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THE UNIVERSITY OF ALBERTA

FACTORS AFFECTING FIRST YEAR GROWTH OF YELLOW PERCH IN DEEP BOREAL LAKES WITH CONTRASTING PRODUCTIVITY

BY

DON H. ABBEY ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

DEPARTMENT OF ZOOLOGY

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Abstract

In order to identify factors responsible for differences in first year growth I sampled age 0 yellow perch (Perca flavescens) from 1985-1987 in four Alberta lakes with similar morphometry but with contrasting productivity. Although first year growth differences have a major impact upon subsequent fish biomass or yield, an accurate prediction of growth requires an integration of factors. I examined patterns of first year growth and size at the end of the season relative to temperature, habitat use, lake productivity, food resources and food selection.

Age 0 perch growth was fitted to the Von Bertalanffy and Gompertz growth models but a logistic model best described the growth of fish in all populations. Populations with rapidly growing individuals reached the inflection point of the logistic curve later, had a longer period of rapid growth, and higher values for asymptotic size. In fitting growth models, I found the most critical periods to be the first 80 days after hatching and at the end of the season.

Divergence in fish size among lakes occurred most rapidly in July, following migration to the littoral zone. This migration was synchronous among all lakes in a given year, occurring at water temperatures between 17 and 21 °C, and at fish sizes exceeding 25 mm total length. However, the largest fish in a given population moved onshore first and the time fish spent in the limnetic zone was inversely

correlated with fish size.

At the end of the growing season, fish in productive lakes were 3.2 times heavier and 1.4 times longer than those in unproductive lakes. Cumulative zooplankton density or biomass or cumulative total gut content biomass explained a significant amount of the variance in fish weight. This demonstrates the importance of food availability to the growth of age 0 yellow perch.

Data from ten lakes in 1988 show that age 0 perch growth can be also be predicted from measures of lake productivity. In evaluating average summer total phosphorus (TP), chlorophyll a (Chl a), zooplankton density and biomass, I found the interaction of TP and Chl a to explain 57% of the variance in fish weight. Predictions of first year growth from lake productivity are strongest at low levels of productivity ($TP < 35\ \mu g \cdot L^{-1}$) which emphasizes the importance of food availability in unproductive lakes.

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Chapter I

General Introduction

Differences in fish biomass or yield among aquatic systems are strongly correlated with first year survival and subsequent recruitment. An important factor in predicting recruitment is the rate of first year growth and the size at the end of the season. Although wide differences in first year fish growth and survival occur among lakes and among years, the factors responsible for these differences remain unclear.

The importance of early life-history stages to subsequent recruitment into adult fish populations was first suggested by Hjort (1914, 1926) and is reviewed by May (1974) and Leiby (1984). Variation in first year survival appears to be a principal cause of recruitment variation in species such as perch (Le Cren 1965; Koonce et al. 1977), walleye (Busch et al. 1975; Forney 1976), capelin (Leggett et al. 1984), and shad (Crecco and Savoy 1985).

There are strong relationships between first year growth and subsequent survival. For example, rapid growth leads to reduced mortality (Keast and Eadie 1984) and facilitates recruitment into the age 1 year class (Gutreuter and Anderson 1985). Fish that grow more quickly are able to capture larger and energetically more profitable prey (Brooks and Dodson 1965; Paloheimo and Dickie 1966; Wong and Ward 1972; Keast and Eadie 1985) which in turn enhances growth. Also, predation risk is usually less for faster growing members of a cohort (Cushing 1974; Hunter 1981; Leiby 1984; Post and Evans 1989a) enhancing survival, although Litvak and Leggett (1992) have recently challenged the widely held belief that larger and older larval fish are less vulnerable to predation. The threat of predation in turn may suppress growth of smaller members of a cohort providing an additional selective advantage for fish with more rapid growth. For example, Werner et al. (1983a) showed that small size-class bluegills exposed to largemouth bass predation moved to a suboptimal habitat which led to a significant depression of individual growth. Another factor relating age 0 growth to subsequent recruitment is that slower growing fish are more susceptible to over-winter mortality (Oliver et al. 1979; Adams et al. 1982; Post and Evans 1989b; Henderson and Cass 1991) due in part to their inability to store sufficient energy reserves.

Recruitment into subsequent year classes appears to be related to first year growth in many fish species (Cushing 1972; Methot 1983; Keast and Eadie 1984; Anthony and Fogarty 1985; Peterman et al. 1988). Identification of the factors responsible for differences in first year growth should lead to better predictions of subsequent recruitment for a given fish species and hence the biomass or potential yield of a given year-class.

In addition to the importance of first year growth to survival and recruitment, some fish species are characterized by populations with wide variations in individual growth rate (Weatherly and Gill 1987). Fish in some of these populations are stunted meaning that their growth rates are well below the potential for the species (Burrough and Kennedy 1979). Differences in individual growth rate may be apparent by the end of the first growing season and the basis for such differences among populations does not appear to be genetic (Weatherly and Gill 1981; Craig 1987; Weatherly 1990). In most cases, the underlying mechanisms responsible for differences in growth rate within the same geographic area have not been identified. The widely held hypothesis that the growth of stunted fish is food limited (Alm 1946; Deedler 1951; Shafi and Maitland 1971; Hanson and Leggett 1985) was tested using a comparative design as described in Chapter V.

My research has been designed to provide insight into factors affecting the growth of age 0 yellow perch (Perca flavescens) by comparing populations from lakes in the same geographical area. To accomplish this objective, I have focused on the growth dynamics of these fish over a four year period in lakes with similar morphometry but contrasting productivity. The following factors relating to the first year growth of perch were examined: (1) A comparison of the patterns of first year growth among lakes. (2) Developing models to describe patterns of growth. (3)

Identifying ontogenetic shifts in habitat use and evaluating the relationship of fish size and growth patterns to these habitat shifts. (4) Evaluating the impact of whole lake productivity and temperature upon growth. (5) Evaluating the influence of food resources on growth.

Yellow perch were chosen for this study because they are important as a game and forage fish (Thorpe 1977; Craig 1987), they are relatively abundant in central Alberta lakes, and they show a wide range of growth rates. Adult perch in the unproductive lakes of this study were known to be stunted when compared to perch in the productive lakes. I wanted to determine whether this pattern of differential growth among lakes started during the first growing season.

The early life history of Perca flavescens in northern lakes begins with spawning soon after ice out (Forney 1971; Amundrud et al. 1974; Collette et al. 1977; Whiteside et al. 1985) when the temperature is between 5° and 14°C (Thorpe 1977). Hatching time is temperature dependent (Hokanson and Kleiner 1974; Guma'a 1978) and usually occurs within 8-20 days after spawning. Newly hatched perch remain in the littoral zone for 7-10 days (Henderson 1977) until the yolk sac is absorbed (Post and McQueen 1988) and then move out to the limnetic zone when surface water temperatures are between 13-18°C (Faber 1967; Whiteside et al. 1985). At this time they are between 6 and 10 mm in length (Wong 1972; Henderson 1977). After 4-8 weeks in the limnetic zone juvenile perch move back into the littoral zone when they are approximately 25-30 mm in length (Wong 1972; Henderson 1977; Kelso and Ward 1977; Post and McQueen 1988; Whiteside et al. 1985). Although the early life history of Perca flavescens is well documented, the reasons for habitat shifts remain unclear. I attempt to clarify the reasons for habitat shifts within the first season in Chapters II and V.

Initially, I followed the sequence of age 0 perch habitat use and related this to fish size and water temperature. These data, presented in Chapter II, permitted comparisons with the literature and among lakes in the same area. My experimental design involved lakes of similar morphometry but contrasting productivity. Growth patterns and habitat use of age 0 perch from two eutrophic lakes with average summer total phosphorus (TP) of 35-60 $\mu g \cdot L^{-1}$ and chlorophyll a (Chl a) concentrations of 15-30 $\mu g \cdot L^{-1}$ were contrasted with patterns of growth and habitat use of fish from two mesotrophic lakes with TP of 12-13 $\mu g \cdot L^{-1}$ and Chl a of 2.5-3.2 $\mu g \cdot L^{-1}$. Use of this comparative approach over a three year period in the same geographical area was designed to provide a data set where factors such as seasonal differences, latitudinal differences, and differences in fish community composition could be separated from other environmental or biotic factors affecting first year growth and subsequent recruitment.

The relationship of fish size to ontogenetic habitat shifts has been investigated for a number of species including Arctic charr, *Salvelinus alpinus* (Naslund 1990), bluegill, *Lepomis macrochirus* (Werner and Hall 1979, 1988; Mittelbach 1981, 1983), European perch, *Perca fluviatilis* (Guma'a 1978; Coles 1981; Treasurer 1988), and yellow perch (Noble 1968, 1972; Kelso and Ward 1977; Whiteside et al. 1985; Post and McQueen 1988). However, these studies are restricted to single systems usually within a single season. This design does not allow for an assessment of among lake differences in fish size, water temperature, fish community structure, or among year differences on the timing of habitat shifts.

I hypothesized that one of the primary factors responsible for the habitat switching of age 0 perch from the limnetic to the littoral zone was food resource availability as suggested by Whiteside et al. (1985). To evaluate this hypothesis, I obtained data on comparative zooplankton densities between these two habitats. The predictions of optimal foraging theory (MacArthur and Pianka 1966) assume that organisms switch habitats when discrete habitat patches of greater profitability are encountered during foraging bouts (Charnov 1976; Parker and Stuart 1976).

Factors affecting habitat switching have been studied intensively for some fish species especially in centrarchids (Werner et al. 1983b; Mittelbach et al. 1988), in coregonids

(Naesje et al. 1991; Sandlund et al. 1992) and in European perch (Persson and Greenberg 1990a, 1990b). However, much of this research has focused on age 1^+ or 2^+ juveniles or adults. Studies evaluating age 0 yellow perch habitat switching in terms of diet choice and habitat profitability are limited to the work of Post and McQueen (1988) in Lake St. George, Ontario. My research, incorporating data from four lakes differing in productivity and zooplankton density was designed to provide a comparative basis for evaluating the above hypothesis.

Mathematical models of fish growth have many applications including predictions of size-at-age for specific cohorts (Allen 1976; Craig 1980), size distributions within cohorts (Wismer et al. 1985; DeAngelis and Huston 1987) and the maximum size individuals within a population could potentially reach (Ricker 1975). These growth models have typically been derived from data on adult fish in populations where sampling was infrequent, often on an annual basis. Some workers have used these models to describe fish growth within a single season (Hamilton and Powles 1979; Post 1987). Predicting seasonal growth of age 0 fish using a model developed to predict asymptotic size or size-at-age of adult fish requires validation of the model prior to the new application. Also, Moreau (1987) indicates that predicting seasonal growth patterns requires intensive sampling over the entire growing season. These conditions for intensive sampling and model validation are dealt with in Chapter III.

In identifying the patterns of first year growth among lakes within a given season and over three growing seasons I obtained data on a weekly or biweekly basis from two weeks after hatching until the end of the growing season. Chapter III fits these data on growth to the Von Bertalanffy, logistic, and Gompertz growth models to evaluate which model best describes age 0 yellow perch growth and to analyze the problems associated with modelling growth within the first season. I integrate data from the literature with my data to show how the timing of sampling affects the choice of a growth model for a given data set. An important objective of this part of my research was to determine whether the general mathematical models used to describe fish growth would adequately describe the growth of age 0 fish. I also wanted to establish guidelines for suitable sampling regimes so that accurate predictions of age 0 fish growth can be made with minimum effort.

The implications of "cascading trophic interactions" (Carpenter et al. 1985; Mills et al. 1987) indicate that both a bottom up and top down control of biomass occurs in aquatic systems (Shapiro 1980; Mills and Schiavone 1982; Carpenter et al. 1987; McQueen et al. 1989). Phytoplankton biomass has been found to be positively correlated with phosphorus concentration (Stockner and Shortreed 1985;

Trimbee and Prepas 1987) as have the biomass of zooplankton (Hanson and Peters 1984) and fish (Hanson and Leggett 1982). Mittelbach et al. (1988) and McQueen (1990) review the implications of these trophic level interactions and Mittelbach et al. (1988) suggests that models with greater predictive power across a productivity gradient will result as populations as well as the resources they use are subdivided into separate size or age classes.

In Chapter IV, the experimental design focuses specifically on age 0 fish in testing the hypothesis that fish size at the end of the season is positively correlated with total phosphorus concentration. Ten lakes were selected in 1988 with similar morphometry but with average summer TP levels ranging from 11-51 $\mu g \cdot L^{-1}$. Water samples for TP and Chl a and zooplankton samples were taken on a monthly basis from each lake from the first of May to the end of August and age 0 perch were collected from each lake at the end of August. This permitted an evaluation of the relationship between age 0 perch size at the end of the season and TP, Chl a, and zooplankton resources to see whether bottom up control was a significant factor in first year fish growth. Chapter IV shows that the size of age 0 perch at the end of the growing season can be predicted from average summer TP and Chl a.

Once I established that divergence in growth rates of age 0 perch populations occurred early in the season, I hypothesized that differences in food resources were the primary factor responsible for these growth differences. Specifically, I wanted to determine if fish in unproductive lakes were experiencing food limited growth. Chapter V presents data supporting the hypothesis of food limited growth.

This interaction between food resources, prey selection and consumption has been investigated for many adult fish populations (Paloheimo and Dickie 1966; Rice et al. 1983). Within a single lake, data on feeding energetics of juvenile fish is available for a number of species including bluegill, *Lepomis macrochirus* (Mittelbach 1981, 1983; Werner and Hall 1988), yellow perch (Mills and Forney 1981; Michaletz et al. 1987; Post and McQueen 1988; Mills et al. 1989), walleye (Forney 1966; Michaletz et al. 1987) and lake whitefish (Taylor and Freeberg 1984). However, comparisons of feeding energetics of age 0 fish among lakes in the same geographical area are lacking. In the four lakes in this study, I have obtained zooplankton data from both the limnetic and littoral zone and analyzed the gut contents of age 0 perch collected in these same zones to identify the impact of zooplankton food resources, prey selection and consumption upon growth rates and size of age 0 perch. Because age 0 perch in this study were almost exclusively planktivorous, this design should determine whether growth was limited by available food.

The unique contributions of this thesis are (1) the high resolution data set on age 0 fish growth in natural environments, (2) the relationship of fish size to habitat switching and to the time spent in a given habitat, (3) the broad spectrum approach where growth patterns are compared in lakes of contrasting productivity over a three year period, (4) the integration of data on TP, Chl *a*, zooplankton density, biomass and species composition with feeding patterns to determine the impact of bottom up trophic level interactions, and (5) the demonstration that growth is food limited in unproductive lakes.

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Chapter II

Interaction between size and habitat use in four age 0 yellow perch populations

Introduction

Ontogenetic shifts in diet or habitat use have been described for many fish species (see review by Werner and Gilliam 1984). However, the factors that trigger the movement of animals from one habitat to another are not well understood. Many investigators have hypothesized that shifts in habitat use depend on predation risk (Werner and Hall 1988) and available resources (Mittelbach et al. 1988; Persson 1990; Persson and Greenberg 1990). Because predation risk and resource availability depend on body size (Mittelbach 1981; Osenberg et al. 1988; Werner and Hall 1988; Hovenkamp 1992), the timing of habitat shifts should be a function of growth rate.

Larval fish should choose a habitat offering the best compromise between minimizing mortality and maximizing growth in their first year. The conditions dictating this choice will often be a function of fish size. Smaller fish are often more susceptible to predation (Nielsen 1980; Werner et al. 1983; Tonn and Paszkowski 1986; Post and Evans 1989a) and are exposed to a larger predatory field than larger fish (Folkvord and Hunter 1986). Increased risk of predation may also limit ingestion rates (Mittelbach 1986; Angradi 1992) further limiting growth. Smaller fish also have lower available energy stores relative to metabolic rate and are probably more susceptible to starvation than larger fish (Ware 1975; Hunter 1981; Buijse and Houthuijzen 1992), especially if zooplankton of a suitable size become limiting (Frank and Leggett 1986). Thus the relationship between growth rate and habitat use needs to be clearly delineated if meaningful predictions of age 0 mortality rates and age-1 recruitment are to be made.

There are few comparative data on the extent of variation in first-year growth of fish among lakes in a limited geographic area. The factors responsible for growth differences in a given geographic area also require further investigation. Differences in first-year growth within a species have been observed when fish from widely differing environments are compared (Shafi and Maitland 1971; Hamilton and Powles 1979; Sinclair et al. 1982). However, the spatial and temporal variability of these data may prevent the linking of variations in first-year growth or survival to environmental factors (Gulland 1965; May 1974, Dahlberg 1979; Fortier and Leggett 1985; Houde 1989). Comparative data on growth patterns of age 0 fish within a single geographic area will assist in separating the effects of climatic factors from biotic factors that affect growth and habitat use.

Within a given geographic area, comparative data on growth rates and/or size-at-age of adult fish are more abundant. Marked differences in fish growth among lakes have been found for populations of bluegill, Lepomis macrochirus (Gerking 1966; Snow 1969; Wiener and Hanneman 1982), white suckers Catostomus commersoni (Trippel and Harvey 1987) European perch Perca fluviatilis (Shafi and Maitland 1971; Rask 1983), and yellow perch Perca flavescens (Grimaldi and Leduc 1973; Ryan and Harvey 1980; Boisclair and Leggett 1989). These differences appear to develop early in life, based on back-calculated lengths for age-1 fish (Ryan and Harvey 1980; Wiener and Hanneman 1982).

Most among-lake comparisons of first-year growth report size at age-1 from back-calculated data (Shafi and Maitland 1971; Goldspink and Goodwin 1979). Snow (1969) reported the size at the end of the first season of growth for eight fish species from Wisconsin lakes but gave no analysis of first-year growth patterns. Only three studies (Bidgood 1973; Post 1987; and Treasurer 1988) have analyzed patterns of first-year fish growth in different lakes in the same geographic area. None of these studies related first-year growth among lakes to ontogenetic niche shifts although Whiteside et al. (1985b) and Post and McQueen (1988) report on ontogenetic distributional patterns of age 0 yellow perch within a single lake.

The purpose of this study was to evaluate the role of climatic factors, lake productivity and fish size on the timing of ontogenetic niche shifts, particularly migration between the limnetic and littoral zones. I quantified the growth differences of age 0 yellow perch within and among four lakes of contrasting productivity over 3 years. The unique comparative approach of this study was designed to identify the relative importance of common environmental factors, such as temperature and photoperiod, from factors differing among lakes, such as lake productivity and fish size, on the timing of ontogenetic niche shifts.

Study Area

Patterns of growth and habitat use of age 0 yellow perch were determined from 1985 to 1987 for four central Alberta lakes: Amisk, Baptiste, Long and Narrow. These lakes are located within a 60 km radius of the Meanook Biological Station near Athabasca, Alberta. The trophic status of the study lakes (as determined by mean summer trophogenic phosphorus; Wetzel 1983) ranged from meso-eutrophic to eutrophic. Mean summer chlorophyll a (Chl a) concentrations ranged from 2.5 to 33.3 $\mu g \cdot L^{-1}$. Total phosphorus (TP) used as an index of lake productivity, ranged from 12 to 13 $\mu g \cdot L^{-1}$ in unproductive Narrow and Long lakes to 34 to 60 $\mu g \cdot L^{-1}$ in productive Amisk and Baptiste lakes. The lakes are all located in glacial till and are surrounded by southern mixed wood boreal forest but have a five-fold range of productivity (Table II-1). Amisk, Baptiste and Long lakes have two distinct basins but the individual basin morphometry is similar among the four lakes.

Materials and Methods

To determine if the time of spawning was equivalent among lakes, ripe female yellow perch were collected during the three field seasons with Windermere perch traps (Le Cren et al. 1972) with 3 cm mesh. Gill nets (5 cm mesh), fyke nets (12 mm mesh), and a bag seine described below were also used. Visual location of egg masses was possible in the clear waters of the two unproductive lakes. During 1986 yellow perch egg masses were collected from Long and Narrow lakes; in 1987, egg masses were collected from Amisk, Long and Narrow lakes. These egg masses were maintained in flow-through aquaria in the laboratory. Temperature of the well water supplying each aquarium was regulated to within 2 °C of lake water temperatures. Embryonic development in the egg masses collected from Long and Narrow lakes in 1986 and 1987 was advanced and hatching of these egg masses commenced within 3 d of collection. Eggs collected in Amisk Lake in 1987 were at the first cleavage stage of development and were maintained for 10 d prior to the onset of hatching. Newly hatched larval yellow perch were measured to determine their total length (TL) at hatching.

Larval yellow perch were collected in the limnetic zone with a midwater trawl, modified from that of Gjernes (1979). The trawl measured 2.25 x 2.26 m at the mouth and was 7.6 m long. The body was constructed from 1.27, 0.64, and 0.32-cm (bar measure) knotless nylon panels with a 0.7-mm mesh plankton net and plankton bucket (0.25-mm mesh) attached to the 30-cm-diameter cod end (Figure II-1). This net was effective in retaining zooplankton in addition to the smallest larval fish (6 mm TL) as a result of the channelled flow pattern created by tapered design and the 0.7 and 0.25 mm mesh at the cod end of the net. Tow speeds with this net averaged 0.6 $m \cdot sec^{-1}$ which precluded catching age-1 and larger yellow perch; however, age 0 perch up to 51 mm TL were routinely caught. The mouth of the net was spread by attaching 6.4-kg weights to each end of a 2.4-m length of 2.5-cm diameter steel pipe at the bottom of the net. Floats attached to a similar pipe at the top of the net provided sufficient buoyancy to keep the net on the surface. The pipe was painted black to reduce its visibility. Since preliminary sampling in 1985 and data from Noble (1972), Lyons (1987) and Post and McQueen (1988) indicated that limnetic larval yellow perch are concentrated between 0 and 2 m, most trawls were done in this stratum of the water column. Deeper trawls, between 2 and 4 m, were made by attaching 2.5-m lines between the surface floats and the top bar of the net.

The trawl was rigged with 6-mm nylon rope (Figure II-2). A current meter from a Clark-Bumpus Sampler was attached to the upper towing bridle prior to each tow. The meter was calibrated with nine replicate 100-m tows (mean, 26.96 units; SD, 0.44) to allow for calculation of the water volume filtered by the net during the collection of each sample.

The trawl was towed by a 4.9-m aluminum boat with a 14.9-kW (20 hp) outboard motor. A 90-cm-high metal frame fastened onto the stern seat of the boat kept the towing line clear of the motor. This line was attached to a hand winch with a drum (2.3-cm diameter; 17.5-cm wide) attached to a movable winch box (40 x 45 x 80 cm) that was secured in the center of the boat.

Amisk Lake (productive) and Narrow Lake (unproductive) were sampled weekly from the end of May through the end of August in 1985 and 1986 and twice monthly over the same period in 1987. Baptiste and Long lakes were sampled from the end of May through the end of August every 3 to 4 weeks in 1985 and twice monthly in 1986 and 1987.

Midwater trawl sampling was continued until the catch of age 0 yellow perch dropped to near zero in a sequence of four tows filtering an average of 1,350 m^3 of water per tow. This point was defined as the end of the limnetic phase for age 0 perch. For each midwater trawl, age 0 perch density ($\# \cdot 1000\ L^{-1}$) was calculated. Due to the large volume of water filtered per tow, fish aggregations due to schooling behavior were not considered to be an important factor affect the estimates of fish density.

Following their movement to the littoral zone, age 0 yellow perch were collected with a bag seine (15.2 x 1.8 m) with 6-mm mesh (bar measure) in the wings and 3-mm mesh in the bag (1.8 x 1.8 x 1.8 m). During 1986 and 1987, a large seine (56 x 3 m) with 9.5 mm mesh (bar measure) was also used. The small seine effectively retained age 0 yellow perch as small as 22 mm TL as indicated by length frequency analysis of catches and visual observations of escapement in the clear water of Narrow and Long lakes. Escape of fish smaller than 25 mm TL was common from the large seine but it effectively retained fish larger than 25 mm TL.

Seining was started in the littoral zone on July 16 1985, July 8 1986, and on June 29 1987. By mid-July age 0 yellow perch were expected to have started their littoral zone migration, based upon the time since hatching and their size in trawl catches in relation to the expected size (≥25 mm TL) at the time of migration based upon data from the literature. Age 0 yellow perch were sampled in mid-October during the three field seasons to determine their size distribution prior to ice formation. Only Amisk and Narrow lakes were sampled in October, 1985; October samples were obtained from all four lakes in 1986 and 1987.

Yellow perch collected in the trawls and seines were killed immediately with a 0.15% aqueous solution of 2-phenoxyethanol and fixed in 4% formalin. When fresh and preserved TLs and weights were compared from three separate sets of age 0 fish, there was no significant change in either length or weight after 7 d in preservative except for one group which did show a significant increase in weight (analysis of variance [ANOVA] $\underline{P}<0.02$) following preservation. All TLs and weights reported are from preserved specimens; no correction factor was applied.

Total lengths of at least 30 preserved age 0 yellow perch from each sample date were measured to the nearest 0.1 mm with a microscope fitted with an ocular micrometer. Blotted wet weights were determined to the nearest milligram. Once the fish exceeded 15 mm TL, vernier calipers were used to measure lengths to 0.1 mm and weights were determined to the nearest 0.01 g.

Weights of yellow perch (6-36 mm TL) collected in Amisk and Narrow lakes in 1985 prior to July 30 were estimated from log length (TL)-log wet weight (W) regression equations. The equation for Narrow lake was log W = 3.87 log TL - 6.303 ($\underline{r}^2=0.98$, $\underline{N}=287$); Amisk Lake was log W = 3 log TL - 6.607 ($\underline{r}^2=0.99$, $\underline{N}=266$). All fish taken from Baptiste and Long lakes in 1985, and as well as the fish collected from all lakes in 1986 and 1987, were weighed and measured directly.

Absolute growth in length ($mm \cdot d^{-1}$) was calculated for each lake over the entire season from the end of May to mid-October. Limnetic and littoral zone growth rates were calculated with the mean length of age 0 yellow perch first caught in the littoral zone and the mean length of fish remaining offshore on the same date to determine the range of growth rates for the limnetic or littoral period. Although the fish remained in the littoral zone through mid-October, growth rates were calculated for the period from the first catch of fish in this zone to the last sample taken near the end of August.

Productivity data for three of the four lakes were obtained from E. E. Prepas (University of Alberta, unpublished data) and from Chambers and Prepas (1988). Total phosphorus and Chl _a_ measurements were carried out from May through August in all of the lakes. Baptiste Lake productivity data for 1985 were obtained from Alberta Environment (Edmonton, Alberta). Total phosphorus was measured with the method of Menzel and Corwin (1965) as modified by Prepas and Rigler (1982). Chlorophyll _a_ levels were determined by the method of Ostrofsky as outlined by Bergmann and Peters (1980). Alberta Environment performed Chl _a_ analyses with the acetone extraction and fluorometric procedure of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965).

Water temperatures were measured with a thermistor (Montedoro-Whitney TC-5C) accurate to 0.1 °C. Measurements were taken at the surface (8 cm) and at 1-m intervals to a depth of 5 m during each sampling period from late May through the end of October.

Results

Size at Hatching

Larval yellow perch (mean TL, 5.70 mm; SD, 0.29 mm; N, 32) hatched from eggs collected in Narrow Lake in 1986 were significantly larger (ANOVA $P<0.001$) than those (mean TL 5.25 mm; SD, 0.20 mm; N, 30) from Long Lake. The TLs of larval yellow perch hatched from eggs collected in Amisk (mean TL, 5.93 mm; SD, 0.21 mm; N, 40), Long (mean TL, 5.92 mm; SD, 0.66 mm; N, 20) and Narrow (mean TL, 6.18 mm; SD, 0.24 mm; N, 49) lakes in 1987 were significantly greater (ANOVA $P<0.001$) than those of newly hatched larvae in Long and Narrow lakes in 1986. Newly hatched larval yellow perch from Narrow Lake in 1987 were significantly larger (ANOVA $P<0.025$) than those from Amisk and Long lakes, which did not differ significantly in size (ANOVA $p>0.75$). These variations in size of newly hatched larval perch may result from variations in the numbers of eggs per adult affecting egg size. In order to identify patterns in egg size or size of larval perch at hatch among lakes more egg masses should be sampled in the littoral zone.

Offshore migration

Newly hatched larval yellow perch were first caught offshore between May 26 and June 4, twenty-six to 29 d after ice out. Trawls were done prior to this time in Amisk Lake in 1985 and 1986 and in Long and Narrow lakes in 1986, but no larval yellow perch were caught. First-caught fish ranged from 6.6 to 8.6 mm TL and from 0.79 to 3.78 mg (Table II-2). When fish were first caught in trawls, the numbers caught ranged from 0 to 20 fish as compared to catches of more than 100 fish per trawl by mid-June. Long and Baptiste lakes were first sampled on June 7, 1985. The TLs of the fish caught on this date as well as the surface water temperatures suggest that larval yellow perch migrated to the limnetic zone of Long and Baptiste lakes prior to June 7.

At the time of limnetic migration, among-year differences in TL and weight within lakes were relatively small (Table II-2). Larval size at limnetic migration did not differ significantly between Amisk and Narrow Lakes in 1986 but larvae from Long Lake were significantly longer (ANOVA $\underline{P}<0.001$; Newman-Keuls $\underline{P}<0.05$) than those from the other two lakes at this time. In Narrow Lake fish were significantly smaller (ANOVA $\underline{P}<0.001$; Newman-Keuls $\underline{P}<0.05$) at the time of limnetic migration in 1985 than fish from Amisk Lake. In 1987, total length at the time of limnetic migration did not differ significantly among three of the four lakes. The exception was Narrow Lake where larval yellow perch were significantly smaller (ANOVA $\underline{P}<0.001$; Newman-Keuls $\underline{P}<0.05$). Larval size at the time of migration to the limnetic zone was smallest in 1987 in all lakes compared to 1985 and 1986 (Table II-3).

Densities of age 0 perch in the limnetic zone during the month of June are shown in Table II-4. In 1985 and 1986, age 0 perch densities in unproductive Narrow Lake were significantly greater (unpaired t-test, $p<0.05$) than those in productive Amisk Lake. However in 1987, June age 0 perch densities Narrow Lake were significantly less than any of the other three lakes. In 1988, densities among lakes did not differ significantly except for age 0 perch in Narrow Lake which exceeded the density of those in Baptiste Lake.

Onshore Migration

Patterns of onshore movement of age 0 yellow perch differed consistently between productive Amisk and Baptiste lakes and unproductive Narrow and Long lakes. The onset of littoral zone migration was essentially synchronous in a given year in all lakes in which sampling frequency was sufficient to permit comparisons (Table II-5). At this time, juvenile fish are distinguished by adult pigmentation patterns and complete fin differentiation and the timing of migration was identified by their disappearance from trawl samples offshore and their appearance in onshore seine samples or in visual surveys of the littoral zone. At the onset of onshore migration, TLs and weights of juvenile yellow perch were similar between productive lakes. However, at this same time, juvenile yellow perch from unproductive Narrow Lake were significantly smaller (ANOVA

$P<0.01$) than those from productive lakes (Table II-5). This indicates that factors other than fish size are responsible for initiating onshore migration.

Onshore migration started in mid-July in 1985 and 1986 and lasted over a period of approximately 7 to 10 d in the productive lakes and 28 to 35 d in the unproductive lakes. The duration of onshore migration was defined as the time from the first catch of age 0 fish in the littoral zone to the time when fish were no longer found in the limnetic zone as determined by a 0-catch in four or more midwater trawl samples. In 1987, onshore migration started at the end of June when the juvenile yellow perch were much smaller in comparison to previous years. The duration of migration in 1987 ranged from 28 d in productive lakes to as long as 40 d in unproductive lakes. This indicates that fish size is an important factor in determining the duration of onshore migration.

During onshore migration, it was possible to catch juvenile yellow perch on the same date both onshore in seines and offshore in trawls. Fish caught in the limnetic zone during the 3 years in any given lake were always significantly smaller (t-test $P<0.05$) than those caught in the littoral zone on the same date (Table II-6), except for Amisk Lake in 1985 where the limnetic zone sample was small and in 1987 where TLs did not differ between zones. Limnetic versus littoral zone size differences are illustrated for Narrow and Baptiste lakes in Figure II-3.

End of Season Size

The size of juvenile yellow perch at the end of the first growing season (October) differed significantly (ANOVA $p<0.001$) between productive and unproductive lakes (Table II-8). Age 0 fish from Amisk and Baptiste lakes were 3.2 times heavier and 1.4 times longer than those from Narrow and Long lakes. In both Amisk and Narrow lakes, over the 3 years, the largest age 0 yellow perch were collected in 1985. Variability in growth among lakes in 1987 was higher than in the previous 2 years. Age 0 perch from Long Lake (unproductive) in 1987 attained only 60% and 18% of the TL and weight, respectively, of Amisk lake (productive) yellow perch. Figure II-4 illustrates the dramatic divergence in fish size over the first season between productive and unproductive lakes.

