A COMPARATIVE STUDY OF THE SEASONAL ENERGY DYNAMICS
OF THE CISCO, *COREGONUS ARTEDII*,
IN THREE MINNESOTA LAKES

A THESIS
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LIST OF FIGURES

Figures are presented at the end of the chapter in which they are discussed. The first number for each figure refers to the chapter in which they appear. Note that the titles of Figs. 4.1.-4.33 have been abbreviated. However, the essential information is provided. These figures all show the seasonal changes of variables in tissues of adult and juvenile ciscos, as indicated.

Fig. No.

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INTRODUCTION

This investigation is a comparison of the seasonal cycles of storage and depletion of energy reserves and the allocation of resources to growth and reproduction in three populations of the cisco, *Coregonus artedii.*

The cisco is a member of the subfamily Coregoninae within the family Salmonidae. Coregonines inhabit a wide variety of habitats in north-temperate latitudes, on the Eurasian and North American continents. The cisco is widely distributed in lakes in the northern United States and Canada. Ciscos are found in habitats ranging from oligotrophic to eutrophic waters, and, although primarily a freshwater fish, may enter coastal waters. Ciscos are generally considered to be planktivores, although they will feed on bottom organisms as well as on items at the water surface, such as winged terrestrial insects. Like many species of fish, they are opportunistic feeders. They may form large aggregations prior to spawning, which takes place in late autumn, in November or December. Some populations are anadromous, migrating up rivers to spawn. The eggs hatch in the spring.

Coregonines as a group, and the cisco in particular, are quite variable in morphometry (Koelz, 1929; Hile, 1937), growth, and life history characteristics (Scott and Crossman, 1973). This study began as an attempt to understand the reasons for the extreme stunting in the of cisco population of Ten Mile Lake and to

investigate the relationship of the slow growth of these fish to certain life history characteristics of this population differed from other populations in the region. Several years before the present study was initiated, my advisor, Professor James C. Underhill, and Merle Johnson of the Minnesota Department of Natural Resources transplantated ciscos from Ten Mile Lake to several lakes that had been reclaimed for stocking with stream trout. In these lakes, the growth of the ciscos was markedly improved, indicating that the cause of stunting was primarily due to environmental conditions that existed in Ten Mile Lake (Underhill, unpublished data; Johnson and Strand, date unknown). Among the differences in life history characteristics noted in the Ten Mile Lake ciscos was the earlier time of spawning. In this lake, the ciscos spawn in late October and early November, nearly one month earlier than in other populations. Further, it was believed that they matured at an earlier age and had a shorter lifespan than other ciscos.

Growth is especially important in fishes since many life history characteristics are directly related to size. Increased size is usually associated with increased fecundity (Bagenal, 1966), generally as a power function (Roff, 1983). Mortality due to predation may decrease with size, resulting in greater longevity, and the age at first maturity is usually, to some extent, determined by size. Thus, the growth rate has direct consequences on fitness (Calow, 1985). The primary impact of

environmental conditions is assumed to be on the growth rate (Stearns and Crandall, 1984), which then affects these life history traits.

Unlike higher vertebrates, growth in fishes is indeterminate, and is responsive to environmental conditions. Among fishes, large intraspecific differences in the growth rate under natural conditions are common and numerous (Weatherley and Gill, 1987). Fish growth can usually be adequately described by asymptotic curves (Ricker, 1979). Thus, the response of growth to altered conditions may be seen as the ability of fishes to approach different asymptotic sizes (Sebens, 1987). This plasticity of fish growth represents a sensitivity of anabolic processes to environmental conditions, especially food and temperature (Caswell, 1983). The wide range of phenotypic expression may stem from an evolutionary experience of fluctuating environments (Mann *et al.*, 1984). This metabolic plasticity is considered to be a trait under natural selection (Stearns and Koella, 1986).

The energy intake of any organism must first meet the maintenance costs of the organism. Above this minimum, surplus energy may be used for growth or reproduction. The allocation of resources to these competing processes is the mechanism that underlies life history differences. This has been most clearly demonstrated by examples of species that undergo migrations. Iteroparous species or populations allocate less stored energy to

reproduction than do semelparous ones (Glebe and Leggett, 1981). The effects of differing environmental conditions on the pattern of allocation in non-migrating species has also received attention. Most often, improvement of environmental conditions has resulted in both increased growth and fecundity, and a decrease in the age at first maturity (Hester, 1964; Bagenal, 1969; Hislop, 1978; Mann and Mills, 1979; Mann et al, 1984; Wooton, 1979,1984; Deacon and Keast, 1987).

The pattern of allocation of resources to growth and reproduction may be obscured by seasonal cycles of energy storage and depletion. These cycles arise because growth and reproduction do not always coincide with periods of abundant resources. Hence, they are often linked to these periods by cycles of energy storage (Pianka, 1976). There have been many studies of such cycles, and their relationship to growth and reproduction. These are discussed in detail later, in appropriate sections. However, intraspecific comparisons of the effects of habitat differences on these cycles, and on their consequences for the allocation of resources, are rare. Where data for more than one population of a species exist, descriptions of important environmental variables are incomplete or lacking. The study by Diana (1983) on northern pike populations is a rare exception. Furthermore, in most studies of cycles of energy storage, the fish is divided into two compartments, somatic and gonadal. The failure to isolate or include various organs or tissues which may

participate in these cycles can obscure details of the processes involved in energy allocation.

The description of seasonal energy cycles in various tissues and organs, and a comparison of the cycles in fish that live in different environmental conditions, could lead to a better understanding of the details of the process of allocation, the mechanisms underlying this process, and of the relationship between this process and the environment. In order to determine the range of phenotypic response of the pattern of energy allocation in the cisco, three populations, whose members exhibited very different growth rates, were chosen for study. The maximum sizes achieved by fish in the different populations span the range observed for ciscos.

In the stunted population of Ten Mile Lake, fish reach a maximum standard length of approximately 125 mm and a weight of 20 g (for ripe females) To my knowledge, this represents the smallest size reported for ciscos. At the other extreme are the fish of Lake Itasca. In this lake, fish reach lengths in excess of 370 mm and weights of 1500 g. This is larger than fish commonly caught in inland lakes of the region, although fish of similar in size have been reported in the Great Lakes, and are common in the Prairie Provinces of Canada (Scott and Crossman, 1973). The fish of the third lake, Elk Lake are of an intermediate size, reaching approximately 310 mm in length and

a weights of 530 g. Ciscos of this size are commonly encountered in the region.

The purpose of this study is to investigate the influence of the environmental conditions that result in these widely varying growth rates on the seasonal cycles of energy storage and and on the allocation of secondary production to growth and reproduction. Several questions are addressed in this work. Among these, the first are descriptive, and involve the determination of the nature of the seasonal cycle of energy accumulation and depletion in the cisco, the identification of the organs and tissues involved in the temporary storage of energy, and whether there are differences in the patterns of utilization of different energy depots.

Related to these are questions concerned with the effects of environmental variables on the seasonal cycles; whether the cycles persist in their general form under varying conditions, or how their expression is modified by these conditions. One might speculate that they might not persist when the growth rate is either greatly reduced or very high. When the growth rate is very low, it could be hypothesized that whatever resources are available should be allocated directly into growth or reproduction, since there are costs associated with energy storage. The formation of energy reserves takes place at the expense of other synthetic processes, such as protein deposition and the building of skeletal materials. There are also costs associated with losses

during energy transformations that occur during the deposition of reserves and again during the mobilization of these reserves. These costs may be manifested as functions of decreased growth, namely, decreased future fecundity, and increased mortality. On the other hand, when resources are abundant, leading to rapid growth, one might expect the appearance of seasonal cycles to be swamped out, with storage tissues being maintained at maximum levels by excess rations. Phenomena such as this have been observed in some populations of Arctic char (Matsuk and Lapin, 1972) and brook trout (Nelson and MacPherson, 1987). These then, are questions regarding the adaptive value of the cycles themselves.

A comparative approach may also provide some of the details of the process of allocation, and whether the pattern of allocation of stored reserves to maintenance, growth and reproduction differs in fish from habitats with greatly different productivity. Of special importance is the question of how the annual allocation to reproduction is affected by environmental conditions, and how differences in allocation are mediated. The study of the status of energy reserves will show whether, when ciscos are limited by resources or environmental stress, somatic tissue is sacrificed in order to produce gonads, as in the stickleback *Gasterosteus aculeatus* (Wooton, 1985), or whether, growth or maintenance is favored and reproduction in limited or curtailed, as in the winter flounder, *Pseudopleuronectes*

americanus (Tyler and Dunn, 1976). Further, this type of study can reveal the consequences of these alternatives. For example, by looking at the energy content of somatic tissues, it is possible to discern whether slow-growing fish suffer extreme depletion as a result of reproductive investment that may lead to post-spawning or overwinter mortality, thereby decreasing longevity. This study will provide insight into how the cisco resolves trade-offs between reproduction and growth.

The habitat conditions that presumably result in the observed differences of growth rate are presented in two chapters. Descriptions of the study lakes follow in Chapter 1. Included are several measures of lake productivity as indices of resource levels. Chapter 2 concerns the vertical distribution of the fish in each lake throughout the year. The seasonal thermal history of the fish, as well as possible limitations caused by low oxygen concentrations may be deduced from this information. In Chapter 3, the age and size of fish from the study populations are discussed. The major part of this endeavor, the comparison of seasonal changes in energy in four compartments, of both mature and juvenile fish from the three lakes, is treated in Chapter 4. Differences in the timing and magnitude of the cycles are described, and an attempt is made to discern the extent to which the cycles are innate, and to what extent they are modified by environmental constraints or those imposed by reproduction. The allocation of energy to growth and reproduction is considered in

relation to these cycles and to the growth rate. In the final chapter, Chapter 5, the significance of these findings is discussed.

CHAPTER 1. CHARACTERIZATION OF LAKE HABITATS

1.1. INTRODUCTION:

The three lakes were chosen for study primarily because of the large differences in growth patterns exhibited by their resident cisco populations. Further, they are in relatively close proximity to one another, which minimizes latitudinal effects, especially major seasonal differences in temperature regimes, which on a global scale are the most important determinants of lake primary productivity (Brylinski and Mann, 1973) and fish production (Schlesinger and Regier, 1982). Logistical considerations were also important.

Various physical and chemical aspects of the three study lakes were investigated in order to describe the habitat available to the ciscos, and to provide a general characterization of lake productivity.

1.2. METHODS:

1.2.1. MORPHOMETRY:

Morphometric measurements were derived from bathymetric maps prepared by the Minnesota Department of Natural Resources. Measurements were converted to metric units (Hodgman, *et al.*, 1959).

Lake surface area (A) was determined as the mean of three tracings using an Ott Compensating Polar Planimeter. The volume (V) of each lake was determined by first determining the area of each depth contour. The volume of each stratum was then calculated according to the formula:

$$V = \frac{h}{3} (A_1 + A_2 + \sqrt{A_1 A_2})$$

where h is the vertical depth of the stratum, A_1 is the area of the upper surface of the stratum and A_2 is the area of lower surface of the stratum. The total lake volume was then determined by summing the volumes of the individual strata (Welch, 1948; Wetzel and Likens, 1979). Mean depth (z) was calculated as the total volume (V) of the lake divided by the area (A). The length of shoreline (SL) was determined using a map measurer. The shoreline development (D_L) was calculated as the ratio of the length of the shore line (SL) to the length of the circumference of a circle with an area equal to that of the lake:

$$D_L = \frac{SL}{2\sqrt{\pi A_0}} \;.$$

1.2.2. PHYSICAL AND CHEMICAL CHARACTERISTICS:

Limnological measurements were made and water samples were collected and analyzed on each of the three lakes at approximately monthly intervals. For convenience, these were scheduled to coincide with the collection of fish samples. Lakes were sampled in the same order each month in order to maintain equal intervals between sampling dates.

TEMPERATURE, DISSOLVED OXYGEN AND TRANSPARENCY:

Profiles of temperature and dissolved oxygen content were made in the deepest part of each lake using a YSI Model 57 Dissolved Oxygen Meter. The meter was calibrated for oxygen concentration each month by comparing values obtained for test samples using the meter with values obtained from standard Winkler titrations as described in the manufacturer's manual.

Transparency, measured with a standard 20-cm diameter Secchi disc, was estimated as the mean of the depths at which the disc disappeared and reappeared upon raising after it had been lowered beyond visability (Wetzel and Likens, 1978).

OTHER CHEMICAL PROPERTIES:

Water samples were collected monthly during the ice-free season. Vertically integrated samples of the water column were collected with 1.27 cm (I.D.) plastic tubing at three sites near the deepest part of each lake. During lake turnover, the water column

was sampled to a depth of 10 m. and during the period of lake stratification, water was collected from the epilimnion, or mixed layer. The three samples were then mixed in a bucket. Part of this pooled sample was then filtered through Gelman type A/E glass fiber filters. The filtrate was used for analysis of pH, conductivity, alkalinity and total dissolved residues and the filters were used for chlorophyll *a* analysis. Unfiltered water was used for determinations of total phosphorous, and total nitrogen. When laboratory analysis could not be performed immediately (total phosphorous, total nitrogen and chlorophyll *a*) samples were frozen with dry ice and placed in a freezer at -24 °C.

Prior to determination of pH and specific conductance water samples were allowed to equilibrate to room temperature. Conductivity (in μmhos) was then measured with a Labline Lectro mhoMeter (Model MC-1, Mark IV) conductivity meter and pH was measured with an Orion Digital Ion Analyzer (Research Model 601A).

Total alkalinity was determined by titration of 50 milliliter (ml) samples with 0.02 N sulfuric acid, using a mixed indicator of bromcresol green and methyl red. Results are expressed as parts per million (ppm) $CaCO_3$.

Total dissolved residues (TDR) was determined for 200 ml samples of filtered water. Samples were evaporated from precombusted and tared porcelain evaporating dishes at 105 °C (American Public Health Association, 1981). Results are presented

as milligrams per liter (mg l-1). Total phosphorous (TP) was determined according to the ascorbic acid procedure following oxidation with potassium persulfate (American Public Health Association, *et al.*, 1981). 100 ml samples were analyzed spectrophotometrically at 885 nm with a Bausch and Lomb Spectronic 70 spectrophotometer. Results are expressed as micrograms phosphate-phosphorous per liter (μg l-1). Total nitrogen (TN) was determined by the cadmium reduction method following digestion with potassium persulphate (American Public Health Association, *et al.*, 1981) using samples collected during lake mixing. This analysis was performed by Dr. Naomi Detenbeck.

Chlorophyll *a* was extracted from filters with methanol and absorbance measured at 665 nm using a Bausch and Lomb Spectronic 70 spectrophotometer, according to the procedure of Holm-Hansen and Reimann (1978). The mean of three replicates for each sample is given as μg chlor *a* l-1.

Figures for this chapter are presented beginning on page 25.

1.3. RESULTS:

1.3.1. MORPHOMETRY:

Lake Itasca (47°13'20" N., 95°11'55" W) and Elk Lake (47°11'20" N., 95°13'45" W) are located within Itasca State Park

in north-central Minnesota. Lake Itasca is the source of the Mississippi River and Elk Lake flows into Lake Itasca via its outlet, Chambers Creek. Ten Mile Lake (46°58'10" N., 94°34'26" W) also contributes to the Upper Mississippi River, mainly through its outlet, the Boy River.

Morphometric features of the three study lakes are summarized in Table 1.1.

Lake Itasca is an irregularly shaped lake consisting of three narrow arms (Fig. 1.1). Thus, although the maximum dimensions are relatively large, the three areas may remain somewhat distinct, as its configuration may limit the effects of wind on mixing. The maximum depth of 13.72 m occurs in the Peace Pipe Vista area, to the north of the East Arm. The maximum depth in each of the three arms of the lake is approximately 10 m. The littoral area, is extensive comprising approximately 40 per cent of the total surface area of the lake.

Elk Lake is a smaller, deeper, subcircular lake (Fig. 1.2), with a surface area one-fourth and a mean depth nearly twice as large as that of Lake Itasca. The volume is approximately half that of the latter. The littoral area is approximately 27 per cent of the total area.

The main body of Ten Mile Lake is roughly subcircular in form, although the presence of several small bays contributes to its somewhat irregular outline (Fig. 1.3). The mean depth of 16.03 m is approximately three times that of Lake Itasca, and the mean

depth of the main body of the lake (excluding three shallow bays with depths under 3 m) is 17.11 m. The littoral area is approximately 20 per cent of the total surface area, including the shallow bays.

The volumes of individual depth strata for the three lakes are given in Appendix A.1.

Table 1.1. Morphometric Characteristics of Study Lakes			
	Lake Itasca	Elk Lake	Ten Mile Lake
Area (hectares)	448	110	1928
Volume (m^3 X 10^7)	2.36	1.08	30.9
Mean Depth (m)	5.26	9.78	16.03
Max. Depth (m)	13.72	29.57	62.79
Max. Length (km)	6.02	1.71	8.17
Max. Breadth (km)	2.67	0.98	3.22
Shoreline (km)	21.95	4.71	33.86
Shoreline Development	2.92	1.27	2.17

1.3.2. PHYSICAL AND CHEMICAL CHARACTERISTICS:

Temperature and dissolved oxygen profiles for the entire period of study are given in Appendices A.2–A.7. Representative profiles are shown graphically in Figs. 1.4 - 1.6.

Dissolved oxygen profiles for Lake Itasca (Fig. 1.4) during summer stratification were basically clinograde (Åberg and Rodhe, 1942; cited in Wetzel, 1983). The metalimnion formed at a shallow depth in Lake Itasca and during summer stratification, its upper boundary was at 4 to 5 m. The hypolimnion became anoxic. Also notable was the depletion of oxygen in the deeper water of Lake Itasca during the winter. This depletion may occur rapidly following ice formation, as can be observed in the profile from December, 1984. In Lake Itasca, spring mixis occurred during May of 1984 and autumnal circulation occurred in the latter half of September in both years.

Oxygen profiles of Elk Lake (Fig. 1.5) were of the clinograde or positive heterograde type with a maximum oxygen concentration in the metalimnion in mid-summer (Åberg and Rodhe, 1942; cited in Wetzel, 1983). The upper boundary of the metalimnion formed at approximately 4 to 5 m, but the temperature gradient was not as steep as in Lake Itasca. The hypolimnion became anoxic in the summer, and there was a noticeable depletion of oxygen in the deeper waters during the winter. This depletion was already evident as early as mid-December in 1984, as in Lake Itasca.

The upper boundary of the metalimnion in Ten Mile Lake formed at approximately 10 m and the thermocline was not nearly as steep as in the other two lakes. The oxygen profile was of the clinograde or positive heterograde type (Åberg and Rodhe,

1942; cited in Wetzel, 1983), with a maximum concentration in the metalimnion in mid-summer (Fig. 1.6). Stratification persisted longer in Ten Mile Lake than in the other lakes, lasting until mid-October. During the last month of stratification (October, 1984), oxygen was depleted in the hypolimnion, which did not, however, become anoxic, except perhaps in the deepest few meters.

Other physico-chemical features are summarized in Table 1.2. Shown are means of values of epilimnetic waters during the period in which the lakes were stratified (top; June through September for Lake Itasca; June through October for Elk Lake and Ten Mile Lake) as well as values for months at the time of autumn mixing (below, in parentheses). Transparency values are means for the entire open water season (May through November) for all lakes. During the period of lake mixing, water samples were taken of the upper 10 m of the water column. Monthly results are included in Appendices A.8-A.12.

Measures of the concentrations of both inorganic and organic nutrients were highest in Lake Itasca and lowest in Ten Mile Lake. Values for Elk Lake were intermediate. Values of specific conductance, total dissolved residues, alkalinity, and total nitrogen were similar in Lake Itasca and Elk Lake, and were markedly lower in Ten Mile Lake. On the other hand, total phosphorus concentrations in Lake Itasca were considerably higher than in the other two lakes, which had similar values.

There was a clear distinction between the three lakes in chlorophyll *a* concentration and Secchi transparency. The chlorophyll *a* concentration in Lake Itasca was more than one and a half times as great as that of Elk Lake and three and a half times as great as that in Ten Mile Lake. The trend in Secchi transparency was the inverse of that observed for chlorophyll *a*, and the differences between lakes were similar in magnitude.

Table 1.2. Limnological Characteristics of Study Lakes

	Lake Itasca	Elk Lake	Ten Mile Lake
Conductivity (μmhos)	248 (260)	219 (260)	180 (151)
TDR (mg/l)	193 (195)	177 (201)	139 (126)
pH	7.98 (8.00)	8.07 (8.11)	7.95 (7.77)
Alkalinity (mg/l)	147 (165)	138 (160)	97 (110)
Total-P (μg/l)	40.04 (45.60)	25.09 (30.93)	22.08 (24.42)
Total-N (μg/l)	-- (630)	-- (635)	-- (373)
Chlorophyll a (μg/l)	13.93 (10.24)	8.46 (15.93)	3.88 (12.11)
Transparency (m)	2.0	3.25	4.67

1.4. DISCUSSION:

Lake Itasca is a relatively large lake; only 15 per cent of Minnesota lakes have a greater surface area. However, its shallow maximum depth is only slighly greater than the median for state lakes (Heiskary, 1985). Because of the depletion of oxygen in the deeper waters during the summer, fish are restricted to the upper 5 m of the water column, where temperatures approach, and in some years exceed, the tolerance limits of ciscos. Summerkills of cisco and other species of fish occur with varying severity in Lake Itasca. Fish may also be limited to the upper strata of the lake during the winter months.

While the area of Elk Lake is near the median for Minnesota Lakes, it is deeper than 94 per cent of state lakes (Heiskary, 1985). Although the oxygen of the hypolimnion is depleted during the summer, a stratum of about 2 m depth in the metalimnion, between 6 and 8 m, remains, in which the dissolved oxygen concentration is adequate for fish and the temperatures do not exceed the tolerance limits of ciscos. Summerkills do not take place in this lake.

Ten Mile Lake is one of the largest and deepest lakes in Minnesota. Its surface area is greater than that of 97 per cent, and it is deeper than 99 per cent of Minnesota lakes. Although the oxygen concentration of the hypolimnion declines during the summer months, that which remains in October is probably

sufficient to support fish, given the low temperatures at these depths. These oxygen concentrations may, however, be limiting to growth. During July and August, temperatures in the epilimnion may be high enough to restrict the distribution of ciscos.

The other limnological features measured have all been used to estimate the trophic status of a lake and some, either singly or combined, have been used to estimate fish yield. The variables measured indicate a consistent trend in general trophic status among the three study lakes, with Ten Mile Lake the least productive, Lake Itasca the most productive, and Elk Lake intermediate between the two.

Values of total phosphorus were similar in Elk Lake and Ten Mile Lake. Values for both lakes fall within the range associated with meso-eutrophic lakes (10-30 μg l^{-1}) according to Wetzel's (1983) classification. The values obtained for Ten Mile Lake are somewhat higher than those measured by FMC Corporation in 1975, but this was probably due mostly to the different methods of sampling. The higher values of epilimnetic total phosphorus in Lake Itasca are within the range found in eutrophic lakes and are consistent with the shallow lake, extensive littoral area and anaerobic hypolimnion in that lake, which may lead to enhanced release of phosphorus from sediments.

Total nitrogen values in Lake Itasca and Elk Lake were similar and are typical of mesotrophic to eutrophic lakes, while

the value obtained from Ten Mile Lake is more typical of oligotrophic to mesotrophic lakes (Wetzel, 1983).

Mean chlorophyll *a* values show perhaps the clearest trend in productivity among the three lakes. The relatively high values for Ten Mile Lake and Elk Lake during times of lake circulation are due to pronounced spring algal blooms (see Appendix 1.11), a common phenomenon in many temperate lakes (Marshall and Peters, 1989). According to Likens's (1975, cited in Wetzel, 1983) classification, Ten Mile Lake and Elk Lake would be classified as mesotrophic, and Lake Itasca as eutrophic. Chlorophyll *a* concentration has been used as a predictor of fish yields (Oglesby, 1977) and of sportfish harvest in lakes and reservoirs of the midwestern United States (Jones and Hoyer, 1982).

The trend in Secchi transparencies of the three lakes is consistent with the that observed for other features. The mean Secchi transparency of Ten Mile Lake, which is greater than 95 per cent of Minnesota lakes, was more than twice as great as that of Lake Itasca and nearly one and a half times as great as that of Elk Lake. Secchi transparency is inversely related to chlorophyll *a* concentration (Megard and Berman, 1990). Readings taken on Ten Mile Lake during this study were generally lower than those taken in 1975 (FMC Corporation). It is not known whether this is indicative of natural year-to-year variation or simply a difference in technique of the observer, which can lead to significant differences (Beeton,1958).

Two other variables that have also been used as indicators of lake trophic status, specific conductance and total dissolved residues, were measured. Dunn (1954, cited in Rawson, 1960) considered lakes with conductivities below 200 μmhos (as is Ten Mile Lake) to be oligotrophic, and those with conductivities greater than this (as are Elk Lake and Lake Itasca) to be eutrophic. As is to be expected, the trend is the same for total dissolved residues. This latter variable, when divided by the mean depth, has been used as an index, the Morphoedaphic Index (MEI) to predict fish yields in lakes (Ryder,1965) and reservoirs (Jenkins, 1982). The MEI for Lake Itasca (36.7) is more than twice that of Elk Lake (18.1) and more than four times as great as that of Ten Mile Lake (8.67). It is realized that the conditions for use of this index are not met by the lakes under consideration, as the populations studied are not exploited, and at least one lake, Lake Itasca, is subject to anomolous environmental conditions (summerkill). Nevertheless, values have been presented because of the widespread interest in the use of this index as a means of predicting the potential fish yield of lakes.

In conclusion, the study lakes differ in their general trophic status and in the habitat available to cisco populations. Ten Mile Lake is a deep, oligo-mesotrophic lake, the least productive of the three study lakes. It has an ample volume of water at cool temperatures that remains oxygenated throughout the year. Elk Lake is more productive, but the habitat available to ciscos

becomes limited in mid-summer due to depletion of hypolimnetic oxygen during lake stratification. Lake Itasca, a shallow, eutrophic lake, is the most productive of the three lakes. Ciscos in this lake are likely to undergo at least some period of stress during summer stratification, because of the high temperatures in oxygenated surface waters which the ciscos must enter as the deeper strata become anoxic. They may also be limited in their vertical distribution during the winter in this lake.

N

9.1
3.0

3.0

3.0

9.1

9.1   3.0

13.7
9.1

0   914   1829
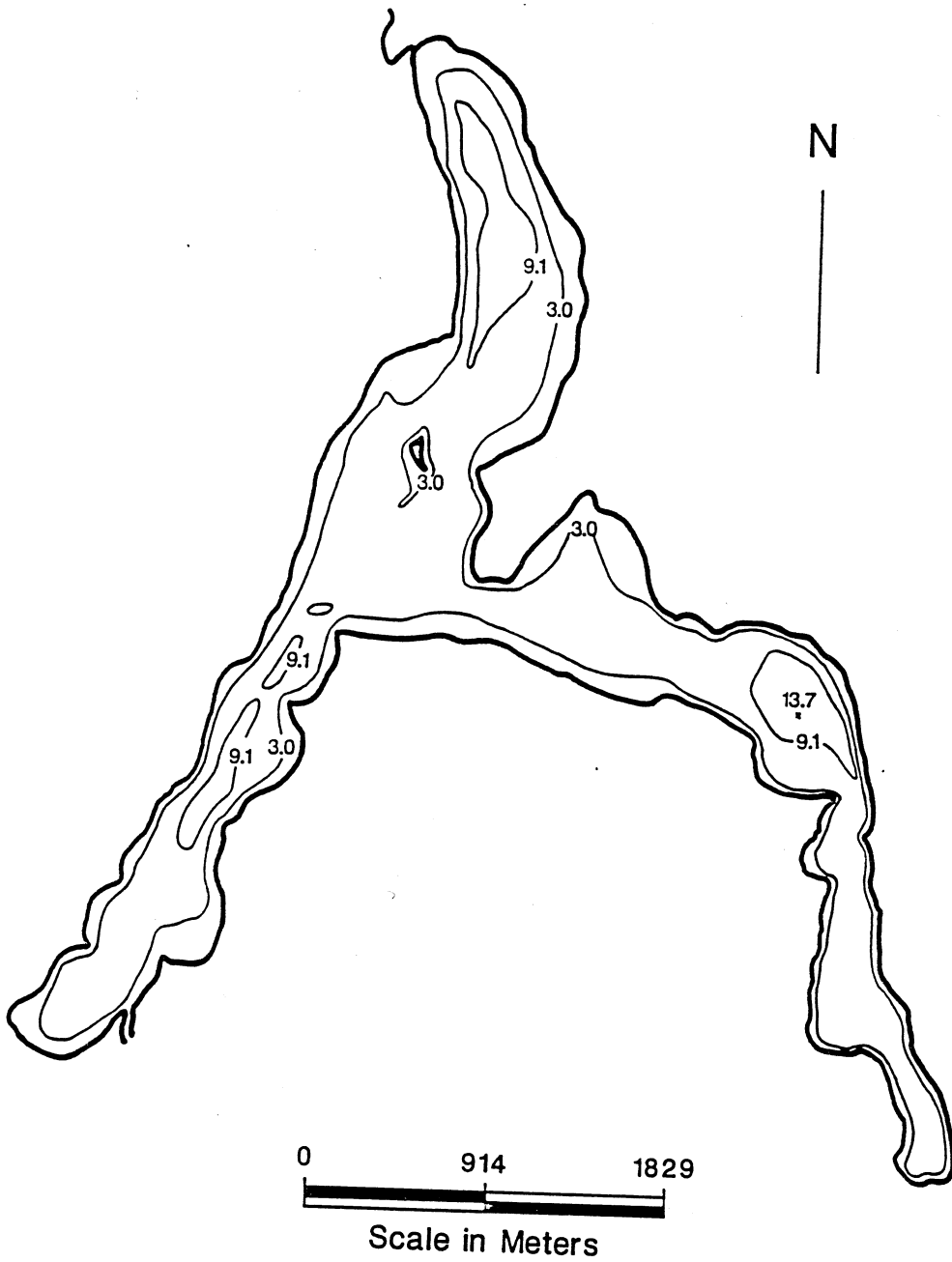
Scale in Meters

Fig. 1.1. Lake Itasca. The depths at contours are in meters.

N

3.0   9.1

15.2

3.0

3.0

15.2   9.1

15.2

3.0   9.1   21.3   27.4   3.0

9.1

0   161   322
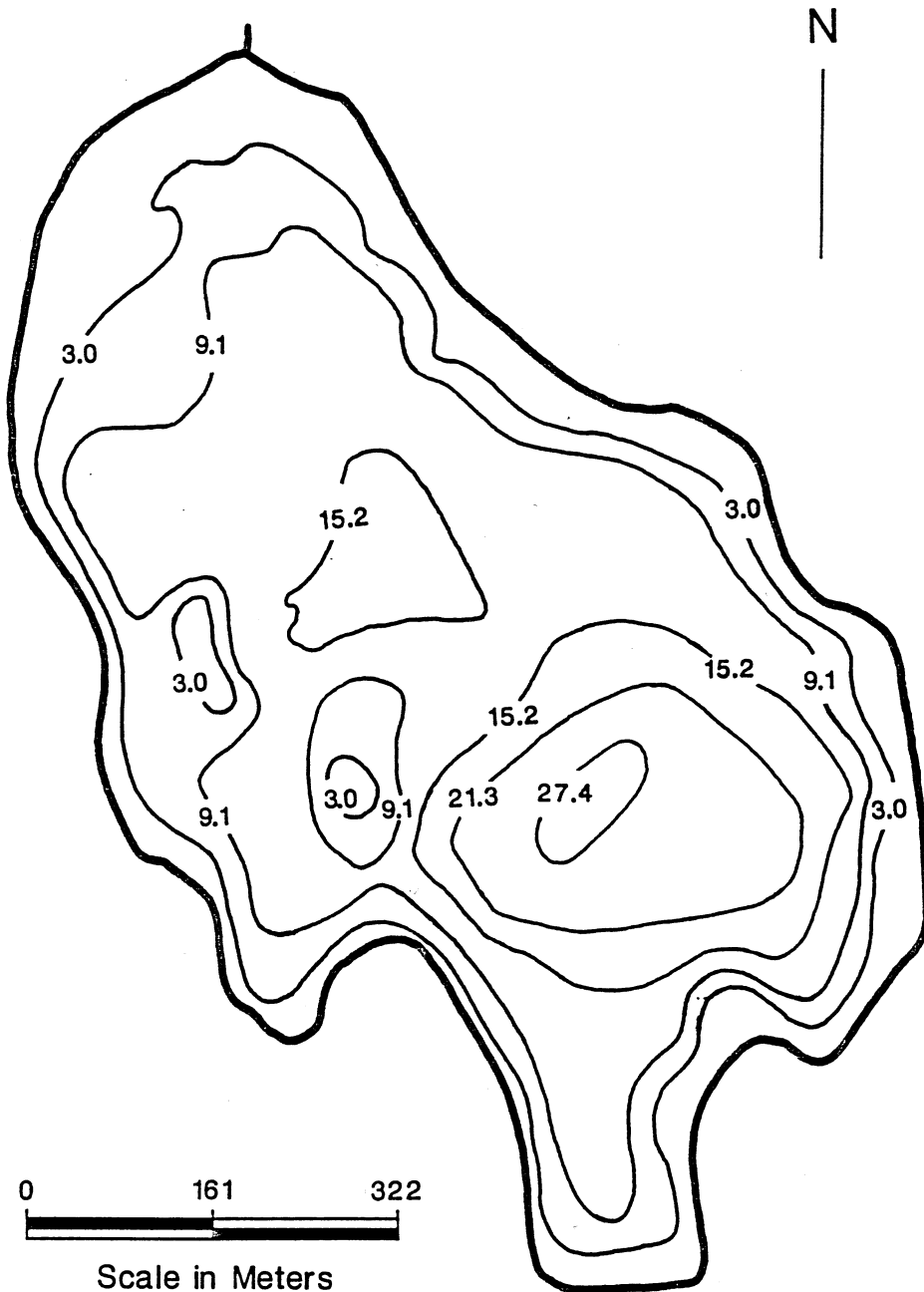
Scale in Meters

Fig. 1.2. Elk Lake. The depths at contours are in meters.
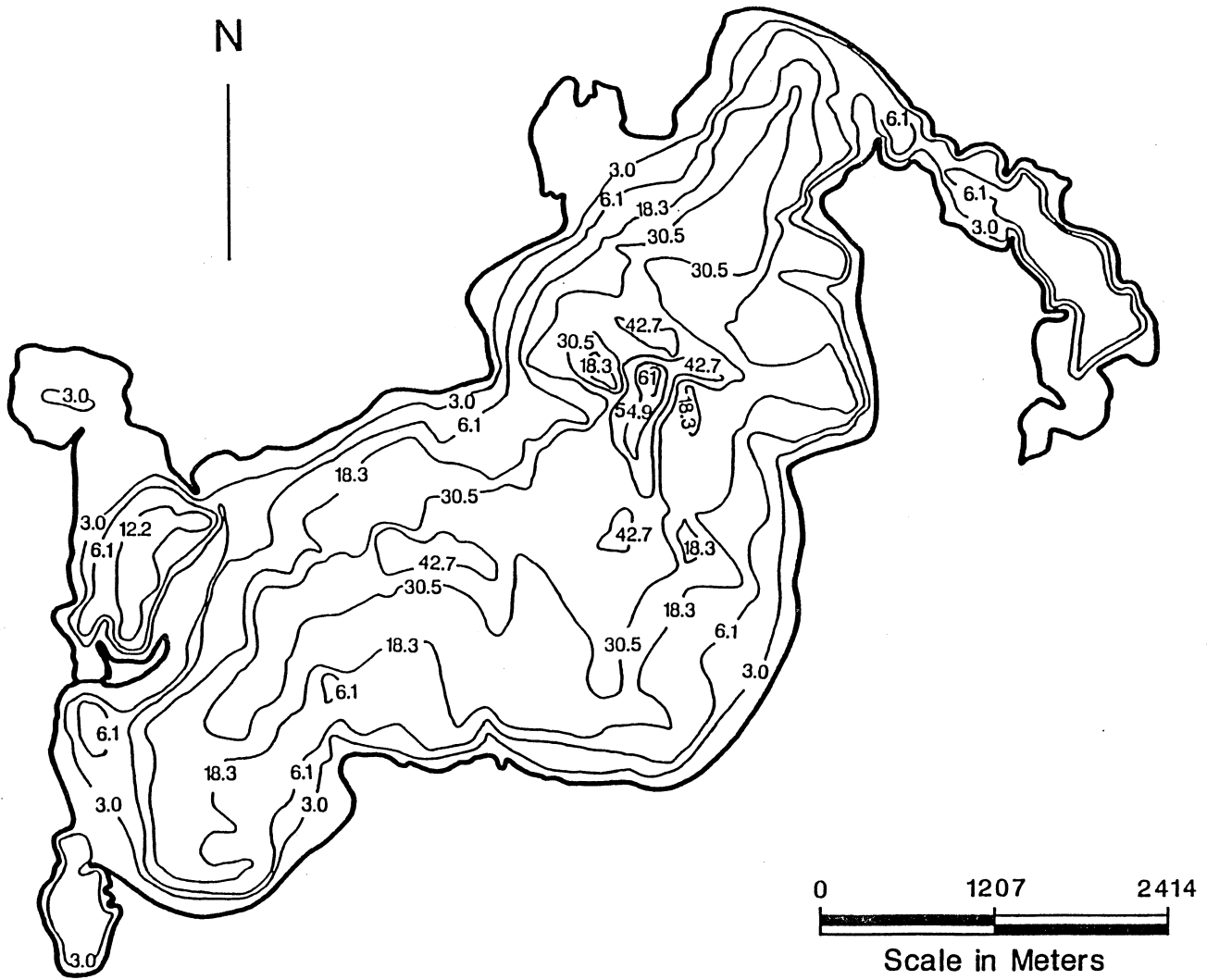
Fig. 1.3. Ten Mile Lake. The depths at contours are in meters.

N

3.0
6.1
18.3
30.5
30.5

6.1

6.1
3.0

3.0
6.1

30.5
18.3

42.7
42.7

61
54.9

18.3

3.0

18.3

30.5
42.7

18.3

30.5
42.7

18.3

30.5

18.3

6.1

3.0

3.0
12.2
6.1

6.1

18.3
6.1

18.3
6.1

3.0

3.0

3.0

| 0 | 1207 | 2414 |

Scale in Meters

Dissolved Oxygen (mg/l)
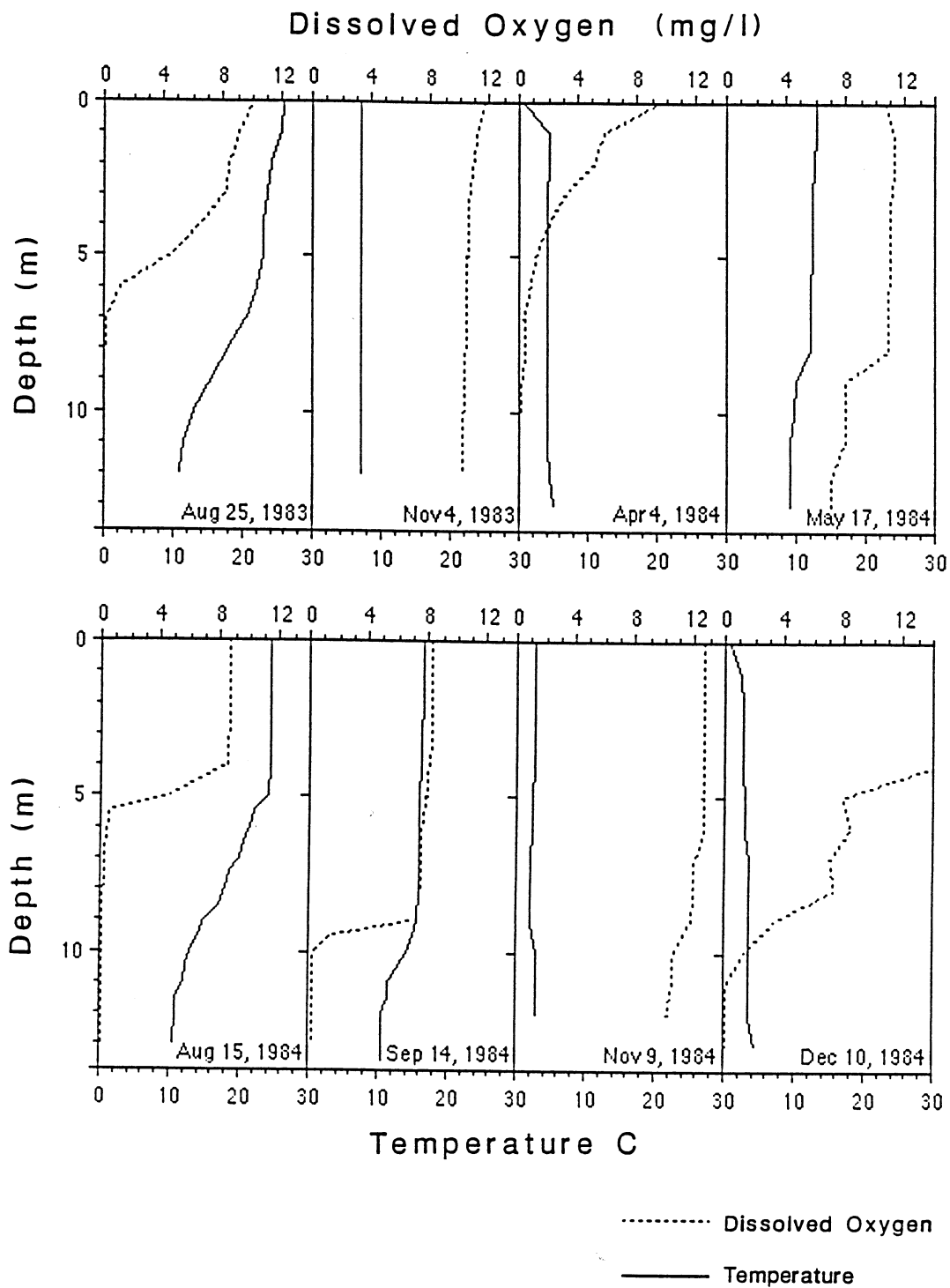
Fig. 1.4. Temperature and Dissolved Oxygen Profiles of Lake Itasca.

Fig. 1.5. Temperature and Dissolved Oxygen Profiles of Elk Lake.

Dissolved Oxygen (mg/l)

Sep 26, 1983

Mar 31, 1984

May 3, 1984

July 5, 1984

Aug 9, 1984

Oct 1, 1984

Nov 6, 1984

Nov 26, 1984

Depth (m)
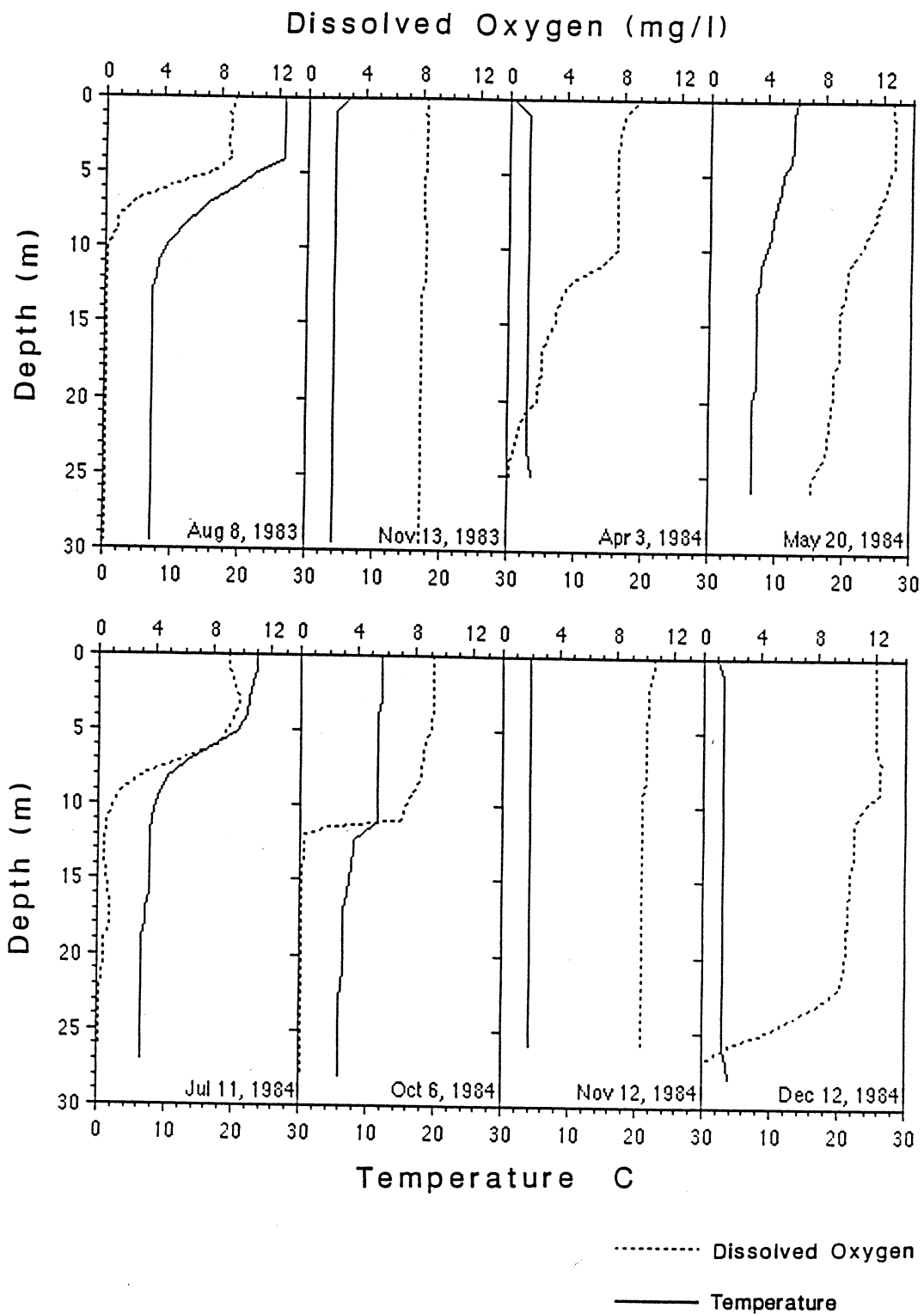
Temperature C

.... Dissolved Oxygen
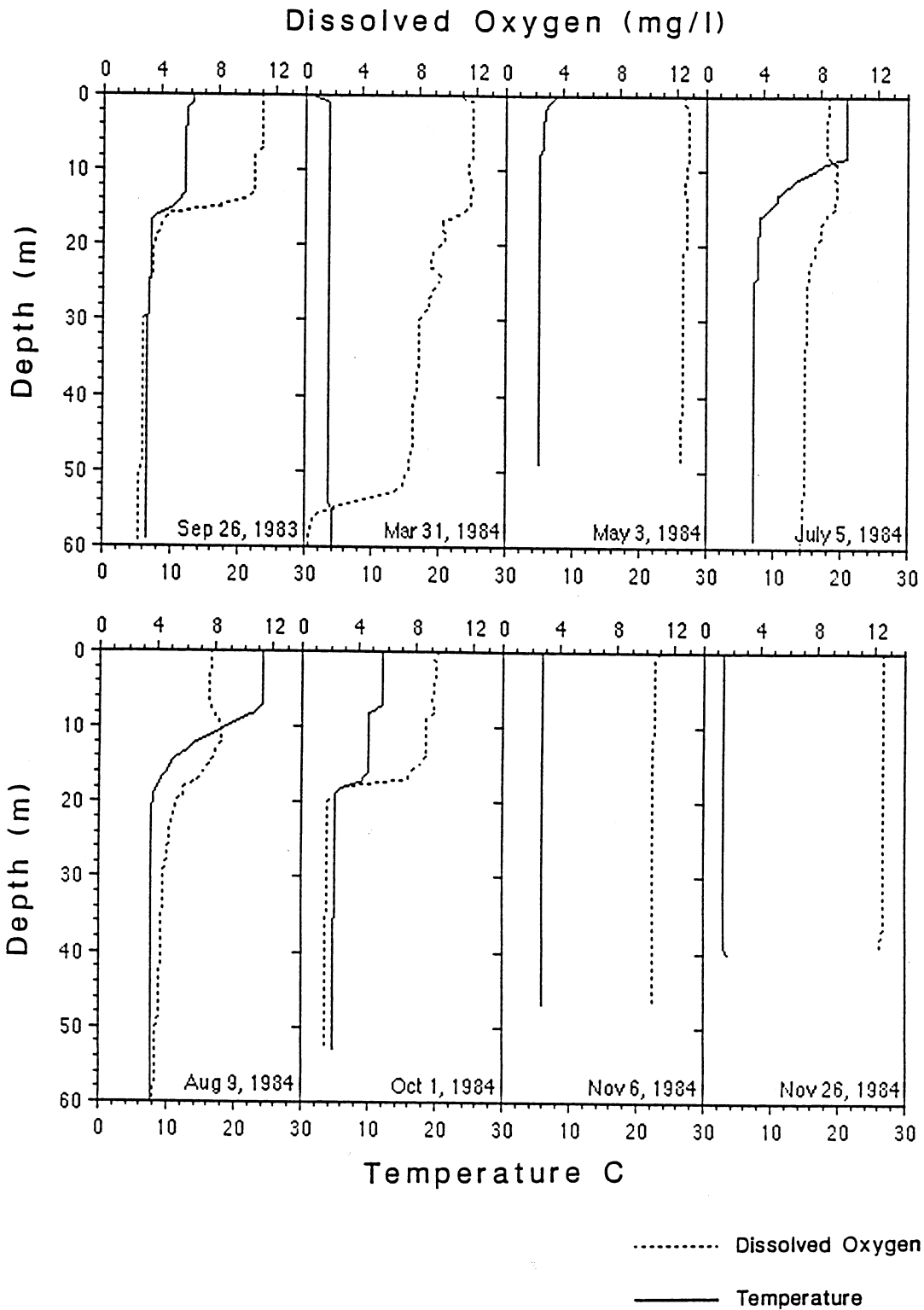
———— Temperature

Fig. 1.6. Temperature and Dissolved Oxygen Profiles of Ten Mile Lake.

CHAPTER 2. VERTICAL DISTRIBUTION

2.1. INTRODUCTION:

An attempt was made to determine the seasonal vertical distribution of ciscos in the three study lakes for reasons of both practical and theoretical interest. Results of these investigations were used to facilitate the capture of fish for tissue analysis. Further, a knowledge of the seasonal changes in the vertical distribution of ciscos would permit an approximate description of the annual thermal history of members of the populations, and would indicate times at which oxygen concentrations might be limiting. For poikilotherms, temperature is of great importance in the determination of physiological and biochemical rates, and exerts a controlling force over metabolic processes (Fry, 1971). Below certain levels, oxygen may limit metabolism and growth, or affect survival. Both of these factors are important in the interpretation of observed growth and reproductive patterns.

The vertical distribution of the cisco, *C. artedii*, has been addressed in many of the classic papers on cisco life history. Authors agree that, in general, temperature and dissolved oxygen concentration are key factors in determining the observed distributions. For example, Hile (1936) suggested that the summer distributions of cisco in lakes in the highlands of Wisconsin were based on temperature and dissolved oxygen

concentrations. In an exhaustive study of cisco distributions in Lake Nipissing, Fry (1937) described both vertical and horizontal movements of ciscos that were closely correlated with changing temperatures and oxygen concentrations. In a survey of 37 lakes in Indiana that contained cisco populations, Frey (1955) concluded that ciscos occupy the coldest waters with adequate oxygen available.

In the Great Lakes and other large lakes, ciscos are pelagic in the spring. Although their distribution may be variable shortly after the disappearance of ice they are found near the surface in the late spring (Koelz, 1929; Dryer and Beil, 1964; Smith, 1956; Fry, 1937). After the surface waters warm, they descend below the thermocline, even if food resources (zooplankton) remain abundant in shallower waters (Dryer and Beil, 1964). They become pelagic again in these lakes in the fall.

The summer distribution of ciscos in smaller lakes has also been described by several authors. The general pattern observed is that ciscos occupy the cooler water of the hypolimnion and gradually move up to the top of this layer, or into the lower portion of the thermocline, as oxygen is depleted in deeper strata (Cahn, 1927; Frey, 1955; Fry, 1937; Hile, 1936; Nelson and Hasler, 1942). Nelson (1970) has described a similar pattern of summer vertical distribution of the cisco in Elk Lake and Lake Itasca, two of the lakes involved in the present study.

2.2. METHODS:

Fish were captured using vertically hung gill nets. In Ten Mile Lake, a single net, 45.7 m deep and 3.66 m wide, with a mesh size of 1.27 cm was used. In Elk Lake, a gang of three nets of different mesh sizes (1.27, 2.54 and 3.81 cm), each 30.48 m deep and 3.66 m wide was used. The bottom of each net was weighted with 1.59 cm diameter steel conduit and the upper end of the net was attached to a wooden pole that was floated at each end by large styrofoam blocks. The nets were held spread apart by 3.96 m lengths of 1.91 cm diameter PVC tubing attached with clips at 5.7 m intervals. The side lines of the net were marked at meter intervals.

Before setting a net, two vertical lines, 3.66 m apart were put into place and drawn taut. Diagonal lines were then set from the tops of, and in the same plane as these to prevent twisting of the net. The net was then lowered along the vertical lines by means of carabiners attached to the ends of the conduit. Any extra netting was tied to the float bar at the top of the net. At Elk Lake, few fish were caught per set night. They were picked by pulling them into the boat allowing the carabiners to slide along the fixed vertical lines, and noting the positions of the fish in relation to the depth markings. The nets were then reset by sliding them back down the lines. This process was carried out for three to five days each month during the ice-free season. At Ten

Mile Lake, where many fish were caught in this net, I found it easier to pull the whole net into the boat and remove the fish on shore. Samples were also collected with vertical nets during the winter at Ten Mile Lake. Except for these samples from winter months, fish caught in the vertical nets were preserved in formalin. Because Lake Itasca is a relatively shallow lake, vertical nets were not used there. The depth of fishing of regular gill nets in this lake was determined from oxygen and temperature profiles and information on the vertical distribution of ciscos in this lake provided by Nelson (1970).

Figures are presented on pages 43-44.

2.3. RESULTS:

Only adult fish were caught in vertical gill nets. In Elk Lake, no fish were caught in the smaller mesh sizes used and in Ten Mile Lake, only adults were vulnerable to the single mesh used there.

In Elk Lake (Fig. 2.1), fish were distributed throughout the water column in May and June. From July through October, 1984 and in August and September of 1983 (the only two months of that year when vertical distribution was determined) ciscos were confined to the upper strata of the lake. In October, 1984 and September, 1983 there was some evidence that ciscos moved downward in the water column with the deepening of the

thermocline at these times. During the height of stratification in both years, August in 1983 and July through September in 1984, fish were captured in vertical nets in the epilimnion, even though temperatures were high at these times. Further, in July, 1984, fish were caught below 10 m, even though the dissolved oxygen concentration was less than1 ppm.

The seasonal pattern of vertical distribution of adult ciscos in Ten Mile Lake is shown in Fig. 2.2. During the winter, ciscos in Ten Mile Lake were distributed throughout most of the water column. In early May, ciscos were concentrated below 20 m, and most fish were caught below 30 m. This occurred in spite of the fact that temperatures were still low in the surface waters (7.5 °C) and the lake was nearly isothermal below 8 m. The vertical distribution of ciscos remained essentially unchanged through early September in 1984. During these months, nearly all fish were caught below 20 m and modes were at 30 m or deeper. In early October, 1984, the mode shifted upward to 27 m and was more pronounced than in the previous months. At this time, oxygen concentrations in the hypolimnetic waters of Ten Mile Lake were low, less than 2 ppm at the depths where cisco were captured. Ciscos inhabited similar depths in early October in the previous year.

2.4. DISCUSSION:

Pelagic fishes generally do not occupy the entire water column. The vertical distribution of fishes may be restricted by a number of factors, such as temperature, oxygen concentration, light, food availability and interactions with other species. Vertical gradients of temperature and dissolved oxygen concentration exist during summer stratification in temperate lakes and have long been considered to play important roles in determining the vertical distribution of fish in general and of ciscos in particular (Juday and Wagner, 1908; Cahn, 1927; Hile, 1936; Fry, 1937; Frey, 1955). Rudstam and Magnuson (1985) approached the problem of cisco (and perch) vertical distribution by considering these two factors as the primary determinants of vertical distribution. They assumed that when possible, ciscos would select their preferred temperature, which was estimated from observations on other coregonids as 12 °C and that ciscos would avoid temperatures in excess of 17 °C, based on Cahn's (1927) experiments. Minimum required oxygen concentrations were estimated as 1.9 ppm at 12 °C and 3.5 ppm at 20 °C. They then compared observed distributions with predictions based on their model, and considered factors other than temperature and dissolved oxygen to be responsible for the deviations observed. Their assumptions appear to be reasonable, and the distributions

of ciscos in the lakes of the present study will be discussed in relation to their analysis.

In general, the distribution pattern of ciscos observed in Elk Lake was similar to that described by Nelson (1970). However, in 1983 and 1984, depletion of oxygen in the hypolimnion occurred earlier, and was more complete than in the years encompassed by his studies. Thus, he noted that ciscos were present at the bottom in early July. In late July he captured ciscos between 7.5 and 11.6 m and in August between 6.1 and 8.5 meters. In his study, the dissolved oxygen concentration at these depths was between 3 and 4 ppm. In contrast, in the present investigation, the oxygen concentration was approximately 2 ppm at 7 m in August, 1983, and at 8 m in August and September of 1984. In spite of this, ciscos were found at approximately the same depths in vertical nets in the present study. It is also of interest that, as in the vertical nets, many ciscos were caught at depths to 11 m in mid-July, 1984 in horizontally set gill nets, although the oxygen concentration at this depth was below 1 ppm.

