THE UNIVERSITY OF ALBERTA

ATTRIBUTES OF MALE AND FEMALE YELLOW PERCH IN MINK LAKE, ALBERTA: EXTERNAL DIFFERENCES, MATURATION, SURVIVAL, ABUNDANCE, AND PRODUCTIVITY

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ATTRIBUTES OF MALE AND FEMALE YELLOW PERCH IN MINK LAKE, ALBERTA: EXTERNAL DIFFERENCES, MATURATION, SURVIVAL, ABUNDANCE, AND PRODUCTIVITY submitted by MARY J. PACKHAM in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

W. C. Mackay
Supervisor

Date December 14, 1987

Abstract

The principal objectives of this study were to evaluate whether differences occurred between adult male and female yellow perch, *Perca flavescens* (Mitchill), in the following demographic characteristics: age at sexual maturity, abundance, rate of growth, survival, biomass and production. The perch population studied was from a small, shallow, eutrophic lake in central Alberta. Perch were caught in Windermere traps or in an otter trawl between May and October during 1981 and 1982. A method was developed to determine the sex of adult perch from external characteristics. The sex of captured and recaptured adults was known, thus allowing separate estimates of abundance, survival, biomass and production for males and females.

Population estimates of the adult fish indicated the presence of 14,806 males and 3,378 females (208 males and 48 females ha^{-1}). The deviation in sex ratio from 1:1 in the adult perch population was attributed to differences between male and female yellow perch in age at sexual maturity and in rates of survival. All males were sexually mature by their fourth year; females matured in their fifth year. Mean annual survival was 0.71 for adult males and 0.37 for adult females.

Methods used by other authors to estimate population sizes of perch during spawning, when sex could be determined by external examination, overestimated the population size of adult yellow perch in Mink Lake by 63 to 90 percent.

Mean biomass and total annual production of adult yellow perch in Mink Lake were low compared to other studies, and were 10.4 kg ha^{-1} and 4.4 kg ha^{-1} yr^{-1}, respectively. Total annual production for adult males and females was 3.4 and 1.0 kg ha^{-1} yr^{-1}, respectively. This study demonstrates large differences between adult male and female perch in survival, abundance, biomass and production.

ACKNOWLEDGEMENTS

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Table of Contents

List of Tables

List of Figures

I. GENERAL INTRODUCTION

The occurrence and magnitude of differences between males and females in attributes such as abundance, biomass and production have not been evaluated for fish. Indeed, few estimates of biomass and production exist (Carlander 1977). If large differences in the biomass and production exist between adult males and females, selection and harvest of appropriate proportions of each sex would be required to guarantee the reproductive success of the population. This need for more intensive management of fisheries resources is now critical as a direct result of increasing human populations, and the subsequent increasing pressures on fish populations by fishermen, especially in remote areas of North America (Lawler 1978). To determine whether differences occur between males and females in abundance, biomass and production, factors involved in their estimation, including growth rate, age at maturity and survival rate should be examined, for each sex.

Differences in abundance, biomass and production between males and females have been evaluated infrequently because the sex of few fish species may be differentiated externally, except briefly during spawning. Where these have been looked at for each sex, the abundance of males and females has been assumed to be equal. The composition of many animal populations deviates, however, from the expected sex ratio of 50 percent males and females, and a constant sex ratio within a single species cannot be assumed (Krebs 1978). In fish, the ratio of adult males to adult females obtained from capture frequencies ranges from 1:32 to 4:1 (Backiel and Zawisza 1968; Clady 1967; Brown 1970; Dadswell 1979).

Differences in the abundance, biomass and production of adult males and females probably do occur for many species of fish owing to the following differences between males and females. Male fish generally mature at an earlier age and at a smaller size than females (Bell *et al.* 1977; Dadswell 1979; Nordeng 1983; Martin-Bergman and Gee 1985), which increases the abundance, biomass and, hence, production of adult males. Females, however, may grow faster (Barton 1980; Martin-Bergman and Gee 1985), achieve a larger ultimate size (Dadswell 1979), and survive better than males with increasing age (Dadswell 1979; Martin-Bergman and Gee 1985). Therefore, females may be more abundant in the oldest age-classes (Bakkala 1970). In addition, relative survival rates may differ between male and female fish (Newsome and Leduc 1975), since each require different amounts of energy for gonadal development, spawning migration and spawning (Belding 1934; Idler and Bitners 1958; Glebe and Leggett 1981).

Yellow perch, *Perca flavescens* (Mitchill), and Eurasian perch, *Perca fluviatilis* L., are biologically equivalent (Thorpe 1977), and may be combined in discussing estimates of perch growth, survival rates, abundance, biomass and production.

Only one researcher has estimated perch production in Canada, although perch are widely distributed (Scott and Crossman 1973), are an important commercial and sport fish (El-Zarka 1959), and in Alberta, are caught more frequently by anglers than any other species (Longmore *et al.* 1982).

In perch, production probably differs between adult males and females, since variations in sex ratio, growth rates, and survival, all factors which affect fish production have been reported. Sex ratio of collections is often unequal and ranges from 2.6:1 in favor of males (Clady 1977), to 1:4 in favor of females (Jellyman 1980). Growth rates may differ between sexes (Hartmann 1975), survival rates are sex specific (Holčik 1977; Craig *et al.* 1979), and production has been reported to differ between sexes at least during spawning (Craig 1980).

Apparent sex ratios of perch reported during sampling or harvesting (Weller 1938; Hile and Jobes 1941; Eschmeyer 1938) probably have been biased owing to difficulties in sampling perch in all locations in a lake and to size selection by gear and anglers. The sexes segregate at different depths and temperatures (Sandheinrich and Hubert 1984), and select different diets (Eschmeyer 1938). Sampling in shallow warm waters favored the collection of female fish (Eschmeyer 1938; Hartmann 1975). Gillnets also select for the larger girth of the faster-growing adult females (El-Zarka 1959), and anglers usually keep the largest fish they capture, which, in the case of perch, are usually females (Clady 1977). Male fish ripen sooner, move to spawning grounds earlier and remain there longer than females (Hile 1936). Collections made during spawning favor males, which are more likely than females to be captured then by traps (El-Zarka 1959; Craig 1974; Jensen 1976; Thorpe 1977), and gillnets (Brazo *et al.* 1975). Thus, when previous researchers have been unable to distinguish the sex of fish from external examination except at spawning, accurate estimates of the relative abundance of adult males and females have not been possible (Thorpe 1974; Jensen 1976; Craig 1977). Understandably, separate estimates of male and female fish populations have not been incorporated into production estimates.

Real variations in sex ratio have been reported infrequently. Males have been reported to be more abundant in slow-growing stocks (Alm 1946; Eschmeyer 1937; 1938; Jensen 1976) and female perch generally are more abundant than males (Thorpe 1974; Jellyman 1980; Viljanen and Holopainen 1982) in fast-growing stocks (Dryagin 1948). A preponderance of female perch has been explained also by their better survival rates after two years of age (Craig 1974), so that at increasingly advanced ages, the sex ratio becomes skewed toward female fish which have longer life spans (Craig 1982).

The goals of this study were to develop a method to distinguish the gender of adult perch externally, and to use this method to enable the estimation and comparison of the abundance, rates of survival, biomass and production for adult male and female yellow perch in Mink Lake.

This thesis is divided into five chapters. In the remainder of the introductory chapter, I will describe the study site and the general methods used. The other four chapters consider the differences between adult male and female yellow perch and include: a method developed and tested for the external determination of sex; a comparison of age at maturity and growth rates; a comparison of the annual survival rates and estimates of abundance, and; a comparison of the estimates of biomass and production.

A. STUDY SITE DESCRIPTION AND GENERAL METHODS

Rationale For Choice of Mink Lake

To estimate the abundance, rates of survival, biomass and production of a species of fish, a lake with specific characteristics is required. These characteristics include small size so that the entire lake can be sampled, and low fish species diversity with the biomass of the target species being largest. In addition, the absence of inflow and outflow prevents tag loss due to fish emigration; no immigration of untagged fish can occur, thus, population size remains constant.

Mink Lake, Alberta, possesses the above required characteristics. The lake is small (7.1 ha), and there is no inflow or outflow. Only five fish species are present; three species were captured during this study. From largest to smallest biomass, the fish species include yellow perch, northern pike, *Esox lucius L.*, and Iowa darter, *Etheostoma exile* (Girard)(this study). One burbot, *Lota lota L.*, and five brook stickleback, *Culaea inconstans* (Kirtland) have been reported in the lake prior to 1981. None were caught in this study, however, and both species are presumed to occur at very low density.

Location, Topography, and Bathymetry of Mink Lake

Mink Lake is located at 53° 31'N, 114°14'W, approximately 70 km west of Edmonton, Alberta (Figure I.1). The lake is situated among rolling hills covered with aspen parkland, characteristic of east-central Alberta, and is partially developed as agricultural land. The lake is comprised of two basins, consisting of 33.6 percent and 66.4 percent, respectively, of the lake surface area, and the rolling topography that surrounds the lake is also observed in the bathymetry of the lake (Figure I.2). Physical data are given in Table I.1.

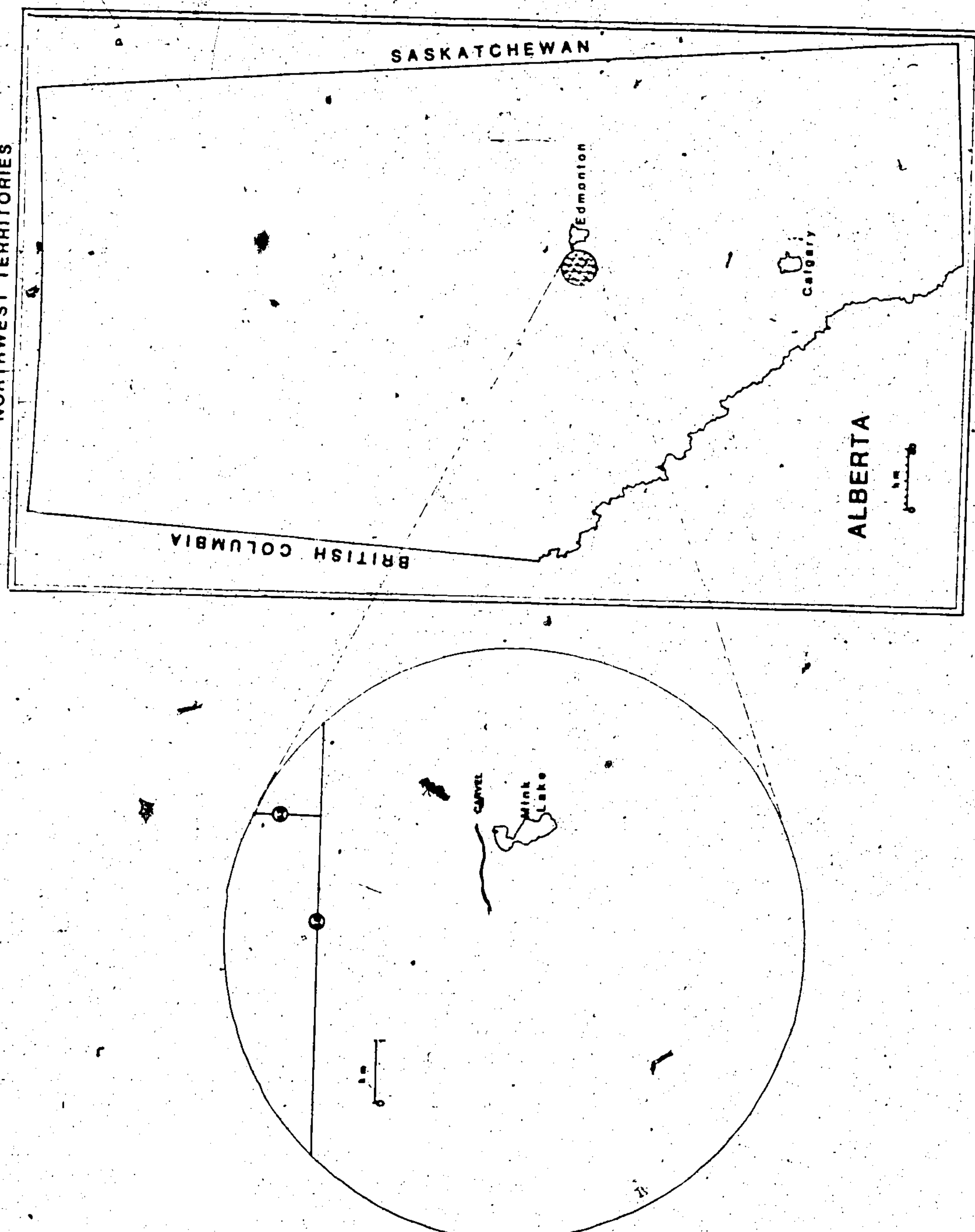

Figure I.1 Location of Mink Lake.

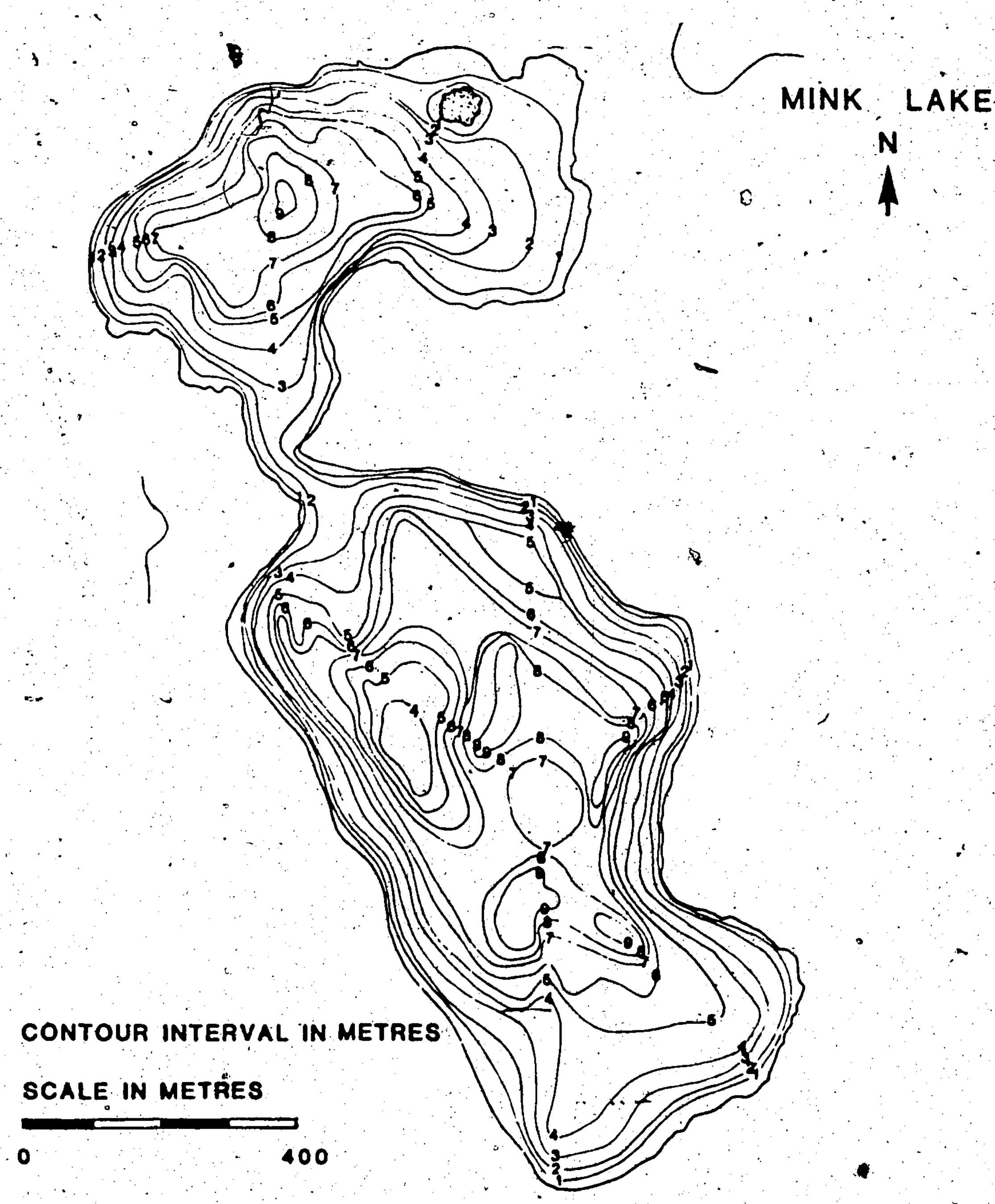

Figure I.2 Bathymetric map of Mink Lake, Alberta.