Discussion

My data show that the time of onshore migration is synchronous among lakes in the same geographic area. Although onshore migration occurred at the same time, age 0 yellow perch from the productive lakes (Amisk and Baptiste) were significantly larger than those from unproductive Narrow Lake. The significant size differences among years and lakes at the time of onshore migration indicate that size is not the proximate factor influencing the onset of onshore migration in these central Alberta lakes. A comparison of the thermal regime in the four lakes over 3 years suggested that a critical minimum temperature of 17 to 21 °C may be the proximate factor for the initiation of onshore migration. This is in close agreement with the available data from the literature, which show that onshore migration occurs at temperatures from 16 to 21 °C with only one exception (Table II-9). The influence of temperature as a factor in triggering onshore migration of age 0 perch requires further study to determine the relationship between lake warming and fish movement.

Photoperiod did not appear to trigger onshore migration of juvenile yellow perch. My results indicate a difference of at least 2 weeks in the onset of littoral zone migration over a 3-year period. Data from the literature (Table II-9) show variation of at least 46 d in the onset of littoral zone migration by juvenile perch. Analysis of these data is difficult as a result of differences in sample design and the time of sampling, location of the lake systems, and among year variability. However, the extent of variation in the timing of onshore migration among these studies supports the argument that photoperiod does not trigger onshore migration. In some cases, migration started prior to the summer solstice (June 21) when photoperiod is increasing. However, in the present study as well as others, onshore migration did not begin until after June 21 when photoperiod was decreasing.

Although my data were not definitive, predator avoidance seemed to be of minor importance in causing juvenile yellow perch to move onshore in unproductive lakes but may be important in productive lakes. The only limnetic piscivores in unproductive Narrow and Long lakes are adult yellow perch. Although adult yellow perch may be cannibalistic (Post and Evans 1989a), they have a very low population density relative to age 0 yellow perch in the two unproductive lakes (W. Jansen, University of Alberta, unpublished data). Predator avoidance could be an important factor triggering the more rapid onshore migration in Amisk and Baptiste lakes. These productive lakes contain walleye Stizostedion vitreum vitreum, and once juvenile yellow perch develop pigmentation and become more visible in open water, predation pressure could increase dramatically (Kelso and Ward 1977). Juvenile yellow perch would then avoid predators more effectively in the structurally complex littoral zone habitat (Werner and Hall 1988).

My data show that differences in limnetic growth among the lakes were not caused by temperature differences. Temperature does markedly affect fish growth (Koonce et al. 1977; Brett 1979; Anthony and Fogarty 1985) but when size comparisons of juvenile yellow perch were made based upon equivalent time periods as measured in cumulative °C·d

(Mills et al. 1989), I found among-lake differences of up to 27.8% and 57.8% in TL and weight, respectively, for 1985 and 1986. This shows that temperature differences among lakes do not explain the divergence in age 0 perch growth in the limnetic zone.

The size of juvenile yellow perch at the time of onshore migration was an important factor affecting the duration of migration. Juvenile yellow perch from the unproductive lakes began moving onshore at the same time but at a significantly smaller size than those from productive lakes. The duration of onshore migration in the unproductive lakes was 1.5 to 4.0 times longer than in the productive lakes. Onshore migration in 1987 occurred at a significantly smaller size among all lakes, and the duration of migration extended 18-21 d longer in the productive lakes and 5-12 d longer in unproductive lakes compared to 1985 and 1986 demonstrating the importance of size to the duration of onshore migration.

Juvenile yellow perch caught offshore in all lakes at the time of onshore migration were significantly smaller than those caught nearshore on the same date. Clearly, larger juvenile fish in a given lake were the first to move into the littoral zone, a pattern also observed by Coles (1981) and Treasurer (1988). However, smaller fish caught in limnetic zone of the productive lakes at the onset of littoral migration were either significantly heavier or did not differ in weight in four out of five cases compared with fish caught in the littoral zone of unproductive lakes at the same time. This indicates that fish size is not the primary factor initiating onshore migration unless a proximate size required to trigger migration differs both among lakes and within a given lake among years.

Although my data indicated that onshore migration is not tightly linked to fish size, a minimum TL of 25 mm and a temperature exceeding 17 °C was reached in all cases before juvenile yellow perch were caught in the littoral zone. This suggests that a size or temperature threshold may need to be reached prior to the onset of migration. In 1987, onshore migration was not completed by [illegible] August in the unproductive lakes, as was the case in Lake St. George in 1984 (Post 1987). Age 0 perch in Long Lake exhibited very slow growth in 1987 (Table II-7) and smaller fish in this population were still present in the limnetic zone at the end of August of that year. Although food resources may be more abundant (Whiteside et al. 1985a) and diverse in the littoral zone, attainment of a minimum size may be necessary to offset the increased risk of more abundant littoral zone piscivores.

In the four study lakes, initial size differences at the time of hatching or during limnetic migration were not reflected in the size differences observed at the end of the first growing season. Yellow perch that hatched in unproductive Narrow Lake were larger in both 1986 and 1987 than those in the other lakes. At the time of migration to the limnetic zone, yellow perch in Narrow Lake were smaller than those from the other lakes in 1987 and not significantly different in size from Amisk Lake yellow perch in 1986.

Variability in growth of larval yellow perch among the lakes during the 7-10-d post-hatch period prior to offshore migration could be caused by differences in water temperature or feeding regime. My results indicated that this early differential growth among lakes is related to lake temperature, but I did not analyze feeding relationships during this period. Between May 6 and May 27, when egg incubation and post-hatch larval development occurred, degree-days among lakes varied, ranging from 237 to 255 in 1987 and from 201 to 220 in 1986. In both years the smallest larval yellow perch at the onset of limnetic migration were from the lake with the lowest number of degree-days. Since exact times for hatching were not available, lower temperatures may also have resulted in delayed hatching and a shorter period for growth prior to offshore migration. Initial growth of the post-hatch yellow perch larvae would increase with increased temperature, if the optimal temperature range for rapid growth and conversion efficiency was not exceeded (Brett 1976), and the amount of food available was sufficient to support maximum consumption rates.

Small age 0 yellow perch from unproductive lakes are less likely to survive to age 1 because size selective mortality (Post and Prankevicius 1987) would be greater than that of larger conspecifics in more productive systems. Size differences at the end of the growing season have a dramatic impact upon overwinter survival and recruitment to age 1 as shown for yellow perch (Post and Evans 1989b), smallmouth bass Micropterus dolomieui (Oliver et al. 1979), sockeye salmon Oncorhynchus nerka (Henderson and Cass 1991) and white perch Morone americana (Johnson and Evans 1990).

At the end of the first season of growth, age 0 yellow perch from the productive lakes in this study were 3.2 times heavier than those from unproductive lakes but comparable in size with age 0 perch from other north temperate lakes (Table II-10). In unproductive Long and Narrow lakes, age 0 perch were much smaller (63% of TL) than fish from all but Dubh Lochan, Scotland and West Blue Lake, Manitoba (Table II-10). These lakes are also unproductive systems with stunted populations of European and yellow perch, respectively (Shafi and Maitland 1971; Ward and Robinson 1974; Kelso and Ward 1977).

Sizes of age 0 yellow perch in the two productive lakes diverged rapidly from those in the unproductive lakes following onshore migration. I hypothesize that the low growth of age 0 yellow perch in unproductive Long and Narrow lakes results from food limitation (Paloheimo and Dickie 1966), lack of suitable size categories of food (Frank and Leggett 1986; Mills et al. 1989) or lack of suitable taxa (Mills and Forney 1981) of zooplankton prey. Resource-limited growth of age 0 fish in productive versus unproductive lake systems is an area requiring further investigation and is addressed in Chapter V of this thesis.

Table II-1. Characteristics of Amisk, Baptiste, Long and Narrow lakes in Alberta, Canada. Total phosphorus (TP) and chlorophyll a (Chl a) concentrations are average summer values over a 4-to 8-year period for the trophogenic zone. Mean depth (z) and maximum depth (MAXz) are in meters.

Lake	Lat. North	Long. West	Area[a] (km²)	Depth[a] (z)	Depth[a] (MAXz)	TP[a] (µg/L)	Chl a[a] (µg/L)
Amisk N	54°35'	112°39'	1.89	[illegible]	30	34.4	14.5
Amisk S	54°35'	112°39'	2.27	19.4	60	37.6	18.7
Baptiste N	54°45'	113°33'	4.74	5.9	15	60.0	33.3
Baptiste S	54°45'	113°33'	4.43	12.7	25	50.8	29.7
Long	54°35'	113°37'	1.62	9.4	30	13.0	3.2
Narrow	54°37'	113°37'	1.14	14.2	35	11.9	2.5

[a] Morphometric and productivity data were obtained from Prepas and [illegible] (1983), Prepas and Vickery (1984), Trimbee and Prepas (1987), Alberta Environment (Edmonton, Alberta) and from E. E. Prepas (University of Alberta, unpublished data).

Table II-2. Mean total length and wet weight of larval yellow perch at the time of migration to the limnetic zones of four lakes in Alberta, Canada. MWT = midwater trawl.

Lake	First date of		Total length (mm)	SD	Wet weight (mg)	SD	$\underline{N}$	Surface H_2O temp (°C)
	MWT	Catch						
			1985					
Amisk	May 31	Jun 3	8.4	1.75	3.31	3.0	94	14.7
Long	Jun 7[a]	Jun 7	8.6	1.28	2.00	1.0	37	16.7
Narrow	May 30[a]	May 30	6.9	0.47	0.89	0.23	15	14.9
			1986					
Amisk	May 21	Jun 4	7.2	0.58	2.02	0.84	46	16.8
Baptiste	May 29[a]	May 29	--	--	--	--	1	17.1
Long	May 18	Jun 3	8.5	0.76	3.78	1.41	62	17.9
Narrow	May 20	Jun 3	7.5	0.60	2.19	0.87	126	17.5
			1987					
Amisk	May 27[a]	May 27	7.0	0.34	1.0	0.2	25	15.1
Baptiste	May 27[a]	May 27	7.2	1.18	1.7	1.11	3	14.4
Long	May 26[a]	May 26	7.2	0.69	1.58	0.61	52	12.7
Narrow	May 26[a]	May 26	6.6	0.79	0.79	0.37	58	14.3

[a] Sampling frequency was not adequate to preclude the possibility of earlier limnetic zone migration

Table II-3. Among year size comparisons (ANOVA followed by Newman-Keuls; $P<0.05$) of the total length (TL) and wet weight (WT) of larval yellow perch at the time of migration to the limnetic zone.

Amisk Lake

ATL85 > ATL86 = ATL87

AWT85 > AWT86 > AWT87

Long Lake

LTL85 = LTL86 > LTL87

LWT86 > LWT85 > LWT87

Narrow Lake

NTL86 > NTL85 = NTL87

NWT86 > NWT85 > NWT87

Table II-4. Mean limnetic zone density (Den.) (#·1000 L^{-1}) of age 0 yellow perch between productive and unproductive lakes during the month of June (JN). A = Amisk, B = Baptiste, L = Long, N = Narrow, M = May, JN = June, JL = July. n = number of midwater trawls during the sampling period.

Unproductive Lakes						Productive Lakes					
Lake	Yr	Period	Den.	SD	n	Lake	Yr	Period	Den.	SD	n
N	85	JN2-JL2	167.0	173.4	32	A	85	JN3-JL3	15.1	17.6	27
N	86	JN2-JL1	730.0	1411.8	196	A	86	JN4-JL2	57.0	73.9	35
L	86	JN3-26	101.8	89.8	7	B	86	JN15-26	20.5	12.4	3
N	87	JN1-JL1	57.7	70.0	23	A	87	JN4-JL2	344.6	523.4	17
L	87	JN17-29	318.7	245.8	9	B	87	JN3-30	136.5	134.7	13
N	88	JN1-28	147.0	61.4	9	A	88	M30-JN27	176.7	234.2	10
L	88	JN1-28	101.7	62.9	7	B	88	JN1-28	43.7	43.9	8

Table II-5. Time of onset of onshore migration of juvenile yellow perch in four lakes in Alberta, Canada. SWT = surface water temperature; Degree (°C)-days: June 2-July 16 1985 and 1986; May 26-July 1 1987. All length and weight comparisons among lakes within years are significantly different (t-test; P>0.05) except as indicated. Total length or weight comparisons from a given lake among years are significantly different except for total length in Baptiste and Long lakes between 1985 and 1986 and in Narrow Lake between 1986 and 1987. JN = June and JL = July.

Lake	Date	SWT (°C)	°C days (d)	Total length (mm)	SD	Wet weight (mg)	SD	N
				1985				
Amisk	JL 17	21.0	785	38.7[c]	2.4	842	192	48
Baptiste	JL 22[a]	22.4	835	36.0[d]	4.3	541[e]	162	14
Long	JL 23[a]	20.6	857	37.6[c,d]	4.4	589[e]	187	50
Narrow	JL 16	20.2	766	32.1	2.1	304	86	99
				1986				
Amisk	JL 17	18.4	801	33.1[f]	2.2	412[g]	135	3
Baptiste	JL 13	18.4[b]	802	35.1[f]	2.3	464[g]	84	30
Long	JL 22[a]	----	717	35.6[f]	2.9	457[g]	122	20
Narrow	JL 15	17.4	787	26.9	2.4	203	64	30

Table II-5. (continued)

1987

Amisk	JL 02	21.3	603	27.4[h]	2.1	219[i]	46	21
Baptiste	JN 30	18.4	576	28.9[h]	3.8	239[i]	91	53
Long	JL 16[a]	19.1	618	32.1	2.5	346	90	34
Narrow	JL 01	19.4	575	25.1	2.2	151	30	9

---

[a] Sampling frequency was not adequate to preclude the possibility of earlier littoral zone migration.

[b] Temperature from July 10 1986.

[c-i] Identical superscripts indicate that total lengths or wet weights do not differ significantly.

Table II-6. Differences in the total lengths and wet weights of juvenile yellow perch caught in the limnetic (Li) and littoral (Lt) zones on the same date. Between-zone differences are significant (*t*-test; $P<0.05$) within a given lake and year except as indicated.

Date	Lake	Zone	Total length (mm)	SD	Wet weight (mg)	SD	*N*
			1985				
Jul 17	Amisk	Li	32.35[a]	8.84	501[a]	445	2
Jul 17	Amisk	Lt	39.23[a]	3.73	913[a]	440	50
Jul 16	Narrow	Li	29.22	2.33	242	81	121
Jul 16	Narrow	Lt	32.10	2.07	304	86	99
Jul 31	Long	Li	28.11	2.57	229	65	41
Jul 31	Long	Lt	42.38	5.27	768	235	50
			1986				
Jul 23	Amisk	Li	28.59	6.19	287	198	14
Jul 23	Amisk	Lt	36.31	3.35	535	150	30
Jul 15	Narrow	Li	23.62	2.24	126	47	144
Jul 15	Narrow	Lt	26.89	2.38	203	64	30
Jul 22	Long	Li	25.29	3.10	168	81	30
Jul 22	Long	Lt	35.59	2.92	456	122	30

Table II-6. (continued)

1987

Jul 02	Amisk	Li	26.79[a]	2.04	196	46	81
Jul 02	Amisk	Lt	27.36[a]	2.12	219	46	21
Jun 30	Bapt	Li	24.66	2.65	144	51	63
Jun 30	Bapt	Lt	28.87	3.82	239	91	53
Jul 01	Narrow	Li	22.37	1.96	95	28	114
Jul 01	Narrow	Lt	25.09	2.22	151	30	9
Jul 16	Long	Li	28.96	3.60	201	45	15
Jul 16	Long	Lt	32.06	2.47	346	91	34

[a] Total length or wet weight differences between zones are not significantly different (*t*-test; *P*>0.05).

Table II-7. Limnetic zone, littoral zone, and seasonal (end of May-mid-October) absolute growth rates for age 0 yellow perch in four lakes in Alberta, Canada.

Lake	Year	Limnetic zone		Littoral zone		Seasonal growth	
		$mm \cdot d^{-1}$	days	$mm \cdot d^{-1}$	days	$mm \cdot d^{-1}$	days
Amisk	1985	0.54-0.69	44	0.76-0.94	35	0.46	130
	1986	0.45[a]-0.60	43	0.49-0.68[a]	33	0.41	130
	1987	0.55-0.56	36	0.58-0.59	52	0.40	138
Baptiste	1986	0.78	28[b]	0.62	39[b]	0.41	120[c]
	1987	0.51-0.64	34	0.50-0.57	56	0.36	136
Long	1986	0.34-0.55	49[b]	0.49-0.89	36[b]	0.25	132
	1987	0.52	34[b]	0.35	55[b]	0.22	139
Narrow	1985	0.48-0.54	47	0.38-0.46	34	0.32	134
	1986	0.38-0.46	42	0.33-0.43	35	0.27	131
	1987	0.44-0.51	36	0.27-0.32	54	0.28	138

[a] Estimated growth rate.

[b] Estimated date for onshore migration.

[c] Data from June 15 to October 13.

Table II-8. End of season comparisons of total lengths and wet weights for age 0 yellow perch populations from four lakes in Alberta, Canada. All length and weight differences among lakes within years are significantly different (*t*-test; $P>0.05$) except as indicated by paired superscripts. All fish from a given lake among years differed significantly in both total length and wet weight except those from Narrow Lake in October 1985 and 1987.

Lake	Date	Total length (mm)	SD	Wet weight (g)	SD	*N*
		1985				
Amisk	Sept 15	68.9^{a}	3.8	2.89	0.55	34
Amisk	Oct 11	68.5^{a}	3.3	3.36	0.53	32
Narrow	Sept 15	49.7^{b}	4.2	1.20^{c}	0.30	24
Narrow	Oct 11	49.8^{b}	0.5	1.10^{c}	0	2
		1986				
Amisk	Oct 12	60.4	3.0	2.25	0.35	50
Baptiste	Oct 11	63.1	3.0	2.51	0.37	37
Long	Oct 13	41.1	5.0	0.70^{d}	0.26	52
Narrow	Oct 12	42.9	3.0	0.75^{d}	0.15	50
		1987				
Amisk	Oct 12	62.3	4.2	2.58	0.52	58
Baptiste	Oct 11	57.4	4.9	1.94	0.57	19
Long	Oct 12	37.2	2.9	0.47	0.13	35
Narrow	Oct 11	45.4	3.9	0.89	0.24	125

Table II-9. Onset of littoral zone migration of juvenile perch in relation to day (D), month (M), and year (Y), fish size (total length), and water temperature. NR = not reported.

Species	Reference	D/M/Y	Total length (mm)	Water temp (°C)
Perca fluviatilis	Guma'a (1978)	14/7/75	25.0	NR
Perca fluviatilis	Coles (1981)	2/7/75	17.0	NR
Perca fluviatilis	Treasurer (1988)	16/6/76	19.9	16
		16/6/77	17.4	13
Perca flavescens	Wong (1972)	29/7/69	27.4	20.5
Perca flavescens	Lin (1975)	26/7/72	42.7	18
		29/6/73	27.6	17
Perca flavescens	Kelso and Ward (1977)	1/8/74	30.0	NR
		1/8/75	30.0	NR
Perca flavescens	Swindoll (1981);	21/6/78	24.9	NR
Perca flavescens	Whiteside et al. (1985b)	5/7/79	23.4	21
		17/6/80	26.0	21
		16/6/81	22.7	NR
Perca flavescens	Post (1987);	27/5/82[a]	16.7	NR
Perca flavescens	Post and McQueen (1988)	17/6/82[b]	30.0	NR

---

[a] Nearshore distribution during the day, offshore at night.

[b] Exclusive nearshore distribution.

Table II-10. End-of-season total length comparisons of age 0 European or yellow perch in north temperate lakes.

Lake	Date	Total length (mm)	Investigator(s)
		Actual data among lakes	
St. George[a]	1985	83.1	Post (1987)
Eaton[a]	1985	87.2	Post (1987)
Harp[a]	1985	64.1	Post (1987)
Dickie[a]	1985	61.3	Post (1987)
Clear[a]	1985	57.3	Post (1987)
Bucks[b]	1965-1967	73.7	Snow (1969)
Hemlock[b]	Mar 1964	68.6	Snow (1969)
Murphy[b]	1965-1966	68.6	Snow (1969)
Red Cedar[b]	1962	61.0	Snow (1969)
Big Gibson[b]	1960	61.0	Snow (1969)
Spruce[b]	Aug 1966	73.7	Snow (1969)
Mille Lacs[c]	Aug 20,1954	63.5	Maloney & Johnson (1957)
Winnibigoshish[c]	Aug 10,1954	55.9	Maloney & Johnson (1957)
		Back calculated data	
26 Lakes[a]	1966-1974	58.4-113.8 (mean, 73.4)	Ryan & Harvey (1980)
La Grande Anse[d]	1965	72.5	Grimaldi & Leduc (1973)
Missisquoi Bay[d]	1965	68.5	Grimaldi & Leduc (1973)
Iles De La Paix[d]	1965	76.5	Grimaldi & Leduc (1973)

Table II-10. (continued)

Hertel[d]	1965	68.0	Grimaldi & Leduc (1973)
St. Joseph[d]	1965	65.0	Grimaldi & Leduc (1973)
Lochan[e]	1966-1967	51.0	Shafi & Maitland (1971)
Lomand[e]	1966-1967	67.0	Shafi & Maitland (1971)
Rostherne[f]	1970	69.5	Goldspink & Goodwin (1979)
Tatton[f]	1970	89.0	Goldspink & Goodwin (1979)
Colemere[f]	1970	88.0	Goldspink & Goodwin (1979)
	Actual data within lakes		
Oneida[g]	1976	65.6	Mills & Forney (1981)
Oneida[g]	1972	56.1	Lin (1975)
Red Lakes[c]	1952-1957	48.9-68.9 (mean, 60.5)	Ney & Smith (1975)
Red Lakes[c]	1962-1967	56.0-75.0 (mean, 65.1)	Ney & Smith (1975)
West Blue[h]	1974	52.5	Henderson (1977)
West Blue[h]	1969	52.9	Wong (1972)

---

[a] Southern Ontario, Canada

[b] Wisconsin, USA

[c] Minnesota, USA

[d] Southern Quebec, Canada

[e] Scotland, United Kingdom

[f] England, United Kingdom

[g] New York, USA

[h] Manitoba, Canada

Figure II-1. Net panel dimensions and mesh sizes of the midwater trawl used to collect age 0 yellow perch.

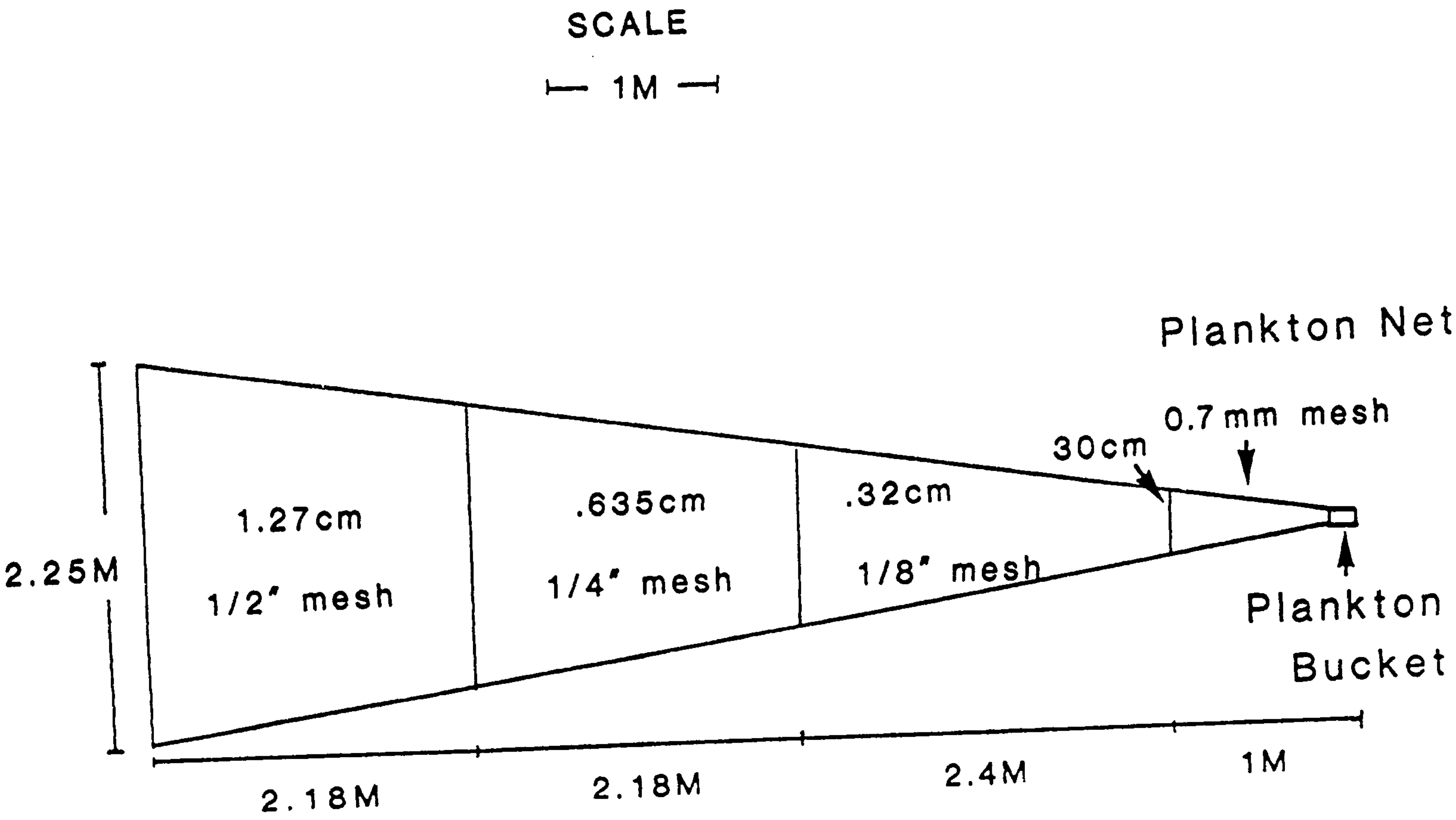

SCALE
1M
Plankton Net
0.7 mm mesh
30cm
1.27cm
1/2" mesh
.635cm
1/4" mesh
.32cm
1/8" mesh
Plankton
Bucket
2.25M
2.18M
2.18M
2.4M
1M

Figure II-2. Rigging of the midwater trawl used to collect age 0 yellow perch. (modified from Gjernes 1979)

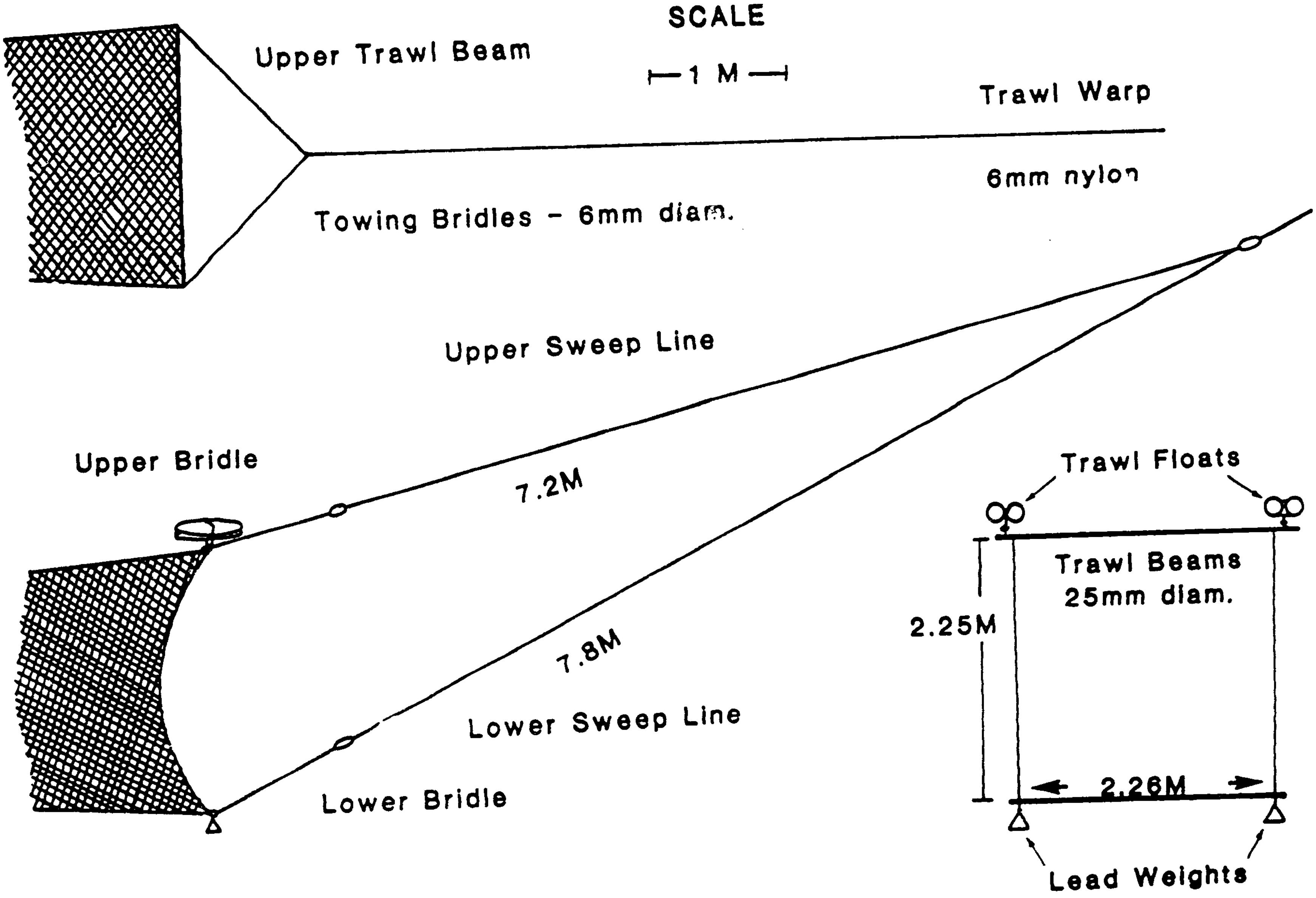
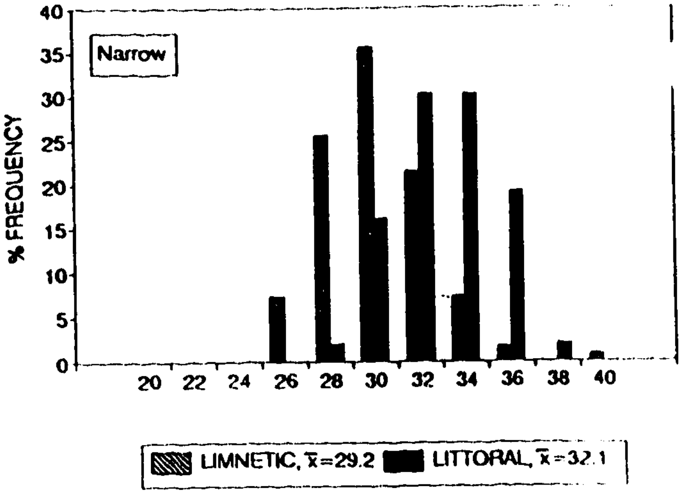
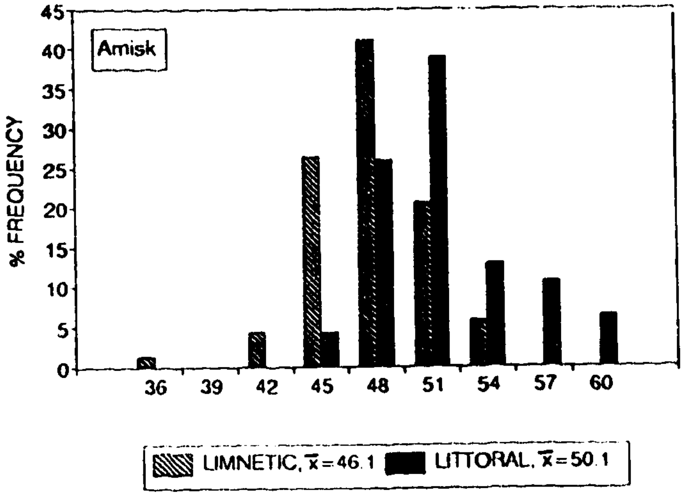

SCALE
1 M
Upper Trawl Beam
Trawl Warp
6mm nylon
Towing Bridles - 6mm diam.
Upper Sweep Line
Upper Bridle
7.2M
7.8M
Lower Sweep Line
Lower Bridle
Trawl Floats
Trawl Beams
25mm diam.
2.25M
2.26M
Lead Weights

Figure II-3. Length distributions of age 0 yellow perch in limnetic and littoral zone habitats in Narrow (July 16 1985), Amisk (July 29 1987), and Baptiste (July 14 1987) lakes, Alberta.