Nelson (1970) observed that occasionally, a small number of fish were caught below the thermocline during summer stratification, but were never caught in epilimnetic waters. In contrast, in the present study, fish were caught in the epilimnion of Elk Lake in both years of the present study. Fish were captured during the night, and this may have been the result of a nocturnal vertical migration of ciscos, in reponse to vertical migrations of

the plankton. Diel vertical migrations of the vendace, *Coregonus albula*, have been documented by several authors (Dembinski, 1971; Enderlein, 1982; Hamrin, 1986; Northcote and Rundberg, 1970). However, although vertical nets were set for 4 or 5 nights, the size of the samples from Elk Lake at these times was small, and conclusions other than that there was a general movement of fish out of the deeper waters during summer stratification are not justified. Regular gill nets were set to encompass the thermocline in these months and yielded large catches on all occasions. It seems likely that most of the ciscos were concentrated in the rather narrow depth strata from approximately 5-8 m at these times, similar to that described by Nelson (1970).

From November to May, adult ciscos in Elk Lake occupied waters at temperatures below their preferred temperature. During summer stratification, they were generally found at depths with temperatures very near to the preferred temperature, except in August and early September, when low oxygen concentration force them to occupy temperatures between 14 and 17 °C. The observations that fish were caught in the epilimnion or in deeper strata below the thermocline (as in July, 1984) may simply be the result of short-term foraging expeditions to these areas.

Ciscos in Ten Mile Lake occupied the entire water column during the winter months and were restricted to hypolimnetic waters during summer stratification. However, for much of the

ice-free season, ciscos in Ten Mile Lake were found in deeper water and hence, at lower temperatures, than would be predicted according to the criteria of Rudstam and Magnuson (1985) described above. In Ten Mile Lake, ciscos were concentrated below 20 m early in May, at temperatures (5 °C) far below their assumed preferred temperature. Similar phenomena have been described in other lakes. In the lakes of southern Wisconsin studied by Cahn (1927), ciscos tended to be associated with the bottom until lack of oxygen forced them to move higher in the water column. Frey (1955) noted that, while in some lakes ciscos occupied the entire hypolimnion during the early months of the ice-free season, in others, such as Green Lake, they remained near the bottom as long as oxygen levels permitted. Further, ciscos in Ten Mile Lake remained at these depths, or at slightly shallower depths, at least until early October, when surface temperatures were near the preferred temperature and when the dissolved oxygen concentration at the depths they inhabited was below 2 ppm. Fry (1937) noted the resistance of ciscos of Lake Nipissing to move into the epilimnion in the fall, even though water temperatures were low at that time. The ciscos of Ten Mile lake thus were not observed to inhabit waters with temperatures greater than 7.5 °C at any time during the year.

Light, distribution of prey items, and bioenergetic considerations may contribute to the explanation of these observations. Light avoidance has been suggested as a factor in

the similar distribution of vendace, *Coregonus albula*, in Swedish lakes (Hamrin, 1986), where a marked vertical migration (upward at dusk, downward at dawn) was observed. In laboratory experiments, brook trout (*Salvelinus fontinalis*) and bluegill sunfish (*Lepomis macrochirus*) selected temperatures other than the preferred temperature to avoid high light intensities (Sullivan and Fisher, 1954; Stuntz, 1975, cited in Rudstam and Magnuson, 1985). The transparency of Ten Mile Lake is relatively high (Chapter 1), and avoidance of light might possibly be a factor involved in depth distribution of ciscos in this lake. This would not, of course, explain why this distribution would occur at night, when the fish were captured. It is not known if the ciscos in this lake migrate upward at night, and information regarding the precise time of capture is lacking. It is possible that the observed distribution is the result of fish being caught at different depths at different times.

Although zooplankton collections were made during the field work, these samples have not yet been enumerated. Thus, no firm conclusions regarding prey distribution or abundance can be made. However, rough estimates of relative abundance in the epi-, meta-, and hypolimnion were attempted. Vertically integrated samples had been collected from three depths: from the top and bottom of the thermocline, and from the lake bottom, to the surface of the lake. Abundance in each of the major strata could then be obtained by subtraction. The volume of settled

zooplankton from each sample was calculated by measuring the height of settled zooplankton in standardized cylindrical containers. The density for each stratum was determined by subtraction. In June and July, zooplankton densities in the metalimnion were approximately twice as great as in the hypolimnion. In May, August and September, densities in the metalimnion and hypolimnion were similar. Zooplankton densities in the epilimnion were similar to those in the hypolimnion in all months except September, when zooplankton were more abundant in the surface waters. Comparisons with samples from the other two lakes indicated that zooplankton densities in Ten Mile Lake were approximately an order of magnitude lower than in either Elk Lake or Lake Itasca. Further, the exceedingly small size of these fish, and the apparently large population size (personal observation) suggests that food may be limiting. If this is the case, these fish may be choosing a temperature lower than the preferred one. This would reduce metabolic costs and could result in better growth (Brett, 1979).

Lake Itasca ciscos are restricted in their summer vertical distribution due primarily to low oxygen concentrations in the metalimnion and hypolimnion and high surface water temperatures. They may also be restricted by low oxygen concentrations in deeper waters during the winter. Winter sample sizes were small, but all fish taken were captured in nets suspended near the surface. From the end of September through

May, conditions exist where the water they may occupy is at temperatures at or below their assumed preferred temperature.

However, from June to August, they were generally caught at depths between 4 and 7 meters. These results are similar to those of Nelson (1970). At these depths, temperatures exceeded the assumed preferred temperature of the species, and at times exceeded the upper avoidance temperature by a considerable amount (up to 24.5 °C). During these periods, fish were also captured in the hypolimnion, which was anoxic or severely depleted of oxygen. In spite of the lack of oxygen at these depths, ciscos in this lake apparently make trips to the bottom to forage, as is evidenced by the appearance of *Chironomid* larvae in gut contents (Nelson, 1970 and J. C. Underhill, personal communication).
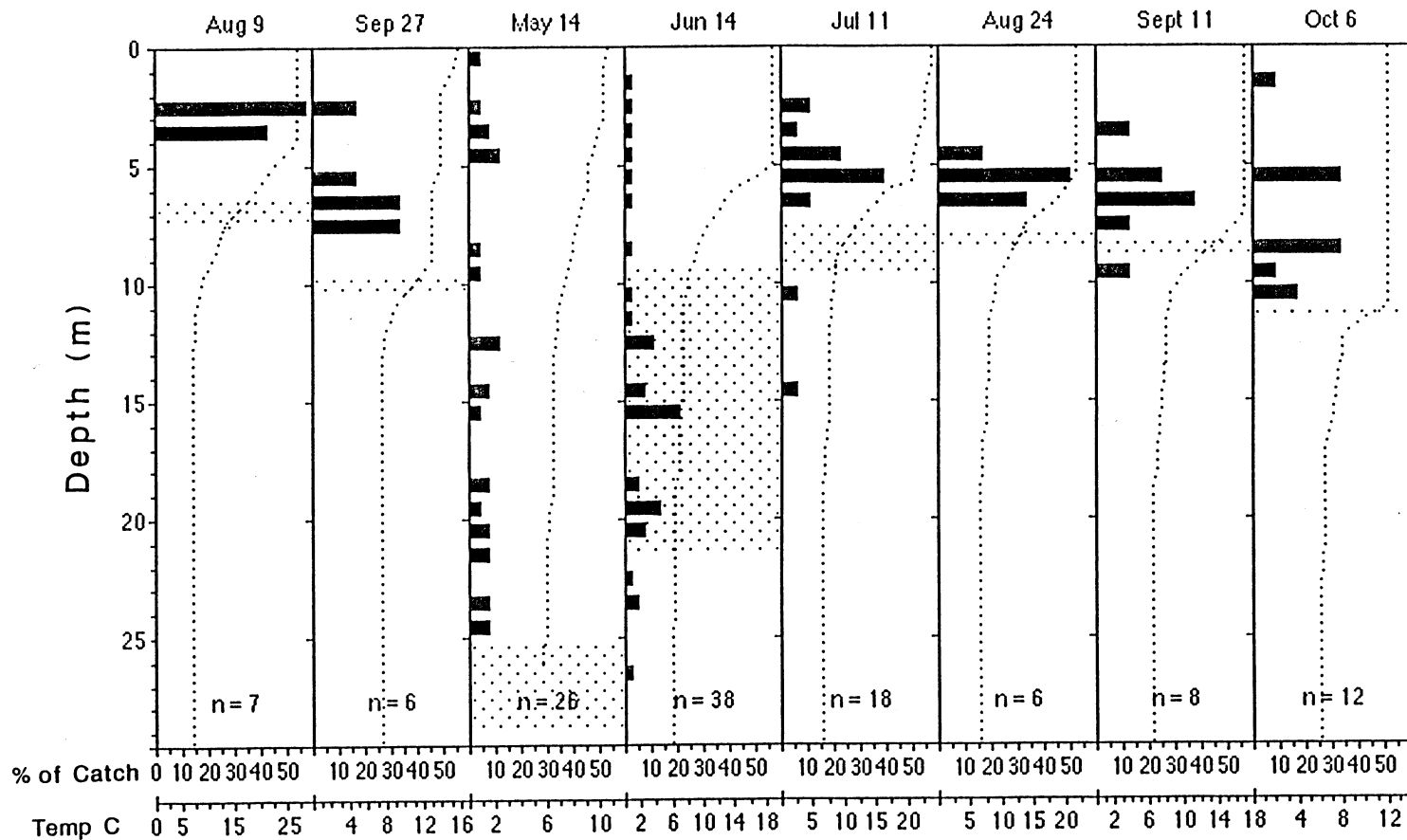
Fig. 2.1. Vertical Distribution of Ciscos in Elk Lake. Bars indicate the per cent of the total catch at each depth interval. Temperature profiles are indicated by dotted lines. The dissolved oxygen concentration at the upper boundary of the stipled areas is 4 ppm, and at the lower boundary it is 2 ppm.
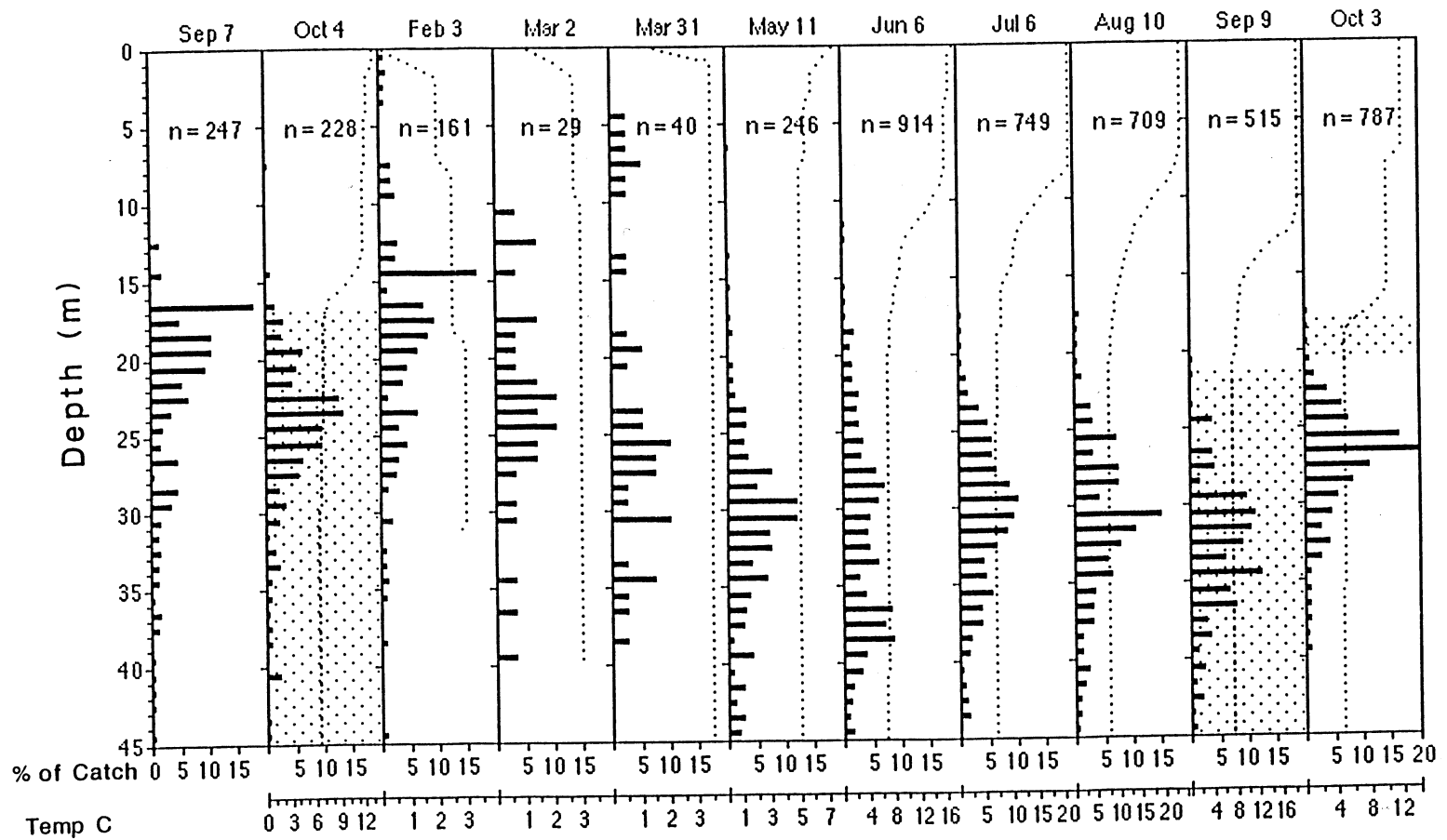
Fig. 2.2. Vertical Distribution of Ciscos in Ten Mile Lake. Bars indicate the per cent of the total catch at each depth interval. Temperature profiles are indicated by dotted lines. The dissolved oxygen concentration at the upper boundary of the stipled areas is 4ppm, and at the lower boundary it is 2ppm.

CHAPTER 3. SIZE AND AGE COMPOSITION

3.1. INTRODUCTION:

Lengths and ages of ciscos from the three study lakes were determined to provide a general description of growth in each lake. They also provided a rationale for grouping samples for tissue analysis and served to identify the age at maturity in the three study populations.

The anatomical structures used for age determination differed for the three populations. Both scales and otoliths were used for age assessment. Since the classic work of Van Oosten (1929) on ageing of ciscos, many workers have applied the technique of age assessment from scales uncritically (Carlander, 1987). However, it has been recognized for some time that using scales for age assessment can lead to underestimates of fish ages, especially in slow-growing fish, and in older fish, whose growth rate decreases, often with the onset of sexual maturation (Beamish and McFarlane, 1987).

Several workers have noted that scale ages can underestimate the age of members of the genus *Coregonus*. Aass's study (1972) comparing otolith and scale readings for *Coregonus albula* suggested the need to look more critically at results determined from scales. Barnes and Power (1984) observed that scale ages underestimated otolith ages in lake whitefish,

Coregonus clupeaformis, and that discrepancies occurred from age 4 or 5 and could be of considerable magnitude. Power (1978) observed ages (as determined from otoliths) of fish of the same species that were up to 35 years older than the previously recorded maximum age using scales. Similar results were obtained by Mills and Beamish (1980), who compared ages determined by fin-rays with scale ages. Ages of up to 21 years have been reported for cisco, *Coregonus artedii* (cited in Beamish and McFarlane, 1987).

Thus, both scales and otoliths were used for age determination of Lake Itasca and Ten Mile Lake fish. Elk Lake fish were processed for tissue analysis first, and at this time, otoliths were not taken from samples. For fish of this lake, scales were used for age assessment. The general methodology was similar in all cases, and is described below.

3.2. METHODS:

3.2.1. FISH COLLECTION:

Fish samples were collected at approximately monthly intervals from September, 1983 to December 1984. At each lake, I tried to obtain several fish of each sex for as many size classes as possible, and especially to obtain both pre-reproductive (juvenile) and sexually mature individuals. Most of the fish used

for tissue analysis were caught with gill nets. All gill nets used were of the sinking type, and were 1.83 m deep, except where noted. The length of netting and mesh sizes used, and number of nights fishing varied from lake to lake and month to month depending on the success of capture of various size classes and time constraints imposed by the sampling regimen. All mesh measurements are given as bar measure. Nets were set just before sunset and were pulled the following morning at approximately 0700-0800 hours.

At Lake Itasca and Elk Lake, nets used were either 76.2 m experimental gill nets containing 15.24 m of each of five mesh sizes (1.27, 1.91, 2.54, 3.81 and 5.08 cm) or combinations of separate 15.24 m panels tied together. These sections were of the same mesh sizes as the experimental nets with the addition of 3.18 and 4.45 cm mesh. The use of these individual panels made it possible to fish for different size groups in different localities or depths and also avoid taking more fish of the larger size classes than were needed. Particularly in Elk Lake, sufficient numbers of larger fish were generally captured in a single night's fishing, whereas it was necessary to set nets for several nights for the smaller size classes.

In Lake Itasca and Elk Lake, nets were generally suspended at various depths. This was done both to avoid the incidental catching of fish such as the brown bullhead (*Ictalurus nebulosus*) and to take advantage of concentrations of ciscos in particular

depth strata, especially during the time of lake stratification. Temperature and dissolved oxygen profiles were taken before setting nets and were used to assist in the determination of the depth of the net sets. Various authors (c.f. Hile, 1936; Fry, 1937; Frey, 1955) have noted the tendency for ciscos to concentrate in zones near the metalimnion in lakes as surface temperatures increase and oxygen is depleted in the hypolimnion and Nelson(1970) studied this phenomenon in these two lakes. Nets were suspended in the coolest strata above waters in which oxygen depletion was evident by attaching 10.16 cm diameter floats with line of the appropriate length at 4.57 m intervals along the float line of the net

Fish from these two lakes were picked from the nets and placed immediately into coolers containing frozen gelatin packs. They were then taken to the laboratory at the Lake Itasca Forestry and Biological Station where Standard and Total Lengths were measured to the nearest millimeter and fish were weighed to the nearest half gram. Fish were then double wrapped in heavy-duty aluminum foil and placed in a freezer at -24 °C.

Gill nets used for collections at Ten Mile lake were of 0.95 and 1.27 cm mesh. In this lake, nets were set on the bottom at depths where results of fishing with vertical gill nets had indicated concentrations of ciscos (see below). Nets of the larger mesh size (15.24 to 30.48 m total length of nets) were only used for one night, and provided adequate samples, generally about

200 to 300 fish per 15.24 meters. However, the smaller mesh size did not capture small fish with equal efficiency, and typically were used for two or three nights. 60.96 meters of net were used each night.

At Ten Mile Lake the procedure was altered in order to ensure proper preservation of the tissues of these fish, which are much smaller than those captured in the other lakes. Removing the fish from the nets took quite some time and it was felt that the tissues might be altered if the nets were picked on the lake, especially during the warmer months. Therefore, the entire net was placed in a cooler with frozen gelatin packs, and the fish were removed on shore. Fish were nearly or completely frozen by the time they were picked from the nets. The first 150 to 200 fish were wrapped in tin foil and placed in a freezer and the rest were preserved in formalin.

This procedure did not permit the weighing and measurement of lengths of fish from Ten Mile Lake at the time of capture. Original lengths and weights were reconstructed from regressions of these variables on lengths and weights measured at the time of processing of a subsample of 38 fish from the October 4, 1983 collection (see Appendix B).

The October 25, 1983 and November 1, 1984 samples from Ten Mile Lake were taken during the spawning run at Ten Mile Lake. Trap nets with 0.95 cm (bar measure) mesh were used to catch these fish.

3.2.2. LENGTH-FREQUENCY DISTRIBUTION:

Length frequency distributions based on Standard Length were constructed for ciscos from Elk Lake and Lake Itasca, using lengths measured at the time of capture. Since Ten Mile Lake fish were not measured until selected for processing of tissues, a length frequency distribution was not constructed for these fish.

3.2.3. AGE DETERMINATION:

Scales were used for age determination of fish from all three populations. They were the primary structure used for the Elk Lake and Lake Itasca populations and were used for comparison with otoliths from Ten Mile Lake fish. Scales were taken from the right side behind the insertion of the dorsal fin.and approximately midway between the lateral line and the dorsal fin. Scale impressions on acetate were made with a Wildco scale press, as described by Smith (1954). Impressions could not be made of scales from the Ten Mile Lake fish, because of their small size and fragile nature. These were cleaned and mounted on glass microscope slides with Sayre's medium (Uphoff, 1948). In general, the criteria for recognizing annuli in the cisco, *Coregonus artedii*, as established by Van Oosten (1929) were used. A description of these characteristics follows in the discussion below.

Otoliths were used as the primary means of age determination for the Ten Mile Lake fish and were used to corroborate ages determined by scales for the fish of Lake Itasca. The fish of Elk Lake were the first to be processed and otoliths were not taken, as difficulties in the determination of ages from scales had not been foreseen. Ages as determined from inspection of scales were compared with those determined from otoliths. Subsamples consisting of 87 fish from Ten Mile Lake and 79 fish from Lake Itasca were used in these comparisons. The samples included fish from different stages of the seasonal cycle and represented several size classes.

Otoliths were examined in two ways. Whole otoliths were cleared in either cedarwood oil or clove oil, and viewed against a dark background using reflected light. Thus, periods of rapid growth were represented by white, opaque bands, and slow growth by translucent hyaline zones (Chilton and Beamish, 1982). Transverse planes were also observed with oblique light after cracking the otolith through the nucleus, grinding with fine (600 grit) wet-and dry paper and clearing with clove oil.

Ages as determined from whole otoliths and those determined by breaking the otolith and viewing transverse sections through the nucleus, were compared, in order to choose the most rapid, yet reliable, method. A sample of 64 fish from Ten Mile Lake were used for this comparison.

The methodology employed for validating ages was similar regardless of the structure used. Since samples representing various size classes were taken at monthly intervals, it was possible to determine the time of annulus formation and to distinguish between true annuli and other checks, by noting the appearance and relative width of monthly increments at the border of the structure. Small fish were analyzed first and each cohort was followed from the fall of 1983 until the end of the study in December, 1984.

Figures are presented on pages 62-66.

3.3. RESULTS:

3.3.1. LENGTH-FREQUENCY DISTRIBUTION:

Most of the monthly collections from Lake Itasca contained either two or three predominant size classes based (Fig. 3.1). Members of the smallest size class were caught only in the later months of both years. Except for the December, 1984 samples, these fish were less than 100 mm standard length, and are not shown. These fish were later determined to be young-of-the-year (see below). Older juveniles were present in the catch from May to December, 1984. These fish measured between 120 and 190 mm SL, depending on the month, and an increase in length during this period was evident. Adult fish fell into two more or less

discrete size classes. Most of the fish belonged to the first of these, which ranged from about 240 to 305 mm SL. As with juvenile fish in this lake, a rather clear increase in size was noted for this group as the sampling season progressed. The second size group of adult fish was less discrete and spanned a broader range of lengths, from about 310 to 375 mm. The few fish captured that were larger than 350 mm are not depicted.

Fish from Elk Lake fell into two major size classes (Fig. 3.2). The smaller size class consisted of fish which ranged from 130 - 155 mm SL in July, 1984 and from 145 - 180 mm SL in October, 1984. These fish were juveniles and it was determined that they represented a single cohort, that of fish in their second year of growth (see below). The other major size group was composed of adult fish. While a progressive increase in length of the smaller size class was evident, no consistent trend could be identified in the larger one.

The range of lengths of Ten Mile Lake fish observed was from 71- 126 mm.

3.3.2. AGE DETERMINATION:

Of the three populations studied, the fish of Lake Itasca were the most amenable to age determination. Fish in this population were characterized by a high growth rate, making it relatively easy to follow the progress of a seasons' growth on the

scales. Annular markings were distinct and could be distinguished from other growth checks. Further, a wide range of sizes of fish were obtained, and ages for different age groups could be verified by following each group through the yearly cycle.

The smallest size class of ciscos in Lake Itasca became vulnerable to the fishing gear in September of both 1983 and 1984. These fish weighed less than 20 g (except for the two collected in December, 1984) and the Standard Length of these fish was from 80-91 mm. The scales of these fish already showed a prominent annulus followed by subsequent growth. The annulus was characterized by crossing over of circuli in the anterior field and by a distinct disruption of circuli in the posterior field. Some of the individuals also showed an accessory check before the annulus, characterized by crowding, and at times, crossing over, of circuli.

The 1983 year class was followed throughout 1984. Crowding of circuli on the edges of scales was first evident in April fish, and a check was formed by May. Rapid growth ensued until the end of July, when crowding was again observed on the scale margins. Rapid growth resumed in September or October, leading to annulus formation at this time. In small fish in this population, two distinct marks were formed each year, once in the late Spring and another in the Autumn.

The next larger group of fish was the most prominent in samples. The Standard Lengths of these fish were between 240

and 310 mm. Annulus formation occurred between September and December in these fish, somewhat later than in the smaller fish. An accessory mark similar to that observed in younger fish, which was characterized by a discontinuity of circuli, especially on the antero-lateral edge, was also present in most of the samples of this size group. This mark was present in fish collected in May and thereafter. At times, it appeared as a continuous thickened line along the length of the anterior field. However, it was often absent on one side of the same scale and was not generally seen on all scales from an individual. Further, it was never seen in the posterior field as was the true annulus. This size class (240 to 310 mm) completed its fourth year of growth by the end of the sampling in 1984.

The age of larger fish was determined as with younger, and thus smaller, fish, by observing the pattern of addition of circuli and annulus formation in succesive months. In these fish, as in the cohort described above, annulus formation occurred sometime between September and December. In many of these fish, little or no addition of circuli took place during the winter months, and only one mark per year, the annulus, was formed.

For Lake Itasca fish, the ages as determined from scales and otoliths were consistent. Of the 79 comparisons made, otolith ages coincided with scale ages in all but 2 cases. In one of these, the fish was quite old, and the scale had been difficult to interpret. In the other, there was a three year discrepancy in ages determined

by the different methods. In this latter case, the length and weight of the individual were much greater than those of similarly aged individuals (Age III). The discrepancy was possibly the result of an error in numbering the scale sample.

In Elk Lake, the results for young-of-the-year and juvenile (Age I) fish were similar to those obtained for Lake Itasca fish. Two distinct marks were observed to have formed in each year. The criteria used for distinguishing annular markings in these fish were the same as those used for Lake Itasca fish. As in these fish, two distinct marks were observed on scales of Elk Lake fish through their fourth year of life. Most of the adult fish from Elk Lake were aged at V to VII years. There was a large amount of overlap in lengths of fish of these ages. In the Age V fish, it was possible to follow the progress of growth around the edge of the scale from month to month In the latter two age groups, this was difficult in some cases, and suggested that in these fish the limit of the relibility of the method was approached.

In Ten Mile Lake fish, ages determined from scales were generally comparable to those determined from otoliths until the formation of the second or third annulus (Fig. 3.3). Scale ages agreed with otolith ages in 59 of the 87 comparisons. In the cases where agreement was not found, otolith ages were greater than scale ages. In nineteen of these cases, scales exhibited three growth periods and otoliths, either four or five. These otoliths had three broad growth zones, while the others were thin. A similar

pattern was observed in the other cases where discrepancies existed. In four cases, scales had two growth zones, while otoliths had three or four, and in six cases, scales had four growth zones, while otoliths had five or six.

The spacing between growth periods on otoliths appeared consistent and otolith ages were judged to be accurate. In general, owing to the thinness of the otolith, ages could be determined from whole otoliths, and except in the largest specimens, these ages agreed well with results from cracked otoliths. Ages determined by these two methods were in agreement in all but one of the 64 comparisons (Fig. 3.3).

In all age classes of Ten Mile Lake ciscos observed, growth (as indicated by the formation of an opaque zone at the edge of the otolith) began between June and July, with an opaque (white) zone first becoming visible on the edge of the otolith in the latter month. A translucent zone became apparent on the edge of the otolith between August and September or October, indicating that growth had ceased. These methods were reliable for fish through age IV, that is, in their fifth year. After this age, it was difficult to distinguish the position and even the presence of growth rings and annuli, due to the extreme thinness of the growth zones.

3.4. DISCUSSION:

3.4.1. LENGTH-FREQUENCY DISTRIBUTION:

Several factors may have led to the predominance of the observed groupings in Elk Lake and Lake Itasca. The gill nets used for capture are well known to influence the size composition of catches through their selective action, which may vary depending on the season of sampling (Hamley, 1975; Pope, et al, 1975). Also, time constraints imposed by a regimen for sampling three lakes obviated the possibility of sampling many habitats and locations in any single lake during each month. As described above, I generally sampled strata in the water column where I expected to achieve high catch rates. This usually produced adequate samples of large, mature fish. However, extra effort had to be expended to catch fish of the smaller size classes, and these were probably underrepresented. For example, Nelson (1970) noted that, as stratification of Lake Itasca progressed, smaller fish remained in areas other than at the deepest part of the lake longer than larger fish, a phenomenon that was described in great detail in Lake Nipissing ciscos by Fry (1937). I was unable to adequately sample these locations. Finally, variations in the success of various year classes, and natural mortality may also have contributed to the observed frequency distributions. For example, the paucity of individuals older than III in Lake Itasca

samples may have been the result of the severe summer-kill that occurred in 1983. Many larger fish were observed on the surface, either dead or dying, in July and August of that year.

3.4.2. AGE DETERMINATION:

Scales were used as the primary structure for age determination for the Lake Itasca and Elk Lake cisco populations. The high degree of consistency in estimates of age based on otolith and scale readings in Lake Itasca fish is consistent with the findings of others (c.f. Van Oosten, 1929; Hile, 1936) that in rapidly growing fish, the age of the individual is accurately represented by pattern of scale markings. The observation that the formation of the annulus occurred at a later time in older fish is consistent with the observations of Hogman (1968), who noted that annuli were formed earlier in younger fish of four coregonine species held in captivity. Accessory checks such as those observed on the scales of Lake Itasca and Elk Lake fish have been noted in the scales of ciscos by Van Oosten (1929), Hile (1936), Smith (1956) and others.

Fish from Ten Mile Lake are extremely slow growing. Several workers have found that age determination from scales in coregonids is difficult when growth rate slows down, typically in older individuals (c.f. Hile, 1936). Others (Aass, 1972; Power, 1978) have found that determinations from scales may

underestimate the age of coregonids, especially when the growth rate is reduced, and have recommended the use of otoliths. The comparison of ages determined from scales and otoliths in Ten Mile Lake fish corroborate these findings. In individuals older than Age I, the ages determined from scales frequently underestimated the age of the fish. There was good correspondence between ages as determined from either whole or cracked otoliths. Skurdal, *et al.* (1985) also found good agreement between ages as determined from whole and cracked otoliths in *Coregonus lavaretus*.

3.4.3. GROWTH IN LENGTH:

The growth rates of individuals differed greatly in the three populations, as did the maximum size attained. These differences were pronounced even at young ages. Growth of Age I fish in all lakes was highly significant ($p < .01$ in all cases, ANOVA). The growth of juveniles from Lake Itasca and Elk Lake was roughly similar, and the lengths of these fish at the end of their second year of life were twice those of Ten Mile Lake juveniles (Fig. 3.4).

The largest adults captured from Ten Mile Lake were considerably smaller than juveniles of the other two lakes. Nevertheless, growth throughout the study period was significant for males through Age IV and females through Age III ($p < 0.01$ in all cases, ANOVA). At the end of their fourth year of life, the

Standard Lengths of Lake Itasca adults were comparable to those of the largest fish caught in Elk Lake, which were considerably older. That growth continued in Lake Itasca fish is indicated by the lengths of the few older fish captured there. The growth of Lake Itasca adults was significant ($p < 0.001$ for both sexes, ANOVA). The change in Standard Length of Age III (in 1984) adults from Lake Itasca and Ten Mile Lake is illustrated in Fig. 3.5. The change in length of Elk Lake adults was not examined. As noted above, a great deal of overlap in length of the age groups was observed. Further, samples for analysis were taken from the predominant size class, as described in the following chapter. The result of this procedure was that, in many months, too few individuals of a particular age class and sex were present to permit the analysis of change in length.
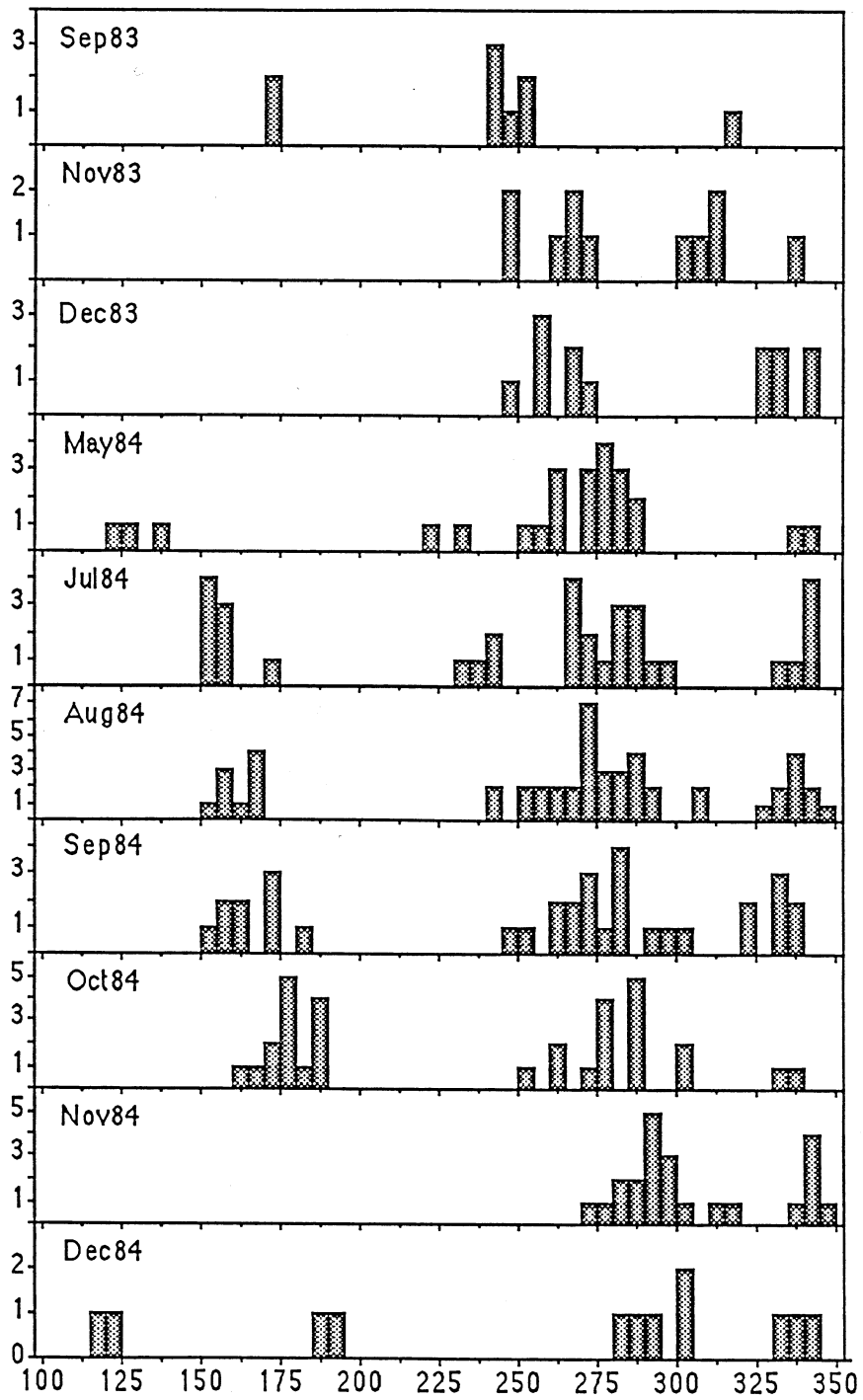
Fig. 3.1. Length-frequency distributions of Lake Itasca ciscos.
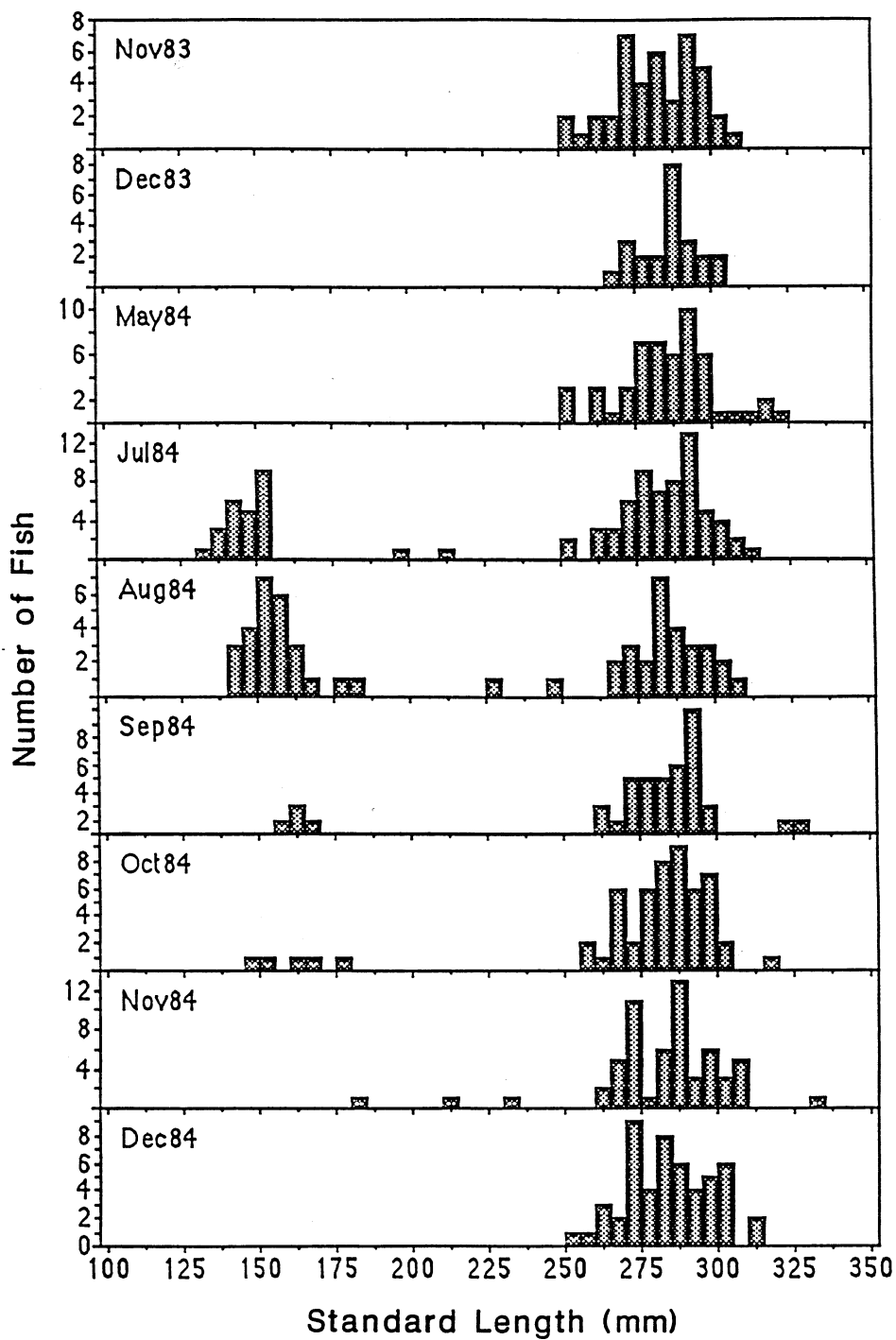
Fig. 3.2. Length-frequency distributions of Elk Lake ciscos.
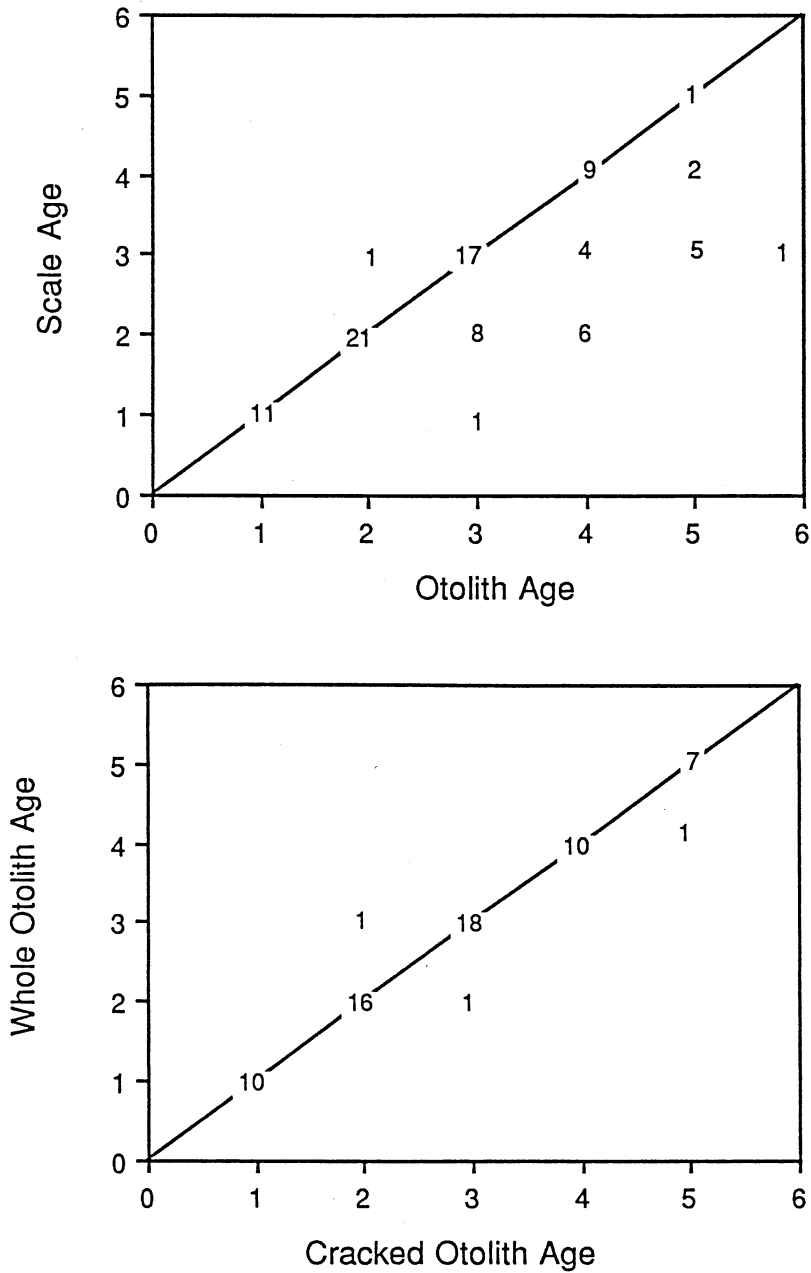
Fig. 3.3. Comparison of age determination methods for Ten Mile Lake ciscos. Top: Comparison of ages determined from scales and from otoliths. Bottom: Comparison of ages determined from whole and cracked otoliths.
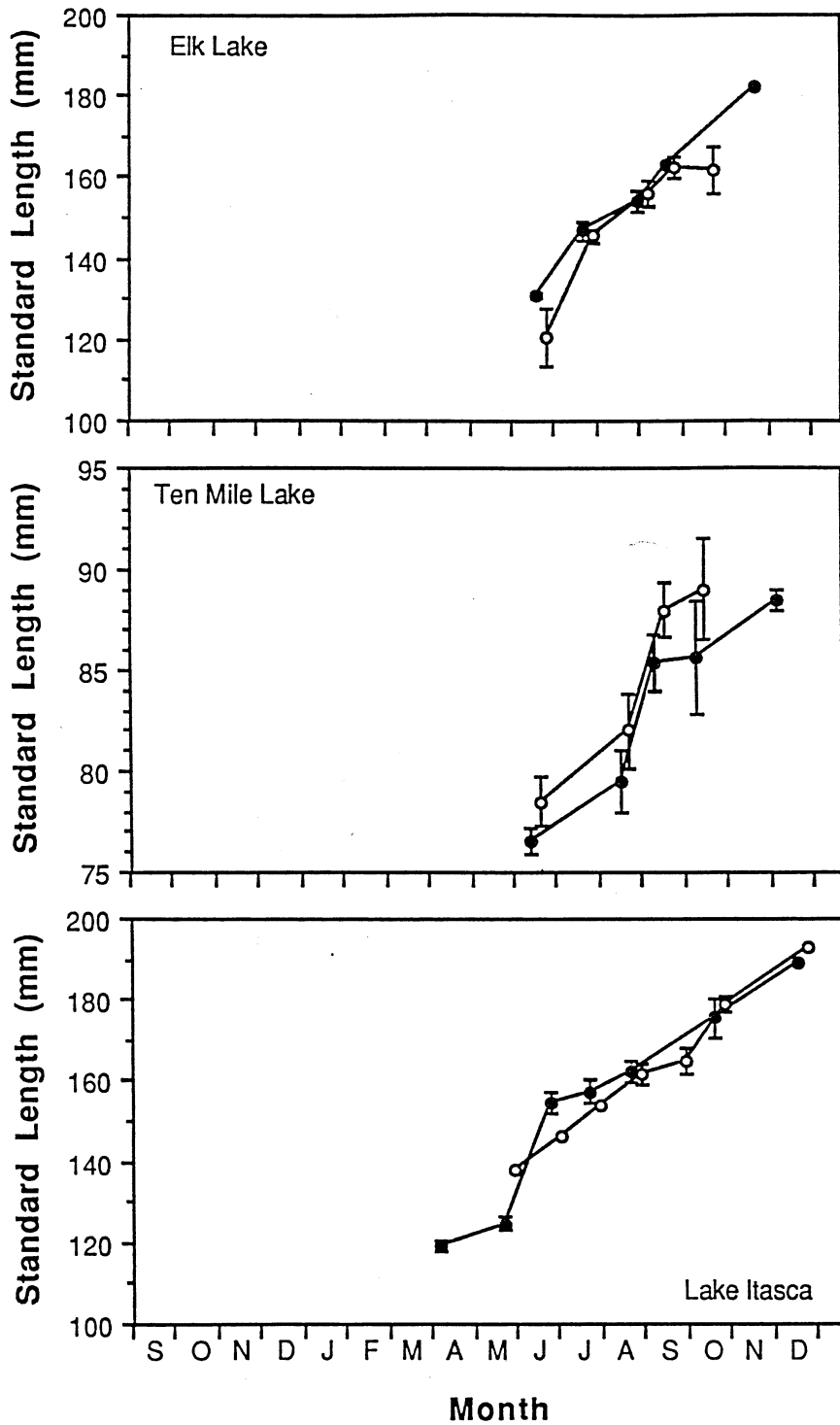
Figure 3.4. Growth in Standard Length of juvenile (Age I) ciscos from Elk Lake (Top), Ten Mile Lake (Center) and Lake Itasca (Bottom).
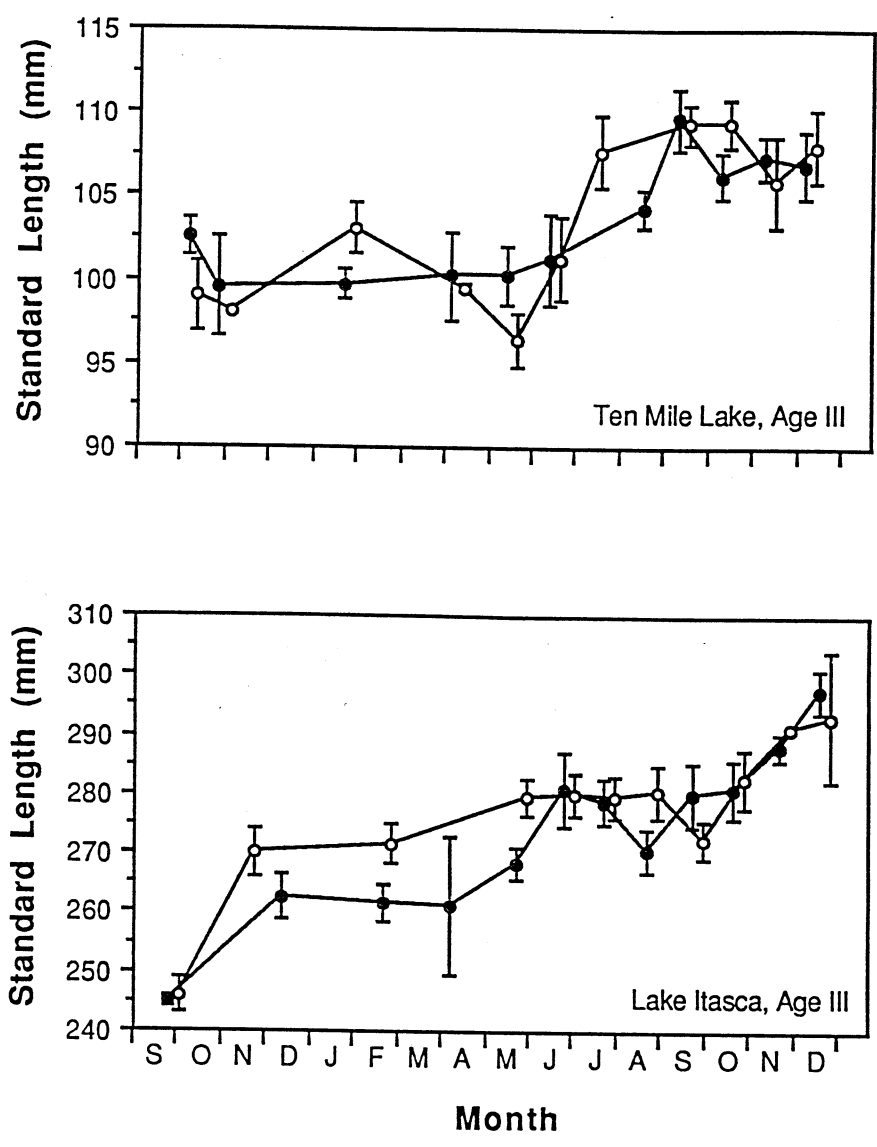
Figure 3.5. Growth in Standard Length of adult (Age III) ciscos from Ten Mile Lake (Top) and Lake Itasca (Bottom).

CHAPTER 4. SEASONAL PATTERNS OF ENERGY ACCUMULATION AND DEPLETION IN TISSUES AND ORGANS

4.1. INTRODUCTION:

The patterns and magnitude of energy accumulation, storage and utilization in fish have been related to the seasonal availability of food resources and the reproductive cycles of fish (Nikolskii, 1963; Shul'man, 1974). Although there have been many studies regarding the seasonal changes in energy reserves of fish, most studies have divided the fish into few compartments, most frequently two: the gonads and some measure of non-gonadal reserves, either muscle, carcass, or somatic tissues combined. Often, only values for the whole fish are presented. Important details of the allocation process may be obscured.

Several organs may be involved in the storage of energy reserves. The most common are the liver, muscle, and visceral deposits, which may be associated with one or more organs (Love, 1970). In the present study, changes in weight, energy density and energy content of these tissues and organs, as well as the gonads were investigated to determine their role in the seasonal energy dynamics of the cisco. Summaries of patterns observed in other species will be discussed in relation to each tissue or organ.

4.2. METHODS:

4.2.1. FISH COLLECTION:

The collection of fish for tissue analysis has been described in Chapter 3.

4.2.2. SELECTION OF FISH FOR TISSUE ANALYSIS:

The choice of samples for tissue analysis was guided by the goal of obtaining a record of the life history of the study populations in terms of energy, by following the seasonal pattern of storage and utilization of energy reserves in different age groups. Most importantly, it was necessary to obtain samples of both immature and adult fish. In practice, choices were determined to some extent by the composition of the catch at each lake and by other constraints imposed by field conditions, which varied between lakes. Ages were determined for fish of all three lakes, and results were incorporated in decisions regarding grouping of samples for analysis. Details of the results of ageing of fish and size composition of the populations were presented in Chapter 3.

Juveniles in their second year of life (Age I) were captured in all three lakes, generally in samples from the latter half of the sampling period. Because young-of-the-year were captured on

only one or two occasions in Elk Lake and Lake Itasca, and samples were very small, data for these fish are not presented.

As noted above, it was not possible to measure lengths and weights of Ten Mile Lake fish at the time of capture. Individuals were thus selected at the time of analysis. Small groups of fish were partially thawed, unwrapped and measured. I tried to obtain at least four fish of each sex for each 10 mm length class, from 80 (and in some months,70) to 120 mm, Standard Length. Ages were then determined, as described below, and fish were grouped accordingly. Because of the method of sampling (by length), and the overlap of size ranges for any given age class, equal representation of all age classes were not obtained for each month. Adult fish aged II- V were analyzed. However, no marked differences in the patterns of energy dynamics were observed between these groups. Therefore, only data from the cohort that was in its fourth year of life in 1984 (Age III fish), which were best represented in most of the monthly samples, are presented.

Adult fish captured in Elk Lake were from 250 and 330 mm Standard Length, with most of these between 270 and 300 mm (see Chapter 3). There was much overlap in length between age groups, and there was some uncertainty in the ageing of older individuals. Therefore, samples for tissue analysis were taken from the more restricted size range (270-300 mm Standard Length). These fish were aged at V-VII years, and do not

represent a single cohort. Approximately eight fish of each sex were analyzed for each month.

Tissue from most of the adults captured from Lake Itasca was analyzed. Data are presented only for those belonging to the predominant cohort which reached Age III in 1984. The sample size varied from month to month depending on the number of fish available.

The sample sizes of fish used for tissue analysis and their dates of collection are given in Appendix C.1. The numbers given are limited to those considered in the present work.

4.2.3. TISSUE ANALYSIS:

BODY COMPARTMENTS ANALYZED:

Fish were removed from the freezer and allowed to thaw partially before dissection. Weights and lengths were measured for comparison to fresh values, and ageing structures were taken. Upon opening the fish, the gross gonadal state was estimated by visual inspection, using a slight modification of the scheme presented in Kesteven (1960). This information was used in conjunction with age assessment to determine age at maturity.

Large fish (> 200 g) were divided into six compartments (tissues) for analysis. These are: liver, digestive tract, gonad, muscle, ventral retroperitoneal fat deposit, and the remainder. Values for the carcass were obtained by combining the values for

muscle, ventral fat deposit, and the remainder of the fish with organs removed. Thus, the carcass represents the whole fish minus the liver, digestive tract and gonads. For smaller fish (<200g), neither muscle fillets nor ventral fat deposits were analyzed separately and values for the carcass were determined directly. The contents of the digestive tract were removed prior to weighing. Muscle tissue was removed as a fillet using a standardized procedure. This was taken from the right side of the fish from just posterior to the opercle to the caudal peduncle, and consisted of both white and red muscle. The ventral fat deposit was taken as an index to a larger fatty deposit found lining the body cavity just beneath the peritoneum. The portion utilized could be removed rather easily from the area just surrounding the ventral midline whereas separation of the deposit from underlying muscle tissue was deemed too difficult in the remainder of the body cavity.

WEIGHT:

Tissues were weighed in pre-dried, and pre-weighed porcelain evaporating dishes. Prior to drying, tissues were divided into small pieces to facilitate drying. This was accomplished either by manual slicing in the case of liver, digestive tract, gonad and ventral fat, or by grinding in a food grinder for muscle and carcass. Tissues were then dried to constant weight at 80 °C (72 hours). The selection of this

temperature for drying was based on tests described in Appendix C.2.

Dried samples were weighed again, to obtain dry weights of tissues, per cent dry matter and per cent water. Samples were then ground in a mortar with pestle, placed in glass scintillation vials and redried at 80 °C for 24 hours. Samples were then processed for caloric content. If processing was delayed, samples were sealed in dessicators and kept in a freezer at -24 °C.

CALORIC DENSITY AND CALORIC CONTENT:

Subsamples of dried tissues weighing approximately 0.5-1.0 g weighed to 0.1 mg were used for analysis of caloric content. In some cases, it was necessary to pool certain tissues because of their small size. These included the liver from all Ten Mile Lake fish and immature (Age I) fish from the other two lakes, and the gonads of all immature fish, mature males from Ten Mile Lake and mature females from Ten Mile Lake in samples taken from January to June, 1984.

The caloric density (cal g^{-1} dry weight) of fish tissues was determined with a Parr Model 1241 Adiabatic calorimeter with a Parr 1680 Master Contol Unit and a Parr Model 1341 Straight Jacket Calorimeter fitted with a temperature transducer. Corrections for acid formation and fuse wire were made according to the instructions of the manual accompanying the apparatus. Based on the results of tests presented in Appendix C.3, which

revealed little variation between replicates, only one determination of caloric density was made for each tissue for each fish. Caloric content, the total calories per tissue or organ, was calculated by multiplying the caloric density of the tissue or organ by its dry weight. Caloric density, expressed on a wet weight basis, was calculated as the caloric content divided by the wet weight of the tissue or organ.

Values of caloric density and caloric content were converted to Joules (1 kcal = 4.186 kJoules), and are reported as energy density (kJ g^{-1}) and energy content (kJ).