Table I.1 Physical and chemical characteristics of Mink Lake.

Physical		Chemical	
Surface Area (km^2)	0.71	Alkalinity ($mg\ L^{-1} CaCO_3$)[a]	149
Volume (m^3)	3.265×10^9	Total Dissolved Solids ($mg\ L^{-1}$)[b]	1186
Mean Depth (m)	3.4	Summer epilimnetic [TP][a] ($mg\ m^{-3}$)	26.6
Maximum Depth (m)	9.7	Summer trophogenic [TP][a] ($mg\ m^{-3}$)	26.9
		Summer chlorophyll *a* ($mg\ m^{-3}$) 1981[a]	5.3
		1982[b]	14.3
		1983[c] N. basin	5.3
		S. basin	5.9
		Summer TN:TP[a]	39

a (Prepas and Trew 1983).
b (Prepas and Vickery 1984).
c (Prepas pers. comm.).

Limnological Characteristics of Mink Lake

Generally, Mink Lake may be considered slightly saline (TDS>500 mg/L) and alkaline, but not heavily colored or turbid (Prepas and Trew 1983). Chlorophyll *a* levels measured over three years ranged from 5.3 to 14.3 mg m⁻³ (Prepas and Trew 1983; Prepas and Vickery 1984; Prepas unpublished), and indicate that Mink Lake is eutrophic (Vollenweider 1979) (Table I.1). Secchi disk readings taken biweekly varied from 1.3 m in August to 9.3 m in June (this study).

Sampling Procedures

Yellow perch were captured at Mink Lake between the months of May and October during 1981 and 1982. Capture techniques can be size selective (Ricker 1975) and vulnerability to traps may increase with increased size of the fish (Latta 1959; Hamley and Regier 1973). Two types of gear with different selectivity (Ricker 1975) were used, therefore, to maximize the precision of the mark and recapture population estimate (Beukema and De Vos 1974). The yellow perch were captured primarily by Windermere perch traps (Worthington 1950), and an otter trawl. The traps are a passive type of fishing gear, i.e. fish actively enter them, whereas fish are picked up by the trawl, which are towed through the water. Helfman (1979) noted that the greatest movements of perch, and the greatest opportunities to catch them in traps, occur at sunset and at sunrise. The traps were set, therefore, each evening of the sampling period between one and two hours prior to sunset, with the funnels parallel to the shoreline. Windermere traps with 1.3 cm diameter mesh and a funnel opening diameter of 8.5 cm capture fish 9.5 cm total length or larger (Craig 1974; LeCren *et al.* 1977). A 5.0 m wide semi-balloon bottom otter trawl with 3.0 cm stretched mesh on the wings and 1.3 cm stretched mesh cod end interliner was used. This trawl size, pulled for five minutes at a speed of 3.4 km hr⁻¹, captures all adult age groups of yellow perch equally, providing reliable indices of relative adult abundance (Nielsen 1983).

In May 1981, a survey was conducted to identify perch spawning sites in Mink Lake, where adults were expected to be concentrated. Six sites were discovered and five were used as locations to set Windermere traps (Appendix I.1). The sixth site was considered to be too close to the boat launch to ensure protection of the traps and the perch captured in them, from vandalism.

By the end of 1981, it was noted that more than half of the adult yellow perch (54 percent, n=1.158) were captured at the north end of the north basin, owing to their concentration there for spawning. Therefore, in 1982, on the basis of the 1981 results, sampling was stratified and conducted equally within two strata: 'A' composed of approximately 10 ha in the north end of the north basin, and 'B' composed of 61 ha, constituting the remainder of the lake (Figure I.3).

Mink Lake was divided into 14 areas (three in Stratum A; areas 12 through 14, and 11 in Stratum B; areas one through 11) in which to set traps or to trawl. For ease of identification of the sampling sites, each of the 14 areas were divided further into four sub-areas, for a total of 56 sub-areas. Sub-areas one and two were less than four metres deep, sub-areas three and four were greater than four metres deep). Based on the observation that during the spring and summer of 1982, that adult perch were captured more frequently in depths less than four metres, sub-area sampling was also stratified to maximize the numbers of fish caught. Traps were set in sub-areas one and two twice as frequently as in sub-areas three and four. Seven groups of traps, comprised of four traps each (equalling 28 traps in total), were set daily in seven of the 14 areas in the lake. To ensure equal fishing effort between the two strata, considering the unequal number of groups of traps (seven), 12 or 16 traps were used in each strata. This number was rotated daily between strata, so that each stratum was fished with 16 traps on alternate nights.

The seven areas in which to set the traps daily, and the places to trawl, were identified according to a table of random numbers. The table was consulted a second time to determine the sub-area within each area in which to place the group of four traps. Each group of four traps was located so that they were all within 50 m of one another. Since the areas were chosen randomly, sometimes two groups of traps were used in the same area. However, no overlap occurred in the placement of two groups of traps in one sub-area. Trawling sites also were chosen randomly except that only depths less than four metres could be used.

The fish were measured for total length (Carlander and Smith 1945), to the nearest millimetre, and the urogenital opening of the perch was examined to determine

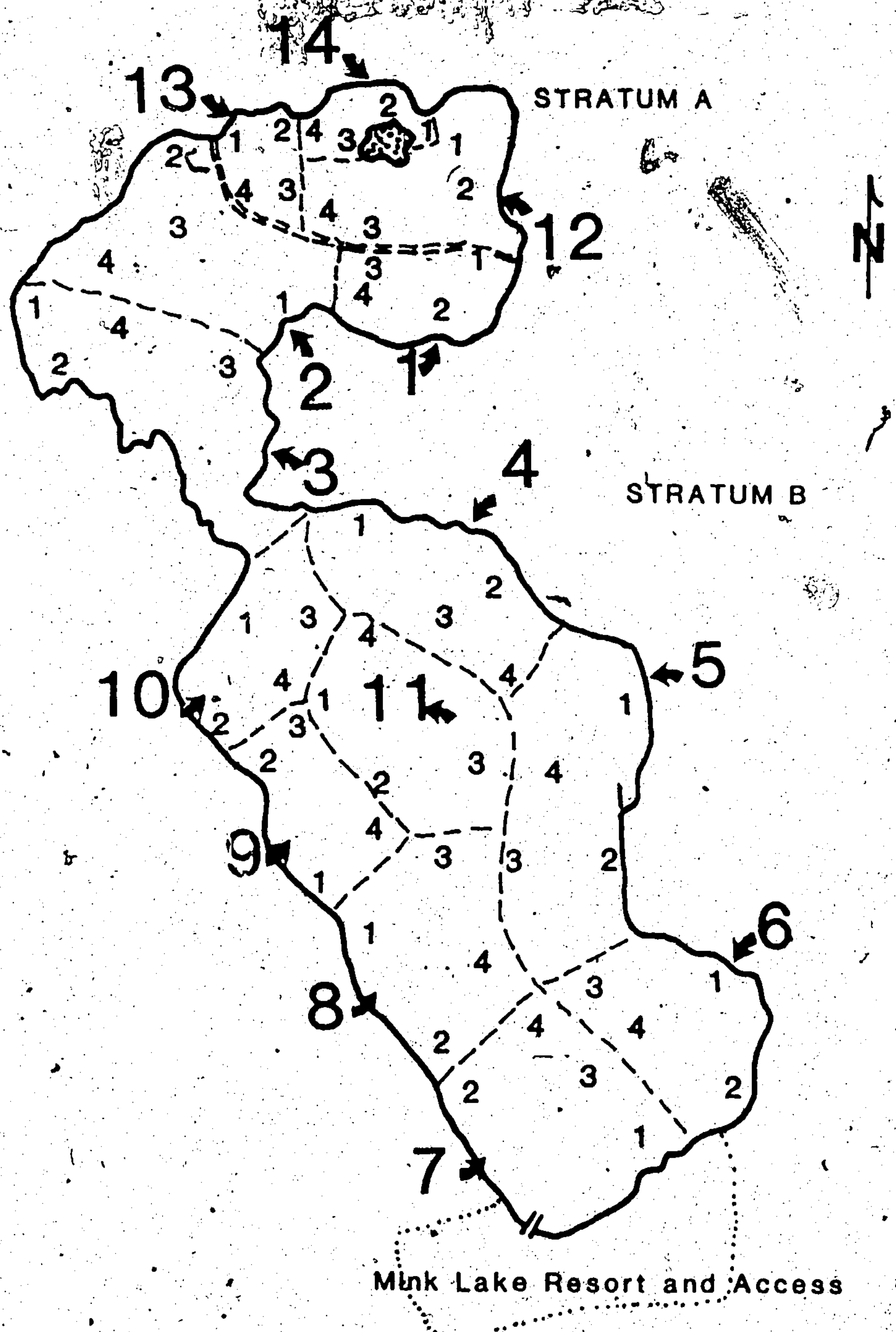

Figure I.3 Sampling design for 1982, Mink Lake indicating 14 areas with four sub-areas within them. In all cases, sub-areas one and two are less than four metres deep and sub-areas three and four are greater than four metres in depth.

the gender of each animal externally (Chapter 2). Numbered spaghetti tags, 3 cm long, (Floy anchor tag FD-67C, Floy Tag Co., Seattle, Washington), yellow in 1981, and blue in 1982, were used to mark the fish. After tagging, the tag was pulled gently to ensure that the 'T' was locked into place behind a neural spine of the vertebral column (Keller 1971). The location of capture, tag number, gear used, number of yellow perch caught per trap or trawl haul, and the number of recaptures were then recorded. Tagged fish were returned to the lake at the site of capture. Five injured fish were released untagged.

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II. EXTERNAL SEX DETERMINATION OF ADULT YELLOW PERCH[1]

A. INTRODUCTION

The determination of sex from external features aids the efficient management of fishery resources. This method is useful for the following purposes: the determination of adult sex ratio; the assessment of potential egg deposition in natural spawning areas (Casselman 1974); the selection of brood stock to increase fingerling production (Parker 1971); the estimation of separate adult male and female population abundance for separate biomass and production estimates, and; the estimation of appropriate proportions of adult males and females for harvest. Further, this method prevents injury to the fish and may be employed during times other than the spawning period.

Accurate techniques to determine the gender of fish externally have been described for a limited number of species of freshwater fish. These include rock bass, *Ambloplites rupestris* (Rafinesque) (Noltie 1985), northern pike, *Esox lucius* L. (Casselman 1974), bluegill, *Lepomis macrochirus* (Rafinesque) (McComish 1968), largemouth bass, *Micropterus salmoides* (Lacepede) (Driscoll 1969; Parker 1971), and fathead minnow, *Pimephales promelas* (Rafinesque) (Flickinger 1969). However, no method has been described to determine externally the gender of yellow perch.

During a mark-and-recapture population study of yellow perch, *Perca flavescens* (Mitchill), in Mink Lake, Alberta, it was necessary to determine gender externally so that various sex-related characteristics of the population, and of individual perch, could be studied at times other than during their spawning period. These included the abundance of adult male and female fish, differences in vulnerability to different types of fishing gear, rates of dispersal from the spawning grounds, rates of survival, adult biomass and production.

The gender of mature perch can be determined during the spawning season in May and June, on the basis of the passage of milt in the male and abdominal distension in the female, however, this method cannot be used to ascertain sex during the remaining

[1] A version of this chapter will be submitted for publication. Packham, M.J. and W.C. MacKay. 1988. Transactions of the American Fisheries Society.

46, non-spawning weeks of the year. Sex-specific characteristics of the fish population cannot be evaluated during the latter period, necessitating the development of an alternate method of sex determination.

The purpose of this study was to develop a non-destructive method of determining the sex of adult yellow perch from external features that could be used year round.

B. MATERIALS AND METHODS

Yellow perch were collected between May and October of 1981 and 1982 from Mink Lake, Alberta (53° 31'N. and 114° 14'W). Windermere perch traps (Worthington, 1950) and an otter trawl were used to capture mature fish.

The effectiveness of using external features for determination of sex was evaluated in two ways. First, accuracy was estimated by determining the sex of 127 mature yellow perch (total lengths 150 to 279 mm), based on external and internal examination of fish collected from July through September in 1981 and 1982. The minimum size represented the size at 100% maturity for adult female perch in Mink Lake (Chapter 3). It was ascertained that the distinguishing female urogenital structure occurred only in adult fish. In the laboratory, each fish was designated male or female on the basis of the external appearance of the urogenital structure (Figure II.1), then given to an assistant who examined the gonads internally and declared the actual sex of the fish. Second, based only on external examination, repeatability was assessed by re-examination of 270 tagged perch at recapture, to compare the sex assigned at the initial time of tagging, with that determined at the time of recapture, up to 14 months later.

C. RESULTS

Some features of the urogenital opening were found to differ consistently between males and females (Figure II.1), and these external characteristics were used to determine the gender of adult yellow perch. In females, the urogenital opening is round; the tissue around it is slightly raised and has a swollen appearance. It is further accentuated by a 1-2 mm wide cream to bright white band that surrounds the opening.

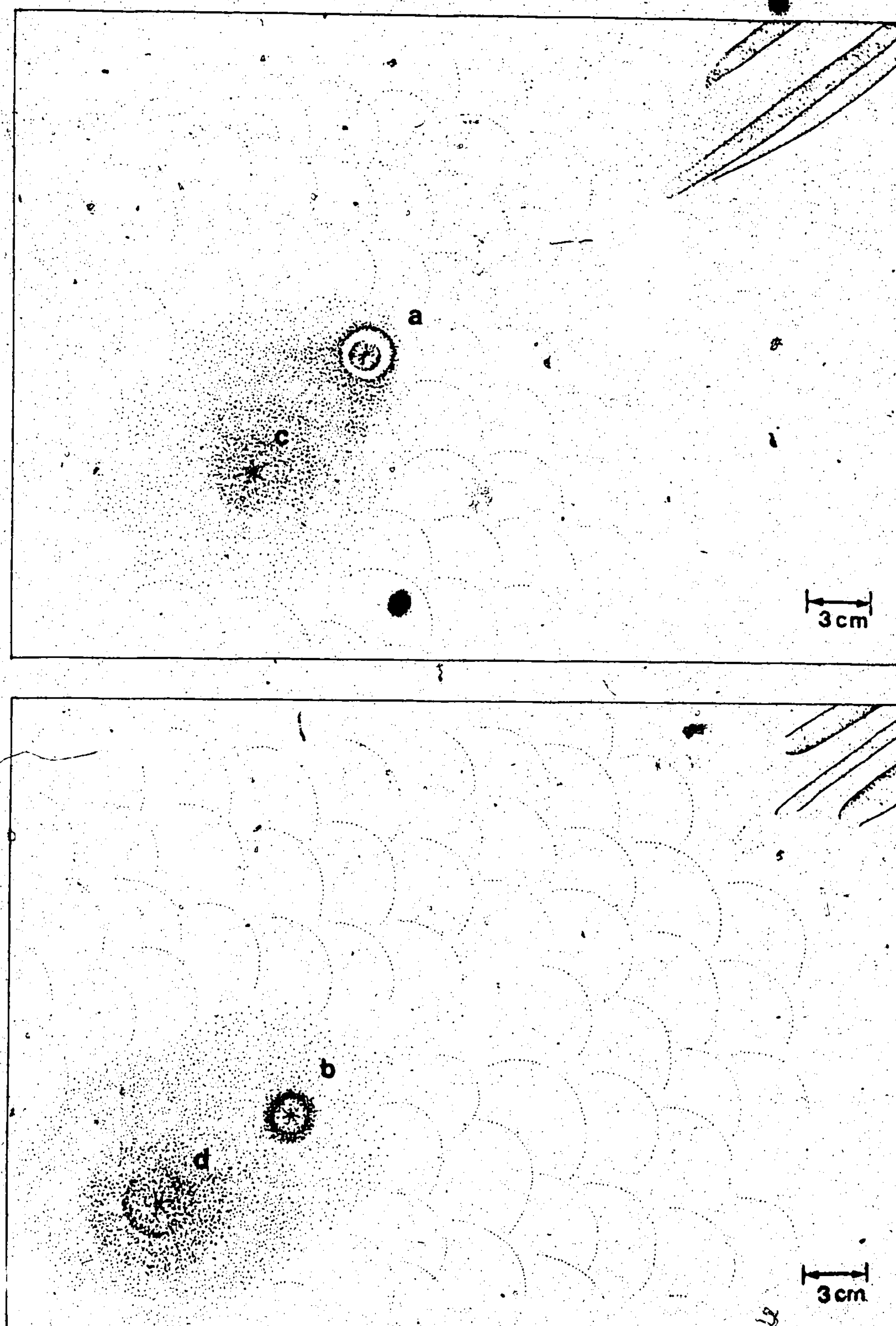

Figure II.1 Ventral view of the urogenital openings of adult female and male yellow perch. Note the raised, white, doughnut-like ring in the female (a) and its absence in the male (b). The anus appears below and to the left of the urogenital opening (c and d).