Narrow
% FREQUENCY
0
5
10
15
20
25
30
35
40
20
22
24
26
28
30
32
34
36
38
40
▨ LIMNETIC, x̄=29.2
■ LITTORAL, x̄=32.1


Amisk
% FREQUENCY
0
5
10
15
20
25
30
35
40
45
36
39
42
45
48
51
54
57
60
▨ LIMNETIC, x̄=46.1
■ LITTORAL, x̄=50.1

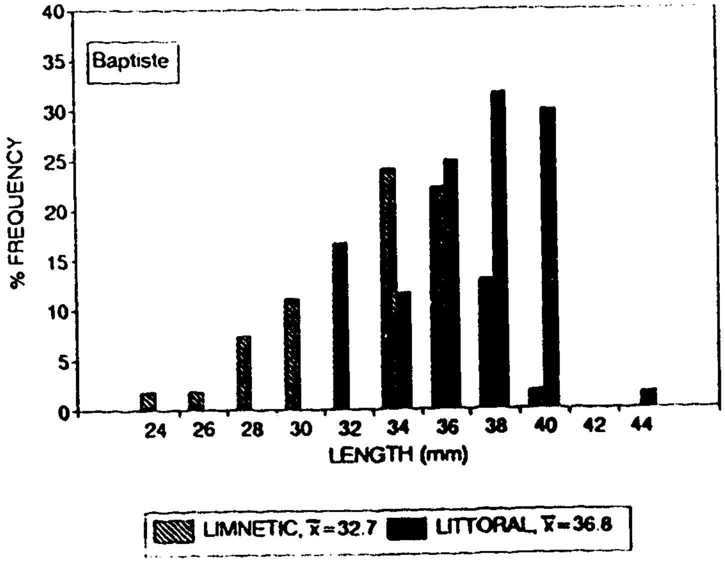
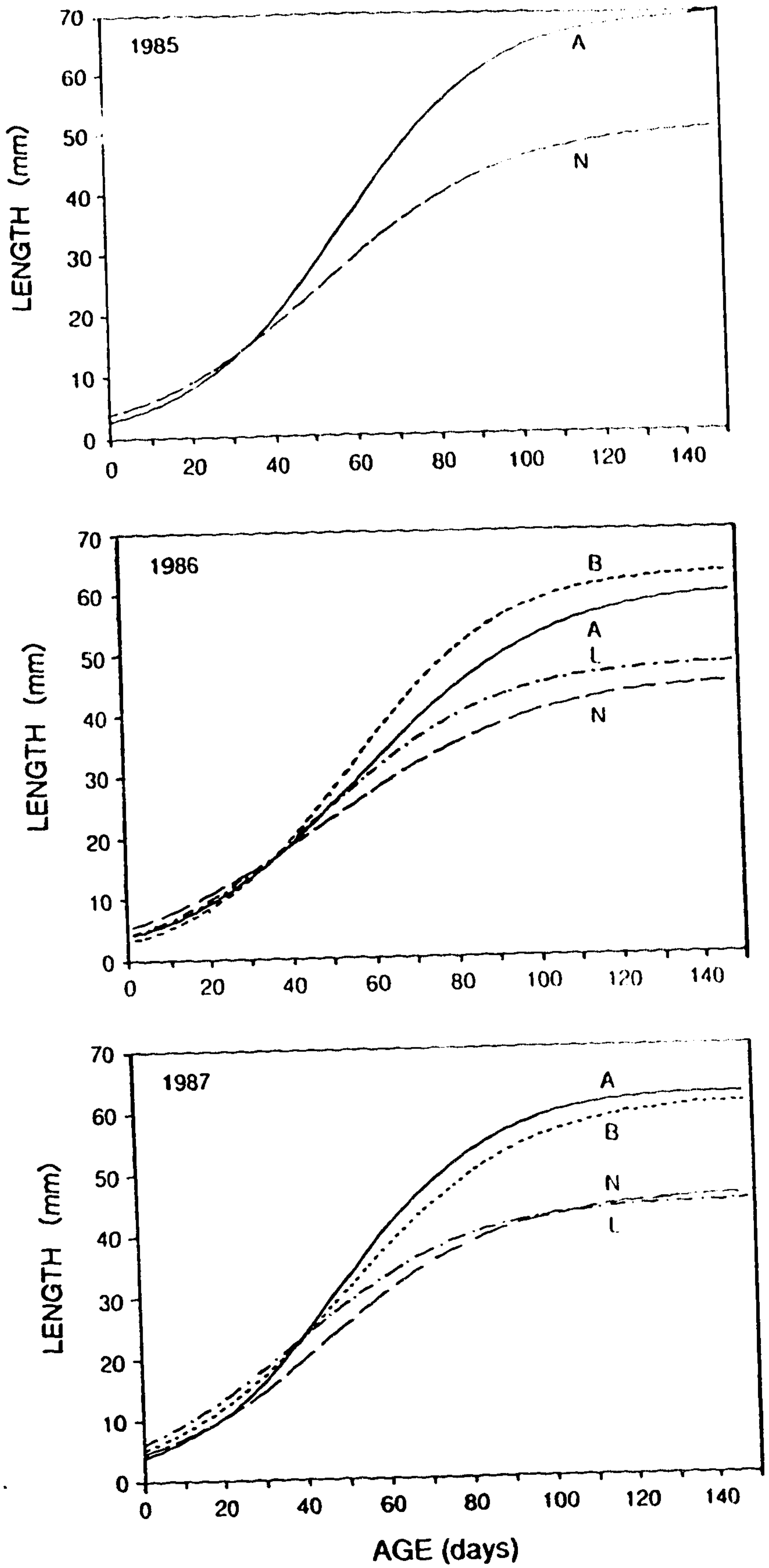

Baptiste
% FREQUENCY
0
5
10
15
20
25
30
35
40
24
26
28
30
32
34
36
38
40
42
44
LENGTH (mm)
▨ LIMNETIC, x̄=32.7
■ LITTORAL, x̄=36.8

Figure II-4. Age 0 yellow perch growth curves for Amisk (A), Baptiste (B), Long (L) and Narrow (N) lakes, Alberta, 1985-1987.


1985
A
N
LENGTH (mm)
0
10
20
30
40
50
60
70
0
20
40
60
80
100
120
140
1986
B
A
L
N
LENGTH (mm)
1987
A
B
N
L
LENGTH (mm)
AGE (days)

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Chapter III

Growth patterns of age 0 freshwater fish - Do the classical growth models adequately describe growth over the first season?

Introduction

Since first year growth is of particular significance to successful age 1 recruitment in fish populations (Post and Evans 1989a, 1989b), meaningful predictions of age 1 recruitment require appropriate descriptions and predictions of age 0 fish growth. Choosing a growth model that is appropriate for predicting seasonal growth patterns requires data based on intensive sampling throughout the growing season, especially in temperate waters (Moreau 1987).

Mathematical models of fish growth are typically used to predict the size at age for a given cohort (Allen 1976; Craig 1980), the size distribution within a cohort (Wismer et al. 1985; DeAngelis and Huston 1987) or the maximum size individuals in a population could potentially reach (Ricker 1975). Models used to predict size at age are typically based upon data from fish populations which were sampled infrequently, usually on an annual basis. However, growth models developed to predict size at age or maximum fish size over the entire life span of fish populations may be inappropriate for describing growth patterns within a given season.

Much of the existing information on fish growth during the first two years is based upon extrapolations from back-calculated data (Shafi and Maitland 1971; Goldspink and Goodwin 1979) which have often been based upon inappropriate models (Francis 1990). Although first year growth patterns have been described for several temperate freshwater fish species, comparisons of age 0 fish growth patterns between lakes in the same geographic area is restricted to three studies (Bidgood 1973; Post 1987; and Treasurer 1988).

This study was designed to compare growth patterns of age 0 yellow perch (Perca flavescens) between lakes of contrasting productivity in the same geographic area and to identify the most appropriate model for [illegible]bing these growth patterns during the first season. The model for individual fish growth was then used to evaluate the differences in growth dynamics among populations. I also predict the size of age 0 fish and the pattern of their growth at any time during the first year.

Materials and Methods

Lake characteristics and sampling protocol

Growth patterns of age 0 yellow perch were determined from 1985 to 1987 for four central Alberta lakes; Amisk, Baptiste, Long and Narrow. These lakes are located within a 60 km radius of Athabasca, Alberta. The lakes are all located in glacial till and are surrounded by southern mixed wood boreal forest but have five-fold range of productivity (Table III-1).

Larval yellow perch (Perca flavescens) were collected in the limnetic zone with a midwater trawl, modified from that of Gjernes (1979). The trawl measured 2.25 x 2.26 m at the mouth and was 7.6 m long. The body was constructed from 1.27, 0.64, and 0.32 cm (bar measure) knotless nylon panels with a 1 mm mesh plankton net and bucket attached to the 30 cm diameter cod end.

Amisk Lake (productive) and Narrow Lake (unproductive) were sampled on a weekly basis from the end of May until the end of August in 1985 and 1986 and biweekly over the same period in 1987. Baptiste Lake (productive), and Long Lake (unproductive) were sampled every 3 to 4 weeks during the 1985 field season and biweekly in 1986 and 1987. Midwater trawl sampling was continued until the catch of age 0 perch dropped to near zero as the juvenile perch moved onshore to the littoral zone. Following this onshore migration, age 0 perch were collected with a 15.2 m by 1.8 m bag seine with 6 mm mesh (bar measure) in the wings and 3 mm mesh in the 1.8 x 1.8 x 1.8 m bag. During 1986 and 1987, a large 56 m by 3 m seine with 9.5 mm mesh (bar measure) was also used.

Seining was started in the littoral zone in mid-July in 1985 and 1986 and at the end of June in 1987. In all three seasons, age 0 perch were sampled in mid-October to determine their asymptotic size prior to ice formation. During 1985, only Amisk and Narrow lakes were sampled in October and in 1986 and 1987, October samples were obtained from all four lakes.

From each sample date, total lengths of preserved age 0 perch were measured to the nearest 0.1 mm using a microscope with an ocular micrometer. Blotted wet weights were determined to the nearest milligram. Once perch exceeded 15 mm in total length, calipers were used to measure lengths to 0.1 mm and weights were determined to the nearest 0.01 g.

Growth analysis

Since the von Bertalanffy, logistic and Gompertz growth models are used extensively in fisheries literature to describe fish growth, I assessed their suitability for describing age 0 growth of yellow perch. These equations are different expressions of a single model with different parameters which determine the shape of a specific curve in relation to an upper asymptote (Schnute 1981; Schnute and Richards 1990).

Specific methods for fitting logistic, Gompertz, or von Bertalanffy equations to a growth curve are described in Ricklefs (1967), Zweifel and Lasker (1976) and Kaufmann (1981). These methods require an estimate of the asymptotic length (L_∞) or asymptotic weight (W_∞) at the end of the growing season, and a recalculation of the size as a percentage of the asymptote. Equations (1), (2) and (3) show the conversion factors (C_w) used to transform the data for logistic, Gompertz and von Bertalanffy models respectively.

(1) $C_w = 0.25 \cdot \ln[(\text{length}/L_\infty)/(1 - \text{length}/L_\infty)]$

(2) $C_w = e^{-1} \cdot \ln[-1(\ln(\text{length}/L_\infty))^{-1}]$

(3) $C_w = 4/9 \cdot \ln(1/3(1-(\text{length}/L_\infty)^{1/3}))$

Estimates of the asymptote (L_∞) are revised until a plot of the conversion factors (C_w) as a function of time yields a straight line with the maximum regression coefficient between C_w and time. The slope (s) of the plot of C_w versus time is directly proportional to the rate constant K for the logistic growth equation where $K = 4 \cdot s$. For the Gompertz equation, $K = e \cdot s$ and for the von Bertalanffy equation $K = 9 \cdot s \cdot 4^{-1}$ (Ricklefs 1967). The inflection point (t_0) of the logistic or Gompertz equation is obtained from the least squares regression equation of C_w versus time by setting $C_w = 0$ and solving for time. For the von Bertalanffy equation, t_0 is calculated in the same manner as above but t_0 represents the point at which the curve intersects the time axis (Moreau 1987). The logistic growth equation (4) is given as:

(4) $L = L_\infty \cdot \{1 + e^{[-K(t - to)]}\}^{-1}$

where L is the predicted length at time t

L_∞ is the asymptotic length at the end of the season

K is the rate constant of the logistic equation

t is the time in days after the estimated time of hatch

t_0 is the inflection point of the logistic equation

The Gompertz growth equation (5), given by Moreau (1987), has equivalent parameters to the logistic equation. However, the shape of the curves differ because the inflection point occurs at an age where 50% and 36.8% of the asymptotic size is reached for the logistic and Gompertz curves respectively (Ricklefs 1967; Moreau 1987).

(5) $$L = L_\infty \cdot \exp\{-\exp[-K(t-t_0)]\}$$

The von Bertalanffy growth equation (6) has equivalent parameters to the logistic equation except for t_0, the point at which the curve intersects the time axis. This equation is given as:

(6) $$L = L_\infty \cdot \{1 - e^{[-K(t - t_0)]}\}$$

Once the parameters for the logistic, Gompertz or von Bertalanffy growth equations are determined, a plot of the curve produced by the growth model is compared with scatter plots of the data. Adjusting the value of K or t_0 in the equations may be necessary to improve the fit of the curve to the actual data. In this analysis individual data on the size of every fish measured was used rather than mean values. Thus weighting of mean values was not necessary when fish sizes from both trawl and seine catches were obtained on the same date.

Using the conversion factors C_w from equations (1), (2), or (3) to accomplish a linear transformation of the data on length or weight, linear plots of transformed length or weight data (C_w) versus time in days after hatch may be compared. Regression equations may be calculated for each of these plots and the most appropriate growth model may then be chosen based upon the equation with the highest regression coefficient.

If a plot for a growth curve is a close fit to actual data obtained from frequent sampling of fish in the population, trends in absolute and relative growth may be extrapolated from the growth model. Using daily length or weight values extrapolated from logistic growth curves fitted to data from weekly sampling of age 0 perch I plotted curves showing absolute growth patterns over the entire first season. These growth patterns were then compared to patterns of habitat use of the age 0 perch from Amisk and Narrow lakes in 1985 and 1986.

Results

Growth Patterns

The general shape of the growth curves during the first season was sigmoidal in all four lakes over the three years of this study. Logistic and Gompertz curves which are sigmoidal in shape were plotted for both length and weight. Logistic curves provided the best fit to the data for length in all cases as indicated by comparing the correlation coefficients for transformed length or weight versus age in Table III-2 and III-3. Both logistic and Gompertz models described growth in weight equally well for productive Amisk and Baptiste lakes in all three seasons and for Narrow Lake in 1987. A logistic model provided the best description of growth in weight in unproductive Narrow and Long lakes in all seasons with the exception of Narrow Lake in 1987.

The simple von Bertalanffy growth model lacks an inflection point and did not fit the sigmoid growth patterns displayed by all the age 0 yellow perch populations in this study. In 1986, although growth in weight showed a sigmoid pattern, growth in length did not show an inflection point in the two unproductive lakes and I fitted a von Bertalanffy curve to these data. Although the correlation coefficients in Table III-2 and III-3 indicated that a logistic model best described growth in length in these two lakes, both Gompertz and von Bertalanffy models also provided a good description of growth in length for 1986 in Narrow and Long lakes (Figure III-1).

The parameters of the logistic and Gompertz growth equations for each lake and season from which weekly or biweekly growth data are available are given in Table III-2 and III-3. The asymptotic length (L_∞) or weight (W_∞) at the end of the first growing season differs substantially between productive and unproductive lakes and provides the best indicator of between lake growth differences. The age of perch at the inflection point t_0 of both the logistic and Gompertz growth curves for length is consistently older within a given season for lakes with higher productivity. This indicates that the most rapid phase of growth in length shown by the steepest portion of the growth curve is occurring later in the season relative to the time of hatching in productive Amisk and Baptiste lakes as compared to unproductive Narrow and Long lakes. A comparison of the shape of the logistic growth curves for length between productive and unproductive lakes shows that the rapid growth phase is sustained for a longer period of time in the productive lakes (Figure III-2). Curves for logistic growth in weight (Figure III-3) indicate that peak growth rates occur around an age of 80 days whereas the peak growth rates for length occur near an age of 50 days. The most rapid growth and largest size at the end of the season occurred in 1985 in both Amisk and Narrow lakes.

Figure III-4 presents data from three lakes fitted to both logistic and Gompertz growth models. Maximum growth in weight as indicated by the inflection point t_o of both the logistic and Gompertz growth curves occurred approximately 30 days later in a given lake compared to the time for maximum growth in length. With the exception of Long Lake, the maximum growth in weight between lakes occurred at a similar time for both productive and unproductive lakes in a given season. Gompertz curves provide the best description of the growth patterns for weight over the first 40 days as shown in Figure III-4. However, I found logistic curves to best describe the growth patterns for length or weight near the end of the season as the asymptotic size is approached.

Although age 0 perch growth patterns over the first season in all four study lakes may be described by a logistic curve, an examination of absolute growth patterns helps reveal important trends (Figures III-5 and III-6). In all three years, absolute growth of larval perch from hatching until after the midpoint of the limnetic phase was slow. At this time, approximately 40 days after hatching, absolute growth in length began increasing rapidly and divergence in length of larval perch from productive and unproductive lakes first became evident (Figure III-2). However, the most rapid divergence in size between lakes occurred after the juvenile perch moved into the littoral zone.

Absolute growth in length peaked 50 to 60 days after hatching in 1985 and 1986 and 40 to 50 days post hatch in 1987 as indicated by the inflection points (t_0) in Tables III-2 and III-3. In 1987, age 0 perch migrated onshore two weeks earlier than in the previous two years. Figure III-5 shows the pattern for absolute growth in length for Amisk and Narrow lakes in 1985 and 1986. In all three years perch from unproductive lakes show an earlier peak for growth in length. Absolute growth in length was within 80% of the maximum for 6 days longer in 1985 and 15 days longer in 1986 in Narrow Lake than it was in Amisk Lake.

Absolute growth in weight peaked approximately 80 days after hatching (Figure III-6) and this peak showed less variance between lakes than did peak growth for length. The peak in weight occurred about 30 days later than the peak growth in length and was sharper. The period over which absolute growth in weight was within 80% of the maximum lasted 21 to 31 days which was 13 to 20 days less than for the equivalent periods for absolute growth in length.

Discussion

My results demonstrate that growth in both length and weight is sigmoidal if sampling is frequent and extends over the entire growing season. When sampling is infrequent or does not extend over the entire growing season, data may be obtained which fit a linear pattern (Noble 1968; Ney and Smith 1975; Treasurer 1988) or a non-sigmoidal pattern such as a von Bertalanffy model (Hamilton and Powles 1979; Post 1987) or an exponential model (Wong 1972; Lin 1975).

Logistic and Gompertz growth patterns

I found a logistic model to best describe the growth of age 0 perch. This finding is supported by the work of Pycha and Smith (1954) and Swindoll (1981) who suggest that the growth of age 0 perch in Red Lakes and Lake Itasca, Minnesota respectively, could be described by a logistic curve. However, they did not fit a growth model to their data. Guma'a (1978) found a logistic model to fit age 0 perch growth in length in Lake Windermere but he did not fit this model to growth in weight.

Although growth in length was best described by a logistic model, both logistic and Gompertz models described growth in weight equally well for productive lakes in all three seasons and for unproductive Narrow Lake in 1987. Both the logistic and Gompertz curves are sigmoid in shape with an upper asymptote and an inflection point (Moreau 1987). The inflection point of the logistic curve occurs at an age where 50% of the asymptotic size is reached so that the two halves of the curve are antisymmetrical. The two parts of the Gompertz curve on either side of the inflection point are not antisymmetrical because the inflection point occurs at an age where 36.8% of the asymptotic size is reached (Ricklefs 1967; Moreau 1987). In higher latitudes where the season for first year growth is short and the absolute growth rates approaching the inflection point are high, it may be difficult to identify the inflection point of a growth curve with enough precision to distinguish between a logistic or Gompertz model. For example, the inflection point for a logistic versus a Gompertz model differed by a maximum of 8 days in Amisk Lake over the three seasons of this study and either model provided a good description for growth in weight.

Although the Gompertz model has been used infrequently to describe fish growth, its relevance in describing the growth of age 0 fish is demonstrated for yellow perch in this study and for anchovy larvae by Hunter (1976) and Zweifel and Lasker (1976). Although growth over the entire season was usually better described by a logistic model, Gompertz models provided the best description of the growth patterns for weight at the beginning of the season.

Von Bertalanffy growth patterns

For growth data to fit the von Bertalanffy curve the highest absolute growth rates must occur at the smallest sizes (Kaufmann 1981). This was not the case in the present study and my results are supported by my reanalysis of Swindoll's (1981) data which show growth rates of age 0 perch in Lake Itasca to peak at an age of 45 and 65 days for length and weight respectively. A von Bertalanffy equation can be fitted to data originating from a sigmoid growth curve if smaller size ranges are not sampled or if the sampling period is long relative to the growth parameter (Yamaguchi 1975). If initial sampling occurs after the inflection point of the growth curve, a sigmoid growth pattern would be missed. If the sampling interval is infrequent, an inflection point could also be overlooked. Either problem would lead to an overestimate of early growth Yamaguchi (1975). Since the von Bertalanffy growth model has no inflection point (Yamaguchi 1975; Zweifel and Lasker 1976), my data indicate that the model is often not applicable to age 0 fish growth which typically has an inflection point early in the season. The model is most suited to the analysis of data describing indeterminate growth over the entire life-span of the organism as is done by Craig (1980) and Jellyman (1980) where sampling is conducted on an annual basis.

Post (1987) fitted a von Bertalanffy model to his data for age 0 perch from five different lakes in Southern Ontario. With the exception of Lake St. George, Post's sampling frequency and time of initial sampling were not adequate to determine if an inflection point occurred in the initial growth period from hatching through the limnetic phase. However he did find that limnetic zone growth rate exceeded littoral zone growth. Although the data from Lake St. George were fitted to a von Bertalanffy model, logistic or Gompertz models were not tested by Post (1987). Age 0 fish growth may be adequately described by the von Bertalanffy model in situations where limnetic zone growth is high relative to littoral zone growth. This was the case for growth in length in Narrow and Long lakes in 1986 as shown in Figure III-1. However, logistic or Gompertz curves provided a better fit for these data and a von Bertalanffy curve did not fit the data for growth in weight which showed distinct inflection points on day 73 and 83 for Long and Narrow lakes respectively. Post (1987) found age 0 perch growth in the limnetic zone of Lake St. George to be high relative to littoral zone growth in 1984 and 1985. He fitted a von Bertalanffy curve to the data for growth in length but did not present an analysis of growth in weight. In Lake Itasca (Swindoll 1981; Whiteside et al. 1985b) and West Blue Lake (Henderson 1977; Kelso and Ward 1977) limnetic zone growth was also high relative to littoral zone growth. These workers did not attempt to fit growth models to their data over the entire season but my reanalysis of Swindoll's data shows that a logistic model best describes both growth in length and weight of age 0 perch in Lake Itasca in 1980. In Lake Windermere, although the growth of age 0 perch in the limnetic zone exceeded that of perch in the littoral zone, Guma'a (1978) was unable to fit a von Bertalanffy model to these data based upon 16 sampling intervals. This frequent sampling identified an inflection point for growth in length and Guma'a (1978) found a logistic model to fit the data.

Exponential growth patterns

First season growth data based upon frequent sampling that may show logistic growth over the entire season is often divided into growth stanzas (time periods) that show exponential growth. My data typically show exponential patterns for growth in weight and linear patterns for growth in length if the sigmoid growth pattern over the entire first season is separated into limnetic and littoral growth stanzas. This type of analysis of age 0 perch growth was done by Guma'a (1978) and by Swindoll (1981). However I found a logistic model to provide an excellent fit for Swindoll's data from 1980 which was based upon 30 sampling intervals from May 6 to August 21. This indicates that if an appropriate growth model is selected and if sampling adequately covers the entire season, growth over a single season need not be divided into separate stanzas.

If the earliest and latest phases of growth within the first season are not adequately sampled, an exponential curve may provide an excellent fit for the data and plots of log length or log weight versus time may be linear. For example, exponential growth patterns for weight of age 0 perch were found by Wong (1972) and Lin (1975) for fish sampled from July 1 to August 31 and from June 14 to August

23 respectively. Lin (1975) fitted growth curves to plots of the natural logarithm of mean weight (ln W) versus time using linear regression and obtained correlation coefficient values (r^2) of 0.99 and 0.98 for 1972 and 1973 respectively. For comparative purposes, I used the same approach to fit growth curves to weight data from Amisk and Narrow lakes between mid-June and August 21, 1986. Over this period, my data for weight also fit an exponential curve and plots of ln W versus time were linear with r^2 values of 0.96 and 0.98 for Amisk and Narrow Lakes respectively. This emphasizes the importance of the duration and timing of sampling in fitting a given data set to a growth model.

Linear growth patterns

Some data on growth in length of age 0 perch has been adequately described by a linear model although none of my data fit this pattern unless samples prior to mid-June and after the end of August were excluded. Treasurer (1988) intensively sampled Loch Kinord from May 17 through to November 16 in 1976, and found a linear pattern for growth in length. Plots of weight versus time were not linear and Treasurer (1988) found littoral zone growth rates significantly higher than those in the limnetic zone. Further analysis of data from Lin (1975) showed that age 0 perch in Oneida Lake exhibited linear growth in length from the end of May to the end of August for both 1972 and 1973.

Lin (1975) found growth in weight for the same periods to be exponential. Noble (1968) states that larval perch growth in the limnetic zone of Oneida Lake was "approximately linear" for 1965 to 1967. However plots of mean larval perch length versus time (May 20-June 25) suggest that an exponential model may fit his 1966 and 1967 data better than a linear model. In Red Lakes, Minnesota, Ney and Smith (1975) found a linear pattern for age 0 perch growth in length for 11 out of 12 years. Their data were restricted to the period from June 30 to August 20 for each season.

Growth patterns and habitat use

My data for age 0 perch indicate that absolute growth rates are lowest during the period from hatching to near the end of the limnetic phase and again at the end of the season. Most rapid growth in length coincided with, or just followed migration of the age 0 perch to the littoral zone and absolute growth in weight peaked approximately one month later. This pattern with an early peak in growth in length followed by a later peak in growth in weight corresponds with the descriptive work on age 0 perch development (Mansueti 1964) where perch larger than 25 mm direct a greater percentage of their energy intake towards increasing body weight rather than length. Whiteside et al. (1985b) suggests that analysis of growth in length may be misleading because initially age 0 perch maximize growth in length and later in the season most of their energy intake is directed towards increasing body weight. This indicates the importance of analyzing data for both length and weight when examining first season growth patterns.

The initial partitioning of energy resources to growth in length may facilitate early swimming performance which is essential for the avoidance of predators and the capture of prey. Later in the season, a shift in partitioning of energy resources to growth in weight would provide adequate energy reserves for survival over the first winter (Post and Evans 1989b). Also, it is possible that initial growth of age 0 perch in this study is limited by a shortage in suitable size categories (Frank and Leggett 1986), type (Mills and Forney 1981) or abundance (Paloheimo and Dickie 1966; Fox 1989; Mills et al. 1989) of food organisms. More rapid growth may be delayed until the fish attain a large enough size (Mittelbach 1981; Keast and Eadie 1985; Persson 1990) to exploit a broader spectrum of food resources available in the littoral zone (Whiteside et al. 1985a).

Choosing and comparing growth models

My data show that choosing an appropriate model for the growth of age 0 fish requires intensive sampling early in the season and should include samples taken in the fall at the end of the growing season. A limitation of the method I used for fitting growth data to a particular model occurred when I attempted to compare the growth rate constant K between different lakes. This rate constant K was derived from the slope of linear plots of transformed length or weight data (C_w) versus time. These transformations depend upon estimates of the asymptotic size which exhibited marked differences between lakes and seasons. This limits comparisons of the slopes of the transformed data or the rate constants K between lakes or seasons to systems with equivalent asymptotic sizes at the end of the season. Cerrato (1990) evaluates the problems associated with statistical comparisons of the parameters of the von Bertalanffy equation and recommends use of the likelihood ratio test in making comparisons between parameters. Cerrato also indicates that sample sizes in excess of 300 individual measurements may be required to produce acceptably low curvature measures when using non-linear criteria to assess the distributional properties of the growth parameters. Additional study is needed to determine the sample sizes necessary for appropriate statistical comparisons of growth parameters derived from field data.

Table III-1. Characteristics of study lakes. Total phosphorus (TP) and chlorophyll a (Chl a) concentrations are average summer values over a four to eight year period for the trophogenic zone. Mean depth (z) and maximum deptn (z_{max}) are in meters. North basin (N), South Basin (S).

Lake	Lat. N	Long. W	Area km²	Depth z	Depth z_{max}	TP $\mu g \cdot L^{-1}$	Chl a $\mu g \cdot L^{-1}$
Amisk N	54°35'	112°39'	1.89	10.7	30	34.4	14.5
Amisk S	54°35'	112°39'	2.27	19.4	60	37.6	18.7
Baptiste S	54°45'	113°33'	4.43	12.7	25	50.8	29.7
Long	54°35'	113°37'	1.62	9.4	30	13.0	3.2
Narrow	54°37'	113°37'	1.14	14.2	35	11.9	2.5

Morphometric and productivity data were obtained from Prepas et al. (1988), Prepas and Vickery (1984), Monitoring Branch, Alberta Environment (unpublished data) and from E. E. Prepas (Dept. of Zoology, University of Alberta, Edmonton; unpublished data).

Table III-2. Comparative growth parameters for logistic growth equations for length (L) and weight (W) of age 0 perch. K is the rate constant of the equation. L_∞ is the asymptotic total length (L) in millimeters or wet weight (W) in milligrams. t_0 is the inflection point of the logistic equation. The slope and correlation coefficient (r^2) are from the regression equation of the linear transformation of (L) or (W) versus time in days after hatch.

Year	Lake	K value	L_∞	t_0	slope	r^2
1985	Amisk (L)	0.0508	70.0	57.5[a]	0.0127	0.927
	Amisk (W)	0.0964	3370	81.8[a]	0.0241	0.897
	Narrow (L)	0.0454	51.0	52.5	0.0116	0.933
	Narrow (W)	0.0854[a]	1230	80.6	0.0246	0.934
1986	Amisk (L)	0.0585[a]	60.5	56.5	0.0116	0.907
	Amisk (W)	0.0933[a]	2250	82.5	0.0187	0.867
	Baptiste(L)	0.0543[a]	63.5	54.9	0.0116	0.846
	Baptiste(W)	0.0688	2700	85.5	0.0153	0.821
	Long (L)	0.0394[a]	45.0	53.7	0.0068	0.605
	Long (W)	0.0707[a]	800	73.0	0.0121	0.654
	Narrow (L)	0.0400[a]	46.0	50.0[a]	0.0073	0.813
	Narrow (W)	0.0615[a]	850	83.3	0.0137	0.790
1987	Amisk (L)	0.0557[a]	62.5	50.4	0.0118	0.883
	Amisk (W)	0.0750	2600	73.0[a]	0.0210	0.830
	Baptiste(L)	0.0471	61.3	50.1	0.0116	0.870
	Baptiste(W)	0.0700	2330	78.8	0.0196	0.829
	Long (L)	0.0480[a]	44.9	39.5	0.0073	0.606
	Long (W)	0.0488	900	90.4	0.0122	0.590
	Narrow (L)	0.0487[a]	45.5	45.5	0.0089	0.878
	Narrow (W)	0.0600	900	80.0[a]	0.0150	0.860

[a] values adjusted to provide the best fit.

Table III-3. Comparative growth parameters for Gompertz and von Bertalanffy growth equations for length (L) and weight (W). t_0 is the inflection point of the Gompertz equation or the point where the von Bertalanffy curve intersects the time-axis. Other symbols are defined in Table III-2.