4.2.4. DATA ANALYSIS:

The seasonal patterns of change in weight, energy content, and energy density were first examined for the significance of overall change during the sixteen months encompassed by the investigation. Data for each sex were examined separately. Means and variances of samples from each lake were calculated and variances were examined for homogeneity using Hartley's F_{max} test (Sokal and Rohlf, 1969). If the variance of the samples for a given variable was determined to be homogeneous, single factor ANOVA was used to detemine the overall significance of seasonal changes. When this condition was not met, the Kruskal-Wallis test was employed. Results of these tests are presented in Appendix D.1. General features of the seasonal patterns were assessed by *a*

posteriori comparisons using Fisher's Protected Least Significant Difference method, and significance of specific changes were assessed by Sheffé's F-test.

Further tests were made by comparing means of variables between what were considered biologically meaningful periods. These periods were: a) spawning to postspawning, b) postspawning to midwinter, c) midwinter to ice-out, or the beginning of the usual growth season (May), d) beginning of the growth season to seasonal maximum, that varied depending on the tissue analyzed, and e) from the seasonal maximum to minimum observed (in the case of the gonads, this was from spawning to post-spawning). These comparisons were thus considered as *a priori* tests. Student's t-test was used to determine the significance of differences in sample means if the variances of the two samples examined in each comparison were determined to be equal using the F-test. When variances were unequal, the Mann-Whitney U-test was utilized. These results are summarized in Appendix D.2.

Differences between sexes for all variables studied, both among adults and juveniles, were examined in months selected to coincide with the limits of the periods described above. Further comparisons were made between juveniles and adults within a given lake, and between fish from the three study lakes. In these latter tests, sexes were examined separately, and only energy density and water content were considered. Differences between

sample means were assessed by Student's t-test or the Mann-Whitney U-test, as described above. Summaries of these comparisons are given in Appendices D.3 and D.4. All appendices of statistical summaries are arranged by tissues, in the same order as presented in the results of this chapter. Additional statistical results are noted in the text. When statistical significance is referred to in the text, it refers to the $\alpha = 0.05$ level.

To avoid repetition, reference to figures and appendices is made at or near the beginning of each section. Figures illustrating changes in wet and dry weight, energy content and energy density expressed on a wet weight basis are included for all tissues examined in adult fish. If the results differed depending on how energy density was expressed, additional figures are provided. Further, since graphs illustrating changes in water content were generally mirror images of the changes in energy density on a wet weight basis, I have usually ommitted these. Fewer graphs are provided for juvenile fish. Data points for females have been shifted 7 days to the right of males from the same sampling date in order to avoid overlap. Figures are presented at the end of the chapter, beginning on page 156.

4.3. RESULTS:

4.3.1.LIVER:

ADULTS:

Distinct seasonal patterns were evident in livers of adult fish of both sexes from all three study lakes. Single factor ANOVA or Kruskal-Wallis tests showed significant changes in all variables studied except for energy density on a wet-weight basis for females of Elk Lake (Appendix D.1.1). Results of additional statistical tests are presented in Appendices D.2.1, D.3.1, and D.4.1).

The seasonal pattern of change in wet weight, dry weight and energy content showed the same features for a given sex within each lake. These patterns were different for males and females, most notably in the large increases of these variables in females that occurred prior to the spawning period in late autumn. Differences between populations were also evident. Changes in wet weight, dry weight, energy content and energy density of adult liver are presented in Figs. 4.1 to 4.4.

MALES:

Livers of adult male fish generally increased in weight and energy content for a variable period of time in spring or early summer, after which these quantities decreased through late autumn. There was some evidence that liver size increased in

males following the spawning period and continued to increase throughout the winter, especially in Lake Itasca fish.

In Elk Lake males, the increase in dry weight from May to August was significant, but changes in wet weight and energy content were not. Relative increases were roughly of the same order of magnitude for these three variables, ranging from 30.5% in wet weight to 56.4% in dry weight. The decreases from August to November of all three variables were significant, and represented a 51% decrease in the energy content of the liver. Increases in liver weight and energy content of Ten Mile Lake males occurred over a shorter period of time, from June to July, and relatively high values of these variables persisted until September. All of these increases were significant. The greatest increase was noted in wet weight (103.57%) and the least in energy content (65%). The subsequent decreases, which took place from July to October, were also significant. In Lake Itasca males, only the increase in liver energy content during the summer, from May to August, was significant, although the increase in dry weight was nearly so (p = .0519, t-test). Significant decreases in these quantities occurred as in the other lakes, from August to October.

From October to December, significant increases in liver dry weight and energy content in Lake Itasca fish, and a significant increase in wet weight of livers of Ten Mile Lake were observed. Livers of Lake Itasca and Elk Lake males exhibited similar

increases in the autumn of the previous year that continued through the winter months. Increases in both wet and dry weight and energy content of Lake Itasca fish were significant from September to December, 1983, and levels in May were similar to those in December. The increases in weight and energy content of Elk Lake males were significant, both from September to December, 1983 and from December, 1983 to February, 1984. However, in Ten Mile Lake, livers of males showed no significant changes in weight or energy content from October of 1983 through June 1984.

In males from both Lake Itasca and Elk Lake, a midwinter (February) peak in liver size and energy content occurred. In Lake Itasca, this peak was not statistically significant, due to the large variance of the February samples. In Elk Lake males, the dry weight of the liver decreased significantly between February and May, but changes in wet weight and energy content were not significant.

The seasonal pattern of changes in energy densities of livers in males from the three lakes were similar. In Elk Lake and Lake Itasca, energy densities increased during the period of growth in size of livers from May to August and subsequently decreased from August to October. In Ten Mile Lake, energy density of liver continued to increase through October, long after increases in liver size had ceased. This explains the prolonged nature of the decrease in energy content during this same period. As in the

males of the other lakes, energy density decreased from October to December. Livers of Elk Lake males had the lowest maximum energy density (6.19 kJ g^{-1} wet weight), and those of Ten Mile Lake the highest (8.08 kJ g^{-1} wet weight). The peak energy density of liver from Lake Itasca males, 7.18 kJ g^{-1}, was intermediate. Single factor ANOVA results indicated that differences between lakes were significant (p = .0013) and Sheffé F-tests showed differences between all lakes to be signficant at the 0.05 level.

The decrease in energy density in the autumn was also evident in 1983 samples, especially in males from Ten Mile Lake. In Elk Lake males, liver energy content also decreased during this time. Although this change was not significant when considered on a wet weight basis, a marked decrease of energy density on a dry weight basis (not shown) was highly significant. In Lake Itasca males, a slight, but not significant decrease in energy density on a dry weight basis occurred between September and November of 1983. However, on a wet weight basis, the energy density of the liver of these fish increased during this time, and continued through February, 1984. Similar increases were also noted in males from Ten Mile Lake and Elk Lake. These values decreased between February and May in male livers from all three lakes, but the decline was not significant in Ten Mile Lake fish.

FEMALES:

The seasonal pattern of growth and energy dynamics of the liver of female fish differed from that of males in all lakes. Differences were also observed between females of the three populations. Some evidence of sexual dimorphism with regard to liver size was also observed, with female livers being larger than those of males, especially during the period prior to and including that of reproduction.

Increases in weight and energy content during the summer season were either prolonged over a longer period than was observed in males or were not significant until a later time. Thus, wet and dry weight of livers of Elk Lake females increased from May to October, while energy content did not increase significantly until September and actually decreased from June to August. The appearance of an early increase in energy content and dry weight between May and June was not statistically significant due to the large variance associated with the June sample. In Ten Mile Lake, increases in wet and dry weight occurred from June through September, as did energy content. It will be recalled that in males, only the latter variable showed a similar time course. In Lake Itasca females, livers decreased in wet weight through August, and changes in dry weight and energy content were not significant until after August, when all three variables increased dramatically.

Relative increases in size during the growth season were smallest in Elk lake fish, and were similar in both sexes, whereas in Lake Itasca, although the increases in female livers took place over a much shorter time period, they were nearly twice as great as in males, and in Ten Mile Lake, where relative increases in liver size were greatest, increases in female livers were substantially greater than those of males, increasing 330% in energy content and 354% in dry weight.

Patterns of energy dynamics in livers in females of Elk Lake and Ten Mile Lake also differed from those of males in the period from September 1983 to the beginning of the summer season of 1984. In Elk Lake females, liver wet and dry weight and energy content decreased sharply from September, 1983 through January, 1984, similar decreases were observed in livers of females from Ten Mile Lake from October to November in 1983. In Elk Lake, these decreases were of the same magnitude as, but appeared to be initiated somewhat earlier than, those following spawning in 1984, whereas in Ten Mile Lake, the magnitude of the changes was smaller in 1983 than in 1984. Increases in these variables followed, leading to a midwinter peak. In Elk Lake this is apparent in February; however changes from January through May were not statistically significant. On the other hand, the increase in liver dry weight that occurred from November, 1983 to January, 1984 and its subsequent decrease from January to May, in Ten Mile lake females were significant. The similar

changes in wet weight and energy content were not statistically significant. Nevertheless, while male livers showed no change from October to May in Ten Mile Lake fish, these variables decreased in female livers during this period.

In contrast, the pattern of change in livers from females in Lake Itasca during this period was similar to that of males in this lake, and increased significantly in wet and dry weight and energy content from September, 1983 through February, 1984. However, the changes were greater than those of males. For example, the energy content increased 128% as compared to a 70% increase in male livers during this time.

In all lakes, the seasonal pattern of change in energy densities of female livers followed the changes in energy content in a general way. However, some differences are notable. In Ten Mile Lake fish, the increase in energy density during the summer began earlier and persisted longer than the increase in energy content. Further, the decrease in energy density in the autumn of 1983, and the subsequent increase until January were more pronounced than the associated changes in energy content. However, the changes in energy density from November, 1983 to May, 1984, were not significant, because of the high variance in the January samples.

Although the overall pattern of seasonal change in energy density on a wet weight basis of livers of Elk Lake females was similar to that of energy content, the only significant changes

occurred between November to December in both years. In Lake Itasca females, the peak in energy density was achieved in August, long before the peak in energy content. Also significant was the sharp decrease in energy density from August to October, the period just prior to spawning.

Maximum values of energy density of liver in females were compared by the Kruskal-Wallis test, which showed lake to be a significant factor (p = .0034). Results of Mann-Whitney U-tests showed the livers of Lake Itasca and Ten Mile Lake females did not differ significantly (p = .873). The peak energy density of liver of Elk Lake females was lower than that of the other two lakes (p = .0039, for both cases).

By and large, energy densities of female liver were similar to those noted for males. Exceptions are discussed below. Results of comparisons between sexes are given in Appendix D.3.1. Contrasts between sexes in adult fish revealed a similar pattern for fish from Elk Lake and Ten Mile Lake. In general, female livers were larger in wet and dry weight and energy content than male livers in months near the reproductive period, and did not differ significantly from male livers near the beginning of the summer. Also, male livers had a higher energy density at some time during the summer season, which was most apparent when the energy density of male livers were at peak values. In Elk Lake fish, the differences in weight and energy content were also apparent in February. At this time, the wet weight of female

livers was significantly greater than that of males and the dry weight and energy content were nearly so (p = .055, U-test, in both cases). However, energy density of female liver was significantly lower than that of males in February, as it was generally during the summer growth period. This difference is especially evident in the August samples (p = .009, t-test). A similar difference in energy density was noted in Ten Mile Lake fish, in October (p = .012, t-test). In Lake Itasca fish, a somewhat different situation was observed. As in the other lakes, female livers weighed more and had a higher energy content in the autumn (October) and, as in Elk Lake, in February. However, they did not differ in these respects in May. Also, energy densities of both male and female livers were similar throughout most of the year, and did not differ significantly in August, when energy densities of both male and female livers were highest. Male livers did have higher energy densities in October. In contrast with the fish of the other two lakes, this occurred at the point of lowest energy density in both sexes.

JUVENILES:

Samples of juvenile fish were obtained only in a few months during the sampling season. A general trend of increasing weight, energy content and energy density followed by a decrease in these variables in the later part of the season was observed, with some exceptions as noted below. To illustrate

these trends, the changes in energy content and energy density are shown in Figs. 4.5 and 4.6, repectively.

The changes in wet and dry weight and energy content of the liver of juveniles from Elk Lake were not significant, although in females, these variables increased from June to August and subsequently decreased through October. Male livers had greater wet and dry weights and a higher energy content in June, but not August. Energy densities of livers of both sexes increased from June to July and did not differ significantly between sexes. Energy density of female liver decreased from July to September. In Ten Mile Lake juveniles, livers increased in wet and dry weight and energy content from June to August in males and from June to October in females. In males these values declined from August to October, but the decreases were not significant. No significant change in energy density was observed for either sex, although mean energy density declined between June and October in both sexes. There were no differences related to sex except that female livers had higher wet weights in June. In Lake Itasca males, liver wet and dry weight, energy content, and energy density increased significantly from April to August. Dry weight, energy content, and energy density decreased from August to October, but only the decreases in energy content and energy density were significant. Juvenile females were only available from August to October. Livers increased significantly in wet weight, but not in dry weight or energy content during this period and

energy density decreased as in males. Male livers weighed more (both wet and dry weights) in June. There were no other differences between the sexes.

Energy density of the liver of juvenile males did not differ from adult males in any of the lakes. In Elk lake, the liver of juvenile males had higher water content than adult fish. Among Ten Mile Lake females, livers of adults had lower water content than those of juveniles in October, but not in June. Adult females also had a higher energy density than juveniles but this was not significant (p = .054, t-test). Livers of juvenile females in Lake Itasca had a higher energy density than adults in October. A similar situation occurred among females in August in Elk Lake.

4.3.2.GONAD:

ADULTS:

Analysis of variance or Kruskal-Wallis Tests indicated significant monthly changes in both sexes of fish from all lakes in all variables studied (Appendix D.1.3). Results of additional statistical tests are given in Appendices D.2.3, D.3.3, and D.4.2).

Gonads in both sexes increased in weight and energy content rather rapidly as the spawning season approached, and these variables decreased precipitously following spawning. During the rest of the year, gonads remained small. In all lakes, males began maturing earlier than females and testes reached

their maximum size earlier than ovaries. These trends are illustrated in Figures 4.7-4.9. Changes in energy density on a wet weight basis are presented in Fig. 4.10 and on a dry weight basis in Fig. 4.11.

TESTES:

The pattern of buildup of gonadal tissue in males is similar in fish of the three lakes, but differences were noted in the timing of maturation and in the length of time during which gonads remained large. In Elk Lake males, gonadal increase in wet weight, dry weight and energy content takes place from May through October, reaching their maximal size approximately one month before spawning. The testes increased by approximately 500% in all three variables during this period. Most of this growth occurred between July and August. The weight and energy content of testes at their maximal values were similar in 1983 and 1984. The testes regressed more rapidly from November to December in 1984 than in the previous season, when the major decrease in gonadal size and energy content took place from December, 1983 to February, 1984.

The period of greatest growth in testes of Lake Itasca fish was from August to September in 1984, somewhat later than in Elk Lake. Dry weight and energy content increased by approximately 400% between May and November. The increase in wet weight was slightly higher. Testes in November, 1984 were

40% larger in wet weight and about 53% larger in dry weight and energy content than in November, 1983. In both years, significant decrease in weight and energy content of the gonads occurred between November and December. The decreases following the 1983 spawning season continued through midwinter. Testes weight and energy content increased between February and May.

In Ten Mile Lake fish, the growth of the testes was more gradual, and took place between June and September, and represented an increase in dry weight and energy content of 168 and 213% respectively. The time of maximal testes size was nearly two months prior to the spawning season in this lake. A major decrease in weight and energy content occurred between September and October, before spawning. Energy content and weight continued to decline through November. Dry weight and energy content were similar in both years, but wet weight was greater in 1984 than in 1983 at this time. Regression of the testes continued through midwinter as in males of the other lakes. As in Lake Itasca, some growth of the testes occurred before spring.

Similarities in the general seasonal pattern of change in energy density of the testes of fish from the three study lakes were observed. In fish from two of the lakes, maximal energy densities occurred during midwinter, in January in Ten Mile Lake and in February in Elk Lake. In Lake Itasca fish, this occurred in May. Following the maximum, there was a sharp decrease in

energy density followed by a period of increase that lasted for a variable period of time, five months in Ten Mile Lake, four in Elk Lake and three in Lake Itasca fish. Though the increase was slight in Elk Lake fish, it was nevertheless significant.

Energy density (wet weight basis) in Elk Lake fish declined from November to December in both 1983 and 1984. This decline was accompanied by a pronounced increase in water content, which masked an increase in energy density on a dry weight basis that occurred between October and November in both years. Values were similar in both years. In Ten Mile Lake fish, a similar decline in energy density on a wet weight basis occurred earlier, between October and November of both years. However, an increase in water content was noted only in 1984. A rise in energy density on a dry weight basis, analogous to that in Elk Lake, also occurred in Ten Mile Lake fish, one month earlier, in October. Values in 1984 were somewhat higher than those of 1983 in this lake. A similar situation existed in Lake Itasca fish in 1983. Although an increase in energy density on both wet and dry weight basis was observed, these were not significant. In 1984, energy density on wet weight basis declined from October through December as water content increased, and no change in energy density on a dry weight basis was observed. Values from both years were comparable. Maximum energy density in testes of Elk Lake fish occurred in February. In Lake Itasca, there appeared to be two peaks, in May and August. These changes

were significant for values of energy density on wet, but not dry, weight basis, and values were higher than those of Elk Lake fish. Similarly, in Ten Mile Lake fish, two peaks were observed, in June and October. Energy densities of testes at the time of spawning in each lake were not significantly different (p = .1122, Kruskal-Wallis Test).

OVARIES:

The pattern of growth of the ovaries was similar in fish from all three lakes. In Elk Lake and Lake Itasca, ovaries increased in weight and energy content from September to November, 1983. In Ten Mile Lake, where spawning occurs earlier, the peak was reached in October. Following spawning, the ovaries regressed until midwinter in fish from all three lakes and then grew from May until November. In Ten Mile Lake, female gonads reached approximately 80% of their final size by September, while in the other two lakes, over 50% of the growth of the ovaries occurred during the last month before spawning. It should be noted that Ten Mile Lake samples were collected during the spawning run in early November whereas Elk Lake fish were collected in mid-November and were nearly ripe. Although no Age III females were collected from Lake Itasca in November, it is likely that they became ripe toward the end of that month, as females collected in October were not yet ripe and those collected in the second week of December were spent.

Further, the few older females that were caught in November samples were not yet ripe at the time of collection.

In Elk Lake, the ovaries reached approximately the same weight in 1984 as in 1983. In Ten Mile Lake and Lake Itasca, ovaries were considerably larger in females in 1984 than in the previous year. The Ten Mile Lake fish probably spawned for the first time in 1983, at Age II, and in Lake Itasca, some, but not all fish of the cohort examined, spawned in 1983.

Energy density on a wet weight basis was lowest in ovaries in the months immediately following spawning, and increased steadily as the size of ovaries increased. In fish from all three lakes, most of the increase in energy density took place two to three months prior to spawning.

In Ten Mile Lake and in Lake Itasca fish collected in 1983, the maximum energy density was reached prior to spawning and decreased as spawning approached. A similar pattern was observed in Ten Mile Lake fish in 1984, when the maximum energy density was reached in September, nearly two months prior to spawning, and a significant decrease in energy density was noted between October and early November, during the spawning run. It is difficult to say whether this also occurred in Lake Itasca fish in 1984, as ripe females were not caught in November. In contrast to the findings in these two lakes, no decrease in energy density on a wet weight basis just prior to spawning was observed in Elk Lake fish in either year.

The decreases in energy density in the ovaries of Ten Mile Lake and Lake Itasca fish resulted from both an increase in water content that occurred at this time and from a change in the composition of organic matter. Energy densities of ovaries, on a dry weight basis, declined from August in Lake Itasca fish and from September in Ten Mile Lake fish, but changes were not significant in Elk Lake fish until the fish were spent. Within a lake, energy densities did not differ between years.

Results of ANOVA indicated a highly significant effect of lake on the energy density of ovaries, both on wet and dry weight basis, at or near the time of spawning (p = .0001 in both cases). When calculated on a wet weight basis, significant differences were found between all three lakes (Sheffé F-test), ovaries of Lake Itasca females having the highest energy density and Ten Mile Lake females, the lowest. Ovaries of Elk Lake females were intermediate, the mean being closer to that of Lake Itasca fish. A similar relationship was observed when the energy densities on a dry weight basis were compared, but values for Lake Itasca and Elk Lake fish were not significantly different (Sheffé F-test). Samples from Elk Lake and Ten Mile Lake were from November, at the time of spawning, and eggs were mature. However, since no females were caught in Lake Itasca during this month, samples from October were used.

In fish of all lakes, ovaries weighed more and had higher energy content than testes in the months prior to and including

the spawning period. This difference was observed as early as February in Elk Lake and May in Lake Itasca, while in Ten Mile Lake, significant differences were not observed until July. During the period of gonadal regression, testes and ovaries were similar in weight and energy content. In Elk Lake this occurred only in December, in Lake Itasca, this equality was evident through midwinter and in Ten Mile Lake it persisted through July, at least for wet and dry weights. As the spawning season approached, higher energy densities were also observed in ovaries than in testes. Again, this appeared to be true for Elk Lake fish at an earlier time than in the other lakes. In Elk Lake, ovaries had higher energy densities than testes in August, a condition that continued until December. In Lake Itasca, this was not observed until September and in Ten Mile Lake until November, during the spawning run. In all three lakes, at some point during the period of gonadal regression, energy density of testes exceeded that of ovaries. This was observed in February in Elk Lake and Lake Itasca fish and in December in Ten Mile lake fish.

GONADOSOMATIC INDEX:

The gonadosomatic index (GSI) was calculated for adult fish using the formula, GSI = G/B X 100, where G is the weight or energy content of the gonad and B, the weight or energy content of the fish. Calculations were made based on wet weight, dry weight and energy content. Maximum values of the GSI were

used for comparison between lakes. These results are summarized in Tables 4.1 and 4.2, below, for males and females, respectively. Note that the values for Lake Itasca females in 1984 are underestimates. The value presented is calculated from data on fish collected in October of that year, as only one ripe female from the Age III cohort was collected prior to spawning in November. Also note that 1984 values for Ten Mile Lake males are from September of that year, when, as noted above, testes weight and energy content were at a maximum.

The GSI of males from Elk Lake and Lake Itasca in both years were similar. In Ten Mile Lake males, the GSI of males was greater in 1984 than in 1983, and was greater than that of males from the other lakes. However, the GSI as presented above, is based on samples taken in September, before the spawning season. When the GSI is calculated based on samples taken in November, 1984, during the spawning run, the values are 0.8556 for wet weight, 0.837 for dry weight and 0.9678 when based on energy content. These levels are comparable to those of males in November, 1983.

Unlike males, the GSI of females varied considerably depending on whether it was based on wet or dry weight or energy content. GSIs calculated on the basis of energy content were nearly twice as great as those based on wet weights in all samples.

Table. 4.1. Gonadosomatic Index in Male Ciscos.

	Elk Lake		Lake Itasca		Ten Mile Lake	
	1983	1984	1983	1984	1983	1984*
Wet Weight	1.99	2.06	2.21	2.25	0.75	1.74
	0.125	0.076	0.102	0.097	0.399	0.141
	9	6	10	14	4	4
Dry Weight	1.91	1.80	1.75	1.79	1.15	2.49
	0.111	0.097	0.074	0.065	0.560	0.229
	8	6	9	13	4	4
Energy Content	2.07	1.92	1.81	1.83	0.99	2.75
	0.112	0.093	0.087	0.065	0.515	0.261
	8	6	9	13	4	4

Table 4.2. Gonadosomatic Index in Female Ciscos.

	Elk Lake		Lake Itasca		Ten Mile Lake	
	1983	1984	1983	1984†	1983	1984
Wet Weight	16.33	13.95	6.73	12.32	6.97	13.30
	1.058	0.648	6.206	0.594	1.164	1.849
	8	7	2	7	4	8
Dry Weight	22.58	19.63	19.21	17.40	9.802	17.73
	1.487	0.921	--	0.966	1.649	2.407
	8	7	1	7	4	8
Energy Content	26.32	23.36	23.35	20.22	10.89	20.28
	1.849	1.185	--	1.326	1.736	2.815
	8	7	1	7	4	8

Tables 4.1 and 4.2. Below each value is the standard error and sample size. * Values are based on pre-spawning fish captured in September, 1984. † Values are based on pre-spawning fish captured in October, 1984.

The GSI for females from Elk Lake were similar from both years. Although conclusions regarding Lake Itasca females are tenuous, it is noteworthy that the GSIs as presented (for October, 1984) are not significantly different from those of Elk Lake fish in November of that year, and it is likely that these are underestimates, as Lake Itasca fish probably spawn in late November and early December. The GSIs of Ten Mile Lake females were nearly twice as great in 1984 as in 1983. The GSIs of Ten Mile Lake females in 1984 are not significantly different from those of Elk Lake fish in that year.

JUVENILES:

Results of ANOVA and Kruskal-Wallis tests are given in Appendix D.1.4 and results of additional statistical tests are given in Appendices D.2.4, D.3.4, and D.4.2. Because of the small size of juvenile gonads, samples from Elk Lake and Lake Itasca were pooled for determination of energy density and content. Samples from Ten Mile Lake fish were too small for analysis of caloric content. Thus, data for dry weight for fish from all three lakes are presented in Fig. 4.11, and for energy density of gonads from Lake Itasca and Elk Lake juveniles in Fig. 4.12.

In Ten Mile Lake males, testes wet and dry weight did not change significantly from June to October, and there was insufficient material to determine energy density or content. In Elk Lake, testes dry weight increased significantly from June to

August. The increases in wet weight and energy content were not significant. The testes of Lake Itasca males increased in wet weight from April to October. Dry weight and energy content increased from April to August and then energy content, but not dry weight, decreased significantly.

Increases in wet and dry weight of ovaries of Ten Mile Lake fish were not statistically significant. In Elk Lake, ovaries of juveniles increased in wet and dry weight and energy content from June to October. Although wet and dry weights of ovaries of Lake Itasca juveniles decreased from August to October, these changes were not significant. In Elk Lake, the energy density of ovaries of juveniles increased from June to August and then decreased from August to October. A similar significant decrease in energy density was also observed in ovaries of Lake Itasca juveniles.

Sexual differences among juveniles varied from lake to lake. In Elk Lake no significant differences were observed in June, whereas in August, ovaries weighed more and had a higher energy content than testes. In Ten Mile Lake, the dry weight of ovaries was nearly three times as great as that of testes and a similar difference in energy content was observed. In October, only the difference in wet weight was significant, although the mean dry weight of ovaries was about four times as great as that of testes. In Lake Itasca, no differences between the sexes was observed in August, but in October, ovaries weighed more and

had higher energy content and water content than testes, which had a higher energy density.

The ovaries of adults in Lake Itasca and Elk lake had a higher energy density than ovaries of juveniles in October, but not in August. Among males, testes of juvenile Elk Lake fish had a higher energy density than adults in August. Although not enough tissue from juveniles was available for calorimetric analysis of Ten Mile Lake fish, the situation was probably similar, as a higher water content in adult testes was observed.

4.3.3. DIGESTIVE TRACT:

ADULTS:

Results from analysis of variance or Kruskal-Wallis tests indicated that significant seasonal changes occurred in all variables investigated in adult fish of all lakes (Appendix D.1.5). Results of additional statistical tests are given in Appendices D.2.5, D.3.5, and D.4.3.

The seasonal pattern of energy dynamics of the digestive tract was similar in fish of both sexes from all three study lakes. A marked increase in wet and dry weights and energy content of the digestive tract occurred for a variable period beginning in May and was followed by a subsequent decrease through November or December to levels similar to those at the start of the summer (Figs. 4.14-4.16). That these changes were largely the

result of accumulation and depletion of lipid reserves is indicated by parallel changes in energy density, both on a wet and dry weight basis. An inverse trend in water content accompanied the changes in energy density (Figs. 4.17, 4.18).

While the overall pattern of energy accumulation and depletion during the course of the ice-free season was similar in all lakes, there were both quantitative and qualitative differences associated with these changes. The magnitude and timing of change in absolute variables (weight and energy content) differed from lake to lake and between sexes within lakes. Further, the observed patterns differed depending on which variable is considered. Some of these points may be illustrated by considering the relative increase in these variables from the beginning of the summer season to their peak values. These are expressed as a percentage of the initial value in May and are presented in the following table.

Table 4.3. Percentage Increases in Mass and Energy Content of the Digestive Tract During the Summer Growth Period.

	Elk Lake		Lake Itasca		Ten Mile Lake	
	Male	Female	Male	Female	Male	Female
Wet Weight (g)	31.1	29.2	39.6	27.9	108.6	77.9
Dry Weight (g)	108.8	35.04	149.2	124.72	162.0	121.17
Energy Content (kJ)	173.4	53.51	173.0	131.7	208.5	147.9

In all cases, the magnitude of accretion was greatest when energy content is the variable observed, followed by dry weight, while wet weight exhibited the smallest change. This is consistent with the fact that increases in energy density also occurred during this period. In all three lakes, the relative increase was greater in males than in females, although only in Ten Mile Lake did comparisons reveal the differences (of wet and dry weight, but not energy content) to be significant when measured at the peak of growth of the digestive tract. However, the energy density of the digestive tracts of females in August was similar to that of males, but only two females were present in this sample, and were omitted from the analysis.

In Elk Lake fish, the energy density of the digestive tract of both sexes at the beginning of summer was lower than that of fish from the other lakes. Initial values in males and females (4.54 and 4.81 kJ g^{-1} wet weight) did not differ significantly. At the the peak of accumulation in August however, males exhibited a higher energy density than females (9.45 and 7.06 kJ g^{-1} wet weight, respectively). The increase in mass, and the proportionally greater increase in lipid content was apparently responsible for the disparity in energy content observed between the sexes in Elk Lake at this time. At this time, the energy content of the digestive tract represented 3.96% of the total energy of the fish in males, and 3.07% in females. Depletion of visceral energy reserves, which occurred through December, resulted in energy densities and total energy content that were not significantly different between the sexes.

In Lake Itasca, the energy densities of the digestive tract of fish of both sexes at the beginning of the growing season were as high as or higher than that achieved by fish of the other lakes at any time (males, 9.00 and females, 9.80 kJ g^{-1} wet weight). These values are not significantly different. Large amounts of lipids were deposited between May and July as is evident from the nearly doubled energy densities achieved by the latter time. This peak occurred one or two months before the peak in energy density in Elk Lake fish. The peaks in energy density on a dry weight basis in Lake Itasca fish persisted until August, when

energy density was also at a peak in Elk Lake males. In Lake Itasca males, the digestive tract at this time accounted for 9.39 % of the total energy content of the fish. In females, 7.13 % of the total energy content of the fish was contained in the digestive tract. Depletion of visceral reserves occurred from August to October in both sexes. There appeared to be some recovery of these reserves between October and December in females (no samples were available from November) and November and December in males. This was evident in both weight and energy content as well as energy density. At this time, values of all variables were similar to those observed in May. It should be noted that December samples sizes were small. Male digestive tracts exhibited a higher energy density on a dry weight basis in October compared to females, which may be indicative of the relatively more rapid utilization of visceral energy stores by females.

Energy densities of the digestive tract of Ten Mile Lake fish in May were intermediate between those of the other two lakes, and did not differ between sexes. These reached their maximum values in September for males and females, (the samples from August females indicated higher values, but were omitted from analysis because of small sample size) and remained high through October, in contrast to the fish of the other lakes. December levels were similar to those in May, as in the fish of the other lakes. However, as in Lake Itasca, but not Elk Lake, energy density on a

dry weight basis was significantly higher in males than in females at this time. The energy content of the digestive tract accounted for up to 8.21% of the total energy content of male fish, and up to 9.67% of that of females.

Comparisons among fish from the three lakes of the peak energy densities of the digestive tract were highly significant (ANOVA, p = .0001, for both males and females). Peak energy densities of digestive tracts of Ten Mile Lake and Elk Lake fish were similar, and those in Lake Itasca fish were significantly greater than in fish of either of the other lakes (Sheffé F-Test). These conclusions were true for both sexes. Energy densities of digestive tracts of fish from all lakes were more similar after most of the energy reserves have been depleted. Comparisons of energy densities at their lowest values at the end of the 1984 season revealed significant differences between lakes for both sexes (ANOVA, p = .0043, males and .0139, females). The energy density of the digestive tract of Lake Itasca and Ten Mile Lake males did not differ significantly, while that of Elk Lake males was significantly lower than that of males from both of the other lakes (Sheffé F-test). A similar situation among females existed. It is interesting to note that among females, the energy density of the digestive tract was highest in Ten Mile Lake fish at this time.

There were differences in the energy dynamics of the digestive tract in adult fish of the three lakes between the time of reproduction and the following spring that influenced the pattern

as presented above for the growing season. In all three lakes, there was some evidence of accumulation of energy reserves during the winter, following spawning in 1983. However, in Elk Lake males and Ten Mile Lake females, these reserves were depleted by the following May. In both males and females of the Lake Itasca population and in females of the Elk Lake population this accumulation resulted in net gains over the winter.

In Elk Lake fish, both dry weight and total energy content of the digestive tract in males and females and wet weight in females increased significantly between November (females) or December (males) of 1983 and February, 1984. In females, most of this occurred between November and December, whereas, in males, the changes were most notable from December to February. These changes were accompanied by a significant increase in energy density on a dry weight basis (on a wet weight basis, the increase is nearly significant, $p = .053$, t-test) in males. In females, changes in energy density during the period through February were not significant, and on a dry weight basis, energy density actually declined somewhat. Changes in wet weight of the digestive tract of both males and females between February and May were not significant. Nor were changes in dry weight or energy content of female digestive tracts. However, the gains in dry weight and energy content that had accrued since December were lost by May in males. These decreases were accompanied by a decrease in energy density. The net result is that at the end of

the winter, the digestive tracts of males are similar in character to their pre-winter condition, whereas in females, a net gain in energy content occurred.

Digestive tracts of both males and females of the Lake Itasca population increased significantly in wet and dry weights, energy content and energy density between September, 1983 and February, 1984. Means for females at this time were higher than for males, but the differences were not significant because of the large variances observed in both sexes. In males, changes between February and May were not significant, whereas in females, declines of approximately fifty percent in weight and energy content as well as a significant decrease in energy density occurred during this time. Nevertheless, the net result in both sexes after the winter was an increase in weight, energy content and energy density of the digestive tract of both sexes. In May, the digestive tracts of males and females did not differ significantly in any of the variables.

Neither wet or dry weight nor energy content changed significantly in fish of the Ten Mile Lake population from November, 1983 through May, 1984. There were, however, indications of increases in the mass of the digestive tract between November, 1983 and January, 1984. While all three variables increased during this time, only the change in dry weight was statistically significant. Perhaps if samples from February were available, this trend would have been more pronounced. In both

sexes, there was an increase in energy density on a wet weight basis. In males this change was significant. This was likely to have been the result of the accompanying decline in water content, which was also significant. In females, the decrease in water content was also significant, although the change in energy density was not. Between January and May, these changes were reversed, and the digestive tracts of Ten Mile Lake fish in May were similar to those in November of the preceding year in the variables studied.

JUVENILES:

Although samples of juvenile fish were available for only a few months of the year, several interesting observations can be made which suggest that patterns of energy accumulation in digestive tract deposits of juvenile fish are similar to those in adult fish. Results of ANOVA and Kruskal-Wallis Tests are given in Appendix D.1.6 and further statistical tests are given in Appendices D.2.6, D.3.6 and D.4.3. The monthly patterns of change in wet weight, dry weight and energy content were similar. Therefore, of these variables, only the changes in energy content are illustrated (Fig. 4.19). Changes in energy density are illustrated in Fig. 4.20.

In males from Ten Mile Lake and Elk Lake increases in weight and energy content were observed through August, but were not significant. However, the increase in energy density was

significant in Ten Mile Lake males. The females of these populations did show significant changes in these variables. Dry weight and energy content increased from June to October and energy density increased from June to September in Ten Mile Lake females. In Elk Lake females, these variables increased significantly from June to August and decreased significantly from August to October. A similar pattern was observed in Lake Itasca males and a decrease was observed in Lake Itasca females from August to October, the only months for which samples were available. The only differences between sexes that were observed were between Lake Itasca fish in August, when males had significantly higher energy density than females and a lower water content.

It appears that the pattern of accumulation and depletion of energy reserves associated with the digestive tract is similar in adult and juvenile fish. In Lake Itasca and Elk Lake, the initial accretion and subsequent depletion of reserves after August, and in Ten Mile Lake, the persistence of the reserves until September are reminiscent of adult patterns in these lakes.

Changes in energy density also appear to have followed patterns similar to those observed in adults, although in some cases, the depletion of reserves in juveniles was more rapid. In Ten Mile Lake, the digestive tracts of adults and juveniles did not differ in energy density or water content in either June or October. The major decrease in energy density in digestive tracts

of Ten Mile Lake adults took place after October, but juveniles were not collected in these months. In Lake Itasca, there were no differences between adults and juveniles in August, but in October, digestive tracts of adult males had a higher energy density than those of juveniles, which had a higher water content. This was a result of the more rapid decrease in energy density in juvenile males. Juvenile females also had a higher water content than adults, but differences in energy density were not significant. Energy densities decreased considerably in both adult and juvenile females between August and October. In Elk Lake, digestive tracts of adult and juvenile males did not differ significantly in June. By August, the digestive tract of adult males had a higher energy density than that of juveniles. Interestingly, the digestive tract of juvenile females had a higher energy density than that of adult fish in June, whereas by August, these values were equivalent. By October, adult females had a higher energy density (dry weight basis) than juveniles, because of the more rapid decline in energy density in the latter. At this time, the energy density of the digestive tract of juveniles of both sexes from Lake Itasca and females from Elk Lake (males were not available) were nearly identical. The energy density of digestive tracts of Ten Mile Lake juveniles was considerably higher than that of juveniles of the other lakes.

4.3.4.CARCASS:

ADULTS:

Seasonal cycles of energy storage and depletion were apparent in carcasses of adult fish from all three lakes. Changes associated with time of year (month) in all variables were significant as judged from the results of analysis of variance or Kruskal-Wallis tests except for the wet weight of carcass in Elk Lake males (Appendix D.1.7). Results of additional statistical tests are given in Appendix D.2.7, D.3.7 and D.4.4.

Adults of both sexes from all three lakes exhibited an accumulation of matter beginning in the early part of the ice-free season, followed by subsequent depletion. The extent of this depletion varied between lakes. Further, the changes that occurred through the winter, following spawning in 1983 differed among lakes. The seasonal patterns of changes in wet weight, dry weight and energy content of adult carcasses are illustrated in Figs. 4.21-4.23. Seasonal patterns of energy density on a wet and dry weight basis are illustrated in Figs. 4.24 and 4.25, respectively.

In Elk Lake fish of both sexes, increases in dry weight and energy content at the beginning of the summer were significant. In males, these occurred between May and August and in females from May through September. The observed increases in wet weight during these periods were not significant, and amounted

to a 10.9% increase in males and a 16.6% increase in females. In contrast, dry weight increased about 40% in both sexes while energy content increased 63.1% in males and 55.9% in females. That these increases are in large part due to the accumulation of lipid is also reflected in the increasing energy density of the carcass during this period, from 4.054 to 6.323 kJ g^{-1} wet weight in males and from 4.316 to 5.984 kJ g^{-1} wet weight in females. In the following months, dry weight, energy content and energy density of carcasses of both sexes decreased to values that did not differ significantly from those at the beginning of the season. Wet weight also decreased in both sexes, but was not significant in females. Similar decreases were observed in the autumn of 1983, which continued throughout the winter until May.

In Ten Mile Lake fish, wet and dry weights and energy content increased significantly from May through September in both sexes. As in Elk Lake fish, the increases were of greater magnitude when energy content was considered (72.7% in males and 97.8% in females) than when either wet or dry weight was considered. The relative increases of these variables were 40.6 and 52.5% wet weight and 59.7 and 82.5% dry weight, for males and females, respectively. Energy density also increased during this time, from 4.1 to 5.18 kJ g^{-1} in males and from 3.899 to 5.386 kJ g^{-1} in females. From September to December, wet and dry weights and energy content decreased in both sexes, but values were higher than at the beginning of summer. The

decrease in wet weight of male carcasses was not significant. A similar decline also took place in the autumn of 1983, but there was also evidence of some winter growth in females. In 1983, male carcass weight (wet and dry) decreased from October to January and energy content decreased from October to November. The decreases in female carcass weight and energy content during this time were not significant. Apparent increases between January and April were not significant in males, but the increases from November to January in the wet weight and energy content of female carcasses were significant. However, these gains were lost by May.

The pattern of energy dynamics in Lake Itasca fish was quite different from that described above for fish from the other two lakes. In both males and females, large increases in wet weight occurred between September and May. Most of this growth took place before February and represented increases of 48.4 and 51.2% in males and females respectively. In males, similar, but relatively smaller changes in dry weight (20.9%) and energy content (30.4%) were evident. In females, data on these variables were lacking, but the magnitude of change in wet weight suggests that similar changes must have occurred. In both sexes, increases were also observed late in 1984. These were not significant in females, but in males, increases in both wet and dry weight were significant. In Lake Itasca fish of both sexes, the summer period of energy accumulation was shorter than in the

other two lakes. Carcass wet weight and energy content in males increased significantly from May to June, by 19 and 34%, respectively, and subsequent decreases prior to spawning were not significant. Dry weight increased steadily through December, and represented a 36% increase from May. In females, significant increases in dry weight (8.1%) and energy content (22.6%) occurred from May to July, and decreases from July to October were significant but changes in wet weight were not. Energy density of carcasses of Lake Itasca fish was at a maximum early in the season (June in males and July in females) and the values of 7.053 and 7.312 kJ g^{-1} wet weight for males and females, respectively, were higher than those observed in fish from the other lakes. Energy density declined from this point through September. It appeared that there was an increase in weight and energy content in females from October to December. However, because of the large variance, these changes were not significant.

In general, the energy density of fish carcasses followed the same pattern as energy content, such that changes in energy content resulted from both changes in mass and in energy density. Comparison (ANOVA) of peak energy density on a wet weight basis revealed significant differences between lakes for both males (p = .0007) and females (p = .0001). The energy density of Ten Mile Lake male carcasses was significantly lower than that of fish from Lake Itasca and Elk Lake, which did not

differ significantly. Differences in peak energy densities of male carcasses, on a dry weight basis, were not significant (p = .1229).

Among females, energy density on a wet weight basis was significantly greater in carcasses of Lake Itasca fish than in fish from the other two lakes, and that of Elk Lake females was higher than that of Ten Mile Lake females. However, when differences in peak energy density on a dry weight basis between females from different lakes are compared, the situation is somewhat altered. Differences between lakes were also significant (p = .0204). However, carcasses of females from Lake Itasca were not significantly different from those of Ten Mile Lake females, and both had significantly higher energy densities on a dry weight basis than Elk Lake females.

Energy densities of carcass reached a maximum earlier in Lake Itasca fish (July) than in the other lakes. Consequently, on a dry weight basis, carcasses of fish from Lake Itasca had similar energy densities to Ten Mile Lake fish in the months near the spawning period, but the values were greater in these fish through the winter and in the early months of the summer season. Energy densities (on a dry weight basis) of carcasses of Elk Lake fish were generally lower than those of Ten Mile Lake fish throughout the growth season. Ten Mile Lake fish had the lowest energy density on a wet weight basis. This was especially apparent in female fish in middle and late winter. Further, in these fish the increase in energy density on a wet weight basis

during the summer growth period was not as great as in the other lakes. This is due to the higher water content in Ten Mile Lake fish than in fish from the other lakes.

At the end of the growth season, when much of the energy reserves of the carcass had been depleted, differences also existed between fish of different lakes. At this time, differences in energy density on a wet weight and dry weight basis were significant among males ($p = .0001$ for both variables) and females ($p = .0007$ and $p = .0017$, respectively). Elk Lake fish exhibited a greater amount of depletion of carcass energy reserves than males from the other two lakes. Lake Itasca males had a higher energy density on a wet weight basis than males of either Elk Lake or Ten Mile Lake, which did not differ significantly. However, carcasses of Elk Lake males had a lower energy density on a dry weight basis than males of the other two lakes. On a dry weight basis, the energy density of carcasses of Lake Itasca and Ten Mile Lake males did not differ significantly. The same relationships were observed in females.

Comparisons between sexes revealed no common pattern among lakes. In Ten Mile Lake, carcass wet weights of males and females differed in October, 1983 and May, 1984. All other variables were equivalent in both sexes in these and other months. In Lake Itasca, female carcasses had higher dry weights and energy content than male carcasses in May. In other months there were no differences in the variables examined. In Elk Lake

there were no significant differences between sexes in September, 1983 or in February, May, August or December of 1984. In November,1983, carcasses of males were heavier (wet and dry weight) and had a higher energy content than females, whereas in September, 1984, the carcasses of females had higher dry weight and energy content and higher energy density than males.

JUVENILES:

Results of ANOVA and Kruskal-Wallis Tests appear in Appendix D.1.8 and results of other statistical tests are given in Appendices D.2.8, D.3.8, and D.4.4. Monthly patterns of changes in dry weight and energy density on wet weight and dry weight bases are illustrated in Figs. 4.26 - 4.28, respectively.

In Elk Lake, the seasonal pattern of accumulation and depletion of mass of the carcass of juvenile fish was similar to that of adults. In contrast, juveniles of Lake Itasca and Ten Mile Lake appeared to continue to accumulate mass through October. However, in Lake Itasca juveniles, energy density of the carcass decreases after August, whereas in Ten Mile Lake fish, carcass energy density continued to increase. In both males and females of Elk Lake, increases in wet and dry weight and energy content occurred from June through August. Increases in energy density on both wet and dry weight basis also occurred during this time, as well as a decrease in water content. In females (no samples of

males were available), wet weight continued to increase until October, but dry weight, energy content and energy density decreased from August to October. The changes in weight and energy content were not statistically significant, but changes in energy density on both wet and dry weight bases were significant, as was the increase in water content that occurred at this time.

In Ten Mile Lake, carcass wet and dry weight and energy content increased from June to October in both sexes. Increases in dry weight and energy content were more than twice as greate as increases in wet weight. A decrease in water content was observed during this period. Energy density increased during this period in both sexes, but was only significant when expressed on a wet weight basis.

Most of the growth of carcasses of juvenile males from Lake Itasca occurred between April and August. Wet and dry weight continued to increase until October. However, energy content decreased, though not significantly, from August to October. Energy density on a dry weight basis decreased from April to October, and on a wet weight basis, from August to October. In females, wet weight increased from August to October, the only months for which samples were available. As in males, changes in dry weight and energy content during this time were not significant , but decreases in energy density were significant.

No significant differences between sexes of juveniles in any of the lakes were detected.

Differences between adults and juveniles in Ten Mile Lake and Elk Lake were significant at the peak of summer growth, in August. In Ten Mile Lake, adult carcasses had higher energy densities on both wet and dry weight bases than juveniles, which had higher water content. This was true also for Elk Lake males. Adult females had higher energy density on a wet, but not dry weight, basis. In both sexes, the carcasses of juveniles had higher water content. There were no significant differences in other months.

In Lake Itasca, adult males had higher energy density on a wet weight basis, and juveniles, a higher water content, in both August and October. Adult males also had a higher energy content on a dry weight basis in October. Carcasses of adult females had a higher energy content on a dry weight basis in October, but differences in other variables were not significant.

4.3.5. MUSCLE AND VENTRAL FAT:

The seasonal energy dynamics of muscle fillets and what I have termed the "ventral fat deposit" were investigated in order to determine their contribution to the overall patterns observed in the carcass. These tissues were only taken from adult fish from Lake Itasca and Elk Lake. Results of ANOVA and Kruskal-Wallis Tests are given in Appendices D.1.9 and D.1.10 for muscle and

ventral fat, respectively. Additional results of other statistical tests are given in Appendices D.2.9 and D.2.10.

MUSCLE:

Although muscle fillets were taken using a standardized method, no attempt was made to obtain all of the muscle of the fish. Thus, only energy densities and water content of muscle tissue were determined. The patterns observed closely approximated those of the carcass. However, in both sexes of both lakes, energy density on a wet weight basis was higher for the carcass than for muscle. That this is a result of the higher water content of muscle is indicated by the fact that the energy density on a dry weight basis is higher in muscle. The seasonal patterns of change in energy density on a wet and dry weight basis are illustrated in Figs. 4.29 and 4.30, repectively.

In both males and females from Lake Itasca, energy densities on both wet and dry weight basis increased significantly from November to February and from May to June and decreased from June (or July, in females) to October. Increases from October to December were not significant. Water content decreased during periods of increasing energy density and increased at other times. Male muscle had a higher water content than that of females in May and July. In May, energy density, on a wet weight basis, of female muscle was significantly greater than that of male muscle.

No differences between sexes were observed in muscle of February and October samples.

The energy density of muscle in Elk Lake fish increased during the summer months (May to August in males and to September in females) as in Lake Itasca fish. However, in Elk Lake fish, muscle energy densities decreased in the autumn of both years. The decrease observed in the autumn of 1983 persisted throughout the winter in 1984. Energy density, on a wet weight basis, of muscle was higher in females, and water content was greater in male muscle in September of both years. In September of 1983, energy density, on a dry weight basis, was also higher in females. There were no significant differences in other months.

Comparisons of the energy density between fish of the two lakes revealed that the muscle of Lake Itasca fish had higher energy densities both at the peak of deposition of energy reserves and in the post spawning period, when reserves were depleted. Comparison of energy densities on both wet and dry weight bases gave similar results. The results of the former comparisons are as follows. In both sexes, the energy density of muscle in Lake Itasca fish was greater than that of Elk Lake fish in the months following spawning (p = .0008 for males and p = .0158 for females, t-test), and in the early summer. Similarly, the peak energy density of muscle of Lake Itasca fish muscle were

higher than energy density than Elk Lake fish (p = .0237 for males and p = .0038 for females, t-test).

VENTRAL FAT:

Distinct seasonal variation was observed in the ventral fat deposits of adult fish of both lakes, although the pattern was somewhat obscured by the high variability in samples from females from Elk Lake. Seasonal variation in wet and dry weight, energy content and energy density on a dry weight basis were not significant for these fish. However, in males from Elk Lake and members of both sexes from Lake Itasca, seasonal changes were significant as determined by analysis of variance or Kruskal-Wallis tests. In general, the patterns observed conformed to the same patterns as those described previously for the carcass. The patterns of change in energy content, and energy density on a wet and dry weight basis are illustrated in Figs. 4.31-4.33. In light of the very high values of energy density that were observed, and the fact that the tissue examined represented only part of the retroperitoneal deposits that line the body cavity, it is likely that that this deposit is important in the temporary storage of energy reserves in these fish.

The ventral fat deposit in males of Lake Itasca increased significantly in wet and dry weight and energy content from November, 1983 to February, 1984. In both males and females, these variables increased significantly from May to June or July

and then decreased from June to September. In males, the later increase in wet weight from August to November was significant, but other changes in either sex were not, due to the large amount of variability of the samples. In both sexes, increases in energy density (both in terms of wet and dry weights) and decreases in water content accompanied increases in weight or energy content. The converse was also true. There were no significant differences between sexes in any of the variables.

In Elk Lake fish, the patterns of energy accumulation and depletion in both sexes appeared to be similar but were not as pronounced in females as in males. None of the changes were statistically significant in females. As in Lake Itasca fish, there was an increase in weight and energy content during the early summer, from May to August, in Elk Lake fish. This was followed by a decrease in these variables through December. This decrease was also evident from September to December in 1983 in males. Changes between December and May were not sigificant in either sex. Changes in energy density generally followed trends in energy content, also as in Lake Itasca fish. Female ventral fat deposits had a higher energy density on a dry weight basis in September and December of 1983, and in December, 1984. Further, in December, 1983, the dry weight and energy density of female ventral fat deposits was greater than that in males, which had a higher water content.

The energy densities obtained reveal the high lipid content of this tissue. On a wet weight basis, the energy density in the ventral fat deposits of Lake Itasca fish reached a maximum of 26.022 kJ g-1 in males, and 25.715 kJ g-1 in females, nearly four times as high as values determined for the carcass. In Elk Lake fish, these values were lower, 22.848 and 21.139 kJ g^{-1}, in males and females, respectively. The differences between both males and females of the two lakes at this time were significant (for males, $p = .0339$, U-test; and for females, $p = .0016$, t-test). At the peak of development in midsummer, the ventral fat deposit represented 2.7% and 2.2% of the total energy content of Lake Itasca males and females, respectively. In Elk Lake fish, 2.2% of the energy content of males and 1.1% of females was located in these deposits. The entire retroperiotoneal deposits must account for a larger percentage at this time.

In the period following spawning, the energy density of the ventral fat deposit declined in fish of both lakes, and the decrease was much more pronounced in Elk Lake fish. The energy density of the fat deposit of Elk Lake males was significantly less than that of Lake Itasca males ($p = .0027$, U-test). Although the means of energy densities in female fat deposits were similar to males in their respective lakes at this time, differences between females were not significant ($p = .070$, t-test) due to the large variation present.

4.4. DISCUSSION:

4.4.1. LIVER:

The liver does not appear to function as a depot for energy storage in ciscos. Typically, it represented approximately 1% or less of the total energy content of the fish and at a maximum accounted for 1.8% (in pre-spawning Ten Mile Lake females). In contrast, in lean fish, such as the cod, *Gadus morhua*, the liver may account for 4.5% of the fresh weight of the fish. Since the fat content of cod liver may reach 75% of its wet weight, while that of the muscle is less than 1%, the liver represents a large portion of the energy reserves in this fish (Jangaard, *et al.*, 1967). Although the contribution of the liver to the energy dynamics of ciscos was small compared to other tissues, distinct seasonal patterns of energy accumulation and depletion were observed in fish from all study lakes. These are probably related to seasonal feeding patterns and to the reproductive cycle.

The increases in liver weight, energy content, and energy density that were observed in adult fish of both sexes from Elk Lake and Ten Mile Lake shortly following ice-out are probably related to the resumption of feeding in fish of these lakes. Similar increases in measures of liver mass or energy content have been observed in spring or early summer in temperate zone fishes. In the northern pike, *Esox lucius*, weight and energy content of the

liver increased following early spring spawning and continued to increase throughout the summer (Medford and Mackay, 1978; Diana and Mackay, 1979). A spring or early summer peak in the liver- somatic index was observed in perch, *Perca fluviatilis*, and largemouth bass, *Micropterus salmoides* (Makarova, 1973; Adams, *et al.*, 1982), and in bluegill sunfish, *Lepomis macrochirus*, this index was correlated with RNA/DNA ratios, an indicator of growth, which reached maximum values in spring (Bulow, *et al.*, 1981).

Further evidence that changes in liver weight are correlated with feeding is provided by controlled laboratory studies. Starvation resulted in a decrease in liver weight in plaice, *Pleuronectes platessa* (Jobling, 1980), and *Tilapia rendalli* (Caulton and Bursell, 1977) and Appelbaum *et al.*, (1986), observed a decrease in cell volume and depletion of glycogen and lipid in the liver of a European whitefish, *Coregonus lavaretus*, during starvation. Liver weight in rainbow trout, *Salmo gairdneri*, increased when rations were increased following starvation or restricted rations (Weatherley and Gill, 1981). Positive correlations of liver weight and fat content of the liver in the winter flounder (*Pseudopleuronectes americanus*), and of liver-somatic index in the largemouth bass (*Micropterus salmoides*) to feeding rate have been observed (Tyler and Dunn,1976; Heidinger and Crawford, 1977).

The lack of increase in liver weight and energy content of ciscos from Lake Itasca between May and August may be related to the higher temperatures in that lake. By June, the lake surface temperature had exceeded 21 °C, and temperatures in the upper 9 meters were well above what I have assumed to be their preferred temperature. A negative correlation of the liver-somatic index and temperature was observed in the largemouth bass (Heidinger and Crawford, 1977). However, deposition of matter was occurring in other tissues (digestive tract and carcass) of the ciscos at this time. The energy content of the livers of Lake Itasca fish had nearly doubled during the preceding winter, and the energy density had increased substantially as well, indicating that lipid was deposited during this time. Perhaps, this was sufficient to meet metabolic needs during the summer months.

Changes in liver that appeared to be related to the reproductive cycle were also evident. The liver of males in all three study lakes decreased in weight and energy content during the latter half of the summer, preceding the attainment of maximum size of the testes. A similar decrease in liver energy content associated with the most rapid phase of testes growth has been observed in the northern pike (Diana and Mackay, 1979). Lizenko *et al.* (1975) observed an increase in per cent fat content of the liver in male vendace, *C. albula*, during the months leading up to spawning. However, total values were not reported. In contrast to the pattern in males, marked increases in weight and

energy content were observed in female ciscos from all three lakes during this same period. This prespawning increase has been observed in Arctic char, *Salvelinus alpinus*, European perch, northern pike and largemouth bass (Matsuk and Lapin, 1972; Makarova, 1973; Diana and Mackay, 1979; Adams *et al.*, 1982). The larger size of female livers during the prespawning period, which is accompanied by an increase in protein, has been associated with the storage of yolk constituents or their precursors, or increased amounts of enzymes required for vitellogenesis (Patzner, 1980; Medford and Mackay, 1979). Most of the yolk protein (vitellogenin) is of hepatic origin, and although this protein is packaged in the oöcytes, little endogenous protein synthesis occurs in the ovary (Wallace and Selman, 1981; Nagahama, 1983). The per cent fat content in female livers in vendace was observed to decrease between August and October (Lizenko *et al.*, 1975), a finding that is consistent with the primarily vitellogenic role of the liver at this time.