Males have a smaller, more oval, and slightly convex urogenital opening, which is pink and may or may not have a pale white center. The raised, white, doughnut-like ring around the urogenital opening of adult females is absent in adult males.

The results from 127 yellow perch examined both externally and internally revealed that external features could be used to determine gender accurately in 98% of the males and 87% of the females (Table II.1). Of 270 yellow perch that were tagged and recaptured between one and 436 days later, there was 90.4% agreement in the sex assignment at tagging and at the time of recapture (Table II.2). There was no significant difference in the accuracy of sex determination for males or females by either method (chi-square=0.15, df=1, P>0.50).

Greater inaccuracy occurred when the external opening was examined more than a few hours after death. When 27 fish were refrigerated overnight and sex was determined from external features the next day, overall accuracy dropped to 78%. Five fish were incorrectly identified as males, since the white band around the female genital opening became faded and the tissue had desiccated and flattened.

D. DISCUSSION

The accuracy of the method developed to distinguish the gender of adult yellow perch externally ranged from 87% for females to 98% for males. This result compared well with other authors' attempts to determine accurately the sex of freshwater fish species from external characteristics (bluegill, -100%, McComish 1968; fathead minnow, 92-97%, Flickinger 1969; largemouth bass, 93-100%, Driscoll 1969; largemouth bass, 51-92%, Parker 1971; northern pike, 91-94%, Casselman 1974).

Repeatability of the method, up to 14 months later, was 90%, suggesting that the characteristics used to distinguish the sexes did not change during the period from May through October. However, the accuracy of this method is limited to adult fish, and this method must be tested on other populations before its generality is known. At Mink Lake, at the time of sexual maturity, the female urogenital opening changes permanently. Before maturity, the female urogenital opening resembles that of an immature or mature male. Since females mature at a larger size than males, only perch larger than the female size at maturity can be accurately distinguished externally. At Mink Lake, this minimum

Table II.1 Agreement of sex determination of adult yellow perch from external and internal examination.

External Examination	Internal Examination	Number	Percent Accuracy	Mean Total Length (mm)
M	M	86	98%	221
F	M[a]	2		218
F	F	34	87%	259
M	F	5		174
Total		127		

a occurred soon after spawning

Table II.2 Repeatability of sex determination of adult yellow perch from external examination at tagging and at recapture.

External Examination at Tagging	External Examination at Recapture	Year Captured 1981	1982	Total
M	M	79	73	152
F	F	67	25	92
M	F	16	3	19
F	M	6	1	7
Total		168	102	270
Repeatability		87.0%	96.1%	90.4%

total length was 150 mm.

A high degree of accuracy and reproducibility can be achieved in determining the sex of adult yellow perch, from the appearance of the urogenital opening.

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III. RATES OF GROWTH, AND AGE AT MATURITY OF MALE AND FEMALE YELLOW PERCH IN MINK LAKE, ALBERTA

A. INTRODUCTION

Growth rates of fish in temperate waters have been investigated for hundreds of years (Ricker 1975; Bagenal and Tesch 1978), but differences in growth between male and female fish have not been incorporated into estimates of fish production unless the population is killed (Chadwick 1976). The growth rate of many species of fish differs between males and females (Barton 1980; Bur 1984; Martin-Bergman and Gee 1985). Such differences could increase or decrease biomass and production estimates of males compared to females.

Factors which may underlie differences in growth rates between males and females include: genetic differences correlated with inherited behavior patterns (Lagler *et al.* 1977), including different activity levels (Thorpe 1977); different metabolic rates (Lagler *et al.* 1977); different diets (Eschmeyer 1938; Hartmann 1975); different prey size preferences (Miller 1983); and different temperature preferences (Gibson 1954; Tsukuda 1960; Hagen 1964). Generally, male fish mature at an earlier age (Scott and Crossman 1973; Barton 1980; Elliott 1985; Martin-Bergman and Gee 1985), and a smaller size than female fish (Dadswell 1979; Nordeng 1983; Helfman *et al.* 1984). Early maturity appears to reduce the growth rate of male fish, so that after maturity males grow more slowly than females (Barton 1980; Bur 1984; Martin-Bergman and Gee 1985). Females have a longer growing season than males (Basimi and Grove 1985), regularly attain a larger size, and enjoy a longer lifespan (Eschmeyer 1950; Le Cren 1951; Dadswell 1979; Shireman and Smith 1983).

Growth rates of yellow perch, *Perca flavescens* (Mitchill), and Eurasian perch, *Perca fluviatilis* L., are biologically equivalent (Thorpe 1977). Growth rates for male and female Eurasian perch have been studied extensively in Britain (Le Cren 1958; Craig 1974), Europe (Rask 1983), and New Zealand (Jellyman 1980). In North America, studies of male and female yellow perch growth have been conducted in eastern Canada (Chadwick 1976), and the United States, where perch are captured during commercial and sport fisheries (Hile and Jobes 1941, 1942; El-Zarka 1959). No work has been done on the growth of male and female perch in western North America, where perch are widely distributed (Scott and Crossman 1973) and are captured more frequently than other species in the sport fishery (Longmore *et al.* 1982).

Differences occur in the size at maturity and growth rates of male somatic and gonadal tissue compared with females in both species. The onset of sexual maturity is related to body size (Love 1980), and males mature at a smaller size a year or more earlier than females (LeCren 1958; Thorpe 1977; Craig 1974; Nyberg 1979; Rask 1983). The size at first maturity for males and females is variable but usually ranges from 50-120 mm and 120-180 mm total length, respectively (Thorpe 1977). Testis weight increases from 0.5% body weight to 3.4-8.0% of the body weight before spawning (Le Cren 1951; Lagler *et al.* 1977). In the maturing female, the ovary increases in size before spawning from 0.5% of body weight to 15.7-31.0% of body weight (Dryagin 1948; Le Cren 1951; Hutchinson 1974). After maturity, male and female perch may exhibit different rates of growth (Newsome and Leduc 1975), or females grow at the same rate as males (Smith 1939; Shafi and Maitland 1971; Neuman 1976). In other lakes, females may exceed the maximum size for males (Craig 1980; 1982), store different amounts of body fat reserves (Newsome and Leduc 1975), and experience a greater longevity than males (Eschmeyer 1937, 1938; Hile and Jobes 1942; Carlander 1950). The lower temperature preference of male perch may account for the slower growth rates and smaller body size of males compared with females of the same age (Sandheinrich and Hubert 1984). Such differences in growth rates between males and females are observed to be related to differences in the abundance of adult perch (Dryagin 1948) and variations in both abundance and growth rates affect separate estimates of male and female production.

Further, differences occur in the timing of growth between males and females. Males may begin their main growth phase three to four weeks earlier than females, and end it two to four weeks earlier with a slower maximum growth rate (Hartmann 1975), in both length and weight (Hile and Jobes 1941; LeCren 1958; Chadwick 1976).

The purposes of this study were to measure the annual growth rate of each sex and age-class in a population of yellow perch in Alberta, to determine whether differences occurred between adult males and females in their rates of growth, and in their size at sexual maturity. Differences between the rates of growth would then be incorporated into the separate estimates of perch production for males and females. Further, the size at 100% maturity for females would provide a size limit above which male and female perch would be tagged. The method developed to determine perch sex externally was limited to adult fish (Chapter 2).

B. MATERIALS AND METHODS

To determine growth rates, 391 adult male and female yellow perch were collected from Mink Lake (53° 31'N. and 114° 14'W), Alberta between May and October during 1981 and 1982 (Chapter 1). The fish were killed with an overdose of the anesthetic 2 phenoxyethanol (MCB Manufacturing, Ohio, USA). Total body length was measured to the nearest millimetre, net weight was determined to the nearest gram (with the stomach removed to reduce the effect of varying stomach fullness on total wet weight), and the sex was recorded. The left opercular bone (Le Cren 1947) was retained for age determination (Chapter 1). The opercula were soaked in hot water (80°C), then wiped clean of skin and associated tissue with a paper towel. They were dried and stored in numbered envelopes. Later the opercular bones were used for age determination (Appendix II.1), and back-calculation of length at the time of formation of each annulus (Appendix II.2). A regression equation for the relationship between total fish length and opercular length was used to back-calculate fish lengths at the time of formation of each annulus (Le Cren 1947) for 100 perch.

For estimates of production, back-calculated length at age must not differ significantly from observed lengths of that age-class in the population (Lee 1912; cited by Ricker 1975). Otherwise back-calculation will not estimate mean length at age accurately for younger age-classes in the population. Such data could not, therefore, be used for production estimates. Since perch growth stops in September (Nakashima and Leggett 1975), 2+ and 3+ fish collected from the lake in October were assigned the ages 3+ and 4+ to represent their age at the time of annulus formation the following spring. To determine if Lee's phenomenon occurred, the lengths (n=35) of 3+ and 4+ back-calculated from 7+ to 9+ fish were compared to the lengths of the 3+ and 4+ fish taken from the lake.

To determine the approximate mean weight at age at the time of annulus formation, for production estimates, the mean weight at age of male and female fish captured in October (n=108) was estimated. The weight of adult male and female fish changes similarly throughout the year (Tanasichuk 1978). Therefore, I assumed that weight loss would occur at a similar rate for adult male and female fish. I further assumed that the mean weight of male and female fish would not increase from October until annulus formation the following spring. Thus, mean weight at age for fish captured in October was assumed to approximate the mean weight at age of fish at the time of annulus formation.

To determine the age and size (length) at maturity for adult male and female yellow perch, percent maturity at each age was estimated from the gonado-somatic indices in fish sampled in September and October of each study year. The gonado-somatic index used was the gonad weight divided by the gut-free somatic body weight, multiplied by 100 (Craig 1974). A gonad weight divided by somatic weight multiplied by 100 (gonado-somatic weight), greater than 0.5 percent indicated that the fish gonad was growing and that the fish would spawn the next spring (Le Cren 1951; Hutchinson 1974; Thorpe 1977).

C. RESULTS

Opercular radius was proportional to fish length (regression equation Y=0.57 + 0.5X; Y and X in millimetres, $r^2 = 0.96$, n=100). Thus, I concluded that opercular bones could be used to back-calculate lengths at earlier ages of individual fish. However, Lee's phenomenon occurred for 3+ and 4+ fish (Student's t-test, P<0.001). Mean back-calculated lengths at 3+ and 4+ from older fish (7+-9+) were smaller than mean lengths at age of fish sampled in October. Therefore, I concluded that size specific mortality was occurring and that back-calculated lengths could not be used as an accurate method to calculate length, or indirectly weight, for the estimates of production of perch in Mink Lake. There were, however, no differences between males and females in mean weight at age in fish captured in October (slopes ANCOVA, P>0.1; elevations ANCOVA, P>0.50). Thus, mean weights from fish collected in October were incorporated into the production estimates (Chapter 5).

To compare the growth of male and female perch at all ages, back-calculated lengths at age were used. I assumed that the mortality rates of the large fish of young year-classes that caused Lee's phenomenon did not differ between immature males and females. There were no significant differences in back-calculated mean total lengths (Table III.1) at individual ages between sexes for either of the two years, or between years (Student's t-tests, P>0.05).

Males matured one to two years earlier (n=33), and at a smaller size, than females (n=35) (Table III.2). Most males (85%) were mature at 1+; by 3+, 100% were mature. Females were 100% mature at age four, although 64% matured at age two. Size at 100% maturity was 105 mm and 150 mm for male and female yellow perch, respectively.

D. DISCUSSION

No significant difference occurred between the growth of male and female perch in length or weight. This finding is in contrast to the majority of previous studies. Generally, female perch grow faster than males (Hile and Jobes 1941; Le Cren 1958; Chadwick 1976; Thorpe 1977). Differences in rates of growth between males and females occur only in lakes where perch grow faster than in Mink Lake. In these lakes, females grow faster than males and females are significantly larger than males at adult ages (Vashro 1975; Chadwick 1976). In lakes with slow-growing populations, difference in growth rate may not occur between males and females until later years (Rask and Arvola 1985). In Mink Lake, in 1981 and 1982, growth of perch was poor according to Tesch's (1955) classification; perch did not reach 160 mm by age 3. Perch growth rates in Mink Lake were also low compared to growth rates of perch in Europe over the range of their distribution (Deelder 1951; Mann 1978; Craig 1980; Jellyman 1980). In addition, perch growth rates in Mink Lake were low compared to perch growth rates in Canada and the United States for all lakes studied (Harkness 1922; Hile and Jobes 1941; Grice 1959; Sheri and Power 1969; Vashro 1975), except two unproductive Canadian lakes (Smith 1939; Chadwick 1976).

Different temperature selection (warm by females, cooler by males; Sandheinrich and Hubert 1984), and different diets (Eschmeyer 1938) may cause differences in perch

Table III. 1. Mean length at-age of yellow perch determined from back-calculations (n in brackets).

age	Female yellow perch 1981	1982	Male yellow perch 1981	1982
1	55.4 ± 3.7(27)	61.3 ± 3.3(45)	58.2 ± 3.1(68)	59.0 ± 2.2(46)
2	88.9 ± 4.3(25)	92.7 ± 4.5(42)	90.5 ± 4.1(63)	90.2 ± 3.0(50)
3	123.9 ± 6.9(25)	119.7 ± 5.9(28)	117.5 ± 5.9(58)	120.9 ± 3.6(47)
4	150.2 ± 14.4(23)	145.2 ± 3.3(21)	143.1 ± 5.2(55)	146.0 ± 3.9(46)
5	171.8 ± 17.9(22)	167.1 ± 10.2(13)	166.4 ± 6.1(47)	172.4 ± 4.4(39)
6	190.3 ± 12.0(21)	191.8 ± 13.2(13)	189.2 ± 10.0(32)	193.8 ± 4.4(30)
7	208.7 ± 15.6(15)	212.0 ± 12.8(12)	205.0 ± 11.2(15)	211.8 ± 6.4(14)
8	229.4 ± 25.0(8)	231.7 ± 26.3(5)	225.6 ± 38.5(6)	228.6 ± 4.8(6)

Table III.2 Age at maturity for female and male yellow pêrch in Mink Lake.

Age class	female perch % mature	male perch % mature
1+	0	85
2+	64	94
3+	82	100
4+	100	100

growth rates between males and females. The lack of difference in growth rates between males and females in Mink Lake may be accounted for in part by their similar distribution (Chapter 4) and similar diet, which is dominated by the small benthic invertebrate *Hyalella azteca*.

Size at sexual maturity fell within the range of fish lengths previously reported. Females were 100% mature at 150 mm mean total length in Mink Lake, and 100% mature between 140 and 240 mm in other lakes (Hile and Jobes 1941; Alm 1946; Thorpe 1974). Males were 100% mature at 105 mm mean total length in Mink Lake, and were 100% mature between 70 and 127 mm in other lakes (Hile and Jobes 1941; Alm 1946; Thorpe 1974). All male and female perch in Mink Lake matured by 3+ and 4+, respectively, as do yellow perch in Canada (Scott and Crossman 1973). However, most authors report age at maturity as 1+ to 2+ for males and 2+ to 3+ for females for both species of perch (Hile and Jobes 1941; Alm 1946; Thorpe 1974).

For the purposes of the production study, growth rate did not differ between the sexes, thus, growth rate did not cause differences in the production of male and female perch in Mink Lake. Further, only male fish 3+ and older, and female fish 4+ and older, could be considered to be mature. The estimation of adult population abundance (Chapter 4) was limited to data from these age groups, owing to the limitations of the external sexing method (Chapter 2).

