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Ecological responses of cisco (*Coregonus artedi*) to hypolimnetic oxygenation in Amisk Lake, Alberta

by

Peter Kofi Mawuena AKU ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **Doctor of Philosophy**

Department of Zoology

Edmonton, Alberta

Fall 1995

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Ecological responses of cisco (*Coregonus artedi*) to hypolimnetic oxygenation in Amisk Lake, Alberta** submitted by **Peter Kofi Mawuena AKU** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy**.

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Dedication

This thesis is dedicated to the ever-loving memory of my mother, Eugenia Yawavi Agbeve. "Dany[illegible], [illegible] dɛ nyuie. Wo luϑɔ na kpɔ gbɔɖemɛ mavɔ" (Beloved mother, rest in peace. May you find eternal rest).

Abstract

I examined responses of cisco (*Coregonus artedi*) to hypolimnetic oxygenation in Amisk Lake during the summers of 1989-1992. One basin of this double-basined eutrophic lake was oxygena s the second basin, and the nearby, untreated Baptiste Lake, served as referen stems. Dissolved oxygen (DO) concentrations in the hypolimnion of both basins of Amisk Lake increased during treatment but were higher in the treated basin than in the reference basin. Hypolimnetic DO in the treated basin remained above concentrations avoided by cisco ($< 1.3 \text{ mg}\cdot\text{L}^{-1}$), but fell below this level by mid-summer in the reference basin. Consequently, cisco habitat extended up to 8 m deeper in the hypolimnion of the treated basin than in the reference basin. Variations in monthly densities suggested that cisco in Amisk Lake also responded to hypolimnetic oxygenation by migrating from the reference basin into the treated basin. This behavioral response, coupled with deeper vertical extensions of fish habitat, resulted in the treated basin supporting a density and biomass of fish that was twice as great as in the reference basin. Higher DO concentrations enabled cisco in the treated basin to feed deeper into the hypolimnion, and incorporate more benthic species into their diets, than those in the reference basin. Increased DO concentrations in both basins resulted in expansion of whole-lake cisco habitat, and whole-lake fish density increased 5-fold and corresponding biomass tripled during treatment. Although prey base for cisco increased during oxygenation, per capita food quantity decreased. Growth rate and condition of cisco in Amisk Lake also decreased during treatment years compared with pretreatment data, suggesting a density-dependent relationship with biomass. In contrast, in untreated Baptiste Lake, where the hypolimnion remained anoxic each summer, cisco were restricted to epilimnetic waters, and density, biomass, and growth rate remained low. These results suggest that through expansion of suitable habitat, hypolimnetic oxygenation can enhance cold-water fish production, especially if combined with regulated fish exploitation.

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Chapter 1

General introduction

General introduction

If available, fish select water strata having environmental conditions most favorable for growth, reproduction, and survival (Magnuson et al. 1979; Matthews et al. 1985; Rudstam and Magnuson 1985). In lakes, vertical gradients of oxygen and temperature are the most critical environmental factors to which fish orient (Coutant 1985, 1990). In many deep eutrophic lakes, large proportions of the water lack adequate dissolved oxygen (DO) concentrations to sustain fish life during much of the year (Bernhardt and Wilhelms 1975; Suthers and Gee 1986; Cowell et al. 1987). Incomplete turnover in spring and fall, combined with decomposition of large quantities of organic matter characteristic of these highly productive lakes, results in oxygen depletion in deep waters, especially during thermal stratification of summer (Bernhardt and Wilhelms 1975; Cowell et al. 1987). Prolonged or severe hypolimnetic oxygen depletion can have severe consequences on fish populations; hypolimnetic anoxia can be catastrophic, resulting in massive fish kills (Frey 1955; Colby and Brooke 1969; Matthews et al. 1985; Rudstam et al. 1993).

Although fish may respond to hypolimnetic deoxygenation by moving upwards in the water column, the extent of such vertical redistribution may be limited by high epilimnetic temperatures for cold-water species such as salmonids (Fast 1973; Fast and Overholtz 1975; Wirth et al. 1975; Coutant 1985; Rudstam et al. 1993). Fish are generally distributed around species-specific depths with upper limits that are temperature-dependent and lower limits that are oxygen- or temperature-dependent (Matthews et al. 1985; Rudstam and Magnuson 1985; Coutant 1985). Because oxygen depletion is most severe in the deeper, colder waters of lakes, favorable habitat for cold-water fishes is most severely affected.

Other biota, such as zooplankton and macroinvertebrates, which are common prey for many cold-water fish, also respond very strongly to vertical gradients of oxygen (Fast 1971; Engel 1976; Taggart 1984). Extended periods of anoxia in the hypolimnion, and at the sediment-water interface, limit zooplankton and profundal macroinvertebrate abundance and biomass (Fast 1971, 1973; Cowell 1984).

Lake aeration is one of several approaches employed by lake managers to increase oxygen concentrations in deep waters. The most common methods of aeration are destratification aeration and hypolimnetic aeration/oxygen injection (McQueen and Lean 1986; Benndorf 1988; Cooke et al. 1993). Destratification aeration destroys thermal stratification and often produces warm isothermal conditions unsuitable for cold-water fish (Fast 1973; Taggart 1984). In contrast, hypolimnetic aeration/oxygen injection allows oxygenation of deep waters with minimal alteration of the natural thermal structure of the water column, and thus should be useful for expanding habitat for cold-water fishes in stratified eutrophic lakes, especially where internal recycling from sediments is the main source of phosphorus load to epilimnetic waters (Fast 1973; Bernhardt and Wilhelms 1975; Taggart and McQueen 1981; Cowell et al. 1987; Ashley 1988).

A 5-yr hypolimnetic oxygenation experiment was conducted in Amisk Lake, a deep, naturally eutrophic lake in which the main source of annual phosphorus input is autochthonus (Prepas 1990). Amisk Lake (54° 35'N, 112° 37'W), located 175 km northeast of Edmonton, is a medium-sized lake ($A_o = 5.2$ km^2) with two basins, a shallower north basin ($Z_{max} = 34$ m), connected by a narrows (sill depth = 11 m) to a deeper south basin ($Z_{max} = 60$ m). Historically, both basins stratified in the summer, with thermoclines ranging within the 5-10 m stratum. Phosphorus release from the anoxic sediments was high, 6-8 mg$\cdot$m$^2\cdot$d^{-1}, resulting in mean hypolimnetic total phosphorus concentrations as high as 150 μg$\cdot$L^{-1}, and this phosphorus-rich water extended well into the metalimnion (Prepas et al., in press). This nutrient-rich condition led to high primary production (mean summer chlorophyll-*a* in the euphotic zone for 1980-1987: 8.7-25.4 μg$\cdot$L^{-1}). High oxygen consumption rates (0.6-1.0 g $O_2\cdot$m$^{-2}\cdot$d^{-1}), combined with incomplete mixing during spring and fall turnovers, led to severe hypolimnetic hypoxia in both basins (Prepas 1990). Year-round liquid oxygen injection into the hypolimnion of the north basin of Amisk Lake started in June 1988 and continued through October 1993. The south basin was not treated and served as a reference.

The goal of the Amisk Lake project was to maintain DO concentrations above 2 mg·L^{-1} year-round throughout the water column of the treated basin, which was expected to enhance cold-water fish and invertebrate habitat. As well, the resulting oxic conditions at the sediment-water interface would reduce internal phosphorus loading and thus reduce the incidence and intensity of summer phytoplankton blooms (Prepas et al., in press).

Although hypolimnetic oxygenation had been successful in increasing hypolimnetic DO concentrations, most previous studies focused on short-term ecological and behavioral responses, such as vertical distributions and dietary responses of stocked fish populations (e.g., Fast 1973; Fast et al. 1975; Fast and Overholtz 1975; Serns 1976; Overholtz et al. 1977; Garrell et al. 1978; Taggart and McQueen 1981; Taggart 1984). Long-term effects, such as changes in growth rate, population structure, density and biomass, and effects on native fish have been rarely evaluated.

In this doctoral thesis, I examine both short- and long-term ecological and behavioral responses of a native fish, cisco (*Coregonus artedi* Lesueur, 1818), to hypolimnetic oxygen injection in Amisk Lake. Cisco is the dominant cold-water fish in Amisk Lake, constituting > 96 % of the pelagic fish assemblage.

The cisco, a member of the family Salmonidae, extends south from Great Bear Lake in the Northwest Territories of Canada, throughout most of Canada, and into the north-central and eastern United States, where its southernmost distribution is reached in northern Indiana, around latitude 41°N (Hile 1936; Frey 1955; Scott and Crossman 1973; Becker 1983). Cisco is primarily a lacustrine species, although it has been reported in large rivers in the Hudson Bay region (Scott and Crossman 1973).

Throughout its range, cisco has been characterized as a pelagic species that prefers well-oxygenated, cool hypolimnetic habitats (Fry 1937; Frey 1955; Scott and Crossman 1973). In general, cisco move in spring and early summer from shallow to deep water below the thermocline, where they remain throughout summer. As the upper waters cool in late summer to early fall, they move back into shallower water (Hile 1936; Fry 1937; Frey 1955; Scott and Crossman 1973; Engel and Magnuson 1976). This seasonal vertical distribution pattern of cisco primarily reflects seasonal changes in vertical profiles of temperature and oxygen. In addition, cisco is generally considered planktivorous, feeding mainly on pelagic zooplankton, but will also prey on macroinvertebrates, including benthic species such as chironomids (Fry 1937; Langford 1938; Engel 1976; Rudstam and Trapp 1987). Thus, the ecology of cisco makes it a more suitable species for evaluating a broader range of ecological and behavioral responses of fish to hypolimnetic oxygenation than in previous studies.

In the first data chapter of this thesis (Chapter 2), I evaluate the efficacy of hypolimnetic oxygen injection in expanding deep-water summer habitat for cisco. I compare the vertical distributions of cisco in relation to differences in DO and temperature profiles between the treated and reference basins of Amisk Lake during periods of oxygen treatment in 1989 and 1990, and following treatment in August, 1994. The patterns in vertical distributions of cisco in Amisk Lake are also compared with those of a cisco population in nearby Baptiste Lake that served as a second unmanipulated system. Finally, I examine the influence of behavioral thermoregulation in cisco, i.e., the selection of habitats within preferred temperature ranges, on realizing the goals of hypolimnetic oxygenation.

Chapter 3 focuses on dietary responses of cisco in Amisk Lake. Here, I compare the diets of cisco with the composition and vertical distributions of their prey between the treated and reference basins during the summers of 1989 and 1992, both within and between years. Data on vertical distributions and abundance of zooplankton were available for 1989 from another study in the Amisk Lake project (Field 1993). Detailed sampling of the zooplankton in Amisk Lake was not possible during the period of detailed monitoring of fish distributions and population structure. Having established fish distribution patterns between 1989 and 1991, I was able to focus again on dietary responses in 1992.

In the last data chapter (Chapter 4), I used data from 1971 (provided by Alberta Environmental Protection, Natural Resources Service) and data collected during the oxygenation to examine growth rate and population structure of cisco during pretreatment and treatment years. In this chapter, I also examine differences in fish density and biomass between the two basins during treatment years, and compare the trends in growth, density and biomass of the Amisk Lake cisco population with those of the cisco population in Baptiste Lake. Finally, Chapter 5 provides general conclusions in which the major findings of this dissertation are discussed and related to changes in the environment and in other trophic levels of Amisk Lake during the study period. I conclude by discussing the contribution of this study to understanding the role of complex trophic interactions in realizing the goals of whole-lake manipulations.

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Chapter 2

Impact of hypolimnetic oxygenation on the vertical distribution of cisco (*Coregonus artedi*) in Amisk Lake, Alberta.

A version of this chapter, co-authored with Lars G. Rudstam and William M. Tonn, has been accepted for publication in Can. J. Fish. Aquat. Sci.

Introduction

Vertical distributions of fish have been correlated with several ecological variables, including temperature, oxygen, light, predator-prey interactions, food availability and internal seiches (Blaxter 1974; Magnuson et al., 1979; Hamrin 1986; Levy et al. 1991). In stratified lakes, dissolved oxygen (DO) concentration can have a strong influence on vertical distributions, particularly during summer (Engel and Magnuson 1976; Rudstam and Magnuson 1985; Suthers and Gee 1986). Hypolimnetic oxygen depletion, combined with warming of epilimnetic waters, can result in some fish being compressed into marginal habitats (Crowder and Magnuson 1982; Coutant 1985, 1990; Matthews et al. 1989). Although the hypolimnion may have suitable temperatures during summer, low DO concentration can exclude cold-water species; hence, in many eutrophic lakes, where hypolimnetic oxygen depletion can be significant, distribution and abundance of cold-water species can be severely limited (Frey 1955; Colby and Brooke 1969; Fast 1973).

Thermal destratification and hypolimnetic aeration/oxygenation are two of several approaches employed by lake managers to increase oxygen concentrations in deep waters of lakes (Cooke et al. 1993). Because hypolimnetic oxygen depletion is strongly coupled with thermal stratification, artificial thermal destratification can eliminate a hypolimnetic oxygen deficit. However, destratification often produces warm isothermal conditions unsuitable for cold-water fish (Fast 1973; Taggart 1984; Ashley 1988). Hypolimnetic oxygen injection or aeration allows oxygenation of deep waters with minimal alteration of the natural thermal structure of the water column, and thus should be useful for expanding habitat for cool- and cold-water fishes in stratified eutrophic lakes (Fast 1973; Fast and Overholtz 1975; Taggart and McQueen 1981).

McQueen and Lean (1986) reviewed 42 published reports of hypolimnetic aeration projects conducted on 16 lakes in North America. Although hypolimnetic aeration has been successful in increasing oxygen concentrations of the hypolimnia, and thus generally improving cold-water fish habitat in these lakes, only seven studies provided data on effects of aeration on fish distributions, and most of them focused on stocked populations (e.g., Fast 1973; Fast et al. 1975; Serns 1976; Overholtz et al. 1977; Garrell et al. 1978). Because of stocking mortality, competition with, and predation by native fishes, evaluation of these results have often been compromised. Therefore, studies that involve natural fish populations are needed for better evaluation of the efficacy of hypolimnetic oxygenation in restoring cold-water fish habitat.

In the present study, I examined the effects of hypolimnetic oxygen injection on the vertical distributions of cold-water fish by quantifying the depth distributions of a native pelagic fish in a double-basined eutrophic lake in which oxygen was injected into the hypolimnion of one basin; the goal of the project was to increase hypolimnetic DO concentration to a point where cold-water fish could use this habitat year-round. The second basin and a nearby, untreated lake served as reference systems. The study focused on cisco (*Coregonus artedi*); because it was the most abundant cold-water fish in the lake, I expected this species to be the primary beneficiary of improved hypolimnetic conditions. I hypothesized that increased DO concentrations in the treated hypolimnion would allow depth distributions of cisco to increase significantly compared with those in the reference basin.

Materials and methods

Study area

Amisk Lake (54° 35'N, 112° 37'W) is a naturally eutrophic lake (mean summer chlorophyll-a (chl-*a*) in the euphotic zone for 1980-1987: 8.7-25.4 $\mu g \cdot L^{-1}$) in central Alberta (Fig. 2-1). It has two basins, a shallower north basin ($A_o = 2.3$ km^2, $Z_{max} = 34$ m), connected by a narrows (sill depth = 11 m) to a deeper south basin ($A_o = 2.8$ km^2, $Z_{max} = 60$ m). Eleven species constitute the fish community, with cisco and yellow perch (*Perca flavescens*) being the dominant pelagic and littoral species, respectively (Prepas 1990). There is an active sport fishery for yellow perch and northern pike (*Esox lucius*), and a small commercial fishery during the fall for coregonids.

Historically, both basins stratify in the summer, with thermoclines ranging within the 5-10 m stratum. Incomplete mixing during spring and fall turnovers and high epilimnetic algal biomass in summer result in high oxygen consumption rates (0.6 - 0.8 g $O_2 \cdot m^{-2} \cdot d^{-1}$) below the thermocline and under ice that have led to severe hypolimnetic hypoxia in both basins during summer and winter (Prepas 1990).

Oxygen injection into the hypolimnion of the north basin of Amisk Lake started in summer 1988 and continued through October 1993. Pressurized pure oxygen was released from an onshore holding tank through 1.5 km of tubing to a set of diffusers located at the deepest point of the basin (34 m; N2 in Fig. 2-1). Oxygenation was year-round, and ranged (mean ± SE) from 0.61 ± 0.03 to 1.3 ± 0.03 $t \cdot d^{-1}$ and 0.50 ± 0.01 to 0.57 ± 0.04 $t \cdot d^{-1}$ of liquid oxygen during thermally stratified and mixed periods, respectively (Prepas and Burke, in press). The south basin was not treated and served as a reference basin.

Baptiste Lake (54° 45'N 113° 33'W) is physically similar but more productive (mean summer chl-*a* in the euphotic zone for 1980-1987: 13.4-50.9 $\mu g \cdot L^{-1}$) than Amisk Lake. High oxygen consumption rates, combined with incomplete turnover during spring and fall, result in anoxia below the thermocline (5-10 m) in summer and under ice. Baptiste Lake has two basins connected by a narrows with a sill depth of 5.5 m; the deeper south basin ($A_o = 4.5\ km^2$, $Z_{max} = 27.5$ m; Fig. 2-1) served as a second reference basin. The fish fauna is similar to that in Amisk Lake (Prepas 1990).

Gill netting

A set of five 3 x 30 m monofilament-nylon vertical gill nets (25, 38, 51, 76 and 102 mm stretch mesh) was set in each basin (sites N2 and S1, Fig. 2-1) of Amisk Lake on successive days, once every 2 wk, along the 30 m contour. Nets were set from July to September 1989, and from May to September 1990; however, because of very low samples sizes from S1 in 1989, gill net catches from that year were not included in my analyses. The 25-m contour in Baptiste Lake (Fig. 2-1) was also sampled from May to September in 1990, but at monthly intervals. The five nets were set next to each other extending from surface to bottom, and checked at 6- to 8-h intervals over 24-h sampling periods. At each inspection, the identity, number, and depth of each species were recorded at 1-m intervals. Total lengths (mm) of all cisco were measured in the field. A minimum of five individuals per 1-cm length class was weighed. The proportions of different size-classes were corrected for both mesh size selectivity and higher encounter probability of larger fish according to Rudstam et al. (1984).

Scales and otoliths from the fish selected for weighing were used for age determination. Toasted sections of otoliths were read in glycerol. Age assignments were compared among three independent readers and precision was determined with the index of average percentage error (APE) (Beamish and Fournier 1981).

Hydroacoustic sampling

Hydroacoustic data on fish size, vertical distributions and abundances in both lakes were collected with a single beam 70 kHz SIMRAD EY-M echo-sounder (full beam angle 11.2°, 0.6 ms pulse duration, 3 pings$\cdot s^{-1}$, 40 Log R time-varied gain). The transducer of the echo-sounder was mounted 1.5 m from the bow and towed 0.5 m below the surface at the side of a 5.5-m boat. Towing speed varied between 1.5 to 2 $m \cdot s^{-1}$.

In 1989, hydroacoustic surveys of 10-15 min durations were conducted in Amisk Lake only, around sites N2 and S1. Survey routes were expanded in 1990 to determine basin-wide distributions (Fig. 2-1). A complete survey in 1990 lasted 25-30 min in the treated basin and 40-45 min in both the reference basin of Amisk Lake and in the south basin of Baptiste Lake. However, technical difficulties prevented completion of the entire survey route on some sampling days. To improve the efficacy of hydroacoustic estimates of fish density and size, I used data only from night surveys (22:30-02:30), when fish were more uniformly dispersed and most of the acoustic scatters were from single fish. During the day, cisco in both lakes school in the water column and in near-shore areas at the same depth layers as occupied at night; schools form at dawn and break up at dusk (P.M.K. Aku and W. M. Tonn, unpubl. data). Cisco in Amisk and Baptiste lakes do not exhibit diel vertical migration. To eliminate the influence of day to day variations in environmental factors on the vertical distributions of fish, I conducted the hydroacoustic surveys in both basins on the same day during each gill netting session. Because my surveys were of short durations, and conducted at periods when the distributions of cisco were expected to be most uniform, I assumed that within-night variations in vertical distributions would be minimal (see also Jurvelius and Heikkinen 1987; Eckmann 1991).

Hydroacoustic signals were recorded on audio cassette tapes. Tapes were digitized and analyzed for fish size and density using the HADAS system (Lindem 1990). Target strength (TS) distributions were obtained by employing the Craig and Forbes (1969) deconvolution technique to remove the effect of the beam pattern. Reference voltages recorded at the beginning of each tape were used to adjust system gains.

The echo-sounder was calibrated each year with a 19-mm steel sphere of TS -48.6 dB. Differences between calibration values of the echo-sounder in 1989 and 1990 were < 1 dB. Repeatability of echo-survey estimates of fish density was determined by comparing mean estimates from three successive 9-min surveys over the same transect.

I estimated fish length from target strength with the equation:

$$L = 10^{(88 - TS)/20}$$

where TS is target strength (dB) and L is fish total length (mm) (Lindem and Sandlund 1984; Bjerkeng et al. 1991). Targets > -46 dB were considered to represent age 1+ and older cisco (fish > 130 mm). Echoes < -46 dB, probably young-of-the-year (YOY) cisco and yellow perch, were excluded from my analyses. TS distributions were split into 2-dB classes beginning at -46 dB. All fish echoes greater than -32 dB were truncated and included in the -32 dB size-class.

For the hydroacoustic data, the number of fish (N) insonified during a survey was calculated as:

$$N = \sum D_i V_i$$

where V_i is the volume of water surveyed in depth layer i within the half-power acoustic beam (using the wedge-shaped model for consecutive pings from Kieser and Mulligan 1984) and D_i is the density of fish in depth layer i.

Temperature and DO profiles

Water temperature and DO data for 1989 were obtained from Webb (1993). Linear interpolations of oxygen measurements surrounding sampling periods were used to obtain DO profiles. In 1990, I used a HYDROLAB™ SURVEYOR II (SVR2-SU), calibrated before and after each sampling session, to measure temperature and DO concentrations at 1-m intervals, from surface to bottom during each fish sampling night. Temperature and DO concentration were measured at S1 and N2 in Amisk Lake, and at B1 and B2 in Baptiste Lake (Fig. 2-1).

Vertical distributions of fish

Vertical distributions (relative abundance) of cisco were compiled at 2-m depth intervals for both gill net and hydroacoustic data and compared to water temperature and DO concentration within and among basins. Data were analyzed at 2-m intervals to improve reliability of the hydroacoustic estimates of abundance because single fish echoes obtained at 1-m intervals were too few for the HADAS method to estimate density with acceptable reliability (Lindem 1990). Quartile depths of vertical distributions of fish were obtained from cumulative percentage frequency distributions of fish against depth. Wave induced surface disturbance contaminated the hydroacoustic data from depths shallower than 4 m on several occasions, therefore to be consistent, I used only fish distributions below 4 m for all analyses. Some cisco were caught in gill nets at depths less than 4 m, but their numbers were never higher than 3% of the total catches.

I also compared the observed vertical distributions of cisco with predictions from a model of vertical distributions of fish, developed by Rudstam and Magnuson (1985) for cisco and yellow perch in Wisconsin lakes. This model predicts the depth distribution of a fish species based on species-specific responses to experimental gradients of oxygen and temperature. A preference index for each depth i (Pref_i) is calculated as the product of a temperature response function (F(T)), and an oxygen response function (G(Ox)):

$$Pref_i = F(T) \cdot G(Ox)$$

F(T) is assumed to be approximated by a normal curve with a mean at the final preferendum temperature and a standard deviation of 2°C (Magnuson et al. 1979). G(Ox) is a step function that is zero below a lower avoidance concentration and one above an upper avoidance concentration. Thus, oxygen below the lower avoidance concentration will completely exclude the fish and oxygen concentrations above the upper avoidance concentration will have no effect on depth selection. The predicted distribution of fish based on temperature and oxygen concentrations can be mapped onto a distribution of fish in space by normalizing these preference values over the whole water column. The proportion of the fish population expected at a given depth i ($Prop_i$) is:

$$Prop_i = \frac{Pref_i}{\sum_{i=1}^{n} (Pref_i)}$$

Species-specific inputs to the Rudstam-Magnuson model (RMM) are a preferred temperature and the upper and lower avoidance DO concentrations. For cisco, Rudstam and Magnuson (1985) assumed a preferred temperature of 12°C, and an upper and lower avoidance DO concentration of 4.4 and 1.9 $mg \cdot L^{-1}$, respectively, at 12°C. I also calculated fish distributions from a uniform distribution model (UDM) for comparisons with distributions predicted from the RMM. The null hypothesis for the UDM was that temperature and oxygen have no limiting effects on fish distributions.

Due to the skewness in vertical distributions of fish, median depths rather than means were used as measures of central tendency of fish distributions. In each year, median depths of fish distributions (MD) were compared between basins with the two-sample median test (Zar 1984). Differences between basins in overall vertical distributions of fish (both observed and predictions from the RMM) were compared in each year with the Komolgorov-Smirnov (K-S) two-sample statistic (D), corrected for large sample size (Sokal and Rohlf 1981). Observed vertical distributions of fish were compared with distributions predicted from the UDM with the K-S uniform distribution goodness-of-fit test. Overlaps between observed and predicted distributions (from both RMM and UDM) were calculated as:

$$O_{hj} = \left[1 - \left(\frac{1}{2} \sum_{i=1}^{n} |p_{hi} - p_{ji}| \right) \right] \times 100$$

where p_{hi} and p_{ji} are proportions of fish at depth i in any pair of basins h and j (Schoener 1969). Overlaps of the observed distributions with the RMM and UDM in each basin (both years) were compared with a paired *t*-test. Angular transformation was used for the *t*-test because some overlap values were less than 30% or greater than 70%.

Post-treatment sampling in Amisk Lake

Oxygen injection into Amisk Lake ceased in October 1993. To determine vertical distributions of fish following the period of oxygenation, I conducted vertical gill net surveys in the treated and reference basins on the nights of August 3 and 4, 1994, respectively; a hydroacoustic unit was unavailable at this time. I also measured temperature and DO profiles during each night as described for 1990.

Results

Temperature and oxygen

Before the onset of thermal stratification (May-June), hypolimnetic DO concentrations were similar in both basins of Amisk Lake in 1989 and 1990 (Prepas and Burke., in press). After establishment of stratification (July through September), hypolimnetic DO concentrations decreased in both basins, but the rate of oxygen depletion was higher in the reference basin than in the treated basin (Fig. 2-2 and 2-3; Appendix A, Table 6-1). In both years, the hypolimnion of the treated basin was 3-5°C warmer than the reference basin but thermal stratification was maintained; these higher water temperatures were apparently induced by the injected oxygen (Fig. 2-2 and 2-3; Appendix A, Table 6-2).

Age and size distributions of fish

The degree of reproducibility within ±1 yr in age assignments was high (APE = 4%, n = 46 in 1989; 5%, n = 97 in 1990) among the three readers. Ages determined from scales and otoliths were identical for fish < 4 yr old. Beyond this age, scale readings were on average, 2 yr less than from otoliths therefore, otoliths were used to establish fish ages. Cisco comprised 94 to 96% of the total gill net catch in both lakes, so I assumed all targets insonified by the echo-sounder were cisco. Based on gill net catches, the pelagic fish population in both lakes consisted of four size (age) groups (Fig. 2-4, A-C), < 130 mm (age 0+, not included in figure), 130-240 mm (1+), 260-320 mm (2+), and > 320 mm (≥ 3+). Fish size estimates from the hydroacoustic method also yielded similar size groups (Fig. 2-4D). Both gill nets and hydroacoustics showed that the adult cisco population in Amisk Lake was dominated by two main size groups: 160-210 mm and > 320 mm (Fig. 2-4A and 2-4B). In Baptiste Lake, the cisco population consisted predominantly of fish > 300 mm (Fig. 2-4C).

Vertical distributions of fish

Vertical distributions of fish obtained with gill nets were usually consistent with distributions obtained from the hydroacoustic method (e.g., Fig. 2-2 and 2-3). Because hydroacoustic data integrate vertical distributions over a larger area and time, they provide more comprehensive information on species distributions than gill nets (Rudstam et al. 1987; Brandt et al. 1991) therefore, I used primarily the hydroacoustic data to investigate cisco distributions. Estimates of fish density from the three successive surveys differed by 2.8, 5.8 and 8.6% of the mean and are typical of precision estimates for the method used (Bagenal et al. 1982; Jurvelius and Heikkinen 1987).

On all sampling dates in Amisk Lake during 1989, maximum depths occupied by cisco were deeper in the treated basin than in the reference basin (Table 2-1). On July 26 and August 9, 1989, there were no differences in either MD or overall distributions of cisco between the treated and reference basins (Table 2-2; Fig 2-2). Overall vertical distributions of fish between the two basins were significantly different on August 23 and September 23 (Table 2-2). Contrary to my prediction, MD and the quartile depth distributions of fish were deeper in the reference basin than in the treated basin on August 23. However, on September 23, MD and quartile depths were deeper in the treated basin than in the reference basin (Table 2-2; Fig 2-2). DO concentrations associated with median depth distributions of fish (MDDO) ranged between 2.1-3.9 and 1.9-2.9 mg·L^{-1}, in the treated and reference basins, respectively; on all dates the MDDOs were greater in the treated basin than in the reference basin (Table 2-3). In contrast, corresponding temperatures associated with median depth distributions of fish (MDT) were higher in the reference basin (11.1-15.9°C) than in the treated basin (9.1-13.3°C). DO concentrations associated with maximum depths occupied by cisco were greater in the treated basin than in the reference basin, ranging between 1.8-3.0 mg·L^{-1} and 1.2-2.1 mg·L^{-1}, respectively (Table 2-1).

Between May 23 and July 25, 1990, when there was little difference in average hypolimnetic DO concentration between basins (Table 2-3; Appendix A, Table 6-1), differences in overall fish distributions in the two basins were either not significant or weakly so (Table 2-2; Fig. 2-3). Distributions of fish in the two basins started to diverge on July 11; however, on July 25, when oxygen supply to the treated basin was shut down temporarily for repairs on the diffuser, both MD and the 25-75 percentile depths became the same in both basins (Table 2-2).

The largest differences in depth distributions of cisco occurred in late summer (August-September) of 1990, which corresponded to the period of the largest differences in hypolimnetic DO concentration between the two basins. During this period, low DO concentration appeared to restrict a higher proportion of fish to shallower depths in the reference basin than in the treated basin (Table 2-2; Fig. 2-3). In August and September, MDs were consistently deeper in the treated basin than in the reference basin and overall fish distributions differed significantly between basins (Table 2-2; Fig. 2-3). DO concentrations associated with MDs ranged between 2.8-3.9 mg·L^{-1} and 0.9-5.9 mg·L^{-1} in the treated and reference basins, respectively (Table 2-3). Corresponding MDTs were higher in the reference basin (12.8-17.3°C) than in the treated basin (11.2-12.3°C) (Table 2-3). From August 23 through September, maximum depths occupied by cisco were deeper in the treated basin than in the reference basin, and associated DO concentration ranged between 1.2-1.8 mg·L^{-1} and 0.8-1.8 mg·L^{-1}, respectively (Table 2-1). Water strata containing the 25-75 percentiles of fish abundance were broader and generally deeper in the treated basin compared with the reference basin (Table 2-2). However, even in the treated basin, where DO concentration was > 1.0 mg·L^{-1} throughout most of the hypolimnion, < 25% of fish insonified were located deeper than 17 m on any sampling day.

Hypolimnetic oxygen depletion was more rapid in Baptiste Lake than in Amisk Lake. Consequently, erosion of maximum depths occupied by cisco was more pronounced in Baptiste Lake than in either basin of Amisk Lake (Fig. 2-5). By the second week of July 1990, water at depths > 8 m was anoxic and fish distributions were restricted to shallower depths where DO concentration was > 1.0 mg·L^{-1}. Late summer (July 30 to September 24) MDs of cisco in Baptiste Lake (both hydroacoustic and gill net) were generally similar to those in the reference basin of Amisk Lake but consistently shallower than those observed in the treated basin (Table 2-2, 2-4). The 25-75 percentile depth ranges were generally narrower and occurred within shallower depths than in either basin of Amisk Lake (Table 2-4). Late summer MDTs ranged between 13.2-19.1°C, with a mean of 16.4 ± 3.0°C. Corresponding MDDOs ranged between 5.3-7.6 mg·L^{-1}, with a mean of 6.0 ± 1.4 mg·L^{-1}. These temperatures and DO concentrations were higher than those in either basin of Amisk Lake, and resulted from fish occupying epilimnetic waters in Baptiste Lake.