I. Gompertz parameters

Year	Lake	K value	L_∞	t_0	slope	r^2
1985	Amisk (L)	0.0374	70.0	45.1	0.0138	0.903
	Amisk (W)	0.0553[a]	3370	74.7	0.0143	0.899
	Narrow (L)	0.0332	51.0	39.2	0.0122	0.884
	Narrow (W)	0.0294	1230	73.3	0.0131	0.890
1986	Amisk (L)	0.0366	60.5	43.9	0.0135	0.875
	Amisk (W)	0.0301	2250	74.6	0.0134	0.861
	Baptiste(L)	0.0390	63.5	39.7	0.0143	0.821
	Baptiste(W)	0.0294	2700	69.5	0.0131	0.811
	Long (L)	0.0331[a]	45.0	37..	0.0075	0.543
	Long (W)	0.0230	800	70.5	0.0085	0.578
	Narrow (L)	0.0231	46.0	34.5	0.0078	0.771
	Narrow (W)	0.0249	850	78.1	0.0091	0.732
1987	Amisk (L)	0.0363	62.5	35.9	0.0133	0.869
	Amisk (W)	0.0311	2600	66.9	0.0138	0.856
	Baptiste(L)	0.0364	61.3	38.0	0.0134	0.844
	Baptiste(W)	0.0404[a]	2330	69.4	0.0135	0.829
	Long (L)	0.0224	44.9	18.5	0.0082	0.564
	Long (W)	0.0219	900	71.0	0.0080	0.530
	Narrow (L)	0.0278	45.5	30.7	0.0102	0.867
	Narrow (W)	0.0233	900	73.0	0.0104	0.861

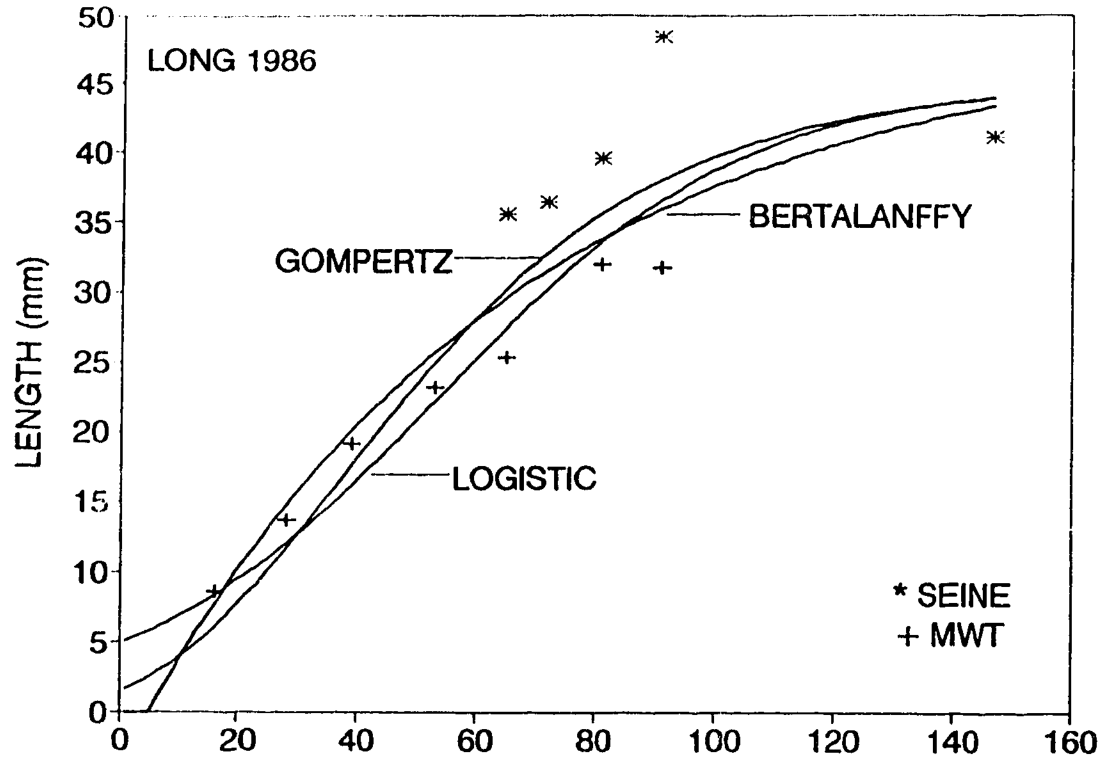
Table III-3. (continued)

II. von Bertalanffy parameters

Year	Lake	K value	L_∞	t_0	slope	r^2
1986	Long (L)	0.0157[a]	48.5	5.0[a]	0.0095	0.542
	Narrow (L)	0.0191	48.0	7.0[a]	0.0085	0.748

[a] values adjusted to provide the best fit.

Figure III-1. Logistic, Gompertz and von Bertalanffy curves for Long and Narrow lake growth in length for 1986. Mean length of fish from seines and midwater trawls (MWT) is plotted separately. Age is in days after hatching.


LONG 1986
LENGTH (mm)
0
5
10
15
20
25
30
35
40
45
50
0
20
40
60
80
100
120
140
160
GOMPERTZ
BERTALANFFY
LOGISTIC
* SEINE
+ MWT

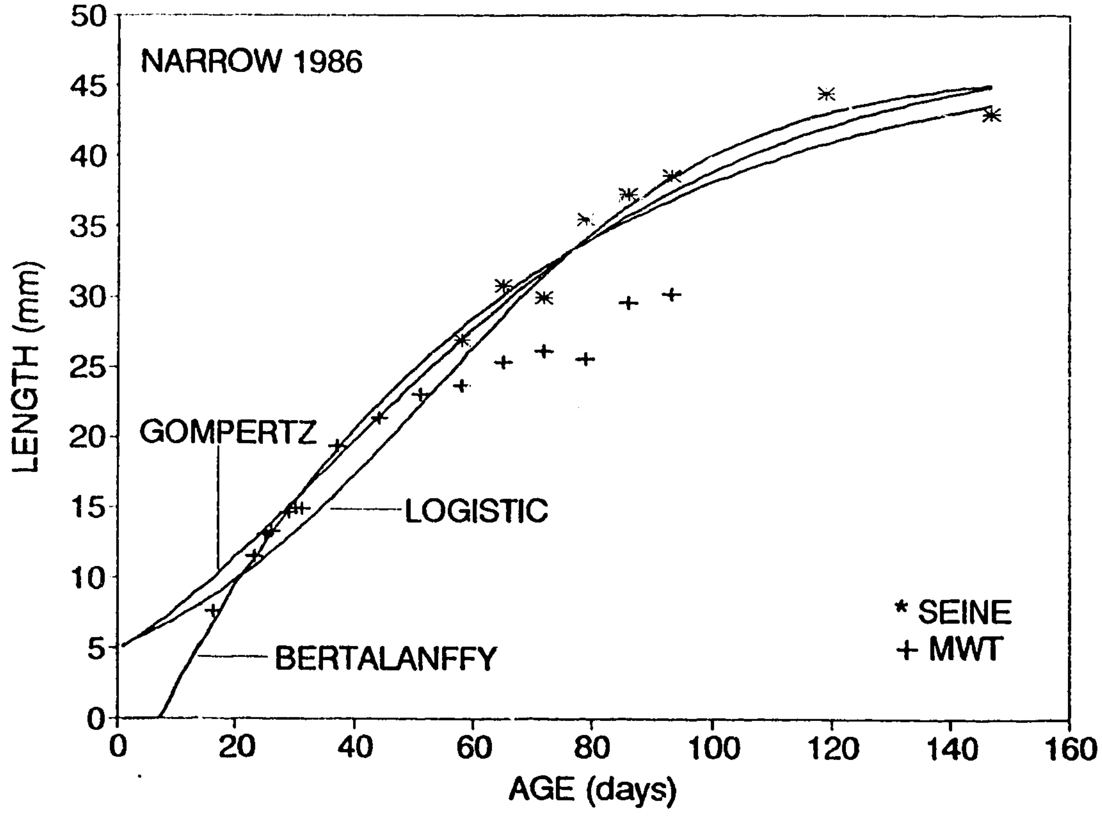
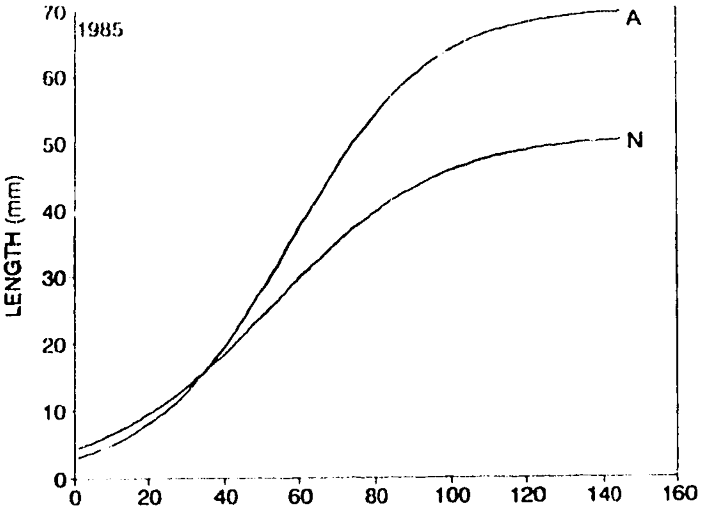
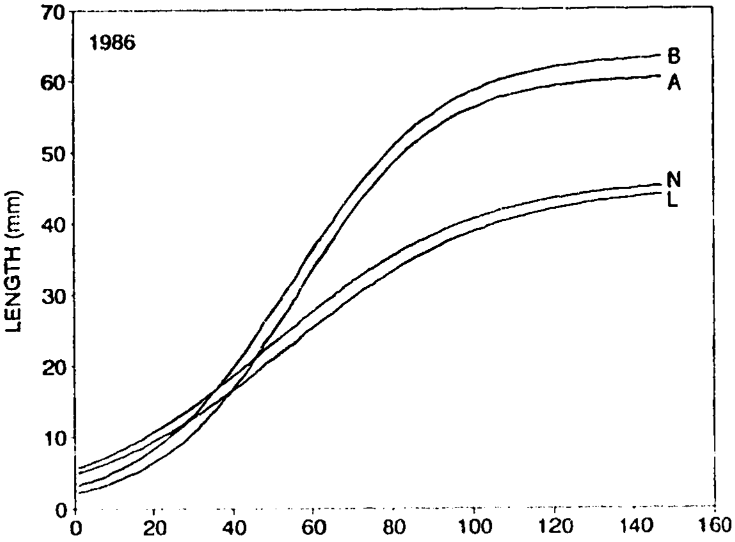

NARROW 1986
LENGTH (mm)
0
5
10
15
20
25
30
35
40
45
50
0
20
40
60
80
100
120
140
160
AGE (days)
GOMPERTZ
LOGISTIC
BERTALANFFY
* SEINE
+ MWT

Figure III-[illegible]. Logistic growth curve for length of age 0 yellow perch from Amisk (A), Baptiste (B), Long (L) and Narrow (N) Lakes 1985-1987. Age is in days after hatching.


1985
LENGTH (mm)
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
140
160
A
N


1986
LENGTH (mm)
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
140
160
B
A
N
L

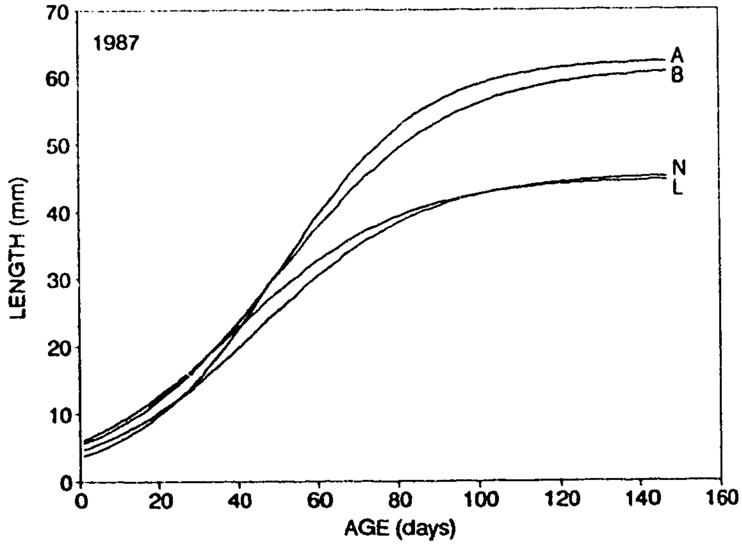
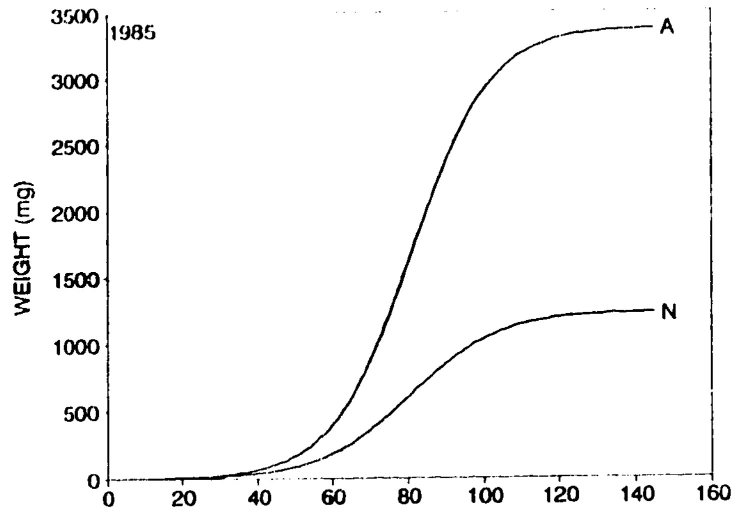
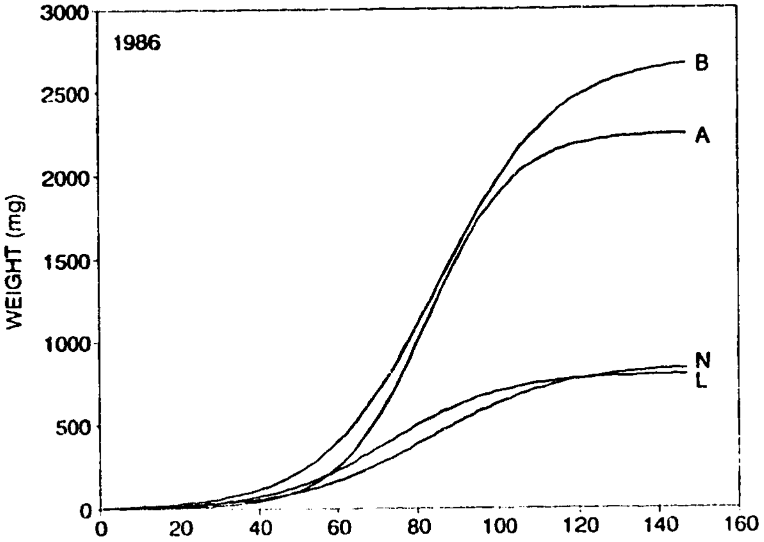

1987
LENGTH (mm)
70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
140
160
AGE (days)
A
B
N
L

Figure III-3. Logistic growth curve for weight of age 0 yellow perch from Amisk (A), Baptiste (B), Long (L) and Narrow (N) Lakes 1985-1987. Age is in days after hatching.


1985
WEIGHT (mg)
0
500
1000
1500
2000
2500
3000
3500
0
20
40
60
80
100
120
140
160
A
N


1986
WEIGHT (mg)
0
500
1000
1500
2000
2500
3000
0
20
40
60
80
100
120
140
160
B
A
N
L

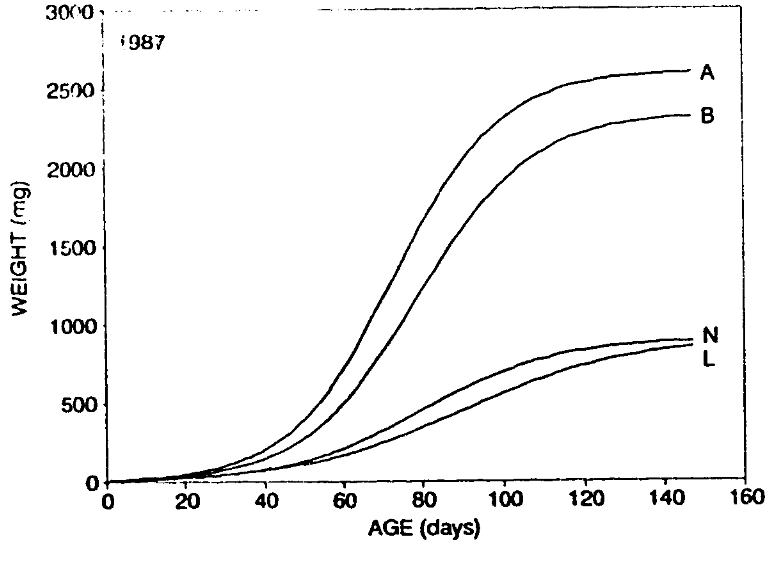
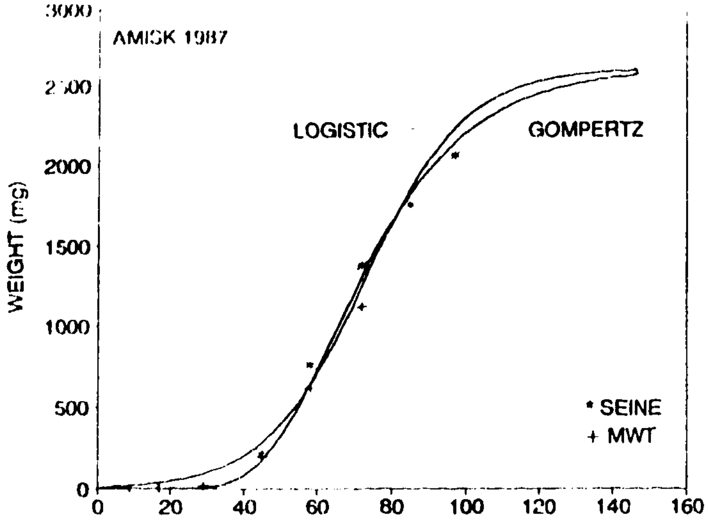
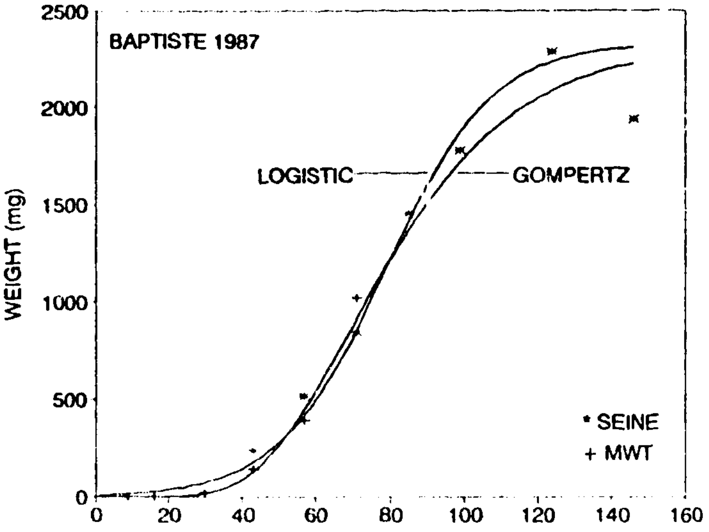

1987
WEIGHT (mg)
0
500
1000
1500
2000
2500
3000
0
20
40
60
80
100
120
140
160
AGE (days)
A
B
N
L

Figure III-4. Logistic and Gompertz growth curves for weight of age 0 yellow perch from Amisk, Baptiste and Narrow Lakes in 1987. Mean length of fish from seines and midwater trawls (MWT) is plotted separately.


AMISK 1987
LOGISTIC
GOMPERTZ
* SEINE
+ MWT
WEIGHT (mg)
0
500
1000
1500
2000
2500
3000
0
20
40
60
80
100
120
140
160


BAPTISTE 1987
LOGISTIC
GOMPERTZ
* SEINE
+ MWT
WEIGHT (mg)
0
500
1000
1500
2000
2500
0
20
40
60
80
100
120
140
160

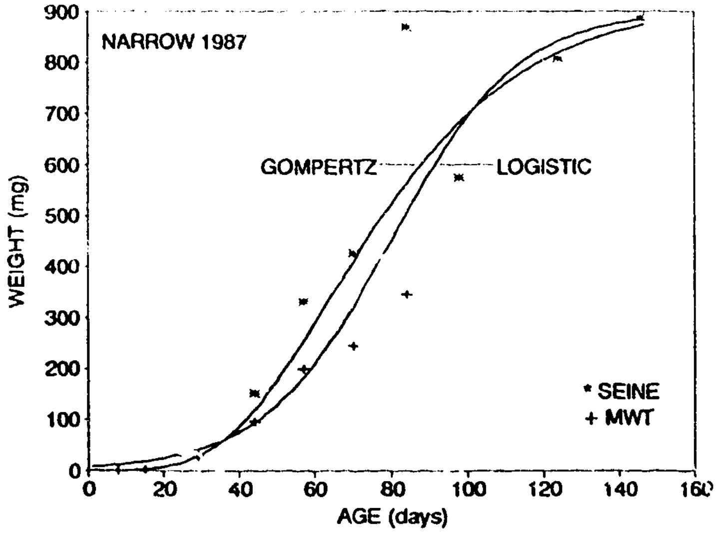
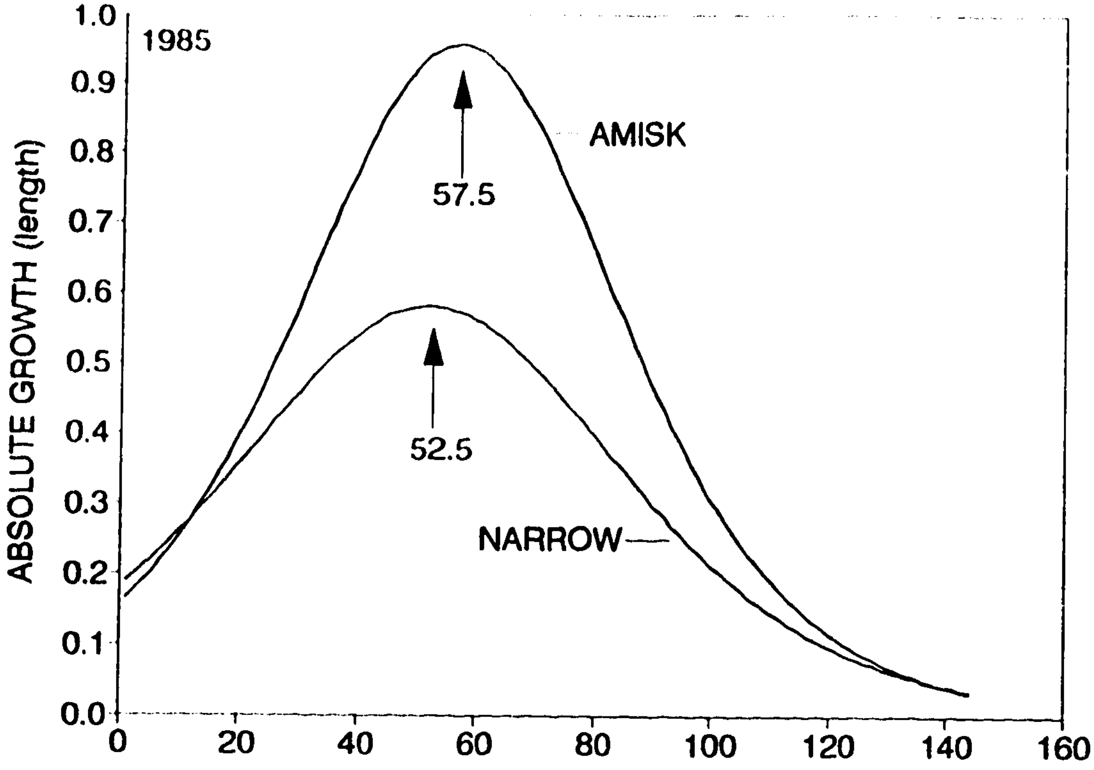
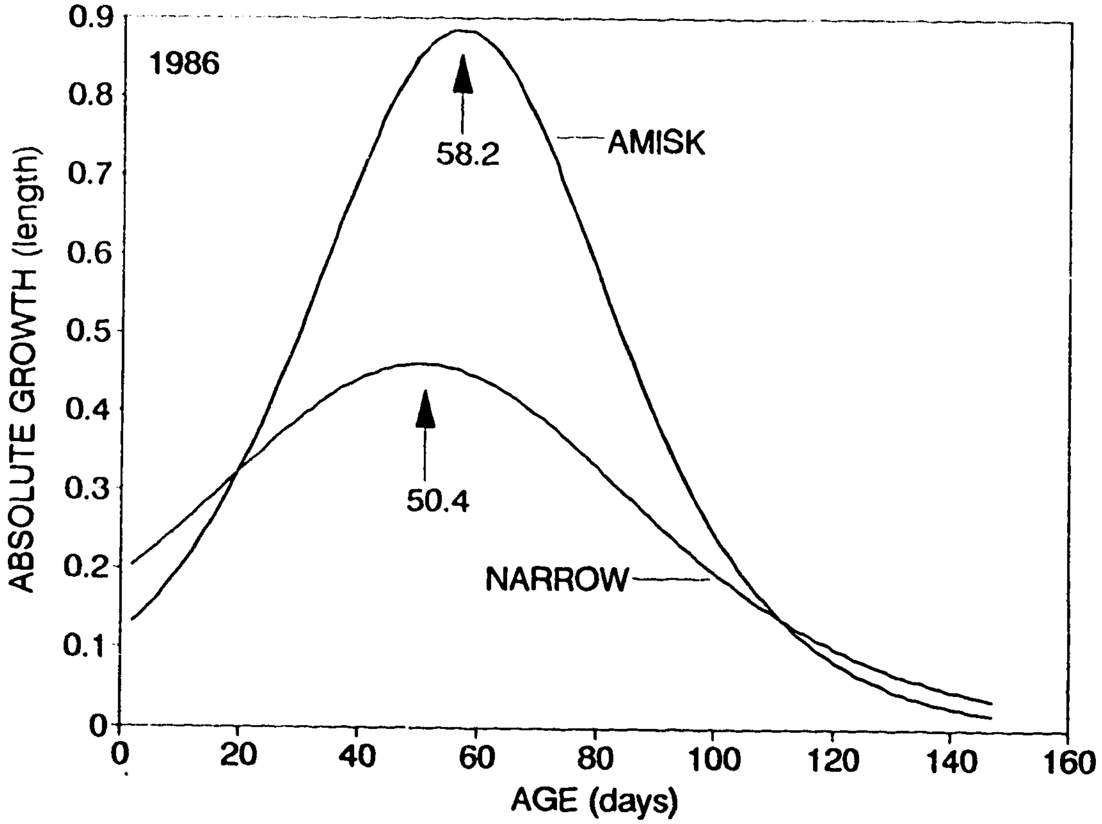
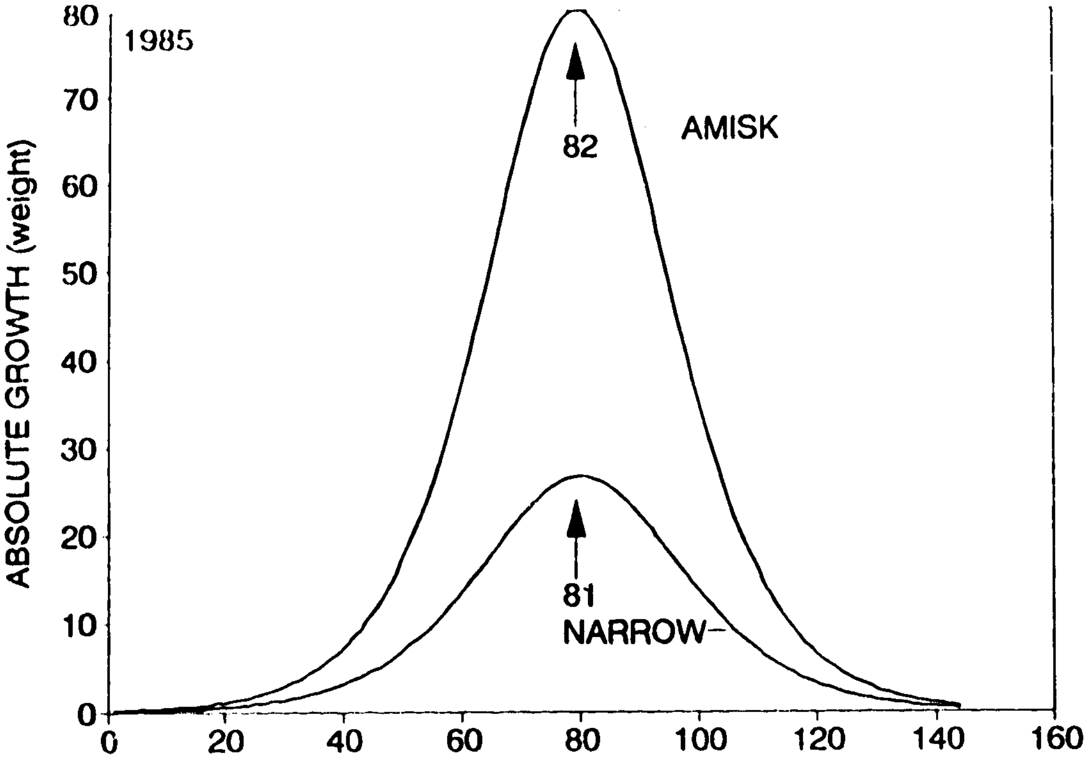

NARROW 1987
GOMPERTZ
LOGISTIC
* SEINE
+ MWT
WEIGHT (mg)
0
100
200
300
400
500
600
700
800
900
0
20
40
60
80
100
120
140
160
AGE (days)

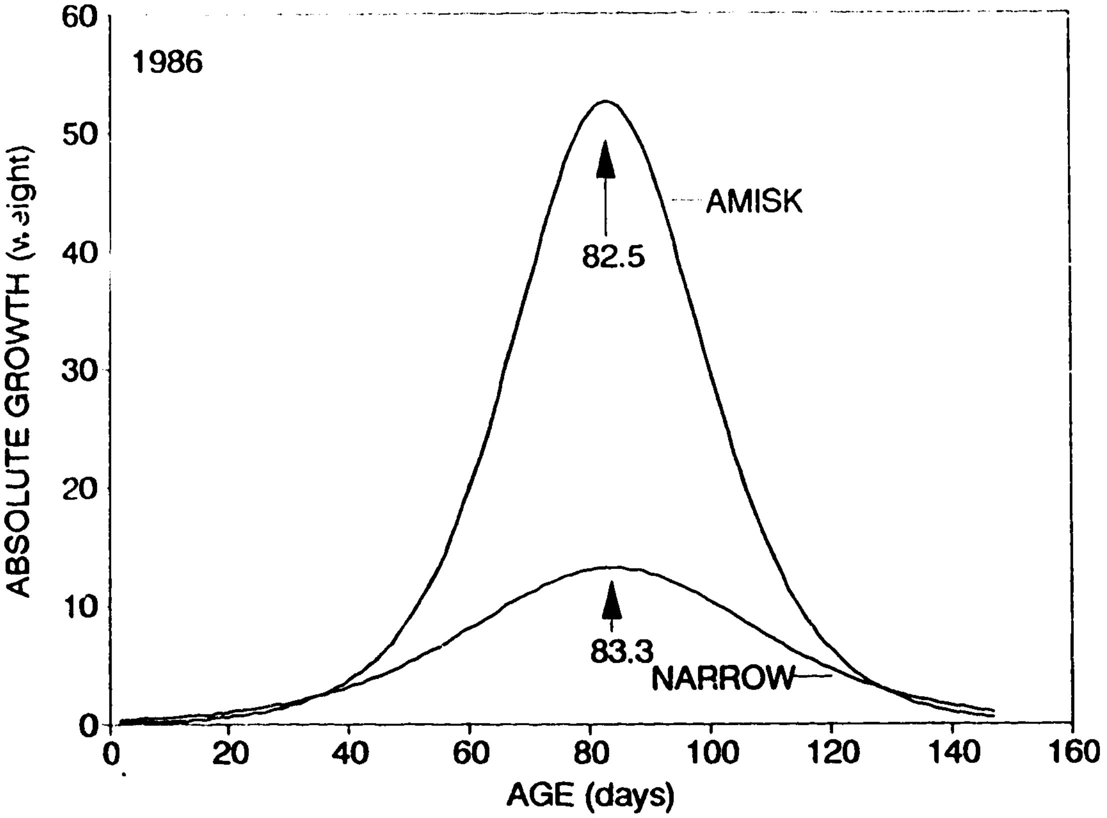
Figure III-5. Absolute growth curves for length (mm·day^{-1}) of age 0 yellow perch from Amisk and Narrow Lakes in 1985 and 1986. The arrows show the inflection points given in days after hatching.


