THE UNIVERSITY OF MANITOBA

BIOLOGICAL AND POPULATION CHARACTERISTICS OF, AND INTERACTIONS BETWEEN AN UNEXPLOITED BURBOT (*LOTA LOTA*) POPULATION AND AN EXPLOITED LAKE TROUT (*SALVELINUS NAMAYCUSH*) POPULATION FROM LAKE ATHAPAPUSKOW, MANITOBA

by

ALLAN CHRISTOPHER DAY

A THESIS

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ABSTRACT

Exploitation history, population characteristics, and biological features of burbot and lake trout were examined in Lake Athapapuskow, 54° 35'N, 101° 35'W, Manitoba, during 1977 and 1978.

Lake trout and burbot had similar depth distributions and were the only large predators found frequently in the hypolimnion. Intermittent commercial fishing for lake trout since 1931 and the development of an intense sport fishery which continues to the present has resulted in a decline in relative abundance and a relatively small mean size of lake trout, and an increase in relative abundance and decrease in mean size of the unexploited burbot.

Growth rates of Lake Athapapuskow lake trout were similar to those of other otolith aged lake trout populations. However, they were in better condition, completed maturation at a younger age, and showed a lower proportion of mature non-spawning females than most other lake trout populations. In contrast, Lake Athapapuskow burbot showed slower growth than any other burbot populations for which I had data and were in poor condition and matured at a late age in comparison to other populations. Relative abundance of burbot in Lake Athapapuskow was high in comparison to other lakes. These anomalies in the population characteristics of Lake Athapapuskow burbot and lake trout were considered as responses to exploitation of lake trout and consequent increase in burbot abundance.

Faster growth of older burbot and lake trout, better condition of older lake trout, greater weight of burbot caught per unit of effort, and lower burbot mortality rates were observed in the middle and north basins than in the less eutrophic south basin. These interbasin differences in the population characteristics of burbot and lake trout were attributed primarily to the more abundant food supply, as indicated by cisco catch per unit effort values, in the middle and north basins than in the south basin.

ACKNOWLEDGEMENTS

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personal support they offered during the writing of this thesis. I express my sincere gratitude to a friend and fisheries biologist, Joe Sigurdson, for encouraging me to undertake this project, for the informative biological studies he did on Lake Athapapuskow prior to this study, and for his assistance in launching this project.

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INTRODUCTION

The sympatric occurrence of burbot and lake trout is common within their North American range. Adults of these species often have similar diets and depth distributions (Rawson 1951; Hackney 1973; Van Oosten and Deason 1938). Larkin (1956) stated that as a consequence of the comparatively few opportunities for specialization in freshwater fish communities, many species tolerate a wide variety of habitats, show flexible feeding habits, and share many resources of their environment with other species. Since burbot and lake trout have similar niches it is expected that changes in the population characteristics of either would be reflected by changes in the population characteristics of the other.

Hackney and Minns (1974) predicted that because of the overlap in diet and distribution of burbot and lake trout in Lake Opeongo, exploitation of one species would result in an increase in abundance of the other. It has been suggested that an apparent increase in burbot abundance in Lake Athapapuskow may be related to a decline in lake trout abundance caused by angling. Knowledge of the status of burbot and lake trout and their interrelationships is needed for management of the lake trout fishing of this lake.

In Lake Athapapuskow, burbot and lake trout are the only large predators found in the hypolimnion during the open water season. In addition, Lake Athapapuskow lake trout have been exploited by commercial and sports fisheries while burbot have been relatively unexploited, and hence, have probably responded to changes in the lake trout population without the complicating effects of exploitation on their own populations. Also, there are historical data on the exploitation, relative abundance, and mean size of both species. These features make Lake Athapapuskow an especially appropriate system in which to study the interactions of burbot and lake trout.

The purposes of this study were:

1. to describe growth, mortality, maturity, length-weight relationships, age and length composition, diet, depth distribution, and trends in mean size and relative abundance of burbot and lake trout in Lake Athapapuskow;
2. to relate these observations to the life history of burbot and the role of burbot in the Lake Athapapuskow fish community;
3. to describe the response of burbot to lake trout exploitation, and the effects of exploitation and burbot on the lake trout population and;
4. to relate burbot and lake trout population characteristics to differences between lake basins in trophy and fish community structure.

MATERIALS AND METHODS

Study Site

Lake Athapapuskow is located at 54^0 35'N, 101^0 35'W,in northern Manitoba. The lake is divided into three basins which are referred to as the south, middle, and north basin (Fig. 1). Mink Narrows connects the south basin with the middle basin. Physical parameters of each basin and the narrows are presented in Table I.

Three water channels connect the south basin with Mink Narrows. The western channel is 3.5 m wide and between 2.5 and 3.0 m deep. The eastern channel is 7.0 m wide and between 1.0 and 1.5 m deep. The centre channel is 7.0 m wide and 2.0 m deep. Only one channel connects Mink Narrows to the middle basin. It is 32.0 m wide, 90.0 m long, and 4.0 m deep. The two channels connecting the middle basin to the north basin are both 46.0 m wide and 5.0 m deep.

Waterflow is from north to south. The majority of inflowing water is supplied by Schist, Mistik, and Pineroot Creeks. Outflowing water leaves the lake through the Goose River.

Lake Athapapuskow lies on the transition between Precambrian and Ordovician rock. The south shore of the south basin is Ordovician, marked by dolomitic limestone.

Figure 1. Contour map of Lake Athapapuskow.

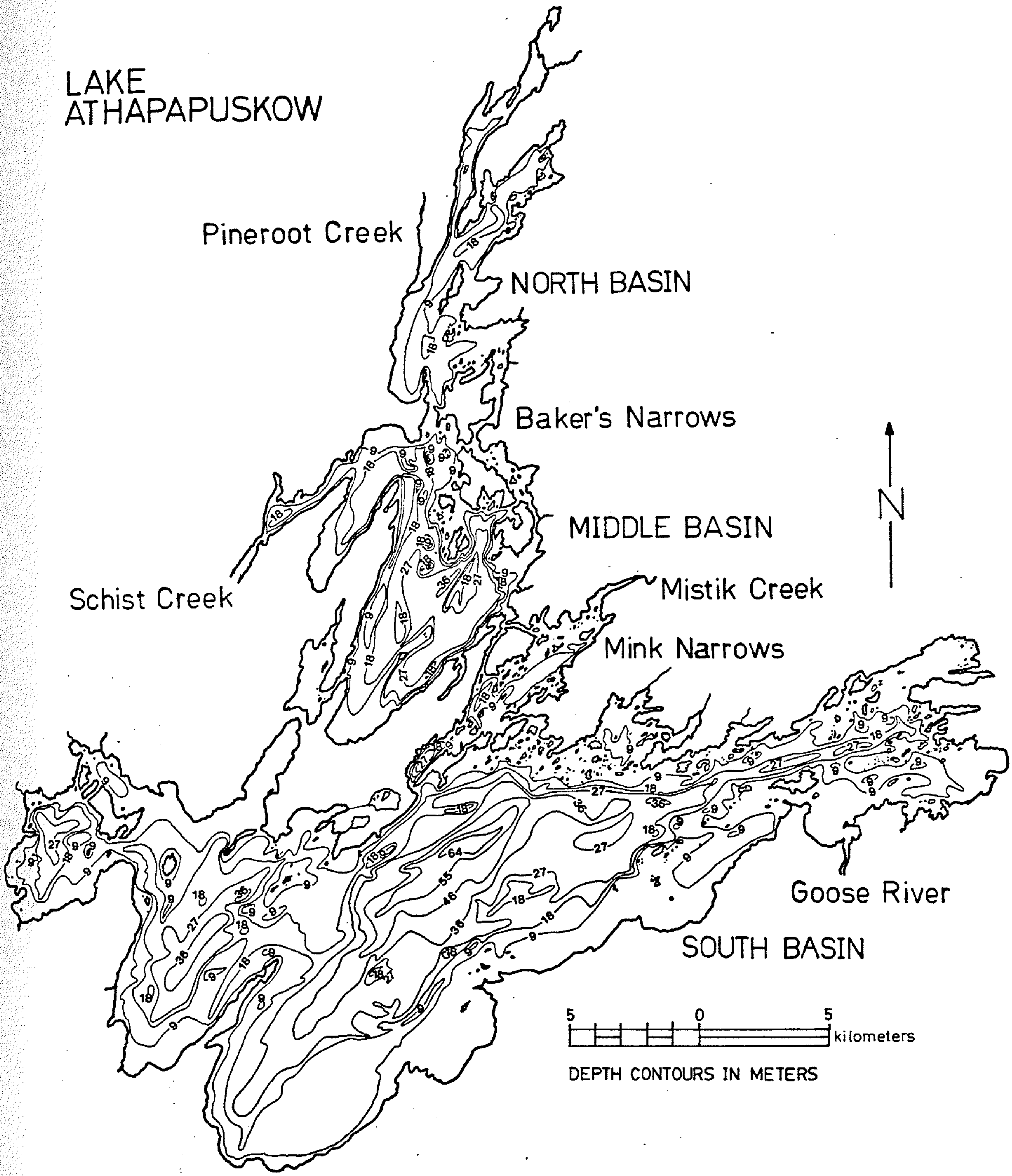

LAKE
ATHAPAPUSKOW
Pineroot Creek
NORTH BASIN
Baker's Narrows
MIDDLE BASIN
Schist Creek
Mistik Creek
Mink Narrows
Goose River
SOUTH BASIN
N
5
0
5
kilometers
DEPTH CONTOURS IN METERS
9
18
21
27
36
46
55
64

Figure 2. Gillnetting stations (1 to 15), successful poisoning sites(P), and unsuccessful poisoning sites (U) in Lake Athapapuskow.

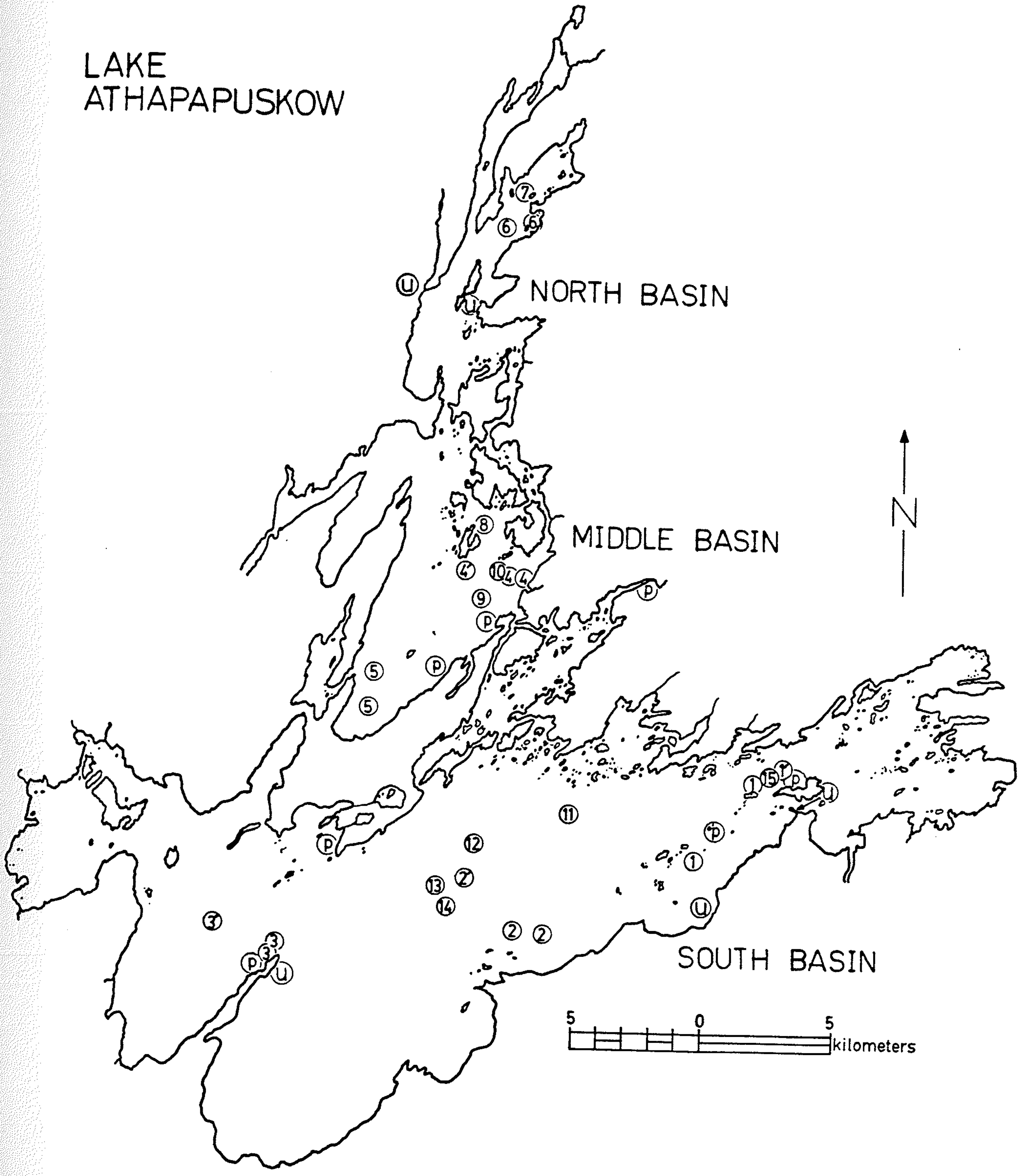

LAKE
ATHAPAPUSKOW
NORTH BASIN
MIDDLE BASIN
SOUTH BASIN
N
5
0
5
kilometers
7
6
6
U
U
8
4
10
4
4
9
P
P
5
5
P
P
P
11
12
13
7
14
3
3
3
P
U
2
2
1
15
1
P
U
P
1
U

Table I. Physical characteristics of Lake Athapapuskow.

	Basins						Mink	
	South		Middle		North		Narrows	
Max. Depth (m)	71.7		40.3		23.0		30.2	
Mean Depth (m)	16.0		14.3		8.0		7.3	
Surface Area (km^2)	187.8		39.3		19.0		8.2	
Contour Surface Area as km^2 and % Total Surface Area	km^2	%	km^2	%	km^2	%	km^2	%
0- 9 m	75.1	39.9	16.3	41.4	11.2	58.8	5.7	69.8
9-18 m	42.8	22.7	8.2	20.8	7.1	37.5	2.1	25.1
18-27 m	25.3	13.4	9.3	23.7	0.7	3.7	0.3	3.6
27-36 m	26.6	14.1	5.4	13.7			0.1	1.6
36-46 m	10.6	5.6	0.4	0.9				
46-55 m	4.4	2.3						
55-64 m	2.4	1.3						
64-72 m	0.6	0.3						
Total Dissolved Solids (mg/l)	258[b]		304[a]		200[a]		265[b]	
Morphoedaphic Index (metric)	11.7		21.3		25.0		36.3	

[a] Data is compiled from Schlick (1973a).

[b] Data is compiled from Kliewer (1969).

Total surface areas and contour surface areas were determined by planimetry.

Contours were recorded using an echo-sounder by R. O. Schlick in 1972.

Mean depth was calculated according to Wetzel (1975).

The remainder of the lake basins are mostly Precambrian, marked by granites and other varieties of igneous rock (Davies et al. 1962). The lake bottom is primarily mud and the shorelines are usually rocky although there are several large sandy beaches. Depth contours are irregular (Fig. 1) and there are many shallow rocky reefs, especially in the south basin.

Secchi Disc Readings and Temperature and Oxygen Profiles

In 1978 each basin was sampled eight times between May 27 and September 7 at stations 2', 4', and 6 (24 m). Secchi disc readings and oxygen and temperature profiles, taken with a Y.S.I. membrane probe, were recorded. Oxygen and temperature profiles taken within a basin at stations other than 2', 4', and 6, were consistent with profiles of the station regularly sampled in that basin.

Thermal stratification of the water column had started by early June and thermoclines were well established by early July in all basins(Figs. 3, 4, and 5). Hypolimnetic and epilimnetic temperatures at any given date were warmest in the north basin and coolest in the south basin. Thermal stratification was most pronounced in the middle basin and least pronounced in the north basin. Maximum thermocline depth was achieved by late August in all basins and was deepest in the south basin and shallowest in the north basin.

South basin oxygen profiles (Fig.8) were orthograde and north basin profiles developed into a clinograde shape as the season progressed (Fig.6). Middle basin profiles were intermediate to those of the other basins but approached a clinograde state by late August (Fig.7). Waters of all strata of the south basin had the highest oxygen content of all three basins and were always saturated or slightly supersaturated. The epilimnion of the middle basin was also saturated or slightly supersaturated, as was its hypolimnion, until early July. Hypolimnetic waters of the middle basin dropped from 85 percent saturation in the bottom strata and 55 percent saturation in the upper strata, by late August. Waters of the north basin contained the least amount of dissolved oxygen of the three basins. By late August north basin epilimnetic waters were saturated. Hypolimnetic waters of the north basin were almost devoid of oxygen by early August. Bottom sediments of this basin had a sulphur smell indicating that they were anaerobic. Sediments of the middle and south basins were nearly odorless and lighter in colour. Although oxygen profiles were not taken at regular intervals in the north basin during 1977, periodic oxygen determinations in the hypolimnion of this basin were an indication that oxygen regimes were similar to those in 1978.

Metalimnetic oxygen maxima (an increase in dissolved oxygen, in excess of normally observed concentrations, in the metalimnion) were observed in early July in the middle and north basins.

Mean secchi disc values for stations 2', 4', and 6 (24 m) were 5.98, 4.35, and 3.65 m respectivley.

Fish Sampling

Gillnets

Gillnets were strung together in a series of panels of varying mesh sizes. Gaps of 3 m were placed between panels to prevent "leading". Large fish may lead along a small mesh net until they are captured by a larger mesh net (Anon. in Hamley 1975).

In 1977, gillnet gangs, 137 m long, were composed of six 22.8 m panels. Stretched mesh sizes of the panels were 2.5, 5.1, 7.6, 10.8, 12.1, and 13.3 cm. Longer gangs (229 m) were composed of five 45.8 m panels of stretched mesh sizes 5.1, 7.6, 10.8, 12.1, and 13.3 cm. Except for the 2.5 cm monofilament mesh, all meshes were made of braided nylon.

In 1978 only 137 m gangs were used. They were composed of six 22.8 m panels of stretched mesh sizes 5.1, 7.6, 8.9, 10.8, 12.1, and 13.3 cm. In the second fishing season the 2.5 cm mesh was omitted due to its inefficiency and the 8.9 cm mesh was added to obtain a better sample of intermediate sized fish.

Figure 3. Temperature profiles in the north basin of Lake Athapapuskow.

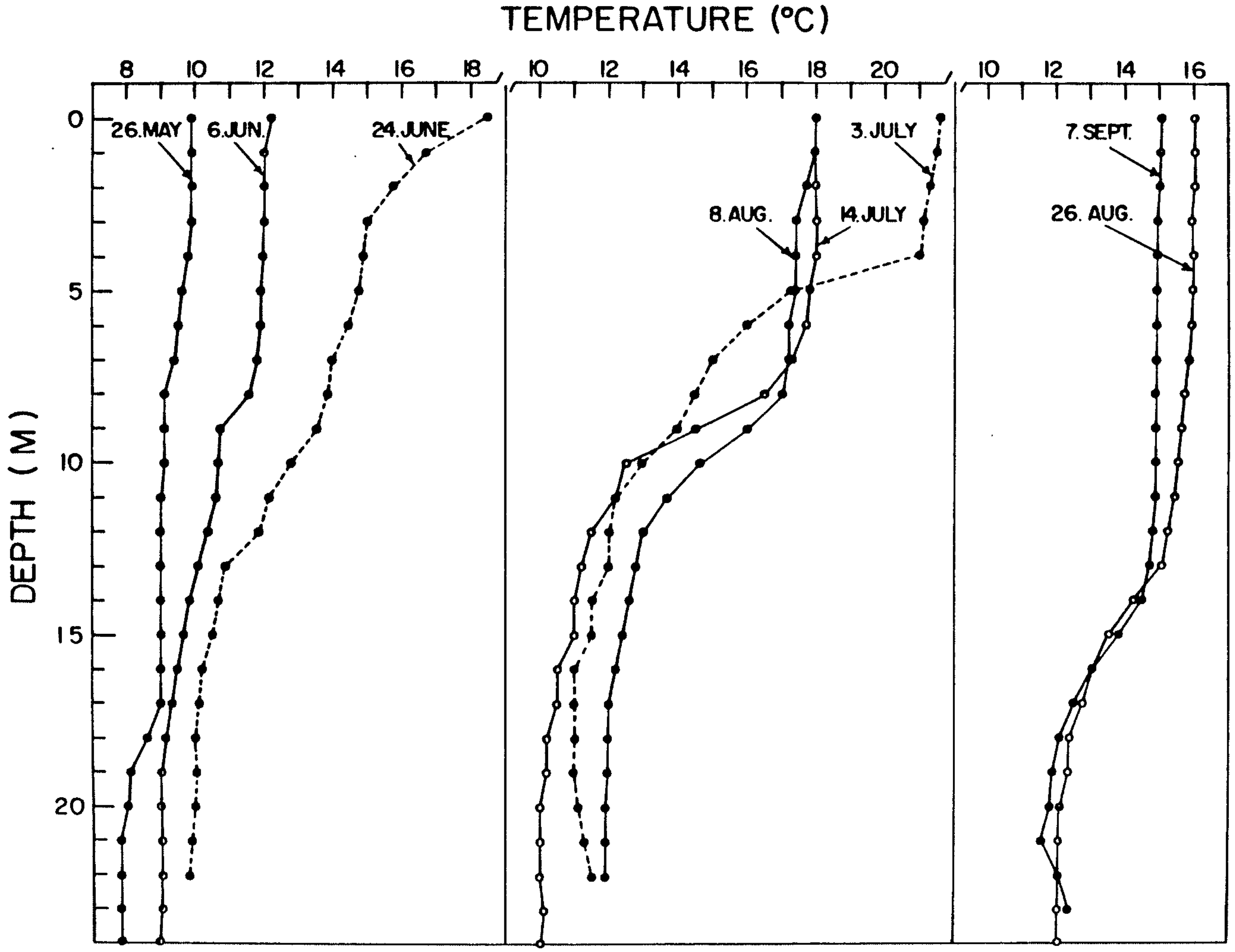

TEMPERATURE (°C)
8
10
12
14
16
18
10
12
14
16
18
20
10
12
14
16
DEPTH (M)
0
5
10
15
20
26.MAY
6.JUN.
24.JUNE
3.JULY
8.AUG.
14.JULY
7.SEPT.
26.AUG.

Figure 4. Temperature profiles in the middle basin of Lake Athapapuskow.

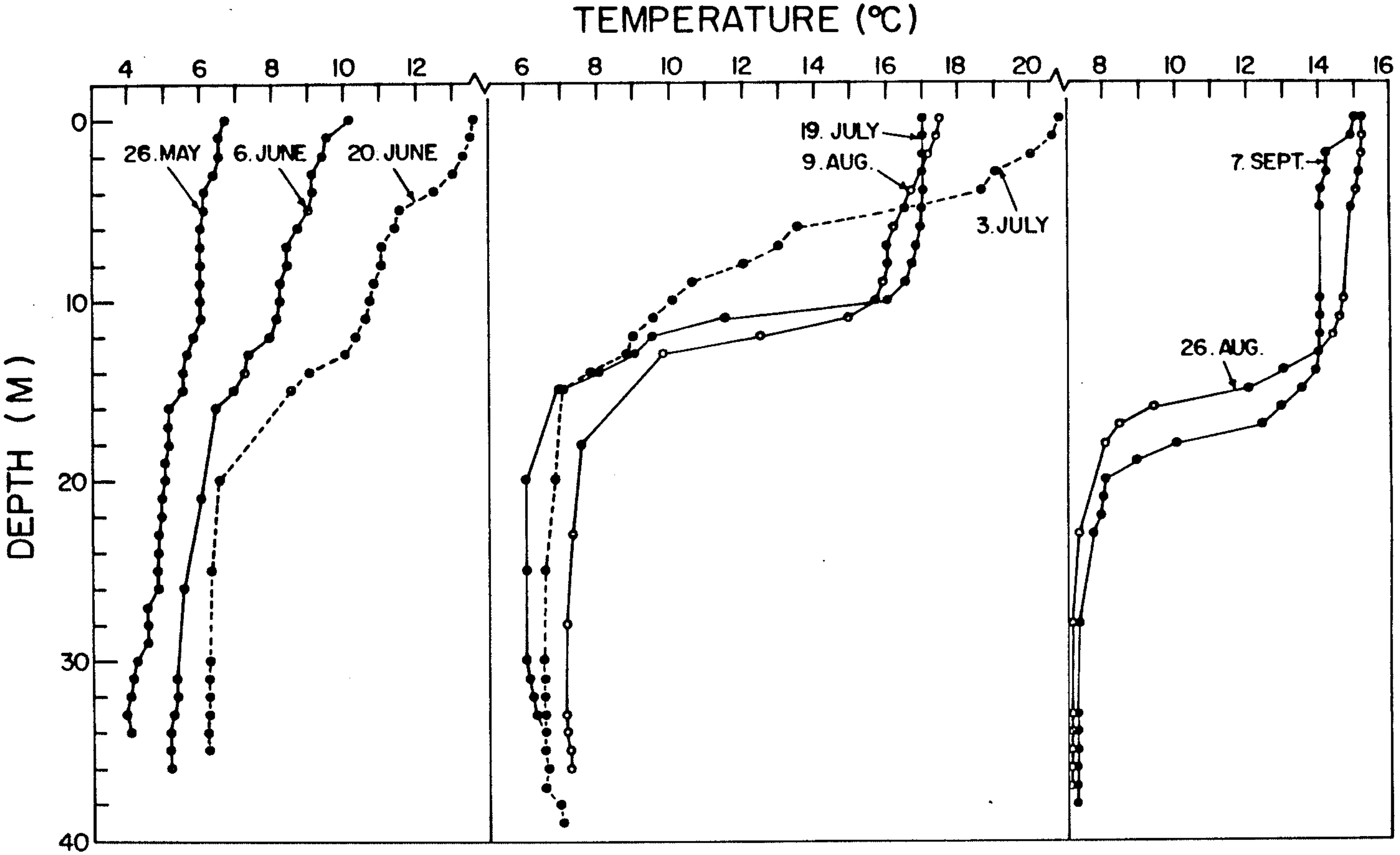

TEMPERATURE (°C)
4
6
8
10
12
6
8
10
12
14
16
18
20
8
10
12
14
16
DEPTH (M)
0
10
20
30
40
26. MAY
6. JUNE
20. JUNE
19. JULY
9. AUG.
3. JULY
7. SEPT.
26. AUG.

Figure 5. Temperature profiles in the south basin of Lake Athapapuskow.

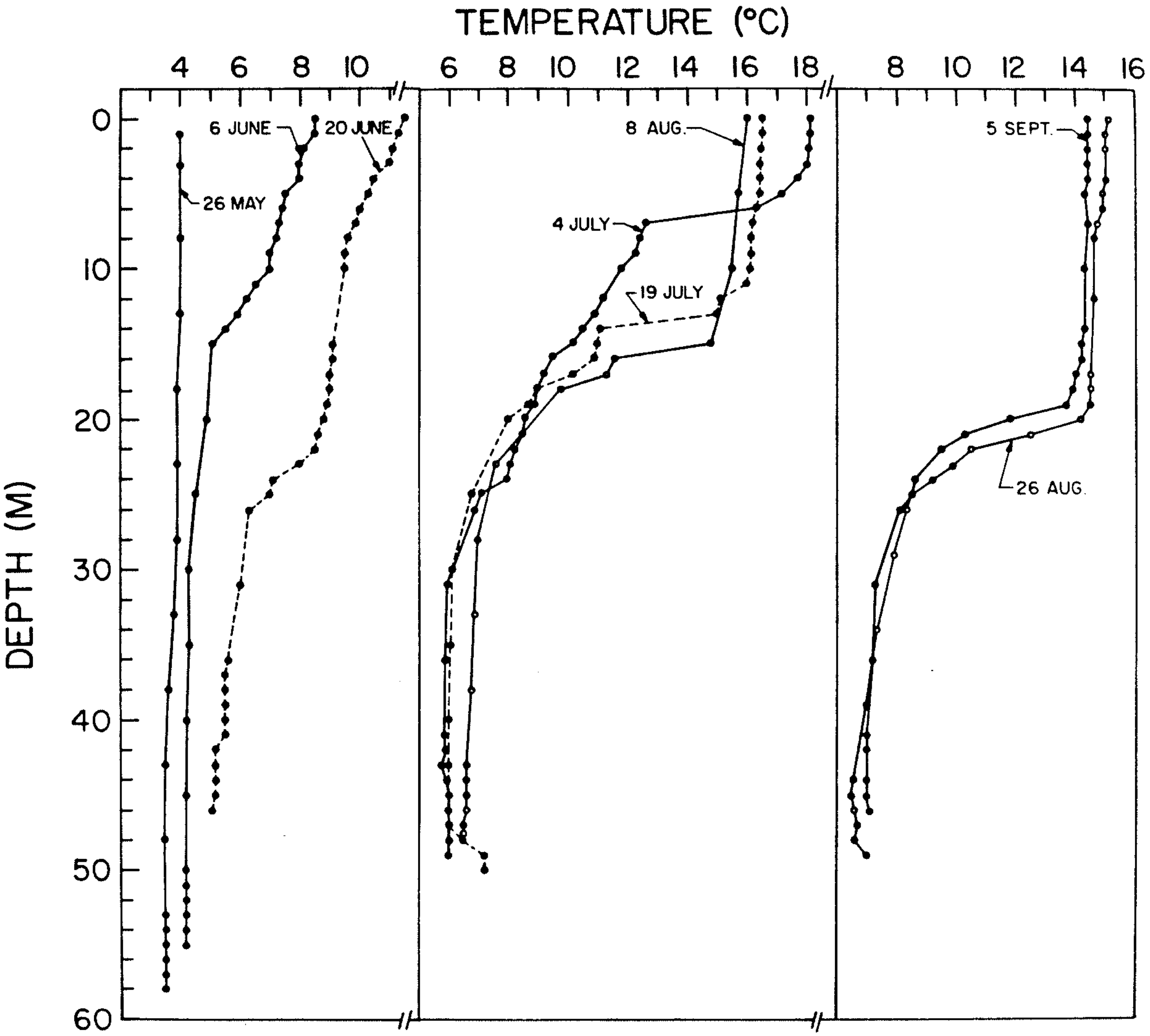

TEMPERATURE (°C)
4
6
8
10
6
8
10
12
14
16
18
8
10
12
14
16
DEPTH (M)
0
10
20
30
40
50
60
6 JUNE
20 JUNE
26 MAY
8 AUG.
4 JULY
19 JULY
5 SEPT.
26 AUG.

Figure 6. Oxygen profiles in the north basin of Lake Athapapuskow.

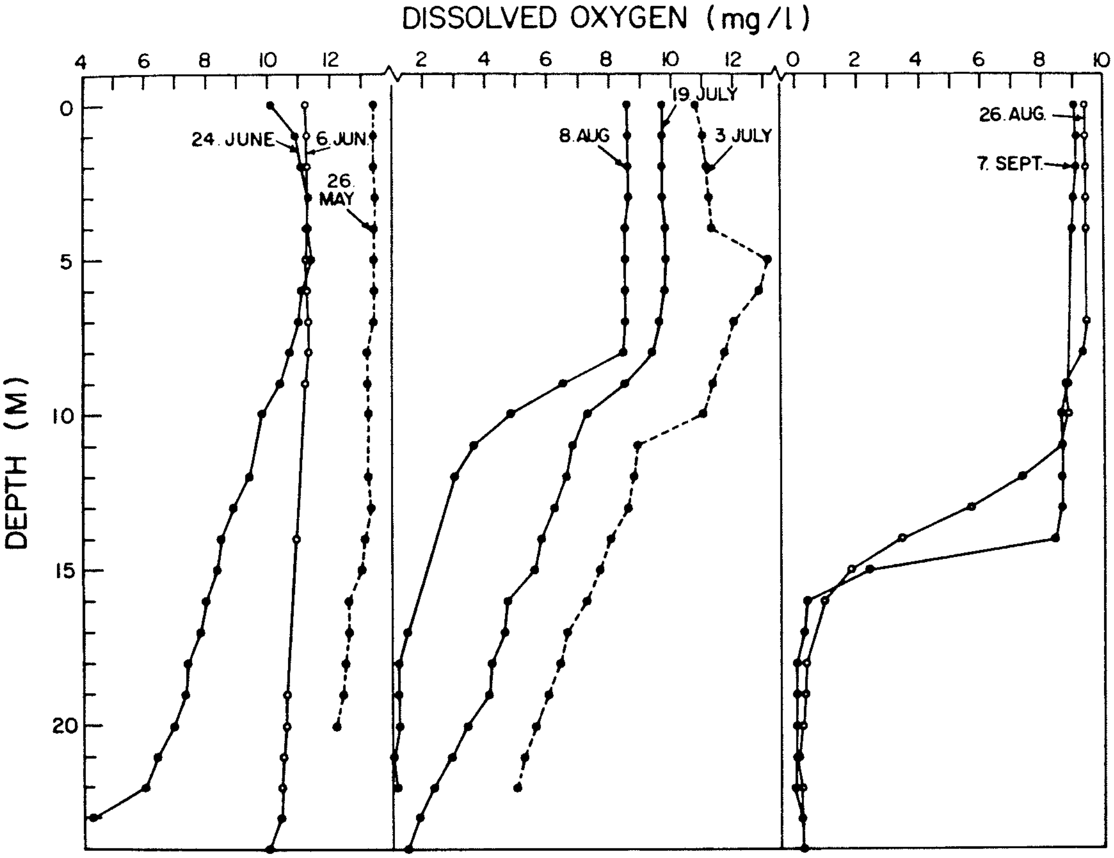
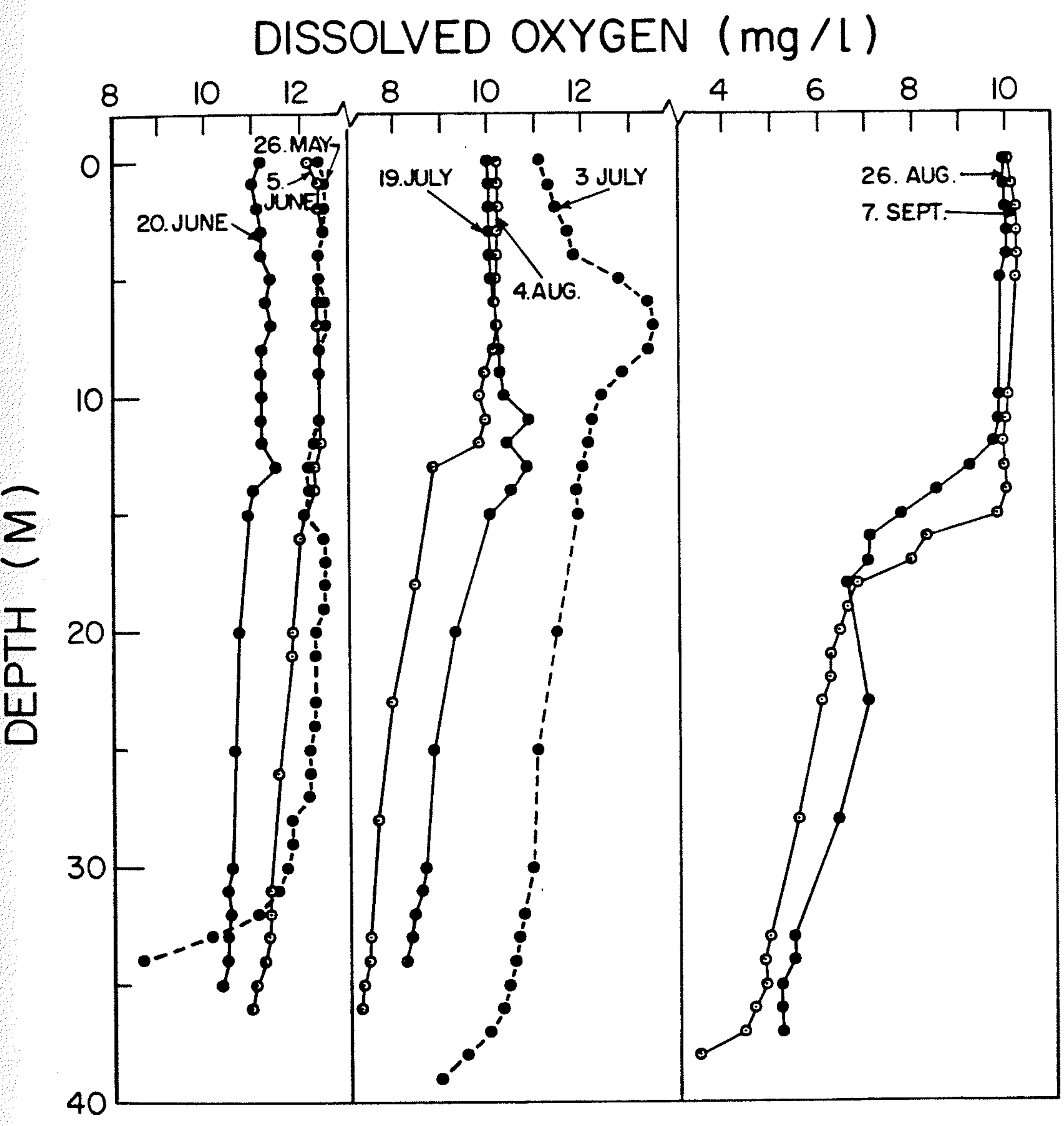
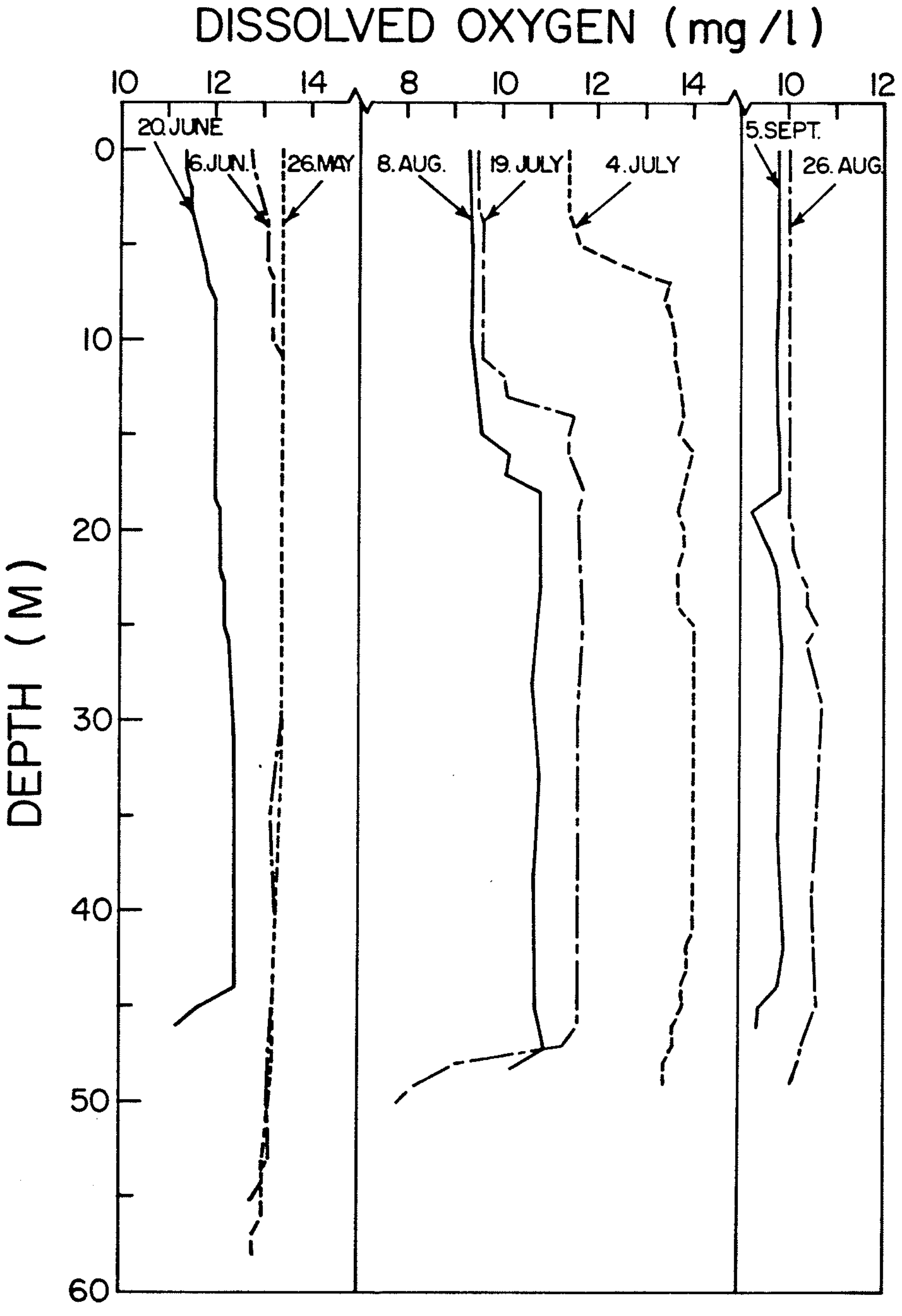

DISSOLVED OXYGEN (mg/l)
4
6
8
10
12
2
4
6
8
10
12
0
2
4
6
8
10
DEPTH (M)
0
5
10
15
20
24. JUNE
6. JUN
26. MAY
19 JULY
8. AUG
3 JULY
26. AUG.
7. SEPT.