Post-treatment vertical distributions in Amisk Lake

On August 3 and 4, 1994, 22 and 37 cisco were caught in the treated and reference basins, respectively. Depth distributions of cisco were similar in both basins, and were limited to the 2-6 m stratum (Fig. 2-6). Temperatures in these waters were also similar in both basins, ranging between 16.8-23.6 °C, well above those associated with fish distributions during treatment years. DO profiles were also similar in both basins, with the water being anoxic at depths deeper than 6 m; DO concentrations dropped from 2.7 mg·L^{-1} at 5 m to 0.7 mg·L^{-1} at 6 m in the treated basin, and from 1.5 mg·L^{-1} at 5 m to 0.5 mg·L^{-1} at 6 m in the reference basin (Fig. 2-6).

Nocturnal metalimnetic oxygen minimum

A nocturnal DO minimum (negative heterograde curve) occurred between 5-11 m in both basins of Amisk Lake on July 11, 1990 (Appendix A, Table 6-1). This hypoxic zone included the metalimnion and top of the hypolimnion. The metalimnetic hypoxia persisted in the reference basin and became more severe by August 23, but was absent in the treated basin (Fig. 2-3). DO concentrations within this hypoxic zone in the reference basin ranged between 1.2-1.3 and 0.8-1.3 mg·L^{-1} on August 11 and 23, respectively. DO concentrations within the corresponding water stratum of the treated basin ranged between 2.7-5.8 and 2.9-8.3 mg·L^{-1} on August 11 and 23, respectively. Daytime measurements did not reveal any DO minimum in the metalimnion of either basin from July through August.

During the period of the negative heterograde oxygen profile, fish in the reference basin exhibited a bimodal vertical distribution, with one mode in the epilimnion, separated from a [illegible] smaller mode in the upper part of the hypolimnion by a zone of fewer fish. This z[illegible]ion corresponded to the metalimnetic hypoxic zone (Fig. 2-3). Tempe[illegible] DO concentrations in the intermediate zone were 12.7°C and 1.3 mg·L^{-1} on August 11 and 13.5°C and 0.9 mg·L^{-1} on August 23, respectively. These DO concentrations are similar to those associated with maximum depth distributions of cisco in both basins whereas the temperatures were similar to MDTs in 1989. The proportion of cisco constituting the hypolimnetic mode decreased with increasing severity of the oxygen minimum. On August 11, 70% of the cisco population in the reference basin was distributed in water shallower than 7 m, but on August 23, this proportion increased to > 80%. In contrast, most fish in the treated basin were at deeper depths where DO concentration remained ≥ 1.3 mg·L^{-1} (Fig. 2-3). This pattern was evident also in gill net catches (Fig. 2-3). Due to the presence of the second mode in deeper water, there was little difference in maximum depths occupied by cisco in the two basins during August (Fig. 2-3). After the metalimnetic oxygen minimum disappeared in September, maximum depths became deeper in the treated than in the reference basin (Table 2-1; Fig. 2-3).

Interaction of temperature and DO

To examine the interactive effect of temperature and oxygen on cisco distributions in Amisk Lake, I considered the mean late summer (last week of July through September) MDTs and MDDOs as indices of the population preferred temperatures and oxygen concentrations, respectively. I compared MDTs and MDDOs between basins in each year, and within and between basins, between years with the standard *t*-test. I used standard deviation (±SD) as the measure of variability around the mean MDTs and MDDOs to make my results comparable to previous studies (Magnuson et al. 1979; Rudstam and Magnuson 1985).

In 1989, there was no significant difference ($P = 0.17$) between mean MDDOs in the treated (2.9 ± 0.6 mg·L^{-1}, n = 4) and reference (2.4 ± 0.5 mg·L^{-1}; n = 4) basins (Table 2-3). Corresponding mean MDTs were also not significantly different ($P = 0.60$) between basins (treated: 11.4 ± 2.0°C; reference: 12.2 ± 2.5°C). However, in 1990, mean MDTs were significantly higher ($P = 0.03$) in the reference basin (14.7 ± 1.9°C; n = 4) than in the treated basin (11.9 ± 0.5°C; n = 4). In spite of the differences in depth and temperature ranges between basins, corresponding MDDOs were similar ($P = 0.88$) in the treated (3.4 ± 0.6 mg·L^{-1}) and reference (3.3 ± 2.5 mg·L^{-1}) basins. Because the MDDOs did not differ either between basins or between years I calculated a preferred DO as the pooled mean for both years. However, because MDTs between the two basins were similar only in 1989, I calculated a preferred temperature as the pooled mean MDT in 1989 and compared MDTs in 1990 with this value using a one-sample *t*-test

DO concentrations associated with maximum depths, and with fish in the hypoxic metalimnion, were also considered as indices of avoidance oxygen concentrations (lower threshold). Due to the dependence of lower threshold DO concentration on temperature (Stewart et al. 1967), I used only DO concentrations that had associated temperatures within ±1 SD of my preferred temperature for calculating an avoidance oxygen concentration (Table 2-1). Further, because fish make rare excursions into extreme thermal and oxygen conditions, and because such rare events can influence average values, averages may not be appropriate as avoidance indices (Stewart et al. 1967; Magnuson et al. 1979); therefore, I calculated avoidance oxygen as the median of the lower threshold DO concentrations.

With the preceding criteria, cisco in Amisk Lake displayed a preferred DO concentration and temperature of 3.0 ± 1.3 $mg \cdot L^{-1}$ (n = 16) and 11.8 ± 2.1°C (n = 8), respectively. Avoidance DO concentration within the preferred temperature range was 1.3 $mg \cdot L^{-1}$ (n = 10). The mean MDT in the treated basin (11.9 ± 0.5°C) in 1990 was similar ($P = 0.41$) to the preferred temperature (from 1989) but the mean MDT from the reference basin in 1990 (14.7 ± 1.9) was significantly higher ($P = 0.03$) than the preferred temperature.

Predicted fish distributions from models

The RMM predicted the general seasonal trend in which depth distributions of cisco decreased after thermal stratification in all three basins (Fig. 2-2, 2-3 and 2-5). The model also predicted the observed bimodal fish distributions related to the metalimnetic hypoxia in the reference basin of Amisk Lake during August 1990 (Fig. 2-3). Despite its ability to predict the general seasonal trend observed, the RMM was less successful in predicting the details of vertical distributions on specific sampling dates. In most cases, the best fits between predicted and observed distributions were realized with a preferred temperature within ±1.5°C of 12°C. The significant differences between RMM predictions and field observations (Table 2-5) were due to cisco occupying deeper depths and with lower DO concentrations than those suggested by the model.

In the two basins of Amisk Lake, overlaps between observed fish distributions and predicted fish distributions from the RMM were generally higher than overlaps between observed fish distributions and fish distributions obtained from the UDM (Table 2-5); this trend was stronger in the reference basin (*P* = 0.004, n = 13) than in the treated basin (*P* = 0.09, n = 13). In Baptiste Lake, overlaps between observed fish distributions and predicted fish distributions from the RMM were not significantly different (*P* = 0.12; n = 5) from overlaps between observed fish distributions and fish distributions from UDM (Table 2-5), but this statistical similarity is more likely an artifact of the small sample size and may underestimate biological implications. From July through September when the hypolimnion was anoxic, overlaps from the RMM were clearly higher than those from the UDM (Table 2-5).

Discussion

Oxygenation and vertical distribution of fish

Hypolimnetic oxygen injection resulted in an expansion of deep-water fish habitat in the treated basin of Amisk Lake during the summers of 1989 and 1990. Although late summer hypolimnetic DO concentration in both basins dropped below prestratification concentrations in both years, oxygen injection reduced the rate of decrease in the treated basin, resulting in deeper distributions of fish. Both maximum and median depth distributions of cisco, which were similar in both basins in early summer, became shallower in the reference basin in concert with hypolimnetic oxygen depletion. The deeper median depth distributions of fish in the reference basin on August 23, 1989 may be due to the availability of adequate DO concentration and temperature (within preferred ranges) throughout most of the upper hypolimnion (Fig. 2-2). However, even on this date, maximum depths remained deeper in the treated basin than in the reference basin.

Vertical distributions of fish during the post-treatment survey in 1994, compared with distributions during 1989-1990, indicate that in addition to the deeper expansion of hypolimnetic habitat in the treated basin than in the reference basin, oxygenation resulted in expansion of whole-lake summer habitat for cisco. Maximum depth distributions of fish in summer were deeper during treatment years than in 1994, ranging between 17-23 m and 13-19 m in the treated and reference basins respectively, for the 1989-1990 treatment period compared with 5-6 m in the two basins during 1994. In August 1994, anoxic water precluded fish distributions below 6 m in both basins, and fish were largely restricted to epilimnetic waters at temperatures well above the preferred range. In contrast, high DO concentrations enabled fish to distribute into midwater in both basins during treatment years; advection of oxygen-rich water from the treated basin into the reference basin resulted in higher midwater DO concentrations in both basins during treatment years compared with pretreatment years

(Lawrence et al., in press; Prepas and Burke in press), and with the post-treatment year. Thus, based on a comparison of maximum depths, potential summer habitat for fish expanded by at least 9 m in both basins, during oxygenation.

The expansion in whole-lake cisco habitat, and the deeper depth ranges occupied by cisco in the treated basin of Amisk Lake compared with the reference basin, are consistent with previous hypolimnetic aeration studies. The first North American hypolimnetic aeration experiment was carried out at Hemlock Lake, Michigan in 1970 (Fast 1973). Before aeration, the deeper water was anoxic and fish trapped at these depths were dead or moribund. During 4 mo of aeration, hypolimnetic DO concentration increased to 9 $mg{\cdot}L^{-1}$ and stocked rainbow trout (*Oncorhynchus mykiss*) were caught well into the hypolimnion. At Ottoville Quarry, Ohio, hypolimnetic DO concentrations increased to > 8 $mg{\cdot}L^{-1}$ during aeration and rainbow trout, previously stocked unsuccessfully due to an anoxic hypolimnion, survived the summer and were largely distributed in the hypolimnion (Fast et al. 1975; Overholtz et al. 1977).

Vertical distributions of fish in Baptiste Lake and in the reference basin of Amisk Lake indicated similar responses to hypolimnetic oxygen depletion, although the oxygen depletion progressed faster in Baptiste Lake than in Amisk Lake. The higher MDTs in Baptiste Lake in late summer suggested that anoxic conditions in the hypolimnion forced cisco into more stressful thermal ranges than in either basin of Amisk Lake. Again, partial treatment effects through water movement between basins could have contributed to the slower oxygen depletion rates in the reference basin of Amisk Lake than in Baptiste Lake (Prepas and Burke, in press).

The occurrence of fish in water deeper than the hypoxic metalimnion in the reference basin of Amisk Lake in August 1990 could have been due to entrapment. During hypolimnetic aeration of Lake Waccabuc, New York, Fast et al. (1975) and Garrell et al. (1978) reported the presence of an anoxic metalimnion but noted that rainbow trout stocked into the hypolimnion moved freely across the anoxic metalimnion into the epilimnion. Similarly, Serns (1976) reported that rainbow trout stocked into the hypolimnion made occasional feeding forays through an anoxic metalimnion into the epilimnion during hypolimnetic aeration. Although fish can make such occasional forays through anoxic metalimnia, restriction of fish movement as a result of hypoxic barriers is well established (Hile 1936; Rudstam and Magnuson 1985; Suthers and Gee 1986), and Fry (1937) reported hypolimnetic entrapment of cisco by a hypoxic metalimnion in Lake Nipissing, Ontario. The hypoxic metalimnion in Amisk Lake was not observed during the day, therefore cisco would have still been able to form schools below this stratum during the day. As schools dispersed at night, fish that did not swim through the metalimnion before DO decreased likely became trapped in the hypolimnion, remaining there as long as DO concentration did not decrease below the avoidance limits.

My study shows that hypolimnetic oxygenation can prevent the development of a hypoxic metalimnion that could restrict fish distributions. The development of a hypoxic metalimnion during hypolimnetic aeration was a major concern in early studies although the impact on cold-water fish distributions remained unresolved (Fast 1973; Wirth et al. 1975; Serns 1976; Garrell et al. 1978). During the aeration of Tory Lake, Ontario, Taggart (1984) observed that an anoxic and toxic (due to H_2S) metalimnion restricted crustacean zooplankton populations to the epilimnion. As a result, Taggart (1984) cautioned that by precluding zooplankton that are food resources for fish from the hypolimnion, an anoxic and toxic metalimnion may limit the effectiveness of hypolimnetic aeration for restoring and enhancing cold-water fish production. A hypoxic metalimnion confined over 70% of fish in the reference basin of Amisk Lake to the epilimnion during August 1990. In contrast, because the metalimnetic hypoxia was eliminated as a result of oxygenation, fish in the treated basin were present throughout the metalimnion and upper hypolimnion.

Influence of temperature and oxygen on fish distributions

The preferred temperature range (11.8 ± 2.1°C) I obtained for cisco in Amisk Lake is comparable to those reported for cisco and other salmonids (11.0-14.9°C) (Magnuson et al. 1979; Rudstam and Magnuson 1985). Also, my preferred DO concentration of 3.0 ± 1.30 mg·L^{-1} is within the lower and upper threshold limits of 1.9-4.4 mg·L^{-1} reported by Rudstam and Magnuson (1985). However, the avoidance DO concentration (1.3 mg·L^{-1}) for cisco in Amisk Lake appears to be lower than the 1.9 mg·L^{-1} proposed by Rudstam and Magnuson (1985). This difference in avoidance DO concentration may be due to methodological differences. Rudstam and Magnuson (1985) used mainly laboratory-determined avoidance values, but such values have been shown to be consistently higher than field values (Christie and Regier 1988).

Comparisons of overall distributions of cisco in the two basins of Amisk Lake in 1989 and 1990 provide insight into the interaction between DO concentration and thermal preferences. At DO concentrations higher than avoidance (1.3 mg·L^{-1}), the depth selected by cisco appeared to be influenced by a combination of thermal and oxygen preferences. For example, although differences in hypolimnetic DO concentration between the two basins of Amisk Lake were more pronounced in 1989 than in 1990, differences in overall patterns of fish distributions were more pronounced in 1990 than in 1989. In 1989, MDs were generally located within the 7-11 m stratum in both basins, and both temperature and DO concentration within this stratum were within preferred ranges in each basin. Temperatures in the 7-11 m stratum were again within the preferred ranges in both basins in 1990 but due to the hypoxic metalimnion in the reference basin, preferred DO concentrations were available only at shallower depths, which were at higher than preferred temperatures. Thus, to obtain the preferred DO concentration in 1990, fish in the reference basin were forced into shallower water at higher and probably more stressful temperatures.

During periods of thermal stratification, hypolimnetic temperatures in the treated basin were within the preferred ranges for cisco, but 3-5°C higher than those in the reference basin. These differences in hypolimnetic temperatures could potentially have led to differences in depth distributions of fish independent of DO concentration. However, my results indicated that within their preferred temperature ranges (9.7-13.9°C), cisco selected a preferred DO concentration range (1.7-4.3 $mg{\cdot}L^{-1}$). Combinations of preferred DO concentrations and temperatures occurred at depths of 7-13 m in the treated basin; therefore, even if preferred temperatures extended throughout the hypolimnion of the treated basin, most of the fish would have been expected to distribute within the 7-13 m stratum instead of at deeper depths, where DO was barely above avoidance concentrations. This expectation seems reasonable since oxygen uptake at avoidance DO concentration (for a given temperature) will be sufficient only to maintain standard metabolism (Stewart et al. 1967; Magnuson et al. 1979); it would have been bioenergetically more costly for cisco in the treated basin to have occupied depths deeper than 13 m. Therefore, the influence of the higher hypolimnetic temperatures in the treated basin on fish distributions relative to the reference basin should have been minimal.

Cisco inhabited water with a lower DO concentration but higher temperature in Amisk Lake than assumed in the RMM, or observed in several northern Wisconsin lakes (Rudstam and Magnuson 1985). In Trout Lake, Wisconsin, larger cisco were concentrated in deep water, at temperatures close to 6°C. Crowder and Magnuson (1982) argued that slow growing, food-limited populations may choose a lower temperature than the "preferred" to optimize growth rates (see also Rudstam and Magnuson 1985). The higher temperatures chosen by the cisco populations in both Amisk and Baptiste lakes is consistent with the faster growth rates of these populations (see Chapter 4), compared with the cisco in Wisconsin lakes.

Although the RMM was less successful in predicting fish densities at specific depths, the differences in overlap indices between the RMM and UDM for the two basins of Amisk Lake emphasize the importance of the interactive effect of temperature and oxygen on vertical distributions of fish. The null hypothesis of the UDM was that temperature and oxygen have no limiting effects on fish distributions. This implies fish densities should be uniform throughout the water column. But because fish distributions were influenced by temperature and oxygen gradients, overlaps of observed distributions were lower with the UDM than with the RMM. Predictions from the RMM were based on fish responses to temperature and oxygen gradients, hence the higher overlap indices. Further, differences between the RMM and UDM overlap indices were more pronounced in the reference basin than in the treated basin, suggesting that the depth distributions of fish were more restricted by temperature and oxygen in the reference basin than in the treated basin.

The selection of preferred temperature and DO concentration ranges by cisco may limit the success of hypolimnetic oxygenation experiments. Thermal and oxygen stratification of the water column can be viewed as presenting a coarse-grained environment to fish with habitat patches of varying qualities. Akin to a consumable resource, the water stratum with a complement of preferred temperature and DO concentration is likely the most profitable patch. Because DO was above avoidance concentrations and temperatures were also largely within the preferred range, the hypolimnion of the treated basin could be considered as having presented a good quality habitat in which fish could distribute freely. However, elevating oxygen in the lower hypolimnion only to concentrations barely above those avoided by cisco was not enough to ensure the use of this habitat patch by fish. Even in the treated basin, fish were often most abundant (encompassing the 25-75 percentiles) within the 7-17 m stratum, the depth stratum within which both temperature and DO concentration were within preferred ranges. Thus, these preferred ranges of temperature and DO, and the distributions of temperature and DO expected in the environment during treatment, are key variables that should be considered during oxygenation experiments.

Results of the Amisk Lake study indicate that hypolimnetic oxygenation can be used to expand potential habitat for cold-water fish in thermally stratified eutrophic lakes; full realization of this potential habitat may, however, be dependent on the availability of preferred DO concentrations and temperatures. In addition, hypolimnetic oxygenation can prevent the development of a hypoxic metalimnion that could restrict fish distributions.

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Table 2-1. Maximum depth distributions of cisco in Amisk Lake during late summer, 1989 and 1990, and associated temperatures and dissolved oxygen concentrations.

Year	Date	Maximum depth (m)		Temperature (°C)		Dissolved oxygen (mg·L^{-1})	
		Treated basin	Reference basin	Treated basin	Reference basin	Treated basin	Reference basin
1989	July 26	21	15	8.1	7.4	3.0	2.1
	Aug. 9	17	15	9.3	8.5	1.8	1.3
	Aug. 23	21	15	9.3	8.5	2.1	1.2
	Sep. 23	17	13	11.2	10.8	2.3	1.9
1990	July 25	21	21	9.6	5.8	3.2	2.1
	Aug. 11	19	19	10.4	6.4	1.8	1.8
	Aug. 23	19	17	10.5	6.1	1.3	1.2
	Sep. 15	15	11	11.5	11.9	1.2	0.9
	Sep. 26	21	13	11.7	11.6	1.8	0.8

Table 2-2. Median, and 25-75 percentile depth distributions of cisco in the treated and reference basins of Amisk Lake, July-September 1989, and May-September 1990, using hydroacoustics (H) and vertical gill net (G) methods. Indicated are results of median tests (χ^2) and of Komolgorov-Smirnov two-sample tests (D) of overall distributions between the two basins. Depths are mid-points of 2-m depth intervals. N for acoustic data is total number of fish in the depth intervals corrected for beam angle, number of pings recorded and total distance surveyed; for gill net, N is total number of fish caught corrected for net selectivity.

			Median depth (m)		25-75 percentile depth (m)				N	
Year	Date	Gear	Treated basin	Reference basin	Treated basin	Reference basin	χ^2	D	Treated basin	Reference basin
1989	July 26	H	11	11	11-13	9-11	3.27^{ns}	0.16^{*}	451	88
	Aug. 9	H	9	9	7-11	7-11	0.06^{ns}	0.05^{ns}	232	77
	Aug. 23	H	7	9	5-9	7-11	26.73^{***}	0.43^{**}	72	63
	Sep. 23	H	11	9	9-11	7-11	12.27^{***}	0.23^{**}	236	237
1990	May 23	H	11	11	7-11	7-15	0.06^{ns}	0.07^{ns}	196	192
		G	--	--	--	--	--	--	--	--
	June 5	H	7	7	5-11	5-13	0.11^{ns}	0.21^{ns}	104	373
		G	9	7	5-11	5-13	--	0.21^{ns}	40	24
	June 20	H	13	11	9-15	9-15	0.52^{ns}	0.10^{ns}	754	596
		G	13	7	9-17	7-11	--	0.36^{*}	87	24
	July 11	H	13	9	7-15	5-13	3.85^{ns}	0.01^{*}	1816	2405
		G	11	11	7-15	7-13	--	0.19^{ns}	46	63
	July 25	H	7	7	5-11	5-11	0.11^{ns}	0.19^{*}	3718	2138
		G	11	11	9-15	7-13	--	0.37^{**}	78	114
	Aug. 11	H	9	5	7-13	5-7	14.43^{***}	0.34^{**}	1398	1611
		G	9	11	7-11	13-15	--	0.41^{**}	115	66
	Aug. 23	H	9	7	5-11	5-7	20.83^{***}	0.38^{**}	1034	841
		G	11	5	9-13	5	--	0.75^{**}	83	61
	Sep. 15	H	11	9	11-13	7-9	62.77^{***}	0.63^{**}	3724	1120
		G	--	--	--	--	--	--	--	--
	Sep. 26	H	13	11	11-17	9-13	39.20^{***}	0.51^{**}	8098	1904
		G	17	--	11-23	--	--	--	1155	--

ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Table 2-3. Dissolved oxygen concentrations and temperatures corresponding to median depths and the 25-75 percentile depth distributions of cisco in Amisk Lake, July-September 1989, and May-September 1990.

		Dissolved oxygen (mg·L^{-1})				Temperature (°C)			
		Median		25-75 percentile		Median		25-75 percentile	
Year	Date	Treated basin	Reference basin	Treated basin	Reference basin	Treated basin	Reference basin	Treated basin	Reference basin
1989	July 26	3.3	2.6	3.7-3.9	2.6-2.9	9.1	15.9	10.6-13.7	10.1-17.3
	Aug. 9	3.3	1.9	3.1-4.0	1.8-2.8	10.3	10.8	9.7-12.6	9.9-13.[illegible]
	Aug. 23	2.1	2.0	1.9-7.5	1.9-2.4	12.7	11.1	10.5-18.2	13.2-16.4
	Sep. 23	3.0	2.9	2.8-3.0	1.7-9.6	13.3	11.1	11.8-13.4	11.5-15.2
1990	May 23	9.6	8.6	9.5-11.9	[illegible]-10.5	6.7	6.9	6.1-9.3	5.8-8.4
	June 5	9.5	8.6	8.5-12.1	[illegible]-11.9	10.0	9	7.7-13.9	6.4-14.8
	June 20	7.3	6.9	7.2-8.3	6.0-7.3	8.4	8.3	6.2-9.5	6.7-9.6
	July 11	5.7	5.0	5.3-5.6	4.7-5.8	9.6	10.7	9.3-13.8	8.6-14.8
	July 25	4.8	3.2	2.9-4.0	3.2-3.3	11.6	12.5	10.6-13.7	10.0-15.9
	Aug. 11	2.8	1.4	2.7-4.6	1.4-3.6	11.2	17.3	10.6-13.4	12.6-17.3
	Aug. 23	4.1	0.9	3.2-8.2	0.9-2.4	11.8	14.5	11.2-19.2	14.5-16.4
	Sep. 15	2.9	5.9	2.1-2.9	5.9-9.2	12.1	14	11.7-12.1	14.0-15.0
	Sep. 26	3.9	5.1	1.8-5.1	0.7-8.0	12.3	12.8	11.9-12.6	11.0-13.5

Table 2-4. Median depths, and 25-75 percentile depth distributions of cisco determined from hydroacoustics (Acoustic) and vertical gill nets (VGN) in Baptiste Lake, May-September 1990. Indicated are dissolved oxygen concentrations and temperatures corresponding to the hydroacoustic data. Depths are mid-points of 2-m depth intervals.

Date	Median depth (m)		25-75 percentile range (m)		N		Dissolved oxygen ($mg \cdot L^{-1}$)		Temperature (°C)	
	Acoustic	VGN	Acoustic	VGN	Acoustic	VGN	Median	25-75%	Median	25-75%
May 25	7	15	5-13	7-15	704	141	7.1	5.9-8.7	7.8	5.9-10.3
June 26	5	9	11	7-11	1759	90	6.3	2.9-6.3	14.4	7.0-14.4
July 30	5	7	5-7	5-9	1359	41	5.3	1.2-5.3	19.1	15.6-19.1
Aug. 28	7	7	7	5-7	2534	38	7.6	7.6	17.0	17.0
Sep. 24	9	7	7-11	5-7	2676	87	5.0	0.5-8.8	13.2	9.5-14.3

Table 2-5. Percentage overlap (O) and Komolgorov-Smirnov statistics (D) of observed vs. predicted (RMM) and, of uniform distribution tests of observed vs. uniform (UDM) distributions of cisco in Amisk (treated basin and reference basin) and Baptiste lakes.

		Amisk Lake									Baptiste Lake			
		Treated basin				Reference basin								
		RMM		UDM		RMM		UDM			RMM		UDM	
Year	Date	O	D	O	D	O	D	O	D	Date	O	D	O	D
1989	July 26	54	0.29^{**}	51	1.64^{**}	54	0.43^{**}	47	1.36^{*}		--	--	--	--
	Aug 9	72	0.13^{**}	59	1.01^{ns}	49	0.41^{**}	50	1.27^{ns}		--	--	--	--
	Aug 23	58	0.35^{**}	53	1.51^{*}	61	0.21^{**}	45	1.27^{ns}		--	--	--	-
	Sep 25	53	0.16^{**}	51	1.46^{*}	85	0.19^{**}	39	1.69^{**}		--	--	--	--
1990	May 23	49	0.50^{**}	66	0.775^{ns}	98	0.02^{ns}	66	0.91^{ns}	May 23	61	0.39^{**}	67	1.93^{**}
	June 5	80	0.16^{ns}	51	1.66^{**}	65	0.35^{**}	55	2.03^{***}		--	--	--	--
	June 20	66	0.24^{**}	69	0.64^{ns}	79	0.51^{**}	70	0.70^{ns}	June 26	48	0.26^{**}	50	2.00^{***}
	July 11	69	0.19^{**}	66	0.82^{ns}	64	0.23^{**}	58	1.12^{ns}		--	--	--	--
	July 25	56	0.44^{**}	50	1.71^{**}	49	0.49^{**}	51	2.29^{***}	July 30	67	0.21^{**}	20	2.50^{***}
	Aug 11	75	0.16^{**}	54	1.21^{ns}	48	0.46^{**}	41	2.60^{***}		--	--	--	--
	Aug 23	55	0.26^{**}	47	1.55^{*}	47	0.20^{**}	33	2.14^{***}	Aug 24	82	0.18^{**}	30	2.21^{***}
	Sep 15	43	0.56^{**}	44	2.07^{***}	73	0.23^{**}	34	2.70^{***}		--	--	--	--
	Sep 26	55	0.45^{**}	46	1.69^{**}	57	0.43^{**}	34	2.09^{***}	Sep 24	66	0.34^{**}	38	1.64^{**}

ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

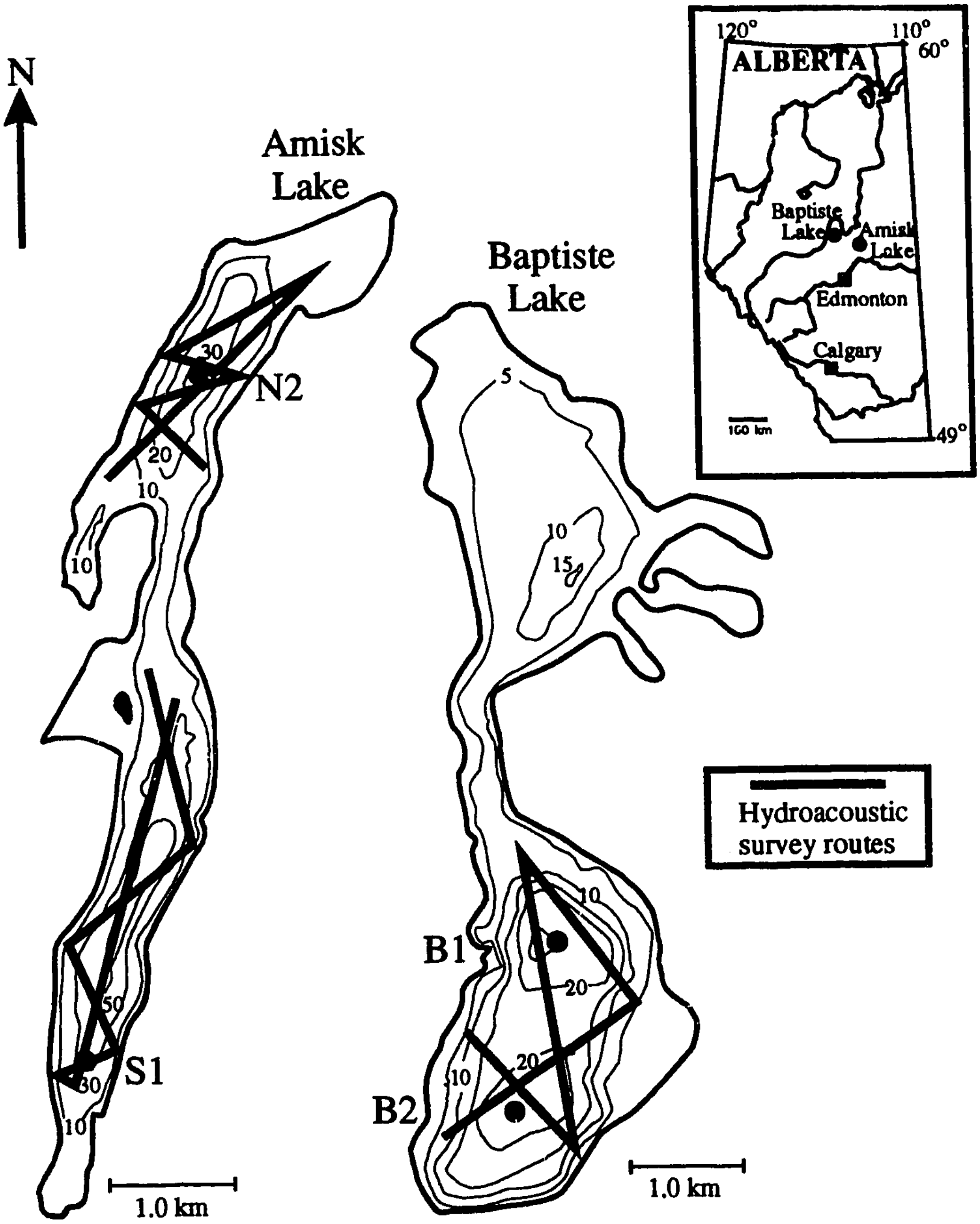


Fig. 2-1. Bathymetric map (with 10-m depth contours) of Amisk and Baptiste lakes, showing sampling sites (black circles: N2, S1, B1, B2) and hydroacoustic survey routes (heavy black lines); the oxygen diffuser was located at site N2. Insert, is map of the province of Alberta.

Fig. 2-2. Vertical distributions of cisco in Amisk Lake, July-September 1989, and associated temperature (Temp.) and dissolved oxygen (DO) profiles on each sampling date. Acoustic: distributions from hydroacoustics; Predicted: distributions predicted from the Rudstam-Magnuson (1985) model.

