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THE UNIVERSITY OF ALBERTA

GROWTH AND FECUNDITY OF BURBOT, *Lota lota* L., IN TWO ALBERTA LAKES.

by

THOMAS DAVID BOAG

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE
STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and reccomend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled: "Growth and Fecundity of Burbot, *Lota lota* L., in two Alberta lakes" submitted by Thomas D. Boag in partial fulfilment of the requirements for the degree of Master of Science in Zoology.

Supervisor

External Examiner

Date 13 April 1989

ABSTRACT

The timing of body growth and the relationship between fecundity and body size in burbot (Lota lota) from Lac Ste. Anne (a shallow, eutrophic lake) and Cold Lake (a deep, meso/oligotrophic lake) were investigated during the winters of 1986/87 and 1987/88. Burbot were sampled by angling through the ice with artificial lures and from commercial catches. The timing of growth was determined by measuring the relative width of light and dark bands on individual otoliths and recording the time of deposition of these bands in burbot from Lac Ste. Anne. Results suggest that somatic growth occurs during winter in adult burbot. Juveniles grew predominantly during summer; however, significant growth in both length and weight occurred during winter.

A comparison of the two populations suggests that Cold Lake burbot were longer-lived and exhibit better condition indices than their conspecifics in Lac Ste. Anne. Males and females did not differ significantly in length or weight within lakes. Burbot in Lac Ste. Anne were longer on average than those in Cold Lake, but were lighter at any given length. There was no significant increase in weight following age 4 in either burbot population sampled. It appears that in the lakes studied, burbot may exhibit a form of determinate growth.

Investigation into aspects of the reproductive biology of burbot suggests that no relationship exists between fecundity (total number of eggs) and body size for burbot in either lake. Ovary weight and egg diameter were correlated positively with body weight in both lakes. Differences in egg size and number were recorded between Lac Ste. Anne and Cold Lake; burbot from the latter produced many small eggs (mean=701,320, n=48), while those from the former produced fewer larger eggs (mean=504,930, n=38). Egg volume was 36.7% larger in fish from Lac Ste. Anne. Taking into account the significant differences in egg size obtained in this investigation as well as the finding of growth in colder water and differences in condition in burbot in the populations investigated, it would appear that Lac Ste. Anne may be a less desirable, more stressful habitat for burbot.

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This study was undertaken under the supervision of Dr. W.C. Mackay, to whom I am most grateful, not only for the opportunity to undertake this study but also for encouragement and advice along the way. I acknowledge gratefully the contributions of Drs. J.S. Nelson, W.M. Tonn, and W.G. Evans who made up my examination committee and offered many valuable comments and critiscisms. I thank Dr. D.A. Boag for editorial help.

I would like to thank especially Messrs. M.G. Sullivan, D. Lowe, and D. Watters of the Fisheries Branch, Alberta Division of Fish and Wildlife, who all contributed time, and effort in collecting burbot for this project. Ms. C. Schweiger and Mr. M. Snyder helped me in the laboratory. Dr. J.M. Hanson contributed his valuable time in angling for burbot and I acknowledge his help and many comments. I am indebted to Dr. J.S. Nelson who loaned me his electrofisher which was useful in the collection of juvenile burbot.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I.GENERAL INTRODUCTION:

Growth in adult fish can be divided into two categories: somatic, which includes growth in skeletal and muscle mass plus the supporting systems, and annual gonadal growth. Fish growth is sigmoidal, characterized by maximum rates between hatching and sexual maturity, during which growth is strictly somatic (Pitcher & Hart 1982). Subsequently, growth is both somatic and gonadal, the relative amounts of each being dependent on the time of year, environmental conditions, and species of fish. Rate of somatic growth typically decreases as a fish approaches maximum age (Pitcher & Hart 1982). All fish are said to show indeterminate growth; that is, they continue to grow somatically over their entire lifespan (Pitcher & Hart 1982). It is generally understood that the extent to which a fish grows within a given season is regulated by a number of factors both biotic and abiotic (Townsend & Calow 1981).

A. FACTORS AFFECTING GROWTH

Food availability (Pitcher & Hart 1982), intra and interspecific competition (Reid 1961), the genetic potential for growth, the effect of parasites, and the plasticity in the allocation of energy into somatic or gonadal growth (Townsend & Calow 1981) are biotic factors that influence growth rates. Brody (1945) and Von Bertallanfy (1957) found that as fish increase in size their growth rate gradually decreases. Thus, the older a fish becomes, the lower its future growth potential (Gerking 1977). Typically, the faster a fish grows, the shorter is its lifespan (Muth 1969). The dominant abiotic factor controlling fish growth is temperature (Brett 1969, Fry 1971, Magnuson et al. 1979, Pitcher & Hart 1982) as it regulates metabolism directly (Sonina 1981).

Temperature

In most fish somatic and gonadal growth occur at maximum rates within specific thermal regimes that can extend over a range of temperatures for a given species (Fry 1968). However, at either end of the optimum range, growth rate decreases (Brett 1971). This phenomenon has been incorporated into the concept of "metabolic scope" in fish (Brett 1971, Magnuson et al. 1979). It states that at temperatures both above and below the thermal optima, food conversion by fish becomes less efficient. Generally, feeding, digestion, and growth rates increase as water temperature increases, but when optimum temperatures are surpassed, growth is again suppressed because so much energy is consumed just in feeding (Brett & Higgs 1970). In juvenile sockeye salmon (<u>Oncorhynchus</u> <u>nerka</u>), low water temperatures suppress rates of digestion, maximum meal size, conversion efficiency (Brett 1971) and hence growth. Thus, one can describe a "zone of efficiency" within the thermal tolerance range (thermal optimum at which maintainance ration is lowest, feeding rate and activity are greatest and hence, conversion efficiency and growth rates are highest) (Metabolic Scope Concept).

In north temperate lakes, fish species distribute themselves in the water column according to specific thermal niches. In the laboratory, Magnuson et al. (1979) found that most fish are not distributed homogeneously along a temperature gradient; each species has its own specific thermal requirements or preferences. For example, Brett (1971) found that young sockeye salmon frequent specific thermal regions of Babine Lake, B.C. when seasonal patterns of temperatures create strata within the lake, enabling these fish to choose their "zone of efficiency". Within the preferred stratum, growth occurs at a maximal rate (Brett 1971) if the optimum temperature is available.

North temperate freshwater fish are subjected to large changes in water temperature, resulting from seasonal climatic cycles, which in turn lead to species specific patterns in their growth and reproduction (Nikolsky 1963). In most north temperate freshwater fish, reproduction and growth occur between ice-out in spring and freeze-up in autumn (Bagenal & Tesch 1978, Pitcher and Hart 1982), being controlled within this period by many factors such as food availability, predation pressure, fish density and temperature changes. Pitcher & Hart (1982) have suggested that somatic growth, concentrated from ice-out to early summer, enables most fish to store sufficient nutrients which in turn, are mobilized during gonad growth later in the year. Hence, it is the seasonal cycling of water temperature and the timing of reproduction that dictates time of year when maximum growth occurs. For most north temperate fish this takes place during spring and summer, when water temperatures are optimal and growth rates are high.

Burbot, Lota lota, are a cold-adapted fish, prefering the coldest zones within lakes (Muth 1973, Hackney 1975), and conventional wisdom suggests they may survive better in water bodies where temperatures remain cold. Species coexisting with burbot such as yellow perch, Perca flavescens, walleye, Stizostedion vitreum, and northern pike, Esox lucius, are described as coolwater species, (Paetz & Nelson 1970, Scott and Crossman 1973), growing primarily when temperatures are warmer during the summer. Thus, the possibilility exists that the pattern of seasonal growth in burbot is different than that exhibited by other north temperate species of freshwater fish. Any differences in the timing of growth should be evident in the bony structures of these fish (Bagenal & Tesch 1978, Pitcher & Hart 1982).

B. FORMATION OF GROWTH ZONES ON BONY STRUCTURES

Seasonal cycling of water temperature is reflected in seasonal zonations or annual marks on bony structures of fish obtained from north temperate regions (Blacker 1974, Pitcher & Hart 1982). The use of these marks in assigning an age to fish is based on the premise that growth does not occur uniformly over the course of one year. Instead, a period of increased growth during spring/summer is followed by one of decreased growth (even cessation) during the autumn/winter months (Blacker 1974, Bagenal & Tesch 1978, Pitcher & Hart 1982, Brothers 1987). Bony structures most commonly used for ageing are scales, cleithra, fin sections and otoliths (Bagenal & Tesch 1978, Jearld 1983, Pitcher & Hart 1982).

Otoliths

Sagittae otoliths, the largest of three pairs of otoliths present in fish, are considered to be the best structures for use in determining the age of most fish, or alternately, for verifying the age obtained when using other bony structures (Blacker 1974, Bagenal & Tesch 1978). Although an element of confusion exists in assigning growth zones to the otolith (see Blacker 1974), it is generally agreed that two alternating growth zones (bands) make up one year's growth on the otolith of most north temperate freshwater (and marine) species (Irie 1960, Chilton & Beamish 1982). Yearly growth zones comprise a "winter" and a "summer" band. The "winter" band is hyaline or transluscent when viewed under transmitted light, and dark when viewed under reflected light. The "summer" band is light or opaque when viewed under reflected light, and dark when viewed under transmitted light (Trout 1954, Blacker 1974, Bagenal & Tesch 1978). This banding pattern is characteristic of fish from temperate climates which show well defined periods of growth during some part of the year. This is in contrast to fish that live in environments that have relatively constant temperatures; they normally do not produce annuli on their otoliths and other bony structures.

It is generally believed that consecutive wide, light (when viewed under reflected light) summer bands, and narrow, dark winter bands are laid down seasonally on the otoliths of north temperate freshwater fish (Trout 1954). This banding occurs in response to changing growth rates, reflecting changing water temperatures; usually increased amounts of food consumed during summer and decreased amounts or no feeding during winter. Burbot possess otoliths that are large and show a clear record of seasonal growth; as a consequence, they can be used to study seasonal growth in this species.

Chapter II of this thesis will address the question of when burbot grow maximally, the results being based on the condition of the otolith and the amount of material laid down seasonally. Additionally, to investigate the influence of the environment on the growth rates of burbot, I compared fish from two lakes of contrasting trophy. This was carried out in an attempt to generate hypotheses concerning what effect lake type may have on the growth of burbot.

C. REPRODUCTION AND FECUNDITY OF FISH

Fish, like all vertebrates, grow to a certain size before attaining sexual maturity (Love 1970). The relationship between the size of a fish (as the result of growth) and its reproductive potential is, for most species, a positive one (Blackett 1973). In fish, absolute fecundity is defined as the number of maturing eggs present in the ovary before spawning (Bagenal 1978, Mance 1986). This includes both maturing oocytes and shed ova because the majority of fish are "batch spawners" (Mance 1986), that is, the ovaries contain batches of oocytes developing asynchronously. Spawning time is species specific, being stimulated proximally by environmental cues that ensure ultimately the hatching of young when environmental conditions are most favorable for their survival (Bone & Marshall 1982).

D. FACTORS CONTROLLING FECUNDITY IN FISH

Body size

Generally, fecundity of fish increases with increased length and weight (May 1967, Love 1970, Bagenal 1978), fecundity being most often a cubic function of length. Once a certain length has been reached, factors associated with the onset of senescence can reduce the number of eggs produced annually (Mance 1986). Characteristically, fecundity is a positive correlate of body weight (Blackett 1973, Ikusemiju et al. 1983). In Eurasian perch (*Perca fluviatilis*), however, the number of eggs per unit somatic weight was inversely related to body length (shorter fish had more eggs per unit body weight than longer fish) (Craig 1974). Bagenal (1978), however, suggested the best predictor of fecundity is total length.

Age

The relationship between age and fecundity in north temperate fishes is highly variable (Gerking 1959, Mance 1986), hence age is the least reliable predictor of fecundity (Mance 1986). The variation in the number of eggs produced by fish within a given age class can be large, as body size in any age class can be highly variable.

Environmental factors

A decrease in fecundity has been associated with poor food quality (Leggett and Power 1969), a function of either reduced primary productivity and/or an increase in intraspecific competition through high population density. Studies of the fecundity of brown trout, Salmo trutta, from productive and unproductive streams suggest that despite differences in ovary weight, fecundity was constant; trout from productive streams simply produced larger eggs (McFadden et al. 1965). In contrast, Stauffer (1976) found that coho salmon, Oncorhynchus kisutch, from a productive lake produced fewer but larger eggs than those from an unproductive lake.

The effect of temperature on fecundity appears to be indirect. Wooton (1979) suggested that fecundity and spawning activity, like growth, are maximized at some species-specific thermal optimum. The time at which ovaries are sampled relative to the time of spawning can also contribute to variation in the number of oocytes counted. In populations of yellow perch from Alberta, Mance (1986) found significant decreases in fecundity over short time periods, probably resulting from the atresia of oocytes.

Of the gadids, the north sea cod, _Gadus morhua_, has been investigated extensively as the result of its economic importance. Oosthuizen and Daan (1974) review much of this literature; it appears that cod are highly fecund, relative to other fish. Fecundity in marine cod is directly related to fish size (Ooshuizen and Daan 1974); as cod become larger, they produce more eggs.

As burbot spawn in mid to late winter, under the ice, their reproductive biology is poorly understood (Clemens 1951b, Muth 1973, Hackney 1975). The literature on burbot fecundity indicates that the relationship between egg numbers and female body size is unclear (Muth 1973). Burbot, like the majority of gadids, are highly fecund, often producing more than 1 million eggs per female (Muth 1973). The possibility of a relationship between lake productivity and fecundity of burbot has never been investigated. In chapter III, I address the effect of lake productivity on fecundity by considering the relationship between body size variables and fecundity of burbot from two lakes of contrasting trophic condition in central Alberta. The information obtained from this portion of the study will aid in the formation of hypotheses concerning fecundity in this species.

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II. THE PATTERN OF GROWTH IN BURBOT (*Lota lota*) FROM CENTRAL ALBERTA

A. INTRODUCTION

The burbot (*Lota lota*) is the only true freshwater cod (Gadidae) (Paetz & Nelson 1970, Scott & Crossman 1973, Hackney 1973). It has a holarctic distribution (Svetivodov 1948, Scott & Crossman 1973), and appears to be a cold-adapted species (Muth 1973) restricted to the arctic and north temperate regions (Scott & Crossman 1973) and, during summer, to the colder regions of lakes and streams (Muth 1973, Christie & Regier 1988). By contrast, a number of coexisting species, such as yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and white sucker (*Catostomus commersoni*), are cool water north temperate species, which frequent the warmer regions of lakes. These latter species grow primarily during the warmest part of the year (summer) (Bagenal & Tesch 1978, Tanasichuk 1979, Diana & Mackay 1979).

Published information on burbot is meagre, although a few studies have dealt with the life history and population dynamics of this fish in eastern North America (Van Oosten & Deason 1938, Bjorn 1940, Clemens 1951a & b, Hewson 1955, Robins & Deubler 1955, Chen 1969, Hackney 1970, Bailey 1972, Muth 1973, Magnin & Fradette 1977). Apart from an intensive study of Alaskan burbot (Chen 1969), northern and western populations of this species have received little attention. These few studies raise a number of questions about the timing and magnitude of growth in this species.

Clemens (1951b) suggested that, unlike most north temperate freshwater fish, burbot grow more in winter than in summer. This suggestion was based on the timing of appearance of dark (decreased growth rate) and light (increased growth rate) bands on the margins of individual otoliths. In most north temperate fish such as pike, a wide, light band represents summer growth, and a narrow, dark band represents winter growth (Trout 1954, Blacker 1974) when viewed under reflected light. The relative widths of the dark and light bands vary within a given otolith in the majority of burbot otoliths studied to date, yet no explanation for this phenomenon exists in the literature. Bailey (1972) reported burbot otoliths having bands of equal width which led him to argue that growth in the population he studied (Lake Simcoe, Ontario) may not cease during winter.

Clemens (1951b) reported a narrow, dark band on the margin of otoliths of burbot collected from April through December in Lake Erie (post spawning). Hackney (1973) reported dark bands present from July to the end of August in Lake Opeongo, Ontario. Conversely, dark bands have been reported on the margins of burbot otoliths collected between December and May and light bands between June and November in Algonquin Park, Ontario (Martin 1941), in Lake Superior (Bailey 1972), in Quebec rivers and lakes (Magnin & Fradette 1977), and June to March in Alaska (Chen 1969).

If Clemens (1951b) and Hackney (1973) are correct, the wide, light band would be formed during winter, suggesting that burbot grow more in winter than in summer. Muller (1960) found light coloured bands around the margins of otoliths in winter, and dark zones during summer in burbot from the Elbe and Olde rivers, supporting this argument. Growth of the otolith takes place around its margins (Blacker 1974), and fastest growth can be observed at the otolith's points (Chilton & Beamish 1982).