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IV. DIFFERENCES IN ABUNDANCE AND RATES OF SURVIVAL BETWEEN ADULT MALE AND FEMALE YELLOW PERCH IN MINK LAKE, ALBERTA

A. INTRODUCTION

Differences in the relative abundance of adult male and female fish in fish samples and harvests, range from 1:32 to 4:1, respectively (Clady 1967; Backiel and Zawisza 1968; Brown 1970; Dadswell 1979). These differences have been attributed to a variety of factors, including a changing environment, and sex-related life-history characteristics such as differences in age at maturity and rates of survival. Females predominate in situations where environmental factors such as food, space, and water conditions are improving (Svärdson 1945), or when intensive and selective fishing or predation occur (Stone 1947; Deason and Hile 1947; Clady 1967; Brown 1970). Adult males may outnumber adult females in the youngest adult age-classes of many species, since males often reach sexual maturity a year or more earlier than females (Coble *et al.* 1979; Barton 1980; Nordeng 1983; Elliott 1985). Females, however, may predominate in the oldest age-classes, since some females survive longer than any males (Dadswell 1979; Martin-Bergman and Gee 1985). Unfortunately, however, sex ratios from separate male and female population estimates are not available.

Variability in the adult sex ratio in collections of the biological equivalent yellow perch, *Perça flavescens* (Mitchill), and Eurasian perch, *Perca fluviatilis* L. (Thorpe 1977) also occur, with males or females predominating. These adult sex ratios range from 1:4 to 2.6:1 (Craig 1974; Clady 1977; Jellyman 1980; Viljanen and Holopainen 1982). They may be real and due to differential age at maturity and rates of growth (Chapter 3), or they may be due only to sampling bias (Chapter 1), and not to actual differences in the population. To estimate adult sex ratio accurately, without sacrificing fish, abundance must be estimated from fish collected after spawning with gear that is not selective for sex or specific depths. Furthermore, a method must be available to distinguish fish sex externally at a time other than the perch spawning period.

Previous studies of relative abundance of male and female adults in populations of perch been hampered by the inability of researcher's to distinguish adult male and female perch, externally, at times other than spawning. Consequently, separate population abundance for males and females has not been estimated. Since adult males are concentrated at spawning and can be identified then by the passage of milt, most estimates of perch population size have focused on estimating numbers of adult males during spawning.

The methods used to estimate adult female abundance at spawning have been indirect and have included the assumption of an equal sex ratio, or doubling the male population estimate to account for the numbers of females present (Le Cren *et al.* 1977). Other authors combined the males and females into one estimate (Craig 1974; Chadwick 1976). However, Craig (1974) noted that this method would result in error in the estimation of animal abundance, as sex ratios were unequal for males and females (Craig 1974). In addition, when these methods were used, males were selectively captured and recaptured, and few females were caught during spawning (Chadwick 1976; Jensen 1976). Thorpe (1974) and Nyberg (1979) attempted to overcome this problem by estimating male abundance at spawning separately, and multiplying this estimate by the sex ratio found by killing fish captured after spawning, to account for females.

In the above studies, problems occurred in meeting assumptions two and three of the population estimate. These involved equal catchability in the first and second sample, and the effect of tagging on recapture frequencies, respectively (Appendix III.1). Further, the lakes studied were large (Thorpe 1974), and the techniques used could not ensure accuracy since the whole lake could not be sampled effectively (Robson and Regier 1964; Craig 1974; Chadwick 1976). The species composition in the lakes studied was also diverse (Thorpe 1974; Chadwick 1976), and this could result in inaccurate individual species biomass (Sumari 1971).

Previous estimates of perch population size have focused on Eurasian perch in Britain (Thorpe 1974), Scandinavia (Nyberg 1979; Jensen 1976; Viljanen and Holopainen 1982; Persson 1983; Rask and Arvola 1985), and the USSR (Holčik 1977). In Canada, only two estimates of yellow perch population size have been conducted (Smith 1939; Chadwick 1976). Both involved poisoning small lakes and counting all the dead fish found.

This is the first study to use mark and recapture to estimate population size for a perch population on the boreal plains in western Canada. Furthermore, this is the first attempt to estimate adult population size and the rates of survival from mark-and-recapture data, separately, for male and female perch. Estimates of juvenile perch populations are difficult and inaccurate owing to their large numbers. Lake-poisoning studies have revealed that the juvenile perch population estimated by mark-and-recapture underestimated the population estimate from poisoning by eight times (Chadwick 1976).

The purpose of this study was to estimate and compare the rates of survival and abundance for adult male and female perch. The sex ratio from the population estimate was compared to the sex ratio of fish taken by the fishing gear. Efforts were made to use a sampling design that alleviated difficulties experienced in previous perch population studies, and to meet all assumptions of the mark-and-recapture population estimate (Appendix III. 1).

B. MATERIALS AND METHODS

The study was begun in early May and continued until October during 1981 and 1982 at Mink Lake, Alberta. Whole lake sampling, random and stratified, was conducted in 1982 (Chapter 1). The two fishing gear used improved the reliability of the population estimate owing to their different selectivity (Beukema and De Vos 1974). The otter trawl actively captured the fish, whereas fish swam into Windermere traps (Chapter 1). Traps could be used at greater depths than the trawl and, hence, more locations than the trawl. Males and females, captured in traps or trawls, were counted, measured for total length and tagged (Chapter 1). Fish sex was determined from external characteristics (Chapter 2). Owing to the fact that this method was limited to mature fish (females were 100% mature at 150mm, males at 105mm), only fish 150mm and larger were tagged. An exception was made for 120-150mm fish if they could be proved to be males by the presence of milt during spawning. Thus, many 3+ males were tagged. During the rest of the year, no mature male fish 120-149mm could be tagged, as they resembled immature females. Therefore, estimates of the numbers of mature male fish were probably low. Fish 105-119mm were considered too small to be tagged and not risk mortality during handling.

Rates of Survival

Mean rates of annual survival between 1981 and 1982 were estimated for male and female yellow perch aged 2+ through 11+ (Ricker 1948; in Ricker 1975, page 126). To provide estimates of the numbers of adult males and females tagged in 1981 that remained in the population at the start of the 1982 season, the numbers of male and female fish tagged in 1981 were reduced separately for each sex to reflect a differential annual mortality rate.

Since a different rate of annual survival had been determined for adult males and females, the rates of survival for individual age-classes of males and females were estimated and compared, to determine how the rates of survival were related to the age and sex of the fish. When the data were available, the rates of survival for individual age-classes of adult male and female yellow perch were estimated two ways. These methods included a comparison of the frequency of recaptures for each age-class between 1981 and 1982 (Ricker 1945, 1948; cited by Ricker 1975, page 123), and a comparison of the abundance of each fully recruited age-class between 1981 and 1982 (Jackson 1939; cited by Everhart and Youngs 1981, page 117).

Population Estimate

The method of Youngs and Heimbuch (1982), based on the assumption of equal distribution of fish per lake surface area, was used to make a preliminary estimate of the number of adult fish per hectare in Mink Lake. Estimates of adult perch per hectare from two other studies were multiplied by the total surface area of Mink Lake. Thus, the preliminary estimate of the numbers of adult perch in Mink Lake was predicted to range from 6446 3+ and older (Thorpe 1974) to 7,202 3+ and older (Tarby 1974) perch. Since male perch have been reported to be 100% mature by 2+ (Thorpe 1977), 2+ fish were included and the estimate was increased to 18,247 (Thorpe 1974). Based on the preliminary population estimate and a 95% probability of a 10% level of precision (Robson and Regier 1964), the number of 2+ and older perch to be marked and to be examined for marks were estimated to be 2,000 and 3,000, respectively. The high level of precision used (10%), was necessary for ratios requiring the use of population numbers for estimates of annual survival (Youngs and Robson 1978).

Schumacher-Eschmeyer (1943) population estimates were conducted and compared for male and female perch. Assumptions of the population estimate (Appendix III.1) that could not be met by sampling design alone were evaluated by chi-square analysis (Youngs and Robson 1978) or Student's t-tests (Appendix III.1). For chi-square analysis, fish length data were grouped into size-classes and converted to age-classes according to the proportions indicated by age-length keys (Ricker 1975)(Appendix III.2).

Sex Ratio

Sex ratio was estimated from the unweighted means of the percentages of males and females captured (Jobes 1952), in 10 individual samples (n=26 to 45). These fish were captured in traps, trawls and seines after spawning was completed, when little selection exists for perch sex by gear (Craig 1974).

Comparison of Mink Lake Population Estimate with Other Authors' Methods

The data obtained by the other authors to estimate adult fe[illegible]e when male and female perch could not be distinguished externally (Craig 1974; Thorpe 1974; Chadwick 1976; Le Cren *et al.* 1977; Nyberg 1979) were compared to data obtained from Mink Lake in the present study. A combined male and female population estimate was compared to separate estimates of male and female abundance, since fish sex was determined externally.

The confidence limits of the separate population estimates were summed in the following way. The sum of the standard error associated with each of the male and female estimates was weighted by the sampling periods in each estimate, and divided by the sum of the sampling periods. This number was multiplied by the t-value at P=0.05, with one degree of freedom subtracted (sampling periods summed minus one). Since the standard error of the Schumacher-Eschmeyer (1943) estimate multiplied by the t-value must be inverted to arrive at the population estimate, the summed standard error multiplied by the new t-value also was inverted. The result was a number that was subtracted or added to the sum of the population estimates to predict the 95%

confidence limits associated with the sum of the two separate population estimates (Prepas pers. comm.).

C. RESULTS

During the 1981 and 1982 study period, the goal of tagging 2,000 adult yellow perch and examining 3,000 adult yellow perch for marks was reached; 2,398 adult yellow perch were tagged, 323 (13.5%) were recaptured, and 3,428 were examined for marks. The locations of capture varied from 10 locations in 1981 to over 40 in 1982, when sampling was random (Appendices III.3 through III.6). In all locations, more adult males were captured, marked and released than females. Both types of fishing gear (traps and trawl), however, captured larger females than males (Figure IV.1).

Rates of Survival

The annual rate of survival between 1981 and 1982 was different between the sexes. Mean adult male survival (71%) was almost twice as high as mean adult female survival (37%) between 1981 and 1982. Combined, the mean adult survival rate was 61%. During the 1981 and 1982 study periods, survival rates for individual age-classes were higher for 9+ females than for 9+ males; however, survival rates were better for males in all other adult age-classes evaluated (Table IV.1).

Population Estimates

All assumptions of the population estimate were met, except that males and females were recaptured at significantly different frequencies in each of the study years (Appendix III.1). This result violated the assumption that marking does not affect the likelihood of capturing an animal. For this reason, adult population abundance was estimated separately for each sex. However, there were no significant differences between gear in the frequency of fish captured or recaptured when data from males and females were separated (Appendix III.1). Therefore, capture data from both gear, the traps and the trawl, were pooled in the population estimates. There was also no difference in the proportions of males and females captured at the two sampling depths

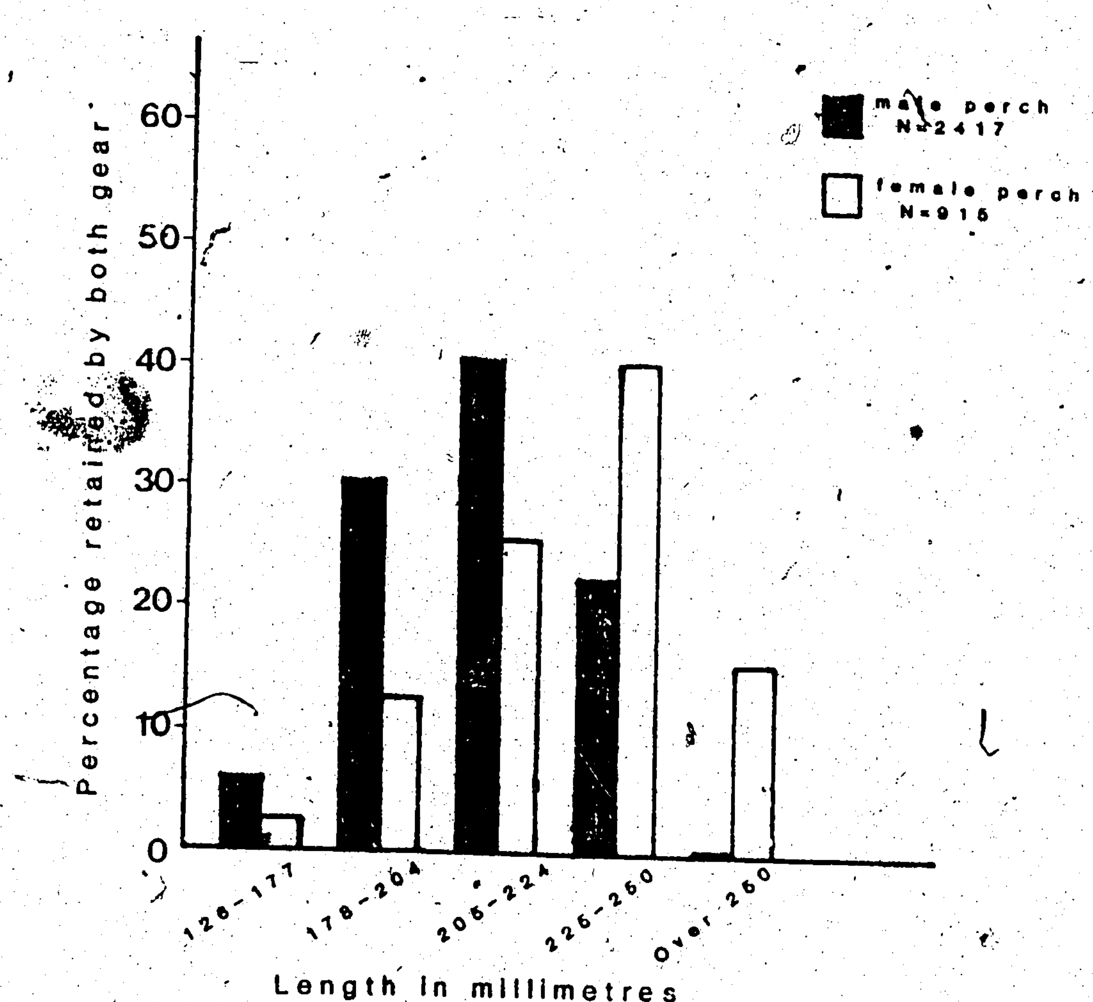

Figure IV.1 Length-frequency histogram for adult male and female yellow perch captured by trap and trawl in 1981 and 1982.

Table IV.1 Rates of survival for adult female and male yellow perch.

Age-class	Female perch 1981 and 1982	Male perch 1981 and 1982
6		0.72[a]
7	0.22[a]	0.49[b] and 0.79[a]
8	0.20[a]	0.27[b] and 0.42[b]
9	0.24[b] and 0.37[b]	0.02[b] and 0.02[b]
mean annual	0.37±0.12[c]	0.71±0.34[c]

[a] Ricker's (1945, 1948) method based on a comparison of the frequency of recapture over two years (recaptures >8).

[b] Jackson's (1939) method based on the age at first recruitment (n >120).

[c] Ricker's (1948) method is based on a series of markings over two years.

in 1982 (67% females; n=358 <4 m; n=82 >4 m), so these data also were pooled in the population estimate.

The numbers of adult male and female perch tagged in 1981 were multiplied by 0.71 and 0.37, respectively, to account for the mean annual rates of survival of adult male and female fish, and to estimate the number of tagged male and female perch remaining in the population at the start of the 1982 season. In this way, it was estimated that 863 tagged males and 239 tagged females were still at large in the population at the start of the 1982 season. The 95% confidence limits for these predictions ranged from 450-1,215 for males, and from 176-316 for females (based on the 95% confidence intervals associated with the estimates of mean annual survival 0.37-1.05 for males; 0.25-0.49 for females, Table IV.1).

The Schumacher-Eschmeyer population estimates were conducted three ways to compare the influence of the estimates of annual survival on the population estimates.

The first estimate was based on mean annual survival from 1981 to 1982 (0.71 for adult males and 0.37 for adult females), the Schumacher-Eschmeyer population estimates indicated the presence of 18,184 adult perch (14,806 adult males and 3,378 adult females) in 1982. Ninety-five percent confidence limits ranged from 10,927-22,956, and 2,194-6,259, respectively (Tables IV.2-3). The combined estimate for adult males and females increased to 20,747 with 95% confidence limits ranging from 16,609-27,631.