Decreases in liver weight during and following spawning occur almost universally (see references above). This post-spawning depletion was seen in fish of both sexes from Ten Mile Lake in both 1983 and 1984, of both sexes from Elk Lake in 1984 and in Elk Lake females in 1983. On the other hand, livers of Lake Itasca fish in both years and Elk Lake males in 1983, did not show signs of depletion of reserves, and in fact, appeared to increase in weight and energy content. This may be of importance

in male fish. Food items were present in the stomachs of these fish, which indicates that the fish were feeding during this period, and results presented above indicate that energy deposition was occurring in other tissues. Whether the observation of increases noted in Lake Itasca females is of significance is open to question, since sample sizes were small (November, 1983 and December, 1984) or missing (November, 1984).

In all ciscos except males from Ten Mile Lake, a midwinter peak in liver weight and energy content was noticeable. Most of the other species discussed above are spring spawners, and when an increase in liver size during the winter has been observed (in perch and northern pike), it occurred in females and was associated with pre-spawning activities. Matsuk and Lapin (1972) observed an increase in the fat content of livers of female Arctic char following spawning in the fall, and attributed this to gonadal resorption and the resumption of feeding. These factors may both also be involved in the observed phenomenon in the cisco.

4.4.2. GONAD:

The development of the gonads of northern temperate fish species that spawn in the fall or early winter is characterized by little growth from post-spawning until midsummer of the following year, followed by a rapid increase to maximum size just prior to spawning (Wooton, 1979). In many species, the male

gonads reach maximum or near maximum size before those of the female, both in fall spawning fish, such as the cisco, and in spring spawning fish, such as rainbow trout (Neves and Brayton, 1982), northern pike (Diana and Mackay, 1979) and European perch (Craig, 1977). In these species, the testes typically reach near maximum size in the autumn and may, as in the perch, actually decrease in weight before spawning. The ovaries continue to mature throughout the winter. Among fall spawners, the temporal difference is, of necessity, of shorter duration. In coregonines, the major portion of testes growth occurs before that of the ovaries. In the pollan, *Coregonus pollan*, the major portion of testes growth occurs between August and September, while that of the ovaries occurs one month later. In both sexes, the gonads continue to grow somewhat until spawning in December (Dabrowski, 1982a). Another pattern was observed in the vendace, *Coregonus albula*. In this species, the testes reach their maximal growth in September, and decline somewhat thereafter, while most ovarian growth takes place between September and December (Dabrowski, 1982b).

Except in Ten Mile Lake fish, the patterns observed in this study were similar to those of other coregonines. It should be noted that although the major portion of the growth of the testes occurred prior to that of ovaries, the total energetic investment in female gonads during these months was greater than that of males.

In Elk Lake males, the major growth of testes occurred from July to August, one month earlier than in males from Lake Itasca, and was complete by October. The observation that the testes of Lake Itasca males decreased in energy content between July and August may indicate that high lake water temperatures may have delayed initial testes development in Lake Itasca males. Excessively high temperatures can induce gonadal regression (Bye, 1984). In Elk Lake and Lake Itasca, the major portion of ovarian growth took place between September and November. The pattern observed in both males and females from Ten Mile Lake was different from that of the other lakes. In males, the testes reached their maximum size in September and then decreased sharply between September and October. Although this is similar to the pattern observed in vendace (Dabrowski, 1982b), the magnitude of the decrease is much greater. It has been observed that the thickness of tubule walls decreases with maturity in two coregonines, *C. albula* and *C. lavaretus* (Dlugosz and Worniallo, 1985; Fuller *et al.*, 1976). This process might account for the loss in mass of the testes in the Ten Mile Lake fish, which mature quite early. Neves and Brayton (1982) observed a similar pattern in rainbow trout that spawn in March. The maximum GSI of male fish was observed in September, after which it declined rapidly. That this pattern is not the result of a bias that might have been introduced by the method of sampling individual fish by size, is indicated by the fact that the same

phenomenon was observed in age II+ and IV+ fish (data not presented), and absolute values of age III+ and IV+ fish were similar. It is also not the result of loss of semen during handling, as the October samples were taken approximately three weeks before the spawning run. The growth of ovaries was nearly complete by September, after which little increase in dry weight or energy content was observed. The growth of ovaries and spawning in a slow-growing population of brook trout occurred earlier than in a fast-growing population (Nelson and McPherson, 1987). The increase in ovarian mass and energy content that occurred between October and spawning in November represents final gonadal maturation. Increases in ovarian weight and energy content occurred during this period in the fish of the other lakes, albeit to a much greater extent. The similarity in timing of this process supports other observations that it is promoted by shortening daylengths and decreasing temperatures (Bye, 1984).

The energy density of testes of ciscos declined following spawning, and increased during the inter-spawning interval. Data for other coregonines indicate that the lipid content of the testes reaches a maximum in August, followed by a decline through the spawning period. In the pollan, the fat content (as per cent dry matter) of testes declined from August to December (Dabrowski, 1982a). Data were not given for other months. In the vendace, total lipid content and per cent lipid of the testes increased from

spring until August, and subsequently declined (Dabrowski, 1982b; Lizenko, *et al.*, 1975).

There are few studies that have followed the seasonal changes in caloric density (or fat content) of the testes in other species. However, the general features of the pattern described have also been observed in American plaice, *Hippoglossoides platessoides* (MacKinnon, 1972), alewife, *Alosa pseudoharengus* (Flath and Diana, 1985), northern pike (Diana and Mackay, 1979), rainbow trout (Neves and Brayton1982), Arctic char (Matsuk and Lapin, 1972), European perch (Craig, 1977) and smelt, *Osmerus mordax* (Foltz and Norden, 1977). Of these, the plaice and European perch show fluctuations similar to those apparent in the ciscos of the study lakes. The significance of these fluctuations is uncertain.

The midwinter increase in energy density of the testes in fish from Elk Lake and Ten Mile Lake is also notable. There is a small fat deposit in the mesentery on the dorsal surface of the testes that at this time may have contributed to the apparent increase due to the small size of the testes. By May, this deposit was no longer visible.

Two general seasonal patterns of changes in the energy density of ovaries have been observed. In some fish, such as plaice (MacKinnon, 1972), alewife (Flath and Diana, 1985) and gizzard shad (Fagan and Fitzpatrick, 1978) energy density, measured on a dry weight basis, increases continually until

spawning. In others, such as the rainbow trout (Neves and Brayton, 1982), smelt (Foltz and Norden, 1977), and northern pike (Diana and Mackay, 1979), the increase in energy density is attenuated, and a decline occurs before spawning. These differences probably reflect differences in timing of deposition of lipid and protein. During the major phase of ovarian growth, both lipid and protein content were observed to increase in the perch (Craig, 1977), plaice, *Pleuronectes platessa* (Dawson and Grimm, 1980) and Arctic char (Matsuk and Lapin, 1972), and lipid and fat-free dry matter (as an estimate of protein content) in the haddock, *Melanogrammus aeglefinus* (Shevchenko, 1972). In two species of coregonine fish, the pollan and the vendace, lipid content, as per cent dry matter, decreased steadily during ovarian maturation, while dry matter, and presumably protein content, increased (Dabrowski, 1982a,b). The pattern may be different in other populations. Lizenko *et al.* (1975) and Lahti (1987) observed that the lipid content of the ovaries of vendace reached a peak in the middle of the maturation process.

There may be a difference in the timing of deposition of lipid and protein in the ovaries of ciscos from the study lakes. The energy density of the ovaries of Elk Lake females increased to its final value and then remained constant. In contrast, in females from Lake Itasca and Ten Mile Lake, the energy density of the ovaries, on a dry weight basis, declined during the period preceding spawning, as it does in the vendace (Lizenko *et al.*,

1975; Lahti, 1987). It will be recalled that the energy density of the liver in Lake Itasca and Ten Mile Lake females also decreased prior to spawning, while the total energy content of the liver increased. The relative proportion of protein deposited at this time may have been greater in fish of these two lakes. In these fish, the synthesis of vitellogenin in the liver and its transfer to the ovaries prior to spawning, results in a higher protein content in both organs, and consequently, to a lower energy density.

The difference in timing of changes in the energy density of the ovaries may be related to the age and prior spawning history of the fish or to environmental effects. Adults examined from Ten Mile Lake and Lake Itasca were spawning for the first or second time and were younger than the adults examined from Elk Lake. It is possible that, as age increases, differences in the timing of deposition of protein and lipid in the ovaries are reduced. This does not appear to be the case in Ten Mile Lake fish. The changes in energy density of ovaries were similar in females within the restricted range of age classes for which data were available, ages II through IV. Further, values of energy density did not differ between age classes from September to December, the months for which data from individual ovaries were available (p values from ANOVA were: 0.5337, 0.2854, 0.1112, and 0.4314). It should be emphasized, however, that the oldest of these fish are still younger than the youngest mature fish in the Elk Lake samples. The fact that Elk Lake fish are exposed to a temperature regime

that more nearly approximates the preferred temperature may have some moderating effect on the partitioning of energy intake. Other differences, notably the relatively smaller increases in energy content of the digestive tract of Elk Lake females, have been noted. However, since the age composition of the fish from the study lakes differed it is not possible to make firm conclusions regarding the cause of the observed differences.

Wooton (1979) presents data on the energy density of ripe ovaries or mature eggs from 60 observations on 50 teleost species. The mean of these determinations was 23.48 kJ g^{-1} dry weight and ranged from 13 to 31 kJ g^{-1}. The ovaries of Ten Mile Lake ciscos (25.74 kJ g^{-1}) had an energy density greater than 70 per cent of these, and those of Elk Lake (26.56 kJ g^{-1}) and Lake Itasca (26.90 kJ g^{-1}) fish were greater than 80 per cent. Significant differences between lakes in the energy density of ovaries were observed. At the time of spawning, ovaries of Ten Mile Lake females had lower energy densities, on both a wet weight and dry weight basis, than fish from either of the other lakes. Ovaries of Lake Itasca females had a higher energy density on a wet, but not dry weight basis than those of Elk Lake fish. This may be due to the difference in sampling time. October females were used to estimate energy density of Lake Itasca ovaries since no females were captured in November. Eggs were not fully mature, and the lack of hydration may have resulted in excessively high values for the ovaries in these fish. Nevertheless,

it is evident that weight-specific energy reserves in Ten Mile Lake ovaries were lower than those of the other lakes.

However, it is uncertain whether or not there are differences between lakes in the energy content per egg. The energy density of the ovary may differ from that of the eggs, as was observed in the medaka, *Oryzias latipes* (Hirshfield, 1980) and in the northern anchovy *Engraulis mordax* (Hunter and Leong, 1981). Few comparative studies have been made regarding differences in the energy content of eggs or ovaries from fish of different populations, or of the effects of environmental factors on these values. The energy density of ovaries of sticklebacks (*Gasterosteus aculeatus*) reported by Wooton (1985) were different from those determined for another population by Meakins (1976). Feeding regime seems to have little effect on the energy content of eggs in the stickleback (Fletcher and Wooton, cited in Wooton,1985) or the northern anchovy (Hunter and Leong, 1981). It will be important to determine the energy content per egg as well as other parameters such as egg size, fat and protein content, in order to assess the significance of the findings presented on this critical stage of development. These factors may influence hatching success and early survival of larval fish. There are many examples of correlations of egg size and subsequent survival of larvae (Miller, 1979).

It is worth noting that even in immature fish, a disparity between sexes in the weight of the gonads was observed. Ovaries of age I fish were larger than testes in all three populations, and while testes growth was variable, ovaries increased markedly in dry weight in both Elk Lake and Ten Mile Lake fish. In fish from Elk Lake and Lake Itasca, the energy density of the ovary decreased between August and November. Although quite small, the ovaries of these fish contained eggs that appeared to be maturing during the late summer. However, by October, it was evident that they would not spawn. It is possible that lipids had been resorbed or, in the case of the ovaries of Elk Lake fish, which continued to increase in dry weight, that protein, rather than lipid, was preferentially deposited.

4.4.3. ENERGY STORAGE TISSUES: THE DIGESTIVE TRACT AND CARCASS:

The patterns of energy storage and utilization in the digestive tract and carcass were similar in many respects. Both are apparently involved in the temporary storage of energy for use in the production of gonads, reproductive activity and maintenance. In field studies such as the present investigation, it is often difficult or impossible to determine for which purpose or purposes these stores are being utilized, as they may coincide temporally. Inferences will be made where possible. Since frequent reference must be made to the changes in both

compartments and to the status of gonadal maturation, they will be discussed together to avoid excessive repetition. The relationships of changes in the three tissues for months during the ice-free season are illustrated in Figs. 4.34 - 4.36. These figures show the mean net changes in energy content of these tissues for the monthly intervals indicated.

Reference in this section will be restricted to changes in energy content. Gerking (1955) observed that weight was not a good measure of growth, since lipid reserves formed a major part of this process. It is possible to observe little or no change in weight due to the inverse relation of lipid and water content of tissues (Flath and Diana, 1982), and even when the seasonal pattern of total body energy content is similar to that based on weight, the variation is relatively greater in the energy storage pattern (MacKinnon, 1972). Significant deposition of lipids occurs in both the carcass and digestive tract in the cisco. Inspection of the graphs (above) illustrating changes in mass and energy content of these tissues reveals the inadequacy of using weight (especially wet weight), as important changes in the tissues may be obscured.

It was pointed out above that in some lean fish, such as the cod and North Sea haddock, the liver is the most important organ for energy storage. It is more common among fishes that muscle tissue and visceral lipid deposits, which are frequently associated with the alimentary tract, serve this function.

Although there have been several studies of the seasonal energy dynamics of fish, relatively few have examined the seasonal changes in fat or energy content of visceral deposits. In some cases, little fat is accumulated on the alimentary tract and caloric values do not change much, as in northern pike (Diana and Mackay, 1979) and plaice (Dawson and Grimm, 1980). In other studies, such as those of Dabrowski (1982a,b) on the pollan and vendace, it is asserted that they are not important since they comprise a small percentage of the total body reserves. Yet, in many fish, both spring and fall spawners, and including the ciscos in this study, lipid deposits associated with the digestive tract play an important role in the energy dynamics of the annual cycle. Before discussing the roles of the carcass and digestive tract in the energy dynamics of the cisco, a few examples of the patterns observed in other fishes will be given to describe important features.

In spring or summer spawners, reserves are built up during the summer and fall, and are used during the winter, for maintenance, gonadal maturation and spawning activities. Tissues are depleted following spawning, and some authors have noted that protein as well as lipid stores may be used.

The energy reserves of the digestive tract and in the carcass of largemouth bass increased from early spring through fall, and were utilized during the winter for metabolic demands and gonad production. Most of the lipid was utilized in early

winter, as indicated by the decrease in caloric densities in December (Adams *et al.*, 1982). During periods of food scarcity, lipid is utilized preferentially, at least initially, in these fish. Protein is also catabolized for energy if these conditions persist (Niimi, 1972). In smelt, both the energy density and total energy content of the digestive tract and carcass reached peaks in October and then decreased. Digestive tract deposits were more important in providing energy during the winter and for gonad maturation. In females up to 86% of the energy stored in these deposits was depleted prior to spawning (Foltz and Norden, 1977). Based on changes in energy density, the digestive tract was considered to be the most important source of energy during overwintering in the rainbow trout (Neves and Brayton, 1982). However, they do not give any data on changes in total energy content of the muscle. Weatherley and Gill (1981) found that visceral fat was completely utilized during even short-term (3 weeks) starvation of rainbow trout. Diana and Mackay (1979) have shown that the muscle of northern pike is utilized for the energy demands of spawning without any change in energy density. This would suggest that muscle tissue, as opposed to some particular component thereof, was probably being utilized. It is likely that this was also the case in rainbow trout. In the alewife, total body energy reached a maximum in October. Losses over the winter were similar in both males and females (23 and 27%, respectively). Spawning-related losses, including develop-

ment of the gonads, were greater (45 and 37%), and fish were severely depleted by early summer (Flath and Diana, 1985).

The growth season for fall spawning species is shortened by the necessity of producing mature gonads and reproducing before winter. The energy content of reserves in fall spawners peaks sometime during the summer and is depleted either prior to or during spawning. In the brook char (*Salvelinus fontinalis*), lipids associated both with the digestive tract and carcass increased from May to August. At this time, 10% of the total body lipids were associated with the digestive tract. The deposits of both compartments were depleted by October or November (Nelson and McPherson, 1987). Muscle and digestive tract fat content increased from July to October in Arctic char and decreased during gonad maturation and spawning in December (Matsuk and Lapin, 1972). An increase in muscle fat content was noted in the early winter.

The fat content of both muscle and intestine increased until August and decreased through spawning in October in *Coregonus lavaretus* (Bolotova, 1976). Dabrowski (1982a,b) analyzed the fat content of the muscle and gonads, but did not consider the intestinal tract to be of importance in the energy dynamics of two coregonines. The intestine was included with the remainder of the fish, so it is difficult to compare his results with those of the present study. In the pollan, 50% of the total increase in fat content occurred between the time of spawning and the following

May, as fish fed during the winter. The rest was accumulated between May and August. In females, most of this was lost between August and November, and was associated with the growth of the ovaries. In males, the greatest depletion occurred from November to December, and was associated with spawning activity. Data for the vendace were collected only between September and November, but Dabrowski (1982b) presents data from Backiel (1952) on vendace from another lake. Vendace accumulated an even greater portion of muscle lipids between January and May than pollan. Peak values appeared to occur in August. In contrast to what he observed in the pollan, vendace of both sexes lost muscle fat at similar rates until November. Between November and December, muscle fat content of females continued to decrease, while that of males increased slightly. Muscle lipids in another population increased in both sexes from May to August, and decreased through October (Lizenko, *et al.*, 1975).

Energy stores were deposited on the digestive tract in fish of both sexes from the three study populations during the early summer, resulting in a marked midsummer peaks in energy content and energy density in all but Elk Lake females. Similar increases in the carcass occurred. Stores were then mobilized at varying rates and values at the time of spawning were similar to those of the previous year, indicating the temporary nature of the

buildup in adults. These patterns are similar to those observed for other fall spawning species.

Visceral energy stores in the ciscos studied may serve as an auxiliary energy source during the buildup of the gonads and during spawning. These stores may be more mobile than others (Neves and Brayton, 1982; Swift, 1955). They probably serve to assist in the conservation of body (carcass) stores, thereby either permitting continued body growth or ameliorating depletion of body energy stores during the reproductive cycle and as environmental conditions change.

In Elk Lake fish, the early growth of the gonads in both sexes was supported from exogenous energy sources, as concurrent increases in the energy content of the carcass occur until September in females and August in males (Fig. 4.34). In females, the proportion of total production accounted for by gonadal production first exceeded that of the carcass between August and September, and digestive tract stores began to be utilized at this time. Losses from both the digestive tract and carcass occurred from September through November, and presumably contributed to the formation and final maturation of the gonad. The increase in energy content of the ovaries during this time amounted to 54.6% of the somatic depletion. Energy from carcass deposits contributed most of the energy used for the formation of the ovaries, as digestive tract losses were only from 5.5% to 6.5% of the total losses. Further losses from the carcass

occurred from November to December and were probably associated with spawning activity. The digestive tract began to accumulate energy reserves during this period. The early use of digestive tract reserves between August and September and the post-spawning replenishment of these reserves suggest that these reserves are more mobile than those of the carcass.

Nevertheless, lipid stores of the digestive tract played a less significant role in Elk Lake females than in the other fish. The peak energy density was lower, and total energy content ceased to increase after June in these fish. This may reflect a proportionately greater diversion of energy to the ovaries during the summer and early fall. The development of the ovaries in Elk Lake fish was more gradual than in females from the other lakes. These features may represent alterations in energy partitioning in older fish.

In Elk Lake males, accretion of energy occurred until August. The major part of testes growth occurred before this time, indicating that exogenous sources were utilized to form most of the gonad. Digestive tract stores may have contributed significantly to the formation of the testes, as 36% of the total energy losses from August to October were contributed by this organ. Testes growth was completed during this time. The increase in testes energy content was only 6.8 % of the somatic depletion during this time, and male somatic losses during the time of gonad formation were only 27% of that of females.

Although losses from both the digestive tract and carcass continued through the post-spawning period, most of the energy for spawning-related activity was provided by the carcass. The costs associated with spawning activity may be high in males. In the pollan, males lost more muscle fat than females during the spawning period (Dabrowski, 1982a). This may be because males reach the spawning ground earlier than females and stay longer. This behavior has been observed in ciscos by several authors (Cahn, 1927; Van Oosten, 1929; Dryer and Beil, 1964). Since the energy content of males and females was similar at the beginning and end of the growth season, it is evident that spawning-related activity was greater in males.

The energy content and energy densities of post-spawning males and females were nearly identical, indicating that total reproductive costs in both sexes were similar. Female carcasses were depleted somewhat earlier than males. This is because female costs are mostly related to formation of the ovaries while male costs are largely associated with spawning activity. The temporary nature of these changes is indicated by the fact that post-spawning values for both sexes were similar to those in May, at the beginning of the summer growth season.

The decline in energy content and energy density from the previous year may demonstrate to year-to-year variation. The summer of 1983 was particularly hot, and the lake stratified earlier than in 1984. The ciscos of Elk Lake were probably

exposed to higher temperatures during the early summer months in 1983. Further, primary production was high in local lakes and prey may have been more abundant. As long as rations were not restricted, these conditions would have resulted in enhanced growth and lipid storage. In brown and rainbow trout, growth rates increased with ration size, and fat content was highest at temperatures that were near estimated physiologically optimum temperatures (Elliott, 1976; Weatherley and Gill, 1983). However, this was not the case in juvenile sockeye salmon, *Oncorhynchus nerka*, and two cyprinid species, *Phoxinus phoxinus* and *Pimephales notatus*. While both protein and fat content increased with ration size in these fish, proportionally more fat was deposited at lower and higher temperatures, with more protein being deposited at temperatures that produced maximum growth rates (Brett et al, 1969; Cui and Wooton, 1988; Gill and Weatherley, 1984). These types of data on Coregonids are lacking.

In Ten Mile Lake fish, the major portion of gonadal growth occurred earlier (between July and September) than in the other lakes, and was probably supported largely by exogenous resources (Fig. 4.35). In females, 77.6% of total production during this period was allocated to ovarian growth and 39.9% of total production was allocated to gondal production in males. The entire growth of the testes, and 80.7% of the growth of the ovaries occurred while the carcass was still accumulating reserves. The early development of the gonad resulted in a much

smaller percentage of depleted reserves being allocated to gonad production. In females, the increase in gonadal energy content between September and November was equal to only 15.3% of the somatic depletion that occurred during this time, much lower than that in the other populations. In males, a decrease in digestive tract energy content roughly equivalent to the increase in that of the testes occurred at this time, and in females, the largest increase in gonadal energy content coincided with the largest decrease in that of the digestive tract, from August to September.

The early allocation to gonad growth of greater proportions of total production, accompanied by the early utilization of stores associated with the digestive tract, resulted in a shortening of the period of growth in length, which ceased in August. Hile (1936) noted that for several populations of cisco, the growing season was shorter in lakes with slower growing fish. In a comparison of two populations of brook char, Nelson and McPherson (1987) observed that growth ceased earlier in the slower-growing population. Further, members of this population spawned earlier, suggesting a similar situation to that in Ten Mile Lake. These factors may result in preventing excessive somatic depletion during spawning, which may be important to overwintering success, as a depletion of reserves in the carcass was observed in females during the latter half of winter.

Unlike the Elk Lake fish, spawning activity was more costly to Ten Mile Lake females than males. The total energy lost from the carcass by females between October and November was twice the amount lost in males. Although part of this cost was related to a significant increase in the size of the ovaries that also occurred at this time, it is likely that energy expenditures associated with spawning are significant in females, which appear in approximately equal numbers as males during the spawning run. The bodies of females were bulging at this time, which may result in costs associated with problems of hydrodynamic performance in small female fish (Miller, 1979). Following spawning, the total energy content of the carcass was similar in both sexes, and was higher than at the same time in the preceding year and at the beginning of the growth season in May. Digestive tract energy content was not significantly different at any of these times. Energy densities of the carcass following spawning were similar in both years and were higher than those in May, whereas energy densities of the digestive tract at all three times were similar. These findings indicate that in Ten Mile Lake fish, the early maturation of the gonads, and early use of digestive tract reserves may provide for the maintenance of energy stores in the carcass.

To a large extent, the patterns of energy storage and utilization of Lake Itasca fish are shaped by the high productivity and severe summer temperature regime of the lake. Most of the

growth of ciscos in this lake takes place between September and May. This is clear from data on length, carcass weight (or energy content) and from the observation that the formation of the annulus on scales takes place in the autumn. Summer increases in energy content of the digestive tract in both sexes and the carcass of females were limited to two months, and that of the carcass of males to only one month (Fig. 4.36). The increase in testes energy content was 5.0 % of the depletion of somatic reserves, slighltly lower than in Elk Lake. As in Elk Lake males, digestive tract energy stores of Lake Itasca males may have contributed significantly to the formation of the testes, as 28% of the total somatic energy lost between August and September, when the majority of testes growth took place, was provided by the stores of the digestive tract. After this, losses in digestive tract stores exceeded those of the carcass and continued to November, after deposition of matter in the carcass had begun again. Thus, in males, visceral stores may be preferentially used to permit the deposition of energy and mass in the carcass. Large losses from visceral energy stores also occurred in these fish between July and August, before the major portion of the testes were formed. Little loss from the carcass was observed during this period. However, a significant amount of energy had been lost by the carcass in the preceding month, probably due to stress caused by the rapid increase in water temperature, which was probably near the tolerance limit of ciscos during this time. The subsequent

loss of energy from the digestive tract may represent physiological acclimation to high temperatures that prevented further losses in carcass energy.

Lake Itasca females did not suffer losses from the carcass from June to July. Females may not be as susceptible to increasing temperatures as males. Fry (1937) observed that male ciscos were the first to seek out cooler waters as surface temperatures rose in Lake Nipissing and were the last to depart the cool hypolimnetic waters as temperatures decreased in the fall. As in males, a significant portion, 39.6%, of the somatic energy losses from July to August were supplied by the stores of the alimentary tract. These costs were most likely the result of maintenance demands, as the ovaries showed only minimal growth during this time. As described above for males, losses from the digestive tract in females continued at least through October, after accumulation in the carcass had resumed. Although not statistically significant, the energy content of female carcasses was lower than that of males in the late autumn. A similar situation was observed in the Arctic char. In these fish, males apparently rely more on energy stores of the digestive tract and females utilize muscle to a greater extent than males (Matsuk and Lapin, 1972).

Most of the energy for ovarian growth in Lake Itasca fish was exogenous in origin. The increase in ovarian energy content during the period from July to September represented only 11.2%

of the somatic depletion that occurred during this time. Most of the ovary was formed between September and October. During this time, only the digestive tract showed a net loss of energy, while increases in the energy content of the carcass and liver resulted in a net gain in somatic reserves. During this period, gonadal production accounted for 94.9% of the total production of Lake Itasca females. Significant increases in the energy content of both the digestive tract and carcass occurred between October and December. Apparently, sufficient food is available during this period to support growth, and costs related to spawning activity in this lake may not be as great as in other lakes. Few fish were caught at this time, and spawning congregations may not have occurred as in the other lakes.

The somatic losses that occurred during late summer and autumn in adult ciscos are related to gonad formation, spawning activity and possibly interference with feeding, caused either by spawning activity or lack of food. These conclusions are supported by several lines of evidence. Ciscos continue to feed during this time and throughout the winter, as food was found in many stomachs, and it is unlikely that they are unable to assimilate efficiently at the low temperatures encountered. Several species of spring spawning fish that are more properly considered cool-water fish (as compared to cold-water ciscos and other salmonids) have been observed to continue growth well into the autumn, including bluegill (Bulow *et al.*, 1981), largemouth bass (Adams *et*

al., 1982), gizzard shad (Pierce et al., 1980), alewife (Flath and Diana, 1985) and walleye (Kelso, 1973). The perch of Lake Windermere continue to grow until November, and female somatic tissue also increases from December to January (Craig, 1977). Other cold-water species often show continued growth into the fall or increases in somatic reserves following spawning. An early spawning population of brook trout exhibited increases in body fat reserves following spawning in October to November (Nelson and McPherson, 1987). Arctic char also exhibited an increase in body fat following spawning (Matsuk and Lapin, 1972). Among coregonines, both the vendace and pollan showed recovery accumulation of fat following spawning and continued deposition through the winter (Dabrowski, 1982 a,b; Lahti, 1987). In the pollan, most of the total annual lipid deposition occurred before May (Dabrowski, 1982a). The major portion of growth of Lake Itasca fish also occurred during months when water temperatures were low, from September to May.

Further evidence that late summer depletion of body energy stores in adults is directly related to reproductive processes comes from observations on juvenile fish. Dry weight and energy content of carcasses of juveniles continued to increase until October (a slight decreasing trend in Elk Lake females was not significant). In two of the lakes, Lake Itasca and Elk Lake, energy densities decreased and energy content remained constant during this time, indicating that lipid was being lost, and that

protein deposition was probably occurring. Losses of visceral energy stores in the late summer and early autumn also occurred in juvenile fish from Lake Itasca and Elk Lake. These stores appear to play a similar role to that in adult fish, and were preferentially used during this period for maintenance of body mass. The lack of decrease in visceral energy stores and carcass energy density in Ten Mile Lake juveniles may be related to the relatively lower maintenance costs associated with low, and comparatively constant temperatures.

The patterns of energy utilization in adult fish during the winter months suggest that growth may have been supported in the early part of the winter, while in the latter half, energy intake was insufficient to meet maintenance costs in any of the populations. While the maintenance of energy stores in Elk Lake and Ten Mile Lake fish in the early part of the winter may have been due largely to resorption of the gonads, the increases observed in Lake Itasca fish were too great, and must have been accounted for by exogenous energy sources. The declines in somatic energy content in the latter half of the winter must have been caused by insufficient feeding at this time, since the temperature throughout the winter was practically constant. Other coregonine populations continue to accumulate muscle fat throughout the winter (cited in Dabrowski, 82a). Northern pike, another species with a boreal distribution, also continue to grow throughout the winter (Diana and Mackay, 1979). Foraging costs

for a piscivore are probably less than those of planktivores, especially at the reduced zooplankton prey densities that might be expected. The assessment of zooplankton abundance and composition should help to clarify this. In Lake Itasca, feeding may have also been reduced due to restrictions imposed by the depletion of oxygen that occurred in the lower depths. The dramatic decreases in the energy content of the digestive tract in these fish may have prevented significant losses in carcass energy content in this population.

Comparisons between populations regarding the utilization of stored energy reserves and the relationship of body energy stores to gonadal tissue were attempted to clarify some of the patterns discussed above. The gonadosomatic indices of mature fish from the three lakes in 1984 were similar, between 1.7 and 2.3% of wet weight in males and12 and14% in females. The values did not differ greatly in terms of energy content either, being from 1.8 to 2.7 % in males and 20 to 23.5 % in females. This similarity in female GSI may reflect limitations imposed by the size of the body cavity. Similarities in GSI are commonly observed within a species and will occur in cases where the weight exponent in allometric equations relating fecundity to body weight is close to 1 (Roff, 1983). This may be expected because fecundity varies as a power function of length, the exponent being about 3 (Bagenal, 1966; Wooton, 1979).

However, while the GSIs of fish from the three populations were similar, the proportion of total annual production allocated to gonadal production were not. These proportions are given in Table 4.4. It can be seen that males from Ten Mile Lake and Lake Itasca allocated similar proportions of annual production to reproduction. In females, the proportion allocated to reproduction was higher in Ten Mile Lake fish. A range is given for Lake Itasca females because no females were caught in November, 1984. It was assumed that gonadal growth would have continued to some extent between October and November. The different values were obtained depending on what assumptions were made about the magnitude of this growth. Elk Lake fish of both sexes invested a much higher proportion of total production to gonadal production, which is consistent with theories that predict a higher reproductive effort in older fish (Williams, 1966).

Table 4.4. Gonadal Production as Percent of Total Annual Production in Mature Ciscos.

	Ten Mile Lake	Lake Itasca	Elk Lake
Male	3.10	3.03	46.95
Female	65.82	44.65 - 51.27	97.83