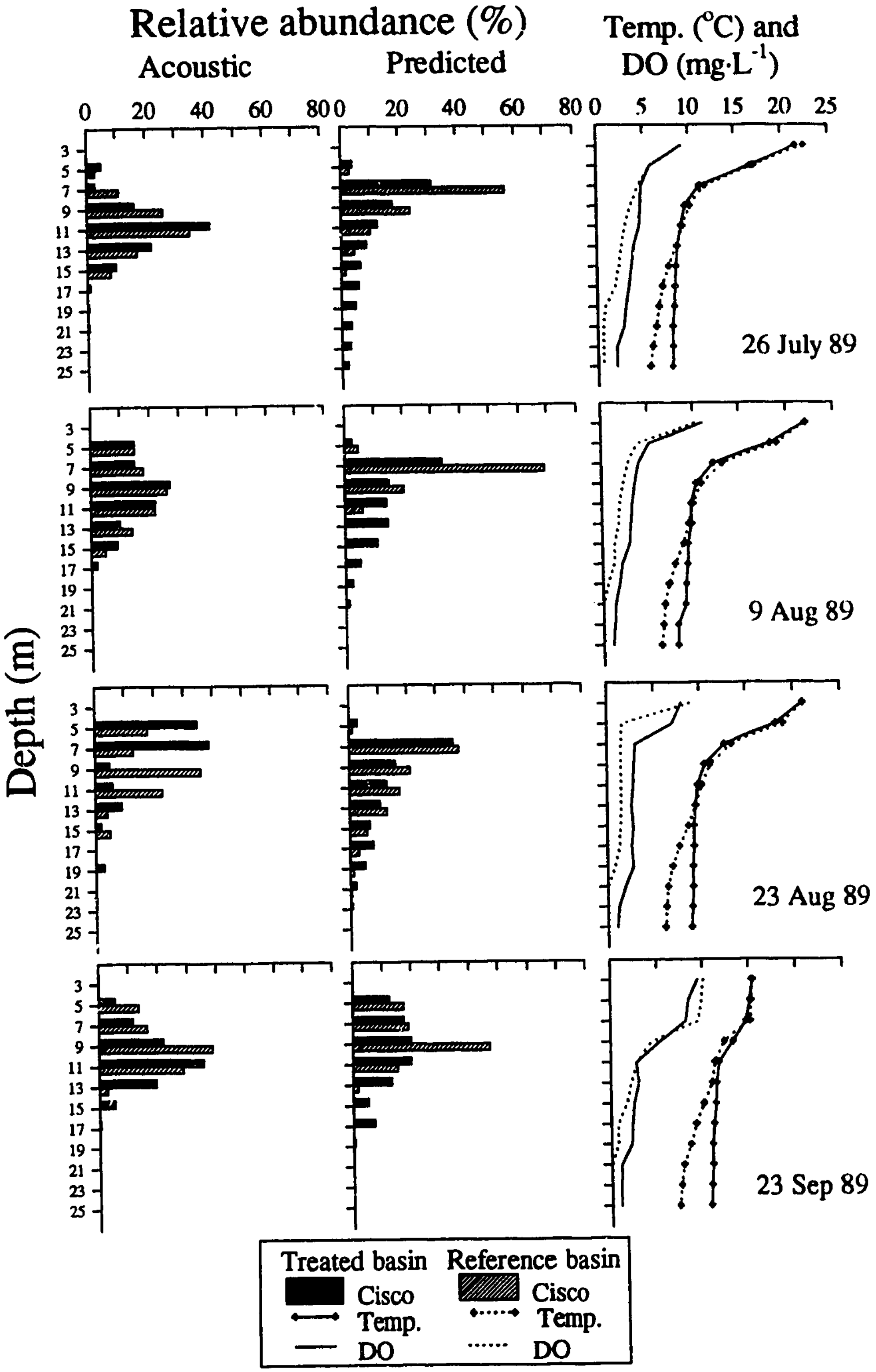

Relative abundance (%)
Acoustic
Predicted
Temp. (°C) and DO (mg·L-1)
0 20 40 60 80
0 5 10 15 20 25
Depth (m)
3 5 7 9 11 13 15 17 19 21 23 25
26 July 89
9 Aug 89
23 Aug 89
23 Sep 89
Treated basin
Reference basin
Cisco
Temp.
DO

Fig. 2-3. Vertical distributions of cisco in Amisk Lake, June-September 1990, and associated temperature (Temp.) and dissolved oxygen (DO) profiles on each sampling date. VGN: distributions from vertical gill nets; Acoustic: distributions from hydroacoustics; Predicted: distributions predicted from the Rudstam-Magnuson (1985) model.

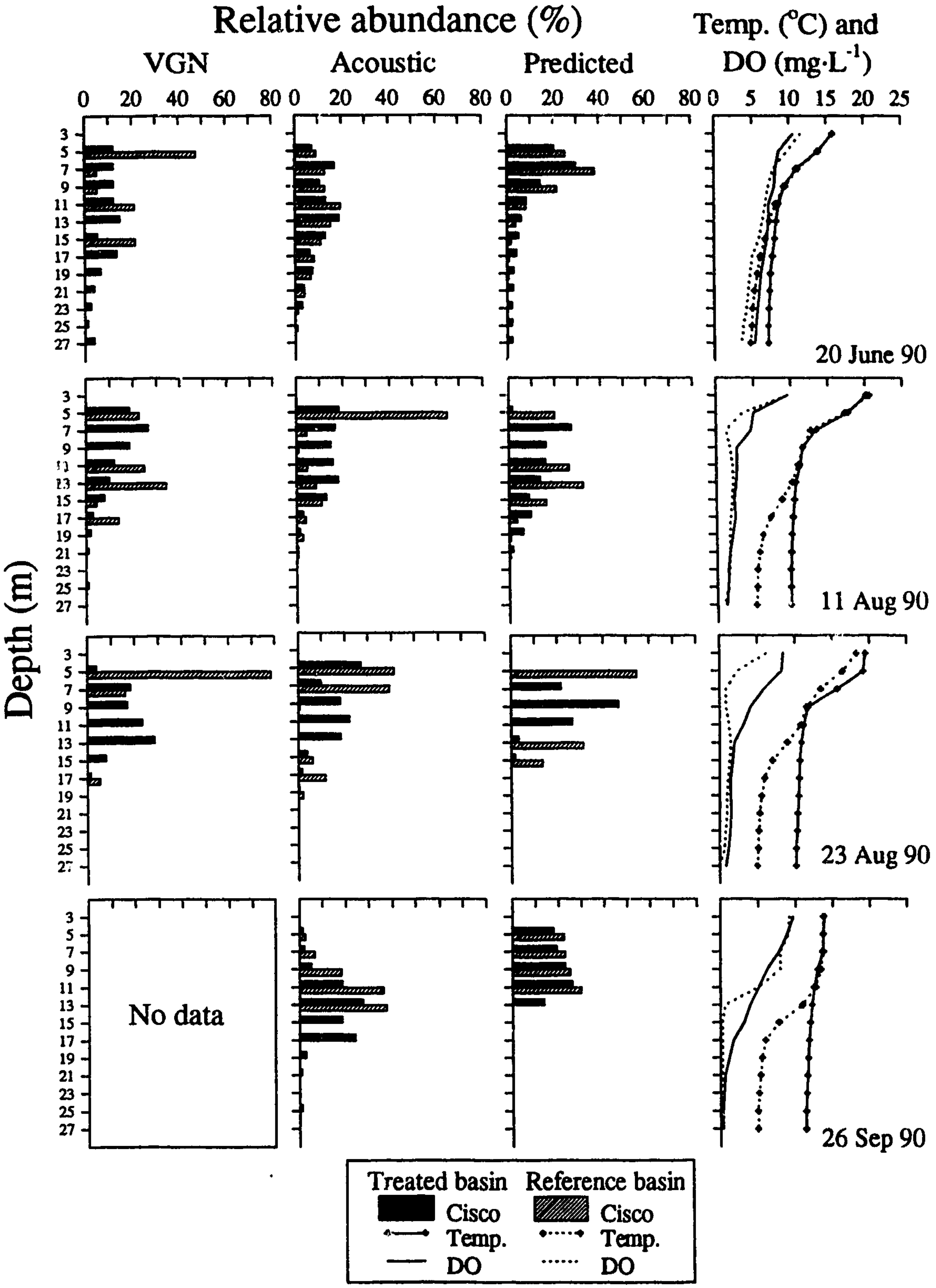

Relative abundance (%)
Temp. (°C) and DO (mg·L⁻¹)
VGN
Acoustic
Predicted
0 20 40 60 80
0 5 10 15 20 25
Depth (m)
3 5 7 9 11 13 15 17 19 21 23 25 27
20 June 90
11 Aug 90
23 Aug 90
26 Sep 90
No data
Treated basin
Reference basin
Cisco
Temp.
DO

Fig. 2-4. Length-frequency distributions of cisco summarized from all gill net catches (corrected for net selectivity) for Amisk (1989, 1990) and Baptiste (1990) lakes. Also shown (panel D) is an example of the distribution of hydroacoustic (Acoustic) estimates of fish size in target strengths (TS) ≥ -46 dB from Amisk Lake (north basin) on July 25, 1989. Top axis of panel D represents lower limits of approximate total lengths corresponding to particular target strengths (mm).

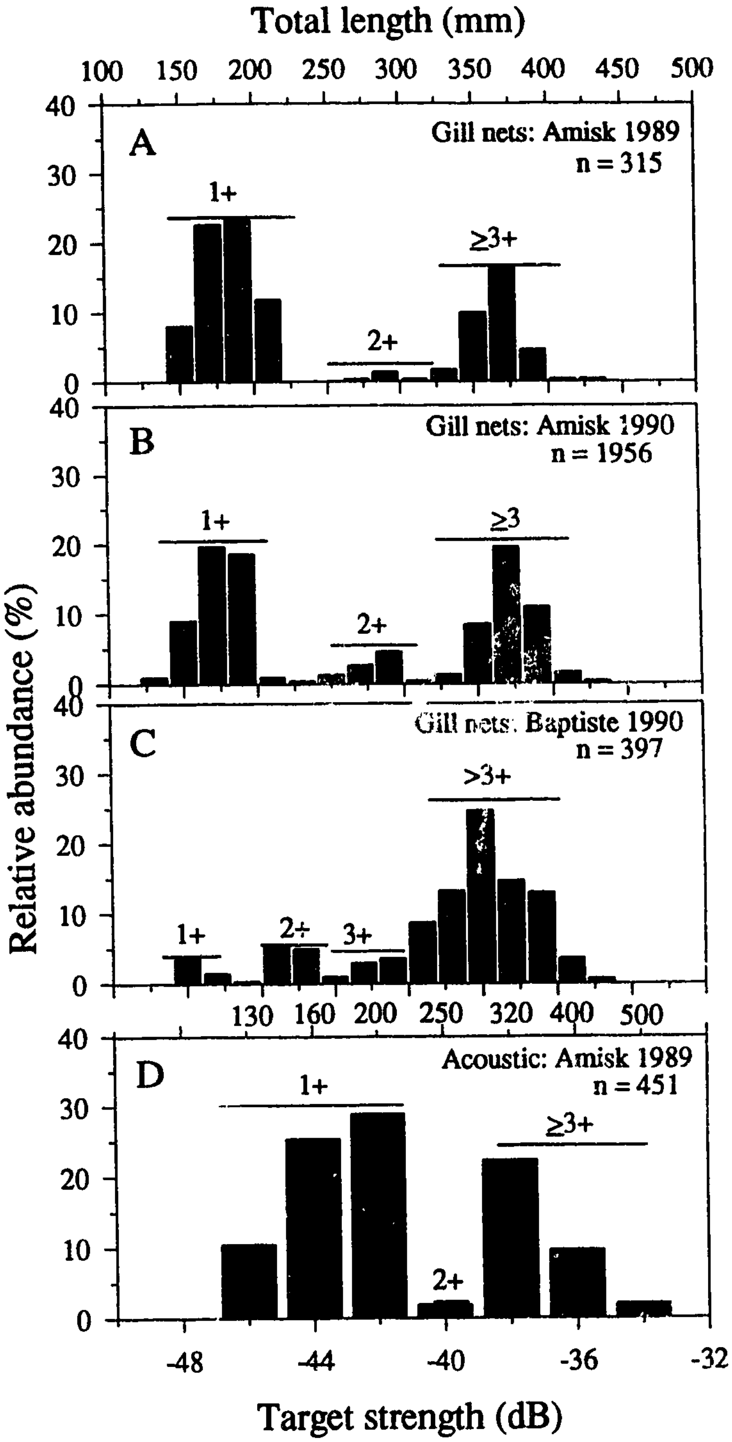
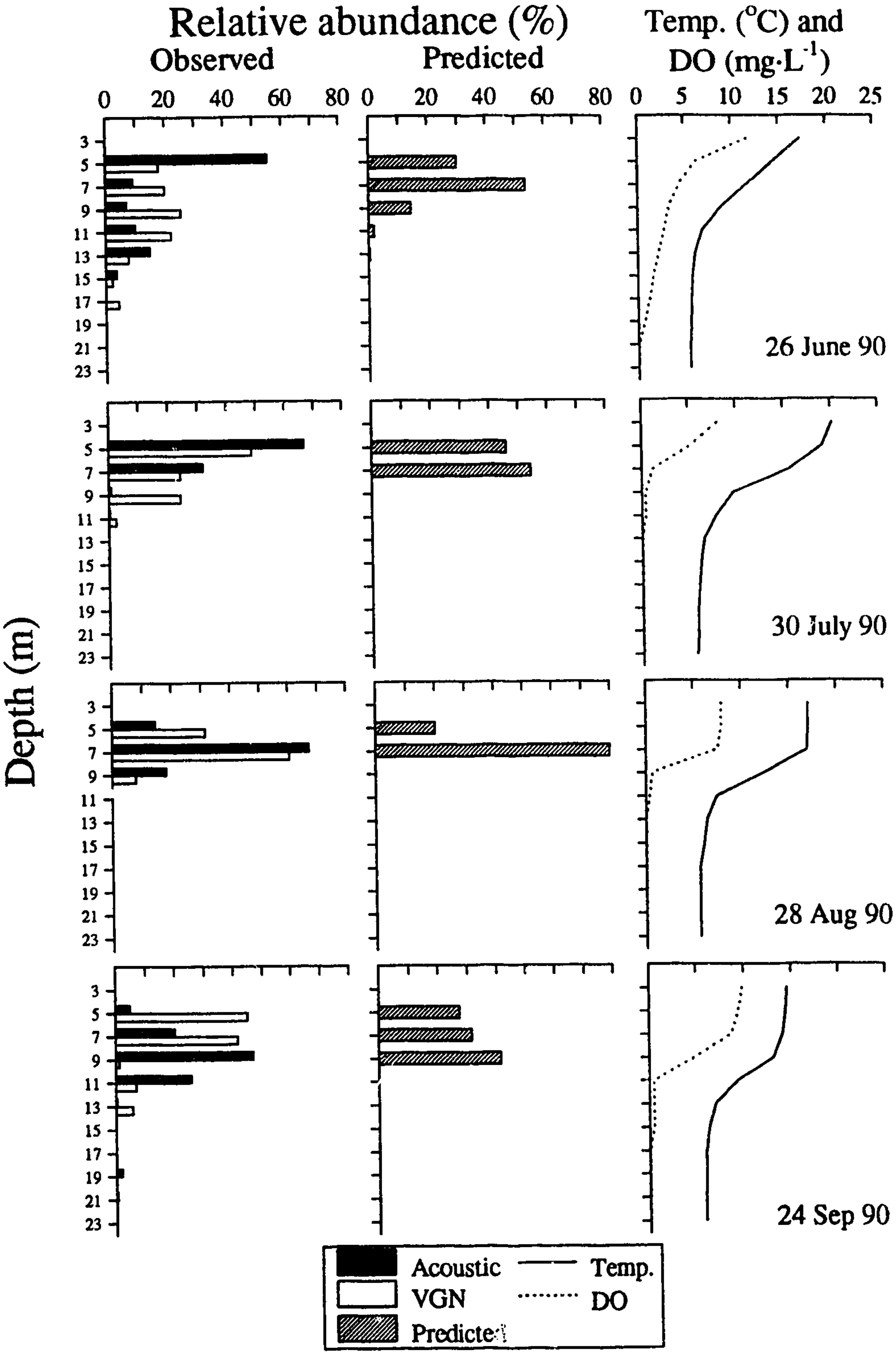

Total length (mm)
100 150 200 250 300 350 400 450 500
A
Gill nets: Amisk 1989
n = 315
1+
2+
≥3+
B
Gill nets: Amisk 1990
n = 1956
1+
2+
≥3
C
Gill nets: Baptiste 1990
n = 397
1+
2+
3+
>3+
130 160 200 250 320 400 500
D
Acoustic: Amisk 1989
n = 451
1+
2+
≥3+
Relative abundance (%)
0 10 20 30 40
-48 -44 -40 -36 -32
Target strength (dB)

Fig. 2-5. Vertical distributions of cisco in Baptiste Lake, June-September 1990, and associated temperature (Temp.) and dissolved oxygen (DO) profiles on each sampling date. Observed: distributions from vertical gill nets (VGN) and hydroacoustics (Acoustic); Predicted: distributions predicted from the Rudstam-Magnuson (1985) model.


Relative abundance (%)
Observed
Predicted
Temp. (°C) and
DO (mg·L⁻¹)
0 20 40 60 80
0 20 40 60 80
0 5 10 15 20 25
Depth (m)
3 5 7 9 11 13 15 17 19 21 23
26 June 90
30 July 90
28 Aug 90
24 Sep 90
Acoustic
VGN
Predicted
Temp.
DO

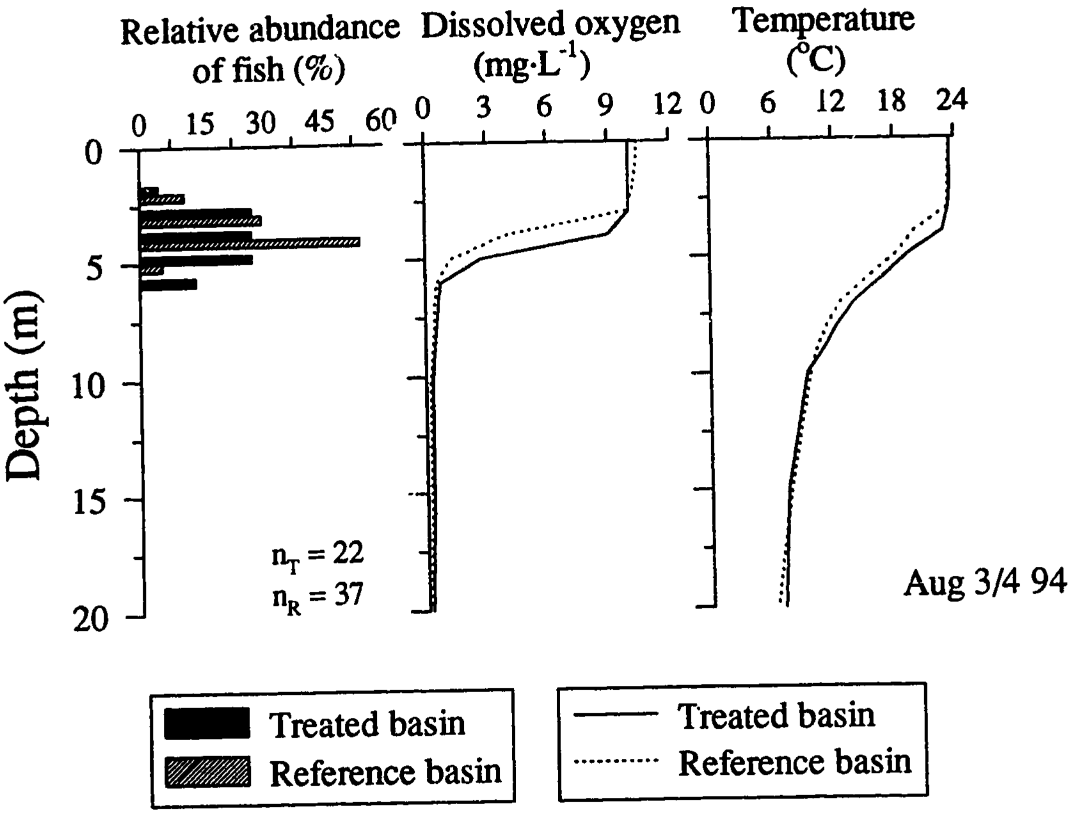


Fig. 2-6. Vertical distributions of cisco, temperature, and dissolved oxygen concentrations in the treated and reference basins of Amisk Lake on August 3/4, 1994. n_T and n_R represent sample sizes in the treated and reference basins, respectively.

Chapter 3

Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco (*Coregonus artedi*) in Amisk Lake, Alberta

A version of this chapter will be submitted for publication, as a manuscript co-authored with William M. Tonn.

Introduction

The cisco (*Coregonus artedi*) is a deep-water salmonid that prefers well-oxygenated, cool hypolimnia of north temperate lakes (Hile 1936; Fry 1937; Frey 1955). However, when they occur in deep eutrophic lakes, hypolimnetic anoxia during summer stratification can force cisco out of the hypolimnion into the metalimnion; high temperatures preclude them from the epilimnion (Fry 1937; Frey 1955). For the zooplanktivorous cisco, this "oxygen-temperature squeeze" of their habitat (Coutant 1985) can drastically reduce the lake volume available for foraging (Fast 1973; Engel 1976; Taggart 1984; Rudstam and Trapp 1987). Although their distributions are also limited vertically in deep eutrophic lakes during periods of thermal stratification (Fast 1971; Engel 1976; Taggart 1984), zooplankton are generally eurythermal and tolerate lower dissolved oxygen (DO) concentrations than cisco. Therefore, both the warm epilimnion and hypoxic hypolimnion can provide refuges against cold-water fish planktivores in these lakes (Herbert 1954; Fast 1971; Pennak 1978).

Beginning in the 1970s, aquatic ecologists have used injection of pure oxygen to artificially increase hypolimnetic oxygen concentrations and to create habitat suitable for year-round survival of fish and their prey organisms (Fast and Overholtz 1975; Overholtz et al. 1977). Hypolimnetic oxygenation is an efficient technique for expanding habitat for cold-water fish in deep eutrophic lakes because it allows for oxygenation of deep waters with minimal alteration to the thermal structure of the water column (Fast 1973; McQueen and Lean 1986; Ashley 1988). In addition to ensuring year-round fish habitat, improved hypolimnetic conditions will result in the restoration or creation of habitat suitable for the invertebrate prey of fish; abundance and biomass of hypolimnetic zooplankton and zoobenthos populations have been observed to increase during hypolimnetic aeration (Fast 1971, 1973; Pastorok et al. 1980).

Although the success of hypolimnetic oxygenation in enhancing cold-water fish populations will be influenced by the availability of prey within the hypolimnion (Taggart 1984), studies that evaluated both fish diet and prey distributions during oxygenation are rare. Of the few studies that described fish diet (Fast 1973; Garrell et al. 1978; Taggart 1984), no quantitative data were presented, neither were comparisons made with untreated nor reference systems.

In the present study, I examined the effects of hypolimnetic oxygenation in Amisk Lake, Alberta on the invertebrate prey and feeding ecology of cisco, which is the dominant cold-water fish in the lake (Aku et al., in press). One basin of this double-basined lake was oxygenated from June 1988 through October 1993 whereas the second basin served as a reference. A major goal of the experiment was to maintain DO concentrations above 2 $mg \cdot L^{-1}$ year-round throughout the water column of the treated basin, and thereby enhance cold-water fish and invertebrate habitat (Prepas and Burke, in press). Here, I compare fish diet composition with zooplankton composition and vertical distributions between the treated and reference basins during the summers of 1989 and 1992. I expected that the improvement of hypolimnetic conditions for both cisco and their prey would enable cisco in the treated basin to feed deeper into the hypolimnion, and incorporate more hypolimnetic prey species in their diets than those in the reference basin.

Methods

Detailed descriptions of the study area and fish sampling procedures are presented in Prepas (1990) and Chapter 2 therefore, only a summary is provided here.

Study area

Amisk Lake (54° 35'N, 112° 37'W) is a naturally eutrophic lake in central Alberta, Canada (Fig. 3-1). It has two basins, a shallower north basin ($A_o = 2.33$ km^2, $Z_{max} = 34$ m), connected by a narrows (sill depth = 11 m) to a deeper south basin ($A_o = 2.82$ km^2, $Z_{max} = 60$ m). Historically, both basins stratified in the summer, with thermoclines located within the 5-10 m stratum (Prepas 1990). High oxygen consumption rates, coupled with incomplete mixing during spring and fall turnovers, have led to severe hypolimnetic hypoxia in both basins (Prepas 1990).

Injection of pure, liquid oxygen into the hypolimnion of the north basin of the lake started in June 1988 and continued year-round through to October 1993. The rate (mean ± SE) of oxygen injection ranged from 0.61 ± 0.03 to 1.3 ± 0.03 $t \cdot d^{-1}$ and 0.50 ± 0.01 to 0.57 ± 0.04 $t \cdot d^{-1}$ during thermally stratified and mixed periods, respectively (Prepas and Burke, in press). The south basin was not treated and served as a reference basin.

Fish sampling

In 1989, vertical distributions of fish were obtained from hydroacoustic surveys. Due to equipment malfunction only dry-chart echograms were available in 1992, therefore, I used vertical gill net catches to determine vertical distributions of fish for this year. Fish samples were collected with a set of five 3 x 30 m monofilament-nylon vertical gill nets (25, 38, 51. 76 and 102 mm stretch mesh) marked at 1-m intervals vertically. Nets were set overnight at sites N2 and S1 on successive days (Fig. 3-1), and inspected after 6-8 h on July 24-25 and August 9-10, in 1989 and monthly, from

June to September, in 1992. I used overnight sets because too few fish were caught at other times during diel surveys (morning, afternoon, dusk and dawn, and inspected after 3-5 h of setting) conducted in 1989 and 1990. Total lengths and overall depth distribution of fish were recorded in the field. When available, up to 5 fish per 1-cm length classes from each depth were stored in plastic bags over ice in coolers, and transported to the laboratory where I recorded the depth at which each fish was caught, measured total length (mm) and weight (g), removed scales and otoliths for aging, and excised stomachs. In 1989, I preserved stomachs individually in 4% buffered formalin. In 1992, stomachs were frozen individually in plastic bags.

For each basin, the total catch at each depth was corrected for net selectivity (Rudstam et al. 1984) and compiled at 2-m depth intervals. Quartile depths of vertical distributions of fish were obtained from cumulative frequency distributions of fish against depth. I used the two-sample Komolgorov-Smirnov statistic (D), corrected for large sample size (Sokal and Rohlf 1981), to compare overall vertical distributions of fish between the two basins.

Water temperature and DO profiles in 1989 were obtained from Webb (1993). In 1992, I used a calibrated HYDROLAB™ SURVEYOR II (SVR2-SU) to measure temperature and DO concentrations at 1-m intervals during each fish sampling night.

Zooplankton sampling

Zooplankton data for 1989 were obtained from Field (1993). Data were available for sites N2 and S1 in the treated and reference basins, respectively, on July 25 (same day as fish sampling) and on August 11 (one day after fish sampling). Density and species composition were determined at 2-m intervals from the surface to within 1 m of the bottom, from samples collected with a 40 L Schindler-Patalas trap fitted with a 64-μm mesh net bucket (Field 1993).

During each fish sampling night of 1992, I collected integrated zooplankton samples at two sites in each basin (N1, N2, S1, and S2; Fig. 3-1), with a 12.7-cm diameter Clark-Bumpus sampler fitted with a 64-μm mesh net, and towed vertically over four depth strata, 2-6, 6-10, 10-15, and 15-20 m, at each site. The four depth strata corresponded to the epilimnion, metalimnion, and upper and mid-hypolimnion, respectively. Maximum depth sampled was selected based on observed maximum depths of fish distributions in 1989-1991. Samples were preserved in a chilled sugar-formalin solution (Prepas 1978). For each sample, the number of individuals per taxon was estimated by counting all individuals in three 5-mL subsamples extracted with an 8-mm diameter pipette, representing 20-50 % of the total sample volume. Estimated densities were expressed as number of individuals per litre. Cladocerans and calanoid copepods were identified to species, using the taxonomic keys of Pennak (1978) and Clifford (1991), whereas the two species of cyclopoid copepods that occur in Amisk Lake, *Diacyclops bicuspidatus thomasi* and *Acanthocycolps vernalis* (Field 1993), were not separated. Cyclopoid copepods were pooled to correspond to the level of identification of stomach contents of fish, where separation of the two species was not possible due to partial digestion.

For the 1992 zooplankton data, I conducted two analyses. First, I used repeated-measures analyses of variance (ANOVA) to examine differences in mean densities of individual taxa and total mean densities of zooplankton between the two basins. For this analysis, data were pooled across the four depth strata. Second, I used two-way ANOVA to determine if densities of each species differed between basins both temporally and by water strata. For these analyses, I pooled data over the 2-6 m and 6-10 m strata, and over the 10-15 m and 15-20 m strata (i.e., above and below the thermocline) and designated them as epilimnion and hypolimnion, respectively. In both analyses, the two sampling sites in each basin were treated as replicates in comparisons between basins. Only taxa with densities $\geq 1.0 \cdot L^{-1}$ were included in analyses. As well, *Diaphanosoma* was not included in statistical analyses because it often occurred in the treated basin only. To ensure additivity of variances, Bartlett's logarithmic transformation was applied to data before analyses (Zar 1984). All statistical analyses were performed using the Statistical Analyses System (SAS Inst. Inc.1989) and, unless noted otherwise, the level of statistical significance is set at $P < 0.05$.

Gut analyses

All fish stomachs were dissected and examined for the presence or absence of food, and the weight (mg) of stomach contents was determined using a Mettler PJ300 balance. Stomach contents were suspended in sugar-formalin solution (Prepas 1978), and the total number of prey items was estimated from two or three subsamples of 1-5 mL. Identification of crustacean prey was similar as for zooplankton samples. In addition, chaoborids and chironomids were identified to genus. When food items were clearly identified as *Daphnia* but could not be identified to species, they were assigned in the same proportion as those identified. In 1992, the first 5-20 whole specimens of each taxon in each stomach were measured using a drawing tube and digitizing tablet.

As a measure of food intake, I calculated stomach fullness by expressing the weight of stomach contents as a percentage of fish weight, i.e., $g \cdot g\ fish^{-1} \times 100$ (Hyslop 1980). Diet composition was quantified as percentage composition by number, where the numbers of each prey type were expressed as proportions of the total number of prey items in each stomach (Hyslop 1980).

To determine if data for dietary analyses could be pooled, I compared diet composition between size-groups of fish within each basin. Fish samples were divided into two size categories, 13.0-24.9 and ≥ 25.0 cm total length, corresponding to age categories ≤ 2+ and ≥ 3+, respectively, based on a natural dichotomy in the population structure; total lengths of 1+ and 2+ overlap and those of ≥3+ fish overlap. Further, 3+ fish were poorly represented in the population. I then used Schoener's (1969) overlap index, O_{hj}, to compare dietary composition between the two size (age) categories:

$$O_{hj} = \left[1 - \left(\frac{1}{2} \sum_{i=1}^{n} |p_{hi} - p_{ji}| \right) \right] \times 100$$

where p_{hi} and p_{ji} are proportions of prey type i in any pair of age categories h and j. This index ranges from 0 to 100, representing no diet overlap to complete overlap, respectively. Overlap > 60% is considered to indicate biologically significant similarity between pairs (Wallace 1981; Martin 1984), therefore, I used this value as the cut-off point for pooling data.

To determine if differences existed in the presence or absence of food in stomachs of large fish compared with small fish throughout the whole lake, I pooled data across all sampling dates and compared the proportions of filled and empty stomachs in the two size categories using the log-likelihood ratio test. Gut fullness was compared between the two basins in each year, and between 1989 and 1992 for July-August period, using two-way ANOVA. Schoener's (1969) overlap index was used to compare differences in diet composition between the treated and reference basins.

I determined if prey eaten by fish reflected differences in numerical proportions of prey in the environment by comparing fish diets with zooplankton samples using Chesson's alpha (α):

$$\alpha = \frac{r_i/p_i}{\sum_{i=1}^{m} (r_i/p_i)}$$

where r_i is the proportion of prey type i in the fish's diet, p_i is the proportion of prey type i in the environment (2-20-m stratum), and m is the number of different prey types in the environment. When $\alpha = 1/m$, a prey type is consumed in proportion to its abundance in the environment; larger values indicate positive selection and smaller values indicate avoidance (Chesson 1978, 1983). I evaluated prey selection for 1992 only because in 1989 zooplankton samples were collected during the day whereas fish samples were collected overnight. All zooplankton taxa encountered in the lake on a given day were included in calculating α.