The second population estimate was based on the 95% confidence intervals for adult male annual survival (0.37 to 1.05) ranged from 8,259-20,458. Population estimates based on the 95% confidence intervals for adult female annual survival (0.25 to 0.49) ranged from 2,926-4,189.

The third population estimate was conducted from data collected only in 1982, when the number of tagged fish in the population was known, and annual survival of individuals tagged in 1981 were not involved. The 1982 estimates of 5,620 males and 3,519 females with 95% confidence limits (4,812-6,754, and 1,940-18,885, respectively) and the combined estimate of 9,094 with 95% confidence limits (6,268-16,560), were lower than those estimated from the 1981 and 1982 data adjusted for annual survival between 1981 and 1982.

Table IV.2 Computations for Schumacher estimates for ages 3-7 male yellow perch in Mink Lake, Alberta, from trap and trawl recaptures during the spring, summer and fall of 1982.

Sampling date	Number caught Ct	Recaptures Rt	Number marked[b]	Marked fish at large Mt[a]	CtMt	MtRt	$CtMt^2$	Rt^2/Ct
May 11-13	517	26	0	863	446,171	22,438	3.85×10^{8}	1.308
May 17-19	239	7	0	863	206,257	6,041	1.78×10^{8}	0.205
May 25-26	23	1	14	877	20,171	877	1.77×10^{7}	0.042
May 31-June 1	65	2	51	928	60,320	1,856	5.60×10^{7}	0.062
June 6-9	70	2	51	979	68,530	1,958	6.71×10^{7}	0.057
June 14-17	96	10	93	1,072	102,912	10,720	1.10×10^{8}	1.042
June 22-27	55	10	45	1,117	61,435	11,170	6.86×10^{7}	1.820
June 29-July 1	51	8	41	1,158	59,058	9,264	6.84×10^{7}	1.250
July 5-7	22	0	11	1,169	25,718	0	3.00×10^{7}	0.000
July 29	11	1	-1	1,168	12,848	1,168	1.50×10^{7}	0.090
August 9-17	45	4	0	1,168	52,560	4,672	6.14×10^{7}	0.355
August 23-25	4	0	0	1,168	4,672	0	5.46×10^{6}	0.000
September 13-15	2	1	0	1,168	2,336	1,168	2.73×10^{6}	0.500
October 2-7	35	2	0	1,168	40,880	2,336	4.77×10^{7}	0.110
October 12-14	34	4	-1	1,167	39,678	4,668	4.63×10^{7}	0.470
Total	1,269	78	304	1,167	1,203,546	78,336	1.16×10^{9}	7.320

[a] Original number tagged in 1981 adjusted by the survival rate per fish sex.

[b] Recaptured fish that were injured during capture were removed from the numbers of tagged fish circulating in the lake.

Schumacher-Eschmeyer estimate (1943) with 95% confidence limits:

$$\frac{1}{\hat{N}} = \frac{\Sigma(MtRt)}{\Sigma(CtMt^2)}$$

$\hat{N}$ = 14,806 The lower confidence limit was 10,927, and the upper limit was 22,956.

Table IV.3 Computations for Schumacher estimates for ages 4-8 female yellow perch in Mink Lake, Alberta, from trap and trawl recaptures during the spring, summer and fall of 1982.

Sampling date	Number caught Ct	Recaptures Rt	Number marked	Marked fish at large Mt^a	CtMt	MtRt	$CtMt^2$	Rt^2/Ct
May 11-13	3	2	0	239	717	478	1.71×10^5	1.333
May 17-19	12	2	0	239	2,868	478	6.85×10^5	0.333
May 25-26	9	0	9	248	2,232	0	5.53×10^5	0.000
May 31-June 1	46	4	40	288	13,248	1,152	3.81×10^6	0.348
June 5-10	57	6	50	338	19,266	2,028	6.51×10^6	0.632
June 14-16	56	2	48	386	21,616	772	8.34×10^6	0.070
June 22-26	21	4	16	402	8,442	1,608	3.39×10^6	0.762
June 28-July 1	13	2	10	412	5,356	1,236	2.21×10^6	0.692
July 5-7	21	0	14	426	8,946	0	3.81×10^6	0.000
July 29	6	1	0	426	2,556	426	1.09×10^6	0.167
August 7-11	26	3	0	426	11,076	1,278	4.72×10^6	0.346
August 23-25	5	1	0	426	2,130	426	9.07×10^5	0.200
Sept. 13-15	1	0	0	426	426	0	1.81×10^5	0.000
October 2-7	14	3	0	426	5,964	1,278	2.54×10^6	0.643
October 12-14	17	3	0	426	7,242	1,278	3.08×10^6	0.529
Total	307	34	187	426	112,085	12,438	4.20×10^7	6.055

[a] Original number tagged in 1981 adjusted by the survival rate per fish sex.

Schumacher-Eschmeyer estimate (1943) with 95% confidence limits:

$$\frac{1}{N} = \frac{\Sigma(MtRt)}{\Sigma(CtMt^2)}$$

N = 3,378 The lower confidence limit was 2,194, and the upper limit was 6,259.

Sex Ratio

In 1982, the adult sex ratio estimated from fish captured in traps, trawl and seine after spawning suggested a sex ratio of 1.9:1 in favor of males (n=350). The sex ratio for fish collected by trawl was 2.6:1 (n=189). The separate Schumacher-Eschmeyer multiple population estimates for adult males and females from 1981 and 1982 data give a sex ratio of 4.4:1.

Comparison of Mink Lake Population Estimate with Other Authors' Methods

When other authors' methods, which included doubling the male estimate and/or the use of data obtained only during perch spawning, were used to estimate the abundance of adult male and female perch in Mink Lake, overestimates of the total population size occurred. This was in comparison to the separate population estimates of adult male and female abundance (Table IV.4). Estimates based on the male estimate and the sex ratio taken at a time other than spawning, or on the combination of male and female data in one estimate, although higher, were within the 95% confidence limits of the separate male and female estimates in this study (5,138-31,230).

D. DISCUSSION

The density of adult yellow perch, estimated from 1981-1982 data, compared well with the density of adult Eurasian perch estimated from mark-and-recapture studies (Jensen 1976; Holčik 1977; Nyberg 1979; Viljanen and Holopainen 1982; Rask 1983; Rask and Arvola 1985). The numbers of adult male perch (3+-7+; 14,806), however, outnumbered adult females (4+-8+; 3,378) in Mink Lake, in 1982, by more than 4:1.

These estimates were based on the capture of more than 20% of the total estimated perch population over a period of 12 months of sampling, over two years. The assumptions of the population estimate were met (Appendix III.1), and the whole lake was sampled in 1982 randomly in a stratified pattern. Hence, the estimate should be very accurate.

Hartmann (1974) noted that stratification by shoals of perch occurred by gender and that females selected warmer shallower waters (Sandheinrich and Hubert 1984). If

Table IV.4 Results of methods used to estimate total adult population abundance when adult males and females could and could not be distinguished.

Method	Population Estimate	Percent Overestimate	Authority
Sexes Distinguished	18,134		this study
Sex Ratio	22,598	Within 95% Confidence Interval	Thorpe 1974
Sexes Combined	20,747	Within 95% Confidence Interval	Craig 1974; Nyberg 1979
Double Males	29,612	63% Overestimate	Le Cren *et al.* 1977
Spawning Data Only	34,584	90% Overestimate	Chadwick 1976; Jensen 1976

Mink Lake was not totally sampled, shoaling by perch could account for the large differences in the abundance of males and females captured. However, the majority of stratified sampling was conducted in the shallower areas, therefore, it is unlikely that the adult female population size was underestimated at Mink Lake. In fact, females occurred in the same proportion in both depth strata.

In fact, the precision of the population estimate was good. The 95% confidence limits or the population estimate were within 20-33% of the estimate. These ranges compared well with Chadwick's (1976), Nyberg's (1979), and Rask's (1983) estimates of combined population abundance with 95% confidence limits ranging between 19-30%, 10-110%, and 2-25%, respectively. The precision of the separate adult male and female estimates, also good, suffered owing to the reduction of numbers of tagged and recaptured fish in the calculations. The 95% confidence limits were within 26-85% of the separate estimates.

The difference in abundance between adult males and females can be attributed to differences in their age at maturity and rates of survival. Adult males matured one to two years earlier than females, and had a mean rate of survival almost twice as high as females. There was, therefore, one abundant age-class (3+) of sexually mature males in the population, which was not represented by mature females. Further, this larger number of adult males survived almost twice as well as adult females.

To determine whether these differences could account for the extent of the differences in the estimates of population size, the importance of the differences in age at sexual maturity and survival rate of males and females was evaluated mathematically. To do this, the estimate of adult male population was manipulated to reflect the older female age at maturity, and the mean rate of annual survival of females, and a new estimate of male population size based on these parameters was calculated. It was assumed that the sex ratio of 0+ and 3+ fish was equal (Craig 1974; Jellyman 1980). To estimate the number of 4+ sexually mature female fish, the number of 3+ males was multiplied by the average annual survival rate for males and females (from this study, 0.61). This number was multiplied by my estimate of the survival of mature females (0.37) to estimate the number of females in each subsequent year (5+-8+). Thus, when the new estimate of female population size for each sexually mature age-class was summed, the original adult male population estimate (14,806, based on the additional year-class of mature males (3+), and the better survival rates compared to those of females), was reduced to 4,748. This new estimate is within the 95% confidence limits of the original estimate of adult female population size (3,398) based on 1981 and 1982 data (2,194-6,259) (Table IV.3).

In populations where fish of one sex mature one or more years earlier than the other sex, the abundance of the earlier maturing sex will be markedly greater than that of the later maturing sex. In this study, males were 100% mature one year earlier than females, which increased the abundance of adult males in the population by 50%, from 9,866 to 14,806, and changed the adult sex ratio from 2.9:1 to 4.4:1.

The mean annual survival rate of adult males in this study was almost twice that of adult females based on mark-and-recapture data collected over two years. To estimate population abundance from 1981 and 1982 data, the mean annual survival estimates for adult male and female perch (0.71±0.34 for males, 0.37±0.12 for females), were used to estimate the number of fish tagged in 1981 that survived to 1982.

To determine if the estimates of male and female survival rates reduced accuracy of the 1982 population estimate, population estimates were calculated based on the 95% confidence limits around the survival rate of each sex. Population estimates based on the extremes of these 95% confidence intervals were usually within the 95% confidence limits of the separate population estimates. Population estimates based on the range of adult male survival were 8,259 and 20,458. This compared well with the 95% confidence limits for the separate adult male population estimate (10,927-22,956). Population estimates based on the range of adult female survival were 2,926 and 4,189. This also compared well with the 95% confidence limits for the separate adult female population estimate (2,194-6,259). Therefore, I assumed that sex-specific survival rates could be used in estimating population size from the 1981-1982 data.

The lower population estimate for the 1982 data only (combined for adult males and females; when survival of fish tagged in 1981 did not affect the estimate), probably was inaccurate due to the small number of fish tagged in 1982 (n=491), and recaptured from that number (n=33; 7%; Youngs and Robson 1978). Therefore, although the 95%

confidence limits ranged from 31%-82%, this estimate of total adult population size probably was not as accurate as that based on the 1981-1982 data adjusted for survival between 1981 and 1982.

This was the first attempt to estimate and compare male and female survival, based on mark-and-recapture data. Other authors have stated that differential annual rates of perch survival between adult males and females may occur, with males (McCormack 1965) or females (Craig 1974) experiencing better rates of annual survival. These authors admitted that their data were limited. Their estimates of sex ratio were based on annual variation in the sex ratios of perch caught in traps during spawning (McCormack 1965), when males are caught in disproportionately high numbers (Thorpe 1977), or from the sex ratio at age from fish collections when few fish were killed (Craig 1974). However, since variations in sex ratio occur (Craig 1974; Clady 1977; Jellyman 1980; Viljanen and Holopainen 1982), it seems reasonable that differential rates of annual survival occur for adult male and female perch.

Although the difference in the mean annual survival rate for adult males and females was large, the combined mean annual survival rate of perch (0.61) in Mink Lake was comparable to estimates of mean annual survival for adult yellow perch from other populations. At Oneida Lake, United States, Noble (1971), Vashro (1975) and Clady (1977) estimated the annual survival of adult perch to be 0.65, 0.63-0.71, and 0.56, respectively. Schneider (1972) estimated the annual survival of adult perch to be 0.59 at Cassidy Lake and Jewett Lake, United States.

In Mink Lake, the high mortality rates among adult female yellow perch compared with adult males may be explained biologically, owing to the high body fat requirements of females during the winter. Newsome and Leduc (1975) suggest that adult females not able to build up sufficiently large fat reserves in summer to meet the energy demands required of ovogenesis and winter maintenance may suffer winter or spring mortality. Newsome and Leduc (1975) do not provide estimates of the mortality rate of adult female perch in lakes where this phenomenon occurs. In Mink Lake, however, where perch growth rates are poor (Chapter 3), adult female winter or spring mortality may occur, although no dead fish were found in Mink Lake from May to October in either study year.

In comparison, with the sex ratio from the population estimates, the sex ratio from three collection techniques combined (traps, trawl, seine), taken after spawning (1.9:1) differed. The sex ratio of perch in adult age-classes older than the age of 4+ (2.9:1), compared well to that estimated from trawl captures (2.6:1). When one sex matures earlier than the other, however, or when gear selects for one sex, determination of adult sex ratio based on this technique, and not on separate population estimates, may be grossly inaccurate. Trawl captures have been reported to reflect the sex ratio of the fish present (Gulland 1983); my results do not support this conclusion. The discrepancy between the sex ratio estimated from the separate population estimates (4.4:1) and the trawl captures (2.6:1), suggests that adult fish of the same age may segregate in Mink Lake, and this segregation may not include all of the smaller, yet mature 3+ male fish. Therefore, adult population estimates based on the male estimate and the sex ratio, even after spawning, will overestimate female abundance.

Methods used by other authors to estimate total fish population size, when males and females could not be distinguished externally, overestimated the abundance of adult perch in Mink Lake, particularly the abundance of the female perch. A 90% overestimate occurred when data were taken only at the time of perch spawning and used in the estimation of population size. When authors assumed that they effectively captured only males, and doubled the male population estimate to account for females in the population, they overestimated total population size by 63%, and the female population size by 332%. The sex ratio method depends on the accuracy of the sex ratio estimated. When the sex ratio based on all sampling gears combined (1.9:1) was applied to the male estimate, the total perch population was overestimated by 25% and the female population size was overestimated by 131%.

Females are harvested selectively in commercial and sport fisheries (El-Zarka 1959). Thus, harvest rates based on the above overestimates of females could deplete the population of adult females, severely reduce the population's reproductive potential, and ultimately reduce total perch biomass and production.

When it is important to manage fish population size for the purposes of determining harvest rates in a commercial or sport fishery, or for brood stock collection (Casselman 1974), therefore, the separation of adult male and female perch population estimates is an improvement since it allows the comparison of abundance and annual survival rate between the sexes.

For these reasons, more time should be spent in developing non-destructive methods of external sex determination. Thus, accurate estimates of annual survival rates and abundance of adult male and female fish can be made during mark-and-recapture studies. In this way, potential overestimates of the total numbers of adult male or female fish in a population will not occur.

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V. BIOMASS AND RATES OF PRODUCTION OF YELLOW PERCH IN MINK LAKE, ALBERTA

A. INTRODUCTION

Information on the biomass and production of yellow perch, *Perca flavescens* (Mitchill), is important in setting harvest rates for commercial and sport fisheries. Unfortunately, very little annual production information is available for perch populations (Carlander 1977). Indeed, in Canada, where perch are widely distributed and important both to the commercial and sport fishermen (Scott and Crossman 1973), only one researcher has estimated their biomass and production (Chadwick 1976). This study involved poisoning the lake and collecting dead fish. However, the lake was not drained so all fish could not be collected. No data are available on differences in biomass and production between males and females estimated from mark-and-recapture studies.