The seasonal pattern of changes in energy density in muscle paralleled the changes observed in the carcass. However, the values were lower on a wet weight basis and greater on a dry weight basis than those of the carcass. The former relationship is indicative of the higher water content of the muscle. The higher ash content of the carcass may be the cause of its lower energy density on a dry weight basis. Further, the amplitude of the changes was smaller in muscle. This may in part be related to changes in the ventral fat compartment, which mimic those of the carcass in timing, but change more, proportionately. The total energy content of this deposit may increase from two to four times during the summer growth period, and at a maximum represented from 2.2-2.7% of the total somatic energy in Lake Itasca males and females respectively and from 2.2 - 1.4% in Elk Lake fish. The ventral deposit may play a significant role in the energy dynamics of these fish, especially if it represents a larger reserve that is continuous throughout the body cavity.
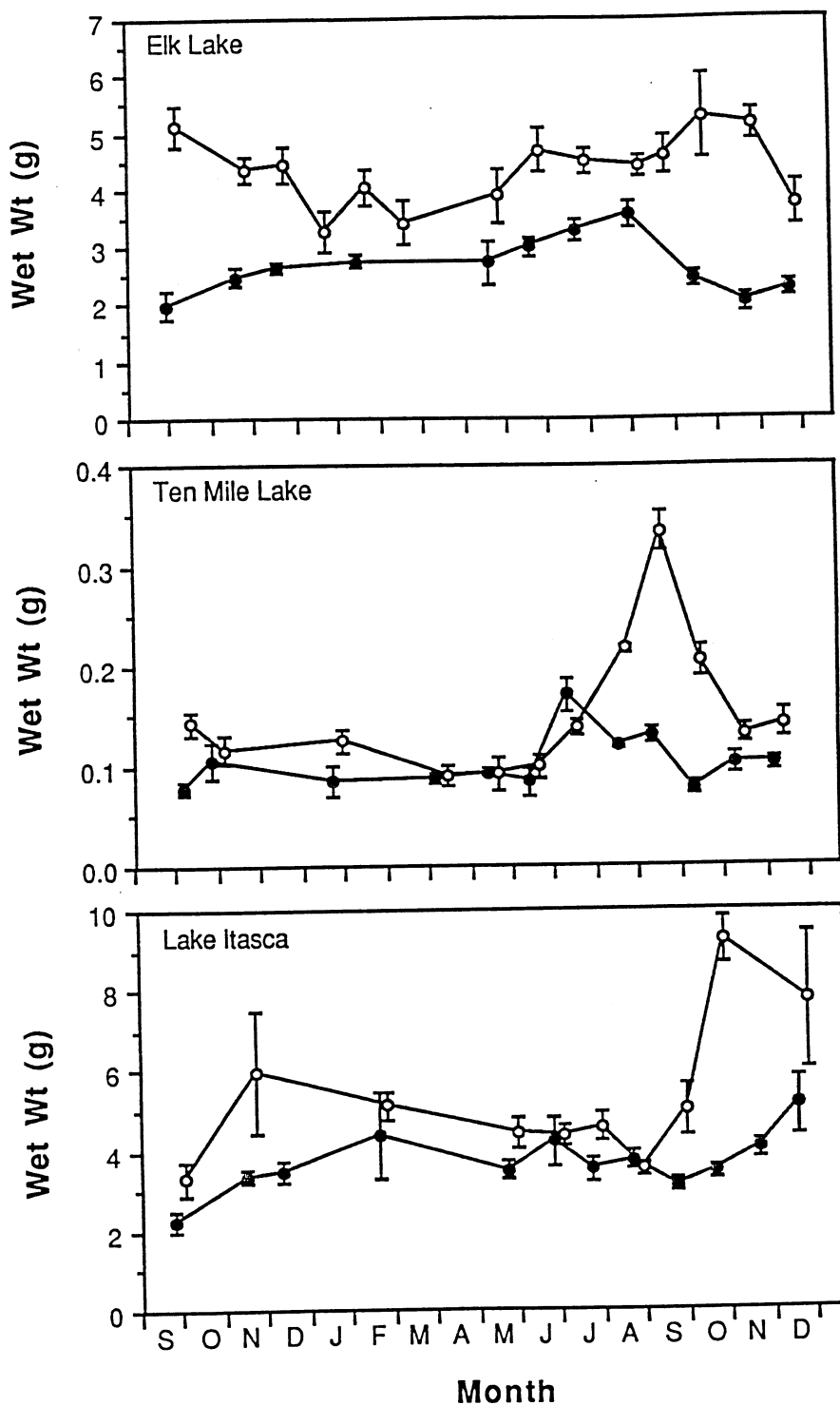
Figure 4.1. Seasonal variation in liver wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
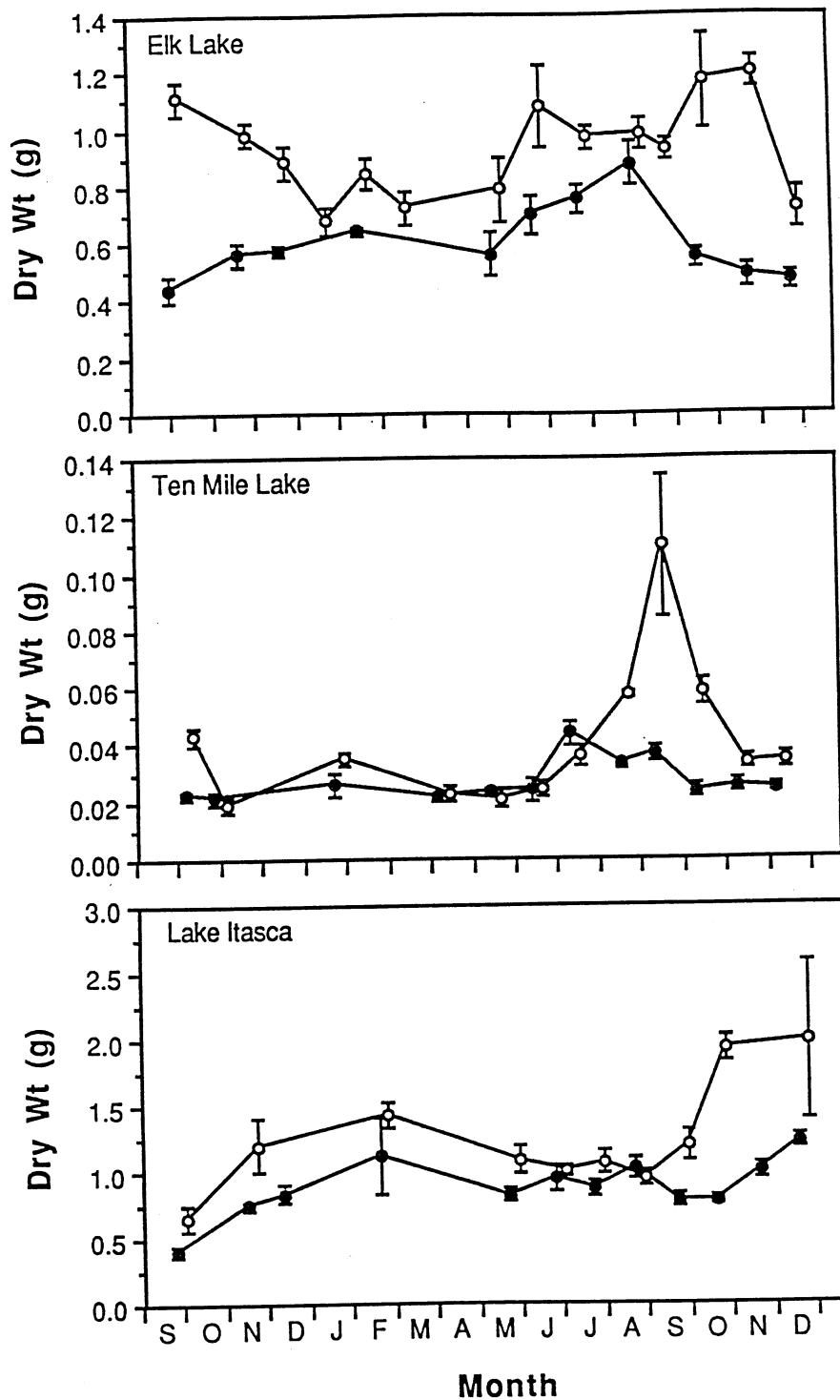
Figure 4.2. Seasonal variation in liver dry weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-○-).
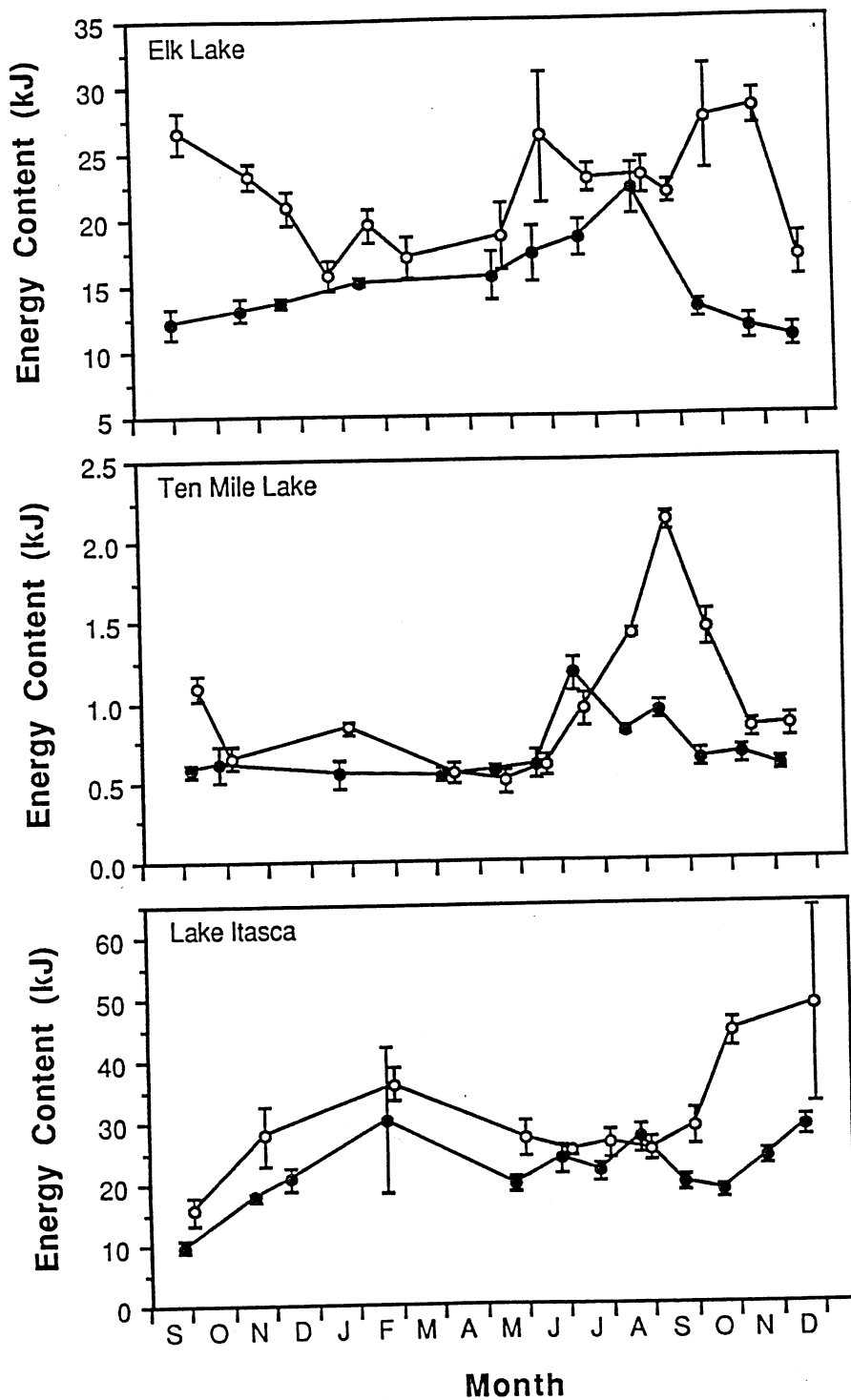
Figure 4.3. Seasonal variation in liver energy content of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
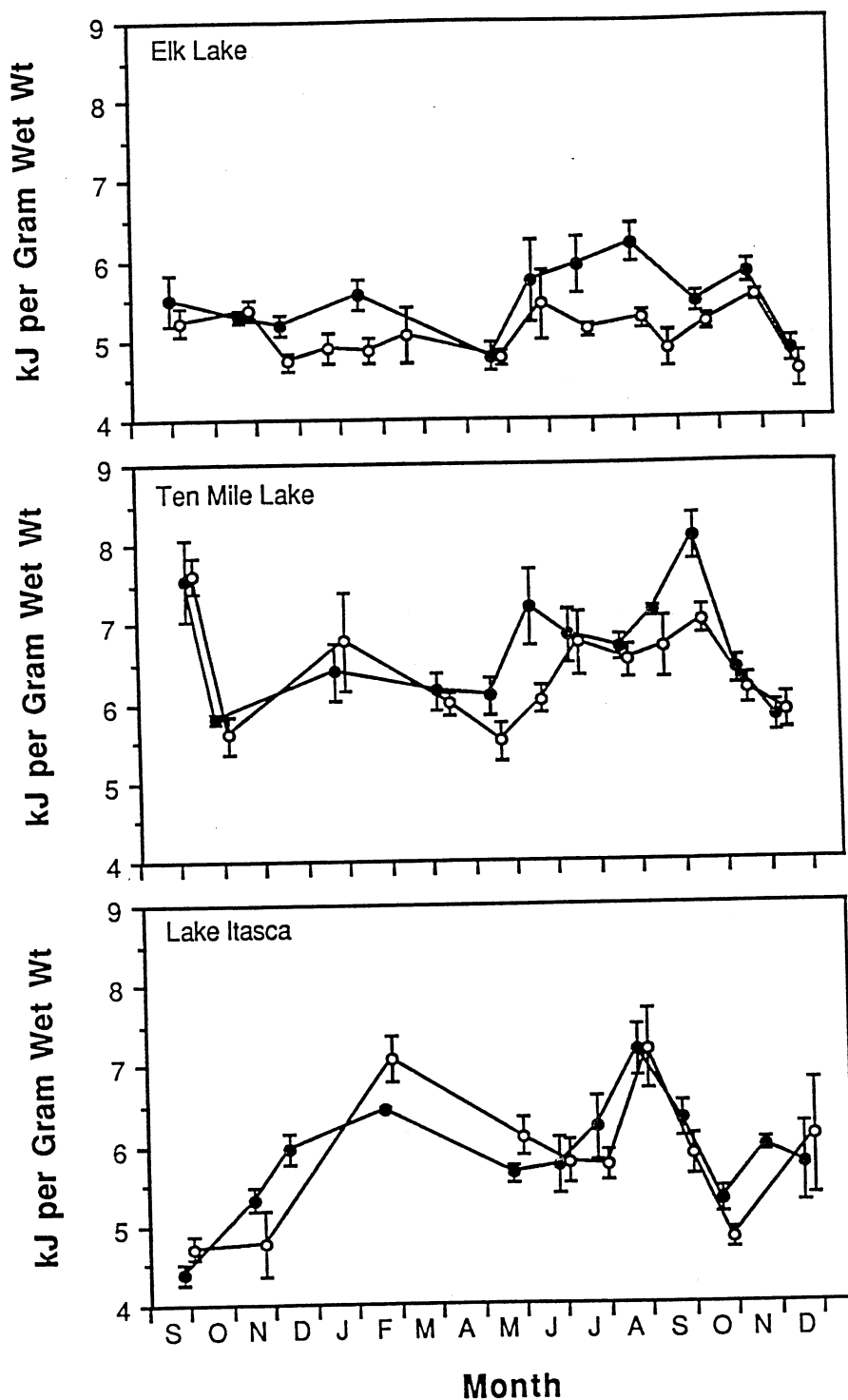
Figure 4.4. Seasonal variation in liver energy density in kJ g⁻¹ wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-○-).
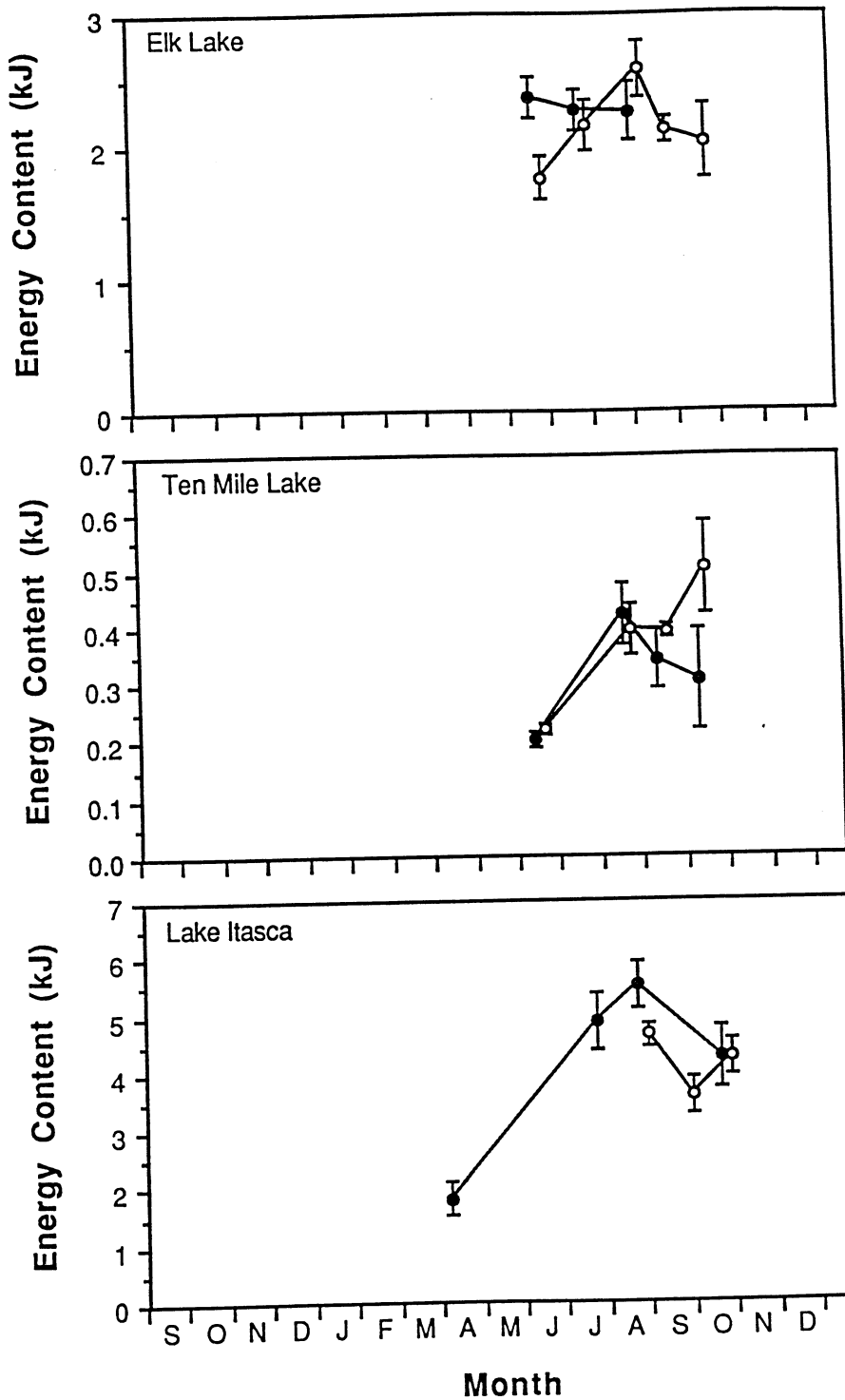
Figure 4.5 Seasonal variation in liver energy content of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-o-).
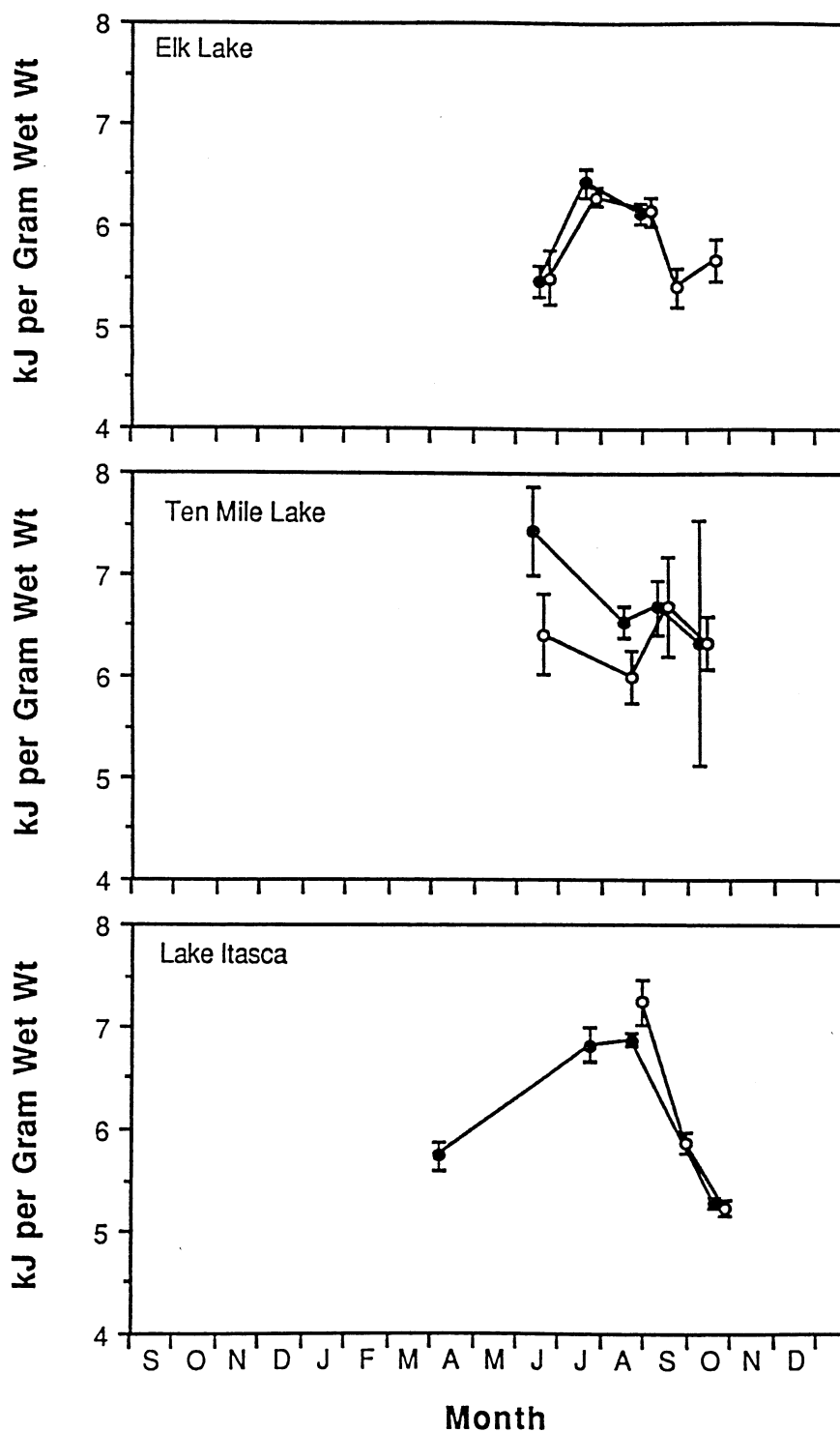
Figure 4.6. Seasonal variation in liver energy density in kJ g^{-1} wet weight of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
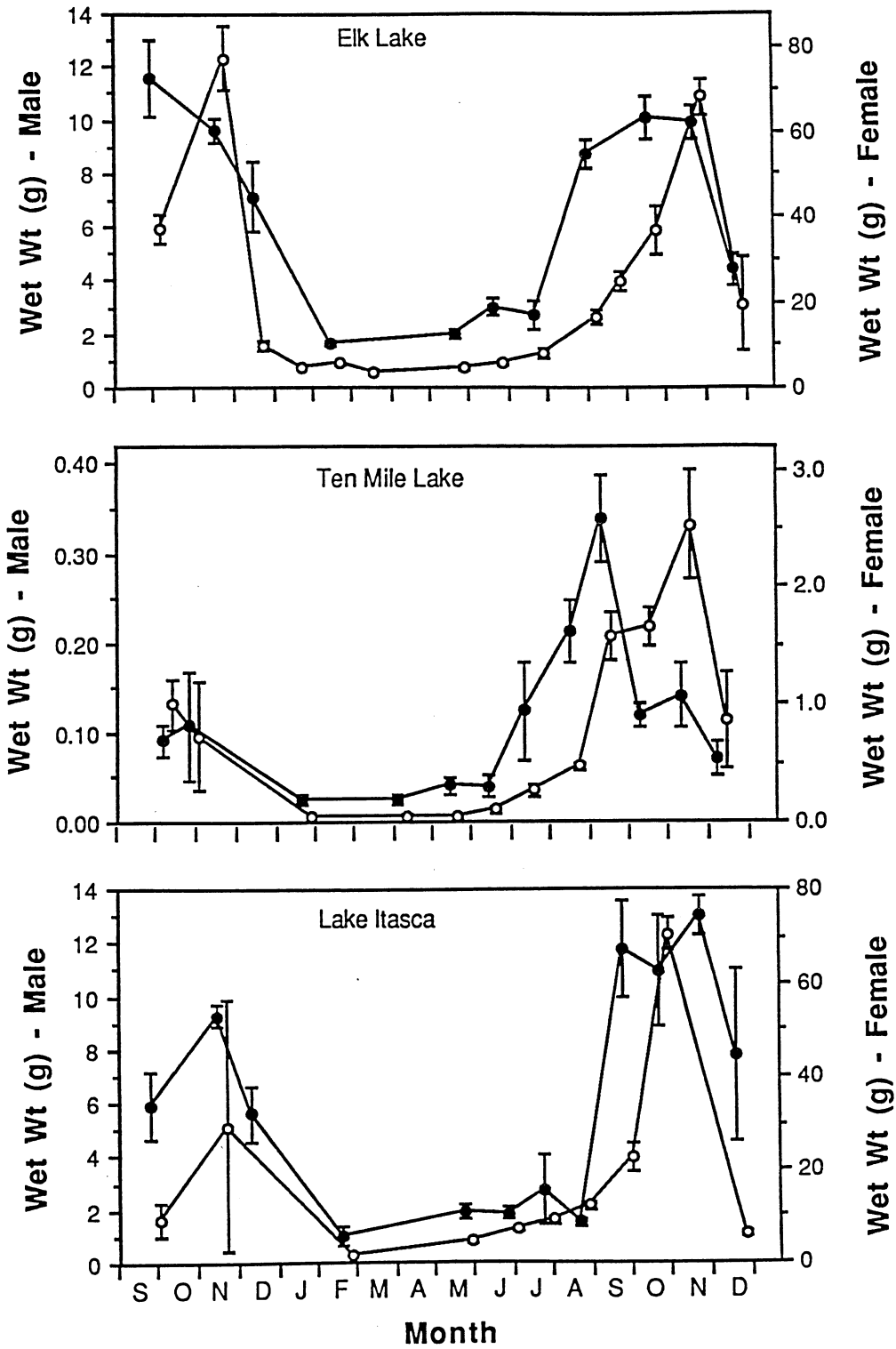
Figure 4.7. Seasonal variation in gonad wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-○-).
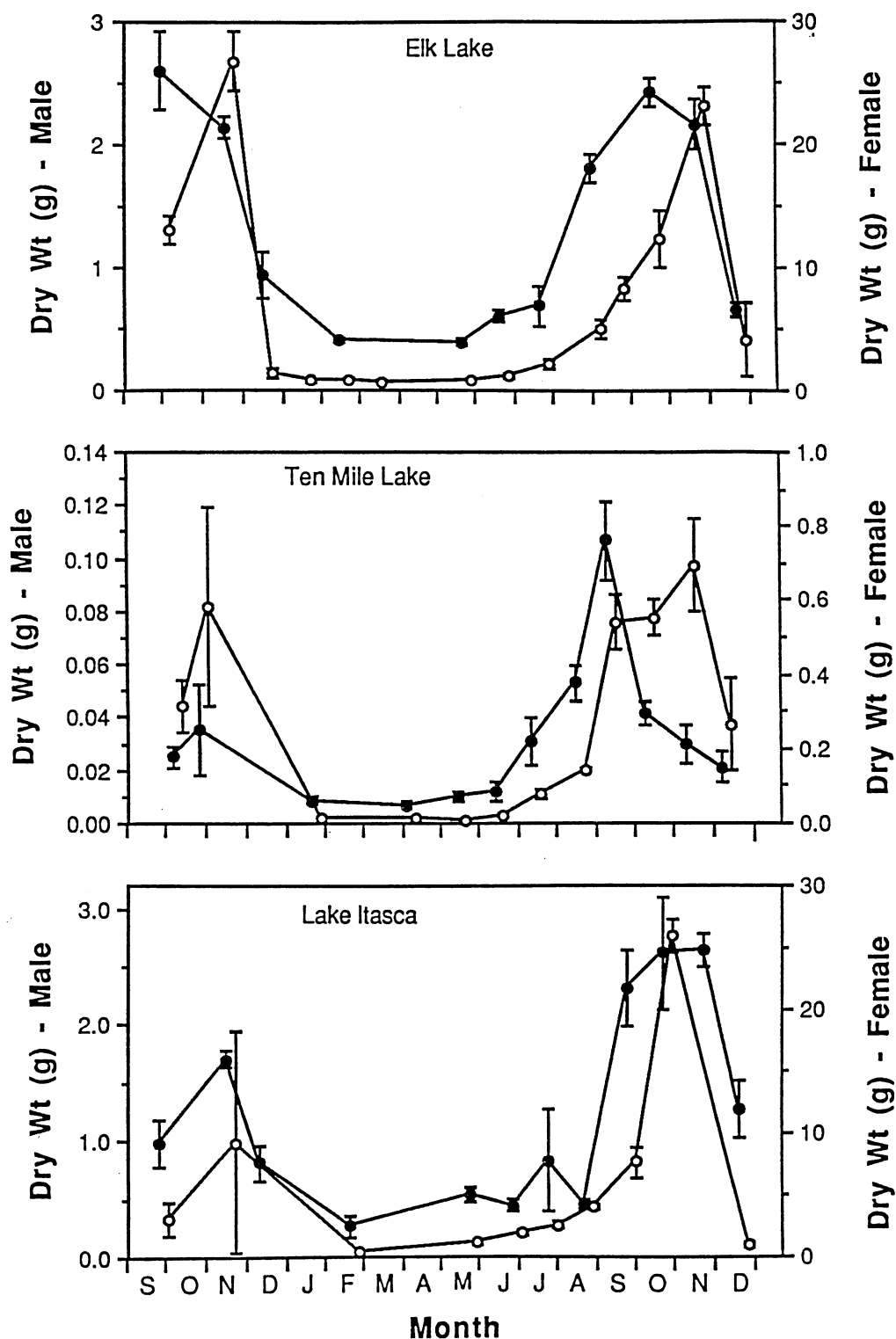
Figure 4.8. Seasonal variation in gonad dry weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
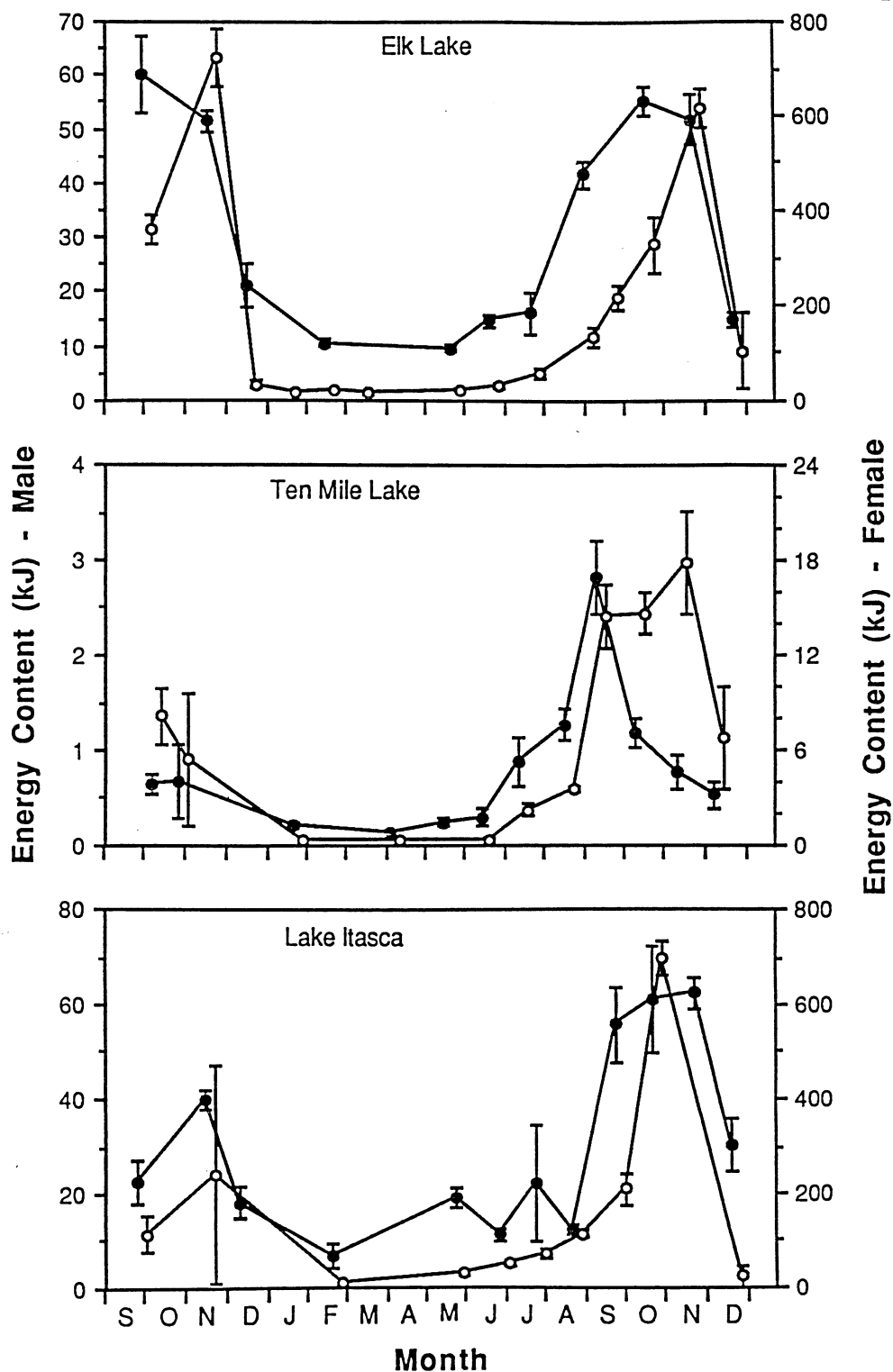
Figure 4.9. Seasonal variation in gonad energy content of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
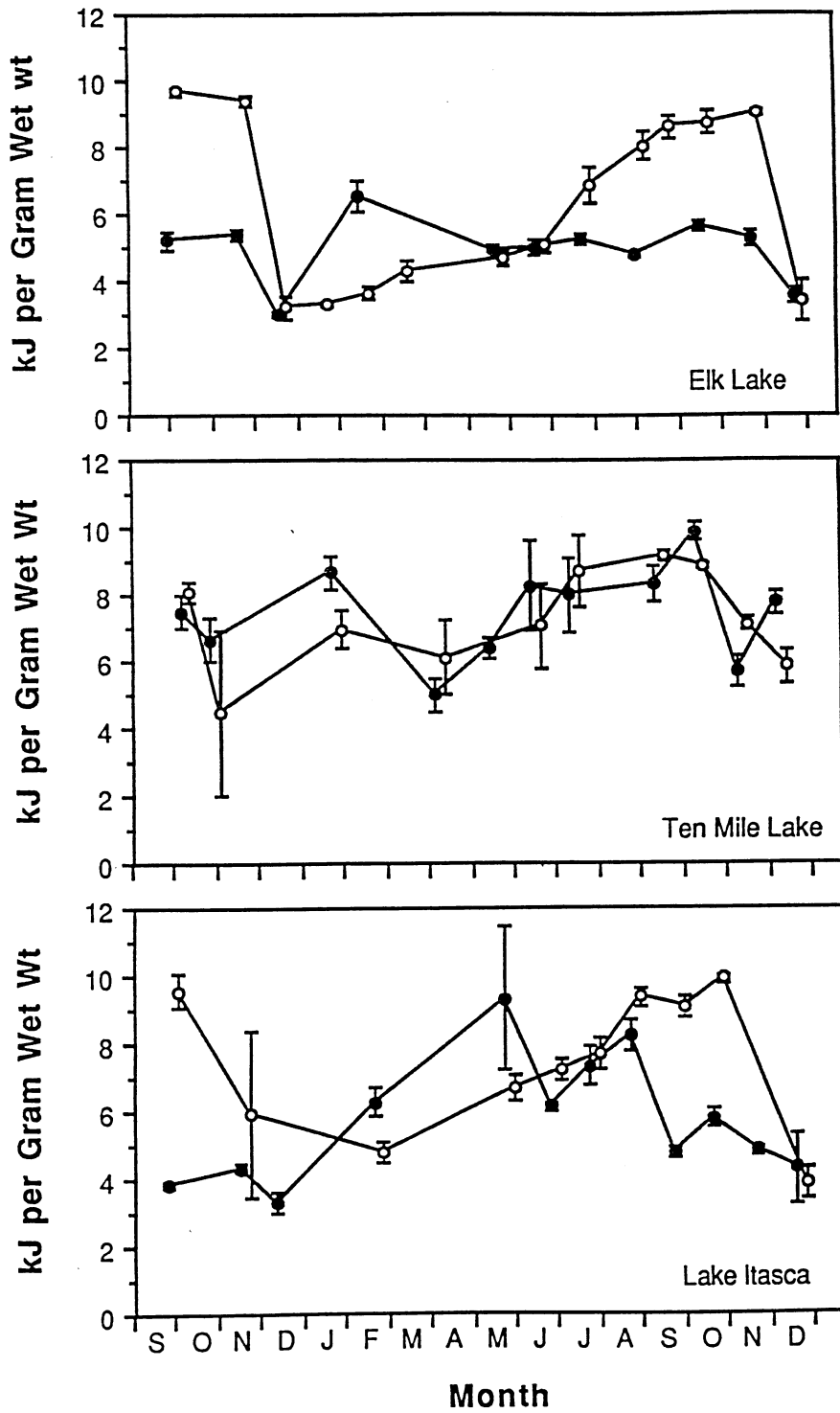
Figure 4.10. Seasonal variation in gonad energy density in kJ g^{-1} wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
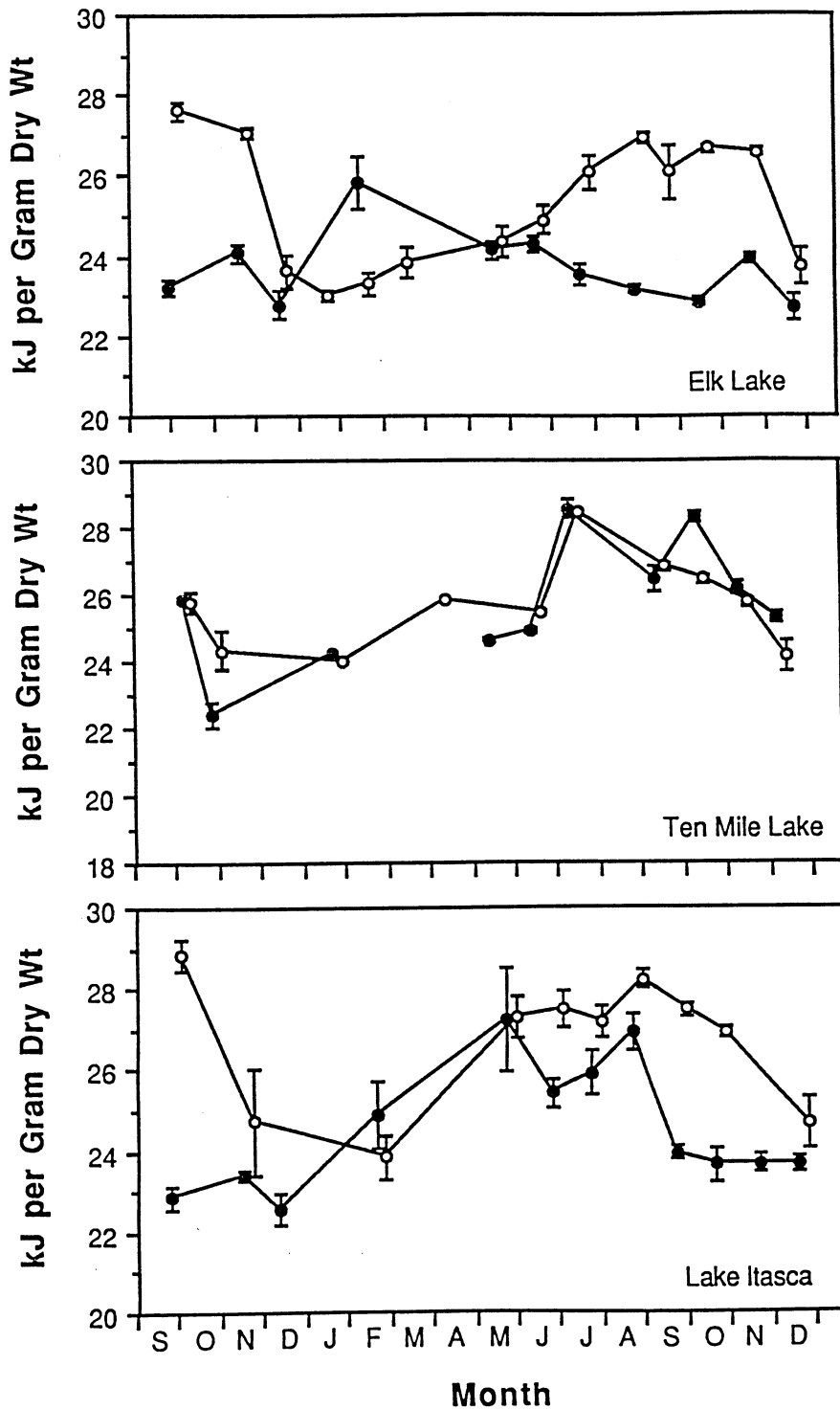
Figure 4.11. Seasonal variation in gonad energy density in kJ g^{-1} dry weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-o-).
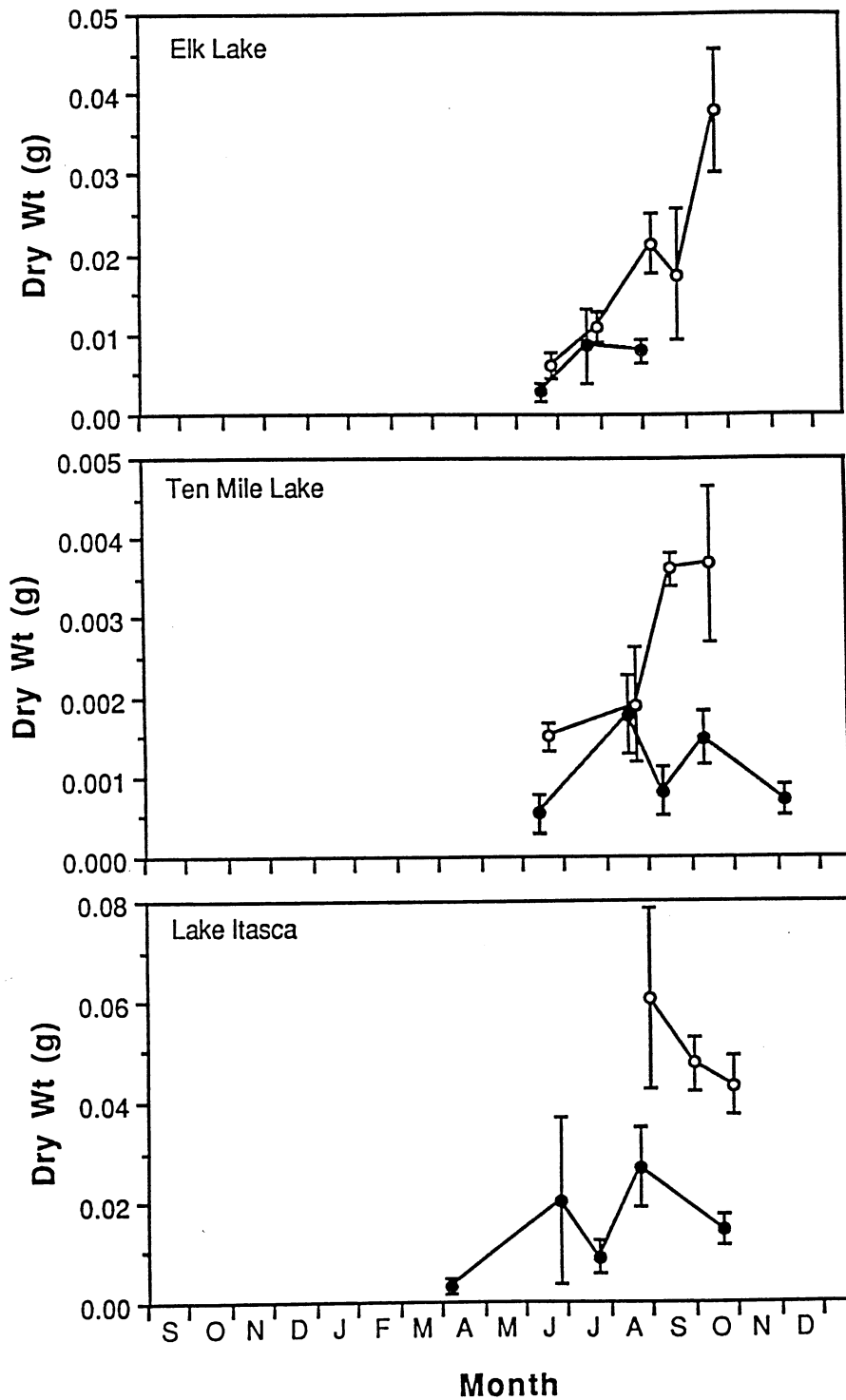
Figure 4.12. Seasonal variation in gonad dry weight of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
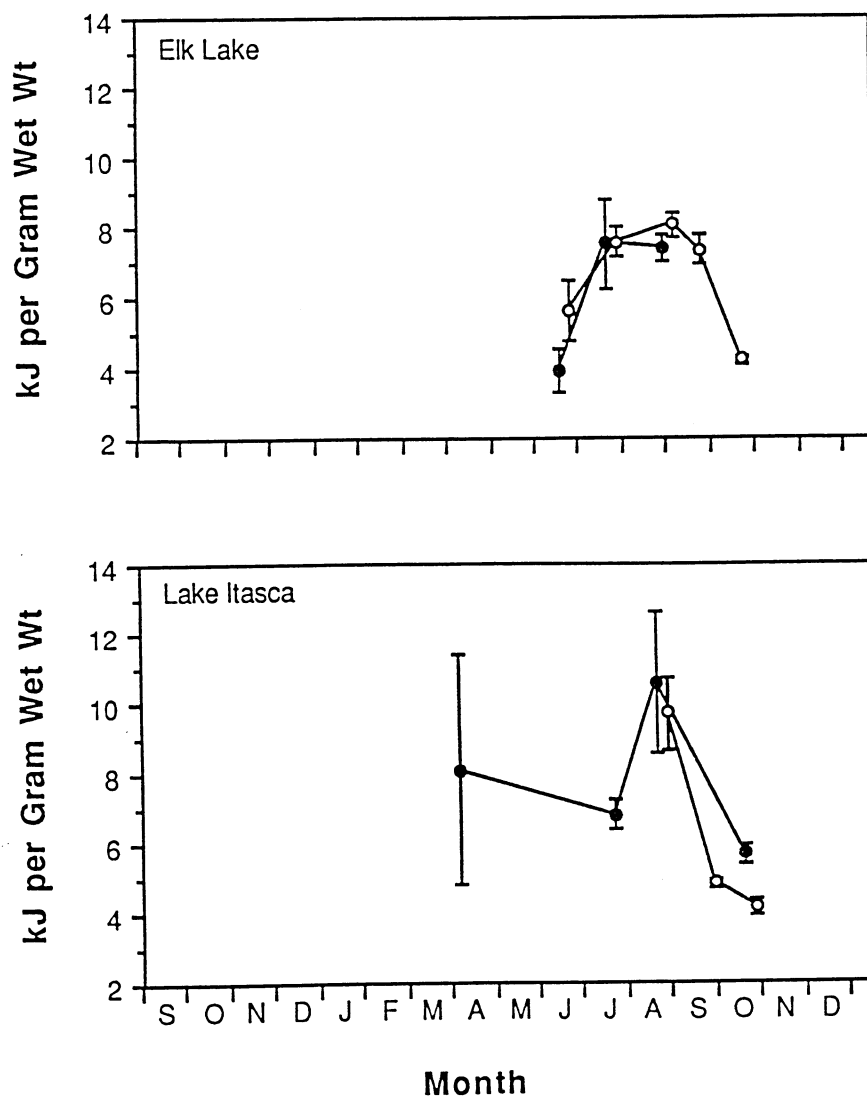
Figure 4.13. Seasonal variation in gonad energy density in kJ g^{-1} wet weight of juvenile ciscos: Elk Lake, top; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
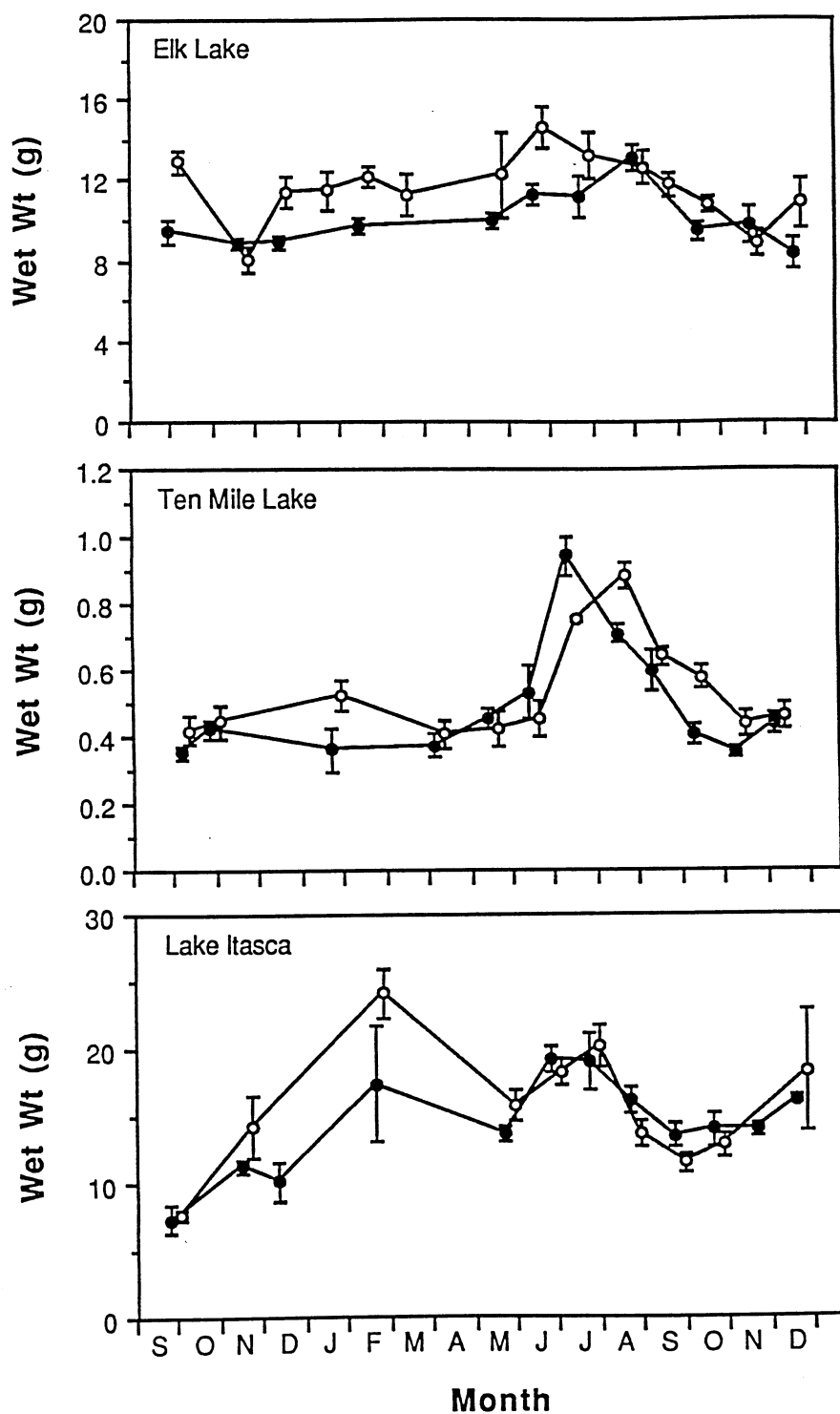
Figure 4.14. Seasonal variation in digestive tract wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-o-).
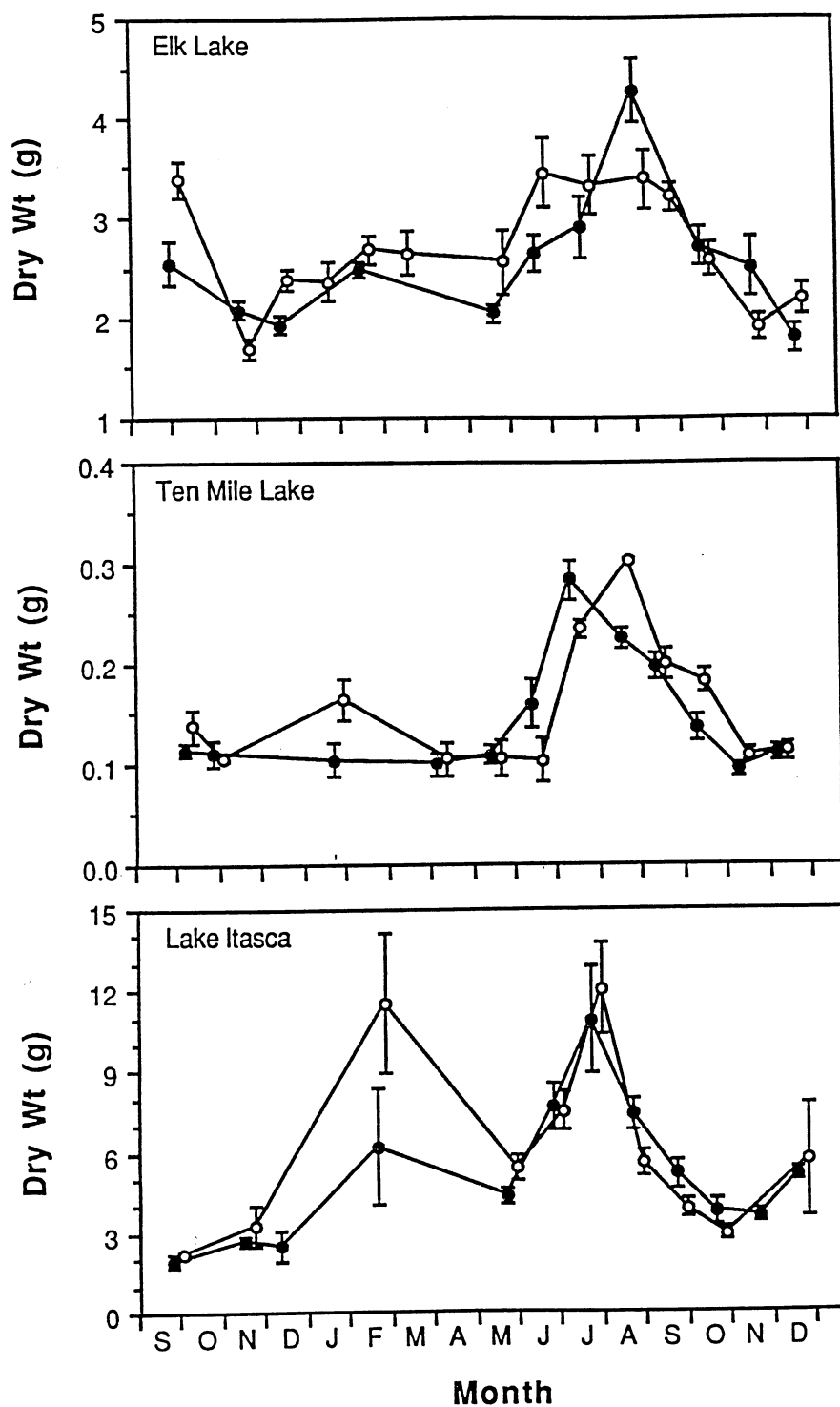
Figure 4.15. Seasonal variation in digestive tract dry weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-○-).
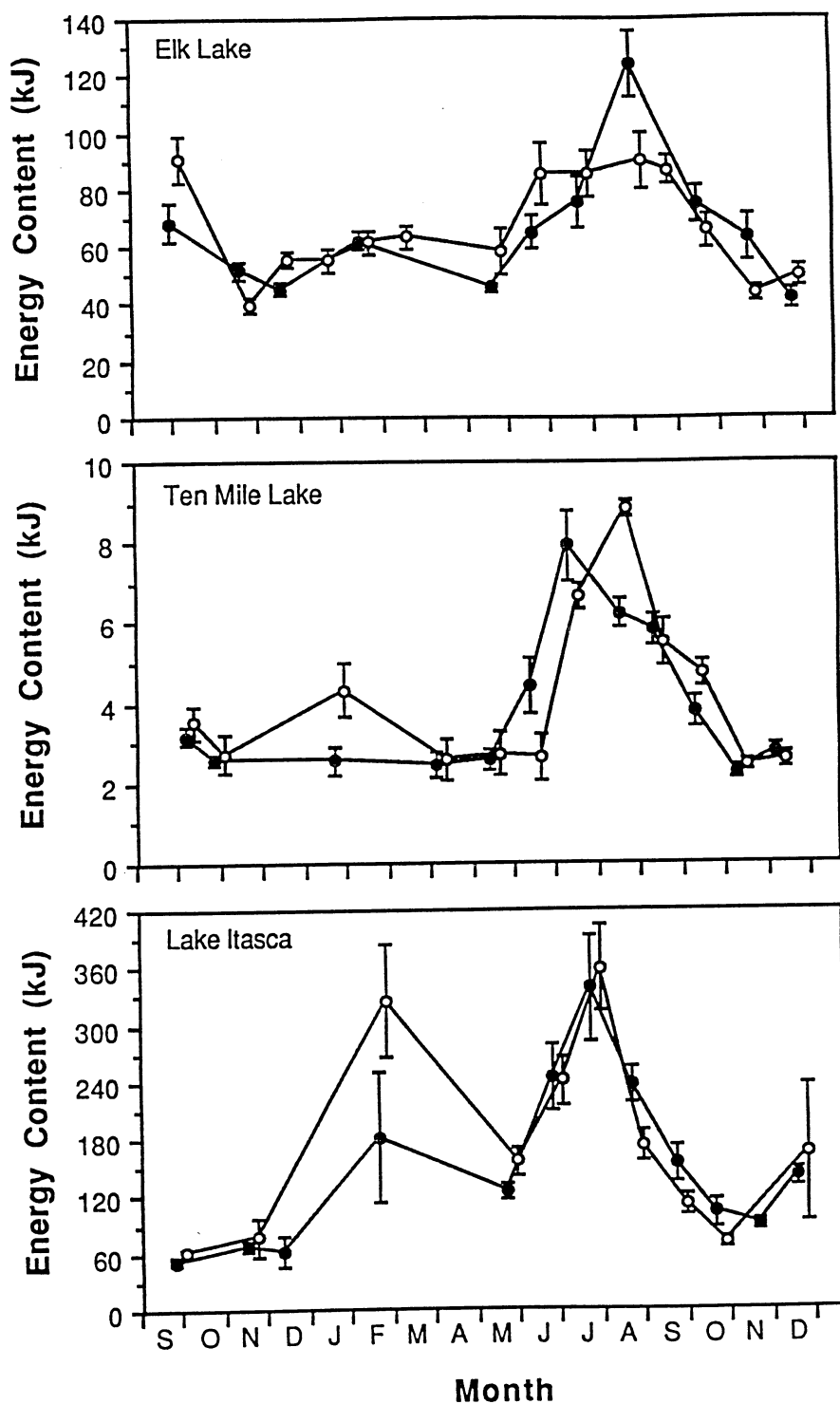
Figure 4.16. Seasonal variation in digestive tract energy content of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
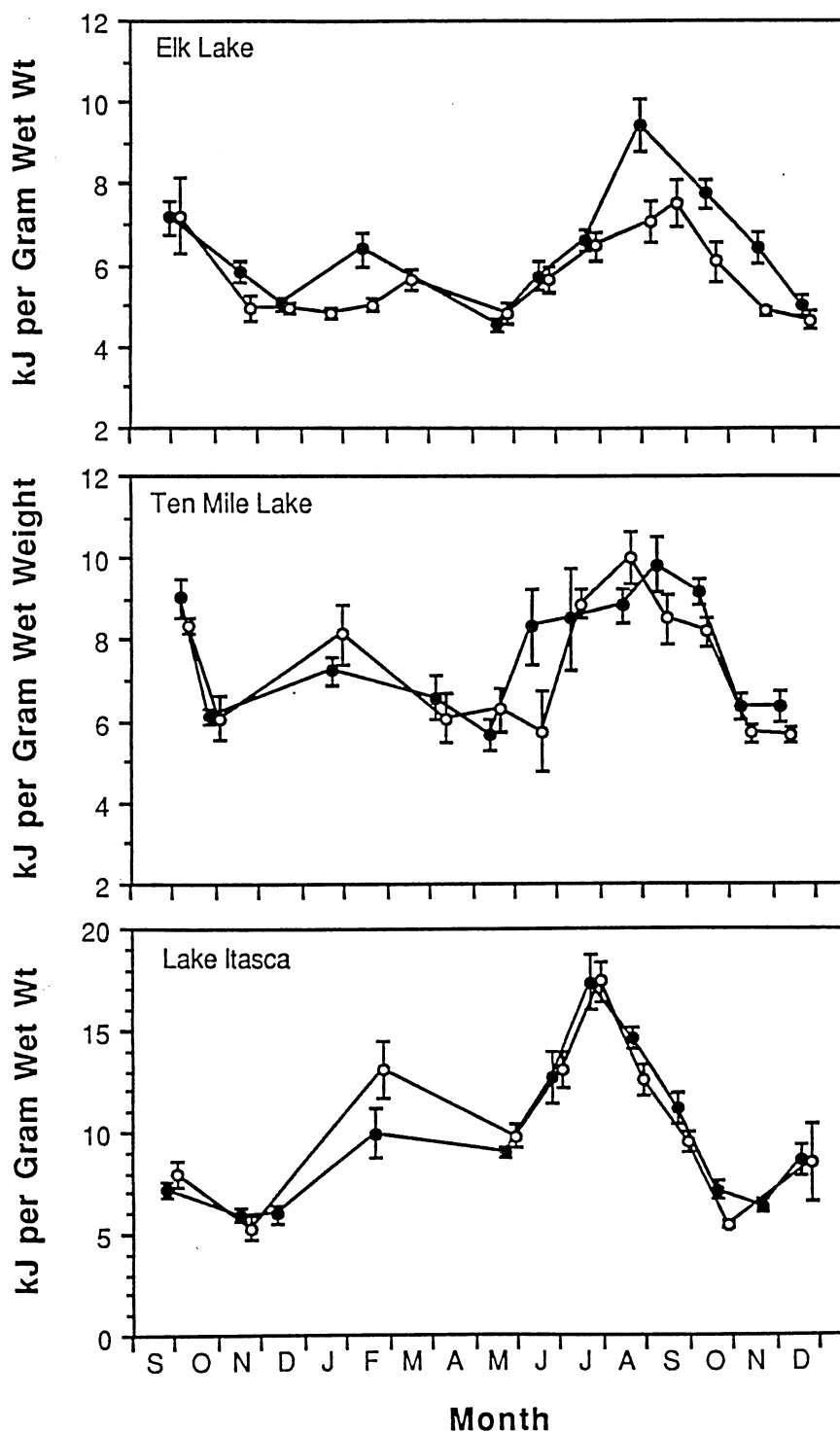
Figure 4.17. Seasonal variation in digestive tract energy density in kJ g⁻¹ wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
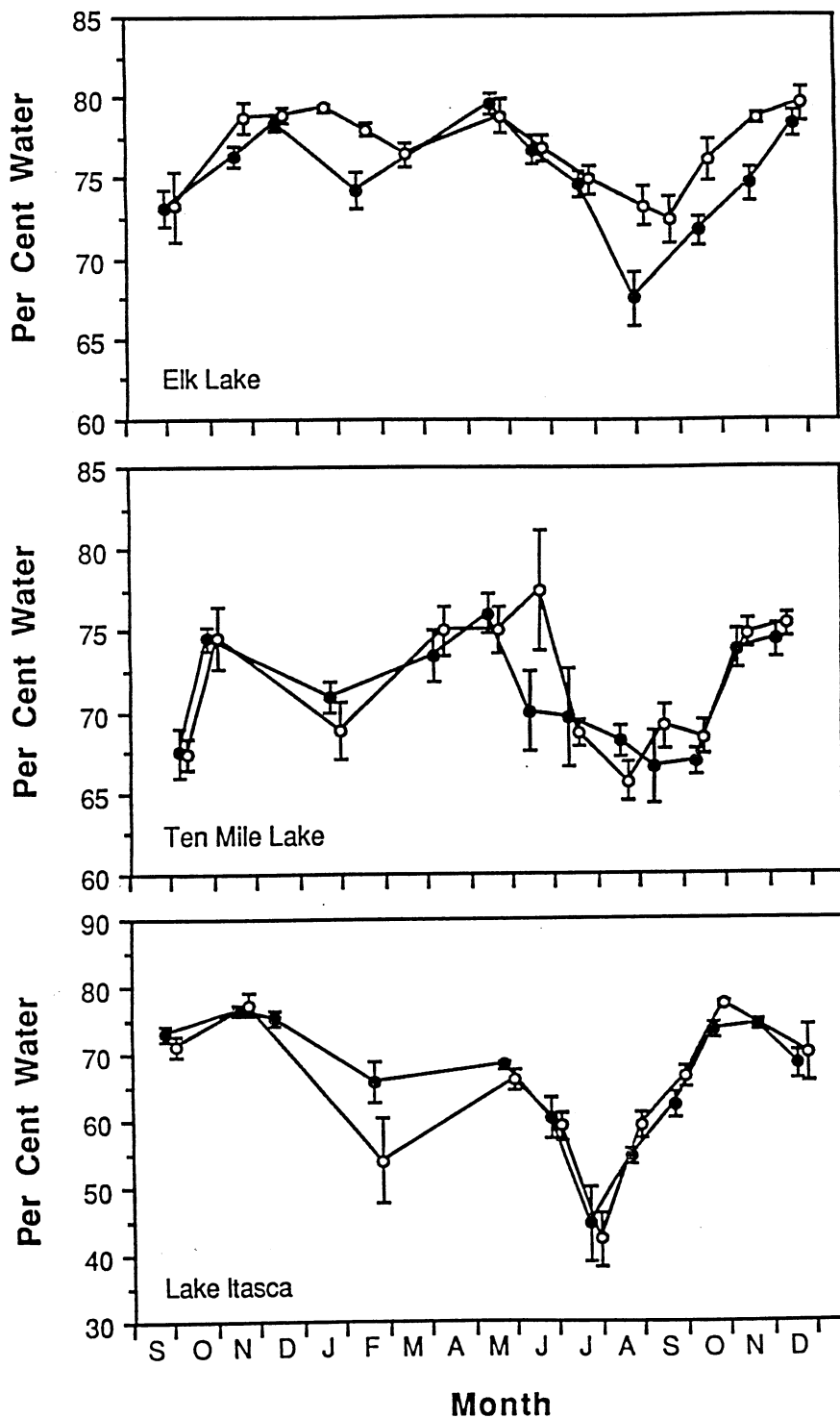
Figure 4.18. Seasonal variation in digestive tract per cent water of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-o-).
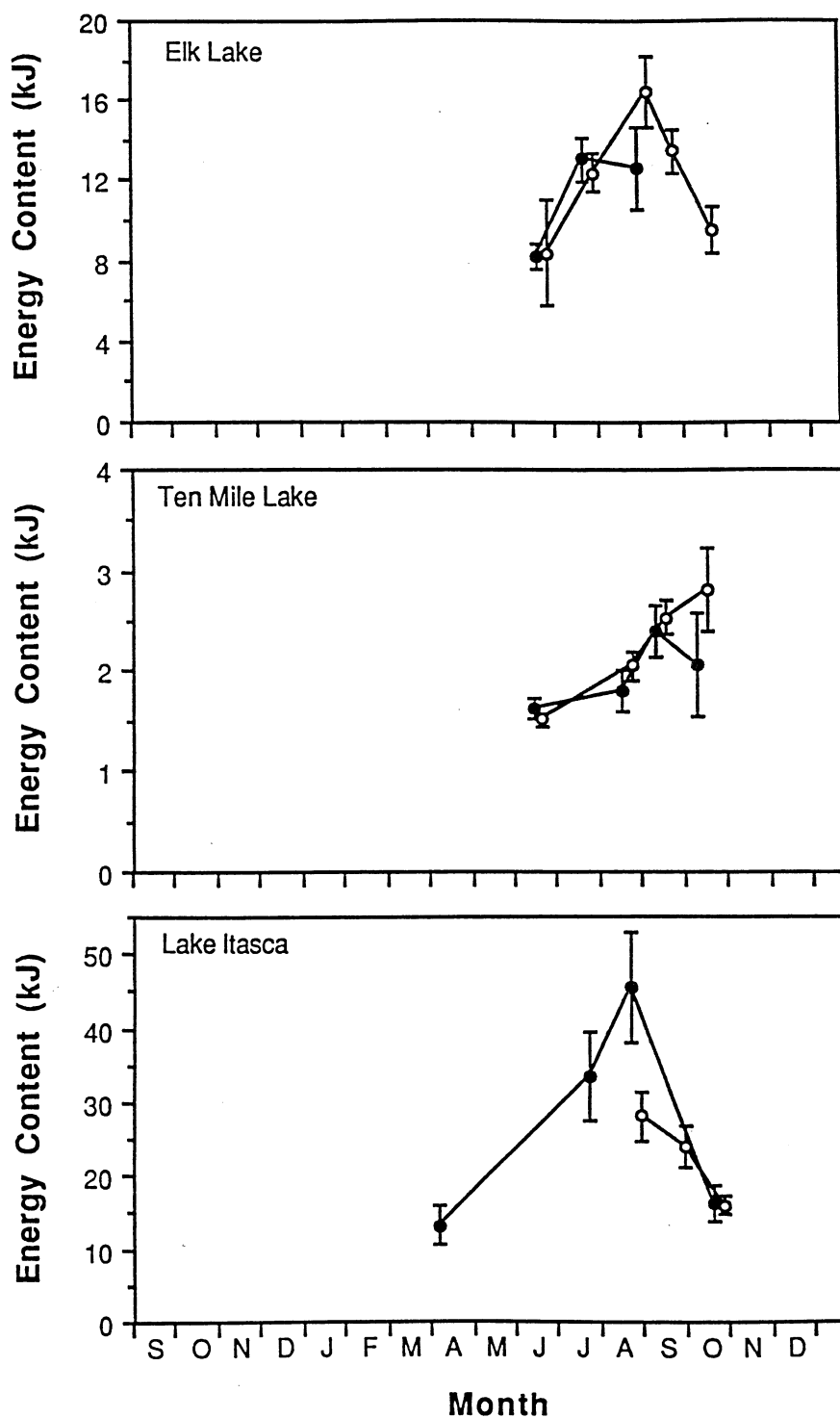
Figure 4.19. Seasonal variation in digestive tract energy content of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
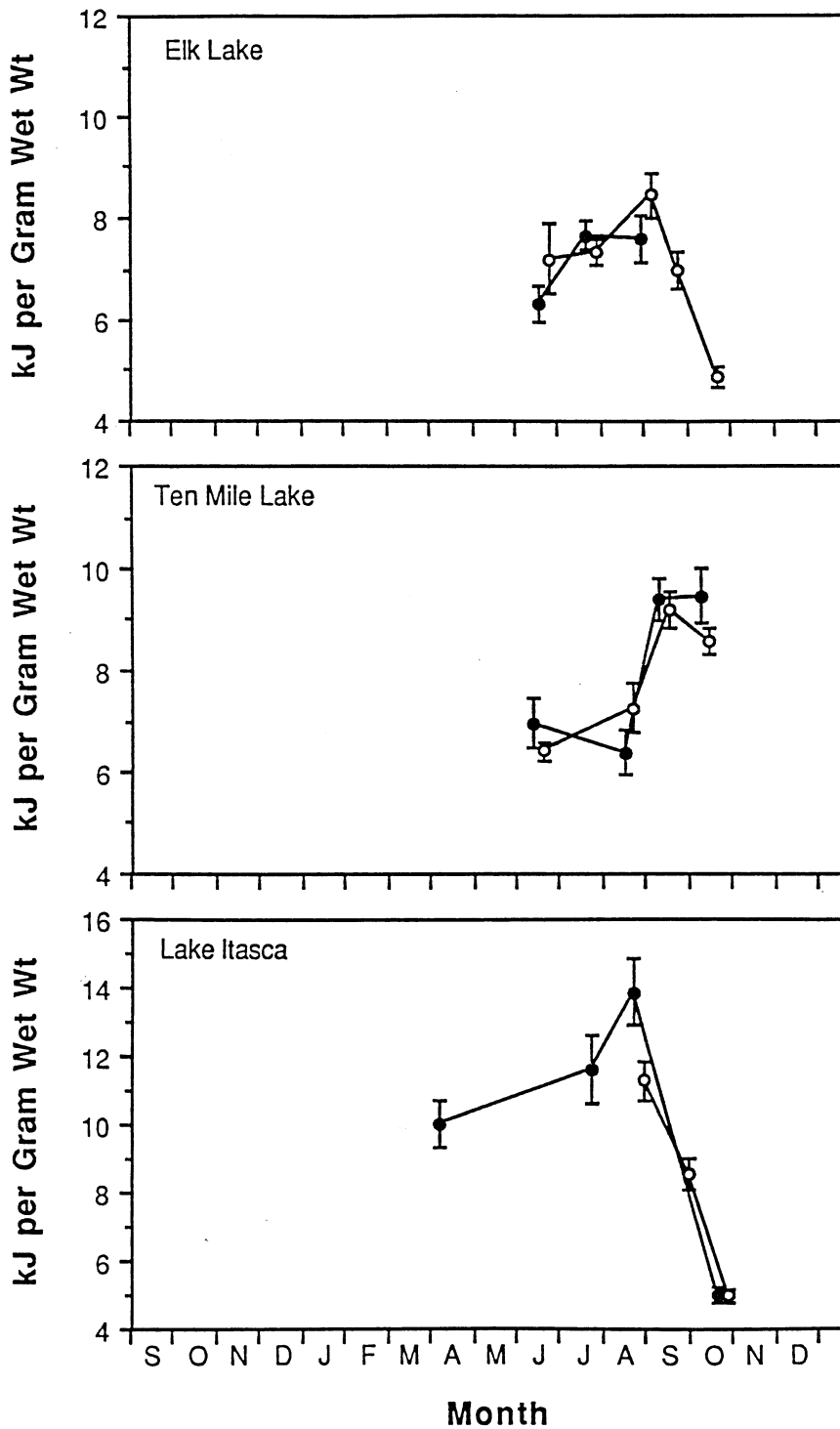
Figure 4.20. Seasonal variation in digestive tract energy density in kJ g-1 wet weight of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (●), females by open circles (-o-).
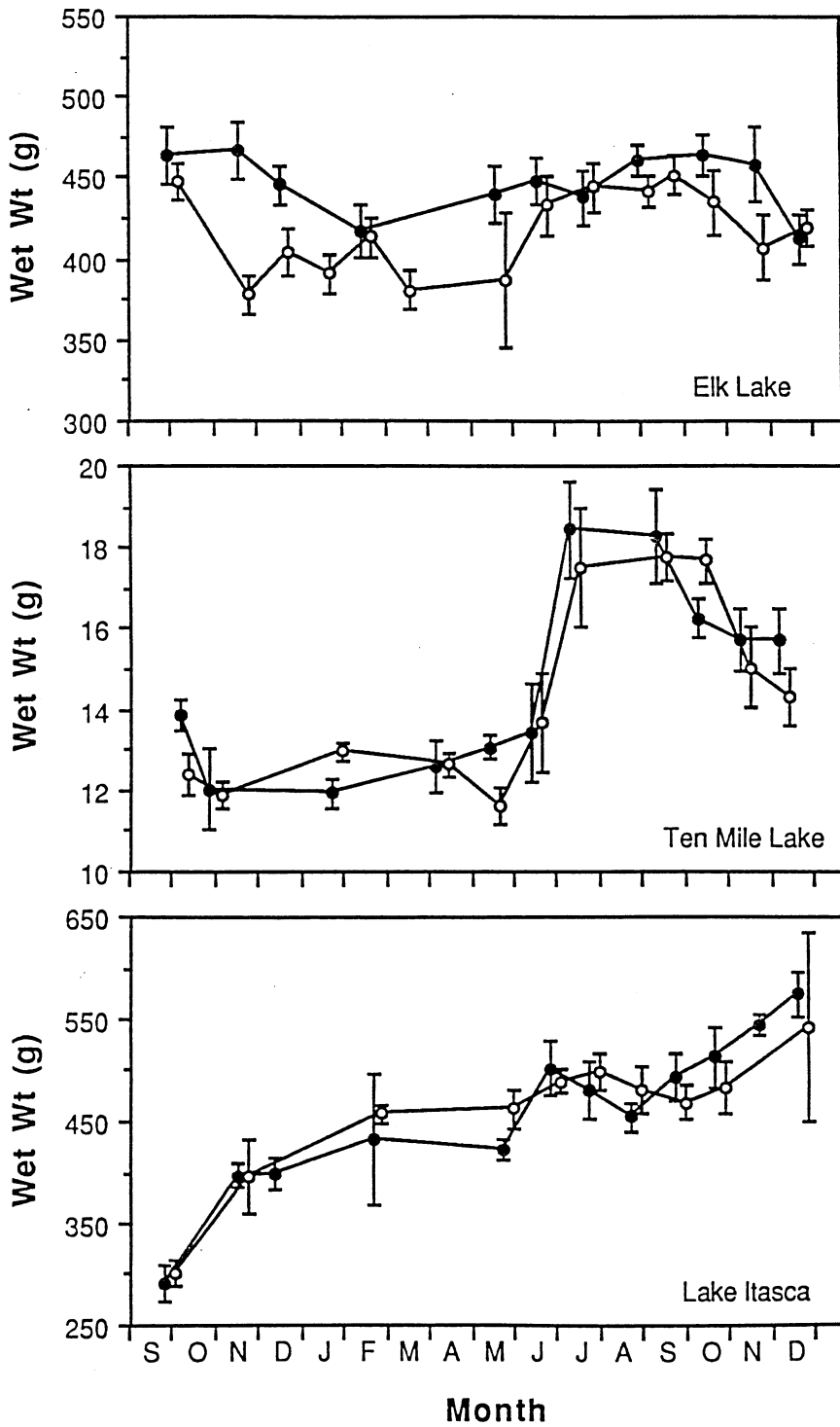
Figure 4.21. Seasonal variation in carcass wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (●), females by open circles (○).
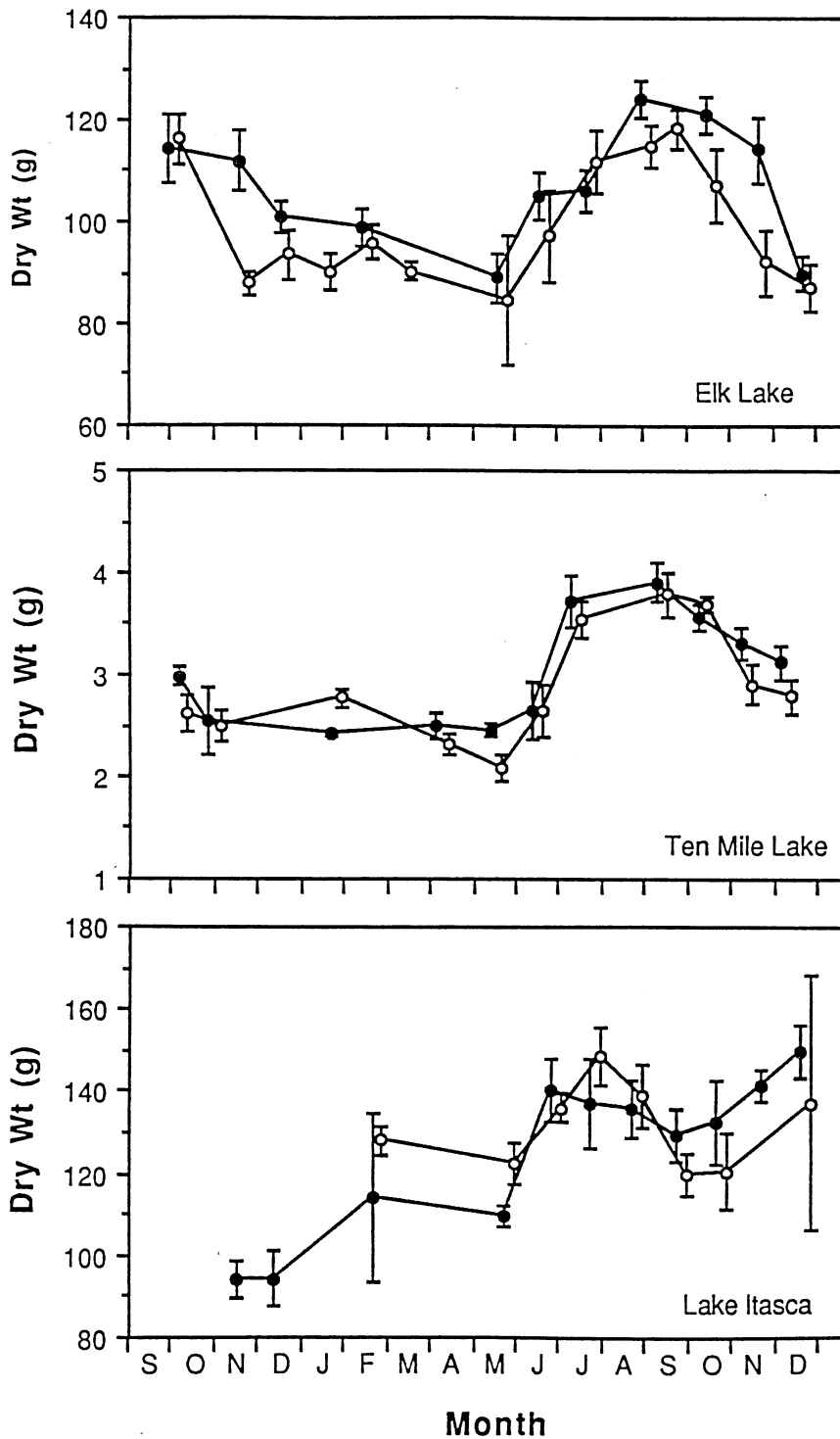
Figure 4.22. Seasonal variation in carcass dry weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
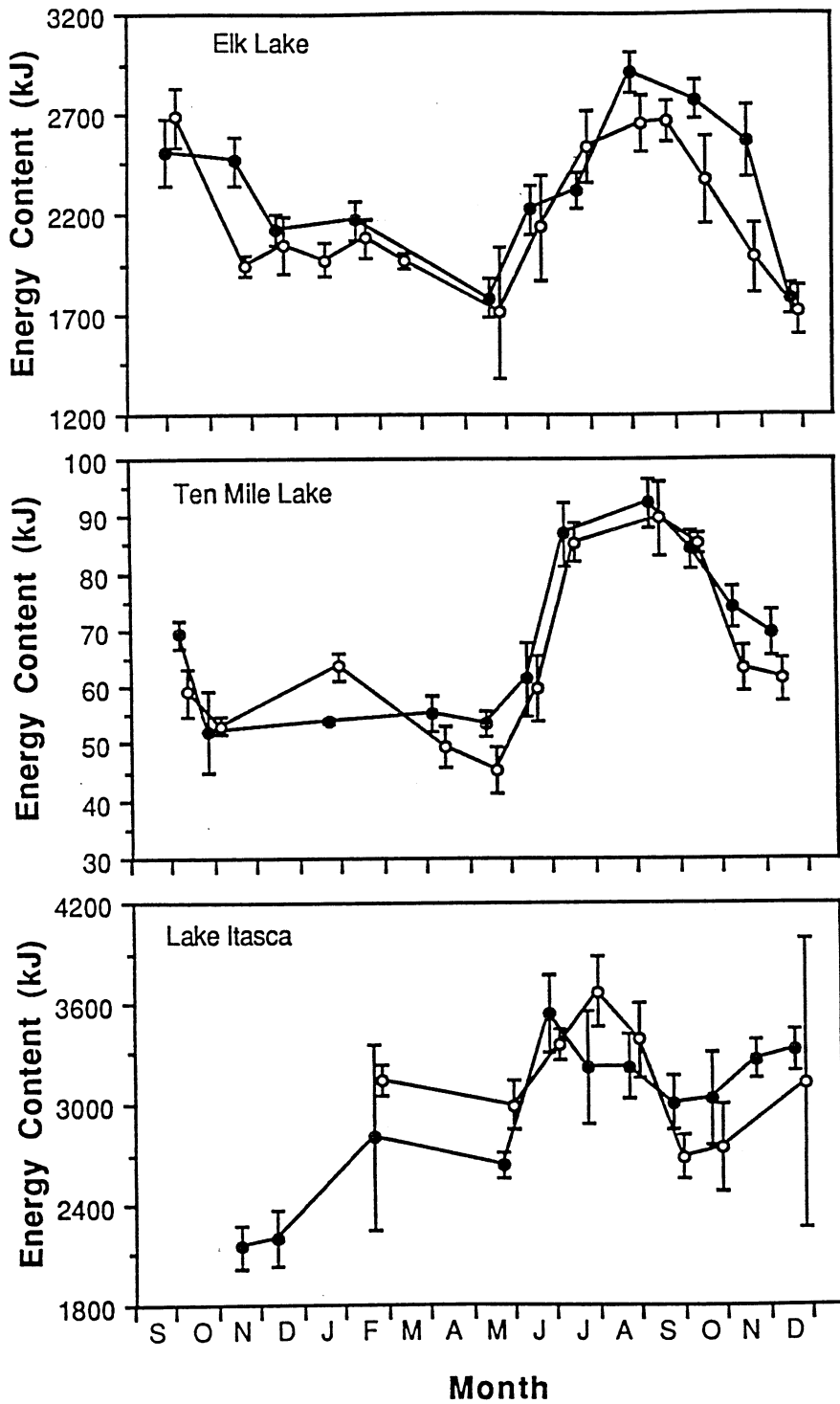
Figure 4.23. Seasonal variation in carcass energy content of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-○-).
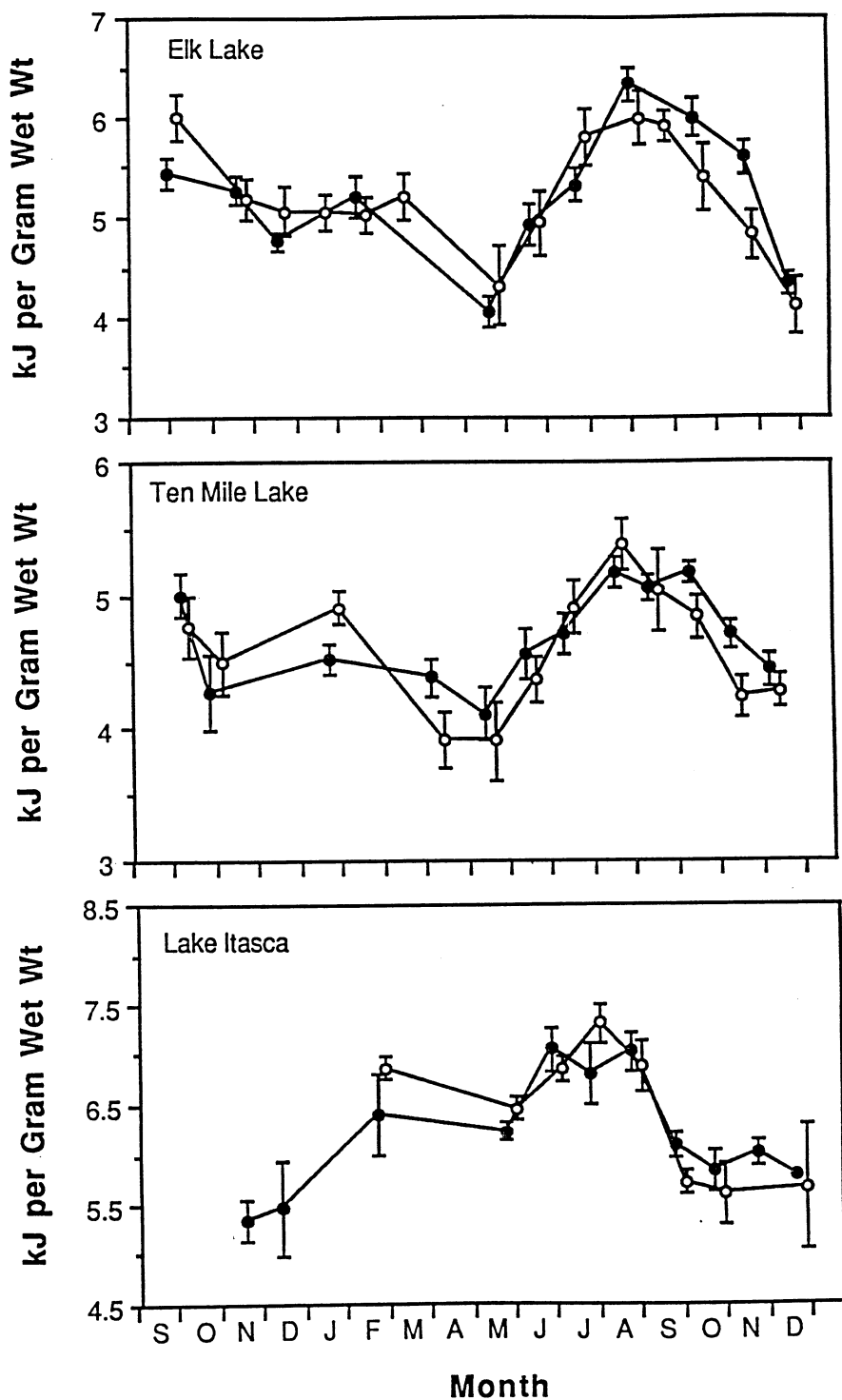
Figure 4.24. Seasonal variation in carcass energy density in kJ g^{-1} wet weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-o-).
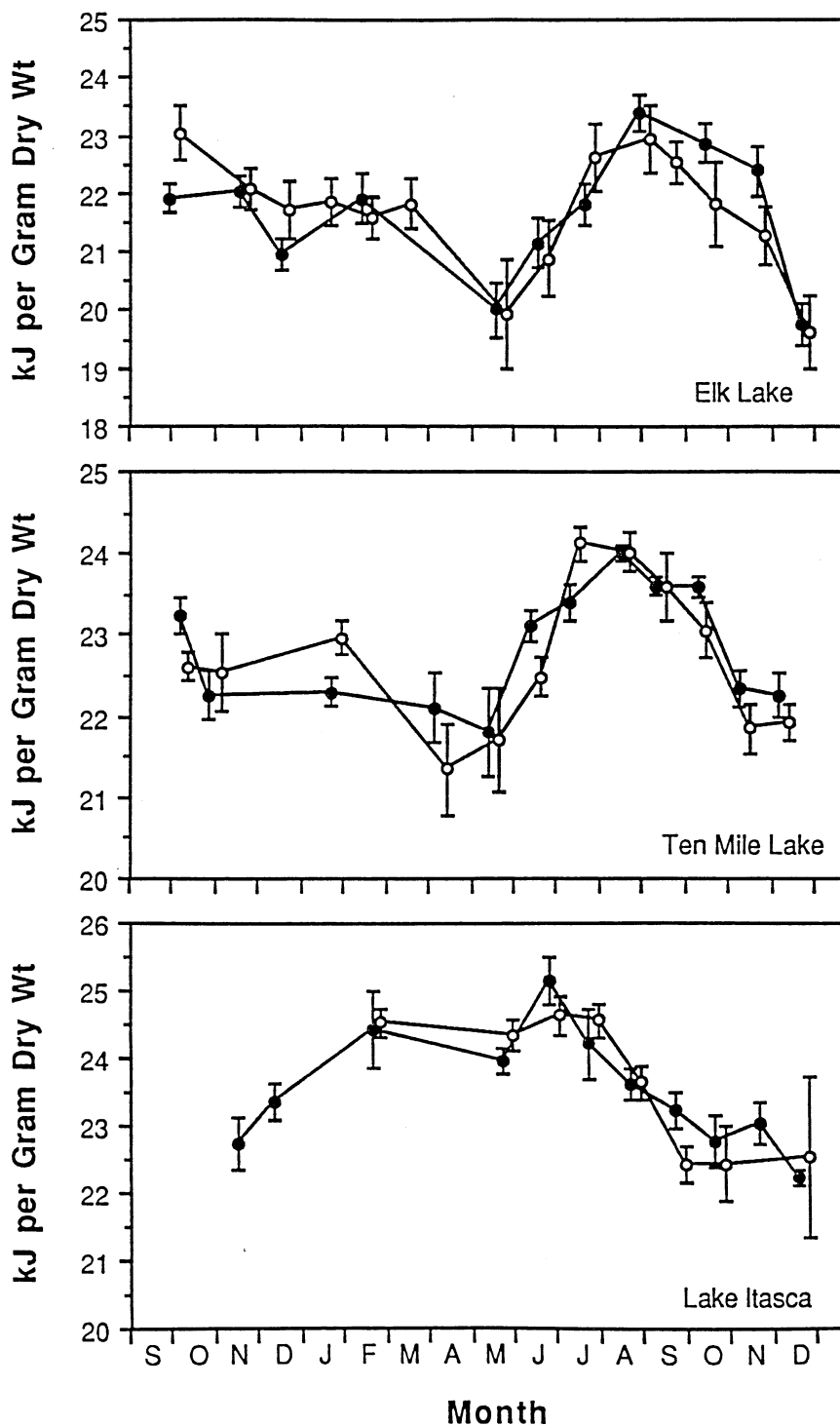
Figure 4.25. Seasonal variation in carcass energy density in kJ g^{-1} dry weight of adult ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
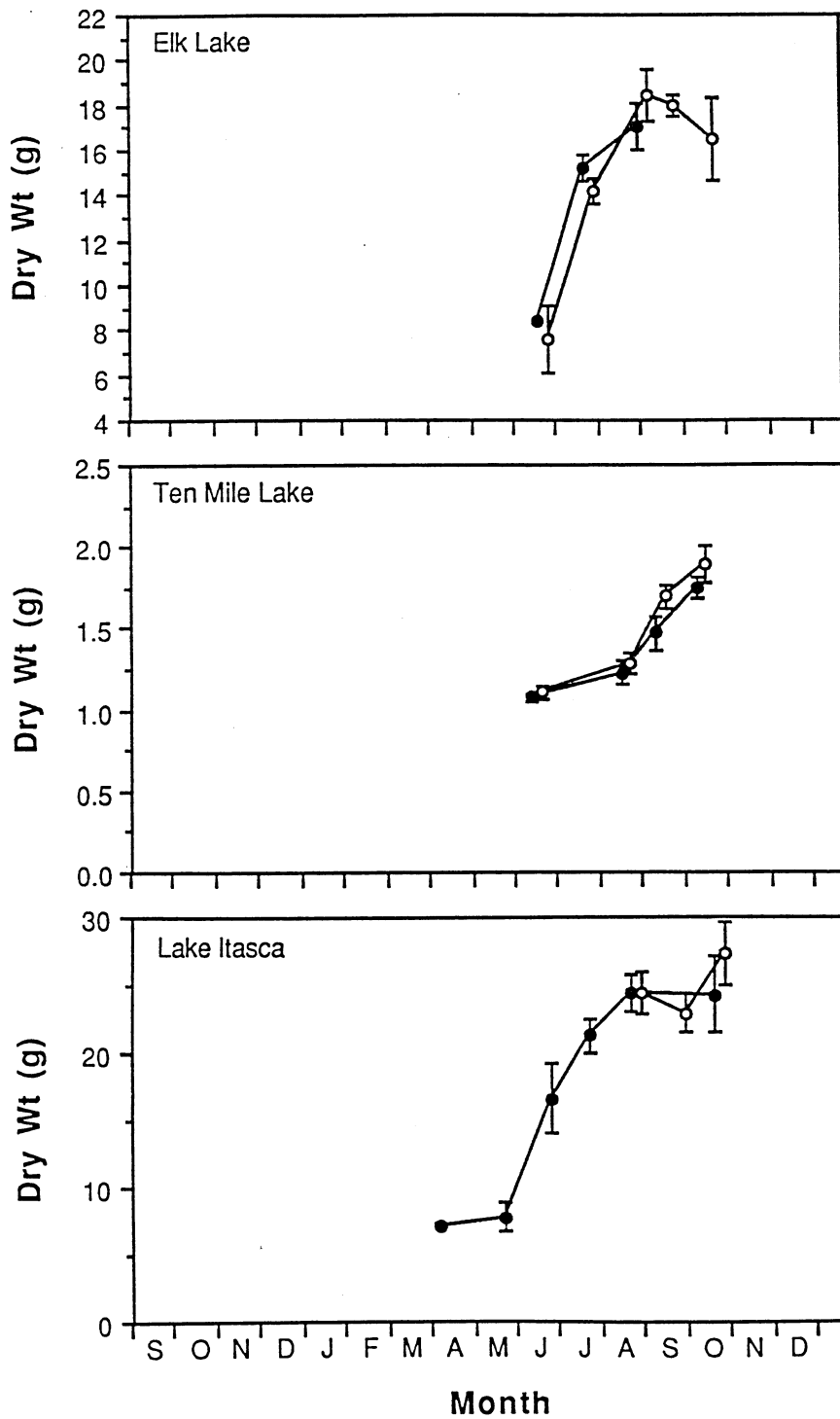
Figure 4.26. Seasonal variation in carcass dry weight of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (•), females by open circles (○).
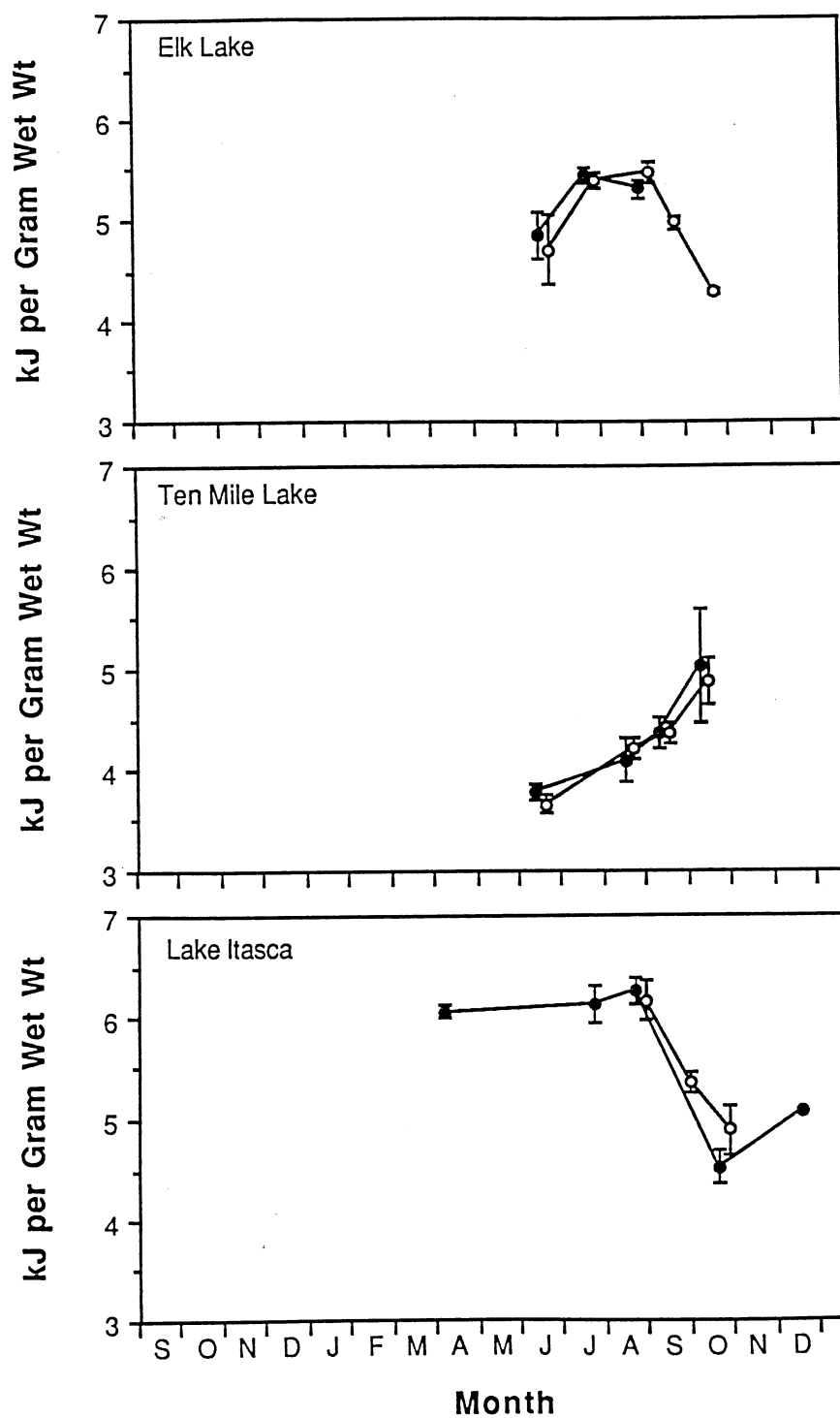
Figure 4.27. Seasonal variation in carcass energy density in kJ g^{-1} wet weight of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-o-).
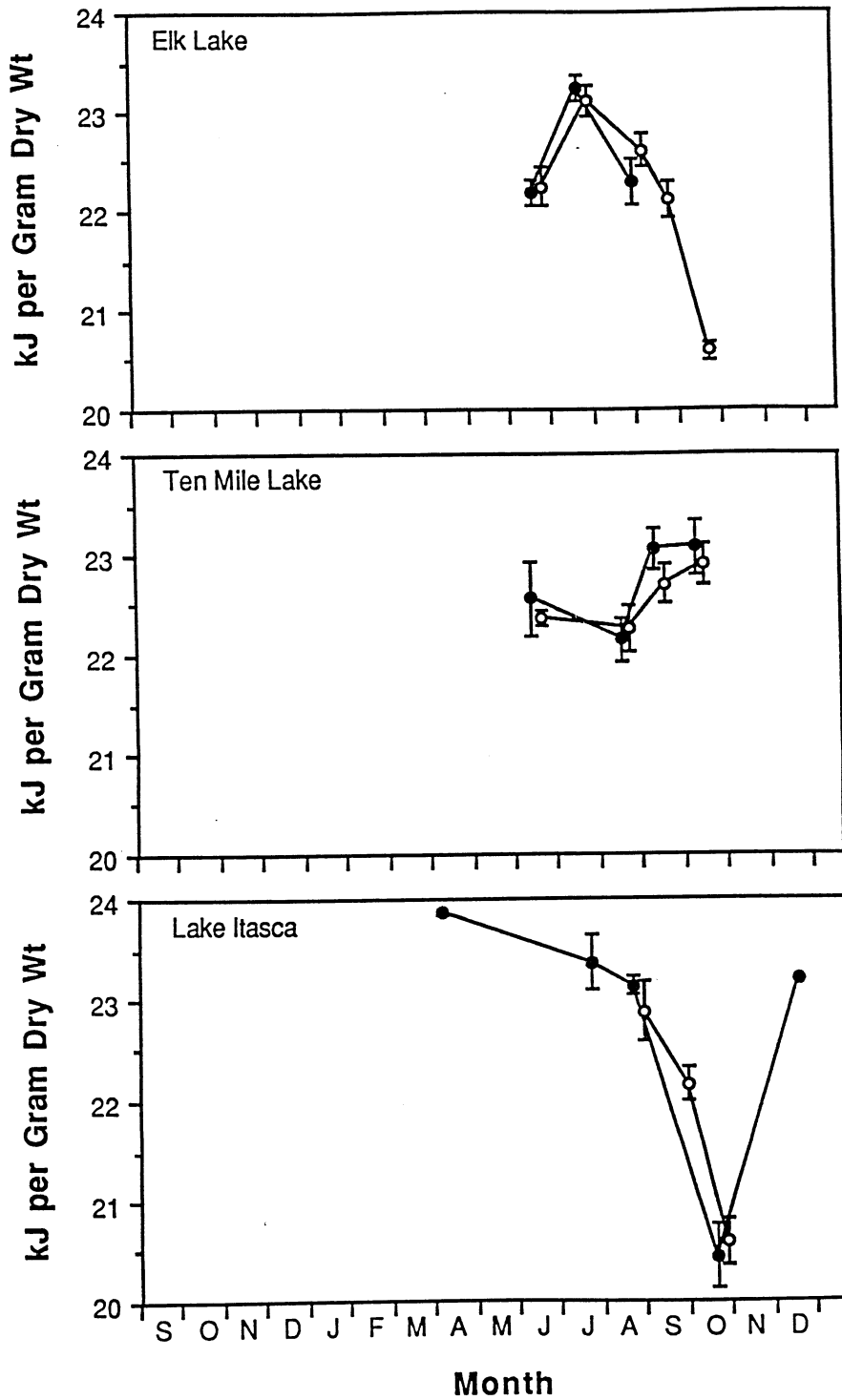
Figure 4.28. Seasonal variation in carcass energy density in kJ g^{-1} dry weight of juvenile ciscos: Elk Lake, top; Ten Mile Lake, center; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-○-).
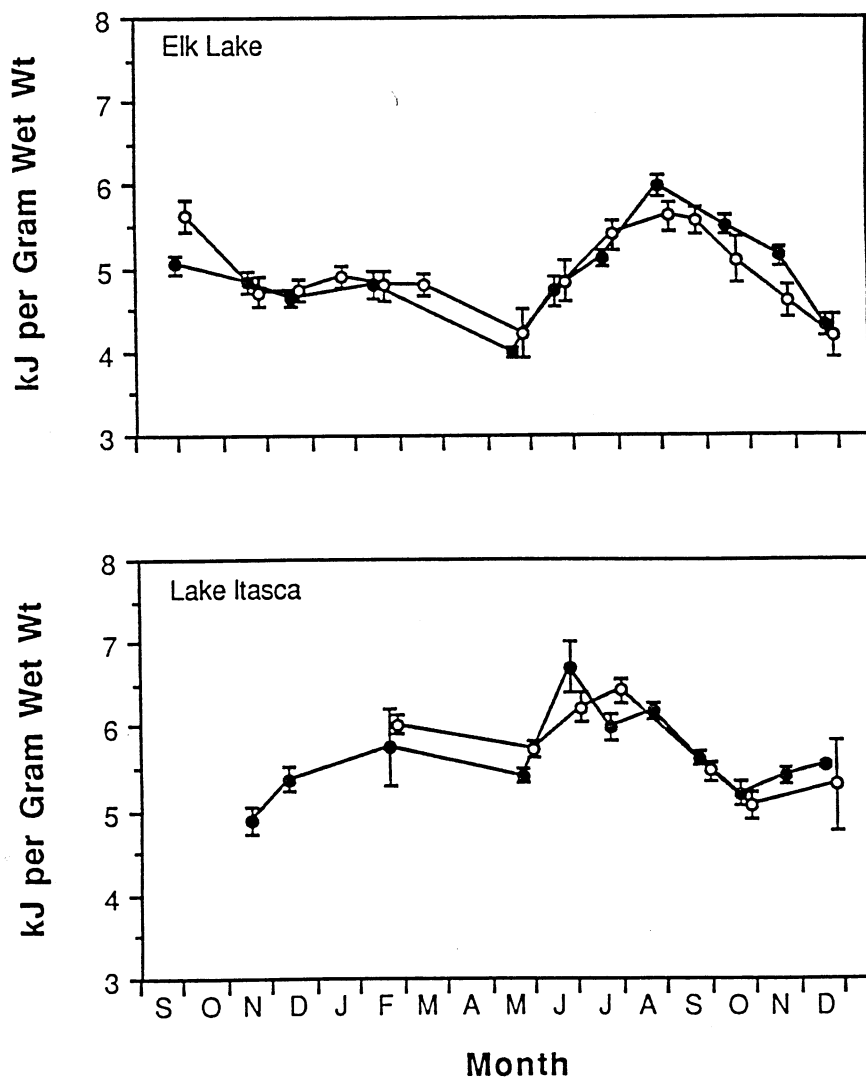
Figure 4.29. Seasonal variation in muscle energy density in kJ g^{-1} wet weight of adult ciscos: Elk Lake, top; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-●-), females by open circles (-○-).
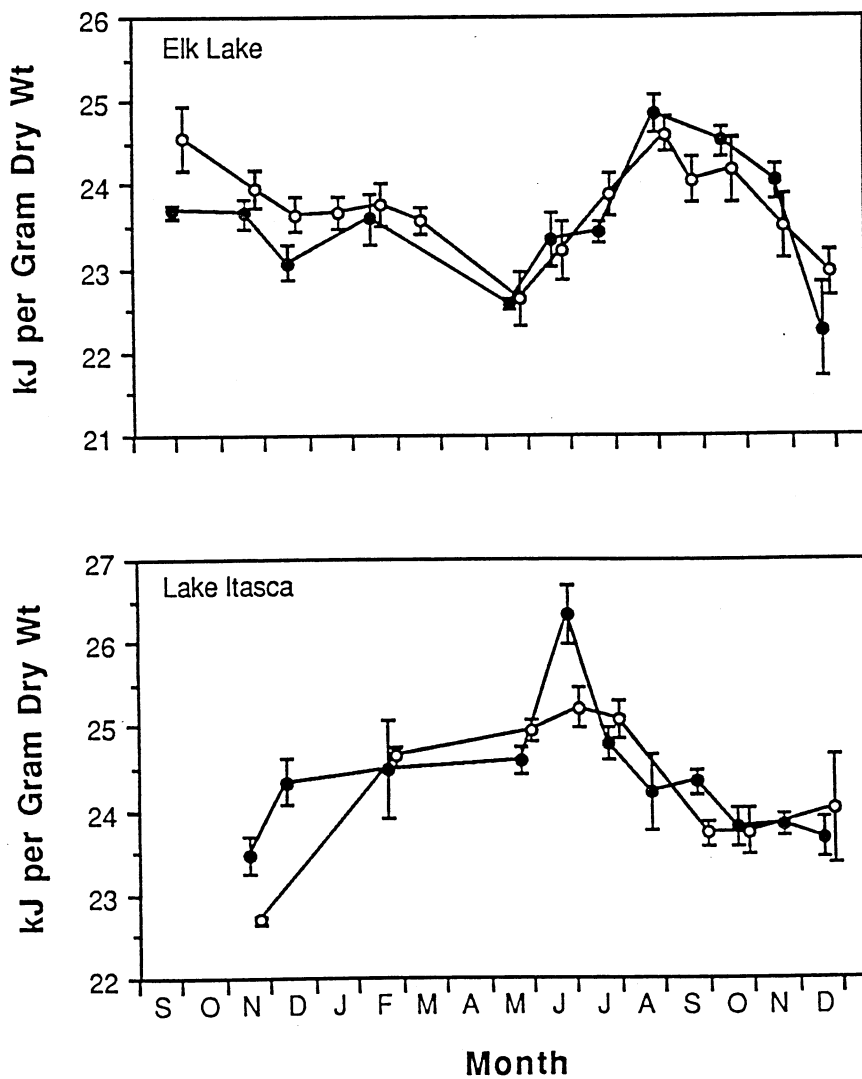
Figure 4.30. Seasonal variation in muscle energy density in kJ g^{-1} dry weight of adult ciscos: Elk Lake, top; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
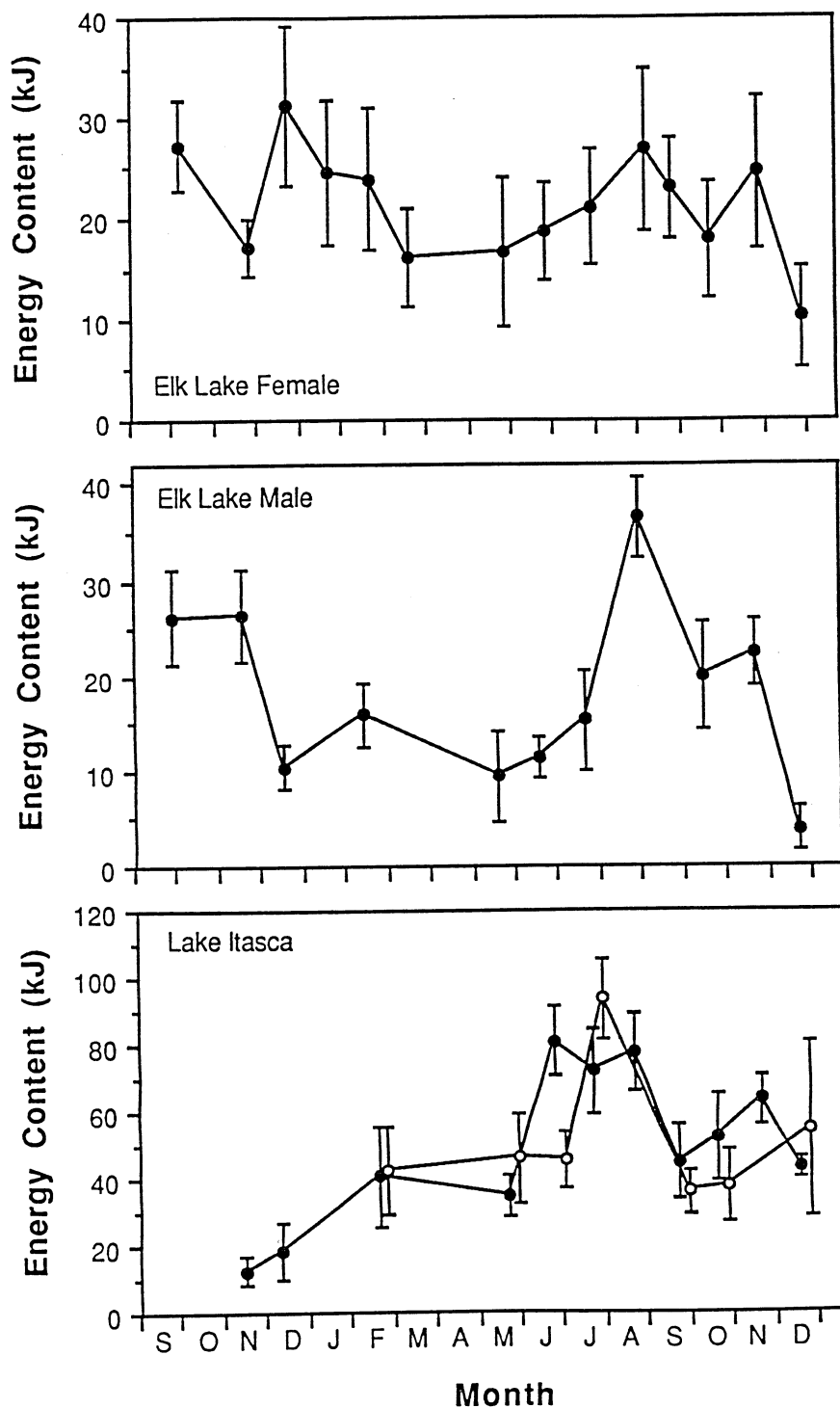
Figure 4.31. Seasonal variation in ventral fat deposit energy content of adult ciscos: Elk Lake females, top; Elk Lake males, center; Lake Itasca, bottom. Shown are means ± 1SE. For Lake Itasca, males are denoted by closed circles (-•-), females by open circles (-o-).
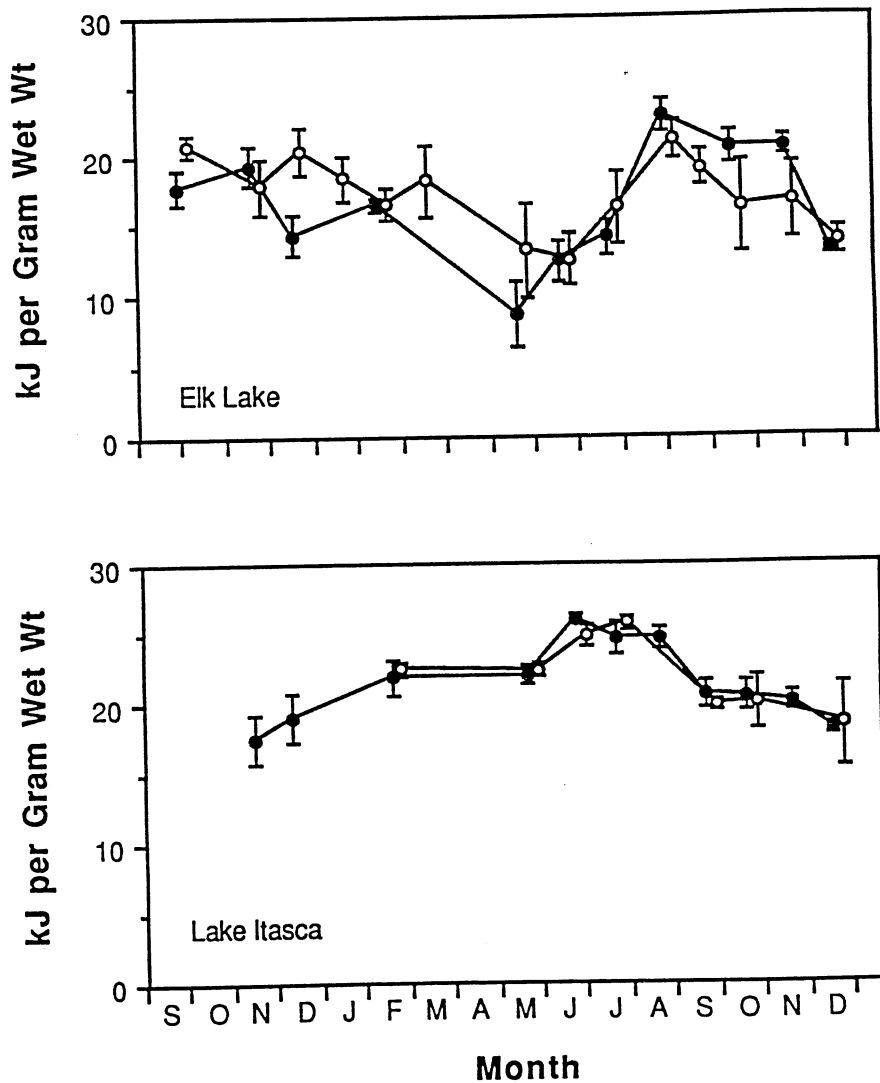
Figure 4.32. Seasonal variation in ventral fat deposit energy density in kJ g⁻¹ wet weight of adult ciscos: Elk Lake, top; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
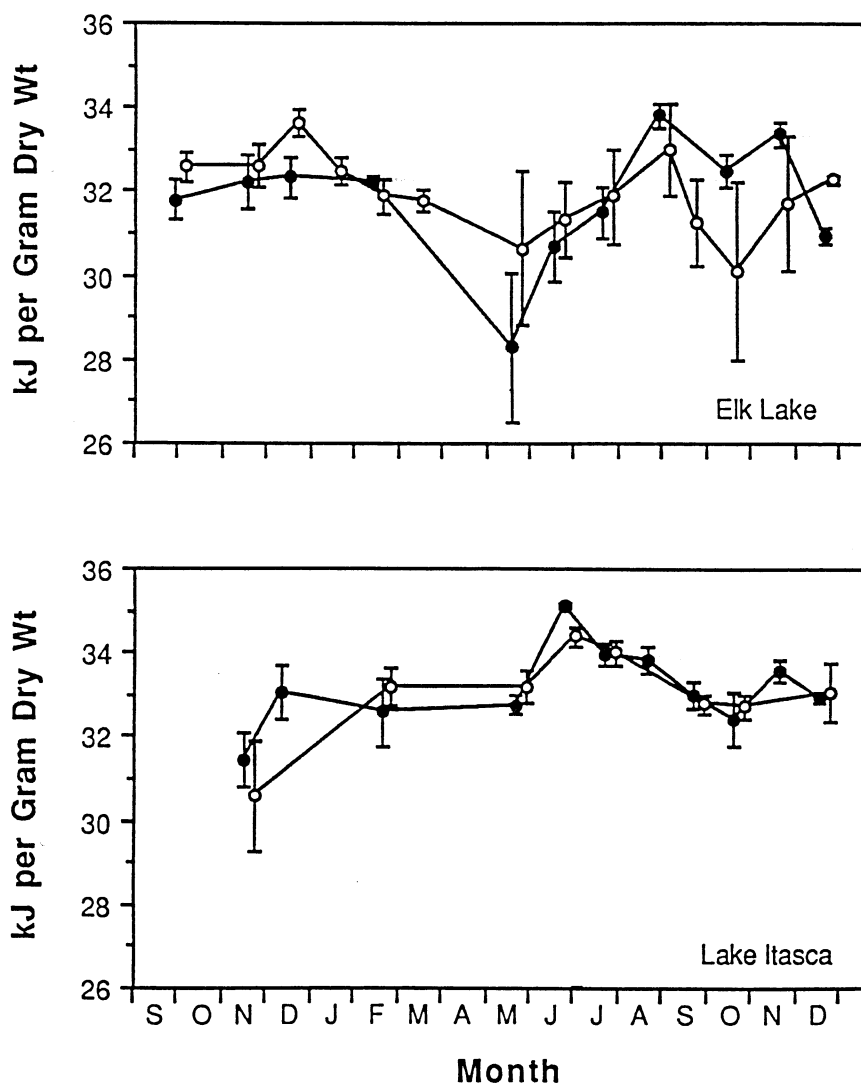
Figure 4.33. Seasonal variation in ventral fat deposit energy density in kJ g^{-1} dry weight of adult ciscos: Elk Lake, top; Lake Itasca, bottom. Shown are means ± 1SE. Males are denoted by closed circles (-•-), females by open circles (-o-).
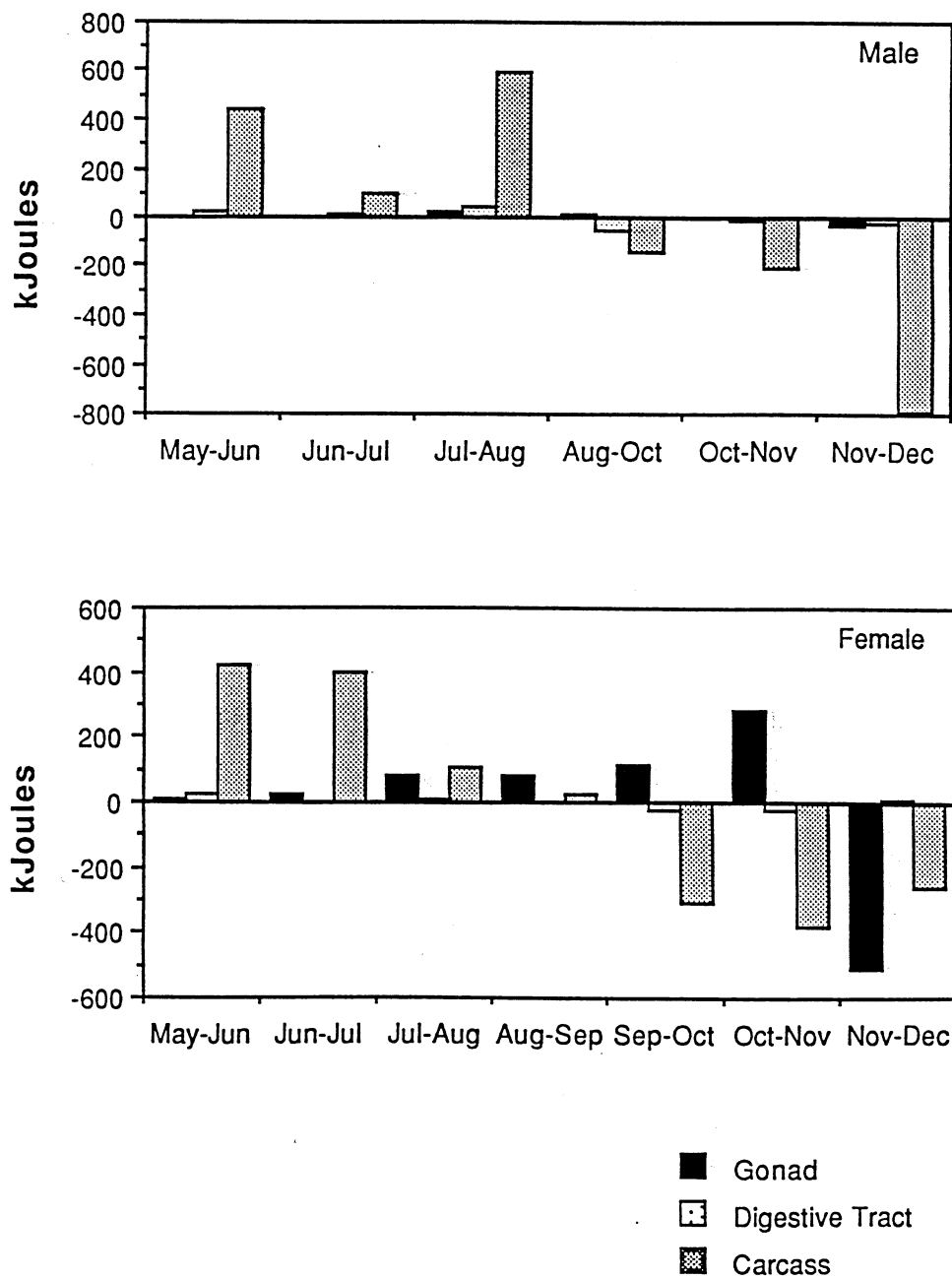
Figure 4.34. Mean net change in energy content of gonad, digestive tract, and carcass of ciscos from Elk Lake, from May to December, 1984. Males, top; Females, bottom.
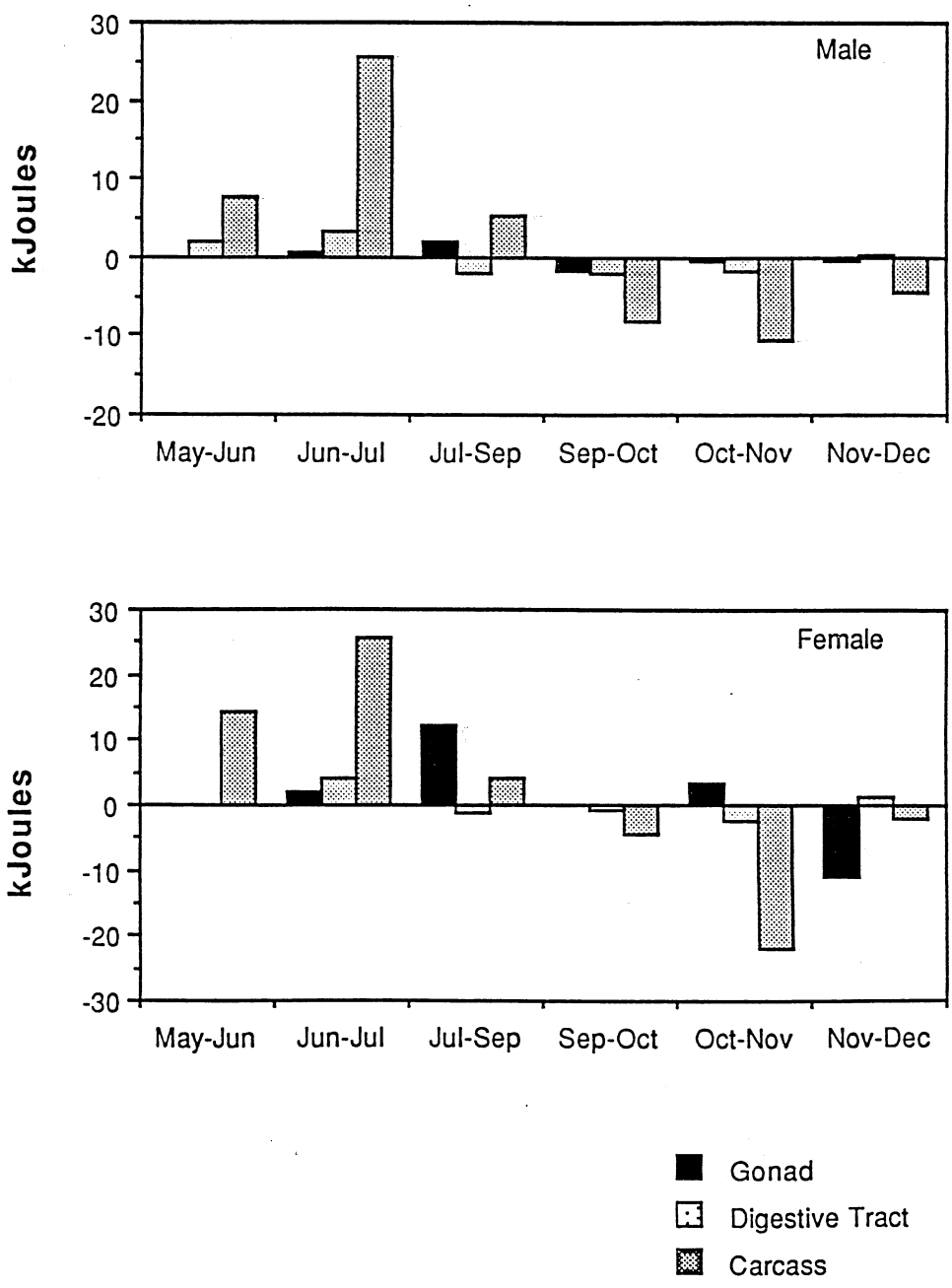
Figure 4.35. Mean net change in energy content of gonad, digestive tract, and carcass of ciscos from Ten Mile Lake, from May to December, 1984. Males, top; Females, bottom.
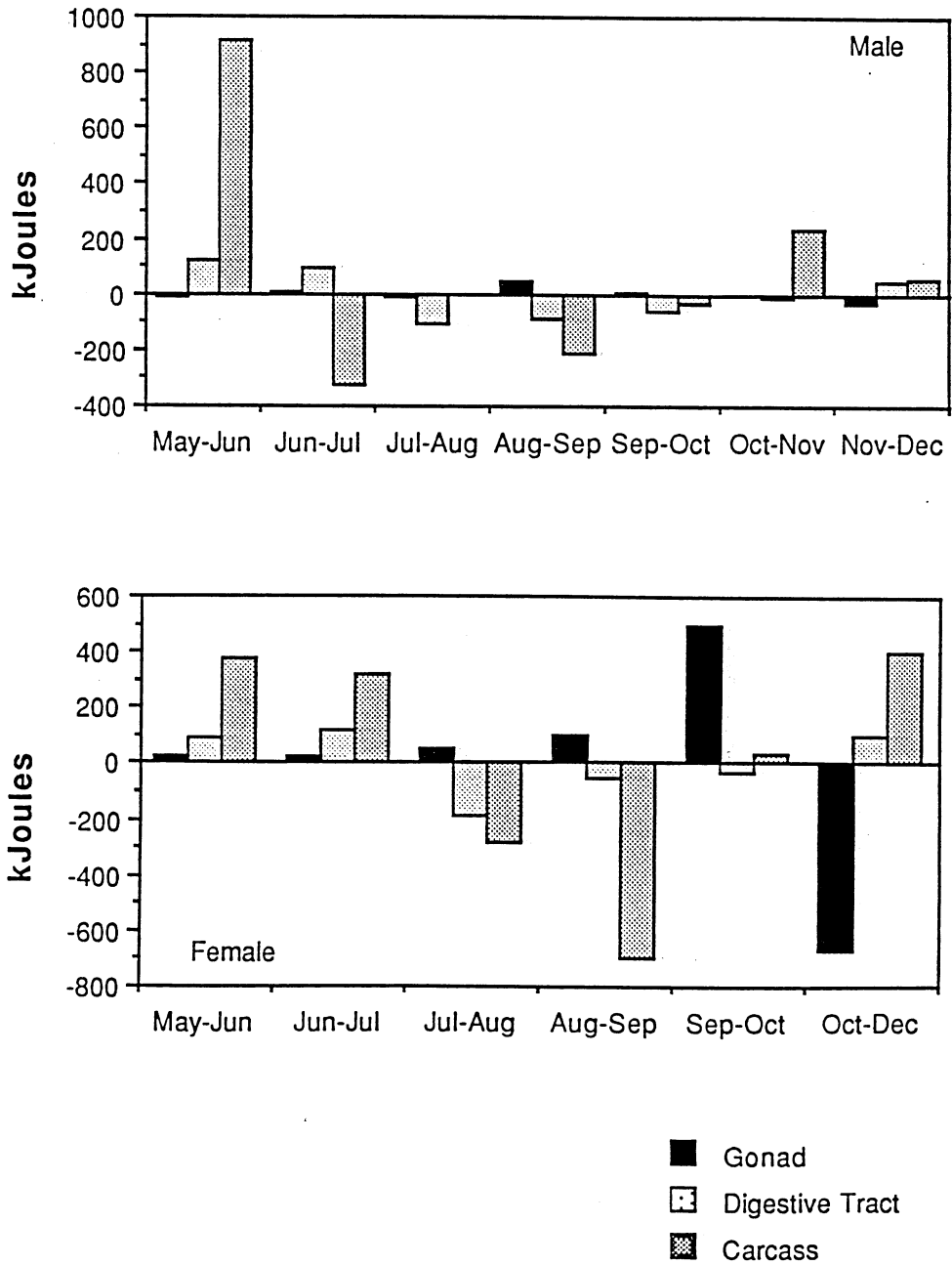
Figure 4.36. Mean net change in energy content of gonad, digestive tract, and carcass of ciscos from Lake Itasca, from May to December, 1984. Males, top; Females, bottom.