Wiggs (1968) found that certain thyroid hormones showed higher activity in adult burbot from Lac Ste. Anne, Alberta, during winter than during summer. Clemens (1951a) and Nikolsk'ii (1954) suggested that burbot may feed more during winter than summer. This was based on the relatively fewer empty stomachs collected during winter than during summer. Muth (1973) found a similar situation in Lake-of-the-Woods, Minnesota. Clemens (1951a), however, cautioned that these observations could be the result of lower digestion rates during winter than summer. Despite the latter comment, the possibility still exists that burbot may grow more in winter than in summer.

The question addressed in this chapter is: can a cold adapted freshwater vertebrate, specifically burbot, grow more during winter, when water temperatures are low, than in summer, when water temperatures are higher? I have stated this question in the form of a null hypothesis which I propose to test with a data set composed of band widths measured on otoliths. The null hypothesis is as follows: Incremental growth on the otolith (representative of growth in the fish) in winter (ice-covered) is equivalent to that in summer (open water) in burbot from central Alberta. Additionally, I will include a comparison of growth between two lakes which differ in thermal regimes and productivity.

B. MATERIALS AND METHODS

Description of study site:

Adult burbot were collected from Lac Ste. Anne ($53^{\circ}43'$ N, $114^{\circ}24'$ W) and Cold Lake ($54^{\circ}35'$ N, $110^{\circ}18'$ W), Alberta, both of which lie in the southern boreal forest region. Nevertheless, they have different physical and trophic characteristics: Cold Lake is a relatively deep oligo/mesotrophic lake, whereas Lac Ste. Anne is a relatively shallow, eutrophic lake (Fig. 1 and Table 1). Both lakes contain large populations of burbot, permitting a comparison between a deep and shallow-lake population. Fish species composition in Cold lake is about double that found in Lac Ste. Anne; larger species found in the former but not in the latter are lake trout (Salvelinus namaycush) and cisco (Coregonus artedii).

Collecting Burbot

Adult burbot were collected from commercial catches taken in Lac Ste. Anne and Cold Lake, mainly during March

Figure 1. Maps of Cold Lake and Lac Ste. Anne, Alberta showing the extent of the littoral zone (< 3m in Lac Ste. Anne, < 5m in Cold Lake: cross-hatched area; based on maximum depth of rooted vegetation.), as well as sampling sites in each lake.

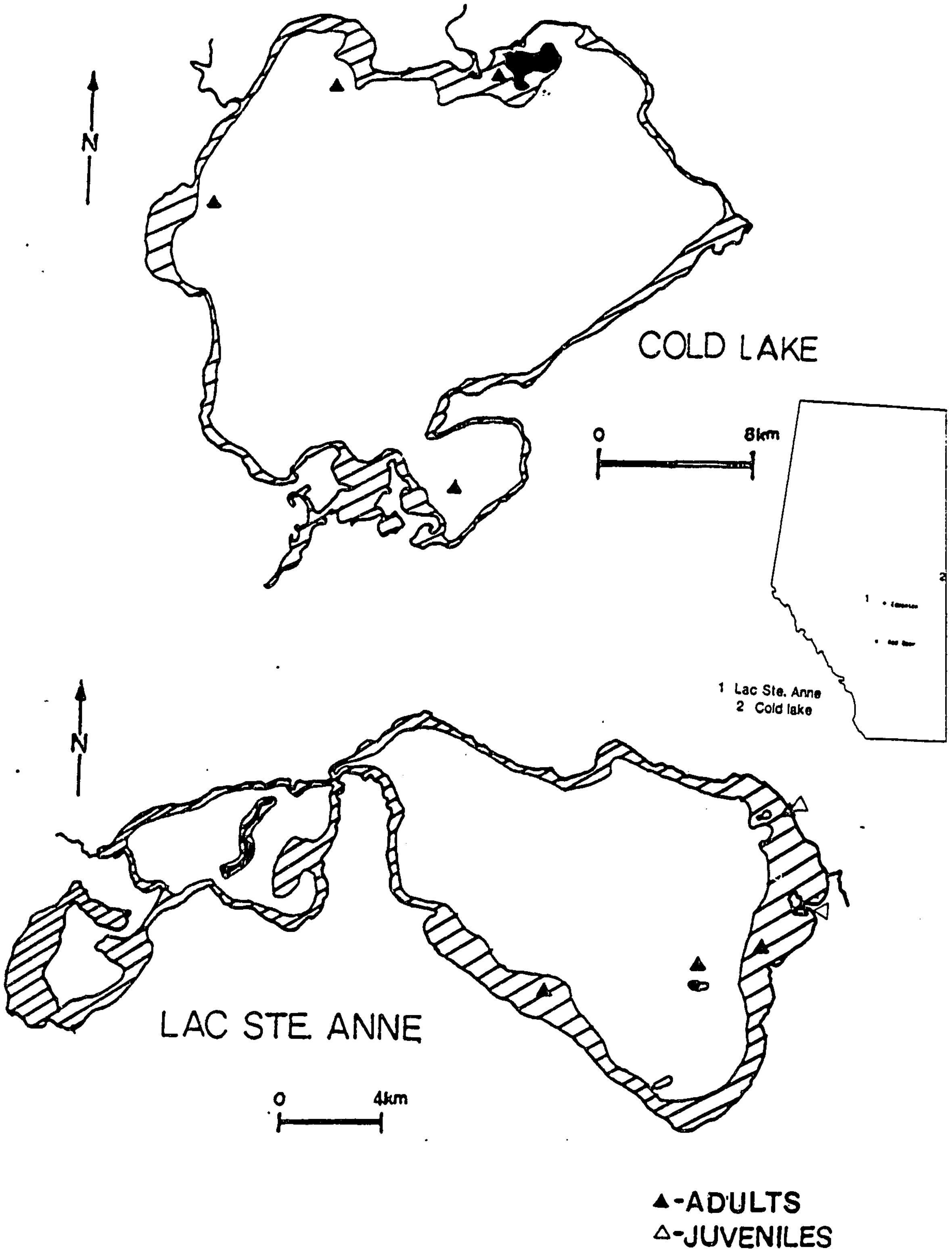

N
COLD LAKE
0
8km
2
1
1 Lac Ste. Anne
2 Cold lake
N
LAC STE. ANNE
0
4km
▲-ADULTS
△-JUVENILES

Table 1: Selected characteristics of Lac Ste. Anne and Cold Lake (*), Alberta.

	Lac Ste. Anne	Cold Lake
Surface area (Km^2)	57.0	372.9
Mean depth (m)	4.8	49.8
Maximum depth (m)	9.0	99.1
% Littoral Area	30.0	7.0
Mean chlorophyll a (ul/L)	30.0	3.2
Mean August temp.(°C) -@ 3m -	20.0	14.0

* Data supplied by Alberta Environment (Atlas of Alberta Lakes)

1987 and 1988 (Appendix 1). These samples were supplemented with fish collected by angling through the ice using artificial lures, particularly at Lac Ste. Anne. Once collected, burbot were frozen and analysis took place later. Analysis of fish involved thawing them, measuring total length (distance from tip of snout to tip of tail), determining sex, recording the weights of liver, gonad, and total body, and retrieving the otoliths.

Juvenile burbot were collected at monthly intervals during the summer from under rocks and floating filamentous algal mats along the margins of Lac Ste. Anne. Fish were captured by hand using a small aquarium dipnet or with a backpack electrofisher (Smith Root, Vancouver, Washington). Individual juveniles were weighed to the nearest 0.1 g, total length was measured to the nearest mm, and their otoliths were removed and saved.

Otolith Preparation:

Sagittae otoliths (the largest pair of three pairs of otoliths present in each inner ear of a fish) were removed from burbot by making an incision in a cross-sectional plane behind the operculum. The section was continued medially across the top of the skull using tin cutters, exposing the otoliths in the sacculi located on each side of the midbrain. The otoliths were retrieved with a pair of forceps. They were rubbed between thumb and forefinger to remove blood and attached membranes, then rinsed with cold water. Once cleaned, otoliths were stored in a 50% glycerine solution in labelled plastic vials (Lawler 1963) or dried in scale envelopes (Wiggs 1968, Magnin & Fradette 1977).

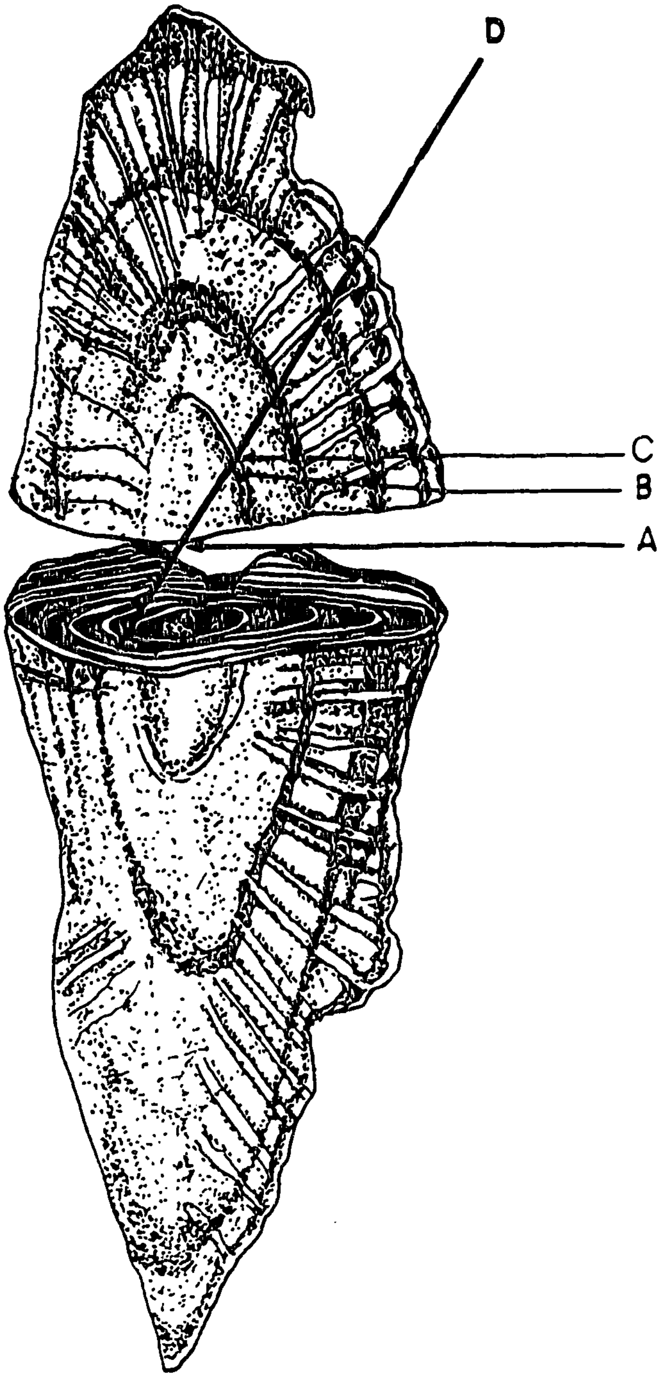
Determining the age of burbot:

The age of a burbot was determined from sectioned (Martin 1941), stained and toasted otoliths (Chilton & Beamish 1982, Brothers 1987) using the following preparation:

Each otolith was held sulcal side up in a pair of forceps such that the origin of the otolith was placed against the edge of the forceps, the longitudinal axis being at right angles to the forceps (Fig. 2). The otolith was then broken in half by applying downwards pressure with thumb and forefinger so that the otolith broke along the margin of the forceps. This accomplished, the broken surface was dipped in water and smoothed using a coarse whetstone. Care was taken not to press too hard as the otoliths broke under too much pressure. An Arkansas stone (fine whetstone) was used to polish the smoothed surface. Again the smoothed surface was dipped in water before being polished.

Once polished, a drop of cedar wood oil was placed onto the polished surface and then this surface was toasted over a Bunsen burner until brown/grey in colour. Cedar wood oil soaks into the polished surface and when toasted, stains black the portion of each annulus containing the greatest concentration of organic material (protein) (Chilton & Beamish 1982, Brothers 1987). The cedar wood oil, added to

Figure 2. Whole gadid otolith (from a hake) showing axis along which seasonal growth was measured (D) (Redrawn from Chilton & Beamish 1982). AB="summer" growth, BC="winter" growth.


D
C
B
A

the otolith surface before toasting, makes the annuli more obvious. Care was taken when toasting the otoliths as it was easy to burn them, causing them to crack and crumble. When cooled, another drop of cedar wood oil was placed on the toasted surface before the section of otolith was mounted on a block of styrofoam (1 cm^3) and viewed through a binocular dissecting microscope (X25). Reflected light was oriented at an angle of 30° to the polished surface of the otolith. Age was determined by counting the number of stained annuli present across the narrowest (slowest growing) portion of the otolith. This part of an otolith gives the most accurate age because it lacks false annuli, present on the wider portions of the otolith, which can confound attempts to assign ages to individuals.

I compared the ages assigned to burbot using toasted otolith cross-sections with those assigned by counting annuli on whole otoliths, and those obtained from annuli on subopercular and opercular bones. To do this, each bony structure was independently assigned an age twice. To avoid any bias, the assignment of age was done blindly by putting 50 numbered scale envelopes containing otoliths, opercular and sub-opercular bones from 50 burbot into a plastic bag. The envelopes were shuffled and removed one at a time without knowledge of which individual the envelope represented: an age was then assigned to each structure. Appendix 3 presents the distribution of ages obtained in the comparison of techniques and the results of the X^2 analysis on the three distributions. There was no significant difference in the distribution of ages obtained (X^2, $P>0.05$).

Validation of Ageing

Otoliths were removed, sectioned, and toasted from burbot of known age (1-year-old), and the location of the annulus noted. Sectioned otoliths from adult fish were compared to those of the 1-year-olds. The annulus closest to the origin in an adult burbot and of similar diameter in cross-section to that of a 1-year-old was considered representative of the first annulus (age 1 year).

Determining Seasonal Growth in Burbot:

To determine the timing and magnitude of growth in juvenile burbot, their total lengths were compared to the diameter of their otoliths over the course of one year. Upon their removal, the colour of the margin of the otolith was noted, and the width of each band on the otolith was measured to the nearest micrometer. The relationship between the colour of the otolith margin and date was used to determine the timing of deposition of each band in burbot. Having done this, deposition of material on the otolith could be related to growth in total length; otolith radius versus length-at-capture.

Measuring otoliths:

An ocular micrometer, calibrated to the nearest 0.01 mm in a binocular dissecting microscope, was used to measure the dimensions of otoliths. Figure 2 illustrates the dimensions recorded on both whole and sectioned otoliths. These dimensions included the axis of measurement - measured from the center of the origin to the outer edge of the otolith at its widest point when viewed across the whole otolith surface (D - Fig. 2). Seasonal growth is shown by measurements: AB (summer), BC (winter), and A + B (annual) (Fig. 2).

Validation of measurements:

Before comparing growth patterns in burbot between lakes, I determined the variation in growth patterns within a single population. This was done by plotting otolith radius against total length to determine the extent to which variation in the former explained variation in the latter (r^2 value). Thirty individuals were selected randomly from each sampling date and their otolith radii measured. Figure 9A shows the relationship ($r^2 = 0.96$) based on nontransformed data. Given that the relationship of total length to otolith radius is highly correlated, one would expect an accurate prediction of total length-at-annulus formation, based only on measurements of otoliths. If total length-at-annulus formation is not significantly different from known length-at-capture, seasonal growth based on the width of "summer" and "winter" bands should also show a strong correlation with fish total length.

To test band widths as predictors of seasonal growth, young-of-the-year burbot from Lac Ste. Anne were collected from April to November and their growth recorded over a period of one year. Young burbot have large otoliths with one to three clearly distinct seasonal bands that are easily seen and measured using an ocular micrometer in a dissecting microscope. Incremental changes in otolith radius were plotted against incremental changes in total length. The colour of the marginal band on each otolith was noted and related to time of capture.

In order to estimate of the proportion of total annual growth occurring in winter and in summer, otoliths from 30 burbot age 6 and younger were selected randomly from Lac Ste. Anne fish. The fish were of the following ages: 6 (n = 5), 5 (n = 11), 4 (n = 21), 3 (n = 27), 2 (n = 30), 1 (n = 30), and zero years (n = 30). The width of light and dark bands on each of the 30 otoliths was measured and expressed as a proportion of the total width of summer plus winter band (Fig. 2).