Figure 7. Oxygen profiles in the middle basin of Lake Athapapuskow.



DISSOLVED OXYGEN (mg/l)
8
10
12
8
10
12
4
6
8
10
DEPTH (M)
0
10
20
30
40
26. MAY
5. JUNE
20. JUNE
19. JULY
3 JULY
4. AUG.
26. AUG.
7. SEPT.

Figure 8. Oxygen profiles in the south basin of Lake Athapapuskow.


DISSOLVED OXYGEN (mg/l)
10
12
14
8
10
12
14
10
12
20. JUNE
6. JUN.
26. MAY
8. AUG.
19. JULY
4. JULY
5. SEPT.
26. AUG.
DEPTH (M)
0
10
20
30
40
50
60

Temporal and Spatial Description of Gillnet Fishing

In 1977 fifteen stations were repeatedly sampled between June 4 and September 10 (Fig. 2). The number of stations allotted to each basin was roughly proportional to its surface area as a fraction of total lake surface area. Stations were positioned within basins so that each identifiable geographic division of a basin would be sampled. Stations 1 to 6 were sampled six times each at both 9.0 m and 18.5 m depths. Stations 7 (18.5 m), 8 (21.4 m), 9 (29.0 m), 10 (18.5 m), 11 (36.6 m), 12 (70.2 m), 13 (57.2 m), 14 (45.8 m), and 15 (18.5 m) were sampled intermittently, 1 to 3 times each, between July 11 and September 10.

All depths sampled at stations 1 to 6 were marked with floats so that depth, direction of set, and location would be identical between sampling dates. Stations 7 to 15 were not marked, therefore, some variance in location and depth is expected between sampling dates at any given station. For the purpose of collection of small sized fish, the 2.5 cm mesh gillnet was set alone in depths between 2 and 3 m on mud, sand, and rock bottoms, and on rocky reefs. These sets were restricted to the south basin.

In 1978 stations 1 to 4 were sampled in order to concentrate fishing effort in the middle and south basins. Relatively good catches in waters $>$18.5 m in 1977 instigated the addition of a deeper sampling location to each station. The deeper locations are labelled 1', 2', 3', and 4' (Fig. 2) and roughly correspond to the deepest waters in the vicinity of each station. Their respective depths are 33.5, 48.5, 36.5, and 39.5 m. Stations were marked by floats. Each of 3 depths at stations 1 to 4 was sampled four times between June 6 and September 6. Stations 1 (9 and 18.5 m), 3 (9 m), and 4 (18.5 m) were sampled beneath the ice between April 28 and May 1 with the 229 m gillnet gangs used in 1977.

All gillnets were set on the bottom. An echo sounder was run during setting to ensure that all net panels were set at the same depth, and that depths were similar between sampling periods. Gangs set in 8 m of water were inspected using S.C.U.B.A. gear. All panels hung well and did not sag or float from the bottom. Gillnets were set in the evening and picked up the following day. The mean set duration was 16 hours.

Rotenone

Rotenone was used to obtain juvenile burbot from shorelines and creek mouths. Poisoning locations are labelled P and U (Fig. 2). Approximately 250 ml of poison (brand name "Chem Fish Synergized", from the Blue Spruce Co., New Jersey) was used at each location.

With the exception of the Mistik Creek site, areas labelled P were small bays, 25 to 50 m in width, characterized by boulder bottoms and an absence of submerged and emergent vegetation. Boulder size varied greatly but was usually between 10 and 30 cm in greatest dimension.

With the exceptions of the Pineroot Creek site and the site on the large point on the southwest shore of the south basin, areas labelled U were characterized by sand bottoms and emergent vegetation.

Fish poisoning was done in 1978 between August 28 and September 4 in 1 to 3 m of water. Rotenone was poured into a plastic bag weighted with a lead sinker. After a 1 cm^2 hole was cut in the bag it was secured by a line and allowed to sink to the bottom. Poison was then dispersed by towing the bag over the bottom in a zig zag pattern towards shore. Fish were collected from deeper areas when they surfaced and from between rocks and debris along the shoreline. All burbot seen were collected. Of other species poisoned, only a small sample of each was collected for identification.

Mistik Creeek was poisoned on September 1, 1977. This site had a section of riffles 40 m long, 30 m wide, and 5 cm to 1 m deep, followed by a pool 2 m deep. Bottom substrate consisted of 10 to 30 cm boulders but was more uneven than littoral lake boulder bottoms. Both submerged and emergent vegetation were present. A 0.6 cm mesh seine net was placed across the pool and rotenone was poured into the head of the riffles 50 m upstream.

Pineroot Creek was poisoned on April 26 and August 31 in 1977. This site had a mud bottom and a thick growth of submerged and emergent vegetation. Water depth was between 1.0 and 1.5 m. A 0.6 cm mesh seine was placed across the creek mouth and rotenone was poured into the creek 200 m upstream.

The site labelled U (Fig. 2) on the southwest shore of the south basin was poisoned on August 25, 1978. Poisoning was done in 3 to 9 m of water. No vegetation was present. The bottom was extremely irregular and composed of large slabs of limestone which varied from 0.5 to 3 m in diameter. At a depth of approximately 9 m the limestone bottom was replaced by silt. With the use of S.C.U.B.A. gear and a plastic bag with a hose attachment, rotenone was dispersed over the bottom and into cavities and crevices.

Fish Measurements

For all fish captured in gillnets, total length of burbot only, fork length, weight, sex, species identification, mesh size, station, station depth, and capture date, were recorded. Three species of ciscoes, *Coregonus reighardi*, *C. hoyi*, and *C. artedii*, encountered in Lake Athapapuskow in this study and in a previous study (Clarke 1969), were treated as a single category. With the exception of burbot, fish collected with rotenone were identified only.

Gillnet caught fish > 0.40 kg in weight were weighed on a 10 kg spring scale accurate to ± 0.05 kg. Fish weighing ≤ 0.40kg were weighed on a 1 kg spring scale accurate to ± 0.005 kg. Fish lengths were measured to within ± 1.0 mm.

Stomachs were removed from all burbot and lake trout and gonads from gillnet caught burbot and lake trout in 1977. Stomachs and gonads were stored in 10% formalin, and later transferred to 30% isopropyl alcohol.

Burbot poisoned on shorelines were preserved intact in the same manner as were stomachs and gonads of the gillnetted fish. Total length, weight, gonad weight, and sex were determined after preservation. Weighing of poisoned burbot and of gonads from all fish was done on a triple beam balance, accurately to ± 1g. Total length was measured to within ± 1 mm.

Otoliths were removed from all lake trout and burbot for aging.

Maturity and Sex Determination

Male burbot and lake trout were identified as mature when their gonads were white and triangular in cross section. Female burbot and lake trout were identified as mature when their gonads contained eggs visible to the unaided eye and were round in cross section. Mature female burbot had ovaries which were a light pink colour and slightly transluscent. Mature female trout had ovaries which were orange in colour and opaque.

Burbot and lake trout were identified as immature when their gonads lay close under the swimm bladder, were ribbon like in appearance, and flat or oval in cross section. Gonads of immature fish were usually clear or transluscent. Eggs could not be seen with the unaided eye in immature female gonads.

For immature fish, it was sometimes not possible to determine sex using gonad shape or colour. In these instances gonads were squashed between glass slides and examined for the presence of egg cells. Male gonad squashes were granular in texture whereas females showed oocytes. Squashes were examined with the aid of an Olympus compound light microscope under magnification up to 400X, as required.

Gonad weights, expressed as percentage of total body weight, were used to verify maturity determinations because there was little overlap between the relative gonad weights of mature and immature fish. Seasonal gonad developement was studied by plotting gonad weight expressed as percentage of total body weight versus date of capture. Separate plots were made for each sex and maturity status within each sex. The above method of studying seasonal gonad development has been used by LeCren (1951) for perch and by Hanson and Wickwire (1967) and Martin (1970) for lake trout.

Diet Analysis

Burbot diet was analysed numerically and volumetrically. For the former, the number of stomachs in which one or more of a given food item was found was expressed as a percentage of non empty stomachs. For the latter, food items of each identifiable taxon in the diet were blotted dry on paper towels and displacement of each taxon was measured in a graduated cylinder. Volume of each taxon was expressed as percentage of the total volume of all stomach contents. Volumetric analysis is best for assessing the energetic and or nutritional significance of diet items while numerical analysis is best for comparing diets between different groups of fish (Windell and Bowen in Bagenal, 1978).

Otolith Reading and Age Determination

Otoliths were removed from lake trout and burbot within a few hours after capture and stored dry in envelopes. In preparation for reading, the lateral faces of otoliths were ground on number 600 grit carborundum. To enhance clarity, especially in the area of the nucleus, otoliths were ground to the depth of the nucleus. The nucleus was the most opaque area and ring deposition patterns in the first few years were less distinct than rings representative of later growth seasons. Each annulus was composed of a hyaline and opaque ring. The interpretation of the robust burbot otolith was greatly improved through grinding.

Lake trout otoliths were ground intact but burbot otoliths were broken through the nucleus along the dorso-vertral axis before grinding (Fig. 9). Since the lateral face of the burbot otolith is concave, grinding it intact would remove its anterior and posterior tips. Otoliths were placed, ground side upwards, in a drop slide filled with benzyl benzoate and viewed under transmitted light with an Olympus compound light microscope at 10X and 100X magnification. Several independent readings of each otolith were made to obtain a consistent annuli count. If a consistent count could not be obtained the fish was not aged. From 541 pairs of lake trout otoliths and 1103 pairs of burbot otoliths examined, age was determined for 498 lake trout and 1082 burbot.

All otolith annuli counts were made on the lateral face of the otolith along the anterio-posterior axis on a radius which extended from the nucleus to the posterior tip. Annulus deposition on this radius was usually clear but when it was not, annuli counts were made on the radius extending from the nucleus to the anterior tip. When otoliths were particularly difficult to read the entire lateral face was used to obtain an annuli count.

In lake trout the first 2 or 3 annuli showed almost no evidence of a hyaline ring and appeared to be composed of opaque material only. The opaque nucleus and first pair of hyaline and opaque rings were counted as the first annulus.

Each successive pair of hyaline and opaque rings was counted as one annulus. Burbot otoliths were interpreted after Chen (1969) and Hackney (1973). Further information on otolith aging and the deposition of hyaline and opaque rings in burbot otoliths is given in Appendix A.

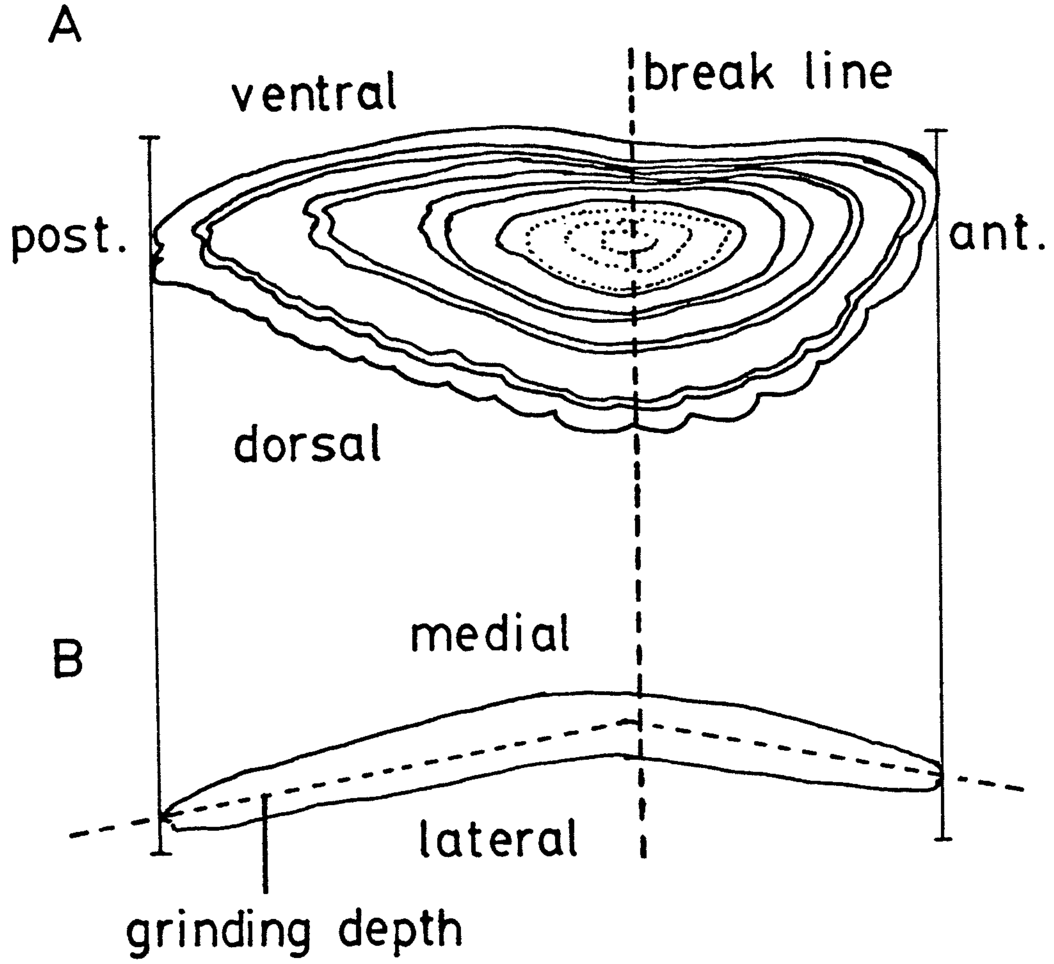
Statistical Analysis

Statistical comparisons were done under the assumption that significant exchange of fish occurred between the north and middle basins but not between the middle and south basins. Therefore, fish were grouped, before analysis, into south group (fish collected in the south basin) and north group (fish collected in the middle and north basins). Burbot collected in Mistik Creek were analysed as a third group because it was not certain what fish stock they represented. A detailed account of the above assumption is presented in the Discussion. All computations were done with Biomedical Computer Programs Statistical Packages, P series (Dixon and Brown 1979).

Growth

Growth of burbot and lake trout in Lake Athapapuskow was examined using population growth rates. These rates are obtained by comparing the mean size of surviving fish at successive ages (Bagenal and Tesch in Bagenal 1978; Ricker 1975) and were presented in this study as plots of mean

Figure 9. Diagramatic presentation of the lateral view (A) and ventral view (B) of a burbot otolith showing planes of breaking (transverse) and grinding (sagittal).


A
ventral
break line
post.
ant.
dorsal
B
medial
lateral
grinding depth

length versus age. Population growth rates give the rate of growth as shown by a population affected by mortality, migration, etc., as opposed to true growth rates which are growth rates of individual fish determined by back calculations (Bagenal and Tesch in Bagenal 1978). As population growth rates are most commonly used for presenting burbot and lake trout growth they were also used in this study. Bagenal and Tesch (in Bagenal 1978) stated that when properly carried out this is the most satisfactory method of presenting growth rates based on age-length data. An account of the assumptions required for the use of population growth rates in this study is presented in Appendix C.

Statistical comparisons of length versus age regressions between sexes within basins and between basins were done using analysis of covariance (ANCOVA) on transformed data. Aptness of age-length data to analysis by linear regression was determined graphically using residual plots according to Neter and Wasserman (1974). They state that a linear model is appropriate if the residuals tend to fall within a horizontal band centred around 0, displaying no systematic tendency to be positive or negative. Residual plots of untransformed burbot and lake trout age-length data indicated that for both species the relationship between age and length was not linear because residuals varied in a systematic fashion between being positive and negative. Therefore, all age-length data were linearized by transformation prior to analysis.

Burbot

After ages and lengths were transformed to their natural logarithms (Ln) residual plots indicated that analysis by linear regression was appropriate. ANCOVA was then used to compare regressions of Ln length versus Ln age between sexes within basins and between basins for fish at ages 0 to 28. For untransformed data, plots of mean length versus age and "t" tests ("t" tests were used for comparison between basins of mean lengths at each age) indicated that growth rates were similar between basins for fish at ages 0 to 10 but different for fish at ages 10 to 28. Consequently, regressions of Ln length versus Ln age for each of the above age groups were analysed in absence of the other group. ANCOVA was used to compare regressions of Ln length versus Ln age between sexes within basins and between basins for fish at ages 10 to 28. For fish at ages 0 to 10, ANCOVA was used to compare regressions of Ln length versus Ln age between sexes within basins. After data for sexes were combined, ANCOVA could not be used to compare regressions of Ln length versus Ln age between basins for fish at ages 0 to 10 because slopes of these regressions were significantly different.

ANCOVA was used to compare regressions of Ln length versus Ln age between sexes of burbot collected in Mistik Creek. After data for sexes were combined regressions were compared among burbot from Mistik Creek and all basins. Ages 0 to 7 were used for these comparisons because the Mistik Creek sample only contained burbot of these ages.

Lake Trout

After lake trout ages were transformed to their reciprocals residual plots indicated that a linear model was appropriate for analysing regressions of length versus 1/age. ANCOVA was then used to compare regressions of length versus 1/age between sexes within basins and between basins for fish at ages 4 to 45. For untransformed data, plots of mean length versus age indicated that growth was similar between basins for fish at ages 4 to 14 but different for fish at ages 14 to 45. Consequently, growth of each of the above age groups was compared between sexes within basins and between basins in absence of the other group. For fish at ages 4 to 14, residual plots indicated that transformation of ages and lengths to their natural logarithms was required before linear regression could be considered an appropriate analysis model. ANCOVA was then used to compare regressions of Ln length versus Ln age between sexes within basins and between basins for fish at ages 4 to 14. For fish at ages 14 to 45, residual plots indicated that transformation of length to its natural logarithm was required before linear regression could be considered an appropriate analysis model. ANCOVA was then used to compare regressions of Ln length versus age between sexes within basins for fish at ages 14 to 45. The use of ANCOVA for comparison between basins of regressions of Ln length versus age was not possible for the above age group because slopes of these regressions were significantly different.

Length-Weight Relationships

Length-weight relationships of both species were determined and compared by using analysis of covariance on plots of log length versus log weight according to LeCren (1951). Comparisons were made between sexes, basins, and years. No attempts were made to analyse seasonal change in length-weight relationships. In addition to comparisons using all age groups, separate comparisons of length-weight relationships were made between sexes within basins and between basins for age groups 0 to 10 and 10 to 28 for burbot and for age groups 4 to 14 and 14 to 45 for lake trout. These comparisons were made because age-length data suggested a between basin divergence in the growth of burbot at age 10 and of lake trout at age 14. Therefore, a corresponding analysis of length-weight relationships at these ages was warranted.

Mortality Rates

Instantaneous mortality rates (Z) of lake trout and burbot were calculated according to Ricker (1975) as the descending slope of the natural logarithm of the frequency of age N versus age N. Instantaneous mortality rates of lake trout, south basin burbot, and middle and north basin burbot, were calculated using frequencies of ages 9 to 45, 11 to 22, and 15 to 27 respectively. After determining Z, survival rates (S) and total annual mortality rates (A) of the above three groups were calculated from the following equation presented by Ricker (1975): $1 - A = S = e^{-Z}$, where e is a constant equal to 2.71828.

Comparisons of Z between sexes, basins, and years were done with a test for the equality of slopes according to Neter and Wasserman (1974). When mortality, growth, and length-weight regressions of burbot and lake trout were compared between basins, sexes, and years within each species, the equality of error variances of compared regressions was tested according to Neter and Wasserman (1974), page 165 .

RESULTS

Gillnet Selectivity

Comparisons of lake trout and burbot length frequency distributions among mesh sizes indicated that for both species the various mesh sizes were selective for different length classes of fish (Figs. 10, 11, 12, and 13). The poor representation of small length classes of burbot and lake trout in all mesh sizes is a feature of catch data derived from gillnets and is due to the inefficiency of gillnets in collecting small fish. Hamley (1975) reviewed the evidence that large mesh sizes are more efficient than smaller.

Gillnet samples of burbot from the south basin contained fish between 8 and 74 cm in total length whereas those from the middle and north basins contained fish between 38 and 80 cm in total length. South basin catches contained relatively greater numbers of small fish of which the greatest proportion were captured in mesh sizes 5.1 to 10.8 cm whereas middle and north basin catches contained relatively greater numbers of large fish of which the greatest proportion were captured in mesh sizes 7.6 to 13.3 cm (Figs. 10 and 11). The selectivity of different mesh sizes for various length classes of burbot is illustrated by: 1) the size frequency histograms of fish caught in various mesh sizes in both basins, which show a relatively large and consistent shift to the right with increasing mesh size (Figs. 10 and 11), and 2) the high squared correlation coefficients for regressions of total length of burbot versus mesh size (Table II). The fact that burbot were usually either girthed or gilled, rather than tangled, probably contributed to the size selectivity of most gillnet mesh sizes used. The main exception was the tangling of large burbot by their maxillae and teeth in 2.5 and 5.1 cm mesh gillnets in the middle and north basins (Fig. 10).

Samples of lake trout caught in gillnets in the south basin contained fish between 14 and 92 cm in fork length whereas those in the middle and north basins contained fish between 29 and 80 cm in fork length. The large range of lake trout length classes caught in all mesh sizes, the relatively small increase in mean lengths of length frequency histograms as mesh size increases, and the absence of strong modal length classes in these histograms indicates that, in all basins, mesh size was not very selective for lake trout length (Figs. 12 and 13). Squared correlation coefficients for regressions of lake trout length versus mesh size were highest in the south basin because a distinct group of lake trout between 20 and 32 cm long were caught in the 5.1 cm mesh gillnet in this basin (Table II, Fig. 13). Lake trout of this length range were infrequently collected in mesh sizes other than 5.1 cm, were almost absent from middle and north basin catches, and were present in south basin catches in 1978 only. Squared correlation coefficients for regressions of lake trout length versus mesh size also indicated that mesh size was not very selective for fish length in the middle and north basins. When the 5.1 cm mesh was excluded from calculations, mesh size was poorly correlated with length in the south basin but the squared correlation coefficient remained unchanged for north and middle basin catches. Lake trout were often entangled in the gillnets by their maxillae and teeth, which probably reduced the selectivity of mesh size for fish length. Johnson (1972, 1976) also found that various mesh sizes were unselective for lengths of lake trout from several Northwest Territories populations.

There is some indication that length frequency histograms of lake trout captured in the south basin are bimodal (Fig. 12). Similar patterns of selectivity curves have also been found for other trout species. Ricker (1942) found a trimodal pattern in gillnet selectivity curves for cutthroat trout (Salmo clarki) and dolly varden (Salvelinus malma) in Cultus Lake. Hamley, in his 1975 review, stated that multimodal selectivity curves may be expected when captures are concentrated at body discontinuities such as maxillae or operculae, as well as the widest part of the body. Modes of large length classes in figure 13 may represent lake trout which were entangled whereas modes of small length classes may represent girthed fish. An alternative explanation of the multimodal histograms in Figure 13 is that the poor representation of length classes between the modes (approximately 44 to 50 cm) may reflect a relatively low abundance of these sizes of fish in Lake Athapapuskow. Method of capture, entanglement or girthing, was not recorded, therefore it was not possible to determine which of the above explanations was appropriate. Approximately the same range of gillnet mesh sizes, used to sample other lake trout populations [Keller Lake (Johnson 1972); Nonacho Lake, Lac la Martre, Maze Lake, Whitefish Lake, Dismal Lake, Wholdaia Lake, Maguse Lake, Beverly Lake, Vaillant Lake (Johnson 1976); Lac la Ronge (Rawson 1961)] were efficient at collecting fish between approximately 44 and 50 cm in length. Poor representation of these length classes in Lake Athapapuskow samples may reflect a relatively low abundance of these length classes in the population. Length frequency histograms of fish caught in the middle and north basins did not show multimodality (Fig. 12). This may be due to the small sample size of lake trout taken in these basins.

Gear selectivity for sex was tested using chi square analysis. The ratio of males to females collected within each basin did not differ significantly from one to one for lake trout, gillnet caught burbot, and rotenone-poisoned burbot (Table III). This indicated that both sexes of lake trout and burbot were equally vulnerable to sampling.

Figure 10. Length frequency distributions of burbot caught in gillnets of given mesh sizes (cm) in the middle and north basins of Lake Athapapuskow. Mean length is indicated by a vertical line.

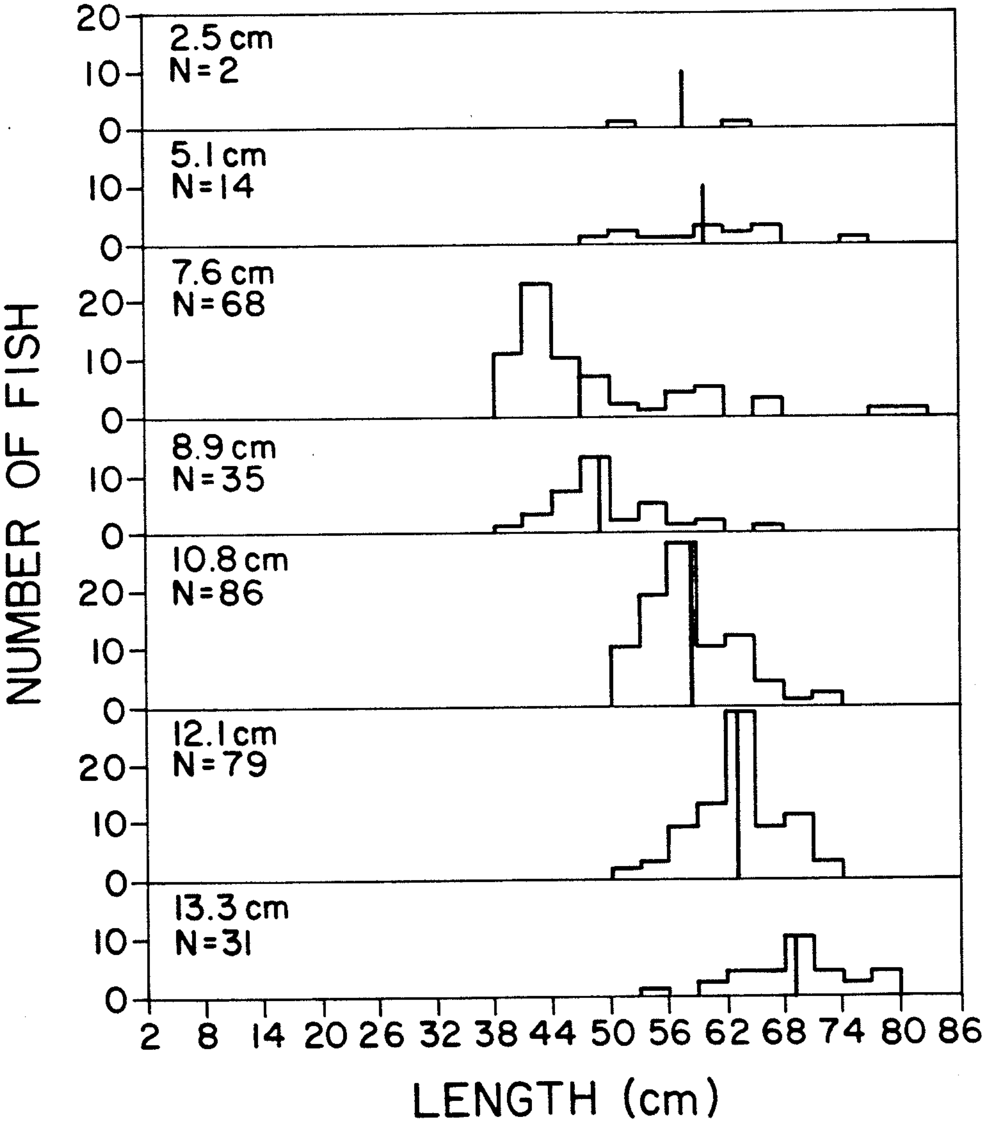

2.5 cm
N=2
5.1 cm
N=14
7.6 cm
N=68
8.9 cm
N=35
10.8 cm
N=86
12.1 cm
N=79
13.3 cm
N=31
0
10
20
NUMBER OF FISH
2
8
14
20
26
32
38
44
50
56
62
68
74
80
86
LENGTH (cm)

Figure 11. Length frequency distributions of burbot caught in gillnets of given mesh sizes (cm) in the south basin of Lake Athapapuskow. Mean length is indicated by a vertical line.

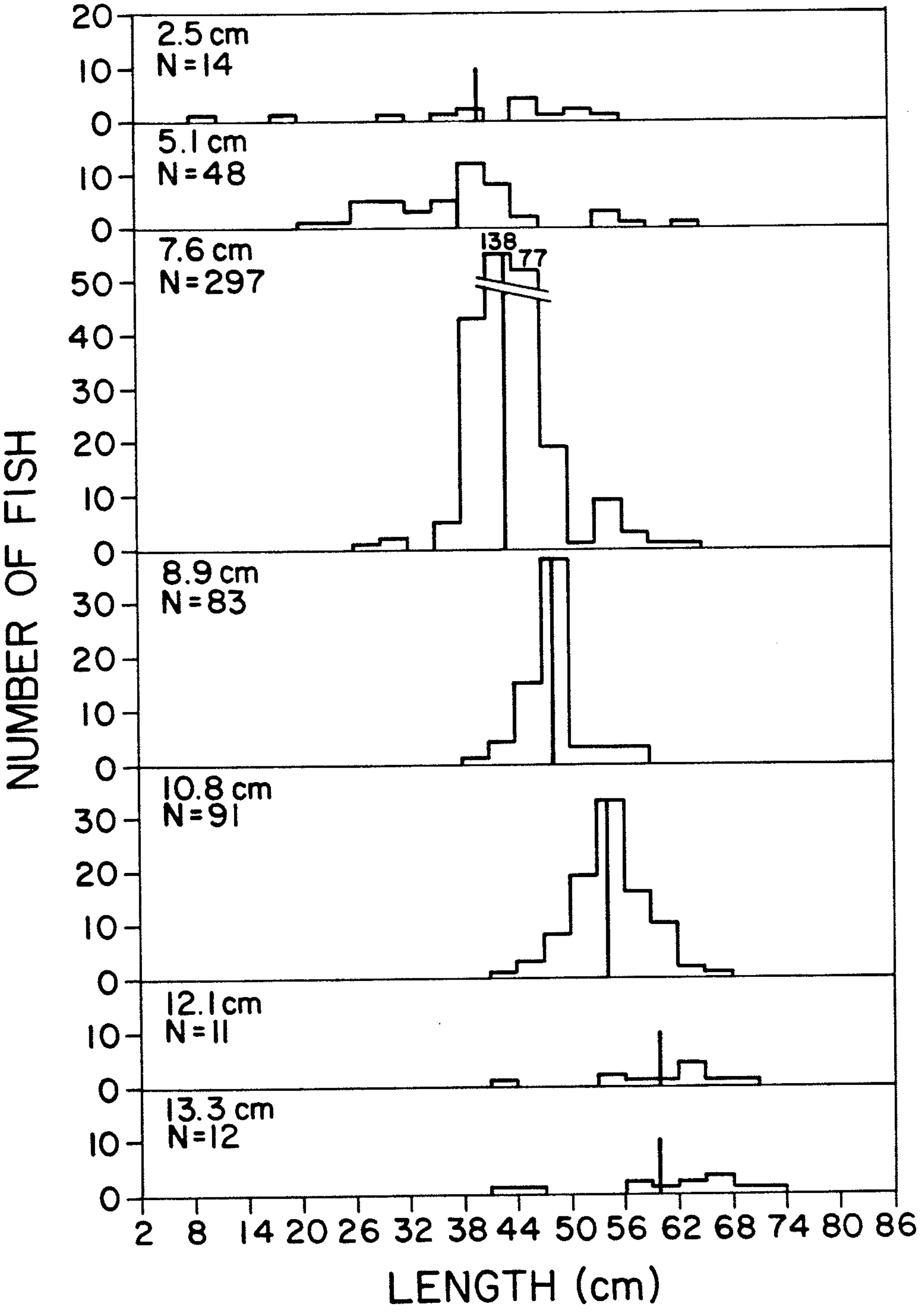

2.5 cm
N=14
5.1 cm
N=48
7.6 cm
N=297
138
77
8.9 cm
N=83
10.8 cm
N=91
12.1 cm
N=11
13.3 cm
N=12
20
10
0
50
40
30
NUMBER OF FISH
2
8
14
20
26
32
38
44
50
56
62
68
74
80
86
LENGTH (cm)

Figure 12. Length frequency distributions of lake trout caught in gillnets of given mesh sizes (cm) in the middle and north basins of Lake Athapapuskow. Mean length is indicated by a vertical line.

Figure 12. Length frequency distributions of lake trout caught in gillnets of given mesh sizes (cm) in the middle and north basins of Lake Athapapuskow. Mean length is indicated by a vertical line.

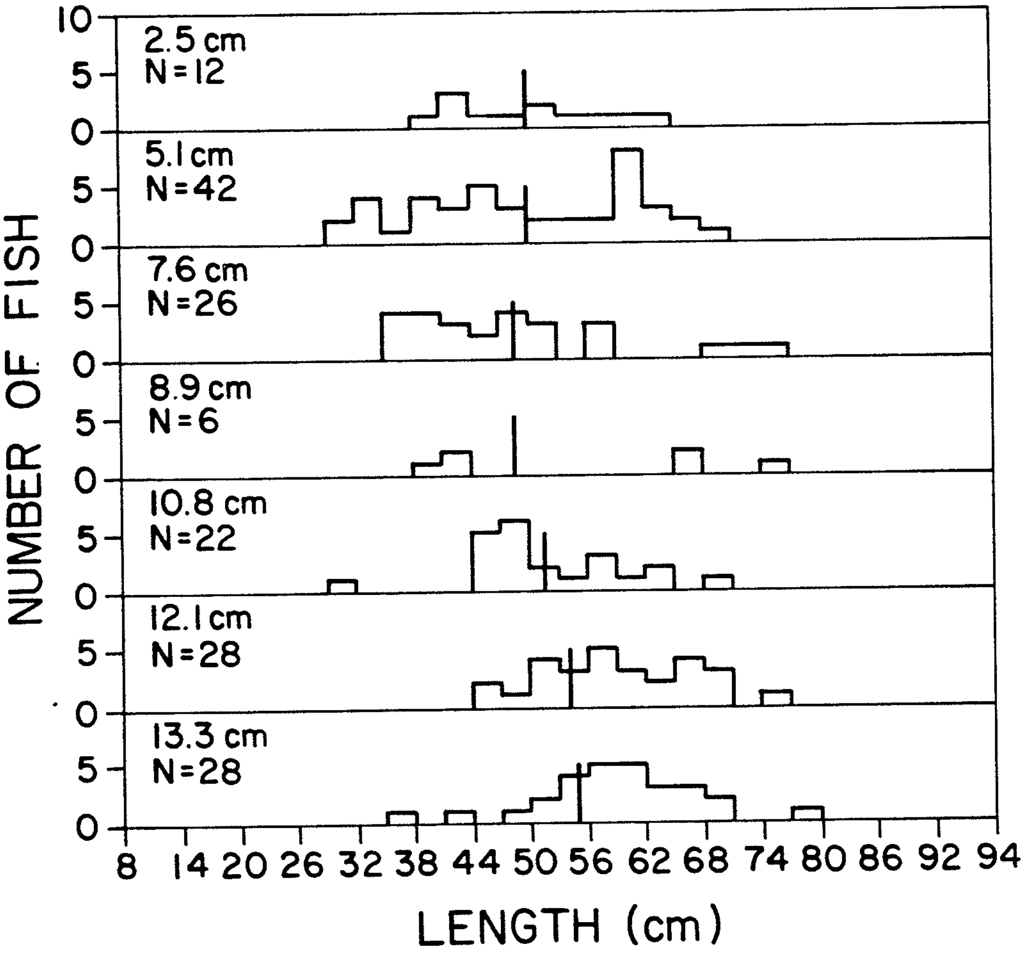

2.5 cm
N=12
5.1 cm
N=42
7.6 cm
N=26
8.9 cm
N=6
10.8 cm
N=22
12.1 cm
N=28
13.3 cm
N=28
10
5
0
NUMBER OF FISH
8
14
20
26
32
38
44
50
56
62
68
74
80
86
92
94
LENGTH (cm)

Figure 13. Length frequency distributions of lake trout caught in gillnets of given mesh sizes (cm) in the south basin of Lake Athapapuskow. Mean length is indicated by a vertical line.

Table II . Squared correlation coefficients (r^2) for regressions of mesh size on length of fish captured in mesh sizes (stretched measure) 2.5, 5.1, 7.6, 8.9, 10.8, 12.1, and 13.3 cm.

		r^2 values	
Basins		all mesh sizes	all mesh sizes except 5.1 cm
Middle and North	Lake Trout	0.12	0.12
South	Lake Trout	0.20	0.08
Middle and North	Burbot	0.34	-
South	Burbot	0.47	-

Table III. Chi-square analysis of the male to female ratio of burbot and lake trout collected in Lake Athapapuskow.

