THE RESPONSES OF A LAKE WHITEFISH (Coregonus clupeaformis) POPULATION TO WHOLE-LAKE FERTILIZATION by


KENNETH HAROLD MILLS

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

## DOCTOR OF PHILOSOPHY

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The responses of an unexploited population of lake whitefish (Coregonus clupeaformis) to increased loadings of phosphorus, nitrogen and carbon were evaluated for four years of fertilization in L226 NE (Lake 226, the northeast basin), the Experimental Lakes Area, Northwestern Ontario. A vinyl sea curtain separated L226 NE from L226 SW (the southwest basin), which received similar additions of nitrogen and carbon over the same time period. In general, L226 NE responded with increased algal and benthic productivity over that in L226 SW though differences between basins were minimal the first year of fertilization. Limnological conditions in L226 SW remained similar to those prior to lake division and fertilization.

Lake whitefish in L226 NE responded with greater growth, higher coefficients of condition, increased recruitment and total elaboration of fish tissue (production) than in L226 SW during the second through the fourth years of fertilization. No response was evident the first year of fertilization. No differences between basins were detected in annual survival for fish $\geq$ age $1^{+}$but greater recruitment in L226 NE was caused by differences in survival under age $1^{+}$. Fecundity of female whitefish may have been greater in L226 NE than SW the second and third years of fertilization, though no differences in fecundity to length ratios were detected in the fourth year. Whitefish production in L226 NE was generally twice that in L226 SW the second through fourth years of fertilization. While differences in growth between basins were a signficant factor in production
differences the second and the third years of fertilization, the greater abundance of whitefish in L226 NE was the primary cause in the fourth year. No major differences in whitefish diet were detected between basins, but increased abundance of dipteran larvae in L226 NE made whitefish production differences possible. Whitefish production and biomass in $L 226$ NE probably had not reached a new equilibrium level by the fourth year of fertilization. Significant year-to-year variations in whitefish production were also present.

The fin-ray method of age determination was used extensively in this study to estimate whitefish growth. A method of backcalculating fish lengths at age was developed using pelvic fin-ray sections. Extensive tests of this method's validity are presented. The implications of errors in aging using whitefish scales are discussed with emphasis on catch-curve survival rates and growth curves.

The Jolly-Seber multiple mark-recapture method was used to estimate whitefish abundances and survival. Extensive tests of the assumptions of the Jolly-Seber method are presented and evaluated for the L226 NE and SW populations. Methods for minimizing the bias introduced in estimates caused by significant tag loss are presented and applied to the L226 NE whitefish data.

The mechanisms used by L226 NE whitefish to respond to increased nutrient inputs were similar to those used by unexploited whitefish populations when first exploited. These mechanisms were also discussed in relation to present theories of lake whitefish population structure and regulation.

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INTRODUCTION

Attempts to increase the fish productivity of natural waters have been a recurring topic of research through the development of fishery biology. An abundant literature base has developed for pond fertilization in both Europe and North America (as reviewed by Vinberg and Lyakhnovich 1969; Neess 1946; Marcioleck 1954; Swingle and Smith 1939; Hasler and Einsele 1948). Intentional fertilization studies of small lakes commenced with Juday et al. (1938), Ball (1948), Langford (1948), Ball and Tanner (1951), Frost and Smyly (1952), Weatherley and Nichols (1955), Smith (1955) and Nelson (1959). Both small lake fertilization and pond experiments have concentrated on responses of stocked populations of relatively young (age $0^{+}$to $2^{+}$), sexually immature fish. In most cases, after one season of nutrient addition, fish populations were harvested and the studies terminated.

More recently, interest in cultural eutrophication has spurred renewed study of the effects of nutrient addition on natural fish populations (Nakashima and Leggett 1975; Colby et a1. 1972; Larkin and Northcote 1969; Lebrasseur et al. 1978). In many cases the mechanisms which these fish populations used to respond to increased nutrient inputs have been confounded with simultaneous perturbations such as commercial exploitation (Nümann 1972; LeCren et a1. 1972), species addition (Grimás et a1. 1972; Maitland 1972; Northcote 1972), or both (Berst and Spangler 1972; Wells and McLain 1972; Hartman and Burgner 1972; and others). Other studies have concentrated on increased production of salmon smolts (Barraclough and Robinson 1972; Hartman and Burgner 1972; Lebrasseur et al. 1978), or commenced after nutrient addition had progressed for many
years (Nakashima and Leggett 1975) when fish populations had apparently reached new equilibrium levels. Little is known of the sequence of responses of an indigenous northern fish population, composed of a large proportion of older, sexually mature individuals (as described by Johnson 1976; Power 1978; Healey 1980) to nutrient addition. As the development of the Canadian North accelerates, responses of these populations will become increasingly important. The purpose of this study was to evaluate changes in an unexploited population of lake whitefish (Coregonus clupeaformis) to increased nutrient addition.

While early studies agreed qualitatively that greater productivity at lower trophic levels leads to higher fish yields (Hasler and Einsele 1948; Ball and Tanner 1951; Weatherley and Nichols 1955), more precise quantification between trophic levels has occurred more recently (McConnell 1963, 1965; Hall et al. 1970; Goodyear et al. 1972; Sreenivason 1964; Hepher 1962; Hrbâcéek 1969; Wolny and Grygierek 1972; Melack 1976; Davies 1980). A secondary goal of this study was to compare primary production and benthic emergence to fish production.

It is difficult to establish adequate control data for whole lake manipulations (Carlander 1966; Hasler and Einsele 1943). One common approach has been to monitor a lake for a year or more and use these data as a baseline to interpret changes in the same lake in subsequent years during and after manipulation (Loftus and Regier 1972; Nakashima and Leggett 1975). A second approach has been to monitor a nearby lake as a control (Ball 1948; Ball and Tanner 1951; Smith 1955). Each technique has shortcomings. An assumption of the first method is that underlying lake productivity does not significantly change from year to year, which is often questionable. For example, Fee (1980) found that
the coefficient of variation for primary production in most ELA lakes was $20 \%$ over a four year study period. Davies (1980) found that dipteran emergence varied substantially between years for individual ELA lakes. The problem with this first method is to show that the response to the manipulation is beyond the natural variation of the lake from year to year. The problems of the second approach are (1) that it is hard to find two exactly identical lakes where fish species composition and age structure are similar, and (2) that the productivity can vary between nearby lakes for the same year (Fee 1979, 1980; Davies 1980). Healey $(1978,1980)$ has used a combination of the above methods in lake whitefish cropping. The above problems can be minimized if double basin lakes are available. For example, Johnson and Hasler (1954) divided a small, two basin dystrophic lake with an earthen wall prior to liming one basin. This technqiue offers advantages over the above other methods: (1) individuals with similar genetic and growth histories are present in both the experimental and control basins, (2) the same species are present in both basins, and (3) the control basin can be used to estimate baseline production for each year of manipulation in the other basin. The lake division technique was used in this study.

I selected six major population parameters to monitor through the study: individual fish growth (length and condition), population size, annual survival rates, fecundity, recruitment and production.

In a nutrient addition study, the carrying capacity, or maximum biomass, of a system is elevated and the fish production should theoretically increase to reach a new carrying capacity for the system. Any of the above parameters can change to accomplish this increase, but rarely have all changed concurrently in previous studies. In some
studies, increased individual growth of juvenile fish was the prime response mechanism to fertilization (Haines 1973; Smith 1955; Ball 1948; Weatherley and Nichols 1955; and others), while survival rates were relatively unchanged. In others (Nelson and Edmondson 1955; Hartman and Burgner 1972; Lebrasseur et al. 1978), increased annual survival was the major response mechanism. Responses of individual fecundity to food availability, and hence nutrient status, have also been documented (Scott 1962; Bagenal 1969; Wootton 1977). Hall et al. (1970) found that recruitment of bluegill sunfish (Lepomis macrochirus) in ponds was correlated with nutrient status. After an initial biomass increase, the new carrying capacity is theoretically sustained each year by fish production which compensates for biomass loss due to natural mortality. This new carrying capacity may be sustained by a different combination of parameters than the initial biomass increase. For example, Hall et al. (1970) and McConnell (1965) showed that growth was the initial parameter used by fish to increase biomass at higher nutrient levels, but that biomass was maintained by adjusting population numbers in later years.

Study site

Lake 226 (hereafter referred to as L226) is a small, double basin lake located in the Experimental Lakes Area, Northwestern Ontario (Cleugh and Hauser 1971). The inflow and outflow of the lake are small and flow intermittently during the summer months. In early June 1973 a sea curtain of vinyl reinforced with nylon ( 60 by 6 m ) was installed to separate the basins (NE and SW, Fig. 1). The wall was securely sealed to the lake sides and bottom with large rocks. Commencing after wall installation in 1973 and continuing through 1980, phosphorus (0.34 $\mathrm{g} \mathrm{m}^{-2} \mathrm{yr}^{-1}$ ), nitrogen ( $1.81 \mathrm{~g} \mathrm{~m}^{-2} \mathrm{yr}^{-1}$ ) and carbon ( $3.46 \mathrm{~g} \mathrm{~m}^{-2} \mathrm{yr}^{-1}$ ) were added in weekly increments during the ice-free season to the NE basin. Nitrogen ( $1.93 \mathrm{~g} \mathrm{~m}^{-2} \mathrm{yr}^{-1}$ ) and carbon ( $3.69 \mathrm{~g} \mathrm{~m}^{-2} \mathrm{yr}^{-1}$ ) were added to the SW basin. Further details of the experiment are well documented elsewhere (Schindler 1974; Schindler and Fee 1974; Davies 1980; Fee 1980). In general, the basin enriched with PNC (L226 NE) developed blue-green algal blooms each year (Findlay and Kling 1975; Findlay 1978) which did not occur prior to enrichment or in the basin receiving only NC (L226 SW). Primary production (Fee 1980), dipteran emergence (Davies 1980) and zooplankton biomass (D.F. Malley, personal communication) have generally been higher in L226 NE than SW through all years of fertilization.

The fish species present in L226 are lake whitefish (Coregonus clupeaformis), pearl dace (Semotilus margarita), finescale dace (Chrosomus neogaeus), redbelly dace (Chrosomus eos), fathead minnow

Figure 1. Bathymetric of L226, based on data collected by I. J. Davies, G. B. Ayles and K. H. Mills.

(Pimephales promelas), and slimy sculpin (Cottus cognatus).

Field sampling procedures

Lake whitefish were collected from L226 from September 1973 to late October 1977 during the ice-free seasons. Fish were collected initially using small mesh ( 9.5 mm ) deepwater trapnets (Beamish 1973), alternating nets between basins at approximately two to three week intervals from September 1973 to September 1975. In 1976 and 1977 nets were fished for this study only in spring and fall. Trapnets were set on gradually sloping areas of the lake bottom with the net pots usually between three and seven meters deep. Since trapnet catch-per-unit effort continually decreased over the course of the study from 21.7 fish per 24 hr set in 1973 to 1.52 in 1977, trapnet catches were supplemented during spring and fall with fish caught using multifilament "experimental" gillnets (connected stretched mesh panels of $11,25,30,33$, 38 and 45 mm ) starting in late September 1975. To minimize mortality from gillnetting, nets were emptied approximately every 15 minutes. Diel gillnetting in September 1975 showed that catches were highest at dusk: all subsequent gillnetting was concentrated during this period. All gillnetted fish were held overnight in pens before sampling to assess short-term gillnetting mortality, which was less than $6 \%$ of the total number of fish caught. Whitefish from trapnet catches were held overnight on four occasions in September 1973 to assess trapnet mortality, which was less than $1 \%$. Since trapnet mortality was so low, fish were subsequently returned to the lake immediately after sampling.

Each whitefish caught was anesthetized with MS-222 (tricaine-methane-sulfonate), weighed to the nearest gram, measured to the nearest mm and sexed if possible. Two tag types were used in L226 NE for marking whitefish, while only one type was used in L226 SW. In September 1973, the first 161 whitefish larger than 220 mm (age $2^{+}$and older) caught in the NE basin were tagged with gun tags (Dell 1968). Modified Carlin tags (White and Beamish 1973) were used subsequently for all tagging in both basins. In May 1975 the minimal length for tagging was raised to 260 mm (age $3^{+}$), because comparisons of length at age between tagged and untagged fish of 220 to 260 mm from fall 1973 to fall 1974 suggested that growth of tagged fish under age 3 was significantly less than that of untagged fish (unpaired $t$ test, $P<0.01$ ). Larger, older fish showed no significant retardation of growth during the same period ( $t$ tests).

All captured fish were partially fin-clipped (2-3 rays) for later aging (Appendix F, Mills and Beamish 1980). Partial clipping of various fins in a systematic fashion according to sampling period was also used for batch marking fish smaller than 260 mm (age $0^{+}$to $2^{+}$) in 1974 to 1977, and fish less than 220 mm (age $0^{+}$and $1^{+}$) in 1973. Partial fin-clipping caused no significant growth retardation (t tests), and rays were easily distinguishable if regenerated.

Lake whitefish larger than 300 mm trapnetted from May 1974 to October 1975 had their stomachs pumped (Seaburg 1957) to identify seasonal changes in diet. To minimize the effects of food scavenged from trapnet floors, only the stomachs of whitefish caught after single night sets were pumped. Fish removed from the nets after sets of two or more nights were not stomach pumped. Trapnets
were usually emptied and whitefish sampled in midmorning (0900-1030 hrs) because a larger quantity and volume of stomach contents was obtained from fish removed from nets in the morning as opposed to the afternoon (1530-1730 hrs).

During the July 1974 sampling period in L226 SW, it became obvious that some whitefish were not recovering adequately prior to release after the sampling procedure (this important problem is addressed in greater detail in Appendix D). The epilimnetic temperature was near $23^{\circ} \mathrm{C}$ at this time, and fish were held and sampled in water at this temperature before release. Commencing during the following sampling period, ice was hauled to the lake to lower water temperatures used for holding and sampling fish whenever epilimnetic temperatures were $12^{\circ} \mathrm{C}$ or greater. This technique was successful (Appendix D).

Age determinations

Age determinations for lake whitefish have usually been made using scales (Healey 1975, 1980; Carlander 1969). Mills and Beamish (1980, Appendix G) have shown that fin-ray ages are superior both in accuracy (describing the true age) and precision (repeatability from one reader to another) to analogous scale ages for L226 whitefish. The fin-ray method of age determination using pelvic and pectoral rays was used in this study. An accurate method of age determination was essential for stratifying a population into age classes to distinguish growth, survival and production differences between basins and years in L226, especially when a large proportion of the population present at the start of the study in each basin was older than $7^{+}$(Fig. 2).

Figure 2. Lake whitefish age frequency distributions for the fall 1973 trapnet catches in L226 according to fin-ray and scale ages. The portion of the catch $\geq$ age $7^{+}$is indicated in the hatched area of each distribution.


Approximately $25 \%$ of the fish captured in L226 NE were older than $7^{+}$ in the 1973 fall sample according to fin-ray ages, while only $1 \%$ were $7^{+}$or older according to scale ages. The comparison was even more extreme for $\mathrm{L} 226 \mathrm{SE} ; 66 \%$ of the fall sample aged older than $7^{+}$using fin-ray sections and only $6 \%$ using scales.

Growth

Yearly growth in length of L226 whitefish was estimated between successive fall sampling periods (September-October). The total number of whitefish caught during each fall sampling period, while large compared to other yearly samples, was usually insufficient to derive relatively precise growth curves from mean length at age data because over 15 age groups were present in each L226 basin. Usually back-calculated lengths at age have been used to meet this problem in the past (Bagenal and Tesch 1978; Everhart et al. 1975; Weatherley 1972). I developed and tested a method for back-calculating whitefish fork-lengths for ages prior to capture using pelvic fin-ray sections (Appendix E). This method was restricted to calculating lengths at annulus formation for fish age $1^{+}$or older, because the initial point where growth initiated in a fin-ray section (called a "focus" on scales (Bagenal and Tesch 1978)), was not distinct. In addition, back calculations were not possible for fish whose pelvic fins had been partially clipped by fall 1974 or 1975 as part of the age validation procedure (Appendix G). For these reasons, yearly whitefish growth was estimated by one of two methods according to fish age at capture.

Growth of whitefish to age $0^{+}$and $1^{+}$from 1973 to 1976 was
estimated from mean length at age data collected during fall sampling. Whitefish growth from hatching (spring) to age $0^{+}$(the following fall) was estimated as the average fork Tength of this age group observed at fall sampling. Fish of the age $0^{+}$age class were caught in relatively large numbers for only the 1973 and 1976 year classes in L226. Fish from the 1974 and 1975 year classes were rarely caught during any sampling period. While a relatively large young-of-the-year (age $0^{+}$) sample was caught in L226 SW during 1973 fall sampling, these fish were released immediately after capture, without recording individual fork lengths, as part of the age validation study. Because the 1974 and 1975 year classes were virtually absent from both $L 226$ basins, and no lengths were recorded for the 1973 year class in L226 SW, growth to age $0^{+}$was only possible for the L226 NE year classes in 1973 and 1976, and for the L226 SW year class in 1976. Whitefish growth from age $0^{+}$ to age $1^{+}$could only be estimated for the L226 NE 1973 year class, because no average length at $0^{+}$was available for the analagous L226 SW fish. Therefore, average lengths at age $1^{+}$were used to compare growth of the 1973 year class between basins, ignoring lengths at age $0^{+}$.

Growth of fish older than age $1^{+}$was estimated by a combination of two methods from 1971 to 1976. Fin-ray sections from the upper portion of the first pelvic ray were used to back-calculate lengths for each different fish caught from fall 1973 to fall 1976, using a modified direct proportionality formula (Tesch 1971; Bagenal and Tesch 1978). Rays from two fins were available for these calculations from many fish, since one was removed at initial marking and the other at recapture one or more years later. Only the fin-rays taken at recapture
were used for these for back-calculations. Back-calculated lengths could then also be compared to actual fork-lengths observed at prior fall sampling as a test of the back-calculation technique's ability to predict previous lengths for individual fish. No significant differences were detected between back-calculated lengths and those observed for the same fish during previous fall sampling ( $t$ test, $P>0.3, n=$ 171). The average error between back calculated lengths and actual observed lengths was $\simeq 8.8 \mathrm{~mm}$ (see Appendix E for a more detailed discussion of the method and tests of its reliability). Growth from one fall to the following fall was calculated as the difference between back-calculated lengths at age for individual fish.

By fall 1974 and 1975, many fish had the leading ray from both pelvic fins removed. Back-calculated lengths were not possible if one of these fish was caught the following fall. Growth was estimated for these fish as the difference between lengths observed from one fall sampling to the following fall. These data were an important source of growth information (56 observations for 1975 and 105 for 1976) because many individuals had both pelvic fins partially removed prior to fall 1976.

One-way analysis of covariance (Snedecor and Cochran 1967; Dixon and Massey 1969) was used to compare whitefish growth between basins for fish older than $1^{+}$. The independent variable was fork length at the beginning of a growth period (fall), and the dependent variable was growth until the following fall. A log transformation of growth linearized the relationship between the variables. The assumption of equality of regression slopes (Steel and Torrie 1960; Dixon and Massey 1969), a critical requirement for covariance analyses was tested and no
significant differences were detected when growth between basins for the same year was compared. This assumption was violated for comparisons between years, so no analyses were conducted for these comparisons. Growth to age $0^{+}$and age $1^{+}$was compared between basins and years using unpaired $t$ tests.

Condition

Condition factors ( $k$ ) were calculated for each fish caught during the course of the study according to the formula:

$$
k=\frac{100 \mathrm{w}}{1^{b}}
$$

where: $w=$ weight in grams
$1=$ fork length in mm
 derived using Ricker's GM functional regression over all L226 whitefish data collected during this study ( $n=1559$ ) (Ricker 1973) Whitefish growth in L226 was allometric, and the slope of the lengthweight relationship was significantly different from $b=3$ ( $t$ test, $P<0.01$ ). While Marciak (1975) has shown condition differences for length classes of bream (Abromis broma) under conditions of increased nutrient inputs, scatter plots of $k$ on length for whitefish from individual sampling periods showed no relationship between a whitefish's length and its condition. Therefore, an average condition factor was calculated for each sampling period and after testing for homogeneity of variance (Bartlett's test, $P>0.42$ ), $t$ tests were used to compare
average condition between basins and between sampling periods (Steel and Torrie 1960). Average condition factors were also calculated for male and female whitefish for sampling periods in the falls of 1975 and 1976. Sample sizes in 1974 for L226 NE were inadequate for comparisons but sufficient numbers were caught in L226 SW.

A potential source of bias in condition estimates can occur when the average condition of fish captured with trapnets is compared to the condition of fish captured in trapnets and gillnets. The tendency for gillnets to select fish of the greatest girth, and therefore condition, among an individual length class is well known (Hamley 1975; Weatherley 1972). This bias is most pronounced when fish are caught by wedging in gillnet mesh (Hamley 1975). Most whitefish in L226 were caught in gillnets by tangling rather than by wedging which greatly reduced this bias. A simple test of gillnet bias in condition estimates was available by comparing average condition of whitefish caught in gillnets during fall sampling in 1975 and 1976 with that of fish caught concurrently in trapnets in the same basin. No significant differences were detected (t tests). Gillnet bias was not a recognizable systematic error in condition estimates.

## Abundance estimates

Throughout this study I have used Jolly's (1965) mark-recapture notation whenever possible. Cormack (1968) provides a table for converting this notation to that of other authors.

Jolly-Seber multiple mark-recapture models (Jolly 1965; Seber
1965) were used to estimate population sizes $\left(\hat{N}_{j}\right)$ for L226 NE and SW
whitefish from fall 1973 to fall 1976 using POPAN, a data maintenance and analysis package for mark-recapture experiments (Arnason and Baniuk 1978). Mark-recapture data for each basin were stratified so that the death-only model could be used on each stratum. This results in more efficient analyses, as judged by smaller standard errors of the estimates, than when data only satisfy the open model, which also allows recruitment (births or new immigrants) entering the population (Arnason and Mills 1980). The whitefish population in each basin was divided into two strata based on fish age determined from fin-ray sections: (1) year classes 1950 to 1972 - all fish age $1^{+}$and older when the study commenced, and (2) the 1973 year class in L226 NE. Age $0^{+}$fish were excluded from all analyses; therefore the first estimate for stratum two fish was in the fall 1974, at age $1^{+}$. Neither the 1973 L226SW, 1974 L226 NE and SW, or the 1975 L226 NE and SW year classes were caught in large enough numbers for analyses similar to that for the 1973 year class in L226 NE.

The particular model, death-only or full, used to form estimates was chosen after data were analyzed to detect violations of the four assumptions underlying these models (Seber 1973). The assumptions, methods used to detect violations of each assumption, and results are summarized in Table 1. A more thorough discussion of each can be found in Appendices A-D. Since methods used to test these assumptions require that each individual fish be tagged with a unique number, analyses were conducted only on the first whitefish stratum in each basin. Two assumption violations were detected: (1) significant tag loss ( $\simeq 18 \% \mathrm{yr}^{-1}$ ) occurred among L226 NE whitefish tagged with gun tags, and (2) heterogeneity of survival was detected among whitefish from

| Assumption | Category | Methods | Results |  |
| :---: | :---: | :---: | :---: | :---: |
|  |  |  | L226 NE | L226 SW |
| Closure <br> (Appendix A) | No emigration |  | - | - |
|  | No immigration |  | - | - |
|  | No recruitment |  | - | - |
| Tag loss (Appendix B) | Gun tags | Appendix ${ }_{\text {" }}$ | * | n/a |
|  | Sew-on tags |  | - | n/a |
| Equal catchability (Appendix C) | Individual samples | Pollock 1965 Carothers 1971 | - |  |
|  | Among all samples |  | - | - |
| Equal survival (Appendix D) | Handling | After Robson 1969 | * | * |
|  | Capture method |  | - | - |
|  | Tagging | , | * | - |
|  | Recapture history | " | - | - |
|  | Age | " | - | - |
|  | Length | " | - | - |
|  | Sex | " | - | - |

two samples in each basin during 1974 (May and June in L226 NE, June and July in L226 SW). Sampling periods where heterogeneous survival existed were omitted from the mark-recapture analyses (the rationale for this is discussed in Appendix D). Results and implications of tag loss are discussed in detail in Arnason and Mills (1980) and Appendix B. Because two tag types were used in L226 NE, each lost at a different rate ( $\simeq 18 \%$ for gun tags and $\simeq 2 \%$ for sew-on tags), heterogeneity of tag loss occurred for the combined data of both tag types. Full model estimates of $\hat{N}_{i}$ are very robust to tag loss and heterogeneity of tag loss when this model is applied to data that satisfy the death-only model (Appendix B, Arnason and Mills 1980). Therefore, full model $\hat{N}_{i}$ will be used for L226 NE stratum one fish and death-only $\hat{N}_{j}$ will be used for L226 SW stratum one and L226 NE stratum two fish.

Arnason and Mills (1980) have devised an alternative method to obtain $\hat{N}_{\mathrm{i}}$ for L226 NE stratum one fish using a combination of deathonly and open model estimates. This method will not be used in this study because estimates cannot be formed for samples between fall sampling periods. Sample sizes of gun-tagged fish were too small to be useful in these intermediate samples, and the method is only applicable to equally spaced samples.

Two modifications of the Jolly-Seber formulae were used prior to any analyses. These were necessary because the variance formulae for the Jolly-Seber estimates are asymptotic - only true when sample sizes $\left(\hat{N}_{j}\right)$ are large and recaptured animals ( $R_{j}$ ) numerous. Manly (1971) has shown that Jolly-Seber $\hat{N}_{i}$ are subject to small sample bias, which leads to erratic and often negatively biased $\hat{N}_{i}$. He has also shown that when sample sizes are small and recaptures few, the upper
confidence interval as estimated by $\hat{N}_{i}+2 \times \operatorname{SE}\left(\hat{N}_{i}\right)$ (Jolly 1965) is an underestimate of the true interval.

The small sample bias in $\hat{N}_{i}$ is well known for other mark-recapture models (Seber 1973) and Jolly-Seber formulae to calculate $\hat{N}_{i}$ were corrected for this bias as described by Seber (1973). This consists of adding one to the number of animals recaptured from any sampling period $\left(R_{j}\right)$ and adding one to the number of animals released from any sample ( $s_{i}$ ), wherever each quantity appears in estimate formulae. As $\mathrm{R}_{\mathrm{i}}$ and $\mathrm{s}_{\mathbf{j}}$ become large, the correction becomes progressively smaller.

The method I chose to adjust the upper confidence interval was the inverse transformation as suggested by Cormack (1968). Otis et a1. (1978) report that this transformation may not completely remove the bias, but others (Arnason and Baniuk 1978) and my own experience indicate that this or other transformations may be valuable. An obvious value of the transformation is to identify those estimates with small sample sizes; the upper confidence interval is greatly expanded. This transformation leaves the lower interval relatively unchanged. The technique is to first derive the confidence interval as:

$$
\begin{aligned}
& 1 / \hat{N}_{i}-1.96 \times S \hat{E}\left(1 / \hat{N}_{i}\right) \text { and } \\
& 1 / \hat{N}_{i}+1.96 \times S \hat{E}\left(1 / \hat{N}_{i}\right)
\end{aligned}
$$

$$
\text { where } \operatorname{SE}\left(1 / \hat{N}_{i}\right)=1 / \hat{N}_{i}^{4} \times \operatorname{Var}\left(\hat{N}_{i}\right)
$$

The formula for $\operatorname{SE}\left(1 / \hat{N}_{i}\right)$ was derived using Seber's (1973) delta method (A. N. Arnason, University of Manitoba, personal communication). The second step is to obtain the final intervals, the inverse of the above interval by back transforming the estimates.

$$
\begin{aligned}
\text { lower interval } & =1 /\left(1 / \hat{N}_{i}+1.96 \times \operatorname{SE}\left(1 / \hat{N}_{i}\right)\right) \\
\text { upper interval } & =1 /\left(1 / \hat{N}_{i}-1.96 \times \operatorname{SE}\left(1 / \hat{N}_{i}\right)\right)
\end{aligned}
$$

While $\hat{N}_{1}$ (September-October 1973) is not available from the full model for L226 NE stratum one whitefish, it can be formed in this particular case from the sum of $\hat{N}_{1 s}$ (formed from capture histories of fish tagged with sew-on tags using the death-only model) with $\mathrm{N}_{1 \mathrm{~g}}$ (the known number of fish tagged with gun tags captured at time one). This is possible because the tag loss rates for sew-on tags, $\approx 2 \% \mathrm{yr}^{-1}$ in L226 NE and $\simeq 1 \% \mathrm{yr}^{-1}$ in L226 SW do not bias $N_{i}$ detectably. Therefore:

$$
\begin{aligned}
\hat{N}_{1} & =\hat{N}_{1 \mathrm{~s}}+N_{1 g} \\
& =518+165 \\
\operatorname{SE}\left(\hat{N}_{1}\right) & =\operatorname{SE}\left(\hat{N}_{1 \mathrm{~s}}\right) \quad \text { where } N_{1 g}=n_{1 g}
\end{aligned}
$$

Because abundance estimates based on mark-recapture methods were unavailable for the 1973 L226 SW and the 1974, 1975 year classes in both basins, trapnet catch-per-unit effort data were used to compare relative abundance of these year classes.

Annual survival rates

The Jolly-Seber death-only model was used to calculate all survival estimates $\left(\hat{\phi}_{i}\right)$ for $L 226$ whitefish. Sampling periods where survival was heterogeneous were omitted from analyses. Capture histories of guntagged fish were excluded also because tag losses may bias $\hat{\phi}_{i}$ (Arnason and Mills 1980).

Annual survival was estimated from analyses using only successive fall sampling periods, 1973 to 1977 . Intervening sampling periods were omitted. Alternative weighted analyses would be very complex and the
loss of information from animals caught in intervening samples is minimal, because most fish were caught during fall sampling periods. To test whether annual survival was a function of whitefish age or length, separate annual $\hat{\phi}_{i}$ were calculated for age groups ( $1^{+}-3^{+}$, $4^{+}-6^{+}, 7^{+}-10^{+}, 11^{+}-25^{+}$) and length groups (176-250 mm, 251-300, 301-450) from the first stratum of whitefish from each basin and for the L226 NE 1973 age class. Further subdividing the data into individual age groups or smaller length groups was not practical because of small sample sizes. Because current versions of the Jolly-Seber model do not allow for interstratum movement, all age and length data for fish captured throughout the study were converted to ages and lengths at fall 1973 using fin-ray age data and back-calculated lengths (Appendix E). These data were then blocked for separate death-only analyses as described above.