Statistical Analyses

To determine whether juvenile burbot grow significantly during winter, a t-test comparing mean length and weight at freeze-up with that at ice-out for the same cohort of fish was carried out. Regression analysis of otolith radius versus time and otolith radius versus total length was carried out on juvenile burbot in order to determine how strong the correlation was between otolith growth and fish growth. Seasonal band width measurements obtained from otoliths were described as a percentage of the total annual deposition on the otolith. Regression analyses of weight, length, and condition versus age of fish from Cold Lake and Lac Ste. Anne were undertaken to determine to what extent growth within lakes differed. Analyses of covariance were used to compare the two populations.

The size distribution of burbot caught by angling was compared with that of netted fish (Table 2), using a X^2 test to determine whether the method of capture was unbiased. Commercial mesh size was the same in both lakes fished: 13.3 cm stretched mesh.

C. RESULTS:

Approximately 250 adult burbot were collected from Lac Ste. Anne and 110 from Cold Lake, Alberta, during the winters of 1986/87 and 1987/88. Appendix I lists capture dates, location, and method of capture of burbot examined in this study. The sampling sites on each lake are shown in Figure 1. Approximately 300 young-of-the-year and 100 1-year-old burbot were collected from rocky, cobble sites (riprap) along the margins of Lac Ste. Anne over the open water season (May - November) of 1987 and April 1988. Angling appears to select for longer burbot (Table 2), as the two size distributions are significantly different ($X^2 = 18.672$, $P<0.05$).

Table 2: Length frequency distributions of angled and gill netted burbot from Lac Ste. Anne, Alberta. Fish caught by angling were significantly longer than those caught by gill net ($X^2=18.8$, $P<0.05$).

Total length interval (mm)	Gill net	Angled
< 520	10	8
521 - 540	7	7
541 - 560	15	12
561 - 580	29	11
581 - 600	20	16
601 - 620	15	15
621 - 640	12	12
641 - 660	9	15
> 661	11	28
	n = 128	n = 124

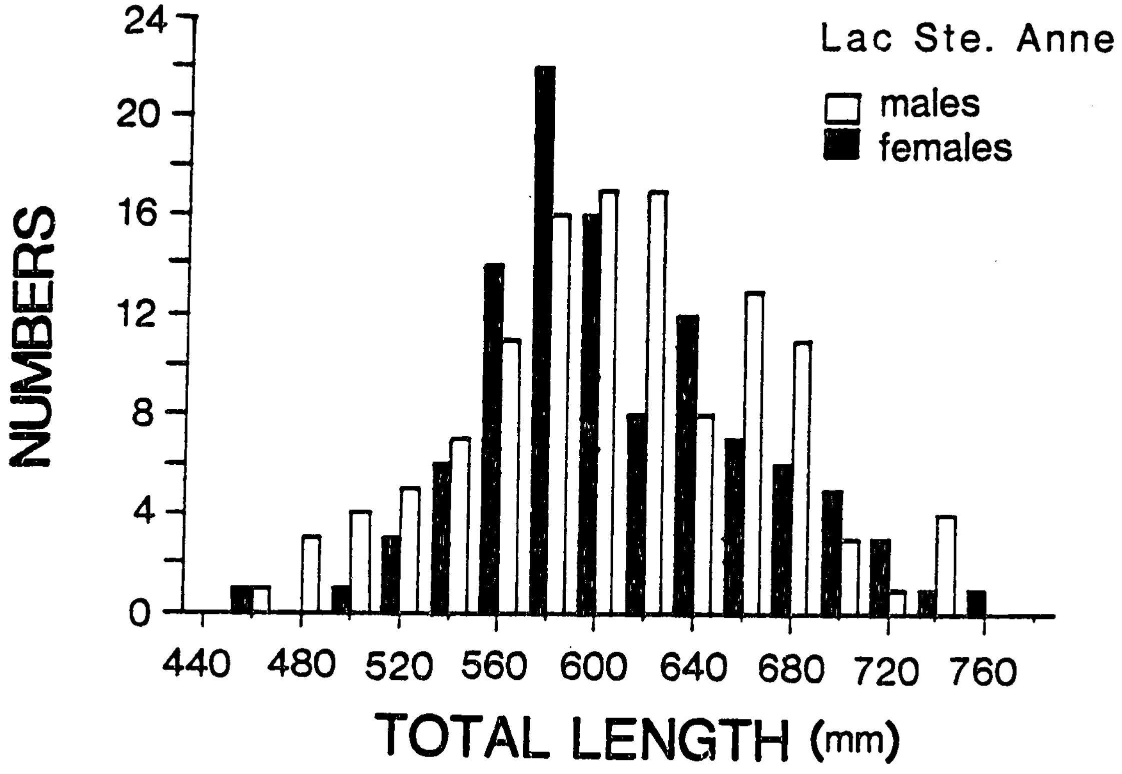
Size Distributions - Adults:

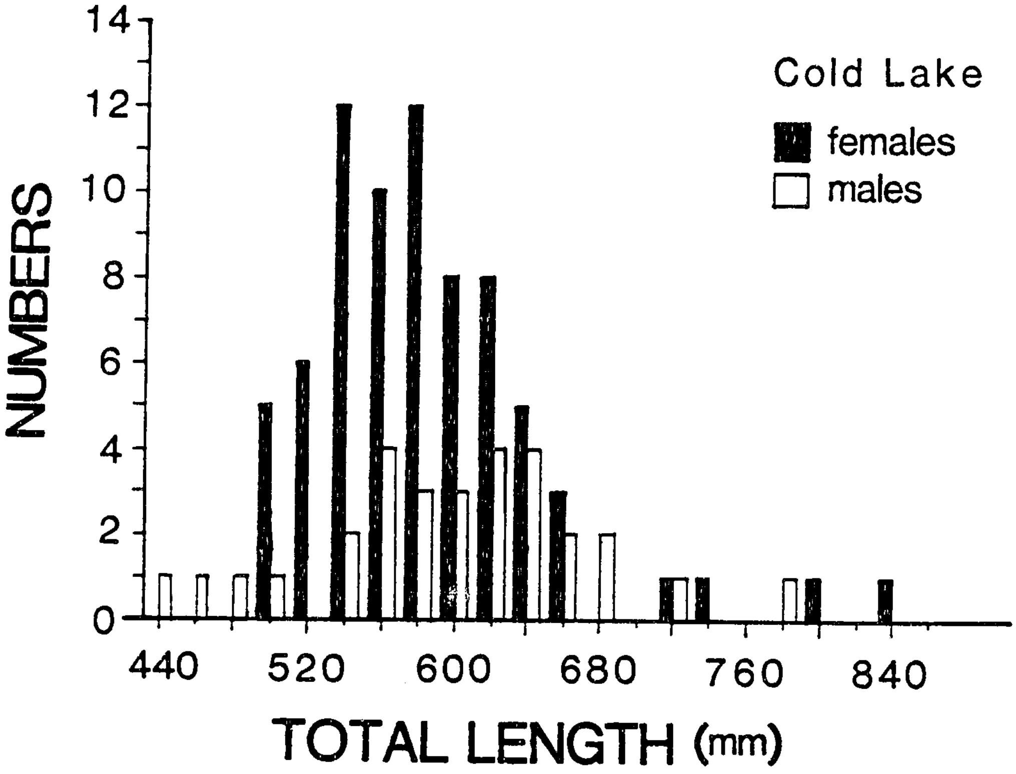
Figure 3 shows the size frequency distributions of male and female adult burbot in samples taken from the populations in Cold Lake and Lac Ste. Anne subject to some exploitation by fishing. Males and females did not differ significantly within lakes in average length (ANOVA, $P>0.05$: Lac Ste. Anne: males - x = 598.7 mm, S.D. = 60.7 mm, females - x = 599.1 mm, S.D. = 55.7 mm; Cold Lake: males - x = 587.0 mm, S.D. = 82.2 mm, females - x = 573.9 mm, S.D. = 61.6 mm). However, burbot in Lac Ste. Anne were significantly longer than those in Cold lake (ANOVA, $P<0.05$) (Fig. 3).

The length-weight regressions for each population studied are shown in Figure 4. As the sexes did not differ significantly in length within lakes, the data for both sexes were combined for further analyses. The relationship between length and weight was significant in both Cold Lake (r^2 = 0.69) and Lac Ste. Anne (r^2 = 0.45) (Fig. 4). Female burbot from Lac Ste. Anne were significantly heavier than males (ANOVA, $P<0.001$); however, no significant difference was found in weight between males and females in Cold Lake (ANOVA, $P>0.05$).

There appeared to be a weak relationship between age and total length (slope significantly different from 0, $P<0.001$) but no relationship between age and total weight in either population (Fig. 5). Condition (a measure of the relative "fatness" of an individual at the time of sampling) can be

Figure 3. Size frequency histograms for each sex of adult burbot collected from Cold Lake and Lac Ste. Anne, Alberta.


Lac Ste. Anne
☐ males
■ females
NUMBERS
0
4
8
12
16
20
24
440
480
520
560
600
640
680
720
760
TOTAL LENGTH (mm)


Cold Lake
■ females
☐ males
NUMBERS
0
2
4
6
8
10
12
14
440
520
600
680
760
840
TOTAL LENGTH (mm)

<u>Figure 4</u>. Length weight scatterplots of sampled adult burbot from Lac Ste. Anne and Cold Lake, Alberta.

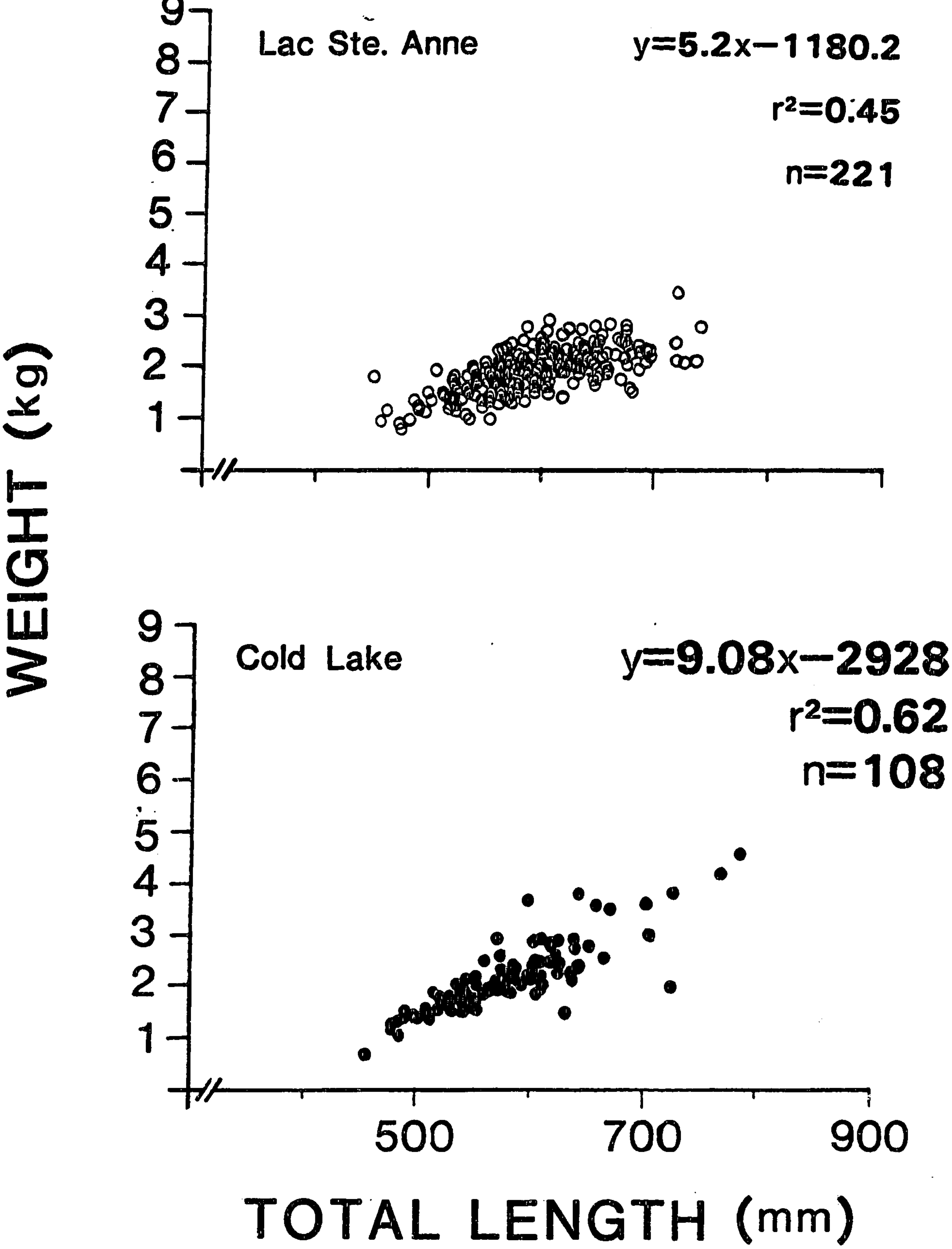
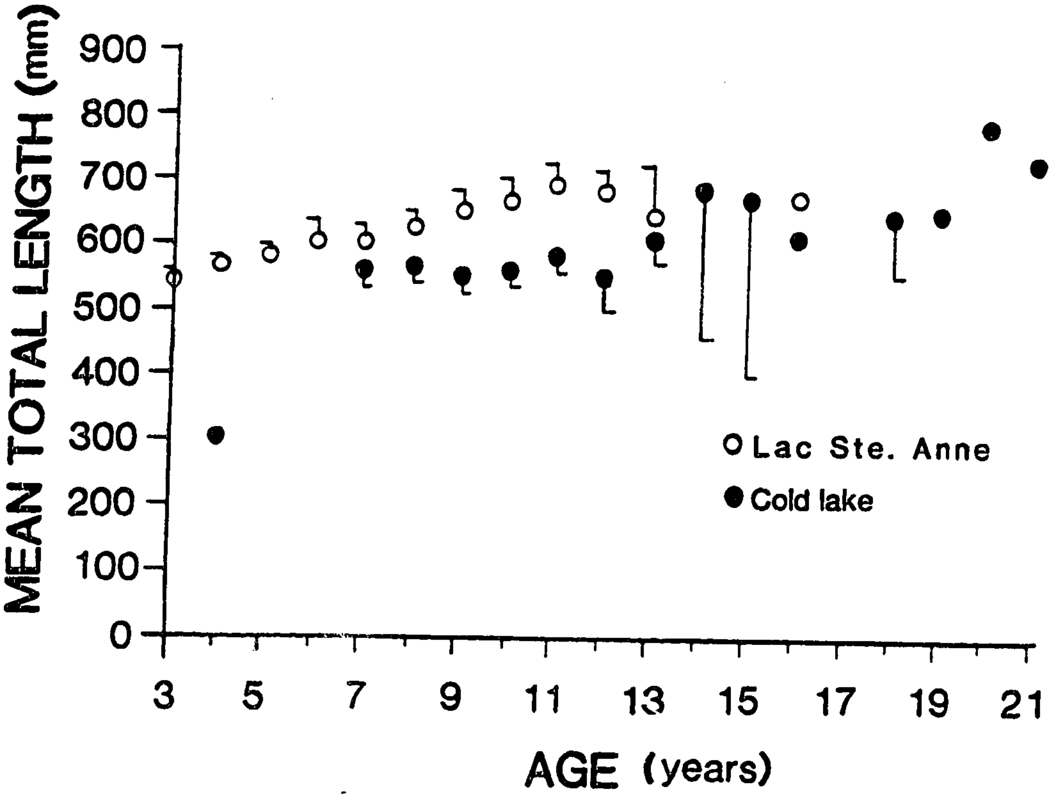
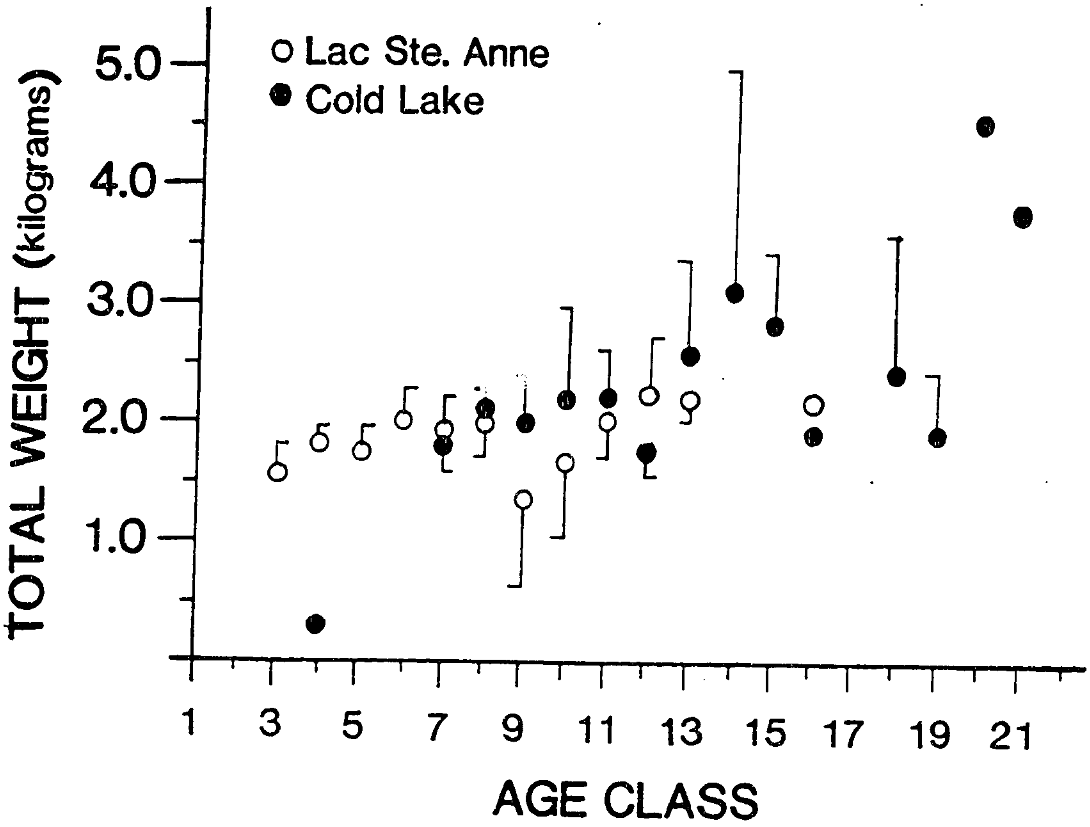

Lac Ste. Anne
y=5.2x−1180.2
r²=0.45
n=221
Cold Lake
y=9.08x−2928
r²=0.62
n=108
WEIGHT (kg)
1
2
3
4
5
6
7
8
9
500
700
900
TOTAL LENGTH (mm)

Figure 5. Relationship between mean total length and mean weight (+/- 95% Confidence Intervals) for adult burbot sampled from Lac Ste. Anne and Cold Lake, Alberta.