Species	Basin	Gear	Total Number			Percentages		χ^2
			Undetermined Sex	Males	Females	Males	Females	
Lota _lota_	north and middle	gillnets	10	152	153	49.8	50.2	0.01
		rotenone	2	56	55	50.4	49.6	0.02
	south	gillnets	8	266	282	48.5	51.5	0.93
		rotenone	0	34	43	44.2	55.8	2.10
Salvelinus namaycush	north and middle	gillnets	11	78	75	51.0	49.0	0.12
	south	gillnets	39	173	177	49.4	50.6	0.09

Ho: proportion of males = $\frac{50}{100}$, proportion of females = $\frac{50}{100}$

reject Ho if $\chi^2 \geq \chi^2_{0.05,\ 1} = 3.84$.

Population Characteristics

Burbot Length Frequency Distributions

Gillnet Caught Burbot. A pronounced difference between basins in length frequency distributions was observed (Fig. 14). Length frequency histograms of fish caught in the south basin were more sharply peaked than were those of fish caught in the middle and north basins. The strongest representation of smaller size classes was observed in the south basin and of larger size classes in the middle and north basins. Mean length of burbot in the middle and north basins (57.0 cm) was significantly greater ($\alpha = .05$, "t" = 17.91) than mean length in the south basin (46.0 cm). The length frequency histogram of burbot caught in the south basin was slightly skewed to the right and the length frequency histogram of burbot caught in the middle and north basins was approximately normal in shape (Fig. 14).

There was a greater overlap between length frequency distributions of gillnet caught and rotenone-poisoned burbot in the south basin than in the middle and north basins.

Rotenone-poisoned Burbot. Juvenile burbot sampled by rotenone poisoning were smallest in the middle and north basins (mean length = 15.6 cm). Mean length of burbot sampled in the south basin (17.9 cm) was larger than that of burbot sampled in the middle and north basins, and the largest mean length was observed in the Mistik Creek sample (mean length = 22.0 cm). The differences in mean lengths among all samples were significant ("t" tests at $\alpha = .05$). Size distributions of burbot collected in Mistik Creek and the middle and north basins were more sharply peaked than that of burbot collected in the south basin (Figs. 14 and 15).

Burbot Age Frequency Distributions

Gillnet Caught Burbot. A pronounced difference between basins in age frequency distributions was oberved (Fig. 16). The age frequency histogram of burbot caught in the south basin was more sharply peaked than was the histogram for burbot caught in the middle and north basins. Mean age of burbot from the middle and north basins (15.3 years) was significantly greater ("t" = 13.61, $\alpha = .05$) than mean age of burbot from the south basin (11.8 yrs). Both age frequency distributions were approximately normal but appeared to be skewed slightly to the right.

As in length frequency distributions, more overlap was observed between age classes of rotenone-poisoned and gillnet caught burbot in the south basin than in the middle and north basins.

Rotenone-poisoned Burbot. All age frequency distributions of poisoned burbot were approximately normal in shape (Figs. 15 and 16). Mistik Creek and south basin distributions appeared to be slightly skewed to the right. Mean age (3.1 yrs) of burbot from the middle and north basins was significantly less than the mean age (4.0 yrs) of Mistik Creek burbot ("t" = 3.79, α = .05) and the mean age (3.8 yrs) of burbot from the south basin ("t" = 4.10, α = .05). There was no significant difference between mean ages of burbot from Mistik Creek and the south basin ("t" test, α = .05).

Lake Trout Age and Length Frequency Distributions

The length frequency histogram of lake trout caught in the south basin was more sharply peaked than that of lake trout caught in the middle and north basins (Fig. 17). The strong representation of 21 to 33 cm lake trout observed in south basin catches was not seen in middle and north basin catches. Lake trout mean length in the middle and north basins (52.8 cm) was significantly greater ("t" = 4.52, α = .05) than mean length in the south basin (48.2 cm).

Age frequency histograms of lake trout are given for the south basin and middle and north basins (Fig. 18). There is great variation within each histogram in year class strength. Both histograms are strongly skewed to the right and have relatively poor representation of year classes 15 to 20. The south basin also has a relatively poor representation of year classes 27 to 29. Strong representation of year classes 4 to 6 (the 21 to 33 cm size group described above) was observed in the south basin. There was no significant difference between mean age of lake trout in the south basin (14.8 yrs) and middle and north basins (14.9 yrs).

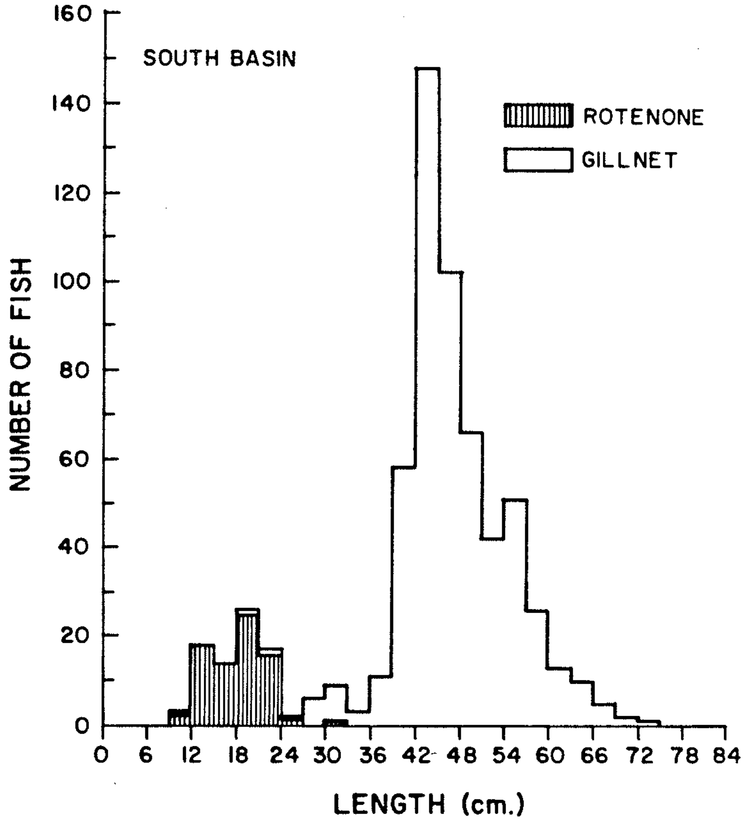
Length-Weight Relationships

When all ages of burbot collected were represented in the analysis there were no significant differences in length-weight regressions between the different years in which fish were caught or between sexes in the middle and north basins. For fish caught in the south basin, there were no significant differences in length-weight regressions between years. After data for 1977 and 1978 were combined the female length-weight regression was significantly greater than that for males in the south basin ("F" = 10.31, $\alpha = .05$). The regression equations are as follows:

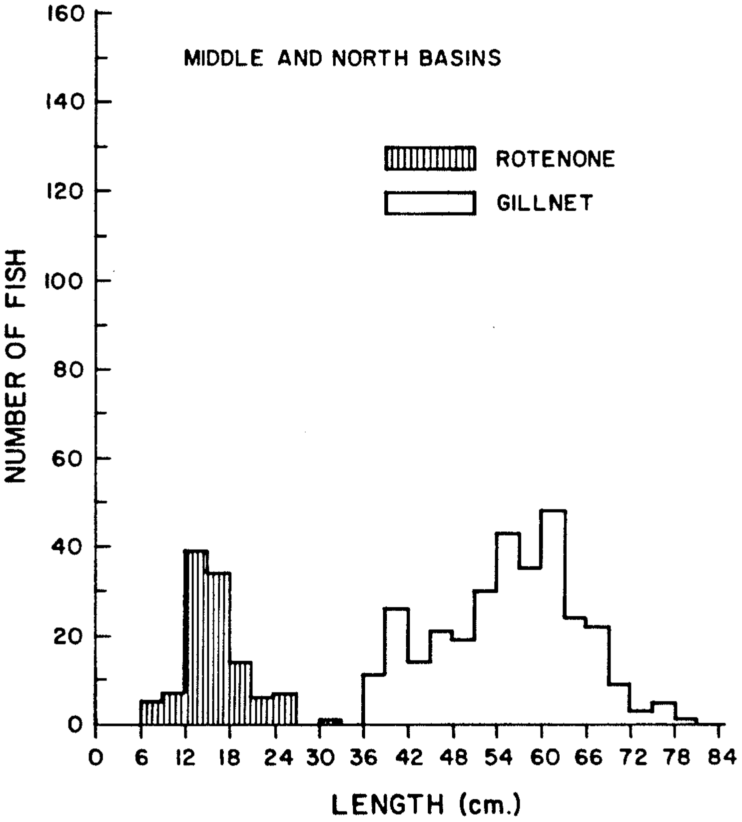
middle and north basins: $\text{Log } W = 3.0024 \text{ Log } L - 2.1990$,
south basin male: $\text{Log } W = 2.9720 \text{ Log } L - 2.1081$,
south basin female: $\text{Log } W = 3.0294 \text{ Log } L - 2.2589$.

Males from the south basin had an adjusted mean weight which was significantly greater than that of middle and north basin burbot ("F" = 7.26, $\alpha = .05$). The length-weight regression of south basin females had a significantly greater slope than the regression of middle and north basin fish ("F" = 7.83, $\alpha = .05$).

Figure 14. Length frequency histograms of burbot caught in the south basin and middle and north basins of Lake Athapapuskow.

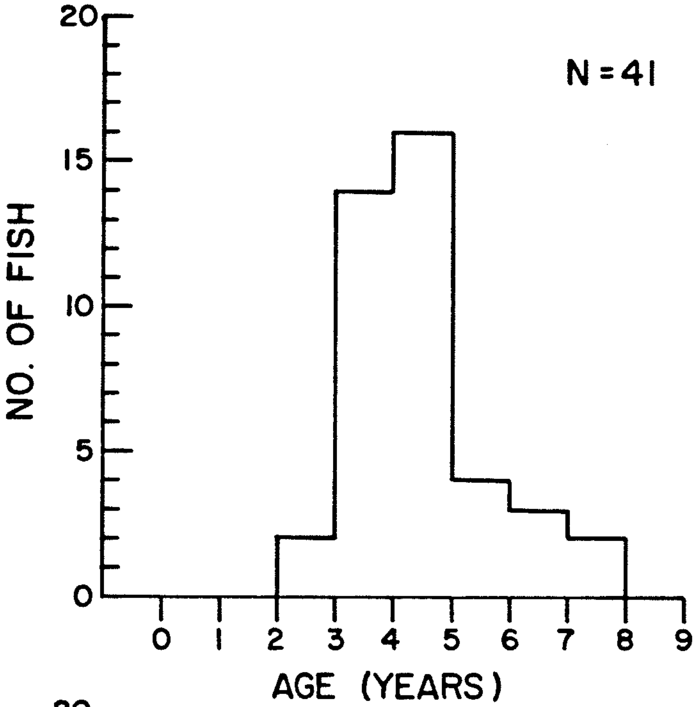


SOUTH BASIN
ROTENONE
GILLNET
NUMBER OF FISH
0
20
40
60
80
100
120
140
160
0 6 12 18 24 30 36 42 48 54 60 66 72 78 84
LENGTH (cm.)



MIDDLE AND NORTH BASINS
ROTENONE
GILLNET
NUMBER OF FISH
0
20
40
60
80
100
120
140
160
0 6 12 18 24 30 36 42 48 54 60 66 72 78 84
LENGTH (cm.)

Figure 15. Age and length frequency histograms of rotenone-poisoned burbot from Mistik Creek.


N = 41
NO. OF FISH
0
5
10
15
20
0
1
2
3
4
5
6
7
8
9
AGE (YEARS)

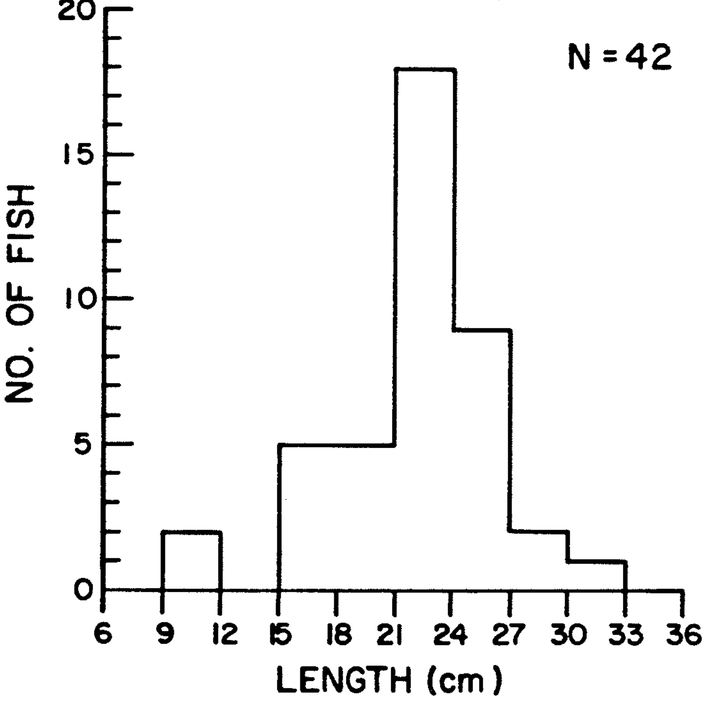
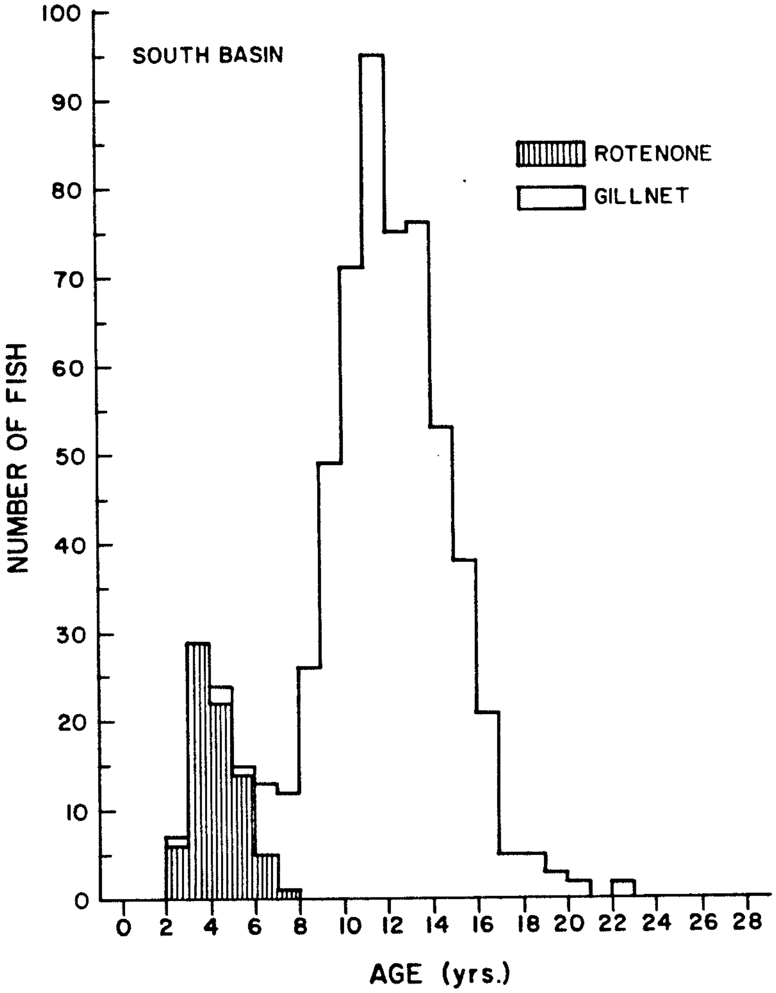

N = 42
NO. OF FISH
0
5
10
15
20
6
9
12
15
18
21
24
27
30
33
36
LENGTH (cm)

Figure 16. Age frequency histograms of burbot caught in the south basin and middle and north basins of Lake Athapapuskow.


SOUTH BASIN
ROTENONE
GILLNET
NUMBER OF FISH
AGE (yrs.)
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28

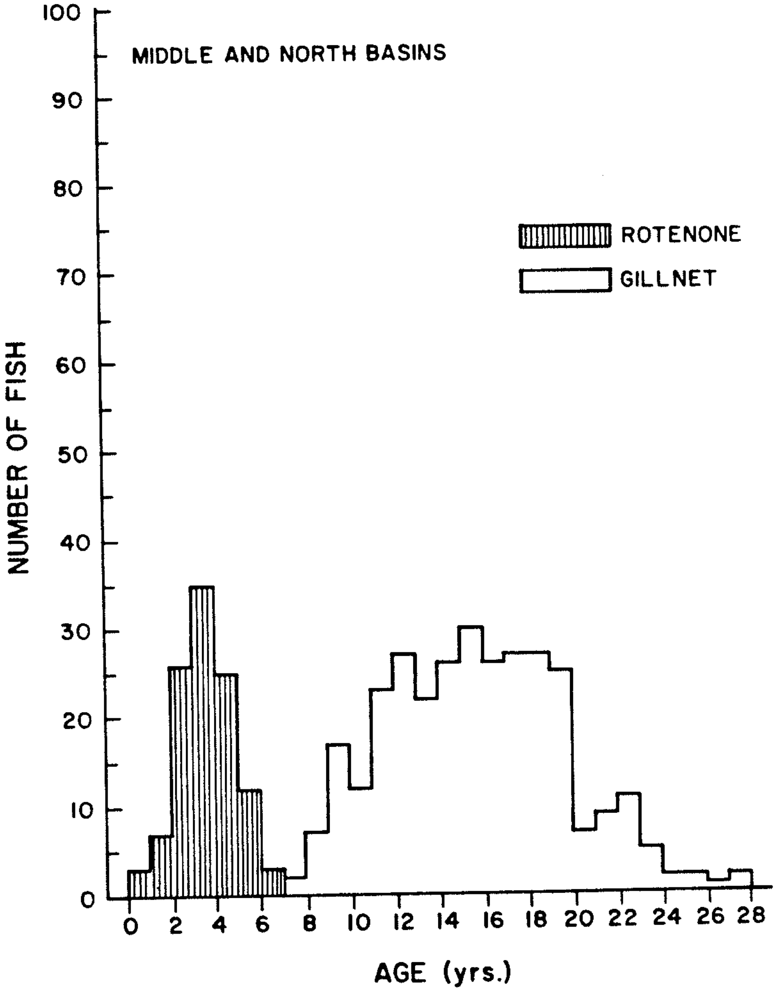
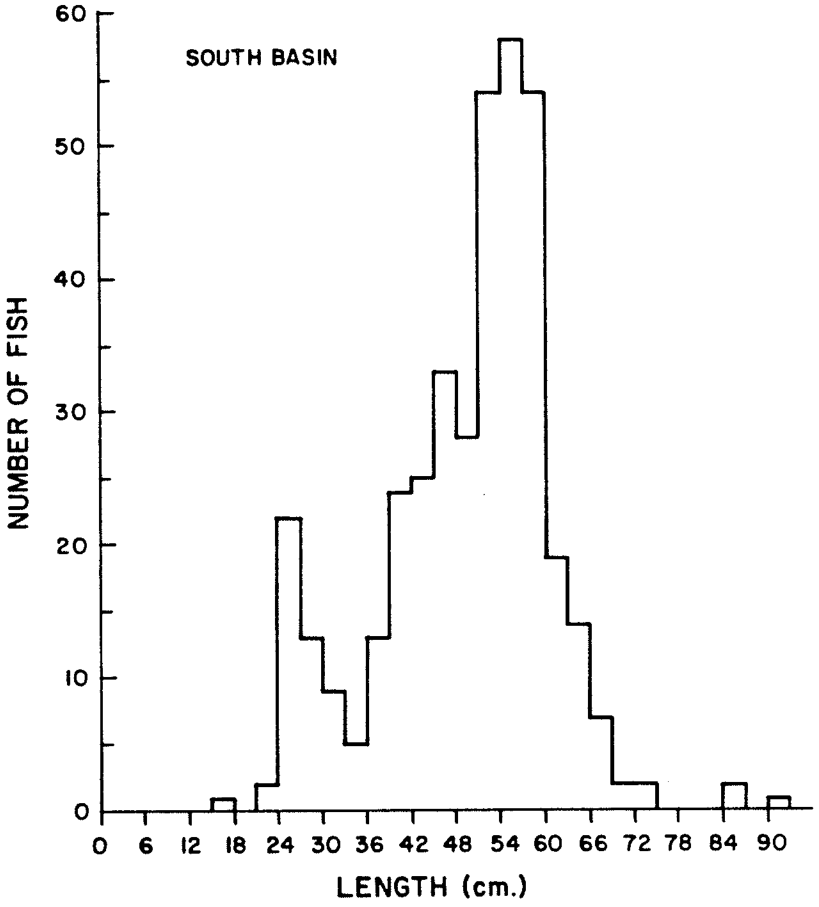

MIDDLE AND NORTH BASINS
ROTENONE
GILLNET
NUMBER OF FISH
AGE (yrs.)
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28

Figure 17. Length frequency histograms of lake trout caught in the south basin and middle and north basins of Lake Athapapuskow.


SOUTH BASIN
NUMBER OF FISH
60
50
40
30
20
10
0
0 6 12 18 24 30 36 42 48 54 60 66 72 78 84 90
LENGTH (cm.)

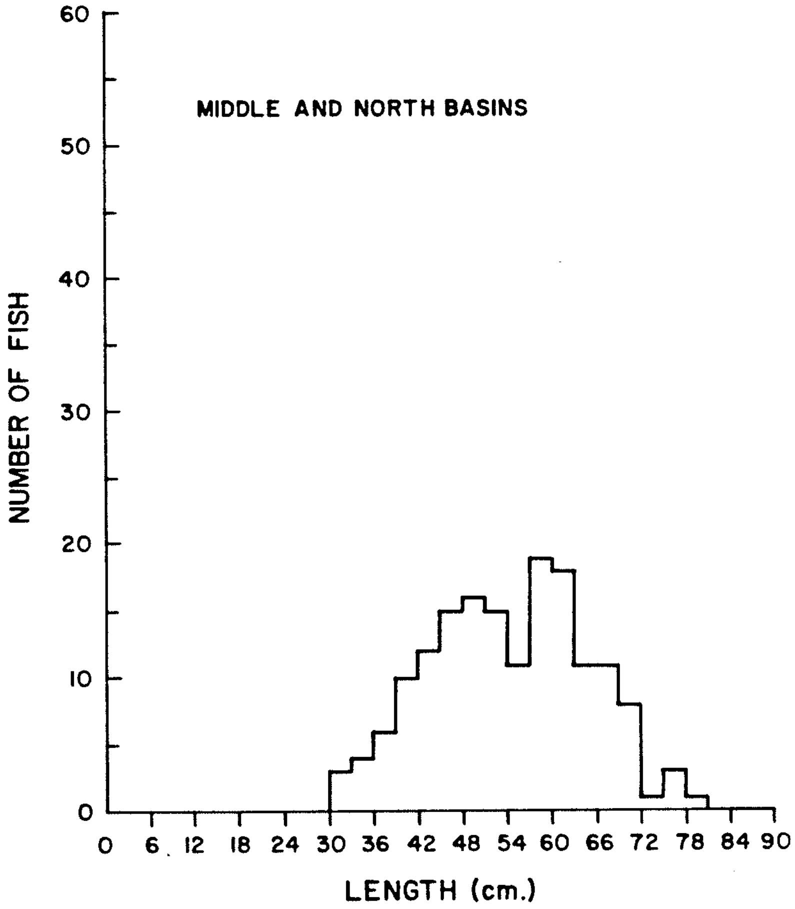
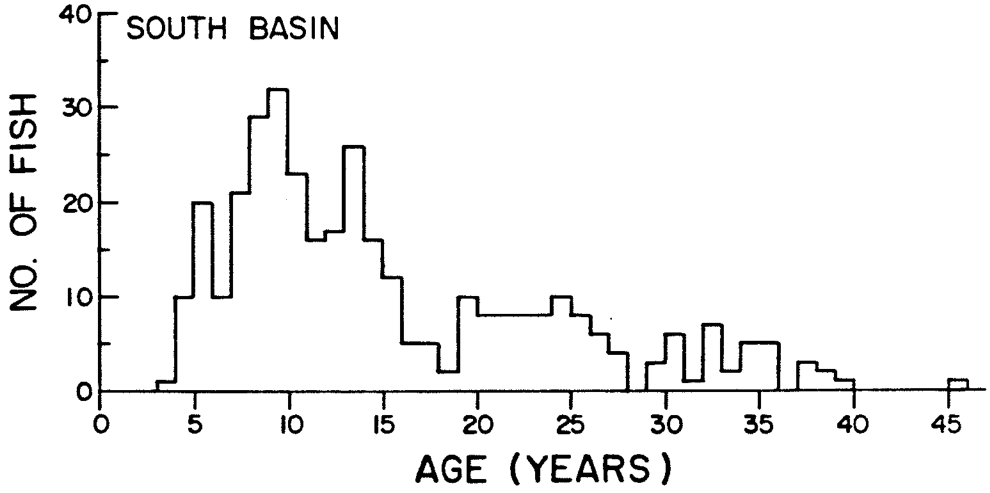
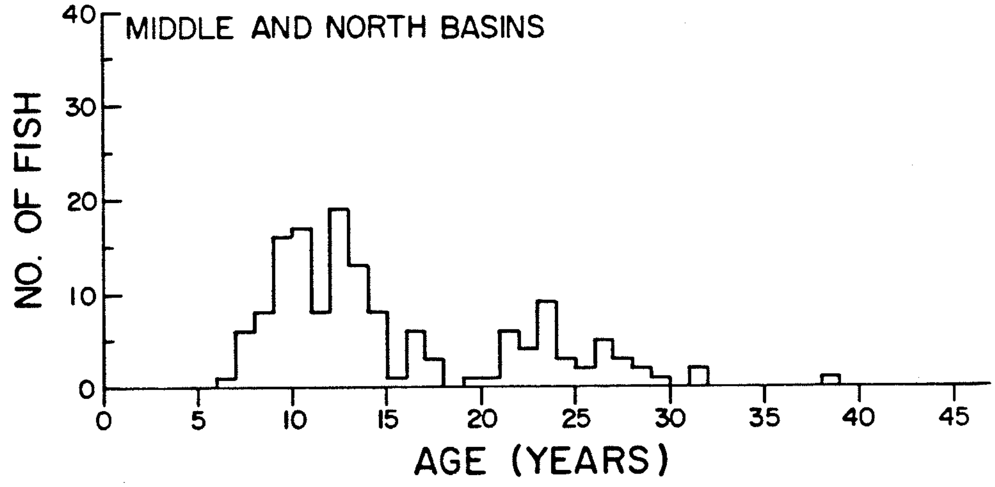

MIDDLE AND NORTH BASINS
NUMBER OF FISH
60
50
40
30
20
10
0
0 6 12 18 24 30 36 42 48 54 60 66 72 78 84 90
LENGTH (cm.)

Figure 18. Age frequency histograms of lake trout caught in the south basin and middle and north basins of Lake Athapapuskow.


SOUTH BASIN
NO. OF FISH
0
10
20
30
40
0
5
10
15
20
25
30
35
40
45
AGE (YEARS)


MIDDLE AND NORTH BASINS
NO. OF FISH
0
10
20
30
40
0
5
10
15
20
25
30
35
40
45
AGE (YEARS)

For fish at ages 0 to 10, there were no significant differences in length-weight relationships between sexes within basins, between basins, or between years. In the south basin, for ages 10 to 28, female length-weight regressions had a significantly greater slope than male regressions ("F" = 5.69, α = .05). In the middle and north basins, for fish at ages 10 to 28, there were no significant differences between length-weight regressions of males and females. For this age group, the slopes of length-weight regressions of south basin males and females were both significantly greater than the regression slope of fish caught in the middle and north basins (at α = .05, "F" values were 10.10 and 8.33 for males and females respectively). When length-weight relationships of other burbot populations were compared to those of Lake Athapapuskow burbot a regression equation was calculated combining data for all basins, both sexes, and both years as follows:

$$\text{Log } W = 3.0099 \text{ Log } L - 2.2015.$$

When age classes of all lake trout collected were represented in the analysis there were no significant differences in length-weight regressions between sexes within basins or between years. When data for each sex and both years were combined, the regression slope for lake trout from the middle and north basins was significantly greater than that for south basin fish ("F" = 19.65,

α = .05). Length-weight regression equations are as follows:

middle and north basins: $\text{Log } W = 3.4382 \text{ Log } L - 2.6540$,

south basin: $\text{Log } W = 3.2267 \text{ Log } L - 2.3014$.

For ages 4 to 14 there were no significant differences in length-weight regressions between sexes within basins, between basins, or between years. For ages 14 to 45 there were no significant differences in length-weight regressions between sexes within basins or between years but when data for each sex and both years were combined adjusted mean weights were significantly greater for fish in the middle and north basins than for fish in the south basin ("F" = 6.22, α = .05). When length-weight relationships of other lake trout populations were compared to those of Lake Athapapuskow lake trout a regression equation was calculated combining data for all basins, each sex, and both years as follows:

$$\text{Log } W = 3.2738 \text{ Log } L - 2.3775.$$

For burbot and lake trout, there were no statistically significant differences between error variances of compared length-weight regressions (α=.05).

Growth

For burbot, ANCOVA indicated that there were no significant differences between sexes within basins or between basins in adjusted mean lengths for fish at ages 0 to 28 (ANCOVA). Divergence of mean length versus age plots at age 10 and significant differences between basins in mean length at ages >10 ("t" tests at $\alpha = .05$) indicated that there was a difference between basins in growth of burbot,beginning at age 10 (Fig. 19). ANCOVA indicated that for ages 10 to 28, middle and north basin burbot were significantly longer at any given age than south basin burbot ("F" = 102.9, $\alpha = .05$). For ages 0 to 10, slope of the plot of Ln length versus Ln age of south basin burbot was significantly greater than that of middle and north basin burbot ("F" = 17.28, $\alpha = .05$). ANCOVA indicated that there were no significant differences between sexes in growth of burbot collected in Mistik Creek. ANCOVA indicated that the growth of Mistik Creek burbot (Fig. 20) did not significantly differ from the growth of south basin or middle and north basin burbot for fish at ages 0 to 7.

For lake trout, ANCOVA indicated that there were no significant differences in growth between sexes within each basin. After data for sexes were combined, the slope of the plot of length versus 1/age of lake trout from the middle and north basins was significantly greater than that of lake trout from the south basin ("F" = 44.40, $\alpha = .05$). Trends in interbasin differences in growth of older fish displayed by burbot (Fig. 19) were also noted for lake trout (Fig. 21). Lake trout age-length relationships start to differ between basins at approximately age 14. Therefore, age groups 4 to 14 and 14 to 45 were analysed separately in absence of the other group. The division of ages into two groups at age 14 was somewhat subjective as confidence intervals for mean lengths at various ages were relatively large and exhibited overlap between basins. This division is partly justified by the abruptness and consistency of the divergence of mean length versus age plots and by the significant differences between basins in mean lengths at ages 23 and 27 (Fig. 21). ANCOVA indicated that for fish at ages 4 to 14 there were no significant differences in growth between sexes within each basin or between basins. For fish at ages 14 to 45, ANCOVA indicated that there were no significant differences in growth between sexes within basins. After data for sexes in this age group were combined, the slope of the plot of Ln length versus age for middle and north basin lake trout was significantly greater than that of south basin lake trout ("F" = 7.11, $\alpha = .05$).

To use ANCOVA for comparison between basins of adjusted mean lengths of older aged lake trout (14+) it was necessary to find age groups for which growth plot slopes did not differ between basins. Slopes of plots of Ln length versus age were significantly different between basins for lake trout at ages 14 to 45 (see above), 15 to 45 ("F" = 6.58,

$\alpha = .05$), and 16 to 45 ("F" = 4.68, $\alpha = .05$), therefore, ANCOVA could not be used for interbasin comparisons of adjusted mean lengths for these age groups. However, ANCOVA was used for comparison of adjusted mean lengths between basins for lake trout at ages 17 to 45 because, for these ages, there was no significant difference between basins in the slopes of the regression of Ln length versus age. ANCOVA indicated that the adjusted mean length of lake trout at ages 17 to 45 was significantly greater for fish caught in the middle and north basins than it was for fish caught in the south basin ("F" = 56.53, $\alpha = .05$). Small sample sizes and large variances in length at age N made "t" tests ineffective for interbasin comparisons of mean lake trout length lengths at various ages.

For burbot and lake trout there were no statistically significant differences between error variances of compared growth regressions (α=.05).

Mortality Rates

The terms Z, S, and A will be used in this section and are defined by Ricker (1975) as follows:

Instantaneous rate of mortality (Z): The natural logarithm (with sign changed) of the survival rate. The ratio of number of deaths per unit of time to population abundance during that time, if all deceased fish were to be immediately replaced so that the population does not change.

Survival rate (S): Number of fish alive after a specified time interval divided by the initial number, usually on a yearly basis:

Annual (or seasonal) total mortality rate (A): The number of fish which die during a year (or season) divided by the initial number.

Having determined Z, the slope of the natural logarithm of the frequency of age N versus age N, A and S were calculated from the equation:

$$1 - A = S = e^{-Z} .$$

Calculated equations are as follows:

$$\text{lake trout: } 1-0.089 = 0.911 = e^{-0.09249} ;$$
$$\text{south basin burbot: } 1-0.366 = 0.634 = e^{-0.45580} ;$$
$$\text{middle and north basin burbot: } 1-0.252 = 0.748 = e^{-0.29010} .$$

Ages used in the calculation of A,S, and Z for the above three groups were 9 to 45, 11 to 22, and 15 to 27, respectively. Catch curves with regression lines fitted to their descending right hand limbs (regression slopes = Z) are presented for burbot (Fig. 22) and lake trout (Fig. 23).

There were no significant differences in burbot instantaneous mortality rates between fish caught in different years or between sexes within basins. After data for each sex and both years were combined, burbot from the south basin had a significantly greater instantaneous mortality rate than middle and north basin burbot ("F" = 19.06, $\alpha = .05$).

There were no significant differences in lake trout instantaneous mortality rates between sexes within basins, between basins, or between years.

For burbot and lake trout there were no significant differences between error variances of compared mortality regressions ($\alpha = .05$).

Maturity

Age and length at which 100 percent of the sampled burbot were mature could not be accurately determined because sample sizes were small at ages and lengths where maturity occurred (Tables IV, V, VI, and VII). Almost all immature burbot were collected on shorelines using rotenone and all mature burbot were collected with gillnets in the main bodies of the lake basins. In all basins most of the burbot collected were mature by age seven. Only five immature fish older than age seven were caught. In the south basin all burbot larger than the 33 to 36 cm length class were mature. In the middle and north basins all burbot larger than the 39 to 42 cm length class were mature.

Percentages of mature lake trout in each age interval and length class are presented in tables VIII and IX respectively. Lake trout older than age 14 and larger than 57 cm were always mature, therefore, data for these fish were not presented in the above tables. The exact age or length class at which 100 percent maturity occurred was not easily determined due to small sample sizes of these classes.

Figure 19. Mean lengths at given ages of burbot caught in Lake Athapapuskow. Half of a 95 percent confidence interval is given for age classes represented by more than two fish. S indicates that mean lengths of fish at a given age are significantly different between basins ("t" tests, $\alpha = .05$).