Results

Zooplankton density and vertical distributions

Detailed information on zooplankton abundance and vertical distribution in 1989 is reported in Field (1993), therefore, only a summary is provided here. During the summer of 1989, the zooplankton communities in both basins were dominated numerically by three cladocerans, *Daphnia longiremis*, *Daphnia galeata mendotae*, and *Bosmina longirostris*, one calanoid copepod, *Skistodiaptomus oregonensis* and two cyclopoid copepods, *Diacyclops bicuspidatus thomasi* and *Acanthocycolps vernalis*. Rare taxa included *Diaphanosoma leuchtenbergianum*, *Leptodora kindtii*, and *Chaoborus* spp. During periods of thermal stratification, *D. g. mendotae*, *Skistodiaptomus* and *Acanthocycolps* resided primarily in the epilimnion whereas *D. longiremis* and *Bosmina* were most abundant in the hypolimnion. *Diacyclops* and *D pulex* were distributed across both layers. In 1989, densities of all major zooplankton taxa were higher at site N2 (treated basin) than at site S1 (reference basin), when densities over the whole water column were compared (Field 1993). However, when only the 2- to 20-m depth stratum was compared (the stratum within which fish were distributed), there were no significant differences in densities between the two sampling sites (*t*-tests) although for most species densities were generally higher at site S1 than at site N2 (Fig. 3-2).

From June through September, in 1992, species composition of the zooplankton communities in both basins were similar to those in 1989 but numerical proportions differed. In 1992, cyclopoid copepods dominated the community in all months, and were twice as abundant as any other taxa (Fig. 3-2). *Leptodora* and *D. pulex* were encountered but their densities were usually $< 1.0 \cdot L^{-1}$. *D. pulex* was encountered in the treated basin from June through August and disappeared thereafter, whereas it occurred in the reference basin from July through September. *Diaphanosoma* was present mainly in the reference basin, attaining a peak density in

August (Fig. 3-2).

Precision was high for the sub-sampling procedure used to estimate zooplankton densities; median CV for thirty of such 3-replicate counts was 8.2 % (range: 1.7-19.7 %). Total zooplankton densities were significantly higher in the reference basin than in treated basin, largely due to cyclopoid copepods, but decreased in a similar pattern between June and September in both basins (Table 3-1; Fig. 3-2). Densities of individual taxa generally varied in similar patterns in both basins over the summer; densities of Cyclopoida, *D. longiremis*, *D. g. mendotae*, and *Bosmina* decreased from July through September whereas *Skistodiaptomus* attained peak densities in August (Table 3-1; Fig. 3-2). Only Cyclopoida and *Skistodiaptomus* dominated zooplankton samples in September; populations of all other taxa collapsed. Although differences in densities between the two basins were not always significant, densities of most zooplankton species except *Bosmina* (the smallest species) were typically higher in the reference than in the treated basin (Fig. 3-2).

With the exception of *Bosmina* on June 23, vertical distribution patterns were similar for all species in both basins (Table 3-2: non-significant interaction effects; Fig. 3-3). Densities of *D. g. mendotae* and *D. longiremis* during June were significantly greater in the epilimnion than in the hypolimnion, whereas *Skistodiaptomus* showed the reverse trend (Table 3-2: layer effects; Fig. 3-3). *Bosmina* was more abundant in the epilimnion than in the hypolimnion of the treated basin on June 23 but this pattern was reversed in the reference basin, and on July 22 densities were similar in both layers of both basins. Cyclopoid copepods were equally abundant in both layers all summer (Table 3-2; Fig. 3-3).

As water temperatures increased and thermal stability strengthened, *D. longiremis* descended into the hypolimnion on July 22 and August 19, whereas *D. g. mendotae* and *Skistodiaptomus* remained predominantly in the epilimnion throughout summer (Table 3-2; Fig. 3-3). When encountered in 1992, *Leptodora* and *D. pulex* typically inhabited the epilimnion and hypolimnion, respectively, and densities of *Diaphanosoma* were twice as high in the epilimnion as in the hypolimnion of the reference basin, on July 22 and August 19. Although there were no consistent patterns for *Bosmina* and *Diaphanosoma* in both basins in 1992, Field (1993) reported significantly higher densities of *Bosmina* in the hypolimnion than in the epilimnion for both basins and the converse for *Diaphanosoma* in 1989, when analyses included samples from depths deeper than the 20-m stratum sampled in 1992. Thus, based on distributions during the present study (Fig. 3-3) and in 1989 (Field 1993), *D. g. mendotae*, *Skistodiaptomus*, *Leptodora*, and *Diaphanosoma* were characterised as epilimnetic species whereas *D. longiremis*, *D. pulex* and *Bosmina* were characterised as hypolimnetic species.

Vertical distributions of fish

Data on vertical distributions of fish in 1989 are provided in Chapter 2, therefore data for 1992 only are provided here.

On all sampling dates in 1992, vertical distributions of fish differed between the two basins (Table 3-3). On June 23, when DO concentrations were high throughout most of the hypolimnion in both basins, median and upper quartile depth distributions of fish were deeper in the reference than in the treated basin. This distribution pattern changed from July through September as hypolimnetic oxygen depletion became more severe in the reference than in the treated basin (Fig. 3-4). During this period, greater proportions of fish in the treated basin occupied deeper water than those in the reference basin (Table 3-3; Fig. 3-4). For example, on August 19, DO concentrations were < 1.0 mg·L^{-1} below 11 m in the reference basin and most cisco were restricted by hypoxia to metalimnetic waters between 5-9 m. In the treated basin, cisco distributed well into the hypolimnion where DO concentrations remained largely above 1.0 mg·L^{-1} (Table 3-3; Fig. 3-4).

Fish diets

Except for the comparison on June 23, 1992, in the treated basin, overlap in diet composition between the two age categories was ≥ 60% (Table 3-4). Based on these results, I pooled samples across age categories for further comparisons.

Nearly half of all stomachs examined in 1989 and 1992 contained food (48 % in 1989, N = 87; 44 % in 1992, N = 340). In both years, higher proportions of younger fish (≤ 2+) had empty stomachs compared with older fish (≥ 3+) (likelihood ratio chi-square; 1989, $\chi^2 = 11.14$, $P = 0.001$; 1992, $\chi^2 = 4.17$, $P = 0.041$).

For the July-August period, cisco in both basins had much fuller stomachs in 1989 than in 1992; in both basins, the amount of food in fish stomachs in 1989 was at least 30 times as high as in 1992 (two-way ANOVA, year $F_{1,168} = 194.66$, $P = 0.004$; Table 3-5). In 1989, stomach fullness varied both between months and basins but these variations were not statistically significant (two-way ANOVA, basin x month $F_{1,37} = 1.24$, $P = 0.273$; Table 3-5). In contrast, stomach fullness differed between basins in 1992, typically being higher in the reference basin than in the treated basin (two-way ANOVA, basin $F_{1,123} = 4.65$, $P = 0.03$; basin x month $F_{3,123} = 2.27$, $P = 0.08$; Table 3-5).

In 1989, the diets of cisco differed between the treated and reference basins (Table 3-6). On July 25, *D. pulex* was the most abundant prey item in diets in the treated basin (Fig. 3-5). Other numerically important prey items included the hypolimnetic species, *D. longiremis*, and the benthic *Chironomus* spp. (> 90 % of chironomids in fish diet belonged to the genus *Chironomus*; W.P. Dinsmore, Dept. of Biological Sciences, Univ. of Alberta, pers. comm.). In contrast, cisco in the reference basin fed almost exclusively on *D. pulex* (Fig. 3-5), which distributed primarily below the epilimnion, but was most abundant in the metalimnion (Field 1993). On August 9, *D. pulex* was again the dominant prey in both basins, with *D. longiremis* also important in the treated basin and *Chaoborus*, an epilimnetic species (at night), important in the reference basin (Table 3-6). On both sampling dates, *D. g. mendotae* was preyed on in the treated basin only.

Diet composition of cisco differed between 1989 and 1992 (Fig. 3-5). The diet spectrum was not only broader in 1992 than in 1989, but numerically dominant taxa also differed between years. Whereas *D. pulex* and *D. longiremis* were the dominant taxa during 1989, Cyclopoida and *D. g. mendotae* dominated in 1992 (Fig. 3-5).

In 1992, similarity in diet composition between the two basins varied temporally. Overlap was high in early summer, but decreased through mid-summer when differences in hypolimnetic DO concentrations between basins were most severe; during fall turnover (September 25) overlap returned to the higher level observed in June (Table 3-6). On June 23, Cyclopoida and *Bosmina* were numerically the most abundant taxa in both the diets and the environment in the two basins (Fig. 3-2, 3-5). On September 25, fish in both basins fed largely on cyclopoid and calanoid copepods, the most abundant taxa in zooplankton samples on this date. Numerical proportions of epilimnetic and hypolimnetic prey species in fish diets differed between the treated and reference basins during stratification (July 22 and August 19; Fig. 3-5). On July 22, fish diets in the treated basin included higher proportions of the hypolimnetic cladoceran, *D. longiremis*, than fish diets in the reference basin (*t*-test, $P < 0.04$). Further, the benthic *Chironomus* occurred exclusively in diets of fish in the treated basin. In contrast, the epilimnetic cladoceran, *D. g. mendotae*, was more abundant in diets of fish in the reference basin than in the treated basin (*t*-test, $P < 0.005$; Fig. 3-5). Similarly, on August 19, the proportion of *D. longiremis* in fish diets was higher in the treated basin than in the reference basin (*t*-test, $P < 0.04$). On this date, fish diets in the reference basin were largely composed of prey species associated with the epilimnion, and the largest cladoceran, *Leptodora*, contributed substantial proportions to the fish diets (Fig. 3-5) in spite of very low densities in the lake.

Except for isolated instances, mean body size of prey did not differ between the two basins (Table 3-7). *Chironomus* and *Leptodora* were the largest and *Bosmina* the smallest prey items consumed. Mean body length of the most dominant prey taxa, Cyclopoida and *D. g. mendotae*, was about 1.0 mm (Table 3-7). Among daphnids, *D. pulex* was the largest, and the calanoid, *Skistodiaptomus oregonensis*, was almost the same body length as *D. pulex*.

Prey selection by cisco reflected patterns in vertical distributions of prey and size-selectivity. The epilimnetic *D. g. mendotae* was positively selected in the reference basin whereas the hypolimnetic *D. longiremis* was positively selected in the treated basin (Table 3-8). Cisco also positively selected for the two large-sized cladocerans, *Leptodora* and *D. pulex* (Table 3-8). Chironomids were considered to be positively selected whenever they occurred in fish diet. *Skistodiaptomus* was positively selected only on September 25, when populations of cladocerans had collapsed.

Discussion

Fish diet and vertical profiles of dissolved oxygen

During hypolimnetic oxygenation in Amisk Lake, higher DO concentrations in the treated basin, relative to those in the reference basin, enabled fish in the treated basin to exploit hypolimnetic food resources that were less available to fish in the reference basin due to hypoxia. Diets of cisco in the treated basin comprised prey items distributed throughout the water column whereas cisco diets in the reference basin consisted largely of epilimnetic prey species. This dietary pattern reflected differences in vertical distributions of cisco between the two basins, especially during mid-summer, when cisco habitat in the treated basin extended into the hypolimnion whereas in the reference basin, cisco habitat was largely restricted to metalimnetic and epilimnetic waters by hypolimnetic hypoxia (Aku et al., in press).

The vertical expansion of foraging habitat in Amisk Lake is consistent with previous aeration studies. During hypolimnetic aeration of Hemlock Lake, Michigan and Ottoville Quarry, Ohio, diets of rainbow trout (*Oncorhynchus mykiss*) stocked into the hypolimnion included *Chaoborus* and *D. pulex*, both of which were associated with the hypolimnion; however, no untreated reference basin was available for comparisons (Fast 1973; Overholtz et al. 1977). Most freshwater zooplankton tend to avoid DO concentrations 0.2 to 1.0 mg·L^{-1} (Herbert 1954; Pennak 1978), whereas for coregonids such as cisco, avoidance DO concentration is 1.3 to 1.9 mg·L^{-1} (Rudstam et al. 1985; Aku et al., in press). Because of their tolerance of lower DO concentrations than cisco, a hypoxic hypolimnion could provide zooplankton with refuge against fish predators during periods of thermal stratification (Fast 1971; Engel 1976; Taggart 1984). In Amisk Lake, increased hypolimnetic DO concentrations, resulting from the oxygen treatment, serve to minimize the volume of the hypoxic refugium for zooplankton as fish in the treated basin distributed into deeper water and used the available food resources. Not surprisingly, densities of hypolimnetic zooplankton species were higher in the lower hypolimnion (> 20 m) compared with the upper hypolimnion (10-20 m) where cisco were most abundant.

At Lake Waccabuc, New York, rainbow trout stocked into the hypolimnion during aeration included benthic chironomids in their diets (Garrell et al. 1978). Similarly, chironomids were included in diets of cisco in the treated basin of Amisk Lake. Chironomid densities were high in both basins of Amisk Lake during oxygenation (Dinsmore and Prepas, in press), therefore, their poor representation in diets of cisco in the reference basin suggests that the better aerated hypolimnion provided additional foraging habitat and food resource for cisco in the treated basin.

Chironomid density and distribution in Amisk Lake during treatment years apparently reflected differences in vertical distributions of cisco between the two basins. Although chironomid densities increased in the profundal zone of both basins in the first year of oxygenation (1988), densities were higher in the treated than in the reference basin at all depths sampled (15, 20, 25 m). However, by 1991, densities at 15 and 20 m became higher in the reference than in the treated basin, and there was no difference between the two basins at 25 m (Dinsmore and Prepas, in press). Hypoxic conditions at 25 m may have provided refuge from fish predation for chironomid, resulting in similar densities at this depth in both basins. Nevertheless, the deeper depth distributions of cisco in the treated basin, coupled with their preference for chironomids, apparently resulted in greater losses of chironomid to fish predation in this basin than in the reference basin, especially within the upper 20 m of the water column where cisco were most abundant. Thus, these studies indicate that through the creation of suitable habitat for both fish and their prey, hypolimnetic oxygen treatment has the potential to improve cold-water fish production.

Fish density and zooplankton community dynamics

The dominance of small-bodied zooplankton in both fish diet and the zooplankton in Amisk Lake in 1992 suggests intensive predatory pressure on the zooplankton community. Whole-lake cisco density increased almost five times in Amisk Lake between 1989 and 1991 (Aku and Tonn 1995). Although quantitative hydroacoustic data were not available in 1992, dry chart echograms indicated that fish densities may have been as high as in 1991, and higher than in 1989, (P.M.K. Aku, unpubl. data). Planktivorous fish have a demonstrated ability to alter the structure and composition of zooplankton communities; fish predation often results in decreased abundance and production of large-bodied zooplankton species (Hrbáček et al. 1961; Brooks and Dodson 1965; Carpenter and Kitchell 1988). Thus, in Amisk Lake, differences in the composition of zooplankton and fish diet between 1989 and 1992 may have been related to differences in predatory pressure; low predatory pressure in 1989 allowed the relatively large daphnids to dominate both zooplankton community and fish diets in 1989, whereas high predatory pressure in 1992 resulted in the elimination of daphnids. Consequently, both the zooplankton community and fish diets were dominated by smaller individuals. Also, in 1992, higher predatory pressure in the treated basin than in the reference basin reflected differences in fish densities that contributed to the lower zooplankton densities in the treated basin compared with the reference basin. During the summers of 1989 to 1991, the treated basin supported a density and biomass of pelagic fish that was at least twice as great as in the reference basin (Aku and Tonn 1995). Dry chart echograms indicated that fish densities were again higher in the treated than in the reference basin in 1992 (P.M.K. Aku, unpubl. data).

Comparison of stomach fullness indices indicate that cisco had access to more food in 1989 than in 1992. This is consistent with the whole-lake increased fish density and biomass between 1989 and 1991 (Aku and Tonn 1995). Similarly, in 1992, the higher fullness indices in the reference basin than in the treated basin is consistent with the treated basin having higher densities of fish than the reference basin. In both instances, food resources likely became more limited as fish densities increased. These observations, coupled with the higher proportions of empty stomachs among young fish compared with adult fish, could have negative influences on growth rate of fish. However, higher fullness indices in the reference basin relative to the treated basin in 1992 contradicts tenets of ideal free distribution (Fretwell and Lucas 1970), suggesting that variations in major environmental factors such as DO concentrations may have influenced fish distributions in ways not yet fully understood; that cisco did not redistribute between the two basins to maximize per capita food acquisition cannot be explained at present.

The feeding repertoire of cisco in Amisk Lake included size-selectivity. In 1992, the large zooplankter, *D. pulex* and *Leptodora*, were rare in both basins but frequently encountered in fish stomachs, and contributed substantially to the fish diet. Similarly, the high proportions of *Chaoborus* and *D. pulex* in cisco diets in 1989 may have resulted from size-selective feeding, although prey selectivity was not determined for that year. Cisco employ two main feeding strategies, particulate feeding and gulping. Particulate feeding entails cisco locating individual prey by sight and attacking (or ignoring) them whereas with gulping, the mouth is opened and closed intermittently and water pumped in while the fish swims, thus, prey are not actively selected (Eggers 1977; Janssen 1978). Both strategies could be used during the day but only the non-selective gulping is used at night during non-visual feeding (Janssen 1978, 1980; O'Brien 1979).

Given these conditions, positive selection for the large cladocerans suggests a diurnal or crepuscular feeding for cisco in Amisk Lake. Although cisco has been described as primarily a nocturnal feeder (Emery 1973; Engel 1976; Janssen 1978), diurnal feeding has also been reported (Rudstam and Trapp 1987), and some of the few samples I collected when nets were set and inspected during daylight hours had food in their stomachs (P.M.K. Aku, unpbl. data). Because during the present study, nets were set at dusk and inspected under daylight in the morning (summer nights being short at the latitude of Amisk Lake), fish caught in nets included individuals that fed visually and selectively at dusk or dawn.

Size-selective feeding by cisco on predaceous invertebrates such as *Leptodora* and *Chaoborus* could have positive effects on the survival and recruitment of juvenile fish. Both *Leptodora* and *Chaoborus* prey on zooplankton, particularly, on small-sized individuals (Lynch 1979; Pastorok 1980; Branstrator and Lehman 1991). Due to mouth gape limitations, larval fish typically also prey on small-sized zooplankton (Anderson and Smith 1971; Davis and Todd 1992), therefore, a potential exists for competition between larval cisco and these invertebrate predators. Thus, by selectively preying on the predaceous invertebrates, cisco may derive not only nutritional benefit, but also an indirect benefit of reducing the number of potential competitors that could act as bottleneck to larval recruitment.

Superimposed on the trophic interactions and oxygen requirements discussed above is the selection of preferred temperatures by cisco (Rudstam and Magnuson 1985; Aku et al., in press). Even in the treated basin of Amisk Lake, where DO concentrations were relatively high throughout most of the deep hypolimnion, cisco were most abundant in metalimnetic and upper hypolimnetic waters (7-17 m), corresponding to their preferred temperature range of 9-14 °C (Aku et al., in press). The advantage of this temperature-mediated depth-specific distribution to realizing the goals of hypolimnetic oxygenation is that fish predatory pressure is reduced on the epilimnetic zooplankton much needed for controlling algal populations. Thus, results of the Amisk Lake study indicate that through the creation of suitable habitat and enhancement of the availability of fish forage organisms in deep water, hypolimnetic oxygenation can be a useful tool for improving both cold-water fish production and water quality in deep eutrophic lakes.

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Table 3-1. Summary of repeated-measures ANOVA comparing mean zooplankton densities between the treated and reference basins of Amisk, June-September, 1992. Only taxa with densities $\geq 1.0 \cdot L^{-1}$ were included in analyses. *Diaphanosoma* was not included because it was not always present in both basins. MS and Error terms were rounded from eight decimal places therefore, F-values may differ if calculated from table. Vertical arrangement of individual species reflect epilimnetic species at the top and hypolimnetic species at the bottom.

	Basin effects			Time effects				
	Basin (df = 1, 2)			Time (df = 3, 6)		Basin x Time (df = 3, 6)		
Taxonomic group	MS	Error	F	MS	F	MS	F	Error
Total	0.061	0.002	39.43*	0.203	7.30*	0.017	0.62^{ns}	0.028
Cyclopoida	0.093	0.001	103.69**	0.271	14.98**	0.016	0.87^{ns}	0.018
D. g. mendotae	0.001	0.014	0.07^{ns}	0.334	11.92**	0.010	0.37^{ns}	0.028
Skistodiaptomus	0.071	0.011	6.14^{ns}	0.215	16.60**	0.001	0.08^{ns}	0.013
Bosmina	0.063	0.014	4.58^{ns}	0.625	8.31**	0.007	0.09^{ns}	0.075
D. longiremis	0.003	0.002	1.21^{ns}	0.204	4.89*	0.042	1.02^{ns}	0.042

ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$

Table 3-2. Summary statistics of two-way ANOVAs comparing mean zoop[illegible] density in the epilimnion and hypolimnion between the treated and reference b[illegible] of Amisk, June-September, 1992. Only species with densities $\geq 1 \cdot L^{-1}$ were included. Vertical arrangement of individual species reflect epilimnetic species at the top and hypolimnetic species at the bottom.

	Effects (df = 1,4)		
	Basin	Layer	Basin x Layer
Taxonomic group	F	F	F
	June 23		
Cyclopoida	0.51^{ns}	3.38^{ns}	0.17^{ns}
D. g. mendotae	0.42^{ns}	10.46*	3.96^{ns}
Skistodiaptomus	4.55^{ns}	14.59*	0.00^{ns}
Bosmina	8.14*	7.68*	19.73*
D. longiremis	7.11^{ns}	77.29**	2.51^{ns}
	July 22		
Cyclopoida	5.97^{ns}	0.77^{ns}	0.35^{ns}
D. g. mendotae	0.30^{ns}	18.06*	3.52^{ns}
Skistodiaptomus	0.74^{ns}	0.02^{ns}	1.82^{ns}
Bosmina	0.10^{ns}	0.01^{ns}	0.00^{ns}
D. longiremis	0.37^{ns}	6.63^{ns}	0.03^{ns}
	August 19		
Cyclopoida	0.40^{ns}	0.07^{ns}	0.00^{ns}
D. g. mendotae	0.83^{ns}	9.72*	0.51^{ns}
Skistodiaptomus	0.15^{ns}	6.31^{ns}	0.05^{ns}
D. longiremis	1.38^{ns}	4.72^{ns}	1.48^{ns}
	September 25		
Cyclopoida	5.95^{ns}	4.12^{ns}	0.47^{ns}
D. g. mendotae	1.21^{ns}	3.45^{ns}	0.00^{ns}
Skistodiaptomus	4.75^{ns}	3.82^{ns}	2.73^{ns}

ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$

Table 3-3. Median, and 25-75 percentile (in brackets) depth distrib[illegible] cisco in the treated and reference basins of Amisk Lake, June-September 1992, using verti[illegible] catches. Indicated are the Kolmogorov-Smirnov two-sample statistics (D) corrected for large [illegible]ze (Sokal and Rohlf 1981), of distributions between the two basins. Depths are mid-points of 2-m depth intervals. N_T and N_R are number of fish in the treated and reference basins, respectively, corrected for gill net selectivity.

	Median depth (m) (25-75 percentile depth)		Maximum depth (m)				
Date	Treated basin	Reference basin	Treated basin	Reference basin	D	N_T	N_R
June 23	7 (5-13)	11 (7-15)	25	23	0.19**	134	155
July 22	15 (11-17)	13 (11-15)	25	17	0.14**	251	284
Aug. 19	9 (7-15)	5 (5-9)	19	15	0.19**	211	100
Sep. 25	15 (11-17)	13 (11-15)	27	19	0.30**	92	43

** = $P < 0.01$

Table 3-4. Diet overlap (Schoener's index, Schoener 1968) between two age categories of cisco in the treated and reference basins of Amisk Lake, in July-August, 1989 and June -September, 1992. N is the number of stomachs analyzed for each age category. When N = 1, overlap was not calculated.

			N	
Basin	Date	Percentage overlap	≤ 2+	≥ 3+
		1989		
Treated	July 25	69.0	6	7
	Aug. 23	--	--	10
Reference	July 25	--	3	1
	Aug. 23	60.2	6	9
		1992		
Treated	June 23	31.7	4	10
	July 22	67.6	13	12
	Aug. 19	83.7	9	6
	Sep. 25	61.6	13	7
Reference	June	--	8	--
	July	--	19	--
	Aug. 19	--	14	--
	Sep. 25	78.3	15	2

Table 3-5. Mass-specific gut contents (mean ± SE; g·g fish^{-1} x 100) of cisco in the treated and reference basins of Amisk Lake in July-August 1989, and June-September, 1992.

	Stomach fullness index		N	
Date	Treated basin	Reference basin	Treated basin	Reference basin
		1989		
July 25	5.25 ± 1.34	3.88 ± 0.81	13	4
Aug. 9	10.62 ± 1.58	5.41 ± 1.39	10	15
		1992		
June 23	0.09 ± 0.03	0.16 ± 0.02	14	8
July 22	0.12 ± 0.02	0.10 ± 0.01	25	19
Aug. 19	0.09 ± 0.02	0.17 ± 0.03	14	14
Sep. 25	0.17 ± 0.02	0.19 ± 0.02	20	17

Table 3-6. Percentage overlap (Schoener's index, Schoener 1968) in diet composition (% by number) of cisco in the treated and reference basins of Amisk Lake, in July-August, 1989 and June -September, 1992. N is the total number of stomachs analyzed for each date.

		N	
Date	Percentage overlap	Treated basin	Reference basin
	1989		
July 25	49.2	13	4
Aug. 9	59.4	10	15
	1992		
June 23	80.6	14	6
July 22	68.5	25	19
Aug. 19	50.0	14	14
Sep. 25	79.7	20	17

Table 3-7. Comparison of mean body length (±SE) of prey in the diet of cisco in Amisk Lake, June-September, 1992. Only prey species which constituted ≥ 1 % (by number) total prey items, on each sampling date are included. Prey items generally arranged vertically by increasing body length.

	Mean body length (mm)			N	
Prey taxon	Treated basin	Reference basin	t-value	Treated basin	Reference basin
		June 23			
Bosmina	0.46 ± 0.00	0.46 ± 0.01	0.17^{ns}	166	61
Cyclopoida	1.17 ± 0.02	0.95 ± 0.03	5.70**	181	61
D. g. mendotae	1.05 ± 0.02	1.08 ± 0.03	0.82^{ns}	32	25
D. pulex	1.20 ± 0.06	1.41 ± 0.07	2.06^{ns}	6	10
Chironomus	13.59 ± 0.44	--	--	2	--
		July 22			
D. longiremis	0.90 ± 0.04			11	--
Cyclopoida	1.05 ± 0.01	0.99 ± 0.02	2.89**	181	158
D. g. mendotae	1.09 ± 0.02	1.03 ± 0.02	1.86^{ns}	60	66
Skistodiaptomus	1.15 ± 0.02	1.24 ± 0.04	2.38*	30	11
D. pulex	1.38 ± 0.03	--	--	47	--
Chironomus	13.35 ± 0.24	--	--	42	--
		August 19			
D. longiremis	1.02 ± 0.27	--	--	20	--
Cyclopoida	1.02 ± 0.02	0.99 ± 0.03	0.95^{ns}	47	54
D. g. mendotae	1.00 ± 0.03	1.03 ± 0.01	0.81^{ns}	20	57
Skistodiaptomus	1.15 ± 0.03	1.22 ± 0.03	1.17^{ns}	13	42
D. pulex	1.47 ± 0.05	1.20 ± 0.03	4.07**	8	38
		September 25			
Cyclopoida	1.14 ± 0.03	1.17 ± 0.03	0.72^{ns}	67	59
Skistodiaptomus	1.27 ± 0.30	1.26 ± 0.02	0.09^{ns}	59	25
D. pulex	--	1.36 ± 0.02	--		34

ns = $P > 0.05$ * = $P < 0.05$; ** = $P < 0.01$

Table 3-8. Selection of the most common zooplankton prey taxa by cisco in Amisk Lake during the summer of 1992. Prey selectivity was described by Chesson's α (mean ± SE; Chesson 1978) for each zooplankton taxon. Critical α is the reciprocal of the number of prey types (m) in the environment on each sampling day; all taxa encountered on a given date were included. α > m^{-1} indicates pref[illegible] In bracket, are number of fish in which prey type was found.

Date	Selectivity index (α)				Critical α (m^{-1})	
	Treated basin	Reference basin	Treated basin	[illegible]	Treated basin	Reference basin
	Daphnia g. mendotae		***Daphnia pulex***			
June 23	0.16 ± 0.08 (5)	0.56 ± 0.08 (8)	0.80 ± 0.07 (4)	1.00 ± 0.20[a] (3)	0.20	0.20
July 22	0.03 ± 0.00 (18)	0.20 ± 0.06 (16)	0.52 ± 0.08 (19)	0.90 ± 0.02 (10)	0.17	0.17
Aug. 19	0.21 ± 0.05 (11)	0.04 ± 0.01 (10)	1.00 ± 0.00[a] (6)	0.34 ± 0.10 (5)	0.20	0.20
Sep. 25	--	0.20 ± 0.24 (11)	--	0.60 ± 0.14 (4)	0.17	0.17
	Daphnia longiremis		**Cyclopoida**			
June 23	0.00 (4)	0.05 ± 0.02 (4)	0.21 ± 0.08 (11)	0.11 ± 0.02 (8)	0.20	0.20
July 22	0.18 ± 0.01 (12)	0.12 ± 0.11 (3)	0.10 ± 0.06 (24)	0.14 ± 0.06 (17)	0.17	0.17
Aug. 19	0.21 ± 0.05 (7)	0.01 ± 0.01 (2)	0.60 ± 0.07 (14)	0.02 ± 0.01 (14)	0.20	0.20
Sep. 25	--	0.07 ± 0.05 (2)	0.36 ± .05 (20)	0.31 ± 0.04 (17)	0.17	0.17
	Skistodiaptomus oregonensis		***Leptodora kindtii***			
June 23	0.16 ± 0.12 (6)	--	--	--	0.20	0.20
July 22	0.02 ± 0.01 (11)	0.13 ± 0.06 (8)	0.77 ± 0.06 (14)	0.18 ± 0.06 (14)	0.17	0.17
Aug. 19	0.11 ± 0.03 (12)	0.02 ± 0.01 (11)	1.00 ± 0.0[a] (5)	0.77 ± 0.06 (14)	0.20	0.20
Sep. 25	0.61 ± 0.05 (20)	0.30 ± 0.06 (16)	1.00 ± 0.0[a] (3)	0.90 (1)	0.17	0.17

[a] = Selectivity (α) assumed to equal 1 because prey type was not encounted in zooplankton sample on given date.