Fecundity estimates

Female whitefish from both basins were collected with gillnets in early October 1976 for fecundity estimates. Fish were killed and ovaries were preserved in Gilson's fluid (Simpson 1951; Bagenal 1967). Ovarian tissue was later decanted from the eggs, eggs were dried to a constant weight, and total counts were determined using Healey's (1975) dry weight proportionality method. Healey found the error in this method compared to total ovarian counts to be approximately $2 \%$ ( $n=13$ ) for lake whitefish from four populations. I found it to be approximately $3 \%(n=10)$ for whitefish from both $L 226$ basins. Mean egg diameters were calculated as the average of twenty-five eggs subsampled
from each fish's ovaries and measured with an ocular micrometer. An unpaired $t$ test was used to compare mean diameters between basins. A one-way analysis of covariance (Dixon and Massey 1969) was used to compare average fecundity between basins where fish fork length was the covariate. While Healey (1978) used scale age as the covariate in his fecundity analyses, most other attempts at relating age to fecundity have been unsuccessful (Bagenal 1978). A much stronger relationship existed between fecundity and fish fork length ( $r=0.923$ ) than fecundity and fish age $(r=0.357)$ for $L 226$ whitefish. Prior to covariance analysis, data were tested for homogeneity of regression slopes as described earlier and no significant differences between slopes weredetected. Both fish length and fecundity were $\log$ transformed prior to analysis.

Food analysis

Stomach contents were preserved in formalin during field sampling and sorted under a binocular microscope to taxonomic group for chironomids and chaoborids and to species for cladocerans and copepods. Stomachs were removed from fish which died after stomach pumping ( $n=7$ ) for later analysis. Examination of these stomachs showed that stomach pumping did not remove all food items, but that the relative proportions of different items which remained after pumping were very similar to the portion removed by stomach pumping.

Numerical analysis of the stomach contents was as described by Windell and Bowen (1978): (1) the average frequency of occurrence method and (2) the average percentage composition method. The
former method was used to estimate the proportion of those sampled which fed on a particular food item while the latter to estimate the average relative abundance of a food item in samples.

## Production estimates

Production (P) of lake whitefish in each L226 basin was estimated from the time of wall installation in late May 1973 to fall 1976 using the Chapman (1967) modification of the Ricker method, where $P=G B$. The instantaneous growth rate is $G$ and $B$ is the average biomass of two adjacent estimates. Annual production was estimated between successive fall sampling periods from fall 1973 to fall 1976, and from late May 1973 to fall 1973. Chapman's method was developed for estimates over short time intervals (Chapman 1967), but also applies for longer time intervals when species life spans are relatively long, survival predictable over extended periods of time and growth exponential (Chapman 1978). Whitefish from $L 226$ meet all three of these criteria. Production estimates were calculated for each of five age groups $\left(1^{+}-3^{+}\right.$, $4^{+}-6^{+}, 7^{+}-10^{+}, 11^{+}-15^{+}$, and $16^{+}-25^{+}$); further subdivision of the data into smaller age groups was not possible because mark-recapture estimates were too imprecise.

Fall population estimates to calculate biomass for each age group were obtained from the sum of (1) separate mark-recapture analyses for each age class group, and (2) proportionality estimates for stratum two fish except the 1973 year class in L226 NE, where mark-recapture estimates as described earlier were used. The $\hat{N}_{i}$ for successive fall sampling periods were obtained after plotting individual $\hat{N}_{j}$ and
$S \hat{E}\left(\hat{N}_{j}\right)$ from analyses of stratum one whitefish and smoothing estimates by eye. All estimates selected for production calculations were within one $S \hat{E}\left(\hat{N}_{i}\right)$ of mark-recapture $\hat{N}_{i}$. Contributions from stratum two whitefish to $\hat{N}_{i}$ from the 1973 year class in L226 SW and the 1974 and 1975 year classes in both basins were obtained using the proportionality methods where the number of these animals is assumed proportional to the number caught in a sample (Gerking 1962; Kelso and Ward 1972; and many others). Results of tests of equal catchibility described under methods used to test mark-recapture assumptions support this technique.

May 1973 abundance estimates for production calculations were not obtained by the methods described earlier which are based on the actual sample of fish captured at each fall sampling period. Because May 1973 was prior to the first mark-recapture period, an indirect method was used to obtain abundance estimates. The average monthly survival rate from the fall 1973 to the fall 1976 samples for both basins was applied to the fall 1973 estimates for each basin to obtain May estimates:

$$
\hat{N}_{\text {May }}=\frac{\hat{N}_{\text {Fall } 1973}}{0.867^{5}}
$$

These back-calculated abundance estimates were based on the assumption that mortality was constant through time in L226 and independent of the season of year. Results from the annual survival estimates indicated that survival was relatively constant from year to year and also between basins. To determine if mortality was constant within years, stratum one whitefish $\hat{N}_{i}$ were plotted with $\operatorname{SE}\left(\hat{N}_{i}\right)$ as a function of time (in months) on semilog paper. A linearly decreasing relationship
between logged estimates and time was evident, supporting the assumption of constant monthly survival.

The production estimates were somewhat conservative because fish lose weight over the winter months and the initial gain in weight in spring back to that of the previous fall was not included in $G$. Estimates of weight at the beginning of each period and gain in weight to the end of the period were calculated by converting growth in length to that in weight using the average length-weight relationship for the populations over the course of the study $(\log W t=3.12 \times \log L-12.05, r=0.987)$.

Growth of whitefish to age $0^{+}$and $1^{+}$

Comparisons of whitefish length at age for $0^{+}$and $1^{+}$are presented in Table 2. No significant differences were detected between mean lengths of $0^{+}$fish between basins or between years. Age $1^{+}$fish in L226 NE were significantly longer than age $1^{+}$fish in L226 SW in 1974.

Growth of whitefish older than age $1^{+}$

Traditionally fish growth has been presented as a function of individual age classes (Ricker 1975; Bagenal and Tesch 1978; Everhart et al. 1975; Carlander 1969). This is sufficient when the number of age groups in a population is small, with large numbers of fish present in each age group. Average growth can then be calculated, usually with fairly small confidence intervals. When there are many age groups present in a population, as in L226 NE and SW, and the absolute number in each age class present is relatively small, growth estimates for individual age classes are sometimes very imprecise (large variance for estimates of mean growth for an age group). In addition, variation in fish length at age usually increases with increasing fish age. Yearly whitefish growth in L226 from 1971 to 1976 is more highly correlated with length at the beginning of the growth season ( $r=$ 0.908 ) than with age ( $r=0.745$ ). If only age classes $11^{+}$and older are considered, the correlation with age is considerably poorer ( $r=$ 0.531 ). For these reasons, growth will be summarized in relation to

Table 2. Mean length at age for whitefish age $0^{+}$and $1^{+}$for fall samples. The $95 \%$ confidence interval is indicated in brackets.

| Age Class | Age | L226 NE | $N$ | L226 SW | $N$ |
| :--- | :--- | :--- | :--- | :---: | :---: |
| 1973 | $0^{+}$ | $92.0( \pm 2.4)$ | 37 | - | - |
|  | $1^{+}$ | $182.4( \pm 2.0)$ | 74 | $173.3( \pm 6.7)$ | 22 |
| 1976 | $0^{+}$ | $93.7( \pm 2.7)$ | 29 | $90.8( \pm 2.4)$ | 14 |

fish length rather than age. The same data expressed with age as the covariate show similar trends, but the precision associated with individual estimates is generally poorer. Precision can be increased by combining growth information from individual age classes, as is done for production estimates.

There were no significant differences in whitefish growth between basins for $1971(F=1.7, P>0.25)$ or $1972(F=0.1, P>0.25)$. This is not surprising because the wall was not installed until early June 1973, and fish could move freely between basins. Most of the variation in growth for these years occurred in fish under 225 mm , ages $1^{+}$to $3^{+}$ (Fig. 3).

There were no significant differences in whitefish growth between basins in 1973, the first year of fertilization ( $F=2.1, P>0.15$ ), but whitefish growth was significantly greater in L226 NE than L226 SW during the second (1974, $F=114.1, P<0.005$ ), third (1975, $F=$ 92.5, $\mathrm{P}<0.005$ ) and fourth (1976, $\mathrm{F}=8.74, \mathrm{P}<0.005$ ) years of fertilization (Figs. 4 and 5). Differences in growth were very pronounced in 1974 and 1975, but only marginal in 1976. Growth differences between basins were apparent in all length groups in 1974 and 1975. Comparable plots based on age groups showed that even fish $16^{+}$to $25^{+}$ showed significantly better growth in the NE than in the SW basin. In 1976, differences between basins were slight for fish under 275 mm , but larger fish grew marginally better in L226 NE.

Whitefish growth in L226 SW from 1973 to 1976 was very similar to prewall growth in 1971 and 1972 (Fig. 6). In general, whitefish grew slightly faster in 1975 than other years of fertilization and marginally greater than 1971 and 1972. Very few fish under 250 mm

Figure 3. Growth of lake whitefish $\geq$ age $1^{+}$for the two years preceding lake division and fertilization. Means and $95 \%$ confidence intervals are plotted for each 25 mm length group.
$\begin{array}{ll}-1972 & N=693 \\ -1971 & N=472\end{array}$

Figure 4. Growth of lake whitefish $\geq$ age $1^{+}$for the first two years of fertilization in L226 NE and SW. Means and 95\% confidence intervals are plotted for each 25 mm length group.


Figure 5. Growth of lake whitefish $\geq$ age $1^{+}$for the third and fourth years of fertilization in L226 NE and SW. Means and $95 \%$ confidence intervals are plotted for each 25 mm length group.


(ars
(WW) H $\perp$ MOYO

Figure 6. Growth of lake whitefish 2age $1^{+}$for all four years of fertilization in L226 SN. Means and 95\% confidence intervals are plotted for 25 mm length groups. The shaded area is drawn from the data in Fig. 3 for $1971-$ 1972 whitefish growth.

were caught in 1975 or 1976 because of the poor recruitment from the 1974 and 1975 year classes.

Whitefish growth in L226 NE was greater each year, 1974 to 1976, than prewall yearly growth, but 1973. growth for both basins was well within the 1971 to 1972 range (Fig. 7). The 1975 growth season was the year of fastest whitefish growth in this basin, as was the case in L226 SW also, with the 1974 growth better than 1976 in L226 NE. Generally, between year differences were most pronounced in length groups 275 mm or larger, approximately the length at sexual maturity for this population.

## Condition

Whitefish condition varied throughout the ice-free season in both basins of L226 in a relatively consistent pattern (Fig. 8). In 1974, condition among fish in both $L 226$ basins was lowest in spring during the earliest sampling periods, increasing through the summer to peak in August and decline in September-October. Van Oosten (1959), Van Oosten and Hile (1949) and others (Carlander 1969) report similar seasonal trends for lake whitefish condition. L226 NE fish followed this pattern in 1975. During 1975, condition of L226 SW whitefish declined throughout the year, though sample sizes for the two early periods were relatively smaller than other 1975 samples ( $n=17$ for May and $N=26$ for June).

There were no significant differences in whitefish condition between basins early in 1974 or 1975, but by the end of July, whitefish in L226 NE were in significantly better condition than L226 SW

Figure 7. Growth of lake whitefish $\geq$ age $1^{+}$for all four years of fertilization in L226 NE. Means and 95\% confidence intervals are plotted for 25 mm length groups. The shaded area is drawn from the data in Fig. 3 for 19711972 whitefish growth.



Figure 8. Condition (k) of L226 whitefish from 1973 to 1976. Mean condition and confidence intervals for each sampling period are plotted.

( $P$ < 0.05). Though confidence intervals about both L226 NE August estimates were fairly large, small sample sizes were not responsible (August 1974, $n=93$; August 1975, $n=42$ ). Condition among fish was in fact quite variable, but well above that in L226 SW. These differences continued into fall sampling both years though differences between basins were not as pronounced. No significant interbasin differences in condition were detected in either 1973 or the 1976 samples. In addition, there were no significant differences in condition between the four years for September-October samples in L226 NE, but condition of whitefish in L226 SW was significantly greater in 1973 and 1976 than in 1974 or 1975 ( $P<0.05$ ).

Female whitefish were in better condition than males during fall sampling in 1974, 1975 and 1976. Female whitefish in L226 NE were in significantly better condition than those in L226 SW in 1975, but no significant difference in female condition between basins was detected in 1976.

Male whitefish in L226 NE were in better condition than in L226 SW in fall 1975 but differences were not significant, probably due to small sample size in L226 NE $(n=8)$. No significant differences between males from different basins were detected in 1976.

Abundance estimates

The statistics used to form estimates for L226 NE stratum one whitefish, those fish $\geq$ age $1^{+}$in fall 1973 (year classes 1950-1972), are located in Table 3, and estimates based on these data are in Table 4. The analogous data for L226 SW whitefish are in Tables 5 and
Table 3. Statistics used to form population estimates for L226 NE whitefish of the 1950-1972 year

| Sample Number (i) | Sampling Dates | $\begin{aligned} & \text { Sample } \\ & \text { Size } \\ & \left(n_{i}\right) \end{aligned}$ | $\begin{aligned} & \text { Recaptures } \\ & \text { in } n_{j} \\ & \left(m_{j}\right) \end{aligned}$ | Number of $n_{i}$ Returned ( s ) | Number of $s_{i}$ Seen Later ( $\mathrm{R}_{\mathrm{i}}$ ) | $\underset{(\%)}{R}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 15 Sep - 11 Oct 1973 | 287 | - | 282 | 146 | 52 |
| 2 | 30 July - 6 Aug 1974 | 74 | 28 | 73 | 55 | 75 |
| 3 | 4 Sep - 1 Oct 1974 | 107 | 48 | 106 | 92 | 68 |
| 4 | 29 May - 11 June 1975 | 98 | 56 | 97 | 58 | 60 |
| 5 | 27 June - 15 July 1975 | 49 | 29 | 48 | 32 | 67 |
| 6 | 12 Aug - 3 Sep 1975 | 10 | 8 | 10 | 7 | 70 |
| 7 | 18 Sep-7 Oct 1975 | 87 | 68 | 86 | 50 | 58 |
| 8 | 29 Apr - 16 May 1976 | 101 | 78 | 99 | 51 | 52 |
| 9 | 19 Sep - 2 Nov 1976 | 154 | 135 | 132 | 38 | 29 |
| 10 | 18 May - 31 Oct 1977 | 68 | 59 | 59 | - | - |
| Total |  | 1035 | 509 | 992 | 509 |  |
| Average |  |  |  |  |  | 59 |

6. The $\hat{N}_{i}$ and associated confidence intervals are plotted in Fig. 9. In general, more stratum one fish were present in L226 NE than L226 SW throughout the study (Fig. 9). Since tag loss was occurring heterogeneously in $L 226 \mathrm{NE}$, the $\hat{N}_{i}$ are probably slight underestimates, based on simulation results for this basin (Appendix B). This would make interbasin abundance differences slightly greater than in Fig. 9. Most $\hat{S E}\left(\hat{N}_{j}\right)$ were between 10 and $20 \%$ of their corresponding $\hat{N}_{i}$. Two exceptions occurred, the August 1975 estimate in L226 NE and the May 1974 estimate in L226 SW. These estimates were based on small sample sizes, both $n_{i}$ and $R_{i}$, and probably reflected small sample bias (Seber 1973), despite the formula modifications described earlier for minimizing this bias. In addition, the May 1974 L226 sample has a smaller $R_{i} / s_{i}$ than other samples early in the experiment, and this suggests possible heterogeneous survival of animals released after tagging.

The statistics and estimates for the L226 NE whitefish 1973 year class of stratum two are in Tables 7 and 8 respectively. The $\hat{N}_{i}$ and associated confidence intervals are plotted in Fig. 9. Most $\hat{N}_{i}$ for L226 NE 1973 year class were not as precise as those for the first stratum, but most $\operatorname{SE}\left(\hat{N}_{i}\right)$ were within $20 \%$ of their associated $\hat{N}_{i}$. The August 1975 sample was probably subject to the same type of sample bias as described for the analagous stratum one estimate. While young-of-the-year whitefish were caught frequently in L226 SW, in 1973, few were caught during subsequent years despite greatly increased effort. The 1974 and 1975 year classes were a negligible component of all trapnet catches from 1974 to 1976. Whitefish from these year classes were present, but the year classes were very weak. The 1976 year class was abundant in both L226 basins and relatively









Figure 9. Population estimates and associated 95\% confidence intervals for whitefish of the 1950 to 1972 year classes (bottom panel), the 1973 year class in L226 NE (middle panel) and a composite summation of the year classes 1950 to 1973 for L226 NE and SW (upper panel).

Estimates in the top panel were formed from (1) those of the two lower panels and (2) estimates for the remaining fish of the 1973 - 1975 year classes based on the proportion of each in fall samples to fish from the 1950-1972 year classes.

Table 7. Statistics used to form population estimates for the 1973 year class of L226 NE whitefish (295 capture histories).

| Sample Number (i) | Sampling Dates | $\begin{gathered} \text { Samp1e } \\ \text { Size } \\ \left(n_{i}\right) \end{gathered}$ | $\begin{aligned} & \text { Recaptures } \\ & i n_{\left(n_{j}\right)} \end{aligned}$ | Number of $n_{i}$ Returned (si) | Number of $\mathrm{s}_{\boldsymbol{j}}$ Seen Later ( $\mathrm{R}_{\mathrm{i}}$ ) | $\mathrm{R}_{\mathrm{i} / \mathrm{\%})}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 4 Sep - 1 Oct 1974 | 72 | - | 72 | 48 | 67 |
| 2 | 29 May - 11 June 1975 | 63 | 7 | 59 | 41 | 69 |
| 3 | 27 June - 15 July 1975 | 144 | 58 | 130 | 65 | 50 |
| 4 | 12 Aug - 3 Sep 1975 | 22 | 10 | 22 | 10 | 45 |
| 5 | 18 Sep - 7 Oct 1975 | 48 | 27 | 47 | 20 | 43 |
| 6 | 29 Apr - 16 May 1976 | 31 | 19 | 30 | 14 | 47 |
| 7 | 19 Sep - 2 Nov 1976 | 88 | 58 | 82 | 18 | 22 |
| 8 | 18 May - 31 Oct 1977 | 44 | 38 | 36 | - | - |
| Total |  | 512 | 217 | 478 | 216 |  |
| Average |  |  |  |  |  | 49 |

$$
\begin{array}{llll}
\text { Table 8. Estimates based on the statistics in Table } 7 \text { for the } 1973 \text { year class of L226 NE whitefish using the } \\
\text { Jolly-Seber death-only model. }
\end{array}
$$

equal numbers of fish were present in each basin.

## Annual survival rates

No significant differences in annual survival ( $\hat{\phi}_{j}$ ) were detected between basins or years in L226 from fall 1973 to fall 1976 (Table 9). While $\hat{\phi}_{i}$ did vary between years and basins, almost all $\hat{\phi}_{i}$ were within one $\operatorname{SE}\left(\hat{\phi}_{i}\right)$ of other estimates. When a $\hat{\phi}_{i}$ was greater than 1.00 , indicating an inadmissible survival estimate (greater than $100 \%$ survival from $\hat{N}_{i}$ to $\hat{N}_{i+1}$ ), the estimate was discarded and because cov $\left(\hat{\phi}_{i-1}, \hat{\phi}_{i}\right)$ was substantial (Jolly 1965), adjacent $\hat{\phi}_{i}$ were also deleted. When $\hat{\phi}_{\boldsymbol{i}}$ were inadmissible, small numbers of $n_{i}$ and $R_{i}$ were usually responsible.

Though $\hat{\phi}_{i}$ for length and age groups did vary considerably between basins and years in some cases, differences were not significant and most $\hat{\phi}_{i}$ were within one $\operatorname{SE}\left(\hat{\phi}_{i}\right)$ of other estimates for length or age groups. In addition, differences were not consistent between years or age groups, and annual survival was therefore not a function of either age or length.

The average annual survival of whitefish of stratum one (the 1950 to 1972 year classes) was 0.74 for L226 NE and 0.76 for L226 SW. The 1973 year class in L226 NE had an average annual survival of 0.82 from 1974 to 1976 when fish were progressing from age $1^{+}$to $3^{+}$. Unfortunately, no mark-recapture $\hat{\phi}_{i}$ were available for the corresponding L226 SW 1973 year class. Some inferences could be drawn from trapnet catch-per-unit effort data though (Fig. 10). There was a marked decline in catch rates of the L226 SW 1973 year class between fall 1973 and fall

Table 9. Annual survival estimates for L226 whitefish using the JollySeber death-only model. Standard errors of the estimates are in brackets. Gun tagged animals were deleted prior to analyses in L226 NE. The number of capture histories used to form estimates is "N". All estimates are for fish from the 19501972 year classes, except where otherwise noted.

|  | Basin | $1973-1974$ | $1974-1975$ | $1975-1976$ | $N$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Total | NE | $.84(.12)$ | $.66(.10)$ | $.71(.10)$ | 296 |
|  | SW | $.76(.09)$ | $.87(.10)$ | $.64(.08)$ | 288 |

Age in 1973

| 0 * | NE | a | .78(.17) | .85(.23) | 336 |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | NE | .88( 23) | .55(.15) | .75(.15) | 160 |
|  | SW |  |  | . $55(.15)$ | 60 |
| 4-6 | NE | b | b | .72(.20) | 37 |
|  | SW | $b$ | b | . $87(.24)$ | 28 |
| 1-5 | NE | .90(.18) | . 59(.12) | .74(.12) | 194 |
|  | SW | .86(.13) | .85(.12) | .62(.09) | 235 |
| 7-10 | NE | . 87 (.23) | .72(.20) | .68(.20) | 59 |
|  | SW |  |  | .63(.10) | 101 |
| 11-25 | NE | .76(.24) | .74(.27) | .82(.31) | 40 |
|  | SW | .63(.13) | .87(.15) | .72(.18) | 92 |
| Length (mm) in 1973 |  |  |  |  |  |
| 176-250 | NE | . 97 (.27) | .74(.27) | . 82(.31) | 40 |
|  | SW | .63(.13) | .87(.15) | .72(.18) | 92 |
| 251-300 | NE | .66(.17) | .68(.19) | .72(.18) | 91 |
|  | SW |  | b | .49(.11) | 92 |
| 301-425 | NE | .82(.16) | .71(.15) | . $92(.25$ ) | 58 |
|  | SW | . 61 (.11) | . $97(.13)$ | .64(.10) | 46 |

* Based on mark-recapture data for the 1973 year class.
${ }^{a}$ No estimate available.
b Inadmissible estimate, $\hat{\phi}_{\mathbf{i}}>1.0$, or biased by adjacent $\hat{\phi}_{\mathbf{i}}>1.0$.

Figure 10. Trapnet catch-per-unit effort data for the 1973-1976 lake whitefish year classes in L226NE and SW. The unit of effort was 100 trap days during fall sampling periods.


1974 (age $0^{+}$to $1^{+}$) and the catch rate stabilized at a very low rate after this time. This decline was not apparent for the 1974 and 1975 year classes, but in general, the catch rates were much lower for these classes also. Based on these catch-per-unit-effort data, the 1973 year class in L226 SW underwent a significantly higher annual loss rate ( $x^{2}$ test, $P<0.01$ ) than the analogous year class in L226 NE between fall 1973 and fall 1974.

## Fecundity estimates

No significant differences were detected between basins for either egg diameters ( $t$ test, $P>0.25$ ) or total fecundities ( $F$ test, $P>0.25$, Fig. 11). There were no consistent differences between basins for either small, relatively young females, or older, larger fish.

## Stomach analyses

Despite small sample sizes, it was obvious that the most important food items in the L226 NE and SW whitefish diets were chaoborids and chironomids. Average percentage composition of stomach contents are presented in Fig. 12; a plot of percentage of stomachs containing various food items shows the same trends. Chaoborids were generally found most often in stomach contents early in the ice-free season and were found less frequently in stomachs during the remainder of the year (Fig. 12). Chironomids were generally found in the stomach contents of most whitefish examined in this study and they were generally the predominant food item present in stomachs from either basin.

Figure 11. Fecundity estimates for L226 whitefish taken in fall 1976 prior to spawning. NE ( $\Delta$ ) . SW ( $\bullet$ )


Figure 12. Average percent composition of whitefish stomach contents by taxonomic group: chaoborids, chironomids, and others (cladocerans, copepods, misc.). Sampling periods are indicated as ( $\mathbf{\Delta}$ ).


Cladocerans and copepods were relatively unimportant components of whitefish diet. Littoral species, such as Latonia setifera and Euryptus Zomellatus, occurred more often and were more numerous in stomach contents than other pelagic species such as Leptodora kindtii, Daphnia galeata mendotae, Holopedium gibberum, and Bosmina Zongirostris. Among copepods, Diaptomus minutus and Mesocyclops edax were found more often than other species. These food items were slightly less important in L226 NE whitefish diet in 1975 than 1974. Other minor components of whitefish diet were leeches, adult dipterans and clams.

No gross changes were evident in whitefish diet between 1974 and the 1975 samples in either basin. Neither were there any distinct differences in diet between basins.

Whitefish production estimates

Annual whitefish production in L226 NE was consistently higher than that in L226 SW from 1973 to 1976, though the yearly totals varied from 38.1 to 63.7 kg for L226 NE and from 13.3 to 30.4 kg for L226 SW (results are summarized in Table 10; more detailed yearly results and intermediate steps in production calculations are located in Appendix F). From May to September-October 1973, L226 NE production was approximately $20 \%$ higher than L226 SW production. Subsequently, whitefish production in L226 NE was more than twice the production in L226 SW for the second to fourth years of fertilization.

In general, population estimates have been the greatest single source of error in other fish production studies (Chapnan 1978), and

|  | 1973 |  | 1974 |  | 1975 |  | 1976 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Age | NE | SW | NE | SW | NE | SW | NE | SW |
| 1-3 | $\begin{array}{r} 23.7 \\ (70.5) \end{array}$ | $\begin{gathered} 13.6 \\ (80.0) \end{gathered}$ | $\begin{gathered} 32.2 \\ (79.7) \end{gathered}$ | $\begin{array}{r} 9.8 \\ (69.6) \end{array}$ | $\begin{gathered} 32.0 \\ (64.6) \end{gathered}$ | $\begin{gathered} 4.6 \\ (47.1) \end{gathered}$ | $\begin{array}{r} 22.3 \\ (72.9) \end{array}$ | $\begin{gathered} 1.8 \\ (64.2) \end{gathered}$ |
| 4-6 | $\begin{gathered} 4.5 \\ (54.9) \end{gathered}$ | $\begin{array}{r} 3.1 \\ (48.4) \end{array}$ | $\begin{gathered} 5.3 \\ (76.7) \end{gathered}$ | $\begin{gathered} 2.2 \\ (43.9) \end{gathered}$ | $\begin{gathered} 16.5 \\ (92.2) \end{gathered}$ | $\begin{gathered} 7.7 \\ (59.9) \end{gathered}$ | $\begin{gathered} 8.3 \\ (43.3) \end{gathered}$ | $\begin{gathered} 3.8 \\ (40.8) \end{gathered}$ |
| 7-10 | $\begin{gathered} 7.8 \\ (56.1) \end{gathered}$ | $\begin{gathered} 6.5 \\ (50.1) \end{gathered}$ | $\stackrel{10.6}{(85.2)}$ | $\begin{gathered} 6.2 \\ (49.0) \end{gathered}$ | $\begin{gathered} 8.2 \\ (97.5) \end{gathered}$ | $\begin{array}{r} 5.4 \\ (68.9) \end{array}$ | $\begin{gathered} 3.8 \\ (59.0) \end{gathered}$ | $\begin{array}{r} 3.5 \\ (47.2) \end{array}$ |
| 11-15 | $\begin{gathered} 2.1 \\ (44.7) \end{gathered}$ | $(47.3)$ | $\begin{gathered} 5.2 \\ (77.4) \end{gathered}$ | $\begin{array}{r} 4.8 \\ (35.2) \end{array}$ | $\begin{gathered} 6.0 \\ (109.7) \end{gathered}$ | $\begin{gathered} 5.4 \\ (57.3) \end{gathered}$ | $\begin{gathered} 2.3 \\ (66.7) \end{gathered}$ | $\begin{gathered} 2.7 \\ (36.2) \end{gathered}$ |
| 16-25 | $\begin{gathered} 0.2 \\ (14.3) \end{gathered}$ | $\begin{gathered} 1.1 \\ (40.7) \end{gathered}$ | $\begin{gathered} 0.3 \\ (45.4) \end{gathered}$ | $\begin{aligned} & 1.1 \\ & (32.0) \end{aligned}$ | $\begin{gathered} 1.0 \\ (82.5) \end{gathered}$ | $\begin{gathered} 1.6 \\ (38.8) \end{gathered}$ | $\begin{gathered} 1.3 \\ (61.3) \end{gathered}$ | $\begin{gathered} 1.5 \\ (29.3) \end{gathered}$ |
| Total | 38.3 | 30.4 | 53.6 | 24.1 | 63.7 | 24.7 | 38.1 | 13.3 |
| Total $\mathrm{g} / \mathrm{m}^{2}$ | 0.46 | 0.38 | 0.64 | 0.31 | 0.77 | 0.32 | 0.46 | 0.17 |
| Average Biomass ( Kg ) | 130.2 | 146.7 | 235.1 | 176.3 | 206.0 | 151.8 | 178.6 | 126.1 |

this was probably also true for $L 226$ estimates. There is probably more error in the 1973 production estimates than those for other time periods because population estimates for May 1973 were calculated indirectly from later mark-recapture $\hat{\mathbb{N}}_{i}$ and $\hat{\phi}_{i}$. Therefore, the interbasin production differences for 1973 were probably less reliable than differences between basins for other years.

Whitefish production estimates for L226 NE and SW for 1973 and 1976 were underestimates, because abundant young-of-the-year whitefish (Fig. 10) were not included in the calculations. Catch rates between basins of young-of-the-year fish were very similar for these years (Fig. 10), so little bias was present when comparing production estimates between basins for 1973 and 1976.

The large production differences between basins from 1974 to 1976 were largely attributable to (1) the numerous 1973 year class in L226 $N E$, and (2) the differences in individual growth between basins from 1974 to 1976.