1985
AMISK
NARROW
57.5
52.5
ABSOLUTE GROWTH (length)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
20
40
60
80
100
120
140
160


1986
AMISK
NARROW
58.2
50.4
ABSOLUTE GROWTH (length)
AGE (days)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
20
40
60
80
100
120
140
160

ure III-6. Absolute growth curves for weight ($mg\cdot day^{-1}$)
age 0 yellow perch from Amisk and Narrow Lakes in 1985
and 1986. The arrows show the inflection points given in
days after hatching.


1985
ABSOLUTE GROWTH (weight)
0
10
20
30
40
50
60
70
80
AMISK
82
81
NARROW
0
20
40
60
80
100
120
140
160


1986
ABSOLUTE GROWTH (weight)
0
10
20
30
40
50
60
AMISK
82.5
83.3
NARROW
0
20
40
60
80
100
120
140
160
AGE (days)

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Chapter IV

Predicting the growth of age 0 yellow perch populations from measures of whole lake productivity

Introduction

Growth rate of fish is highly variable among lakes and identifying the factors responsible for this variability is essential for predicting fish growth. Although trophic level interactions have been used to predict fish production or biomass in aquatic systems, this community level approach has not been applied to predicting fish growth.

Determining the relative importance of trophic level interactions on fish production or biomass in aquatic systems has stimulated active research and discussion (Mills and Schiavone 1982; McQueen et al. 1986; Carpenter et al. 1987; Mills and Forney 1988). Extending the analysis of trophic level relationships to specific aspects of community structure or dynamics should improve predictions of the response of a given species to trophic level perturbations (Shapiro 1980; Scavia and Fahnenstiel 1988).

Models predicting the nature of interactions among trophic levels in aquatic systems have been developed for different levels of trophic interactions. Phytoplankton biomass has been found to be positively correlated with phosphorus concentration (Stockner and Shortreed 1985; Trimbee and Prepas 1987) as have the biomass of zooplankton

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--1. A version of this chapter has been published. Abbey and MacKay 1991. Freshwat. Biol. 26:519-525.

(Hanson and Peters 1984) and fish (Hanson and Leggett 1982). The implications of "cascading trophic interactions" (Carpenter et al. 1985; Mills et al. 1987) suggest both a bottom-up and top-down control of the biomass at any given trophic level (McQueen et al. 1989). Mittelbach et al. (1988) and McQueen (1990) review the implications of these trophic level interactions and Mittelbach et al. (1988) suggest that models with greater predictive power across a productivity gradient will result when populations as well as their resources are subdivided into separate size or age classes. Assuming that resources are limited, the response of a population to increases in primary productivity should be an increase in individual growth rate or increased population density. Either response would result in increased population biomass unless mortality rates increased concurrently. In natural systems, accurate seasonal estimates of primary productivity or phytoplankton population density are difficult or costly to obtain. However total phosphorus or chlorophyll a levels are easily obtained in aquatic systems and provide good estimates of primary productivity (Fee 1979; Smith 1979).

I hypothesized that the size of age 0 yellow perch (*Perca flavescens* Mitchill) at the end of August could be predicted as a function of the following independent variables: average summer total phosphorus (TP) and chlorophyll a (Chl a) concentrations, zooplankton density and biomass, and degree-days. I examined the extent to which these variables could explain variation in age 0 yellow perch size at the end of the season in 10 central Alberta lakes. I present a predictive model for the end of season size of age 0 yellow perch as a function of average summer TP and Chl a.

Materials and Methods

Ten deep boreal lakes in cental Alberta were selected with similar morphometry (Table IV-1) but with average summer TP and Chl a levels ranging from 11-51 and 1.4-20 $\mu g \cdot L^{-1}$ respectively. North and South Skeleton Lake were treated as separate bodies of water because they consist of two distinct basins separated by a 1.2 km channel less than 2 m deep. Water samples were taken for TP and Chl a analysis and water temperatures were recorded on a monthly basis from each lake from the first of May to the end of August 1988. Since the ten lakes in this study were similar in morphometry and in the same geographic area, similar temperature regimes among lakes were expected. However, each temperature in each lake was monitored to control for degree-day (°C·d) differences.

Water temperatures were measured during each sampling period at the surface (8 cm) and at 1-m intervals to a depth of 5 m using a calibrated thermistor (Montedoro-Whitney TC-5C) with a precision of 0.1 °C. Mean temperatures over the

6 depth intervals were used to calculate cumulative degree-days from 1 May to the end of August for each lake. To determine the accuracy of these estimates, degree-days were calculated from daily median temperatures at a depth of 2 m obtained from a Ryan temperature recorder in Narrow Lake and compared with degree-day estimates based upon temperatures recorded during the 5 sampling intervals in this lake. Degree-day estimates based upon the 5 sampling intervals in Narrow Lake were within 3.9% of actual degree-day values obtained from daily median temperatures using a Ryan recorder.

Integrated water samples were taken to a depth of 1% light penetration for TP and Chl a analysis. Total phosphorus was measured using the method of Menzel and Corwin (1965) as modified by Prepas and Rigler (1982). Chl a levels were determined by Ostrofsky's method outlined by Bergmann and Peters (1980).

Zooplankton were collected using a 30 cm diameter plankton net with 243 μm mesh. Vertical tows were taken in each lake from 0-6 m in the limnetic zone at the end of June and from 0-3.2 m over a depth of 4 m in the littoral zone at the end of July. Two replicate tows were made at each sampling site. Zooplankton were preserved with a 6% sucrose, 2% formalin solution. Taxonomic identification was to suborder for the subclass Copepoda: Cyclopoida and Calanoida and to genera for Cladocera. Zooplankton were measured using an ocular micrometer fitted in a stereo dissecting microscope. Zooplankton density was determined by two replicate counts made from each of two random subsamples of 300-500 organisms taken from each zooplankton tow. Zooplankton biomass ($\mu g \cdot L^{-1}$) estimates were then derived using regressions relating dry weight (μg) to TL (mm) for each major taxa of zooplankton (McCauley 1984; Culver et al. 1985).

Age 0 yellow perch were collected with a beach seine from each lake between August 22 and 26, killed with an overdose of anaesthetic (0.15% 2-phenoxyethanol) and preserved in 8% formalin. Total lengths (TL) of preserved age 0 yellow perch from each lake were measured to the nearest 0.1 mm with calipers. Blotted wet weights were determined to the nearest milligram.

Stepwise multiple linear regression was used to determine the relation between fish size at the end of August and the independent variables Chl a, TP, total zooplankton density, zooplankton density by taxa and size group, total zooplankton biomass and degree-days. Variables which did not contribute significantly in predicting fish size were not retained in the regression model. The breakdown of zooplankton density was based on five taxonomic groups (calanoids, cyclopoids, rotifers, Daphnia, and cladocerans excluding Daphnia and Leptodora) and four size groups ($x < 0.5$, $0.5 \leq x < 1.0$, $1.0 \leq x < 1.5$, $x \geq 1.5$ mm).

In Amisk, Baptiste, Long and Narrow lakes, age 0 perch were collected near the end of August in every year from 1985 to 1992. In every year, length and weight data obtained near the end of August were adjusted to give size estimates for August 28. This was done using an appropriate logistic growth model developed in Chapter III. Data from these lakes was combined with the 1988 data from the six other lakes in this study to evaluate the relationship between fish size at the end of the season and TP, Chl a, and degree-days. This approach enabled me to determine whether consistent patterns in fish size occurred among lakes or among years.

Results

Stepwise multiple regression showed that a significant ($P < 0.05$) amount of the variation in wet weight (WT) of age 0 yellow perch could be explained by the interaction of TP, Chl a, and density of calanoid copepods (Cal) between 1.0 and 1.5 mm in length. The last variable did not contribute significantly to explaining the variation in total length (TL) of age 0 yellow perch. The regression equations were:

$$TL = 1.10(TP) - 1.78(Chl\ a) + 34.00 \qquad R^2=0.61 \quad (1)$$

$$WT = 120.66(Cal) + 79.42(TP) - 150.53(Chl\ a) + 148.18 \qquad R^2=0.80 \quad (2)$$

Removal of calanoid density from equation (2) reduced the coefficient of determination (R^2) from 0.80 to 0.57 thus:

$$WT = 95.76(TP)-150.65(Chl\ \underline{a})+70.22 \qquad R^2=0.57 \quad (3)$$

The contribution of total zooplankton density or biomass in explaining the variance in age 0 yellow perch size at the end of the season improved when fish from lakes with TP exceeding 37 $\mu g \cdot L^{-1}$ were excluded from the data set. With this restriction, regression models predicting fish size at the end of August improved dramatically (Table IV-2).

The sizes of age 0 yellow perch at the end of August in relation to the trophic level parameters TP, Chl a, zooplankton density and biomass are given in Table IV-3. The variance in the size of age 0 yellow perch at the end of the season was much greater as TP increased (Figure IV-1). This figure suggests that there may be an optimum level of TP at which age 0 perch weight maximized. Two factors may account for this pattern. In the most productive lakes of this study, spottail shiners were abundant. These planktivores are a competitor of age 0 perch and may suppress the growth of perch. Also, high nutrient levels increase phytoplankton densities as indicated by Chl a concentrations (Table IV-3). Reduced light penetration would limit the depth of the photic zone as well as the effective feeding depth for planktivores. Total zooplankton biomass could be reduced as well.

My eight year data set showed that a significant amount of the variance in TL or WT of age 0 perch on August 28 was explained by either TP or Chl *a*. Stepwise multiple regression models were used to predict TL or WT as a function of TP, Chl *a*, and degree-days. In all cases, either TP or Chl *a* were found to be significant predictors of TL or WT but the degree-day variable never showed a significant correlation with the dependent variables. In fact in 1988, when cumulative degree-days were the highest for the 1985-1988 period, end of season WT of age 0 perch was lowest for that period in Amisk, Baptiste, Long and Narrow lakes (Table IV-4).

The contribution of either TP or Chl *a* in explaining the variance in TL or WT was similiar but in no case did both variables contribute significantly in a multiple regression model. The correlation coefficient between TP and Chl *a* is 0.89 which may be why independent effects cannot be seen. When all lakes and years were included in single linear regression models (n=37), the regression equations were:

$$TL = 0.366(TP) + 43.19 \qquad R^2=0.43 \quad (4)$$

$$TL = 0.509(Chl\ a) + 47.89 \qquad R^2=0.40 \quad (5)$$

$$WT = 35.15(TP) + 806.42 \qquad R^2=0.37 \quad (6)$$

$$WT = 50.93(Chl\ a) + 1235.68 \qquad R^2=0.38 \quad (7)$$

These results indicate that predictions of age 0 perch size at the end of the season are equally valid whether TP or Chl *a* are the independent variables. These results also show that predictions of fish size among years is possible using bottom-up trophic level indicators.

Discussion

The variability in the relationship between age 0 yellow perch size at the end of August and lake productivity (as indicated by average summer TP), increased as lake productivity increased. This suggests that in less productive lakes, the growth of planktivorous fish may be food limited because zooplankton biomass and density have been shown to depend upon TP (Hanson and Peters 1984). My data support the hypothesis of food limited control if the three lakes with TP exceeding 37 $\mu g \cdot L^{-1}$ were excluded. In this case, total zooplankton density or biomass alone predict from 43-63 % of the variance in age 0 yellow perch size at the end of the season (Table IV-2).

In highly productive lakes, planktivorous fish may experience a food surplus and their growth would be determined by physiological or environmental factors or community level interactions independent of bottom-up control. Cisco (Coregonus artedii Lesueur), whitefish (Coregonus clupeiformis Mitchill) and spottail shiners (Notropis hudsonius Clinton), all important planktivores, were not present in unproductive Long and Narrow lakes. However, with the possible exception of Ghost Lake, one or more of these potential competitors of age 0 perch were present in all the other study lakes. Walleye (*Stizostedion vitreum* Mitchill), an important predator of yellow perch, were present in all the study lakes with TP > 34 $\mu g \cdot L^{-1}$, with the possible exception of Ghost Lake. The reduced complexity in fish community structure in less productive lakes increases the likelihood that bottom-up measures of productivity will accurately predict fish growth in these systems.

Downing et al. (1990), in assessing data on production by fish communities from the literature, found that the conversion of phytoplankton into fish production is several orders of magnitude more efficient in oligotrophic systems than in eutrophic ones. This would be expected in oligotrophic systems if fewer trophic links were present or if bottom-up control was operating and food was limiting. Sprules and Munawar (1986), in assessing plankton size spectra in relation to ecosystem productivity, found that in eutrophic ecosystems, nutrients entering at a high rate are cycled quickly through fast-growing nannoplankton to produce relative high abundances of zooplankton. These high densities of zooplankton should support a greater biomass of planktivorous fish. However, if food were present in excess in eutrophic systems, conversion efficiencies into fish growth would be low because a greater fraction of the biomass in lower trophic levels would be channelled directly to the detrital food web. This indicates that predicting fish growth in eutrophic systems from bottom-up measures of productivity alone may not be a suitable approach.

Mills et al. (1989) found a significant relationship between the biomass of *Daphnia* and the growth of age 0 yellow perch. These authors used an 11 year data set from Oneida Lake, New York to calculate the mean biomass of five zooplankton species groups on three equivalent cumulative temperature dates corresponding to mid-July, mid-August and early-October. My data for zooplankton density and biomass from each of the 10 lakes were based upon two sampling dates. The high variance in zooplankton densities within and among lakes reduced my ability to predict fish size from these data. Calanoid density was the only zooplankton variable which explained a significant amount of the variation in WT of age 0 yellow perch. Although more frequent and intensive zooplankton sampling would result in better predictions of fish size, the costs and time involved in sampling and analysis would not be justifiable for lake management purposes.

The contribution of zooplankton density or biomass in predicting age 0 fish size would be expected to be greater than that of Chl *a* or TP as a result of the direct trophic link between these fish and zooplankton. I did find TP to explain a significant amount of the variance in total zooplankton density or biomass (r^2 = 0.46 and 0.49 respectively). Although the link between fish size and zooplankton density or biomass was stronger when the three lakes with the highest productivity were excluded, a significant relationship was only found between TL and zooplankton biomass.

Boisclair and Leggett (1989a) found that differences in food consumption explained a significant proportion of the variability in yellow perch growth rates among 12 Quebec lakes for age-1 fish but not for age-2 or age-3 fish. These authors suggested that factors other than food consumption, such as prey type and prey availability (Boisclair and Leggett 1989b) or total fish community density (Boisclair and Leggett 1989c), were responsible for among population variability in growth of age-2 and age-3 yellow perch. These data emphasize that models developed to predict fish growth or production must be validated for a given size or age-category of fish.

My data show that average summer TP and Chl a are good predictors of age 0 yellow perch size at the end of the growing season. Although equation (3) explains less of the variance in WT of age 0 fish at the end of August, it is a model which is more suitable for fish management than equation (2) because zooplankton sampling and analysis are not required. Since all 10 experimental lakes were of similar basin morphometry and located in the same geographic area, temperature regimes were similar among lakes and degree-days did not contribute significantly in explaining fish size at the end of the first season. When examining trends among years in four lakes, I found no correlation at all between degree-days and age 0 perch size on August 28. In fact, the smallest seasonal sizes occurred in 1988 when the highest cumulative degree-days occurred. It seems clear that variables other than degree-days are much more important in the growth of age-0 perch at least in these lakes which occur in the same area.

The application of this model to aquatic systems in other geographic areas would require that the size of age 0 yellow perch be determined at a time when cumulative degree-days were equivalent (see Mills et al. 1989). Alternatively, the model could be modified to include temperature as one of the predictors of end-of-season size differences. Temperature was not included in the present model because degree-days varied less than 6.3% among the lakes in 1988.

In eutrophic systems, first year fish growth is less predictable from bottom-up trophic level indicators. In these systems, data on more complex community level interactions including top-down effects should be evaluated prior to developing a model predicting fish growth, yield or production.

Table IV-1. Characteristics of the 10 study lakes in Alberta, Canada. Mean depth ($\underline{z}$) and maximum depth (MAX$\underline{z}$) are in metres.

Lake	Latitude North	Longitude West	Area (km^2)	Depth ($\underline{z}$)	Depth (MAX$\underline{z}$)
Amisk N	54°35'	112°37'	2.33	10.8	34
Baptiste S	54°45'	113°33'	4.74	11.9	27
Garner	54°12'	111°44'	6.19	8.1	15
Ghost	54°53'	113°37'	1.98	4.8	14
Hanmore	54°17'	112°31'	2.67	8.3	25
Lodge	54°43'	112°26'	2.50	6.6	22
Long	54°34'	113°38'	1.62	9.4	28
Narrow	54°35'	113°37'	1.14	14.4	38
Skeleton S	54°37'	112°43'	6.13	6.6	11
Skeleton N	54°38'	112°42'	2.16	13.1	17

Table IV-2. A comparison of coefficients of determination ($\underline{r}^2$) and the significance level (p) for the slope (s) of the relationship between age 0 yellow perch total length (Ln) or wet weight (Wt) as predicted from total phosphorus (TP), chlorophyll a (Chl a), total zooplankton density (Zpd) or biomass (Zpb).

Variables		All Lakes			Lakes with TP < 37 $\mu g \cdot L^{-1}$		
Dep.	Ind.	s	$\underline{r}^2$	p	s	$\underline{r}^2$	p
Ln	TP	0.27	0.29	0.11	0.61	0.76	0.01
Ln	Chl a	0.27	0.07	0.45	1.48	0.58	0.05
Ln	Zpd	0.08	0.29	0.11	0.12	0.48	0.08
Ln	Zpb	0.01	0.25	0.14	0.02	0.63	0.03
Wt	TP	25.34	0.30	0.10	58.20	0.84	0.004
Wt	Chl a	26.88	0.09	0.41	150.23	0.72	0.02
Wt	Zpd	7.07	0.25	0.14	10.08	0.43	0.11
Wt	Zpb	0.80	0.20	0.19	1.55	0.52	0.07

Table IV-3. Total length (TL) and weight (WT) of age 0 yellow perch at the end of August in 10 central Alberta lakes. Total phosphorus (TP) and chlorophyll a (Chl a) concentrations are average summer values (n=5). Zooplankton density and biomass are mean values for limnetic and littoral zone samples taken at the end of June and July respectively. Degree days (°C·d) are given from May 1 to August 24, 1988.

						Zooplankton		
Lake	TL (mm)	WT (mg)	n	Chl a ($\mu g \cdot L^{-1}$)	TP	Density ($\# \cdot L^{-1}$)	Biomass ($\mu g \cdot L^{-1}$)	°C·d
Amisk	53.4	1762	84	10.2	34.3	64.47	566.9	2010
Baptiste	47.3	1238	100	19.5	46.8	70.84	927.2	1949
Garner	57.2	2462	11	10.4	34.3	30.34	263.9	1994
Ghost	53.5	1746	98	10.4	38.3	24.61	226.0	2046
Hanmore	51.2	1463	100	2.9	16.3	24.95	220.1	1927
Lodge	55.5	1760	100	3.9	23.6	32.59	440.1	2039
Long	41.8	767	100	2.0	11.6	2.66	9.4	2049
Narrow	38.6	583	100	1.4	10.9	0.30	1.1	2022
Skeleton S	58.1	2217	100	8.6	35.2	87.96	296.0	1977
Skeleton N	50.2	1468	73	17.9	40.1	131.94	909.7	1992

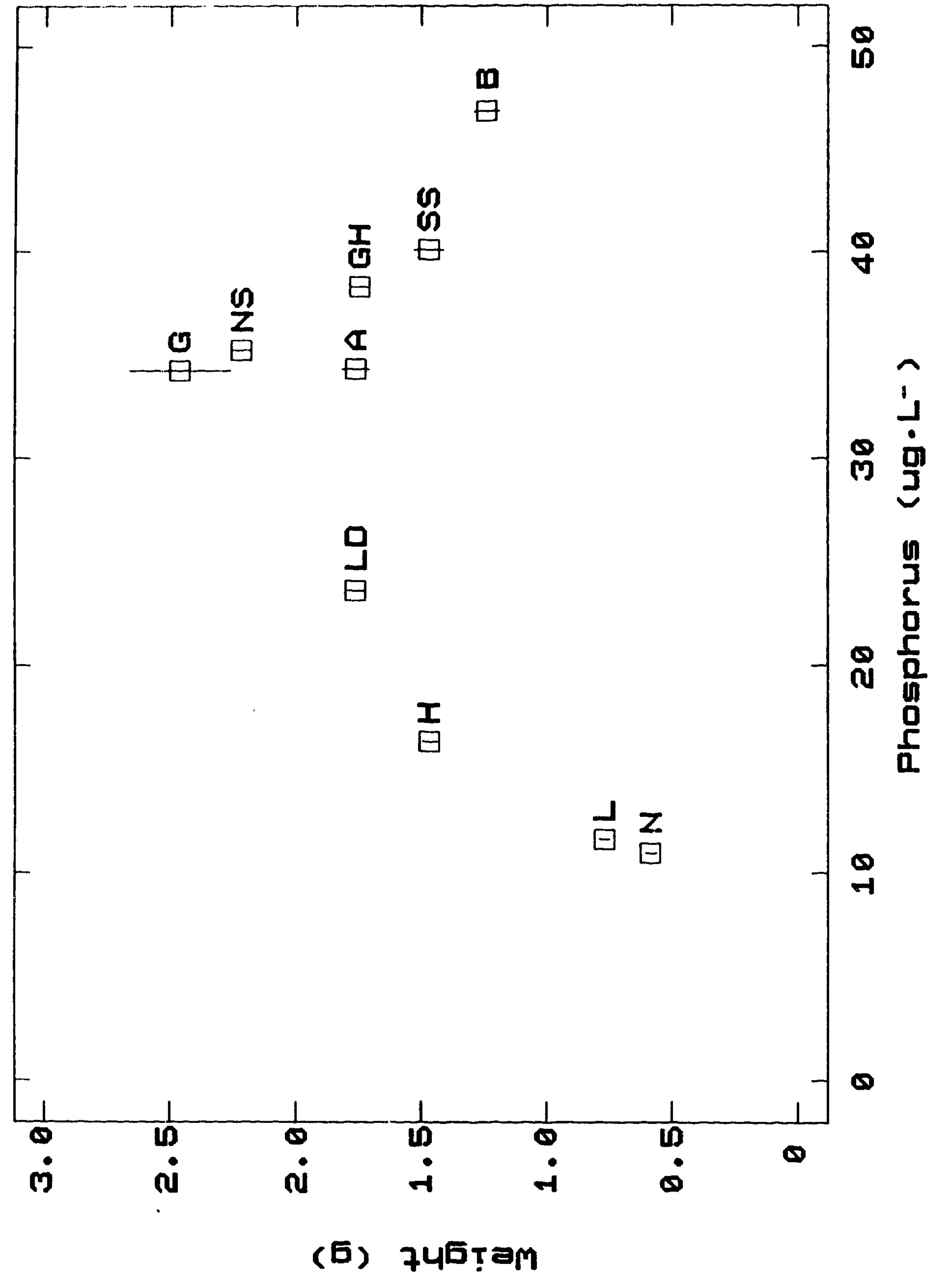
Table IV-4. Among year and among lake size comparisons of age 0 yellow perch in 10 central Alberta lakes. Total length (TL) and weight (WT) estimates are for August 28 in all cases. Total phosphorus (TP) and chlorophyll a (Chl a) concentrations ($\mu g \cdot L^{-1}$) are average summer values. Degree days (°C·d) are given from May 7 to August 28 in all years.

LAKE	YEAR	TL (mm)	WT (mg)	Chl a	TP	°C·d
AMISK	1985	66.2	3225	13.3	28.4	1935
AMISK	1986	58.5	2137	8.7	26.2	1940
AMISK	1987	60.7	2485	18.2	26.9	1951
AMISK	1988	53.7	1788	10.2	34.3	2020
AMISK	1989	58.0	2167	10.0	29.9	
AMISK	1990	58.1	2086	11.4	35.7	
AMISK	1991	62.1	2560	7.1	30.2	
AMISK	1992	58.5	2302	11.3	30.2	
BAPTISTE	1985	52.6	1336	30.3	50.8	1982
BAPTISTE	1986	60.3	2479	24.2	41.3	1944
BAPTISTE	1987	57.1	1821	25.5	55.1	1950
BAPTISTE	1988	47.8	1318	19.5	46.8	2041
BAPTISTE	1989	64.1	3009	24.9	48.5	
BAPTISTE	1990	70.3	3856	24.9	48.5	
BAPTISTE	1991	64.3	2990	24.9	48.5	
BAPTISTE	1992	57.6	2290	24.9	48.5	
LONG	1986	50.6	1158	3.9	13.2	1880
LONG	1987	44.3	891	3.0	19.4	1990
LONG	1988	42.6	779	2.0	11.6	2124
LONG	1989	46.2	1023	3.0[a]	14.7[a]	
LONG	1990	43.7	825	3.0[a]	14.7[a]	
LONG	1991	47.1	1050	3.0[a]	14.7[a]	
LONG	1992	42.8	769	3.0[a]	14.7[a]	
NARROW	1985	48.1	1663	2.4	13.6	1901
NARROW	1986	42.7	738	2.7	10.5	1919
NARROW	1987	43.9	796	2.0	11.8	1897
NARROW	1988	38.8	605	1.4	10.9	2095
NARROW	1989	44.0	1503	1.9	11.8	
NARROW	1990	50.5	1202	1.1	13.9	
NARROW	1991	49.8	1270	2.5	11.7	

NARROW	1992	51.2	1499	2.2	10.1	
GHOST	1988	54.1	1797	10.4	38.3	2155
HANMORE	1988	51.3	1477	2.9	16.3	1966
LODGE	1988	55.8	1786	3.9	23.6	2095
SKELETON S	1988	50.5	1494	17.9	40.1	2033
SKELETON N	1988	58.4	2243	8.6	35.2	2050
GARNER	1988	57.4	2497	10.4	34.3	2034

[a] average value based on 1986-1988 data

Figure IV-1. Wet weight of age 0 yellow perch at the end of August 1988 in 10 central Alberta lakes in relation to average summer total phosphorus ($\mu g \cdot L^{-1}$). Vertical bars denote standard error. Lake codes: A = Amisk; B = Baptiste; G = Garner; GH = Ghost; H = Hanmore; LD = Lodge; L = Long; N = Narrow; NS = Skeleton N; SS = Skeleton S.


Weight (g)
3.0
2.5
2.0
1.5
1.0
0.5
0
Phosphorus (ug·L⁻)
0
10
20
30
40
50
G
NS
A
GH
SS
B
LD
H
L
N

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Chapter V

The interaction between zooplankton resources, food selection and consumption upon the growth of age 0 yellow perch in lakes of contrasting trophic status.

Introduction

The wide variations in individual growth rate which occurred among yellow perch populations in a small geographic area were related to lake productivity (Abbey and Mackay 1991). These differences in growth appeared to be directly caused by differences in the quality or quantity of available food in a given lake. Divergence in growth among lakes occurred five to six weeks after hatching in yellow perch when perch were entirely planktivorous and growth was most rapid. This feature provideed an opportunity to measure both the quantity and quality of food available and food consumption in populations showing a wide range of age 0 fish growth.

The interaction between growth and food resources, food selection and consumption has been investigated for many adult fish populations (Paloheimo and Dickie 1966; Rice et al. 1983). Within a given lake, data relating body size or growth to feeding energetics of juvenile fish is available for bluegill, Lepomis macrochirus (Mittelbach 1981, 1983), walleye (Forney 1966; Michaletz et al. 1987), lake whitefish, Coregonus clupeaformis (Taylor and Freeberg 1984) and European perch, Perca fluviatilis (Guma'a 1978; Coles

1981; Treasurer 1988).

Previous studies of age 0 yellow perch growth and feeding were restricted to the laboratory (Confer and Lake 1987; Mills et al. 1989a) or focus on a single season (Post 1987) or on a single lake if over more than one season (Lin 1975; Ney and Smith 1975; Noble 1975; Henderson 1977; Mills and Forney 1981; Whiteside et al. 1985; Michaletz et al. 1987; Post 1987; Mills et al. 1989b). This study is unique in that factors responsible for differences in body size and growth of age 0 fish in their natural habitat are compa among lakes over a three year period.

In the four lakes in this study, species composit zooplankton from both the limnetic and littoral zones were compared with the gut contents of age 0 perch to identify the relationships between zooplankton food resources, food selection and consumption. I hypothesize that size differences of age 0 perch among lakes in a given geographic area the primary factor is a result of differences in food resources. My research, incorporating data from four lakes differing in productivity, is designed to provide a comparative basis for evaluating this hypothesis.

Materials and Methods

This study was carried out between 1985 and 1988 in four central Alberta lakes; Amisk, Baptiste, Long and Narrow. These lakes are located within a 60 km radius of

Athabasca, Alberta and have average summer total phosphorus (TP) and chlorophyll a (Chl a) levels in the range of 11-47 and 1.4-19.5 $\mu g \cdot L^{-1}$, respectively. Age 0 yellow perch were collected in the limnetic zone with a midwater trawl and in the littoral zone with a bag seine. In 1985 and 1986, five or six zooplankton and fish samples were taken in both Amisk and Narrow lakes at regular intervals between the end of June and the end of August. During 1987, all four study lakes were sampled for zooplankton and fish on three occasions from the end of June to the end of July during the period of maximum fish growth. Stomach contents were analyzed from 10-30 randomly chosen fish caught at an equivalent time and from the same region of the lake as the zooplankton samples. In 1985, 1987 and 1988, zooplankton samples were taken on selected dates between July 10 and August 5 in both the limnetic and littoral zones to allow for comparisons of zooplankton densities between zones when age 0 perch were moving to the littoral zone. Concurrent zooplankton samples were also taken from both the littoral and limnetic zones in Amisk Lake on June 12 and 26, 1985, prior to the time of onshore migration.

Age 0 yellow perch collected in trawls or seines were immediately killed with an overdose of anaesthetic (0.15% 2-phenoxyethanol) and preserved in 8% formalin. Total lengths (TL) of preserved fish were measured to the nearest 0.1 mm and blotted wet weights were determined to the nearest milligram. In age 0 perch less than 20 mm TL, where the stomach is not clearly differentiated, the alimentary canal was removed and the gut contents from the anterior part of the esophagus to the first intestinal inflection were removed for analysis. In fish greater than 20 mm TL, gut content analysis was restricted to the contents of the stomach.

For each fish, the number and taxa of all prey items in the gut were recorded and a random sample of up to 15 organisms of each taxon was measured using the method of Culver et al. (1985) using a microscope fitted with an ocular micrometer. Taxonomic identification was to genus for Cladocera and to suborder: Cyclopoida and Calanoida, for the order Copepoda. Prey items were grouped into four size categories (< 0.5, $0.5 - < 1.0$, $1.0 - < 1.5$, and ≥ 1.5 mm) and seven general taxonomic groupings: Bosmina, Daphnia, Leptodora, other cladocerans, copepods, rotifers, and all others. In Long and Narrow Lakes, Leptodora were usually not present and when found they were grouped with others. In Amisk and Baptiste lakes, rotifers were rare and if found they were grouped with others. The same taxonomic and size groupings were used in analyzing zooplankton samples.

Zooplankton were collected using a 243 μm mesh plankton net with a 30 cm mouth diameter. Limnetic zone samples consisted of replicate vertical tows made from 6 m to the surface. Littoral zone samples were replicate tows from

0.8, 2.8, and 4.8 m to the surface over the 2, 4 and 6 m depth contours in each lake except in 1988 where only the 2 and 4 m depth contours were sampled. Samples were preserved in situ with a cold 6% sucrose, 2% formalin solution. Subsequent processing involved removal of organisms exceeding 4-5 mm for separate identification and measurement, dilution to a fixed volume (50, 80, 100 or 200 mL), mixing and duplicate volumetric subsampling (1-5 mL). The objective of subsampling was to obtain between 200 and 600 organisms from the original sample. As a result of the low zooplankton densities in Long and Narrow lakes subsampling was often unnecessary and the entire zooplankton sample was analyzed. The number and taxa of all prey items in the subsample were recorded and a random sample of up to 15 organisms of each taxa was measured using microscope with an ocular micrometer.

Zooplankton density was determined from counts of two random subsamples taken from each zooplankton tow. For both lake zooplankton and stomach contents, pooled samples were used to determine the relative abundance in each of the seven taxonomic groupings. Zooplankton biomass ($\mu g \cdot L^{-1}$) estimates were derived using regressions relating dry weight (μg) to TL (mm) for each major taxa of zooplankton (McCauley 1984; Culver et al. 1985). Gut content biomass ($\mu g \cdot fish^{-1}$) was estimated using the same regression equations for zooplankton taxa with aquatic insect weights being estimated using the techniques of Smock (1980).

Cumulative zooplankton density or biomass and cumulative gut content biomass estimates were obtained as follows. Mean zooplankton density, biomass or gut content biomass estimates for each sampling date in a given lake were summed over sequential sampling dates. This value provided an estimate of cumulative densities or biomass over any given period where more than one sampling interval had occurred. In any given season or period, the sampling intervals among lakes were equivalent so that cumulative estimates among lakes could be compared.