MEAN TOTAL LENGTH (mm)
900
800
700
600
500
400
300
200
100
0
3
5
7
9
11
13
15
17
19
21
AGE (years)
○ Lac Ste. Anne
● Cold lake


TOTAL WEIGHT (kilograms)
5.0
4.0
3.0
2.0
1.0
1
3
5
7
9
11
13
15
17
19
21
AGE CLASS
○ Lac Ste. Anne
● Cold Lake

represented by an index (total weight (g)/ (total length cm)^3). A comparison of these values for fish from Lac Ste. Anne and from Cold Lake showed a significant difference (ANCOVA, $P<0.05$) (Fig. 6). Cold Lake fish were "fatter" at age 7 and older (Fig. 6). Even though fish from Lac Ste. Anne grow faster in length than fish from Cold Lake, they were not heavier because of the difference in condition factor.

Based on the sampled fish, burbot apparently live longer in Cold Lake than in Lac Ste. Anne (Table 3). Thus, burbot in Lac Ste. Anne appear to grow faster, to live shorter lives, and to be in poorer condition in weight at most ages than their counterparts in Cold Lake.

Size Distributions - Juveniles:

Juvenile burbot rapidly colonized rip-rap sites from which they had been previously removed by sampling. These sites consisted primarily of rock and larger cobble piles located along the shore at Lac Ste. Anne. Juvenile burbot were not observed moving during daylight, therefore, it is assumed that movement along shore margins is primarily nocturnal. The highest concentration of juvenile burbot was found at the land/water interface, where individuals would hide under rip-rap, larger cobbles, and boulders. Individuals were often found deep within rip-rap sites, having swum "inland" distances of 15 cm or more from the contact of water with the shoreline. One-year-old burbot

Figure 6. Relationship between an index of condition (Total weight (g)/total length (cm^3) and age for sample of burbot collected from Lac Ste. Anne and Cold Lake, Alberta. Wide confidence intervals (95%) arise from sample size of 5 or fewer individuals.

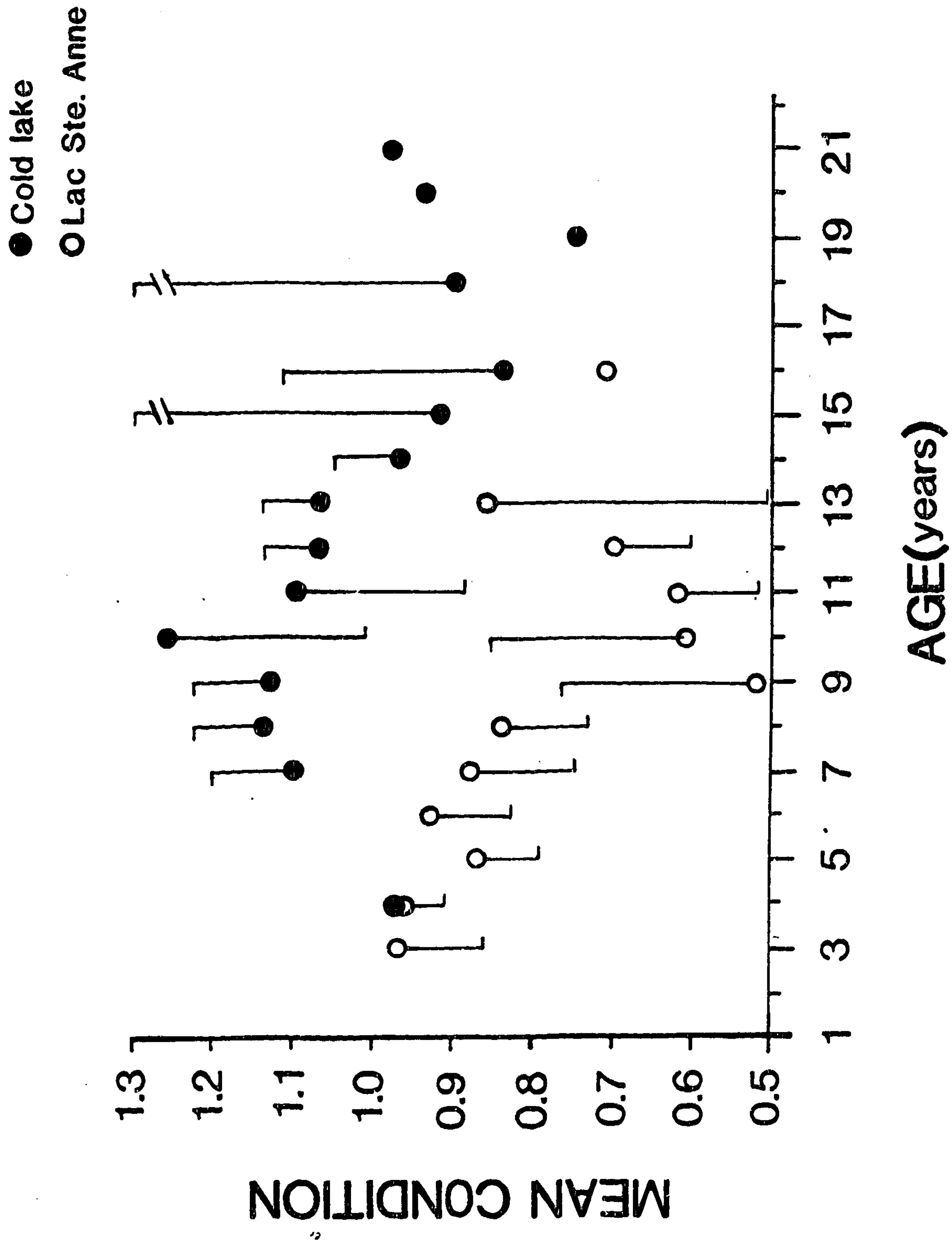

● Cold lake
○ Lac Ste. Anne
MEAN CONDITION
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
1
3
5
7
9
11
13
15
17
19
21
AGE(years)

Table 3: Frequency distribution of ages of burbot sampled from Lac Ste. Anne and Cold Lake, Alberta.*

Age class	Lac Ste. Anne	Cold Lake
3	40	0
4	53	1
5	33	0
6	25	0
7	24	13
8	23	19
9	14	15
10	10	11
11	10	17
12	9	4
13	4	16
14	0	3
15	0	2
16	1	1
17	0	0
18	0	3
19	0	2
20	0	1
21	0	1

* Frequency distribution of ages are significantly different: $X^2=126.3$, df=7, $P<0.001$.

captured along the shoreline of Lac Ste. Anne show were significantly longer (12.1%) at ice-out in April than they had been as young-of-the-year at freeze-up in mid-November (t-test, t = 2.484, 106df, P<0.01) (Fig. 7). Weight frequency distributions followed the same trend (t-test, t = 3.968, 106df, P<0.01) (Fig. 8); 1-year-old burbot were 36.7% heavier at ice-out in April than they had been at freeze-up the preceding November (Fig. 8).

Total length and weight within age cohorts of juvenile burbot was highly variable; differences of up to 40mm were recorded within a given age cohort at a given time of sampling (Fig. 7 and 8). Over the course of 8 sampling dates, standard deviations of individual age class means of total length and total weight ranged from 7.5% to 13.7% for the former and 10.1% to 42.9% for the latter.

Otolith/Body Size Relationships in Juveniles

In order to estimate seasonal growth in burbot from changes in the width of marginal bands on the otolith, it was imperative to show that growth in length was also reflected in growth of the otolith. Figure 9A illustrates the relationship between body length and otolith radius. There was a strong statistically significant (r^2=0.96, P<0.001) relationship between the length of juvenile burbot and the radius of their sagittae otoliths. Figure 9B illustrates the change in otolith radius over time (months). Growth of the otolith slowed during the winter; nevertheless,

Figure 7. Length frequency histograms for young-of-the-year (0+) and 1-year-old (1+) burbot sampled at various times over the season of open water in Lac Ste. Anne, Alberta. Arrows represent mean, scale for frequency is on Fig. 8. Numbers in each sample are listed in parentheses.

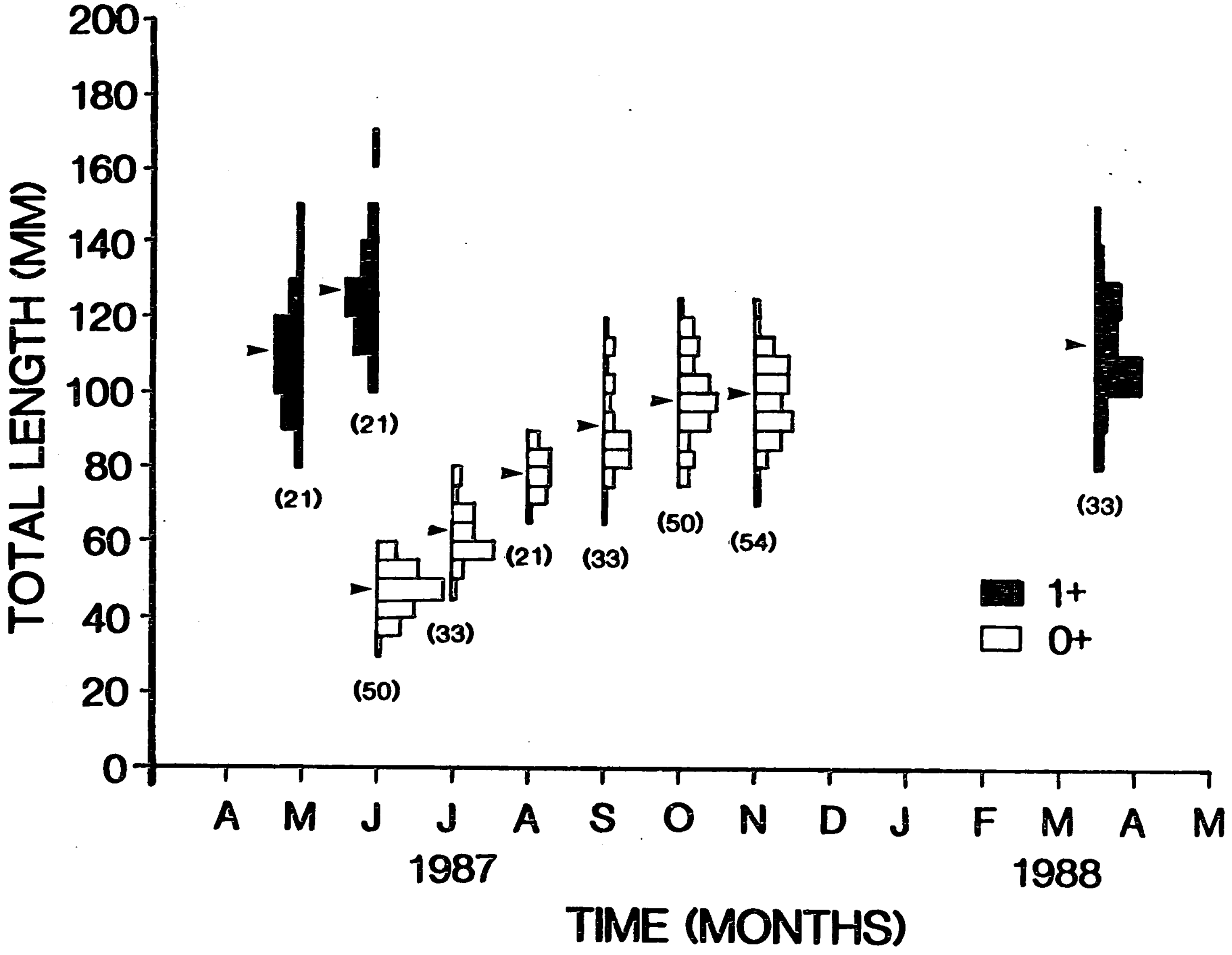

TOTAL LENGTH (MM)
0
20
40
60
80
100
120
140
160
180
200
(21)
(21)
(50)
(33)
(21)
(33)
(50)
(54)
(33)
1+
0+
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1987
1988
TIME (MONTHS)

Figure 8. Weight frequency histogram for young-of-the-year (0+) and 1-year-old (1+) burbot sampled at various times throughout the open water season in Lac Ste. Anne, Alberta. Arrows represent means. Numbers in each sample are listed above the frequency distributions.