CHAPTER 5. CONCLUSION

A great deal of variation in growth was observed in the cisco populations studied. In this chapter an account of these differences is presented as well as a general consideration of the cycles of storage and depletion that accompany this plasticity. The relationships of these cycles to some aspects of cisco life history are discussed.

5.1. THE GROWTH OF CISCOS IN THE THREE STUDY LAKES:

The growth rates exhibited by the three populations studied represent the range observed for the species. These differences can largely be explained by current understanding of the effects of biotic and abiotic factors on fish growth. Of the factors that influence the growth of fishes the three most important are temperature, resource availability (ration size), and oxygen concentration, which may restrict the access of fish to certain areas and hence limit growth. The relationships of these factors to growth will be briefly discussed and inferences will be made regarding the general growth of fish from the study populations.

Temperature has long been acknowledged as an important factor influencing the growth of fishes. In field studies, the effects of temperature were often inferred or related to temperature regimes suitable for growth. For example, in a long-term study of

the perch of Lake Windermere, temperature, measured as degree-days over 14 °C, accounted for two-thirds of the year-to-year variation in growth rate (Le Cren, 1958).

The effects of temperature on growth have also been studied in the laboratory. Typically, at a given level of feeding, there is an optimum temperature, at which the growth rate is maximal. At temperatures that are either higher or lower than this temperature, growth is reduced. This type of relationship has been observed for several species, including sockeye salmon (Brett *et al.*, 1969), brown trout, *Salmo trutta* (Elliot, 1975a,b), largemouth bass (Niimi and Beamish, 1974), and bluntnose minnow, *Pimephales notatus* (Gill and Weatherley, 1984).

Oxygen may be limiting to growth if it falls below certain concentrations. There is a nearly linear increase in growth up to an oxygen concentration of about 4 to 5 ppm for several species. At concentrations above this level, no further improvement of growth occurs (Brett, 1979).

Following Rudstam and Magnuson (1985), the optimal temperature has been assumed to be approximately 12 °C for adult ciscos. This estimate may be low, as ciscos are probably the most temperature-tolerant of the coregonines. The upper temperature limit of adults may be presumed to be between 17 and 20 °C. Cahn (1927) showed that adult ciscos actively avoid temperatures in excess of 17 °C, and field observations of several authors (Fry, 1937; Frey, 1955; Nelson, 1970) suggest these

temperatures represent the upper part of their tolerance range. As in many species, the temperature tolerance of early life history stages is higher than that of adults. Edsall and Colby (1970) determined the upper lethal limit of juvenile ciscos to be 26 °C, while in larval stages the lethal temperature was 19.8 °C (McCormick *et al.*, 1971). Incredibly, the maximum growth rate of larval ciscos continued to rise almost to this temperature.

The temperature regimes experienced by the ciscos of the study lakes differed greatly. Throughout summer stratification in Elk Lake, a stratum of water with sufficient oxygen and at temperatures below the presumed upper limit for ciscos was always present. The fact that ciscos were caught at higher temperatures than would be predicted may be related to foraging patterns or to relatively low oxygen concentrations in the lower metalimnion. They may select a higher temperature with more available oxygen. It is perhaps noteworthy that depletion of energy stores began in August and September, when this situation occured.

In Lake Itasca, the effects of high temperatures on growth were obvious. During the midsummer months, a significant loss of body reserves occurred that was probably the result of increased metabolic demands incurred at these temperatures. Reduced summer growth in *C. pollan* was attributed to high water temperatures (Dabrowski, 1985). Low ambient temperatures during fall and winter did not preclude growth in

Lake Itasca fishes. The decline in growth in the latter half of winter may have been due to reduced oxygen concentrations in deeper waters, which may have limited foraging ability.

The observed depth distribution of Ten Mile Lake fish shows that they spend the entire growth season at temperatures between 7 and 8 °C, well below the predicted temperature. The empirical results of Brett *et al.* (1969) and Elliott (1975a,b) and the predictions of various models based on bioenergetics (Kitchell *et al.*, 1977; Sebens, 1987) indicate that temperature differences of relatively small magnitude can lead to large differences in growth rates and maximum sizes. The low temperatures inhabited by Ten Mile Lake fish probably contribute to their small maximum size.

The relation of ration size to growth has been studied in many species. Generally, the growth rate increases curvilinearly with ration size, reaching some maximum rate at satiation rations (Brett, 1979). The interaction of ration size and temperature is of particular interest. In studies on the sockeye salmon (Brett *et al.*, 1969) and brown trout (Elliott, 1975a,b), the optimal temperature for growth was observed to decrease with decreasing ration size. This occurs due to the relatively higher maintenance costs at higher temperatures, and suggests that at low levels of energy intake, fish can achieve maximum growth by moving into cooler waters.

In the current study, the relative availability of food has been inferred from data on nutrient conditions (phosphorus, conductivity, etc.) and productivity of lower trophic levels (chlorophyll *a*). As noted above, fish production has been correlated to lake productivity. Further, it has been demonstrated that lake fertilization may result in increased growth, as well as the enhancement of condition and increased production, in the closely related lake whitefish, *Coregonus clupeaformis* (Mills, 1985) and another salmonid, the sockeye salmon, *Oncorhynchus nerka* (Hyatt and Stockner, 1985). In both of these studies, the enhancement of growth was related to increases in prey items correlated with changes observed at lower trophic levels.

It is likely that the availability of food in the three study lakes follows the general order of productivity described earlier. Although zooplankton collections have not yet been enumerated, a rough comparison of samples from the three lakes was attempted by measuring the settled volumes of plankton in containers of equal diameter. When vertically integrated samples of the entire water column were compared, the zooplankton densities in Lake Itasca were at least an order of magnitude greater than those in Ten Mile Lake, and those in Elk Lake were approximately half as great as those in Lake Itasca. The location of prey in relation to that of the fish probably resulted in an even greater difference of food availability. As mentioned above, in at least two of the summer months, zooplankton in Ten Mile Lake

appeared to be more heavily concentrated in the metalimnion than in the hypolimnion, where the ciscos were found. In Elk Lake, the zooplankton are concentrated just below the thermocline during the months of lake stratification (Dr. Robert Megard, personal communication), and are available to the ciscos which are concentrated in the metalimnion. Ciscos in Lake Itasca appear to utilize the entire water column, even during periods of unfavorable thermal conditions. Chironomid midge larvae are found in the stomach contents of Lake Itasca ciscos when the hypolimnion is anoxic (Nelson, 1970 and personal observation). Differences in prey abundance are likely to be important in determining the observed difference in growth rates.