The 1973 year class dominated production in L226 NE as these fish moved from age $1^{+}$in 1974 to $3^{+}$in 1976 (Table 10). Over $56 \%$ of the total production in L226 NE was due to the age $1^{+}$to $3^{+}$group from 1974 to 1976, while only $27 \%$ of the total production in L226 SN was due to this age group over the same time period. Age $1^{+}$to $3^{+}$fish were much more abundant and were growing faster in L226 NE than their counterparts in L226 SW.

Even though the $1^{+}$to $3^{+}$age group dominated production in L226 NE from 1974 to 1976, production of older fish was also generally greater in L226 NE than SW (Table 10). These differences were certainly minimal for age group $7^{+}$or older in 1976, but were very striking for 1974 and
1975. Growth of L226 NE whitefish was generally 30 g per fish greater than that in L226 SW whitefish for fish older than $3^{+}$in 1974 and 1975. This difference in whitefish growth between basins continued into 1976 for fish age $11^{+}$or older. Therefore, sexually mature whitefish, generally age $5^{+}$to $6^{+}$and older, contributed significantly to the production differences between $L 226$ basins.

## DISCUSSION

Lake 226 was changed in two ways in early June 1973: (1) a wall was installed, which divided the lake into two basins, and (2) fertilization of both basins began. The object of this study was to evaluate the effects of fertilization on L226 whitefish, but before this is possible, the potential confounding influences of the wall on L226 whitefish must be appraised to establish a baseline for interpreting fertilization effects.

A recent controversy has developed about the structure and regulation of unexploited whitefish populations (Johnson 1976; Power 1978). Comparative population dyanamics studies such as Healey's $(1978,1980)$ whitefish exploitation experiments and my study of the effects of eutrophication on a whitefish population provide data to evaluate mechanisms of response of lake whitefish to ecosystem manipulations. Both experiments provide insight into the regulation of unexploited whitefish populations.

I will therefore discuss:
(1) effects of wall installation on the limnology of L226
(2) effects of wall installation on L226 whitefish
(3) effects of fertilization on L226 SW whitefish
(4) effects of fertilization on L226 NE whitefish
(5) whitefish production in L226 NE and SW and that at lower trophic levels
(6) similarities between responses of whitefish to nutrient addition and exploitation
(7) implications of the L226 whitefish study for the theory of structure and regulation of whitefish populations.

Effects of the wall on the limnology of L226

In late May 1973, a plastic wall was installed in L226, separating the L226 basins. This wall was later replaced, in mid-June, with a heavy vinyl sea curtain. If primary production differences were present between basins prior to wall installation, interbasin water mixing probably canceled this difference. However, with wall installation in 1973, interbasin water mixing was minimized, which would accentuate any intrinsic productivity differences.

Fee (1979) hypothesized that primary production in L226 NE was slightly greater than L226 SW prior to fertilization, if interbasin water mixing was ignored. Fee has shown that primary production in non-fertilized ELA lakes was related to the ratio of area of epilimnetic sediments to water volume. This ratio was slightly higher in L226 NE than SW; therefore Fee predicted that production would be slightly higher in L226 NE than SW. His hypothesis was supported indirectly by Davies (1980) who observed that dipteran emergence was related to area of epilimnetic sediments.

Alternately, Vollenweider (1976), Dillon and Rigler (1974) and Schindler et al. (1978) have shown that there was an inverse relation between flushing rate and primary production. The flushing rate of L226 NE was higher than L226 SW. Both basins have similar watersheds, but L226 NE also received water from L226 SW causing the total difference. The higher flushing rate for L226 NE would probably lower its productivity conpared to L226 SW.

The primary production differences hypothesized by Fee would be canceled by differences between basins in flushing rates. Fee did
hypothesize that any interbasin differences would be minimal.
Therefore a conservative approach to interpretation of interbasin differences in whitefish population parameters would be to view baseline production prior to fertilization in L226 NE as marginally greater than in L226 SW. I chose this approach.

Effects of the wall on the whitefish of L226

The wall installation in early June 1973 effectively segregated L226 whitefish into two populations, one in each basin. Only one tagged fish was caught in a basin other than where tagged between fall 1973 and fall 1977. The segregation of the L226 whitefish population into two components could have disrupted spawning activities or divided the population extremely unevenly, to confound interpretation of the effects of nutrient addition.

The wall could have isolated whitefish in one basin from the traditional spawning site in the other basin. A strong year class could have occurred in one basin while a year class failure, entirely unrelated to lake fertilization, could have occurred in the other basin. Fortunately, this did not occur (Fig. 10). The occurrence of strong and weak year classes coincided between basins. Strong year classes occurred in 1973 and 1976 in both basins, while weak year classes occurred in 1974 and 1975. Whitefish of the 1973 year class had hatched and probably some dispersal between basins had occurred prior to wall installation, but the coincident strong 1976 year class in both basins showed that year class failures in 1974 and 1975 were not related to wall installation. One weak year class
followed by a second was somewhat unusual for L226, based on a composite age frequency distribution for all L226 whitefish (Fig. 13), but also occurred in 1966 and 1967. Year class fluctuations were an integral component of the $L 226$ whitefish population dynamics prior to wall installation.

Since the wall apparently did not affect year class occurrence in either basin, one could argue that two isolated subpopulations of whitefish, each confined to one basin, existed prior to wall installation. The channel separating L226 basins was small and very shallow. Whitefish are traditionally regarded as stenotherms which prefer cooler waters (Scott and Crossman 1974; Carlander 1969), so epilimnetic temperatures for much of the ice-free season would confine fish to the hypolimnion of each basin for much of the year. Interbasin fish movement may not have occurred at other times of the year. Two observations refute this argument. First, a zipper holding sections of the wall together separated in late August in 1978 and was not repaired until mid-September 1978. Many fish, judged from recaptures of tagged animals in late September 1978, exchanged basins. Second, when backcalculated growth of whitefish was compared between basins for 1971 and 1972, no significant differences were detected despite very large sample sizes. If two subpopulations were genetically isolated prior to fertilization, this would probably be reflected in growth differences between basins.

The L226 whitefish population was probably divided unevenly at wall installation. More whitefish were present in L226 NE than SW in fall 1973 (Fig. 7), and there was indirect evidence that no unusual mortality occurred in either basin between early June and September-

Figure 13. Composite age frequency distribution for L226 NE and SW whitefish population at fall 1973, derived from the age structure of individual animals used for markrecapture analyses from 1973-1976.


0ctober 1973. First, whitefish survival was relatively constant from fall 1973 to fall 1976 both between years and between basins (Table 9). If differences in mortality did not occur from fall 1973 to fall 1976, when production levels of both whitefish (Table 10) and other trophic levels (Fee 1980; Davies 1980) varied widely, it is highly unlikely that differences occurred from May 1973 to fall 1973. Second, if compensatory mortality (Ricker 1975; Everhart et al. 1975) had occurred between basins (the occurrence of increased growth to compensate for increased mortality, or growth depression to compensate for higher survival), it is not reflected in growth at fall 1973. No significant interbasin differences in whitefish condition or growth were detected in fall 1973, and if survival had been better in L226 NE over this period, it probably would be reflected in one of these parameters (Weatherley 1972).

Effects of fertilization on L226 SW whitefish

The hypothesis tested by the L226 experiment was that there would be no detectable response to high inputs of nitrogen ( $N$ ) and carbon (C) without the presence of phosphorus (P) (Schindler and Fee 1974). Ultimately the response of L226 SW whitefish to $N$ and $C$ was tied to the response of lower trophic levels. I will briefly discuss the effects of $N$ and $C$ on these lower trophic levels, and then the response of L226 SW whitefish.

Only small amounts of limnological data were collected from L226 prior to wall installation. In addition, portions of the L226 wall failed for short periods during two years of this study, twice in early

1973 and once in late summer 1977. Substantial epilimnetic water mixing probably occurred both years. This would partially bias results for each year as shown by total $P$ mass balances for each year. Total P for the ice-free periods of both years, 1973 and 1977, were at least $50 \%$ higher than other years of fertilization in L226 SW from 1973 to 1977 (D. W. Schindler, Freshwater Institute, unpublished data). It was probable that other minor interbasin water mixing occurred through the study, either between floats at the curtain top or through other small openings along the curtain top. The only limnological information collected prior to 1973 was in L226 NE during 1971 when water chemistry data (Schindler and Fee 1974; D. W. Schindler, Freshwater Institute, unpublished data), phytoplankton composition and biomass (Findlay 1975) and zooplankton composition (D. F. Malley, Freshwater Institute, unpublished data) were collected. The SN basin was not sampled in 1971. Zooplankton and phytoplankton species composition were very similar between L226 NE in 1971 and subsequent years in L226 SW after wall installation. Summer epilimnetic chlorophyll concentrations were somewhat higher in L226 SW from 1973 to 1977 than in L226 NE in 1971, but total epilimnetic P concentrations showed the reverse trend (D. W. Schindler, Freshwater Institute, unpublished data). Based on these observations, it is unlikely that lower trophic levels responded to increased $N$ and $C$ loadings with an increase in production.

Only limited whitefish data were available for interpretation of effects of $N$ and $C$ additions over prefertilization conditions. Whitefish growth data for 1971 and 1972 (Fig. 3) were very similar to L226 SW whitefish growth data from 1973 to 1976 (Fig. 6). Other
nutrient addition studies (Hall et a1. 1970; Nikolsky 1963; Vinberg and Lyakhnovich 1965; Haines 1973; Smith 1969; and others) showed that individual fish growth was a sensitive response indicator of a fish population to nutrient additions. The absence of pronounced growth differences between the 1971-1972 whitefish data and the 1973-1976 data indicated strongly that L226 SW whitefish did not respond to $N$ and $C$ additions.

Other studies have shown that pond fertilization was only effective when phosphorus additions accompanied nitrogen (Vinberg and Lyakhnovich 1976; Marciolek 1954; Neess 1949). Juday et al. (1938) added many different fertilizers to a northern Wisconsin lake, but responses to fertilization occurred only when $P$ was a component of the annual fertilization. Because the response of L226 SW whitefish to $N$ and $C$ was not detectable, and the response of other limnological parameters was minimal or absent, 1973-1976 L226 SW whitefish data and data from 1971-1972 for both basins will be used as a control for interpretation of the effects of $P, N$ and $C$ additions on L226 NE whitefish.

## Effects of fertilization on L226 NE whitefish

Increased phosphorus loading in L226 NE was reflected in: (1) increased growth of individual fish, (2) increased survival of the 1973 year class, (3) possible differences in fecundity between similar sized fish, and (4) fish production differences between basins. I will discuss each of these responses separately.

Individual fish growth
Increased growth of L226 NE whitefish was an important reponse to P, N and C additions. No response was present the first year of fertilization. Very pronounced differences occurred between basins in the second and third years of fertilization, 1974 and 1975, but decreased substantially in 1976.

Interpretation of growth results between basins for 1973 (Fig. 4) is somewhat puzzling. Because more fish were present in L226 NE than SW in fall 1973, it could be argued that the lack of growth differences between basins actually represented a response to phosphorus additions in L226 NE. The basis of this argument is that if no response were present (no production differences between basins), the larger whitefish population present in L226 NE in 1973 (Fig. 9) should show slower growth than the smaller population in L226 SW to have production balance between basins. An inverse relationship between growth and population numbers is well documented in fishery literature (Everhart et al. 1975; Weatherley 1972; Vinberg and Lyakhnovich 1965; Nikolsky 1963). An alternative explanation is that the similarity in growth between basins is a direct consequence of the small morphometric primary and benthic production differences between basins described earlier, which would be reflected in whitefish growth after wall installation. The chlorophyll concentrations present throughout the 1973 ice-free season in each L226 basin support this second interpretation (Schindler and Fee 1974). Chlorophyll concentrations were very similar between basins until late August, when L226 NE responded to $P$ fertilization for approximately one month. Most growth occurred between mid-May and late August for L226 whitefish, so there was inadequate time for
the algal bloom in late August 1973 to be converted first into organic matter and then into chironomid biomass to be ingested by whitefish. In addition, response to change in nutrient loading is not instantaneous (as discussed later); a new equilibrium phosphorus level would probably not be reached the first year of nutrient addition. A weak response (or no response) would be the normal situation.

The differences in whitefish growth between basins were very pronounced in 1974 and 1975, and occurred in all age groups. The response of sexually immature fish was not surprising. Many other lake studies with stocked trout (Smith 1959, 1969; Ball and Tanner 1951; Weatherley and Nichols 1955), or young sockeye salmon (Nelson 1959; LeBrasseur et a1. 1978) have shown similar increased growth for young fish. Pond fertilization studies (Winberg and Lyakhnovich 1965; Hall et al. 1970; Marciolek 1954; McConnell 1965; Haines 1973) were almost always conducted with stocked populations of young immature fish.

The response of whitefish growth in sexually mature, older fish was as striking as that for younger fish. These differences were very pronounced in 1974 (Fig. 4) and 1975 (Fig. 5). In addition for both years, older fish in L226 NE were in better condition than similar sized fish in L226 SW (Fig. 8). Describing growth in terms of fish length understates the importance of these differences for older fish. A small change in length converts to a greater change in weight for a large fish than an equal length change for a small fish. In general, the response of older fish to nutrient addition has not been well documented elsewhere. Even fish age $11^{+}$to $25^{+}$showed an obvious growth response clearly evident on their fin-ray sections. Some
animals which showed very poor growth for the three to five years prior to fertilization responded with one year's growth equal to the prior three to five combined. It is obvious that without a reliable method of age determination, the response of older fish would probably have been obscured. Others have speculated that growth increased for mature fish when nutrient additions occurred to lakes. Leach et al. (1977) reported some increases in growth of mature percids from European lakes as eutrophication progressed, and Colby et al. (1972) suggested general increases in coregonid growth in eutrophic lakes. Both these studies are confounded by concurrent species additions or exploitation. In a lightly exploited yellow perch (Perea flavescens) population, Nakashima and Leggett (1975) found no significant growth differences in either mature or immature fish between the eutrophic southern arm of Lake Memphramagog, Quebec, and the more northern oligotrophic arm of the lake. Perch growth in this lake was at a maximum for the area and apparently has not changed appreciably from 1963 to 1973. They hypothesized that there was no scope for increased growth in this population; the perch had already reached their zoogeographic limit for the area. Whitefish in L226 were also near their zoogeographic growth maximum for the ELA area when compared to data for five other ELA populations (Fig. 14), but substantial increases still occurred to raise the growth curve well above the previous maximum for the area. The response of older, larger fish to nutrient addition has apparently been ignored because either (1) the only species of interest was a stocked population of fry or fingerlings, or (2) age determination errors obscured the response, or (3) the responses of older fish were assumed insignificant because these animals were only a small component of the population.

Figure 14. Growth curves for five populations of ELA lake whitefish. All populations were sampled with gillnets in 1975 except $L 226$ which was sampled with trapnets in 1973 and trapnets-gillnets in 1976. The numbers to the right of each curve correspond to the ELA lake number where fish were obtained. Healey's (1975) summary of the previously reported whitefish growth data is indicated between the dotted lines.


FIN-RAY AGE

The increase in growth was not related to any major change in L226 NE whitefish diet (Fig. 12). Dipterans became slightly more important in whitefish diet and fewer zooplankton were consumed, but no major shift occurred to a new food resource.

## Annual survival

Annual survival rates of whitefish were not significantly different either between basins or between years (Table 9). The average across basins and years (0.75) was very similar to the catch curve rate (0.73) reported by Mills and Beamish (1980, Appendix G) based on the age structure of the September 1973 catch. The similarity between the two estimates is encouraging; it supports the hypothesis that annual survival has not changed for the whitefish population of $L 226$ with the addition of the wall and fertilization. The relatively constant annual survival of fish age $1^{+}$or older agreed with Bell et al. (1977), who found similar results for lake whitefish of Lesser Slave Lake, Alberta. In another fertilization study, Dobbins and Boyd (1976) found no difference in survival of fish stocked in a series of ponds fertilized at five different levels using $P$ and $K$. Similar results were obtained in other pond fertilization studies (Hall et al. 1970; Vinberg and Lyakhnovich 1969).

Even though I could detect no significant differences in annual survival between basins for fish older than $1^{+}$, there is the possibility that my sample sizes were not adequate to detect differences. Reversing this question, one can ask: given my sampling intensity, how small an actual difference could be detected in $\hat{\phi}_{j}$ ? I conducted a number of mark-recapture simulations similar to those in Appendix B
varying the actual $\phi_{i}$ but using other population parameters similar to those for $L 226$ whitefish. In general, I found that my sampling intensity was sufficient to show changes in $\hat{\phi}_{i}$ of approximately $5 \%$, or in this case of about 0.04 units of $\hat{\phi}_{j}$. Based on these simulations, the lack of consistent significant differences between basins was not due to small sample sizes.

Annual survival did vary between basins for younger fish, age $0^{+}$ to $1^{+}$of the 1973 year class (Fig. 10); annual survival was substantially lower in L226 SW than NE. In addition, the average fork length and condition of the 1973 year class at age $1^{+}$was significantly greater in L226 NE than L226 SW. The strength of a whitefish year class in L226 was apparently determined before age $1^{+}$and the natural mortality rate was nearly constant through the following years.

The results for the 1973 year class were consistent with the observations of others for regulation of year class strengths. The mechanism regulating abundance of perch in the upper and lower portions of Lake Memphramagog also occurred in the first year of life, with relatively similar survival between areas of the lake during subsequent years. Though there was apparently greater juvenile mortality in the more productive Lake Memphramagog south basin than in the oligotrophic north basin, many more young-of-the-year perch were still present in the south basin. The result was a marked difference in perch abundance between areas of the lake in spite of the greater juvenile mortality in the southern eutrophic basin. Nelson and Edmondson (1959) and Mathieson (1972) also showed a general correlation between a source of nutrient addition, the number of decomposing salmon carcasses, and subsequent year class strength and average length of salmon at smolt stage. They also found
a positive correlation between salmon smolt survival and size. Nikolsky (1963) cited other examples of positive correlations between fish survival and fish condition or length.

An even more relevant question than whether the L226 sampling intensity was high enough to detect survival differences is: was there sufficient scope in the range of natural variation for whitefish survival rates for $\hat{\phi}_{i}$ to increase? Annual survival was apparently very high in L226 prior to years of nutrient enrichment. Healey (1975) listed natural mortality rates for many lake whitefish populations and the $\hat{\phi}_{\mathbf{i}}$ for the L 226 whitefish were very close to the upper limit of this range, discounting the major mortality of L226 whitefish between ages $0^{+}$and $1^{+}$. All Healey's annual mortality rates were derived from catch curve data and were based on scale ages of whitefish. These mortality rates may be underestimates due to aging errors (Mills and Beamish 1980, Appendix G). Mills and Beamish (1980, Appendix G) presented catch curve survival rates for seven unexploited populations of lake whitefish based on fin-ray ages using the Robson and Chapman (1961) method, and the L226 rate was one of the highest of these rates regardless of whether the catch curve rate or the mark-recapture rates were considered. It was certainly possible that annual survival of whitefish older than $1^{+}$did not increase significantly in L226 NE because whitefish were already at an upper limit of the natural survival range before lake division and fertilization began.

Fecundity
While no significant difference in fecundity at length was detected between basins in 1976 (Fig. 11), differences may have occurred in 1974
and 1975. In general, there is a positive correlation between fecundity at length and fish condition (Bagenal 1978; Weatherley 1972; Nikolsky 1963). Whitefish spawning occurred after September-October sampling in L226; fish condition was significantly greater in L226 NE than SW for 1974 and 1975 during these fall periods. While no comparative data were available for 1974, female whitefish in L226 NE were in significantly better condition than those in L226 SW in 1975. This suggests that fecundity at length could have been greater in L226 NE than SW for 1974 and 1975. Annual variations in fecundity at length are well documented for whitefish and other species. Healey (1978) has shown significant annual variations in fecundity at length for four lake whitefish populations in the Northwest Territorities, and similar annual variations have been reported for other marine and freshwater species (as summarized in Bagenal 1978). Other studies have also shown that fecundity varies with food supply (Wootton 1977; Tyler and Dunn 1976; Bagenal 1969; Woodhead 1960; Alm 1952). The response to increased food supply was usually immediate, the same growth season as the increase in food supply. It is likely that if I had obtained whitefish ovaries from both basins in 1974 and 1975, I would have detected fecundity differences.

Fecundity of the total whitefish population was probably greater in L226 NE than SW from 1974 to 1976, as an indirect result of the growth differences between basins. Because the fecundity of an individual fish was directly correlated with its length (Fig. 11), the increased growth of older, sexually mature fish in L226 NE over SW fish in 1974 and 1975 led to indirect differences in total fecundity between basins. For example, based on Figs. 4, 5 and 11, a female whitefish
first reaching sexual maturity in L226 NE in 1973 at a fork length of 300 mm (age $6^{+}$) would increase in length and fecundity to 326 mm ( 8,000 eggs) in 1974, 350 mm (11,500 eggs) in 1975 and 363 mm ( 13,000 eggs) in 1976. The same fish in L226 SW would be 312 mm ( 6,500 eggs) in 1974, 329 mm ( 8,000 eggs) in 1975 and 339 mm (9,700 eggs) in 1976. Even though there were only minor differences in whitefish growth in 1976 between basins, the cumulative increments from previous years in L226 NE still led to a substantial fecundity difference between basins.

## L226 whitefish production and its relation to lower trophic levels

Fish production is ultimately a function of production at lower trophic levels (Odum 1957; Lindemann 1942). In recent years many researchers have correlated fish production, or commercial fishery yield, with primary production or chlorophyll concentrations (Hall et a1. 1970; Melack 1976; Hrbáček 1969; Davis and Warren 1965; McConne11 1963, 1965; Dobbins and Boyd 1976; and many others), benthic production or biomass (Gerking 1962; Hall et al. 1970; Hrbacek 1969; Vinberg and Lyakhnovich 1965), or zooplankton production and biomass (Hall et al. 1970; Hrbáček 1969; Vinberg and Lyakhnovich 1965; Smith 1969; Goodyear et al. 1972). The L226 experiment is somewhat unique; primary production, epilimnetic chlorophyll concentrations, dipteran emergence and whitefish production have been measured over a series of years (Fig. 15). As in the above studies, there was generally good correlation between average epilimnetic chlorophyll concentrations and annual whitefish production in L226 ( $r=0.86, P<0.01, n=8$ ), or between dipteran emergence and whitefish production ( $r=0.77, P<0.05, \mathrm{n}=8$ ). The relationship between whitefish production and primary production was not as

Figure 15. Annual average epilimnetic chlorophyll concentrations, primary production, dipteran emergence and whitefish production for L226 from 1973 to 1976. Chlorophyl1 concentrations are from Schindler and Fee (1974) and D. W. Schindler, Freshwater Institute, unpublished data. Primary production data are from Fee (1980). Dipteran emergence data are from Davies (1980) and I. J. Davies, Freshwater Institute, unpublished data.
(大) L226 NE
(0) L226 SW




pronounced ( $r=0.67, P>0.05, n=8$ ), but the relationship improved if only data from L226 SW and the first two years of fertilization of L226 NE were considered ( $r=0.85, P<0.05, n=6$ ). Primary production and whitefish production were inversely related for L226 NE in 1975 and 1976.

A plausible explanation for the L226 NE primary production and whitefish production data for 1975 and 1976 was that a "use lag" (McConnell 1963) was present. For example, primary production (and chlorophyll concentrations) increased from 1973 to 1974; this was reflected in increased whitefish production from 1974 to 1975. Primary production and chlorophyll concentrations decreased from 1974 to 1975; this was reflected in a decrease in whitefish production from 1975 to 1976. A one year lag improved the correlation between whitefish production and primary production ( $r=0.90, P<0.01, n=6$ ) and similar lags have been previously described in other studies (Vinberg and Lyakhnovich 1965; Lellák 1965; Wolny and Giereck 1972). These lags have generally been attributed to the time needed for conversion of dead algae to benthic biomass for fish consumption. The "time lag" explanation breaks down somewhat for 1976 data though. Based on L226 NE primary production data which increased from 1975 to 1976, whitefish production should increase from 1976 to 1977 . Chlorophyll concentrations decreased from 1975 to 1976, indicating that whitefish production should decrease over this same period. Unfortunately, or fortunately, L226 NE whitefish production for 1977 is not presently available to resolve this dichotomy.

Another anomolous datum, which is somewhat easier to explain, is the extremely low L226 NE dipteran emergence in 1976. Whitefish biomass
in L226 NE increased rapidly during the first years of fertilization (Table 10), which would exert a very heavy predation pressure on dipterans, the predominant food item in whitefish diet (Fig. 12). Therefore, even if dipteran emergence was somewhat lower in L226 NE than SW in 1976, dipteran production was still probably greater in L226 NE.

A shortcoming of many of the early lake fertilization studies (summarized by Marciolek 1954) was that fertilizations were conducted generally over a one year period, and the response of fish growth or yield measured the same year. Some one year experiments were successful in increasing trout yield or growth (Tanner 1960; Weatherley and Nichols 1956) ; others gave poor responses (as summarized by Wagner and Parker 1973). Response lags, as described above, were used sometimes to explain the poor growth and yield response of fish in fertilization experiments. Probably of greater importance is the realization that a sudden increase in nutrient loading (or decrease) puts the lake into a disequilibrium and a certain number of years of sustained nutrient additions (or reductions) are necessary before a new equilibrium state is reached. Water renewal time for a lake $\left(\tau_{W}\right)$ is a critical component of this response (Vollenweider 1975; Dillon and Rigler 1974; D. W. Schindler, Freshwater Institute, unpublished data). Newbury et al. (1980) estimated the average water renewal time for L226 as 4.2 yrs. L226 NE has a faster renewal time than L226 SW as described earlier and it was probably somewhere between 4.2 yrs (similar water renewal times between basins) and 2.1 yrs (twice as fast in L226 NE as SW). Using the method of Schindler et al. (1978), the equilibrium annual total phosphorus concentrations ( $\Sigma \overline{\mathrm{F}}$ ) can be predicted for L226 NE (Fig. 16).

Figure 16. The predicted and observed rates of average total annual phosphorus ( $\Sigma \overline{\mathrm{F}}$ ) equilibrium for L226 NE. Actual data are indicated by "x". The equilibrium phosphorus level was calculated after the $I_{p} V_{0}^{-1}$ relationship for ELA lakes reported by Schindler et al. (1978). Where $I_{p}$ is total quantity of phosphorus received by the lake in milligrams and $V_{0}$ is the volume of outflow in cubic metres (inflow + precipitation - evaporation). The model used to predict $\Sigma \overline{\mathrm{P}}$ was:

$$
\begin{aligned}
& C_{t}=C_{e}+\left(C_{0}-C_{e}\right) e^{-t / t_{w}} \\
& \text { where }= \\
& C_{t}= \text { predicted } \Sigma \bar{P} \\
& C_{e}= \text { expected equilibrium } \Sigma \bar{P} \\
& \text { calculated from } I_{p} V_{o}^{-1} \\
& C_{0}= \text { initial } \Sigma \bar{P} \text { before change } \\
& \text { in } P \text { loading } \\
& t_{W}= \text { water renewal time in years } \\
& t= \text { time in years }
\end{aligned}
$$

(after D. W. Schindler, Freshwater Institute, unpublished data).


A simple model of the form $Y=A-B \exp (-k t)$ (Crowe and Crowe 1969) has been used previously to accurately model the response of Lake Washington to decreased $P$ inputs and the response of L227, ELA, to increased P loadings (D. W. Schindler, Freshwater Institute, unpublished data). This model was used for the disequilibrium period in $L 226$ NE (Fig. 16). Based on results from this model, it was not surprising that there was little or no growth response the first year of fertilization in L226 NE, and that equilibrium $\Sigma \bar{P}$ levels would not be reached until the third to fifth years of fertilization, depending on the true ${ }^{\tau} w$. If a lag is present for conversion of $P$ to fish production, it is likely that L226 NE whitefish production and biomass had not reached equilibrium in this study. During the years of detectable response to P additions in L226 NE, 1974-1976, average lake whitefish biomass averaged 33\% higher in L226 NE than SW (Table 10). At equilibrium, the difference would probably be greater.

Responses of lake whitefish populations to exploitation and nutrient addition

Both cropping and nutrient addition experiments give insight into the mechanisms used by unexploited fish populations to return to predisturbance conditions. In both situations, a deficit is created between the carrying capacity of the environment and the whitefish stock present. In a cropping experiment, this difference is created by reducing the whitefish stock. In a nutrient addition experiment, the difference is created by increasing the carrying capacity of the lake. With extreme exploitation, a whitefish population age structure
is changed drastically from the unexploited state to one which is very different from that of L226 at the beginning of this experiment. Under less intensive exploitation, the whitefish age structure present after cropping can be very similar to the pre-exploitation age structure and the L226 NE age structure at the start of nutrient addition.

In 1973 and 1974, Healey $(1978,1980)$ cropped three lakes at rates of 10,20 and $30 \%$ respectively and monitored a fourth as control. He measured the response of each experimental lake to cropping from 1975 to 1978 and evaluated year-to-year variation in parameters used in the L226 study: whitefish growth, recruitment and fecundity. Prior to cropping, the whitefish population structure present in all four lakes was similar to that present in L226 at the beginning of the nutrient addition experiment. The whitefish population age structure after cropping in those lakes cropped at 10 and $20 \%$ was very similar to that before cropping, while the whitefish population age structure of the heavy exploited third lake was very differnet from the precropping age structure. Few old fish remained.

Healey $(1978,1980)$ found that whitefish responded to exploitation by increased growth, increased fecundity at length, and increased recruitment. Whitefish from L226 NE responded similarly, though the fine details of some responses were significantly different. Healey (1980) found increased growth over pre-exploitation levels in all exploited lakes, though he reports these changes were not significant for older, mature fish (Healey 1978). Increased growth was evident for L226 NE whitefish, and increases extended significantly to older, mature fish. Though no significant interbasin differences in fecundity at length were apparent in L226 in 1976, indirect evidence suggested that
an increase in L226 NE whitefish fecundity did occur in earlier years, and that total population fecundity for $L 226$ NE whitefish was greater than L226 SW all three years. Healey's (1980) data for whitefish fecundity in exploited lakes show pronounced year-to-year variation in whitefish fecundity at length. This apparently also occurred in L226 NE, though the supporting evidence was circumstantial.