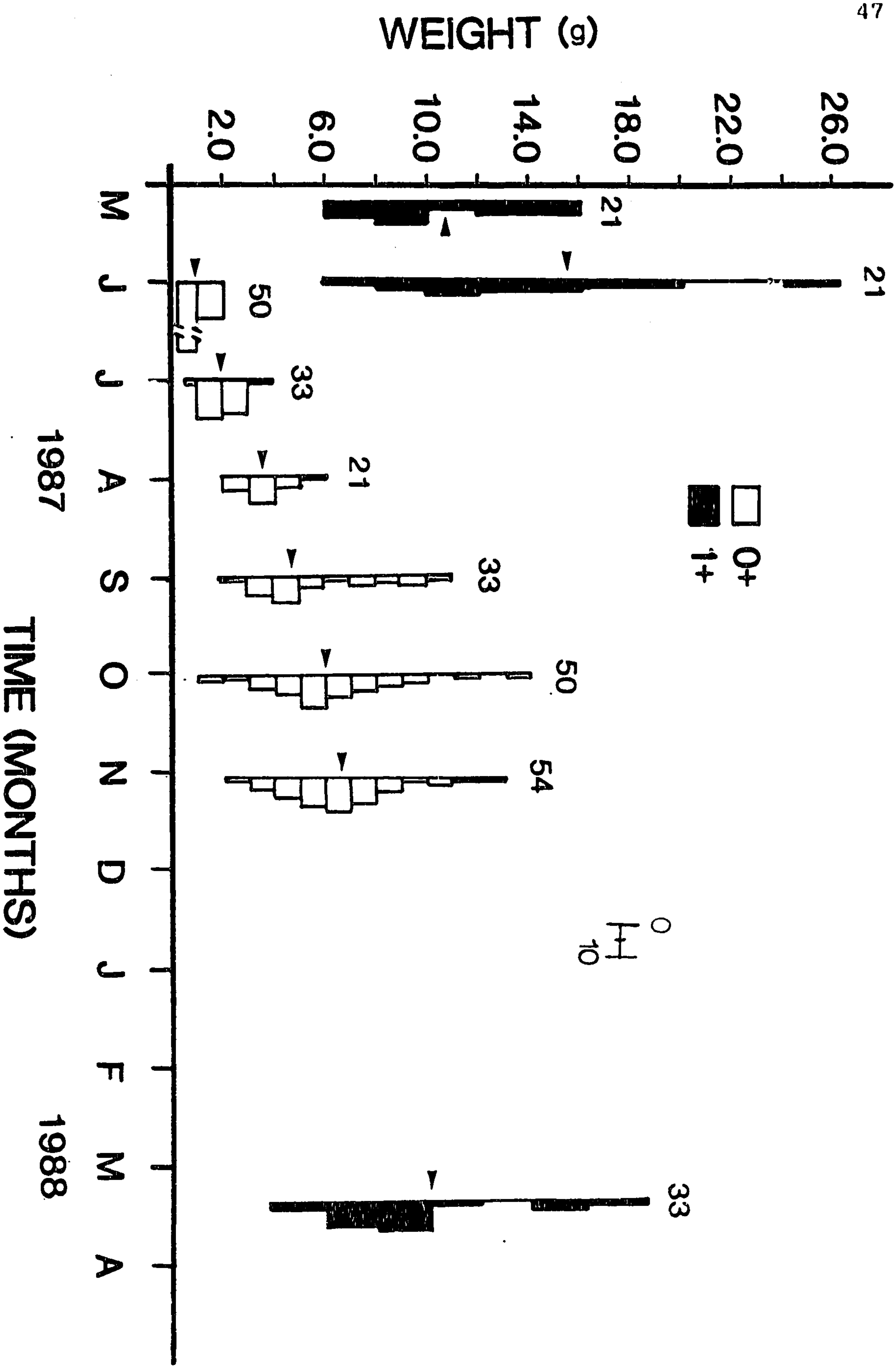
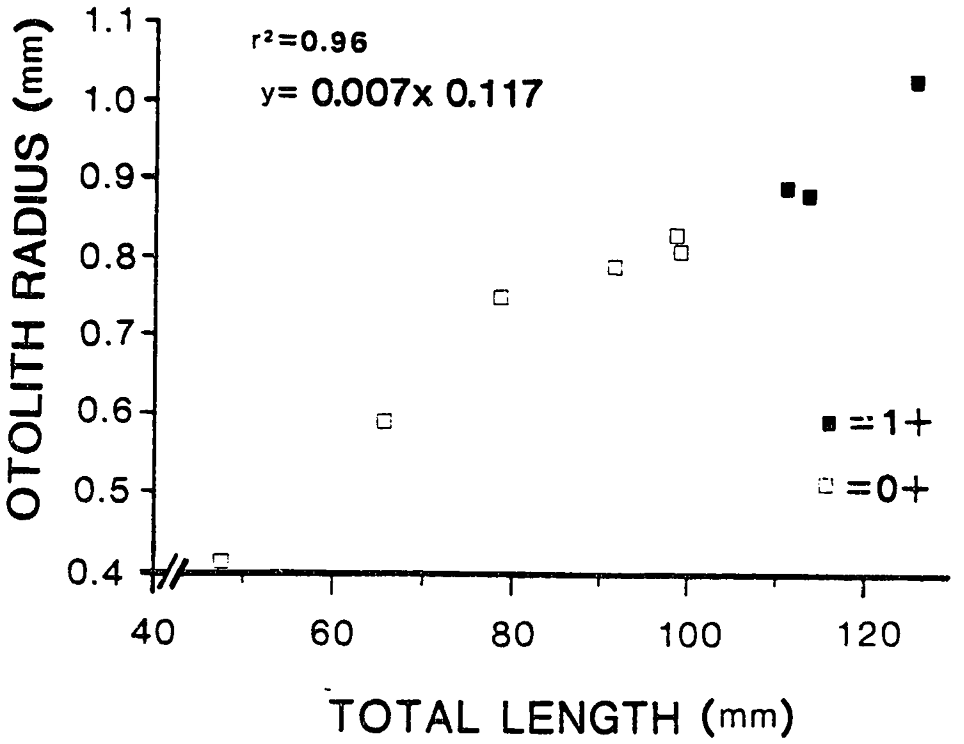
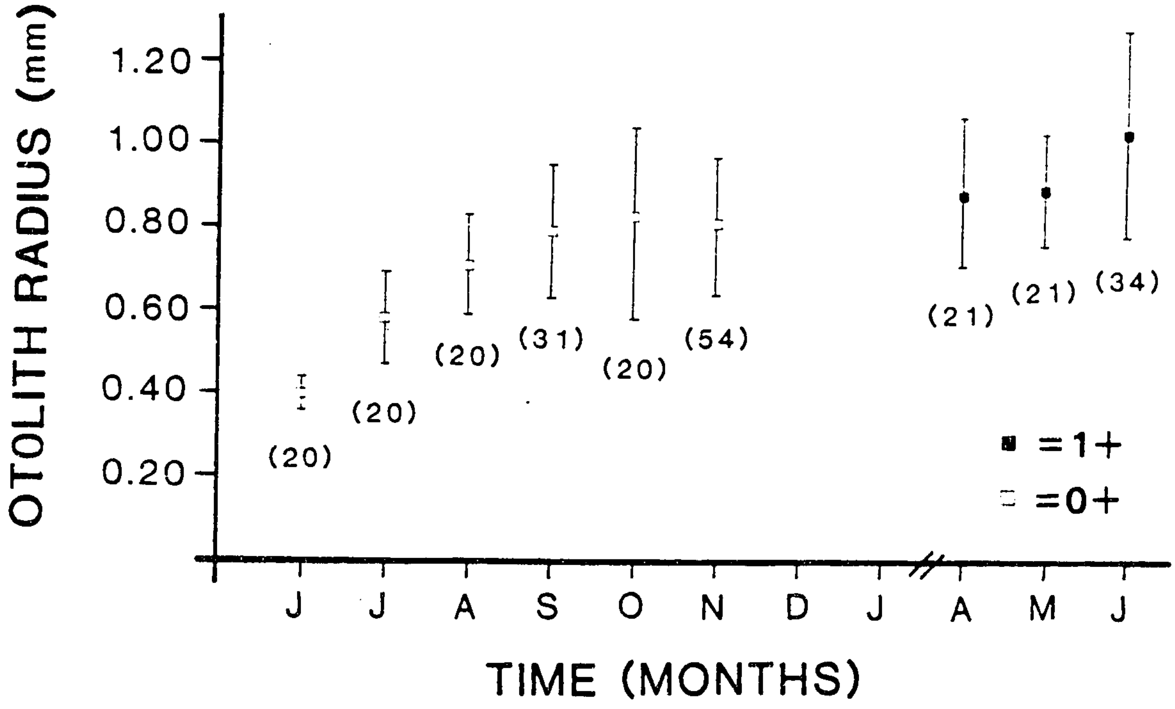

WEIGHT (g)
2.0
6.0
10.0
14.0
18.0
22.0
26.0
M
J
J
A
S
O
N
D
J
F
M
A
1987
1988
TIME (MONTHS)
21
21
50
33
21
33
50
54
33
0+
1+
0
10

Figure 9A. Regression of otolith radius against total length for juvenile burbot from Lac Ste. Anne, Alberta. Each point represents the mean value for approximately 25 individuals.

Figure 9B. Growth in otolith radius (mean +/- 95% Confidence Intervals) over time for juvenile burbot sampled from Lac Ste. Anne, Alberta.


r²=0.96
y= 0.007x 0.117
OTOLITH RADIUS (mm)
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
■ =1+
□ =0+
40
60
80
100
120
TOTAL LENGTH (mm)


OTOLITH RADIUS (mm)
1.20
1.00
0.80
0.60
0.40
0.20
(20)
(20)
(20)
(31)
(20)
(54)
(21)
(21)
(34)
■ =1+
□ =0+
J
J
A
S
O
N
D
J
A
M
J
TIME (MONTHS)

the otolith increased in size throughout the summer and winter (Fig. 9B).

Otolith margins in juveniles were light for most of the summer, fall, and spring (Fig. 10). Only during mid-August was a dark band laid down (n = 21). By September the margin was light again in all of 33 otoliths examined.

Adults appeared to differ in the timing of growth. Their otolith margins were light in colour from early November through to late March. The sample of adults obtained in early November (n = 3) all had otoliths the fastest growing points (Fig. 2) of which were light coloured with the rest of the otolith's margin being dark. The opposite case occurred in mid-May (n = 7), when the otolith points (Fig. 2) were dark, but the rest of the otolith margin was light (Fig. 10). For the months when both age cohorts (immature: <3 and mature: >3) were represented, only during August did they have similarily coloured margins, suggesting a temporal difference in growth patterns between sexually immature and mature fish.

Growth in summer predominates in juvenile burbot up to age 3 years (Fig. 11). At age 3, burbot become sexually mature and the width of dark and light bands is approximately equal; growth in summer matches growth in winter. From age 4 onward, dark bands become predominate, the proportion of total annual otolith increment made up by the dark bands becoming greater than that comprising light bands. The

Figure 10. Relationship between season and the proportion of the otolith margins coloured either dark or light in adult (> 3+ years) and juvenile (< 3+ years) burbot from Lac Ste. Anne, Alberta. Deviations from the 100% horizontal indicate a transition from one colour to the other. Otolith edges at the extreme points grow fastest (Fig. 3), hence they are first to show change in colour. Each point represents the average colour of the majority of otolith margins examined within a given sample. The mid-November sample (n=3) was obtained from Bangs Lake, and that in early December (n=20), from Wolff Lake; both are found close to Cold Lake, Alberta.

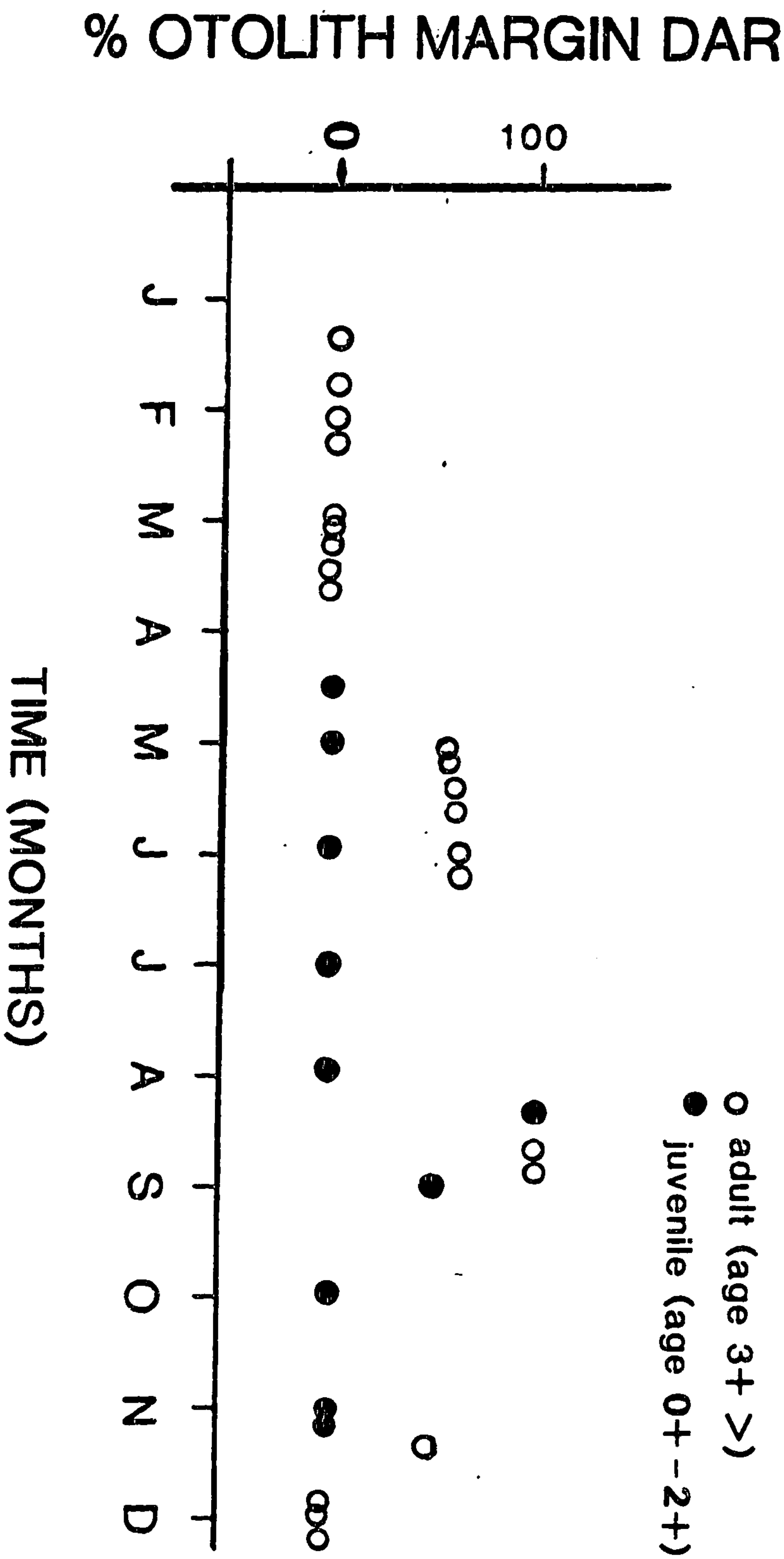
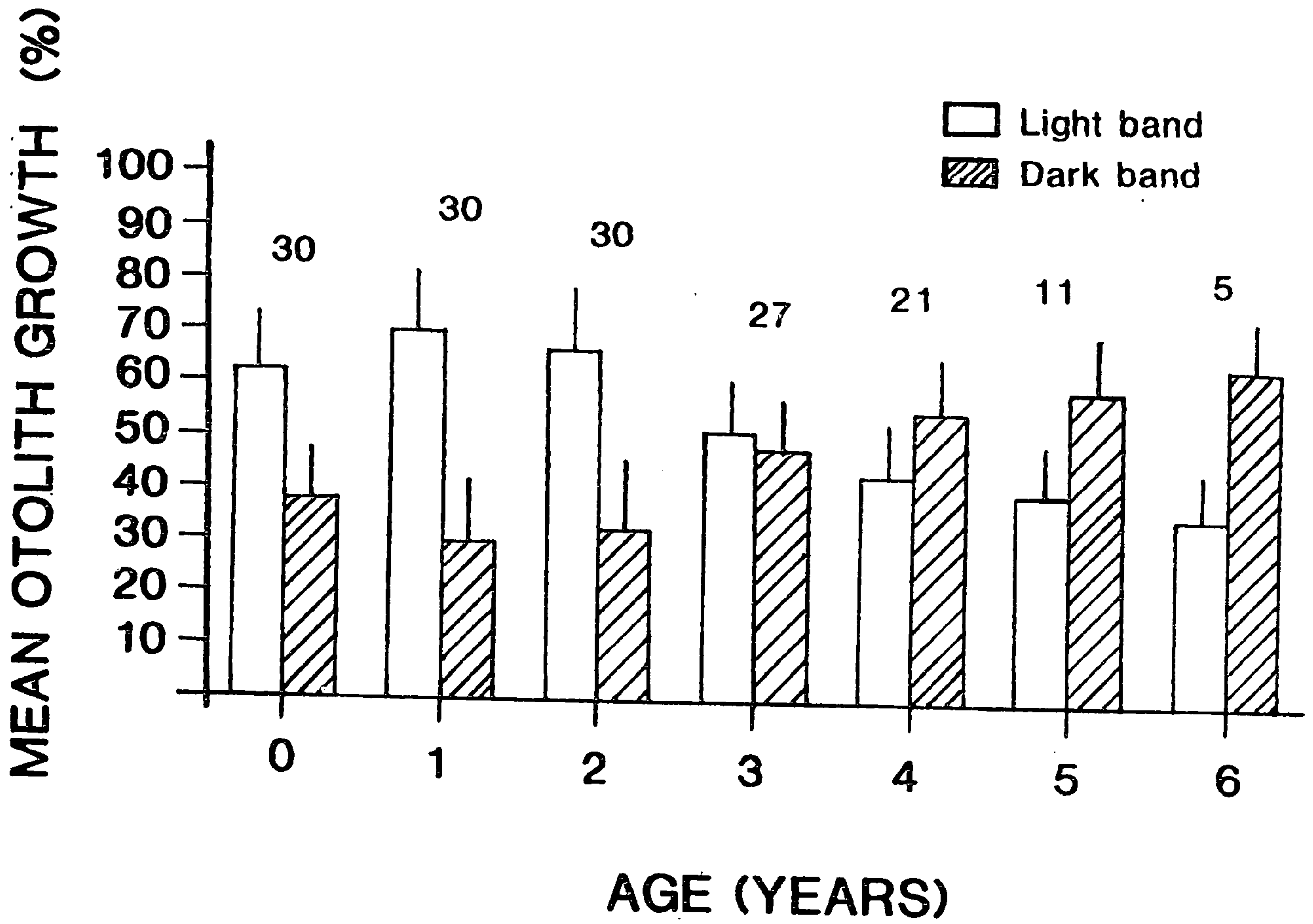

% OTOLITH MARGIN DARK
0
100
J
F
M
A
M
J
J
A
S
O
N
D
TIME (MONTHS)
○ adult (age 3+ >)
● juvenile (age 0+ - 2+)

Figure 11. Proportion of the otolith grown during summer (ice-out to freeze-up, open bars) and winter (freeze-up to ice-out, hatched bars) in samples of burbot ranging in age from 0 to 6 years taken from Lac Ste. Anne, Alberta. Vertical bars represent 95% confidence intervals. Amount of growth is determined from measurements of band widths obtained from whole otoliths.