The type of prey available in the three study lakes is also likely to affect the growth rate of ciscos. The availability of larger prey items may result in improved foraging efficiency, and selection of larger prey has been demonstrated in several species, including the lake whitefish, *Coregonus clupeaformis*, which exhibited a preference for larger *Daphnia* in experiments conducted by Seghers (1975). Selection of larger prey has been shown to result in a greater energy intake per unit time in sunfish (summarized in Werner, 1984). Crowder (1981) quantified the costs and benefits of feeding on various sizes of prey for the bloater, *Coregonus hoyi*. Costs were lowest for the largest prey (*Mysis relicta*), and increased dramatically for small prey.

Nelson (1970) conducted a qualitative and quantitative study of the food habits of ciscos in Lake Itasca and Elk Lake. In the former lake, *Chaoberus* and *Chironomus* dominated the gut contents. Daphnids and *Leptodora* were the most common crustaceans, and although copepods were commonly encountered, they formed a small portion of the total volume of stomach contents. In Elk Lake, the items were similar, but *Leptodora* was more prominent, and *Chaoberus* may have contributed less to the total diet. However, in these fish there was much unidentifiable material, which he suggested may have been *Chaoberus*. They were readily apparent in many of the lake zooplankton samples and I have encountered them in the stomachs of many fish. The abundance of large prey items probably contributed to the good growth observed in these populations. The presence of a variety of organisms of various sizes, including small copepods, in the diets of these fish may reflect an abundant food supply. Mills *et al.* (1989) noted that at low ration levels, growth of 0-Age yellow perch was best when fed *Daphnia* that were within a restricted size range (1.4-1.8mm), whereas when rations were superabundant, no relationship of growth to prey size was observed.

The food habits of Ten Mile Lake cisco have not yet been studied. However, a qualitative inspection of lake zooplankton samples indicated that the diet of Ten Mile Lake ciscos must have been composed nearly entirely of small copepods (0.5-1.0 mm),

as these dominated all samples. Cladocerans were extremely rare, and when encountered, were small. The zooplankton community of Lower LaSalle Lake, another lake in the same region with a stunted population of ciscos, is also composed largely, if not entirely of copepods (personal observation). The lack of large prey items may restrict the growth of Ten Mile Lake fish. When large prey are rare, the advantages large fish have in searching for and handling prey diminish, and increased metabolic costs associated with larger size may outweigh them (Mittlebach, 1983). Using an energetics model for brook trout, Kerr (1971) concluded that trout must have access to increasingly larger prey in order to achieve large body size. Although in some cases small prey, including copepods, may provide more nutritional benefit than larger prey (Confer and Lake,1987), the low prey abundance and the predominance of small, elusive prey in Ten Mile Lake probably contribute to the slow growth observed. Further, these conditions may lead to the observed vertical distribution of Ten Mile Lake ciscos. The selection of a lower ambient temperature under conditions of limited resources was observed in juvenile sockeye salmon by Brett (1971), who suggested that growth could be maximized by the increase in conversion efficiency that resulted from decreased maintenance costs at low temperatures.

Finally, differences in population density may be involved in the different growth patterns of fish in the three study lakes. An inverse relationship of growth and density of ciscos and the

closely related lake whitefish has been observed in small lakes, where alterations of local conditions contributed to changes in density, and in populations exposed to commercial exploitation.

In four lakes in the northeastern highlands of Wisconsin, density was the only factor Hile (1936) found to be correlated with differences in growth. Rudstam (1984) studied some of the same lakes many years later, using the same type of sampling gear and methods as those used by Hile. He found that density had decreased and growth had increased. The decrease in density was presumed to be caused by an increase in predation on cisco by introduced piscivores (muskellunge, *Esox masquinongy* and walleye, *Stizostedion vitreum*). Clady (1967) found that growth of cisco increased in Birch Lake, Michigan, as density declined over a 20 year period. Similar responses of growth attributable to differences in density have also been observed in the congeneric lake whitefish. For example, Bidgood (1973) compared the whitefish populations in two eutrophic lakes. In one of the lakes, increased angling and the destruction of predator habitat that occurred with shoreline development resulted in decreased predator populations. He attributed the decline in size of whitefish in this lake to an increase in density that presumably resulted from decreased predation.

Changes in the growth of cisco associated with changes in density have also been observed in populations subjected to commercial exploitation. Carlander (1943) reported increased

growth increments in ciscos following increased exploitation in Lake of the Woods, Minnesota, and the changes in size of cisco in Lake Superior observed by Dryer and Beil (1964) were likely related to increasing exploitation that occurred in the fishery (Selgeby, 1982). Hoff and Serns (1983, cited in Rudstam, 1984) observed a decrease in growth of ciscos following a substantial decline in exploitation in Pallette Lake, Wisconsin.

An analyses of 14 exploited whitefish populations indicated that increased fishing pressure resulted in increased growth (Jensen, 1981). Healey (1980) experimentally subjected four populations of whitefish to different levels of exploitation. He observed that growth increased in the exploited populations and that the degree and persistence of the increase was proportional to the intensity of exploitation.

Attempts to estimate the size of the cisco populations by mark-recapture methods were not successful, either because of high mortality associated with the stress of capture and marking, (Elk Lake), or because too few marked individuals were recaptured to permit an estimation of abundance (Ten Mile Lake). However, a comparison of the number of fish caught per meter of net gives some insight into the relative densities of the populations. For each lake, only the mesh sizes to which adult fish were vulnerable were included. No attempt was made to correct for different catchabilities of the different meshes in each lake.

The most illuminating comparison was that of the month of August, 1984. In this month, the fish in Lake Itasca and Elk Lake were concentrated in a narrow depth stratum of water, and in a confined area of each lake. In both cases, fewer than one fish per meter of net were caught (0.52 and 0.85 fish per meter in Lake Itasca and Elk Lake, respectively). In Ten Mile Lake, the net was set at 28 m, near the mode of the depth frequency distribution. The catch per meter of net (33.3 fish) was nearly two orders of magnitude greater than in the other lakes. This probably underestimates the difference in density between this lake and the other two, as the fish in Ten Mile Lake were not nearly as concentrated in their depth distribution. In the vertical net, ciscos were caught over a depth range of 30 m. It is likely that the high density of this population results in intraspecific competition that leads to the stunted condition of the ciscos in this lake

5.2. SEASONAL CYCLES OF ENERGY ACCUMULATION AND DEPLETION:

The seasonal patterns of energy storage and depletion in several compartments of the cisco were examined in this study. Changes in the energy content of the liver are related to metabolic demands associated with feeding and the production of materials for gonadal formation and maturation. However, as it amounts to less than 2% of the total energy content of the fish at

a maximum, and does not appear to serve as a energy storage depot.

It has been shown that both the digestive tract and the carcass participate in the temporary seasonal storage of energy reserves. In the latter compartment, both muscle tissue and ventral fat deposits are involved. The stores associated with the digestive tract may be less essential and therefore utilized more readily than stores associated with the carcass. There was much greater variation between fish from the different lakes in peak energy densities of the digestive tract than of the carcass, and at the end of the year, following spawning, the visceral reserves in all three populations were rather completely depleted. In fish from Ten Mile Lake and Elk Lake, the depots of the digestive tract were utilized before those of the carcass, and also began to accumulate energy before the carcass near the end of the year. This suggests that stores associated with the digestive tract are more mobile than those of the carcass. They may be utilized to permit continued growth, as was observed in juveniles of Lake Itasca and Elk Lake, or to prevent the depletion of other somatic reserves, as was observed in adults from Lake Itasca. Reserves of both the digestive tract and carcass may be utilized during the formation of the gonads. Although most of this energy comes from the carcass, the digestive tract of males from Lake Itasca and Elk Lake contributed a significant portion of the total energy utilized during the time of formation of the testes.

A well defined seasonal pattern of energy storage and depletion was observed in fish of the three populations studied, in spite of differences in their growth rates. Although some important differences have been noted, the presence of a common general pattern, in both juveniles and adults, indicates the importance of the cycle itself, and one must conclude that it has some adaptive value. The overall similarity of the patterns of the observed cycles, in spite of the marked variation in growth, is consistent with the assertion that seasonal accumulation of energy and the subsequent depletion of tissues is part of a suite of adaptive traits that characterize the life history of a species (Iles, 1974). The seasonal energy dynamics of a species may be innate. There is evidence that this is true for the growth process. Underlying seasonal cycles of growth, perhaps stimulated by changing photoperiod, have been observed in brown trout and in four species of coregonines (Swift, 1955; Hogman, 1968). In these experiments, these cycles were not related to temperature or food availability.

However, the timing of the seasonal energy cycles suggest that the ultimate causes of the cycles may be related to food availability (Shul'man, 1974; Nikolskii, 1963). Energy storage is a means of transferring ecosystem productivity foraged at one point (in time or space) for expenditure at another (Pianka, 1976). Thus, the organism is effectively insulated from the

immediate effects of resource fluctuations and can maintain presumably optimal partitioning in the face of these fluctuations.

Lipids are the most common energy storage material. Carbohydrates constitute only a small fraction of total fish composition (Love, 1970) and more energy can be obtained per unit weight of lipid than of protein. Deposition of protein is also more costly than that of lipid (Jobling, 1985), and may represent a substantial portion of metabolic costs. That changes in lipid content were responsible for the cycles observed in the three populations is indicated by the fact that changes in energy density parallelled those of total energy content in the major storage organs. The temporary storage of lipids occurs at the expense of other synthetic processes, such as protein growth and the buildup of skeletal materials. Thus, there may be a cost in mortality and future fecundity associated with energy storage. However, without energy stores, starvation could occur if resource levels were insufficient to supply maintenance demands (Sibley and Calow, 1987). Depletion of energy stores has been implicated in winter mortality in brook trout (Cunjak et al., 1987) and yellow perch (Newsome and Leduc, 1975). The persistence of seasonal cycles of storage in the extremely slow-growing population of Ten Mile Lake suggests that they may serve to maintain somatic reserves at a certain level to prevent such depletion.

The amplitude of the cycles may depend on the magnitude of periodic energy demands, on the amplitude of fluctuations in the abundance of resources, or in the level of resource availability. Species that undergo extensive migrations, during which little or no food is taken, typically exhibit more pronounced changes in lipid (or energy) content than those that do not (Shul'man, 1974). Seasonal cycles of energy storage (as measured by energy density) in northern populations (Ohio) of gizzard shad, *Dorosoma cepedianum*, are more pronounced than those in southern populations in Texas (Pierce *et al.*, 1980; Fagan and Fitzpatrick, 1978). This is presumably because the more moderate climate of the south led to more constant availability of prey resources. Similarly, among five species of rockfish, the amplitude of fat cycles was greater in northern populations (Guillemot, *et al.*, 1985), where more restricted upwelling may lead to a more well-defined seasonal variation in food supply. Matsuk and Lapin (1972) observed greater seasonal variation in the proportion of fat in a population of Arctic char feeding on poorer resources (mollusks) than in a piscivorous one. Of two populations of brook trout, there was more depletion in the slower-growing population, which inhabited poorer waters (Nelson and McPherson, 1987).

In the cisco populations studied, the situation may be more complex. Variation in energy content and energy density of the carcass was greatest in Elk Lake fish, and values of the latter were lowest in this lake. This may be be related to the higher

reproductive effort, possibly associated with age, in these fish. Relative changes in fish of Ten Mile Lake and Lake Itasca, which were the same age, were similar despite the great difference in growth rates. It is possible that if the Lake Itasca fish did not undergo periods of thermal stress, the variation observed would have been greater. However, it is also possible that the appearance of a storage cycle would be swamped out by excess resources under a more favorable temperature regime. When one considers the digestive tract, the changes in energy density of the Lake Itasca fish are greater than in either of the other lakes.

Similarities in the seasonal cyles in all populations were evident, and the cycles persisted in their general form regardless of differences in growth rates. However, differences were observed, and have been related to local habitat conditions and differences between members of the three populations. Thus, it is difficult to make generalizations based on the current evidence. When populations are compared, habitats must be adequately described, fish should have similar reproductive histories, and distinctions between sites of energy storage should be made.

5.3. SEASONAL CYCLES AND REPRODUCTION:

Stored energy may be used for growth, maintenance, or reproduction. Most authors have stressed the importance of energy storage in relation to the reproductive cycle. Gonad

formation and maturation is generally a process with strict time limits that may require extensive expenditure. There may not be a significant connection between somatic energy storage and reproduction in some tropical and subtropical fish (DeVlaming, *et al.*, 1978; Hails, 1983). However, in most temperate zone fishes, the transfer of materials from somatic stores to the ovaries may be important in permitting the maturation of gonads and spawning to take place at a time that is appropriate for embryos and larvae even though food availability may be unfavorable for the adults (Wooton, 1979). Further, rapid somatic growth and ovarian development are often incompatible, and there tends to be a seasonal division between periods of growth and gonad (especially ovarian) development (Iles, 1974).

Energy not utilized for maintenance or activity, that is, surplus energy or energy available for production, can be used for either growth or reproduction. Thus, many authors assume that there is a direct trade-off between the two. Energy channelled into gonads at one point may detract from future fecundity, or may lead to increased mortality (Ware, 1982).

It is assumed that patterns of allocation of resources between reproduction and growth are responsive to selection and that differences in these patterns occur in ways that maximize fitness. In many fishes, the reproductive rate is sensitive to available energy (Ware, 1984). Several experimental studies have investigated the relationship of food supply and fecundity, or

some other meausre of reproductive output. The dry weight of eggs and total egg production in the haddock, *Melanogrammus aeglifinus*, increased with feeding levels (Hislop, *et al.*, 1978), and at reduced ration levels, there was a balance between somatic growth and reproduction. Similarly, in the winter flounder, ovarian development is sacrificed for maintenance of somatic tissue when rations are reduced (Tyler and Dunn, 1976). Studies of the brown trout and rainbow trout indicate that increased rations lead to improved growth and fecundity (Bagenal, 1969; Scott, 1962). Further, reduced rations resulted in smaller eggs, and lower dry weight, lipid, and protein content at the swim-up fry stage in the rainbow trout (Knox, *et al.*, 1988). Reduced rations also resulted in reduced offspring and reduced large and medium-sized oöcytes in the poeciliid, *Lebistes reticulatus* (Hester, 1964).

Direct comparisons with other studies is not possible, since fecundity of the ciscos in the study lakes was not determined. Nevertheless, the allocation of energy to reproduction differed between lakes, and appeared to be influenced by environmental conditions. However, the proportion of surplus energy allocated to production may be largely determined by age and previous reproductive history.

In Ten Mile Lake, where food resources were presumed to be low, allocation of energy input to the gonads and soma occurred concurrently. The major portion of gonadal growth was

supported from exogenous energy sources and input to the gonad ceased when the soma began to be depleted. Shortage of food may affect reproductive investment by restricting the recruitment of new oöcytes, as was observed in the winter flounder (Tyler and Dunn, 1976). This is consistent with observations on other coregonids. Egg maturation in the vendace, *Coregonus albula*, is asynchronous (Dlugosz and Worniallo, 1985) and the number of oöcytes recruited increased as the summer season progressed in *Coregonus lavaretus* (Fuller and Scott, 1976).

As in Ten Mile Lake, most of the growth of the gonads in Lake Itasca fish was supported largely from exogenous energy sources and took place during times when somatic growth was also occurring. Although food resources for ciscos in Lake Itasca were high, investment in reproduction may be limited by unfavorable summer temperatures. However, in spite of severe losses in somatic reserves during this period, some ovarian growth was maintained. The accumulation of energy reserves during the previous fall and winter led to high energy densities of the major storage depots, which may have permitted continued gonadal maturation in spite of otherwise unfavorable conditions. Some species of fish may forego reproduction in the face of food shortage or other stressful circumstances, and atresia of the gonads may occur. The evidence from the Ten Mile Lake and Lake

Itasca populations suggest that ciscos maintain some reproductive investment in spite of unfavorable circumstances..

Reproductive effort, estimated as the proportion of total annual production allocated to the gonads, was lower in ciscos from Ten Mile Lake and Lake Itasca than in those from Elk Lake. This may be a result of changing patterns of allocation with age. This is supported by the observation that in these two lakes gonadal growth is supported largely by exogenous energy sources, while in the older fish of Elk Lake, ovarian maturation occurred at the expense of somatic reserves. However, the differences in reproductive effort may have been the result of the earlier cessation of gonadal formation in the slow-growing fish of Ten Mile Lake, and the early depletion of stores in Lake Itasca fish caused by high summer temperatures. The lack of fish of similar ages from all populations precludes a conclusion on this matter.

Lifetime fecundity is also affected by the frequency of spawning and the age at first maturity. Ration size may influence the frequency of spawning in some fish. In the convict cichlid, *Cichlasoma nigrofasciatum*, higher rations led to an increased number of spawnings as well as to increases in fecundity and egg size (Townshend and Wooton, 1984). In the stickleback, *Gasterosteus aculeatus*, the effect of ration on fecundity was primarily exerted on the number of spawnings, whereas the

number of eggs per spawning depended on fish size (Wooton, 1979). In both of these cases, low rations resulted in severe depletion of somatic stores. In contrast to the situation described earlier for the winter flounder, the strategy observed in the stickleback was to maintain ovarian growth at the expense of somatic tissues. In this short-lived fish, mortality following the period of spawning is high. Mann *et al.* (1984) observed the reproduction of three species of fish from habitats of low and high productivity. The slower-growing populations in the former produced only one batch of eggs per year, while those in the latter produced several batches per year.

Non-annual spawning has been observed in coregonid populations that inhabit waters in the northern parts of their range (Kennedy, 1953; Power, 1978; Morin *et al.*, 1982). In Elk Lake, this may occur rarely and only in older fish. A few fish in poor condition were caught during the summer months that were not developing ovaries. In Ten Mile Lake, a few fish were caught in April that had ripe eggs in their ovaries. Apparently they had not spawned in the previous year and had not resorbed the eggs. However, similar fish were not encountered in the limited samples from subsequent months that were examined, which may indicate that this phenomenon is a rare occurrence. Further, several fish that were marked during the 1983 spawning run were recaptured during the run in the following year, suggesting

that these fish spawn annually. In a landlocked population of Arctic char in which fish do not breed annually, fish that were beginning to develop gonads in the spring had higher somatic caloric densities than fish that were not developing gonads, indicating that an energy deficit may preclude annual spawning (MacCallum and Regier, 1984). The fact that spawned ciscos in Ten Mile Lake did not show pronounced depletion of somatic reserves is consistent with the annual spawning of members of this population. Examination of remaining frozen and preserved samples that were not included in the present study may clarify these observations.

Direct costs associated with reproduction, such as depletion of somatic tissues, may lead to increased mortality, and thus affect lifetime fecundity. This is most obvious in semelparous fish such as Pacific salmon. It has been demonstrated that gonadectomized salmon do not degenerate (Calow, 1977). Adult fathead minnows (*Pimephales promelas*) that breed at age I have a lower survival rate than those that delay reproduction until the following year (Markus, 1934). Increased reproductive effort led to increased mortality in the medaka (Hirshfield, 1980). Some fish such as the American plaice and northern pike, may metabolize their own flesh (not just lipid reserves) to sustain reproduction (Roff, 1983; Diana and Mackay, 1979). In the former species, a condition known as "jellied flesh", that is characterized by an

extremely high water content, occurs in older fish and may be associated with increased mortality.

The carcass of Ten Mile Lake fish had the lowest energy density and the highest water content of the fish studied. They also appeared to have the shortest lifespan of the three populations. No fish older than age V were found. It is possible that depletion of somatic tissues following spawning in older fish are the cause of this decrease in longevity. The flesh of several old (greater than age VII) fish from Elk Lake had a peculiar consistency and tended to fall apart, even when fresh. These fish were not forming gonads, and this condition may represent severe depletion of body tissues. The caloric density of the carcass following spawning was lowest and the reproductive effort was highest, in adult fish in Elk Lake. These findings are consistent with the observations cited, that as reproductive effort increases with age, direct costs to survival may be incurred. It would be enlightening to see whether protein was utilized during the pre-spawning depletion in these fish.

The age at maturity may have a large effect on the lifetime fecundity of organisms and thus on the fitness of organisms. Considerable attention has been paid to the question of whether fish mature at a given age or at a given size. This is essentially a question of the relative importance of genetic and environmental factors in determining the age at maturity. Alm's (1959) extensive study presents evidence that suggest both are involved.

He concluded that when different strains or species (including coregonids) are compared, the smaller ones mature earlier, and the larger ones later, suggesting that genetic differences are involved. However, within a particular group, larger fish mature earlier. Further, he cites evidence that suggests that the degree of genetic determination may vary between species. Thus, in the transplantation experiments of Oloffson (1934) *Coregonus. albula* matured at the same age even though their growth rate had increased, but transplantation of *C. lavaretus* resulted in more rapid growth and earlier maturity (Svärdson, 1951). Others, such as Nævdal, *et al.* (1978), have observed that genetics plays a predominant role in the determination of age at maturity.

Many studies have indicated the importance of environmental effects on growth and age at maturity. For example, in brown trout (Bagenal, 1969; Scott, 1962) pumpkinseed, *Lepomis gibbosus*, (Deacon and Keast, 1987), and three species of fish studied by Mann *et al.* (1984), decreased age at maturity was associated with better food resources and better growth. Among coregonids, Svärdson (1951) found that transplanted *Coregonus albula* grew better and matured at an earlier age, and Miller (1956) found that a population of lake whitefish responded to exploitation by increased growth and earlier maturity. Perhaps the best illustration of the interaction of genetic and environmental factors in the determination of age at maturity are the studies on the platyfish, *Xiphophorus maculatus*,

summarized by Policansky(1983). In this fish, age at maturity is controlled by a single locus, with six alleles. However, for a given genotype, there is a range of ages and sizes at which maturity may occur.

Throughout their geographic range, ciscos exhibit a wide range of age at first maturity, from ages I to V or VI. In most populations, individuals become mature between II and IV. In Clear Lake, Wisconsin, most ciscos were mature during their second year of life (I). In Green Bay, Lake Michigan (Smith, 1956), Lake of the Woods, Minnesota (Carlander, 1943), Saginaw Bay, Lake Huron (Van Oosten, 1929), Lake Erie (Clemens, 1922) and Trout, Silver and Muskellunge Lakes, Wisconsin (Hile, 1936), most or all fish were mature at age II, and some fish were mature at age I in all lakes except Lake Erie. Some fish matured at age II and all were mature by the following year in Irondequoit Bay, New York (Stone, 1937) and Lake Oconomowoc, Wisconsin (Cahn, 1927). In Lake Ontario, fish began maturing at age II and most fish were mature by age IV. In Hudson Bay, a similar situation was described by Dymond (1933). In several Manitoba lakes, Bajkov (1930) found that most fish were mature by their fifth year (IV). At the northern extremes of their range, ciscos mature somewhat later. Most ciscos were mature in Great Bear Lake at the end of their fifth or sixth year (IV-V) and in the La Grande River in the James-Hudson Bay region at age VI (Morin et al, 1982).

The ciscos of the three study lakes probably mature at ages II-III. In Lake Itasca, all males and approximately 50% of the females were mature in their third year (age II). All were mature by age III. Although sample sizes for some ages (particularly II) were small for some months, it appears that a similar situation exists in Ten Mile Lake. Very few fish between the ages of I and V were caught in Elk Lake. All that can be said is that some females do mature at age II and others do not. The pattern and spacing of annuli on scales of Elk Lake fish through their fourth year was similar to that observed on scales of fish from Lake Itasca, which also suggests that maturity may be reached at a similar age. Admittedly, these data are not robust. Nevertheless, there does not appear to be any marked difference in the age at maturity in the three populations. One might conclude from this and the results of Hile (1936) that, at least within a restricted geographical area, ciscos mature at the same age, regardless of their rate of growth.

The effects of environmental limitations on the lifetime fecundity of ciscos act primarily by influencing annual reproductive investment. Longevity may also be limited in conditions of scarce resources. The age at maturity and the duration of the interspawning interval appear to be unaffected by varying environmental conditions.

SUMMARY

Seasonal patterns of energy accumulation and depletion were studied in three populations of the cisco, *Coregonus artedii*. Changes in wet and dry weight, total energy content, and energy density of the liver, digestive tract, gonad and carcass were examined over a sixteen month period, from September, 1983 to December, 1984. The patterns observed were related to age and habitat differences and the relationship of environmental differences to energy allocation to growth and reproduction were discussed.

1. THE CISCO POPULATIONS AND THEIR HABITATS:

The habitats occupied by the three populations were differed greatly and individuals from these populations exhibited very different growth rates. Lake Itasca is a large, shallow, eutrophic lake. The ciscos grow rapidly in this lake and reach a maximum length (SL) of 375 mm and a maximum weight of approximately 1500 g. They undergo a period of thermal stress for about two months during the summer. Die-offs of varying severity occur during this time. Elk Lake is a small, deep, meso- to meso-eutrophic lake. Ciscos reach lengths of about 310 mm and maximum weights of 550 g. No die-off occurs in this lake. Ten Mile Lake is a large, very deep, oligo- to oligo-mesotrophic lake.

The ciscos in this lake are extremely stunted, reaching a maximum length of 125 mm and a maximum weight of just 20 g.

In Lake Itasca, the hypolimnion becomes anoxic, and surface waters reach lethal, or near lethal, temperatures during the summer. Thus, ciscos are restricted to a very narrow stratum of water. In Elk Lake, ciscos are distributed throughout the water column until June. Throughout the remainder of the summer, they are restricted to the metalimnion at depths between 5 and 8 m. During much of this time, the temperature of the waters they occupy is near their preferred temperature. In Ten Mile Lake, ciscos occupy the entire water column throughout the winter. Around the time of ice-out, they migrate down to depths of 20-30 m, where they remain until the autumn. They spend the entire year at temperatures less than 7.5 °C.

2. SEASONAL ENERGY DYNAMICS OF TISSUES:

Tissues of both juveniles and adults were examined. Juveniles (Age I) were present in samples from all three lakes, from June to October, 1984. Adults were chosen from the predominant age or size class in each lake. In Lake Itasca and Ten Mile Lake, adults analyzed were from the cohort that reached Age III in 1984. All males and approximately half of the females in these lakes matured in the previous year, at Age II. In Elk Lake, most of the fish captured belonged to a single size class, from

270-300 mm SL. More than one cohort was represented in these samples and these fish were older than the adults from the other two lakes.

Distinct seasonal cycles of energy storage and depletion were observed in all fish, a fact which attests to the adaptive value of these cycles. Differences were attributed to age or environmental conditions, and are discussed below.

2.1. LIVER:

The energy content of the liver never exceeded 2% of the total energy content of the fish. Hence, it probably does not function as an energy storage tissue. In both Elk Lake and Ten Mile Lake adults, a pronounced increase in weight and energy content of the liver occurred at the beginning of the ice-free season. In Lake Itasca adults, the liver had markedly increased in weight and energy content during the previous winter. In males, a decrease in the energy content of the liver occurred later in the summer, during the time of formation of the testes. In females, a large increase in liver weight and energy content occurred prior to spawning.

In Ten Mile Lake and Lake Itasca females, this increase was accompanied by a decrease in energy density, probably associated with the process of vitellogenesis. In Elk Lake females, no such change was observed.

In juveniles, the weight, energy content and energy density increased, and then decreased from June to October.

2.2. GONAD:

Maturation of the testes occurred before that of the ovaries in adults from all lakes. The testes reached their maximum weight about one month before spawning in Elk Lake and Lake Itasca fish and two months prior to spawning in Ten Mile Lake fish. In females from Elk Lake and Lake Itasca, the major portion of ovarian growth took place by October, but increases in weight and energy content continued until spawning, in November. In Ten Mile Lake females, most of the growth of the ovaries was complete by September, nearly two months before spawning. The growth of ovaries was somewhat more gradual in Elk Lake fish than in fish from the other lakes. Gonadosomatic indices at the time of spawning were similar for fish from all lakes.

A decrease in the energy density of the ovaries was observed in Lake Itasca and Ten Mile Lake ciscos prior to spawning, suggesting that deposition of yolk proteins occurred at this time. In Elk Lake fish, no decrease in energy density was noted. The observations that the ovaries develop more gradually in Elk Lake fish, and that no decrease in energy density occurred prior to spawning in either the liver or the ovaries suggest that the process of vitellogenesis is moderated with age.

The energy density of the ovaries of Ten Mile Lake fish was significantly lower than that of fish from the other lakes.

Among juveniles, the ovaries were larger, and grew more, than the testes in all lakes.

2.3. DIGESTIVE TRACT:

The digestive tract serves as a temporary energy storage depot in ciscos, comprising up to 10% of the total energy content of the fish. The weight and energy content of the digestive tract increased from the beginning of the open-water season in juveniles and adults from all three lakes. These deposits were subsequently depleted by October. Similar changes in energy density were observed. The peak energy density of the digestive tract of Lake Itasca fish was nearly twice that of the other fish.

In Elk Lake females, the increase in energy content was of short duration. This was probably related to the earlier utilization of energy for the formation of the ovaries. In Lake Itasca fish, the decline in energy content began with the onset of summer thermal stress, somewhat earlier than in fish from the other two lakes. There was some evidence that energy was stored in the digestive tract during the first half of the winter in all three populations.

In juveniles from Elk Lake and Lake Itasca, similar patterns of increase in energy stores followed by depletion were observed. In Ten Mile Lake juveniles, no depletion had occurred by October.

The energy stores of the digestive tract may be used preferentially, and may serve to either permit continued growth of other body tissues or prevent their depletion. They were completely utilized by late autumn in all fish except juveniles from Ten Mile Lake.

2.4. CARCASS:

The carcass of ciscos also exhibits a seasonal pattern of energy accumulation and depletion. In all populations, an increase in weight and energy content began in May, at the beginning of the ice-free season. Energy stores were then utilized, leading to depletion by the end of the year. In both Lake Itasca and Ten Mile Lake fish, a net gain in energy content occurred, whereas, in Elk Lake fish, all energy stores were utilized. Depletion of carcass energy stores began earliest in Lake Itasca fish, at the time of summer temperature stress. A marked increase in the energy content of Lake Itasca fish occurred during the winter.

The energy density of the carcass of Elk Lake fish was the same at the end of the year, following spawning, as at the beginning of the ice-free season. In Ten Mile Lake fish, the energy density was higher, and in Lake Itasca fish, lower, at the end of the season. Nevertheless, the peak energy density of the carcass was highest in Lake Itasca fish. The energy density of the carcass was lowest, and the water content highest, in Ten Mile

Lake fish. These conditions may lead to reduced longevity in this population.

Energy storage depots of the carcass include both the muscle and ventral fat deposit.

3. SEASONAL ENERGY CYCLES AND REPRODUCTION

Most of the energy for the maturation of the gonads of ciscos from Ten Mile Lake and Lake Itasca came from exogenous sources, whereas in Elk Lake fish, especially females, body energy stores were depleted during gonadal formation. In both males and females from Elk Lake a much greater proportion of total annual production was invested in reproduction. These differences may have been the result of the differences in ages of the fish.

Under conditions which lead to slow growth (Ten Mile Lake), gonadal production ceased early. Spawning also occurred earlier than in the other lakes. This may serve to prevent excessive depletion of other body reserves. Gonadal production in Lake Itasca fish may be limited by unfavorable summer thermal conditions, as a large portion of energy reserves were utilized during this time. Under more favorable conditions, such as those that exist in Elk Lake, the formation of the gonads was more gradual.

The major differences in lifetime fecundity between the three populations are due to differences in annual gonadal production and longevity. Annual fecundity is related to size and Ten Mile Lake ciscos have shorter life spans than fish from the other populations. Age at maturity and the inter-spawning interval appeared to be similar in the three populations.

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APPENDICES

Appendix A.1. Volume of Depth Strata in Study Lakes

Depth Strata (m)	Volume (m^3)		
	Ten Mile Lake	Elk Lake	Lake Itasca
0-3.05	52,745,064	2,991,261	11,693,888
3.05-4.57	22,284,322	1,274,031	4,568,759
4.57-6.096	20,063,480	1,203,950	3,548,669
6.096-9.14	36,685,876	2,048,628	3,334,564
9.14-12.19	32,485,201	1,497,002	424,946
12.19-15.24	28,827,062	864,797	17,621
15.24-18.29	25,156,897	70,152	(13.72 m)
18.29-21.34	21,827,005	402,441	
21.34-24.38	17,984,219	271,373	
24.38-27.43	15,352,005	118,309	
27.43-30.48	11,933,700	8,923	
30.48-33.53	9,313,077	(29.57m)	
33.53-36.58	6,686,824		
36.58-42.67	4,413,716		
42.67-48.77	2,212,080		
48.77-54.86	869,703		
54.86-60.96	252,752		
60.96-63.39	7,895		
Total vol (m^3)	309,100,878	10,750,866	23,588,448

Appendix A.2. Temperature (°C) Profiles of Lake Itasca.

Date	Aug 25	Sept 25	Nov 4	Jan 11	Feb 8	Mar 8	Apr 4	Apr 26	May 17	Jun 20	Jul 18	Aug 15	Sept 14	Oct 9	Nov 9	Dec 10
Depth (m)																
0	26	14	7	0	0.5	0	1	10	13	21.5	24	24.5	16.5	12.5	2.8	1
1	25.5	14	7	1	1	1.5	4.5	10	12.8	21.5	23.5	24.5	16.5	12.5	2.8	2.5
2	24	14	7	1.5	2	2.5	4.5	10	12.7	21.5	23.5	24.5	16.5	12.5	2.8	2.8
2.5																
3	23.5	13.5	7	1.5	2.5	2.5	4	9.25	12.5	20.5	23	24.5	16.3	12	2.8	2.8
3.5																
4	23	13.5	7	2	2.5	2.75	4	8.25	12.5	20	22	24.5	16.3	12	2.8	2.8
4.5																
5	23	13	7	2.5	3	3	4	6.5	12.3	19.5	22	24	16	11.5	2.5	3
5.5												22				
6	22	13	7	2.75	3.25	3.5	4	6.25	12.1	18.5	21.5	21.5	16	11.5	2.5	3
6.5												20.5				
7	20.5	12.5	7	3	3.5	3.5	4	5	12	17.5	19	20	16	11.5	2	3.5
7.5											17.5	18.5				
8	18	12.5	7	3	4	3.5	4	4.75	12	15.5	17.5	18	16	11.5	2	3.5
8.5											15	17				
9	15.5	12.5	7	3	4	3.5	4	4.5	10	13.5	14	15	15.5	11.5	2	3.5
9.5											13	14	15			
10	13	12	7	3	4	3.5	4	4.5	9.6	11.5	12.5	13	14	11.5	3	3.5
10.5											11.5	12.5	13			
11	11.5	12	7	3.5	4	3.5	4	4.25	9.2	10.5	10.5	12	11.5	11.5	3	3.5
11.5												11	11.5			
12	11	12	7	4	4	4	4.5	4.25	9	10.5	10.5	11	10.5	11.5	3	3.5
13				4.5	5	5	5		9		10	10.5	10.5			4.5
13.5					5								10.5	11.5		

Appendix A.3. Dissolved Oxygen (mg/l) Profiles of Lake Itasca.

Depth (m)	Aug 25	Sept 25	Nov 4	Jan 11	Feb 8	Mar 8	Apr 4	Apr 26	May 17	Jun 20	July 18	Aug 15	Sept 14	Oct 9	Nov 9	Dec 10
0	10	8.5	11.6	11.2	8.5	7.7	9.6	12.9	10.6	8.9	7.7	8.6	8.2	9.7	12.6	14.3
1	9	8.1	11.1	11.2	8.2	7.1	5.7	13	11.1	8.9	7.7	8.6	8.2	10	12.6	14.1
2	8.4	7.8	10.8	11.2	7.5	6.1	4.9	12.8	11.3	9	7.7	8.6	8.2	10	12.6	14.1
2.5																
3	8.1	7.8	10.6	11.2	6.7	4.6	3	12	11	8.9	7.7	8.5	8.2	10	12.6	14.1
3.5																
4	6.5	7.9	10.6	8.6	5.8	3.7	1.9	9.4	11	8.3	7.4	8.5	8	9.5	12.6	14.1
4.5																
5	4.5	7.7	10.4	6.6	2.6	1.9	1.15	6.6	11	5.9	7.1	4.7	7.9	8	12.5	7.8
5.5												0.6				
6	1.1	7.7	10.4	4.4	2.2	0.6	0.7	5.7	10.8	3.85	6.8	0.4	7.6	7.4	12.6	8.4
6.5												0.3				
7	0.15	7.7	10.4	2.6	0.3	0.25	0.3	1.7	10.8	1.8	0.5	0.3	7.5	7	12	7
7.5												0.3				
8	0	7.7	10.3	1.2	0.2	0.2	0.5	1.5	10.8	0.65	0.4	0.2	7.4	7.2	12	7.3
8.5												0.2				
9	0	7.7	10.3	1.2	0.8	0.2	0.1	1.2	8	0	0.4	0.2	7.1	7.2	11.6	3.3
9.5												0.2	1.4			
10	0	7.7	10.2	1.2	1.3	0.2	0.1	1	7.9	0	0.4	0.2	0.3	6.9	10.6	1.2
10.5												0.2	0.3			
11	0	7.7	10.2	0.25	0.4	0.2	0.1	0.8	7.8	0	0.4	0.2	0.3	5.8	10.4	0.2
11.5												0.2	0.3			
12	0	7.7	10	0.1	0.3	0.2	0	0.2	7		0.35	0.2	0.3	3.8	10.2	0.2
13	0			0.05	0.2	0.2	0		7		0.35	0.2	0.3	2.7		0.2
13.5	0				0.2											

Appendix A.4. Temperature (°C) Profiles of Elk Lake.

Date	Aug 8	Sept 26	Nov 13	Jan 13	Feb 9	Mar 9	Apr 3	May 2	May 20	Jun 13	Jul 11	Aug 23	Sept 11	Oct 6	Nov 12	Dec 12
Depth (m)																
0	26.5	16	6.2	0.5	0.5	0.5	0.5	6	13	19	23.5	22	16.5	12	4	2
1	26.5	15	4	1	1	1	3	5.5	12.5	19	23.5	22	16.5	12	4	3
2	26.5	14	4	1	1.5	2	3	5.5	12.5	19	23	22	16.5	12	4	3
3	26.5	13.5	4	1	1.75	2	3	5.5	12.5	18.5	22.5	22	16.5	12	4	3
4	26.5	13.5	4	1	1.75	2	3	5.5	12	18.5	22	22	16.5	11.5	4	3
5	22.5	13.5	4	1.5	2	2	3	5.5	11	18.5	21	21.5	16.5	11.5	4	3
5.5												21.5	16.5	11.5	4	3
6	19	13	4	1.5	2	2	3	5.5	10.5	14	17	19.5	16.5	11.5	4	3
6.5												18.5	16.5	11.5	4	3
7	15.5	13	4	2	2	2.25	3	5.5	10	11.5	13.5	15.5	16.5	11.5	4	3
7.5												14	16	11.5	4	3
8	13	13	4	2	2.5	2.5	3	5.5	9.5	10	10.5	13.5	15	11.5	4	3
8.5												11.5	13	11.5	4	3
9	11	13	4	2	2.5	2.5	3	5.5	9	9	9.5	11.3	11.5	11.5	4	3
9.5												10	10	11.5	4	3
10	9	11	4	2	2.5	2.5	3	5.5	8.5	8	8.5	9	9.5	11.5	4	3
10.5												8.9	8.5	11.5	4	3
11	8	9	4	2	2.75	2.75	3	5.5	7.5	7.5	8	8.5	8.5	11.5	4	3
11.5												8	8	10	4	3
12	7.5	8	4	2.5	2.75	2.75	3	5.5	7.5	7.5	7.5	8	8	8.5	4	3
12.5														8	4	3
13	7	7.5	4	2.5	2.75	2.75	3	5.5	7	7.5	7.5	8	8	8	4	3
14	7	7.5	4	2.5	2.75	2.75	3	5.5	7	7.5	7.5	8	7.75	7.5	4	3
15	7	7.5	4	2.5	2.75	2.75	3	5.5	7	7.5	7.5	7.5	7.5	7.25	4	3
16	7	7.5	4	2.5	3	2.75	3	5.5	7	7	7.5	7.5	7.25	7	4	3
17	7	7.5	4	2.5	3	3	3	5.5	7	7	7	7	7	6.5	4	3
18	7	7.5	4	2.5	3	3	3	5.5	7	7	7	7	7	6.5	4	3
19	7	7.5	4	2.5	3	3	3	5.5	7	6.5	6.5	6.5	6.5	6.5	4	3
20	7	7.5	4	2.5	3	3	3	5.5	6.5	6.5	6.5	6.5	6.5	6.5	4	3
21	7	7.5	4	2.5	3	3	3	5	6.5	6.5	6.5	6.5	6.5	6.5	4	3
22	7	7.5	4	2.5	3	3	3	5	6.5	6.5	6.5	6.5	6.5	6.25	4	3
23	7	7.5	4	2.5	3	3	3	5	6.5	6.5	6.5	6.5	6.5	6	4	3
24	7	7.5	4	2.5	3.25	3	3.25	4.5	6.5	6.5	6.5	6.5	6.5	6	4	3
25	7	7.5	4	2.5	3.25	3	3.5	4.5	6.5	6	6.5	6.5	6.5	6	4	3
26	7	7.5	4	2.5	3.25			4	6.5	6	6.5	6.5	6.5	6	4	3
27	7	7.5	4	2.5	3.25					6	6.5	6.5		6		3.5
28	7	7.5	4	2.5	3.25							6.5		6		3.75
29	7	7.5	4	2.5	3.25							6.5				
29.5	7	7.5	4	2.5	3.25							6.5				

Appendix A.5. Dissolved Oxygen (mg/l) Profiles of Elk Lake.

Date	Aug 8	Sept 26	Nov 13	Jan 13	Feb 9	Mar 9	Apr 3	May 2	May 20	Jun 13	Jul 11	Aug 23	Sept 11	Oct 6	Nov 12	Dec 12
Depth (m)																
0	8.9	8.6	8.2	11	9.5	9.2	9	9.5	12.5	9.4	9.1	8.2	8.25	9.2	10.6	12
1	8.5	8.5	8.1	10.6	8.9	8.9	8	9.5	12.6	9.4	9.1	8.15	8.4	9.2	10.4	12
2	8.6	8.5	8.3	10.4	8.5	8.3	7.7	9.4	12.7	9.4	9.4	8	8.4	9.2	10.2	12
3	8.4	8.5	8.2	10.2	8.3	8.2	7.6	9.3	12.7	9.3	9.7	8	8.4	9.2	10.2	12
4	8.6	8.4	8.2	9.6	8.2	8.1	7.6	9.3	12.7	9.3	9.4	8	8.4	9	10	12
5	7.5	8.2	8.1	9.2	8.1	8	7.6	9.2	12.4	9.3	8.9	7.8	8.3	8.9	10	12
5.5												7.7				
6	4.4	8.2	8.1	9	7.7	7.8	7.4	9.1	12.1	9.7	8.3	5.9	8.2	8.5	10	12
6.5												5.5				
7	2.05	7.9	8.1	8.6	7.4	7	7.5	9	11.7	7.8	5.9	4.45	7.85	8.4	10	12.2
7.5												3.6	5.6			
8	0.8	7.5	8.1	8.4	7.2	6.9	7.5	8.8	11.4	5.3	3.1	1.9	2.1	8.35	10	12.2
8.5												1	0.3			
9	0.7	7.2	8.2	8.3	7	6.1	7.6	8.8	10.8	3.95	1.7	0.5	0.3	7.8	9.8	12.1
9.5												0.3	0.25			
10	0.2	2.75	8.2	8	6.6	5.6	7.6	8.8	10.4	3.55	0.9	0.3	0.25	7.3	9.8	11
10.5												0.3	0.25			
11	0.15	0.25	8.2	7.7	6.4	5.3	6.5	8.8	9.6	3.2	0.6	0.25	0.25	6.8	9.8	10.5
11.5												0.25	0.25	1.8		
12	0.15	0.2	8.2	7.6	6.2	5	4.55	8.75	9.5	3.1	0.35	0.25	0.25	0.3	9.8	10.4
12.5													0.25			
13	0.15	0.2	8	7.4	5.9	4.7	3.65	8.75	9.4	3	0.35	0.25	0.25	0.25	9.8	10.4
14	0.15	0.2	8	7.2	5.7	4.5	3.3	8.65	9	3	0.35	0.25	0.25	0.2	9.8	10.1
15	0.15	0.2	8	7.2	5.4	4.35	3.1	8.5	9	3.05	0.55	0.25	0.25	0.2	9.8	10.1
16	0.15	0.2	8	7.2	5.2	4.3	2.6	8.5	9	3	0.7	0.25	0.2	0.2	9.8	10
17	0.15	0.2	8	7.2	4.4	4	2.15	8.5	9	3.05	0.8	0.25	0.2	0.2	9.8	10
18	0.15	0.2	8	7.2	4	3.55	2.3	8.4	8.6	3.05	0.8	0.25	0.2	0.2	9.8	9.9
19	0.15	0.2	8	7.2	3.5	3.2	2.05	8.4	8.7	2.8	0.4	0.25	0.2	0.2	9.7	9.9
20	0.15	0.2	8	7.2	2.75	2.7	2	8.1	8.5	2.9	0.4	0.25	0.2	0.2	9.7	9.8
21	0.15	0.2	8	7.2	2.35	1.95	1.1	7.5	8.4	2.65	0.25	0.25	0.2	0.2	9.7	9.6
22	0.15	0.2	8	7.2	1.95	1.3	0.7	7.2	8.3	2	0.2	0.25	0.2	0.15	9.7	9.3
23	0.15	0.2	8	7.2	1	0.6	0.35	6.7	8.1	1.45	0.15	0.25	0.2	0.15	9.7	8
24	0.15	0.2	8	7.2	0.7	0.25	0.2	5.4	7.8	1.3	0.15	0.25	0.2	0.15	9.7	6.3
25	0.15	0.2	8	7.2	0.7	0.15	0.1	4.7	7.2	0.4	0.15	0.25	0.2	0.15	9.7	4.2
26	0.15	0.2	8	7.2	0.95			3.4	7.2	0.3	0	0.25	0.2	0.15	9.7	1.6
27	0.15	0.2	8	7.2	0.35					0.05	0	0.2		0.15		0
28	0.15	0.2	8	7.2	0.25							0.2		0.15		0
29	0.15	0.2	8	7.2	0.25							0.2				
29.5	0.15	0.2	8	7.2	0.25							0.2				

Appendix A.6. Temperature (°C) Profiles of Ten Mile Lake.

Date	Sept 26	Feb 4	Mar 4	Mar 5	Mar 31	May 3	June 9	July 5	Aug 9	Sept 4	Oct 1	Nov 6	Nov 26
Depth (m)													
0	13.3	0	1	0	1	7.5	17.5	21	24	19	12	6	3
1	13.3	1	2	2.5	3.5	6.5	16.5	21	24	19	12	6	3
2	12.4	2	2.8	3.3	3.5	6	16.5	21	24	19	12	6	3
3	12.4	2	2.8	3.3	3.5	6	16.5	21	24	19	12	6	3
4	12.4	2	2.8	3.3	3.5	5.5	16	21	24	19	12	6	3
5	12.1	2	2.8	3.3	3.5	5.5	16	21	24	19	12	6	3
6	12.1	2	2.8	3.3	3.5	5.5	16	21	24	19	12	6	3
7	12.1	2	2.8	3.3	3.5	5.5	16	21	24	19	12	6	3
8	12	2.5	2.8	3.3	3.5	5	16	21	23	19	10	6	3
9	12	2.5	2.8	3.3	3.5	5	15.5	17.5	21	19	10	6	3
10	12	2.5	3	3.3	3.5	5	13.5	16	18.5	19	10	6	3
11	12	2.5	3	3.3	3.5	5	12.5	13.5	16.5	19	10	6	3
12	12	2.5	3	3.3	3.5	5	11	12	14	18	10	6	3
13	12	2.5	3	3.3	3.5	5	9.5	10.5	13	14	10	6	3
14	11.5	2.5	3	3.3	3.5	5	9	10.5	11.5	12	10	6	3
15	10.2	2.5	3	3.3	3.5	5	8.5	9.5	10.5	10	10	6	3
16	8	2.5	3	3.3	3.5	5	8	8	10	9	10	6	3
17	7.2	2.5	3	3.3	3.5	5	8	8	9	8.5	9	6	3
18	7.1	2.5	3	3.3	3.5	5	7.5	8	8.5	8.5	6	6	3
19	7	3	3	3.3	3.5	5	7.5	7.5	8	8	5	6	3
20	7	3	3	3	3.5	5	7	7.5	8	8	5	6	3
21	7	3	3	3	3.5	5	7	7.5	7.5	7.5	5	6	3
22	7	3	3	3	3.5	5	7	7.5	7.5	7.5	5	6	3
23	7	3	3	3	3.5	5	7	7.5	7.5	7.5	5	6	3
24	7	3	3	3	3.5	5	7	7.5	7.5	7.5	5	6	3
25	6.7	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
26	6.7	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
27	6.7	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
28	6.7	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
29	6.7	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
30	6.6	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
31	6.6	3	3	3	3.5	5	7	7	7.5	7.5	5	6	3
32	6.6	2	3	3	3.5	5	7	7	7.5	7.5	5	6	3
33	6.6	1.5	3	3	3.5	5	7	7	7.5	7.5	5	6	3
34	6.6	0.5	3	3	3.5	5	7	7	7.5	7.5	5	6	3
35	6.6	0.5	3	3	3.5	5	7	7	7.5	7.5	5	6	3
36	6.6	0.5	3	3	3.5	5	7	7	7.5	7.5	4.8	6	3
37	6.6	0.5	3	3	3.5	5	7	7	7.5	7.5	4.8	6	3
38	6.6	0.5	3	3	3.5	5	7	7	7.5	7.5	4.8	6	3
39	6.6	0.5	3	3	3.5	5	7	7	7.5	7.5	4.8	6	3.5
40	6.5	0.5	3	3	3.5	5	6.5	7	7.5	7.5	4.8	6	
41	6.5	0.5		3	3.5	5	6.5	7	7.5	7.5	4.8	6	
42	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8	6	
43	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8	6	
44	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8	6	
45	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8	6	
46	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8	6	
47	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8		
48	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8		
49	6.5	0		3	3.5	5	6.5	7	7.5	7.5	4.8		
50	6.5	0		3	3.5		6.5	7	7.5	7.5	4.8		

Appendix A.7. Dissolved Oxygen (mg/l) Profiles of Ten Mile Lake.

Date	Sept 26	Feb 4	Mar 4	Mar 5	Mar 31	May 3	Jun 9	Jul 5	Aug 9	Sept 4	Oct 1	Nov 6	Nov 26
Depth													
0	11	9.6	11	14.4	10.5	12.4	9	8.4	7.7	8.3	9.5	10.8	12.5
1	11	10.6	11.9	14	11.6	12.5	9	8.5	7.7	8.2	9.2	10.6	12.5
2	11	10	11.6	14	11.7	12.7	9	8.5	7.7	8.2	9.3	10.6	12.5
3	11	10	11.5	14.1	11.6	12.6	9.2	8.4	7.6	8.2	9.3	10.6	12.5
4	11	9.4	11.4	14.2	11.6	12.7	9.4	8.4	7.6	8.2	9.2	10.6	12.5
5	11	9	11.4	14.2	11.6	12.7	9.4	8.4	7.6	8.2	9.2	10.6	12.5
6	11	8.8	11.4	14.4	11.6	12.7	9.4	8.4	7.6	8.2	9.1	10.6	12.5
7	11	8.8	11.4	14.4	11.6	12.7	9.4	8.4	7.5	8.2	9.1	10.6	12.5
8	10.5	8.6	11.4	14.6	11.6	12.7	9.4	8.4	7.8	8.2	9.3	10.6	12.5
9	10.5	8.4	10.7	13.8	11.4	12.6	9.6	8.9	8	8.2	8.7	10.6	12.5
10	10.4	8.3	10.7	13.8	11.4	12.6	9.8	9.1	8.4	8.2	8.7	10.6	12.5
11	10.4	8.3	10.6	13.8	11.4	12.5	10	8.9	8.4	8.1	8.6	10.5	12.5
12	10.4	8.2	10.6	13.8	11.6	12.5	10.2	9.1	8.4	8	8.6	10.5	12.5
13	10.4	8.1	11	13.8	11.5	12.5	10.3	9.1	8	8	8.6	10.5	12.5
14	9.8	8.1	10.6	13.8	11.5	12.6	10.2	8.9	7.8	7.7	8.6	10.5	12.5
15	8.1	8	10.6	12	11.4	12.6	9.8	8.9	7.5	6.7	8.3	10.5	12.5
16	4.5	8	10.8	11.8	10.8	12.6	9.8	8.2	7.2	5.7	7.5	10.5	12.5
17	4	7.8	9.7	11.8	9.6	12.6	9.6	8	6.7	5.2	7.3	10.5	12.5
18	3.8	7.8	10.4	11.6	9.6	12.6	9.4	7.9	5.8	5	2.7	10.5	12.5
19	3.6	7.7	10.6	10.2	9.7	12.6	9.3	7.8	5.8	4.5	2.4	10.5	12.5
20	3.4	7.7	10.2	9.9	9.5	12.6	9.1	7.6	5.2	4.2	1.8	10.5	12.5
21	3.4	7.5	9.2	9.6	8.9	12.3	9	7.5	5.2	4	1.8	10.5	12.5
22	3.4	7.4	9.1	10.1	8.8	12.4	8.9	7.3	4.9	3.9	1.8	10.5	12.5
23	3.4	7.3	9	10.4	8.8	12.4	8.9	7.2	4.85	3.9	1.8	10.5	12.5
24	3.4	7.3	9.2	10.5	9.3	12.4	8.9	7.2	4.8	3.7	1.8	10.5	12.5
25	3.1	7.2	10	10.2	9.3	12.4	8.9	7	4.8	3.6	1.8	10.5	12.5
26	3.1	7.1	10.2	10.2	8.9	12.4	8.9	7	4.7	3.5	1.8	10.5	12.5
27	3.1	7.3	10.2	9.9	8.7	12.4	8.9	7	4.6	3.5	1.8	10.5	12.5
28	3.1	7.2	10	9.9	8.6	12.4	8.9	7	4.5	3.5	1.8	10.5	12.5
29	3.1	7	9.8	9.8	8.2	12.4	8.8	7	4.5	3.5	1.8	10.5	12.5
30	2.8	7	9.4	9.6	7.9	12.4	8.8	7	4.5	3.5	1.8	10.4	12.5
31	2.8	6.8	9.2	9.8	8	12.4	8.8	7	4.5	3.5	1.8	10.4	12.5
32	2.8	6.8	8.5	9.6	8	12.4	8.8	7	4.5	3.5	1.8	10.4	12.5
33	2.8	6.8	7.7	8.3	8	12.4	8.8	6.9	4.4	3.5	1.8	10.4	12.5
34	2.8	6.9	7.9	8.5	8	12.3	8.8	6.9	4.4	3.5	1.8	10.4	12.5
35	2.8	6.9	7.2	8	8	12.3	8.8	6.9	4.3	3.5	1.7	10.4	12.5
36	2.8	7.6	7.2	7.6	8	12.3	8.8	6.8	4.3	3.4	1.7	10.4	12.5
37	2.8	7.3	6.7	7.5	7.8	12.3	8.8	6.8	4.3	3.4	1.7	10.4	12.3
38	2.8	7.2	6.5	7.4	7.8	12.3	8.8	6.9	4.3	3.4	1.7	10.4	12.2
39	2.8	7.1	5.8	7.2	7.8	12.3	8.8	6.9	4.2	3.3	1.7	10.4	12.2
40	2.7	6.8	5.6	7.2	7.7	12.3	8.8	6.8	4.2	3.3	1.7	10.4	7.2
41	2.7	6.5		7.2	7.6	12.3	8.7	6.8	4.2	3.3	1.7	10.4	
42	2.7	7.2		7	7.6	12.3	8.7	6.8	4.2	3.1	1.7	10.4	
43	2.7	7.1		6.9	7.6	12.3	8.7	6.8	4.2	3	1.7	10.4	
44	2.7	7.2		6.7	7.6	12.3	8.6	6.8	4.2	3	1.7	10.4	
45	2.7	7		6.6	7.5	12.3	8.7	6.8	4.2	3	1.6	10.4	
46	2.7	7.2		6.7	7.5	12.3	8.7	6.8	4.1	3	1.6	10.4	
47	2.7	7.1		6.7	7.5	12.3	8.7	6.8	4.1	3	1.6	10.2	
48	2.7	6.7		6.6	7.3	12.3	8.7	6.8	4.1	3	1.6		
49	2.7	6.9		6.4	7.3	12.3	8.7	6.8	4	3	1.6		
50	2.5	6.2		6.3	7.2		8.6	6.8	3.9	2.9	1.7		

Appendix A.8. Limnological Characteristics of Lake Itasca

Date	Conductance (μmhos)	Total Dissolved Residues (mg/l)	pH	Alkalinity (mg/l)	Total-P (μg/l)	Chlor a (μg/l)	Transparency (m)
5/1/84*	265	0.193		186	38.4	9.86	1.55
6/25/84	224	0.196	7.8	155	42.5	18.33	2.20
7/21/84	268	0.185	7.8	142	41.8	12.56	1.65
8/17/84	275	0.189	8.0	143	31.2	9.00	1.85
9/14/84	225	0.204	8.1	148	44.6	15.81	1.85
10/10/84*	260	0.197	8.0	147	43.2	10.62	2.75

Note: Asterisk (*) denotes lake is mixing.