Most of the previous studies that measure fish production considered salmonids living in streams, in the United Kingdom, the United States (Chapman 1978) and New Zealand (Allen 1951). Estimates of salmonid production in streams range between 0.2-7.2 kg ha^{-1} yr^{-1} (Allen 1951; Cooper and Scherer 1967; Le Cren 1969; Elliott 1985). Production estimates for species in lakes are rare. For northern pike in lakes, production estimates range between 0.02-0.06 kg ha^{-1} yr^{-1} (Kipling and Frost 1970; Backiel 1971). Production values for adult Eurasian perch, *Perca fluviatilis* L., and yellow perch, which may be compared directly (Thorpe 1977), are higher than those of salmonids or northern pike, and range between 0.26-26.3 kg ha^{-1} yr^{-1} (Thorpe 1974; Chadwick 1976; Clady 1977; Rask and Arvola 1985, Table V.1).

Various factors, such as species diversity, fishing pressure, and habitat changes affect fish biomass and rates of production. In lakes where perch is the only species, biomass for all age classes ranged from 39 to 215 kg ha^{-1}, but in lakes with other species, perch biomass was under 65 kg ha^{-1} (Carlander 1977). Fishing pressure may complicate seasonal variations in biomass and productivity (Kelso and Ward 1977). Decreases in habitat diversity, water level and water temperature may lower fish biomass and production (Portt *et al.* 1986). Inadequate sampling techniques may prevent all fish habitats from being sampled (Chadwick 1976), and artificially lower the estimate

Table V.1 Density and total annual production rates for adult Eurasian and yellow perch estimated by mark and recapture.

Locality	Number of Perch (ha^{-1})	Total Production P ($kg\ ha^{-1}\ yr^{-1}$)	Authority
Red Deer Lake (Canada)	7(>3+)	0.26	Chadwick (1976)
Lake Vitalampa (Sweden)	262-597(>2+)	0.4-0.6	Nyberg (1979)
Horkkajärvi Lake (Finland)	1,360 (>2+)	4-8	Rask and Arvola (1985)
Lake Suomunjärvi (Finland)	312 (>3+)	6-8	Viljanen and Holopainen (1982)
Oneida Lake (USA)	5-137(2-3+)	9-19	Vashro (1975)
Cub Lake (USA)	3-81 (>3+)	19-26	Clady (1977)
Loch Leven (England)	257 (2-9+)	21	Thorpe (1974)

of total annual production.

Overestimates of population abundance and, consequently, production (Chadwick 1976) may be caused by behavioral differences between the sexes at the time of sampling. When perch are captured only during spawning for population estimates, gear such as traps (Craig 1974) and gillnets (Brazo *et al.* 1975) select for males (Thorpe 1977). Hence, disproportionately large numbers of tagged males inflate estimates of total population size and lead to overestimates of their rates of production (Chadwick 1976; this study).

The inability of researchers to differentiate male and female perch at a time other than spawning (Chapter 2), has prevented them from comparing biomass and production for adult male and female perch. Production probably differs markedly between adult male and female perch, however, since differences in life-history characteristics, which affect estimates of prodution, occur between the sexes. These include: age at maturity (Craig 1974; Thorpe 1977); growth rates (Hile and Jobes 1941; Chadwick 1976; Craig 1980, 1982); survival (Craig 1974; this study), especially in the oldest age-classes (Eshmeyer 1937, 1938; Craig 1982); abundance (this study by population estimates), and; sex ratio (Craig 1974; Clady 1977; Jellyman 1980; Viljanen and Holopainen 1982; this study).

The few studies of yellow perch production conducted in North America have not been sufficiently rigorous to yield good production estimates. In Canada, Chadwick (1976) estimated the rates of production of all age-classes of perch by poisoning a small (6.2 ha) lake and collecting dead fish. He noted that eight times the juvenile fish estimated to be in the lake by mark-and-recapture were collected. However, only half of the adult fish, marked by fin-clipping immediately before lake poisoning, were recovered. This result suggests that a large proportion of all adult poisoned fish, perhaps half, were not recovered, which would lead to an overestimate of population abundance and fish production. In the USA, Vashro (1975) estimated production of the first three age-classes of perch in eutrophic Oneida Lake. The number of 1+ and 2+ fish were estimated from the density determined by trawl. Only the 3+ fish population estimates were made by a mark-and-recapture technique. Unfortunately, Oneida Lake is large (206.7 km^2), and has over 50 fish species. Both these factors could result in underestimates of the estimate of total annual production of perch (Carlander 1977). Clady (1977) estimated production for perch in a smaller lake (Cub Lake, 11.3 ha). He sampled fish using only one sampling method, and the limitations of the electroshocker prohibited him from sampling waters greater than two metres in depth. Both factors may cause an underestimate of adult perch population size and production, since electrofishing may sample only a subpopulation of fish (Schneider 1971), and adult perch regularly inhabit waters deeper than two metres (Thorpe 1977). For these reasons, a lake was chosen for this study that had low fish species diversity and little fishing pressure, and that could be fully sampled.

The present study is the first to estimate adult yellow perch biomass and production in western Canada. It is also the first to estimate the rates of production separately for males and females from separate estimates of their abundance. Although the greatest production occurs in the youngest age-classes (Thorpe 1974; Vashro 1975), only the 100% mature adult age-classes of perch were considered in this study, since mortality rates are high (Clady 1977), and the number and growth rates of young fish are difficult to determine (Chadwick 1976; Nyberg 1979).

B. METHODS AND MATERIALS

Yellow perch were captured in Windermere perch traps and an otter trawl and samples of fish were measured for total length (Chapter 1) and weighed. Sex of marked fish was determined by the method described in Chapter 2.

To estimate the rates of production for adult fish, the age at sexual maturity was determined for males and females. Back-calculated data could not be used in the estimation of mean weight at age for production estimates as Lee's phenomenon occurred. Therefore, mean weight at age was estimated from adult perch collected in October (n=108) (Chapter 3). Population estimates of adult male (3+-7+) and female (4+-8+) yellow perch (Chapter 4), were used as the total abundance of adult male and female perch. Population estimates for each adult age-class 4+ and older were estimated from the size distribution of perch captured by an otter trawl (Noble 1972). Age was judged from the left opercular bone (Chapter 3) of 391 fish (Appendix III.2). Size of the fish was converted to an estimated age using age-length keys (Ricker 1975).

The numbers of 3+ male perch were derived from the estimated abundance of 4+ males adjusted for mean annual male survival rate (0.71) the previous year (Chapter 4). The methods of Ricker (1946) were used in the computation of biomass and total annual production.

C. RESULTS

Mean biomass and total annual production were different for adult male and female yellow perch. Adult male perch contributed 78% of the total annual production in Mink Lake, or almost four times that of adult females. The greatest proportion of production within each sex was contributed by 5+ fish. Both 5+ age-classes contributed 57% to the total annual rates of production (Tables V.2 and V.3). Mean biomass and total annual production for males and females combined was 10.39 kg ha^{-1} and 4.42 kg ha^{-1} yr^{-1} (Table V.4).

D. DISCUSSION

The estimated biomass of adult perch (10.39 kg ha^{-1}) was low compared with those for other lakes and ponds in North America (Carlander 1977). It was, however, within the range of adult perch biomass for lakes with poor perch growth (Table V.1) which ranged from 8.2-21 kg ha^{-1} (Chadwick 1976; Nyberg 1979; Viljanen and Holopainen 1982).

The total annual production for adult male and female perch in Mink Lake (4.42 kg ha^{-1} yr^{-1}), also was within the lower part of the range of those previously reported (Table IV..1). It was much lower than the production reported by Thorpe (1974) for Loch Leven, although adult perch densities were similar (Tables IV.1 and IV.4). The rates of fish production are related to both abundance and rates of growth. Hence, the low density (Chapter 4) and poor rates of growth of perch in Mink Lake (Chapter 3) probably are responsible for the low rate of fish production estimated. Growth rates of yellow perch did not differ significantly between the sexes in Mink Lake (Chapter 3) and hence did not influence the rates of production of adult females relative to adult males.

The estimate of total annual production of adult males exceeded that of adult females by a factor of 4.5 in one year in Mink Lake. This large difference between the

Table V.2 Computations of mean biomass and total annual production for adult male yellow perch in Mink Lake.

Variables[a]	Age Classes 3		4		5		6		7	Lake Total	Total $P\ ha^{-1}$
N	4940		3502		2818		2597		949	14 806	208
$\overline{w}$	21.5		31.5		37.0		89.5		117.5		
B'	106.21		110.31		104.27		232.43		111.51		
Z		0.344		0.217		0.082		1.01			
G		0.382		0.161		0.880		0.272			
H		0.038		-0.056		0.798		-0.748			
$(e^H - 1)/H$		1.019		0.973		1.530		0.704			
$\overline{B}$		108.23		107.33		159.53		163.63		538.72	7.58
P		41.34		17.28		140.86		44.51		243.99	3.44

[a] Variables are defined in Appendix IV-1.

Table V.3 Computations of mean biomass and total annual production for adult female yellow perch in Mink Lake.

Variables[a]	Age Classes 4		5		6		7		8	Lake Total	Total P ha^{-1}
N	879		845		708		609		336	3378	48
$\overline{W}$	31.5		37.0		89.5		117.5		132.3		
B'	27.69		31.26		63.37		71.56		44.45		
Z		0.039		0.177		0.151		0.595			
G		0.161		0.883		0.272		0.119			
H		0.122		0.706		0.121		-0.476			
$(e^H - 1)/H$		1.064		1.453		1.063		0.796			
$\overline{B}$		29.46		45.42		67.36		56.96		199.20	2.81
P		4.74		40.11		18.32		6.78		69.95	0.98

[a] Variables are defined in Appendix IV.1.

Table V.4 Summary of mean biomass and total annual production estimates for adult male and female yellow perch in Mink Lake.

Variables[a]	Age Classes 3	4	5	6	7	8	Lake Total	Total P ha⁻¹
N							18,183	.256
$\overline{B}$	108.23	136.79	204.95	230.99	56.96		737.92	10.39
P	41.34	22.02	180.97	62.83	6.78		313.94	4.42

[a] Variables are defined in Appendix IV.1.

sexes in total annual production is related to equivalent differences in the estimates of adult male and female abundance (Chapter 4) (adult sex ratio of 4.4:1 in favor of males).

Chadwick (1976) noted that adult female perch contributed 56% of production at Red Deer Lake. This result is in contrast to those at Mink Lake where males contributed a larger proportion to total annual production (78%), than the females. Chadwick's results probably were inaccurate. Few fish (n= 103) were involved in the estimates of adult annual production and the population estimates, on which production is based, overestimated the numbers of adult fish in the lake by eight times, owing to sampling error (Chadwick 1976).

Rates of production are dependent on the abundance, rates of survival and growth of the fish (Vashro 1975), therefore, variations in any of these factors between sexes could influence the relative production of male and female fish. Theoretically, the better growth rates of adult female fish in most populations (Thorpe 1977; Jellyman 1980), would increase their production relative to that of males, especially in fast-growing populations where females predominate (Dryagin 1948). Large numbers of adult male fish, which often mature earlier than females (Thorpe 1977; Craig 1974; Nyberg 1979), however, would increase male production in the younger adult age classes. I suggest that since differences in these life history characteristics occur for many species of fish (Chapter 1), differences between their adult male and female production also occur, as in this study.

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VI. CONCLUDING DISCUSSION

The combined estimates of adult male and female perch survival, abundance, biomass and productivity confirmed other authors' results. Separate estimates for each sex, however, which were conducted for the first time, indicated that, at Mink Lake, adult males survived better, were more abundant, and had a larger biomass and greater production than adult females.

Separate estimates for each sex were possible owing to the development of a method to determine the gender of adult yellow perch. The method was based on external differences in the appearance of the urogenital structure, and was used successfully at times other than perch spawning, during May through October of this study.

Separate estimates of adult abundance suggested a sex ratio of 4.4:1 in favor of males. The large difference in abundance of adult males and females was attributed to differences in the age at maturity, and in the rates of survival between the sexes, but not to differences in growth rates. Males matured one year earlier than females, which increased their adult abundance by 50%, compared with adult females. Adult males also survived almost twice as well as females, which augmented their already inflated numbers.

The difference in abundance and, consequently, biomass and production between adult males and females was not caused by differences in behavior between sexes or by inadequacies in sampling techniques. Shoals did not stratify by gender, depth or diet preference. These results are in contrast with those of Hartmann (1974) and Sandheinrick and Hubert (1984), respectively. In Mink Lake, males and females were mixed throughout the lake, except when males were concentrated for spawning.

Adult sex ratio estimated from data taken after spawning from all gears (Jobes 1952 method; 1.9:1), and from trawls (Thorpe's 1974 method; 2.9:1), overestimated the numbers of females present compared with the sex ratio estimated from the separate population estimates (4.4:1). Sex ratio of the 4+ and older fish (2.6:1), was closest to that estimated from trawl data. This ratio appears to omit the 3+ mature males, so that data obtained from trawls do not reflect the adult sex ratio present. This finding is in contrast to Gullands' (1983) results. The similarity between these sex ratios suggests that perch in Mink Lake may stratify by size (age). When one sex matures a year or more earlier than the other, however, sex ratio estimated from trawl captures is inaccurate for adult population estimates.

Other authors' methods to estimate female perch abundance, from spawning data (such as doubling the male estimate [Le Cren *et al.* 1977], combining the male and female estimate [Craig 1974], and, the male estimate multiplied by sex ratio taken after spawning [Thorpe 1974]), probably have overestimated female, and sometimes total perch abundance. These comparisons were made using data obtained from perch in Mink Lake and this finding suggests that the above population estimates were made when researchers depended on the following erroneous assumptions: sex ratio 1:1; accurate population estimates could be made using data taken predominantly during spawning, and; sex ratio taken by killing fish after spawning reflects the actual sex ratio of the population.

Overharvests will occur when commercial or sport fish harvest rates of perch are based on the assumption of equal sex ratio of adults, yet females are taken selectively by anglers and gillnets, owing to their larger size (El Zarka 1959), and females are less abundant than males, owing to their greater rates of mortality (this study).

The differences in survival rate, when males survive better than females, may be related to differences in energy required for reproduction (Newsome and Leduc 1975). This study also notes that, although adult males survive almost twice as well as adult females in general, some females survive longer than all males. The largest oldest fish in a population, therefore, would be females.

The total annual production of adult perch in Mink Lake was 4.42 kg ha^{-1} yr^{1}, which was within the lower range of those estimates previously reported for yellow and Eurasian perch from mark-and-recapture data. Adult males, however, contributed four and a half times more production than adult females, for one year.

In summary, the ability to determine accurately, and externally, the gender of adult yellow perch has resulted in a clearer understanding of the differential demography of males and females within a population, including their rates of survival, and population size, which ultimately determine biomass and production. Although perch density and growth rates were comparable to other studies, subtle differences in parameters such as age at maturity and survival between adult males and females accounted for great differences in their abundance and, therefore, their biomass and production.