MEAN OTOLITH GROWTH (%)
100
90
80
70
60
50
40
30
20
10
30
30
30
27
21
11
5
0
1
2
3
4
5
6
AGE (YEARS)
□ Light band
▨ Dark band

smallest adult fish captured by both angling and gillnetting was 3 years old. Two-year-olds captured in mid-October had no visible gonad, thus it is assumed that maturity most likely occurs at age 3.

D. DISCUSSION

Timing of Growth in Burbot

Data obtained in this study suggests that adult burbot in Lac Ste. Anne grow more in winter than in summer. Adult burbot appear to grow predominantly from mid-November to May. Adults probably put energy into gonad growth in late summer and early fall, after which somatic growth (growth in length) predominates during winter.

Juveniles appear to grow maximally during the summer with growth rate slowing down in mid-August but increasing again between September and mid-November. Chen (1969) noted a similar temporal shift in deposition of material on the otoliths of juvenile burbot during the summer in Alaska. This study suggests that it is only during August that adults and juveniles exhibit a similar pattern of growth. Therefore it appears that a temporal shift in growth may follow the onset of sexual maturity (age 3) in this species. Lack of significant growth in August probably reflects the negative impact on growth produced by very warm water temperatures experienced by juvenile burbot living in shallow water.

In five of seven other studies, a light band (indicating increased growth rate) made up the marginal increment of adult burbot otoliths during the winter (Table 6). Although there is some variation in the timing of deposition of the light and dark bands, there is a strong trend toward increased growth in this species throughout the winter months when water bodies at these latitudes are ice-covered (Table 6) and maximum water temperature is 4°C. The apparent growth of burbot during the winter shown in this study and others (Table 6), based on the timing of formation of the opaque band on the margin of the otolith, suggests that this growth pattern may be consistent throughout the south-western part of its distribution. In contrast, Clemens (1951b) and Chen (1969) found that the formation of a light band on the marginal increment of the otolith of burbot took place from June to November. These observations, which appear to contradict the results obtained in this study, may reflect one of two possibilities. A common source of confusion prevalent in studies of otoliths has been the inconsistent use of terms to describe the colour of seasonal bands based on the type of light source used by the researcher. The colour of the light and dark bands depends upon the nature of the light source (transmitted versus reflected light). It may very well be that the colour of the bands observed by the afore-mentioned authors were reversed. For example, Martin (1941) reported on the use of the otolith for assigning age

Table 6. The timing of deposition of the light band on the otolith marginal increment recorded in different studies.

Lake	Time of Deposition	Researcher
Lake Opeongo, ONT.	Sept. - February	Hackney (1975)
Lake Superior, ONT.	Dec. - May	Bailey (1972)
Lake Erie, ONT.	June - March	Clemens (1951b)
Lake Opeongo, ONT.	"summer"	Martin (1941)
Susquehanna River, N.Y.	"late winter" - May	Robins et.al (1955)
Elbe & Oder Rivers, GERMANY	"winter"	Muller (1960)
Tanana River, ALASKA	June - March	Chen (1969)

to burbot and states that "light was focussed to a point on the side of the otolith just below the broken surface," which may mean it was transmitted causing light bands (under reflected light) to appear dark and the converse. Chen (1969) studied burbot at the northern edge of their range, hence the overall colder climate at his study site may have changed the periods of maximal growth for this species; the period of ice cover and colder water temperatures are extended at such latitudes.

Thermal Requirements of Burbot

Data obtained in this study and by others (Table 6) suggests that burbot have lower thermal requirements than other boreal freshwater fish. Christie & Regier (1988) describe thermal niches for a number of Great Lakes and Saskatchewan fish species. The fishes they described (walleye, Stizostedion vitreum, northern pike, lake whitefish Coregonus clupeaformes, and lake trout) were also found living sympatrically with burbot in at least one of the lakes I studied (Cold Lake). The thermal optima for growth in these species spans 11.7 to 23.5°C (Christie & Regier 1988). Burbot are described as a cold-water offshore species (Muth 1973, Hackney 1975). The evidence presented in this study and in others (Table 6) suggests that the thermal optimum for growth may be considerably lower in burbot than it is in other north temperate freshwater fish.

Corroborating evidence for growth of burbot in winter as compared to summer comes from a number of studies of the water temperatures they appear to prefer and from feeding studies (Table 6). Muth (1973) suggested that burbot frequent areas of Lake-of-the-Woods, Minnesota, that lie on the 10°C isotherm (over the open water season). When water temperatures exceed 10°C, burbot appeared to be absent from these warmer locations (during the late summer and autumn months) (Muth 1973). Muth (1973) suggested that their absence from these waters may indicate an adverse effect on growth rate in this species when exposed to periods of warmer temperatures. Hackney (1975) reported that burbot in Lake Opeongo, Ontario were absent from strata warmer than 13°C.

Growth rates of burbot appeared to decline markedly in Lac Ste. Anne following sexual maturity (Fig. 5). Clemens (1951b) acknowledged a marked retardation in the growth rate of burbot following age 3. Whether this was the result of a dietary change or of attaining sexual maturity was unknown.

In his study of burbot in Lake-Of-The-Woods, Minnesota, Muth (1973) noted a reduction in feeding during summer months (July to September) and an increase in feeding during winter months (October, December, January, and March), based on the volume of stomach contents and frequency of empty stomachs. If not merely a function of differential rates of digestion, these observations support the findings in this study of increased somatic growth of burbot during winter which presumably must mean increased rates of feeding.

Population Characteristics

Burbot sampled from Lac Ste. Anne and Cold Lake showed similar weight-length regressions, although this relationship was stronger in Cold Lake than in Lac Ste. Anne. Regression equations describing the two populations were not significantly different; however, weights for any given length proved more variable in Lac Ste. Anne than in Cold Lake. The variation in weight explained by length (r^2 values) are, nevertheless, weaker than expected in both lakes. Magnin & Fradette (1977) found much stronger length-weight relationships in the majority of burbot populations investigated in Quebec. The reason for this is unknown; it cannot be attributed to sample size as Magnin and Fradette (1977) had similar N values to those in this study.

No differences were observed in growth rate in terms of total length between male and female burbot in either lake. Clemens (1951b) found that female burbot in Lake Erie grew faster than males once they reached 4 years of age. Chen (1969) found a similar situation in Alaska after age 10. Hackney (1973) reported that there were no differences in the growth rates of the sexes in burbot up to age 10, from Lake Opeongo, thereafter female growth slowed, but male growth appeared to stop. Magnin & Fradette (1977) found no difference in growth between the sexes in their study of burbot in Quebec, nor did Robins & Deubler (1955) in the Susquehanna River, New York.

The rate of growth in both length and weight of burbot from Lac Ste. Anne and Cold Lake declined significantly after age 3. That is, growth up to age 3 was rapid (up to 54.5 cm in length, and 1576 g in weight); following sexual maturity growth rate declined abruptly. As there was no significant difference between the average weight of 3-year-old burbot and burbot aged 10 - 13 years (in Lac Ste. Anne) and 10 - 16 years (in Cold Lake), it appears that burbot in this study may exhibit a form of determinate growth, growing rapidly in length and weight to sexual maturity, losing this growth potential thereafter as they begin to reproduce. To my knowledge this phenomenon, observed in both populations studied, has not been observed in other fish.

Another potential explanation for these data is that differential mortality occurs after sexual maturity with the more rapidly growing individuals dying before the slower growing, smaller fish (Muth 1969). This would mean that only the smallest individuals survived into old age. Gill net selectivity could account for the lack of growth following sexual maturity. Table 3, indicating the length-frequency distributions of angled and gill netted burbot, shows that angled burbot were longer on average. It is unlikely, however, that gill netting biased the sample of burbot obtained even though it appeared to select for smaller, slower growing individuals in any given age class. Clemens (1951b) found that growth was rapid up to age 3 and 4 in Lake

Erie. At this time growth slowed but accelerated again after age 4. This phenomenon was attributed to the onset of sexual maturity and a shift in diet. Chen (1969) found that burbot in Alaska continue to grow throughout their life, although growth rate decreases following sexual maturity.

Burbot sampled from Cold Lake were slower growing, yet lived longer than their counterparts in Lac Ste. Anne. This phenomenon is generally true for most species of fish (reviewed in Pitcher and Hart 1982). The two lakes have markedly different morphometric and trophic characteristics. The longevity of Cold Lake burbot may be attributed to the thermal regime of the lake. It is clear that during the summer, Cold Lake has a relatively, as well as absolutely, larger area of preferred habitat for burbot; it is larger, colder and deeper than Lac Ste. Anne. Furthermore, the possibility exists that because Cold Lake has a significantly smaller littoral zone than Lac Ste. Anne, burbot can exist in their preferred thermal niche for longer periods of time each year in the former than in the latter. This would enable these fish to avoid the potential stressful conditions encountered in Lac Ste. Anne where the above conditions do not hold and where avoidance of the extensive littoral zone may lead to increased intraspecific competition as well as possible anoxic conditions in the remaining reduced area available to them under warm, summer conditions.

Data gathered in this study supports the hypothesis that burbot, a cold-adapted freshwater cod, following sexual maturity grow more somatically in winter when water temperatures are cold than in summer when temperatures are warm. Although Cold Lake burbot may have been longer lived than their conspecifics in Lac Ste. Anne, their higher condition indices suggest that the former may be a more suitable habitat.

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III. THE RELATIONSHIP BETWEEN FECUNDITY, BODY SIZE, AND LAKE TYPE IN BURBOT (*Lota lota*).

A. INTRODUCTION

Burbot (*Lota lota*), are highly fecund relative to other north temperate freshwater fish (Lawler 1963). They produce large gonads and have a high fecundity which is a characteristic of the family (Gadidae) to which they belong (May 1967, Oosthuizen & Daan 1974). The reproductive biology of burbot (*Lota lota*) has been investigated by a number of authors (Bjorn 1940, Chen 1969, Bailey 1972, Hackney 1973). However, the information generated was usually fragmentary and often contradictory in nature. Bjorn (1940), in a preliminary study of burbot in Wyoming, reported a trend of decreasing fecundity (total number of eggs) with increasing fish size, but his sample size was very small (n=4). Bailey (1972) found a similar trend stating that "fecundity in burbot is not clearly related to length or weight," but again the sample size was not large (n = 8). Chen (1969) investigated spawning time and maturity in Alaskan burbot, however, little work was carried out on fecundity and the results are inconclusive. These trends appear to contradict the normal pattern found in freshwater fish in which fecundity increases with increasing fish size (Bagenal 1978). Studies of marine cod (*Gadus morhua*) also indicate that fecundity increases with increasing fish size (Powles 1958, Botros 1962, May 1967, Joakimsson 1969, Shopka 1971, Oosthuizen & Daan 1974). Because the sample sizes were small in the studies of burbot fecundity, the relationship between body size (length and weight) and fecundity in this species requires further investigation.

It is well known that in fish, productivity is a function of lake trophic condition (Wetzel 1983). For the majority of fish, the time of sexual maturation is a function of size. Hence fast growing fish mature earlier than their slower growing counterparts (Bagenal 1978). Hence, bigger fish produce more eggs.

Growth rate of fish seems to be closely tied to the productivity of their habitat; fish from lakes of higher productivity exhibit faster growth rates, and because they are larger at any given age than their slower growing counterparts from less productive systems, are more fecund (Bagenal 1978, Pitcher & Hart 1982). Nevertheless, the best predictor of fecundity is total length (Bagenal 1978); the longer the individual, the more eggs it produces.

Published interlake comparisons of fecundity in burbot are few. Differences have been recorded in Alaska (Chen 1969); however, no explanation for the differences was offered. The effect of lake trophic condition on the fecundity of burbot is unknown. The purpose of this study was to compare fecundity of burbot from two lakes with differing primary productivity and differing growth rates.

B. METHODS AND MATERIALS

Collecting burbot

Adult burbot were sampled from commercial gill net (13.3 cm stretched mesh size) catches in Cold Lake and Lac Ste. Anne predominantly during March, approximately one week before spawning took place. Both lakes lie within the southern boreal forest region of Alberta (Fig. 1). Angling through the ice with artificial lures supplemented the sample from Lac Ste. Anne.

The following parameters were recorded from individual burbot: total length (mm), total weight (g), gonad weight (g), and sex. Otoliths were removed as described in chapter II, and stored in scale envelopes to determine the age of each individual. Ovaries were removed and preserved in order to determine fecundity at a later date.

Ovary Preparation:

Ovaries were removed from freshly thawed adult female burbot, and fixed by placing them in 750 mL or 1 L glass jars filled with Gilson's fluid (Simpson 1951). Each ovary was cut open along its long axis to accelerate the fixation and subsequent separation of ova from extraneous ovarian tissue. Ovaries were left standing in Gilson's fluid for 2 to 3 weeks with the container being inverted every week to facilitate even fixation of the tissues.

After 4 weeks, jars were shaken vigorously to break the ovaries apart and loosen the eggs from surrounding connective tissue and capillaries. Once shaken, the contents of individual jars were poured into an aquarium dipnet whose square mesh = 0.5mm; sufficiently small to prevent egg loss during the rinsing. Cold tap water was used to flush old Gilson's fluid and dissociated tissue (e.g., blood) through the net. Rinsing was continued until water draining from the net was clear. Once rinsed, ovaries were returned to their respective jars, covered with fresh Gilson's fluid, and left standing for a further 4 to 6 weeks. The longer the eggs were left in the fixative the harder they became and the easier they were to handle. Once the eggs were well fixed (appearing slightly brownish-yellow in colour), ovaries were gently rerinsed and coarse particles removed by pouring the contents of each jar onto plastic mosquito screening (mesh size = 1.5mm^2) stretched over a 4-l pail and anchored with an elastic band. Water was poured slowly onto the ovary while it was gently agitated mechanically. The coarse particles (e.g., ovarian wall) left behind on top of the screen were discarded, while the eggs passed through the mesh into the pail, were ready to be counted.

Subsampling Eggs

To estimate the total egg production by an individual fish, I devised a procedure for quantitatively subsampling and then counting the eggs. It was neccessary to subsample eggs because of the time committment necessary to count individually the large numbers of eggs present in each fish. Cleaned eggs were washed into a 1 L graduated cylinder through a funnel and the volume of both eggs and water recorded. The contents of the graduated cylinder were then transferred to a 1 L beaker.

Preliminary experimentation with a known number of eggs (10,000) suggested that a volumetric ratio of 1:5 (eggs:water) yielded the best estimate of egg numbers following subsampling (Appendix 3). Eggs remaining in the cylinder were washed into the beaker with sufficient water to obtain the desired egg:water ratio.

Once the transfer of eggs was completed, the contents of the beaker were stirred in a figure-eight manner with a glass rod. This created a homogenous suspension of eggs in the water column and minimized settling of the eggs before the subsamples were taken. A 1 mL automatic pipette, with a tip 6 mm inside diameter, was used to draw up two 1-ml subsamples of eggs and water. The subsample was obtained before the suspension of eggs in the water column began to settle. In order to minimize subsample variance, the pipette was pushed downwards through the water column as the subsample was being drawn into the pipette, allowing an even suspension of eggs to be drawn into the pipette.

Determining fecundity

To count the number of eggs in a 2 ml subsample, each subsample was placed in a plastic Petri dish with a bottom surface area of 2123.72 mm^2. The bottom was subdivided into 67, 25 mm^2 squares, etched into its underside. Each square was numbered from 0 to 66. As the bottom of the Petri dish was circular, its entire surface could not be covered with squares. Along the outer margins of the dish were areas not bounded by squares. Eggs situated in these areas were not counted. Eggs were distributed in a uniform layer across the bottom of the Petri dish by physically tapping and gently swirling the dish.

Counting eggs

Eggs were counted on a black background under reflected light using a binocular dissecting microscope. In order to decide the cells in which eggs were to be counted, 10 random numbers, between 0 and 66, inclusive, were taken from a table of random numbers. These numbers were matched to their counterpart squares on the bottom of the Petri dish, and the number of eggs in each of the identified squares was counted. Eggs that were oriented on lines making up the grid on the bottom of the Petri dish were included in the egg count only if greater than 50% of the egg lay on the inside of the square being counted.