Responses of whitefish recruitment to cropping and nutrient addition were very similar. In both studies, year classes already present at the time of manipulation (ages $0^{+}$and $1^{+}$in Healey's lakes, age $0^{+}$ in L226 NE) became a dominant factor in later catch curves. Healey's sampling gear, gillnets, did not permit assessment of abundance levels for these $0^{+}$and $1^{+}$fish in his lakes at the time of exploitation, while the trapnet catch-per-unit effort data from L226 showed that a differential mortality between ages $0^{+}$and $1^{+}$for the 1973 year class was responsible for later abundance differences. Healey's (1980) data were consistent with this L226 observation for the 1973 year class. Very large recruitment of young fish already present in the population at the time of exploitation occurred in all three manipulated whitefish populations, while little recruitment of these fish occurred in the control lake.

The duration of increased growth and recruitment in Healey's moderately exploited populations was also similar to that in L226 NE. The growth response had abated in both lightly exploited populations three years after the cropping, and recruitment of new year classes dominated overall production. In L226 NE a marked growth response occurred for two years, but by the third year differences in abundance between L226 basins were more important to overall production than growth responses.

Application of L226 results to the theory of the structure and regulation of northern whitefish populations

Johnson (1976) and Power (1978) present conflicting hypotheses to explain the structure and regulation of unexploited northern fish populations. Catches from these populations are characterized by (1) many fish of relatively uniform large size, forming a dominant mode in population catch curves of age or length, and (2) many fish of relatively old age. The traditional explanation for this type of catch curve is that gear selectivity, especially when using gillnets, is responsible for the abridged number of fish below the dominant mode (Ricker 1975; Everhart et al. 1975; Beverton and Holt 1957). Selectivity of gillnets in exploited populations is well documented (see Hamley 1975 for a recent review). Johnson (1976) presents many gillnet catch curves from unexploited northern populations which do not fit the more traditional form (Fig. 17); he also found similar catch curves using other fishing gear. Length frequency distributions for both Healey's (1980) whitefish prior to exploitation and L226 whitefish prior to nutrient addition were similar to those of Johnson. After presenting Johnson's hypothesis to explain these catch curves, I will examine Power's alternative hypothesis. It is difficult to test either Johnson's or Power's hypotheses for unexploited populations. Manipulation experiments such as Healey's or the L226 fertilization provided indirect tests for some of the mechanisms proposed by Johnson and Power to regulate whitefish abundance and growth.

Figure 17. Typical gillnet selectivity of four mesh sizes for lake whitefish from (A) an exploited population (after Regier and Robson 1966), and (B) an unexploited population (after Johnson 1976).

## Johnson's hypothesis

Johnson (1972, 1976) hypothesizes that unimodal and bimodal catch curves are representative of the whitefish populations present in unexploited northern lakes. He suggests that population regulation occurs via a complex growth and mortality sequence among whitefish. The largerwhitefish of the dominant mode suppress the growth of smaller fish. This suppression may take the form of relegation of smaller whitefish to marginal habitats where their survival is lower (Johnson 1976). The dominant fish group is a closed population with relatively constant number and low mortality rate. Subordinate fish filter into the dominant mode as older fish die. This explains the presence of many age groups in the dominant mode; fish enter the mode at different ages.

There are some difficulties that arise from Johnson's hypothesis, and with the data he uses to support his hypothesis. The first is that there are few confirming data for the aging methods he used for many of the whitefish populations. Accurate aging, or at least fairly accurate aging, for a large proportion of the catch from a lake is extremely important for forming catch curves based on age frequency distributions. A possible extension of this problem is that many of Johnson's (1976) catch curves have rapidly declining right hand portions, indicating high mortality rates for much of this dominant mode. It is difficult to conceive of a mechanism for supressing younger, smaller fish when a large portion of the dominant mode is undergoing high mortality. Second, it is necessary to assume that fish essentially do not grow for a period of years, and then grow very rapidly to the approximate modal length of the dominant group. There is some evidence of individuals moving from the subordinate mode to the dominant mode in
many of Johnson's length frequency distributions, but he presents no detailed growth histories for intermediate sized animals to support his hypothesis. Third, it is difficult to conceive of a mechanism that would allow only some members of the subordinate group access to the empty spaces in the dominant fish group, while suppression of other members continues. Behavorial studies, under conditions of limited space, have shown that dominant fish can suppress the growth of subordinates (Magnuson 1962; Noakes 1978) but lakes are substantially larger than laboratory aquaria. If subordinates are relegated to marginal habitats as Johnson hypothesizes, then behavioral factors may be responsible for a hierarchy within the subordinate fish mode, which in turn may determine which fish advance later to the dominant mode. Spatial segregation also is difficult to prove in field studies when it involves catching very young fish. Certain fishing gear, such as electroshocking, catch many small fish in shallow water, but catch few fish in deeper pelagic waters.

## Power's hypothesis

Power (1978) hypothesizes that the age frequency distributions observed many times for unexploited northern populations are artifacts, produced by grossly underaging many individuals in a catch. He believes that unimodal or bimodal length frequency distributions for these populations are the result of natural variation in length at age, and cites a model similar to Baranov's (1918, as cited in Ricker 1975) to show that bimodal length frequency distributions are the natural consequence of low annual mortality, low growth rates, and increasing variance in length of fish with older age.

Power believes the use of scales in Johnson's and other studies results in grossly underaging many fish. In his opinion, the mode present in many of Johnson's distributions may be the point where the aging method fails. Fish would cluster around this point forming a prominent mode. He believes sectioning otoliths is a more reliable method for aging slow growing northern populations, though he presents no comparisons between scale and otolith ages for the whitefish populations he examined. Usually when discrepancies occur between otolith and scale ages for an individual fish, the otolith age is preferred (Johnson 1976; Power 1978; and others). Power concludes from his data that no dominant mode among older fish exists, but curves are very similar to the classical catch curve (Fig. 17). He concludes that no complex growth or mortality sequence is necessary to explain the length and age frequency distributions from northern unexploited populations, only slow growth coupled with low mortality over much of a fish's life. The unimodal or bimodal length frequency distributions are then simply the outcomes of variance in fish length for each age group increasing as a function of fish age. He proposes that population regulation occurs among young fish by density dependent predation from other fish species, intraspecific density-dependent predation, or competition between young fish.

There are some underlying problems with Power's hypothesis. First, he presents no confirming evidence for otolith ages. He does reference a paper where otolith ages for lake trout were approximately twice corresponding scale ages, but trout scales are generally much harder to age than those of whitefish (Johnson 1976). There are no comparisons of otolith and scale ages for individual whitefish. A more important
problem is inadequate sample sizes, especially for his three whitefish populations ( $n=2,15$ and 27 respectively). Constructing age frequency distributions from the sample of 27 fish distributed among 55 age groups necessitates the running averages and multiplying length frequencies he uses to obtain reasonable looking catch curves. Other multiplication factors or calculating running averages over a different number of age groups might give very different results, and by inference very different mortality rates.

Implications of Healey's cropping experiment and the L226 nutrient addition experiment for Johnson's and Power's hypotheses

Healey (1980) concluded that results from his cropping experiments were more consistent with Johnson's hypothesis than Power's for three reasons. First, variations in whitefish growth were more closely related to year class than growth year in his populations. Fish of one year class (or age class) grew consistently faster over two or more years than fish of other year classes also present. This observation supports Johnson's view of a complicated pattern of growth, where some individuals grow faster than others present at the same time. Second, periods of good recruitment of young fish were associated with declines in numbers of adult fish. Good recruitment occurred only in the exploited lakes where adults had been removed. Third, catchability of young fish increased in exploited populations. The many young fish which were recruited into the exploited populations were present prior to exploitation but caught only rarely. All three observations agree with the population regulating mechanisms proposed by Johnson. Healey used scale aging for whitefish, and catch curves
for his three whitefish populations prior to exploitation were very similar to Johnson's (1976). He dismissed the occurrence of gross aging errors for his populations primarily on the strength of good agreement between scale ages determined by different readers and supports this by mark-recapture results. Four of eight recaptured whitefish had ages at recapture the correct numbers of years greater than at release. Mills and Beamish (1980, Appendix G) point out that agreement between readers represents consistency of age determinations, not accuracy. Mills and Beamish also present age comparison data between treatments of scale ages (from different readers) and between these scale ages and fin-ray ages. Fin-ray ages were generally greater than scale ages, while agreement between scale readings was sometimes very good between readers. It is certainly possible, based on Power's (1978) and Mills and Beamish's (1980) results that Healey has underestimated the severity of aging errors for these whitefish populations. These errors would not seriously bias the three generalizations cited above because these were based on relatively young fish, under age five, where fewer aging errors are likely to occur (Mills and Beamish 1980, Appendix G).

I interpret the results of the $L 226$ fertilization experiment to support Power's hypothesis for the structure of unexploited northern whitefish populations, and to support Johnson's hypothesis for the regulation of these populations.

I found that the unimodal length-frequency distribution present throughout the study in L226 SW and the bimodal distribution in L226 NE were a consequence of the low mortality rate of adult whitefish, slow growth of adult fish and the many age groups present in the population
beyond sexual maturity. Both age frequency and length frequency catch curves for L226 NE and SW whitefish were very similar to those hypothesized by Power. The bimodal curves in L226 NE were caused by the highly successful 1973 year class which resulted from fertilization.

No complex growth and mortality sequence was necessary to explain L226 whitefish age frequency and length frequency distributions. Whitefish mortality was constant over the three years of this study for fish older than $1^{+}$. While Healey (1980) found growth related more strongly to age classes than growth years, I found the reverse for whitefish in L226 (Figs. 6 and 7). Generally when high yearly growth was present for some age (or length) classes in L226, it was also present for almost all of the other age (or length) classes also present that year. I found no evidence for greater mortality of older adult whitefish than younger adult fish, which is necessary under Johnson's hypothesis.

Power predicted a clustering of fish about the age where the aging technique breaks down in age based catch curves. He believed this was responsible for the dominant mode in Johnson's age frequency distributions, though he presented no data to support this generalization. I found a distinct mode in L226 whitefish scale age catch curves from ages $4^{+}$to $7^{+}$similar to that in Fig. 2, the point where scale aging broke down for this population (Mills and Beamish 1980, Appendix G). This mode was absent in fin-ray based age frequency distributions. Plots for other unexploited whitefish populations reported in Mills and Beamish (1980, Appendix G) were similar, though the scale age where the mode occurred varied between populations.

The structure of L226 NE and SW whitefish populations is regulated by highly variable mortality among young fish. Regulation occurred in
fish under age $1^{+}$either through year class failures or greater mortality of fish from age $0^{+}$to $1^{+}$. Both Healey's results and results for L226 whitefish support the hypothesis that food availability limits the recruitment of whitefish. Healey found good recruitment only after many adult fish had been removed from exploited whitefish populations. Good recruitment in L226 NE occurred when more dipterans, the major whitefish food resource, were present (Fig. 15). Power suggests that cannibalism or predation limit fish recruitment for northern fish populations. I found no evidence of cannibalism among L226 whitefish, and no significant predators were present in L226. The slimy sculpin was a potential predator, but I found only dipterans in sculpin stomachs, examined periodically throughout the study. These observations support Johnson's hypothesis for older fish suppressing the growth of younger, smaller fish, though the evidence is circumstantial.

The role of fish behavior in limiting production or in the regulation of fish population size is only beginning to receive attention (Noakes 1978). Many studies support the hypothesis that dominant individuals can affect changes in subordinates' growth and survival. Dominance hierarchies for many fishes have been demonstrated repeatedly (see Noakes 1978 for a review) and artificial crowding has intensified dominance interactions for mosquitofish, Gombusia holbrooki (Martin 1975). There is evidence in salmonids that subordinate fish are forced to move more, feed less, and consequently suffer a much higher mortality rate than dominant fish (Backiel and LeCren 1978; Chapman 1966; Miller 1958; Noakes 1978). Rainbow trout (Salmo gairdnemi) will show territorial and/or dominance behavior when a restricted quantity of food is present, but these actions disappear when the amount of available
food is increased (Landless 1976). Magnuson (1962) showed that aggressive behavior in the medaka (Oryzias latipes) was largely responsible for growth differences among individuals under conditions of restricted food or space. Aggressive behavior is not necessarily an essential component of this interaction for some species. For example, Eaton and Farley (1974) showed that larger zebrafish (Brachydanio rerio) were more efficient food gatherers than smaller fish when limited food was available. No aggressive behavior was present. Under conditions of adequate food, such as the initial increases in benthic biomass in L226 NE, enhancement of feeding or social facilitation, common in domestic animals (Scott 1969) may also occur. The significance of gregarious feeding behavior has often been postulated for fish (as reviewed by Noakes 1978). These interactions may disappear later after the fish biomass has reached its new carrying capacity. Certainly this could be an explanation for the decreasing importance of growth differences after the first two years of fertilization in L226 NE and for the absence of growth differences for Lake Memphramagog perch along the production gradient present in the lake. Results of the $L 226$ fertilization with those of Johnson (1976) and Healey (1978) strongly suggest that behavioral regulation of population size occurs in unexploited whitefish populations.

It might be argued that different mechanisms are operating in ELA whitefish populations than the more northern populations of Healey (1978, 1980), Johnson (1972, 1976) or Power (1978). Certainly the maximum age Power found for lake whitefish ( $57^{+}$) was approximately twice the maximum age observed for L226 whitefish, but Erickson (1980) showed that extremely old whitefish also exist in southeastern Manitoba,
near ELA. Healey (1975) showed that many unexploited southern whitefish populations grow at least as fast as northern populations. Mills and Beamish (1980, Appendix G) also found no differences in mortality rates between northern and southern unexploited whitefish populations. It is only logical to conclude that the same mechanisms for limiting the abundance and growth of northern arctic populations operate for more southern populations also.

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Appendix A. The closure assumption

The closure assumption is a basic assumption of the Jolly-Seber and other mark-recapture models (Seber 1973, Ricker 1975). In the most general case, for the "open" or sometimes called the "full" model, this assumption consists of no non-permanent emigration of individuals out of and back into the population within the study period. Births, or new immigrants, are estimated by the model as new entries into the population. In the Jolly-Serber "death-only" model, the closure assumption is extended to include no immigration of individuals into the population within the study period. It is obvious that a population which meets this extended closure assumption for the death-only model, also meets the assumption for the full model.

Lake 226 is a small lake with one inlet entering the west end of the lake from a diffuse source. The outlet from L226 is small, approximately 10 cm deep where it originates from the lake and a small waterfall along its course blocks any immigration into L226 from L468 (Cleugh and Hauser 1971). Both inlet and outlet run normally only during three to four months of the seven month ice-free season. Immigration into or non-permanent emigration from L226 is therefore highly unlikely. Both the full model or the death-only model, if new recruits are excluded, are appropriate for $L 226$ whitefish.

The possibility of interchange of fish between basins must also be considered when evaluating the closure assumption. Divers ensured that there were no major or minor openings from one basin into the other when the wall was installed, early June 1973, by burying the wall bottom in lake sediments and securing the wall sides continuously from bottom
to surface along lake shores with boulders. In addition, divers examined the wall from time to time between 1974 and 1977; only one small hole was found resulting from the splitting of a zipper joining sections of the wall (in July 1977). This hole was promptly repaired. In addition, floats which supported the wall top were periodically repaired to minimize water exchange between basins. Evidence of fish exchange between basins can only come from the capture histories of individually tagged fish. By winter 1974, over $45 \%$ of all whitefish caught in L226 NE and over 30\% in L226 SW were previously tagged and by winter 1975, over 78\% of all whitefish in L226 NE and over $65 \%$ in L226 SW were marked. Only one tagged whitefish, in 1975, was caught in a basin other than where it was tagged over the five year study period. No significant whitefish interchange occurred between basins.

The Jolly-Seber death-only model was initially chosen to calculate abundance estimates $\left(\hat{N}_{\mathfrak{j}}\right)$ and survival rates $\left(\hat{\phi}_{\mathbf{i}}\right)$ for $L 226$ whitefish from each basin because an estimate of $N_{1}$ can be obtained. No direct estimate of $N_{1}$ is available using the open model. The open model estimates are generally less precise than their closed model equivalents because an estimate of new entries entering the population during the study is also generated. New entries were excluded from analyses of the L226 whitefish population on the basis of ages from fin-ray sections (Mills and Beamish 1980, Appendix G). Arnason and Mills (1980) show that there is a gain in precision obtained by this subdivision of the population. New entries occurring during the study were separated for additional analyses using the death-only model.

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Appendix B. Tag loss, its effects on Jolly-Seber estimates and methods for correcting estimates

## INTRODUCTION

Implicit to multiple mark-recapture techniques is the assumption that animals do not lose their marks. While it is well known that tag loss can bias estimates of population size $\left(\hat{N}_{i}\right)$ and survival ( $\hat{\phi}_{j}$ ) (Cormack 1968), the relative magnitude of bias that a given tag loss rate produces in individual estimates is unknown. Arnason and Mills (1981) present explicit methods for calculating bias in Jolly-Seber estimates when the tag loss rate is known and occurs homogeneously throughout the population. These methods are only asymptotically correct, when sample sizes become "large" and recapture rates "high" (Seber 1973). Since "large" and "high" cannot be specifically defined, biases calculated analytically by the methods of Arnason and Mills (1981) should be confirmed by simulations. In addition, Arnason and Mills (1981) methods deal specifically with cases where the tag loss rate is homogeneous among tagged animals alive at a given time. If the tag loss rate is heterogeneous, such as when two tag types are used in a mark-recapture experiment and each is lost at a significantly different rate, simulations provide an empirical method for assessing tag loss bias where other explicit techniques do not exist. The purpose of this appendix was to (1) calculate tag loss rates from field data for two different tag types, (2) assess the bias introduced in Jolly-Seber death-only and open model $\hat{N}_{i}$ and $\hat{\phi}_{i}$ by the loss of each of these tag types, and (3) assess the bias introduced in estimates
when both tag types are used in combination in a mark-recapture experiment.

MATERIALS AND METHODS

Estimates of tag loss rates

Two types of individually numbered tags were used to mark lake whitefish (Coregonus clupeaformis) in a mark-recapture experiment spanning six years in Lake 226 (referred to as L226 hereafter), the Experimental Lakes Area, northwestern Ontario (Cleugh and Hauser 1971). L226 is a small ( 16.1 ha, $Z_{\max } 14.7 \mathrm{~m}$ ) double basin lake divided into halves (L226 NE and L226 SW) using a vinyl curtain.

Floy FD-68B gun tags (De11 1968) were used to mark 161 whitefish captured and released during fall 1973 in L226 NE. Modified Carlin sew-on tags (White and Beamish 1972) were used to mark the remaining whitefish caught in L226 NE from fall 1973 to fall 1977. When animals lost tags, the sew-on tag was used to remark animals. This sew-on tag was used in L226 SW from 1973 to 1977; gun tags were not used in this basin. In addition to numbered tags, each fish was marked with a partial pelvic fin clip which was not regenerated during the course of the study. While fish were captured and released continuously from 1974 to 1977 during the ice-free seasons, more than $69 \%$ were caught each year during a three week period each fall. Tag loss rates were estimated using only this fall data; intervening sampling periods were omitted.

When tag loss occurred, the type of tag lost was easily identified
by the scar each left on the fish. The gun tag left a scar only on the side of the fish where it was injected through the pterygiophores beneath the dorsal fin. The sew-on tag left a scar on both sides of the animal where the surgeon's needle was inserted during tagging. All animals which lost tags were retagged with sew-on tags. Indirect evidence that one could reliably distinguish between tag types lost on the basis of scar tissue comes from L226 SW where no animals were tagged with gun tags. Of the fish recaptured from this basin that had lost tags, none had a tag scar on only one side of the fish as attributed to gun tags in L226 NE. All had scars on both sides of the fish beneath the dorsal fin.

The Robson-Regier (1966) model was used to estimate a tag loss rate for those animals tagged with gun tags. While this model was initially developed for removal sampling, where all animals were killed at recapture, it was still applicable when recaptured animals were returned to the population (Arnason and Mills 1980). The necessary conditions to use this model are that (1) recaptured animals that have lost tags are subsequently retagged so they are not confused with other animals who have lost tags, (2) for all animals captured and exhibiting tag loss, the time when they were first captured and tagged is known, and (3) tag loss occurs at a homogeneous rate per unit time throughout the experiment.

The Robson-Regier model was also used to estimate tag loss rates for animals initially tagged with sew-on tags in both basins. Since fish were marked throughout the study with this type of tag, the model is not strictly appropriate since it was developed for estimating a tag loss rate for animals marked only during the first sampling period.

At this time alternative models do not exist, so the tag loss rate for sew-on tags can be calculated as follows (Arnason and Mills 1980):
(1) Construct a standard trellis diagram as in Ricker (1975) for the number of observed tag retentions for each year of study.
(2) Distribute the total number of animais that have lost tags among these strata in (1) according to the proportion of each caught and retaining tags in each sample.
(3) Carry out the analysis as described in Robson and Regier (1966).

Simulation methods for determining bias in $\hat{N}_{i}$ and $\hat{\phi}_{i}$ from loss of a single tag type at a homogeneous rate

Bias is the systematic error between the actual true value of a parameter and an estimated value of that parameter (Arnason and Baniuk 1978). The size of a bias (in expectation) can be defined as:

$$
\begin{aligned}
\text { Bias } & =\text { Estimated value }- \text { True value } \\
& =\hat{N}_{i}-N_{i} \text { or } \\
& =\hat{\phi}_{i}-\phi_{i}
\end{aligned}
$$

Mark-recapture computer simulations (Arnason and Baniuk 1978) were used to determine the bias introduced in $\hat{N}_{i}$ and $\hat{\phi}_{i}$ from tag loss for a population similar to L226 NE whitefish. Preliminary L226 NE whitefish population parameters were used to construct the simulations where:

$$
\begin{aligned}
N_{1}= & \text { true population at time } 1,683 \text { fish } \\
\phi_{i}= & \text { true survival rate between sampling } \\
& \text { periods, } 0.75
\end{aligned}
$$

$$
\begin{aligned}
P_{i}= & \text { probability an animal is captured, } \\
& 0.22, \text { at each sampling period } \\
1= & \text { total number of samples, each assumed } \\
& \text { to be one year apart, } 6
\end{aligned}
$$

New entries, or births, were not allowed in simulations; the populations were "closed", only subject to dilutions by death. Seven tag loss rates were tested: $0,5,10,20,40$ and $60 \%$ loss between each pair of successive sampling periods. Nine independent simulations were run using the Jolly-Seber "death-only" model and the Jolly-Seber "open" model (Jolly 1965, Seber 1973). The simulation technique (Arnason and Baniuk 1978) can be outlined briefly as follows:
(1) The initial number of animals, 683 was first generated.
(2) A sample was drawn from this population and returned after being marked.
(3) The population underwent mortality at the specified rate.
(4) The marked subset underwent tag loss at the specified rate; animals that lost tags joined the unmarked subset.
(5) A sample was drawn from the population, recaptured animals were tabulated, unmarked animals were marked and all animals were then returned to the population.
(6) Steps three to five were repeated until the sample number equaled the total number specified.
(7) $\hat{N}_{i}$ and $\hat{\phi}_{i}$ were formed from the statistics gathered during the simulations along with $\hat{N}_{\mathfrak{i}}$ and $\hat{\phi}_{\mathbf{i}}$ determined from the known parameters.

A11 simulations were stochastic, so successive $\hat{N}_{i}$ and $\hat{\phi}_{i}$ for individual replications (experimental runs with the same true parameters but
different random number streams) will vary slightly. After nine replications, average values for $N_{i}, \phi_{i}, \hat{N}_{j}, \hat{\phi}_{i}$, and their standard errors were calculated. The standard errors were formed using the individual $\hat{N}_{i}$ and $\hat{\phi}_{i}$ over the nine replications.

The criteria used to judge bias in $\hat{N}_{i}$ and $\hat{\phi}_{i}$ were:
(1) The relative size of the estimated bias, or

$$
\overline{\hat{N}}_{i}-\bar{N}_{i} \text { or } \overline{\hat{\phi}}_{i}-\phi_{i}
$$

where the average sign implies means over nine replications.
(2) Whether the bias was consistently positive or negative over successive $\hat{N}_{i}$ or $\hat{\phi}_{i}$.
(3) Whether the bias was significantly different from "zero".

A bias was judged significant if it exceeded:
$1.96 \times$ standard error of the estimated bias Arnason and Baniuk (1978) discuss this in greater detail.

Simulation methods for determining bias in $\hat{N}_{i}$ and $\hat{\phi}_{i}$ from a population where both tag types are used and tag loss is heterogeneous

In the case where two tag types were present in a population, and each was lost at a different rate, generalized simulations at a variety of tag loss rate combinations as used in the previous section were impractical. In this case, each subpopulation marked with a different tag type was introduced as a cohort, with different tag loss rates for each cohort:
cohort 1-161 animals all captured and tagged at time 1 subjected to the gun-tag loss rate, $18 \%$ per year.

$$
\begin{aligned}
\text { cohort } 2- & 487 \text { animals captured and tagged through- } \\
& \text { out the simulation subjected to the sew- } \\
& \text { on tag loss rate, } 1 \% \text { per year. }
\end{aligned}
$$

Other parameters were the same as described for the simulations of the previous section. The populations were closed; no births were allowed. Twenty-five separate simulations were run for both the open and deathonly Jolly-Seber models. The criteria used to judge bias in $\hat{N}_{i}$ and $\hat{\phi}_{\boldsymbol{j}}$ were as described in the previous section.

## RESULTS

Estimates of tag loss rates for each tag type

Gun tags (Table B.1) were lost at a much higher rate than sew-on tags (Tables B. 2 and B.3). The retention rate for gun tags was estimated as 0.824 (standard error $=0.017$ ), or if expressed as a loss rate, $17.6 \%$ per year. The retention rates for sew-on tags were similar between L226 NE and L226 SW, 0.984 (S.E. $=0.005$ ) and 0.989 (S.E. $=$ 0.004 ) respectively (or loss rates of $1.6 \%$ and $1.1 \%$ per year). The observed proportions of animals retaining tags were very similar to theoretical values generated from the Robson-Regier model (Tables B. 1 to B.3) and goodness of fit tests confirmed that this model was adequate for the data (gun tags: $\chi^{2}=0.70, p>0.75,3$ df; sew-on tags L226 NE: $x^{2}=0.93, p>0.75$, 3df; sew-on tags L226 SW: $x^{2}=$ $0.57, p>0.75,3 d f)$.

Table B.1. Tag retention frequency of gun tags from L226 NE whitefish. The expected retention for each sample is also presented, based on results from the Robson-Regier (1966) model where the retention rate $(\hat{r})=0.824$, $\operatorname{SE}(\hat{r})=0.017$.

| Sample time <br> after release <br> $(t)$ | Year | $R_{i}$ | $L_{i}$ | Retention <br> $R_{i} /\left(R_{i}+L_{i}\right)$ | Expected <br> retention <br> $(r t)$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 1974 | 60 | 11 | 0.845 | 0.824 |
| 2 | 1975 | 53 | 25 | 0.679 | 0.679 |
| 3 | 1976 | 42 | 36 | 0.538 | 0.559 |
| 4 | 1977 | 12 | 13 | 0.480 | 0.461 |

Table B.2. The tag retention trellis (A) and estimated tag retention frequency of sew-on tags (B) for L226 NE whitefish. The distribution of tag losses among release strata ( $j$ ) is indicated in parentheses. The expected retention for each sample is also presented based on Robson-Regier (1966) model results where the retention rate $(\hat{r})=0.984, S E(\hat{r})=0.005$.

A

| Year of <br> release <br> $(j)$ | New tags <br> added | 1974 | 1975 | 1976 | 1977 |
| :--- | :---: | :---: | :---: | :---: | :---: |
| 1973 | 122 | $48(0)$ | $49(1)$ | $56(2)$ | $11(1)$ |
| 1974 | 68 |  | $53(1)$ | $71(2)$ | $16(1)$ |
| 1975 | 39 |  |  | $54(1)$ | $23(1)$ |
| 1976 | 56 | 48 | 102 | 181 | 61 |
| Total retentions |  | 2 | 5 | 4 |  |
| Total losses |  |  |  |  |  |

B

| Sample time <br> after release <br> $(t)$ | $R_{i}$ | $L_{i}$ | Retention <br> $R_{i} / R_{i}+L_{i}$ | Expected <br> retention <br> $(r t)$ |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 166 | 3 | 0.982 | 0.984 |
| 2 | 143 | 4 | 0.973 | 0.969 |
| 3 | 72 | 3 | 0.960 | 0.953 |
| 4 | 11 | 1 | 0.917 | 0.938 |

Table B.3. The tag retention trellis (A) and estimated tag retention frequency of sew-on tags (B) for L226 SW whitefish. The distribution of tag losses among release strata ( $j$ ) is indicated in parentheses. The expected retention of each sample is also presented based on Robson-Regier (1966) model results where the retention rate $(\hat{r})=0.989, \operatorname{SE}(\hat{r})=0.004$.

## A

| Year of <br> release <br> $(j)$ | New tags <br> added | 1974 | 1975 | 1976 | 1977 |
| :--- | :---: | :---: | :---: | :---: | :---: |
| 1973 | 85 | $48(0)$ | $43(0)$ | $30(0)$ | $19(1)$ |
| 1974 | 198 |  | $81(1)$ | $75(2)$ | $31(1)$ |
| 1975 | 71 | 28 |  |  | $33(1)$ |
| 1976 | 0 | 124 | $13(1)$ |  |  |
| Total retentions of recapture |  |  |  |  |  |
| Total losses |  |  |  | 3 | $6(0)$ |

B

| Sample time <br> after release <br> $(t)$ | $R_{i}$ | $L_{i}$ | Retention <br> $\left(R_{i} / R_{i}+L_{i}\right)$ | Expected <br> retention <br> $\left(\hat{r}^{t}\right)$ |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 168 | 2 | 0.988 | 0.989 |
| 2 | 131 | 3 | 0.978 | 0.978 |
| 3 | 61 | 1 | 0.984 | 0.967 |
| 4 | 19 | 1 | 0.950 | 0.957 |

Bias introduced in $\hat{N}_{i}$ and $\hat{\phi}_{i}$ by each tag type: the death-only model

Many $\hat{N}_{i}$ were inflated as a result of tag loss (Table B.4), and in general death-only $\hat{N}_{i}$ were very susceptible to bias from tag loss. The first relatively large bias in $\hat{N}_{\mathrm{j}}$ occurred between 5 and $10 \%$ tag loss per year. This was also the point when biases became consistent, always resulting in significantly larger $\hat{N}_{i}$ than true $\hat{N}_{j}$. The biases of $\hat{N}_{i}$ for early sampling periods were generally greater than those of later $\hat{N}_{i}$ regardless of tag loss rate.