Data Analysis

For each collection period, linear- and stepwise multiple-regression analysis was used to determine the dependence of (a) age 0 yellow perch total length or wet weight, and (b) absolute or relative growth rate on the following independent variables: cumulative degree days, cumulative total zooplankton density, cumulative total zooplankton biomass, and the cumulative biomass of all food or of selected taxa in the gut.

The absolute growth rate (GRa) and relative growth rate (GRr) of age 0 yellow perch between pairs of samples were calculated. $GRa = (Wt_2-Wt_1) \cdot n^{-1}$ and $GRr = (Wt_2-Wt_1) \cdot (Wt_1 \cdot n)^{-1}$ where Wt is the mean wet weight (mg) of age 0 fish at collection time 2 and 1 respectively and n is the number of days between collections.

An index of stomach fullness (K_f) was calculated for each individual fish where K_f = [dry weight of gut contents (μg)]·[wet weight of the fish (mg)]$^{-1}$ (Fox 1989). On each sampling date, an index of cumulative stomach fullness (K_{fc}) was also derived for each population where K_{fc} = [mean cumulative dry weight of gut contents (μg)]·[mean wet weight of all fish sampled (mg)]$^{-1}$

Plots showing percent frequency by weight of each taxonomic group in the guts were compared within lakes and among lakes for each collection period, and with lake means generated by averaging data over all collection periods in that year.

The proportion of prey consumed were compared with the proportion available in the environment using the Manly/Chesson index (Chesson 1978, 1983). In this index the value of α_i is interpreted as the proportion of the diet which would consist of food type i if all food types were present in equal numbers in the environment. The model chosen assumes no appreciable change in prey density over a given sampling period. This is an acceptable limitation because zooplankton and fish samples were taken at nearly the same points in time and changes in prey density caused by consumption are likely to be insignificant compared to the total number of prey present in the natural environment.

The Manly/Chesson index was chosen because the value of

α_i does not change with food density unless consumer behavior changes (Chesson 1983). Another index of food selection (Strauss 1979) is widely used in feeding studies. Strauss' index was deemed inappropriate for use in this field study because comparisons among experiments require that relative abundances of available prey are similar (Chesson 1983; Ready et al. 1985).

Results

Predicting age 0 yellow perch size and growth

My data show that age 0 yellow perch size during the first season of growth can be predicted from food availability or from indicators of feeding activity. Differences in age 0 perch size among lakes with contrasting productivity could be predicted from available zooplankton density or biomass in all four lakes.

In predicting total length, wet weight, and absolute growth of age 0 yellow perch, I used cumulative zooplankton density or biomass, cumulative total gut biomass, or cumulative degree days. The results of these predictions based on stepwise multiple regression analysis are given in Table V-1.

Predicting Length or Weight

The best predictor of age 0 yellow perch wet weight or total length on a given date was cumulative total gut biomass in 1985 and 1986. In 1987 cumulative zooplankton density and cumulative degree days were the best predictors of length or weight of fish in (a) the littoral zone or in (b) combined littoral/limnetic samples. Cumulative total gut biomass was the only significant predictor of fish length or weight in the limnetic zone in 1987.

One way of assessing the fish production capacity of a given lake system is to look at fish size at a given point in time in relationship to food availability. On any given date over the three year period, cumulative zooplankton density or biomass explained a significant amount ($R^2=0.34$, $P=0.0004$) and ($R^2=0.31$, $P=0.0008$) respectively, of the variance in fish weight in the study lakes. This demonstrates the importance of food availability to the cumulative weight gain of age 0 yellow perch.

I also evaluated fish size near the end of the season in relationship to food availability. Cumulative zooplankton density explained a significant amount ($R^2=0.78$, $P=0.002$) of the variance in fish weight at the end of August in 1985 and 1986 and at the end of July in 1987. This relationship between age 0 yellow perch weight and cumulative zooplankton density is shown in Figure V-1.

To determine the relative importance of different zooplankton taxa in the gut in predicting age 0 perch weight, four data variables were evaluated. These four variables included the cumulative dry weight biomass of

Bosmina, Copepods, *Daphnia*, and other Cladocerans in the gut. When evaluated with stepwise multiple regression, prediction of fish weight from combinations of these four variables did not markedly improve the R^2 values over those obtained in a simple regression model based on cumulative total gut biomass (Table V-2). Also, the limited improvement provided by this approach may be offset by problems with increased sensitivity to variations in abundance of specific taxa. This problem is illustrated in samples including fish collected in the littoral zone of Narrow Lake on July 14, 1987. The guts of these fish were packed almost exclusively with the cladoceran *Polyphemus* and this anomaly dramatically reduced the ability of all the regression models which included these data in predicting fish weight.

Predicting growth

The only significant predictor of absolute growth of age 0 yellow perch in 1985 and 1986 was cumulative total gut biomass. In 1987 cumulative zooplankton density or biomass were the only significant predictors of absolute growth. In 1986, only 30% of the variance in absolute growth was explained by cumulative total gut biomass (Table V-1). This low coefficient of determination (R^2) in 1986 may be caused by a sharp drop in total gut biomass for fish collected in both lakes near the end of August in 1986. Zooplankton density in Amisk Lake at the end of August 1986 was only one third that of 1985 suggesting the possibility of a period of food limited growth in Amisk Lake. Mean total zooplankton density in Narrow Lake was significantly less in 1986 compared to 1985 (unpaired t-test; $p<0.05$) and zooplankton densities on the five separate sampling dates were consistently low. Therefore I expected growth of fish in Narrow Lake in 1986 to be more limited by food than in 1985. However, no differences were found between 1985 and 1986 in either mean gut biomass or cumulative gut biomass over the summer. This suggests that the reduced growth of Narrow Lake fish in 1986 could result from a greater proportion of energy being spent searching for prey than in 1985 when prey were more abundant.

Fish size versus prey density and biomass

Indicators of age 0 yellow perch growth (weight or relative growth) show consistent patterns among all lakes when related to zooplankton density or biomass (Figures V-2, V-3). In Amisk or Baptiste Lakes, age 0 perch gut content biomass on a given date was either significantly higher or not significantly different from fish in Narrow or Long Lakes. The only exception to this pattern was on July 14/15, 1987 when Narrow Lake fish exhibited a significantly higher gut biomass than fish from Amisk Lake. On this date, 98.6% of the total gut biomass of age 0 perch from the littoral zone of Narrow Lake consisted of Polyphemus which was present in extremely high numbers. Age 0 perch exhibit consistent schooling behavior. At a given point in time, the tendency of a school to exploit a profitable food patch could explain why a given sample of fish could have an unusually high level of food in the gut even though individuals in the population have a long term trend of low growth.

Stomach fullness index

Indices of stomach fullness were not useful in predicting body weight. No consistent patterns were found in attempts to predict fish weight from an index of stomach fullness, K_f (total gut biomass·fish weight^{-1}) or from K_{fc} (cumulative total gut biomass·fish weight^{-1}). There was a great deal of scatter between either variable K_f or K_{fc} and fish weight and a significant relationship occurred in only 3 out of 11 cases.

Although stomach fullness indices exhibited high variance and were not useful in predicting body weight, these indices were generally higher in productive than in unproductive lakes. The stomach fullness index K_f followed a similar trend to that of total gut biomass with fish in Amisk and Baptiste Lakes generally having values that were significantly higher or no different from fish in Narrow and Long Lakes. However, there were two dates in 1985 and one in 1987 (reflecting the peak in Polyphemus in the gut) when fish in Narrow Lake did have significantly higher indices of stomach fullness than fish from Amisk Lake.

Gut content composition and prey selection

It appears that fish from productive Amisk and Baptiste Lakes were generally not food limited since zooplankton are abundant and fish in these lakes exhibited a high level of selectivity in their diet. Figures V-4 and V-5 show the percent frequency by dry weight of different zooplankton taxa in the gut. In all three years, Daphnia dominated the gut content biomass in Amisk Lake with Baptiste Lake exhibiting the same pattern in 1987. Amisk and Baptiste Lakes are highly productive and have zooplankton densities which are typically 5-20 times greater than the zooplankton density in unproductive Narrow and Long Lakes. In Narrow Lake, Copepods, Bosmina, Daphnia, and other Cladocerans were all important components in the diet with no single group being consistently dominant either within or among years.

Table V-3 shows the mean Manly/Chesson preference values for the six zooplankton groups found in age 0 yellow perch guts. Selection by fish of Bosmina was significantly higher in all three years in Narrow Lake as compared with Amisk Lake. Daphnia was more strongly selected for in Amisk Lake in 1986 and 1987 than in Narrow Lake. In 1985, selection for Daphnia was nearly twice as high in Narrow

Lake compared to Amisk Lake. However, as shown in Figure V-4, biomass of Daphnia in fish guts was twice as high in Amisk Lake as compared to Narrow Lake. This indicates that the density of Daphnia in the zooplankton was much higher in Amisk Lake. Manly/Chesson indices for selection of Cladocerans ranged between 0.06 and 0.33 with mean values being nearly twice as high in Amisk and Baptiste Lakes compared with Narrow and Long Lakes. However, there were no consistent differences among lakes or years in the percent frequency of Cladoceran biomass in gut contents. In comparing seasonal mean Manly/Chesson indices for copepods among lakes and years, the values in six of eight cases were very low when compared with the actual percent frequency of copepods in the total gut biomass. This indicates active feeding selection against copepods which were abundant in the zooplankton.

Contrasting patterns between the littoral and limnetic zones

Zooplankton densities in both the limnetic and littoral zones were compared on selected dates in 1985, 1987 and 1988 (Table V-4). Littoral zone zooplankton densities were significantly higher in three cases, lower in three cases and no different from zooplankton densities in the limnetic zone in 11 cases (unpaired t-test). No difference was found between limnetic and littoral zone zooplankton densities with Wilcoxon's rank sum test (P=0.05). These comparisons were made when age 0 yellow perch were migrating from the limnetic to the littoral zone which started around July 15 in 1985 and 1988, and around July 1 in 1987. The high level of variance in the zooplankton data precluded any identification of trends in littoral versus limnetic zone food availability. I was unable to determine if migration to the littoral zone in early July would be a beneficial strategy either productive or unproductive lakes. Two comparisons of zooplankton densities between limnetic and littoral zones prior to onshore migration were made in Amisk Lake in 1985 but these comparisons were insufficient in number to identify trends.

Discussion

This study clearly demonstrates that the size and absolute growth of age 0 yellow perch during the first season can be predicted from either food availability or gut content biomass. Since estimates of zooplankton density, zooplankton biomass or gut content biomass typically exhibit high levels of variance, the best predictions of fish size or growth were obtained from cumulative estimates of these three variables over the growing season.

In this study, lakes in the same geographical area with similar morphometry were sampled over four consecutive seasons. Within a given season, differences in temperature regimes among lakes were small. Significant correlations were found in all cases between end of season fish size and cumulative °C·days but the lack of variance in temperature regimes among lakes reduced the impact of °C·d as a useful predictor of end of season size. However, the temperature regime of a given lake is a major factor in determining fish growth (Schneider 1973; Brett 1979) and the impact of temperature should be evaluated in any predictive model. This is essential when growth predictions are being made among systems with different temperature regimes.

The significant correlations between age 0 perch weight on a given date or end of season weight and cumulative zooplankton density demonstrate the importance of bottom-up trophic level control. If comparisons were made only among highly productive lakes this relationship would not be expected to show up because fish may not be food limited in highly productive lakes.

A number of field studies have attempted to demonstrate food limited growth in fish populations (Rask 1983; Keast and Eadie 1985; Whiteside et al. 1985) but have not been definitive because systems with a wide range of productivity were not included. Mills et al. (1989b) were able to demonstrate significant relationships between age 0 yellow perch weight and (1) the cumulative biomass of Daphnia and (2) zooplankton body size. Although Oneida Lake is a eutrophic system where food might not be limiting, their design used an 11 year field data set, and minimized variance by measuring time in degree-days and focused on Daphnia which is an extremely important organism in the diet of age 0 perch in this lake. Noble (1975) also found growth of age 0 perch in Oneida Lake to be significantly correlated with Daphnia abundance. It is possible that even in systems with a surplus of potential food strong selection by fish for a preferred food item or size class may allow for reasonable predictions of fish size based upon the abundance of that item.

The rapid divergence in weight of fish among lakes results from consistently higher relative growth rates in productive versus unproductive lakes as shown in Figures V-2 and V-3. This pattern may be explained by the consistently higher zooplankton density and biomass found in the productive lakes in all three years. Although several studies have suggested a linkage between age 0 fish size and the density of suitable prey (Noble 1975; Lasker and Zweifel 1978; Houde and Schekter 1981; Lemly and Dimmick 1982; Crecco and Savoy 1985; Keast and Eadie 1985; Kiorboe and Munk 1986; Fox 1989), the impact of lake productivity on this relationship has only been demonstrated by Abbey and MacKay (1991). The results in this chapter show that lake productivity impacts subsequent trophic levels resulting in increased zooplankton densities and higher rates of growth for age 0 yellow perch.

Even though my data show that a significant amount of the variance in fish size is explained by lake productivity or by available food, assuming a linear relationship between these variables and fish size may be inappropriate. Keckeis and Schiemer (1992) showed that assimilation efficiency of three species of larval and juvenile cyprinids at low food densities was approximately twice that of well-fed groups. Post (1990) found that the sensitivity of growth rate to changes in prey availability is greater in small than in large fish. This implies that small age 0 perch in unproductive Long and Narrow Lakes may be sensitive to variance in zooplankton density but may partially compensate for food limitation by increasing assimilation efficiencies.

Populations with low individual growth rates resulting from low zooplankton densities might be limited to small prey as a result of their restricted gape size (Schael et al. 1991). My data show that gape limited foraging is not responsible for divergence in fish size between productive and unproductive lakes. Data from Schael et al. (1991) indicate that age 0 perch 14-18 mm in length select prey greater than 0.5 mm in length. I found zooplankton between 0.5 and 1.0 mm to be the dominant size group in all lakes from 1985-1987. I also found that divergence in size of age 0 perch did not begin until after the fish exceeded 18 mm in length.

Being limited to small prey is generally considered to be a disadvantage (Brooks and Dodson 1965; Paloheimo and

Dickie 1966; Keast and Eadie 1985) and bluegill have been shown to exhibit a preference for large prey with increases with prey density (Bartell 1982; Werner et al. 1983). However, some studies (Bence and Murdoch 1986; Parrish and Margraf 1991) found small prey to be more profitable than large prey. This is contrary to the predictions of O'Brien et al.'s (1976) apparent size model and to optimal foraging predictions with respect to prey size but is consistent with other research on feeding selectivity of young planktivores (cf. Walton et al. 1992). Nutritional differences among available prey may explain selection for smaller prey (Confer and Lake 1987; Mills et al. 1989b). Although I have not evaluated prey size selection in this chapter, I did find productive Amisk and Baptiste lakes to consistently show a higher percentage of zooplankton exceeding 1.0 mm in size than in unproductive Long or Narrow lakes. Additional analysis on feeding selectivity needs to be done to determine if age 0 perch in the productive lakes are benefiting from these larger prey.

On the other hand, Economou (1987) suggests that in a food limited environment, bigger larval or juvenile fish may experience greater foraging difficulties than small fish resulting from their higher absolute food requirements and the scarcity of large prey. This is contrary to current theory that small fish are more likely to experience: (1) food deprivation at low food densities caused by reduced reaction distances and swimming ability (Blaxter 1986; Webb and Weihs 1986), (2) increased risk of starvation and predation (Miller et al. 1988), and (3) a tradeoff in habitat use between foraging success and safety (Werner et al. 1983; Holbrook and Schmitt 1988; Gotceitas and Colgan 1990b). Recent evidence indicates that in some cases, predation risk for older and larger larval fish may be higher than that of younger, smaller fish (Litvak and Leggett 1992). My data does not address the predation risk to age 0 perch in relation to fish size. However, in Long and Narrow lakes the absence of limnetic zone predators and the low density of potential predators (Northern pike and adult yellow perch) in the littoral zone, suggests that age 0 perch in these lakes are probably not altering their foraging behavior in these two lakes as a result of predation pressure. I did not evaluate the potential impact of invertebrate predators such as <u>Chaoborous</u>, corixids or notonectids upon age 0 perch. In Amisk and Baptiste lakes, age 0 perch are exposed to a broader field of piscivores (Northern pike, adult perch and walleye) present in greater densities than in Long or Narrow lakes. However Amisk and Baptiste lakes also have much higher zooplankton densities and a greater percentage of zooplankton in larger size categories than Long or Narrow lakes so predation pressure is unlikely to be a factor limiting growth.

My data indicate that predictions of fish size or growth in unproductive systems should be based upon the density or biomass of all zooplankton in the environment or in the gut. I found significant relationships in all three years between age 0 perch weight on a given date and the cumulative biomass of specific taxa in the gut as shown in Table V-2. However, in unproductive Long and Narrow Lakes, age 0 perch were opportunistic feeders as shown in Figures V-4 and V-5 with no zooplankton taxa being consistently dominant in the diet. In all lakes, copepods, Daphnia, and cladocerans were the most important taxa in the diet. Daphnia was consistently the dominant taxa in the diet of age 0 perch in productive lakes. In unproductive lakes, copepods, cladocerans and occasionally Bosmina were important dietary items along with Daphnia. In the absence of consistent diet selectivity, all taxa should be included in predictive models. Predictions of fish size or growth based on specific zooplankton taxa such as Daphnia (e.g., Noble 1975; Mills and Forney 1981; Mills et al. 1989b) or nauplii (Lemly and Dimmick 1982), or specific size categories of prey (Frank and Leggett 1986; Mills et al. 1989a; Miller et al. 1990) are only appropriate when fish show consistent diet selectivity. Werner and Hall (1974) found that fish exhibited size selectivity for prey at high prey densities but ate prey as encountered at low densities. Emlen (1966) indicates that animals should be more selective when satiated. The consistent dominance of Daphnia in the diet of age 0 perch in productive Amisk and Baptiste lakes suggests that fish exhibit greater diet selectivity with higher lake productivity.

In unproductive Narrow Lake, cumulative zooplankton density explained a significant amount of the variance in fish weight on a given date in both 1985 and 1986. In productive Amisk Lake, a significant relationship was not found between fish weight and zooplankton density in 1985 and this relationship was of marginal significance ($p=0.048$) in 1986. At some point, higher available food density should have no additional impact on fish size or growth because satiation will restrict further feeding. MacKenzie et al. (1990) estimated that marine fish larvae ingestion rates were independent of food density at levels > 185 $\mu g \cdot L^{-1}$. I found mean zooplankton biomass in productive lakes to vary considerably among years as shown in Figure V-2 and V-3 but consistent patterns emerge. In 1985, zooplankton biomass was the highest for all three years and age 0 perch reached their maximum size in that year in both Amisk and Narrow lakes. In Narrow and Long lakes, mean seasonal zooplankton biomass ranged between 2.5 and 16.7 $\mu g \cdot L^{-1}$ except in 1985 when it was 95.9 $\mu g \cdot L^{-1}$ in Narrow Lake. In Amisk and Baptiste lakes, mean seasonal zooplankton biomass ranged between 360.4 and 927.8 $\mu g \cdot L^{-1}$ except in 1987 when it was 167.5 $\mu g \cdot L^{-1}$ in Amisk Lake. If the estimates of MacKenzie et al. (1990) relating ingestion rates to food density apply to age 0 perch, growth of these fish should be independent of food density in Amisk and Baptiste lakes. However, laboratory derived values of food ingestion rates may not accurately represent the response of larval fish in nature. Further investigations of the relationships between fish growth, food density and biomass, assimilation efficiency and satiation levels in natural systems are needed. However, the level of sampling intensity and analysis required to adequately quantify these relationships and the large number of variables in natural environments provides a substantial challenge in understanding these relationships.

My data indicate that predicting absolute or relative growth at a given point in time over the season is much more difficult than predicting length or weight. This was expected because growth rates are continuously fluctuating in response to environmental variation. On the other hand, the fish length or weight on a given date is the cumulative sum of all growth to that date and the impact of small-scale temporal and spatial environmental fluctuation (Fortier and Leggett 1984; Owen 1989; Rose and Leggett 1990) would be much less important than long term trends. Therefore, if growth comparisons are made among lakes, the time period over which the comparison is made should be in the order of weeks or months and should be equivalent among systems. Boisclair and Leggett (1989a; 1989b) found the most effective growth predictors of yellow perch from 12 lakes and three year classes (I+, II+, and III+) to be the percent contribution of a given prey type to the diet rather than the mean weight of prey consumed. This approach is similar to using cumulative prey density or biomass in growth predictions rather than mean values from each sampling date.

Although indices of stomach fullness K_f or K_{fc} were not useful in predicting fish weight, these measures followed a general trend shown between productive and unproductive lakes. In 13 out of 16 cases K_f values were significantly higher in productive versus unproductive lakes. One reason for the high variance in K_f values is that they would be susceptible to patchiness of prey in both feeding activity and effort. This patchiness would be accentuated in a schooling population such as age 0 perch where the probability of encountering zooplankton patches should be enhanced (Pitcher 1986). Estimates of zooplankton density or biomass based on a random sampling strategy would have a lower likelihood of being affected by patchiness than K_f values where fish are actively searching for and selecting zooplankton patches.

Although this study was not designed to address the question of variance in feeding success in response to differences in density of zooplankton patches, I did observe consistent schooling behavior of the age 0 perch which may enhance the probability that individual fish will find profitable food patches. Fish have been shown to be sensitive to differences in food availability between patches (Wildhaber and Crowder 1991). Holbrook and Schmitt (1992) found that selective use of available patches by striped surfperch (Embiotoca lateralis) lead to different diets and marked differences in body size. In the case of surfperch, access to the most profitable patches was determined by intraspecific competition (Holbrook and Schmitt 1992) but patch selection or the time spent in profitable patches could be determined by other factors related to body size such as predation risk (Mittelbach and Chesson 1987; Sih 1987; Gotceitas and Colgan 1990a).

In this study, I initially found no significant relationships between age 0 perch size and zooplankton density or biomass. My initial analysis was based on a sequence of sampling dates with discrete estimates of fish size and zooplankton density or biomass for each date. These estimates of zooplankton density or biomass on a given sampling date exhibited high levels of variance. Cumulative estimates of these variables exhibited equally high levels of variance but I was able to show significant relationships between cumulative zooplankton density or biomass and fish size. Zooplankton are known to be patchy in distribution (Owen 1981, 1989; Jenkins 1988) and integrated sampling techniques may underestimate zooplankton densities actually present in the microhabitat chosen by larval fish (Leggett

1986; Jenkins 1988; Owen 1989). Also growth is a cumulative process so data on feeding activity over time are essential in order to determine the impact of feeding upon growth. Future studies on the feeding energetics of fish in natural environments should include spatial and temporal patchiness as an important design variable.

Table V-1. Coefficients to predict age 0 yellow perch length (mm), weight (mg) and absolute growth from cumulative degree days (°C·d), cumulative zooplankton density (Zpd) (#·L^{-1}) or biomass (Zpb) (µg·L^{-1}) and cumulative total gut biomass (GB) (µg·fish^{-1}). Order of addition of variables in stepwise regression is shown as a superscript. Non-significant variables ($P>0.05$) were excluded.
T = Midwater Trawl and S = Seine.

Dep. Var.	Yr	°C·d	Zpd	Zpb	GB	slope	R^2
Weight							
T&S	85				0.653	-16.07	0.956
T&S	86				0.117	78.47	0.977
T&S	87	0.500^2	7.286^1	-0.214^3		-342.79	0.963
T	87				0.164	186.33	0.797
S	87	0.593^2	5.910^1	-0.211^3		-353.30	0.969
Length							
T&S	85	0.020^2			0.006^1	3.50	0.969
T&S	86	0.013^2			0.002^1	10.04	0.981
T&S	87	0.017^2	0.123^1	-0.003^3		10.36	0.978
T	87				0.004	27.20	0.732
S	87	0.019^2	0.077^1			10.25	0.963
Absolute Growth							
T&S	85				0.014	4.64	0.722
T&S	86				0.002	5.50	0.297
T&S	87		0.320^1	-0.009^2		6.22	0.835
T	87		0.300			3.78	0.785
S	87		0.265^1	-0.011^2		9.22	0.753

Table V-2. Coefficients to predict age 0 yellow perch weight (mg) from cumulative dry weight biomass of *Bosmina* (Bsmn), Copepods (Copd), *Daphnia* (Daph), and other Cladocerans (Clad) in the gut. Nonsignificant variables ($P>0.05$) were excluded. Order of addition of variables in stepwise regression is shown as a superscript. Cumulative total gut biomass (GB) ($\mu g \cdot fish^{-1}$) was also used to predict fish weight in a simple regression model. T = Midwater Trawl and S = Seine.

Dep. Var.	Yr	Copd	Daph	Clad	slope	R^2	n
Weight							
T&S	85		1.070		75.12	0.961	11
T&S	86		0.121^1	0.295^2	62.44	0.982	10
T&S	87	2.937			133.44	0.454^b	12
T	87		0.113^2	0.726^1	168.66	0.941	12
S	87^a			1.476	309.00	0.850	11

Dep. Var.	Yr	GB	slope	R^2	n
Weight					
T&S	85	0.653	-16.07	0.956	11
T&S	86	0.117	78.47	0.977	10
T&S	87	0.110	225.25	0.515^b	12
T	87	0.164	186.33	0.797	12
S	87	0.058	352.47	0.217^b	12

[a] excludes Narrow Lake - no significant relationship when including Narrow Lake.

[b] R^2 values lowered due to extremely high levels of *Polyphemus* found in Narrow Lake fish in the littoral zone on July 14, 1987.

Table V-3. Means of individual preference values (Manly/Chesson index) for age 0 yellow perch from four central Alberta lakes 1985-1987. Values above 0.167 indicate positive selection. Values less than 0.167 indicate negative selection.

Yr	Lake	N	Bsmn	Copd	Daph	Clad	Lept^{l} Rtfr^{r}	Other
85	Amisk	5[a]	0.05	0.19	0.18	0.33	0.15^{l}	0.09
85	Narrow	6	0.29	0.09	0.34	0.06	0.04^{r}	0.19
86	Amisk	5	0.003	0.06	0.40	0.23	0.14^{l}	0.17
86	Narrow	5	0.18	0.19	0.20	0.13	0.01^{r}	0.29
87	Amisk	3	0.04	0.04	0.14	0.16	0.20^{l}	0.35
87	Baptiste	3	----[b]	0.04	0.16	0.18	0.35^{l}	0.27
87	Narrow	3	0.253	0.07	0.03	0.20	0.26^{r}	0.18
87	Long	3	0.15	0.04	0.32	0.10	0.21^{r}	0.18

[a] number of sample dates each of which included 20+ fish.

[b] Bosmina were not present in the plankton samples.

Table V-4. Comparative zooplankton densities (Zpd) ($\# \cdot L^{-1}$) in the limnetic and littoral zones on the same date. Unpaired t-test comparisons: S = significant, NS = not significant at the 0.05 level. JN = June, JL = July, AG = August, A = Amisk, N = Narrow, B = Baptiste, L = Long.

			Limnetic Zone			Littoral Zone			t-test	
Lake	Yr	Date	Zpd	SD	n	Zpd	SD	n	P-value	
A	85	JN 12[a]	76.0	13.0	4	102.6	29.8	16	$p<0.2$	NS
		JN 26[a]	110.1	34.5	4	67.3	16.3	16	$p<0.01$	S
		JL 10	31.4	8.4	4	32.3	15.5	16	$p>0.9$	NS
		AG 05	45.7	4.6	4	71.5	35.6	16	$p<0.2$	NS
N	85	JL 15	14.0	1.1	2	21.2	5.4	5	$p<0.2$	NS
A	87	JL 15	28.0	1.7	2	110.5	35.8	2	$p<0.1$	NS
		JL 29	47.5	0.2	2	2.2	0.3	2	$p<0.01$	S[b]
B	87	JL 15	28.0	9.4	2	35.9	3.7	2	$p<0.4$	NS
		JL 28	47.7	4.8	2	45.6	10.9	2	$p<0.9$	NS
N	87	JL 14	0.3	0.03	2	0.5	0.01	2	$p<0.01$	S
		JL 27	0.5	0.04	2	1.6	0.7	2	$p<0.2$	NS
L	87	JL 16	5.7	0.7	2	8.5	3.2	2	$p<0.4$	NS
		JL 27	1.4	0.1	2	0.2	0.02	2	$p<0.01$	S[b]
A	88	JL 26	63.9	6.7	2	95.0	21.8	2	$p<0.4$	NS
B	88	JL 25	58.1	14.6	2	56.8	13.0	2	$p>0.9$	NS
L	88	JL 25	2.3	0.4	2	4.2	0.2	2	$p<0.05$	S
N	88	JL 25	0.3	0.005	2	0.4	0.01	2	$p<0.01$	S

[a] These dates were prior to littoral zone migration

[b] Littoral zone zooplankton density less than Limnetic zone

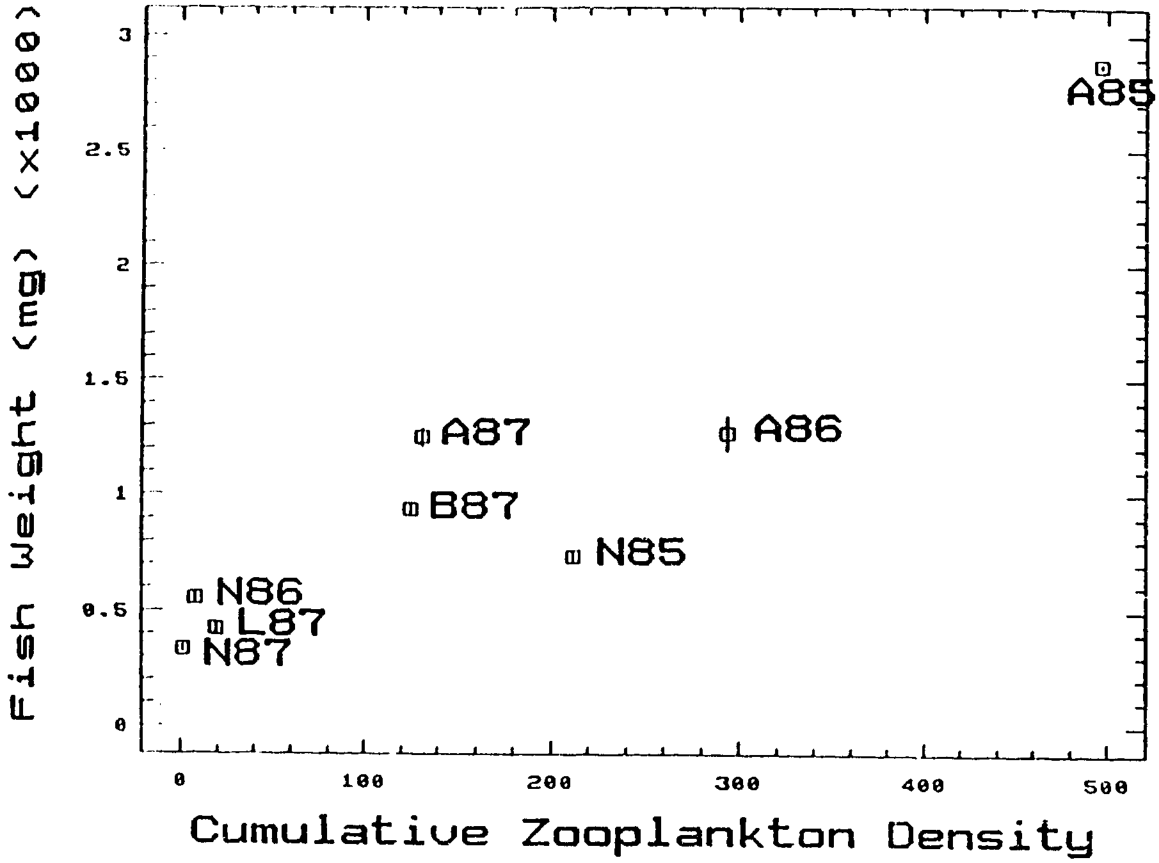


Figure V-1. Age 0 yellow perch weight (August 19-21, 1985 and 1986, July 27-29, 1987) versus cumulative zooplankton density (#·L^{-1}). In 1985 and 1986, zooplankton sampling was done 5-7 times between June 11 and August 21. In 1987, three zooplankton samples were taken between June 29 and July 29.

Figure V-2. Changes over time in (a) mean wet weight; (b) relative growth; (c) zooplankton density ($\# \cdot L^{-1}$); (d) zooplankton biomass ($\mu g \cdot L^{-1}$); and (e) cumulative gut content biomass ($\mu g \cdot fish^{-1}$) for Amisk and Narrow Lakes in 1985 and 1986.