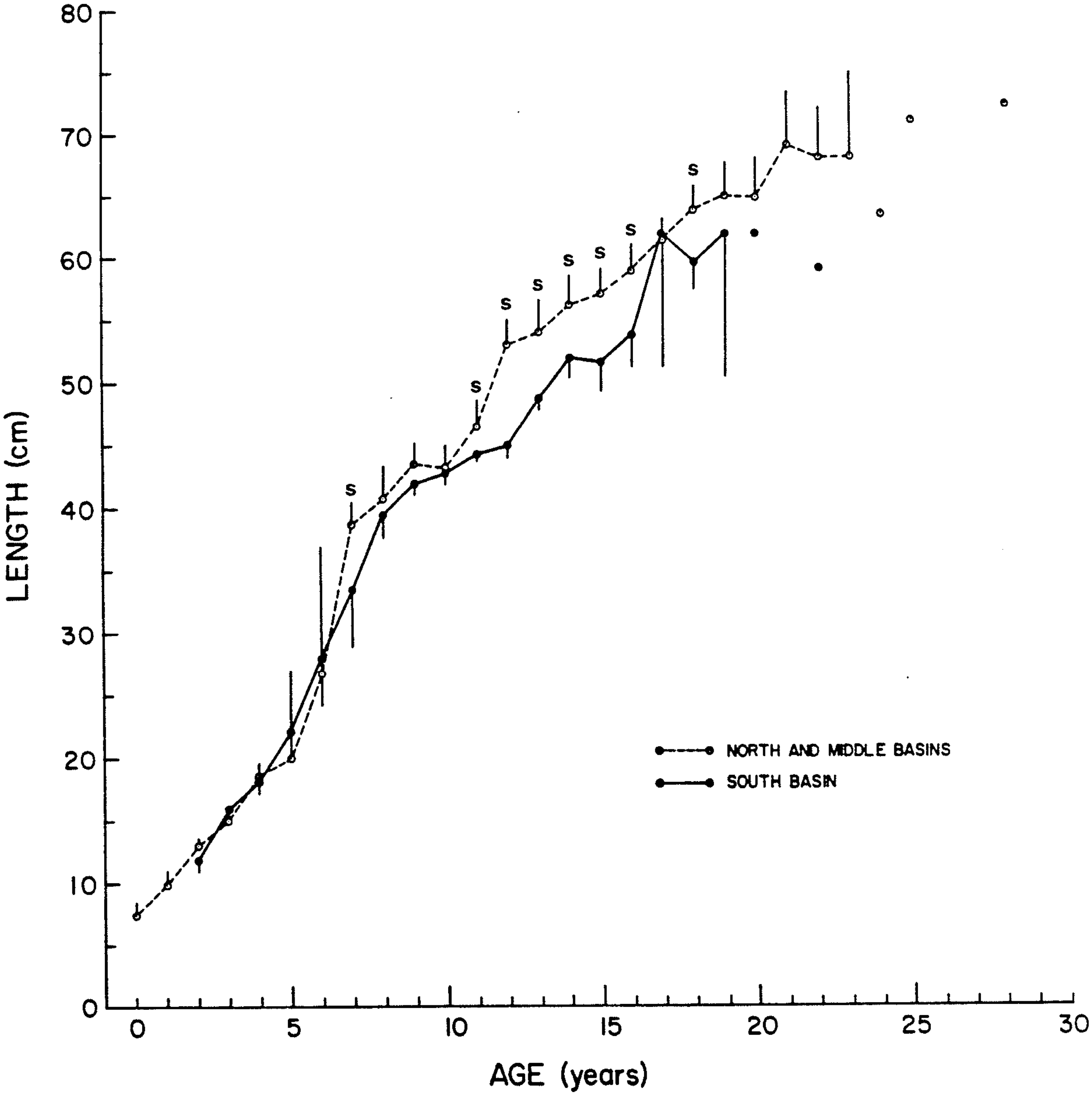
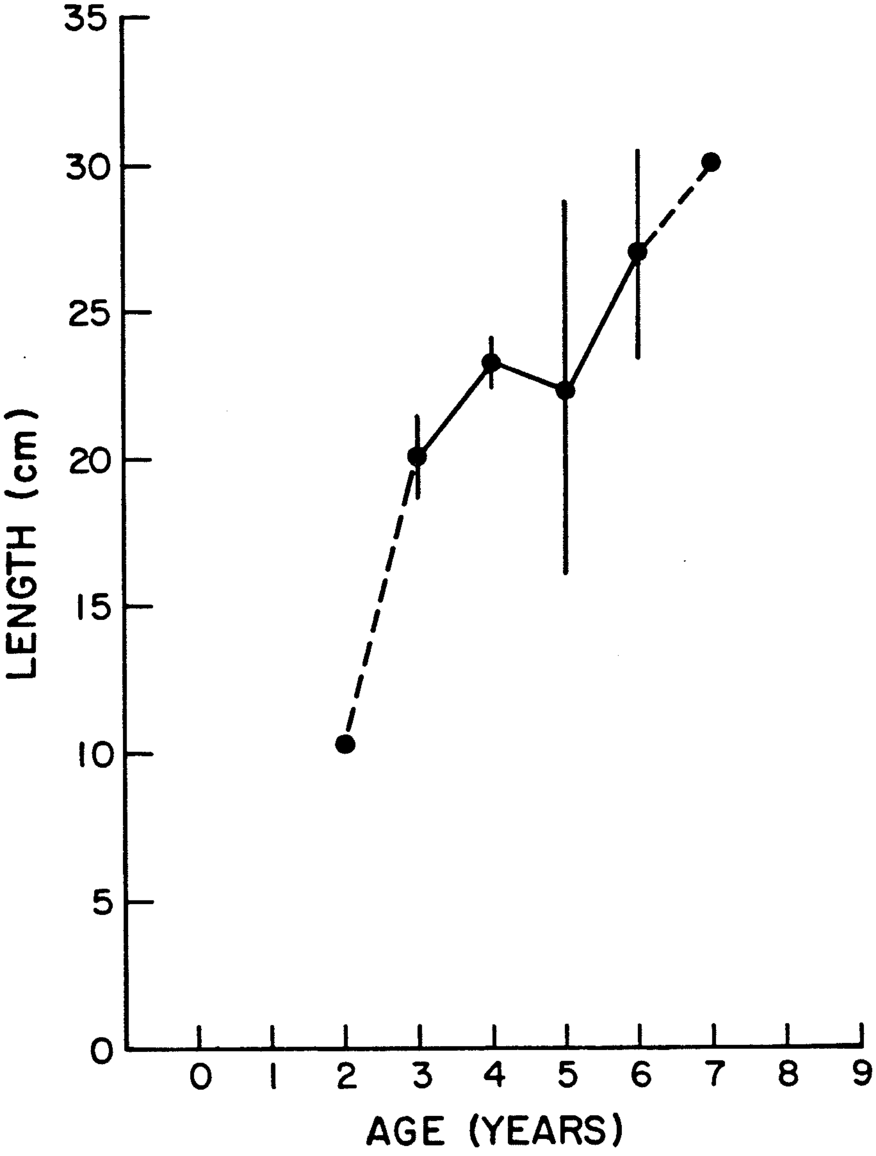
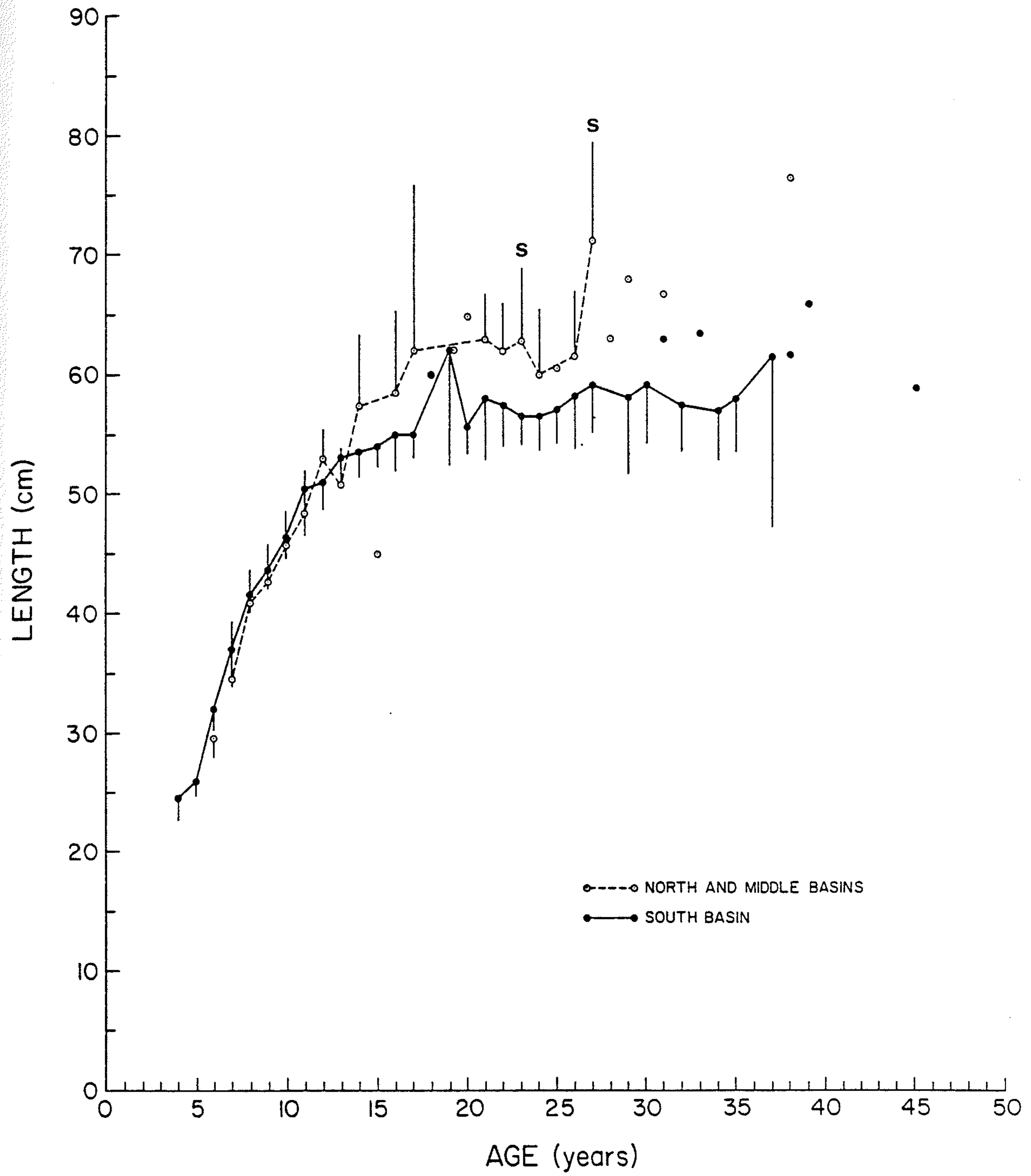

LENGTH (cm)
0
10
20
30
40
50
60
70
80
AGE (years)
0
5
10
15
20
25
30
s
s
s
s
s
s
s
s
s
NORTH AND MIDDLE BASINS
SOUTH BASIN

Figure 20. Mean lengths at given ages of burbot caught in Mistik Creek. Confidence intervals are given for age classes represented by more than two fish.



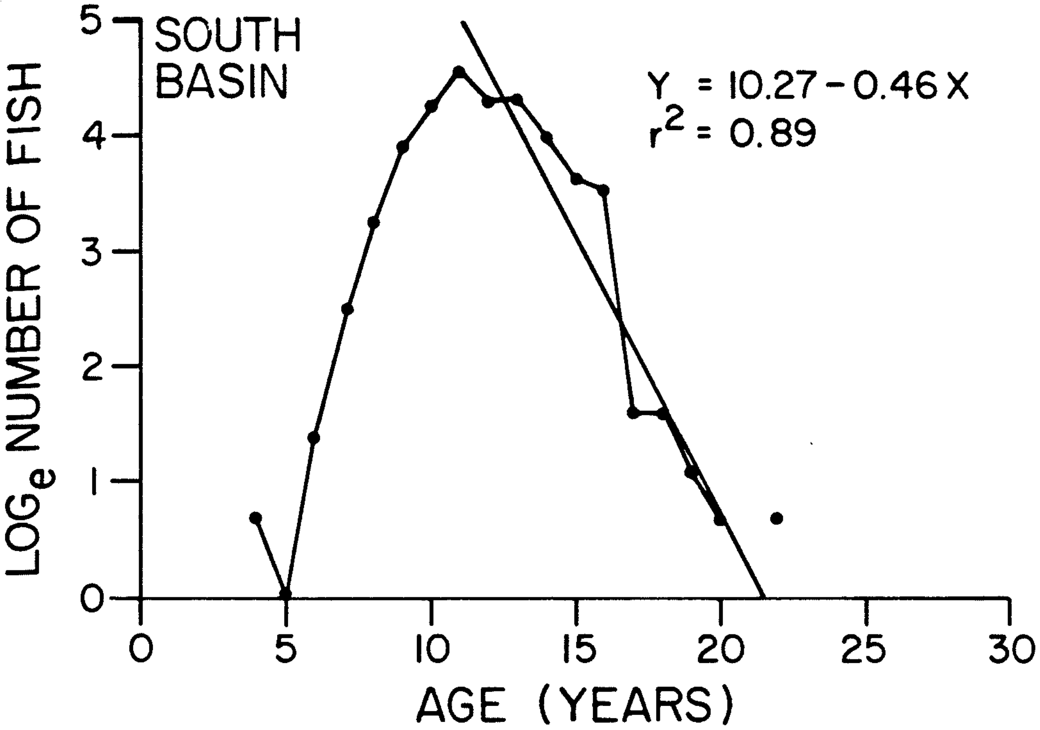
35
30
25
20
15
10
5
0
LENGTH (cm)
0
1
2
3
4
5
6
7
8
9
AGE (YEARS)

Figure 21. Mean lengths at given ages of lake trout caught in Lake Athapapuskow. Half of a 95 percent confidence interval is given for age classes represented by more than two fish. S indicates that mean lengths of fish at a given age are significantly different between basins ("t" tests, $\alpha = .05$).



LENGTH (cm)
AGE (years)
0
10
20
30
40
50
60
70
80
90
0
5
10
15
20
25
30
35
40
45
50
S
S
NORTH AND MIDDLE BASINS
SOUTH BASIN

Figure 22. Catch curves for burbot caught in Lake Athapapuskow. Regression lines are fitted to the descending right hand limbs of the curves (regression slopes = Z).


SOUTH
BASIN
Y = 10.27 - 0.46 X
r2 = 0.89
LOGe NUMBER OF FISH
5
4
3
2
1
0
0
5
10
15
20
25
30
AGE (YEARS)

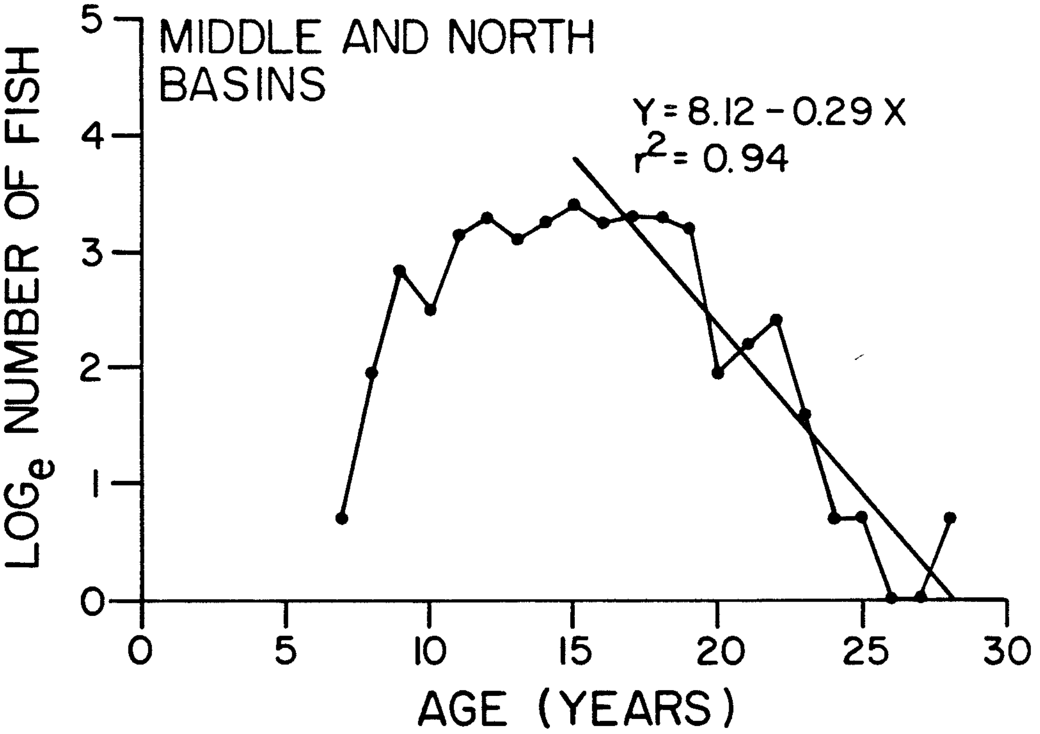
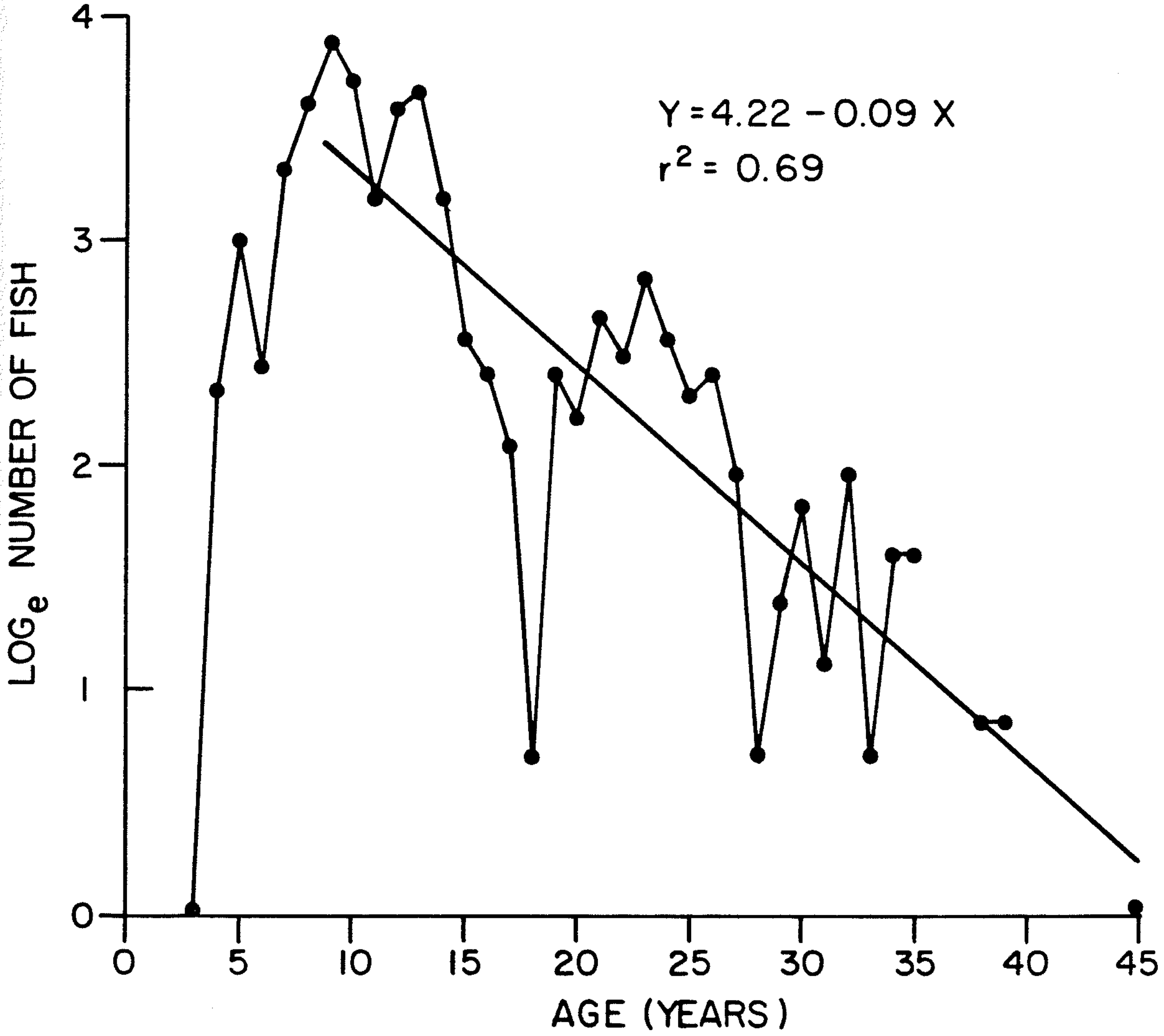

MIDDLE AND NORTH
BASINS
Y = 8.12 - 0.29 X
r2 = 0.94
LOGe NUMBER OF FISH
5
4
3
2
1
0
0
5
10
15
20
25
30
AGE (YEARS)

Figure 23. Catch curve for lake trout caught in Lake Athapapuskow. A regression line is fitted to the descending right hand limb of the curve (regression sope = Z).


Y = 4.22 − 0.09 X
r² = 0.69
LOGe NUMBER OF FISH
0
1
2
3
4
AGE (YEARS)
0
5
10
15
20
25
30
35
40
45

Lake trout of both sexes in the 51 to 54 cm and larger size groups were always mature. All males caught in the middle and north basins were mature at ages ≥ 12 whereas all males caught in the south basin were mature at ages ≥ 11. All females caught in the middle and north basins were mature at ages ≥ 14 whereas all females caught in the south basin were mature at ages ≥ 13. The earliest observed maturation occurred approximately four to five years prior to the age at which 100 percent of the sampled fish were mature, at lengths of about 45 to 48 cm.

Seasonal Gonad Development

Gonads of immature lake trout showed no trends in weight increase as the summer progressed (Fig. 24). Ovary weight of mature female lake trout increased rapidly throughout the summer (Fig. 25).

Five mature female lake trout which were above the size and age of maturity observed for this population, sampled between August 13 and 23, 1978, had abnormally low ovary weights (Fig. 25) and small egg diameters. Egg diameters were approximately 1.0 to 1.5 mm whereas other mature females sampled during this period contained eggs of about 3 mm in diameter. Abnormally small relative ovary weights and egg diameters are an indication that the above mature females would not have spawned during the year in which they were collected. Their ages and fork lengths were, 12 years

Table IV. Catch frequencies at given ages of mature and immature burbot caught in the south basin of Lake Athapapuskow.

Age (Years)	Rotenone ≤3.5 Meters (Shore Lines)		Gillnets 9 Meters		Gillnets ≥18.5 Meters	
	Immature	Mature	Immature	Mature	Immature	Mature
0						
1						
2	6		1			
3	29					
4	22		1		1	
5	14				1	
6	5				1	7
7	1					9
8						25
9						49
10				1		70
11						93
12				1		75
13				1		76
14				1		53
15				2		38
16				2		21
17				1		5
18						5
19						3
20						2
21						
22						2

Table V. Catch frequencies at given ages of mature and immature burbot caught in the middle and north basins of Lake Athapapuskow.

Age (Years)	Rotenone $\leq$3.5 Meters (Shore Lines) Immature	Mature	Gillnets 9 Meters Immature	Mature	Gillnets $\geq$18.5 Meters Immature	Mature
0	3					
1	7					
2	26					
3	33					
4	25					
5	12					
6	3					
7					1	1
8					2	4
9						17
10					1	11
11				2		22
12				2	1	25
13						21
14				1		25
15				1		29
16				1		26
17				2		27
18				1		27
19						25
20						7
21						9
22				2		10
23						5
24						2
25						2
26						1
27						1
28						2

Table VI. Catch frequencies at given length intervals of mature and immature burbot caught in the south basin of Lake Athapapuskow.

Length Interval (CM)	Rotenone ≤3.5 Meters (Shore Lines)		Gillnets 9 Meters		Gillnets ≥18.5 Meters	
	Immature	Mature	Immature	Mature	Immature	Mature
6 - 9						
9 - 12	2		1			
12 - 15	19					
15 - 18	14		1			
18 - 21	24					
21 - 24	16				1	
24 - 27	1					1
27 - 30						6
30 - 33	1		1		2	4
33 - 36						3
36 - 39						11
39 - 42				2		58
42 - 45					2	114
45 - 48						102
48 - 51				2		65
51 - 54				2		42
54 - 57						51
57 - 60				1		26
60 - 63						13
63 - 66						10
66 - 69						5
69 - 72						2
72 - 75				1		1
75 - 78						
78 - 81						

Table VII. Catch frequencies at given length intervals of mature and immature burbot caught in the middle and north basins of Lake Athapapuskow.

Length Interval (CM)	Rotenone ≤3.5 Meters (Shore Lines)		Gillnets 9 Meters		Gillnets ≥18.5 Meters	
	Immature	Mature	Immature	Mature	Immature	Mature
6 - 9	4					
9 - 12	7					
12 - 15	37					
15 - 18	34					
18 - 21	14					
21 - 24	6					
24 - 27	7					
27 - 30						
30 - 33	1					
33 - 36						
36 - 39					1	
39 - 42					3	14
42 - 45					1	20
45 - 48						19
48 - 51				1		17
51 - 54						20
54 - 57				4		34
57 - 60				4		39
60 - 63				2		36
63 - 66				1		44
66 - 69						28
69 - 72						17
72 - 75						6
75 - 78						4
78 - 81						5

Table VIII. Percentage of mature fish in the total catch of each age class of lake trout caught in Lake Athapapuskow.

	North and Middle Basins								South Basin							
Age	Males				Females				Males				Females			
(Years)	N	Immat.	Mat.	% Mat.	N	Immat.	Mat.	% Mat.	N	Immat.	Mat.	% Mat.	N	Immat.	Mat.	% Mat.
4									3	3	0	0	4	4	0	0
5									8	8	0	0	5	5	0	0
6	1	1	0	0					6	6	0	0	4	4	0	0
7	2	2	0	0	4	4	0	0	6	6	0	0	11	11	0	0
8	1	1	0	0	6	6	0	0	15	10	5	33.3	12	12	0	0
9	6	4	2	33.3	10	9	1	10.0	18	9	9	50.0	13	13	0	0
10	9	6	3	33.3	7	5	2	28.6	8	4	4	50.0	12	6	6	50.0
11	5	1	4	80.0	2	1	1	50.0	4	0	4	100.0	11	1	10	90.9
12	10	0	10	100.0	9	3	6	66.7	8	0	8	100.0	7	3	4	57.1
13	8	3	5	62.5	5	1	4	80.0	9	2	7	77.8	16	0	16	100.0
14	3	0	3	100.0	4	0	4	100.0	7	0	7	100.0				

Table IX. Percentage of mature fish in the total catch of each length interval of lake trout caught in Lake Athapapuskow.

Length	North and Middle Basins								South Basin							
Interval	Males				Females				Males				Females			
(CM)	N	Immat.	Mat.	% Mat.	N	Immat.	Mat.	% Mat.	N	Immat.	Mat.	% Mat.	N	Immat.	Mat.	% Mat.
15-18									1	1	0	0				
18-21									0	0	0	0				
21-24									2	2	0	0	2	2	0	0
24-27									3	3	0	0	7	7	0	0
27-30									7	7	0	0	4	4	0	0
30-33	2	0	0	0	1	1	0	0	5	5	0	0	2	2	0	0
33-36	1	0	0	0	3	3	0	0	4	4	0	0	0	0	0	0
36-39	4	0	0	0	3	3	0	0	6	6	0	0	8	8	0	0
39-42	2	0	0	0	8	8	0	0	13	12	1	7.7	13	13	0	0
42-45	4	0	0	0	7	7	0	0	4	4	0	0	8	8	0	0
45-48	6	4	2	33.3	7	6	1	14.3	21	7	14	66.7	16	16	0	0
48-51	15	5	10	66.7	2	0	2	100.0	19	3	16	84.2	12	2	10	83.3
51-54	5	0	5	100.0	8	2	6	75.0	14	0	14	100.0	20	0	20	100.0
54-57					6	0	6	100.0								

and 49.6 cm, 14 years and 49.7 cm, 27 years and 56.5 cm, 31 years and 62.7 cm, and 38 years and 54.5 cm. These "non spawners" were close to the age at which maturity occurred or they were relatively old. Three mature female lake trout exhibited abnormally large relative gonad weights. Their ages and fork lengths were, 26 years and 59.9 cm, 26 years and 61.5 cm, and 22 years and 54.5 cm. They were relatively old but not as old as the 3 oldest "non spawners". Data (Fig. 25) indicates that the majority of mature female lake trout would have spawned during the year in which they were collected.

Relative testes weights of mature male lake trout increased at a lower rate than relative ovary weights of mature females and did not increase in weight after early August (Fig. 25). At all sampling periods male gonads constituted a much smaller proportion of body weight and were relatively more variable in weight than female gonads.

Gonad weights (expressed as percentage body weight) of burbot remained unchanged as the sampling season progressed and, therefore, were not presented graphically. However, relative gonad weights differed between mature and immature fish. Mean burbot gonad weights expressed as percent bodyweight ± 95 percent confidence intervals were 0.36 ± 0.04 for mature males, 0.23 ± 0.11 for immature males, 0.83 ± 0.12 for mature females, and 0.44 ± 0.16 for immature females. It appeared that burbot gonad development was negligible from the time at which spawning was completed to at least early September. The majority of synthesis of gonadal products must, therefore, occur after early September and prior to spawning time (early spring).

Although relative gonad weight was not used as a criterion for assigning maturity status the limited overlap between relative gonad weights of mature and immature lake trout (Figs. 24 and 25) and burbot supports the validity of maturity status assignments based on visual examination of gonads (see Methods).

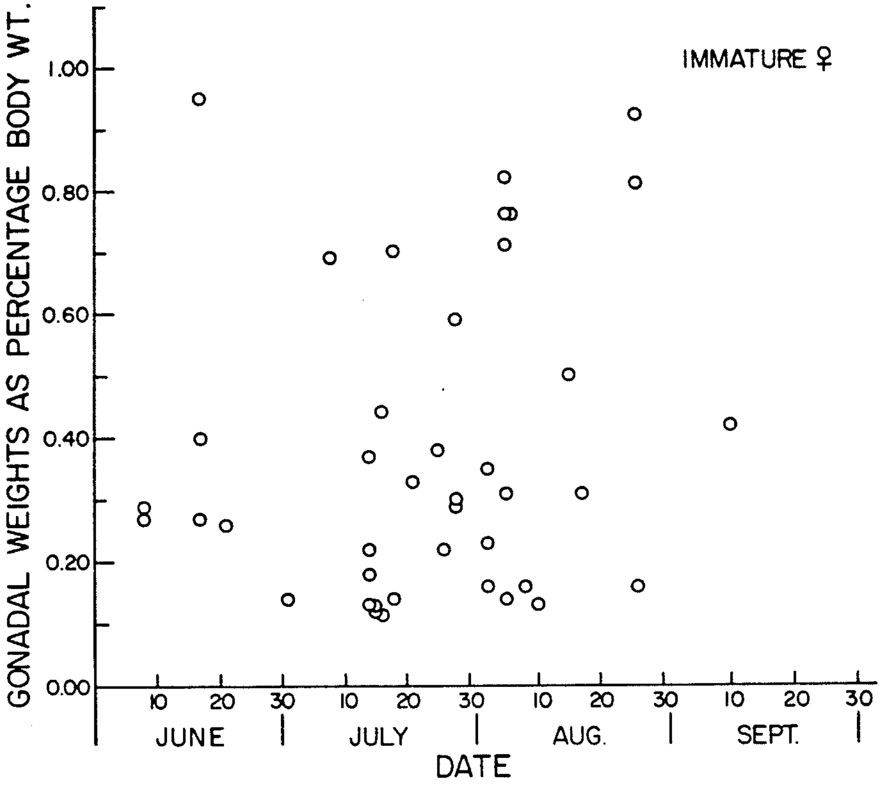
Mean Weights of Burbot and Lake Trout

Mean weights of burbot captured by gillnets appear to have decreased between 1971 and 1978 (Table X). This decrease is most pronounced in the south basin between 1976 and 1978.

Mean weights of lake trout captured by gillnets were relatively stable between 1971 and 1978 (Table X). Mean weights of lake trout from the south basin and from all basins combined were lowest in 1978. Low 1978 mean weights of lake trout were caused by a distinct group of small lake trout captured in 5.1 cm mesh gillnets in the south basin during 1978 (Fig. 13).

The mean weight of burbot captured by gillnets in 1977 and 1978 was significantly greater ("t" = 18.40, $\alpha = .05$) in the middle and north basins (1.27 kg) than in the south

Figure 24. Relationship between date and relative gonad weight of immature female and male lake trout caught in Lake Athapapuskow.


IMMATURE ♀
GONADAL WEIGHTS AS PERCENTAGE BODY WT.
1.00
0.80
0.60
0.40
0.20
0.00
10
20
30
10
20
30
10
20
30
10
20
30
JUNE
JULY
AUG.
SEPT.
DATE

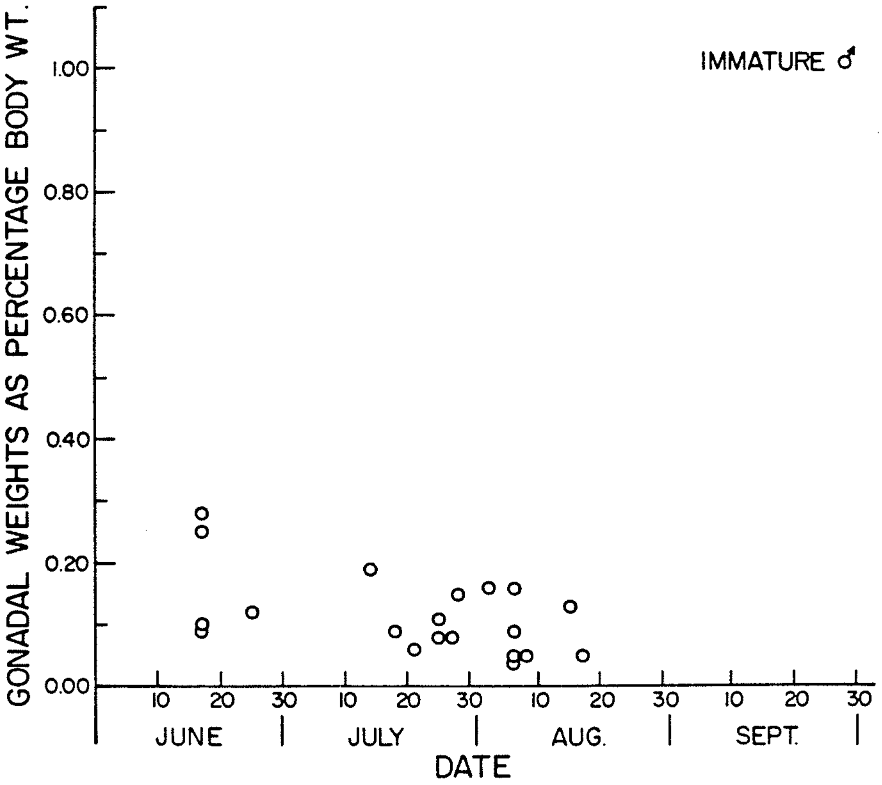
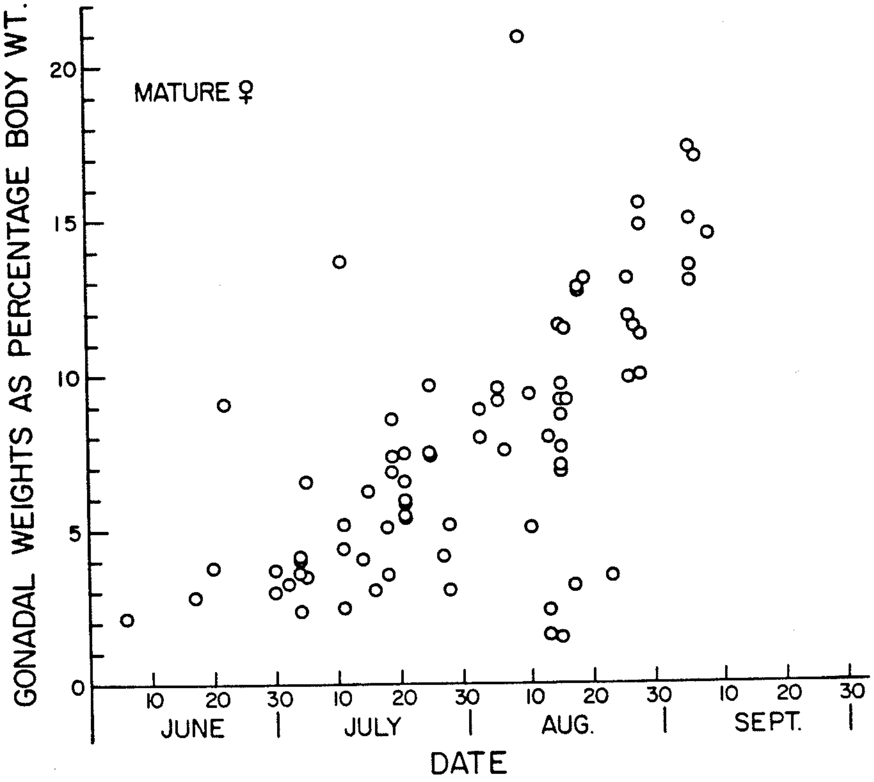
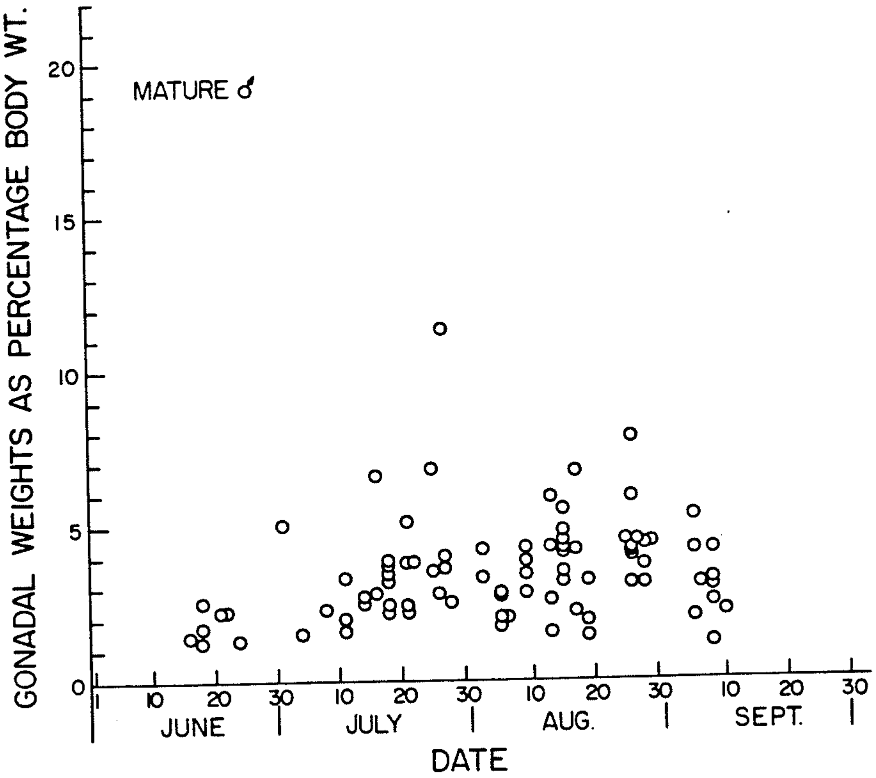

IMMATURE ♂
GONADAL WEIGHTS AS PERCENTAGE BODY WT.
1.00
0.80
0.60
0.40
0.20
0.00
10
20
30
10
20
30
10
20
30
10
20
30
JUNE
JULY
AUG.
SEPT.
DATE

Figure 25. Relationship between date and relative gonad weight of mature female and male lake trout caught in Lake Athapapuskow.


MATURE ♀
GONADAL WEIGHTS AS PERCENTAGE BODY WT.
0
5
10
15
20
10
20
30
10
20
30
10
20
30
10
20
30
JUNE
JULY
AUG.
SEPT.
DATE


MATURE ♂
GONADAL WEIGHTS AS PERCENTAGE BODY WT.
0
5
10
15
20
1
10
20
30
10
20
30
10
20
30
10
20
30
JUNE
JULY
AUG.
SEPT.
DATE

basin (0.65 kg). The mean weight of lake trout captured in 1977 and 1978 was significantly greater ("t" = 4.93, α = .05) in the middle and north basins (2.19 kg) than in the south basin (1.62 kg).

Abundance Estimates of Burbot and Lake Trout

The relative density of burbot and numerical percentage of burbot in the total catch were higher in 1977 and 1978 than in 1971, but relative biomass has remained fairly constant (Table XI).

All lake trout abundance estimates were higher in 1971 than they were in 1977 and 1978. Abundance estimates of lake trout appear abnormally low for 1977. Sampling effort in the middle and north basins constituted 31, 44, and 32 percent of the sampling effort utilized in 1971, 1977, and 1978 respectively. Lake trout were more abundant in the south basin than in the middle and north basins. Therefore, low 1977 lake trout abundance estimates (Table XI) may be explained by the greater sampling effort employed in the middle and north basins in 1977 than in 1971 and 1978.

Combined relative density of all species appeared to increase between 1971 and 1978 (Table XI) and was greatest in the middle and north basis (Table XII).

Lake Trout Harvests

A commercial gillnet fishery operated on Lake Athapapuskow from 1931 to 1943 and in 1956 and 1957 (Schlick, 1973a). Lake trout catches and catch per license for each year of commercial fishing are presented in Figure 26. Catch and catch per license were calculated from commercial fishery records presented by Schlick (1973a). Year class frequencies or relative year class strengths given in Figure 26 were derived from lake trout sampled in this study. For example, if a 17 year old lake trout was captured in 1977 it was assumed to have hatched in 1960 and was subsequently assigned to the 1960 year class.

Catch per license was stable for the first two years of fishing, declined in 1933, and rose to its highest value in 1934 (3300 kg). Between 1934 and 1940 catch per license remained relatively stable and total catch steadily increased. After 1940 catch and catch per license dropped rapidly and by 1943 the fishery experienced its lowest catch per license value. It is unlikely that a wartime decrease in fishing effort per license could account for low catches during 1940 to 1943 because the weight of whitefish caught per license increased during this period. This indicated that fishing effort per license did not decrease during 1940 to 1943. For lake trout, catch per license values in 1956 and 1957 were low, although the total catch was high (15000 kg in 1956 and 32700 kg in 1957). This indicated that lake trout abundance had not increased appreciably since 1943 even though the fishery was closed from 1944 to 1955.

The large variance of the frequencies of year classes obscured interpretation of trends in relative year class strength. A decline in year class strength was expected as age increased because of mortality (Fig. 26). The representation of 1958 through 1962 year class was abnormally small in all basins. This period of poor year class representation was preceded by a period (1956 and 1957) characterized by high commercial yields and a low abundance suggested by low catch per license values.