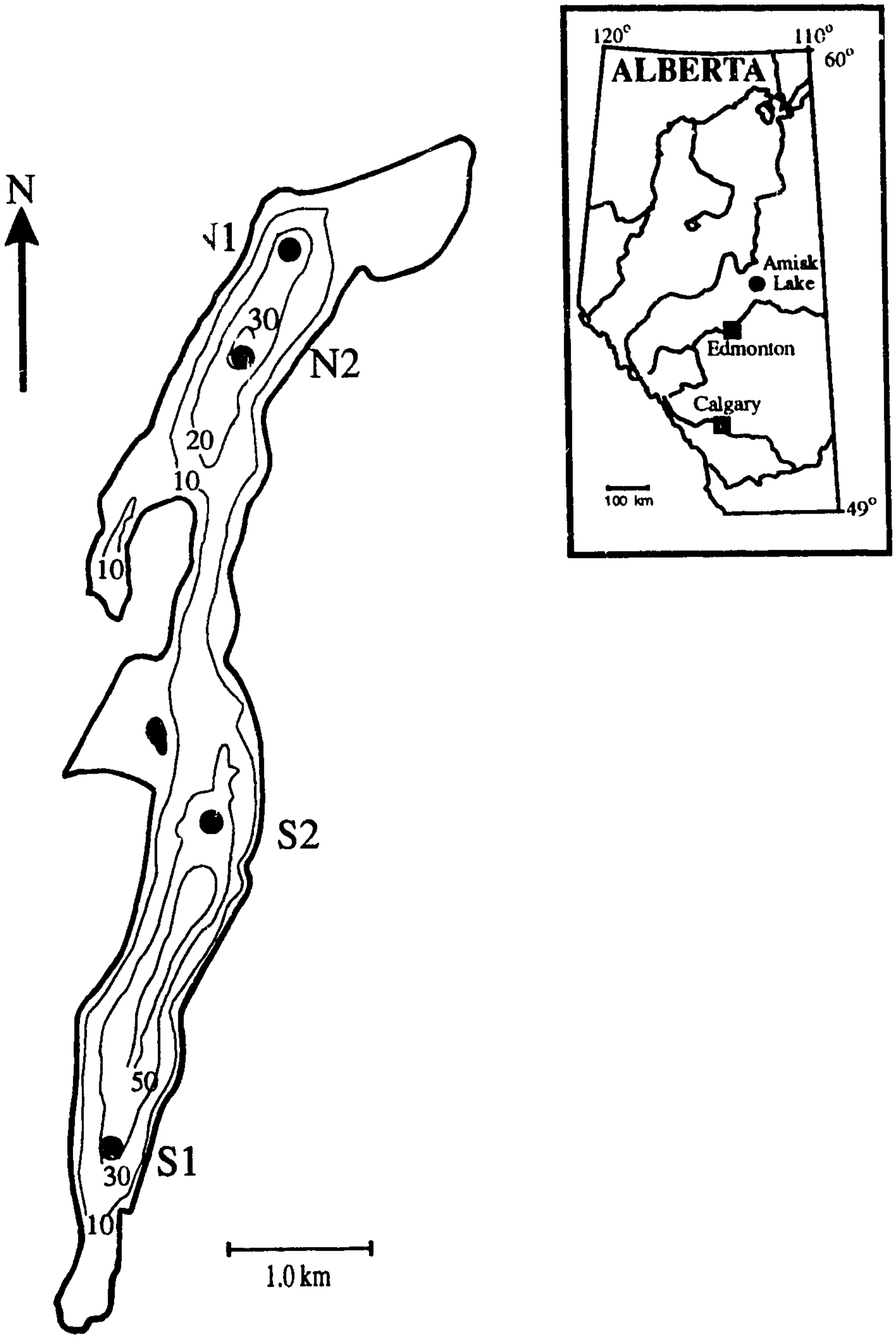


Fig. 3-1. Bathymetric map (with 10-m depth contours) of Amisk Lake showing sampling sites (black circles: N1, N2, S1, S2); the oxygen diffuser was located at site N2. Insert, is map of the province of Alberta.

Fig. 3-2. Mean (±SE) monthly density of zooplankton within the 2-20 m stratum in the treated and reference basins of Amisk Lake, July-August, 1989, and June-September, 1992. SE is for 2-m interval estimates at one sampling site per basin in 1989, and estimates from two sampling sites per basin in 1992. Total = all taxa pooled; D. lon = *Daphnia longiremis*; D. gal = *Daphnia galeata mendotae*; Bos = *Bosmina longirostris*; D. pul = *Daphnia pulex*; Cyc = Cyclopoida; Ski = *Skistodiaptomus oregonensis*; Dia = *Diaphanosoma leuchtenbergianum*; Lep = *Leptodora kindtii*. Note the difference in scale of the vertical axis for *D. longiremis* and Cyclopoida.

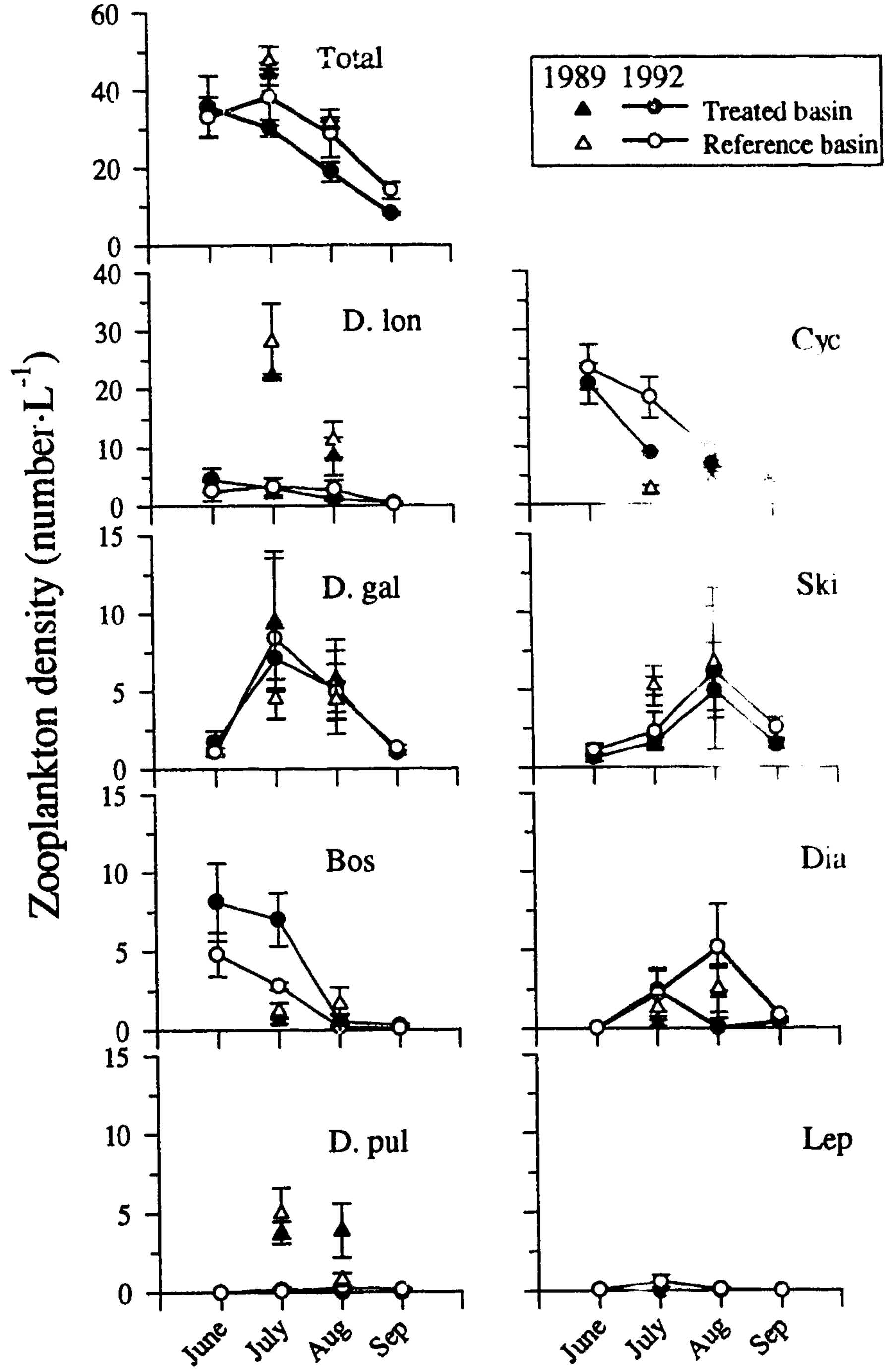

Total
D. lon
Cyc
D. gal
Ski
Bos
Dia
D. pul
Lep
1989 1992
▲ —●— Treated basin
△ —○— Reference basin
Zooplankton density (number·L^{-1})
60
40
20
0
40
30
20
10
0
15
10
5
0
15
10
5
0
15
10
5
0
June
July
Aug
Sep
June
July
Aug
Sep

Fig. 3-3. Mean (±SE) monthly density of zooplankton within the epilimnion (Epi: 2-10 m) and hypolimnion (Hypo: 10-20 m) in the treated and reference basins of Amisk Lake, June-September, 1992. Samples were collected from two sampling sites per basin. Cyc = Cyclopoida; D. gal = *Daphnia galeata mendotae*; Ski = *Skistodiaptomus oregonensis*; Dia = *Diaphanosoma leuchtenbergianum*; Bos = *Bosmina longirostris*; D. lon = *Daphnia longiremis*; Note variation in scale of the vertical axes. Arrangement of species beyond Cyclopoida on the horizontal axes, reflect epilimnetic species to the left and hypolimnetic species to the right.

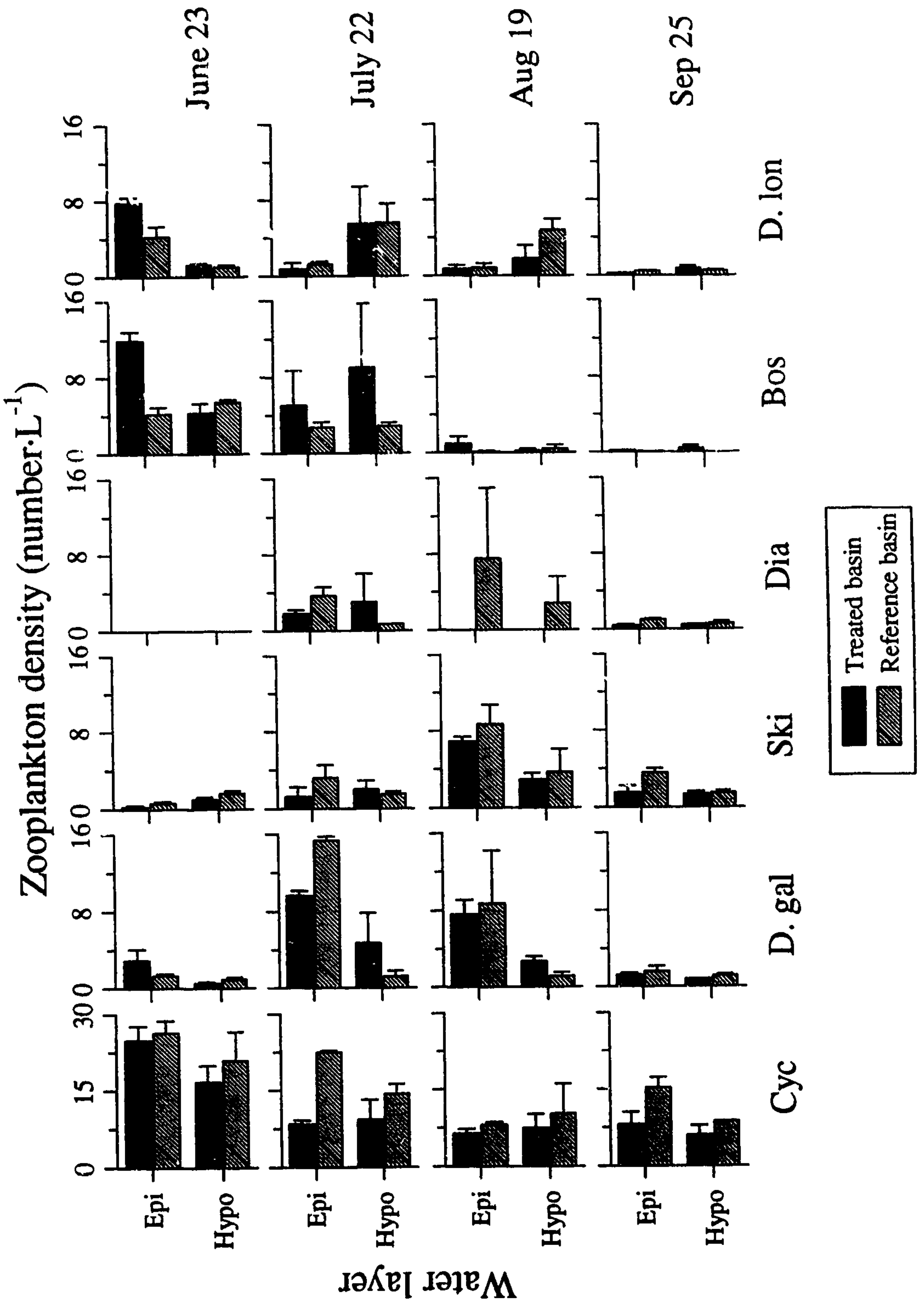

Zooplankton density (number·L⁻¹)
Water layer
June 23
July 22
Aug 19
Sep 25
D. lon
Bos
Dia
Ski
D. gal
Cyc
Epi
Hypo
0
8
16
0
15
30
Treated basin
Reference basin

Fig. 3-4. Vertical distributions of cisco, determined from gill net catches in the treated and reference basins of Amisk Lake, June-September, 1992, and associated temperature (Temp.) and dissolved oxygen (DO) profiles on each sampling date. n_T and n_R represent sample sizes in the treated and reference basins, respectively, corrected for gill net selectivity using the size-encounter probability method (Rudstam et al. 1984).

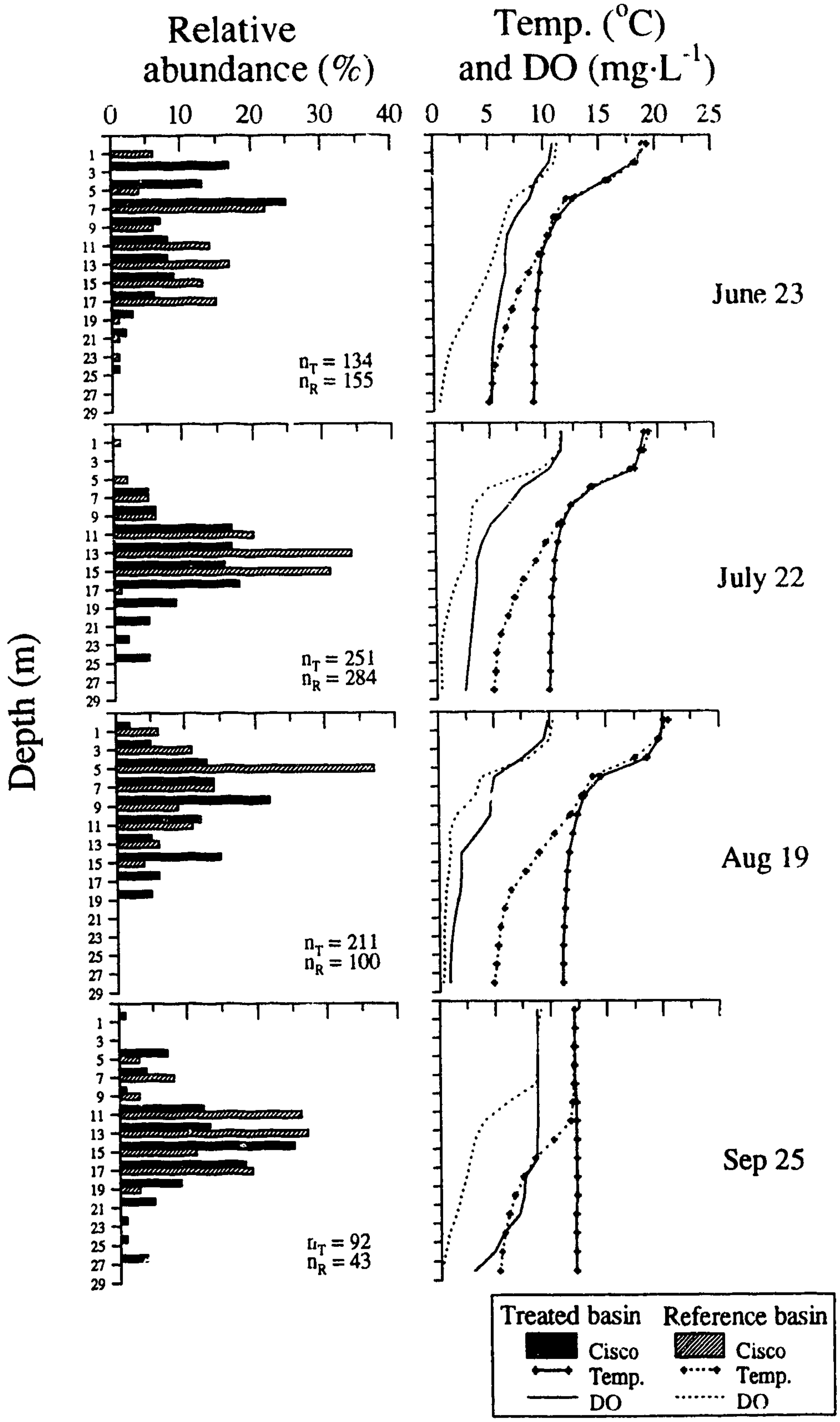
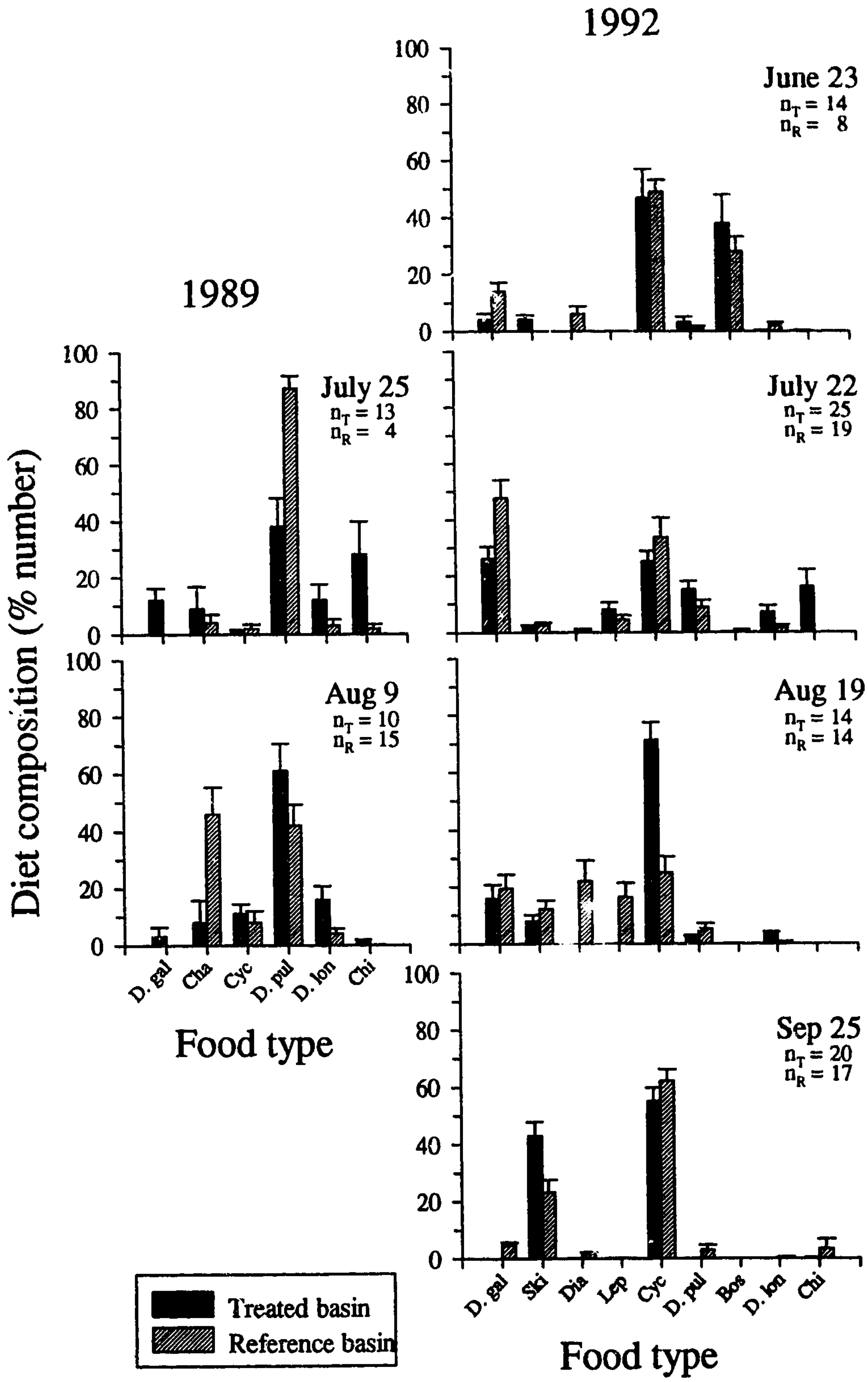

Relative abundance (%)
Temp. (°C) and DO (mg·L⁻¹)
0
10
20
30
40
0
5
10
15
20
25
Depth (m)
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
June 23
n_T = 134
n_R = 155
July 22
n_T = 251
n_R = 284
Aug 19
n_T = 211
n_R = 100
Sep 25
n_T = 92
n_R = 43
Treated basin
Cisco
Temp.
DO
Reference basin
Cisco
Temp.
DO

Fig. 3-5. Taxonomic composition (% number) of prey in diets of cisco in Amisk Lake, July-August, 1989, and June-September, 1992. D. gal = *Daphnia galeata mendotae*; Cha = *Chaoborus* spp.; Ski = *Skistodiaptomus oregonensis*; Dia = *Diaphanosoma leuchtenbergianum*; Lep = *Leptodora kindtii*; Cyc = Cyclopoida; D. pul = *Daphnia pulex*; Bos = *Bosmina longirostris*; D. lon = *Daphnia longiremis*; Chi = *Chironomus* spp. Arrangement of prey type on the horizontal axes reflect epilimnetic taxa to the left and hypolimnetic taxa to the right. n_T and n_R represent sample sizes in the treated and reference basins, respectively.


1992
1989
Diet composition (% number)
100
80
60
40
20
0
June 23
n_T = 14
n_R = 8
July 25
n_T = 13
n_R = 4
July 22
n_T = 25
n_R = 19
Aug 9
n_T = 10
n_R = 15
Aug 19
n_T = 14
n_R = 14
Sep 25
n_T = 20
n_R = 17
D. gal
Cha
Cyc
D. pul
D. lon
Chi
Food type
D. gal
Ski
Dia
Lep
Cyc
D. pul
Bos
D. lon
Chi
Food type
■ Treated basin
▨ Reference basin

Chapter 4

[1]Changes in population structure, growth rate, and biomass of cisco (*Coregonus artedi*) during hypolimnetic oxygenation in Amisk Lake.

A version of this chapter will be submitted for publication, as a manuscript co-authored with William M. Tonn.

[1] Data on density and biomass only from Amisk Lake has been published in Archiv. Hydrobiol. Spec. Issues Advance Limnol. 46: 453-464, as proceedings of the Fifth International Symposium on Biology and Management of Coregonid Fishes.

Introduction

In stratified productive lakes, high epilimnetic temperatures and hypolimnetic deoxygenation, particularly during summer, can drastically reduce the volume of suitable fish habitat, forcing fish into marginal or restricted zones. Epilimnetic waters may have adequate dissolved oxygen (DO) concentrations, but high temperatures during summer can prevent occupation of the epilimnion by certain fishes (Fry 1937; Magnuson et al. 1979; Rudstam and Magnuson 1985). For these cold-water species, optimal habitat may exist in such lakes only during cooler months. Hence, habitat choice, production and even survival of such fishes can be severely limited by hypolimnetic oxygen depletion (Hile 1936; Frey 1955; Colby and Brooke 1969).

Hypolimnetic oxygenation is one of several techniques employed to increase deep water oxygen concentrations with minimal alterations to thermal structure of the water column (Fast and Overholtz 1975; Taggart and McQueen 1982). Maintaining thermal stability and relatively high hypolimnetic DO concentrations has several advantages to cool- and cold water fish. Low hypolimetic temperatures and high DO concentrations not only create suitable habitat for year-round survival of fish, but because higher temperatures increase metabolic oxygen demand, fish will also derive metabolic cost reductions by occupying the cold hypolimnion (Brett 1971; Garrell et al. 1977). In addition, improved hypolimnetic conditions will result in habitat suitable for the invertebrate prey of fish; abundance and biomass of hypolimnetic zooplankton and zoobenthos populations have been observed to increase during hypolimnetic aeration (Fast 1971, 1973; Pastorok et al. 1980). It is also generally assumed that an expanded hypolimnetic habitat will enhance cold-water fish production, particularly during summer, because of the alleviation of crowding within epilimnetic strata (Pastorok et al. 1980).

Although the primary target of most oxygenation studies is to stimulate cold-water fish production, changes in growth rate, density and biomass have been rarely evaluated. Most studies have instead focused on changes in vertical distributions of fish in response to changes in DO concentrations (e.g., Fast and Overholtz 1975; Brynildson and Serns 1977; Overholtz et al. 1977; Aku et al., in press). Of the few studies that reported changes in growth rate (Fast 1973; Overholtz et al. 1977; Garrell et al. 1978), limited quantitative evaluations were conducted, probably because studies were of short duration.

A 5-yr hypolimnetic oxygenation (1988-1993) program was conducted in one of the two basins of Amisk Lake, Alberta, which provided a year-round well-oxygenated hypolimnion for cisco (*Coregonus artedi*). Cisco, the dominant cold-water, zooplanktivorus fish in Amisk Lake, constituted >96% of the pelagic fish assemblage during this period (Aku et al., in press). Here, I examine the responses of cisco to the increase in hypolimnetic oxygen concentration in Amisk Lake. First, I compare the growth rates of cisco before and during treatment years. Second, I compare cisco density and biomass between the treated and untreated basins, and lastly, I compare the trends in growth, density and biomass of the Amisk Lake cisco population with those of the cisco population in nearby Baptiste Lake, which served as an unmanipulated reference system.

Materials and methods

A detailed description of the study area and fish sampling procedures is presented in Prepas (1990) and Chapter 2 of this thesis, therefore only a summary is provided here.

Study areas

Amisk Lake (54° 35'N, 112° 37'W) is a naturally eutrophic lake in central Alberta, Canada (Fig. 4-1). It has two basins, a shallower north basin (A_o = 2.33 km^2, Z_{max} = 34 m), connected by a narrows (sill depth = 11 m) to a deeper south basin (A_o = 2.82 km^2, Z_{max} = 60 m). Historically, both basins stratified in the summer, with thermoclines ranging within the 5-10 m stratum (Prepas 1990). Baptiste Lake (54° 45'N 113° 33'W) is physically similar but more productive than Amisk Lake (Fig. 4-1). It also stratifies in the summer, with thermoclines ranging within the 5-10 m stratum and has two basins connected by a narrows with sill depth 5.5 m (Prepas 1990). High oxygen consumption rates, combined with incomplete mixing during spring and fall turnovers, have led to severe hypolimnetic hypoxia in both lakes (Prepas 1990).

Oxygen injection into the hypolimnion of the north basin of Amisk Lake started in summer 1988 and continued through October 1993. Oxygenation was year-round, and ranged (mean ± SE) from 0.61 ± 0.03 to 1.3 ± 0.03 $t \cdot d^{-1}$ and 0.50 ± 0.01 to 0.57 ± 0.04 $t \cdot d^{-1}$ of liquid oxygen during thermally stratified and mixed periods, respectively (Prepas and Burke, in press). The south basin was not treated and served as a reference basin. The south basin of Baptiste Lake (A_o = 4.47 km^2, Z_{max} = 27.5 m) served as a second reference basin.

Limnological data

Volume-weighted hypolimnetic DO concentration data from 1987-1989 were provided by E.E. Prepas and co-workers (Dept. of Biological Sciences, Univ. of

Alberta, unpubl. data). Water samples for analyses of DO concentration were collected at variable depths from 3 m to the bottom in 1987, and at 2-m intervals from 3-18 m and 3-m intervals beyond 18 m, in 1988-1989. Water samples were analyzed by a modified Winkler method (Carpenter 1965), and linear interpolations were used to obtain DO concentration profiles from surface to bottom. In 1987-1989, samples were collected during daytime, either on the same day or during the same week as fish sampling. From 1990 through 1992, I used a HYDROLAB™ SURVEYOR II (SVR2-SU), calibrated before and after each sampling session, to measure temperature and DO concentrations at 1-m intervals, from surface to bottom during each fish sampling night. I used data from 1987 to represent the pretreatment condition; data from 1988 through 1992 were considered as treatment years.

I calculated mean monthly hypolimnetic DO concentrations, from June to September of each year, for each basin in Amisk Lake, and for Baptiste Lake. Data for September was available for only 1989-1992 and 1990-1992 for Amisk and Baptiste lakes, respectively. The hypolimnion was defined as starting from the bottom of the metalimnion at a depth where change in temperature first became $< 1\ ^{\circ}\mathrm{C}\cdot\mathrm{m}^{-1}$. To assess the effect of the oxygenation on DO concentration, I compared monthly mean hypolimnetic DO concentrations between the pretreatment and treatment periods, within each basin of Amisk Lake, with ANOVA (Proc GLM, SAS) and Dunnett's multiple comparison test, treating 1987 as the "control" group. For each month, I used a paired *t*-test to compare DO concentrations between the two basins of Amisk Lake using sampling years as blocks.

Experimental vertical gill netting

Fish samples were collected with a set of five 3 x 30 m monofilament-nylon vertical gill nets (25, 38, 51, 76 and 102 mm stretch mesh). In Amisk Lake, nets were set along the 30 m contour in each basin (sites N2 and S1, Fig. 4-1) on successive days, once every two weeks from July to August 1989, and from May to September in 1990-1992. In Baptiste Lake, the 25-m contour was sampled at monthly intervals from May to September in 1990-1992. Nets were set next to each other and checked at 6- to 8-h intervals over 24-h sampling periods.

Hydroacoustic sampling

Fish distributions, density and biomass estimates were derived primarily from hydroacoustic data because such data provide more complete temporal and spatial information on fish distributions than gill nets (Thorne 1983; Rudstam et al.1987; Eckmann 1991).

Night time (22:30-02:30) hydroacoustic surveys were conducted in both basins of Amisk Lake and in Baptiste Lake, once a month, during the netting periods. Because varying light intensity strongly influences fish behavior and spatial distributions (Blaxter 1974; Helfman 1981), and can bias population estimates derived from hydroacoustic data (Luecke and Wurtsbaugh 1993), surveys for density and biomass estimates were conducted on moonless nights. Hydroacoustic data were obtained with a single beam 70 kHz SIMRAD EY-M echo-sounder (full beam angle 11.2°, 0.6 ms pulse duration, 3 pings·s^{-1}, 40 Log R time-varied-gain). Fish echoes were recorded on audio cassette tapes and analyzed for fish size and density using the HADAS software (Lindem 1990). The HADAS program uses a modification of the Craig and Forbes (1969) algorithm to remove the effect of the beam pattern, and analysis is based on the size distribution of single fish echoes. By assuming that target strength (TS) distribution of single fish is representative of all fish, energy from both single and multiple echoes (echo integration values) is converted to estimate total fish density (Eckmann 1991; Hansson 1993).

Target strength was transformed to fish length with the equation $L = 10^{(68 - TS)/20}$, where TS is the lower limit of a range of target strengths (dB) and L is total length (cm) of fish (Jurvelius and Heikkinen 1987; Bjerkeng et al. 1991). Cisco comprised > 96% of the total gill net catch in both lakes, therefore I assumed all targets insonified were cisco. Because the smallest cisco caught was 10 cm, I considered targets ≥ -48 dB (fish > 10.0 cm) to represent cisco. Echoes < -48 dB, were considered noise, and excluded from my analyses. All echoes > -32 dB were truncated and included in the -32 dB size class. Due to equipment malfunctioning, no hydroacoustic data are provided for 1992.

Age determinations

Because cisco are exceptionally sensitive to handling stress, my attempts at marking them to examine inter-basin movement were unsuccessful. However, mark-recapture studies I conducted on yellow perch (*Perca flavescens*) indicated considerable movement between the two basins. Although yellow perch in Amisk Lake are mainly littoral and limited to the upper 8 m, I considered that pelagic cisco could also move between the two basins. Further, because the sill between the two basins is 11 m and allows advection of some hypolimnetic water from the treated basin into the reference basin (Lawrence et al. in press), there should be little hindrance to fish movement between basins, even within hypolimnetic waters. Therefore, for age and growth rate determinations, I considered cisco in both basins of Amisk Lake as belonging to the same population.

Fish age was determined from scales and otoliths of specimens collected in May 1990-1992 in both lakes. Scale samples were removed from the left side between the posterior edge of the dorsal fin and the lateral line and mounted between two acetate slides. In collaboration with R. Mandryk (Dept. of Biological Sciences, Univ. of Alberta), we developed a technique of preparing permanent mounts of otoliths. Otoliths were read either in glycerol from broken and toasted sections or from 20-30 μm sections permanently mounted in LKB historesin. To enhance readability, otolith sections were stained in methylene blue before mounting. Scales and otolith sections were read with a dissecting microscope at 6-40x magnifications.