To determine how many squares were necessary to count in order to obtain a reasonable estimate of the number of eggs/subsample, 95% confidence intervals were calculated for 5 through 10 squares. The coefficient of variation was 4% when egg counts were done on 10 squares (Appendix II).

Therefore, counting the eggs in 10 squares would yield accurate, reproducible counts with minimal variation.

Since the surface area of the bottom of the Petri dish covered by the squares was 1675 mm^2 (25 mm X 67), and the total surface area of the petri dish was 2123.72 mm^2, I calculated the total number of eggs in the Petri dish as the mean number of eggs per square multiplied by 84.956 (67 X (2123.72/1675)).

To determine the number of eggs within an ovary, the total number of eggs in the Petri dish was multiplied by half the total volume that the eggs and water displaced in the 1 L beaker. (2 mL were subsampled from the total volume of the egg suspension). Egg diameters from unpreserved ovaries were measured to the nearest micrometer using a binocular dissecting microscope with an ocular micrometer.

Analyses

Comparisons of fecundity and egg size beween lakes was undertaken using regression analysis. Fecundity versus body size parameters were plotted and tested for their significance. Gonado-somatic-indices were plotted using frequency histograms and the resulting distributions compared using X^2 analysis. Mean GSI's between lakes were compared using t-tests.

C. RESULTS

Body Size - Fecundity Relationships

Among female burbot from Lac Ste. Anne, there was no apparent relationship between body size variables and fecundity variables, apart from a weak, statistically significant relationship between total weight and ovary weight (Table 4 & Fig. 13). By contrast, female burbot from Cold Lake showed a weak, statistically significant relationship between total weight and a number of derived fecundity variables (Table 5). These relationships were not evident in Lac Ste. Anne.

Gonad Size

The distributions of Gonado-Somatic Indices (GSI = gonad weight(g)/total weight) for males and females sampled from Cold Lake (n = 96) and Lac Ste. Anne (n = 196) are presented in Figure 12. Male and female GSI did not differ significantly within Cold Lake at the time of capture (X^2 = 9.061, df= 9, $P>0.05$). In Lac Ste. Anne, however, male and female GSI differed significantly (X^2 = 35.655, $P<0.05$); females had larger gonads (Mean female GSI=0.182, s=0.092; Mean male GSI=0.158, s=0.072). As GSI's were dissimilar in Lac Ste Anne, each sex was compared separately between lakes. Male GSI was not significantly different between lakes (X^2 = 13.240, $P>0.05$); however, the distribution of female GSI's was significantly different (X^2 = 108.500, $P<0.001$), with female burbot from Lac Ste. Anne having as higher GSI than their counterparts in Cold Lake (t-test, t = 6.301, $P<0.001$). It appears, therefore, that burbot in Lac Ste. Anne produce

Table 4: r^2 values for regressions of body size parameters and age against condition and ovary weight.

	Lac Ste. Anne				Cold Lake			
	Age	Total Length	Weight	Somatic Weight	Age	Total Length	Weight	Somatic Weight
Ovary weight	0.35^{**}	0.28^{**}	0.63^{**}	0.45^{**}	0.10	0.37^{**}	0.71^{**}	0.66^{**}
Condition	0.00	0.31^{**}	0.06	0.04	0.01	0.09	0.42	0.47
Somatic Condition	0.00	0.30^{**}	0.05	0.06	0.02	0.07	0.43^{*}	0.52

* Slope of regression is statistically significant ($P<0.05$).

** Slope of regression is statistically significant ($P<0.01$).

Table 5: r^2 values derived from regressions of burbot body size parameters and age against fecundity from Lac Ste. Anne and Cold lake, Alberta.*

	Lac Ste. Anne				Cold Lake			
	Age	Total Length	Weight	Somatic Weight	Age	Total Length	Weight	Somatic Weight
Fecundity	0.08	0.00	0.21	0.20**	0.02	0.00	0.00	0.00
Fecundity/ ovary wt.	0.03	0.00	0.01	0.00	0.04	0.20**	0.35**	0.36**
WT Specific Fecundity	0.01	0.00	0.04	0.04	0.01	0.14*	0.37**	0.37**
TL Specific fecundity	0.02	0.03	0.10	0.09	0.00	0.04	0.02	0.02
Somatic WT specific fecundity	0.01	0.00	0.04	0.06	0.01	0.13*	0.36**	0.38**

* As on Table 4.

Figure 12. Frequency histogram of Gonado-Somatic Indices of burbot sampled approximately one week before spawning from Lac Ste. Anne and Cold Lake, Alberta. Males and females significantly different only in Lac Ste. Anne (X^2=35.66, P<0.001)

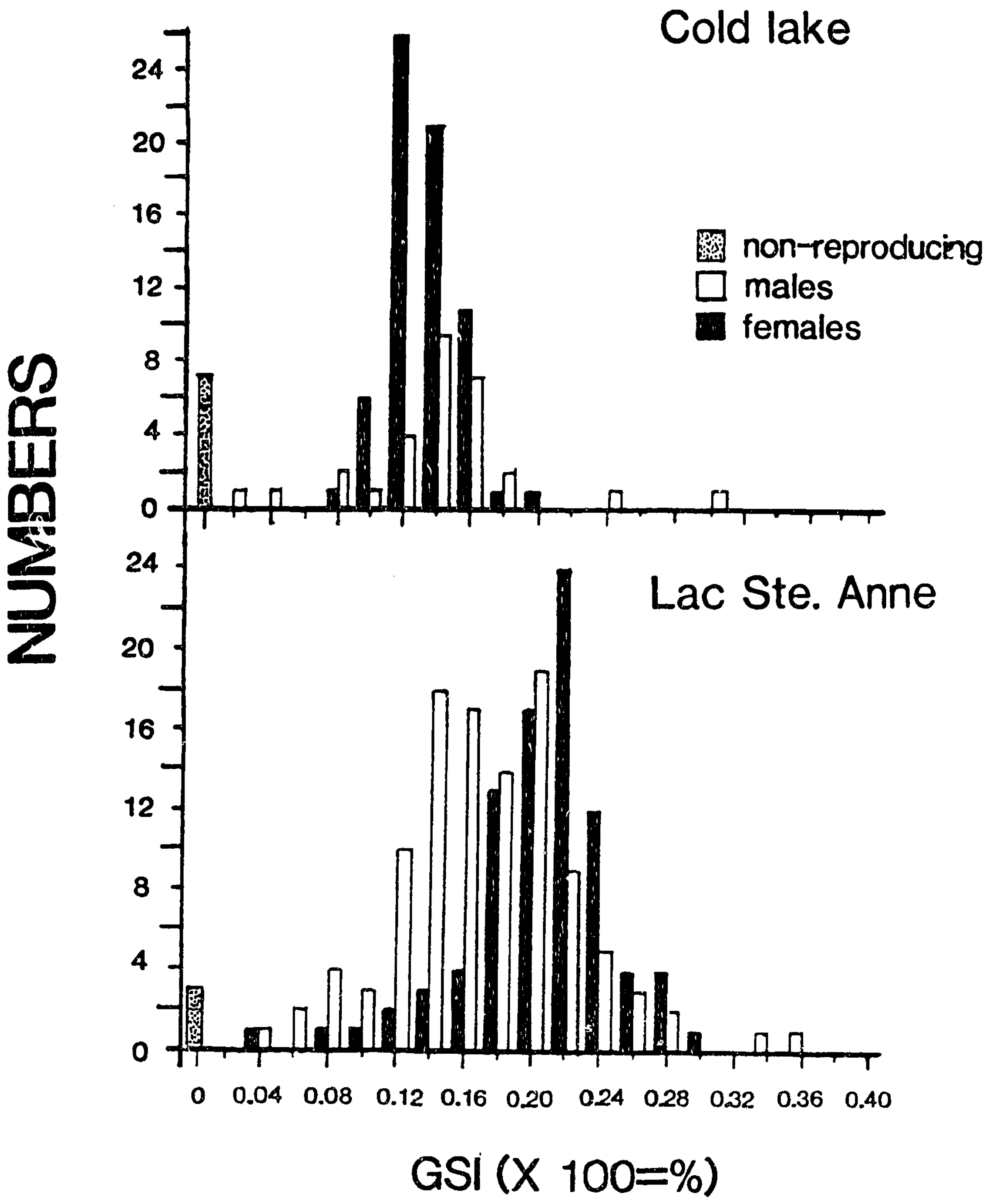
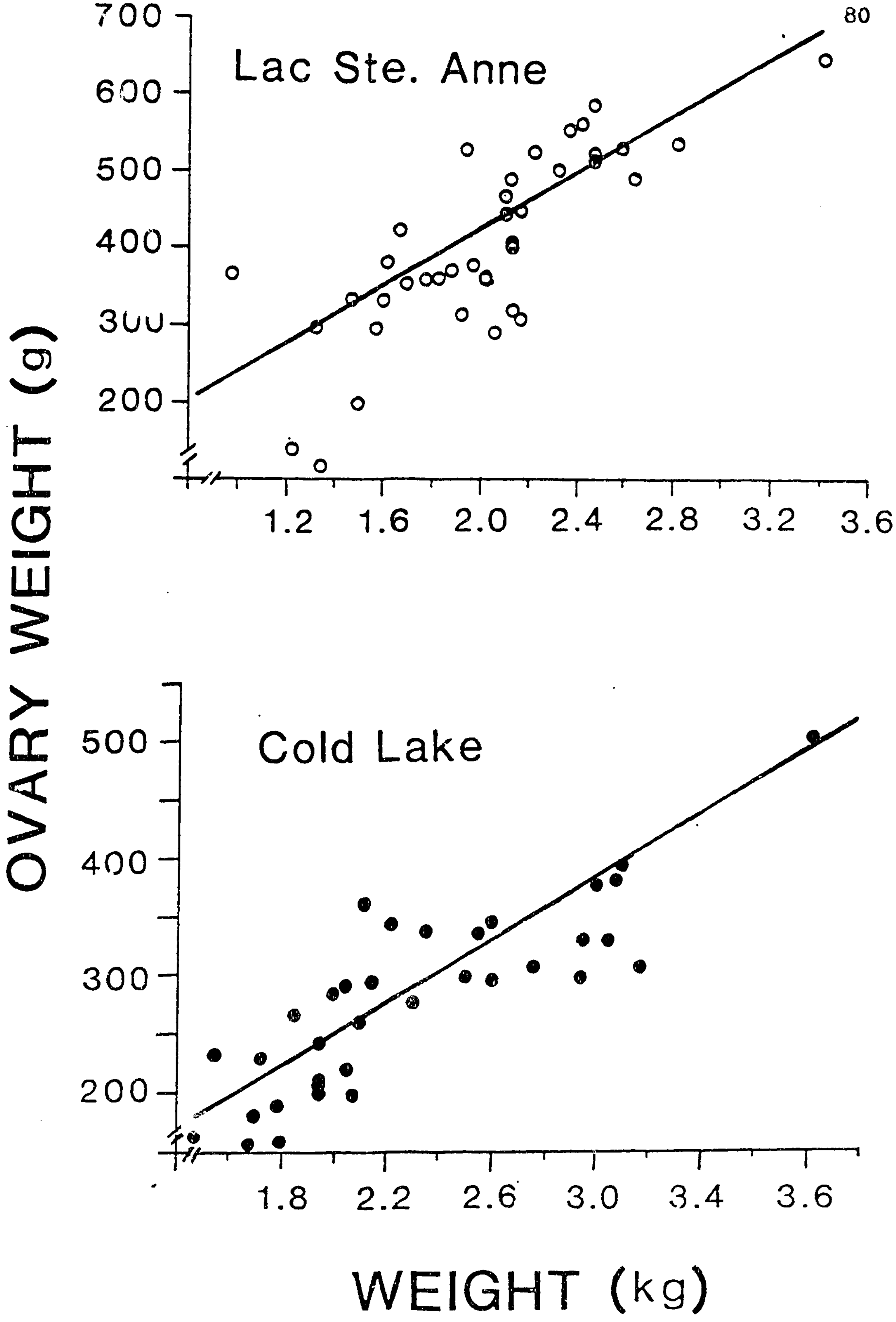

Cold lake
Lac Ste. Anne
non-reproducing
males
females
NUMBERS
GSI (X 100=%)
0
4
8
12
16
20
24
0.04
0.08
0.12
0.16
0.20
0.24
0.28
0.32
0.36
0.40

Figure 13. Scatterplot of ovary weight against total body weight for burbot sampled from Lac Ste. Anne and Cold Lake, Alberta. Both slopes and lines are highly significant ($P<0.001$).


Lac Ste. Anne
700
600
500
400
300
200
1.2
1.6
2.0
2.4
2.8
3.2
3.6
Cold Lake
500
400
300
200
1.8
2.2
2.6
3.0
3.4
3.6
OVARY WEIGHT (g)
WEIGHT (kg)

larger ovaries than their counterparts in Cold Lake (Fig. 12).

In both lakes a small percentage of the adult population sampled had undeveloped gonads which made it impossible to determine their sex. These individuals comprised 0.5% of the Cold Lake sample and 1.5% of the Lac Ste. Anne sample. All these fish were large (in excess of 1 Kg), and aged 4 - 11 years (Fig. 12: "non-reproducing"). Adult male burbot having ripe gonads (n = 3) were collected by mid-November (Bangs Lake). Females captured shortly thereafter however, possesed ovaries that were only partially developed (Wolff Lake).

Burbot spawned in Lac Ste. Anne on about the 14th of March over the course of two winters of sampling. Burbot sampled from commercial fisheries during March 9 and 10 were all ripe. Burbot angled on March 16 were spent. The literature states that burbot spawn between November and April throughout most of their range (Cahn 1936, Bjorn 1940). Burbot in Cold Lake spawn during the third week of March, based on similar criteria to those used for Lac Ste. Anne.

Spawning

Burbot were observed in Lac Ste. Anne during the morning through holes (25 cm in diameter) drilled in the ice. They were in schools of up to six individuals swimming together in a V-pattern in shallow water (< 2m) over a sandy bottom. Actual spawning was not observed, however, it was noted that by late morning, water in the holes through which burbot were angled turned cloudy. Earlier that morning, the water was clear; clouding of the water could be attributed to the release of milt by spawning adult males. Burbot appeared to be highly active and were caught throughout the morning. By noon, angling success had declined, although burbot were still seen swimming past the observation holes.

Fecundity of Burbot

There appeared to be no correlation between fecundity and body size parameters in either of the two lakes (Tables 4 and 5). Plots of total length versus fecundity, total weight versus fecundity, and age versus fecundity, all gave regression lines the slope of which did not differ significantly from 0 except in Lac Ste. Anne where fecundity is positively correlated with total weight (r^2=0.20, P<0.01) (Tables 4 & 5).

Fecundity of burbot, as measured by numbers of eggs per ovary, was significantly different between the two lakes sampled (t-test, t=-4.1458, P<0.001). Mean fecundity in Lac Ste. Anne was 504,930 (s^2=52,902x10^6) eggs, mean fecundity in Cold Lake was 701,320 (s^2=40,628x10^6) eggs.

Egg size

The mean egg diameter of a female burbot from Lac Ste. Anne (n = 12) is 0.925 mm, and 0.792 mm from Cold Lake (number of females = 12). These mean values are significantly different (t-test, P<0.001). Females in Lac Ste. Anne produce eggs that are 36.7% larger in volume than their counterparts in Cold Lake. Plots of egg diameter versus total length and weight both yielded positive relationships (Figs. 14A & B).