Mean annual commercial harvest of lake trout from Lake Athapapuskow was 19650 kg/yr (Schlick, 1973a). A creel census indicated that the 1975 annual angler harvest was 41900 kg/yr (Sigurdson and Scaife, 1975a). Surface area of Lake Athapapuskow is 26596 ha. Therefore, mean annual commercial harvest per hectare was:

$$\frac{19650}{26596} = 0.74 \text{ kg/ha/yr},$$

and the 1975 estimate of angler harvest per hectare was:

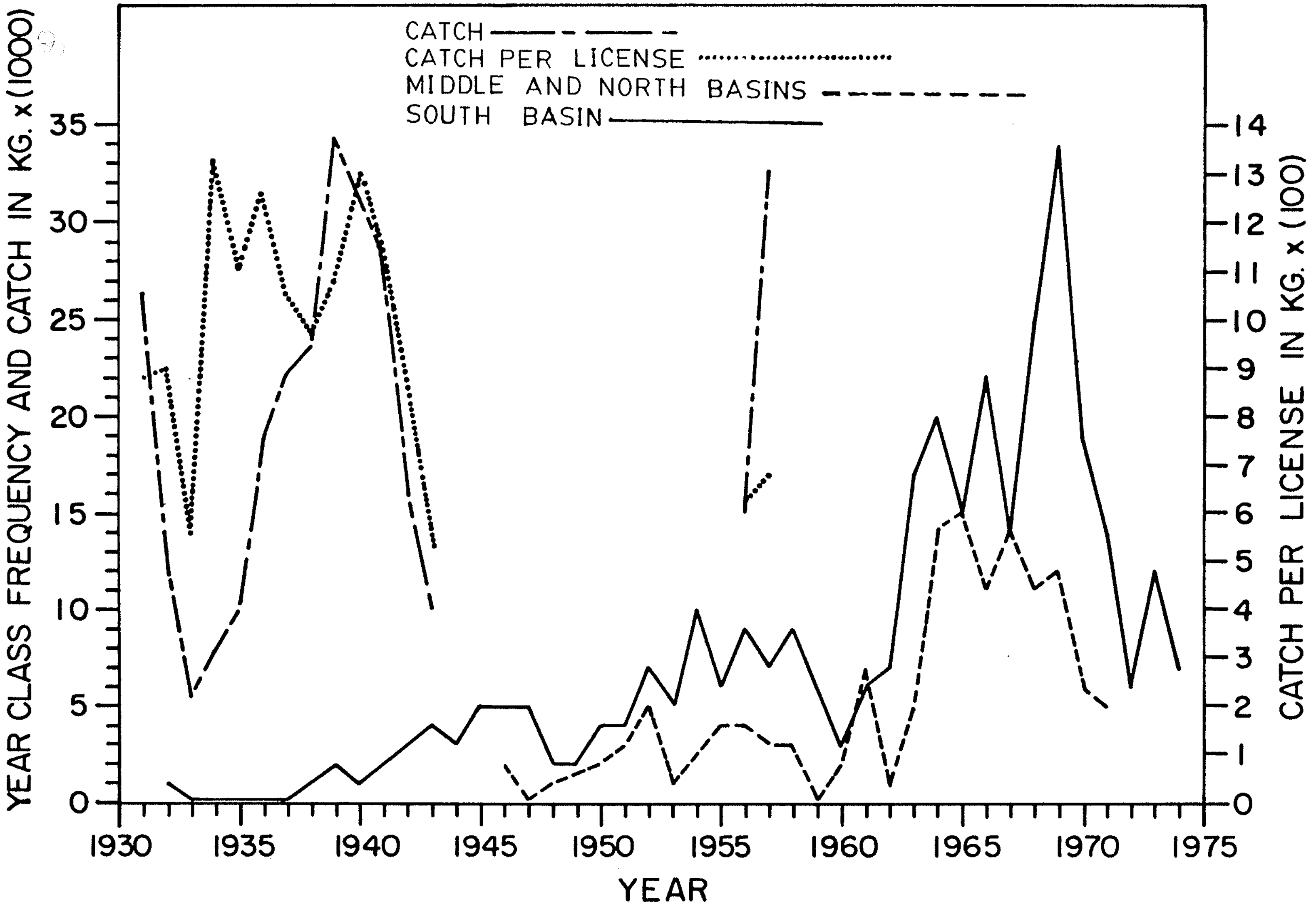
$$\frac{41900}{26596} = 1.58 \text{ kg/ha/yr}.$$

Table X. Mean weights by year, of lake trout and burbot caught in gillnets in Lake Athapapuskow. Sample sizes are given in parenthesis.

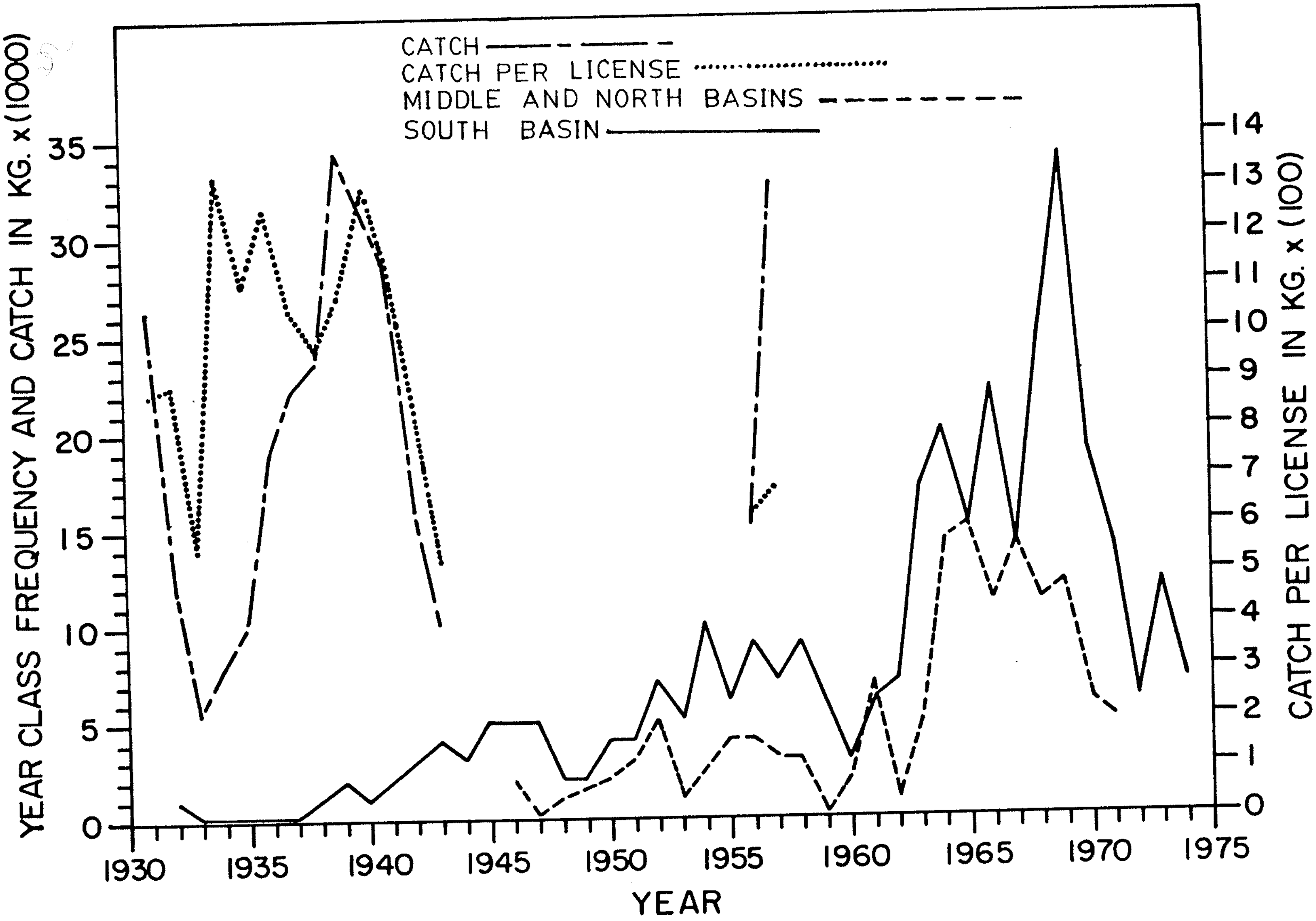
	Mean Weight (kg)					
	Burbot			Lake Trout		
Year	S. Basin	M. and N. Basins	All Basins	S. Basin	M. and N. Basins	All Basins
1971	- (-)	- (-)	1.13 (125)	- (-)	- (-)	2.00 (254)
1975	- (47)	- (26)	1.00 (73)	- (33)	- (3)	2.16 (36)
1976	1.05 (64)	1.42 (31)	1.17 (95)	1.64 (43)	3.07 (3)	1.74 (46)
1977	0.69 (332)	1.41 (169)	0.93 (501)	1.78 (179)	2.20 (115)	1.95 (294)
1978	0.61 (224)	1.10 (146)	0.80 (370)	1.49 (210)	2.16 (49)	1.61 (259)

Data for 1971, 1975 and 1976 are from Schlick (1973a), Sigurdson and Scaife (1975b), and Wright (1976) respectively.

Figure 26. Commercial gillnet catch per license, and year class frequencies of lake trout from Lake Athapapuskow. Year class frequencies are determined from fish sampled in 1977 and 1978.



CATCH
CATCH PER LICENSE
MIDDLE AND NORTH BASINS
SOUTH BASIN
YEAR CLASS FREQUENCY AND CATCH IN KG. x (1000)
0
5
10
15
20
25
30
35
CATCH PER LICENSE IN KG. x (100)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
1930
1935
1940
1945
1950
1955
1960
1965
1970
1975
YEAR


CATCH
CATCH PER LICENSE
MIDDLE AND NORTH BASINS
SOUTH BASIN
YEAR CLASS FREQUENCY AND CATCH IN KG. x (1000)
0
5
10
15
20
25
30
35
CATCH PER LICENSE IN KG. x (100)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
1930
1935
1940
1945
1950
1955
1960
1965
1970
1975
YEAR

Other Biological Characteristics

Diets of Burbot and Lake Trout

Table XIII best illustrates diet preference of burbot as values presented for each taxon are a measure of frequency of feeding on that taxon. Table XIV best illustrates the energetic or nutritional significance of each taxon found in the burbot diet. Sampling at shorelines and Mistik Creek was limited to the last week in August in each year, therefore, it may be expected that the results for diet of burbot from these two areas will be biased by the failure of the short sampling period to represent seasonal fluctuations in diet taxa availability. Almost all burbot caught in the main bodies of the lake basins were sexually mature and all burbot caught at shorelines and Mistic Creek were sexually immature, therefore, further discussion in this section will be in reference to the diets of mature and immature fish.

Orconectes virilis and *Mysis relicta* were the most frequently eaten invertebrates by mature burbot (Table XIII) whereas the former was the most frequently eaten invertebrate by immature burbot caught on lake shorelines. All mature burbot which had fed on *O. virilis* were captured at a depth of about 9 meters. The sculpin component of the immature burbot diet consisted entirely of *Cottus cognatus* whereas mature burbot fed more frequently on *Myoxocephalus thompsoni* than on the former species. Other well represented taxa in the diets of immature burbot were Ephemeroptera

Table XI. Abundance estimates by year (expressed as numerical percentage of the catch, relative density, and relative biomass) of burbot, lake trout, and all species caught in gillnets in Lake Athapapuskow.

	Burbot			Lake Trout			All Species		
	1971	1977	1978	1971	1977	1978	1971	1977	1978
Total Number Caught	125	501	370	257	294	259	2351	4796	3112
Numerical % of Catch	5.32	10.45	11.89	10.93	6.13	8.82	100	100	100
Total Weight Caught (kg)	313	468	296	513	573	413	-	-	-
Number of Effort Units	57	99	62	57	99	62	57	99	62
C.P.U.E.[a] Expressed as:									
Relative Density (fish/U.E.)	2.19	5.06	5.97	4.51	2.97	4.17	41.25	48.44	50.19
Relative Biomass (kg/U.E.)	5.49	4.72	4.77	9.00	2.97	6.66	-	-	-

[a] Catch per unit of effort equals number or weight of fish caught in 137 m. of gillnet fished overnight.

Data for 1971 are from Schlick (1973a).

Table XII. Relative Density (fish/U.E.) and relative biomass (kg/U.E.) of fish caught in gillnets in Lake Athapapuskow.

	South Basin		North and Middle Basins	
Total number of meters of gillnets fished	13,419		8,664	
Approximate number of gangs fished	98		63	
Species	Number Caught	Relative Density	Number Caught	Relative Density
Coregonus clupeaformis	1641	16.74	1783	28.30
Coregonus sp. (cisco)	139	1.42	495	7.86
Salvelinus namaycush	389	3.97	164	2.59
Esox lucius	29	0.30	102	1.62
Catostomus catostomus	328	3.35	0	0.00
Catostomus commersoni	655	6.68	438	6.95
Lota lota	556	5.68	315	4.98
Perca fluviatilis	196	2.00	143	2.27
Stizostedion vitreum	189	1.93	259	4.11
all species combined	4200	42.86	3708	58.86
	Weight Caught (kg)	Relative Biomass	Weight Caught (kg)	Relative Biomass
Salvelinus namaycush	632	6.44	359	5.70
Lota lota	366	3.73	399	6.33

---

* One unit of effort equals 137 m of gillnet fished overnight.

and Trichoptera nymphs, *Hyallela sp.*, *Rhinicthys cataractae*, *Etheostoma nigrum*, and unidentified cyprinids. Immature burbot caught in Mistik Creek fed most frequently on black fly larvae (Simuliidae) and Odonata larvae. Fish were poorly represented in their diets.

Immature burbot fed more frequently on a wider variety of invertebrates than did mature burbot but, mature burbot fed more frequently on a wider variety of fish. With the exception of *O. virilis*, no taxon was well represented in the diets of both mature and immature burbot. There was no apparent overlap between sizes of *O. virilis* eaten by mature and immature burbot.

Volumetric representation of fish in the burbot diet exceeded that of invertebrates for all burbot sampled (Table XVI). The exception was Mistik Creek burbot for which invertebrates represented the greatest volume of the diet. The greatest percentage volumes of taxa in the diets of mature burbot were represented by ciscoes, *Coregonus clupeaformis*, *M. thompsoni*, and *O. virilis*. *C. cognatus*, *R. cataractae*, *Perca fluviatilis*, and *O. virilis* constituted by volume the majority of the diet of immature burbot. *O. virilis* was the only taxon for which strong volumetric representation was noted in both mature and immature burbot diets. Cannibalism was rare. Of the 974 burbot stomachs examined only one contained another burbot.

Although lake trout stomachs were not analysed, four lake trout collected at various depths, locations, and dates from the south basin each had the caudal fin of a burbot protruding from its mouth. All lake trout were relatively large (61.0, 63.0, 64.0, and 71.4 cm). Total lengths of the nearly undigested burbot (38.4, 40.0, 40.7, and 44.0 cm) approximated the most common lengths of burbot collected by gillnets in the south basin.

Since I did not sample lake trout stomachs, burbot may have been common in lake trout diets, but have gone unnoticed when they were fully swallowed.

Depth Distributions of Burbot and Lake Trout

Fishing effort was equal among depths and fishing periods within a basin but was three times greater in the south basin than in the middle basin, because fish were collected from three stations in the south basin and from only one station in the middle basin. Comparisons between basins of absolute numbers of fish collected at a given depth or fishing period have, therefore, not been justified. Figures 27, 28, and 29 were based on 1978 data because inconsistencies in temporal and spatial distribution of fishing effort in 1977 made comparisons of fish distributions between different depths and fishing periods invalid.

Burbot in the south basin were most abundant at all fishing periods at depths ≥ 33.5 m and were also abundant in the 18.5 m depth samples from July 18 onward (Fig. 27). In the middle basin, burbot were most abundant in 18.5 m or ≥ 33.5 m sampling depths depending on the fishing period. Burbot occurred in shallow waters (9.0 m) infrequently, usually in late June, in both basins.

Lake trout were most abundant at the sampling depth of 18.5 m in the south basin between June 27 and July 2 (Fig. 28). Lake trout abundance was similar between depths of 18.5 and ≥ 33.5 m for the remainder of the season, although it became slightly greater at ≥33.5 m depths between July 18 and July 25 and between August 4 and August 21. With the exception of the earliest sampling period when they appeared equally distributed among all sampling depths, almost all middle basin lake trout were collected from 18.5 m depths (Fig. 28). Lake trout occurred in shallow waters infrequently in both basins, usually in late June.

Pronounced differences between depth distributions of burbot and lake trout occurred in the south basin between June 27 and July 2. At this time burbot were concentrated at ≥ 33.5 m and lake trout were concentrated at 18.5 m. In the middle basin burbot were relatively abundant at ≥ 33.5 m but lake trout were rarely collected at this depth (Figs. 27 and 28).

Depth distributions of burbot and lake trout were similar in both basins but burbot were most abundant at ≥ 33.5 m and lake trout were most abundant at 18.5 m (Fig. 29).

Table XIII. Burbot diet taxa expressed as percentage frequency of occurrence in stomachs containing food.

	Lake Athapapuskow		Mistik Creek		Lake Athapapuskow Shorelines	
Item	%	N	%	N	%	N
Total number of stomachs:	100	788	100	36	100	186
Empty stomachs:	44	347	11	4	30	56
No. of stomachs with food:	56	441	89	32	70	130
Fish						
Coregonus sp. (Ciscoes)	9.75	43				
Coregonus clupeaformis	0.91	4				
Unidentified coregonids	1.81	8				
Myoxocephalus thompsoni	9.52	42				
Cottus cognatus	1.59	7			27.69	36
Stizostedion vitreum	0.23	1				
Perca fluviatilis	0.23	1			3.08	4
Catostomus catostomus	0.23	1				
Lota lota	0.23	1				
Pungitius pungitius	4.31	19			0.77	1
Percopsis omiscomaycus	0.23	1			0.77	1
Percina caprodes			3.13	1		
Rhinichthys cataractae			3.13	1	2.31	3
Notropis hudsonius					1.54	2
Unidentified cyprinids					3.08	4
Etheostoma nigrum					3.85	5
Unidentified fish	35.83	158			3.85	5
Invertebrates						
Orconectes virilis	11.11	49			23.08	30
Hyalella sp.	2.27	10			8.46	11
Mysis relicta	12.47	55				
Amphipoda	0.91	4				
Cladocera			3.13	1	2.31	3
Ostracoda					0.77	1
Simuliidae			81.25	26		
Diptera	1.36	6			0.77	1
Plecoptera					2.31	3
Neuroptera	0.68	3				
Ephemeroptera	3.85	17			11.54	15
Trichoptera					7.69	10
Odonata			21.88	7		
Unidentified Insects	0.23	1	6.25	2	9.23	12
Hirudinea					1.54	2
Oligochaeta					0.77	1
Gastropoda			3.13	1		
Porifera	0.23	1				
Misc. (including fish eggs, debris)	39.23	173	18.75	6	26.15	34

Table XIV. Burbot diet taxa expressed as percentage of total volume (ml) of all stomach contents.

Item	Lake Athapapuskow			Mistik Creek			Lake Athapapuskow Shorelines		
	%	Vol.	N	%	Vol.	N	%	Vol.	N
Total number of stomachs:	100		788	100		36	100		186
Empty stomachs:	44		347	11		9	30		56
Number of stomachs examined:	56		441	89		32	70		130
Total volume of stomachs:	100	2873.15		100	49.50		100	102.6	
Fish									
Coregonus sp. (Ciscoes)	30.17	866.75							
Coregonus clupeaformis	7.97	229.00							
Unidentified coregonids	4.02	115.50							
Myoxocephalus thompsoni	4.79	137.60							
Cottus cognatus	0.72	20.70					58.97	60.50	
Stizostedion vitreum	0.45	13.00							
Perca fluviatilis	0.28	8.00					3.22	3.30	
Catostomus catostomus	1.04	30.00							
Lota lota	2.26	65.00							
Pungitius pungitius	1.15	33.00					0.10	0.10	
Percopsis omiscomaycus	0.19	5.50					3.02	3.10	
Percina caprodes				3.43	1.70				
Rhinichthys cataractae				1.41	0.70		6.53	6.70	
Notropis hudsonius							0.59	0.60	
Unidentified cyprinids							1.95	2.00	
Etheostoma nigrum							1.75	1.80	
Unidentified fish	23.84	685.00					1.36	1.40	
Invertebrates									
Orconectes virilis	16.89	485.20					12.04	12.35	
Hyalella sp.	0.08	2.40					0.68	0.70	
Mysis relicta	1.96	56.40							
Amphipoda	0.14	4.00							
Cladocera				0.20	0.10			P*	
Ostracoda								P	
Simuliidae				85.15	42.15				
Diptera	0.02	0.60						P	
Plecoptera							0.49	0.50	
Neuroptera		P							
Ephemeroptera	0.07	2.20					0.75	1.00	
Trichoptera							0.39	0.40	
Odonata				7.47	3.70				
Unidentified insects	0.03	0.80		1.21	0.40		0.78	0.80	
Hirudinea							0.29	0.30	
Oligochaeta								P	
Gastropoda					P				
Porifera		P							
Misc. (including fish eggs, unidentified debris)	3.92	112.50		1.51	0.75		6.87	7.05	

---

*When diet taxa were present but too small for volumetric measurement they were expressed as P.

Differences between species in depth distribution were most pronounced in the middle basin. Few lake trout and many burbot were collected at $\geq$ 33.5 m in this basin. Differences between basins in depth distributions of either species were most pronounced for lake trout as this species was abundant at $\geq$ 33.5 m in the south basin and rarely collected at this depth in the middle basin.

While mature burbot seldom occurred at depths less than 18.5 m, immature burbot were restricted to shorelines and the mouths of creeks (Tables IV, V, VI, and VII).

Collections of rotenone-poisoned fish contained burbot only when rock and boulder bottom shorelines were sampled. Poisoned shorelines at which burbot were collected are labelled P and poisoned shorelines which did not yield burbot are labelled U (Fig. 2). All P sites were characterized by rock and boulder bottoms and all U sites, with the exception of the site near the large point on the southwest shore of the south basin, which is described in methods, were characterized by sand and/or mud bottoms.

Lake trout were never present in collections of rotenone-poisoned fish from shorelines or the mouths of creeks. Lake trout would be susceptible to rotenone, therefore, their absence from these collections indicates that they were not in this habitat during the sampling period.

Table XV gives the abundance of eight species at 9.0 and 18.5 m sampling depths in the north basin (station 6) in

1977. After July 21, whitefish, lake trout, and burbot abundance decreased markedly in 18.5 m amples. Since a corresponding increase in abundance after July 21 at 9.0 m was observed for whitefish but not for lake trout and burbot, the latter two species probably left the basin.

Community Structure

Gillnet catches were composed predominantly of benthic feeders (lake whitefish, longnose sucker, and white sucker) and deepwater predators (burbot and lake trout). Shallow water predators (yellow perch, walleye, and northern pike) were poorly represented in gillnet catches. Yellow perch, trout-perch, spottail shiner, sculpin, lake chub, and cisco were under-represented in gillnet catches as they were less susceptible to capture by gillnets and were captured by only one or two of the smallest mesh sizes (Table XVI). Lake chub and longnose sucker were well represented in south basin cathces but absent from middle and north basin catches. Relative abundance of most species exhibited appreciable variation between years (Table XVI). Variance between 1977 and 1978 relative abundance estimates can be attributed to differences in mesh sizes used in gillnet gangs and to spatial and temporal differences of sampling between years (see methods).

Gillnet catches at depths $\geq$ 18.5 m were composed predominantly of lake trout, burbot, lake whitefish, cisco, and longnose sucker. Catches at 9 m were composed predominantly of yellow perch, walleye, northern pike, cisco, and white sucker.

Lake whitefish, cisco, walleye, and northern pike were most dense in the middle and north basins whereas lake trout were most dense in the south basin. The relative density of burbot was similar between basins but the relative biomass of burbot was greatest in the middle and north basins (Table XII).

Collections of rotenone-poisoned fish made along shorelines in the middle basin were composed of burbot, logperch, trout-perch, yellow perch, spottail shiner, slimy sculpin, white sucker, and longnose dace. In the south basin these collections were composed of burbot, trout-perch, yellow perch, slimy sculpin, white sucker, longnose dace, longnose sucker, johnny darter, and lake chub.

Quantitative assessment of shoreline communities was not attempted. Usually in excess of 100 individuals of each species were poisoned and often several hundred were seen in the poisoned area. Longnose sucker, lake chub, and johnny darter were absent from all shorelines poisoned in the middle basin. Spottail shiner and logperch were absent from all shorelines poisoned in the south basin. With the exception of spottail shiner, yellow perch, and lake chub, all species collected on shorelines were primarily benthic foragers.

Figure 27. Capture frequency of burbot at three depths and four fishing periods in Lake Athapapuskow, 1978.

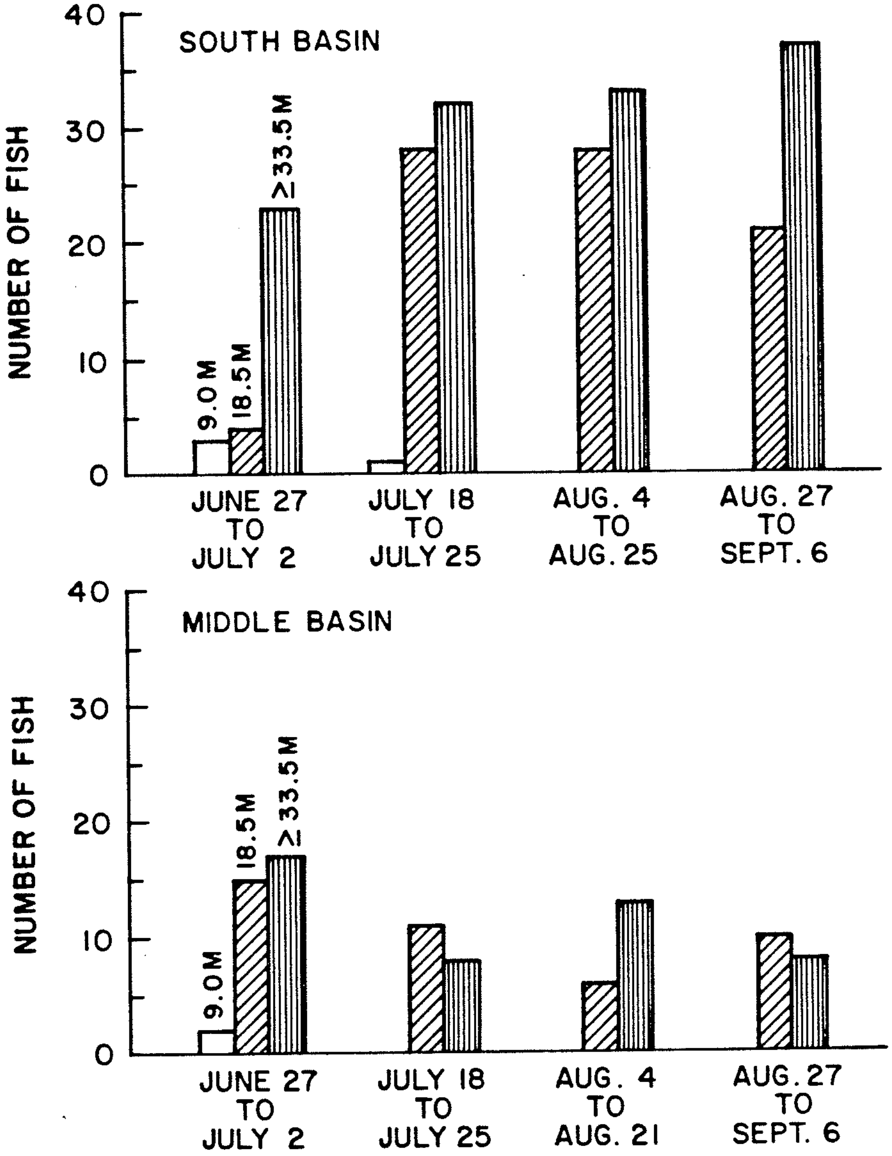
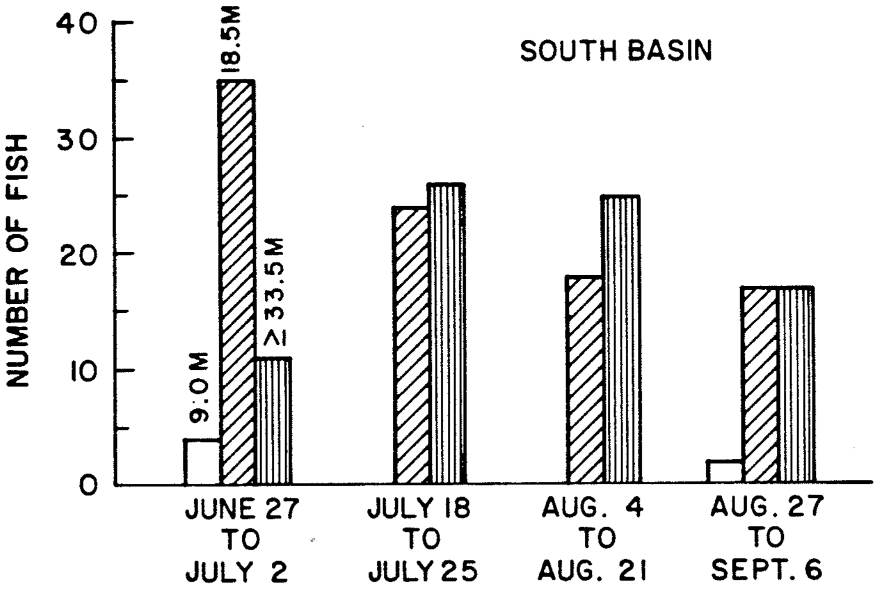

SOUTH BASIN
NUMBER OF FISH
0
10
20
30
40
9.0 M
18.5 M
≥ 33.5 M
JUNE 27 TO JULY 2
JULY 18 TO JULY 25
AUG. 4 TO AUG. 25
AUG. 27 TO SEPT. 6
MIDDLE BASIN
NUMBER OF FISH
0
10
20
30
40
9.0M
18.5M
≥ 33.5 M
JUNE 27 TO JULY 2
JULY 18 TO JULY 25
AUG. 4 TO AUG. 21
AUG. 27 TO SEPT. 6

Figure 28. Capture frequency of lake trout at three depths and four fishing periods in Lake Athapapuskow, 1978.


SOUTH BASIN
NUMBER OF FISH
0
10
20
30
40
9.0M
18.5M
≥ 33.5M
JUNE 27 TO JULY 2
JULY 18 TO JULY 25
AUG. 4 TO AUG. 21
AUG. 27 TO SEPT. 6

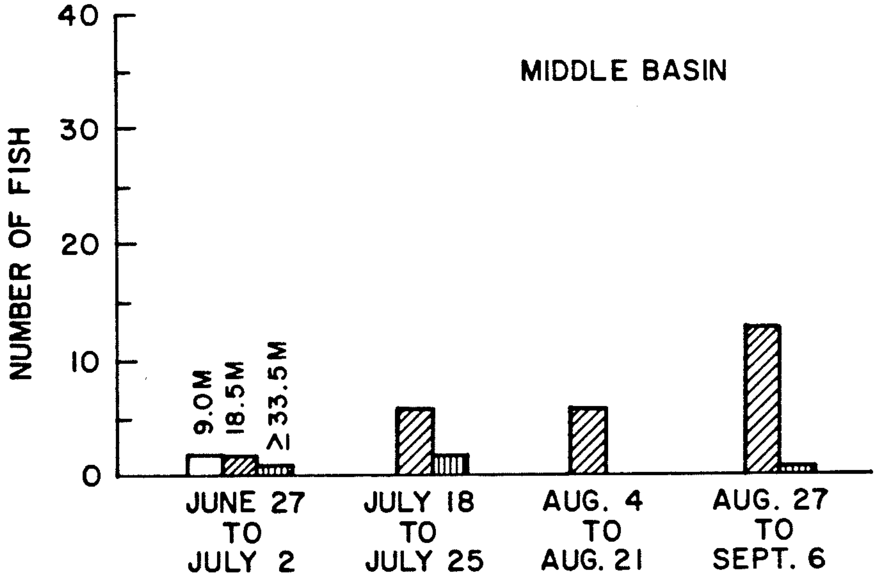
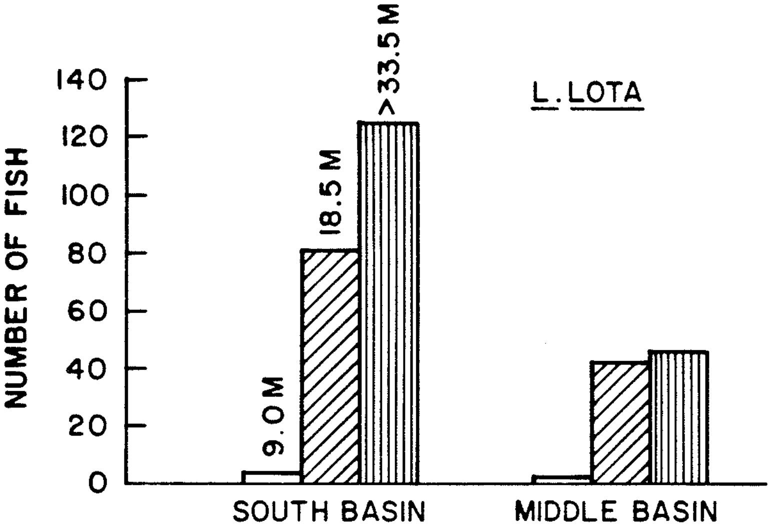
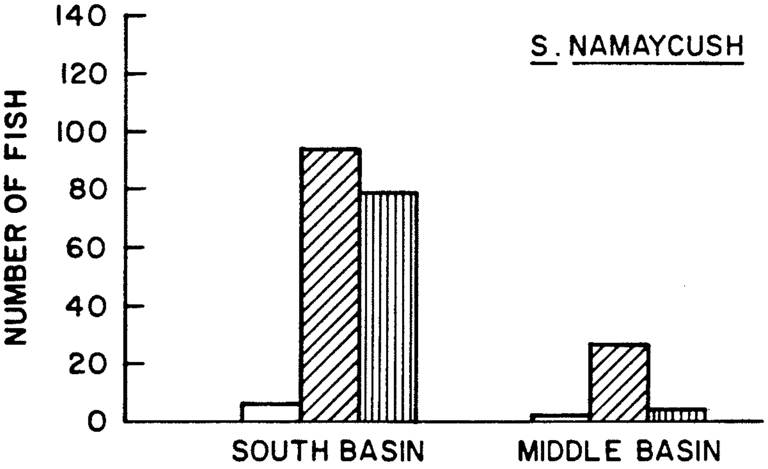

MIDDLE BASIN
NUMBER OF FISH
0
10
20
30
40
9.0M
18.5M
≥ 33.5M
JUNE 27 TO JULY 2
JULY 18 TO JULY 25
AUG. 4 TO AUG. 21
AUG. 27 TO SEPT. 6

Figure 29. Capture frequency of burbot and lake trout at three depths in Lake Athapapuskow, 1978.



140
120
100
80
60
40
20
0
NUMBER OF FISH
9.0 M
18.5 M
>33.5 M
L. LOTA
SOUTH BASIN
MIDDLE BASIN



140
120
100
80
60
40
20
0
NUMBER OF FISH
S. NAMAYCUSH
SOUTH BASIN
MIDDLE BASIN

Table XV. Gillnet catch in the north basin of Lake Athapapuskow (station 6) in 1977.

Depth	Sampling Date	Burbot	Lake Trout	Whitefish	Cisco	White Sucker	Northern Pike	Pickerel	Perch
9 metres	June 25	0	1	4	23	9	4	2	1
	July 11	0	1	5	5	5	0	1	0
	July 21	0	0	6	16	10	2	4	3
	August 5	0	0	1	3	21	0	13	25
	August 20	0	0	21	6	6	2	4	2
	Sept. 8	0	6	9	9	11	0	2	46
18.5 metres	June 26	4	1	11	8	0	0	0	0
	July 11	3	8	45	25	0	1	0	0
	July 21	8	12	25	30	1	0	3	0
	August 5	1	7	12	24	0	0	0	0
	August 20	0	0	1	0	0	0	0	0
	Sept. 8	0	0	0	14	0	1	0	0

Table XVI. Total number caught and numerical percentage of total catch (relative abundance) of each species caught in gillnets in Lake Athapapuskow.

	Total 1977		Total 1978		% 1977		% 1978	
	South Basin	Middle and North Basin	South Basin	Middle Basin	South Basin	Middle and North Basin	South Basin	Middle Basin
Lota lota	332	169	224	146	14.6	6.7	11.6	12.3
Salvelinus namaycush	179	115	210	49	7.9	4.6	10.9	4.1
Coregonus clupeaformis	732	1015	909	768	32.2	40.2	47.1	64.9
Coregonus sp. (Cisco)	105	466	34	29	4.6	18.5	1.8	2.4
Catostomus commersoni	396	316	259	122	17.4	12.5	13.4	10.3
Catostomus catostomus	173	---	155	---	7.6	---	8.0	---
Esox lucius	14	82	15	20	0.6	3.2	0.8	1.7
Stizostedion vitreum	73	209	116	50	3.2	8.3	6.0	4.2
Perca fluviatilis	190	143	6	---	8.4	5.7	0.3	---
Myoxocephalus thompsoni	2	---	---	---	0.09	---	---	---
Cottus cognatus	3	---	---	---	0.1	---	---	---
Couesius plumbeus	65	---	---	---	2.9	---	---	---
Percopsis omiscomaycus	8	1	---	---	0.4	0.4	---	---
Notropis hudsonius	---	8	---	---	---	0.3	---	---
Total	2272	2524	1928	1184	100	100	100	100

DISCUSSION

Gillnet Selectivity

The selection for different sizes of fish by gillnets of various mesh sizes may affect estimates of population characteristics that imply random sampling (Hamley 1975). Hamley (1975) defines selection as any process that causes the probability of capture to vary with the characteristics of the fish. He defines selectivity as a quantitative expression of selection which traditionally means selection by size. He classified methods of estimating selectivity into five basic types. These are; 1) direct estimates, 2) indirect estimates, 3) the determination of selectivity by inference from girth measurements or 4) from mortality estimates, and 5) the comparison of size distributions of fish caught in each mesh size. Direct estimates are made by comparing size distributions of gillnet catches with size distributions of a known population. These estimates could not be made in this study because the actual size distributions of the sampled populations were not known. Data were available for indirect estimates of selectivity but these estimates were not calculated because they assume that the selectivity curves for all mesh sizes have the same shapes and heights. This assumption was first made by Baranov

(1914). Hamley (1975) stated that criticism of this assumption was first made by Ricker (1949) who observed that the youngest fish (the most abundant in the population) were not the most abundant in gillnet catches. Recent work has refuted Baranov's assumption of geometric similarity among selectivity curves of various mesh sizes (Regier _et_ _al_. 1969; Hamley and Regier 1973; Hamley 1972). These authors found that larger mesh sizes caught fish of a size for which they were selective more efficiently than smaller mesh sizes caught fish of a size for which they were selective. Inference of selectivity from girth measurements assumes that a fish will be caught if its head girth is smaller but maximum girth larger than the mesh perimeter. If other means of capture are ignored, maximum and head girth measurements can be used to predict selectivity before any gillnet fishing is done (Hamley 1975). Lake Athapapuskow lake trout, however, were often caught by entanglement, not girthing. In any case, head and maximum girth measurements were not made in this study. Hamley (1975) stated that estimates of fishing mortality can be used to estimate gear selectivity (DeLury 1947; Hamley 1972) if calculations are done separately for each size class of fish. He stated that this method assumes that catchability remains constant during sampling. Its disadvantages are the difficulty of obtaining adequate sample sizes and satisfying the above assumption. This method is applicable when a closed population is fished intensively so that catch per unit of effort decreases as the population is reduced. This method could not be used in estimating selectivity in Lake Athapapuskow because sample sizes were too small. Also, since sampling was not intensive it was unlikely that it would have any measureable affect on the population size of burbot or lake trout in Lake Athapapuskow. Consequently, gillnet selectivity in this study was examined by comparing size distributions of fish captured in various mesh sizes (Figs. 10, 11, 12, and 13). Hamley (1975) cautions that this method gives only a rough idea of selectivity because the catch of fish in a length class depends on the abundance of that length class and on the selectivity of each mesh size for that length class. Since actual length class abundances of burbot and lake trout in Lake Athapapuskow are unknown, as are the vulnerabilities of these length classes to gillnets of various mesh sizes, inferences on gillnet selectivity based on the heights of length frequency histograms in figures 10, 11, 12, and 13 cannot be made.