Appendix A.9. Limnological Characteristics of Elk Lake

Date	Conductance (μmhos)	Total Dissolved Residues (mg/l)	pH	Alkalinity (mg/l)	Total-P (μg/l)	Chlor a (μg/l)	Transparency (m)
5/1/84*	218	0.199		176	28.8	22.79	2.25
6/18/84	170	0.166	7.7	140	30.3	6.78	3.65
7/11/84	185	0.185	7.9	136	26.5	4.43	3.25
8/23/84	263	0.176	8.2	134	21.9	4.25	4.1
9/11/84	240	0.199	8.1	143	20.5	9.44	4.08
10/8/84	235	0.162	8.2	135	26.3	9.42	3.8
11/12/84	260	0.177	8.1	144	32.4	9.06	3.05

Note: asterisk (*) signifies lake is mixing

Appendix A.10. Limnological Characteristics of Ten Mile Lake

Date	Conductance (μmhos)	Total Dissolved Residues (mg/l)	pH	Alkalinity (mg/l)	Total-P (μg/l)	Chlor a (μg/l)	Transparency (m)
5/3/84*	160	0.139		122	30.3	21.3	4.4
6/9/84	167	0.151	7.86	105	24.2	6.60	5.5
7/5/84	212	0.158	7.72	87	–	3.04	5.4
8/9/84	204	0.106	8.17	100	24.4	2.18	3.3
9/4/84	190	0.144	8.08	97	25.1	3.05	3.55
10/1/84	130	0.138	7.93	94	14.6	4.54	5.2
11/6/84*	151	0.113	7.77	97	25.2	2.91	5.35

Note: Asterisk (*) indicates lake is mixing

Appendix A.11. Monthly Values of Chlorophyll *a* in the Study Lakes

Lake							
	Date	5/1	6/25	7/21	8/17	9/14	10/10
Itasca		9.86 (1.34)	18.33 (7.81)	12.56 (0.39)	9.00 (0.94)	15.81 (1.96)	10.62 (1.09)

	Date	5/1	6/18	7/11	8/23	9/11	10/8	11/12
Elk		22.79 (8.05)	6.78 (1.54)	4.43 (1.64)	4.25 (0.08)	9.44 (0.71)	9.42 (2.93)	9.06 (0.64)

	Date	5/3	6/11	7/8	8/11	9/3	10/3	11/6
Ten Mile		21.3 (7.74)	6.6 (2.10)	3.04 (1.06)	2.18 (0.91)	3.05 (1.35)	4.54 (3.61)	2.91 (0.60)

Shown is mean monthly chlorophyll *a* in $\mu g \; l^{-1}$ (SD in parentheses); n=3 except for the following: September-Elk Lake (n=2); May,August and September-Ten Mile Lake (n=4).

Appendix A.12. Secchi Transparency (m)

Lake Itasca		Elk Lake		Ten Mile Lake	
Date	Depth (m)	Date	Depth (m)	Date	Depth (m)
9/23/83	1.4	9/26/83	3.4		
11/4/83	1.8	11/13/83	2.7		
1/11/84	5.7	1/13/84	4		
2/8/84	6.2	2/9/84	4.4		
3/8/84	4.9	3/9/84	4.5	3/4/84	5.3
4/4/84	4.5	4/3/84	3.9	3/31/84	6.0
4/26/84	2.1	4/26/84	2.2	5/3/84	4.4
4/29/84	1.55	5/2/84	2.25	6/9/84	5.5
5/17/84	1.8	5/20/84	1.8	7/5/84	5.4
6/20/84	2.2	6/13/84	3.65	8/9/84	3.3
7/18/84	1.65	7/11/84	3.25	9/4/84	3.55
8/15/84	1.85	8/23/84	4.1	10/1/84	5.2
9/14/84	1.85	9/11/84	4.08	11/6/84	5.35
10/9/84	2.75	10/6/84	3.8		
11/9/84	2.35	11/12/84	3.05		
12/10/84	3.55	12/12/84	4.55		

Appendix B. Conversion of Lengths and Weights of Ten Mile Lake Ciscos.

As explained in Chapter 4, ciscos from Ten Mile Lake were not weighed and measured at the time of capture. Thus it was necessary to reconstruct the values of these variables from regression analysis.

Thirty-eight fish from the collection made on October 4, 1983 were weighed and measured in the field and then frozen. These were later thawed and remeasured and reweighed at the same time as other fish from Ten Mile lake were being processed. Regressions of weight and length at the time of processing on original weight and length were performed.

The regression equations and values of R^2 for the parameters were:

Weight: $W_P = .931W_O + 0.455$ $R^2 = 0.988$

Standard Length: $L_P = 1.007L_O - 2.471$ $R^2 = 0.962$

Total Length: $L_P = 1.018L_O - 5.342$ $R^2 = 0.968$,

where the subscript 'O' denotes the original (field) measure and 'P' is the measure at the time of processing.

Appendix C.1. Fish Collection Dates and Sample Sizes.

Sample sizes reflect only the number of fish used for tissue analysis from age groups used in this study. Month refers to month cited in text; date is the middle date for the sampling period.

Appendix C.1.1. Elk Lake Sampling Dates and Sample Sizes.

Month	Date	Juvenile Male	Female	Adult Male	Female	Totals
September	9/27/83			7	8	15
November	11/13/83			10	8	18
December	12/14/83			8	8	16
January	1/11/84				6	6
February	2/9/84			4	6	10
March	3/9/84				4	4
May	5/15/84			5	4	9
June	6/15/84	4	3	8	10	25
July	7/14/84	10	14	8	6	38
August	8/25/84	13	11	10	6	40
September	9/12/84		4		9	13
October	10/7/84		5	9	6	20
November	11/16/84			6	7	13
December	12/14/84			6	7	13
	Totals	27	37	81	95	240

Appendix C.1.2. Lake Itasca Sampling Dates and Sample Sizes.

| | | Juvenile | | Adult | | |
Month	Date	Male	Female	Male	Female	Totals
September				2	4	6
November	11/4/83			10	2	12
December	12/25/83			6		6
February	2/17/84			3	5	8
April	4/1/84	3				3
May	5/10/84			10	8	18
June	6/6/84			4	6	10
July	7/6/84	7		5	10	22
August	8/10/84	4	5	13	6	28
September	9/8/84		8	7	7	22
October	10/2/84	6	8	7	7	28
November	11/1/84			14		14
December	12/28/84			2	2	4
	Totals	20	21	83	57	181

Appendix C.1.3. Ten Mile Lake Sampling Dates and Sample Sizes.

| | | Juvenile | | Adult | | |
Month	Date	Male	Female	Male	Female	Totals
October	10/4/83			6	4	10
November	10/25/83			4	3	7
January	1/17/84			3	5	8
April	4/1/84			5	6	11
May	5/10/84			4	5	9
June	6/6/84	4	4	5	8	21
July	7/6/84			3	3	6
August	8/10/84	4	4	7*	2	17
September	9/8/84	5	4	3	3	15
October	10/2/84	3	3	8	6	20
November	11/1/84			6	8	14
December	11/28/84			9	9	18
	Totals	16	15	63	62	156

* Total Energy content is not available for some tissues of these fish, due to a laboratory accident. In these cases, only energy density is presented.

Appendix C.2. The Effects of Drying Temperature on The Caloric Content of Fish Tissues

INTRODUCTION:

The major aims of this thesis involve the determination of energy content, which is closely related to lipid content. Thus, it was important to determine the effects, if any, of different drying temperatures on the caloric density of various tissues.

Recommendations regarding drying temperatures are based on considerations of how lipids are affected by the process. Some authors recommend drying at lower temperatures to prevent loss of volatile fatty acids (Prus, 1975; Sawicka,1975). However, others have recommended higher temperatures, noting that at low temperatures drying time is greatly increased, and can result in progressive decomposition of fats (Paine, 1971; Gorecki, 1975).

Practical considerations were also important. It had previously been determined that drying samples to constant weight at 80 °C took 72 hours, whereas 120 hours were necessary at 50 °C. This was not a trivial consideration given the large numbers of fish that were to be sampled.

METHODS:

Several samples of muscle, remainder (the carcass minus muscle fillet and ventral fat deposit), ovary and intestine were

tested for the effects of drying temperature on caloric density. Samples were mixed well by hand or in a blender, and divided into two subsamples. One of these was dried at 50 °C and the other at 80 °C. Samples were burned in a calorimeter as described above, in Chapter 5. For each tissue, the results were treated as paired samples and compared using Student's t-Test. Since there was no *a priori* reason to expect one set to yield higher values, the test was two-tailed.

RESULTS:

A summary of results is given in the following table:

Comparison of the caloric content of selected tissues dried at different temperatures. Shown are means and standard deviations (in parentheses).

		Drying Temperature			
Tissue	n	50 °C	80 °C	Mean diff.	p
Muscle	9	5344.93 (147.29)	5584.66 (231.77)	239.73	0.0021
Remainder	9	5031.97 (219.55)	5106.55 (281.99)	74.58	0.1276
Ovary	6	6128.86 (335.74)	6287.61 (281.05)	158.75	0.0451
Digestive Tract	8	5620.33 (231.51)	5812.66 (328.35)	192.33	0.0142

In three of the four tissues, significant differences in caloric density were observed between paired samples, and in all cases the values of samples dried at 80 °C were higher than those dried at 50 °C.

DISCUSSION:

The higher caloric values obtained at the higher drying temperatures may have resulted from several causes. The degradation of fats due to prolonged drying at the lower temperature may have been greater than the loss of volatile fats at the higher temperature. Also, it is possible that at the lower temperature, the removal of water from samples was less efficient. Water may remain bound in the tissue, which would lead to an estimate of dry weight that was too high, thereby resulting in a low estimate of caloric content. Strange and Pelton (1987) also found that samples dried at lower temperatures (48 h at 60 °C) had higher apparent dry weights and thus lower gross energy values than those dried at higher temperatures (24 h at 60 °C and overnight at 105 °C). In either case, the more accurate method would be the one which results in the higher caloric value. Thus, the higher temperature, 80 °C, was used for drying tissue samples.

Appendix C.3. Replicate Determinations of the Caloric Density of Fish Tissues

Two tests were conducted in order to determine whether it would be necessary to analyze replicates for determination of caloric density of fish tissues. In the first of these, two subsamples of tissues from each of several fish were analyzed. These were compared using Student's T-test for paired samples. Results are presented in the table below. Given are means, standard deviations (in parentheses), the mean difference of the paired groups, the number of samples (n) and the value of p.

Replicate Determinations of Caloric Density, Test 1.					
Tissue	sample 1	sample 2	Mean diff	n	p
Muscle	5609.56 (157.77)	5617.02 (178.06)	7.464	11	0.6322
Remainder	5296.52 (401.72)	5266.77 (426.94)	29.755	10	0.4678
Ovary	6440.84 (194.31)	6453.74 (221.65)	12.90	5	0.4460
Testes	5468.23 (189.05)	5466.93 (187.11)	1.296	7	0.9291
Digestive Tract	6256.19 (644.18)	6300.41 (700.48)	44.21	12	.2367
Liver	5637.99 (118.88)	5612.48 (119.37)	25.51	6	0.3088

It is clear that differences between replicates were not significant for any of the tissues examined.

The second test involved examining the coefficients of variation of six replicate determinations of the caloric content of sample of a given tissue. Tissues analyzed were muscle, remainder (whole fish minus liver, digestive tract, gonads, muscle fillet and ventral fat deposit), testes and digestive tract. The coefficients of variation in all cases were quite low: 0.577, 1.705, 0.361, and 0.657 respectively.

On the basis of these tests, it was decided that the determination of caloric content for only one subsample would be sufficient.

Appendix D. Results of Statistical Tests.

This appendix contains summaries of result of statistics used to analyze data on fish tissue weights, energy density, energy content and water content. There are four subsections:

SECTION D.1. RESULTS OF ANOVA AND KRUSKAL-WALLIS TESTS.

These tests were conducted to determine the overall significance of seasonal changes in the variables investigated. The type of test is indicated in the second column of the table; if there is no entry, ANOVA on the untransformed data was used; if log is entered, the ANOVA was performed on log-transformed data, and if KW is entered, results are from the Kruskal-Wallis Test. Also given is the p-value for the test, the F-value for ANOVAS or the H value for Kruskal-Wallis Tests, and the number of groups and total samples involved in the analysis of each case.

SECTION D.2. SIGNIFICANCE OF SEASONAL CHANGES.

This section contains the results of tests comparing specific months that comprise the limits of periods of the year deemed biologically meaningful, as explained in the methods section of Chapter 4.

In this section, results for males and females are given in a single column, and are separated by a slash (/), with information

pertaining to males on the left, and females on the right. Arrows are used at times to denote the extension of the time period under consideration to the particular month noted, when different from the months listed in the column heading. At times, there may be more than one month listed for one or both of the limits of the time period under consideration. When this occurs, the month to the left of the slash(/) indicates the month used as the limit for males, and that to the right of the slash, for females. When the particular month differed depending on the variable in question, the limit of the period under consideration is simply referred to as "Peak". The reader may readily determine which month was used by referring to the graphs in the main body of the text.

SECTION D.3. COMPARISONS BETWEEN SEXES.

This section contains comparisons between sexes of the variables studied. Juveniles and adults are considered separately.

SECTION D.4. COMPARISONS BETWEEN ADULTS AND JUVENILES.

Comparison of individuals of a given sex and within a given lake are presented in this section.

In all sections, tables are arranged by tissue, in the order in which they are presented in the text.

In sections D.2-D.4, symbols denoting statistical significance are the same and are as follows: asterisks (*) denote the fact that a t-test was performed. A single asterisk (*) indicates significance at the $\alpha = .05$ level, and a double asterisk (**) indicates significance at the $\alpha = .01$ level. A cross (†) is used to denote cases where the Mann-Whitney U-test was used. A single cross (†) indicates significance at the $\alpha = .05$ level and a double cross (††) indicates significance at the $\alpha = .01$ level. "NS" means the comparison was not significant, and "NA" means that the particular test does not apply. It may indicate that the limits of a time period were extended to another month, or. more usually, that the test could not be performed, because of lack of samples.

App. D.1.1. Liver, Adults: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M		0.0001	5.2191	11	56
	F		0.0001	18.9295	11	59
Dry Weight	M		0.0001	6.1265	11	56
	F		0.0001	17.3636	11	58
PerCent Water	M	KW	0.0013	28.9428	11	56
	F	KW*	0.0033	26.3767	11	58
kJ/g-Dry Weight	M		-	-	11	pooled
	F		-	-	11	pooled
kJ/g-Wet Weight	M		0.0001	6.9532	11	56
	F		0.0001	4.7219	11	57
Energy Content	M		0.0001	6.3781	11	56
	F		0.0001	22.3645	11	57
LAKE ITASCA						
Wet Weight	M		0.1021	1.7583	9	73
	F		0.0001	17.5900	8	53
Dry Weight	M	log	0.0027	3.3960	9	72
	F		0.0001	13.9987	8	53
PerCent Water	M		0.0001	5.4842	9	73
	F		0.0001	11.0904	8	53
kJ/g-Dry Weight	M	KW	0.0001	48.7104	10	78
	F		0.0001	5.5295	8	53
kJ/g-Wet Weight	M	KW	0.0003	31.2800	10	77
	F		0.0001	9.7815	8	53
Energy Content	M	KW	0.0019	26.1855	10	77
	F		0.0001	8.9640	8	53
ELK LAKE						
Wet Weight	M		0.0001	7.1397	11	81
	F		0.0075	2.4466	14	95
Dry Weight	M	log	0.0001	8.0570	11	79
	F	log	0.0001	4.2464	14	94
PerCent Water	M		0.0139	2.4670	11	79
	F		0.0044	2.6168	14	94
kJ/g-Dry Weight	M	KW*	0.0028	26.8483	11	75
	F	KW	0.2621	15.7645	14	93
kJ/g-Wet Weight	M	KW	0.0006	31.1234	11	75
	F	KW	0.0010	34.4921	14	93
Energy Content	M	KW	0.0001	43.8478	11	75
	F	log	0.0001	4.1189	14	93

App. D.1.2. Liver, Juveniles: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M		0.0153	5.2351	4	16
	F	log	0.0020	9.7255	4	15
Dry Weight	M		0.0566	3.3259	4	16
	F	log	0.0007	12.5340	4	15
PerCent Water	M	log	0.4313	0.9875	4	13
	F		0.9139	0.1701	4	15
kJ/g-Dry Weight	M		-	-	4	pooled
	F		-	-	4	pooled
kJ/g-Wet Weight	M	KW	0.3248	3.4691	4	16
	F		0.6190	0.6157	4	15
Energy Content	M	log	0.0766	2.9356	4	16
	F	log	0.0008	12.1213	4	15
LAKE ITASCA						
Wet Weight	M		0.0102	5.2665	4	20
	F	KW	0.0354	6.6810	3	21
Dry Weight	M		0.0084	5.5355	4	20
	F		0.1056	2.5533	3	21
PerCent Water	M		0.0001	16.2504	4	20
	F		0.0001	20.7346	3	21
kJ/g-Dry Weight	M		-	-	4	pooled
	F		-	-	3	pooled
kJ/g-Wet Weight	M		0.0001	37.5297	4	20
	F		0.0001	59.1590	3	20
Energy Content	M		0.0043	6.5258	4	20
	F		0.0700	3.1223	3	20
ELK LAKE						
Wet Weight	M	KW	0.3186	2.2878	3	27
	F	KW	0.4535	3.6630	5	37
Dry Weight	M	KW	0.6302	0.9233	3	27
	F	KW	0.4286	3.8362	5	37
PerCent Water	M		0.1864	1.8031	3	27
	F		0.0768	2.3333	5	37
kJ/g-Dry Weight	M		-	-	3	pooled
	F		-	-	5	pooled
kJ/g-Wet Weight	M		0.0013	8.8272	3	27
	F		0.0010	6.0558	5	36
Energy Content	M	KW	0.8147	0.4100	3	27
	F	KW	0.2555	5.3259	5	36

App. D.1.3. Gonad, Adults: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M	log	0.0001	4.8994	11	56
	F	log	0.0001	13.8505	11	59
Dry Weight	M	log	0.0001	6.3837	11	56
	F	KW	0.0001	40.8932	11	58
PerCent Water	M	log	0.0067	2.9189	11	56
	F		0.0707	1.8895	11	58
kJ/g-Dry Weight	M	*	0.0001	44.7617	3	18
	F	KW*	0.0019	20.9327	7	33
kJ/g-Wet Weight	M		0.0001	6.1580	11	56
	F	KW*	0.0001	38.9590	11	56
Energy Content	M		0.0001	12.2884	11	56
	F	*	0.0003	32.6913	11	56
LAKE ITASCA						
Wet Weight	M	KW	0.0001	52.2923	9	73
	F	KW	0.0001	42.7121	8	53
Dry Weight	M	KW	0.0001	49.7172	9	73
	F	KW	0.0001	42.8864	8	53
PerCent Water	M	KW	0.0001	57.0077	9	73
	F	KW	0.0001	38.1828	8	53
kJ/g-Dry Weight	M	KW	0.0001	49.1616	10	74
	F	log	0.0001	10.5122	8	51
kJ/g-Wet Weight	M	KW	0.0001	59.4988	10	73
	F	KW*	0.0001	39.0567	8	52
Energy Content	M	KW	0.0001	50.6578	10	73
	F	log	0.0001	73.6557	8	52
ELK LAKE						
Wet Weight	M	KW	0.0001	60.7832	11	80
	F	KW*	0.0001	84.2026	14	96
Dry Weight	M	log	0.0001	40.1679	11	78
	F	KW*	0.0001	80.6185	14	95
PerCent Water	M		0.0001	23.1609	11	78
	F	KW*	0.0001	80.6235	14	95
kJ/g-Dry Weight	M	KW	0.0001	47.4372	11	78
	F	KW	0.0001	71.9139	14	93
kJ/g-Wet Weight	M	log	0.0001	29.7093	11	78
	F	KW	0.0001	80.1281	14	93
Energy Content	M	KW	0.0001	63.1088	11	78
	F	KW	0.0001	80.2216	14	93

App. D.1.4. Gonad, Juveniles: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M		0.0902	2.7918	4	15
	F		0.0961	2.7111	4	15
Dry Weight	M		0.1259	2.3749	4	15
	F		0.0260	4.7582	4	15
PerCent Water	M		0.2438	1.6313	4	14
	F		0.4602	0.9264	4	15
kJ/g-Dry Weight	M		-	-	-	insuff. tissue
	F		-	-	-	insuff. tissue
kJ/g-Wet Weight	M		-	-	-	insuff. tissue
	F		-	-	-	insuff. tissue
Energy Content	M		-	-	-	insuff. tissue
	F		-	-	-	insuff. tissue
LAKE ITASCA						
Wet Weight	M		0.0611	3.0081	4	20
	F		0.4438	0.8501	3	21
Dry Weight	M	log	0.0006	11.3326	4	20
	F		0.4471	0.8420	3	21
PerCent Water	M	KW	0.0323	8.7863	4	20
	F	KW	0.0013	13.2805	3	21
kJ/g-Dry Weight	M		-	-	4	pooled
	F		-	-	3	pooled
kJ/g-Wet Weight	M	KW*	0.0458	8.0078	4	17
	F	KW	0.0007	14.6494	3	21
Energy Content	M		0.0184	4.4709	4	20
	F	KW	0.3384	2.1669	3	21
ELK LAKE						
Wet Weight	M	KW	0.1193	4.2520	3	20
	F	log	0.0001	14.4067	5	33
Dry Weight	M	KW	0.0352	6.6939	3	20
	F	KW	0.0019	17.0330	5	33
PerCent Water	M	KW	0.0944	4.7199	3	20
	F	KW	0.0091	13.4977	5	33
kJ/g-Dry Weight	M		-	-	3	pooled
	F		-	-	5	pooled
kJ/g-Wet Weight	M		0.0385	3.9700	3	26
	F	KW	0.0054	14.6821	5	32
Energy Content	M	KW	0.1479	3.8229	3	26
	F	log	0.0001	9.6600	5	32

App. D.1.5. Dig. Tract, Adults: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M		0.0001	11.5007	11	55
	F		0.0004	4.1134	11	59
Dry Weight	M		0.0001	13.5982	11	55
	F	KW	0.0005	31.2079	11	58
PerCent Water	M		0.0001	5.2108	11	56
	F	log	0.0003	4.2376	11	58
kJ/g-Dry Weight	M	*	0.0001	9.9933	11	60
	F		0.0001	10.3504	11	58
kJ/g-Wet Weight	M		0.0001	7.0197	11	56
	F		0.0001	4.9728	11	58
Energy Content	M		0.0001	14.9433	11	56
	F		0.0001	8.4463	11	58
LAKE ITASCA						
Wet Weight	M		0.0001	5.1560	9	73
	F	log	0.0001	22.5428	8	53
Dry Weight	M	log	0.0001	18.0376	9	73
	F	log	0.0001	25.8157	8	53
PerCent Water	M	log	0.0001	23.9154	9	73
	F	KW	0.0001	41.2735	8	53
kJ/g-Dry Weight	M	KW	0.0001	61.7698	10	79
	F		0.0001	12.0916	8	53
kJ/g-Wet Weight	M	log	0.0001	46.7014	10	78
	F	log	0.0001	33.2404	10	55
Energy Content	M	log	0.0001	22.0380	10	78
	F	log	0.0001	31.2571	8	53
ELK LAKE						
Wet Weight	M		0.0001	5.7421	11	81
	F		0.0001	4.0998	14	95
Dry Weight	M	log	0.0001	11.9039	11	80
	F	log	0.0001	9.6762	14	95
PerCent Water	M	log	0.0001	11.8676	11	80
	F	KW	0.0001	45.9456	14	95
kJ/g-Dry Weight	M	log	0.0001	20.4187	11	79
	F	KW	0.0001	54.4617	14	95
kJ/g-Wet Weight	M	log	0.0001	16.2017	11	79
	F	KW	0.0001	50.2254	14	95
Energy Content	M	log	0.0001	14.5787	11	79
	F	log	0.0001	10.5644	14	94

App. D.1.6. Dig. Tract,Juveniles: ANOVA and Kruskal-Wallis Tests

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M		0.2895	1.4041	4	16
	F		0.0727	3.0739	4	15
Dry Weight	M		0.4651	0.9099	4	16
	F		0.0073	6.8283	4	15
PerCent Water	M		0.0175	5.0202	4	16
	F		0.0630	3.2668	4	15
kJ/g-Dry Weight	M	-				
	F	KW	0.0056	12.5760	4	15
kJ/g-Wet Weight	M		0.0007	11.7975	4	16
	F		0.0227	4.7836	4	15
Energy Content	M		0.2243	1.6786	4	16
	F		0.0047	7.7498	4	15
LAKE ITASCA						
Wet Weight	M		0.0230	4.1829	4	20
	F		0.0357	4.0330	3	21
Dry Weight	M		0.0099	5.3054	4	20
	F		0.1495	2.1162	3	21
PerCent Water	M	log	0.0001	18.5802	4	20
	F		0.0001	50.5422	3	21
kJ/g-Dry Weight	M		0.0001	33.2170	4	20
	F		0.0001	113.7944	3	21
kJ/g-Wet Weight	M	log	0.0001	37.6778	4	20
	F	log	0.0001	77.9798	3	21
Energy Content	M	log	0.0034	6.9006	4	20
	F		0.0104	5.9518	3	21
ELK LAKE						
Wet Weight	M	KW	0.1527	3.7582	3	27
	F	log	0.0294	3.0886	5	37
Dry Weight	M	KW	0.1941	3.2790	3	27
	F	KW	0.0908	8.0216	5	37
PerCent Water	M	KW	0.2852	2.5092	3	27
	F		0.0001	9.2358	5	37
kJ/g-Dry Weight	M	log	0.0687	3.0001	3	27
	F		0.0001	10.0738	5	37
kJ/g-Wet Weight	M	log	0.2088	1.6733	3	27
	F	log	0.0001	11.7268	5	37
Energy Content	M	KW	0.1545	3.7356	3	27
	F		0.0195	3.4192	5	37

App. D.1.7. Carcass, Adults: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M	log	0.0001	6.4507	11	56
	F	KW*	0.0004	31.9900	11	60
Dry Weight	M	KW*	0.0002	33.8061	11	56
	F		0.0001	7.9494	11	58
PerCent Water	M		0.0003	4.3132	11	56
	F		0.0012	3.6366	11	58
kJ/g-Dry Weight	M		0.0001	7.6354	11	56
	F		0.0004	4.1514	11	58
kJ/g-Wet Weight	M		0.0001	5.0180	11	56
	F		0.0006	3.9463	11	58
Energy Content	M	KW*	0.0001	38.4131	11	56
	F		0.0001	9.7587	11	58
LAKE ITASCA						
Wet Weight	M		0.0001	7.9383	9	73
	F		0.0001	7.2195	8	53
Dry Weight	M	log	0.0001	7.2684	9	70
	F		0.0107	3.2243	7	49
PerCent Water	M	KW*	0.0001	43.0385	9	70
	F		0.0001	13.6506	7	49
kJ/g-Dry Weight	M		0.0002	4.3116	10	74
	F		0.0001	9.7449	7	48
kJ/g-Wet Weight	M		0.0001	8.7891	10	73
	F		0.0001	11.9397	7	48
Energy Content	M		0.0001	5.4697	10	74
	F		0.0022	4.2033	7	48
ELK LAKE						
Wet Weight	M		0.2888	1.2285	11	80
	F		0.0059	2.5193	14	95
Dry Weight	M		0.0001	6.1320	11	77
	F		0.0001	4.6333	14	89
PerCent Water	M		0.0001	17.6024	11	76
	F		0.0001	6.3060	14	89
kJ/g-Dry Weight	M		0.0001	10.3898	11	77
	F		0.0003	3.4557	14	88
kJ/g-Wet Weight	M		0.0001	16.5455	11	76
	F		0.0001	5.2963	14	88
Energy Content	M		0.0001	9.9251	11	77
	F	*	0.0001	4.9472	13	84

App. D.1.8. Carcass, Juveniles: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
TEN MILE LAKE						
Wet Weight	M		0.0102	5.9112	4	16
	F		0.0001	18.0482	4	15
Dry Weight	M	log	0.0003	14.0023	4	16
	F		0.0001	24.8524	4	15
PerCent Water	M	KW	0.0254	9.3110	4	16
	F		0.0008	12.2164	4	15
kJ/g-Dry Weight	M		0.0956	2.6600	4	16
	F		0.1258	2.3755	4	15
kJ/g-Wet Weight	M		0.0364	3.9265	4	16
	F		0.0005	13.9095	4	15
Energy Content	M	log	0.0004	13.0246	4	16
	F		0.0001	24.2424	4	15
LAKE ITASCA						
Wet Weight	M	KW*	0.0107	11.1946	4	20
	F		0.0082	6.3450	3	21
Dry Weight	M	KW*	0.0346	8.6303	4	20
	F		0.2428	1.5330	3	20
PerCent Water	M		0.0001	20.9308	4	20
	F	KW	0.0474	6.0994	3	21
kJ/g-Dry Weight	M	KW	0.0046	12.9939	4	20
	F		0.0001	26.3107	3	21
kJ/g-Wet Weight	M	KW*	0.0061	12.3993	4	20
	F		0.0013	9.8240	3	21
Energy Content	M	KW*	0.0380	8.4262	4	20
	F		0.5896	0.5441	3	21
ELK LAKE						
Wet Weight	M	log	0.0001	23.0152	3	27
	F		0.0001	10.0381	5	37
Dry Weight	M	KW	0.0019	12.5559	3	27
	F	KW	0.0014	17.7413	5	37
PerCent Water	M	KW	0.1265	4.1346	3	27
	F	KW	0.0006	19.5134	5	37
kJ/g-Dry Weight	M	KW	0.0046	10.7662	3	27
	F	log	0.0001	28.1569	5	36
kJ/g-Wet Weight	M		0.0239	4.3813	3	27
	F	KW	0.0008	19.0016	5	36
Energy Content	M	KW	0.0044	10.8709	3	27
	F	log	0.0001	12.9766	5	36

App. D.1.9. Muscle, Adults: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
LAKE ITASCA						
PerCent Water	M		0.0001	9.2431	9	62
	F		0.0001	14.3094	7	44
kJ/g-Dry Weight	M		0.0001	10.3452	10	65
	F		0.0001	10.2059	6	43
kJ/g-Wet Weight	M		0.0001	9.0639	10	62
	F		0.0001	14.3536	6	43
ELK LAKE						
PerCent Water	M		0.0001	17.8260	11	78
	F		0.0001	7.3983	14	89
kJ/g-Dry Weight	M	KW	0.0001	51.8992	11	78
	F		0.0009	3.1442	14	89
kJ/g-Wet Weight	M		0.0001	19.6907	11	78
	F		0.0001	5.9622	14	89

App. D.1.10. Ven. Fat, Adults: ANOVA and Kruskal-Wallis Tests.

	Sex		p	F or H	# groups	# samples
LAKE ITASCA						
Wet Weight	M		0.0001	6.8962	9	73
	F		0.0022	4.1705	7	49
Dry Weight	M	log	0.0009	4.0848	9	56
	F		0.0005	5.1846	7	48
PerCent Water	M	log	0.0001	6.5589	9	56
	F		0.0001	6.8286	7	41
kJ/g-Dry Weight	M	KW	0.0011	27.6316	9	56
	F	log	0.0018	4.8736	6	40
kJ/g-Wet Weight	M	KW*	0.0026	25.3395	9	56
	F	KW*	0.0001	26.6056	6	40
Energy Content	M		0.0001	4.8468	9	56
	F		0.0025	4.5411	6	40
ELK LAKE						
Wet Weight	M		0.0455	2.0059	11	81
	F		0.9542	0.4301	14	95
Dry Weight	M	log	0.0001	4.1968	11	80
	F		0.5337	0.9229	14	93
PerCent Water	M		0.0001	11.1558	11	77
	F		0.0106	2.3811	14	83
kJ/g-Dry Weight	M	KW	0.0004	31.8961	11	66
	F	KW	0.2426	16.1216	14	79
kJ/g-Wet Weight	M	log	0.0001	8.7216	11	65
	F		0.0431	1.9248	14	79
Energy Content	M		0.0001	4.6370	11	75
	F		0.6259	0.8316	14	88

Appendix D.2.1. Liver, Adults: Seasonal Changes

Elk Lake

	Sept-Dec	Dec-Feb	Feb-May	May-Peak	Peak-Dec
Wet Weight	*/**	*/NS	NS/NS	NS/*	**/*
Dry Weight	*/**	*/NS	NS/NS	*/**	**/**
Energy Content	NS/†	*/NS	NS/NS	NS/NS	**/**
kJ/g-Wet Weight	NS/NS	NS/NS	*/NS	**/NS	**/*
kJ/g-Dry Weight	**/NS	NS/NS	NS/NS	†/NS	**/NS
Per Cent Water	NS/NS	*/NS	NS/NS	**/**	**/†

Lake Itasca

	Nov-Feb	Feb-May	May-Aug	Aug-Oct/Nov	Oct/Nov-Dec
Wet Weight	*/*	NS/*	NS/*	NS/††	NS/NS
Dry Weight	*/*	*/**	NS/NS	**/**	**/NS
Energy Content	NS/*	NS/NS	††/NS	††/**	**/**
kJ/g-Wet Weight	*/*	NS/*	†/*	††/††	NS/*
kJ/g-Dry Weight	**/NS	NS/NS	**/NS	††/††	NS/*
Per Cent Water	*/**	*/**	**/NS	*/**	NS/*

Ten Mile Lake

	Oct-Nov	Nov-May	May-Peak	Peak-Oct/Dec	Male-Oct-Dec
Wet Weight	NS/NS	NS/NS	*/**	**/**	*
Dry Weight	NS/**	NS/NS	**/†	**/*	NS
Energy Content	NS/*	NS/NS	*/**	**/*	
kJ/g-Wet Weight	*/**	NS/NS	**/**	**/**	
kJ/g-Dry Weight	-	-	-	-	
Per Cent Water	NS/*	NS/NS	NS/NS	*/*	**

Note: * and † = significant at .05; ** and †† = significant at .01
    See text for further explanation

Appendix D.2.2. Liver, Juveniles:
Seasonal Changes

Elk Lake

	Jun-Aug	Aug-Oct
Wet Weight	NS/NS	NA/NS
Dry Weight	NS/NS	NA/NS
Energy Content	NS/NS	NA/NS
kJ/g-Wet Weight	**/*	NA/NS
kJ/g-Dry Weight	NS/NA	NA/NA
Per Cent Water	NS/NS	NA/NS

Lake Itasca

	Apr-Aug	Aug-Oct
Wet Weight	**/NA	NS/NS
Dry Weight	**/NA	NS/NS
Energy Content	**/NA	NS/NS
kJ/g-Wet Weight	**/NA	**/**
kJ/g-Dry Weight	NA/NA	NA/NA
Per Cent Water	**/NA	**/**

Ten Mile Lake

	Jun-Aug	Aug-Oct
Wet Weight	†/†	NS/NS
Dry Weight	†/†	NS/NS
Energy Content	*/-->Oct	NS/†<--Jun
kJ/g-Wet Weight	NS/NS	NS/NS
kJ/g-Dry Weight	NA	NA
Per Cent Water	NS/NS	NS/NS

Note: * and † = significant at .05; ** and †† =
significant at .01. See text for further explanation.

Appendix D.2.3. Gonad, Adults: Seasonal Changes

Elk Lake

	Sept-Dec	Dec-Feb	Feb-May	May-Oct/Nov	Oct/Nov-Dec
Wet Weight	*/††	††/††	NS/NS	††/††	**/†
Dry Weight	**/††	††/†	NS/NS	††/††	**/**
Energy Content	**/††	††/**	NS/-->	**/††<-Jan	††/**
kJ/g-Wet Weight	††/††	††/-->	**/-->	*/††<-Jan	*/††
kJ/g-Dry Weight	NS/††	**/-->	*/-->	**/**<-Jan	††/††
Per Cent Water	**/††	††/†	*/*	**/††	**/††

Lake Itasca

	Nov-Feb	Feb-May	May-Jun/Jul	Jun/Aug-Peak	Peak-Dec
Wet Weight	**/NS	NS/-->	NS/-->	††/††<-Feb	*/†
Dry Weight	**/NS	NS/-->	NS/-->	**/††<-Feb	**/†
Energy Content	**/NS	**/-->	**/-->	††/††<-Feb	**/†
kJ/g-Wet Weight	**/**	NS/-->	NS/-->	†/**<-Feb	NS/**
kJ/g-Dry Weight	NS/**	NS/**	NS/NS	NS/NA	NS/†<-Aug
Per Cent Water	**/NS	NS/-->	†/-->	††/**<-Feb	<-AugNS/**

Ten Mile Lake

	Oct-Apr/May	May-Peak	Peak-Nov/Dec
Wet Weight	*/**	†/††	**/*
Dry Weight	*/†	†/††	**/*
Energy Content	††/†	†/†	**/*
kJ/g-Wet Weight	**/NS	**/†	**/*
kJ/g-Dry Weight	pooled/NA	NA/†	NA/*
Per Cent Water	NS/NS	NS/NS	*/**

Note: * and † = significant at .05; ** and †† = significant at .01
    See text for further explanation

Appendix D.2.4. Gonad, Juveniles: Seasonal Changes

Elk Lake

	Jun-Aug	Aug-Oct
Wet Weight	*/**-->Oct	
Dry Weight	*/**-->Oct	
Energy Content	NS/†-->Oct	
kJ/g-Wet Weight	NS/**	NA/††
kJ/g-Dry Weight	NA/NA	NA/NA
Per Cent Water	**/NS	NA/NS

Lake Itasca

	Apr-Aug	Aug-Oct
Wet Weight	*/NA	NS/NS
Dry Weight	†/NA	NS/NS
Energy Content	†/NA	†/NS
kJ/g-Wet Weight	††/NA	††/††
kJ/g-Dry Weight	pooled	pooled
Per Cent Water	*/NA	†/††

Ten Mile Lake

	Jun-Aug	Aug-Oct
Wet Weight	NS/NS	NS/NS
Dry Weight	NS/NS	NS/NS
Energy Content	NA	NA
kJ/g-Wet Weight	NA	NA
kJ/g-Dry Weight	NA	NA
Per Cent Water	NS/NS	NS/NS

Note: * and † = significant at .05; ** and †† = significant at .01. See text for further explanation.

Appendix D.2.5. Digestive Tract, Adults: Seasonal Changes

Elk Lake

	Sept-Dec	Dec-Feb	Feb-May	May-Peak	Peak-Dec
Wet Weight	NS/**	NS/**	NS/NS	††/NS	**/††
Dry Weight	*/**	**/**	**/NS	††/NS	**/††
Energy Content	**/††	**/**	**/NS	††/*	††/††
kJ/g-Wet Weight	††/*	**/NS	**/NS	††/*	††/††
kJ/g-Dry Weight	**/*	**/NS	**/NS	††/*	**/††
Per Cent Water	**/*	NS/NS	NS/NS	††/*	**/**

Lake Itasca

	Sep/Nov-Feb	Feb-May	May-Peak	Peak-Nov/Oct	Oct/Nov-Dec
Wet Weight	*/††	NS/**	**/*	**/††	NS/NS
Dry Weight	**/†	NS/††	††/††	††/††	NS/†
Energy Content	†/†	NS/††	††/††	**/††	NS/†
kJ/g-Wet Weight	**/*	NS/*	††/**	**/††	NS/†
kJ/g-Dry Weight	**/*	NS/NS	**/**	††/**	NS/*
Per Cent Water	NS/†	NS/†	††/††	††/††	NS/†

Ten Mile Lake

	Oct-Nov	Nov-Jan	Jan-May	May-Peak	Peak-Nov
Wet Weight	NS/NS	NS/NS	NS/NS	**/†	**/**
Dry Weight	NS/NS	NS/†	NS/NS	**/**	**/**
Energy Content	NS/NS	NS/NS	NS/NS	**/**	†/**
kJ/g-Wet Weight	**/**	*/NS	*/NS	**/*	**/**
kJ/g-Dry Weight	**/*	NS/NS	NS/NS	*/*	NA/**
Per Cent Water	**/*	*/*	*/*	NS/*	NS/**

Note: * and † = significant at .05; ** and †† = significant at .01
See text for further explanation

Appendix D.2.6. Digestive Tract, Juveniles: Seasonal Changes

Elk Lake

	Jun-Aug	Aug-Oct
Wet Weight	NS/NS	NA/NS
Dry Weight	NS/NS	NA/NS
Energy Content	NS/NS	NA/*
kJ/g-Wet Weight	NS/NS	NA/††
kJ/g-Dry Weight	NS/NS	NA/††
Per Cent Water	NS/NS	NA/**

Lake Itasca

	Apr-Aug	Aug-Oct
Wet Weight	*/NA	NS/*
Dry Weight	*/NA	*/*
Energy Content	†/NA	†/††
kJ/g-Wet Weight	*/NA	†/††
kJ/g-Dry Weight	†/NA	**/**
Per Cent Water	*/NA	†/**

Ten Mile Lake

	Jun-Aug	Aug-Oct
Wet Weight	NS/NS	NS/NS
Dry Weight	NS/*	NS/NS
Energy Content	NS/*	NS/NS
kJ/g-Wet Weight	NS/**-->Sep	**/NS
kJ/g-Dry Weight	†/NS	NA/*
Per Cent Water	NS/NS	NS/NS

Note: * and † = significant at .05; ** and †† = significant at .01. See text for further explanation.

Appendix D.2.7. Carcass, Adults: Seasonal Changes

Elk Lake

	Sept-Dec	Dec-Feb	Feb-May	May-Peak	Peak-Dec
Wet Weight	NS/**	NS/NS	NS/NS	NS/NS	*/NS
Dry Weight	NA/**	NA/NS	Nov<-*/NS	**/*	**/**
Energy Content	*/**	NS/NS	NS/NS	**/*	**/**
kJ/g-Wet Weight	**/*	*/NS	**/NS	**/**	**/**
kJ/g-Dry Weight	*/NS	NS/NS	*/NS	**/*	**/**
Per Cent Water	NS/**	NS/NS	**/NS ،	**/**	**/**

Lake Itasca

	Nov-Feb	Feb-May	May-Jun/Jul	Jul-Aug/Sep	Aug/Sep-Dec
Wet Weight	NS/**	Sep<-**/NS	*/NS	NS/NS	**/NS
Dry Weight	NS/NA	NS/NA??	**->Dec/*	NA/**	NA/NS
Energy Content	NS/NA	Nov<-*/NS	**/*	NS/*	NS/NS
kJ/g-Wet Weight	*/NA	NS/*	**/**	NS/**	NS/NA
kJ/g-Dry Weight	*/NA	NS/NS	**/NS	**/**(Oct)	NS/NS
Per Cent Water	*/NA	NS/*	**/**	**->Dec/**	NA/NS

Ten Mile Lake

	Oct/Nov-Jan	Jan-May	May-Peak	Peak-Dec
Wet Weight	*/*	NS/*	**/**	NS/**
Dry Weight	*/NS	NS/NS	**/**	*/**
Energy Content	NA/*	Oct<-**/**	†/**	*/**
kJ/g-Wet Weight	Oct-May-->	**/NS	**/*	**/*
kJ/g-Dry Weight	Oct-May-->	*/NS	††/*	††/**
Per Cent Water	Oct-May-->	**/*	**/*	**/*

Note: * and † = significant at .05; ** and †† = significant at .01
      See text for further explanation

Appendix D.2.8. Carcass, Juveniles: Seasonal Changes

Elk Lake

	Jun-Aug	Aug-Oct
Wet Weight	††/**->Oct	NA/NA<-Jun
Dry Weight	††/**	NA/NS
Energy Content	††/**	NA/NS
kJ/g-Wet Weight	**/*	NA/††
kJ/g-Dry Weight	††/*	NA/**
Per Cent Water	*/**	NA/††

Lake Itasca

	Apr-Aug	Aug-Oct
Wet Weight	**->Oct/NA	NA/**
Dry Weight	**/NA	NS/NS
Energy Content	†/NA	NS/NS
kJ/g-Wet Weight	NS/NA	**/**
kJ/g-Dry Weight	†/NA	†/**
Per Cent Water	NS/NA	**/NS

Ten Mile Lake

	Jun-Oct
Wet Weight	*/**
Dry Weight	†/**
Energy Content	**/**
kJ/g-Wet Weight	†/**
kJ/g-Dry Weight	NS/*
Per Cent Water	†/**

Note: * and † = significant at .05; ** and †† = significant at .01. See text for further explanation.

Appendix D.2.9. Muscle, Adults: Seasonal Changes

Elk Lake

	Sept-Dec	Dec-Feb	Feb-May	May-Aug/Sep	Aug/Sep-Dec
kJ/g-Wet Weight	**/**	NS/NS	**/NS	††/**	**/**
kJ/g-Dry Weight	*/*	NS/NS	†/†	††/**	**/**
Per Cent Water	**/**	NS/NS	**/NS	**/**	**/**

Lake Itasca

	Nov-Feb	Feb-May	May-Peak	Peak-Aug/Oct	Aug/Oct-Dec
kJ/g-Wet Weight	NS/NA	<-Nov*/NS	**/*	**/**	NS/NS
kJ/g-Dry Weight	NS/NA	<-Nov**/NS	**/NS	**/**	NS/NS
Per Cent Water	*/NA	NS/**	**/**	**/**	NS/NS

Note: * and † = significant at .05; ** and †† = significant at .01
See text for further explanation

Appendix D.2.10. Ventral Fat Deposit, Adults: Seasonal Changes

Elk Lake

	Sept-Dec	Dec-Feb	Feb-May	May-Aug	Aug-Dec
Wet Weight	*/NS	NS/NS	NS/NS	NS/NS	**/NS
Dry Weight	**/NS	NS/NS	NS/NS	**/NS	**/NS
Energy Content	*/NS	NS/NS	NS/NS	**/NS	**/NS
kJ/g-Wet Weight	<-Nov*/NS	NS/NS	†/NS	**/*	†/**
kJ/g-Dry Weight	NS/*	NS/*->Mar	*/NS	††/NS	*/NS
Per Cent Water	*/NS	NS/NS	†/NS	**/*	**/**

Lake Itasca

	Nov-Feb	Feb-May	May-Peak	Peak-Aug/Oct	Aug/Oct-Dec
Wet Weight	*/NA	NS/NS	**/*	**/**	**/NS
Dry Weight	*/NA	NS/NS	**/*	**/**	**/NS
Energy Content	*/NA	NS/NS	**/*	NS/**	NS/NS
kJ/g-Wet Weight	NS/NA	NS/NS	**/**	**->Dec/**	NA/NS
kJ/g-Dry Weight	NS/NA	NS/NS	**/NS	*/**	NS/NS
Per Cent Water	NS/NA	NS/NS	NS/**	NS/††->Dec	**/**

Note: * and † = significant at .05; ** and †† = significant at .01
See text for further explanation

Appendix D.3.1. Liver, Adults: Comparisons Between Sexes

Elk Lake

	Sept	Nov	Feb	May	Oct	Dec
Wet Weight	**	**	*	NS	††	††
Dry Weight	**	**	NS	NS	††	†
Energy Content	**	**	NS	NS	††	**
kJ/g Dry Wt	NS	NS	NS	NS	NS	NS
kJ/g Wet Wt	NS	NS	*	NS	NS	NS
PerCent Water	NS	NS	*	NS	NS	NS

Lake Itasca

	Feb	May	July	Oct
Wet Weight	NS	*	NS	**
Dry Weight	NS	*	NS	**
Energy Content	NS	*	NS	††
kJ/g Dry Wt	NS	NS	NS	†
kJ/g Wet Wt	NS	NS	NS	*
PerCent Water	NS	*	NS	NS

Ten Mile Lake

	Oct	May	Sep	Dec
Wet Weight	**	NS	**	*
Dry Weight	**	NS	**	*
Energy Content	**	NS	**	NS
kJ/g Dry Wt	-	-	-	-
kJ/g Wet Wt	NS	NS	NS	NS
PerCent Water	NS	NS	NS	NS

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.3.2. Liver, Juveniles:
Comparisons between sexes.

Elk Lake

	Jun	Aug
Wet Weight	**	NS
Dry Weight	*	NS
Energy Content	*	NS
kJ/g Dry Wt	-	-
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Lake Itasca

	Aug	Oct
Wet Weight	†	NS
Dry Weight	†	NS
Energy Content	NS	NS
kJ/g Dry Wt	-	-
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Ten Mile Lake

	Jun	Oct
Wet Weight	**	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	-	-
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Note:* and † = significant at .05;
    ** and †† = significant at .01.
  See text for further explanation.

Appendix D.3.3. Gonad, Adults: Comparisons Between Sexes

Elk Lake

	Sept	Nov	Dec	Feb	May	Aug	Sep	Dec
Wet Weight	††	††	NS	†	†	††	††	††
Dry Weight	††	††	NS	†	†	††	††	NS
Energy Content	††	††	†	**	†	††	††	NS
kJ/g Dry Wt	**	**	NS	**	NS	**	††	NS
kJ/g Wet Wt	**	**	NS	**	NS	††	**	NS
PerCent Water	**	**	NS	**	NS	††	**	NS

Lake Itasca

	Sept	Feb	May	July	Oct
Wet Weight	NS	NS	**	**	**
Dry Weight	NS	NS	**	**	**
Energy Content	NS	NS	*	**	††
kJ/g Dry Wt	**	NS	NS	NS	††
kJ/g Wet Wt	**	*	NS	NS	††
PerCent Water	NS	*	NS	NS	**

Ten Mile Lake

	Oct	May	Sept	Nov	Dec
Wet Weight	†	NS	NS	††	NS
Dry Weight	†	NS	NS	††	NS
Energy Content	†	-	†	††	NS
kJ/g Dry Wt	NS	-	-	-	-
kJ/g Wet Wt	NS	-	NS	†	**
PerCent Water	NS	NS	NS	**	**

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.3.4. Gonad, Juveniles:
Comparisons between sexes.

Elk Lake

	Jun	Aug
Wet Weight	NS	**
Dry Weight	NS	††
Energy Content	NS	**
kJ/g Dry Wt	NS	-
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Lake Itasca

	Aug	Oct
Wet Weight	NS	**
Dry Weight	NS	**
Energy Content	NS	**
kJ/g Dry Wt	NS	-
kJ/g Wet Wt	NS	**
PerCent Water	NS	*

Ten Mile Lake

	Jun	Oct
Wet Weight	*	*
Dry Weight	*	NS
Energy Content	*	-
kJ/g Dry Wt	-	-
kJ/g Wet Wt	NS	-
PerCent Water	NS	NS

Note: * and † = significant at .05;
      ** and †† = significant at .01.
   See text for further explanation.

Appendix D.3.5. Digestive Tract, Adults: Comparisons Between Sexes

Elk Lake

	Sept	Nov	Feb	May	Aug	Dec
Wet Weight	**	NS	**	NS	NS	NS
Dry Weight	**	*	**	NS	NS	NS
Energy Content	NS	**	**	NS	NS	NS
kJ/g Dry Wt	NS	*	*	NS	*	NS
kJ/g Wet Wt	NS	*	**	NS	*	NS
PerCent Water	NS	*	**	NS	*	NS

Lake Itasca

	Sept	Feb	May	July	Oct
Wet Weight	NS	NS	NS	NS	NS
Dry Weight	NS	NS	NS	NS	NS
Energy Content	NS	NS	NS	NS	NS
kJ/g Dry Wt	NS	NS	NS	NS	**
kJ/g Wet Wt	NS	NS	NS	NS	NS
PerCent Water	NS	NS	NS	NS	*

Ten Mile Lake

	Oct	May	July	Dec
Wet Weight	NS	NS	*	NS
Dry Weight	NS	NS	*	NS
Energy Content	NS	NS	NS	NS
kJ/g Dry Wt	NS	NS	NA	**
kJ/g Wet Wt	NS	NS	NS	NS
PerCent Water	NS	NS	*	NS

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.3.6. Digestive Tract, Juveniles: Comparisons Between Sexes

Elk Lake

	Jun	Aug
Wet Weight	NS	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	NS	NS
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Lake Itasca

	Aug	Oct
Wet Weight	NS	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	NS	NS
kJ/g Wet Wt	*	NS
PerCent Water	*	NS

Ten Mile Lake

	Jun	Oct
Wet Weight	NS	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	NA	NA
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Note: * and † = significant at .05;
    ** and †† = significant at .01.
  See text for further explanation.

Appendix D.3.7. Carcass, Adults: Comparisons Between Sexes

Elk Lake

	Sept	Nov	Dec	Feb	May	Aug	Sep	Dec
Wet Weight	NS	**	*	NS	NS	NS	NS	NS
Dry Weight	NS	**	NS	NS	NS	NS	*	NS
Energy Content	NS	**	NS	NS	NS	NS	*	NS
kJ/g Dry Wt	NS	NS	NS	NS	NS	NS	NS	NS
kJ/g Wet Wt	NS	NS	NS	NS	NS	NS	*	NS
PerCent Water	NS	NS	NS	NS	NS	NS	**	NS

Lake Itasca

	Sept	Feb	May	July	Oct
Wet Weight	NS	NS	NS	NS	NS
Dry Weight		NS	*	NS	NS
Energy Content		NS	*	NS	NS
kJ/g Dry Wt		NS	NS	NS	NS
kJ/g Wet Wt		NS	NS	NS	NS
PerCent Water		NS	NS	NS	NS

Ten Mile Lake

	Oct	May	July	Dec
Wet Weight	*	*	NS	NS
Dry Weight	NS	NS	NS	NS
Energy Content	NS	NS	NS	NS
kJ/g Dry Wt	NS	NS	NS	NS
kJ/g Wet Wt	NS	NS	NS	NS
PerCent Water	NS	NS	NS	NS

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.3.8. Carcass, Juveniles: Comparisons between sexes.

Elk Lake

	Jun	Aug
Wet Weight	NS	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	NS	NS
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Lake Itasca

	Aug	Oct
Wet Weight	NS	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	NS	NS
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Ten Mile Lake

	Jun	Oct
Wet Weight	NS	NS
Dry Weight	NS	NS
Energy Content	NS	NS
kJ/g Dry Wt	NS	NS
kJ/g Wet Wt	NS	NS
PerCent Water	NS	NS

Note: * and † = significant at .05;
    ** and †† = significant at .01.
  See text for further explanation.

Appendix D.4.1. Liver: Comparisons Between Juveniles and Adults

Elk Lake

	Jun		Aug		Oct
	Male	Fem	Male	Fem	Fem
kJ/g Dry Wt	-	-	NS	**	-
kJ/g Wet Wt	NS	NS	NS	**	NS
PerCent Wate	††	NS	NS	*	NS

Lake Itasca

	Aug		Oct	
	Male	Fem	Male	Fem
kJ/g Dry Wt	-	-	-	-
kJ/g Wet Wt	NS	NS	NS	*
PerCent Wate	NS	NS	NS	NS

Ten Mile Lake

	Aug		Oct	
	Male	Fem	Male	Fem
kJ/g Dry Wt	-	-	-	-
kJ/g Wet Wt	NS	NS	NS	NS
PerCent Wate	NS	NS	NS	*

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.4.2. Gonad: Comparisons Between Juveniles and Adults

Elk Lake

	Jun		Aug		Oct
	Male	Fem	Male	Fem	Fem
kJ/g Dry Wt	-	-	-	-	-
kJ/g Wet Wt	NS	NS	††	NS	††
PerCent Water	NS	NS	††	NS	††

Lake Itasca

	Aug		Oct	
	Male	Fem	Male	Fem
kJ/g Dry Wt	-	-	-	-
kJ/g Wet Wt	NS	NS	NS	**
PerCent Water	NS	NS	NS	**

Ten Mile Lake

	Aug		Oct	
	Male	Fem	Male	Fem
kJ/g Dry Wt	-	-	-	-
kJ/g Wet Wt	-	-	-	-
PerCent Water	*	NS	NS	NS

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.4.3. Digestive Tract: Comparisons Between Juveniles and Adults

Elk Lake

	Jun Male	Jun Fem	Aug Male	Aug Fem	Oct Fem
kJ/g Dry Wt	NS	NS	*	NS	†
kJ/g Wet Wt	NS	*	*	NS	NS
PerCent Water	NS	*	*	NS	NS

Lake Itasca

	Aug Male	Aug Fem	Oct Male	Oct Fem
kJ/g Dry Wt	NS	NS	**	NS
kJ/g Wet Wt	NS	NS	**	NS
PerCent Water	NS	NS	**	*

Ten Mile Lake

	Aug Male	Aug Fem	Oct Male	Oct Fem
kJ/g Dry Wt	NS	NS	NA	NS
kJ/g Wet Wt	NS	NS	NS	NS
PerCent Water	NS	NS	NS	NS

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.

Appendix D.4.4. Carcass: Comparisons Between Juveniles and Adults

Elk Lake

	Jun Male	Jun Fem	Aug Male	Aug Fem	Oct Fem
kJ/g Dry Wt	NS	NS	**	NS	NS
kJ/g Wet Wt	NS	NS	**	*	NS
PerCent Water	NS	NS	**	**	NS

Lake Itasca

	Aug Male	Aug Fem	Oct Male	Oct Fem
kJ/g Dry Wt	NS	NS	**	*
kJ/g Wet Wt	*	NS	**	NS
PerCent Water	*	NS	**	NS

Ten Mile Lake

	Aug Male	Aug Fem	Oct Male	Oct Fem
kJ/g Dry Wt	**	**	NS	NS
kJ/g Wet Wt	**	**	NS	NS
PerCent Water	**	**	NS	NS

Note: * and † = significant at .05; ** and †† = significant at .01.
See text for further explanation.