Tag loss had no detectable effect on most survival estimates (Table B.5). With the exception of the extreme tag loss rate of $60 \%$, generally $\hat{\phi}_{i}$ were rarely significantly different from true $\hat{\phi}_{i}$. Other significant differences at lower tag loss rates showed no consistent pattern. Use of either tag type would not result in detectable bias in $\hat{\phi}_{i}$.

Bias introduced in $\hat{N}_{\boldsymbol{j}}$ and $\hat{\phi}_{\boldsymbol{i}}$ by each tag type: the open model

Open model $\hat{N}_{i}$ were very robust to violations of the no tag loss assumption regardless of the tag loss rate (Table B.6). No estimate of $N_{1}$ is available using this model, but succeeding $\hat{N}_{i}$ showed no perceptible bias.

Open model $\hat{\phi}_{\mathbf{i}}$ were in general sporadic at tag loss rates greater than or equal to $5 \%$ per year (Table B.7). Many times $\hat{\phi}_{i}$ were significantly less than true $\hat{\phi}_{i}$. In general, as the tag loss rate increased, negative bias of $\hat{\phi}_{\boldsymbol{j}}$ became larger.

Table B.4. Average bias of population estimates $\left(\hat{N}_{j}\right)$ from true $N_{i}$ over nine independent simulations at each tag loss rate, using the JollySeber "death-only" model. See text for a more detailed explanation.

| Sample <br> (i) | Average true population$\begin{aligned} & \text { size } \\ & \left(\bar{N}_{j}\right) \end{aligned}$ | Tag loss rate |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 0.0 | 0.01 | 0.05 | 0.10 | 0.15 | 0.20 | 0.40 | 0.60 |
| Average bias of $\mathrm{N}_{i}$ |  |  |  |  |  |  |  |  |  |
| 1 | 683 | 15 | 17 | $105 *$ | 258* | $375 *$ | 419* | 1330* | 2666* |
| 2 | 511 | 24 | -16 | $38 *$ | 171 * | $224 *$ | $278 *$ | 779 * | $2242{ }^{*}$ |
| 3 | 382 | -10 | 0 | 36 | $82^{*}$ | $169 *$ | 211 * | $444 *$ | 1056* |
| 4 | 289 | -17 | 21 | 6 | 47 | $74 *$ | 158* | $243 *$ | 979* |
| 5 | 218 | 8 | 35 | 77 | 17 | $35^{*}$ | $110^{*}$ | $144 *$ | 256* |

${ }^{*}$ Significant difference between $\bar{N}_{i}$ and $\overline{\hat{N}}_{j}, p<0.05$.
Table B.5. Average bias of survival estimates ( $\overline{\hat{\phi}}_{j}$ ) from true $\phi_{i}$ over nine independent simulations at each tag loss rate using the JollySeber "death-only" model. See text for a more detailed explanation.

| Sample <br> (i) | True survival rate $\left(\phi_{i}\right)$ | $0.0 \cdot 0.01$ | 0.05 | Tag 10 0.10 | ss rate 0.15 | 0.20 | 0.40 | 0.60 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Average bias of $\hat{\phi}_{\mathbf{i}}$ |  |  |  |  |  |  |
| 1 | 0.75 | 0.02-0.04 | -0.05 | -0.02 | -0.05 | -0.03 | -0.08 | 0.06 |
| 2 | 0.75 | -0.05 0.02 | 0.01 | -0.07* | 0.01 | 0.02 | -0.08 | -0.20 * |
| 3 | 0.75 | -0.02 0.05 | -0.03 | -0.03 | -0.08 | $-0.12^{*}$ | -0.13 * | $-0.12^{*}$ |
| 4 | 0.75 | 0.02-0.01 | 0.03 | -0.04 | -0.04 | -0.08 | 0.11 | -0.25 |

* Significant difference between $\phi_{i}$ and $\overline{\hat{\phi}}_{i}, p<0.05$.

Table B.6. Average bias of population estimates $\left(\hat{N}_{j}\right)$ from true $N_{i}$ over nine independent simulations at each tag loss rate using the JollySeber "open" model. See text for a more detailed explanation.

| Sample <br> (i) | $\begin{gathered} \text { Average true } \\ \text { population } \\ \text { size } \\ \left(N_{i}\right) \end{gathered}$ | 0.0 | 0.01 | 0.05 | $\begin{gathered} \text { Tag } 10 \\ 0.10 \end{gathered}$ |  | 0.20 | 0.40 | 0.60 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Average bias of $\hat{N}_{i}$ |  |  |  |  |  |  |  |
| 1 | 683 | a | a | a | a | a | a | a | a |
| 2 | 513 | 46 | -43 | -49 | -27 | 30 | 30 | 105 | 38 |
| 3 | 384 | -7 | - 1 | - 8 | -33 | -6 | 35 | 6 | -71 |
| 4 | 289 | 46 | -28 | -22 | 30 | -2 | 10 | 13 | -92 |
| 5 | 216 | 16 | - 1 | 17 | -25 | 2 | 6 | -54 | $-94 *$ |

${ }^{\text {a }}$ No estimate available.

* Significant difference between $\bar{N}_{i}$ and $\overline{\hat{N}}_{i}, p<0.05$.
Table B.7. Average bias of survival estimates ( $\hat{\phi}_{\mathbf{j}}$ ) from true rates over nine independent simulations of for a more detailed explanation.

| Sample (i) | Average true survival rate $\left(\bar{\phi}_{\mathbf{j}}\right)$ | 0.0 | 0.01 | 0.05 | Tag los 0.10 | rate 0.15 | 0.20 | 0.40 | 0.60 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 0.75 | -0.007 | -0.016 | -0.029 | $-0.124^{*}$ | $-0.106^{*}$ | $-0.132^{*}$ | -0.189* | -0.384* |
| 2 | 0.75 | 0.043 | 0.004 | -0.022 | -0.059 | $-0.052^{*}$ | -0.087 | $-0.294^{*}$ | $-0.535^{*}$ |
| 3 | 0.75 | -0.037 | -0.051 | $-0.107^{*}$ | -0.051 | -0.098* | -0.187* | -0.280 * | -0.480 * |
| 4 | 0.75 | 0.076 | 0.028 | $0.082^{*}$ | -0.451* | -0.147 | -0.478* | -0.350 * | $-0.565^{*}$ |
| Significant difference between $\bar{\phi}_{i}$ and $\overline{\hat{\phi}}_{i}, \mathrm{p}<0.05$. |  |  |  |  |  |  |  |  |  |

Bias introduced in $\hat{N}_{j}$ and $\hat{\phi}_{i}$ when both tag types were present and lost heterogeneously

Death-only model $\hat{N}_{i}$ were severely inflated due to tag loss (Table B.8) while death-only $\hat{\phi}_{i}$ were not perceptively biased. Generally, early $\hat{N}_{i}$ were more biased than later estimates.

Open model $\hat{N}_{i}$ were generally not perceptively biased (Table B.9) except $N_{1}$, which was an underestimate by approximately $8.8 \%$. Open model $\hat{\phi}_{\mathfrak{j}}$ were significantly biased for two periods and three of the four $\hat{\phi}_{\boldsymbol{i}}$ were underestimates.

## DISCUSSION

The $18 \%$ gun tag loss rate and the one to two percent sew-on tag loss rate determined in this study were well within the range of those previously reported. Tag loss has varied from essentially no tag loss (MacCrimmon and Robbins 1979) to over $70 \%$ per year (Armstrong and Blackett 1966) using other tagging methods. White and Beamish (1972) reported tag loss rates after three years of $17 \%$ for smallmouth bass (Micropterus dolomieui) and $0.6 \%$ for white sucker (Catostomus commersoni) using similar sew-on tags. Carline and Brynildson (1972) found that brook trout (Salvelinus fontinalis) lost gun tags at rates of 5.7 and $2.0 \%$ for two independent trials of eight months each. Any conversion of Carline and Brynildson's rates to annual rates for comparison to the whitefish gun-tag loss rate is probably misleading. Their study occurred over winter months when little fish growth was occurring. Catch records for $L 226$ whitefish indicated that most tag loss occurred

Table B.8. Results of 25 simulations when tag loss was heterogeneous ( $r_{1}=$ $.824, r_{2}=.984$ ) using the death-only model.

| Time <br> (i) | $\overline{\hat{N}}_{i}$ | $\bar{N}_{i}$ | Bias $N_{i}$ | $\left.\underset{\times 1.96}{\operatorname{SE}(\text { Bias }} \overline{\hat{N}}_{j}\right)$ | $\overline{\hat{\phi}}_{i}$ | $\bar{\phi}_{i}$ | $\mathrm{Bi}_{\hat{\phi}_{i}}$ | $\begin{gathered} \operatorname{SE}\left(\text { Bias } \hat{\phi}_{i}\right) \\ \times 1.96 \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 740 | 648 | $92^{*}$ | 26 | . 742 | . 748 | -. 006 | . 045 |
| 2 | 546 | 486 | 61 * | 30 | . 753 | . 750 | . 003 | . 057 |
| 3 | 407 | 365 | $43^{*}$ | 30 | . 759 | . 757 | . 002 | . 059 |
| 4 | 312 | 273 | $37 *$ | 23 | . 675 | . 747 | -. 072 | . 078 |
| 5 | 212 | 205 | 7 | 22 |  |  |  |  |

Significant difference between $\bar{N}_{i}$ and $\overline{\hat{N}}_{i}, p<0.05$.

Table B.9. Results of 25 simulations when tag loss was heterogeneous ( $r_{1}=$ .824, $r_{2}=.984$ ) using the open model.

| Time <br> (i) | $\overline{\hat{N}}_{i}$ | $\bar{N}_{i}$ | ${\stackrel{\text { Bias }}{N_{i}}}^{\text {and }}$ | $\left.\underset{\times 1.96}{\operatorname{SE}(\operatorname{Bias}} \overline{\hat{N}}_{i}\right)$ | $\overline{\hat{\phi}}_{i}$ | $\phi_{i}$ | $\mathrm{B}_{\hat{\phi}_{\dot{j}}}$ | $\begin{gathered} \operatorname{SE}\left(\operatorname{Bias} \overline{\hat{\phi}}_{i}\right) \\ \times 1.96 \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | - | 648 |  |  |  |  |  |  |
| 2 | 442 | 485 | $-43 *$ | 31 | . 675 | . 748 | -. 073 * | . 045 |
| 3 | 367 | 363 | 4 | 34 | . 737 | . 748 | -. 011 | . 055 |
| 4 | 287 | 270 | 7 | 30 | . 753 | . 744 | . 009 | . 076 |
| 5 | 188 | 202 | -14 | 22 | . 644 | . 749 | $-.105^{*}$ | . 080 |
| 6 | - | 153 |  |  |  | . 755 |  |  |

* Significance difference between $\bar{N}_{i}$ and $\overline{\hat{N}}_{i}$ or $\bar{\phi}_{i}$ and $\overline{\hat{\phi}}_{j}, p<0.05$.
during the summer months when fish are actively growing. Carline and Brynildson's estimates are therefore probably underestimates if converted to annual rates.

The simulations invoiving homogeneous tag loss indicate that the use of gun tags would seriously bias death-only mode $1 \hat{N}_{i}$ and open model $\hat{\phi}_{i}$. The simulations also show that either model could be used to form $\hat{N}_{i}$ and $\hat{\phi}_{i}$ for animals tagged with the sew-on tags. The bias is particularly crucial for the death-only model $\hat{N}_{i}$. As a general rule, in any multiple mark-recapture experiment, $\hat{N}_{i}$ for samples occurring early in the study have smaller standard errors, and therefore greater precision than later $\hat{N}_{i}$ if true survival is in fact high (say $\phi_{i}=0.5$ or greater) and sampling intensity is relatively constant at reasonable levels (say $P_{i}=0.1$ or more). The obvious result of this is that when interpreting a string of successive $\hat{N}_{j}$, much greater confidence is placed in the early $\hat{N}_{j}$. Since early $\hat{N}_{i}$ are also those most subject to tag loss bias, large interpretive errors could result. The simulations show that these early $\hat{N}_{i}$ can be significantly biased at tag loss rates as low as $5 \%$ per year. It is therefore essential that tag loss be very low if the death-only model $\hat{N}_{i}$ are used.

The results of the simulations show that under conditions of homogeneous tag loss, even at low rates, significantly biased deathonly $\hat{N}_{i}$ can occur, but that even in the presence of substantial homogeneous tag loss, valid $\hat{N}_{i}$ can be formed using the open model on a population which is in fact "closed". In this case, the estimate of births ( $\hat{B}_{j}$ ) that the open model produces may be a rough estimate of the number of fish that have lost tags, though the standard errors associated with $\hat{B}_{i}$ are usually so large that $\hat{B}_{i}$ are essentially
meaningless. In general, most Jolly-Seber $\hat{B}_{j}$, even under ideal simulation conditions when there are no violations of any assumption, are very poor unless a very large proportion of the population is caught in each sample (say $P_{i}>0.4$ ).

Valid $\hat{\phi}_{i}$ can be formed more readily with the death-only model than with the open model under conditions of homogeneous tag loss. Open model estimates of $\hat{\phi}_{\dot{i}}$ are generally underestimates because they are the product of the true $\hat{\phi}_{i}$ and the tag retention rate. While death-only $\hat{\phi}_{i}$ are slightly negatively biased (Arnason and Mills 1980), this bias is negligible, usually within the precision of $\hat{\phi}_{i}$ (bias << standard error of $\hat{\phi}_{j}$ ).

The results of the simulations under the particular set of conditions of heterogeneous tag loss show that if the open model is used when the population is in fact closed, estimates are fairly robust. Only one biased $\hat{N}_{i}$ was detected, but the bias was small and could well be within the experimental standard error of the estimate. This situation could occur in many field studies, where one high loss tag type is abandoned for another low loss type during the experiment. The bias tag loss heterogeneity introduces in $\hat{N}_{i}$ would probably be slight. Based on these simulation results, the open model should be used to form $\hat{N}_{j}$ for L226 NE whitefish where tag loss was occurring at a heterogeneous rate.

The simulations involving tag loss lead to two obvious questions:
(1) If open model $\hat{N}_{i}$ are more robust to violations of the no tag loss assumption, why not use the open model exclusively to derive $\hat{N}_{i}$ when in fact the death-only model is more appropriate?
(2) Since the open model $\hat{N}_{j}$ are very robust to tag loss when the population is closed, how robust to tag loss are open model $\hat{N}_{i}$ when births are in fact occurring (the population is open)?

The answer to the first question is two-fold. First, an estimate of the population size is available for the first sample using the death-only model while it is not available using the open model. The first $\hat{N}_{i}$ that can be formed is for the second sample using the open model. Second, since the open model estimates an additional parameter, $\hat{B}_{j}$, compared to the death-only model, the precision associated with open model $\hat{N}_{i}$ and $\hat{\phi}_{\boldsymbol{j}}$ is much poorer than death-only estimates. When mark-recapture data are collected associated with minimal tag loss, it is generally more efficient to use the death-only model than the open model.

The answer to the second question is more complicated than the evaluation of tag loss on the closed population since an additional parameter, $\hat{B}_{i}$, is added. Arnason and Mills (1980) discuss the theoretical bias in each parameter under these conditions. Some preliminary simulations (Mills, unpublished data) with the same $\hat{\phi}_{j}, N_{l}, P_{j}$ as in the previous death-only simulations, indicate that when births occur at a constant rate equal to the death rate, that $\hat{N}_{i}$ are only slightly positively biased and probably due to small sample bias rather than than tag loss (Arnason and Mills 1981). This bias is very small and not significant compared to the precision of $\hat{N}_{i}$. The $\hat{\phi}_{\mathfrak{i}}$ under these conditions are sometimes biased in a similar fashion to the open model estimates for the closed population, but that associated precision levels are poor. The $\hat{B}_{\mathbf{i}}$ are erratic, sometimes reflecting the combina-
tion of new recruits and animals that have lost tags, and other times much larger than true values. Theoretical analyses (Arnason and Mills 1980) show $\hat{B}_{i}$ estimate a complicated function of $B_{i}$ (the true recruits), tag losses (artificial recruits to the unmarked population) and $N_{i}$. Because the standard errors of $\hat{\mathrm{B}}_{\mathrm{i}}$ are almost always large, the estimates are of dubious value.

Tag loss can significantly bias $\hat{N}_{i}$ and $\hat{\phi}_{i}$. Every effort should be made to minimize tag loss in mark-recapture population studies. There is a great volume of previously published tag loss rates for many tag types. These should be used as a guide for tag choice for a species. In addition, all fish should be double tagged. This can consist of one numbered tag and a batch mark such as a fin clip as used in this study. In a more recent study using lake trout (Salveiinus namaycush), Welch and Mills (1981) tagged fish with sew-on tags and batch marked these fish in two ways. First, by partially clipping a fin and second, by puncturing dorsal fin-rays systematically according to the sampling period when captured. The puncture heals to form a prominent lump where the ray was pierced. In this way, an entire fish's capture history can be read from the rays of the dorsal fin. Even is a fish loses its tag, the information necessary for the JollySeber models is still available and the tag loss will not bias any estimates.

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Appendix $C$. Tests of the assumption of equal catchability

## INTRODUCTION

Almost all current mark-recapture techniques require that every individual alive in a population at a particular sample time has the same probability of being captured in that sample. More specifically, in actual experiments this assumption usually means that once an animal is tagged, the probability of recapturing this animal is the same as for other untagged animals or tagged animals, and that animals do not become trap shy after being recaptured on multiple occasions. Documented violations of this assumption are numerous (see Cormack 1968 for a review), but Buck and Thoits (1965) is a classic example. In this experiment, 15 ponds were drained after conducting mark-recapture experiments. The population estimates obtained from the Peterson model were compared with the actual number of fish counted after the ponds were drained. A substantial portion of many populations were uncatchable, resulting in population estimates which were as much as $78 \%$ under the true numbers. As a general rule, violations of this assumption involving trap avoidance by marked animals result in smaller numbers of recaptures for individual sampling periods and subsequent overestimates of $\hat{N}_{i}$ using the Jolly-Seber models (Arnason and Baniuk 1978; Otis et al. 1978). Where unequal catchability is due to some animals having a much higher than average probability of being caught or some animals having zero probability of being caught, the reverse occurs, giving underestimates of $\hat{N}_{j}$.

## MATERIALS AND METHODS

Various tests have been proposed to evaluate the hypothesis of equal catchability for multiple mark-recapture experiments (Seber 1973), but the Leslie-Carothers test (Carothers 1971,1973 ) has replaced others as a general test of equal catchability over the entire string of samples (i) in an experiment (Seber 1973). It makes more efficient use of markrecapture information and is more general in its application than previous tests. In particular, the data matrix used for calculation of the test statistic can be modified according to the closure assumptions of the mark-recapture model used for data analysis (Table C.1). Generally, the more restrictive the model, the larger the data base for analysis and therefore the more powerful the analysis. It is essentially a randomization test, similar to Cochran's test for related observations (Conover 1971).

The Leslie-Carothers test of equal catchability was applied to the individual capture histories from tagged animals for both L226 NE and SW. Since the populations in each basin were stratified to be "closed", subject to death-only, capture histories were modified to reflect the known presence of animals at sample time one even though they may have been seen for the first time later. Changes in the data blocks from the standard data format are illustrated in Table C.1. Since the data blocks used in this analysis were large, the Carother's suggested minimal mean number of captures per individual per block for the test was reduced from 1.5 to 0.98 . In addition, data used in this test should satisfy the closure (death-only) assumption and the no tag loss assumption. To satisfy the no tag loss assumption, capture histories

Table C.1. Capture histories for five fish arranged for (A) the "full" Jolly-Seber model and (B) the "death-only" Jolly-Seber model, prior to forming blocks for the Leslie-Carothers test of equal catchibility. If an animal is seen at time (i), then a " 1 " is recorded. If an animal is not seen at time (i), a "0" is recorded.

| Fish \# | Capture history |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Time | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|  |  |  |  |  |  |  | A |  |  |  |  |  |
| 1 |  | $1{ }^{\prime}$ | 0 | 1 | 0 | 0 | 0 | 0 | 0 | $1{ }^{\prime}$ |  |  |
| 2 |  |  | $1{ }^{\prime}$ | 0 | 0 | 0 | 1 | $1{ }^{\prime}$ |  |  |  |  |
| 3 |  |  |  | $1{ }^{1}$ | 1 | 0 | 0 | $1{ }^{\prime}$ |  |  |  |  |
| 4 |  |  |  | $1^{\prime}$ | 0 | 0 | 0 | 0 | 1 | $1{ }^{\prime}$ |  |  |
| 5 |  |  |  |  |  |  |  |  |  | $1^{\prime}$ | 0 | $1{ }^{\prime}$ |
|  |  |  |  |  |  |  | B |  |  |  |  |  |
| 5 |  | 0 * | 0 * | $0^{*}$ | 0 * | $0^{*}$ | 0 * | 0 * | $0^{*}$ | 1 | 0 | $1{ }^{\prime}$ |
| 1 |  | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | $1^{\prime}$ |  |  |
| 4 |  | 0 * | $0^{*}$ | 1 | 0 | 0 | 0 | 0 | 1 | $1{ }^{\prime}$ |  |  |
| 2 |  | 0 * | 1 | 0 | 0 | 0 | 1 | $1{ }^{\prime}$ |  |  |  |  |
| 3 |  | $0^{*}$ | 0 * | 1 | 1 | 0 | 0 | $1{ }^{\prime}$ |  |  |  |  |

1' Captures which do not contribute to the test.
$0^{*}$ Additional capture history data due to known presence of animals prior to first capture.
from gun-tagged fish, were removed prior to analyses.
While the Leslie-Carothers test is a general test covering the entire study, Pollock (1975) suggests constructing two-by-two contingency tables to test equal catability for each individual sample (i). These tests utilize the complete capture histories of animals to calculate the number of animals alive at (i) as the sume of those captured at (i) plus those captured for the first time in subsequent sampling periods. The tests are independent, and individual $x^{2}$ can be added as an overall test of equal catchability. Before individual contingency tables were constructed, data were abridged to satisfy the other Jolly-Seber death-only model assumptions as in the LeslieCarothers test. In general, $\left(m_{i}\right)$ and $\left(n_{j}\right)$ must be fairly large throughout the study to form meaningful tests. The Pollock tests are useful for testing for specific causes of unequal catchability, and so are a useful supplement to the general Leslie-Carothers test. The test in Table C. 3 stratifies the data into marked and unmarked classes, and hence tests if mark status affects catchability. Similarly, other stratifications (e.g. by age, sex, etc.) can be used (White 1975).

RESULTS

No heterogeneous catchability was detected in either the NE or SW basin whitefish data (Tables C. 2 and C.3). Block sizes were extremely large for the Leslie-Carothers test, resulting in extremely powerful tests.

Table C.2. Summary of Leslie-Carothers test of equal catchibility for L226 NE and SW whitefish.

| Block | No. <br> Rows | No. <br> Columns | Mean no. capture/row <br> Observed <br> (var.) | Expected | $x^{2}$ | dfProb. <br> levei |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| L226 NE |  |  |  |  | 214.8 | 218 | 0.50 |
| 1 | 57 | 9 | $1.82(0.015)$ | 1.96 |  |  |  |
| 2 | 89 | 8 | $1.54(0.007)$ | 1.40 |  |  |  |
| 3 | 41 | 7 | $0.98(0.019)$ | 1.14 |  |  |  |
| 4 | 32 | 5 | $1.44(0.020)$ | 0.91 |  |  |  |

$\begin{array}{llllll}\text { L226 SW } & 198.2 & 183 & 0.76\end{array}$

| 1 | 55 | 9 | $1.95(0.014)$ | 1.86 |
| :--- | :--- | :--- | :--- | :--- |
| 2 | 95 | 8 | $1.36(0.006)$ | 1.30 |
| 3 | 34 | 7 | $1.09(0.022)$ | 1.11 |

Table C.3. Comparisons of capture frequencies of marked and unmarked whitefish to detect unequal catchability. An example table (A) using Jolly's (1965) notation and results (B).

A

|  | Seen at i Not seen at i |  |
| :---: | :---: | :---: |
| Known number unmarked and alive in population | S. $1\left(\mathrm{n}_{10}\right)$ | N. $1 \underset{\left(\sum_{j>2} n_{10}\right)}{ }$ |
| Known number marked and alive in population | S. $2\left(\mathrm{~m}_{\mathrm{i}}\right)$ | N. $2\left(z_{i}\right)$ |

B

| Basin | Date | Sample (i) | 5.1 | S. 2 | N. 1 | N. 2 | $x^{2}$ | df |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| L226 NE | July 74 | 4 | 46 | 11 | 193 | 62 | 0.63 | $1^{\text {a }}$ |
|  | Sept 74 | 5 | 59 | 31 | 134 | 73 | 0.02 | 1 |
|  | June 75 | 6 | 38 | 36 | 92 | 94 | 0.45 | 1 |
|  | July 75 | 7 | 20 | 23 | 72 | 118 | 1.07 | 1 |
|  | Aug 75 | 8 | 2 | 5 | 70 | 142 | 0.06 | 1 |
|  | Sept-0ct 75 | 9 | 19 | 49 | 51 | 97 | 0.88 | 1 |
|  | May 76 | 10 | 23 | 56 | 28 | 80 | 0.23 | 1 |
|  | Sept-Oct 76 | 11 | 19 | 102 | 7 | 16 | 3.29 | 1 |
|  |  |  |  |  |  |  | 6.63 | $8^{\text {b }}$ |
| L226 SW | May 74 | 2 | 22 | 9 | 251 | 46 | 3.74 | 1 |
|  | Aug 74 | 5 | 42 | 5 | 209 | 57 | 2.80 | 1 |
|  | Oct 74 | 6 | 63 | 26 | 146 | 62 | 0.01 | 1 |
|  | May 75 | 7 | 25 | 25 | 121 | 99 | 0.40 | 1 |
|  | July 75 | 8 | 26 | 17 | 95 | 114 | 3.26 | 1 |
|  | Sept-0ct 75 | 9 | 40 | 73 | 55 | 65 | 2.61 | 1 |
|  | May 76 | 10 | 17 | 45 | 38 | 84 | 0.26 | 1 |
|  | Sept-0ct 76 | 11 | 32 | 94 | 6 | 18 | 0.01 | 1 |
|  |  |  |  |  |  |  | 13.09 | 8 |

a
the $P .05=3.84$
b the $\mathrm{P} .05=15.5$

The value of using two techniques for capture-recapture of L226 whitefish is clear. Trapnet catch-per-unit effort (C/f) dropped progressively in both basins throughout the study (Table C.4). This implies that either changes in catchability, heterogeneous survival, or changes in activity were occurring. While heterogeneous survival was occurring in early summer 1974 (Appendix D), no additional periods of unequal survival were detected during the remainder of the study to explain the decreasing $\mathrm{C} / \mathrm{f}$ using trapnet data. The supplementary gillnetting in 1975 through 1977 apparently compensated for the trapnet bias.

While simulations have shown the Leslie-Carothers test to be fairly efficient (Carothers 1971), both it and Pollock's tests are limited to detecting differences in catchability between only the first capture and last recapture of animals for the full Jolly-Seber model, and only between the first sampling period and the last recapture in the deathonly model. The tests will not detect unequal catchability for a group of animals which may be marked, but become completely uncatchable, never recaptured throughout the experiment. These animals would probably be detected during tests of survival heterogeneity (Appendix B), since they would be treated in the model as mortalities.

A more severe situation occurs when a subset of the population has zero catchability, fish present in a lake but never caught throughout the study. The only method for detecting this type of unequal catchability would be by draining the lake,as Buck and Thoits (1965) did in ponds. In a lake as small as L226, where two types of netting

have occurred intensively throughout the lake over a five year period, it is highly unlikely that a group of whitefish could exist without being caught eventually.

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## Appendix D. Tests of the assumption of equal survival

## INTRODUCTION

Almost all mark-recapture methods require that each animal has the same probability of surviving from time (i) to (i+1) as any other animal. Examples of survival heterogeneity are numerous (see Cormack 1968 or Ricker 1975 for reviews), but its effects on results from Jolly-Seber models are relatively unknown. Manly (1970) has shown that the Jolly-Seber model is fairly robust to age-dependent mortality, though high infant mortality may bias estimates. Arnason and Baniuk (1978) suggest estimates of population size ( $\hat{N}_{i}$ using Jolly's 1965 notation) are robust to failure of this assumption, but it can have serious effects on the accuracy and meaning of survival estimates ( $\hat{\phi}_{i}$ ). Manly's conclusions were based on a limited number of simulations using either increasing mortality with fish age, or very high infant mortality followed by homogeneous mortality at later age. Arnason and Baniuk's conclusions were based on theoretical considerations.

I used Arnason and Baniuk's simulation methods to determine the extent of bias introduced in both "full" and "death-only" Jolly-Seber model estimates when heterogeneous survival occurred. I used simulation parameters similar to those in Appendix $B\left(\hat{\phi}_{\mathbf{i}}=0.75, N_{1}=700, \mathrm{P}_{\mathbf{i}}=\right.$ $0.22, B_{i}=0$ ). I simulated a form of heterogeneous mortality by setting survival for all animals captured and released from sample three $\left(S_{i}\right)$ to $25 \%$ to sample four. Animals caught at time three experienced a higher rate of mortality than other animals caught through the study or
other animals present in the population but not caught at time three. These simulations (Table D.O) showed that both death-only and full model $\hat{N}_{3}$ were severely biased by this heterogeneous mortality. In addition, the survival estimates from sample two to sample three $\left(\hat{\phi}_{2}\right)$ were consistently greater than $100 \%$ for all simulations (severely biased), and the survival estimates from sample three to sample four $\left(\hat{\phi}_{3}\right)$ were significant underestimates. While the full model was an acceptable alternative to the death-only model when tag loss was present (Appendix B), both models produced seriously biased estimates under conditions of heterogeneous survival. Simulations of other, more serious forms of heterogeneous survival with baseline parameters similar to those of Table C. 1 gave similar results; both $\hat{N}_{j}$ and $\hat{\phi}_{i}$ can be seriously biased by heterogeneous survival. In addition, Arnason and Baniuk (1978) have proposed alterations in Jolly-Seber formulae to compensate for heterogeneous survival, but results from these analyses under conditions of heterogeneous survival similar to Table 1 show little gain in robustness of model estimates.