Age assignments were compared among three independent readers, and precision was determined with the index of average percentage error (APE) (Beamish and Fournier 1981). Ages determined from scales and otoliths were identical for fish < 4 yr old. Beyond this age, the number of annuli counted on different scales of a single fish were variable, and 1-4 yr less than ages determined from otoliths, therefore, otoliths were used to establish fish ages. Because year-class distribution among samples was variable among years, I pooled samples collected in May of all three years to calculate mean size-at-age. Pooling was also necessary to increase sample size, particularly among older ages. Relative strength of a year-class was then calculated as the proportion of fish that an individual year-class comprised in the pooled sample. I used a *t*-test to compare size-at-age between the Amisk Lake and Baptiste Lake cisco populations.

Length-frequency distributions were used to validate age distribution among fish ≤ 3 yr by assigning ages to prominent length modes. Age validation was not possible among older fish due to overlapping size distributions.

Growth rate determinations

To determine if growth rate of cisco was affected by the oxygenation, I compared the first three annuli (at ages 1-3) laid on scales before, and during, treatment periods (Fig. 4-2). Because age interpretations from scales and otoliths were identical for fish < 4 yr old, and scales were easier to process than otoliths, I used scales to determine growth rates. To have sufficient representation of growth during treatment years, I used scale samples collected in 1991 and 1992. Growth during the first three years of the 1985 and preceding year-classes was considered "pretreatment" growth. Thus, fish from the 1985 year-class caught in 1992 were 7 yr old, and would have laid their third annulus in spring of 1988. Growth of the 1988 and later year-classes was considered "treatment" growth because all their growth occurred during the treatment period. Individuals from the 1986 and 1987 year-classes contributed to growth measurements during both periods, e.g., for the 1986 year-class, growth in years one (1986) and two (1987) was pretreatment growth whereas growth in year three (1988) was treatment growth.

Scales were photographed using high contrast Kodak film (Tech Pan 2415) at 12x and 18x magnifications, and measured with a Sigma Scan digitizing tablet. A stage micrometer was also photographed at the two magnifications and used for calibrations during measurement. Scale radii, from focus to edge, were measured along five axes for each of 98 randomly selected scales (two scales per fish), to determine variation in scale radius. An axis bisecting the dorsal region (between the anterolateral and posterolateral ridges) showed the least variation and was selected for further growth measurements.

The distance from focus to annulus i (one of the first three annuli), and from focus to the scale's edge for fish older than 3 yr, was measured along the selected axis for five scales per fish and averaged to provide radius length (S_i) for each fish (Fig. 4-2). Annual growth increment (A_i) for each fish was then calculated as the distance between adjacent radii. Thus, whereas S_1, S_2 and S_3 represent radii at ages one, two and three, respectively, corresponding annual growth increments (A_i) were $A_1 = S_1$, $A_2 = S_2 - S_1$ and $A_3 = S_3 - S_2$. For each year-class, A_is were then averaged to obtain an average annual growth increment for each of the first three years.

My approach of measuring growth directly from annuli increments rather than from back-calculations is similar to the linear model approach to growth calculations proposed by Weisberg and Frie (1987). These authors suggested that most of the information on the growth history of an individual fish is contained in the increment between annuli on scales and other bony structures, and can be used as direct measures of intrinsic (age or size) and extrinsic (environmental or management practices) effects (see also Weisberg 1993). They assumed that inter-annuli distance is proportional to growth; if this distance is large, growth is large; if it is small, growth is less, thus comparisons between good and bad years can be made.

I used one-way ANOVA to determine if growth at a given A_i (i.e., for a specific age interval, for example, between ages 1 and 2) varied between years (i.e., among year-classes) during pretreatment and treatment periods. Where the ANOVA showed significant differences, I used the Student-Neuman-Keuls multiple range test (SNK) to determine which years were different. For each A_i, there were no significant differences among year-classes during the pretreatment period, therefore I calculated an average pretreatment A_i for each of the three growth years by pooling across year-classes. I then used the Dunnett's multiple comparison test to compare A_is, during treatment years with the corresponding pretreatment A_i to determine if growth differed between treatment and pretreatment years.

Comparison of length-weight relationships

To determine if condition of fish in Amisk Lake differed between pretreatment and treatment periods, I used analysis of covariance to compare length-weight relationships of cisco during the two periods. Pretreatment length-weight data, collected at similar time periods as during treatment years, were available only for May 1971 (provided by Alberta Environmental Protection, Natural Resources Service). Because fish condition varies with maturity, season, age and size, treatment data were restricted to samples collected in May, and to fish within the same size range (26.0-40.0 cm) as those in the 1971 sample. Although fish condition also varies with sex, I did not differentiate between sexes because sex was not reported for the 1971 data. Further, Carlander (1945) reported that body growth of cisco is not sexually dimorphic during pre-spawning period, when all my samples were collected. There were no significant differences among length-weight relationships for samples collected in May of 1990, 1991, and 1992, therefore I pooled data from all three years for comparison with 1971.

Population structure

The number of cisco caught in gill nets on each sampling day was recorded and their total lengths measured. I derived selectivity curves for my gill nets with the "length-dependent encounter probability" method developed for cisco by Rudstam et al. (1984). This method is based on the assumption that the probability of catching a fish of size l in a net of mesh size m may be separated into two independent probabilities: (1) encounter probability $P(E_l)$, the probability that the fish will encounter the net, (2) retention probability ($P(R_{lm})$), the probability that the fish will be retained by the net.

The coefficients of selectivity I obtained varied between 0.20 and 1.31 for 10.0 cm to 43.0 cm fish, the size range of cisco present in my study lakes (Appendix B, Fig. 7-1). The low selectivity coefficients of smaller fish suggest that the gang of nets was biased against them, therefore I grouped catches into 1-cm intervals and corrected for net selectivity to give a more accurate representation of population structure of cisco in the lakes.

Density and biomass of fish

Corrected length-frequency distributions were used to divide the cisco populations into three size groups, with total fish length ranges of 10-24.9, 25.0-34.9, and ≥ 35.0 cm. To estimate density and biomass, I pooled TS from hydroacoustic surveys also into three groups, -48 to -41, -40 to -38, and ≥ -37 dB, corresponding to the three fish length ranges, respectively. I examined the hydroacoustic data for autocorrelation of fish density estimates using three surveys, selected randomly, from the 1991 data set. Each survey was analysed for fish density at four time-steps, i.e., in

2-min, 4-min, 5-min, and 6-min data blocks and their mean lag-one autocorrelation coefficients were compared. The 5-min time-step (equivalent to 900 pings) was selected for further analyses because it had the least variable autocorrelation coefficients that were consistently < 20 % (see Williamson 1982; MacLennan and Mackenzie 1988). However, data from Baptiste Lake in August 1991 was analysed using a 10-min time step because single fish resolution was too low at the 5-min step to allow for reliable estimates of densities from the energy in multiple echoes. Parameters used in the hydroacoustic data analyses are summarized in Appendix B (Table 7-1 and 7-2).

Estimates of mean (±SE) fish density (fish·ha^{-1}) were calculated for the three size-classes within the 3-30 m water stratum during each 5 min of sampling. Biomass (kg·ha^{-1}) for each size-class was obtained by multiplying densities by the mean weight of cisco in that size-class derived from gill net catches in each year. Total densities and biomasses were then obtained by summation.

To investigate monthly variation in density and biomass, I used data from 1990 and 1991 for Baptiste and Amisk lakes, respectively, because these were the only years for which I had data for the full June-September period. Also, because data were available for August and September only for Amisk Lake in all three years, 1989-1991, I used data from these months to determine whole-lake changes in density and biomass between years. For this analysis, I combined surveys conducted in the two basins of Amisk Lake on a particular date by pooling the separate 5-min block sets and treating the data as though they came from one continuous survey. The cut-off point of -48 dB used for the hydroacoustic estimates meant that, progressively more young-of-the-year (YOY) cisco will be included in my estimates between June and September as fish grow. Because temporal variations in recruitment and growth bias comparisons of density and biomass derived from hydroacoustic surveys conducted at long time intervals (Hansson 1993), I compared whole-lake estimates separately for August and

September, to keep among-year comparisons to surverys conducted during similar periods of the growing season. Similarly, for Baptiste Lake, I used data for August only to compare density and biomass between 1990 and 1991; data were available from June through September in 1990 but for June and August only in 1991.

Due to the lack of pretreatment estimates of density and biomass, as well as the impracticality of replicating whole-lake experiments (Hurlbert 1984) such as the Amisk Lake experiment, application of inferential statistics was kept to minimum and was used not to assess treatment effects but rather to determine if there were real differences in density and biomass between the two locations (basins), and if the temporal (month) trends observed could have occurred independent of location (basin). In this regard, I used a two-way nested ANOVA to compare the 1991 monthly estimates of cisco densities and biomass between the two basins of Amisk Lake. I considered the sampling months and the two basins as fixed effects, and the 5-min blocks as a random effect that was nested within month and basin. To ensure additivity of variances, Bartlett's logarithmic transformation (Zar 1984) was applied to the data before analyses.

Results

Changes in hypolimnetic dissolved oxygen concentration

During the pretreatment year, mean monthly (June to August) hypolimnetic DO concentrations were similar in both basins of Amisk Lake and the hypolimnion was anoxic in July and August (Fig. 4-3). After initiation of oxygen treatment in 1988, monthly DO concentrations increased in both basins and DO concentrations during treatment years were significantly greater than the pretreatment DO concentrations (Dunnett's *t*-test, Table 4-1; Fig. 4-3). However, for each year during the treatment period, mean monthly DO concentrations were significantly greater in the treated basin than in the reference basin (paired *t*-test, Table 4-2; Appendix A, Table 6-3). Between 1989 and 1992, mean hypolimnetic DO concentrations remained above 2 $mg \cdot L^{-1}$ in the treated basin throughout summer but in the reference basin, DO concentrations usually dropped to < 1 $mg \cdot L^{-1}$ in August. In Baptiste Lake, high hypolimnetic DO concentrations occurred only in June and the water was generally anoxic from July through September. Although there was considerable annual variation in Baptiste Lake, there were no significant differences in mean DO concentrations in June between 1987-1992 (Fig. 4-3; Appendix A, Table 6-5).

Age distribution and population structure

Ages of cisco in both lakes ranged between 1-16 yr (Table 4-3). At all ages (except age 13), average length tended to be greater in Amisk Lake than in Baptiste Lake (Table 4-3). Nevertheless, in both lakes, there was considerable overlap in size-at-age among older fish ($\geq$ 4 yr). This overlap is also evident in length-frequency histograms as there were no distinct modes among fish $\geq$ 4 yr (Fig. 4-4). Sizes among younger age groups were more discrete (Table 4-3).

Based on size-at-age distributions, the cisco populations in both lakes fall into five age groups, age 0+, 1+, 2+, 3+, and $\geq$ 4+ (Fig. 4-4). In Amisk Lake, the population was composed largely of the 1+, and ≥ 4+ groups in 1989 and 1990 (except in September of 1990 when large numbers of 0+ were caught), with intermediate groups poorly represented. Although the 1+ group remained as a substantial proportion of the population in 1991 and 1992, representation of the intermediate groups increased whereas the proportion of the ≥ 4+ group declined. In Baptiste Lake, the population in 1990 was composed largely of the ≥ 4+ group, but in succeeding years, the 1+ group dominated the population (Fig. 4-4). In particular, the high abundance of 1+ fish in the 1992 populations indicated a strong 1991 year-class in both lakes.

Growth rate and condition

In Amisk Lake, age assignments to modal length-classes showed a general decrease in body size of juvenile fish in successive years, particularly, the 1+ and 2+ cohorts, but decrease in body size was not evident in the Baptiste Lake population (Fig. 4-4). In Amisk Lake, mean annual increment of fish scales during each of the first three years of life differed significantly during treatment years (1988-1991; Table 4-4). Scale increment in the first year (A_1) was similar for the early years of treatment (the 1988 and 1989 year-classes) and the pretreatment period, but decreased significantly, and consecutively in the later years of treatment (1990 and 1991, *P*s < 0.05, SNK), and compared with the pretreatment period (Dunnett's *t*-test, Table 4-5; Fig. 4-5). Similarly, A_2 decreased significantly in successive years between 1989 and 1991 ($P < 0.05$, SNK), and were significantly lower in 1989 and 1991 than pretreatment increment, however, A_2 for 1990 was not significantly different from pretreatment A_2. Although ANOVA indicated a significant difference in A_3 among the three treatment years (Table 4-4), paired comparisons did not reveal significant differences among individual years (*P*s > 0.05, SNK). Mean annual scale increment in the third year was least variable between treatment and pretreatment periods. Of the three A_3s estimated during treatment period, only the 1991 estimate differed significantly from the pretreatment estimate (Dunnett's *t*-test, Table 4-5; Fig. 4-5). The decrease in A_1 and A_2 of the Amisk Lake population is consistent with the decrease in modal lengths of the 1+ and 2+ age groups in the length-frequency histograms (Fig. 4-4).

In Baptiste Lake A_2 and A_3 varied from year-to-year but did not differ significantly between 1984 and 1991 (Fig. 4-5). First year scale increment differed among year-classes but not in a distinctive pattern; subsets corresponding to pretreatment (1984-1987) and treatment (1988-1991) periods in Amisk Lake differed significantly within but not between periods ($P < 0.05$, SNK). Mean annual scale increments for each of the first three years was lower in Baptiste than in Amisk Lake (Fig. 4-5). Slower growth rates in Baptiste compared with Amisk Lake is consistent with the differences observed in size-at-age (Table 4-3).

Length-weight relationships differed significantly between the 1971 sample and the treatment period samples ($P < 0.0001$, *t*-test). For a given length, fish were heavier (in better condition) in 1971 than during treatment period (Fig. 4-6).

Fish density and biomass

Except for August 1989, monthly estimates of cisco density and biomass were consistently greater in the treated than in the reference basin of Amisk Lake during the study period, typically being at least twice as high in the treated as in the reference basin (Fig. 4-7). In each year, peak fish densities occurred in September but the timing of peak biomass varied among years and was not always associated with peak density. However, for the 3-yr period, both peak density and biomass (mean ± SE) of 7410 ± 1017 fish·ha^{-1} and 1127 ± 56 kg·ha^{-1}, repectively, occurred in September 1990 (Fig. 4-7), and coincided with the dominance of YOY cisco (> 80%) in gill net catches (P.M.K. Aku, unpubl. data).

In 1991, cisco density and biomass generally decreased in the reference basin of

Amisk Lake as summer progressed but increased in the treated basin (Fig. 4-7). This reciprocal change between basins resulted in highly significant basin x month interaction terms for both density and biomass indicating that the temporal patterns were influenced by differences between the two basins (Table 4-6). In Baptiste Lake, density and biomass also increased progressively during the summer of 1990 (Fig. 4-7).

Based on estimates in August of each year, whole-lake fish density (mean ± SE) in Amisk Lake increased almost five times, from 353 ± 44 to 1872 ± 509 fish·ha^{-1}, between 1989 and 1991, while biomass tripled over the same period, from 102 ± 15 to 380 ± 105 kg·ha^{-1} (Fig. 4-8). Whole-lake estimates derived from surveys conducted in September also exhibited an increasing trend between 1989 and 1991 but the patterns were different. Unlike the August estimates which showed a steady increase in successive years, the peak density and biomass (3162 ± 944 fish·ha^{-1} and 507 ± 140 kg·ha^{-1}, respectively) of the September estimates occurred in 1990; both density and biomass increased six times between 1989 and 1990 but only five and three times respectively, between 1989 and 1991 (Fig. 4-8). Because YOY fish were typically < 13 cm it is likely that using an average weight based on TS distributions of fish length 10 to 25 cm may have resulted in overestimating the biomass of YOY fish. In view of this bias, I consider whole-lake estimates derived from the August surveys as better estimates than those derived from September surveys when YOY fish were most abundant. In contrast with the steady and substantial increases observed in Amisk Lake, there were no appreciable changes in the August estimates of cisco density and biomass in Baptiste Lake; density and biomass varied from 1888 ± 528 fish·ha^{-1} and 234 ± 32 kg·ha^{-1}, respectively, in 1990 to 2218 ± 653 fish·ha^{-1} and 189 ± 61 kg·ha^{-1} in 1991.

Discussion

Changes in fish distributions, density and biomass

Hypolimnetic oxygenation resulted in increased DO concentrations in the hypolimnion of Amisk Lake during the summers of treatment years relative to pretreatment years, and to Baptiste Lake. Although DO increased in both basins of Amisk Lake, concentrations were significantly higher in the treated basin than in the reference basin. Concurrent with higher DO concentrations, greater density and biomass of fish were supported in the basin that received oxygenation than in the reference basin. The greater areal estimates of density and biomass of cisco may indicate a more suitable hypolimnetic habitat in the treated basin compared with the reference basin. Cisco in Amisk Lake avoid water with DO concentrations < 1.3 $mg{\cdot}L^{-1}$ (Aku et al., in press) and differences in depth distributions of cisco between the two basins were more pronounced in late summer when hypolimnetic DO in the reference basin fell below this avoidance concentration. Thus, as a result of higher DO concentrations, hypolimnetic habitat for cisco during the summer extended 2-8 m deeper in the treated basin than in the reference basin between 1989 and 1991 (Aku et al. in press; see also Appendix B, Table 7-3 and 7-4), which may have enabled the treated basin to support a higher fish density and biomass than the reference basin.

Whole-lake estimates indicated that fish density and biomass increased dramatically, and consecutively in Amisk Lake from 1989 through 1991 that may be related to a general expansion in whole-lake cisco habitat during treatment years resulting from increased DO concentrations; increased DO concentrations in the reference basin resulted from advection of oxygen-rich water from the treated (Lawrence et al., in press). In contrast, fish density and biomass remained similar in 1990 and 1991 in Baptiste Lake where there had been no change in the oxygen regime. Although increased density and biomass could result from biological processes unrelated to oxygenation (Hansson 1993), comparison of fish distributions indicated that summer habitat for cisco expanded at least 9 m deeper during treatment years than in 1994 (post-treatment) when hypoxic conditions limited cisco in both basins to the top 6-m stratum. In addition, higher DO concentrations and better aerated sediments enabled cisco in the treated basin to feed deeper into the hypolimnion, and on benthic species (Aku and Tonn 1995). During the study period, depth distributions and densities of hypolimnetic zooplankton species and biomass of benthic macroinvertebrates also increased in both basins of Amisk Lake, with increases being more pronounced in the treated basin than in the reference basin (Field and Prepas, in press; Dinsmore and Prepas, in press). Cisco in the treated basin included higher proportions of the hypolimnetic cladoceran, *Daphnia longiremis*, in their diets than did those in the reference basin. In addition, benthic chironomids occurred predominantly in the diets of cisco in the treated basin only. A consequence of increased available prey base would be that the treated basin could have supported a higher biomass than the reference basin and this could have contributed to the increase in whole-lake biomass.

Changes in density and biomass of cisco in the two basins of Amisk Lake during the summer of 1991 suggest that fish in the reference basin avoided hypoxic conditions as summer progressed by moving into the better oxygenated treated basin. In the absence of catastrophic events, fish density and biomass should increase increase temporally due to recruitment of YOY fish and accretion, (Hansson 1993). However, this was not the case in the reference basin of Amisk Lake, instead, density and biomass decreased. Since the major difference between the two basins during this period was in their hypolimnetic DO concentrations, the systematic temporal decrease in the reference basin in contrast with the increase in the treated basin indicates a behavioral response to the improved habitat conditions in the treated basin. The temporal pattern observed in Baptiste Lake during the summer of 1990 may also reflect responses related to availability of oxygen, reinforcing the behavioral response hypothesis.

Although I do not have data on oxygen conditions in the north basin of Baptiste Lake, this basin has a higher macrophyte coverage than the south basin, is shallower than the south basin, and anoxic hypolimnetic water reaches up to 7 m during summer compared with 10 m in the south basin (Prepas 1990). Hence, higher respiratory oxygen consumption during the night, when my hydroacoustic surveys were conducted, coupled with a smaller volume of well-oxygenated water, could force cisco to move from the north basin into the relatively better aerated south basin similar to that observed in Amisk Lake.

Changes in population structure and growth rate

The differential success of treatment-period year-classes between the two lakes suggested that oxygenation enhanced fish survival in Amisk compared with Baptiste Lake. For example, strong year-classes occurred in both Amisk and Baptiste lakes in 1990 and 1991, and dominated cisco populations in the subsequent year in both lakes (Fig. 4-4). However, whereas the 1990 year-class in Amisk Lake continued to contribute substantially to the population in 1992, the 1990 year-class in Baptiste Lake was poorly represented in 1992. Regional pulses of strong year-classes are typical of coregonid populations, and have been correlated with weather events (Miller 1952; Lawler 1965; Healey 1980). Thus, the occurrence of strong year-classes in both lakes in 1990 and 1991 could be a regional event; the proximity of Amisk and Baptiste lakes would suggest that weather conditions would influence recruitment similarly in both lakes. However, from his study of variations in year-class strength of cisco populations in several northern Wisconsin lakes, Hile (1936) suggested that year-class success is dependent on local events within a lake. Therefore, the higher survival of the 1990 year-class in Amisk compared with Baptiste Lake may reflect such local events, the most significant being most likely related to differences in oxygen regime.

Comparison of length-weight relationships between 1971 and the treatment period showed that cisco were in better condition during 1971 than during treatment years. The poorer conditions of fish during treatment years compared with the pretreatment period could be the result of a combination of increased densities resulting from the oxygenation and weak exploitation. The higher conditions in 1971 may have been a compensatory response to higher exploitation rates. Commercial harvest of cisco in Amisk Lake averaged 8,560 $kg \cdot yr^{-1}$ between 1944-1966, and rose to a peak of 13,170 $kg \cdot yr^{-1}$ for 1966-1973, but the fishery has since been restricted, resulting in rates of 2,860 $kg \cdot yr^{-1}$ by 1987 (H. Norris, Alberta Environmental Protection, Natural Resources Service, unpubl data). Although there are no estimates of commercial harvest during treatment years, there has been a steady decline in the harvest since 1987 and the Amisk Lake population could be considered unexploited (H. Norris, pers. com.).

Changes in growth rate of fish can be used to assess the effect of environmental manipulations. If growth at a given age varies haphazardly between years, differences may be attributed to natural year-to-year variations in the environment but if growth rate increases or decreases systematically, the changes may be due to either a systematic sampling bias or to some other time trend that could be attributed to an environmental or management change (Weisberg and Frie 1987; Weisberg 1993). Previous hypolimnetic studies provide very limited information on changes in growth rates of fish. The few that did so all reported increases in growth during oxygenation (Fast 1973; Overholtz et al. 1977; Garrell et al 1978), but in all cases, no data were provided, and no comparisons were made with pretreatment growth rates. Therefore, the decrease in growth rate of cisco in Amisk Lake during treatment period compared with the pretreatment period was somewhat unanticipated but should not have been surprising.

The more favorable conditions of increased, suitable hypolimnetic habitat coupled with increases in food base may have led to an expectation of increased growth rate in Amisk Lake. However analyses of guts collected in 1989 and 1992 indicated that higher proportions of cisco ≤ 3 yr had empty stomachs compared with older fish suggesting exploitative advantage of larger fish over the smaller ones (P.M.K. Aku, unpubl., Chapter 3). Thus, an increase in fish density, coupled with strong recruitment events, apparently led to intraspecific competition for food that culminated in depressing growth rates. An inverse relationship between growth and density of fish populations is well established (Townsend 1989; Tonn et al. 1994) and density-dependent growth has been reported for cisco populations (Hile 1936; Carlander 1945; Hoff and Serns 1983). Variations in growth rates occur naturally in unexploited fish populations (Healey 1980), as evident from the Baptiste and pretreatment Amisk Lake populations. However, the systematic decrease in growth rate of the Amisk Lake population in treatment years but not during pretreatment period suggests a negative indirect influence of the oxygen treatment.

Because the Amisk Lake study is the first whole-lake oxygenation experiment to monitor fish density and biomass, the changes observed from 1989 to 1991 were not easily comparable with other aeration studies. Nevertheless, in parallel with increased hypolimnetic DO concentrations, fish density and biomass increased in Amisk Lake suggesting that, through expansion of suitable summer habitat for fish, hypolimnetic oxygenation could allow a lake to support higher density and biomass of fish. Improved habitat conditions could also enhance fish survival. The manipulation also underlined the importance of density-dependent interactions; because benefits derived from hypolimnetic oxygenation, such as enhanced fish survival and increased densities, may lead to negative effects on growth rates of fish in unexploited populations, higher sustainable yields could be attained if oxygenation is combined with other lake management practices such as regulated exploitation rates.

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Table 4-1. Summary of Dunnett's multiple comparison test of mean monthly hypolinmetic dissolved oxygen concentrations between pretreatment (1987, designated as "control') and treatment years in the treated and reference basins of Amisk Lake. Degrees of freedom (df) for all comparisons is 18.

		Treated basin		Reference basin	
Month	Group Comparison	Difference between means	MSE	Difference between means	MSE
June	1990 - control	6.227*	1.1106	3.955*	0.3105
	1992 - control	6.142*		1.980*	
	1991 - control	3.494*		1.964*	
	1989 - control	3.135*		1.395*	
	1988 - control	1.983^{ns}		-0.320^{ns}	
July	1990 - control	4.474*	0.5259	3.152*	0.2394
	1992 - control	4.405*		1.707*	
	1989 - control	3.660*		1.667*	
	1991 - control	2.223*		1.355*	
	1988 - control	1.950*		0.412	
August	1992 - control	2.411*	0.3375	1.250*	0.0869
	1989 - control	2.143*		1.033*	
	1991 - control	2.031*		0.715*	
	1990 - control	1.935*		0.442^{ns}	
	1988 - control	0.766^{ns}		0.330^{ns}	

ns = $P > 0.05$; * = $P < 0.05$

Table 4-2. Paired comparison of mean monthly hypolimnetic dissolved oxygen concentrations between the treated and reference basins of Amisk Lake during treatment years (1988-1992)

Month	Mean difference	SE of mean	*t*-value	df	*P*
June	2.54	0.453	5.60	4	0.005
July	2.04	0.311	6.56	4	0.003
August	1.46	0.299	4.88	4	0.008
September	1.38	0.642	2.14	3	0.122

Table 4-3. Comparisons of mean (±SE) total length (cm) at age, of cisco populations in Amisk and Baptiste lakes, calculated from pooled samples collected in May of 1990, 1991, and 1992. Also provided are the student t-statistics (*t*-value).

	Amisk Lake		Baptiste Lake		
Age (yr)	N	Total length (cm)	N	Total length (cm)	*t*-value
1	73	14.1 ± 0.19	16	13.9 ± 0.24	0.35^{ns}
2	76	22.3 ± 0.22	45	19.3 ± 0.51	6.19***
3	36	28.3 ± 0.47	13	27.0 ± 1.07	1.27^{ns}
4	2	33.5 ± 0.85	16	31.7 ± 0.27	2.13^{ns}
5	1	36.7	21	33.5 ± 0.29	--
6	8	36.7 ± 0.46	17	34.1 ± 0.34	4.29***
7	27	38.1 ± 0.23	18	35.1 ± 0.31	8.04***
8	34	38.5 ± 0.26	9	35.8 ± 0.48	4.61***
9	22	39.0 ± 0.30	16	37.2 ± 0.36	3.68***
10	4	39.9 ± 0.60	5	37.4 ± 0.54	3.06*
11	5	39.6 ± 0.64	7	37.9 ± 0.32	2.55*
12	1	41.6	5	38.3 ± 0.57	--
13	6	40.2 ± 0.93	4	40.2 ± 0.73	0.12^{ns}
14	3	40.9 ± 1.45	3	38.4 ± 1.13	1.36^{ns}
15	5	40.3 ± 0.53	--	--	--
16	1	42.7	1	38.1	--

ns = $P > 0.05$; * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$

Table 4-4. ANOVA table for the comparison of growth rate of cisco in the first three years of life during treatment years in Amisk Lake, and first year growth during 1984-1991 in Baptiste Lake. A_1, A_2, and A_3 represent annual growth during the first, second and third years, respectively. ANOVA for A_2 and A_3 for Baptiste Lake not shown because there were no significant differences between years.

Lake	Annual growth	Source	df	Sum of squares	Mean square	F value	P
Amisk	A_1	Model	3	779329.06	259776.40	25.66	0.0001
		Error	96	971765.13	10122.55		
		Total	99	1751094.19			
	A_2	Model	2	673110.25	336555.10	27.05	0.0001
		Error	72	895877.54	12442.74		
		Total	74	1568987.80			
	A_3	Model	2	209891.68	104945.84	5.05	0.0122
		Error	33	686266.40	20795.95		
		Total	35	896158.09			
Baptiste	A_1	Model	7	219492.33	31356.05	7.93	0.0001
		Error	57	225409.83	3954.56		
		Total	64	444902.15			

Table 4-5. Summary of Dunnett's multiple comparison of growth rate of cisco between treatment and pretreatment (control) years in Amisk Lake. A_1, A_2, and A_3 represent annual growth during the first, second and third years, respectively.

Annual growth	Group comparison	Simultaneous lower confidence limit	Difference between means	Simultaneous upper confidence limit	df	MSE
A_1	1988 - control	-37.78	68.72^{ns}	175.22	136	10770.73
	1989 - control	-49.57	7.60^{ns}	64.78		
	1990 - control	-185.15	-126.09*	-67.04		
	1991 - control	-290.93	-210.93*	-129.70		
A_2	1989 - control	30.72	138.79*	246.87	112	12001.18
	1990 - control	-52.67	5.35^{ns}	63.37		
	1991 - control	-222.42	-158.17*	-91.91		
A_3	1990 - control	-31.12	97.94^{ns}	227.00	71	16580.48
	1988 - control	-205.88	22.06^{ns}	250.01		
	1991 - control	-170.17	-91.46*	-12.74		

ns = $P > 0.05$; * = $P \leq 0.05$

Table 4-6. ANOVA table for the comparison of density estimates of cisco between the two basins of Amisk Lake during the summer of 1991. ANOVA table for biomass not provided because results are the same as for density.

Source	df	Sum of squares	Mean square	F value	P
Model	51	19346.31	379.34	2.12	0.0006
Error	104	18570.49	178.56		
Corrected total	155	37916.79			
		Type III SS			
Basin	1	9329.03	9329.03	52.25	0.0001
Month	3	486.00	162.00	0.91	0.4403
Basin x month	3	3023.13	1007.71	5.64	0.0013
Block (basin x month)	44	4811.82	109.36	0.61	0.9655

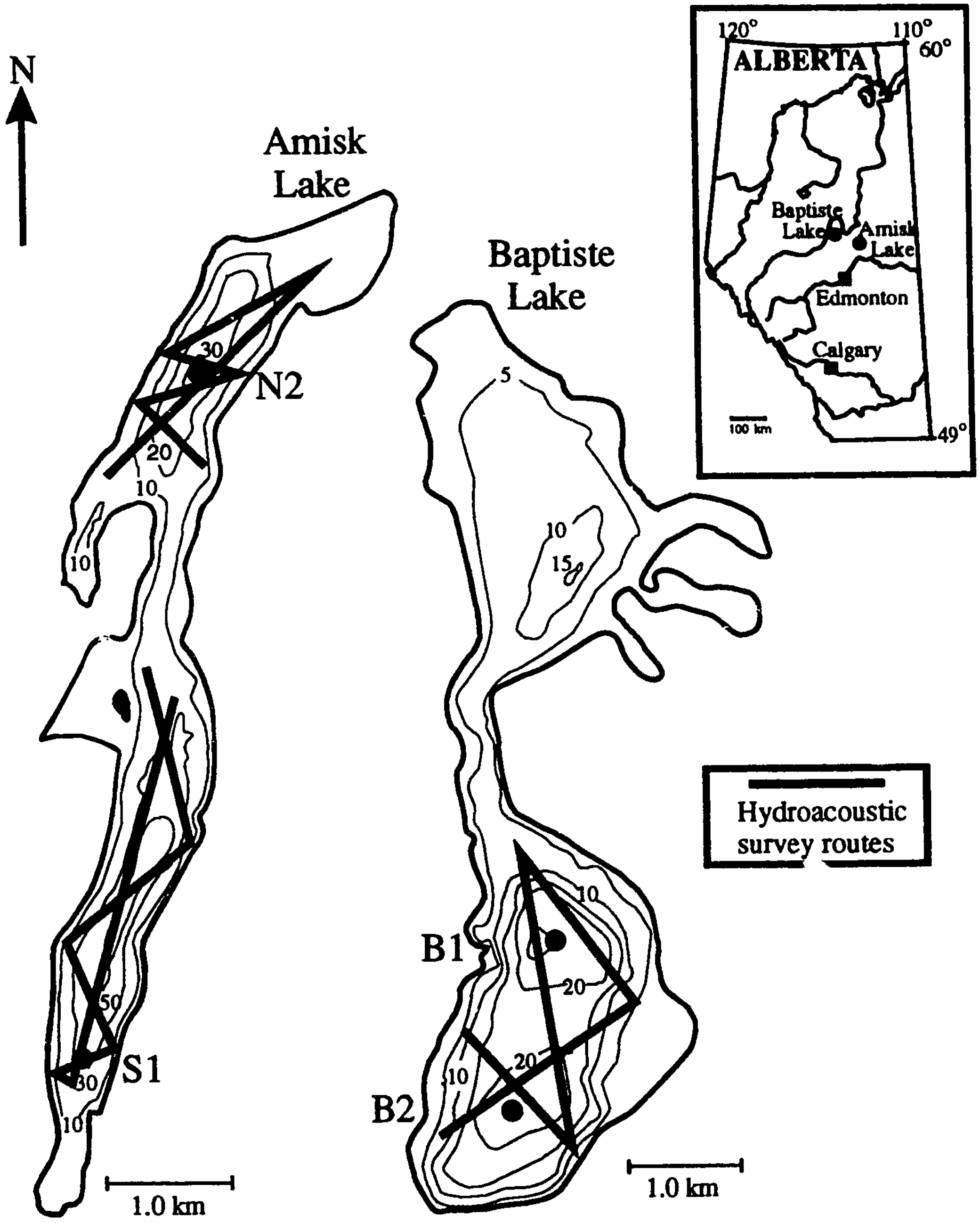


Fig. 4-1. Bathymetric map (with 10-m depth contours) of Amisk and Baptiste lakes, showing sampling sites (black circles: N2, S1, B1, B2) and hydroacoustic survey routes (heavy black lines); the oxygen diffuser was located at site N2. Insert, is map of the province of Alberta.