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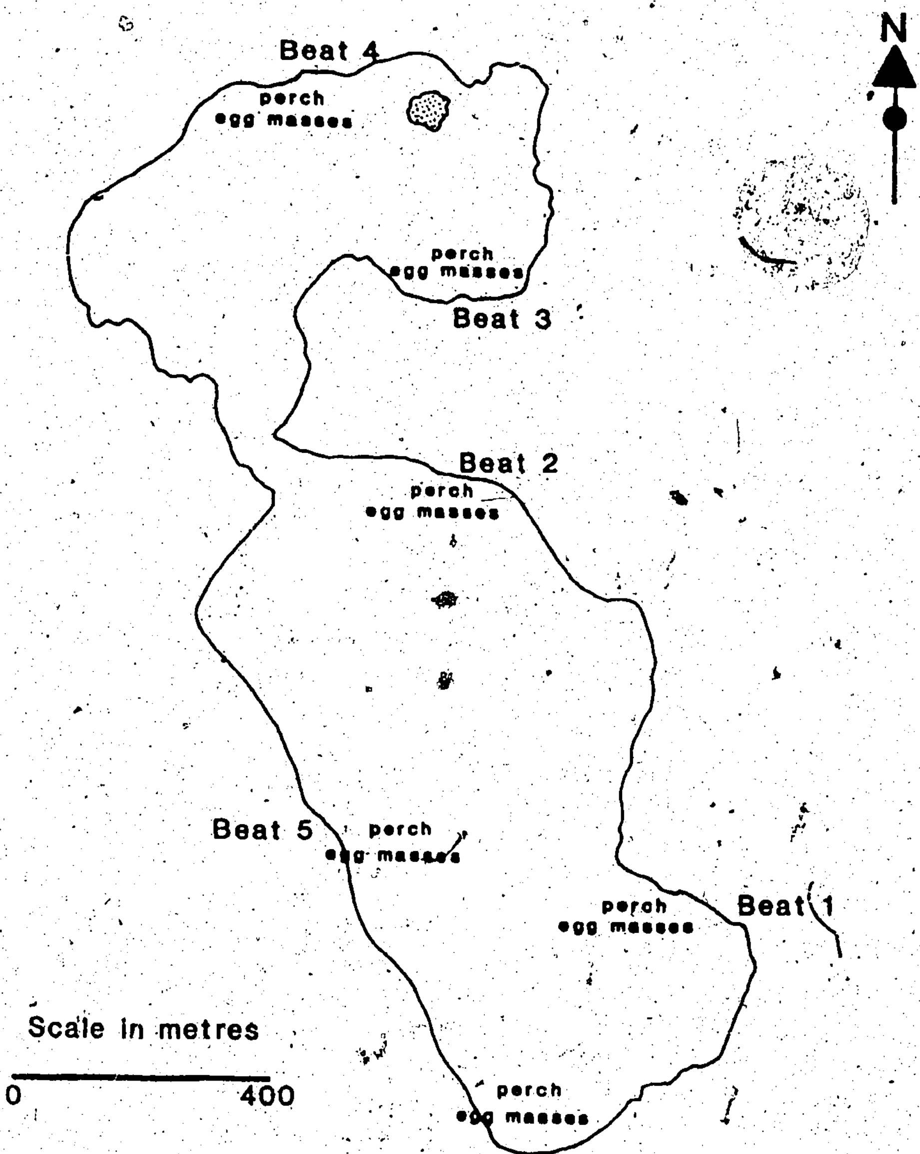
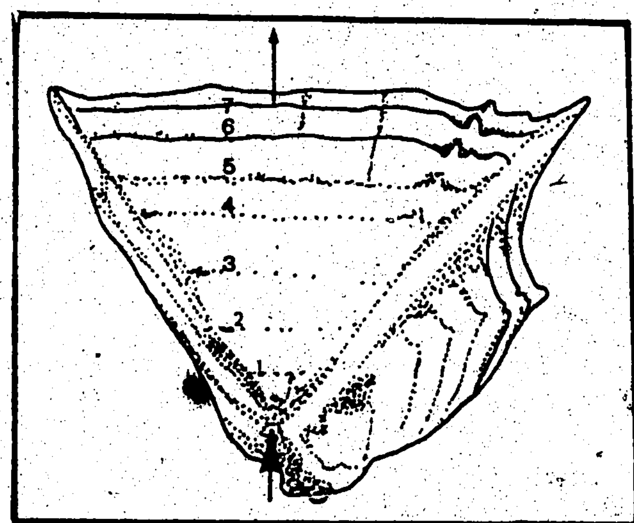
VII. APPENDIX I



APPENDIX I.1

Spawning sites of yellow perch in 1981 were used as beats one through five for trapping in 1981. Traps were set in groups of four.

VIII. APPENDIX II



APPENDIX II. 1

Drawing of an opercular bone used for age determination of perch. Arrows mark the focus and direction used when measuring an operculum. Ages are indicated in years of growth (redrawn from Norris 1984).

APPENDIX II.2

Methods used in Back-calculation

Data for back-calculation were collected in the following way:

1. An image of the opercular bone was projected on a white wall;
2. Cardboard strips placed on the wall were marked to indicate the focus and each annulus, and;
3. The distance from the focus to each annulus was measured and used to calculate total length at earlier ages [from a regression equation for the relationship between total body length and opercular length (LeCren 1947; Craig 1974)], with a correction made for magnification of the projection. This required that the distance between the projector and the wall remain constant. The intercept of the regression equation was used to compensate for the length of the fish before the first annulus was laid down.

IX. APPENDIX III

APPENDIX III.1

How Assumptions of the Population Estimate Were Evaluated at Mink Lake and Results of the Evaluations.

Assumptions of the population estimate were taken from Seber (1982).

1. Assumption one states that the population is closed, so that the estimate is constant. This assumption was met; at Mink Lake there is no inflow or outflow and there was no immigration of untagged fish or emigration of tagged fish during the study.

2. The second assumption states that there is equal catchability in the first and second sample. This is the most crucial assumption, since it concerns equal vulnerability of all individuals to the catching method (Cormack 1969), and is affected by the behavior of the fish (Beukema and De Vos 1974). Other researchers have violated this assumption by capturing fish only during spawning (Thorpe 1974; Jensen 1976), when gear captures sexually mature males in disproportionately large numbers (Craig 1974), and by baiting traps (Chadwick 1976), which may cause fish to re-enter traps more frequently than by chance. To evaluate assumption two in this study, all data were examined to determine if males, females or different size-classes of fish had different vulnerability to the sampling gear, or if recruitment of newly mature individuals to the small size classes affected the ratio of marked and unmarked fish in the second year of the study.

   a. To determine if different selectivity operated between age-classes, the ratio of recaptured to unmarked fish in each size-class was examined by chi-square analysis to determine if there was a difference in the proportion of recaptured fish in each of the five size-classes. If the proportion was not the same, all sizes of fish were not equally catchable (Youngs and Robson 1978). At Mink Lake, there were no significant differences between gear in the frequency of male and female perch captured and recaptured in the five adult size-classes in 1981 for males (chi-square= 4.38, df=4, n=983, P>0.25), or females (chi-square=6.33, df=3, n=526, P>0.05), or in 1982 for males (chi-square=5.03, df=3, n=310, P>0.10), or females (chi-square= 0.02, df=2, n=199, P>0.99).

b. To determine if new recruitment to the population in the second year of the study affected the proportion of size-classes caught, the proportion of unmarked to marked fish in the five size-classes in the second year of the study was compared by chi-square analysis. A large proportion of unmarked fish in the small size-classes would suggest first recruitment of a new size-class to the population (Youngs and Robson 1978). At Mink Lake, there was no significant difference in the proportions of marked and unmarked male and female perch in the sample caused by the recruitment of young unmarked fish to the gear in 1982 (chi-square= 7.35, df=4, n=1199, P>0.10 for male perch; chi-square=0.68, df=4, n=285, P>0.95 for female perch).

3. The third assumption states that tagging does not affect recapture frequencies of fish by mortality, or by trap avoidance or selection by fish. Violation of assumption three occurred in previous studies when marking by clipping a fin caused increased mortality (Chadwick 1976; Jensen 1976; Nyberg 1979).

a. Tags were chosen according to the literature to reduce the effects of tagging on the survival, rates of growth and feeding behavior of the perch. Spaghetti tags, yellow or blue in color, anchored between the dorsal fin and the lateral line were recommended for mark-and-recapture studies with fish (Keller 1971; Greenland and Bryan 1974; Laird and Stott 1978). These tags cause negligible mortality, attract few predators, and do not interfere with feeding. The results of the tagging experiment indicated that tagging did not affect survival or total weight in the short term. Nine tagged and nine control perch of matched size were held in the laboratory for five weeks. The fish were measured for total length and wet weight, and tagged in the same manner as in the field. They were held in identical flow-through tanks in North Saskatchewan River water (17±1°C) (fish originally held for the above experiment in Mink Lake were stolen). Mortalities were recorded and after-experiment weights were taken for comparison with pre-experiment values There was no significant difference in the survival or the change in total wet weight of fish due to tagging (Student's t-test, t=0.34, df=14, P>0.50). Further, at Mink Lake, no dead tagged fish were found or reported.

b. A comparison of the frequency of recapture between males and females, and between males and females caught in two different fishing gear was made by chi-square analysis. At Mink Lake, a difference did occur between sexes in the frequency of recapture in 1981 and 1982. Females were recaptured significantly more frequently than males in 1981. Males were recaptured significantly more frequently than females in 1982 (chi-square=12.45, df=1, n=1613, P<0.005, and chi-square=5.42, df=1, n=552, P<0.025, respectively).

c. To determine if fish selected or avoided gear after tagging, the frequency of fish captured and recaptured by both gear in 1982 was compared. A significant difference would suggest that fish were selecting or avoiding a gear. However, at Mink Lake, there was no difference in the frequency of recapture between gear for females or males (chi-square; n=285, P>0.90 and n=1199, P>0.05, respectively).

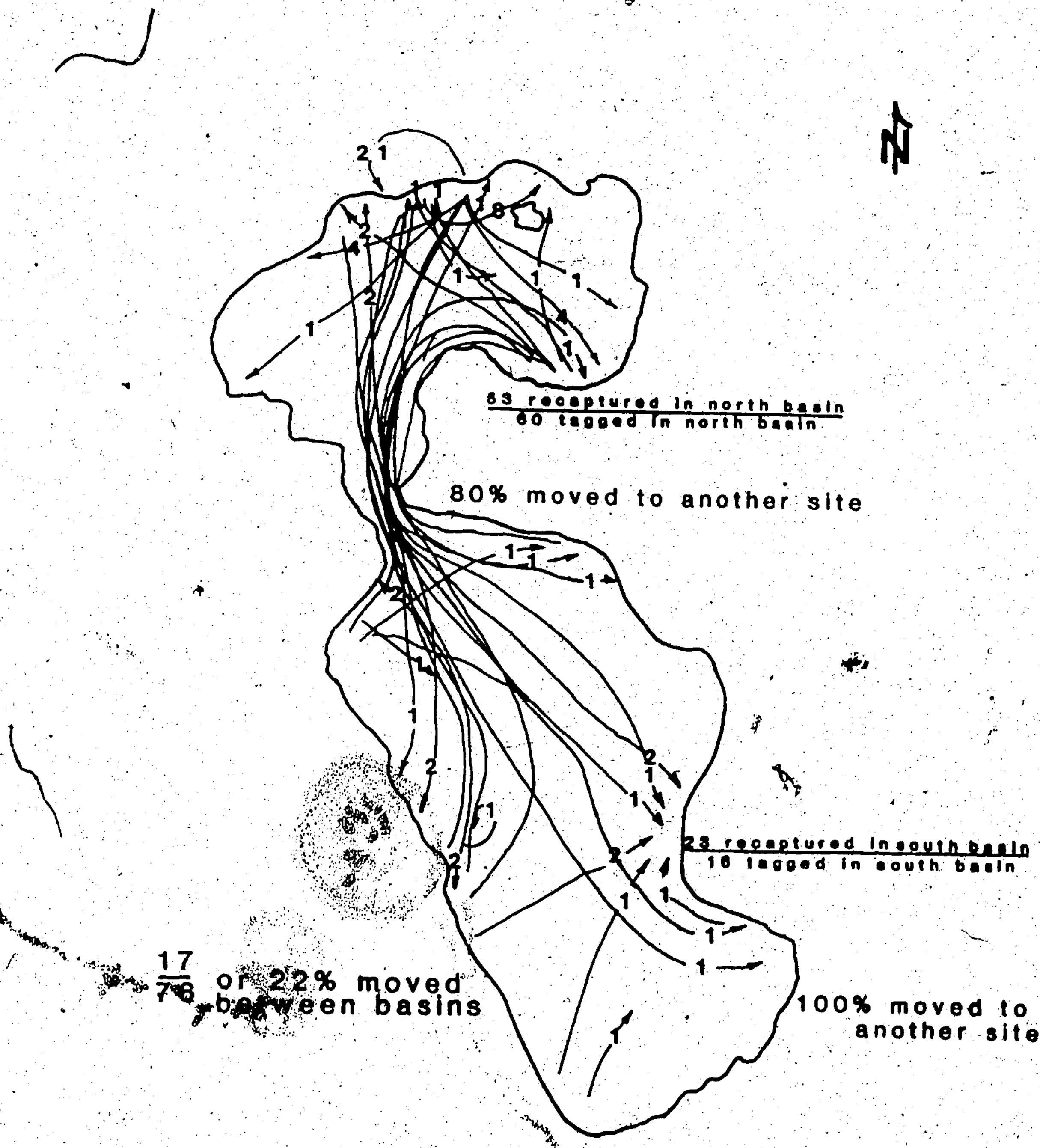
4. To meet the fourth assumption, that tagged fish were mixed randomly among the untagged fish, recapture data were analysed to determine if fish tagged in 1981 were mixed among untagged fish by 1982. In 1982, sampling in the lake was designed to be random, which met the assumption of random mixing (Jackson 1939; Lagler and Ricker 1942; Ricker 1945, 1955).

   a. Multiple recapture data, i.e., from fish that were captured more than once in 1981, were tested by comparing the relative frequencies of multiple recapture to the number of fish tagged (Craig 1974; Nyberg 1979). Chi-square analysis comparing the frequency of multiple recaptures to the number of fish tagged for each sex suggested that there was no difference in the proportions of fish captured or recaptured up to three times. Thus, at Mink Lake, it was assummed that tagged adult female and male perch were mixed randomly among untagged perch during 1981 (chi-square= 3.45, df=2, n=653, P>0.15, and chi-square=3.76, df=2, n=1198, P>0.15, respectively).

   b. The average time for tagged perch to move from the tagging site to another in 1981 was estimated. The number of fish that moved to another site but were not recaptured, then returned to the original site, could not be evaluated in this study. In 1981, at Mink Lake, perch were tagged at five areas by traps and five areas by trawl. The distance between the tagging areas ranged from 100 m to 1,000 m (closely situated within the north basin compared with the farthest areas between the north and south basins). After tagging, these 10 areas were sampled for the presence of tagged animals, and many perch were recaptured at the site of tagging. However, movement was observed within days of tagging, and the incidence of movement differed between male and female perch. Female perch remained only a short time at the site of spawning/tagging, but the males remained longer. Fifty percent of females recaptured two days or more after tagging were recaptured in an area other than the one in which they had been tagged, indicating that they had moved (n=54). Fifty percent of males recaptured six days or more after tagging also had moved (n=36) to another area.

c. To determine whether tagged fish were moving throughout the lake, and mixing among untagged fish within a year after tagging, the frequency of movement of tagged fish within and between the two basins in Mink Lake was evaluated. By 1982, 80% (n=60) of the fish tagged in 1981 in the north basin, and 100% (n=16) of the fish tagged in the south basin had moved to another area, and 22% (n=76) had moved between basins (Appendix III, Figure III.1).

5. To evaluate the fifth assumption, that fish are not likely to lose their marks, since tag loss produces overestimates of population size (Arnason and Mills 1981), fish should be double tagged in a separate experiment using two different tags. For this study, the literature was consulted to determine methods to reduce tag loss by choice of tag and handling. The tags were chosen for size, type and color, and placed between the spinous dorsal fin and lateral line to engage the interneurals (Black 1957; Muir 1963; Keller 1971; Greenland and Bryan 1974; Laird and Stott 1978; Tranquilli and Childers 1982). All perch were examined to determine the incidence of tag loss (the presence of scar tissue in the area of tag insertion, Ebener and Copes 1982) midway between the lateral line and the spinous dorsal fin. There was no evidence of tag loss in the location of tag insertion. However, in 1.5% of the recaptured fish (four in 1982), the 2 cm long numbered plastic tag had broken off, leaving only the anchor 'T' (5 mm of clear plastic tag, 1 mm in diameter was visible). Although these fish could not be identified individually, since their numbered tag was missing, they still could be included in the total number of marked fish within their size-class and sex.



Appendix III, Figure III.1

Movement of yellow perch captured in Mink Lake between basins between 1981 and 1982.

Three years after tagging, after the completion of the study, tagged fish were reported by fishermen, indicating that tags were well retained in the perch musculature when locked behind neural spines.

6. All fish were recaptured by the author to meet the last assumption that all recaptured fish were recorded.

APPENDIX III.2

To determine the age composition of the adult fish, an age-length key was constructed from the age at length for sampled fish according to the methods of Ricker (1975). A table giving the proportion of each age within a certain length category was used to convert the observed length distribution of tagged fish to age. Age-length keys were divided between May 17 - July 29 and July 29 - October 14, 1982, to account for yellow perch growth during the summer and to increase accuracy of the predictions of age at length. The lengths were divided into 5 mm intervals, and begun at 105 mm (the first length of maturity for males) and continued to 275 mm (the largest size with fish subsampled).

APPENDIX III.2 continued

Key for assigned age at length for female yellow perch (proportion of length at a given age based on subsamples taken between May 13 and July 29 in 1982).