Tests of the assumptions of equal survival using real populations of animals are usually limited by small sample sizes and low recapture rates. Robson (1969) has suggested using two-by-two contingency tables to test this assumption for detecting increased mortality among newly marked animals. Capture-recapture data for $L 226$ whitefish were adequate to test the equal survival assumption for a wide range of causes of unequal survival defined below:
(D.1) Handling effects: whether an animal's survival was influenced by the sequence of events after capture (anesthetization, weighing, tagging, etc.).

Table D.0. Results of 25 simulations using the Jolly-Seber full and deathonly models when survival heterogeneity was occurring between sample times three and four. Survival of animals captured and released from sample three was $25 \%$, while all other animals had survival rates of $75 \%$. See text for a more complete explanation.

| Time <br> (i) | $\overline{\hat{N}}_{i}$ | $\bar{N}_{i}$ | $\stackrel{\text { Bias }}{i}$ | $\left.\underset{\times 1.96}{\operatorname{SE}(\operatorname{Bias}} \overline{\hat{N}}_{i}\right)$ | $\overline{\hat{\phi}}_{i}$ | $\Phi_{i}$ | Bias $\bar{\phi}_{i}$ | $\underset{\times 1.96}{\mathrm{SE}(\text { Bias }}{ }_{\mathrm{i}}^{\left.\overline{\hat{\phi}}_{i}\right)}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Full Model |  |  |  |  |  |  |  |  |
| 1 |  | 700 |  |  | 0.74 | 0.75 | -0.01 | 0.05 |
| 2 | 524 | 527 | -3 | 54.9 | $\geq 1.00^{\text {a }}$ | 0.75 | $\geq 0.25^{\text {b }}$ | - ${ }^{\text {c }}$ |
| 3 | 1235 | 395 | $840 *$ d | 534.3 | 0.27 | 0.64 | $0.37^{* d}$ | 0.04 |
| 4 | 253 | 253 | 0 | 31.8 | 0.71 | 0.75 | -0.04 | 0.08 |
| 5 | 1.69 | 191 | -22 | 19.6 |  |  |  |  |
| 6 |  | 144 |  |  |  |  |  |  |
| Death-only Model |  |  |  |  |  |  |  |  |
| 1 | 700 | 700 | 0 | 25.5 | 0.74 | 0.75 | 0.01 | 0.02 |
| 2 | 514 | 522 | -8 | 20.0 | $\geq 1.00^{\text {a }}$ | 0.75 | $\geq 0.25$ | - ${ }^{\text {c }}$ |
| 3 | 1027 | 392 | $635^{* d}$ | 111.3 | 0.25 | 0.64 | $0.39^{\star d}$ | 0.03 |
| 4 | 241 | 249 | -8 | 20.0 | 0.73 | 0.75 | 0.02 | 0.08 |
| 5 | 183 | 189 | -6 | 22.2 |  |  |  |  |
| 6 |  | 142 |  |  |  |  |  |  |
| ${ }^{\text {a }}$ Estimate 21.00 , reset to 1.00 . |  |  |  |  |  |  |  |  |
| ${ }^{\text {b }}$ Minimal bias, since $\overline{\hat{\phi}}_{i}$ was $\geq 1.00$. |  |  |  |  |  |  |  |  |
| ${ }^{\text {c }}$ No estimate possible, since $\hat{\phi}_{i} \geq 1.00$. |  |  |  |  |  |  |  |  |

(D.2) Method of capture: whether animals gillnetted at (i) had a different survival rate than animals trapnetted at (i).
(D.3) Tagging: whether animals first tagged at (i) had a different survival rate after release than animals previously tagged (Robson's (1969) "type 1" loss).
(D.4) Previous capture history: whether the total number of times an animal was recaptured prior to (i) affected its survival after release.
(D.5) Whitefish age: whether an animal's survival rate after release was correlated with his age.
(D.6) Whitefish length: whether whitefish survival after release was correlated with size at capture.
(D.7) Whitefish sex: whether males have a different survival rate than females after sampling and release.

MATERIALS AND METHODS

All tests of the equal survival assumption require that individual capture histories are collected for each whitefish; therefore, only data from tagged whitefish were used for these tests. In addition, data should have previously satisfied (A) the closure assumption, (B) the no tag loss assumption, and (C) the equal catchability assumption Since the presence of newly recruited whitefish from the 1973 to 1977 year classes violated the closure assumption, they were excluded from all tests used to detect survival heterogeneity. In addition, these animals were batch marked, so that individual capture histories were not available. Similarly, whitefish tagged with gun tags violated the
no tag loss assumption and these were also excluded. If these data were included, test results would be confounded; significant results could occur either because of differential survival or tag loss among strata.

Contingency tables (Robson 1969; Seber 1973) were constructed to test each of the individual causes of survival heterogeneity $D .1$ to D.7. The test statistic was $x^{2}$; the level of significance was the $5 \%$ level and all tests were two tailed except D.1, which was one tailed. Yates correction for continuity was not used; recent authors (summarized in Conover 1971) have shown that its use makes $x^{2}$ overly conservative.

In general, individual contingency tables were constructed for each sampling period (i) as follows: the animals released ( $s_{j}$ ) from sample (i) were divided into two or more subgroups based on the presence or absence of an attribute and recaptures from this sample ( $R_{\mathbf{j}}$ ) were tabulated for each subgroup. An example contingency table for each test is presented in the results section. The criteria used to form subgroups for each test are discussed below:
(D.1) Handling: a population subset which has been captured $\left(n_{i}\right)$, sampled and released ( si ) may have a lower survival rate than fish not caught in the sample $\left(n_{j}\right)$. If fish die during the capture-sampling procedure, the Jolly-Seber estimates can be adjusted for this type of loss on capture, but if fish die of handling stress after release, a more serious problem occurs. The problem can be difficult to diagnose, especially if animals initially swim away from the release site apparently normally. Unless the general recapture rate is high over the population study period, there is little hope of
detecting this type of survival heterogeneity. If, in general, the recapture rate is high for most sampling periods, but low for a few, excessive handling mortality may have been occurring for these latter periods.

A test of the above situation is possible using an approximate one tailed $x^{2}$ test described by Conover (1971). Contingency tables are constructed for consecutive pairs of sampling periods, (i) and (i-1). The test follows the form outlined in Table D.1. It is based on the assumption that animals caught at (i-1) undergo the additional mortality between (i-1) and (i) that animals caught at (i) escape. Therefore, more animals from (i) should be seen from $(i+1)$ to the end of the experiment than from ( $i-1$ ) over the same time period.

An example of the above may clarify this test further:
(a) a sample is drawn from a population at time one and animals are returned to the lake. A sample is drawn at time two and fish are also returned to the lake. In this case (i) is second sample and (i-1) is the first sample.
(b) the numbers of recaptures from each period are tabulated from time three to the end of the string of samples. These recaptures are represented below by "*n:

| sample time | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $i$ | $*$ | $*$ | $*$ | $*$ | $*$ |
|  | $i-1$ |  | $*$ | $*$ | $*$ | $*$ | $*$ |

(c) if the proportion of recaptures relative to the number released is greater for (i-1) than
for (i), the test is run. The assumption is that a higher proportion of the animals released from sample two should be recaptured from time three to time seven than those from sample one over the same time period. Animals released from sample one undergo mortality between times one and two prior to the capture of sample two. If the reverse occurs, then animals handled and released at time two have probably undergone a higher mortality than those released from sample one.

Since each sampling period can contribute to two tests, a significant result for a sampling period (i) indicates that the following test, (i) with (i+1) may be severely biased and should be viewed with caution. A further pairing of ( $i-1$ ) and ( $i+1$ ) should be performed since the heterogeneous survival at (i) may bias any other test in which (i) is involved.
(D.2) Method of capture: trapnets and gillnets were used during sampling periods in Sept.-Oct. 1975, May 1976 and Sept.Oct. 1976. Subgroups for tests were fish caught gillnetting and those caught using trapnets. Because $x^{2}$ tests were independent, individual $x^{2}$ from each test are additive to give a more powerful overall test.
(D.3) Initial tagging mortality: subgroups for each (i) consisted of newly tagged animals ( $n_{i 0}$ ) and animals which were tagged previously ( $m_{f}$ ).
(D.4) Previous capture history: fish released at (i) were grouped into classes according to the number of times previously seen: once, twice, three or more times. When sample sizes were very small for individual classes, samples were combined. Since this test is identical to $D .3$ for sample times early in the experiment, samples two and three were omitted from this analysis.
(D.5) Whitefish age: whitefish were aged using fin-ray sections (Mills and Beamish 1980, Appendix G). These ages were converted into age in Sept.-Oct. 1973. Since capture-recapture frequencies were low for individual age classes, subgroups were formed as follows:

| Group | $\frac{\text { Age in } 1973}{1^{+}-3^{+}}$ |
| :---: | :---: |
| 2 | $4^{+}-6^{+}$ |
| 3 | $7^{+}-10^{+}$ |
| 4 | $11^{+}-15^{+}$ |

Group
55

Age in 1973
$16^{+}-25^{+}$
(D.6) Whitefish length: all whitefish lengths at first capture were converted to lengths in Sept.-Oct. 1973 using backcalculated lengths based on fin-ray ages (Appendix E). Whitefish were then subgrouped as follows:

| Group | Fork length in 1973 (mm) |
| :---: | :---: |
| 1 | $176-250$ |
| 2 | $251-300$ |
| 3 | $301-350$ |
| 4 | $351-425^{+}$ |

The unequal length intervals are a result of small sample sizes in groups one and four.
(D.7) Whitefish sex: whitefish were sexed during fall sampling periods in L226 SW in 1974, 1975 and 1976 and in L226 NE in 1975 and 1976. Sex was determined by gently squeezing the fish's abdomen, resulting in egg or milt expulsion. Not all fish were ripe since most spawning occurred at ice-up, after fall sampling. Sample sizes for this test were very small. Subgroups for the test consisted of males and females released at each (i). Since individual test were independent, individual $x^{2}$ were combined to give a more powerful test.

RESULTS
Results for each test D. 1 to D. 7 are presented in the corresponding Tables D. 1 to D.7, and summarized in Table D.8. Survival heterogeneity was detected for May and June 1974 in L226 NE, and for June and July
(m) wlu nulawiun tur (B). signiticant differences are indicated by "*".


Table D.2. Comparisons of trapnetting and gillnetting to detect heterogeneity of survival due to capture method. An example Table (A) with notation used in (B). Significant differences are indicated by "*".
(A)

|  | seen <br> later | not seen <br> later |
| :--- | :--- | :--- |
| Caught by gillnet at (i) | G.1 | G.2 |
|  | Caught by trapnet at (i) | T.1 |

(B)

| Basin | Date | Sample (i) | G. 1 | G. 2 | T. 1 | T. 2 | $x^{2}$ | DF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| NE | Sep-Oct 1975 | 9 | 17 | 12 | 26 | 16 | 0.08 | 1 |
|  | May 1976 | 10 | 9 | 6 | 33 | 19 | 3.67 | 1 |
|  | Sep-0ct 1976 | 11 | 22 | 41 | 22 | 23 | 1.08 | 1 |
|  | Total |  |  |  |  |  | 4.73 | 3 |
| SW | Sep-0ct 1975 | 9 | 14 | 14 | 61 | 25 | 3.65 | 1 |
|  | May 1976 | 10 | 24 | 29 | 4 | 2 | 1.05 | 1 |
|  | Sep-Oct 1976 | 11 | 32 | 52 | 7 | 12 | 0.01 | 2 |
|  | Tota 1 |  |  |  |  |  | 4.71 | 3 |
| NE \& SW |  |  |  |  |  |  | 9.44 | 6 |

Table D.3. Comparisons of recapture frequencies to detect survival heterogeneity due to initial tagging mortality (Robson's type 1 loss). An example table (A) with notation used in ( $B$ ).

First seen at (i)
Seen previously
(A)
seen not seen
later later

| F.1 | F.2 |
| :---: | :---: |
| R.1 | R.2 |

(B)

| Basin | Date | Sample <br> (i) | F.1 | F.2 | R.1 | R.2 | X $_{1}^{2}$ DF |
| :--- | :--- | ---: | ---: | ---: | ---: | ---: | ---: |
|  | May 74 | 2 | 6 | 11 | 9 | 1 | $10.36_{*}^{*}$ |
|  | June 74 | 3 | 10 | 31 | 4 | 2 | 4.41 |
|  | July 74 | 4 | 32 | 12 | 10 | 2 | 0.57 |
|  | Sep 74 | 5 | 35 | 21 | 22 | 11 | 0.17 |
|  | June 75 | 6 | 22 | 16 | 25 | 14 | 0.75 |
|  | July 75 | 7 | 14 | 6 | 15 | 8 | 0.11 |
|  | Aug 75a | 8 | 1 | 0 | 3 | 3 | - |
|  | Sep-0ct 75 | 9 | 13 | 5 | 24 | 26 | 3.12 |
|  | May 76 | 10 | 9 | 10 | 29 | 29 | 0.05 |
|  | Sep-0ct 76 | 11 | 3 | 10 | 29 | 64 | 0.69 |
|  |  |  |  |  |  |  |  |
|  | May 74 | 2 | 13 | 8 | 5 | 4 | 0.11 |
|  | June 74 | 3 | 29 | 44 | 11 | 6 | 3.43 |
|  | July 74a | 4 | 5 | 6 | 1 | 0 | - |
|  | Aug 74 | 5 | 26 | 12 | 5 | 2 | 0.02 |
|  | Oct 74 | 6 | 38 | 18 | 24 | 9 | 0.23 |
|  | May 75 | 7 | 12 | 9 | 20 | 7 | 1.52 |
|  | July 75 | 8 | 14 | 8 | 10 | 7 | 0.11 |
|  | Sep-0ct 75 | 9 | 14 | 14 | 50 | 32 | 1.04 |
|  | May 76 | 10 | 5 | 6 | 23 | 25 | 0.67 |
|  | Sep-0ct 76 | 11 | 5 | 11 | 26 | 53 | 0.01 |
|  |  |  |  |  |  |  |  |

[^0]Table D.4. Comparisons of recapture frequencies to detect heterogeneity of survival due to number of times an
(A)

(B)
No. of Times
Captured Previously
○ $-\sim{ }^{+}$

| Basin | Date | Sample (i) | S. 0 | S. 1 | S. 2 | S. 3 | N. 0 | N. 1 | N. 2 | N. 3 | $x^{2}$ | DF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| L226 NE | July 74 | 4 | 32 | 10 |  |  | 12 | 2 |  |  | 0.57 | 1 |
|  | Sep 74 | 5 | 40 | 20 |  |  | 21 | 11 |  |  | 0.98 | 1 |
|  | June 75 | 6 | 23 | 18 |  |  | 23 | 11 |  |  | 1.03 | 1 |
|  | July 75 | 7 | 15 | 6 |  |  | 19 | 4 |  |  | 0.75 | 1 |
|  | Aug 75 | $8^{\text {a }}$ |  | 2 | 1 |  | 1 | 1 | 1 | 1 |  |  |
|  | Sep-0ct 75 | 9 | 17 | 17 | 5 |  | 4 | 10 | 7 |  | 5.26 | 2 |
|  | May 76 | 10 | 9 | 15 | 15 |  | 12 | 14 | 9 |  | 1.82 | 2 |
|  | Sep-0ct 76 | 11 | 3 | 17 | 8 | 4 | 10 | 22 | 17 | 11 | 0.30 | 3 |
| L226 SW | July 74 | $4^{\text {a }}$ |  |  |  |  |  |  |  |  |  |  |
|  | Aug 74 | 5 | 26 | 5 |  |  | 12 | 2 |  |  | 0.01 | 1 |
|  | 0ct 74 | 6 | 43 | 21 |  |  | 20 | 4 |  |  | 2.18 | 1 |
|  | May 75 | 2 | 11 | 13 |  |  | 12 | 9 |  |  | 0.60 | 1 |
|  | July 75 | 8 | 17 | 8 |  |  | 10 | 4 |  |  | 0.05 | 1 |
|  | Sep-Oct 75 | 9 | 20 | 31 | 17 |  | 18 | 18 | 6 |  | 2.85 | 2 |
|  | May 76 | 10 | 6 | 18 | 6 |  | 7 | 14 | 8 |  | 0.82 | 2 |
|  | Sep-Oct 76 | 11 | 6 | 8 | 14 | 5 | 10 | 16 | 20 | 12 | 1.06 | 3 |

a Insufficient sample size.

Table 0.5. Comparisons of recapture frequencies to detect survival hetergeneity due to age of whitefish. An
example table (A) with notation for $(B)$.

| (A) |  |  |  |
| :---: | :---: | :---: | :---: |
| Group | Age | seen later | not seen later |
| 1 | 1-3 | S. 1 | N. 1 |
| 2 | 4-6 | S. 2 | N. 2 |
| 3 | 7-10 | 5.3 | N. 3 |
| 4 | 11-15 | 5.4 | N. 4 |
| 5 | 16-25 | S. 5 | N. 5 |

(B)

| Basin | Age | Sample (i) | S. 1 | 5.2 | S. 3 | S. 4 | S. 5 | N. 1 | N. 2 | N. 3 | N. 4 | N. 5 | $x^{2}$ | DF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| L226 NE | Sep 73 | 1 | 36 | 15 | 12 | 10 |  | 32 | 3 | 7 | 4 |  | 6.38 |  |
|  | May 74 | 2 | 3 | 7 | 7 10 | 3 |  | 2 | 9 | 13 | 10 |  | ${ }_{0}^{6.38} 0$ | 1 |
|  | June 74 | 2 |  | 2 | 10 | 2 |  |  | 13 | 9 | 11 |  | $7.82{ }^{\text {* }}$ | 2 |
|  | July 74 | 4 | 25 | 6 | 11 |  |  | 6 | 1 | 7 |  |  | 1.70 | 2 |
|  | Sep 74 | 5 | 23 | 9 | 14 | 11 |  | 13 | 5 | 9 | 5 |  | 0.27 | 3 |
|  | June 75 | 6 | 32 | 8 | 6 |  |  | 19 | 7 | 4 | 5 |  | 0.51 | 2 |
|  | July 75 | 7 a | 14 | 5 | 3 | 7 |  | 10 | 1 | 1 | 2 |  | 2.20 | 3 |
|  | Aug 75 | $8^{\text {a }}$ | 1 |  | 2 | 7 |  | 1 | 2 | 1 | 1 |  | 2.20 | 3 |
|  | Sep-0ct 75 | 9 | 20 | 7 | 8 | 4 |  | 13 | 5 | 7 | 3 |  | 0.22 | 3 |
|  | May 76 | 10 | 20 | 7 | 7 | 3 |  | 23 | 3 | 7 | 5 |  | 2.31 | 3 |
|  | Sept-Oct 76 | 11 | 17 | 5 | 5 | 4 |  | 37 | 12 | 19 | 6 |  | 1.49 | 3 |
| L226 SW | Oct 73 |  | 8 | 8 | 20 | 13 | 6 | 5 | 1 | 10 | 11 | 2 | 5.45 |  |
|  | May 74 | 2 |  | 6 | 5 | 5 | 6 | 5 | 2 | 16 | 11 | 2 | 5.45 2.05 | 4 2 |
|  | June 74 | 3 a | 4 | 6 | 15 | 11 |  | 12 | 9 | 16 | 18 |  | 2.41 | 3 |
|  | July 74 | $4^{\text {a }}$ | 4 | 1 | 4 | 1 |  | 12 | 2 | 16 4 | 18 |  | 2.41 | 3 |
|  | Aug 74 | 5 | 14 | 3 | 6 | 7 |  | 6 | 7 | 1 | 1 |  | 6.55 |  |
|  | Oct 74 | 6 |  | 19 | 14 | 20 | 8 |  | 12 | 4 | 7 | 3 | 1.89 | 3 |
|  | May 75 | 7 |  | 17 | 4 | 8 |  |  | 9 | 3 | 7 |  | 0.68 | 2 |
|  | July 75 | 8 | 9 |  |  | 6 |  | 15 |  | 12 | 10 |  |  | 2 |
|  | Sep-0ct 75 | 9 | 15 | 11 | 20 | 13 | 5 | 14 | 7 | 11 | 13 | 1 | 4.46 | 4 |
|  | May 76 | 10 | 4 | 6 | 10 | 7 |  | 6 | 7 | 10 | 8 |  | 0.30 | 3 |
|  | Sep-Oct 76 | 11 | 6 | 7 | 10 | 5 | 3 | 15 | 12 | 15 | 14 | 6 | 1.24 | 4 |

[^1]Table D.6. Comparisons of recapture frequencies to detect survival heterogeneity due to fish length when


Table D. 7 Comparisons of recapture frequencies to detect survival heterogeneity due to sex of an animal. A representative Table (A) with notation used in (B). Significant results are indicated by "*"
(A)
seen not seen
later later

| males seen at $(i)$ | S.1 | N.1 |
| ---: | :---: | :---: |
| females seen at (i) | S.2 | N.2 |

(B)

| Basin | Date | S.1 | S.2 | N.1 | N.2 | $x^{2}$ | DF |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| L226 NE | Sep-0ct 1975 | 6 | 11 | 4 | 2 | 0.15 | 1 |
|  | Sep-0ct 1976 | 5 | 22 | 4 | 14 | 0.09 | 1 |
|  | Total |  |  |  |  | $\frac{1}{2.24}$ | $\frac{2}{2}$ |
| L226 SW | Oct 1974 | 4 | 10 | 4 | 4 | 1.03 | 1 |
|  | Sep-0ct 1975 | 10 | 14 | 5 | 5 | 0.60 | 1 |
|  | Sep-0ct 1976 | 9 | 19 | 13 | 13 | 1.70 | 1 |
|  | Tota1 |  |  |  |  | 3.33 | 3 |
| NE \& SW |  |  |  |  |  | 3.57 | 5 |

Table D.8. Summary of test results for the assumption of equal survival for each sampling period due to
7 different causes. Significant differences in survival (*), no detectable differences ( - ), ).

| Basin |  | D. 1 Handling | D. 2 <br> Capture <br> Method | $0.3$ <br> Tagging | D. 4 <br> Capture History | D. 5 Age | D. 6 Length | D. 7 Sex |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| L226 NE | Sep 1973 |  |  |  |  | - | - |  |
|  | May 1974 | * |  | * |  | - | - |  |
|  | June 1974 | * |  | * |  | - | * |  |
|  | July 1974 | - |  | - | - | - | - |  |
|  | Sep 1974 | - |  | - | - | - | - |  |
|  | June 1975 | - |  | - | - | - | - |  |
|  | July 1975 | - |  | - | - | - | - |  |
|  | Aug 1975 | - |  | a | a | a | a |  |
|  | Sep-0ct 1975 | - | - | - | - | - | - | - |
|  | May 1976 | - | - | - | - | - | - |  |
|  | Sep-Oct 1976 | - | - | - | - | - | - | - |
|  | 1977 |  |  |  |  |  |  |  |
| L226 SW | 0ct 1973 |  |  |  |  | - | - |  |
|  | May 1974 | - |  | - |  | - | - |  |
|  | June 1974 | * |  | - |  | - | - |  |
|  | July 1974 | * |  | a | a | a | a |  |
|  | Aug 1974 | - |  | - | - | - | - |  |
|  | Oct 1974 | - |  | - | - | - | - |  |
|  | May 1975 | - |  | - | - | - | - |  |
|  | July 1975 | - |  | - | - | - | - |  |
|  | Sep-0ct 1975 | - | - | - | - | - | - | - |
|  | May 1976 | - | - | - | - | - | - |  |
|  | $\begin{aligned} & \text { Sep-0ct } 1976 \\ & 1977 \end{aligned}$ | - | - | - | - | - | - | - |

1974 in L226 SW. Handling mortality was detected also for L226 NE whitefish sampled in May and June 1974 along with age related mortality for June 1974.

## DISCUSSION

Capture, tagging and later release of many fish species without excessive sampling mortalities is partially dependent on the water temperature used for holding fish during sampling procedures (Nikolsky 1963). As the lake epilimnetic temperature rises from early spring to late summer, sampling mortalities increase. Detecting losses during sampling at high water temperatures is straightforward; fish generally die during sampling procedures. A more subtle situation occurs when fish appear to swim away satisfactorily after sampling, only to die shortly thereafter. It was obvious that fish were not reviving during the July 1974 sampling period in L226 SW when epilimnetic temperatures were above $20^{\circ} \mathrm{C}$. Commencing with the following sampling period, July 1974 in L226 NE, the water temperature in containers used for sampling procedures was lowered below $10^{\circ} \mathrm{C}$ by using ice. After constructing initial $x^{2}$ similar to those in D. 1 for detecting handling mortality after October 1974, it was obvious that this procedure was effective and that handling mortality of fish that appeared heal thy on release was occurring before July 1974 sampling. This mortality was detected for fish sampled when epilimnetic temperatures were above $15^{\circ} \mathrm{C}$. Therefore, during subsequent sampling in 1975, 1976 and 1977, ice was used to lower the temperature of water used for field sampling when epilimnetic temperatures were above $12^{\circ} \mathrm{C}$. The handling mortality was probably responsible for the
survival heterogeneity detected by test D. 3 for L226 NE whitefish in May and June 1974; mortality was greatest among newly tagged fish. The age related heterogeneity in June 1974 in L226 NE was also probably the result of handling mortality. This type of heterogeneity was not present in any other sampling period throughout the study, and the interrelationship between mortality and age for the sample was complicated; both younger and older fish suffered higher mortality than those of intermediate age.

Inflated or erratic $\hat{N}_{i}$ result for (i) where survival heterogeneity occurs (Fig. D.1). The bias is large and makes interpretation of other $\hat{N}_{\mathbf{i}}$ difficult. In addition, many $\hat{\phi}_{\mathbf{i}}$ are inadmissible, greater than 1.0 ( $100 \%$ survival). This might convince an investigator that some undetected recruitment was occurring into the population and that the death-only model should be abandoned in favor of the open model, which allows for recruitment. Estimates of birth $\left(\hat{B}_{j}\right)$ would probably be inconsistent and hard to interpret.

Compensating for survival heterogeneity can take two forms:
(1) Analyses that are robust to some failures in the equal survivorship assumption are available (Arnason and Baniuk 1978). These techniques give $\hat{N}_{i}$ and $\hat{\phi}_{\boldsymbol{i}}$ that are somewhat less biased than those from unmodified analyses, but may result in a large loss of information or be no improvement over unmodified estimates. This may take the form of a loss in the precision of $\hat{N}_{i}$ (Mills unpublished data). Arnason's procedure also requires the loss of $\hat{N}_{1}$ and $\hat{\phi}_{1}$.
(2) An alternative is to omit data from samples when the assumption is violated. Strictly speaking, if only handling mortality is

Figure D.1. Population estimates and confidence intervals for L226 NE whitefish of the 1950-1972 age classes from 1973 to 1975. Estimates where survival heterogeneity was detected are indicated by ( $\diamond$ ). Capture histories histories of gun-tagged fish were deleted prior to analysis. The asymmetric confidence intervals are due to the inverse transformation used to correct bias in the Jolly-Seber formulae.

detected, and there is also no evidence of survival heterogeneity between animals caught at (i) based on some attribute such as tag status, all capture histories should be deleted where animals were caught at (i). Obviously a large amount of capture information can be lost using this method.
(3) A third alternative is to omit only those sampling periods where the assumption is violated. If only some capture histories are affected by the survival heterogeneity, such as those animals that are newly tagged at (i), omitting the sampling period will delete all capture histories where animals were first seen at (i) and not seen again. This technique also offers the advantage of leaving other capture information from an animal's capture history to contribute to the analysis. There is a substantial gain in information using this method over the second technique.

The third alternative was the one followed for L226 whitefish. Handling mortality affected animals which were first tagged at (i) while a large number of fish sampled at (i) that were previously tagged were seen again later (Table D.3). This method minimized the amount of information lost by data deletion. The number of fish whose data histories were deleted from L226 NE was 42, and from L226 SW was 34 . Since these fish were known present prior to the sampling periods when survival heterogeneity occurred, estimates for these periods could be modified to account for these animals. I chose not to make these changes since relatively similar numbers of fish were deleted from each basin. Any corrections would be similar between basins.

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Appendix E. A simple method for back-calculating lengths of lake whitefish using fin-ray sections

## INTRODUCTION

Back-calculations of length at age data have been used for many years to obtain estimates of fish growth using scales (Tesch 1971; Everhart et al. 1975). Similar measurements have been made on other bony structures (DeBont 1967), but to date annual marks on fin-ray sections as a basis for predicting fish length have not proved reliable (Tesch 1971). Because scale ages are unreliable for many lake whitefish populations (Mills and Beamish 1980), then back-calculations based on these ages are also many times unreliable. The purpose of this study was to find a method for back-calculating lengths from fin-ray sections, and establish its reliability using a whole lake mark-recapture experiment.

## MATERIALS AND METHODS

Fin-rays were obtained from lake whitefish in Lake 226 (hereafter referred to as L226) from 1973 to 1976 during a mark-recapture study of the effects of nutrient addition on whitefish populations. Details of the fin-ray aging technique and tests of its validity are reported in Mills and Beamish (1980).

Fin-rays have not been used previously for back-calculations, probably for three reasons: (1) the initial point of growth, the "focus" on scales, is not distinguishable on fin-ray sections, (2) the shape of a fin-ray cross-section can change as a fish grows, and (3) as sections are cut
progressively farther from the base of the fin, the number of distinguishable annuli can change, as does the shape of some fin-ray sections. These problems were minimized by: (1) using the first annulus as an origin for measuring fin-ray lengths; (2) using the same plane of the upper part of the first pelvic ray for all back-calculations, and (3) only using one of the first five sections cut closest to the base of the pelvic fin. The upper portion of the first pelvic ray (Fig. E.1) showed a minimal change in shape as fish growth progressed. Growth of this section was linearly related to growth in length of the fish (Fig. E.2). To test whether the number of annuli in a section change in relation to how close a section is cut from the base of a pelvic fin, fin-rays from 20 whitefish of a variety of lengths were sectioned until only one-third of each remained. The number of annuli observed in the upper part of the first ray did not change over approximately one-third the length of the first fin-ray and usually the first five sections make up less than one-tenth the length of the ray, leaving a large margin for error. No significant differences occurred between total cross-section fin-ray length and between distances to individual annuli within these sections among the five sections for these twenty fish.