Gillnet selectivity most seriously misrepresented the abundances of length classes smaller than the modal length classes of histograms in figures 14 and 17. It was expected that these small fish would be more abundant than larger fish, however, the above histograms indicated they were less abundant. The abundance of length classes greater than or equal to modal length classes of these histograms will not represent the abundance of these larger classes in the population if there are differences among these classes in vulnerability to the gear.

As gillnets are not very selective for lake trout, with the exception of lake trout between 20 and 32 cm in length, the relative abundances of length classes greater than or equal to modal classes in figure 17 probably approximates the abundance of these length classes in the sampled population. The relative abundance of the distinct group of small lake trout (20 to 32 cm) probably greatly underestimates the abundance of this size range in the sampled population because they were caught almost exclusively in the 5.1 cm mesh gillnet in 1978 in the south basin whereas other size classes were caught in several mesh sizes and in all basins (Figs. 12, 13, and 17) in both years. For lake trout, the modal length classes are between 51 and 60 cm in the south basin and between 57 and 63 cm in the middle and north basins (Fig. 17). The plots of mean length versus age (Fig. 21) become asymptotic at these lengths in the respective basins. Therefore, these length intervals would be expected to encompass a greater range of ages, and by implication, include more fish at or above these lengths than below them. The fact that growth becomes asymptotic at the length class which is represented by a strong modal size group in each basin further supports the contention that the gillnet catches at and beyond these size classes approximate the abundance of these size groups in the lake. An analagous conclusion can not be drawn for burbot because their growth is almost linear. Faster growth of burbot in the middle and north basins (Fig. 19), however, would infer that gillnet samples from these basins will contain relatively greater numbers of larger fish than samples from the south basin. This is, indeed, the case (Fig. 14). Therefore, gillnet samples of burbot are probably reliable indicators of relative abundances of length classes in the sampled populations.

Comparisons between basins of population characteristics derived from gillnet samples are probably valid because identical mesh sizes were fished in all basins at similar dates and depths, and a large range of fish sizes were caught in all basins. Also, there was considerable overlap between basins in the range of ages and sizes of fish caught. Therefore, it seems unlikely that selectivity varied between basins.

Gillnet selectivity can bias estimates of population characteristics other than size and age distributions of sampled fish. Ricker (1975) stated that, if sampling is more effective for fish of intermediate size, it will select more of the larger members of younger age groups and more of the smaller members of older age groups. If, in Lake Athapapuskow, gillnets select for intermediate sized fish, the growth of younger fish will be overestimated and the growth of older fish will be underestimated. It was not possible to determine if gillnets were selective for intermediate sized fish, therefore, conclusions on the effects of gillnet selectivity on estimates of population growth rates of lake trout and burbot can not be made.

Mortality rate estimates can also be affected by the selectivity of gillnets for fish size because this rate can be size dependent (Ricker 1969, 1975). The larger fish in a year class often have a different, usually greater, mortality rate than the smaller fish (Ricker 1975). Comparisons of mortality rates of burbot between basins may, therefore, be criticized because younger age groups were used to calculate mortality rates in the south basin (ages 11 to 22) than in the middle and north basins (ages 15 to 28). These comparisons are justified in part, by the high squared correlation coefficient values of regressions used to calculate these estimates and by the large overlap between basins in ages used to calculate mortality rates (Fig. 22).

Ricker (1975) stated that if larger fish are more vulnerable to a given gear than smaller fish, older fish will be over represented in the catch and estimates of mortality will be too small. It was not possible to determine if there were differences in vulnerability to gillnets among age classes used to calculate burbot mortality rates. Therefore, no conclusions can be made about the effects of gillnet selectivity on estimates of burbot mortality rates. As discussed later, the validity of estimates of lake trout mortality rates in Lake Athapapuskow is doubtfull even if the effects of gillnet selectivity on these rates are ignored. Therefore, it is not necessary to consider the effects of gear selectivity on estimates of mortality rates for this species.

Basin Trophy

Ryder (1965) developed a morphoedaphic index (M.E.I.), based on mean depth and total dissolved solids, as an estimate for the potential fish production of north-temperate lakes. He proposed that a M.E.I. of about 6.6 appeared to separate oligotrophic from eutrophic lakes. He stated that the index range for mesotrophic lakes was narrow and probably did not exceed 1.4 units. Ryder (1972) classified 11 lakes as oligotrophic in which the M.E.I. varied from 0.4 for Lake Superior to 11.7 for Lac la Ronge. The morphoedaphic indexes of the south, middle, and north basins of Lake Athapapuskow are 11.7, 21.3, and 25.0 respectively. These indexes indicate that the south basin is less eutrophic and has a lower potential for fish production than the middle and north basins. I excluded Schlick's (1973a) total dissolved solid values for Schist Creek when calculating the M.E.I. of the middle and north basins. Schist Creek is a relatively small isolated area not representative of any major lake basin (Fig. 1). It had comparatively high total dissolved solid levels (376 mg/l), possibly due to the effluent it receives from the town of Flin Flon.

Oxygen profiles were consistent with M.E.I. values because they also indicated that the south basin was less eutrophic than the middle and north basins. Oxygen profiles of the south basin of Lake Athapapuskow were orthograde (Fig. 8) whereas those of the middle and north basins were clinograde (Fig. 7). Oxygen profiles termed orthograde (after Aberg and Rodhe 1942) are rarely found in dimictic lakes and are characteristic of extremely unproductive lakes or moderately oligotrophic lakes during the very early stages of summer stratification (Wetzel 1975; Ruttner 1953; Hutchinson 1957). Oxygen profiles termed clinograde (after Aberg and Rodhe 1942), are characteristic of eutrophic lakes (Wetzel 1975; Ruttner 1953; Hutchinson 1957), and were observed in the middle and north basins (Figs. 6 and 7).

Greater relative densities of whitefish, cisco, northern pike, white sucker, perch, and walleye and a greater relative biomass of burbot in the middle and north basins than in the south basin (Table XII) indicated that the M.E.I. of each basin was a valid indicator of that basin's potential for fish production. Similarly, Martin (1966) found that the yield of lake trout from Happy Isle, Merchants, Redrock, and Opeongo Lakes in Algonquin Park, Ontario, was directly proportional to the M.E.I. values of these lakes. However, the relative density and biomass of lake trout was greatest in the south basin (Table XII) even though the M.E.I. of this basin was lower than those of the middle and north basins. This discrepancy may be due to more intense exploitation of lake trout in the middle and north basins than in the south basin (see Discussion: Evidence for Overfishing of Lake Athapapuskow Lake Trout). A greater removal of fish in the middle and north basins could reduce relative density and biomass estimates to below what would be expected based on the M.E.I. values.

Fish Exchange Between Basins

Prior to data analysis it was assumed that negligible exchange of fish occurred between the south and middle basins and substantial exchange occurred between the middle and north basins. Several observations suggest that pooling of data from the middle and north basins is justified. These are: 1) the decline in catch of lake trout and burbot after mid July in nets set at 18.5 m in the north basin, 2) the lack of any correlated increase in catch in nets set in shallower depths at this time suggesting that burbot and lake trout left this basin, rather than moving to shallower water (Table XV), and 3) the establishment of anoxic conditions in the hypolimnion in the north basin at this time (Fig. 6). All of these, and the existence of two relatively large deep connections between the north and middle basins suggested that burbot and lake trout moved from the north basin to the middle basin when the hypolimnion of the north basin became anoxic. If fish moved from the north to the middle basin an increase in catch per unit of effort in the middle basin may have been expected at this time, but was not observed. Although this movement probably occurred, it may not have been reflected by an increase in catch per unit of effort in the middle basin because the number of fish which moved into the middle basin was relatively small in comparison to the number of fish which were in the middle basin prior to this movement. This explanation is supported by the following facts. Almost all burbot and lake trout were caught in habitat $\geq$ 18.5 m in depth (Figs. 27, 28, and 29) and there is 22 times more habitat $\geq$ 18.5 m in depth in the middle basin than in the north basin (15.1 ha in the middle basin versus 0.7 ha in the north basin (Table I). If densities of resident fish were similar between basins before movement, the addition of the proportionally smaller number of fish from the north basin to the middle basin would have made too small a difference in the density of fish in the middle basin to be detected in gillnet catches.

Exchange of fish between the south and middle basins is likely impeded by the almost complete separation of these basins. In warm seasons the shallowness of water passages between these basins may inhibit the movement of coldwater fish because of a thermal barrier. Ice (approximately 1.2 m thick) may restrict or block these passages in winter.

Franzin and Clayton (1977) studied the frequencies of alleles of genes governing electrophoretic phenotypes of lake whitefish muscle glycerol-3-phosphate dehydrogenase (G-3-PDH) and lactate dehydrogenase (LDH). Based on differences between allele frequencies of whitefish caught in the south and middle basins it is unlikely that significant exchange of whitefish occurs between these basins (W.G. Franzin, pers. comm.). Kliewer (1969) found significant differences between the south and middle basins in whitefish gillraker numbers, length, and spacing.

The presence in the south basin and absence in the middle and north bsins of lake chub, longnose sucker, and johnny darters, and the presence in the middle and north basins and absence in the south basin of spottail shiners and logperch, suggests that there is little movement of most fish species between the south and middle basins.

Consistently observed significant differences between south basin and middle and north basin burbot and lake trout morphologies (Appendix B, Table II) and population characteristics further substantiates the assumption that negligible exchange of these species occurs between the south basin and middle and north basins.

Depth Distribution of Burbot Size and Maturity Classes

As stated in results, mature burbot seldom occurred at depths less than 18.5 m whereas immature burbot were restricted to shorelines and the mouths of creeks (Tables IV, V, VI, and VII). Because immature burbot were less susceptible to capture by gillnets, their rarity in habitats other than shorelines may be due to sampling error. Mature burbot were probably susceptible to collection by poisoning because several very large immature burbot were collected in this manner. Therefore, the absence of mature burbot from shoreline collections indicated that they probably did not inhabit these areas. This is further supported by the lower abundance of mature burbot in the 9.0 m depth gillnet samples than in the $\geq$ 18.5 m gillnet samples (Tables IV, V, VI, and VII).

Although immature burbot were not very susceptible to capture by gillnets the number captured by gillnets at 9.0 and $\geq$ 18.5 m was considerably less than expected if these abundant age classes were well represented in deep water. The rapid decline in representation of burbot greater than approximately 20.0 cm in length in shoreline catches and the poor representation of burbot between lengths of 20.0 and 40.0 cm at all sampling sites coupled with the observations that all south basin burbot were mature at lengths $\geq$ 36.0 cm and all middle and north basin burbot were mature at lengths $\geq$ 42.0 cm (Tables VI and VII), suggested that burbot left the shoreline habitat prior to maturity, matured in areas between shorelines and approximately 18.5 m, and inhabited waters ≥ 18.5 m after maturity. The occurrence of small immature burbot in the shallow shoreline habitat has been noted in several populations. Johnson (1975) reported that burbot taken in warm shallow water in Great Bear Lake were less than 200 mm in length. Hanson and Quadri (1980) captured young-of-the-year burbot on the shorelines of islands in the Ottawa River. In Heming Lake young-of-the-year burbot were poisoned on shorelines (Lawler 1963). Hackney (1973) stated that in Lakes Opeongo and Lavieille young burbot probably begin joining the offshore community of adult burbot by the end of their second summer.

The concentration of adult burbot into deep cool habitat during summer has been noted not only in Lake Athapapuskow (Figs. 27 and 29) but also in Great Slave Lake (Rawson 1951), Lake Michigan (Pearse 1921), and Lake Nipissing (Harkness and Fry 1940).

As noted among burbot from Lake Athapapuskow, cannibalism is extremely rare in lacustrine burbot populations (Hackney 1973; Lawler 1963; Hewson 1955; Clemens 1951a; Bailey 1972; McCrimmon and Devitt 1954; Van Oosten and Deason 1938). This may be due to differences in distribution of young and adults. This relationship may change during winter when young and adults inhabit similar depths (Hackney 1973). He notes that in some fluvial populations (Yukon and Tanana

Rivers, Chen 1969) in water with temperatures that do not stratify, cannibalism is common.

Burbot Condition and Temperature Preferences

Based on the assumption that heavier fish are in better condition than lighter fish at a given length, the condition of burbot and lake trout from Lake Athapapuskow was compared to the condition of fish from other areas. For these comparisons, equations for the regression of log weight versus log length were used to calculate weights of 45 cm burbot and 55 cm lake trout (Tables XVII and XVIII). The above lengths approximated the midpoint of the data ranges from all areas considered. Errors involved with comparison of fish weights estimated for lengths which were not close to the midpoint of all data ranges would be extreme because; 1) weights estimated from length-weight regressions will, in part, be determined by regression slopes and regression slopes varied among populations, 2) slopes of length-weight regressions will, in part, be determined by the range of data from which these regressions were derived and data ranges varied among populations, and 3) for length-weight regressions, the variance in weight at a given length is characteristically greatest at the limits of the data range.

Estimated weights of 45 cm burbot were greatest in large lakes at all latitudes (Erie, Winnipeg, Superior, Simcoe, and Lake of the Woods) and smaller lakes which occur north of 45^0N latitude (Opeongo, Saint-Louis, and Deux-Montagnes). Estimated burbot weights were least in small lakes south of 45^0N latitude (Ring, Ocean, Trail, and Boysen), in populations which occur near the northern limits of the North American range of burbot (Interior Alaska and Great Slave Lake), and in rivers (Grand Riviere in Quebec and the upper Tanana and Yukon River drainages in interior Alaska) (Table XVIII).

Since Lake Athapapuskow is both large and north of 45^0N latitude, it would be expected that the estimated weight of 45 cm burbot from this lake would be relatively high, as are those from northern lakes and large southern lakes. Instead, it is less than those of 11 other populations and similar to the estimated weights of 45 cm burbot from small lakes south of 45^0N latitude, rivers, and populations near the northern limits of the North American range of burbot. (Table XVII).

The condition of adult burbot may be more directly related to lake temperature regimes rather than to lake size and latitude since in the range of burbot, large lakes at all latitudes and smaller northern lakes will have relatively colder habitats within them than do rivers and small southern lakes. The absence of burbot populations south of 40^0N latitude (Scott and Crossman 1973; Lee et al. 1980) may be due to their preference for a cold water habitat in which adults appear to be in good condition.

Chen (1969) stated that the condition of winter prespawning burbot was better than that of summer burbot. Miller (1970a) reported that condition factors of Ocean Lake burbot were lowest in summer and fall and were possibly due to higher water temperature at these times. He found that burbot condition was best in winter, even after spawning. He noted that during the summer burbot were trapped most successfully at night at the mouths of drainage inlets where water temperaturs were 2.2^0 to 6.11^0 C cooler than the lake water. Kennedy (1940) trapped burbot migrating from a rapidly warming shallow lake into a cooler deeper lake in spring and early summer. Robins and Deubler (1955) state that, at the southern periphery of its range, burbot survival is dependent on the availability of cool, deep lakes or headwater creeks and springs. They reported that burbot distribution in the Susquehanna River was restricted to cooler tributaries in the uppermost reaches of the river.

Unlike adults, juvenile burbot are usually found in warm shallow water. Crossman _et_ _al_. (1953) found that under laboratory conditions yearling burbot preferred a temperature of 21^0 C. In Lake Athapapuskow, mature burbot were caught in deep water at temperatures which never exceeded 12^0 C and were most often between 4^0 and 8^0 C whereas immature burbot were caught in shallow water at temperatures between 15^0 and 21^0 C. Clady (1976) reported that in Oneida Lake, a lake situated on the southern periphery of the burbot range in which summer temperatures often exceed 24^{0}C, there was a disproportionately great abundance of larval burbot in relation to adults. He states that the great abundance of the young which are more tolerant to high temperatures than adults, may contribute to the persistence of this cold-water species in eutrophic environments.

Burbot Growth

In general, burbot from populations north of 53^0 N latitude grow more slowly than burbot from more southern populations (Figs. 30, 31, 32, and 33). Slow growing southern populations were from Ring and Trail lakes, both with surface areas less than 60 ha, and from streams (Torrey Creek, upper reaches of the Susquehanna River) situated on the southern periphery of this species' range. Slow growth of these populations and of northern populations may be related to water temperature extremes to which they are subjected.

Lake Athapapuskow burbot grew more slowly than burbot from all other populations for which I had growth data. This may be due to the apparent increase in abundance of burbot in Lake Athapapuskow if an increase in abundance has resulted in an increase in intraspecific competition for food. Unfortunately, the little information on burbot abundance in other populations makes it difficult to comparatively assess the abundance of burbot in Lake

Table XVII. Length-weight relationships of 17 burbot populations.

Location	North Lat.	West Long.	Method of Calculation	Units		Calculated Weight in grams at 45 cm	Data range in cm
				Weight	Length		
Lake Erie	42°	81°	graphically*	-	-	832	27-67
Lake Winnipeg (South)	52°	47°	$\text{Log } W = 2.65 \text{ Log } L - 3.0706$	lb	in	784	41-79
Lake Winnipeg (North)	52°	47°	$\text{Log } W = 3.18 \text{ Log } L - 3.7695$	lb	in	720	37-82
Lac Saint-Louis	45°	73°	$\text{Log } W = 2.45 \text{ Log } L - 3.67$	gr	mm	677	24-64
Lake Superior	47°	87°	$\text{Log } W = 2.82335 \text{ Log } L - 3.35697$	lb	in	667	8-74
Lake of the Woods	49°	94°	$\text{Log } W = 2.7484 \text{ Log } L - 4.468$	gr	mm	666	2-82
Lake Simcoe	44°	79°	graphically*	-	-	658	33-85
Lake Opeongo	45°	78°	$\text{Log } W = 3.0119 \text{ Log } L - 5.1737$	gr	mm	657	34-73
Lac des Deux-Montagnes	45°	74°	$\text{Log } W = 2.56 \text{ Log } L - 3.99$	gr	mm	634	20-56
Great Slave Lake	61°	113°	$\text{Log } W = 2.51 \text{ Log } L - 3.86328$	gr	mm	626	21-68
Ring Lake	43°	109°	$\text{Log } W = 3.001 \text{ Log } L - 3.622$	lb	in	604	2-87
Lake Athapapuskow	54°	101°	$\text{Log } W = 3.0099 \text{ Log } L - 2.2015$	gr	cm	595	6-81
Ocean Lake	43°	108°	$\text{Log } W = 2.715 \text{ Log } L - 3.273$	lb	in	593	20-92
La Grande Riviere	53°	77°	$\text{Log } W = 2.94 \text{ Log } L - 5.06$	gr	mm	550	28-72
Trail Lake	43°	109°	$\text{Log } W = 2.8934 \text{ Log } L - 3.472$	lb	in	528	2-67
Interior Alaska	63°-66°	141°-148°	$\text{Log } W = 2.95527 \text{ Log } L - 2.18341$	gr	cm	504	9-97
Boysen Reservoir	43°	108°	$\text{Log } W = 2.688 \text{ Log } L - 3.397$	lb	in	412	7-96

* When equations were not given in the original paper, weight at length was calculated by fitting the best line to plots of log weight on log length.

Erie (Clemens 1951b', Winnipeg (Hewson 1955), Simcoe (McCrimmon and Devitt, 1954), Opeongo (Hackney 1973), Superior (Bailey 1972), Ring, Ocean, Trail, Boysen (Miller 1970a, 1970b), Saint-Louis, LaGrande Riviere, Deux-Montagnes (Magnin and Fradette 1977), Lake of the Woods (Muth and Smith 1974), Great Slave (Bond and Turnbull 1973), Interior Alaska (Chen 1969)

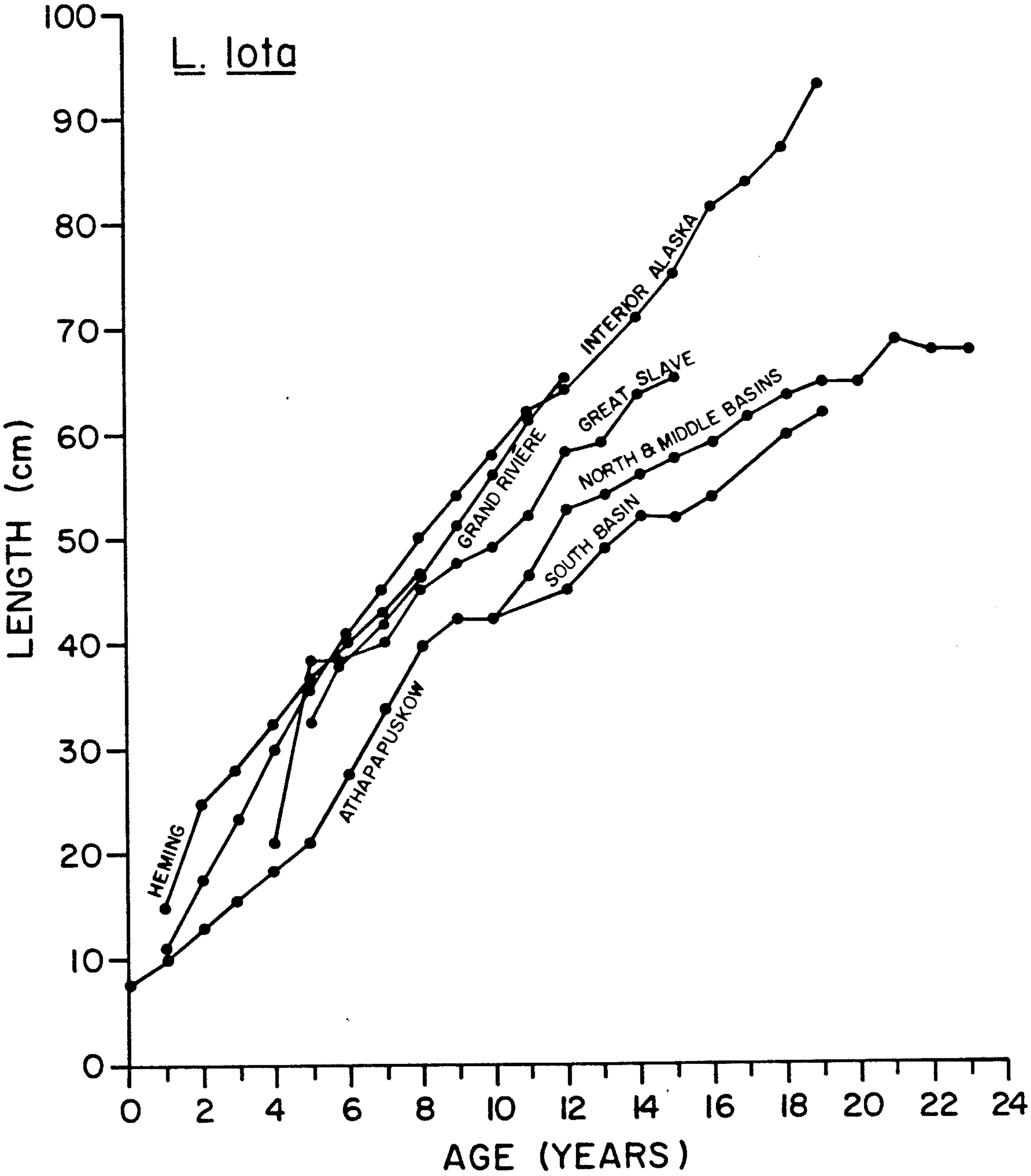
Athapapuskow. However, relative abundance estimates can be used as the basis for some comparisons. In several northern Saskatchewan lakes (Reindeer, Ile a la Crosse, Lac la Ronge, Amisk, Great Slave, Athabasca, Cree (Rawson 1957); MacKay, Hebden (Koshinsky 1965); Wollaston (Rawson 1959); Black (Johnson 1971); Little Bear (Johnson 1963) the percentage of burbot in the total catch of all species or relative abundance of burbot, ranged between 0.5 and 5.5 percent. The relative abundance of burbot in Lake Athapapuskow was 10.45 percent in 1977 and 11.89 percent in 1978.

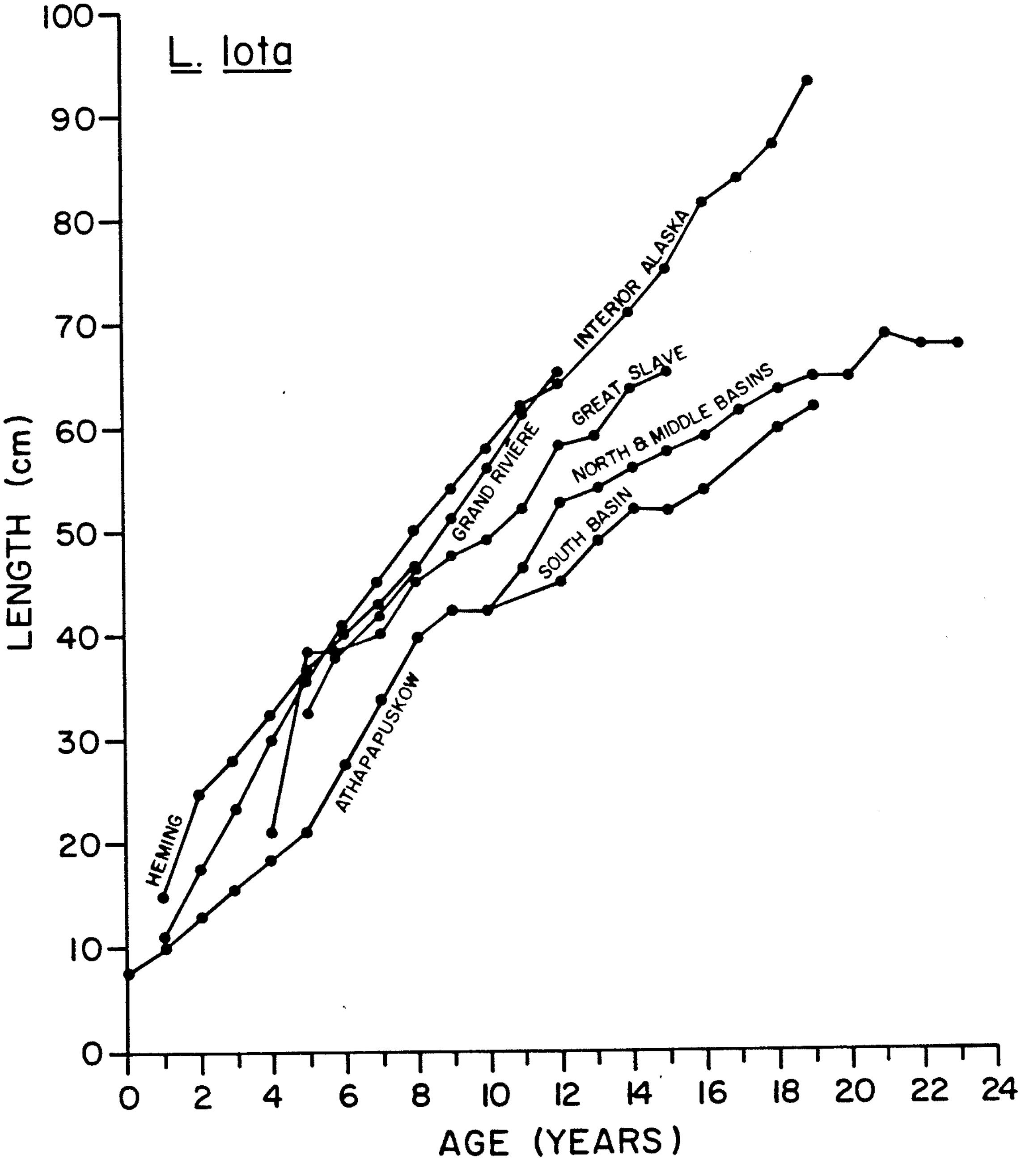
Burbot Maturity

Studies on the maturity of burbot have yielded varied and often conflicting results. Male burbot matured at smaller sizes than females in Lake Superior (Bailey 1972), Ring Lake (Bjorn 1940), and Lake Erie (Clemens 1951b). However, Hewson (1955) found that in Lake Winnipeg female burbot could mature at a younger age than males. Size and age at maturity were not compared between sexes for Lake Athapapuskow burbot because samples of sizes and ages at which maturity occurred were too small.

Maturity was reported to be associated more with age than with size in burbot from Ring Lake, Trail Lake, and Boysen Reservoir (Miller 1970b) but Hewson (1955) stated that maturity of Lake Winnipeg burbot was more closely associated with size rather than with age. Chen (1969) noted that

Figure 30. Growth of burbot from Lake Athapapuskow and four populations north of 53° N latitude. Sources: Interior Alaska (Chen 1969); Heming Lake (Lawler 1963); Great Slave Lake (Bond 1974); Grand Riviere (Magnin and Fradette 1977).


L. lota
LENGTH (cm)
AGE (YEARS)
0
10
20
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24
HEMING
ATHAPAPUSKOW
GRAND RIVIERE
INTERIOR ALASKA
GREAT SLAVE
NORTH & MIDDLE BASINS
SOUTH BASIN


L. lota
LENGTH (cm)
AGE (YEARS)
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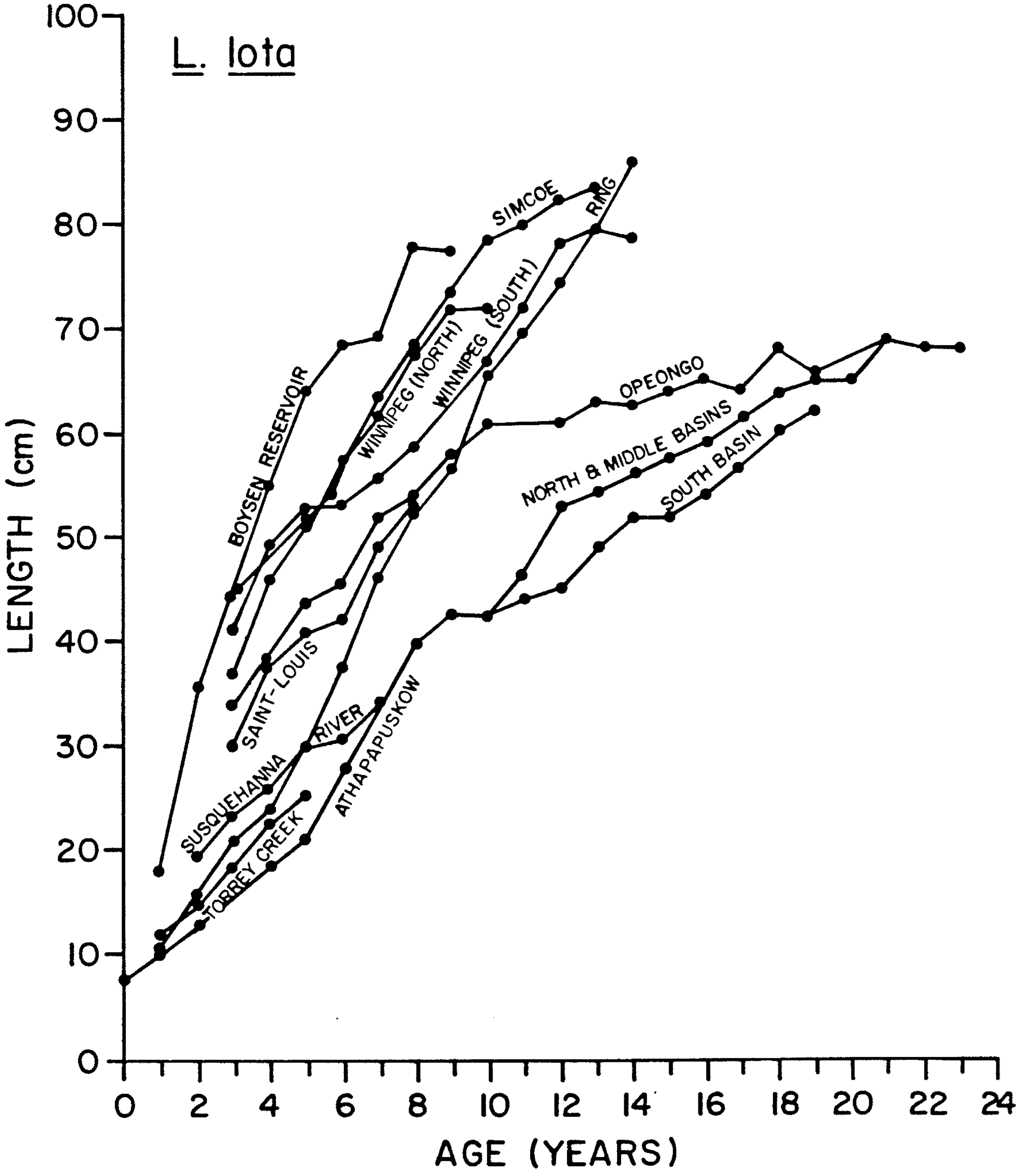
18
20
22
24
HEMING
ATHAPAPUSKOW
GRAND RIVIERE
INTERIOR ALASKA
GREAT SLAVE
NORTH & MIDDLE BASINS
SOUTH BASIN

Figure 31. Growth of burbot from Lake Athapapuskow and nine populations south of 53° N latitude. Sources: Boysen Reservoir, Torrey Creek, Ring Lake (Miller 1970a, 1970b); Lac Saint-Louis (Magnin and Fradette 1977); Lake Winnipeg (Hewson 1955); Lake Simcoe (McCrimmon amd Devitt 1954); Lake Opeongo (Hackney 1973); Susquehanna River (Robins and Deubler 1955).



L. lota
LENGTH (cm)
AGE (YEARS)
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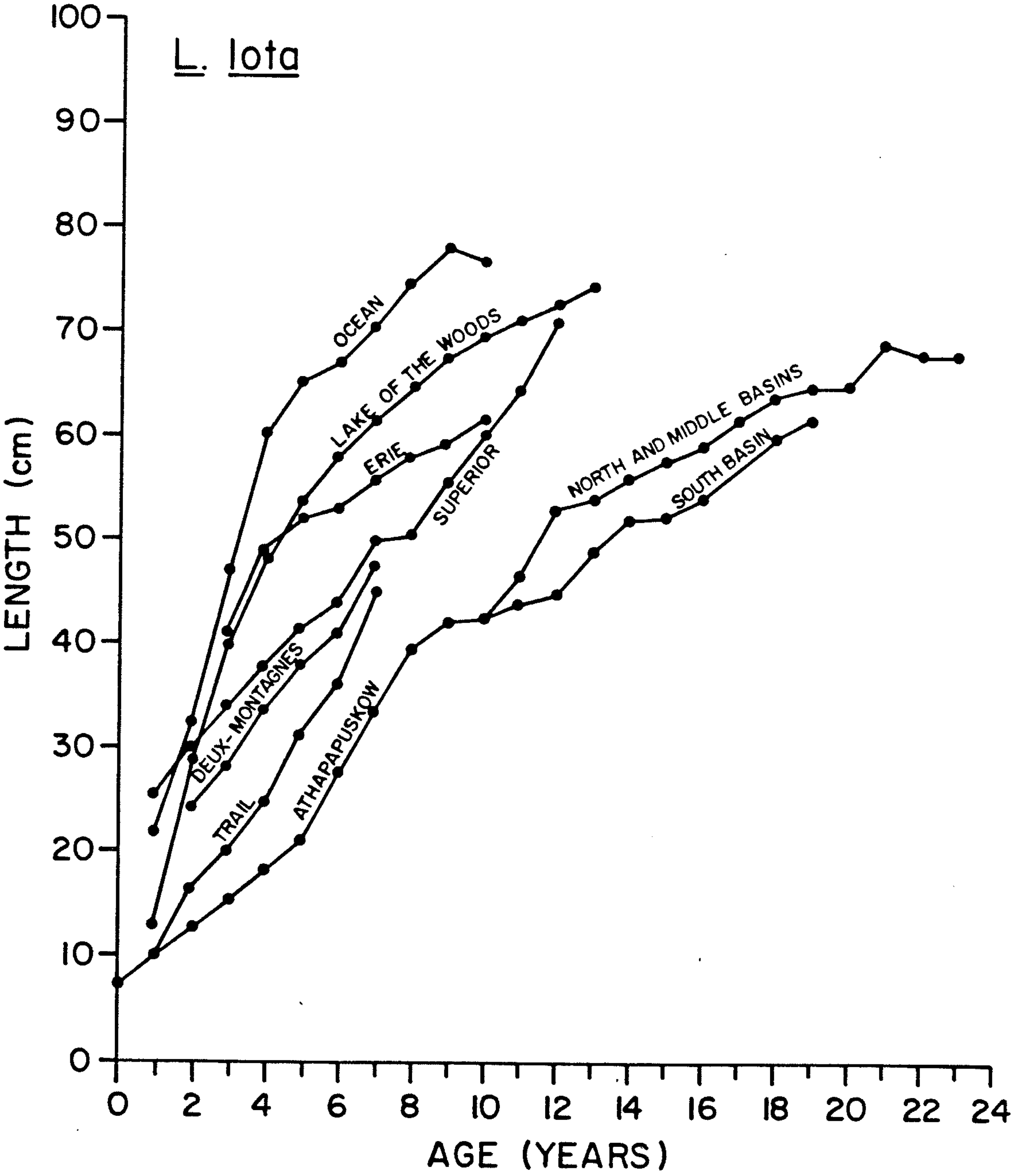
30
40
50
60
70
80
90
100
0
2
4
6
8
10
12
14
16
18
20
22
24
BOYSEN RESERVOIR
WINNIPEG (NORTH)
WINNIPEG (SOUTH)
SIMCOE
RING
OPEONGO
NORTH & MIDDLE BASINS
SOUTH BASIN
SAINT-LOUIS
SUSQUEHANNA
RIVER
TORREY CREEK
ATHAPAPUSKOW

Figure 32. Growth of burbot from Lake Athapapuskow and six populations south of 49^0 N latitude. Sources: Trail Lake, Ocean Lake (Miller 1970a, 1970b); Lac des Deux Montagnes (Magnin and Fradette 1977); Lake Superior (Bailey 1972); Lake of the Woods (Muth and Smith 1974); Lake Erie (Clemens 1951b).