Fig. 4-2. Scale of a 9 yr old cisco (age determined from otolith) from Amisk Lake caught in May 1991 showing the first three annuli used in calculating growth rates.

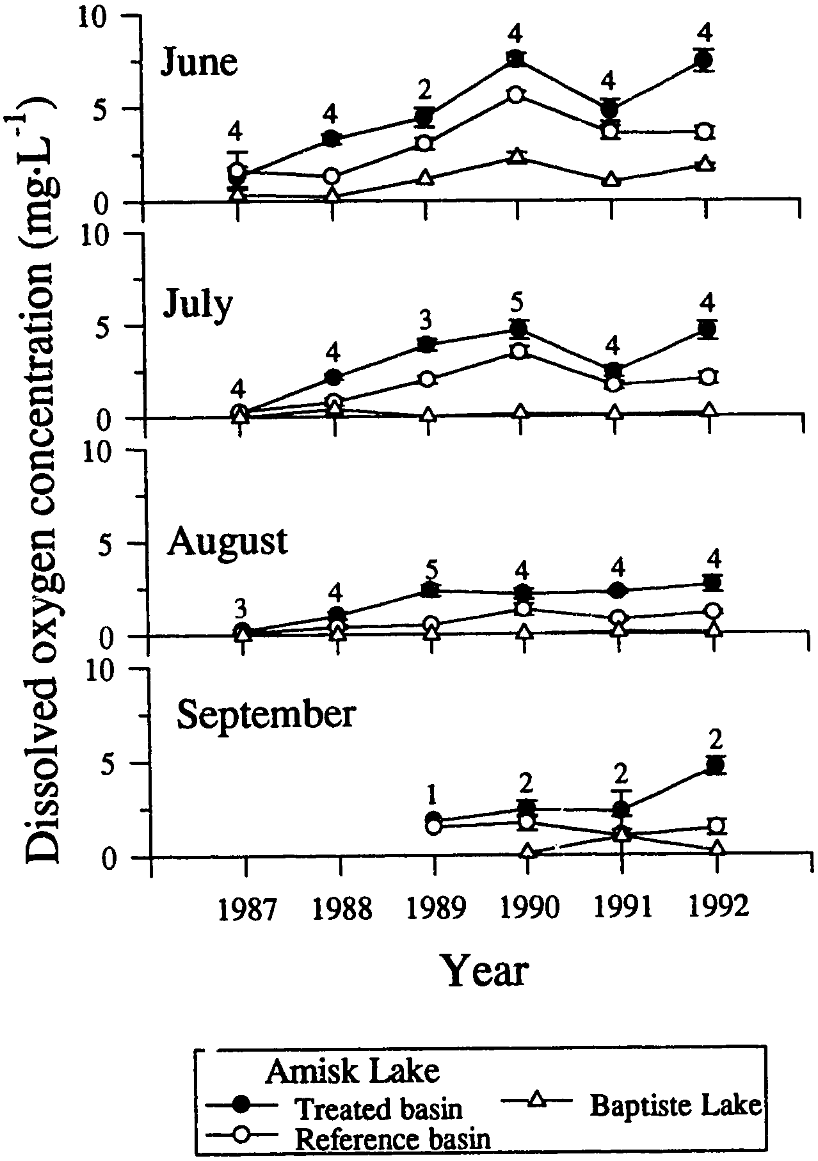
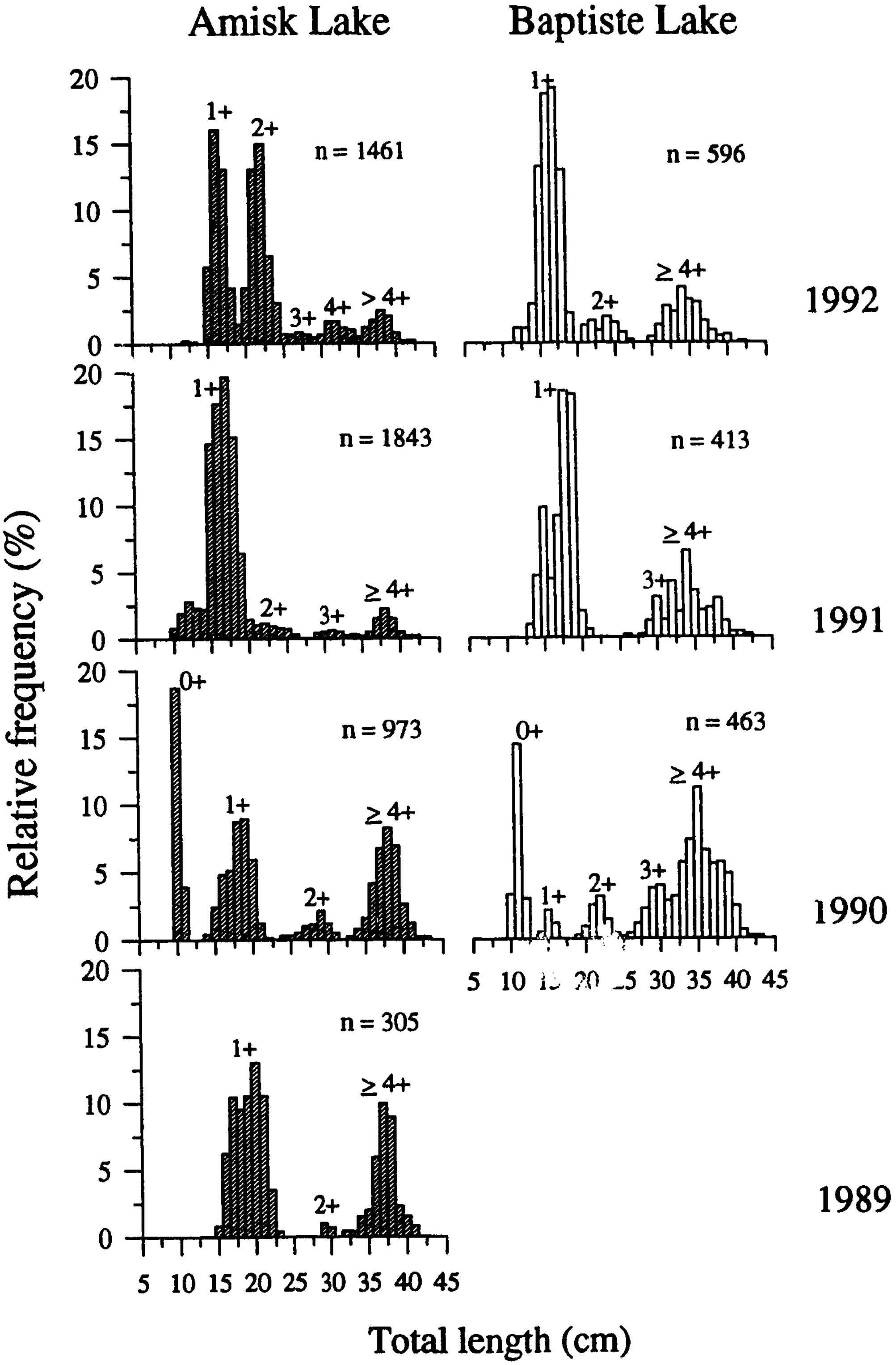


Fig. 4-3. Mean (±SE) monthly (June-September) hypolimnetic dissolved oxygen concentrations in Amisk and Baptiste lakes, from 1987-1992. Indicated are the number of sampling dates used in calculating means for Amisk Lake basins. Sample sizes for Baptiste Lake were two sampling dates per month, except for July and August, 1987, for which only single sampling dates were available.

Fig. 4-4. Length-frequency distributions of cisco in Amisk and Baptiste lakes during the summers of 1989-1992 (Baptiste Lake was not sampled in 1989). Frequencies were corrected for gill net selectivity using the size-encounter probability coefficient (Rudstam et al. 1984). Indicated are ages assigned to modal length classes, and corrected sample size (n).


Amisk Lake
Baptiste Lake
Relative frequency (%)
Total length (cm)
1992
1991
1990
1989
n = 1461
n = 596
n = 1843
n = 413
n = 973
n = 463
n = 305
1+
2+
3+
4+
> 4+
≥ 4+
0+
0
5
10
15
20
5 10 15 20 25 30 35 40 45

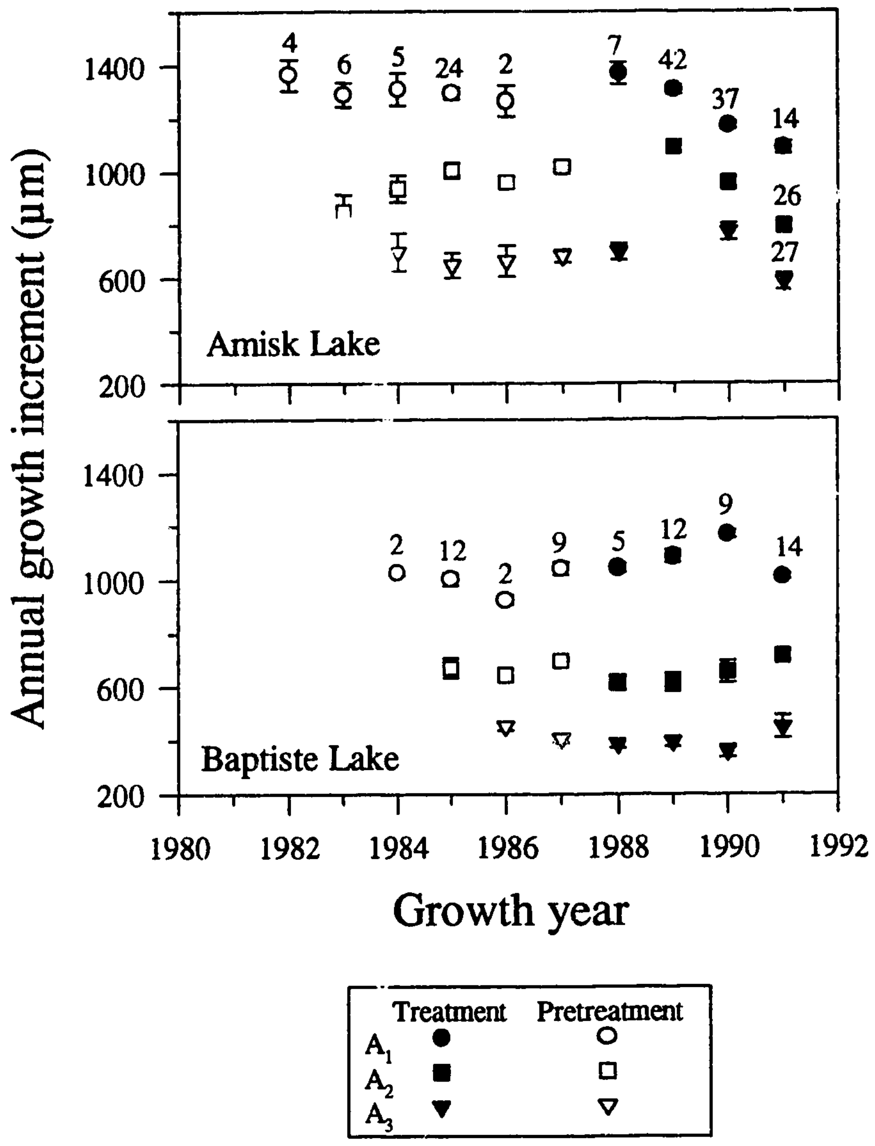


Fig. 4-5. Mean (±SE) annual growth increments on scales of cisco during the first three years of life (A1, A2, A3) in Amisk and Baptiste lakes during treatment and pretreatment years. Samples were collected from Amisk Lake in 1991-1992, and from Baptiste Lake in 1992. Sample sizes are number of fish from a year-class.

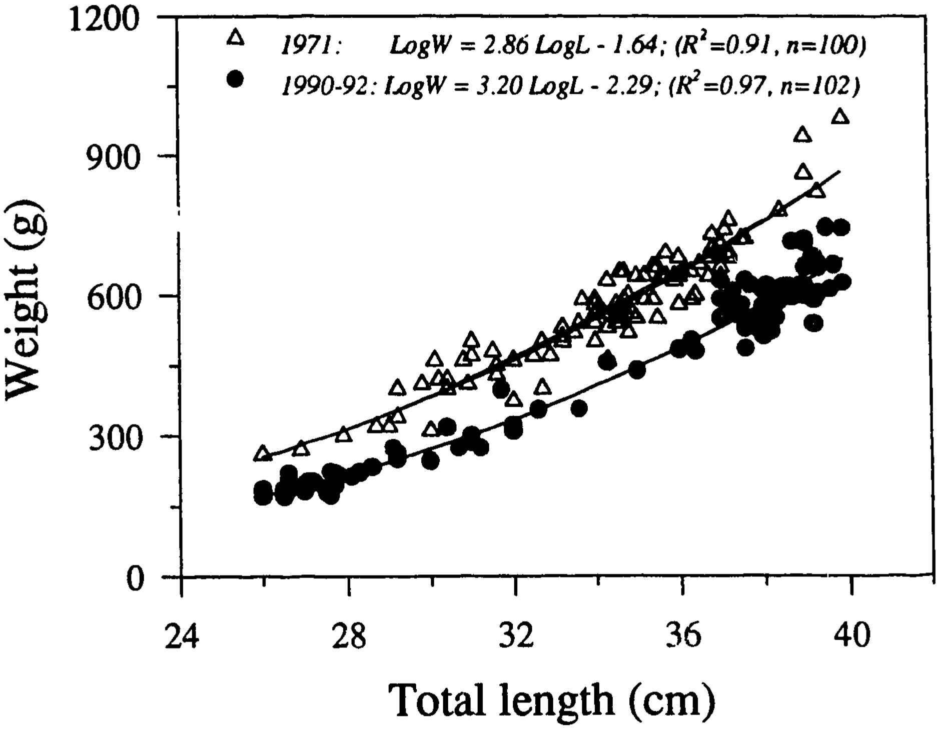
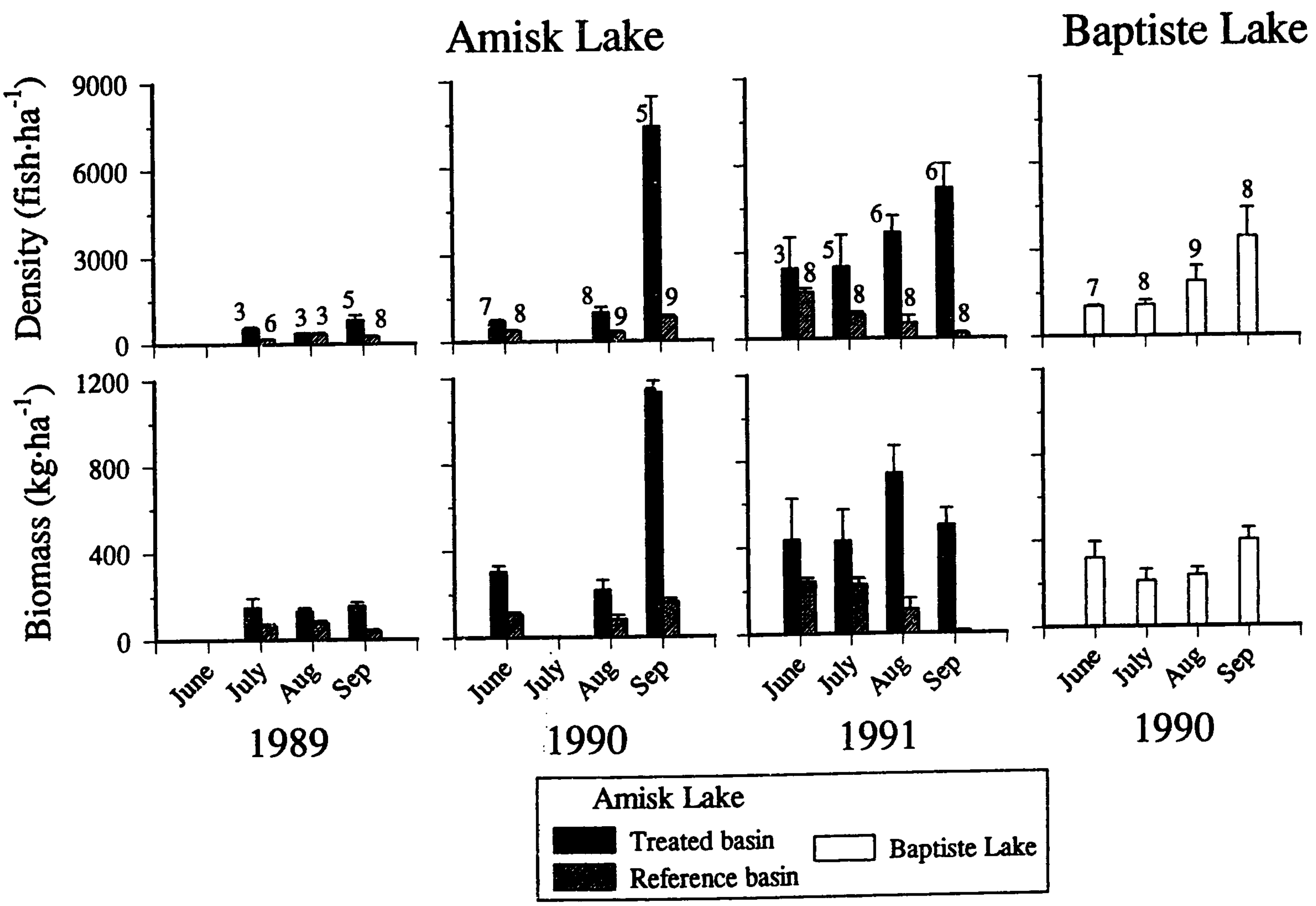


Fig. 4-6. Length-weight relationships of cisco in Amisk Lake from pretreatment (1971) and treatment (1990-1992, pooled) years. Only samples collected during May of each period were used. Equations are log-transformed length-weight linear regressions; LogL represents $\log_{10}$ total length (cm) and LogW is $\log_{10}$ weight (g).

Fig. 4-7. Mean (±SE) monthly density and biomass of cisco in the two basins of Amisk Lake during the summers of 1989 to 1991, and in Baptiste Lake during the summer of 1990. Sample sizes are the number of 5-minute hydroacoustic sampling units used to calculate means.


Amisk Lake
Baptiste Lake
Density (fish·ha-1)
9000
6000
3000
0
Biomass (kg·ha-1)
1200
800
400
0
3
6
3 3
5
8
7
8
8
9
5
9
3
8
5
8
6
8
6
8
7
8
9
8
June
July
Aug
Sep
1989
1990
1991
1990
Amisk Lake
Treated basin
Reference basin
Baptiste Lake

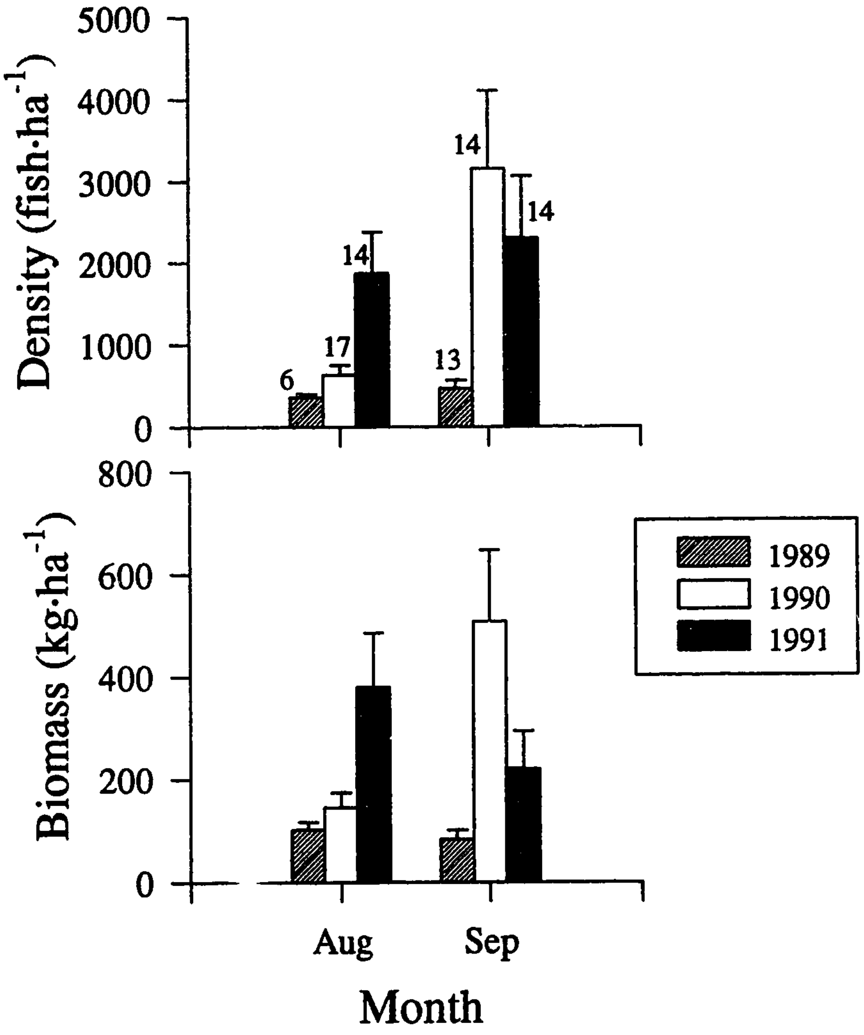


Fig. 4-8. Mean (±SE) monthly density and biomass of cisco in Amisk Lake from 1989-1991. Bar labels represent the number of 5-minute hydroacoustic sampling units used to calculate means.

Chapter 5

General discussion and conclusions

General discussion and conclusions

Hypolimnetic oxygenation resulted in increased DO (dissolved oxygen) concentrations in the deep waters of Amisk Lake from 1988 through 1993, relative to pretreatment and post-treatment years, and to nearby, untreated Baptiste Lake (Prepas and Burke, in press). In response to increased DO concentrations in Amisk Lake, summer habitat for the cold-water cisco expanded into the upper hypolimnion during treatment years compared with the post-treatment year (1994); maximum depth distributions of cisco during summer were up to 9 m deeper in treatment years compared with the post-treatment year. In contrast, the hypolimnion of untreated Baptiste Lake remained anoxic throughout summer, and cisco were restricted to epilimnetic waters.

During treatment years, the most discernable differences in vertical distributions of fish between the treated and reference basins of Amisk Lake occurred during peak thermal stratification in late summer. Cisco in Amisk Lake avoided water with DO concentrations < 1.3 mg·L^{-1} (Chapter 2). Although DO concentrations increased in the reference basin due to advection of oxygen-rich water from the treated basin, hypolimnetic DO concentrations remained significantly higher in the treated basin than in the reference basin throughout the study period (Lawrence et al., in press; Prepas and Burke, in press). Indeed, hypolimnetic DO remained above avoidance concentration throughout summer in the treated basin, but fell below it by mid-August in the reference basin. With higher DO concentrations, late summer habitat for cisco extended up to 8 m deeper in the hypolimnion of the treated basin than in the reference basin.

However, elevating DO in the lower hypolimnion of Amisk Lake to concentrations barely above those avoided by cisco was not enough to ensure their use of this habitat. Cisco response to hypolimnetic oxygenation was influenced by the selection of water with preferred (optimum) temperatures and DO concentrations.

Cisco were generally most abundant at depth strata within which both temperature and DO concentrations were within the preferred ranges. This suggests that the magnitude of alteration introduced into the environment, combined with behavioral and physiological requirements of fish, are key variables that should be considered during oxygenation experiments. Although previous hypolimnetic aeration studies reported increased depth distributions of fish (e.g., Fast 1973; Overholtz et al. 1977; Garrell et al. 1978), the Amisk Lake fish study is the first to link the exploitation of an expanded hypolimnetic habitat to both oxygen and temperature preferences among cold-water fish. Controlled laboratory experiments that vary both DO concentrations and temperature may provide additional understanding of fish responses to the interactive effects of these factors.

Hydroacoustic data indicated that cisco in Amisk Lake also responded to hypolimnetic oxygenation by migrating from deteriorating oxygen conditions in the reference basin into the better aerated treated basin as summer progressed. This behavioral response, coupled with the deeper vertical extensions of fish habitat, resulted in the treated basin supporting a density and biomass of fish that was at least twice as great as in the reference basin.

Although a primary target of most oxygenation studies is enhanced cold-water fish populations, long-term effects, such as changes in growth rate, population structure, density, and biomass, have not been quantified, because previous studies were of short duration (1-2 yr). The relatively long duration of the Amisk Lake experiment (5 yr) allowed for the evaluation of some of these long-term effects. Whole-lake increases in density and biomass were the most dramatic changes to the cisco population in Amisk Lake during oxygenation. Concurrent with the increased DO concentrations and expanded habitat, whole-lake fish density increased almost five-fold, and corresponding biomass tripled, during the first three years of treatment. However, this increased fish production may have contributed to decreased growth rates and condition of fish during treatment years compared with pretreatment data. In contrast, in nearby, untreated Baptiste Lake, where there had been no change in the oxygen regime, density, biomass, and growth rate of cisco did not change.

Although the manipulation indicated that benefits derived from hypolimnetic oxygenation, such as increased densities, may lead to reduced growth rates of fish in unexploited populations, this should not undermine the efficacy of hypolimnetic oxygenation as a tool for enhancing cold-water fish populations. Improved habitat conditions could also enhance fish survival and recruitment that will affect population structure, and thereby influence future production. High sustainable yields of fish could be attained if oxygenation is combined with other lake management practices, such as regulated exploitation rates (see Healey 1980).

Advection of oxygen-rich water from the treated basin may have reduced the rate of hypolimnetic oxygen depletion in the reference basin of Amisk Lake, thereby minimizing differences in DO concentrations and fish responses. Due to the difficulty in replicating whole-lake experiments, most such studies employ reference systems to determine whether the system being manipulated changed or not (Hurlbert 1984; Carpenter 1993). Using Baptiste Lake as a second reference system helped elucidate some of the changes to the ecology of cisco in Amisk Lake (e.g., expanded hypolimnetic habitat, enhanced survival, increased biomass, and decreased growth rates) that may have been influenced by the oxygen treatment.

Concurrent with fish responses, there were changes at other trophic levels in Amisk Lake during the oxygen treatment that provided an opportunity to examine interactions between these trophic levels and fish. During treatment years, the spring mixed period lasted several weeks (> 4 wk) longer than during pretreatment years, and the euphotic zone, which was previously limited to epilimnetic depths, extended into the metalimnion (Webb et al., in press; M.D. Agbeti, Dept. of Biological Sciences, Univ. of Alberta, unpubl. data). Although increased phytoplankton biomass in deep water during treatment years may be largely related to changes in these physical factors (Webb et al., in press), indirect effects of fish may also have played a role. Nutrient excretion by zooplanktivorous fish can increase nutrient recycling and thereby increase phytoplankton biomass (Kitchell et al. 1975; Lamarra 1975; Reinertsen et al. 1986). Therefore, the increased biomass and deeper depth distributions of cisco during treatment years could have resulted in higher nutrient excretion rates that facilitated algal growth in deeper waters.

During treatment years, the phytoplankton community in Amisk Lake shifted from a cyanobacterial dominated assemblage to diatom- and cryptophyte-dominated assemblage (Webb et al., in press; M.D. Agbeti, unpubl. data). Because cryptophytes and diatoms are more desirable food sources than cyanobacteria for zooplankton (Kerfoot 1987; Vanni and Temte 1990), the shift in phytoplankton assemblage should have enhanced zooplankton production that should translate, through zooplanktivory, into higher biomass of deep water fish species. Thus, the increased biomass of cisco in Amisk Lake during treatment years may have been supported by increased zooplankton production. Increases in zooplankton standing crop may have been masked by increased fish predation pressure, particularly within metalimnetic and upper hypolimnetic waters where cisco were most abundant. In such situations, evidence of increased zooplankton production may be sought from changes in life history parameters such as size at maturity, clutch size and reproductive output. Severe fish predation increases fertility and reproductive output among cladoceran zooplankton (Culver et al. 1984; Sorano et al. 1993), therefore, future oxygenation studies aimed at enhancing both fish and zooplankton populations should include evaluations of zooplankton production and not only biomass.

The oxygen treatment in Amisk Lake also influenced interactions between cisco and their food resources. Higher DO concentrations enabled cisco in the treated basin to feed deeper into the hypolimnion, and more on benthic species, than those in the reference basin. Although zooplankton and benthic macroinvertebrate prey for cisco increased initially during oxygenation (Field and Prepas, in press; Dinsmore and Prepas, in press), increased fish density apparently resulted in a substantial reduction in per capita food levels in later years. Reduced per capita food levels could have contributed to the decrease in growth rate of the Amisk Lake cisco during treatment years.

The interaction between zooplankton and planktivorous fish is the cornerstone of the top-down concept in lake management (Hrbáček 1961; Brooks and Dodson 1965; Shapiro and Wright 1984; Carpenter et al., 1987). Among the several ecological variables that can be altered in whole-lake manipulations, a reduction in predatory pressure on zooplankton is essential to maximize filtration capacity of herbivorous zooplankton (McQueen et al. 1989; Kerfoot 1987; Crowder et al. 1988). Reducing the densities of planktivorous fish has been the typical approach used to reduce zooplankton losses. Although planktivorous fish biomass increased during the Amisk Lake oxygenation, reduction in zooplankton losses to fish predation was achieved through alternative means. The oxygenation expanded hypolimnetic habitat, enabling cisco to distribute into, and spend most of the time in deeper water. The result of this habitat shift by cisco likely was reduced predatory pressure on zooplankton species within the euphotic zone.

Because oxygenation was initiated to reduce internal nutrient recycling, the Amisk Lake experiment may be considered a bottom-up approach to lake management. However, the linkages between the various trophic levels re-emphasises the notion that both bottom-up and top-down effects operate simultaneously to influence the structure and function of aquatic ecosystems (Mills and Forney 1988; Carpenter et al. 1987; McQueen et al. 1989; Demelo et al. 1992). Because of the multiple linkages and complex interactions that occur in these ecosystems, exact predictions are not always possible during whole-lake manipulations. Through monitoring physical, chemical and biological responses during the whole-lake oxygenation experiment in Amisk Lake, including those of planktivorous fish, some of the changes that did occur were identified, and this should help aquatic ecologists gain insights into the complexity of lacustrine food webs, and in formulating management guidelines.