Fin-ray measurements were made using a compound microscope with a screen at $160 x$ magnification. The relationship between individual whitefish fork length and fin-ray length was linear but not directly proportional, so back-calculations were made according to the modified direct proportionality formula (Bagenal and Tesch 1978):

$$
1_{i}-c=\frac{f_{i}}{f} \times(1-c)
$$

where: $1_{i}=$ length of fish when annuli "i" was formed

Figure E,1, The upper portion of the first pelvic fin-ray at $160 x$. The plane of the ray used for back calculation is indicated by (--).


Figure E.2. The relationship between fin-ray section length in cross section, as defined in Figure E.1, and corresponding fork length for 920 different whitefish from L226. Cross-sections were measured as in Figure E. 1 using a screen attachment on a microscope (160x).


$$
\begin{aligned}
1= & \text { length of fish at time fin-ray was removed } \\
f_{i}= & \text { length to annulus " } i \text { " on the fin-ray } \\
f= & \text { total fin-ray cross-section length } \\
c= & \text { correction factor needed because the relationship } \\
& \text { between fish length and fin-ray length is not directly } \\
& \text { proportional. }
\end{aligned}
$$

Four values of "c" were compared to determine which gave the minimal error between back-calculated fork-lengths and those observed in the field for the same fish. Lengths back-calculated from fin-rays from recaptured fish were compared to fork lengths observed for the same fish at initial marking one to three years earlier. The value of " $c$ " is usually derived from a regression of fish length on fin-ray section length; "c" is the intercept on the length axis. Two values of "c" were calculated using the regression method, the first using the geometric regression (Steel and Torrie (1960) of fish length on fin-ray radius ( $c=153$ ) and the second, using Ricker's (1973) functional regression ( $c=138$ ). The value of " $C$ " also should be that length when growth of the structure first occurs after first annulus formation. The other two values of "c" were based on averages calculated from observed fork lengths of whitefish. The first was the average length of whitefish in fall sampling prior to first annulus formation ( $c=95$ ) in 1973. The second was the average length of whitefish immediately after annulus formation during spring sampling prior to any observed growth on the fin-rays in 1974 ( $c=111$ ). The 1973 year class was the only successful year class between 1973 and 1976 which could be followed through first annulus formation in this study.

## RESULTS AND DISCUSSION

Back-calculated lengths using " $c$ " derived from Ricker's functional regression on the average varied less from corresponding observed lengths than other values of "c" (Table E.1). The value of "c" calculated from the geometric regression gave back-calculated lengths that were consistently greater than actual lengths observed for the same fish during previous sampling. Ricker (1973) predicts that this will occur when using the geometric regression for back calculations. In this case, the use of the geometric regression to derive " $c$ " would result in underestimates of whitefish growth during years prior to capture.

The other two estimates of "c", 95 and 111 mm were based on observed lengths of whitefish immediately prior and just after first annulus formation. Both these values of "c" give consistent underestimates of length at age for $L 226$ whitefish and would result in overestimates of whitefish growth. Since theoretically the true value of "c" would be the average length immediately prior to growth in the fin-ray after annulus formation and $c=111$ give consistent underestimates, the true value of "c" should be greater than 111, observed in May 1974. The next field observations for fish age 1+ in 1974 was in July 1974, when growth was clearly evident on the fin-rays. Fish averaged 156 mm at this time, so the true value of "c" should be between 111 and 156. The estimate from the functional regression, 138, is therefore a very realistic value for " $c$ ".

Many authors have observed that back-calculated lengths show consistent irregularities (Bagenal and Tesch 1978). Lee's phenomenon, the tendency for back-calculated lengths at a given age to be smaller, the

Table E.1. The mean differences between back-calculated fork lengths and corresponding lengths observed during field sampling one, two and three years earlier for four values of " $c$ ", the correction factor used in the back calculation formula. All lengths are for fall sampling periods (September October). Significant differences are indicated by (*) for $p<0.05$ and ( $* *$ ) for $p<0.01$.

| c | 1 yr | 2 yr | 3 yr | Combined |
| :---: | :---: | :---: | :---: | :---: |
|  |  | Sign of difference considered |  |  |
| 95 | $5.48^{* *}$ | $7.85^{*}$ | 5.30 | $6.50^{*}$ |
| 111 | $3.15^{*}$ | $4.33^{* *}$ | $9.03^{*}$ | $4.69^{*}$ |
| 138 | -0.07 | $-4.87^{*}$ | -2.12 | -2.38 |
| 153 | -8.09 | $-6.00^{* *}$ | -5.65 | $-6.76^{*}$ |

Sign of difference ignored

| 95 | 7.39 | 12.08 | 22.73 | 12.03 |
| ---: | ---: | ---: | ---: | ---: |
| 111 | 6.52 | 10.01 | 11.17 | 8.89 |
| 138 | 6.42 | 10.68 | 10.36 | 8.79 |
| 153 | 13.19 | 11.33 | 13.65 | 12.49 |


| Sample sizes | 67 | 71 | 33 | 171 |
| :--- | :--- | :--- | :--- | :--- |

older the fish from which they are computed, is probably the best known of these irregularities. There was no evidence of Lee's phenomenon for L226 whitefish using fork lengths from fin-ray sections and $c=138$.

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Appendix F. Production calculations from May 1973 to SeptemberOctober 1976 for L226 NE and SW whitefish

| Table F. 1 | L226 NE | May 1973 - Fall 1973 |
| :---: | :---: | :---: |
| Table F. 2 | L226 SW | May 1973 - Fall 1973 |
| Table F. 3 | L226 NE | Fall 1973 - Fall 1973 |
| Table F. 4 | L226 SW | Fall 1973 - Fall 1974 |
| Table F. 5 | L226 NE | Fall 1974 - Fall 1975 |
| Table F. 6 | L226 SW | Fall 1974 - Fall 1975 |
| Table F. 7 | L226 NE | Fall 1975 - Fall 1976 |
| Table F. 8 | L226 SW | Fall 1975 - Fall 1976 |
| Where: |  |  |

Production $(P)=$ the instantaneous growth rate $(G) \times$ average biomass ( $\bar{B}$ )

Average biomass $(\bar{B})=$ the average of the biomass present at time one $\left(B_{0}\right)$ and time two $\left(B_{1}\right)$

Instantaneous growth rate $(G)=\log$ of the average weight at time two - log of the average weight at time one Average weight for an age group was calculated from the average length for that age group using the length-weight relationship for the entire number of $L 226$ whitefish caught from fall 1973 to fall 1976

Average lengths for an age group were formed the average back-calculated length for an age group at fall sampling, supplimented by direct observation for fish where back-calculations were impossible

Estimates of number for each age group ( $N_{0}$ and $N_{1}$ ) were formed as the sum of two components:
(a) stratum one fish, determined from separate mark-recapture analyses using the Jolly-Seber full model for L226 NE and the death-only model for L226 SW. Estimates were plotted with $\pm 1$ standard error of the estimates for an age group from 1973 to 1976, and a line was eye-fitted. Appropriate stratum one population estimates for production estimates were read from the eye-fitted line.
(b) stratum two fish, determined from a Jolly-Seber death-only analysis for stratum two fish of the 1973 year class for L226 NE plus a proportion estimate for the remaining 1974-1975 year classes in L226 NE. The L226 SW estimates were based entirely on proportion estimates. Proportion estimates were formed as:

$$
\begin{aligned}
N_{i 2}= & \hat{N}_{i 1} \times n_{i 1} / n_{i 2} \\
& \hat{N}_{i 1} \text { is the appropriate Jolly-Seber } \\
& \text { estimate and the subscripts } 1 \text { and } \\
& 2 \text { refer to strata }
\end{aligned}
$$

Table F.1. Estimated whitefish production for L226 NE from May 1973 to fall (September-October 1973).

| Age Class | Date | Average L.ength (mm) | Average <br> Weight (gm) | Ins tantaneous Growth Rate (G) | Number $\left(N_{0}\right)$ $\left(N_{j}\right)$ | Instantaneous Mortality Rate (z) | Biomass <br> ( Kg ) | Average Biomass ( Kg ) | $\begin{aligned} & \text { Production } \\ & (\mathrm{Kg}) \end{aligned}$ | $\begin{aligned} & \text { Production } / \mathrm{m} \\ & (\mathrm{gm}) \end{aligned}$ | $\begin{aligned} & \text { Production } / N_{0} \\ & (\mathrm{gm}) \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fall } 1973 \end{aligned}$ | $\begin{aligned} & 207.8 \\ & 248.0 \end{aligned}$ | $\begin{aligned} & 101.0 \\ & 175.7 \end{aligned}$ | 0.5535 | $\begin{aligned} & 336 \\ & 295 \end{aligned}$ | 0.1301 | $\begin{aligned} & 33.9 \\ & 51.9 \end{aligned}$ | 42.9 | 23.7 | 0.28 | 70.5 |
| 4-6 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fall } 1973 \end{aligned}$ | $\begin{aligned} & 273.6 \\ & 293.7 \end{aligned}$ | $\begin{aligned} & 238.8 \\ & 247.8 \end{aligned}$ | 0.2207 | $\begin{aligned} & 82^{*} \\ & 72 \end{aligned}$ | 0.1301 | $\begin{aligned} & 19.6 \\ & 21.5 \end{aligned}$ | 20.6 | 4.5 | 0.05 | 54.9 |
| 7-10 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fa11 } 1973 \end{aligned}$ | $\begin{aligned} & 296.2 \\ & 313.6 \end{aligned}$ | $\begin{aligned} & 306.0 \\ & 365.7 \end{aligned}$ | 0.1783 | $\begin{aligned} & 139^{*} \\ & 122 \end{aligned}$ | 0.1305 | $\begin{aligned} & 42.5 \\ & 44.7 \end{aligned}$ | 43.6 | 7.8 | 0.09 | 56.1 |
| 11-15 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fall } 1973 \end{aligned}$ | $\begin{aligned} & 327.5 \\ & 339.0 \end{aligned}$ | $\begin{aligned} & 418.7 \\ & 466.2 \end{aligned}$ | 0.1075 | $\begin{aligned} & 47^{*} \\ & 41 \end{aligned}$ | 0.1366 | $\begin{aligned} & 19.7 \\ & 19.1 \end{aligned}$ | 19.4 | 2.1 | 0.03 | 44.7 |
| 16-25 | May 1973 <br> Fall 1973 | $\begin{aligned} & 356.6 \\ & 364.1 \end{aligned}$ | $\begin{aligned} & 545.9 \\ & 582.7 \end{aligned}$ | 0.0654 | $\begin{aligned} & 7^{*} \\ & 6 \end{aligned}$ | 0.1542 | $\begin{aligned} & 3.8 \\ & 3.5 \end{aligned}$ | 3.7 | 0.2 | <0.01 | 14.3 |
| Total |  |  |  |  |  |  | $\begin{array}{r} 119.5 \\ 40.7 \end{array}$ | 130.2 | 38.3 | 0.46 |  |

Table F.2. Estimated whitefish production for L226 SW from May 1973 to fall 1973 (September-October).

| Age Class | Date | Average <br> Length (mm) | Average Weight (gm) | Ins tantaneous Growth Rate (G) | $\begin{gathered} \text { Number } \\ \left(N_{0}\right) \\ \left(N_{\mathbf{i}}\right) \end{gathered}$ | Instantaneous Mortality Rate (z) | $\begin{gathered} \text { Biomass } \\ (\mathrm{Kg}) \end{gathered}$ | Average Biomass (Kg) | Production (Kg) | Production/m (gm) | $\underset{(\mathrm{gm})}{\text { Production } / N_{0}}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fal1 } 1973 \end{aligned}$ | $\begin{aligned} & 217.2 \\ & 258.8 \end{aligned}$ | $\begin{aligned} & 116.1 \\ & 200.7 \end{aligned}$ | 0.5473 | $\begin{aligned} & 170^{*} \\ & 149 \end{aligned}$ | 0.1318 | $\begin{aligned} & 19.7 \\ & 29.9 \end{aligned}$ | 24.8 | 13.6 | 0.17 | 80.0 |
| 4-6 | May 1973 <br> Fall 1973 | $\begin{aligned} & 275.6 \\ & 293.3 \end{aligned}$ | $\begin{aligned} & 244.2 \\ & 296.5 \end{aligned}$ | 0.1942 | $\begin{aligned} & 64^{\star} \\ & 56 \end{aligned}$ | 0.1335 | $\begin{aligned} & 15.6 \\ & 16.6 \end{aligned}$ | 16.1 | 3.1 | 0.04 | 48.4 |
| 7-10 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fa11 } 1973 \end{aligned}$ | $\begin{aligned} & 295.3 \\ & 312.5 \end{aligned}$ | $\begin{aligned} & 302.8 \\ & 361.7 \end{aligned}$ | 0.1776 | $\begin{aligned} & 128^{\star} \\ & 112 \end{aligned}$ | 0.1316 | $\begin{aligned} & 38.7 \\ & 35.0 \end{aligned}$ | 36.7 | 6.5 | 0.08 | 50.1 |
| 11-15 | $\begin{aligned} & \text { May } 1973 \\ & \text { Fall } 1973 \end{aligned}$ | $\begin{aligned} & 324.2 \\ & 336.7 \end{aligned}$ | $\begin{aligned} & 405.6 \\ & 456.3 \end{aligned}$ | 0.1176 | $\begin{aligned} & 129^{\star} \\ & 113 \end{aligned}$ | 0.1324 | $\begin{aligned} & 52.3 \\ & 51.6 \end{aligned}$ | 52.0 | 6.1 | 0.08 | 47.3 |
| 16-25 | May 1973 Fall 1973 | $\begin{aligned} & 377.7 \\ & 385.5 \end{aligned}$ | $\begin{aligned} & 653.4 \\ & 696.4 \end{aligned}$ | 0.0636 | $\begin{aligned} & 27^{*} \\ & 24 \end{aligned}$ | 0.1178 | $\begin{aligned} & 17.6 \\ & 16.7 \end{aligned}$ | 17.1 | 1.1 | 0.01 | 40.7 |
| Total |  |  |  |  |  |  | $\begin{aligned} & 143.9 \\ & 149.8 \end{aligned}$ | 146.7 | 30.4 | 0.38 |  |

Table F.3. Estimated whitefish production for L226 NE during 1974 (September-0ctober 1973 to September-October 1974).

| Age Class | Date | Average <br> Length (mm) | Average Weight (gm) | Instantaneous Growth Rate (G) | Number $\left(\mathrm{N}_{\mathrm{o}}\right)$ $\left(N_{j}\right)$ | Instantaneous Mortality Rate <br> (z) | Biomass ( Kg ) | Average Biomass (Kg) | Production ( Kg ) | Production/m (gm) | $\begin{aligned} & \text { Production/ } I_{0} \\ & (\mathrm{gm}) \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | $\begin{array}{ll} \text { Fall } 1973 \\ \text { Fall } 1974 \end{array}$ | $\begin{aligned} & 248.1 \\ & 283.7 \end{aligned}$ | $\begin{aligned} & 175.8 \\ & 267.2 \end{aligned}$ | 0.4190 | $\begin{aligned} & 404.8 \\ & 310.0 \end{aligned}$ | 0.2668 | $\begin{aligned} & 71.1 \\ & 82.8 \end{aligned}$ | 77.0 | 32.2 | 0.39 | 79.7 |
| 4-6 | $\begin{aligned} & \text { Fall } 1973 \\ & \text { Fall } 1974 \end{aligned}$ | $\begin{aligned} & 316.9 \\ & 340.7 \end{aligned}$ | $\begin{aligned} & 377.6 \\ & 473.5 \end{aligned}$ | 0.2261 | $\begin{aligned} & 69.4 \\ & 44.1 \end{aligned}$ | 0.4534 | $\begin{aligned} & 26.2 \\ & 20.9 \end{aligned}$ | 23.5 | 5.3 | 0.06 | 76.7 |
| 7-10 | $\begin{array}{ll} \text { Fall } 1973 \\ \text { Fall } 1974 \end{array}$ | $\begin{aligned} & 352.9 \\ & 373.3 \end{aligned}$ | $\begin{aligned} & 528.5 \\ & 629.8 \end{aligned}$ | 0.1755 | $\begin{array}{r} 123.9 \\ 87.2 \end{array}$ | 0.3513 | $\begin{aligned} & 65.5 \\ & 54.9 \end{aligned}$ | 60.2 | 10.6 | 0.13 | 85.2 |
| 11-15 | Fall 1973 <br> Fall 1974 | $\begin{aligned} & 369.2 \\ & 385.0 \end{aligned}$ | $\begin{aligned} & 608.5 \\ & 693.9 \end{aligned}$ | 0.1313 | $\begin{aligned} & 67.2 \\ & 55.2 \end{aligned}$ | 0.1968 | $\begin{aligned} & 40.9 \\ & 38.3 \end{aligned}$ | 39.6 | 5.2 | 0.06 | 77.4 |
| 16-25 | $\begin{array}{ll} \text { Fall } 1973 \\ \text { Fall } 1974 \end{array}$ | $\begin{aligned} & 381.5 \\ & 391.1 \end{aligned}$ | $\begin{aligned} & 674.0 \\ & 728.9 \end{aligned}$ | 0.0783 | $\begin{aligned} & 6.0 \\ & 4.0 \end{aligned}$ | 0.4055 | $\begin{aligned} & 40.4 \\ & 29.2 \end{aligned}$ | 34.3 | 0.3 | $<0.01$ | 45.4 |
| Total |  |  |  |  |  |  | $\begin{aligned} & 244.1 \\ & 226.1 \end{aligned}$ | 235.1 | 53.6 | 0.64 |  |

Table F.4. Estimated whitefish production for L226 SW during 1974 (September-October 1973 to September-October 1974).

| Age Class | Date | Average Length (mm) | Average Weight (gm) | Instantaneous Growth Rate (G) | Number $\begin{aligned} & \binom{N_{0}}{\left(N_{j}\right.} \end{aligned}$ | Instantaneous Mortality Rate (z) | Biomass (Kg) | Average Biomass ( Kg ) | Production (Kg) | Production/m (gm) | $\begin{aligned} & \text { Production } / I_{0} \\ & (\mathrm{gm}) \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | Fall 1973 <br> Fall 1974 | $\begin{aligned} & 237.2 \\ & 270.1 \end{aligned}$ | $\begin{aligned} & 152.8 \\ & 229.2 \end{aligned}$ | 0.4057 | $\begin{aligned} & 140.6 \\ & 116.6 \end{aligned}$ | 0.1872 | $\begin{aligned} & 21.5 \\ & 26.7 \end{aligned}$ | 24.1 | 9.8 | 0.13 | 69.6 |
| 4-6 | Fall 1973 Fall 1974 | $\begin{aligned} & 304.5 \\ & 318.4 \end{aligned}$ | $\begin{aligned} & 333.3 \\ & 383.1 \end{aligned}$ | 0.1393 | $\begin{aligned} & 49.0 \\ & 38.0 \end{aligned}$ | 0.2542 | $\begin{aligned} & 16.3 \\ & 14.6 \end{aligned}$ | 15.4 | 2.2 | 0.03 | 43.9 |
| 7-10 | Fal1 1973 <br> Fall 1974 | $\begin{aligned} & 341.5 \\ & 354.1 \end{aligned}$ | $\begin{aligned} & 477.2 \\ & 534.0 \end{aligned}$ | 0.1125 | $\begin{array}{r} 127.4 \\ 94.0 \end{array}$ | 0.3040 | $\begin{aligned} & 60.1 \\ & 50.2 \end{aligned}$ | 55.5 | 6.2 | 0.08 | 49.0 |
| 11-15 | Fal1 1973 <br> Fall 1974 | $\begin{aligned} & 351.5 \\ & 360.7 \end{aligned}$ | $\begin{aligned} & 521.9 \\ & 566.1 \end{aligned}$ | 0.0812 | $\begin{array}{r} 136.0 \\ 83.0 \end{array}$ | 0.4938 | $\begin{aligned} & 71.0 \\ & 47.0 \end{aligned}$ | 59.0 | 4.8 | 0.06 | 35.2 |
| 16-25 | Fall 1973 <br> Fall 1974 | $\begin{aligned} & 380.6 \\ & 386.8 \end{aligned}$ | $\begin{aligned} & 669.4 \\ & 703.9 \end{aligned}$ | 0.0503 | $\begin{aligned} & 35.0 \\ & 30.0 \end{aligned}$ | 0.1542 | $\begin{aligned} & 23.4 \\ & 21.1 \end{aligned}$ | 22.3 | 1.1 | 0.01 | 32.0 |
| Total |  |  |  |  |  |  | $\begin{aligned} & 192.3 \\ & 159.6 \end{aligned}$ | 176.3 | 24.1 | 0.31 |  |

Table F.5. Estimated whitefish production for L226 Ne whitefish during 1975 (September-October 1974 to September-October 1975).

| Age Class | Date | Average Length (mm) | Average <br> Weight (gm) | Instantaneous Growth Rate (G) | Number $\left(\mathrm{N}_{0}\right)$ $\left(N_{j}\right)$ | Instantaneous Mortality Rate (z) | Biomass ( Kg ) | Average <br> Biomass ( Kg ) | Production (Kg) | $\begin{aligned} & \text { Production/m } \\ & (\mathrm{gm}) \end{aligned}$ | $\begin{aligned} & \text { Production } / N_{0} \\ & (\mathrm{gm}) \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 229.1 \\ & 262.8 \end{aligned}$ | $\begin{aligned} & 137.2 \\ & 210.5 \end{aligned}$ | 0.4283 | $\begin{aligned} & 496.0 \\ & 387.0 \end{aligned}$ | 0.2482 | $\begin{aligned} & 68.0 \\ & 81.5 \end{aligned}$ | 74.8 | 32.0 | 0.38 | 64.6 |
| 4-6 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 296.3 \\ & 423.3 \end{aligned}$ | $\begin{aligned} & 306.3 \\ & 406.1 \end{aligned}$ | 0.2822 | $\begin{aligned} & 179.0 \\ & 153.0 \end{aligned}$ | 0.1569 | $\begin{aligned} & 54.8 \\ & 62.7 \end{aligned}$ | 58.5 | 16.5 | 0.20 | 92.2 |
| 7-10 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 331.7 \\ & 356.2 \end{aligned}$ | $\begin{aligned} & 435.5 \\ & 544.0 \end{aligned}$ | 0.2226 | $\begin{aligned} & 84.0 \\ & 68.0 \end{aligned}$ | 0.2113 | $\begin{aligned} & 36.6 \\ & 37.0 \end{aligned}$ | 36.8 | 8.2 | 0.10 | 97.5 |
| 11-15 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 352.9 \\ & 377.0 \end{aligned}$ | $\begin{aligned} & 528.4 \\ & 649.8 \end{aligned}$ | 0.2069 | $\begin{aligned} & 55.0 \\ & 45.0 \end{aligned}$ | 0.2007 | $\begin{aligned} & 29.1 \\ & 29.2 \end{aligned}$ | 29.2 | 6.0 | 0.07 | 109.7 |
| 16-25 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 379.3 \\ & 397.7 \end{aligned}$ | $\begin{aligned} & 66.19 \\ & 768.0 \end{aligned}$ | 0.1487 | $\begin{array}{r} 12.0 \\ 7.0 \end{array}$ | 0.5390 | $\begin{aligned} & 7.9 \\ & 5.4 \end{aligned}$ | 6.7 | 1.0 | 0.01 | 82.5 |
| Total |  |  |  |  |  |  | $\begin{aligned} & 196.4 \\ & 215.8 \end{aligned}$ | 206.0 | 63.7 | 0.77 |  |

Table F.6. Estimated whitefish production for L226' SW during 1975 (September-0ctober 1974 to September-October 1975).

| Age Class | Date | Average Length (mm) | Average Weight (gm) | Instantaneous Growth Rate (G) | Number $\left(N_{0}\right)$ $\left(N_{j}\right)$ | Instantaneous Mortality Rate (z) | Biomass $(\mathrm{Kg})$ | Average Biomass ( Kg ) | Production (Kg) | $\begin{aligned} & \text { Production/m }(\mathrm{gm}) \end{aligned}$ | $\begin{gathered} \text { Production } / N_{0} \\ (\mathrm{~mm}) \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 245.6 \\ & 272.5 \end{aligned}$ | $\begin{aligned} & 170.4 \\ & 235.6 \end{aligned}$ | 0.3240 | $\begin{aligned} & 98.0 \\ & 50.0 \end{aligned}$ | 0.673 | $16.7$ | 14.2 | 4.6 | 0.06 | 47.1 |
| 4-6 | Fall 1974 <br> Fall 1975 | $\begin{aligned} & 293.0 \\ & 312.8 \end{aligned}$ | $\begin{aligned} & 295.6 \\ & 362.6 \end{aligned}$ | 0.2040 | $\begin{aligned} & 128.0 \\ & 103.0 \end{aligned}$ | 0.2173 | $\begin{aligned} & 37.8 \\ & 37.3 \end{aligned}$ | 37.6 | 7.7 | 0.10 | 59.9 |
| 7-10 | $\begin{array}{ll} \text { Fall } 1974 \\ \text { Fall } 1975 \end{array}$ | $\begin{aligned} & 329.2 \\ & 347.2 \end{aligned}$ | $\begin{aligned} & 425.5 \\ & 502.2 \end{aligned}$ | 0.1658 | $\begin{aligned} & 78.0 \\ & 63.0 \end{aligned}$ | 0.2136 | $\begin{aligned} & 33.2 \\ & 31.6 \end{aligned}$ | 32.4 | 5.4 | 0.07 | 68.9 |
| 11-15 | $\begin{array}{ll} \text { Fall } 1974 \\ \text { Fall } 1975 \end{array}$ | $\begin{aligned} & 341.2 \\ & 355.4 \end{aligned}$ | $\begin{aligned} & 475.8 \\ & 540.2 \end{aligned}$ | 0.1270 | $\begin{aligned} & 95.0 \\ & 75.0 \end{aligned}$ | 0.2364 | $\begin{aligned} & 45.2 \\ & 40.5 \end{aligned}$ | 42.9 | 5.4 | 0.07 | 57.3 |
| 16-25 | Fall 1974 Fall 1975 | $\begin{aligned} & 373.5 \\ & 382.0 \end{aligned}$ | $\begin{aligned} & 631.0 \\ & 677.2 \end{aligned}$ | 0.0707 | $\begin{aligned} & 42.0 \\ & 29.0 \end{aligned}$ | 0.3704 | $\begin{array}{r} 26.5 \\ 19.6 \end{array}$ | 23.1 | 1.6 | 0.02 | 38.8 |
| Total |  |  |  |  |  |  | $\begin{aligned} & 159.9 \\ & 140.8 \end{aligned}$ | 150.2 | 24.7 | 0.32 |  |

Table F.7. Estimated whitefish production for L226 NE during 1976 (September-0ctober 1975 to September-0ctober 1976).

| Age Class | Date | Average Length (mm) | Average Weight (gm) | Instantaneous Growth Rate <br> (G) | Number $\begin{aligned} & \left(N_{0}\right) \\ & \left(N_{i}\right) \end{aligned}$ | Instantaneous Mortality Rate (z) | Biomass ( Kg ) | Average Biomass (Kg) | Production (Kg) | Production/m (gm) | $\begin{aligned} & \text { Production } / N_{0} \\ & (\mathrm{gm}) \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | Fall 1975 Fall 1976 | $\begin{aligned} & 248.1 \\ & 282.7 \end{aligned}$ | $\begin{aligned} & 175.8 \\ & 264.3 \end{aligned}$ | 0.4082 | $\begin{aligned} & 306.0 \\ & 210.0 \end{aligned}$ | 0.3765 | $\begin{aligned} & 53.8 \\ & 55.5 \end{aligned}$ | 53.7 | 22.3 | 0.27 | 72.9 |
| 4-6 | Fal1 1975 Fall 1976 | $\begin{aligned} & 316.9 \\ & 331.2 \end{aligned}$ | $\begin{aligned} & 377.6 \\ & 433.4 \end{aligned}$ | 0.1378 | $\begin{aligned} & 191.8 \\ & 111.2 \end{aligned}$ | 0.5451 | $\begin{aligned} & 72.4 \\ & 48.2 \end{aligned}$ | 60.3 | 8.3 | 0.10 | 43.3 |
| 7-10 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 352.9 \\ & 366.8 \end{aligned}$ | $\begin{aligned} & 528.5 \\ & 596.2 \end{aligned}$ | 0.1206 | $\begin{aligned} & 65.0 \\ & 49.0 \end{aligned}$ | 0.2826 | $\begin{aligned} & 34.3 \\ & 29.2 \end{aligned}$ | 31.8 | 3.8 | 0.05 | 59.0 |
| 11-15 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 369.2 \\ & 383.3 \end{aligned}$ | $\begin{aligned} & 608.5 \\ & 684.3 \end{aligned}$ | 0.1174 | $\begin{aligned} & 35.0 \\ & 27.0 \end{aligned}$ | 0.2595 | $\begin{aligned} & 21.3 \\ & 18.5 \end{aligned}$ | 19.9 | 2.3 | 0.03 | 66.7 |
| 16-25 | Fall 1975 Fall 1976 | $\begin{aligned} & 381.5 \\ & 394.8 \end{aligned}$ | $\begin{aligned} & 674.0 \\ & 750.6 \end{aligned}$ | 0.1076 | $\begin{aligned} & 21.0 \\ & 13.0 \end{aligned}$ | 0.4796 | $\begin{array}{r} 14.1 \\ 9.8 \end{array}$ | 12.0 | 1.3 | 0.15 | 61.3 |
| Total |  |  |  |  |  |  | $\begin{aligned} & 195.9 \\ & 161.2 \end{aligned}$ | 178.6 | 38.0 | 0.46 |  |

Table F.8. Estimated whitefish production for L226 SW during 1976 (September-October 1975 to September-October 1976).

| Age Class | Date | Average Length (mm) | Average Weight (gm) | Instantaneous Growth Rate (G) | Number ( $\mathrm{N}_{\mathrm{O}}$ ) $\left(N_{i}\right)$ | Instantaneous Mortality Rate (z) | Biomass $(\mathrm{Kg})$ | Average <br> Biomass ( Kg ) | Production ( Kg ) | $\underset{(\mathrm{gm})}{\text { Production } / \mathrm{m}}$ | $\underset{(\mathrm{gm})}{\text { Production } / N_{0}}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1-3 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 234.2 \\ & 267.1 \end{aligned}$ | $\begin{aligned} & 146.8 \\ & 221.4 \end{aligned}$ | 0.4106 | $\begin{aligned} & 28.0 \\ & 21.0 \end{aligned}$ | 0.2877 | 4.1 4.6 | 4.4 | 1.8 | 0.02 | 64.2 |
| 4-6 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 304.5 \\ & 318.4 \end{aligned}$ | $\begin{aligned} & 333.3 \\ & 383.1 \end{aligned}$ | 0.1393 | $\begin{aligned} & 94.0 \\ & 62.0 \end{aligned}$ | 0.9162 | $\begin{aligned} & 31.3 \\ & 23.8 \end{aligned}$ | 27.5 | 3.8 | 0.05 | 40.8 |
| 7-10 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 341.5 \\ & 354.1 \end{aligned}$ | $\begin{aligned} & 477.2 \\ & 534.0 \end{aligned}$ | 0.1125 | $\begin{aligned} & 74.0 \\ & 50.0 \end{aligned}$ | 0.3920 | $\begin{aligned} & 35.3 \\ & 26.7 \end{aligned}$ | 31.0 | 3.5 | 0.04 | 47.2 |
| 11-15 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 351.5 \\ & 360.7 \end{aligned}$ | $\begin{aligned} & 521.9 \\ & 566.1 \end{aligned}$ | 0.0812 | $\begin{aligned} & 75.0 \\ & 49.0 \end{aligned}$ | 0.4257 | $\begin{aligned} & 39.1 \\ & 27.7 \end{aligned}$ | 33.4 | 2.7 | 0.03 | 36.2 |
| 16-25 | Fall 1975 <br> Fall 1976 | $\begin{aligned} & 380.6 \\ & 386.8 \end{aligned}$ | $\begin{aligned} & 669.4 \\ & 703.9 \end{aligned}$ |  | $\begin{aligned} & 50.0 \\ & 37.0 \end{aligned}$ |  | $\begin{aligned} & 33.5 \\ & 26.0 \end{aligned}$ |  |  |  |  |
| Total |  |  |  |  |  |  | $\begin{aligned} & 143.3 \\ & 108.8 \end{aligned}$ | 126.1 | 13.3 | 0.17 |  |

Appendix G. A comparison of fin-ray and scale age determinations for lake whitefish (Coregonus clupeaformis) and their implications for estimates of growth and annual survival ${ }^{1}$

## ABSTRACT

Fifteen populations of lake whitefish (Coregonus clupeaformis) were sampled to compare the fin-ray and scale aging techniques. There was good agreement between aging methods in fast growing populations, but usually fin-ray ages were larger than scale ages in slow growing populations. The validity of each aging method was tested by comparing finray and scale ages taken from three populations of whitefish when marked and when recaptured at least one year later. When growth was rapid, recaptured fish formed annular marks on both fin-rays and scales. When growth was slower, annular marks were distinguished on fin-ray sections more often than on scales of recaptured fish. When growth was extremely poor, annular marks on scales of recaptured fish were rarely distinguishable, but still recognizable on the majority of fin-ray sections. When fin-ray ages were consistently larger than scale ages for a given population, fin-ray based estimates of annual survival were higher and growth slower than corresponding scale age based estimates. In general, the finray method was more reliable than the scale method for aging lake whitefish.
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36: 534-544.