L. lota
LENGTH (cm)
AGE (YEARS)
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10
20
30
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80
90
100
0
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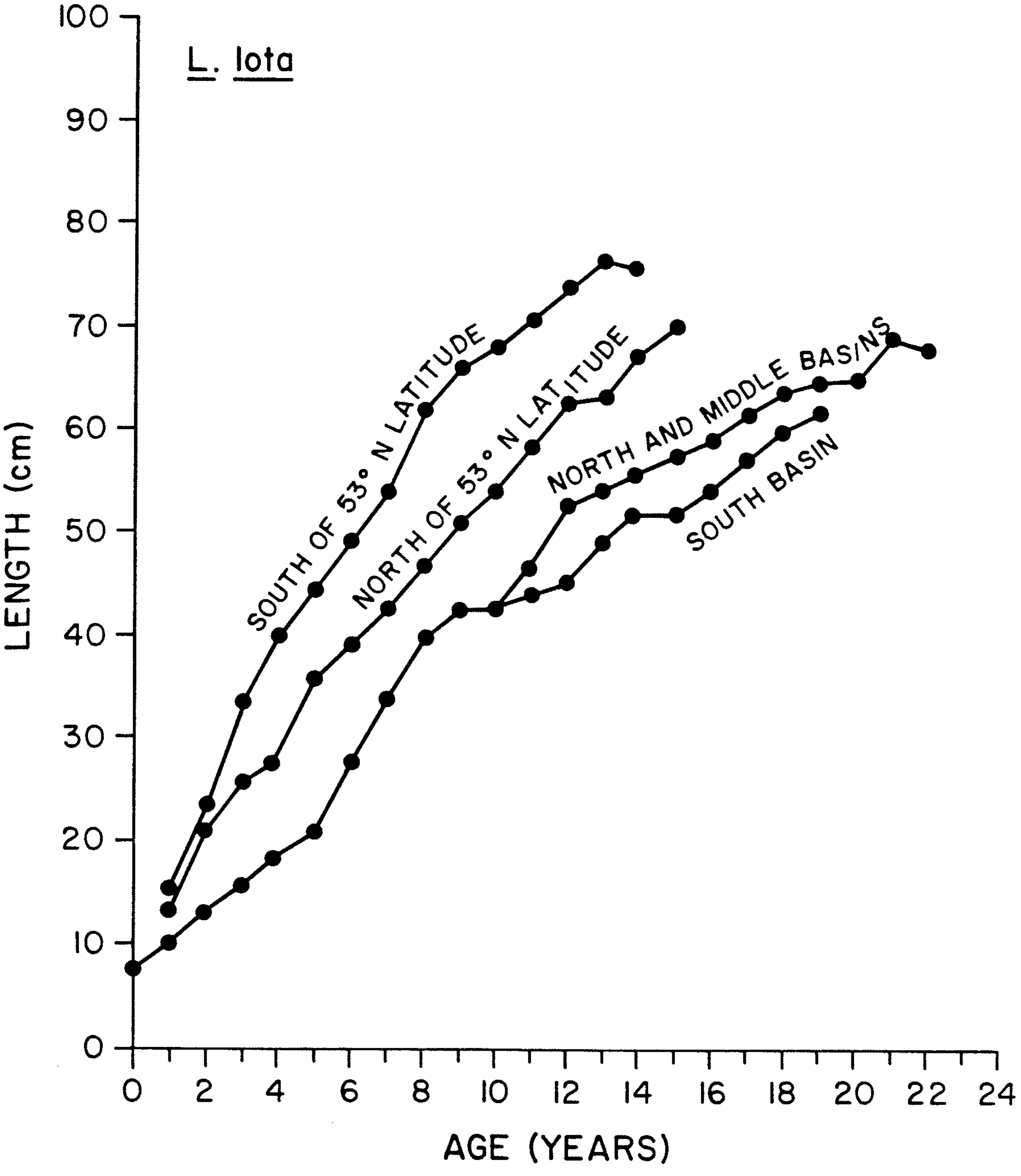
4
6
8
10
12
14
16
18
20
22
24
OCEAN
LAKE OF THE WOODS
ERIE
SUPERIOR
DEUX-MONTAGNES
TRAIL
ATHAPAPUSKOW
NORTH AND MIDDLE BASINS
SOUTH BASIN

Figure 33. Plots of mean length versus age for burbot from Lake Athapapuskow, populations north of 53° N latitude, and populations south of 53° N latitude. Mean lengths for each of the latter two groups are derived from pooled mean lengths of all populations in that group. Sources: see figures 30, 31, and 32.


L. lota
LENGTH (cm)
AGE (YEARS)
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100
0
2
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6
8
10
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14
16
18
20
22
24
SOUTH OF 53° N LATITUDE
NORTH OF 53° N LATITUDE
NORTH AND MIDDLE BASINS
SOUTH BASIN

there is a tendency for burbot in high latitudes to mature at later ages than those in low latitudes.

Burbot mature at ages ranging from 1 year in Lake Superior (Bailey 1972) to 6 or 7 years in the Tanana River (Chen 1969) and Vilyui River (Kirilov 1962). Size at onset of sexual maturity ranges from 155 mm in Torrey Creek (Miller 1970a) to between 560 and 630 mm in the Vilyui River (Kirilov 1962). Burbot in Lake Athapapuskow mature at a relatively late age (6 to 7 years). Lengths at which maturity occurs (between 330 and 360 mm in the south basin and 390 and 420 mm in the middle and north basins) are intermediate in the range of lengths at which burbot from other populations mature. Late maturity of Lake Athapapuskow burbot may be a response of this population to its increasing abundance (Table XI) and apparently high abundance when compared to the abundances of burbot populations from northern Saskatchewan.

Lake Trout Condition

Lake trout condition was compared among populations in the same manner as burbot condition. For the 16 populations of lake trout examined, estimated weight of 55 cm lake trout from Lake Athapapuskow was greater than the estimated weights of 55 cm lake trout from 10 other populations (Table XVIII). The relatively high weight of 55 cm lake trout from Lake Athapapuskow may be a consequence of exploitation since removal of lake trout would decrease intraspecific competition for food. There appeared to be no simple relationship between lake trout condition and the latitudes at which they occurred (Table XVIII).

Lake Trout Maturity

Healey (1978a) reported that mean sizes and ages at which maturity first occurred, at which 50 percent of the fish were mature, and at which 90 percent of the fish were mature as 450 mm and 12 years, 502 mm and 16.8 years, and 578 mm and 19 years for female lake trout from populations north of 60^{0} N latitude, and 490 mm and 7.7 years, 507 mm and 9.4 years, and 595 mm and 11.5 years for female lake trout from more southern populations. For the same maturity groups given above, he listed mean sizes and ages at maturity as 482 mm and 6.6 years, 512 mm and 8.0 years, and 610 mm and 8.6 years for female lake trout from exploited populations, and 443 mm and 10.3 years, 502 mm and 12.8 years, and 536 mm and 14.6 years for female lake trout from unexploited populations. He only considered female maturation because males are more difficult to assign to a particular stage of maturity. He concluded that populations of lake trout north of 60^{0} N latitude matured at smaller sizes and older ages than more southern populations, and unexploited populations of lake trout may mature at smaller sizes and older ages than exploited populations. He cautions that the validity

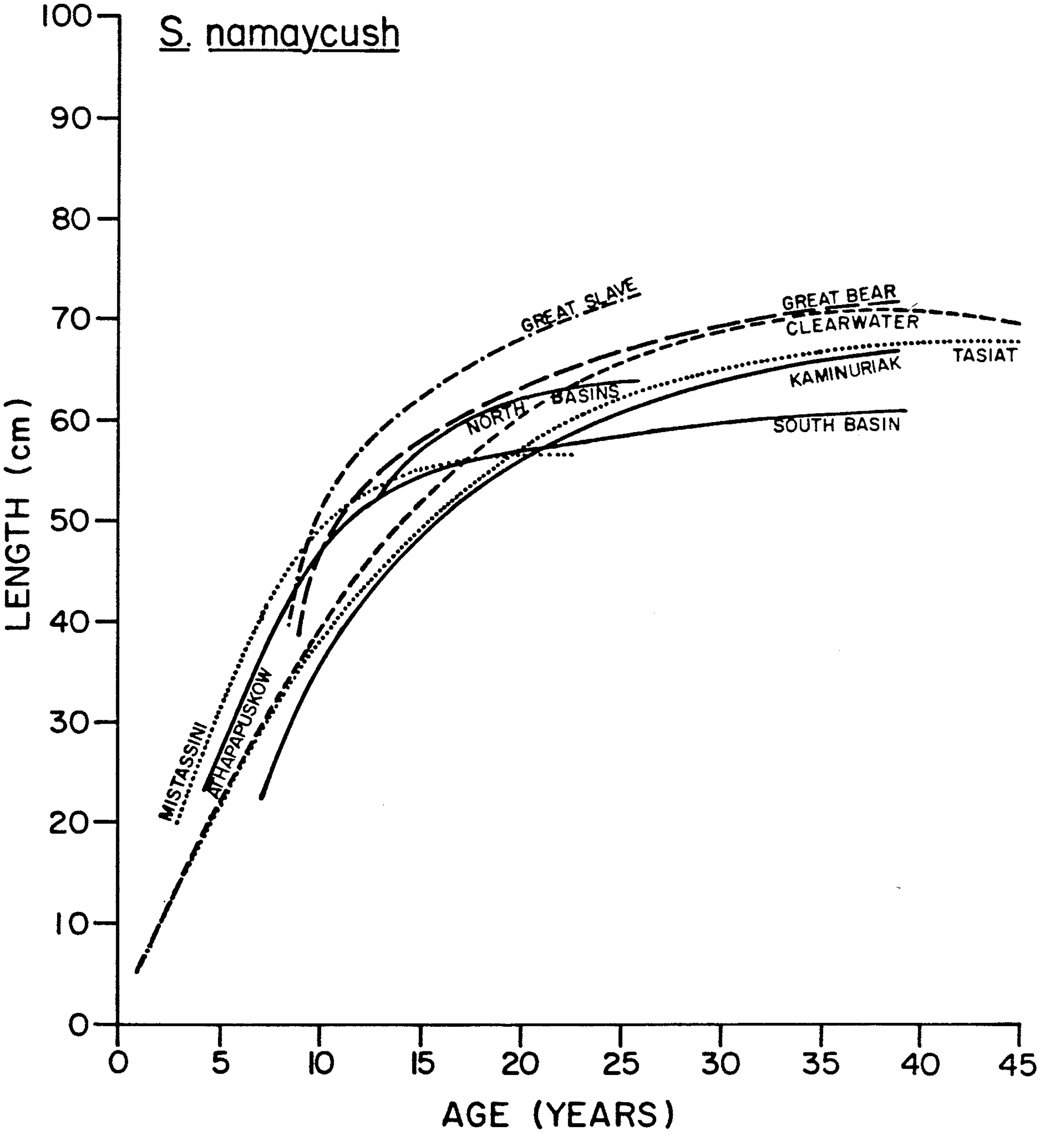
Table XVIII. Length - weight relationships of 16 Lake Trout populations.

Location	North Lat.	West Long.	Method of Calculation	Units Weight	Units Length	Calculated Weight in grams at 55 cm	Date range in cm
Swan Lake	52°	115°	graphically*	-	-	2700	15 - 76
Lac La Ronge	55°	104°	graphically*	-	-	2242	20 - 102
Lake Opeongo (1955-61)	45°	78°	Log W = 3.37522 Log L - 2.65266	oz	in	2191	32 - 65
Lake Superior (siscowets)	47°	87°	Log W = 3.387 Log L - 3.890	lb	in	2105	30 - 86
Lake Athabasca	59°	109°	graphically*	-	-	2101	49 - 72
Lake Athapapuskow	54°	101°	Log W = 3.2738 Log L - 2.3775	gr	cm	2090	15 - 92
Lake Tahoe	39°	120°	graphically*	-	-	2055	43 - 89
Keller Lake	63°	121°	Log W = 2.8921 Log L - 1.7288	gr	cm	2016	7 - 100
Great Bear Lake	65°	120°	Log W = 2.752 Log L - 4.2487	gr	mm	1962	21 - 112
Kaminuriak Lake	62°	95°	Log W = 3.1883 Log L - 5.4478	gr	mm	1947	22 - 67
Hottah Lake	65°	118°	Log W = 3.09 Log L - 5.1960	gr	mm	1869	18 - 98
Lake Opeongo (1937-1949)	45°	78°	Log W = 3.09839 Log L - 2.37848	oz	in	1758	32 - 65
Lake Superior	47°	87°	Log W = 3.191 Log L - 3.765	lb	in	1536	10 - 104
Namaycush Lake	70°	108°	Log W = 2.6133 Log L - 1.3878	gr	cm	1446	5 - 100
Cold Stream Pond	44°	70°	graphically*	-	-	1422	40 - 71
Great Slave Lake	61°	113°	Log W = 3.448 Log L - 6.3070	gr	mm	1386	13 - 98

* When equations were not given in the original paper, weight at length was calculated by fitting the best line to plots of log weight on log length.

Athabasca (Rawson 1947), La Ronge (Rawson 1961), Tahoe (Hanson and Wickwire 1967), Opeongo (Martin 1970), Superior (Eschmeyer and Phillips 1965), Kaminuriak (Bond 1975), Keller (Johnson 1972), Great Bear, Great Slave (Falk et al. 1973), Hottah (Wong and Whillans 1973), Cold Stream Pond (DeRoche and Bond 1955), Namaychush (Johnson 1976), Swan (Paterson 1968).

Figure 34. Growth curves of seven Lake Trout populations. Sources: Lake Mistassini (Dubois and Lagueux 1968); Clearwater Lake, Lake Tasiat (Power 1978); Kaminuriak Lake (Bond 1975); Great Bear and Great Slave Lakes (Falk *et al*. 1973).


S. namaycush
LENGTH (cm)
AGE (YEARS)
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25
30
35
40
45
GREAT SLAVE
GREAT BEAR
CLEARWATER
TASIAT
KAMINURIAK
NORTH BASINS
SOUTH BASIN
MISTASSINI
ATHAPAPUSKOW

of his conclusions are weakened by the observation that all unexploited populations of lake trout for which data are available are from north of 60^{0} N latitude. His age at maturity means are derived from scale ages and therefore cannot be compared to maturation ages of Lake Athapapuskow lake trout. A disagreement between lake trout ages derived from scales and otoliths was demonstrated by Dubois and Lagueux (1968). They stated that male and female lake trout from Lake Mistassini that were aged by scales matured at 5 and 7 years respectively and, when aged by otoliths, at 7 and 9 years respectively. In comparison to other populations for which otolith age data are available, the age at onset of maturity of Lake Athapapuskow lake trout is similar, but fish mature faster and, therefore, are 100 percent mature at relatively young ages (Table XIX). When compared to Healey's mean lake trout sizes at maturation the size at onset of maturity of Lake Athapapuskow lake trout (450 to 480 mm) was similar to that of other populations but the size above which 100 percent of the population was mature (510 to 540 mm) was relatively small.

Fry (in Falk _et_ _al_. 1973) found that in Lake Opeongo, lake trout size at maturation decreased as fishing pressure increased. This contradicts Healey's statement that unexploited lake trout populations are on the average smaller at maturity. Falk _et_ _al_. (1973) stated that lake trout maturation dates appear to fluctuate according to the density of the population occurring at ages in excess of the age of maturation. They stated that in populations where there are many old fish the population appears to limit itself by suppression of maturity for a longer period of time.

As a result of changes in the diet of lake trout from Lake Opeongo, due to the introduction of cisco, Martin (1970) reported that fish matured at larger sizes and older ages. This may, in part, account for the observation that lake trout in the middle and north basins of Lake Athapapuskow, where cisco density is greater than in the south basin, mature one year later than south basin lake trout.

In Lake Athapapuskow the relatively young age and small size above which 100 percent of the lake trout population is mature would allow a large proportion of the population to be mature and, therefore, increase its reproductive potential. This enhancement of the reproductive potential of Lake Athapapuskow lake trout may imply that small size and young age at maturity are consequences of exploitation. Healey (1978b) showed that the fecundity and, therefore, the reproductive potential of lake trout from four lakes increased as exploitation increased.

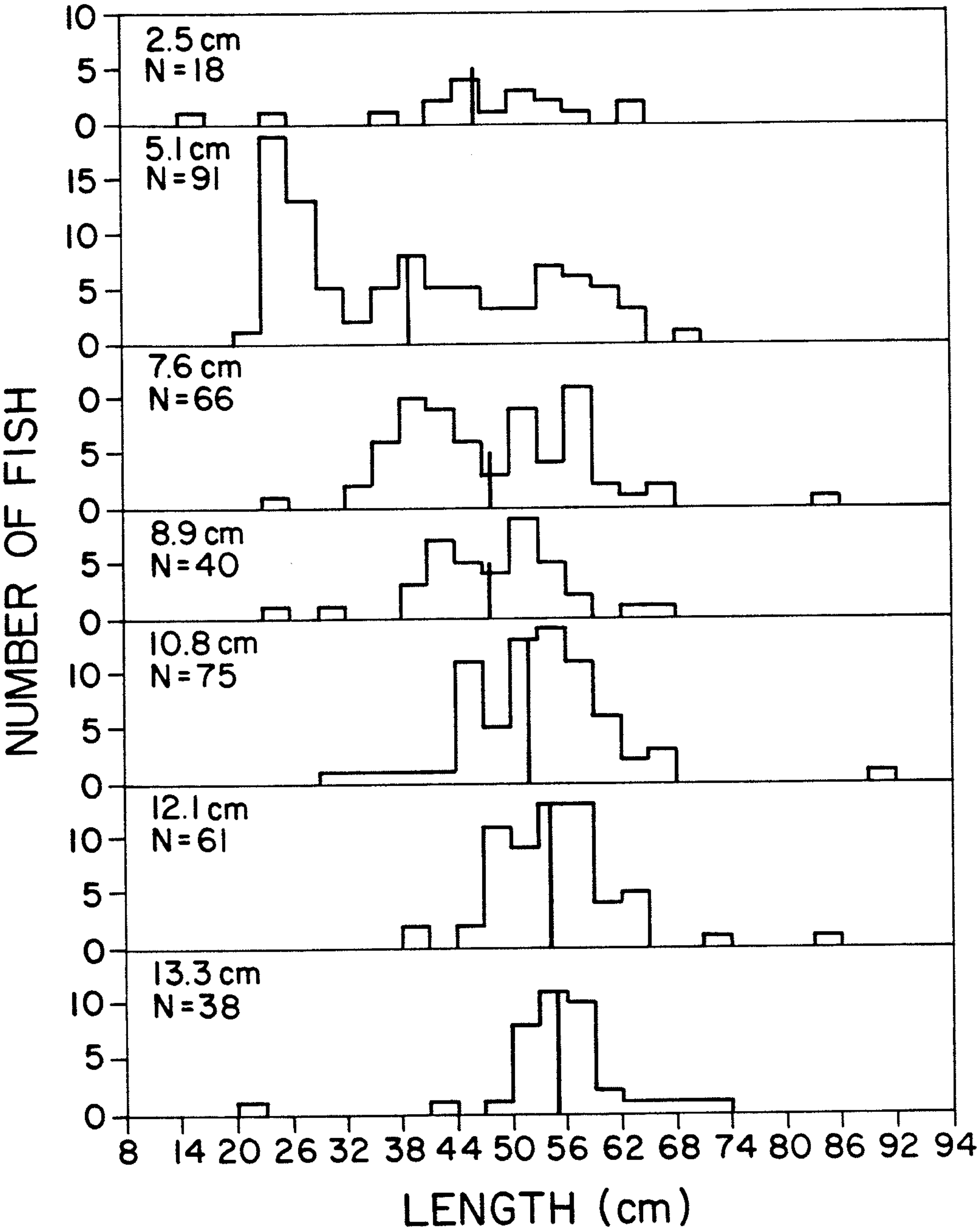
Intermittent spawning is a feature of many lake trout populations. In the following lakes the percentage of mature female lake trout which spawned in any one year was 33 percent in Keller (Johnson 1972), 36 percent in Great

Bear (Miller and Kennedy 1948), 50 percent in Great Slave (Kennedy 1954), 83.4 percent between 1937 and 1945 and 98 percent between 1955 and 1965 in Lake Opeongo (Martin 1970), and 92 percent in Lac la Ronge (Rawson 1961). Dubois and Lagueux (1968) reported that in Lake Mistassini mature female lake trout probably spawn once every two years. In Kaminuriak Lake 67 percent of mature females older than 25 years spawned in any one year (Bond 1975). In Lake Athapapuskow trends in seasonal increase in weight of female gonads (Fig. 25) and egg size suggested that very few mature females did not spawn in 1977. Healey (1978a) stated that intermittent spawning is most common in unexploited lake trout populations that are north of 60° N latitude but also occurs in some southern populations.

In Lake Athapapuskow the high proportion of mature females which spawn in any one year may be a response to exploitation and would increase the reproductive potential of the population.

Interbasin Differences in Population Characteristics of Burbot and Lake Trout.

Interbasin difference in population characteristics of burbot and lake trout may be related to differences in trophic state between basins. Slower growth of older burbot and lake trout in the south basin than in the middle and north basins may be attributed to the greater abundance of burbot and lake trout food (ciscoes) in the middle and north


2.5 cm
N = 18
5.1 cm
N = 91
7.6 cm
N = 66
8.9 cm
N = 40
10.8 cm
N = 75
12.1 cm
N = 61
13.3 cm
N = 38
NUMBER OF FISH
0
5
10
15
8
14
20
26
32
38
44
50
56
62
68
74
80
86
92
94
LENGTH (cm)

basins. The growth rate of adult lake trout increased in Lake Opeongo after ciscoes were introduced into this lake (Martin 1970). Greater abundance of cisco in the middle and north basins than in the south basin is indicated by cisco catch per unit effort which is more than five times greater in these basins than in the south basin (Table XII). The trophic state of the south basin would likely limit the abundance of burbot and lake trout food to a greater degree than would the more eutrophic state of the middle and north basins. It is notable that the greatest interbasin difference in catch per unit effort is for ciscoes, which, as plankton feeders, are trophically closer to the primary producer level than are piscivorous species. Ciscoes were the dominant item in the diet of adult gillnet caught burbot in Lake Athapapuskow. They constituted 30.17 percent by volume of their diet (Table XIV). According to Sigurdson and Scaife (1975b), ciscoes were the most frequently found taxon in the stomachs of Lake Athapapuskow lake trout and burbot. Ciscoes are the dominant item in the diet of adult lake trout in most cases (Martin 1970; Clemens _et al_. 1923; Clemens _et al_. 1924; Dymond 1928; Hacker 1956; Rawson 1961; Dryer _et al_. 1965). When compared to piscivorous lake trout, planktonivorous lake trout grow more slowly, do not reach as great a size or age, and mature at a smaller size and younger age (Martin 1966).

Table XIX. Age in years at sexual maturity of lake trout from five lakes. All ages are determined from otoliths.

Lake	Sex	Earliest Age at Maturity	Percentage Mature at Age							Number of Years Between Maturity Onset and 100% Maturity
			23%	25%	50%	67%	75%	84%	100%	
Kaminuriak										
	M	13						14-27		>14
	F	19	19-24			25.35				>16
Mistassini										
	M	7							15	8
	F	9							17	8
Great Bear										
Great Bear Lodge	M+F	10			13		15		18	8
Great Bear Lake Lodge	M+F	12			13		16		22	10
Cameron Bay Lodge	M+F	12			14				15	3
Great Slave										
Great Slave Lake Lodge	M+F	8		9	10		16		24	16
Frontier Lodge	M+F	8			8		11		18	10
Athapapuskow										
Middle and North Basins	M	9							12	3
	F	9			11				14	5
South Basins	M	8			9				11	3
	F	10			10				13	3

Data from Bond (1975) Kaminuriak, Dubois and Lagueux (1968) Mistassini, and Falk et al. (1973) Great Bear and Great Slave Lakes.

Interbasin differences in growth of burbot and lake trout were most evident among older, mature fish and first occurred at approximately age 14 for lake trout and age 10 for burbot (Figs. 19 and 21). The absence of interbasin differences in growth of young burbot ($<$10 yr.) may be due to an abundance of benthic, littoral fauna in all basins. No observations of juvenile lake trout diets were made, but the similar growth pattern suggests that their growth may also have been limited to a lesser extent by food abundance than was the growth of adult lake trout.

Prey of small burbot collected on shorelines and in Mistik Creek was sometimes taxonomically similar but always much smaller in size than prey of larger burbot and was therefore probably at a lower trophic level than the prey of larger burbot. Feeding regimes of young and old burbot differed because habitat of young burbot was predominantly littoral whereas older burbot were mainly in profundal habitats (Tables IV, V, VI, and VII). The similarity between basins of younger burbot and lake trout length-weight relationships and the interbasin differences in length-weight relationships of older burbot and lake trout supports the suggestion that feeding regimes of older fish differ between basins more than do feeding regimes of younger fish. Growth rates of younger, smaller lake trout and burbot may be more independent of basin trophy than growth rates of older fish. Therefore, interbasin differences in trophic state will be manifested mostly by interbasin differences in growth of older fish.

The greater abundance of cisco in the middle and north basins than in the south basin may explain why older lake trout are heavier at any given length in the middle and north basins than in the south basin. Martin (1970) stated that the length-weight relationship of adult lake trout in Lake Opeongo improved after the introduction of cisco into this lake. Trends in length-weight relationships of burbot are opposite to those of lake trout, such that older burbot are heavier at any given length in the south basin than in the middle and north basins. Factors other than basin trophy and food abundance must influence length-weight relationships, as seen from the contradictory correlations between burbot and lake trout length-weight relationships with interbasin differences in trophic state and the relative abundance of cisco. Better condition of burbot in the south basin than in the middle and north basins may be related to greater intraspecific competition for food in the middle and north basins since their relative biomass in these basins is almost two times greater than in the south basin (Table XII). Given that lake trout are heavily exploited in Lake Athapapuskow it is doubtful that their length-weight relationships are influenced by intraspecific competition for food to the extent that they are in burbot.

Interbasin differences in lake trout and burbot population growth rates (Figs. 19 and 21) were probably not due to temperature differences since hypolimnions of the middle and south basins, where these species were mainly found (Figs. 27, 28, and 29), had similar temperature regimes (Figs. 4 and 5). Although hypolimnetic temperatures of the north basin were considerably warmer (Fig. 3) fish were sampled in this basin only during 1977, and they apparently disappeared from the hypolimnion by mid July (Table XV) due to anoxic conditions in that year. There are not sufficient data to compare growth of north basin fish with growth of fish from other basins. Pooling of the small numbers of north basin fish with the middle basin sample probably does not significantly affect the growth rates.

The greater relative abundance of older and larger burbot in the middle and north basins than in south basin, as indicated by gillnet catches (Figs. 14 and 16), is probably a result of lower mortality rates and faster growth of burbot in the middle and north basins.

Length frequency distributions of lake trout were similar between basins except that in the south basin there was a stronger representation of modal length classes, and a distinct group of smaller fish (Fig. 17). Stronger representation of modal length classes in the south basin is attributed to the growth of south basin lake trout because it is at lengths in these modal classes (approximately 50 to

60 cm) that growth of south basin lake trout approaches an asymptote (Fig. 21). The distinct group of small lake trout caught in the south basin and absence of a similar group of fish caught in north and middle basins (Fig. 17) may be due to asynchronous recruitment between basins, or recruitment failure in the middle and north basins.

It is difficult to separate the effects of basin trophy and exploitation on the population characteristics of lake trout. Heavy exploitation will probably mask relationships between these characteristics and basin trophy. Therefore, proposed relationships between interbasin differences in trophic state and population characteristics of lake trout are obscure. Burbot in Lake Athapapuskow are essentially unexploited (Schlick 1973b; Sigurdson and Scaife 1975a), therefore, their population characteristics probably reflect differences in basin trophy.

Evidence for Overfishing of Lake Athapapuskow Lake Trout

Lake Trout Yields

Healey (1978a) calculated yields for five hypothetical lake trout populations. Hypothetical populations were assigned ranges of mortality and growth rates exhibited by known populations. He felt that the calculated yields were unrealistic because the distribution of biomass among age classes in lake trout populations is poorly understood. When combined with information on population density, productivity, and permissable total mortality he suggested that sustainable lake trout yields would range from 0.2 kg/ha/yr for populations with a low standing stock of mature fish and slow growth to a maximum of 0.5 kg/ha/yr for populations with a large standing stock of mature fish and rapid growth. He concluded that under ordinary circumstances yields would not likely exceed 0.5 kg/ha/yr in any lake. He listed the following known stable yields, which agree with his calculated limit. Prior to the introduction of the lamprey, stable yields of the Great Lakes ranged from 0.24 kg/ha/yr from Lake Superior to 0.58 kg/ha/yr from Lake Michigan. Lawrie and Rahrer (1972) suggested that constant traditional yields from Lake Superior may not have represented lake trout stability if stock after stock was depleted as fishermen moved to different areas of the lake. In Lake Athabasca yields averaged 0.28 kg/ha/yr between 1930 and 1960. Yields in Lake Opeongo and Lac la Ronge averaged 0.33 and 0.45 kg/ha/yr respectively. Healey also indicated that overfishing may occur when yields are lower than 0.5 kg/ha/yr. The Great Slave Lake lake trout population began to fail after ten years of yields ranging from 0.37 to 0.67 kg/ha/yr during which a yield of 0.5 kg/ha/yr was exceeded in 1949 only (Keleher 1972; Bond and Turnbull 1973). Hartman (1972) states that lake trout from the deep oligotrophic eastern basin of Lake Erie were overexploited by annual catches exceeding 40000 kg in the late 1800's and few have been taken in this lake since the mid 1930's. Smith (1972) listed the highest recorded yield of lake trout from Lake Erie as 0.25 kg/ha/yr and from Lake Ontario as 0.26 kg/ha/yr. Christie (1972) attributes the collapse of lake trout stocks in Lake Ontario at the turn of the century to overfishing.

In Lake Athapapuskow, an average commercial lake trout harvest of 0.74 kg/ha/yr or a total of 19700 kg/yr for a 15 year period (Schlick 1973a) and estimated angler (sport fishing) harvests of 1.58 kg/ha/yr or a total of 41900 kg/yr (Sigurdson and Scaife 1975a) are in great excess of any proposed sustainable yield and also exceed yields which were high enough to overfish any other population for which data exists. Sigurdson and Scaife (1975a) censused 2874/16304 = 17.6 percent and 8280/41900 = 19.8 percent of the estimated total annual number of anglers and estimated total annual harvest of lake trout respectively. The census was intense, therefore, the total annual harvest estimate is realistic. Sigurdson and Scaife estimated total annual number of anglers from their own studies and Hoole's (1970) data on the outdoor recreational use of Lake Athapapuskow. Estimates of total annual lake trout harvests taken by three categories of anglers (campground = 22850 kg, lodge = 18100 kg, cottage = 950 kg) were calculated as the product of mean weight of angled lake trout, mean number of fish caught per angler, and estimated total annual number of anglers.

Using Healey's estimate of 0.5 kg/ha/yr as the largest likely sustainable yield, Lake Athapapuskow could support removal of no more than 25596 ha x 0.5 kg/ha/yr = 13300 kg/yr, and, in fact, probably could not support a yield that high since the growth rate is slow compared with other populations (Fig. 34).

The Commercial and Sport Fishery

An abrupt decline in lake trout catch per license, beginning in 1941, followed nine years of commercial exploitation (Fig. 26). In 1943, the commercial fishery experienced its lowest catch per license and was closed from 1944 to 1955. When the commercial fishery was reopened in 1956 and 1957, low catch per license suggested that lake trout abundance had not appreciably increased since the closure.

Healey (1978a) estimated that densities of mature lake trout are small, generally less than one fish per hectare. Heavy exploitation and consequent removal of a large proportion of mature lake trout from Lake Athapapuskow may decrease spawning success to the extent that periods of heavy exploitation are subsequently reflected by poor year class strengths due to the removal of potential spawners. Since lake trout are slow growing and have multi-aged spawning populations, it may take many years for recruitment to replace all ages of spawners removed by exploitation.

The poor representation of year classes between approximately 1958 and 1962 may be due to removal of spawners during the period of commercial fishing in 1956 and 1957. The effect of the 1956-57 fishery on spawner density may have been even more serious because large total catches (15000 and 32700 kg in 1956 and 1957 respectively) were taken when catch per license values suggested low lake trout abundance (Fig. 26). Also, the unknown effects of the sport fishery harvest must be added to the effects of commercial fishing on lake trout.

Johnson (1972, 1976) suggested that, in northern lake trout populations, the pool of prerecruitment fish is limited. In Healey's (1978a) description of the decline of the western population of lake trout in Great Slave Lake he stated that the breeding population may have been destroyed before it could be replaced by immature fish if intensive exploitation occurred at a time when immature fish were very scarce.

It is expected that a significant proportion of angled lake trout were immature because a low percentage of fish were released after capture (Table XX) and mean length of angled lake trout (51.4 and 51.6 cm in 1968 and 1975 respectively) were in the smallest size class (51 to 54 cm) in which 100 percent of the fish were mature (Table IX). The above lengths of angled lake trout were estimated using the length-weight equation of Lake Athapapuskow lake trout given in Table XIX and mean weights of angled lake trout given in Table XX. It is concluded that the distribution of lengths of angled lake trout around their means would probably be composed of a significant proportion of immature fish. In Lake Athapapuskow the duration and frequency of periods of poor lake trout recruitment will likely increase if the replacement of harvested mature fish is prevented by the synchronous harvest of immature fish.

Creel census data for 1968 and 1975 indicates that lake trout abundance is declining (Table XX). The decrease between 1968 and 1975 in numerical percentage of lake trout in the angled catch may indicate a decrease in lake trout abundance as suggested by Sigurdson and Scaife (1975b) or a shift in angler focus to other species. The latter explanation may also reflect a decrease in lake trout abundance as it is expected that anglers would pursue other species if the quality of lake trout fishing declined. The increase in number of lake trout caught per angler hour between 1968 and 1975 suggests that anglers did not shift to other species, but rather continued to fish for lake trout while catching an increasing proportion of other species. It should be noted that angling techniques for trout changed between 1968 and 1975, leading to a marked improvement in efficiency of catching lake trout.

It is probable that the middle and north basins of Lake Athapapuskow have been more heavily exploited than the south basin. Access is better and there is more cottage and resort development near these basins. Strong winds are more likely to prevent fishermen utilizing the larger south basin. In an aerial survey conducted between June 26 and September 16, 1968, 89 angling parties on the middle and north basins and 118 on the south basin were counted (Schlick 1973b). Therefore, 43 percent of the observed fishing effort was on the middle and north basins, which constitute ony 23 percent of the total surface area of the lake (Table 1). Differences in fishing effort between basins may explain why there are fewer age classes (Fig. 18), lower catch per unit effort (Table XII), and lower relative abundance (Table XVI) of lake trout in the middle and north basins than in the south basin.

Effects of Exploitation on the Population Characteristics of Lake Trout

The estimated annual total mortality rate of Lake Athapapuskow lake trout was 9 percent. This is much lower than the range of 17 to 92 percent for 26 lake trout populations given by Healey (1978a). Healey states that these rates will be too high because age estimates were based on scale reading which tends to underage lake trout as demonstrated by Dubois and Lagueux (1968) for lake trout from Lake Mistassini, Quebec. I calculated total annual mortality rates of lake trout, from age frequency histograms given by Dubois and Lagueux (1968), and found that rates

Table XX. Summary of data on lake trout angling in Lake Athapapuskow in 1968 and 1975.

	Year	
	1968	1975
no. lake trout caught per angler hour	0.14	0.18
numerical % of lake trout in angler catch	57.03	35.38
numerical % of angled lake trout released	5.6	12.9
mean weight (kg) of lake trout caught	1.68	1.70
number of lake trout censused	288	4871
estimated annual angler harvest (kg)	-	41900

Data was obtained by creel census in 1968 (Schlick, 1973b) and 1975 (Sigurdson and Scaife, 1975a).

based on scale age and otolith age data were 23 and 14 percent respectively. The 14 percent mortality rate of Lake Mistassini lake trout indicated that the mortality rate of Lake Athapapuskow lake trout may be similar to those of other populations, rather than much lower.

Heavy exploitation of Lake Athapapuskow lake trout can be taken in an argument against the validity of the low estimated mortality rate of these fish. When calculating mortality rate as the slope of the natural logarithm of the frequency of age N versus age N it is assumed that recruitment is constant from year to year and that survival rate does not change with age. Deeply concave and multimodal age frequency histograms (Fig. 18) indicate that survival rate increases with age and that recruitment is not constant from year to year and perhaps is cyclical. In Lake Opeongo (Martin and Fry 1973) and in Great Slave Lake (Kennedy 1954) statistically significant year to year changes in lake trout instantaneous mortality rates were found. Martin and Fry reported that in Lake Opeongo there appears to be roughly an eight year cycle of strong and weak year classes. Healey (1978a) stated that sources of error in estimating lake trout mortality rates weaken one's confidence in the accuracy of these estimates.

Mortality rates calculated from catch curves are generally expected to increase with exploitation because as older fish are harvested the proportion of younger fish increases resulting in an increase in slope of the descending right hand limb of the curve. The calculated mortality rate would not increase with exploitation if all age classes in the descending right hand limb of the catch curve were exploited in proportion to their abundance. If younger fish were exploited at a proportionally greater intensity than older fish, calculated mortality rates would decrease even though true mortality rates may be increasing. This may explain the low estimated mortality of Lake Athapapuskow lake trout since, as mentioned earlier, mean size of angled lake trout in this lake is small. Angling in Lake Athapapuskow may have simply resulted in a lowering of the lake trout catch curve (Fig. 23), leaving the descending slope of the curve the same or even less, causing a falsely low mortality estimate.

Mean weights of gillnet caught lake trout were the same in 1971 and 1977 (Table X). The lower mean weight observed in 1978 was probably due to the relatively greater sampling effort in the south basin in which mean size of lake trout is smaller (Table X), growth is slower (Fig. 21), and a large group of young fish reached recruitment size for the 2.5 cm mesh gillnet in that year (Fig. 13).

Keleher (1972) showed that during a 20 year period on Great Slave lake the mean weight of commercially caught lake trout declined from 4.5 kg in the western basin and 3.2 kg in the eastern basin to 3.4 and 2.5 kg in the western and eastern basins respectively. He noted that lake trout size appeared to decline continually and not approach a steady state. In Lake Athapapuskow mean weights of angled lake trout were similar in studies conducted during 1968 (1.68 kg) and 1975 (1.70 kg).

Johnson (1976) listed mean lengths of gillnet caught lake trout from 19 Northwest Territories lakes as ranging from 515 to 759 mm. Rawson (1961) reported mean lengths ranging from 586 to 604 mm for Lac la Ronge lake trout in various years and Falk _et_ _al_. (1973) reported that mean lengths and weights of lake trout from two Great Slave Lake fishing lodges were 687 mm and 5.83 kg, and 561 mm and 2.45 kg. They also gave mean lengths and weights of lake trout from three Great Bear Lake lodges of 732 mm and 4.67 kg, 675 mm and 3.62 kg, and 620 mm and 2.72 kg. By comparison, the observed mean length and weight of south basin Lake Athapapuskow lake trout (482 mm and 1.62 kg) are smaller than any of the above values. Mean sizes of middle and north basin lake trout (528 mm and 2.19 kg) exceed only Johnson's two lowest length values.

The small average size of angled and gillnet caught lake trout from Lake Athapapuskow is likely the result of exploitation but may be partly explained by the small size at which curves from lake trout growth data become asymptotic (Figs. 21 and 34). Although growth in older trout is slow, particularly in the south basin of Lake Athapapuskow, growth of north basin fish is similar to that observed in other lakes (Fig. 34) in which mean size is greater.