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Chapter 6

Appendix A: Dissolved oxygen and temperature data for Amisk and Baptiste lakes

Table 6-1. Dissolved oxygen (mg·L^{-1}) profiles in the treated (site N2) and reference (site S1) basins of Amisk Lake on fish sampling nights in 1990, measured with a HYDROLAB™ SURVEYOR II.

Treated basin (site N2)

Depth (m)	May 23	June 5	June 20	July 11	July 25	Aug. 11	Aug. 23	Sep. 15	Sep. 26
0	13.9	13.0	11.9	13.6	11.1	11.0	8.9	10.1	9.8
1	13.9	12.7	11.8	13.6	10.9	11.0	8.9	10.0	9.8
2	13.9	12.4	12.2	13.5	9.3	10.8	8.7	9.7	9.7
3	13.9	12.4	11.7	13.6	7.6	10.2	8.5	9.1	9.6
4	13.8	12.2	9.6	13.4	4.3	9.0	8.4	8.9	9.0
5	13.6	12.1	9.1	12.2	2.7	4.9	8.3	8.5	8.7
6	12.7	10.4	8.5	7.9	3.3	5.1	8.2	7.8	8.1
7	11.9	9.7	8.0	5.9	5.0	5.4	7.0	6.2	7.7
8	11.0	9.4	8.3	5.2	4.7	3.8	4.8	5.1	6.7
9	10.2	9.1	8.3	5.3	4.6	2.9	4.3	3.9	6.0
10	9.5	9.0	8.4	6.2	3.9	2.7	4.0	3.3	5.2
11	9.5	8.8	7.7	6.3	3.9	2.8	3.4	3.3	4.9
12	9.6	8.2	7.4	6.1	3.9	2.7	2.9	2.4	4.2
13	9.0	7.7	7.4	5.7	3.7	2.6	2.0	1.2	3.7
14	8.4	7.4	7.3	5.6	3.8	2.8	1.9	1.1	3.5
15	8.3	7.3	7.2	5.3	3.7	2.6	1.9	1.1	2.8
16	8.2	7.2	7.1	5.3	3.6	2.5	1.8	1.0	1.9
17	8.0	7.0	6.8	5.2	3.6	2.5	1.4	1.1	1.7
18	7.8	7.0	6.7	5.0	3.5	2.5	1.5	1.0	1.3
19	7.7	7.0	6.4	4.9	3.5	2.3	1.5	0.8	1.0
20	7.7	6.9	6.3	4.9	3.4	2.1	1.6	0.6	0.8
21	7.6	6.9	6.1	4.7	3.2	1.9	1.6	0.5	0.6
22	7.5	6.8	6.0	4.5	3.2	1.7	1.6	0.4	0.5
23	7.4	6.7	5.9	4.5	3.1	1.7	1.5	0.3	0.5
24	7.3	6.5	5.7	4.3	2.9	1.5	1.4	0.2	0.4
25	7.3	6.4	5.7	4.3	2.7	1.5	1.2	0.2	0.4
26	7.3	6.3	5.5	4.2	2.6	1.4	1.2	0.2	0.4
27	7.3	6.1	5.5	4.2	2.3	1.3	1.0	0.2	0.4
28	7.3	6.1	5.4	4.1	2.3	1.3	0.9	0.2	0.3
29	7.3	6.1	5.3	4.1	2.2	1.3	0.8	0.2	0.3
30	7.3	6.1	5.2	4.1	2.2	1.2	0.8	0.2	0.3

Table 6-1 continued.

Reference basin (site S1)

Depth (m)	May 23	June 5	June 20	July 11	July 25	Aug. 11	Aug. 23	Sep. 15	Sep. 26
0	12.7	12.1	11.8	13.2	12.0	11.1	9.2	10.1	9.4
1	12.7	12.1	11.8	13.3	11.9	11.0	7.9	9.5	9.3
2	12.7	12.1	11.8	13.0	11.0	11.0	7.8	9.5	9.0
3	12.7	12.1	11.8	10.0	10.4	10.5	6.5	9.4	9.2
4	12.7	12.0	11.5	7.6	8.2	8.6	5.9	9.3	9.2
5	12.7	12.0	10.2	6.1	4.5	1.8	3.2	9.2	9.1
6	12.1	11.9	9.4	5.5	1.9	1.2	1.6	9.2	9.0
7	11.4	9.0	8.4	5.1	2.0	1.3	1.0	9.2	9.0
8	10.8	8.3	7.7	4.8	2.2	1.6	0.8	9.1	8.9
9	10.1	7.7	7.5	4.9	2.5	1.8	0.9	8.6	8.4
10	9.5	7.4	7.1	5.1	3.2	2.1	1.1	3.2	7.7
11	9.1	7.1	7.0	5.2	3.3	2.2	1.2	0.9	5.9
12	8.7	6.9	6.8	5.2	3.4	2.3	1.3	0.5	4.3
13	8.1	6.8	6.5	5.1	3.4	2.3	1.4	0.3	0.8
14	7.5	6.6	6.4	5.0	3.5	2.3	1.6	0.3	0.5
15	7.4	6.5	6.1	4.9	3.6	2.2	1.5	0.2	0.3
16	7.3	6.2	5.8	4.5	3.6	2.0	1.4	0.3	0.3
17	7.1	6.1	5.2	4.3	3.3	2.0	1.2	0.4	0.3
18	6.9	6.0	5.2	3.9	3.0	1.9	1.1	0.6	0.3
19	6.7	5.9	4.9	3.5	2.7	1.8	1.1	0.4	0.3
20	6.5	5.8	4.7	3.3	2.6	1.8	1.0	0.3	0.3
21	6.3	5.6	4.6	3.3	2.6	1.9	1.0	0.4	0.3
22	6.1	5.5	4.5	3.1	2.6	1.8	1.0	0.3	0.3
23	5.9	5.4	4.3	3.0	2.5	1.8	0.9	0.2	0.3
24	5.7	5.4	4.2	3.0	2.4	1.7	0.8	0.2	0.3
25	5.7	5.3	4.1	2.8	2.2	1.6	0.7	0.2	0.3
26	5.7	5.3	4.0	2.5	2.0	1.3	0.6	0.2	0.3
27	5.6	5.2	3.9	2.4	1.9	1.2	0.5	0.2	0.3
28	5.6	5.2	3.7	2.1	1.8	1.1	0.6	0.2	0.3
29	5.6	5.0	3.7	2.0	1.7	0.9	0.4	0.2	0.3
30	5.6	5.0	3.7	2.0	1.7	0.9	0.4	0.2	0.3

Table 6-2. Temperature (°C) profiles in the treated (site N2) and reference (site S1) basins of Amisk Lake on fish sampling nights in 1990, measured with a HYDROLAB™ SURVEYOR II.

Treated basin (site N2)

Depth (m)	May 23	June 5	June 21	July 11	July 27	Aug. 12	Aug. 20	Sep. 15	Sep. 26
0	11.2	14.9	17.8	21.3	21.0	22.6	19.7	15.0	13.9
1	11.1	14.9	17.7	20.8	20.9	22.6	19.7	15.0	13.9
2	10.7	14.8	17.0	20.5	20.3	21.2	19.7	15.0	13.9
3	10.5	14.8	16.4	20.3	19.1	20.4	19.5	15.0	13.9
4	10.4	14.4	15.5	19.8	17.0	19.9	19.3	15.0	13.9
5	10.4	14.3	14.6	18.2	15.0	18.9	19.3	14.9	13.8
6	10.3	13.4	13.1	16.2	12.3	16.5	19.2	14.7	13.7
7	10.0	10.7	11.6	14.5	11.8	14.3	18.2	14.7	13.6
8	8.5	9.4	10.5	13.0	11.5	12.4	13.2	13.3	13.6
9	7.9	8.8	9.6	11.7	11.3	11.8	12.0	12.7	13.3
10	7.1	8.4	9.3	10.7	11.0	11.2	11.6	12.5	12.9
11	7.0	7.9	8.8	10.3	10.7	11.2	11.3	12.2	12.6
12	6.3	7.5	8.6	9.9	10.5	11.2	11.1	11.9	12.5
13	6.3	7.2	8.4	9.7	10.3	10.5	10.9	11.7	12.3
14	6.3	6.9	8.3	9.5	10.2	10.5	10.8	11.6	12.2
15	6.1	6.8	8.2	9.3	10.1	10.4	10.7	11.5	12.1
16	6.1	6.7	8.1	9.2	9.9	10.3	10.6	11.4	12.1
17	6.1	6.6	7.9	9.1	9.8	10.2	10.6	11.3	11.9
18	6.0	6.6	7.8	9.0	9.8	10.1	10.5	11.3	11.8
19	5.9	6.5	7.6	8.9	9.7	10.0	10.5	11.2	11.7
20	5.9	6.5	7.5	8.8	9.7	9.9	10.4	11.2	11.7
21	5.8	6.4	7.5	8.8	9.6	9.8	10.4	11.1	11.6
22	5.8	6.3	7.4	8.8	9.6	9.8	10.3	11.1	11.6
23	5.7	6.3	7.4	8.7	9.5	9.8	10.3	11.1	11.6
24	5.7	6.3	7.3	8.7	9.4	9.8	10.2	11.0	11.5
25	5.7	6.3	7.3	8.7	9.4	9.8	10.2	11.0	11.5
26	5.7	6.2	7.3	8.7	9.4	9.7	10.2	11.0	11.5
27	5.7	6.2	7.3	8.6	9.4	9.7	10.2	10.9	11.4
28	5.7	6.2	7.3	8.6	9.4	9.7	10.1	10.9	11.4
29	5.6	6.2	7.3	8.6	9.4	9.7	10.1	10.9	11.4
30	5.5	6.2	7.3	8.6	9.4	9.7	10.1	10.9	11.4

Table 6-2 continued.

Reference basin (site N2)

Depth (m)	May 23	June 5	June 20	July 11	July 25	Aug. 11	Aug. 21	Sep. 15	Sep. 26
0	10.0	15.1	17.0	19.8	21.1	23.1	18.6	15.0	13.7
1	10.0	15.1	17.0	19.7	21.0	23.1	18.6	15.1	13.5
2	9.8	15.0	16.9	18.5	19.9	23.0	18.6	15.1	13.8
3	9.5	15.0	16.5	17.2	19.4	21.4	18.4	15.1	13.8
4	9.3	14.9	15.4	16.3	18.3	19.9	18.1	15.1	13.8
5	9.0	14.9	14.6	15.3	16.8	18.8	17.1	15.1	13.8
6	8.6	14.7	13.7	14.4	14.9	15.7	15.7	15.0	13.8
7	8.4	9.7	11.9	13.1	12.9	13.0	14.5	15.0	13.8
8	8.3	8.3	10.4	11.7	12.0	12.3	12.6	15.0	13.8
9	8.1	7.5	9.9	11.0	11.3	11.8	11.8	14.8	13.6
10	7.9	7.2	9.3	10.4	10.7	11.3	11.3	13.3	13.4
11	7.3	6.8	8.6	9.8	10.2	11.0	11.0	11.9	13.1
12	6.6	6.5	8.0	9.4	9.8	10.7	10.5	11.2	12.4
13	6.1	6.5	7.6	8.9	9.3	10.3	9.4	10.4	11.6
14	6.0	6.3	7.4	8.3	8.9	9.9	8.5	9.5	10.3
15	5.9	6.1	7.0	7.4	8.4	9.1	7.6	9.1	8.4
16	5.7	5.9	6.7	6.9	7.8	8.4	6.8	8.7	7.4
17	5.7	5.7	6.4	6.6	7.3	7.6	6.1	8.1	6.5
18	5.6	5.6	6.0	6.2	6.7	6.9	5.9	7.5	5.7
19	5.4	5.5	5.9	5.9	6.4	6.4	5.7	6.8	5.7
20	5.3	5.3	5.7	5.7	6.1	6.0	5.5	6.4	5.5
21	5.2	5.2	5.5	5.6	5.9	5.8	5.4	6.0	5.4
22	5.1	5.1	5.2	5.3	5.7	5.7	5.3	5.6	5.3
23	5.1	5.0	5.1	5.2	5.6	5.5	5.2	5.5	5.3
24	5.0	5.0	5.0	5.2	5.4	5.4	5.2	5.3	5.2
25	5.0	4.9	5.0	5.1	5.3	5.3	5.1	5.2	5.1
26	5.0	4.9	4.9	5.0	5.2	5.3	5.0	5.1	5.0
27	5.0	4.8	4.9	4.8	5.1	5.2	5.0	5.0	4.9
28	5.0	4.8	4.8	4.9	5.0	5.2	5.0	5.0	4.9
29	5.0	4.8	4.8	4.9	5.0	5.1	5.0	4.9	5.0
30	5.0	4.8	4.7	4.8	4.9	5.1	4.9	4.8	4.9

Table 6-3. Dissolved oxygen (mg·L^{-1}) profiles in the treated (site N2) and reference (site S1) basins of Amisk Lake on fish sampling nights in 1991, measured with a HYDROLAB™ SURVEYOR II.

Treated basin (site N2)

Depth (m)	June 13	July 11	July 23	Aug. 15	Aug. 28	Sep. 12	Sep. 26
0	10.6	10.3	10.8	11.2	10.9	10.1	8.8
1	10.6	10.3	10.7	10.8	10.8	9.9	8.8
2	10.6	10.3	10.9	11.1	10.2	9.9	8.6
3	10.6	10.3	10.8	11.1	9.9	9.7	8.5
4	9.1	9.3	10.5	9.6	9.0	9.2	8.4
5	7.5	8.4	7.4	7.9	4.2	8.0	8.4
6	7.2	7.5	6.8	5.4	2.1	6.3	8.3
7	7.0	6.6	5.9	5.1	4.8	3.6	8.1
8	6.7	5.7	5.4	4.7	4.5	2.6	7.9
9	6.3	5.4	4.3	4.5	4.2	3.5	7.7
10	5.9	5.1	2.9	3.3	3.8	3.4	7.6
11	5.8	4.6	3.7	3.0	3.2	2.6	7.2
12	5.7	4.2	4.8	2.7	2.9	1.4	6.7
13	5.9	3.7	3.9	2.4	2.2	1.2	6.3
14	6.1	3.2	3.5	1.8	1.4	1.0	5.9
15	6.1	3.4	3.3	1.8	1.4	0.8	4.5
16	6.0	3.5	2.4	1.9	1.4	1.3	3.7
17	5.3	3.2	2.3	1.9	1.4	1.4	3.4
18	4.6	2.9	2.3	1.7	1.4	0.9	2.8
19	4.5	2.8	2.4	1.7	1.3	0.8	2.5
20	4.5	2.6	2.2	1.7	1.5	0.6	2.2
21	4.4	2.5	2.1	1.7	1.7	0.8	1.9
22	4.2	2.5	1.9	1.6	1.3	0.7	1.5
23	3.9	2.6	1.7	1.5	1.2	0.6	1.1
24	3.7	2.6	1.7	1.4	1.1	0.5	0.9
25	3.7	2.5	1.6	1.2	1.1	0.4	0.8
26	3.7	2.4	1.5	1.2	1.0	0.3	0.7
27	3.8	2.3	1.4	1.2	0.8	0.3	0.6
28	3.7	2.1	1.4	1.2	0.7	0.2	0.5
29	3.7	2.1	1.3	1.1	0.7	0.2	0.5
30	3.6	2.0	1.2	1.1	0.7	0.2	0.4

Table 6-3 continued.

Reference basin (site S1)

Depth (m)	June 13	July 11	July 23	Aug. 15	Aug. 28	Sep. 12	Sep. 26
0	10.6	10.3	10.6	11.1	10.5	10.0	8.9
1	10.6	10.3	10.6	10.9	10.5	9.3	8.6
2	10.6	10.3	10.7	11.1	10.4	9.4	8.4
3	10.6	10.3	10.7	11.1	10.4	9.3	8.1
4	9.6	9.1	10.6	11.1	10.1	9.2	7.8
5	8.5	7.9	8.6	10.8	10.1	9.1	7.6
6	7.8	6.4	5.4	3.7	1.1	9.0	7.4
7	7.2	4.9	3.2	2.3	0.6	9.0	7.3
8	6.5	3.5	2.0	1.9	0.5	7.7	7.1
9	6.0	3.3	2.0	1.5	0.5	1.9	6.9
10	5.5	3.1	2.0	1.1	0.5	0.8	6.2
11	5.4	3.0	2.1	1.0	0.5	0.5	2.7
12	5.3	3.0	2.2	1.0	0.3	0.3	1.8
13	5.1	2.9	2.2	0.9	0.3	0.3	1.0
14	4.9	2.8	2.1	0.9	0.3	0.2	0.8
15	5.0	2.6	2.0	0.9	0.2	0.2	0.7
16	5.1	2.4	2.0	1.0	0.2	0.2	0.5
17	4.9	2.6	1.4	0.7	0.2	0.2	0.4
18	4.7	2.8	1.2	0.8	0.2	0.0	0.3
19	4.4	2.6	1.2	0.7	0.2	0.0	0.3
20	4.0	2.5	1.1	0.5	0.0	0.0	0.3
21	3.6	2.3	1.0	0.4	0.0	0.0	0.3
22	3.3	2.1	0.7	0.4	0.0	0.0	0.3
23	3.0	1.9	0.7	0.4	0.0	0.0	0.3
24	2.6	1.7	0.6	0.4	0.0	0.0	0.3
25	2.5	1.4	0.5	0.4	0.0	0.0	0.3
26	2.4	1.1	0.3	0.3	0.0	0.0	0.0
27	2.2	0.8	0.3	0.3	0.0	0.0	0.0
28	1.9	0.9	0.3	0.3	0.0	0.0	0.0
29	1.6	0.9	0.3	0.3	0.0	0.0	0.0
30	1.3	0.9	0.3	0.3	0.0	0.0	0.0

Table 6-4. Temperature (°C) profiles in the treated (site N2) and reference (site S1) basins of Amisk Lake on fish sampling nights in 1991, measured with a HYDROLAB™ SURVEYOR II.

Treated basin (site N2)

Depth (m)	June 13	July 11	July 23	Aug. 15	Aug. 28	Sep. 12	Sep. 26
0	14.5	21.4	21.7	23.3	19.2	14.9	12.1
1	14.4	21.3	20.7	23.3	19.2	14.9	12.1
2	14.3	21.1	19.8	23.3	19.1	14.9	12.1
3	14.2	21.0	19.6	22.5	18.6	14.9	12.0
4	14.1	17.5	19.3	20.0	18.7	14.8	12.0
5	9.4	16.5	17.2	18.2	17.6	14.5	12.0
6	9.1	12.1	11.6	15.4	14.4	13.0	12.0
7	9.1	10.4	10.6	12.4	11.6	12.2	11.9
8	9.1	9.2	9.7	11.2	11.1	11.5	11.8
9	7.9	9.2	9.5	10.6	10.9	11.1	11.7
10	7.6	9.1	9.1	10.1	10.6	10.9	11.6
11	7.6	8.7	9.0	9.8	10.3	10.7	11.6
12	7.5	8.5	8.7	9.5	10.1	10.5	11.4
13	7.4	8.2	8.5	9.3	9.9	10.4	11.3
14	7.0	8.0	8.4	9.2	9.8	10.2	11.2
15	6.8	7.7	8.2	9.1	9.7	10.1	10.9
16	6.6	7.6	8.1	8.9	9.6	10.0	10.8
17	6.4	7.5	7.9	8.9	9.5	9.9	10.7
18	6.3	7.4	7.8	8.8	9.4	9.8	10.6
19	6.2	7.2	7.8	8.7	9.3	9.7	10.5
20	6.2	7.2	7.7	8.6	9.3	9.6	10.5
21	6.1	7.1	7.6	8.6	9.3	9.6	10.4
22	6.1	7.1	7.5	8.5	9.2	9.6	10.4
23	6.0	7.1	7.5	8.5	9.1	9.6	10.3
24	6.0	7.1	7.4	8.5	9.1	9.5	10.3
25	6.0	7.0	7.4	8.4	9.1	9.5	10.3
26	6.0	6.9	7.4	8.4	9.1	9.5	10.2
27	6.0	6.9	7.3	8.4	9.0	9.5	10.2
28	6.0	6.9	7.4	8.4	9.0	9.5	10.2
29	6.0	6.8	7.4	8.4	9.0	9.5	10.2
30	6.0	6.8	7.4	8.4	9.0	9.5	10.2

Table 6-4 continued.

Reference basin (site S1)

Depth (m)	June 13	July 11	July 23	Aug. 15	Aug. 28	Sep. 12	Sep. 26
0	14.5	20.8	21.7	23.1	19.0	14.8	12.2
1	14.5	20.6	21.6	23.1	19.1	14.8	12.1
2	14.3	20.5	20.7	23.0	19.0	14.8	12.1
3	14.3	20.4	20.6	22.8	18.9	14.7	12.0
4	14.3	19.5	19.8	22.8	18.7	14.7	11.9
5	14.2	15.2	17.6	22.4	18.4	14.7	11.9
6	14.1	12.3	13.8	14.7	14.7	14.7	11.8
7	14.1	10.3	11.3	11.6	12.2	14.7	11.8
8	9.7	9.4	9.9	10.8	1.2	14.4	11.7
9	9.1	8.8	9.2	10.2	10.7	11.9	11.7
10	7.8	8.5	8.9	9.9	10.5	11.1	11.1
11	7.4	8.3	8.4	9.6	10.1	10.7	10.7
12	6.9	7.9	8.1	9.2	9.6	10.2	10.4
13	6.5	7.7	7.6	8.9	8.7	9.5	10.0
14	6.0	7.0	7.0	8.5	7.9	9.1	9.8
15	5.4	6.8	6.7	8.1	7.2	8.3	9.8
16	5.2	5.7	6.4	7.5	6.4	7.2	9.5
17	5.1	5.3	5.8	6.8	5.5	6.4	9.2
18	4.9	5.0	5.2	6.4	5.2	5.9	8.7
19	4.8	4.8	4.9	5.6	4.8	5.4	7.9
20	4.7	4.6	4.6	5.2	4.7	5.0	7.1
21	4.5	4.3	4.5	4.9	4.6	4.8	6.3
22	4.2	4.2	4.3	4.6	4.4	4.6	5.5
23	4.2	4.2	4.2	4.4	4.3	4.6	5.2
24	4.1	4.0	4.2	4.4	4.2	4.5	4.8
25	4.1	4.0	4.1	4.3	4.1	4.5	4.7
26	4.1	3.9	4.1	4.2	4.1	4.4	4.5
27	4.1	3.8	4.0	4.2	4.0	4.3	4.5
28	3.9	3.8	4.0	4.1	4.0	4.2	4.3
29	3.7	3.8	4.0	4.1	4.0	4.1	4.3
30	3.7	3.8	4.0	4.0	4.0	4.1	4.2

Table 6-5. Dissolved oxygen and temperature profiles in Baptiste Lake on fish sampling nights in 1990, measured with a HYDROLAB™ SURVEYOR II. Values are averages from two sampling sites. Depths are mid-points of 2-m intervals.

Depth (m)	June 30	Aug. 19	Sep. 25
Dissolved oxygen ($mg \cdot L^{-1}$)			
1	9.3	10.5	10.2
3	9.3	7.6	8.5
5	6.8	2.0	7.9
7	4.2	4.0	7.7
9	1.2	0.0	7.1
11	0.5	0.0	1.1
13	0.0	0.0	0.3
15	0.0	0.0	0.0
17	0.0	0.0	0.0
19	0.0	0.0	0.0
21	0.0	0.0	0.0
Temperature (°C)			
1	20.0	22.5	13.3
3	17.1	21.4	12.5
5	15.0	19.6	12.3
7	13.0	15.6	12.3
9	9.3	10.6	12.1
11	6.4	7.8	8.9
13	5.8	6.3	6.0
15	4.8	5.4	5.2
17	4.3	5.2	5.0
19	4.0	5.1	5.0
21	4.0	5.0	5.0

Chapter 7

Appendix B: Hydroacoustic data on abundance and distribution of cisco in Amisk and Baptiste lakes.

Table 7-1. Parameters of the hydroacoustic data used in fish density and biomass estimates in Amisk Lake; pings analyzed are the total number of pings recorded during each survey, single fish echoes are the total number of single fish echoes ≥ -48 dB, percentage single fish is the percentage of total echo energy attributable to single fish targets and 5-minute intervals represents the number of 5-minute time steps analyzed for each survey.

		Treated basin					Reference basin				
				Percentage single fish					Percentage single fish		
Year	Date	Pings analyzed	Single fish echoes	Median	Range	5-minute intervals	Pings analyzed	Single fish echoes	Median	Range	5-minute intervals
1989	July 26	2700	1619	64.8	63.8-86.5	3	5400	1049	89.2	83.0-100	6
	Aug. 9	2700	1110	83.7	67.1-96.4	3	[illegible]	1007	91.9	80.1-92.2	3
	Sep. 23	4500	4176	66.2	62.9-77.9	5	7200	1695	75.5	19.5-95.8	8
1990	June 20	6630	3016	99.2	97.3-100	7	7440	2721	[illegible]	76.5-97.4	8
	Aug. 11	7690	2529	76.3	52.4-94.8	8	9005	2190	85.[illegible]	63.2-92.7	9
	Sep. 26	5320	5969	24.7	19.7-53.3	5	8930	4497	70.3	49.8-92.8	9
1991	June 13	2900	2542	65	54.4-85.2	3	6590	8956	73.[illegible]	62.8-82.1	7
	July 11	4420	3390	74.7	23.9-82.9		7770	5785	83.8	62.7-89.7	8
	Aug. 15	5540	5530	38.4	35.9-76.6	6	7440	2172	75.9	37.5-88.1	8
	Sep. 12	5750	3582	27.3	19.4-32.0	6	7640	3620	81.1	42.5-81.1	8

Table 7-2. Parameters of the hydroacoustic data used in fish density and biomass estimates in Baptiste Lake; pings analyzed are the total number of pings recorded during each survey, single fish echoes are the total number of single fish echoes ≥ -48 dB, percentage single fish is the percentage of total echo energy attributable to single fish targets and 5-minute intervals represents the number of 5-minute time steps analyzed for each survey.

				Percentage single fish		
	Date	Pings analyzed	Single fish echoes	Median	Range	5-minute intervals
1990	June 22	6740	2850	83.3	59.2-92.5	7
	July 25	7480	1382	76.0	59.8-8[illegible].3	8
	Aug. 27	8060	1586	50.1	32.[illegible]-66.7	9
	Sep. 24	7670	3222	46.0	37.4-83.6	8
[a]1991	Aug. 19	4620	756	--	9.2-16.1	2

a = analyzed at 10-min time steps.

Table 7-3. Vertical distributions of cisco (fish·ha^{-1}) in Amisk Lake during the summer of 1990, determined form hydroacoustic surveys. Depths are mid-points of 2-m intervals.

Depth (m)	May 23	June 5	June 20	July 11	July 25	Aug. 11	Aug. 23	Sep. 15	Sep. 26
Treated basin									
5	73	48	66	409	1751	350	440	264	89
7	73	25	156	300	1530	322	161	277	151
9	52	24	97	238	721	285	292	272	401
11	19	13	121	241	496	304	357	1559	1458
13	44	12	173	402	303	346	297	1799	2167
15	34	5	119	420	186	249	60	423	1466
17	65	2	57	243	133	54	23	30	1906
19	40	0	69	110	89	24	5	5	205
21	7	0	34	41	126	6	0	0	65
23	8	0	27	20	49	0	0	21	8
25	0	6	0	11	0	0	0	1	71
27	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0
Reference basin									
5	18	132	39	555	1011	1042	294	355	30
7	25	104	56	363	104	70	279	316	83
9	28	42	56	206	191	11	2	612	224
11	11	19	85	278	258	74	1	292	449
13	12	14	66	325	232	133	1	4	468
15	14	24	48	242	140	173	43	2	0
17	24	15	35	105	76	64	83	7	0
19	9	10	28	44	25	39	13	0	0
21	0	16	17	13	7	4	0	0	1
23	1	14	4	9	0	0	0	0	0
25	2	7	3	2	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0

Table 7-4. Vertical distributions of cisco (fish·ha^{-1}) in Amisk Lake during the summer of 1991, determined form hydroacoustic surveys. Depths are mid-points of 2-m intervals.

Depth (m)	June 13	July 11	July 23	Aug. 15	Aug. 28	Sep. 12	Sep. 26
Treated basin							
3	172	379	57	242	0	31	77
5	152	1311	820	526	538	156	44
7	272	817	1921	1298	786	1225	48
9	591	343	2327	1967	1030	3631	137
11	424	84	962	874	288	1146	219
13	259	79	507	192	74	36	256
15	139	95	221	34	3	29	352
17	148	51	128	9	0	0	264
19	79	41	77	1	0	23	30
21	86	10	31	0	0	0	5
23	194	19	0	4	0	206	0
25	4	91	0	0	0	0	0
27	0	0	0	0	0	0	0
Reference basin							
3	26	313	86	27	74	110	101
5	84	368	514	252	27	202	97
7	247	271	273	796	48	74	128
9	440	248	54	380	7	0	387
11	458	278	22	35	0	0	168
13	452	211	12	0	0	0	0
15	289	77	11	0	0	0	0
17	127	11	5	0	0	0	0
19	21	0	0	0	0	0	0
21	7	0	0	0	0	0	0
23	2	0	0	0	0	0	0
25	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0

Table 7-5. Vertical distributions of cisco (fish·ha^{-1}) in Baptiste Lake during the summer of 1991, determined form hydroacoustic surveys. Depths are mid-points of 2-m intervals

Depth (m)	June 30	Aug. 19	Sep. 25
3	393	594	121
5	822	242	50
7	196	65	48
9	21	0	161
11	0	0	5
13	0	0	16
15	0	0	24
17	0	0	0
19	0	0	0
21	0	0	0

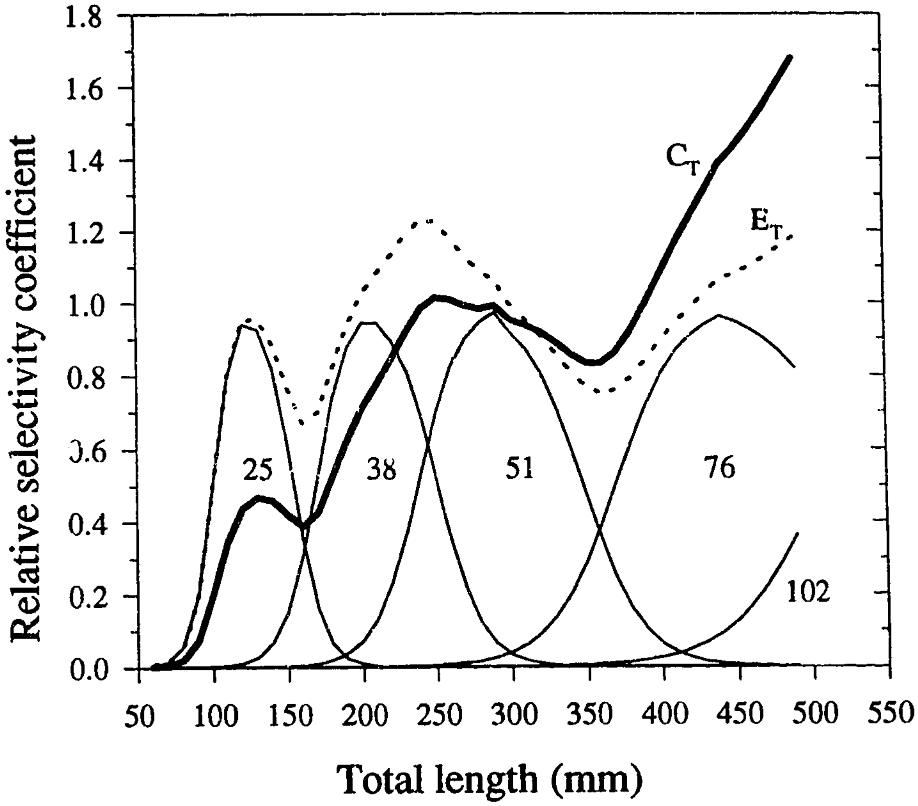

Fig. 7-1. Relative selectivity curves derived for cisco in Amisk and Baptiste lakes using the size-encounter probability method (Rudstam et al. 1984). Indicated are the selectivity curves for each net (stretch mesh sizes 25, 38, 51, 76, and 102 mm) E_T is encounter probability for the whole-set of nets assuming the probability of encountering a net, *P*(E), is constant. C_T is the selectivity for the whole set of nets assuming *P*(E) is an exponential function to the power 0.8 of fish length.