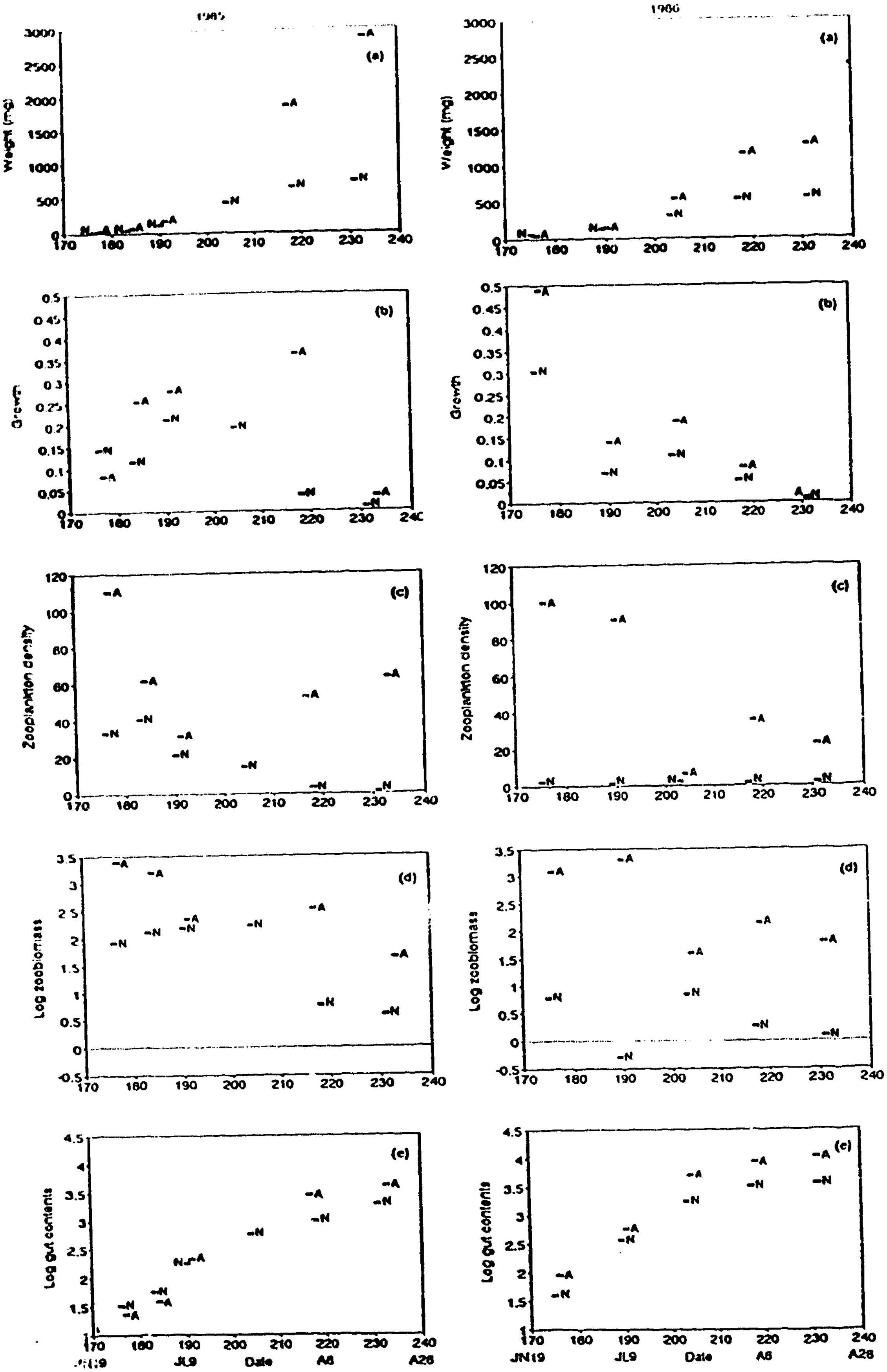
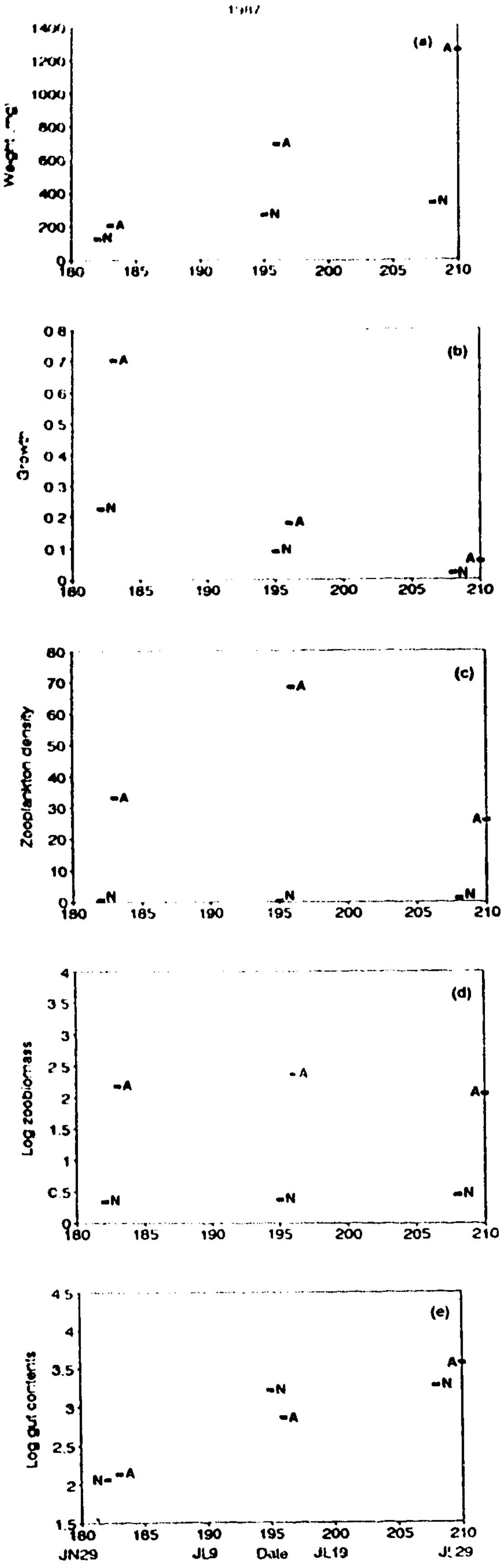
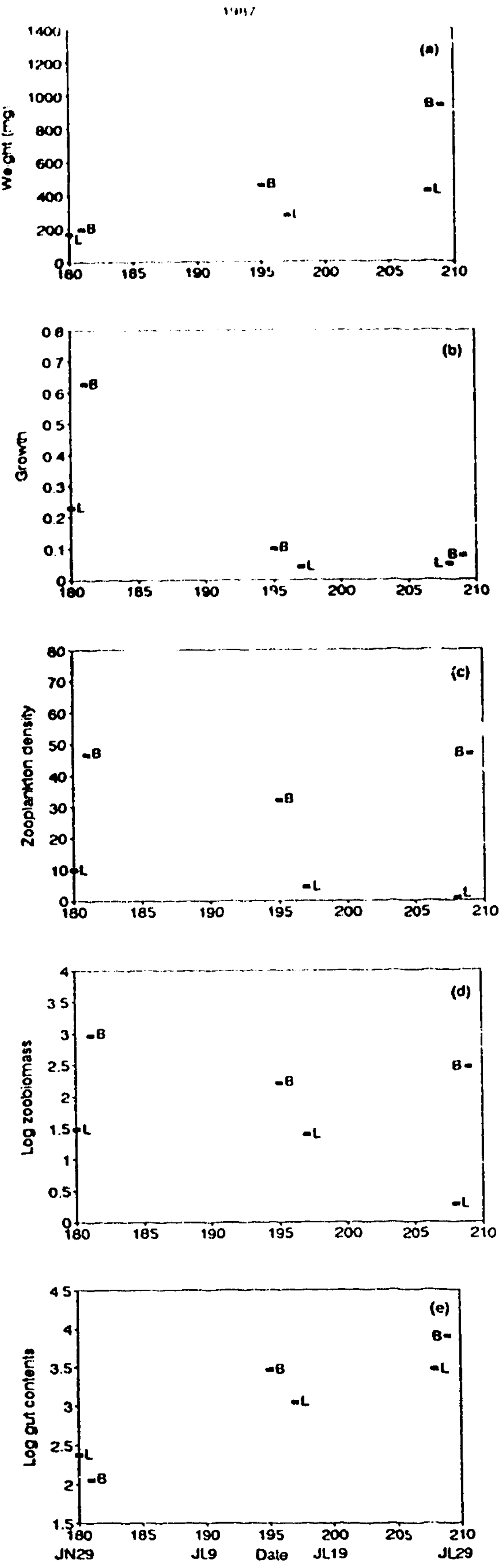
1985
1986
(a)
Weight (mg)
0
500
1000
1500
2000
2500
3000
(b)
Growth
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
(c)
Zooplankton density
0
20
40
60
80
100
120
(d)
Log zoobiomass
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
(e)
Log gut contents
1
1.5
2
2.5
3
3.5
4
4.5
170
180
190
200
210
220
230
240
JN19
JL9
Date
A8
A28
A
N

Figure V-3. Changes over time in (a) mean wet weight; (b) relative growth; (c) zooplankton density ($\# \cdot L^{-1}$); (d) zooplankton biomass ($\mu g \cdot L^{-1}$); and (e) cumulative gut content biomass ($\mu g \cdot fish^{-1}$) for Amisk and Narrow Lakes and for Baptiste and Long Lakes in 1987.


1987
(a)
Weight (mg)
0
200
400
600
800
1000
1200
1400
A
N
(b)
Growth
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
A
N
(c)
Zooplankton density
0
10
20
30
40
50
60
70
80
A
N
(d)
Log zoobiomass
0
0.5
1
1.5
2
2.5
3
3.5
4
A
N
(e)
Log gut contents
1.5
2
2.5
3
3.5
4
4.5
A
N
180
185
190
195
200
205
210
JN29
JL9
Date
JL19
JL29


1987
(a)
Weight (mg)
0
200
400
600
800
1000
1200
1400
B
L
(b)
Growth
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
B
L
(c)
Zooplankton density
0
10
20
30
40
50
60
70
80
B
L
(d)
Log zoobiomass
0
0.5
1
1.5
2
2.5
3
3.5
4
B
L
(e)
Log gut contents
1.5
2
2.5
3
3.5
4
4.5
B
L
180
185
190
195
200
205
210
JN29
JL9
Date
JL19
JL29

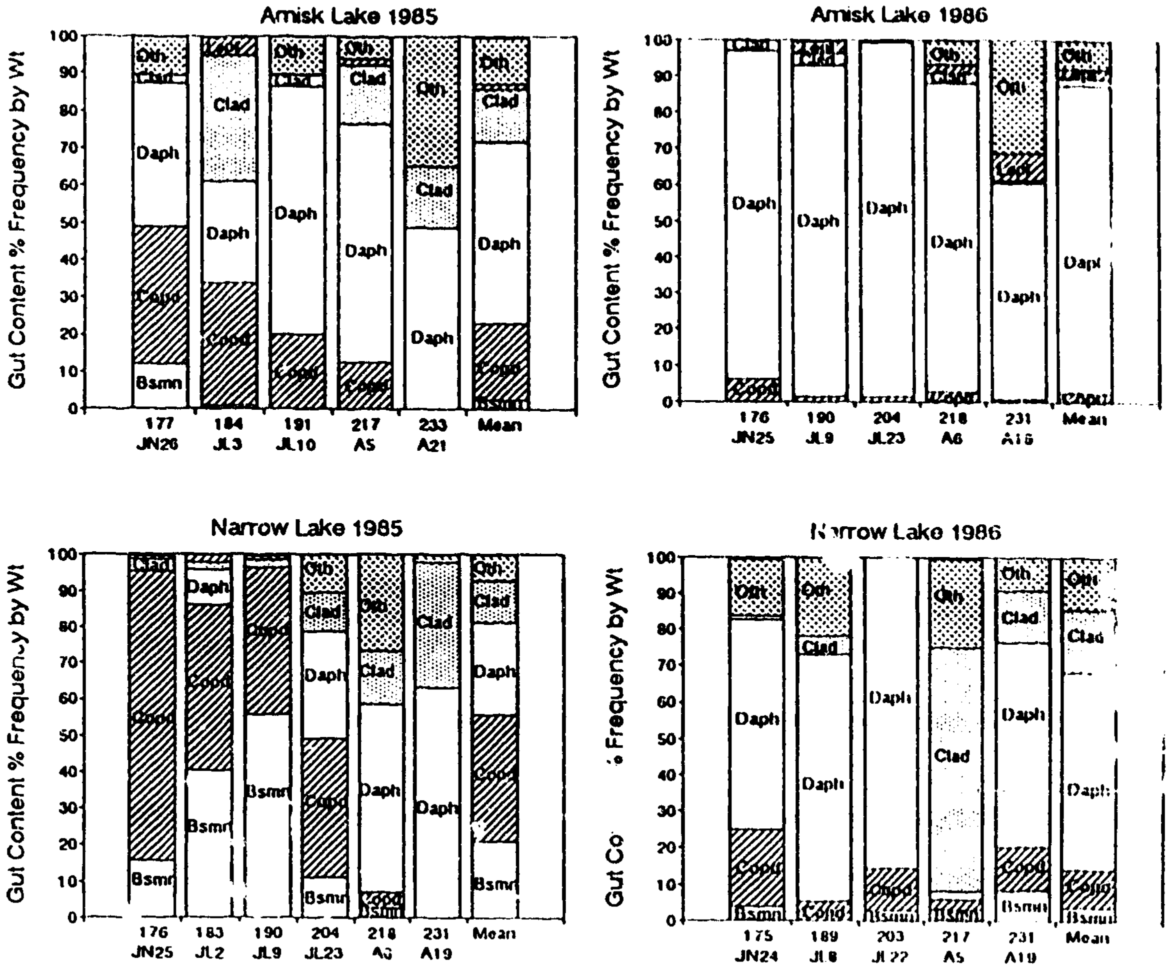


Figure V-4. Percent frequency by dry weight of different zooplankton taxa in the gut. Amisk and Narrow Lakes 1985 and 1986. JN = June, JL = July, A = August, Bsmn = *Bosmina*, Copd = Copepods, Daph = *Daphnia*, Clad = Cladocerans, Lept = *Leptodora*, Oth = Other.

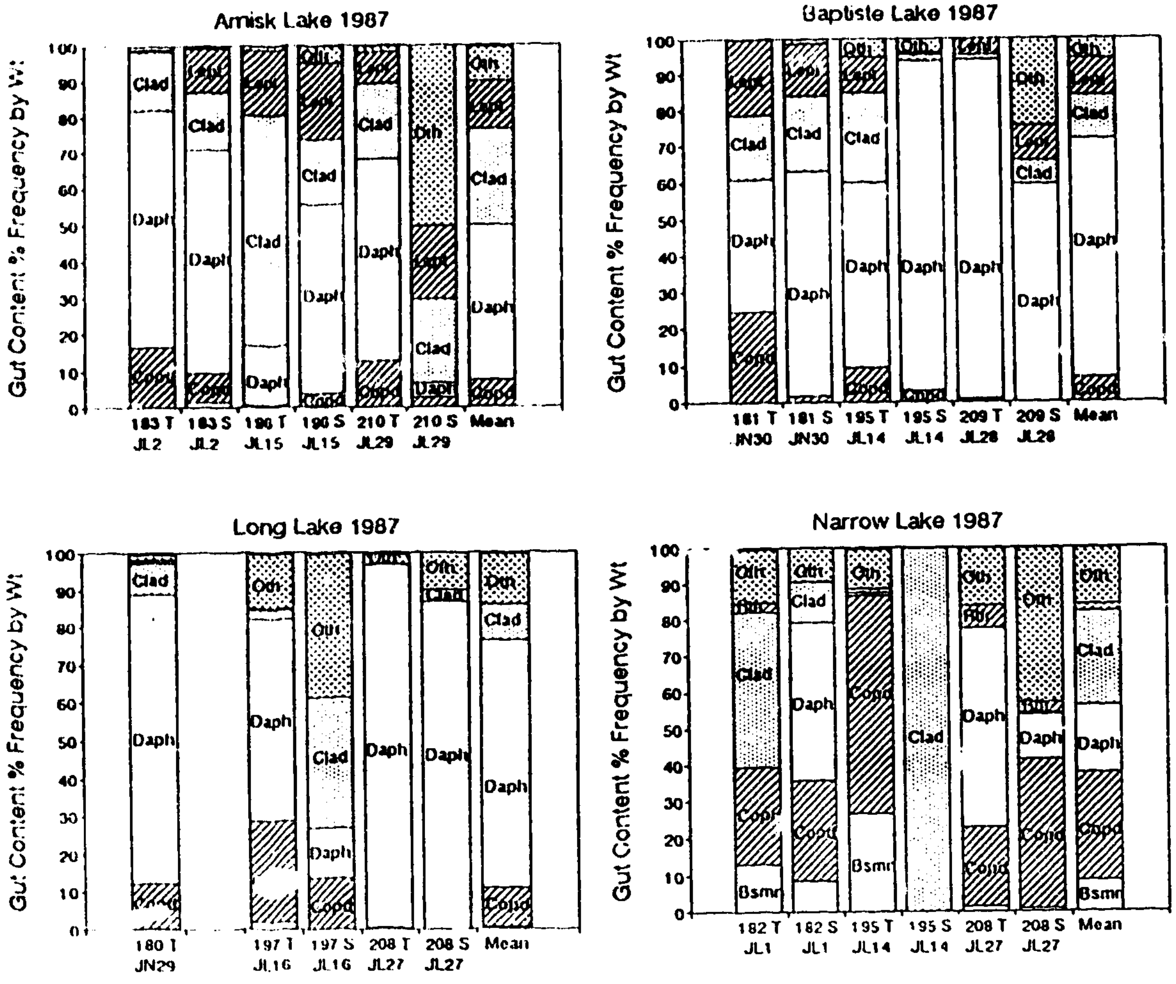


Figure V-5. Percent frequency by dry weight of different zooplankton taxa in the gut. Amisk, Baptiste, Long, and Narrow Lakes 1987. JN = June, JL = July, A = August, Bsmn = Bosmina, Copd = Copepods, Daph = Daphnia, Clad = Cladocerans, Lept = Leptodora, Rtfr = Rotifers, Oth = Other.

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Chapter VI

General Discussion

This thesis provides the most thorough and long term comparative examination of the early life history and growth yet available for any north-temperate freshwater fish. I show that age 0 yellow perch in unproductive lakes experience food limited growth. I also integrate data on lake productivity and trophic level relations and demonstrate that the size of age 0 perch at the end of the season can be predicted from average summer TP or Chl a or from cumulative zooplankton density or gut content biomass.

Reasons for ontogenetic habitat shifts

Previous studies of age 0 yellow perch have identified the early life history sequence of this species (Forney 1971; Wong 1972; Amundrud et al. 1974; Collette et al. 1977; Henderson 1977; Kelso and Ward 1977; Whiteside et al. 1985; Post and McQueen 1988). These studies show a consistent ontogenetic habitat shift which has also been documented for other species including European perch (Guma'a 1978; Coles 1981; Treasurer 1988), Arctic charr (Naslund 1990) and bluegill (Werner and Hall 1979; 1988; Mittelbach 1981, 1983). The restriction of the above studies to single systems usually within a single season has not allowed these workers to clearly identify the reasons for these ontogenetic habitat shifts.

I found that age 0 perch size at hatching showed no consistent differences among lakes, and the timing of offshore migration to the limnetic zone was the same among lakes within a given season. Divergence in growth rate of age 0 perch among the four populations first occurred in the limnetic zone. However, the rate of divergence in growth was greatest in late July following migration to the littoral zone. Synchronous limnetic and littoral zone sampling at the time of migration showed that larger fish moved onshore first. Also, fish in productive lakes where growth was rapid completed this migration in a much shorter time frame than fish in unproductive lakes where growth was slow. Chapter II demonstrates that size differences within and among lakes directly affect the duration of habitat use in the limnetic zone but not the onset of littoral zone migration. My data do not clearly delineate one specific causal factor responsible for the onset of littoral zone migration. However, data in Chapter II show that important factors in all populations of age 0 perch include body size (25-30 mm TL), water temperature (17-21 °C). It may be that these and other factors such as resource availability contribute in a cumulative way to the actual triggering of the event.

Patterns of growth

Modelling and predicting fish growth is an important part of fisheries science. However, growth models derived from data on adult fish populations for the purpose of predicting asymptotic size (Ricker 1975), size distributions within a cohort (Wismer et al. 1985; DeAngelis and Huston 1987), or size-at-age (Allen 1976; Craig 1980) should be validated prior to their use in other applications. Hamilton and Powles (1979) and Post (1987) used the von Bertalanffy model to describe age 0 fish growth within a given season. Treasurer (1988) divided first season growth into stanzas and also used a log transformation in order to fit a linear model to his data. I wanted to determine whether growth over the first season could be described without separating the data into growth stanzas and I wished to determine if the logistic, Gompertz or von Bertalanffy models could be used in this application.

Growth in length or weight of age 0 yellow perch from the four populations studied were best described by a logistic model. The von Bertalanffy model was not suitable for describing first year growth if data near the beginning of the season was included. In productive lakes, the Gompertz model described growth in weight as well as a logistic model. A unique contribution of this thesis is weekly or biweekly sampling in four lakes over three separate growing seasons. Most previous studies on individual growth in North-temperate fish populations fail to include age 0 fish or lack the resolution necessary for the identification of growth patterns. Guma'a (1978) is one of the few studies to identify a first year growth pattern with an inflection point. The identification of an inflection point requires that intensive sampling be initiated near the beginning of the growing season and that subsequent sampling be continued once or twice monthly until growth rates begin to decline near the end of the season. In order make meaningful comparisons among growth patterns in different systems relevant data on environmental conditions, habitat and community interactions should also be available.

Populations exhibiting the most rapid growth in length reached the inflection point of the logistic curve later, and experienced a longer period of rapid growth when compared to populations with slow growth. However, in all lakes, fish were essentially similar in size at hatch, and growth during the first 30 days was equivalent among lakes. This pattern suggests that fish in unproductive lakes may become food limited early in the season just prior to the time of fish size divergence among lakes.

Predicting growth from lake productivity

Since predicting the potential yield of fish from a particular aquatic system is an important goal of fisheries managers (Rawson 1952, 1955; Ranta and Lindstrom 1989), a number of models have been developed to predict fish biomass or yield, the most prominent of which is the morphoedaphic index (Ryder et al. 1974). Hanson and Leggett (1982) compare the morphoedaphic index with other models developed to predict fish yield incorporating factors such as primary production (Oglesby 1977), macrobenthos standing crop (Matuszek 1978), or total phosphorus (Hanson and Leggett 1982). Although the morphoedaphic index or similar models are useful predictors of total fish yield or biomass, these models fail to predict fish yield at the species level especially in lakes of similar size and water quality (Ranta and Lindstrom 1989). Predicting fish yield at the species level should be possible if the growth of that species can be predicted. However, with the exception of Abbey and MacKay (1991), previous predictions of fish growth have required extensive data on trophic level relationships (ie. Mills et al. 1989). My results, which also evaluate data on trophic level relationships, show that age 0 perch growth can be predicted from TP and Chl a.

I found growth in length and weight of age 0 yellow perch from ten central Alberta lakes in 1988 to be best predicted by average summer TP and Chl a. Chapter IV indicates that the following variables: (a) total zooplankton density or biomass, (b) zooplankton density by predominate taxa or size group, and (c) degree days did not contribute significantly in predicting fish size at the end of August. I did find cumulative zooplankton density to be a significant predictor of age 0 perch size and rate of growth (Chapter V) in 1985, 1986 and 1987. It is evident that the high levels of variance often encountered in estimating zooplankton densities may prevent the use of these data in predictive models. However, use of cumulative zooplankton densities reduces the problems caused by high variance providing a variable with useful predictive power. Chapter IV shows that if highly productive lakes (TP >38 $\mu g \cdot L^{-1}$) were excluded from the 10 lake data set zooplankton density or biomass alone predicted from 43 to 63% of the variance in fish size at the end of the season. Several factors may explain the tighter link between available food and fish size in lakes with TP < 38 $\mu g \cdot L^{-1}$. An obvious explanation may be that food is limiting in these lakes but not in more productive lakes. Also in more productive lakes, community level interactions are more complex with more species of competing planktivores and more species of potential predators present. Finally, in food limited environments, assimilation efficiencies may be higher (Keckeis and Schiemer 1992) and the sensitivity of growth rate to changes in prey availability is greater in small (slower growing) than in large fish (Post 1990). Any of these factors could have a dramatic impact on the relationship between available food and fish size.

Fish growth as a function of food resources

Previous studies on the feeding energetics of age 0 fish indicate that prey size (Mills et al. 1989a; Munk 1992) or prey profitability (Osenberg 1988; Tsai 1991) are important predictors of growth. Kiorboe and Munk (1986) have shown in laboratory studies that larval herring growth rates increased asymptotically with prey density and that larger larvae were more efficient in converting ingested food into growth. Mills et al. (1989b) also demonstrate the importance of prey density to age 0 perch growth. Since growth of larval and juvenile fish is more sensitive to variation in temperature and prey availability than are adults (Post 1990), determining the impact of prey density on age 0 growth patterns is of particular importance. By choosing lakes of contrasting productivity but with similar morphometry within the same area I was able to assess the impact of prey density on growth in natural systems where temperature differences were minimal.

This study shows that either cumulative zooplankton density or gut content biomass are significant predictors of age 0 yellow perch size and rate of growth during the first season. In all three years, zooplankton densities were 5-20 times greater in productive versus unproductive lakes. Gut content biomass of fish in productive versus unproductive lakes was also significantly higher or no different in every case but one. Greater feeding selectivity was shown by fish in productive lakes with *Daphnia* consistently being dominant. In unproductive lakes, gut contents typically consisted of diverse taxa with no consistent patterns.

Although my data show that age 0 fish in unproductive lakes experience food limited growth, the point at which ingestion rate or growth rate becomes independent of food density has not been established. As indicated by MacKenzie et al. (1990), rates for fish ingestion derived in the laboratory cannot be reliably extrapolated to the wild. Also, the point at which a given fish species becomes food limited in one system may differ from other systems as a result of the following factors: (1) Temperature regime, (2) size or species composition of prey, (3) fish community structure affecting both competition and predator/prey interactions and (4) habitat structure. These differences emphasize that although the probability for food limited growth increases as lake productivity decreases, predicting a specific point at which food limitation occurs is not possible.

Optimal foraging theory and food limited environments

During the time of age 0 perch migration to the littoral zone, I found total zooplankton densities in the littoral zone to be significantly greater than or not significantly different from those in the limnetic zone in 13 out of 15 cases. This agrees with the predictions of optimal foraging theory (MacArthur and Pianka 1966; Pyke et at. 1977) which assumes that organisms switch habitats when discrete food patches of greater profitability are encountered during foraging bouts (Charnov 1976; Parker and Stuart 1976). For this strategy to be effective, organisms must sample potential feeding sites with a frequency relating to the time scale on which the abundance or size distribution of potential prey respond to differences in primary production or environmental changes (Pyke et al. 1977). Jachner (1991) analyzed habitat partitioning among age 0 European perch, smelt, and roach and found an inverse relationship between diet overlap and habitat overlap. Determining the degree of diet overlap between age 0 perch found in the limnetic versus the littoral zone habitat would be helpful in assessing the reasons for this habitat switch.

Previous studies evaluating age 0 yellow perch habitat switching in terms of diet choice and habitat profitability are limited to the work of Post and McQueen (1988) in Lake St. George, Ontario. In contrast to my findings of greater or no different zooplankton densities in the littoral versus the limnetic zone, Post and McQueen (1988) found that the littoral zone in Lake St. George had fewer and smaller zooplankton prey than the limnetic zone at the time when age 0 perch were moving onshore. Post and McQueen's results appear to contradict the predictions of optimal foraging theory and they suggest that this onshore migration may result from the genetic programming of the species. However, it is possible that the fish are able profit from the switch through effective use of microhabitats. If so, large fish may more effectively profit from the structurally complex littoral zone than small fish as a result of greater reaction distances and swimming ability (Blaxter 1986; Webb and Weihs 1986) and greater resistance to starvation and predation (Miller et al. 1988). This may also explain why I found larger age 0 perch moving onshore first. Ultimately, the habitat chosen should represent a tradeoff between foraging success and safety (Holbrook and Schmitt 1988; Gotceitas and Colgan 1990). Data on broad scale temporal or spatial habitat shifts are available for many fish populations but few studies have been done on small scale habitat adjustments which may provide optimal conditions for fish growth and survival.

This research identifies several areas which require more investigation: (1) Are fish in unproductive lakes with limited food spending more time/energy searching for food and/or sampling their environment for suitable food patches than fish in productive lakes where food in not limited? (2) How effectively do fish in natural environments sample and use food patches? (3) What is the impact of competition and predation on the foraging efficiency of fish in natural environments? (4) What is the mechanism by which food is limiting growth? With respect to (3), age 0 perch in the limnetic zone of Narrow Lake were significantly more dense but were exposed to a much smaller predatory field than those in Amisk Lake. With respect to (1) and (4), data from Narrow Lake suggests that growth differences between 1985 and 1986 resulted from more energy spent searching for prey and not directly from the amount of prey ingested.

In conclusion, fisheries managers face significant challenges in predicting recruitment and if effective management decisions are to be made the following data should be considered essential: (1) Fish community structure, (2) Lake morphometry, (3) Lake productivity as indicated by total phosphorus and chlorophyll _a_, (4) Cumulative degree days over the growing season, (5) Estimates of abundance and size-at-age of year-classes with special emphasis on pre-reproductive cohorts.

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Appendix 1. Density (#·1000 m^3) estimates of limnetic zone age 0 perch based on midwater trawl samples. Depth intervals 2 - (0-2 m), 4 - (2-4 m), SD - standard deviation, n - number of trawls, Volume - total water filtered (m^3).

Date	Depth	Density	SD	n	Volume
Amisk 1985					
May 31	2	0	0	2	5224
Jun 3	2	9.74	6.28	4	10448
Jun 12	2	17.14	12.02	6	15284
Jun 13	2	4.84	4.37	4	9444
Jun 19	2	14.30	7.00	4	10748
Jun 26	2	8.73	5.15	4	9572
Jul 3	2	30.60	31.75	5	13808
Jul 10	2	10.86	14.86	4	12906
Jul 17	2	0.16	0.28	4	13542
Amisk 1986					
May 21	2	0	0	5	9704
May 28	2	0	0	4	6054
Jun 4	2	3.58	3.74	6	14644
Jun 10	2	14.83	7.41	3	3840
Jun 19	2	71.83	37.66	6	6802
Jun 25	2	37.04	50.19	9	19054
Jul 2	2	105.97	98.18	11	12036
Jul 9	2	6.63	13.07	11	21800
Jul 23	2	1.78	2.06	5	11416
Amisk 1987					
May 27	2	3.15	2.08	3	9580
Jun 4	2	4.13	1.30	3	6812
Jun 4	4	10.87	7.23	3	7650
Jun 16	2	147.49	402.57	8	11518
Jul 2	2	777.65	681.72	6	8268
Jul 15	2	56.80	56.23	6	6754
Jul 29	2	75.77	105.32	6	7010
Aug 11	2	0	0	6	7368
Amisk 1988					
May 30	2	2.61	2.87	4	4495
Jun 27	2	292.77	240.33	6	6732
Jun 27	4	2.46	3.21	7	8610
Jul 26	2	50.52	45.28	4	6074

Appendix 1. Cont... Density (#·1000 m^3) estimates of limnetic zone age 0 perch based on midwater trawl samples.

Date	Depth	Density	SD	n	Volume
Baptiste 1986					
May 29	2	0.23	0.40	4	4352
Jun 15	2	26.50	0	1	1076
Jun 26	2	17.99	14.5	2	6582
Jul 10	2	0.15	0.26	4	12960
Baptiste 1987					
May 27	2	0.22	0.23	4	13288
Jun 3	2	1.49	0.35	3	7798
Jun 3	4	4.95	5.25	3	7280
Jun 17	2	151.66	149.00	6	7764
Jun 30	2	215.09	74.26	4	5152
Jul 14	2	11.45	17.73	4	4962
Jul 28	2	11.45	11.79	6	6312
Aug 11	2	0	0	6	6882
Baptiste 1988					
Jun 1	2	43.70	58.60	4	4488
Jun 28	2	43.73	20.47	4	4788
Jul 25	2	17.25	14.93	4	6078
Long 1986					
May 18	2	0	0	6	3596
Jun 3	2	44.99	56.74	4	4362
Jun 15	2	218.30	0	1	748
Jun 26	2	157.21	74.11	2	2524
Jul 10	2	237.39	148.88	2	2286
Jul 22	2	132.80	0	1	2656
Aug 7	2	234.49	46.38	2	3978
Aug 17	2	43.62	6.34	2	2780
Long 1987					
May 26	2	5.12	3.36	4	9272
Jun 17	2	521.95	118.07	5	6036
Jun 29	2	64.67	48.43	4	5334
Jul 16	2	3.46	3.62	4	4762
Jul 27	2	23.49	18.02	4	5264
Aug 10	2	2.43	2.20	4	4930

Appendix 1. Cont... Density (#·1000 m^3) estimates of limnetic zone age 0 perch based on midwater trawl samples.