The difference between lake trout abundance estimates for 1977 and 1978 is explained by the difference between years in the distribution of sampling effort among the lake basins (see Results: Abundance Estimates of Burbot and Lake Trout). It is concluded that the best estimate of lake trout abundance for this study lies somewhere between 1977 and 1978 values and, therefore, indicates a decline from 1971 values (Table XI). This decline is undoubtably a consequence of exploitation.

As stated earlier, the relatively good condition of lake trout in Lake Athapapuskow, the early age at which 100 percent of the sampled fish are mature, and the low percentage of mature females with underdeveloped gonads which indicated that they would not spawn, all may be consequences of exploitation. Also, periods of poor recruitment can be related to the commercial fishery (see Discussion: Evidence for Overfishing of Lake Athapapuskow Lake Trout).

Burbot and Lake Trout Interactions

In Lake Athapapuskow, intensive lake trout exploitation may have caused an increase in burbot abundance because of the similarities in habitat and food requirements of these two species. If such a correlated change in abundance has occurred these species must share a limited resource. Hackney (1973) and Hackney and Minns (1974) described competition for food between lake trout and burbot in the south arm of Lake Opeongo by means of a simulation model of biomass dynamics and food consumption which predicted an increase in lake trout yields as burbot fishing rates increase.

In Lake Athapapuskow, all estimates of lake trout abundance have declined between the 1971 study and my 1977-1978 study. At the same time, the catch per unit effort and relative abundance of burbot have increased, but the relative biomass of burbot has remained approximately the same (Table XI). Relative biomass may remain constant while catch per unit effort increases if mean weight of burbot decreases (Table X). The constant relative biomass of burbot, coupled with increasing catch per unit effort and relative abundance of this species, and the continuing decline in lake trout abundance due to fishing pressure all imply that burbot abundance and biomass are not at present limited by interaction with lake trout, but rather, that burbot growth, and hence biomass, are probably limited by intraspecific competition for food. The limitation of burbot growth and biomass by intraspecific competition for food is also indicated by the fact that in the middle and north basins, where the abundance of the dominant item (ciscoes) in the diet of burbot is much greater than in the south basin, burbot growth is faster (Fig. 19) and they have a greater relative biomass (Table XII). Exploitation of burbot would probably not result in an increase in lake trout abundance in Lake Athapapuskow since lake trout abundance appears to be limited primarily by exploitation. If as suggested, the slow growth of Lake Athapapuskow burbot (Figs. 30, 31, 32, and 33) and their decreasing mean size have resulted in a stable burbot biomass when the number of burbot caught per unit of effort has been increasing, their exploitation may initially not result in a decrease in biomass if responses to this exploitation and consequent decrease in density are an accelerated growth rate and an increase in mean size.

Although historical changes in the abundance of burbot and lake trout in Lake Athapapuskow indicated that they share resources there is also evidence which suggests that their niches do not totally overlap. Both lake trout and burbot were uncommon at shallow depths, but became more common in the 18.5 and $\geq$ 33.5 m nets. However, burbot continued to increase in abundance in the $\geq$ 33.5 m nets, even in the middle basin where at that depth lake trout rarely occurred. In the south basin, lake trout were somewhat less abundant at $\geq$ 33.5 m than 18.5 m (Figs. 27, 28, and 29). In the middle basin, the large difference in abundance between burbot and lake trout at $\geq$ 33.5 m may be the result of an apparently greater tolerance of low oxygen concentrations by burbot, such as those found in deep waters of the middle basin (Fig. 7). Cameron (1973) gives evidence that burbot blood has a high oxygen affinity. Additionally, body form, apparent differences in swimming ability, and observation of the tendency for burbot to be caught near the lead line in gillnets more frequently than lake trout, all indicate that burbot are probably more sedentary and spend more time near the bottom, while lake trout are more active swimmers and occur often in midwater.

Evidence presented in this study indicates that the decline in abundance of lake trout in Lake Athapapuskow is due to exploitation and not to an increase in the abundance of burbot. The exploitation of lake trout is reflected in the population characteristics of burbot because these species share resources in the lake. Although the abundance of burbot has increased, they have simply responded to the decline in lake trout density.

If this lake is to be maintained as a lake trout sport fishery the harvest of lake trout must be severely restricted. If this is not possible because of social or economic reasons the harvest of lake trout may be reduced indirectly by switching the emphasis of the sport fishery to walleye, northern pike, or a stocked salmonid.

Sampling of lake trout and burbot in Lake Athapapuskow should be continued because it would allow the predictions of this study to be tested. Data generated from this sampling could be used to construct a more refined mathematical model of burbot and lake trout interactions and responses to lake trout exploitation.

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Appendix A

AGE DETERMINATION OF BURBOT AND LAKE TROUT

Burbot

If otoliths are used for aging fish it must be shown that the frequency of annular markings is a product of fish age only. Otoliths of temperate zone fish show a pattern of alternating clear or hyaline rings, which contain crystaline calcium carbonate embedded in an organic matrix, and opaque rings, which contain much more organic matter than hyaline rings (Pannella 1974). Pannella (1971, 1974) has shown that these alternating bands are deposited seasonally. Also, finer rings exist on otoliths of a wide variety of fish species and are correlated with daily growth increments (Taubert and Coble 1977; Scott 1973; Brothers et al. 1976; Ralston 1976; Struhsaker and Uchiyama 1976; and Pannella 1971, 1974).

Otoliths are best for age determination of burbot because burbot scales are minute, embedded, and lack annuli, and annular marks on burbot opercular bones are difficult to interpret (Chen, 1969). McCrimmon and Devitt (1954) found otoliths to be the most workable and accurate means of burbot age determination. All previous burbot studies have used otoliths as the primary aging structures. Burbot sagittae (the largest and most commonly used otoliths for aging) used in this study were up to 15 mm long and usually had well marked annuli.

There is some variance between burbot populations in the timing of hyaline and opaque ring deposition in otoliths. Hyaline rings are laid down in summer on the otoliths of burbot from Lake Opeongo (Martin 1941), the Elbe River (Koops 1959, and Muller 1960), the Oder River (Muller 1960), and southwestern Lake Superior (Bailey 1972). Clemens (1951) states that in Lake Erie hyaline bands are deposited on burbot otoliths between June and March. Tanana River burbot probably deposit hyaline bands on their otoliths in April and May (Chen, 1969). Muth and Smith (1974) reported that burbot from Lake of the Woods deposited hyaline bands on their otoliths between early summer and November. Opaque rings were laid down in winter on otoliths of burbot from the Elbe and Oder Rivers (Muller 1960) and southwestern Lake Superior (Bailey 1972). Opaque bands are deposited on the otoliths of burbot from, the Susquehanna River between late winter and May (Robins and Deubler 1955), the Yukon River between late June and early September (Chen 1969), Ocean Lake in February, March, and April (Miller 1970), and the Elbe River between September and May (Koops 1959).

There is also variance between age and size classes within burbot populations in the timing of the deposition of hyaline and opaque rings on otoliths. Chen (1969) found that between late June and early September burbot from the Yukon River which were greater than 300 mm in length had hyaline otolith margins but had opaque margins when less than 300 mm in length. Burbot captured during January and February in Lake Simcoe had hyaline otolith margins when they were older than 3 years whereas younger burbot had opaque otolith margins (McCrimmon and Devitt 1954). Hackney (1973) reported that hyaline otolith margins were noted in older burbot from Lake Lavieille but not in young-of-the-year burbot even as late as October. The first few hyaline rings in otoliths of burbot from interior Alaska are more or less opaque and, therefore, difficult to distinguish from opaque material (Chen 1969).

In otoliths of Lake Athapapuskow burbot a marginal hyaline band was apparent in early June. Its width was maximum at the end of the sampling period in early September. Unlike other year classes, the otoliths of young-of-the-year burbot were entirely opaque. If the first hyaline zone of burbot otoliths is not deposited until the second summer the boundary between the first hyaline zone and second opaque zone marks the end of a growth period consisting of the first and second summers and first winter. Each successive pair of hyaline and opaque bands represents a 12 month growth period. In this study, and in studies conducted by Chen (1969) and Hackney (1973), the above boundary was used to specify one year old fish when, in fact, they were one year plus one summer old.

Lake Trout

Most of the early studies of lake trout used scales for aging but in recent studies (Power 1978; Bond 1975; Falk *et al*. 1973) aging has usually been done with otoliths. Doubt has been cast on the validity of scale ages especially for long lived and slow growing fish such as lake trout. Dubois and Lagueux (1968) found that after lake trout had matured otoliths continued to register annuli whereas scales did not. Their findings may explain why lake trout ages determined from scales usually indicate that fish are fast growing, short lived, and have linear growth whereas lake trout ages determined from otoliths usually indicate that fish are slow growing, long lived, and have growth which becomes asymptotic with increasing age. Scott and Crossman (1973) stated that lake trout age determination using scales is difficult for ages over eight years. Otoliths were used to age lake trout in this study. Lake Athapapuskow lake trout growth was compared only to populations for which ages were determined from otoliths (Fig. 34).

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Appendix B

BURBOT TAXONOMY AND INTERBASIN COMPARISONS OF BURBOT AND LAKE TROUT MORPHOLOGIES

Introduction

Morphological measurements were taken primarily as indirect indicators of interbasin exchange of lake trout and burbot in Lake Athapapuskow. Burbot morphological measurements were also taken for bearing on the validity of assigning burbot to a subspecific rank. Hubbs and Schultz (1941), Chen (1969), and Pivnicka (1970) have recognized subspecies of burbot based largely on geographic variation in the caudal peduncle ratio, while Lindsey (1956) and Lawler (1963) feel that this variation is clinal and does not justify the recognition of separate subspecies.

Materials and Methods

In 1978 caudal peduncle height and length (Hubbs and Schultz 1941) was measured on 335 gillnet caught burbot, of which head lengths (Scott and Crossman 1973) and interorbital widths (Pivnicka 1970) were also measured on 229 of them. Caudal peduncle height and length was measured on 189 poisoned burbot. Interorbital width and head length (Scott and Crossman 1973) was measured on 228 lake trout.

Measurements on gillnet caught burbot and lake trout were taken with a compass and read to ± 1.0 mm accuracy on a ruler. Measurements on poisoned burbot were taken with a dial caliper accurate to ± 0.05 mm. Burbot total length and lake trout fork length (Scott and Crossman 1973) were key morphological measurements because they were used in the analysis of growth, and the relationships between length and morphological character variation.

The relationships between total length and the following morphological character ratios were examined for burbot using regressions of total length versus ratios of, head length to total length, interorbital width to head length, peduncle length to total length, peduncle height to peduncle length, and peduncle height to total length. The relationships between fork length and the following morphological character ratios were examined for lake trout using regressions of fork length versus ratios of, head length to fork length, interorbital width to head length, and interorbital width to fork length. For burbot and lake trout, the significance of the slopes of the above regressions was tested using analysis of regression.

Comparison of mean character ratios between basins was done using analysis of covariance because length frequency distributions of burbot and lake trout differed between basins and analysis of regression indicated that character ratios were significantly dependent on length. Regressions of head length versus total length, interorbital width versus head length, peduncle length versus total length, peduncle height versus peduncle length, and peduncle height versus total length, were compared between basins for burbot. Regressions of head length versus fork length, interorbital width versus head length, and interorbital width versus fork length, were compared between basins for lake trout.

Character ratio means ± 95 percent C.I. were calculated for each basin but not used for between basin comparisons of morphologies.

Results

There was a significant linear relationship between morphological character ratios and length for the majority of characters studied (Table I). Middle and north basin fish showed fewer significant regressions than did south basin fish. Smaller sample sizes undoubtably weakened statistical confidences of middle and north basin regressions.

Table I. Morphological variation in relation to burbot total length and lake trout fork length, of fish collected in the middle and north (M + N) and south (S) basins of Lake Athapapuskow. For each regression line Y = ratio and X = total length or fork length in cm.

Species	Ratio	Basins	Ratio Versus Length Regression	R	F Statistic	Ratio Mean ± 95% C.I. (X 100)
Lota lota	head length to total length	M + N	Y = .01656X + 19.919	0.16	2.22	20.8 ± 2.0
		S	Y = .00339X + 21.075	0.03	0.09	21.2 ± 2.0
	interorbital width to head length	M + N	Y =-.01983X + 29.304	-0.09	0.79	28.2 ± 4.0
		S	Y = .05955X + 24.371	0.24	8.85*	27.2 ± 2.0
	peduncle length to total length	M + N	Y = 0.1292X + 8.019	0.33	29.00*	8.5 ± 2.0
		S	Y = 0.2741X + 7.451	0.52	103.65*	8.5 ± 0.8
	peduncle height to peduncle length	M + N	Y =-.14101X + 73.424	-0.34	32.45*	68.3 ± 9.8
		S	Y =-.16270X + 77.066	-0.35	37.39*	70.8 ± 7.8
	peduncle height to total length	M + N	Y =-.00317X + 5.869	-0.12	3.31	5.8 ± 0.7
		S	Y = .00675X + 5.724	0.24	17.60*	6.0 ± 0.5
Salvelinus namaycush	head length to fork length	M + N	Y = .01216X + 24.142	0.03	0.03	24.7 ± 2.0
		S	Y = .02897X + 22.431	0.18	5.75*	23.8 ± 2.0
	interorbital width to head length	M + N	Y = .06342X + 26.334	0.25	2.06	29.3 ± 4.2
		S	Y = .03002X + 28.269	0.15	3.93*	29.7 ± 3.9
	interorbital width to fork length	M + N	Y = .01936X + 6.282	0.27	2.36	7.2 ± 2.0
		S	Y = .01713X + 6.244	0.30	17.67*	7.0 ± 0.8

* indicates a significant regression at $\alpha = .05$

Table II. Comparison of morphologies of burbot and lake trout from the middle and north (M+N) and south (S) basins of Lake Athapapuskow.

Species	Regression Y on X	Basins	Analysis of Covariance			
			Adjusted Mean (adj. $\bar{X}$ in cm)	Slope	F Statistic	
					adj. $\bar{X}$	Slope
Lota	head length on	M + N	10.308	0.216	11.19*	0.12
lota	total length	S	10.542	0.214		
	interorbital width	M + N	2.947	0.268	14.73*	3.33
	on head length	S	2.847	0.293		
	peduncle length	M + N	3.253	0.089	0.00	4.58*
	on total length	S	3.252	0.092		
	peduncle height	M + N	2.148	0.612	35.43	6.90*
	on peduncle length	S	2.269	0.647		
	peduncle height	M + N	2.151	0.056	55.54	34.93*
	on total length	S	2.267	0.061		
Salvelinus	head length on	M + N	11.63	0.247	5.41*	0.22
namaycush	fork length	S	11.22	0.256		
	interorbital width	M + N	3.30	0.260	1.43	9.20*
	on head length	S	3.35	0.300		
	interorbital width	M + N	3.40	0.081	1.54	0.20
	on fork length	S	3.33	0.072		

* indicates a significant difference between basins of adjusted means or slopes at $\alpha = .05$.

For almost all characters examined, there was a significant difference between basins for the regressions of character Y variables versus character X variables (Table II). A significant difference between basins in adjusted means indicated that character Y values were different between basins at any given character X value. A significant difference between basins in slopes of Y versus X indicated that the rate of change of character Y values as character X values increased was different between basins.

Character ratios are presented in the literature as means, therefore, character ratio means ± 95 percent C.I. were calculated (Table I) for Lake Athapapuskow burbot and lake trout for comparison with other populations.

Discussion

Interbasin Comparisons of Fish Morphologies

The significant interbasin differences in burbot and lake trout morphologies (Table II), indicated that little exchange of these species occurs between the south basin and middle and north basins of Lake Athapapuskow.

Burbot Taxonomy

Burbot are distributed across northern Eurasia and North America, including Alaska and the Pacific Slope (McPhail and Lindsey 1970; Scott and Crossman 1973). The key character used in distinguishing subspecies of burbot has been the ratio of caudal peduncle length to caudal peduncle height. Based largely on this ratio, Hubbs and Schultz (1941) recognized Lota lota leptura in northwestern North American and Lota lota maculosa in the southeast. Lindsey (1956) and Lawler (1963) noted that this ratio increased towards the north and west but felt that it was a clinal variation and did not justify the recognition of two subspecies. They proposed that all burbot should be referred to as Lota lota. Chen (1969) and Pivnicka (1970) suggested that trends in burbot caudal peduncle ratios were not clinal and recognized two subspecies in North America. Chen called the northwest form Lota lota leptura and Pivnicka called this form Lota lota lota while both authors referred to the southeast form as Lota lota lacustris. Caudal peduncle ratios of the northwest form are about 1.7 to 1.95 and for the southeast form, about 1.3 to 1.4 (Chen 1969). A large boundary zone between the two proposed subspecies is characterized by intermediate peduncle ratios and lies between approximately 100 and 130 W longitude. Caudal peduncle ratios (1.46 in the middle and north basins and 1.41 in the south basin) place Lake Athapapuskow forms in Lota lota lacustris if this subspecies is valid.

Hubbs and Schultz (1941) found no apparent variation in burbot caudal peduncle ratios due to age and Chen (1969) found little relationship between the caudal peduncle ratio and standard length, sex, and vertebral number. In Lake

Athapapuskow the burbot caudal peduncle ratio was significantly correlated with length (Table I). Relationships between the caudal peduncle ratio and length may not have been observed in populations other than those in Lake Athapapuskow because samples from these populations are usually small and/or rarely contain younger fish. If the variation of the caudal peduncle ratio, as illustrated by the 95 percent confidence intervals in table I, and the correlation of this ratio with length are characteristic of other populations they may be highly significant for interpretation of the taxonomic validity of burbot subspecies.

Other morphometric characters of Lake Athapapuskow burbot (head length, interorbital width, peduncle length, and peduncle height) were not interpreted as being characteristic of a subspecies because there are no well marked geographical trends in the variations of these characters.

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Appendix C

POPULATION GROWTH RATES OF BURBOT AND LAKE TROUT

Population growth rates are obtained by comparing the mean size of surviving fish at successive ages (Bagenal and Tesch in Bagenal 1978; Ricker 1975). The use of popuation growth rates to estimate rate of increase in size from year to year assumes that there is little difference between year classes in respect to rate of growth and that the fish are a random sample of the age classes involved (Ricker 1975). The former assumption can be tested by comparing sizes of fish at the same age sampled in two or more successive years (Ricker 1975).

In this study the use of population growth rates for the analysis of burbot and lake trout growth and the pooling of 1977 and 1978 data prior to analysis is justified because plots of mean length versus age are similar between years (Figs. 1, 2, 3, and 4).

Figure 1. Mean lengths at given ages of burbot caught in the middle and north basins of Lake Athapapuskow in 1977 and 1978. Half of a 95 percent confidence interval is given for age classes represented by more than two fish.

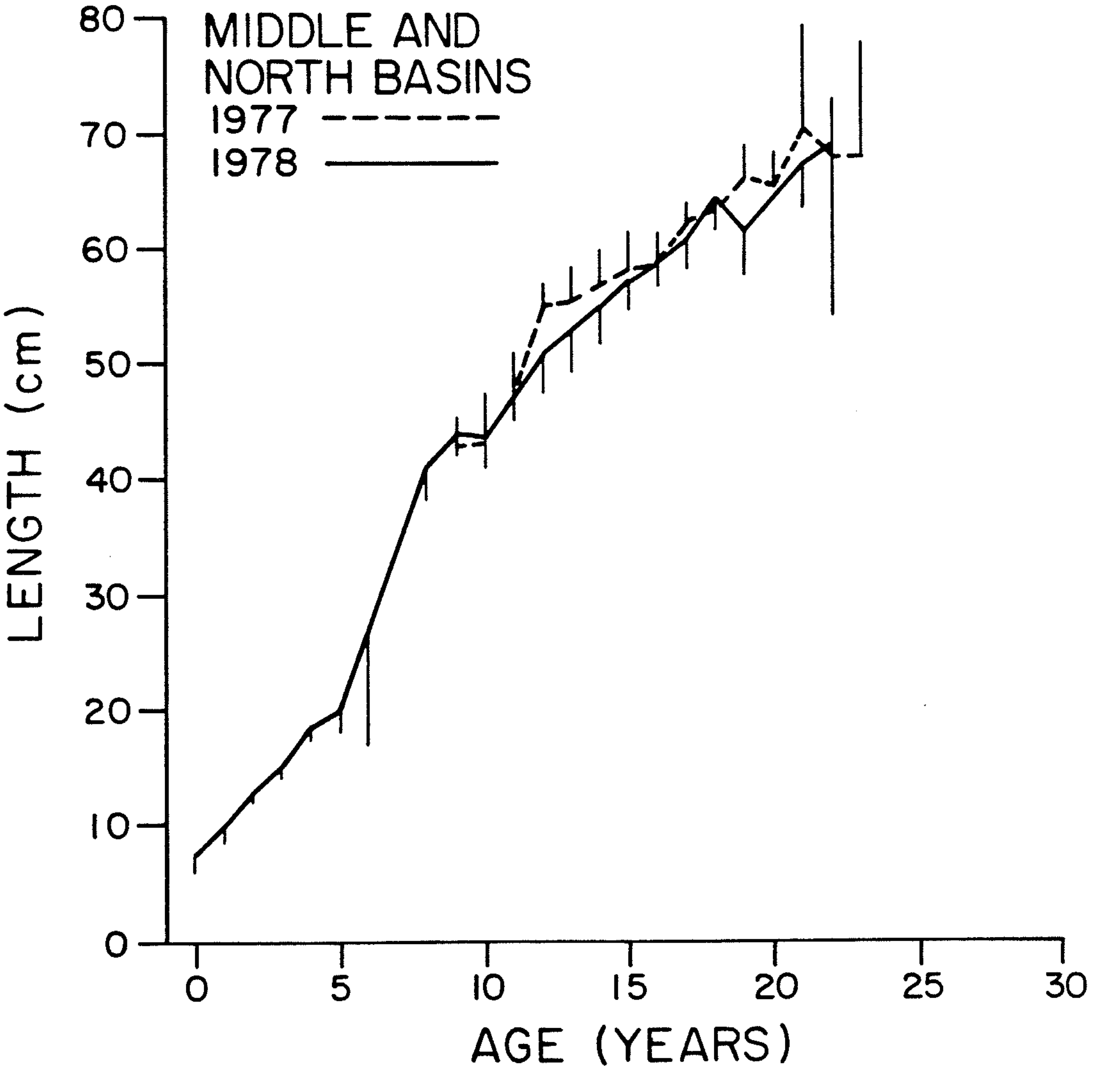

MIDDLE AND NORTH BASINS
1977
1978
LENGTH (cm)
0
10
20
30
40
50
60
70
80
0
5
10
15
20
25
30
AGE (YEARS)

Figure 2. Mean lengths at given ages of burbot caught in the south basin of Lake Athapapuskow in 1977 and 1978. Half of a 95 percent confidence interval is given for age classes represented by more than two fish.

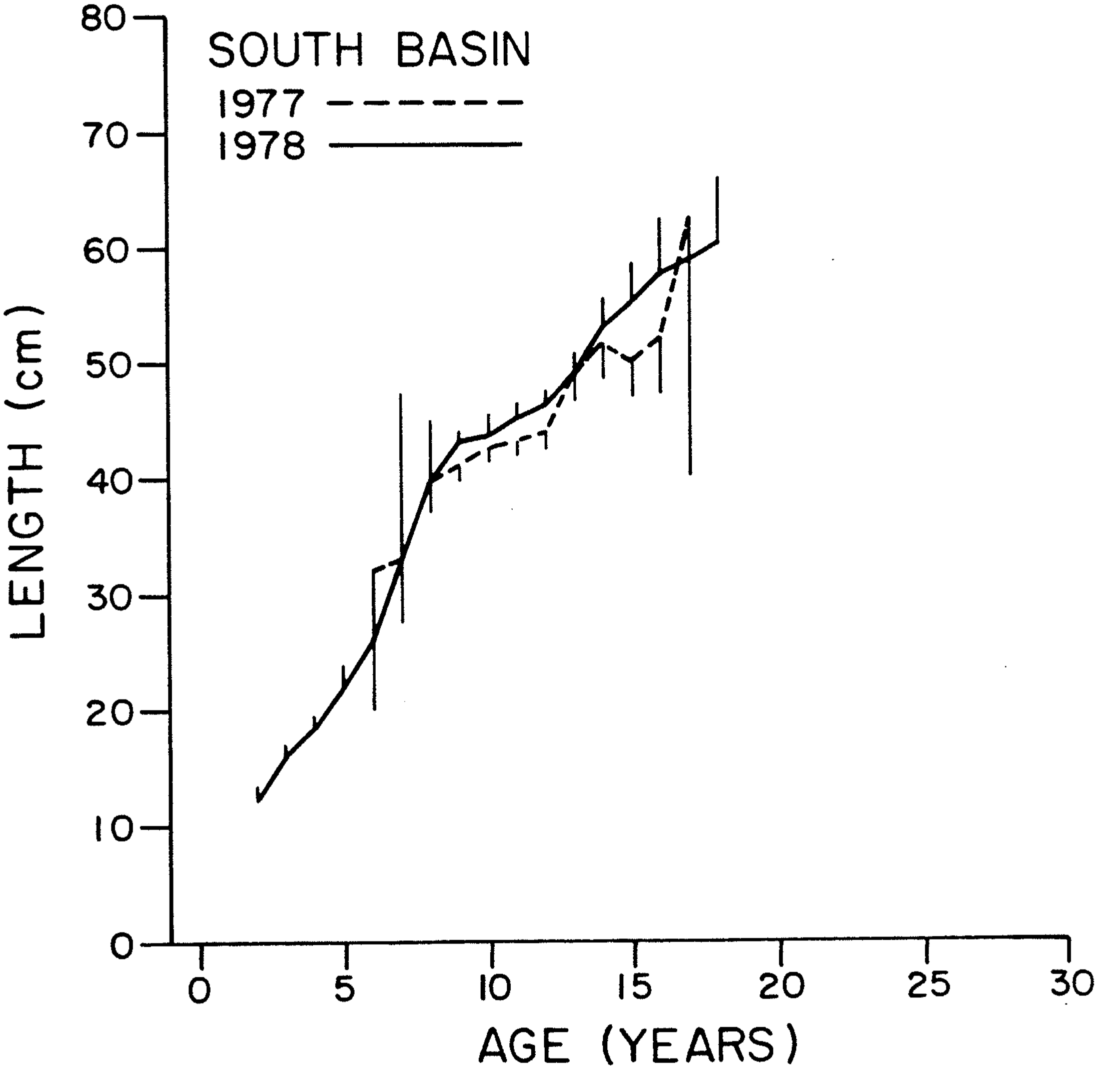

SOUTH BASIN
1977
1978
LENGTH (cm)
AGE (YEARS)
0
10
20
30
40
50
60
70
80
0
5
10
15
20
25
30

Figure 3. Mean lengths at given ages of lake trout caught in the middle and north basins of Lake Athapapuskow in 1977 and 1978. Half of a 95 percent confidence interval is given for age classes represented by more than two fish.

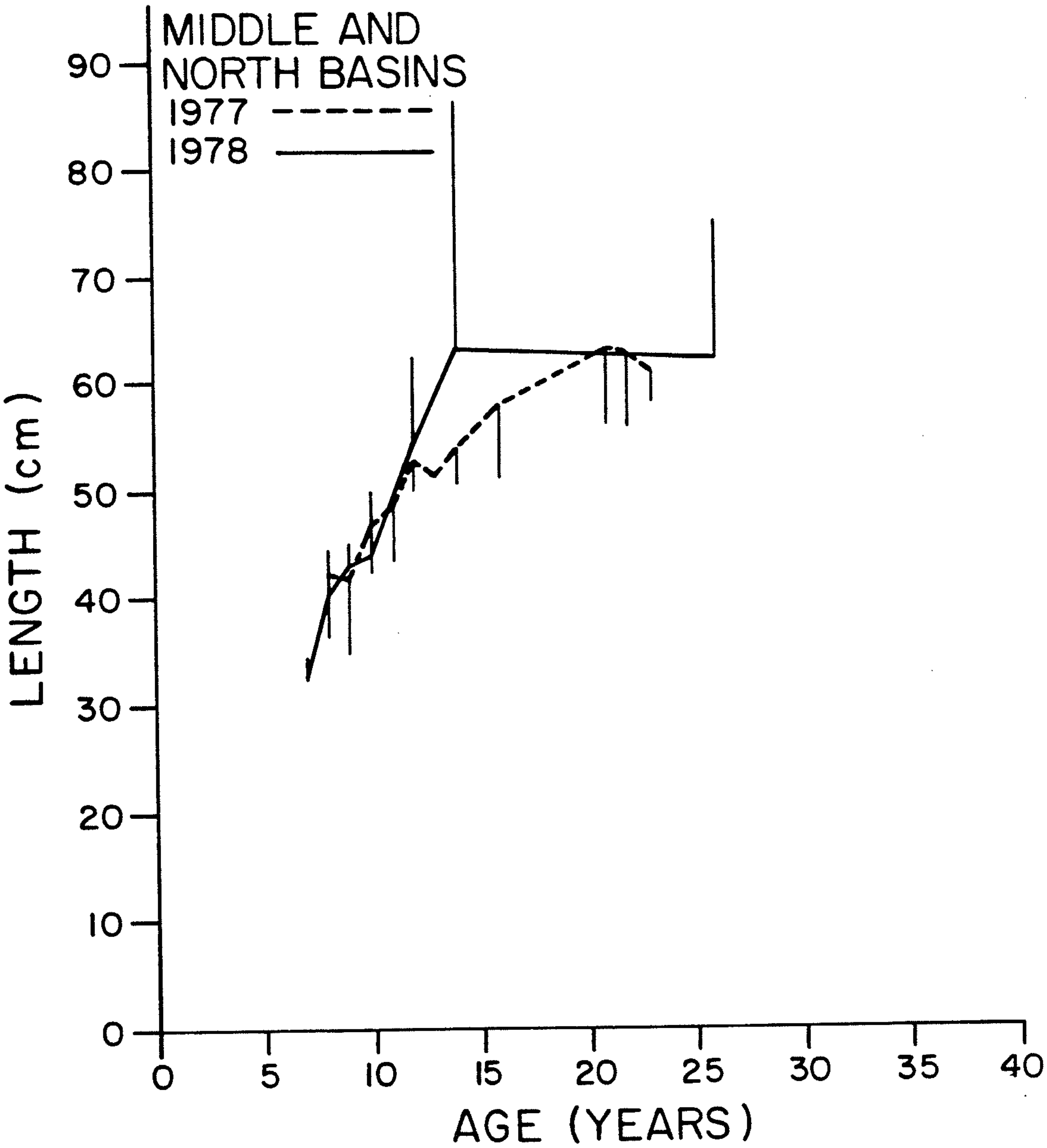
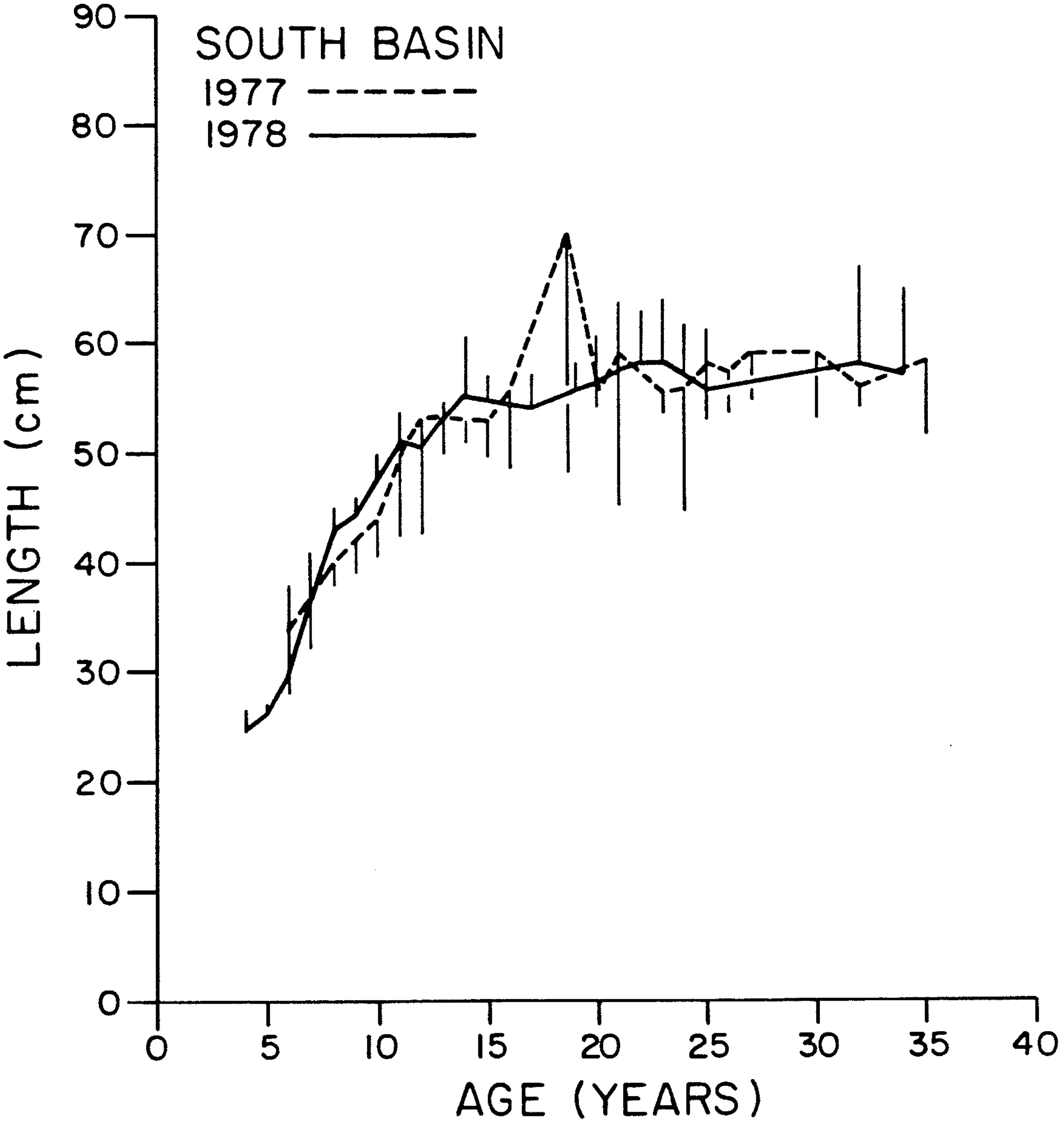

MIDDLE AND
NORTH BASINS
1977
1978
LENGTH (cm)
0
10
20
30
40
50
60
70
80
90
AGE (YEARS)
0
5
10
15
20
25
30
35
40

Figure 4. Mean lengths at given ages of lake trout caught in the south basin of Lake Athapapuskow in 1977 and 1978. Half of a 95 percent confidence interval is given for age classes represented by more than two fish.


SOUTH BASIN
1977
1978
LENGTH (cm)
AGE (YEARS)
0
10
20
30
40
50
60
70
80
90
0
5
10
15
20
25
30
35
40

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Appendix D

AGE-LENGTH DATA FOR BURBOT AND LAKE TROUT

Tables I, II, and III summarize age-length data of Lake Athapapuskow burbot and lake trout and are presented for a more direct examination of the growth of these species and for comparison with growth in other populations.

Table I. Mean length (cm) at age (years) plus or minus 95% confidence intervals, of burbot from Lake Athapapuskow.

	South Basin			Middle + North Basins		
Age	N	Mean	95% C.I.	N	Mean	95% C.I.
0				3	7.5	1.12
1				7	9.9	1.28
2	7	12.0	1.15	26	13.0	0.59
3	29	16.0	0.87	35	15.1	0.62
4	24	18.3	1.13	25	18.5	1.26
5	15	22.0	1.81	12	20.0	2.25
6	13	27.9	3.69	3	26.9	10.46
7	12	33.3	4.34	2	38.7	6.99
8	26	39.6	1.76	7	40.9	2.53
9	49	42.0	0.83	17	43.6	1.74
10	71	42.8	0.84	12	43.3	1.87
11	95	44.3	0.76	23	46.5	2.22
12	75	45.0	0.94	27	52.9	2.11
13	76	48.9	1.15	22	54.1	2.71
14	53	52.1	1.61	26	56.3	2.33
15	38	51.7	2.38	30	57.3	2.02
16	21	53.8	2.92	26	58.9	1.94
17	5	62.1	10.89	27	61.4	1.70
18	5	59.7	2.35	27	63.8	1.81
19	3	61.9	11.46	25	64.8	2.66
20	2	62.0	73.06	7	64.8	2.96
21				9	69.1	4.37
22	2	60.35	60.35	11	68.1	3.97
23				5	68.2	6.90
24				2	63.7	90.85
25				2	70.9	113.08
26				1	66.0	
27				1	66.5	
28				2	72.3	0.64

Table II. Mean length (cm) at age (years) plus or minus 95% confidence intervals, of burbot from Mistik Creek.

Age	N	Mean	95% C.I.
0			
1			
2	2	10.2	10.2
3	14	20.1	1.3
4	16	23.2	0.8
5	4	22.2	6.4
6	3	27.2	3.6
7	2	30.2	26.0

Table III. Mean length (cm) at age (years) plus or minus 95% confidence intervals, of lake trout from Lake Athapapuskow.

South Basin								Middle and North Basins							
Age	N	$\bar{X}$	95% C.I.	Age	N	$\bar{X}$	95% C.I.	Age	N	$\bar{X}$	95% C.I.	Age	N	$\bar{X}$	95% C.I.
1				21	8	58.1	5.29	1				21	6	63.0	3.78
2				22	8	57.4	3.53	2				22	4	62.1	3.85
3				23	8	56.6	2.49	3				23	9	62.9	5.90
4	10	24.6	1.88	24	9	56.7	2.92	4				24	3	60.2	5.51
5	20	25.9	1.08	25	8	57.1	2.93	5				25	2	60.5	6.35
6	10	32.0	4.26	26	6	58.3	4.52	6	1	29.6		26	5	61.16	5.44
7	21	37.0	2.87	27	4	59.3	4.18	7	6	34.6	4.8	27	3	71.3	8.26
8	29	41.6	1.43	28	0			8	8	41.2	2.58	28	2	63.2	17.15
9	32	43.3	1.62	29	3	57.9	6.25	9	16	42.8	3.16	29	1	68.2	
10	23	46.5	1.86	30	6	59.3	5.06	10	17	45.7	3.18	30	2	66.8	28.59
11	16	50.4	4.00	31	1	62.7		11	8	48.4	3.56	38	1	76.5	
12	17	51.1	2.38	32	7	57.4	4.03	12	19	53.2	2.37				
13	26	53.1	1.98	33	2	63.5	31.77	13	13	50.9	3.21				
14	16	53.5	2.13	34	5	56.9	4.26	14	8	57.5	5.93				
15	12	53.9	1.82	35	5	57.9	4.61	15	1	45.0					
16	5	55.2	3.22	36	0			16	6	58.5	6.80				
17	5	54.9	2.00	37	3	61.6	14.24	17	3	62.1	13.91				
18	2	59.7	10.80	38	2	61.8	31.2	18	0						
19	10	61.9	9.47	39	1	66.0		19	2	62.0	50.82				
20	8	55.7	2.35	45	1	58.8		20	2	64.9	14.61				