T.Length	Tagged n=246	Age 1	2	3	4	5	6	7	8	9	Subsample Aged n=77
10.5-11.4			1.0								1
11.5-12.4			.4	.6							7
12.5-13.4			.55	.44							10
13.5-14.4			.33	.66							6
14.5-15.4				.7	.3						10
15.5-16.4				.11	.88						9
16.5-17.4					1.0						5
17.5-18.4					.5	.5					2
18.5-19.4					1.0						1
19.5-20.4											0
20.5-21.4					1.0						1
21.5-22.4											0
22.5-23.4						.14	.86				7
23.5-24.4						.25	.38	.38			8
24.5-25.4							.33	.66			3
25.5-26.4								.50	.50		2
26.5-27.4								1.0			2
>27.5							.33	.33	.33		3

APPENDIX III.2 continued

Key for assigned age at length for female yellow perch (proportion of length at a given age based on subsamples taken between July 29 and October 14 in 1982).

T.Length	Tagged n= [illegible]	Age 1	2	3	4	5	6	7	8	9	Subsample Aged n=95
10.5-11.4			1.0								2
11.5-12.4			1.0								3
12.5-13.4			1.0								7
13.5-14.4			.62	.38							8
14.5-15.4				.75	.25						8
15.5-16.4				.21	.64	.14					14
16.5-17.4					1.0						7
17.5-18.4						1.0					2
18.5-19.4						1.0					2
19.5-20.4											0
20.5-21.4								1.0			1
21.5-22.4							.5		.5		2
22.5-23.4							.8	.2			5
23.5-24.4						.08	.08	.69	.16		13
24.5-25.4							.42	.42	.14		7
25.5-26.4						.11	.11	.44	.11	.22	9
26.5-27.4								1.0			5
>27.5											0

APPENDIX III.2 continued

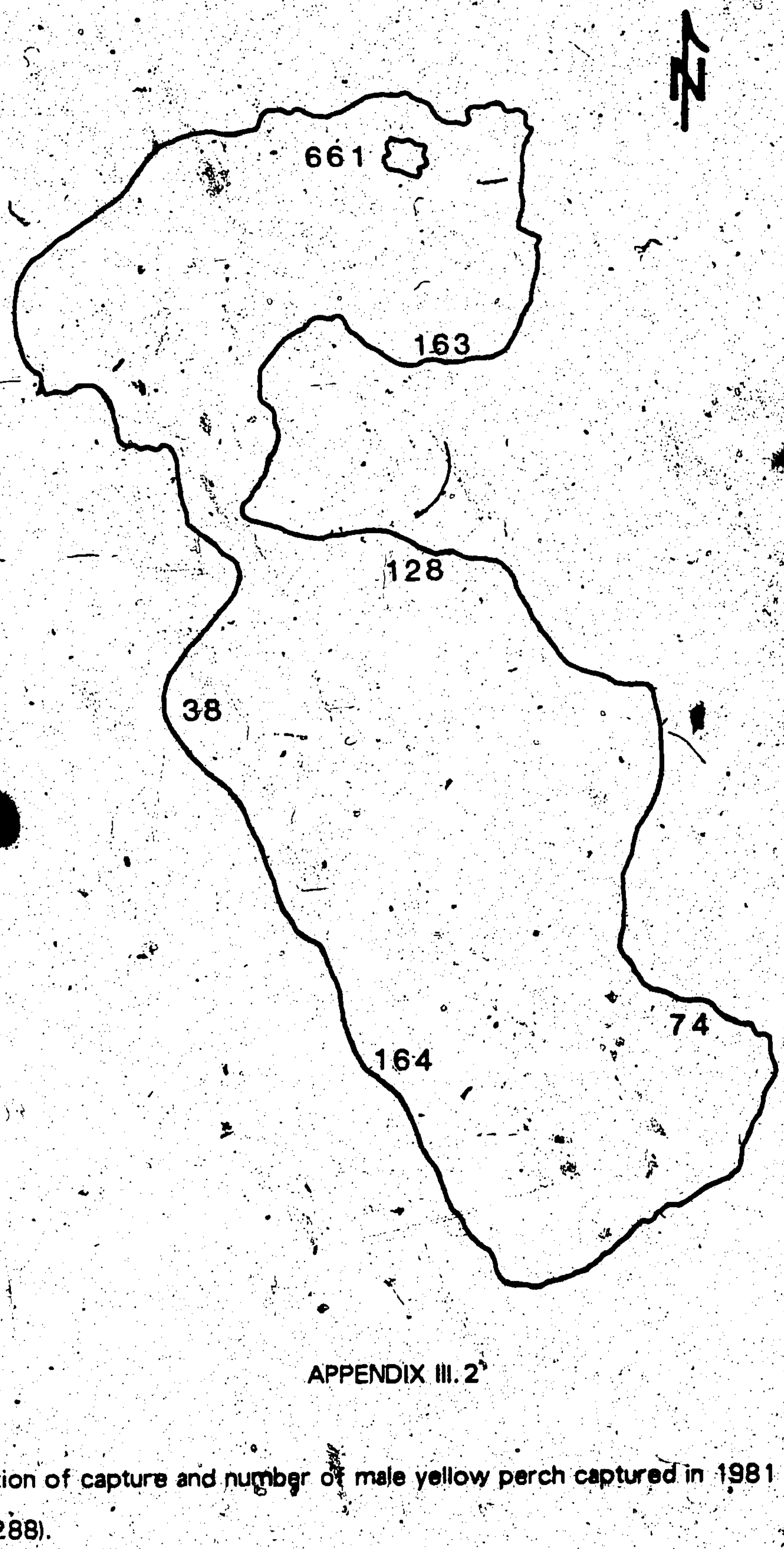
Key for assigned age at length for male yellow perch (proportion of length at a given age based on subsamples taken between May 13 and July 29 in 1982).

T.Length	Tagged n=1291 Age 1	2	3	4	5	6	7	8	9	Subsample Aged n=85
10.5-11.4	.5	.5								2
11.5-12.4		.67	.33							3
12.5-13.4		.5	.5							2
13.5-14.4			1.0							3
14.5-15.4			.66	.33						3
15.5-16.4			.33	.66						9
16.5-17.4			.75	.25						4
17.5-18.4				.5	.5					2
18.5-19.4				.25	.75					4
19.5-20.4				.22	.56	.22				9
20.5-21.4				.06	.27	.55	.05	.06		18
21.5-22.4				.07	.47	.40	.07			15
22.5-23.4						.83	.17			6
23.5-24.4						.5	.25	.25		4
24.5-25.4						1.0				1
25.5-26.4										0
26.5-27.4										0
>27.5										0

APPENDIX III.2 continued

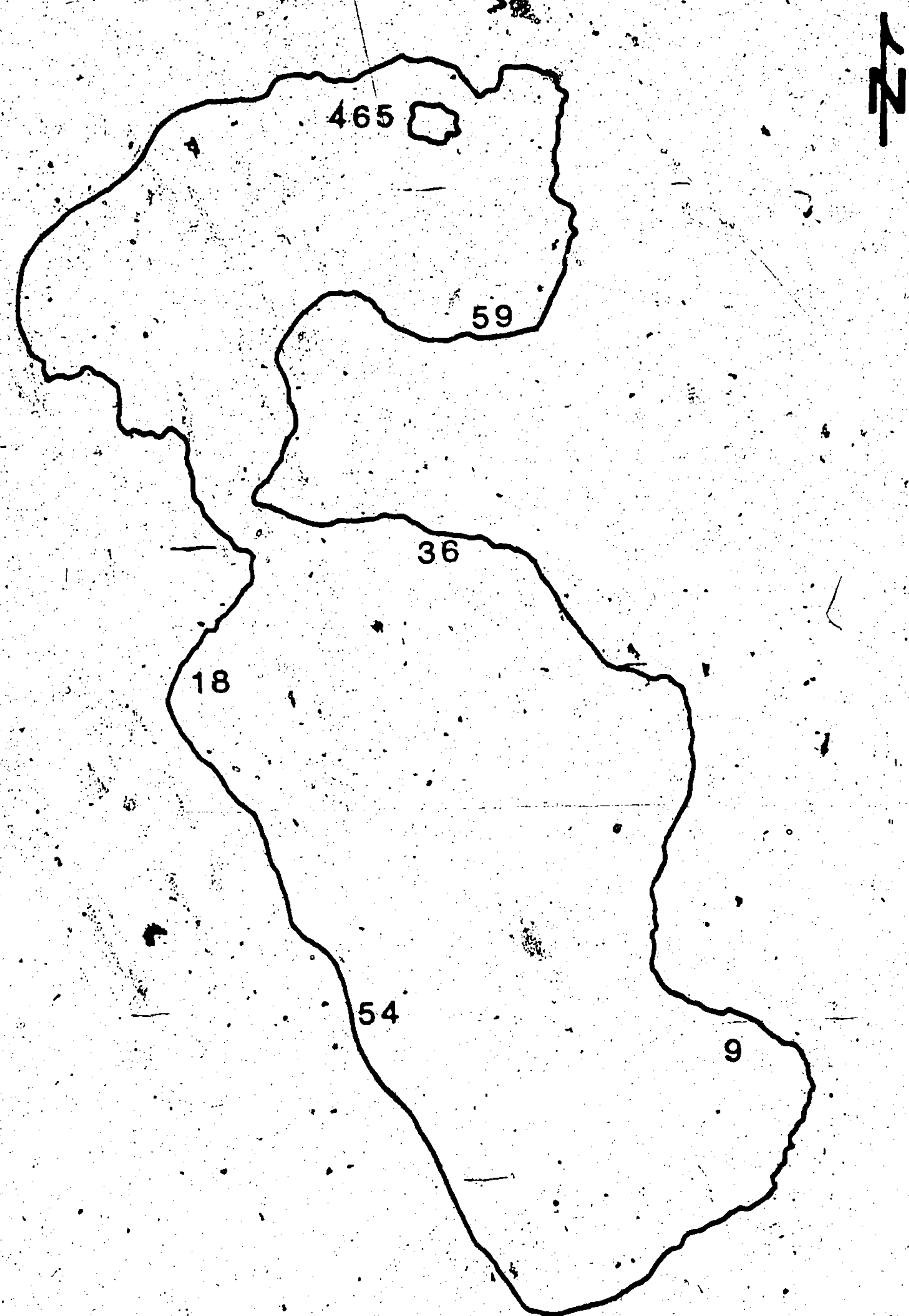
Key for assigned age at length for male yellow perch (proportion of length at a given age based on subsamples taken between July 29 and October 14 in 1982).

T.Length	Tagged n=150	Age 1	2	3	4	5	6	7	8	9	Subsample Aged n=126
10.5-11.4		1.0									4
11.5-12.4			1.0								2
12.5-13.4			.84	.16							6
13.5-14.4			.7	.3							10
14.5-15.4			.62	.25	.13						8
15.5-16.4				1.0							6
16.5-17.4				.6	.4						5
17.5-18.4				.6	.4						5
18.5-19.4				.25	.75						4
19.5-20.4					.25	.25	.5				4
20.5-21.4						.43	.30	.22	.04		23
21.5-22.4						.13	.25	.44	.13	.06	16
22.5-23.4						.17	.22	.17	.35	.08	23
23.5-24.4						.20	.20	.40	.20		5
24.5-25.4							.5	.5			2
25.5-26.4								1.0			1
26.5-27.4							.5		.5		2
>27.5											0



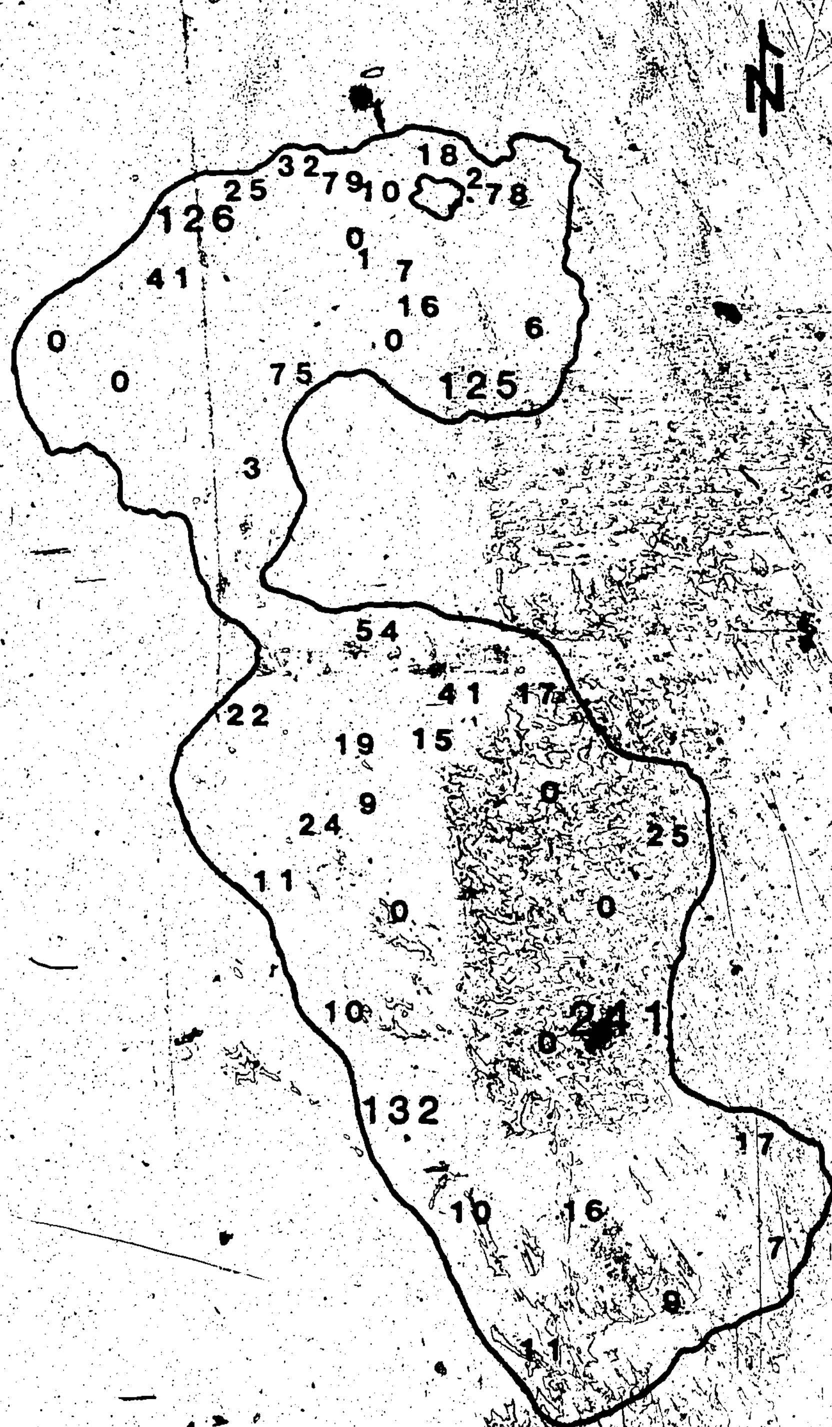
APPENDIX III.2

Location of capture and number of male yellow perch captured in 1981 (n=1288).



APPENDIX III.3

Location of capture and numbers of female yellow perch captured in 1981 (n=641).



APPENDIX III.4

Location of capture and numbers of male yellow perch captured in 1982 (n=1334).

APPENDIX III.5

Location of capture and numbers of female yellow perch captured in 1982 (n=269).

X. APPENDIX IV

APPENDIX IV.1

Definitions of the Symbols Used in the Estimation of Production.

To estimate production, according to the methods of Ricker (1946), the following calculations were required:

1. N_i - the number of fish in each age group i at the time of collection;
2. $\overline{w}_i$ - the mean weight in g of each group i at the time of collection;
3. B_i - the initial biomass in kg of each age group i at the time of collection which equals $N_i\overline{w}_i / 1000$;
4. Z - the instantaneous mortality rate which equals $-(\log_e N_i - \log_e N_{i-1})$;
5. G - the instantaneous growth rate which equals $\log_e \overline{w}_i - \log_e \overline{w}_{i-1}$;
6. H - the rate of increase in biomass which equals $G - Z$;
7. $\overline{B}$ - the mean biomass in kg which equals $B_i(e^H - 1)/H$.
8. P - the total production in kg which equals $G\overline{B}$.