## INTRODUCTION

The purpose of this study was to compare the scale and fin-ray methods of age determination for lake whitefish (Coregonus clupeaformis), examine the validity of each method in whole lake mark-recapture experiments, and discuss some consequences of aging errors on estimates of growth and annual survival.

Scales are the traditional structures used for aging lake whitefish and most other freshwater teleosts (Everhart et al. 1975), but tests of the method's validity are conflicting. Van Oosten (1923) and Hogman (1968) held lake whitefish under artificial conditions to determine whether annuli were formed yearly on scales. Van 0osten could identify annuli on scales held under constant conditions in aquariums, and Hogman found two distinguishable marks formed on scales of fish held in hatchery pools. Neth (1955) compared scale ages of lake whitefish at release with those at recapture one year later in a whole lake study and found most fish formed one annulus, but felt that older, slower growing individuals might be underaged. Sych (1971) compared scale ages from Swedish coregonids with known ages and found frequent underaging in many populations. Crowding of annuli, failure of annulus formation, resoprtion or difficulties in interpretation of scales are widespread for in vivo populations (see Carlander (1974) for a review).

The scale method has rarely been compared with other methods of aging. Notable exceptions are Aass (1972) who compared otolith and scale ages using the cisco Coregonus aZbuZa, Beamish and Harvey (1969) who compared fin-ray and scale ages using the white sucker (Catostomus commersoni), and Power (1978) who compared scale and otolith ages for
lake whitefish. All three studies showed that when differences between aging methods occurred, scale ages were usually lower than corresponding ages determined by the alternative method.

Alternatives to scale aging are available for most species, but generally researchers have resorted to these only when scale aging was very difficult. Deelder and Williamsee (1973) showed that fin-rays were acceptable alternatives to scales for many European species. Cuerrier (1951) showed fin-ray aging was feasible for lake whitefish and this aging method was chosen as an alternative for this study.

Age composition data are necessary for calculating many population parameters, but rarely are errors in ages considered a serious source of bias. The argument frequently used is that errors would affect only a small portion of a sample, generally old individuals which make up only a small part of the population (Le Cren 1974).

MATERIALS AND METHODS

Lake whitefish were collected from 15 Canadian lakes using gillnets in all lakes. Trapnets were also used in L226 (Lake 226). Seven lakes were located within the Experimental Lakes Area, Ontario. The other eight were located across central and north-western Canada. Two lakes, L226 and L302, were divided into halves using vinyl walls for whole lake experiments in eutrophication (Schindler and Fee 1974). Lakes were selected to represent wide ranges of surface area, maximum depth, and geographical location (Table G.1). Only South Bay, Manitoulin Island, was sampled in Lake Huron. In other lakes larger than $1,000 \mathrm{~km}^{2}$ whitefish were gathered from more than one location.

Table G.l. Location, whitefish sample size, and some physical characteristics of the study lakes.

| Lake | Location | Surface area ( $\mathrm{km}^{2}$ ) | Maximum depth (m) | Sample size |
| :---: | :---: | :---: | :---: | :---: |
| Bell | $46^{\circ} \mathrm{N}, 81{ }^{\circ} \mathrm{W}$ | - | - | 36 |
| Clay | $50^{\circ} \mathrm{N}, 93^{\circ} \mathrm{W}$ | 30 | 24 | 111 |
| Dezadeash | $61^{\circ} \mathrm{N}, 137^{\circ} \mathrm{W}$ | 77 | 8 | 213 |
| ELA: 122 |  | <1 | 13 | 200 |
| 226 |  | $<1$ | 15 | 410 |
| 259 |  | 1 | 20 | 43 |
| 302 | $49^{\circ} \mathrm{N}, 93^{\circ} \mathrm{W}$ | <1 | 14 | 76 |
| 305 |  | $<1$ | 33 | 37 |
| 310 |  | <1 | 20 | 78 |
| 468 |  | 3 | 25 | 82 |
| Great Slave | $62^{\circ} \mathrm{N}, 114^{\circ} \mathrm{W}$ | 27,195 | 625 | 62 |
| Huron | $45^{\circ} \mathrm{N}, 32^{\circ} \mathrm{W}$ | 59,596 | 229 | 164 |
| Opeongo | $45^{\circ} \mathrm{N}, 48^{\circ} \mathrm{W}$ | 59 | 52 | 100 |
| Southern Indian | $57^{\circ} \mathrm{N}, 99^{\circ} \mathrm{W}$ | 2,250 | 37 | 415 |
| Winnipeg | $52^{\circ} \mathrm{N}, 98^{\circ} \mathrm{W}$ | 24,500 | 37 | 308 |

After fish were weighed, fork length recorded, and sex determined where possible, at least three scales and two fin-rays were removed from each fish. Scales were taken from either the first or second row above the lateral line beneath the posterior portion of the dorsal fin (Johnson 1976, Healey 1975, Hogman 1968, and others). Fin-rays were clipped from either a pelvic or pectoral fin as close to the base of the fin as possible. Ages determined from pectoral and pelvic fins from the same fish do not differ significantly (Mills, unpublished data).

To determine whether whitefish formed one annulus per year on both scales and fins, fish captured in L226 and L302 were marked and returned to their respective capture locations after sampling. Fish with fork lengths greater than 15 cm were tagged with either individually-numbered dart or modified spaghetti tags (White and Beamish 1972). A minimum of one year elapsed after release of marked fish before recaptures were sampled again during routine fall trapnetting and gillnetting.

Three additional scales were removed from recaptured fish from the same area as those taken previously, and at least two fin-rays were removed from the unclipped pelvic fin for use in age determinations. Rays were removed from a pectoral fin of fish which had had both pelvic fins clipped previously. Clipped fin-rays did not regenerate on whitefish larger than 22 cm and in smaller fish the regenerated rays were deformed and easily recognizable. Regenerated fin-rays or scales were not used for any age determinations. All age determinations using fin-rays or scales were made without reference to lengths of fish or previously assigned ages.

Scales were read by scale readers in whatever manner each thought appropriate. All readers had extensive prior experience in aging
whitefish; two had routinely aged whitefish for over 20 years using scales. Van Oosten $(1923,1929)$ established the criteria used for annulus determination: the crowding of circuli, "cutting over" of circuli on the antero-lateral fields, or both (Bell et al. 1977, Christie 1963, Edsall 1960, and others). Six different readers read the same set of scales taken from L310 whitefish. Three collaborated for one set of readings; the others read the scales independently. Sets of scales taken from lakes other than L310 were aged by one or another of the above readers. The same individual read all scales taken from L226 and L302 whitefish for each of the three years of sampling.

Fin-rays were mounted in clear epoxy, dried and sectioned with jewelers' saws using $7 / 0$ or $8 / 0$ blades. Individual sections about 0.5 mm thick were brushed clean and mounted on slides for age determinations under a compound microscope. The translucent zone which appeared as a clear ring extending completely around the center of individual rays under transmitted light was considered an annulus. Fin-ray annuli were similar in appearance to those described by Beamish (1973), Beamish and Harvey (1969), and Scidmore (1953) for white sucker. Two individuals read fin-ray sections from L310 fish independently and sets of fin-ray sections from other lakes were read by one or the other of these readers. The same individual read a11 L226 and L302 fin-ray sections.

I chose growth curves and annual survival estimates to demonstrate some effects of aging disagreements on population parameters. These were calculated for populations where more than 70 whitefish were sampled. Smaller sample sizes resulted in aberrant growth curves and age-frequency distributions unsuited for catch curve analysis. Growth curves were constructed from mean length at age data using each aging method.

Survival was estimated by catch curve analysis (Robson and Chapman 1961) using length frequency distributions based on each aging method.

RESULTS

Comparisons of Fin-Ray and Scale Ages

Agreement between fin-ray and scale ages was generally poor for most populations (Table G.2). The 15 populations could be separated into two groups based on agreement between pairs of corresponding fin-ray and scale ages.

The first group consisted of five populations and was characterized by generally good agreement between aging methods. Either pairs of finray and scale age agreed for most individuals or differences between the ages were rarely greater than one year. Fish collected from Clay Lake, Lake Huron, Lake Winnipeg, Bell Lake and L122 (Fig. G.1) comprised this group. Few individuals from all five populations were aged older than six by either method of aging.

The second group was composed of the 10 remaining populations and was characterized by poor agreement between aging methods and many comparisons where fin-ray ages were more than 1 year greater than scale ages. Many individuals were aged as eight or older using fin-rays. Few were aged as old as eight using scale ages.

The poorer the agreement was between methods of aging in the second group, the younger the age classes which showed consistent differences. In populations where agreement between methods was approximately $35-50 \%$, as in L226 (Fig. G.1), fin-ray ages were consistently greater than scale

Table G.2. Summary of percent agreement between pairs of fin-ray and scale ages for lake whitefish from 15 populations.

| Lake | Scale = <br> fin-ray | $\begin{aligned} & \text { Scale }= \\ & \text { fin-ray } \\ & \pm 1 \text { yr } \end{aligned}$ | Scale > <br> fin-ray | $\begin{aligned} & \text { Fin-ray } \\ & >\text { scale } \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: |
| Huron | 93 | 100 | 2 | 5 |
| Clay | 79 | 96 | 7 | 14 |
| Winnipeg | 55 | 88 | 19 | 26 |
| Bell | 42 | 72 | 19 | 39 |
| 122 | 30 | 75 | 18 | 52 |
| 226 | 47 | 60 | 3 | 50 |
| 302 | 41 | 59 | 1 | 58 |
| Southern Indian | 27 | 56 | 9 | 64 |
| Opeongo | 26 | 40 | 1 | 73 |
| Dezadeash | 23 | 48 | 1 | 77 |
| Great Slave | 23 | 60 | 21 | 56 |
| 259 | 18 | 47 | 1 | 79 |
| 468 | 16 | 29 | 0 | 84 |
| $310^{1}$ | 15 | 49 | 5 | 79 |
| 305 | 8 | 11 | 0 | 92 |

1 The best agreement between fin-ray and scale readers.

Figure G.1. Comparisons of fin-ray, scale age pairs for lake whitefish from four populations. The Lake Huron and Lake 122 plots are representative of group 1 populations. The Dezadeash Lake and Lake 226 plots are representative of group 2 populations. See text for complete explanation. Numbers represent individual pairs of ages falling in each age category. The diagonal line indicates comparisons where fin-ray ages $=$ scale ages. Comparisons where scale ages > fin-ray ages are above the line; comparisons where fin-ray ages > scale ages are below the line.

ages, starting at scale ages of four or five. In populations where agreement was $30 \%$ or less, like Dezadeash Lake (Fig. G.1), consistent differences in aging started at scale ages of two or three. Individuals with greater scale ages could have fin-ray ages two or three times those of the corresponding scale ages.

The L310 population sample exhibited poor agreement between methods and was well suited for an examination of replicability between readers. Agreement between fin-ray readers (61\%) was better than agreement between any combination of scale readers ( $44 \%$ ). The best agreement between any combination of fin-ray and scale readers was $15 \%$ and the worst agreement was $6 \%$. While the fin-ray ages of one reader were slightly higher than those of the second, the differences were much less than those between scale readers. The variation in age assigned a particular fish was sometimes large, as much as 14 years between a fin-ray and a scale age. See Beamish et a7. (1976) for a more detailed discussion of these results.

Fish length was a poor indicator of fish age for L310 whitefish, as was generally true for other populations in this second group. While the smallest individuals were normally younger than the largest ones, large variations in age within 1 cm length groups obscured any clear relationship. More variation within these length groups was apparent using fin-ray ages rather than scale ages in the L310 sample, by as much as 11 years, but scale ages also varied widely, by as much as eight years.

Age Validation for L226 and L302 Lake Whitefish

Of the 923 marked whitefish released in L226 during 1973 and 1974, 195 were recaptured in 1974 and 1975 for age comparisons. Of the 61
marked whitefish released in L302 in 1975, 29 were recaptured for age comparisons in autumn 1976. Results from the two separate basins of L302 were combined because the wall permitted intermixing of fish between basins. Results from the two basins of L226 are discussed separately because there was no interchange of fish between basins.

Comparisons of age at release and age at recapture for L226 NE showed that both aging methods were valid (Table G.3). New annuli on both fin-rays and scales were very clear (Fig. G.2). While on the average, fin-ray aging gave more reliable results than scale aging, no bias was present in the number of recapture scale ages which were either greater or less than that predicted knowing the scale age at marking.

Comparisons of age at release and age at recapture showed that fin-ray aging was valid and scale aging questionable in L226 SW (Table G.3). New annuli on fin-rays were very clear but new annuli on scales were frequently unclear or apparently absent. This was most pronounced in fish recaptured two years after release (Fig. G.3).

Comparisons of age at release and recapture in $L 302$ showed that the fin-ray method was of questionable value and the scale method invalid (Table G.3). New annuli on fin-rays were many times compressed to the old but were distinguishable in the majority of cases. New annuli on scales were rarely detected (Fig. G.4).

## Growth

Growth curves based on scale ages (Fig. G.5) fell within the range reported for other lake whitefish populations (Healey 1975). Growth curves based on fin-ray ages could be extended to older age groups more

Table G.3. Summary of differences in age of individual whitefish determined at initial marking (M) to later recapture (R) using the fin-ray and scale ageing techniques. The number of individuals whose change in age ( $R-M$ ) equaled the number of winters between marking and recapture is indicated by "*".

| Lake | $\begin{gathered} \text { Change in } \\ \text { age } \\ (R-M) \end{gathered}$ | No. recaptured 1 year after release |  | No. recaptured 2 years after release |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Scales | Fin-rays | Scales | Fin-rays |
| $\begin{aligned} & \mathrm{L} 226 \\ & \mathrm{NE} \end{aligned}$ | $-2(\leq) 1$ | 2 | 1 |  |  |
|  | -1 | 1 |  |  |  |
|  | 0 | 8 | 1 |  |  |
|  | 1 | $42^{*}$ | $68{ }^{*}$ | 7 | 1 |
|  | 2 | 9 | 2 | $29 *$ | $37^{*}$ |
|  | $3(\geq)^{2}$ |  |  | 3 |  |
| $\begin{aligned} & \mathrm{L} 226 \\ & \mathrm{SW} \end{aligned}$ | -2 ( 5 ) | 1 | 1 |  |  |
|  | -1 | 3 |  | 1 |  |
|  | 0 | 13 | 1 | 6 |  |
|  | 1 | $34 *$ | 56 * | 21 | 2 |
|  | 2 | 5 | 1 | $3 *$ | $23 *$ |
|  | $3(\geq)$ | 3 |  | 1 |  |
| L302 | -2 ( $\leq$ |  | 1 |  |  |
|  | -1 | 3 |  |  |  |
|  | 0 | 19 | 10 |  |  |
|  | 1 | $2^{*}$ | $18{ }^{*}$ |  |  |
|  | 2 |  |  |  |  |
|  | $3(\geq)$ |  |  |  |  |

[^2]Figure G.2. Scales and pelvic fin-ray sections from a L226 NE whitefish taken at marking ( $A, C$ ) and recapture ( $B, D$ ) one year later. Annuli are indicated by $(-)$. Both scales and fin-ray sections were aged three at release and four a recapture.

A


Figure G.3. Scales and pelvic fin-ray sections from a L226 SW whitefish taken at marking ( $\mathrm{A}, \mathrm{C}$ ) and recapture $(B, D)$ two years later. Annuli are indicated by $(-)$. Both scales and fin-ray sections were aged three at release. The fin-ray sections were aged five at recapture while the scales were aged four.


Figure G.4. Scales and pelvic fin-ray sections from a L302 whitefish taken at marking ( $A, C$ ) and recapture ( $B, D$ ) one year later. Annuli are indicated by $(-)$. Both scales and fin-ray sections were aged five at release. The fin-ray sections were aged six at recapture while scales were aged five.


Figure G.5. A summary of individual comparisons between fin-ray and scale age based growth curves for 11 populations. A, the range of growth where fin-ray ages and scale ages resulted in very similar growth curves. B, the range where fin-ray age based curves differed from scale based curves starting at age four or five. $C$, the range where fin-ray age based curves differed from those of scales starting at age two or three. Dots indicate the previously reported range of whitefish growth based on scale ages (Healey 1975).

readily than those derived from scales and in many cases these indicated slower growth. The 11 populations could be divided into three groups based on comparisons between pairs of fin-ray and scale growth curves.

The first group was made up of four populations which had similar fin-ray and scale growth curves and were generally located in the upper range of whitefish growth (Fig. G. 5A). Three of these populations (Lake Huron, Lake Winnipeg and Clay Lake) exhibited very rapid growth rates and contained larger individuals than other populations. The L122 population also showed good agreement between scale and fin-ray growth curves, but somewhat slower growth.

The second group was made up of three populations whose fin-ray growth curves indicated moderately slower growth than those derived from scales (Fig. G.5B). The scale growth curves for these populations, Southern Indian, L226 and L302, were generally in the middle range of whitefish growth. The L226 population (Fig. G.6) is representative of this group and shows that differences between growth curves due to aging methods start at age four, the age of sexual maturity for this population. Slower growth after sexual maturity using fin-ray ages was a common characteristic of this group.

The third group was made up of four populations whose fin-ray growth curves indicated much slower growth than those derived from scales (Fig. G.5C). The scale growth curves for these populations were generally in the lower range of whitefish growth. The Dezadeash, Opeongo, L310 and L468 populations had fin-ray curves that indicated much poorer growth than those derived from scales with differences starting in age groups before sexual maturity. The Dezadeash Lake population, representative of this group (Fig. G.6), showed that differences in growth curves can

Figure G.6. Growth curves determined from fin-ray ( $O$ ) and scale $(\Delta)$ mean lengths at age for Dezadeash Lake and L226. The dashed lines are eye-fitted growth curves based on scale ages, the solid lines based on finray ages. Brackets represent the $95 \%$ confidence limits on each mean fork length at age.

occur in fish as young as age two, well before sexual maturity. These populations were composed almost entirely of small whitefish from many age groups. Few individuals larger than 30 cm were present.

Annual Survival

Annual survival rates calculated from age data and previously published rates for the same populations are presented in Table G. 4 for 11 of the populations. My catch curve rates and previously published rates based on scale ages agree well. For four populations survival estimates using fin-ray ages agreed well with corresponding scale estimates. In most populations fin-ray estimates were much higher than scale estimates. In only two cases was the scale based annual survival greater than its fin-ray counterpart. Generally, fin-ray survival rates were greater than those using scales and could be as much as twice the corresponding scale estimates. Two mark-recapture annual survival estimates independent of age data are available for comparison with catch curve rates. Both mark-recapture estimates are similar to fin-ray estimates for Lake Huron and L226. The scale survival estimate was similar to the mark-recapture estimate for Lake Huron, but well below the mark-recapture estimate for L226.

DISCUSSION

Whitefish Age Determination

A common method employed by many researchers to determine the level

Table G.4. Annual survivorship rates for 11 whitefish populations using catch curves based on scale and fin-ray ages from Fig. 2. The upper group is composed of populations undergoing moderate and heavy exploitation; the lower group of populations undergoing light exploitation or unexploited. Other independent estimates are presented for comparison where survivorship $=1$ - total mortality rate.

| Lake | Annual Survival |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Scale age 95\% | Fin-ray age 95\% | Scale Literature values | Mark recapture |
| Huron | $.17 \pm .11$ | $.19 \pm .12$ | . 071 - . $38^{2}$ | $.11{ }^{6}$ |
| Clay | $.46 \pm .08$ | $.48 \pm .08$ |  |  |
| 122 | $.49 \pm .05$ | . $43 \pm .06$ |  |  |
| Winnipeg | . $52 \pm .06$ | $.50 \pm .06$ | . $04-.50^{3}$ |  |
| 468 | $.27 \pm .10$ | $.68 \pm .08$ |  |  |
| 302 | $.35 \pm .11$ | $.64 \pm .10$ |  |  |
| Dezadeash | $.44 \pm .08$ | $.60 \pm .07$ |  |  |
| Opeongo | $.49 \pm .07$ | . $75 \pm .05$ | $.41-.59^{4}$ |  |
| 226 | . $59 \pm .04$ | . $73 \pm .04$ |  | $.75^{7}$ |
| Southern Indian | $.60 \pm .04$ | . $70 \pm .04$ | $.30-.57^{5}$ |  |

1 Budd and Cucin 1962.
2 Cucin and Regier 1965.
3 Davidoff et al. 1973.
4 Ricker 1947, dwarf form excluded
${ }^{5}$ Ayles 1976.
6 Spangler 1970.
7 Mills, unpublished data, Jolly-Seber estimate averaged for 3 years' data.
of confidence placed in a set of age determinations is to read the same set more than once, comparing ages for individual fish and reporting percentage agreement between sets of ages, or reaging individuals where disagreements occur. Ricker (1975) suggests that $80-90 \%$ agreement between sets is good. Only the results from the Lake Huron sample, the fastest growing population, exhibited this level of agreement between methods. Both Neth (1955) and Christie (1963) found close to $80 \%$ agreement between sets of scale ages for other relatively fast growing populations. For slower growing populations, we found agreement between methods or readers to be much lower. But even if agreement between sets of age determinations is good, it does not constitute validity for an aging technique. It only indicates consistency of the readers, clarity of the annuli, or both.

Comparisons of percent agreement between sets of age determinations can be an unreliable statistic with which to judge consistency between aging methods. For example, the L122 sample showed poor agreement between aging methods (30\%) but rarely was the difference between aging methods greater than one year. More importantly, there was little consistent bias between aging methods. The resulting growth curves and survivorships using either method of aging were almost identical. Despite the poor agreement between aging methods, the effects on parameters calculated from these ages was minimal. The $L 226$ data showed better agreement between aging methods (47\%) than the L122 data, but a consistent bias was present between the two aging methods. Fin-ray ages were generally greater than scale ages (Fig. 1). The resulting growth curves and survivorships for $L 226$ whitefish showed large differences depending on which method of aging was used. Despite better agreement
between aging methods in L226 than L122, there were great differences in the parameters calculated from the age data depending on which method of aging was used. Percent agreement only assesses whether ages determined by one method equal those of another, without quantifying the magnitude of differences.

Aging techniques for each population of interest should be validated in situ. This certainly is not possible in most cases. I suggest instead that scales and fin-rays be examined for a lake whitefish population to determine if one method consistently results in greater ages than the other. Simple data plots like Fig. G. 1 are more valuable for assessing aging accuracy than percent agreement between aging methods. A simple glance at Fig. 1 indicates whether there is a significant and consistent bias between the two methods, the magnitude of the bias, and at what age consistent differences first occur. 0toliths (Power 1978) or some other bony structure might also be used. Otolith ages for lake whitefish can agree well with fin-ray ages for some populations (personal communication, K. Machniak, Department of Fisheries and Oceans, Freshwater Institute), but it is necessary to sacrifice fish to obtain otoliths and they are not as conveniently removed as a few fin-rays. The processes involved in deposition of scales are different from those of fin-rays or bone (Simkiss 1974). Therefore, an alternative method of age determination also has a physiological basis.

If consistent differences between fin-ray and scale ages occur, we believe the fin-ray ages are more dependable than scale ages. The different growth regimes in L226 and L302, combined with the age validation possible in these lakes, provide a plausible explanation for the aging disagreements found between different methods used for
many lake populations. The productivity of L226 NE is much higher than that of L226 SW or L302 (Schindler and Fee 1974, Fee 1979). Marked whitefish grew faster in L226 NE (averaging $31 \mathrm{~mm} /$ year), slower in L226 SE (16 mm/year), and slowest in L302 (1 mm/year). After a year of good growth, as in L226 NE, distinguishable annuli are formed on both scales and fin-rays. Under conditions of moderate growth, as in L226 SW, annuli are easily distinguishable on fin-rays, but not on scales. When growth is minimal, annuli are rarely distinguishable on scales, and not always apparent on fin-ray sections. Combinations of years of good, moderate, or minimal growth could easily explain the large differences in scale and fin-ray ages present in many of the lake whitefish populations of Table G.2.

Some Implications of Aging Errors on Whitefish Growth, Survivorship and Management

Since fin-ray ages are correct more often than scale ages, then when consistent differences occur between the methods, parameters based on fin-ray ages should be more reliable than those based on scale ages. The good agreement between the mark-recapture and catch curve survival estimates for L226 supports this (Table G.4). This has important implications for lake whitefish management.

Carlander (1974) has shown that over-estimates of growth often result from aging errors. Growth of populations in the middle and lower range of whitefish growth was overestimated using scales (Fig. G.5). All of these populations were also unexploited except that of Southern Indian Lake, which is only lightly exploited (Ayles 1976). All these
populations contained large numbers of older individuals, beyond age eight. While our data based on fin-ray ages are not as extensive as those based on scale ages for many whitefish populations, it is very likely that growth rates of other slower growing lake whitefish populations have been overestimated using scales.

When scale and fin-ray ages differed markedly for a population, the annual survival based on fin-rays was higher than that using scales. Populations which showed the greatest difference between fin-ray and scale based annual survival were the unexploited or lightly exploited populations (Table G.4). All previous estimates of survivorship for unexploited populations are from scale age structure data (Healey 1975). It is very likely that these previous estimates were very conservative, underestimating the true rates.

When using fin-ray ages, an inverse relationship between growth and survivorship was apparent. Slow growing populations had high survivorships. Fast growing populations had low survivorships. If growth and survivorship were calculated using scale ages, no relationship was apparent. Healey (1975) also found little correlation between survivorship and growth in an extensive review of whitefish population dynamics based on scale ages. I believe that errors in aging whitefish using scales might have obscured this relationship.

While our data show that scale age determinations are acceptable for moderately or heavily exploited populations, and unacceptable for lightly or unexploited populations, others which are in transition from relatively unexploited to heavily exploited could also show errors due to aging. Current management practice for northern lake whitefish fisheries is to crop the populations more intensively. Many of these
populations exhibit relatively slow growth rates. There is sufficient evidence to suggest that an increase in harvest will produce an increase in growth rate for lake whitefish (Healey 1975). The use of scale ages instead of fin-ray ages for populations such as L226 or Dezadeash Lake (Fig. G.6) before and after cropping could result in false conclusions about the effects of increased cropping. While scale ages might show an increase in length at age for young age groups after increased harvest, the full impact on older age classes might be lost because larger sized, initially underaged fish were removed (Fig. G.7A). Similarly, there is sufficient evidence to suggest lake whitefish respond to increased cropping by a decline in age at maturity (Healey 1975). This could also be obscured by errors from scale ages (Fig. G.7B). If we are to have predictive management of lake whitefish and other fish populations, we must recognize that significant, widespread aging errors are possible and that these errors can introduce significant bias in parameters used for management decisions.

Figure G.7. Some possible consequences of incorrect scale aging under conditions of changing exploitation: (A) growth curves and ( $B$ ) age at sexual maturity. Condition before exploitation (a) and after (b).



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[^0]:    * Insufficient sample size.

[^1]:    ${ }^{a}$ Insufficient sample sizes.

[^2]:    ${ }^{1}$ The age at recapture was 2 years or less than at marking.
    2 The age at recapture was 3 years or greater than at marking.