D. DISCUSSION

Fecundity of Burbot

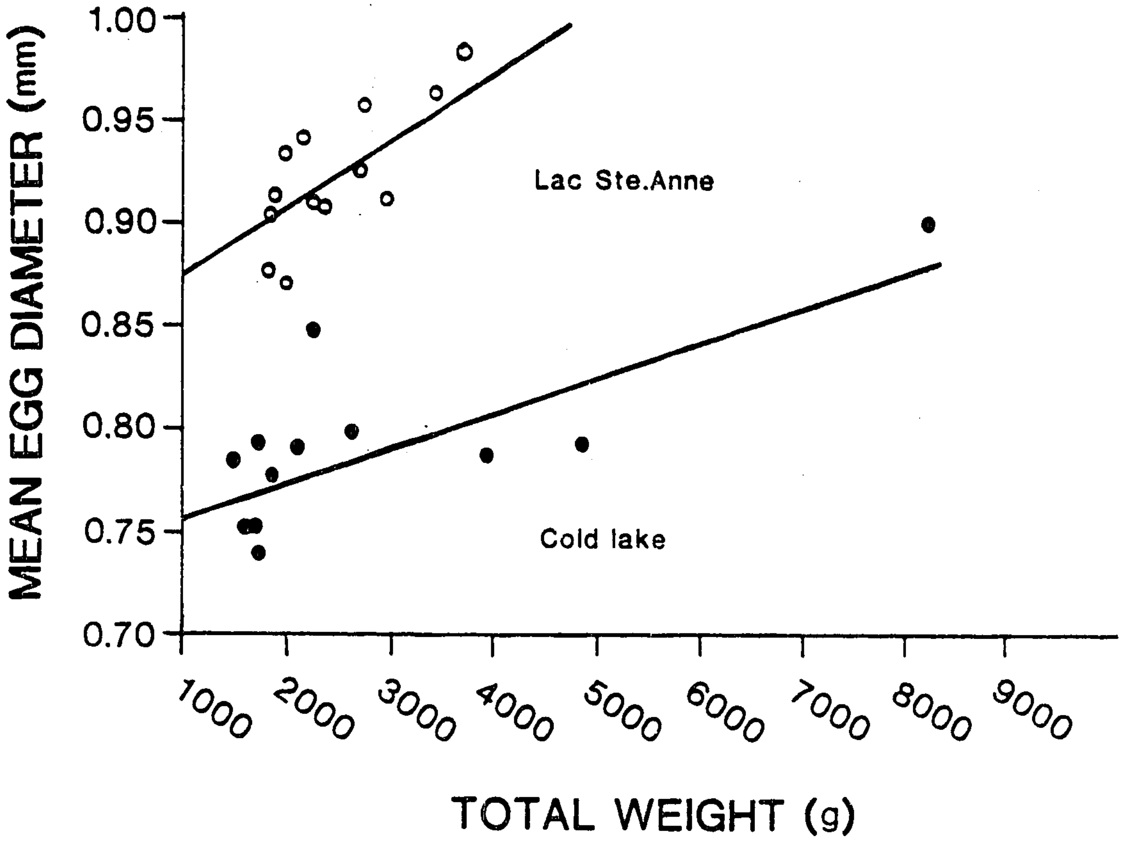
Fecundity of burbot examined in the present study was not related to either body size or age. These results are similar to those obtained by Bjorn (1940) and Bailey (1972), although their conclusions were based on much smaller sample sizes. In the lakes I studied, burbot appear to produce eggs in varied numbers independently of their weight and total length. This situation differs from the usual pattern found in fish in which fecundity is correlated positively with size of mature fish (Bagenal 1978).

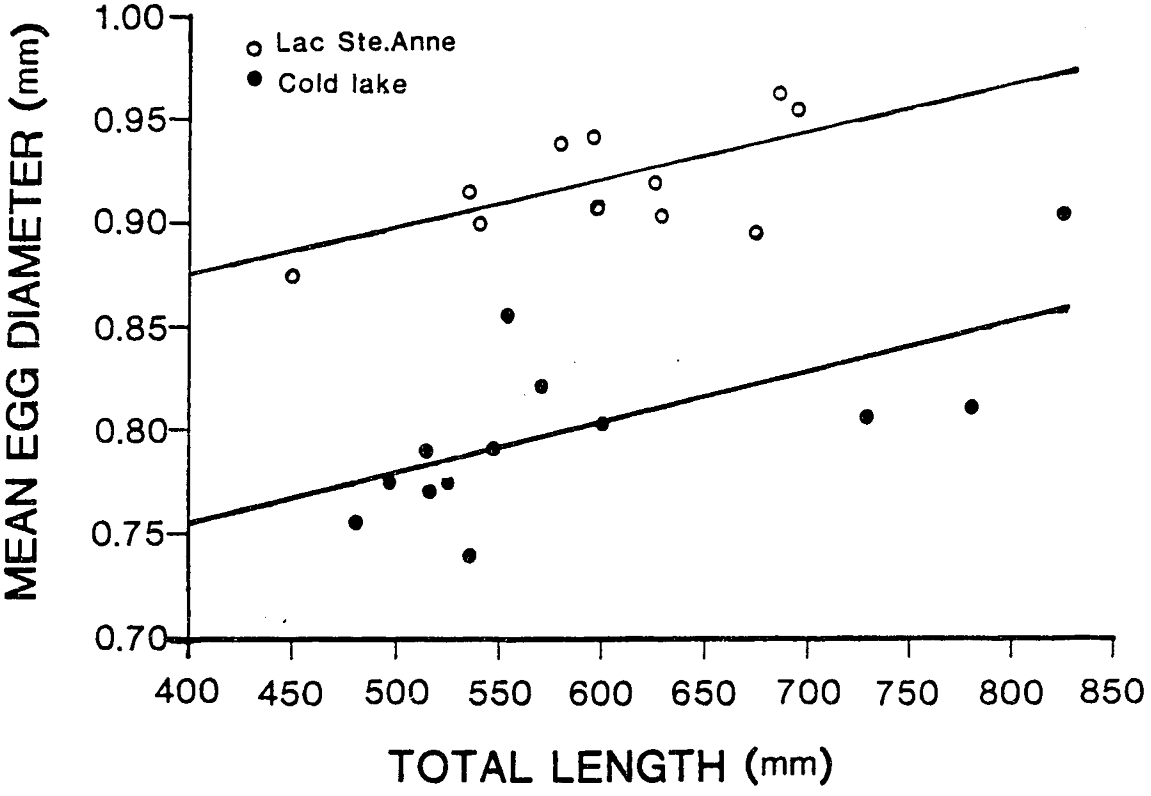
Ovary weight was found to be correlated positively with somatic and total body weight (Fig. 13): as burbot become larger, they develop a larger ovary. This relationship was similar in both burbot populations investigated. This is not surprising as there is an effect of autocorrelation between these two variables. However, somatic weight was equally correlated, suggesting that there is a direct relationship between these two variables.

The relationship between ovary weight and body weight

Figure 14A. Scatterplot of egg diameter against total weight in burbot sampled from Lac Ste. Anne ($y=1.629^{-5}x+ 0.751, r^2=0.58$, $P<0.01$) and Cold Lake ($y=3.275^{-5}x + 0.842$, $r^2=.25$, $P<0.05$).

Figure 14B. Scatterplot of egg diameter against total length in burbot sampled from Lac Ste. Anne ($y=2.218^{-4}x + 0.666$, $r^2=0.37$, $P<0.01$) and Cold Lake ($y=2.431^{-4}x + 0.775$, $r^2=0.40$, $P<0.01$), Alberta.


MEAN EGG DIAMETER (mm)
1.00
0.95
0.90
0.85
0.80
0.75
0.70
Lac Ste.Anne
Cold lake
1000
2000
3000
4000
5000
6000
7000
8000
9000
TOTAL WEIGHT (g)


MEAN EGG DIAMETER (mm)
1.00
0.95
0.90
0.85
0.80
0.75
0.70
○ Lac Ste.Anne
● Cold lake
400
450
500
550
600
650
700
750
800
850
TOTAL LENGTH (mm)

differed between the two populations examined, but testes weight to body weight ratios did not differ (Fig. 12). Male GSI does not appear to be significantly different between the two lakes.

Male burbot mature earlier than females in the two populations investigated. As sample sizes were small, it is difficult to conclude whether these findings are significant. However, Chen (1969) found burbot in Alaska matured by late summer; Hackney (1973) recorded mature gonads during autumn in Lake Opeongo, Ontario. It appears that male burbot ripen before females in Alberta. Hackney (1973), McCrimmon (1959), and Bjorn (1940) found a similar situation in Ontario.

Fecundity Estimates from Lac Ste. Anne and Cold Lake

Estimates of the fecundity of burbot differed significantly in the two lakes studied. Burbot from Lac Ste. Anne produce fewer eggs than their counterparts in Cold Lake, yet they develop a larger ovary. Conversely, ovaries were smaller in Cold Lake, yet held many more eggs.

These discrepancies may be explained by taking into account the significant difference in egg size between fish from the two lakes studied. Burbot in Lac Ste. Anne produce eggs which are 36.7% larger in volume than those produced by Cold Lake burbot. Therefore, burbot ovaries from Lac Ste. Anne contain fewer, larger eggs, than ovaries from burbot in Cold Lake. It is unlikely that the developmental state of the eggs was different at the time of sampling in each lake since the fish from Cold Lake were collected 9 to 11 days after those in Lac Ste. Anne. Hence, the eggs from Cold Lake should have been the more mature (larger) on the basis of time of sampling.

Age at Maturity

Burbot in Lac Ste. Anne mature by age 3. The youngest burbot captured by angling were 3 years old and possessed large ovaries. Two-year-old burbot captured by electrofishing at freeze-up (n = 4) lacked developed gonads. As only one fish less than age 7 was caught in Cold Lake (Table 3), it is impossible to determine the age at sexual maturity there. Hewson (1955) stated that body weight determined when maturity was reached in this species. Based on the assumption that this also holds true for burbot in Cold Lake and that the growth pattern for these same fish is similar to that in Lac Ste. Anne, it is not unreasonable to assume the Cold Lake fish also were mature by age 4. Hackney (1973) found that burbot in Lake Opeongo mature at age 3 as did McCrimmon and Devitt (1955) in Lake Simcoe. Clemens (1951b) found that burbot matured during their 3rd, 4th and 5th year in Heming Lake, Manitoba. Chen (1969) reported that burbot matured in their 6th and 7th year in Alaska. It appears that burbot in Lac Ste. Anne mature at an age similar to their conspecifics in the east. If one compares the age distributions of burbot sampled in this study (Table 5), there exists the possibility that burbot in Cold Lake mature later than those from Lac Ste Anne. Chen (1969) noted that burbot at the southern edge of their range mature earlier than those in his study. Data in this study based on age-at-maturity appear to conflict, at least partially with Chen's (1969) finding.

Spawning in a single population of burbot appears to take place over a short period of time and seems to be highly synchronous. During both sampling years, spawning time was identical to the day. This suggests that some physical signal such as photoperiod is important in synchronising spawning activity. Further research needs to be undertaken on this aspect as data obtained in this study is not strong enough to warrant further discussion.

The difference in egg size observed between lakes may be attributed to their physical and limnological characteristics. As both lakes are dramatically different in these characteristics (Table 1), lake trophic status may have a dramatic effect on both growth and fecundity of burbot in north-central Alberta. Mann and Mills (1979) state that fish living in harsh environments often modify their reproductive strategies to maximize the survival of their young. Burbot in this study exist close to the south-western edge of their range. As a result, burbot in Cold Lake exist in a more stable environment, relative to fluctuating temperature conditions in the much shallower Lac Ste. Anne, which is more likely similar to what this species experiences further north in its range.

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IV. CONCLUDING DISCUSSION

Results obtained in this study, suggest that somatic growth in sexually mature burbot occurs predominately during the winter (Fig. 13), when water temperatures and primary productivity are low. This contrasts with what is known about the general growth pattern in most north temperate freshwater fish which grow mainly during spring and summer when water temperatures and primary productivity are high (Pitcher and Hart 1982). Thus during winter, most north temperate freshwater fish become relatively inactive, their metabolism reduced dramatically as the result of cold water temperatures (Pitcher & Hart 1982). Burbot are reported to forage actively during the day in winter (Muller 1973), when light intensity is reduced because of the ice and snow cover present and forage fish are lethargic and may be highly vulnerable to predation. This evidenced by large numbers of forage fish found in their stomachs prior to and following spawning (Clemens 1951a, Nikolsky 1954, pers. obs.). During summer, burbot are reported to feed at night on fish that are nocturnally quiescent (Roberts 1975). This seasonal shift in activity pattern has been well documented (Muller 1973, Kroneld 1974). Findings in this study and other corroborating evidence from the literature (Muller 1960, Clemens 1951a & b, Chen 1969) suggest that burbot may have different thermal requirements from the majority of other north temperate freshwater fish.

Somatic growth in immature burbot (up to age 3) is rapid, most occurring during summer, but also appearing to continue throughout the winter, although at a slower rate (Figs. 9 & 10). Hence it appears that there is a temporal shift in growth following sexual maturity in this species; mature fish growing predominantly during the winter, and immatures during summer. In Alaska, Chen (1969) found a similar growth pattern for immatures in the Tanana River.

As the smallest sexually mature individuals collected over the two winters of this study were 3 years old, it is assumed that burbot mature at this age in Lac Ste. Anne. This trend is similar to that observed in eastern populations of burbot (Hewson 1955, McCrimmon and Devitt 1955, Clemens 1951b, Hackney 1975). Burbot in Lac Ste. Anne appeared not to grow significantly in length following age 4; growth rate following sexual maturity declined significantly. Such is not the case in eastern populations previously cited. The dramatic decline in growth rate following sexual maturity most likely reflects the metabolic demands imposed on an individual in developing a large gonad (up to 36% of body weight in burbot from Lac Ste. Anne - Fig. 14). Mann and Mills (1979) state that fish modify their reproductive strategies in order to cope with changing environmental stresses. Burbot investigated in this study existing close to the southwestern edge of their range may face a thermal regime and predation pressure that is selecting for gonad output over somatic growth. These stresses are different in their eastern counterparts, which must invest more energy in somatic growth and less in gonadal growth.

The size of eggs from female burbot in Lac Ste. Anne were significantly larger (36.7% larger in volume) and fewer in number than those from Cold Lake fish. Bagenal (1969) states that there is a direct relationship between egg size and the probability of fry survival: large eggs should produce large fry. Following hatching in the littoral zone (Mansfield et al. 1983), burbot fry move offshore (Abbey, unpublished data 1986, Boag pers. obs. 1986). This move is most likely associated with the need to find sufficient food of appropriate size and possibly to avoid predation pressure from inshore predators. The significant difference observed in egg size between lakes suggests that conditions faced by fry upon hatching may be more demanding in Lac Ste. Anne than those faced by conspecifics in Cold Lake. If burbot spawn in similar habitats in both lakes, larger eggs in Lac Ste. Anne may provide fry with the extra energy required to reach the pelagic zone which is considerably more distant in Lac Ste. Anne than it is in Cold Lake (Fig. 2 and Table 1). Cold Lake also has cisco which is a pelagic plankton feeder. It is possible that burbot in Cold Lake produce more eggs relative to those in Lac Ste. Anne in response to greater predation pressure from these fish.

It appears there may be a relationship between lake trophic condition, somatic growth beyond sexual maturity, and reproductive output in burbot. The short-lived nature of this species in Lac Ste. Anne, their poorer body condition, and the production of larger eggs, suggest that burbot must invest more energy in reproduction than their counterparts in Cold Lake. In terms of a thermal niche, Lac Ste. Anne seems to provide a poorer environment for this species. It is likely that burbot growth and reproductive energetics are associated closely with lake trophic condition (depth and primary productivity), however further research into this question is required. Furthermore, the effect of lake trophic condition on the reproductive biology of burbot, specifically fecundity needs also to be further investigated.

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Appendix 1. Capture dates of adult burbot sampled over the winters of 1986 - 1987 and 1987 - 1988.

Date	Lake	Number of burbot
11/01/87	Lac Ste. Anne	1
25/01/87		7
08/02/87		8
06/03/87		44
10/03/87		61
14/03/87		10
16/03/87		18
05/03/88		5
06/03/88		14
09/03/88		68
11/03/88		9
13/03/88		6
14/03/88		3
18/03/87	Cold Lake	50
19/03/88		59
16/11/87	Bangs Lake	3

Appendix II: Egg counts from 10, 2 mL subsamples from a known number of eggs (n=10,000) and resulting difference expressed as a percentage.

Subsample #	Mean # eggs per square	Number of eggs in a subsample
1	4.6	390.5
2	6.7	568.8
3	4.2	356.6
4	4.3	365.1
5	5.3	450.0
6	5.7	483.9
7	4.2	356.6
8	4.1	348.1
9	4.7	399.0
10	5.2	441.5
		Mean = 416.01

Total # eggs in hypothetical ovary = 10,008 in 50 mL of water
Actual number of eggs counted = (416.01)(25 mL) = 10,400
% Difference = (10,400 - 10,008)/10,008 = 3.92%
Therefore, error using this counting technique is less than 5%.

Coefficient of variation calculated for 10 - 2 mL subsamples from an ovary selected at random.

Ovary #COLD-11
Mean #eggs/subsample = 2612
s^2 = 13,380
s = 115.67

Coefficient of variation = (s/mean #eggs)(100)=(0.044)(100)
= 4.4%

Appendix III. Frequency distribution of ages obtained using 3 different techniques.

Age	Opercular	Sub-Opercular	Sectioned Otolith
7	4	3	4
8	2	4	5
9	7	7	3
10	8	6	5
11	9	14	15
12	7	5	6
13	3	4	5
14	2	2	2
15	0	0	0
16	0	0	0
17	1	1	1
18	1	1	1

Null hypothesis = Age distributions obtained are similar
Alternate hypothesis = Age distributions are different

X^2,0.05, 9df = 15.507
X^2 Calc = 6.907

Therefore, do not reject null hypothesis at alpha = 0.05; the distributions are similar.