Date	Depth	Density	SD	n	Volume
Long 1988					
Jun 1	2	97.64	41.87	3	3366
Jun 28	2	104.78	74.68	4	4666
Jul 25	2	154.64	136.01	4	5738
Aug 23	2	13.56	10.11	4	4574
Narrow 1985					
May 30	2	5.32	0	1	2792
Jun 2	2	240.37	119.62	2	5584
Jun 5	2	44.94	59.79	3	8376
Jun 9	2	67.20	20.76	7	18550
Jun 10	2	41.52	26.90	4	11204
Jun 18	2	207.56	97.63	4	12292
Jun 22	2	348.67	154.84	2	5952
Jun 25	2	640.87	140.42	2	5114
Jul 2	2	159.53	100.53	8	16950
Jul 9	2	90.97	49.80	4	8460
Jul 16	2	85.19	115.15	4	7982
Jul 23	2	18.55	23.53	4	10740
Jul 30	2	26.13	17.41	4	11050
Aug 6	2	2.45	2.12	4	13088
Aug 13	2	0.24	0.14	4	13252
Narrow 1986					
May 20	2	0	0	8	17466
May 27	2	0	0	6	7276
Jun 3	2	41.67	28.41	6	7070
Jun 10	2	111.33	134.69	12	13280
Jun 12	2	360.64	336.54	25	79370
Jun 13	2	718.79	756.21	34	97832
Jun 16	2	1935.38	3888.06	34	113792
Jun 17	2	597.20	637.84	20	57314
Jun 17	4	956.53	1811.91	17	45940
Jun 18	2	555.85	492.92	33	105794
Jun 24	2	438.65	204.17	20	73402
Jul 1	2	264.50	372.41	12	15830
Jul 8	2	312.17	390.08	12	12912
Jul 15	2	12.43	82.34	7	9998
Jul 22	2	195.70	74.15	10	13336
Jul 27	2	52.30	57.44	10	13176
Aug 5	2	14.40	13.02	10	11330
Aug 12	2	15.96	6.35	10	11958
Aug 19	2	5.96	3.19	8	10090

Appendix 1. Cont... Density (#·1000 m^3) estimates of limnetic zone age 0 perch based on midwater trawl samples.

Date	Depth	Density	SD	n	Volume
Narrow 1987					
May 26	2	6.68	5.31	4	10038
Jun 2	2	21.29	15.85	11	16392
Jun 16	2	61.76	63.23	9	12028
Jul 1	2	82.73	83.43	8	12510
Jul 14	2	57.79	41.94	8	12020
Jul 27	2	82.36	82.82	8	13002
Aug 10	2	2.72	4.80	8	9144
Narrow 1988					
Jun 1	2	88.19	18.30	3	3366
Jun 28	2	33.53	14.55	6	7382
Jun 28	4	176.46	53.72	6	6806
Jul 25	2	134.85	59.16	3	5380
Aug 23	2	42.78	11.26	2	2377

Appendix 2. Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992. T - midwater trawl, S - beach seine, SD - standard deviation, n - sample size.

Date	Method	Length	SD	Weight	SD	n
Amisk 1985						
Jun 3	T	8.4	1.8	3	3	94
Jun 12	T	10.5	1.4	7	4	194
Jun 13	T	10.4	1.2	6	3	41
Jun 19	T	12.9	1.5	14	6	127
Jun 26	T	14.5	1.8	22	10	72
Jul 3	T	19.1	2.1	61	24	172
Jul 10	T	25.4	3.8	180	88	72
Jul 17	T	32.4	8.4	501	445	2
Jul 17	S	39.2	3.7	913	440	50
Jul 24	S	41.6	0	1080	0	1
Jul 28	S	50.8	2.6	1230	235	50
Aug 5	S	55.1	2.3	1875	254	38
Aug 14	S	59.6	3.5	1962	337	46
Sep 15	S	69.0	3.8	2893	549	34
Oct 11	S	68.5	3.3	3362	530	32
Baptiste 1985						
Jun 7	T	10.0	1.4	5	3	25
Jul 4	T	20.7	2.7	74	32	35
Jul 22	S	36.0	4.3	541	163	14
Aug 16	S	50.6	3.7	1135	252	41
Garner 1985						
Jun 17	T	12.0	2.3	14	7	23
Jul 15	T	26.0	3.8	191	91	7
Aug 15	S	55.4	2.5	1742	264	31
Long 1985						
Jun 7	T	8.6	1.3	2	1	37
Jul 4	T	19.7	2.4	65	31	100
Jul 23	S	37.6	4.4	589	187	50
Jul 31	T	28.1	2.6	229	65	41
Jul 31	S	42.4	5.3	768	235	50
Narrow 1985						
May 30	T	6.9	0.5	0.88	-	14
Jun 2	T	7.9	0.7	1.5	-	112
Jun 5	T	9.1	0.8	3	1	62
Jun 9	T	10.4	1.0	4	2	365
Jun 10	T	10.7	0.7	5	1	188

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Narrow 1985 - continued						
Jun 18	T	13.9	0.9	13	3	200
Jun 23	T	15.7	0.9	22	5	100
Jun 25	T	16.6	1.0	26	7	100
Jul 2	T	19.1	1.5	47	14	554
Jul 9	T	24.2	1.9	117	36	196
Jul 16	T	29.2	2.3	242	81	121
Jul 16	S	32.1	2.1	304	86	99
Jul 23	T	32.3	1.9	352	83	90
Jul 23	S	35.1	2.2	434	124	50
Jul 30	T	34.7	2.5	358	91	151
Jul 30	S	38.7	3.1	546	158	50
Aug 6	T	35.6	3.1	443	137	31
Aug 6	S	41.9	3.2	660	167	50
Aug 13	T	37.9	1.6	510	69	3
Aug 13	S	43.1	4.3	648	219	58
Aug 19	S	45.0	3.8	735	183	63
Sep 15	S	49.8	4.2	1225	298	24
Oct 11	S	49.9	0.5	1100	0	2
Amisk 1986						
Jun 4	T	7.2	0.6	2	0.8	46
Jun 10	T	9.5	1.7	6	4	50
Jun 19	T	13.3	0.9	26	6	90
Jun 25	T	17.7	1.4	50	25	136
Jul 2	T	22.2	1.7	114	30	179
Jul 9	T	24.2	2.6	148	61	57
Jul 17	S	33.1	2.3	412	135	3
Jul 23	T	28.6	6.0	287	191	14
Jul 23	S	36.3	3.3	535	150	30
Jul 30	S	43.5	2.4	890	182	30
Aug 6	S	46.6	3.8	1141	283	30
Aug 12	S	42.6	6.0	814	393	37
Aug 19	S	49.2	5.6	1267	538	47
Sep 14	S	59.0	3.5	2098	374	50
Oct 12	S	60.4	3.0	2247	345	50
Baptiste 1986						
Jun 15	T	13.3	0.9	25	6	30
Jun 26	T	20.7	2.2	78	22	30
Jul 13	S	35.1	2.3	464	84	30
Jul 24	S	40.8	2.3	709	120	30
Aug 7	S	52.0	2.4	1507	198	30
Aug 11	S	52.5	2.6	1511	244	35

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Baptiste 1986 - continued						
Aug 21	S	59.2	3.0	2197	413	30
Sep 13	S	63.4	3.1	2642	452	14
Oct 11	S	63.1	3.0	2510	373	37
Long 1986						
Jun 3	T	8.5	0.8	4	1	62
Jun 15	T	13.7	1.0	29	6	31
Jun 26	T	19.1	3.2	67	37	30
Jul 10	T	23.1	2.4	123	46	60
Jul 22	T	25.3	3.1	168	81	30
Jul 22	S	35.6	2.9	456	122	30
Jul 29	S	36.4	5.7	551	284	30
Aug 7	T	31.9	5.1	327	158	50
Aug 7	S	39.5	4.9	661	275	50
Aug 17	T	31.7	3.0	319	93	60
Aug 17	S	48.4	4.0	1126	227	49
Oct 13	S	41.1	5.0	704	262	52
Narrow 1986						
Jun 3	T	7.6	0.1	2.2	0.9	126
Jun 10	T	11.5	0.9	12	4	205
Jun 12	T	13.0	0.8	20	5	179
Jun 13	T	13.3	0.9	21	5	313
Jun 16	T	14.6	1.0	30	7	206
Jun 17	T	14.9	1.2	32	8	152
Jun 18	T	14.8	1.2	36	10	170
Jun 24	T	19.3	0.0	63	18	178
Jul 1	T	21.4	1.9	87	27	180
Jul 8	T	23.1	2.1	123	45	180
Jul 15	T	23.6	2.2	126	47	144
Jul 15	S	26.9	2.4	203	64	30
Jul 22	T	25.3	2.6	173	80	153
Jul 22	S	30.7	4.3	309	103	24
Jul 29	T	26.1	2.6	177	64	137
Jul 29	S	30.0	2.1	276	72	30
Aug 5	T	25.6	2.6	158	56	133
Aug 5	S	35.5	6.0	525	260	17
Aug 12	T	29.5	4.3	287	147	148
Aug 12	S	37.2	5.3	547	234	92
Aug 19	T	30.1	3.8	270	114	59
Aug 19	S	38.5	4.0	551	184	50
Sep 14	S	44.4	3.8	823	230	50
Oct 12	S	42.9	3.0	753	153	50

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Amisk 1987						
May 27	T	7.0	0.3	1	0.2	25
Jun 4	T	8.6	0.7	3	0.6	71
Jun 16	T	13.7	1.1	17	6	108
Jul 2	T	26.8	2.0	196	46	81
Jul 2	S	27.4	2.1	219	46	20
Jul 15	T	38.2	4.9	620	205	88
Jul 15	S	41.2	4.0	763	257	20
Jul 29	T	46.1	3.0	1118	225	68
Jul 29	S	50.1	3.8	1377	372	46
Aug 11	S	55.2	2.8	1756	333	97
Aug 23	S	57.4	3.4	2066	473	70
Oct 12	S	62.3	4.2	2584	518	58
Baptiste 1987						
May 27	T	7.2	1.2	1.7	1.1	3
Jun 3	T	8.2	0.9	2.1	0.8	45
Jun 17	T	14.6	1.4	21	8	198
Jun 30	T	24.7	2.7	144	51	63
Jun 30	S	28.9	3.8	239	91	53
Jul 14	T	32.7	3.3	390	116	54
Jul 14	S	36.8	2.1	516	88	60
Jul 28	T	44.9	2.6	1023	190	64
Jul 28	S	44.0	4.2	847	275	100
Aug 11	S	52.3	4.1	1454	361	97
Aug 25	S	56.7	3.6	1782	371	100
Sep 19	S	61.0	5.2	2287	601	50
Oct 11	S	57.4	4.9	1939	569	19
Long 1987						
May 26	T	7.2	0.7	1.6	0.6	52
Jun 17	T	17.0	2.3	43	16	100
Jun 29	T	25.0	3.2	162	75	85
Jul 16	T	29.0	3.6	201	45	15
Jul 16	S	32.1	2.5	346	91	34
Jul 27	T	33.0	4.2	357	164	59
Jul 27	S	36.7	3.8	482	135	30
Aug 10	T	27.7	2.2	178	36	12
Aug 10	S	44.4	3.4	853	222	48
Aug 23	S	44.3	6.0	891	403	101
Oct 12	S	37.2	2.9	474	133	35

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Narrow 1987						
May 26	T	6.6	0.8	1	0.1	58
Jun 2	T	8.8	0.8	3	1	89
Jun 16	T	15.3	1.2	28	7	212
Jul 1	T	22.4	2.0	95	28	114
Jul 1	S	25.1	2.2	151	30	9
Jul 14	T	27.6	2.1	198	50	91
Jul 14	S	32.2	1.9	331	69	50
Jul 27	T	30.3	2.6	244	71	86
Jul 27	S	35.8	3.3	426	123	50
Aug 10	T	33.2	2.3	345	74	22
Aug 10	S	43.5	3.0	868	228	2
Aug 24	S	39.8	2.8	574	121	101
Sep 19	S	43.5	2.6	807	230	3
Oct 11	S	45.4	3.8	888	239	125
Amisk 1988						
May 30	T	8.7	0.4	5.8	2.5	10
Jun 27	T	22.0	1.9	102	31	95
Jul 26	T	38.9	2.2	636	116	60
Jul 26	S	40.4	3.7	708	222	51
Aug 24	S	53.4	5.0	1762	485	84
Baptiste 1988						
Jun 1	T	9.1	0.7	6	2	131
Jun 28	T	21.2	2.4	91	38	95
Jun 28	S	27.4	3.0	214	56	38
Jul 13	S	35.3	2.1	479	98	50
Jul 25	T	37.8	4.5	608	212	42
Jul 25	S	38.5	3.7	603	183	50
Aug 8	S	43.4	4.8	849	324	32
Aug 22	S	47.3	6.0	1238	501	100
Sep 23	S	54.4	4.7	1727	459	99
Garner 1988						
Aug 24	S	57.1	4.4	2462	637	11
Ghost 1988						
Aug 21	S	53.5	3.1	1746	333	98

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Hanmore 1988						
Aug 24	S	51.2	3.2	1463	299	100
Lodge 1988						
Aug 23	S	55.5	3.2	1760	326	100
Long 1988						
Jun 1	T	11.2	0.9	7	2	100
Jun 28	T	24.0	2.0	132	36	91
Jul 25	T	31.6	3.0	308	86	60
Jul 25	S	31.4	2.0	296	62	33
Aug 23	T	38.4	4.4	581	170	62
Aug 23	S	41.8	3.3	767	179	100
Narrow 1988						
Jun 1	T	9.3	1.1	4.5	2.2	152
Jun 28	T	20.0	1.8	57	20	131
Jul 25	T	25.2	2.4	151	42	59
Jul 28	S	37.6	3.8	568	192	50
Aug 23	T	28.8	3.5	244	81	100
Aug 23	S	38.6	4.6	583	206	100
South Skeleton 1988						
Aug 23	S	50.2	5.6	1468	503	73
North Skeleton 1988						
Aug 23	S	58.1	3.5	2217	391	100
Amisk 1989						
Aug 27	S	57.9	4.0	2160	621	38
Baptiste 1989						
Aug 27	S	64.0	4.9	2966	729	98
Long 1989						
Aug 27	S	46.0	5.1	1019	393	102

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Narrow 1989						
Aug 27	S	43.9	5.1	872	320	100
Amisk 1990						
Aug 29	S	58.1	3.8	2094	445	98
Baptiste 1990						
Aug 28	S	70.3	3.9	3856	751	76
Long 1990						
Aug 28	S	43.7	3.3	825	184	115
Narrow 1990						
Aug 28	S	50.4	5.1	1202	370	120
Amisk 1991						
Aug 28	S	62.1	3.2	2561	417	108
Baptiste 1991						
Aug 28	S	64.3	4.2	2994	657	63
Long 1991						
Aug 28	S	47.1	3.7	1046	211	52
Narrow 1991						
Aug 28	S	49.8	4.3	1274	381	94
Amisk 1992						
Aug 24	S	57.9	2.9	2250	376	114
Baptiste 1992						
Aug 24	S	57.0	3.4	2196	395	103

Appendix 2. Cont... Total length (mm) and wet weight (mg) of age 0 yellow perch caught 1985-1992.

Date	Method	Length	SD	Weight	SD	n
Long 1992						
Aug 24	S	42.4	3.1	756	211	113
Narrow 1992						
Aug 24	S	50.6	6.3	1472	615	119

Appendix 3. Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1985	Amisk	May 10	S	8.4	1
		May 14	S	8.4	1
		May 15	S	11.2	2
		May 20	S	13.8	3
		May 22	S	15.0	3
		May 31	S	13.2	2
		Jun 3	S	14.7	4
		Jun 7	S	15.2	2
		Jun 9	S	14.3	1
		Jun 10	S	14.1	1
		Jun 12	S	14.8	6
		Jun 13	S	14.6	4
		Jun 19	S	16.1	4
		Jun 26	S	16.3	4
		Jul 1	S	20.1	1
		Jul 3	S	20.4	5
		Jul 3	2-4	19.4	4
		Jul 4	S	21.1	1
		Jul 9	S	21.7	1
		Jul 10	S	22.7	4
		Jul 17	S	21.0	4
		Jul 21	S	21.2	1
		Jul 24	S	20.2	4
		Jul 31	S	23.3	1
		Aug 12	S	17.4	1
		Aug 14	S	17.7	3
		Aug 21	S	16.1	1
		Sep 14	S	12.5	1
		Oct 11	S	8.0	2
1985	Baptiste	Jun 7	S	15.5	2
		Jul 4	S	21.2	4
		Jul 22	S	22.5	2
		Aug 16	S	17.7	1
1985	Garner	Jun 17	S	14.6	2
		Jul 15	S	20.5	3
		Aug 15	S	18.3	3
1985	Long	Jun 7	S	16.7	1
		Jul 4	S	22.0	2
		Jul 23	S	20.7	2
		Jul 31	S	19.8	3
		Aug 19	S	18.1	1
		Sep 15	S	14.1	1
		Oct 10	S	7.4	1

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1985	Narrow	May 9	S	7.0	1
		May 13	S	9.6	1
		May 15	S	9.4	1
		May 28	S	14.9	1
		May 29	S	14.9	1
		Jun 2	S	14.4	1
		Jun 5	S	16.6	3
		Jun 9	S	15.5	7
		Jun 10	S	15.1	4
		Jun 18	S	15.6	4
		Jun 23	S	16.0	2
		Jun 25	S	14.5	2
		Jul 2	S	20.0	4
		Jul 2	2	19.1	1
		Jul 9	S	20.1	4
		Jul 16	S	20.2	4
		Jul 23	S	20.1	5
		Jul 30	S	20.0	6
		Aug 6	S	20.5	6
		Aug 13	S	17.1	6
		Aug 19	S	18.9	1
		Sep 15	S	13.3	1
		Oct 11	S	7.1	2
1986	Amisk	May 6	S	10.4	1
		May 6	1	8.2	1
		May 7	S	10.2	2
		May 7	1	7.8	2
		May 12	S	9.9	2
		May 12	1	8.3	2
		May 13	S	9.9	3
		May 13	1-2	9.5	4
		May 21	S	9.0	4
		May 21	1-2	8.9	8
		May 28	S	13.4	4
		May 28	1-2	12.8	8
		Jun 4	S	16.8	6
		Jun 4	1	16.6	6
		Jun 10	S	19.3	3
		Jun 10	1-2	19.3	6
		Jun 19	S	18.2	3
		Jun 19	1-2	18.1	6
		Jun 25	S	18.7	4
		Jun 25	1-2	18.4	8
		Jul 2	S	19.6	6
		Jul 2	1-2	19.2	12

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1986	Amisk	Jul 9	S	18.3	5
		Jul 9	1	18.2	5
		Jul 23	S	18.5	1
		Aug 6	S	21.3	1
		Aug 6	1-2	20.9	2
		Oct 12	S	9.2	1
		Oct 12	1-2	8.9	2
1986	Baptiste	May 5	S	6.7	1
		May 5	1	6.2	1
		May 29	S	17.1	4
		May 29	1-2	16.3	8
		Jun 15	S	17.7	1
		Jun 15	1-2	17.6	2
		Jun 26	S	17.1	1
		Jun 26	1-2	17.1	2
		Jul 10	S	18.6	2
		Jul 10	1-2	18.3	4
		Aug 7	S	20.5	1
		Aug 7	1-2	19.6	2
		Oct 13	S	10.0	1
		Oct 13	1	9.0	1
1986	Long	May 13	S	11.0	1
		May 14	S	4.9[a]	1
		May 18	S	12.7	3
		May 18	1-2	11.2	6
		May 26	S	13.5	1
		May 26	1	13.5	1
		Jun 3	S	17.9	3
		Jun 3	1-2	17.9	6
		Jun 15	S	16.8	1
		Jun 15	1-2	16.2	2
		Jun 26	S	17.6	2
		Jun 26	1-2	17.5	4
		Jul 10	S	18.6	2
		Jul 10	1-2	18.5	4
		Aug 7	S	22.0	2
		Aug 7	1-2	20.4	4
		Aug 17	S	20.0	2
		Oct 13	S	8.0	2
		Oct 13	1-2	8.0	4

[a] Wind event caused turnover of water column

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1986	Narrow	May 8	S	8.5	2
		May 8	1	7.7	2
		May 11	S	8.5	2
		May 11	1-2	8.2	3
		May 12	S	8.1	2
		May 12	1	8.1	2
		May 14	S	4.7[a]	1
		May 18	S	11.5	1
		May 18	1	10.2	1
		May 20	S	11.8	8
		May 20	1-2	11.3	16
		May 27	S	14.1	7
		May 27	1-2	13.5	12
		Jun 3	S	17.5	6
		Jun 3	1-2	17.3	12
		Jun 10	S	19.1	12
		Jun 10	1-2	18.9	24
		Jun 12	S	17.5	8
		Jun 12	1-2	17.4	16
		Jun 13	S	17.3	11
		Jun 13	1-2	17.0	22
		Jun 16	S	16.5	6
		Jun 16	1-2	16.5	4
		Jun 17	S	18.2	9
		Jun 17	1-2	17.6	18
		Jun 18	S	17.8	8
		Jun 18	1-2	17.5	12
		Jun 24	S	17.4	8
		Jun 24	1-2	17.0	16
		Jul 1	S	18.7	6
		Jul 1	1-2	18.5	12
		Jul 8	S	18.1	6
		Jul 8	1-2	17.9	12
		Jul 15	S	17.4	6
		Jul 15	1-2	17.4	10
		Jul 22	S	20.1	5
		Jul 29	S	18.5	7
		Jul 29	1-2	18.5	14
		Aug 5	S	20.7	3
		Aug 6	S	20.1	1
		Aug 6	1-2	19.8	2
		Aug 12	S	21.0	4
		Aug 12	1	21.0	2
		Aug 19	S	18.8	4

[a] Wind event caused turnover of water column

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1986	Narrow	Sep 14	S	13.3	1
		Sep 14	1-2	13.3	2
		Oct 12	S	8.2	1
		Oct 12	1-2	8.2	2
1987	Amisk	May 6	S	8.1	0
		May 27	S	15.1	3
		May 27	1-3	13.5	6
		Jun 4	S	13.5	5
		Jun 4	1-5	11.1	8
		Jun 16	S	17.0	8
		Jun 16	1-5	16.4	16
		Jul 2	S	21.3	6
		Jul 2	1-5	20.4	15
		Jul 15	S	18.1	8
		Jul 15	1-5	16.5	16
		Jul 29	S	24.1	8
		Jul 29	1-5	21.2	20
		Aug 11	S	17.4	7
		Aug 11	1-5	17.1	18
		Aug 23	S	16.9	1
		Aug 23	1-5	16.6	5
		Oct 12	S	10.5	1
		Oct 12	1-5	10.4	4
1987	Baptiste	Apr 30	S	9.0	2
		Apr 20	1-5	5.5	8
		May 4	S	10.2	2
		May 27	S	14.4	8
		May 27	1-3	13.8	12
		Jun 3	S	13.4	6
		Jun 17	S	16.9	8
		Jun 17	1-5	16.6	15
		Jun 30	S	18.5	11
		Jun 30	1-5	17.9	24
		Jul 14	S	18.8	4
		Jul 14	1-5	17.2	8
		Jul 15	S	19.6	4
		Jul 15	1-5	18.8	8
		Jul 28	S	24.0	9
		Jul 28	1-5	20.9	29
		Jul 30	S	23.3	4
		Jul 30	1-5	21.7	19
		Aug 11	S	18.1	5
		Aug 11	1-5	17.6	13

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1987	Baptiste	Aug 25	S	17.2	3
		Aug 25	1-5	17.0	15
		Aug 27	S	17.5	6
		Aug 27	1-5	16.9	21
		Oct 11	S	10.9	1
		Oct 11	1-5	10.9	5
1987	Long	May 7	S	12.2	1
		May 7	1-2	11.6	2
		May 15	S	10.8	2
		May 17	S	13.5	2
		May 17	1-3	13.0	3
		May 26	S	12.2	2
		May 26	1-3	11.8	4
		May 27	S	15.6	3
		May 27	1-3	13.9	4
		Jun 17	S	17.5	4
		Jun 17	1-5	17.3	6
		Jun 29	S	18.8	4
		Jun 29	1-5	17.8	8
		Jul 1	S	21.1	3
		Jul 1	1-5	18.6	10
		Jul 16	S	19.1	4
		Jul 16	1-5	18.7	8
		Jul 27	S	22.6	4
		Jul 27	1-5	20.7	10
		Aug 10	S	18.4	4
		Aug 10	1-5	18.0	10
		Aug 23	S	17.6	1
		Aug 23	1-5	16.7	5
		Oct 12	S	10.5	1
		Oct 12	1-5	10.5	5
1987	Narrow	Apr 30	S	9.9	2
		Apr 30	1-3	9.0	4
		May 1	S	9.3	2
		May 1	1-5	7.6	6
		May 5	S	7.8	3
		May 5	1-5	7.3	11
		May 6	S	8.3	1
		May 6	1	8.3	1
		May 7	S	8.9	2
		May 7	1-5	7.3	4
		May 17	S	11.5	2
		May 17	1-2	11.5	2
		May 26	S	13.7	8
		May 26	1-3	12.7	12

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1987	Narrow	Jun 2	S	12.9	5
		Jun 2	1-5	11.9	13
		Jun 16	S	17.0	8
		Jun 16	1-5	16.9	16
		Jun 29	S	19.1	8
		Jun 29	1-5	18.1	16
		Jul 1	S	19.4	16
		Jul 1	1-5	18.1	32
		Jul 14	S	18.3	8
		Jul 14	1-5	16.7	13
		Jul 27	S	22.4	11
		Jul 27	1-5	20.9	35
		Jul 29	S	22.3	4
		Jul 29	1-5	21.4	20
		Aug 10	S	18.6	8
		Aug 10	1-5	18.1	20
		Aug 12	S	17.3	1
		Aug 12	1-5	17.4	5
		Aug 24	S	16.8	4
		Aug 24	1-5	16.6	20
		Oct 11	S	10.3	2
		Oct 11	1-5	10.3	5
1988	Amisk	Apr 27	S	5.9	1
		Apr 27	1-5	5.8	5
		May 30	S	15.5	1
		May 30	1-5	15.3	5
		Jun 27	S	20.1	2
		Jun 27	1-5	18.9	5
		Jul 26	S	22.9	2
		Jul 26	1-5	21.2	5
		Aug 24	S	19.4	2
		Aug 24	1-5	18.4	5
1988	Baptiste	Apr 25	S	5.8	2
		Apr 25	1-5	5.6	10
		Apr 26	S	6.2	1
		Apr 26	1-5	5.1	3
		May 20	S	12.3	1
		May 20	1-5	12.2	3
		Jun 1	S	15.6	4
		Jun 1	1-5	15.3	10
		Jun 28	S	22.7	4
		Jun 28	1-5	20.2	10
		Jul 13	S	18.5	1

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1988	Baptiste	Jul 25	S	19.3	4
		Jul 25	1-5	18.7	10
		Aug 8	S	18.6	1
		Aug 8	1-5	18.4	3
		Aug 21	S	18.9	2
		Aug 21	1-5	18.7	5
		Aug 22	S	18.3	2
		Aug 22	1-5	18.1	10
		Sep 23	S	10.4	1
		Sep 23	1-5	10.3	3
1988	Garner	Apr 27	S	8.1	1
		Apr 27	1-5	8.0	5
		May 31	S	14.5	2
		May 31	1-5	14.5	5
		Jun 29	S	20.6	2
		Jun 29	1-5	19.5	5
		Jul 27	S	20.9	2
		Jul 27	1-5	20.2	5
		Aug 25	S	20.0	2
		Aug 25	1-5	18.3	5
1988	Ghost	Apr 25	S	8.8	1
		Apr 25	1-5	8.2	5
		May 31	S	15.6	2
		May 31	1.5	15.5	5
		Jun 29	S	21.5	2
		Jun 29	1-5	20.5	5
		Jul 27	S	21.2	2
		Jul 27	1-5	20.0	5
		Aug 21	S	18.2	2
		Aug 21	1-5	17.9	5
1988	Hanmore	Apr 27	S	6.0	1
		Apr 27	1-5	5.5	5
		May 31	S	14.3	2
		May 31	1-5	14.3	5
		Jun 29	S	19.9	2
		Jun 29	1-5	19.6	5
		Jul 27	S	20.6	2
		Jul 27	1-5	19.6	5
		Aug 25	S	19.3	2
		Aug 25	1-5	18.5	5

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1988	Lodge	Apr 27	S	8.2	1
		Apr 27	1-5	8.0	5
		May 30	S	15.4	1
		May 30	1-5	15.4	5
		Jun 27	S	20.3	2
		Jun 27	1-5	19.1	5
		Jul 26	S	23.0	2
		Jul 26	1-5	20.6	5
		Aug 24	S	18.8	2
		Aug 24	1-5	18.2	5
1988	Long	Apr 26	S	9.4	1
		Apr 26	1-5	8.7	5
		Apr 28	S	9.9	1
		Apr 28	1-5	9.5	5
		Jun 1	S	16.1	2
		Jun 1	1-5	15.5	5
		Jun 28	S	21.1	1
		Jun 28	1-5	19.8	5
		Jul 25	S	20.9	2
		Jul 25	1-5	20.1	5
		Aug 22	S	18.8	1
		Aug 22	1-5	18.7	5
		Aug 23	S	18.9	2
		Aug 23	1-5	18.6	5
1988	Narrow	Apr 26	S	5.9	1
		Apr 26	1-5	5.8	5
		Apr 28	S	9.5	1
		Apr 28	1-5	9.1	9
		Jun 1	S	15.6	3
		Jun 1	1-5	15.4	5
		Jun 28	S	20.7	2
		Jun 28	1-5	19.6	5
		Jul 25	S	20.8	2
		Jul 25	1-5	20.1	5
		Aug 8	S	19.2	1
		Aug 8	1-5	19.2	3
		Aug 23	S	18.3	1
		Aug 23	1-5	18.2	5

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1988	S. Skeleton	Apr 27	S	6.0	1
		Apr 27	1-5	5.9	5
		May 30	S	15.0	1
		May 30	1-5	15.0	5
		Jun 27	S	22.2	4
		Jun 27	1-5	19.0	10
		Jul 4	S	18.8	2
		Jul 4	1-5	18.7	5
		Jul 26	S	24.0	2
		Jul 26	1-5	20.0	5
		Aug 24	S	18.8	2
		Aug 24	1-5	18.0	5
1988	N. Skeleton	Apr 27	S	8.4	1
		Apr 27	1-5	7.7	5
		May 30	S	14.9	1
		May 30	1-5	14.9	5
		Jul 4	S	19.4	2
		Jul 4	1-5	19.1	5
		Jul 26	S	22.9	2
		Jul 26	1-5	20.0	5
		Aug 24	S	19.4	2
		Aug 24	1-5	18.4	5
1989	Amisk	Aug 27	S	13.5	1
		Aug 27	1-5	13.2	5
1989	Baptiste	Aug 27	S	13.7	1
		Aug 27	1-5	13.6	5
1989	Long	Aug 27	S	13.4	1
		Aug 27	1-5	13.4	5
1989	Narrow	Aug 27	S	13.4	1
		Aug 27	1-5	13.4	5
1990	Amisk	Aug 29	S	16.8	1
1990	Baptiste	Aug 28	S	18.0	2
1990	Long	Aug 28	S	18.5	1
1990	Narrow	Aug 28	S	18.3	1

Appendix 3. Cont... Water temperatures (°C) in study lakes 1985-1992. S - surface temperature at 20 cm. n - number of samples.

Year	Lake	Date	Depth	Temp	n
1991	Amisk	Aug 28	S	20.0	1
1991	Baptiste	Aug 28	S	22.0	1
1991	Long	Aug 28	S	20.0	1
1991	Narrow	Aug 28	S	18.8	1
1992	Amisk	Aug 23	S	18.0	1
1992	Baptiste	Aug 23	S	18.0	1
1992	Long	Aug 23	S	17.7	1
1992	Narrow	Aug 23	S	18.0	1