.0003	75.92**	0.9955**
31.7-2.8.70	Y	28	4.0229	0.0017	2366.44**	0.9942**
15-17.8.70	S	31	4.1692	0.0013	3134.71**	0.9951**
29-30.8.70	S	37	6.5147	0.0006	11429.25**	0.9980**
29.9.70	S	31	3.0968	0.0007	4361.68**	0.9965**