Factors Influencing Growth and Survival
of Yellow Perch from Saginaw Bay, Lake Huron

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FACTORS INFLUENCING GROWTH AND SURVIVAL
OF YELLOW PERCH FROM SAGINAW BAY, LAKE HURON[1]

Ronald J. Salz

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by

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A thesis submitted in partial fulfillment

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TABLE OF CONTENTS

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LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The yellow perch (Perca flavescens) population from Saginaw Bay has historically supported a large commercial fishery. Presently the population, which is dominated by small, unharvestable fish, exhibits both slow growth and high mortality past age four. Large energetic costs associated with reproduction and parasitism have a negative effect on yellow perch body growth and survival. Most somatic growth occurred between spawning (May) and onset of gonad production (August). Percent water (visceral and somatic) decreased from June-August, suggesting some seasonal storage of lipids by yellow perch. Surplus body energy was depleted after August as gonads matured and parasite incidence increased. Surplus body energy, condition, and parasite incidence varied by location within inner Saginaw Bay. Yellow perch collected from deeper sites (Au Gres and Blackhole) had more surplus body energy than perch from the shallow, eutrophic Wildfowl Bay. Females grew faster than males after maturation but also contained more water (%) in both the viscera and soma. Back-calculation analysis showed strong evidence for negative size-selective mortality where only the largest individuals from each cohort survived to age five or six. These results suggest that energy depletion mortality may be more significant than fishing mortality in

determining the present population structure found in yellow perch from Saginaw Bay. The interrelationship between large reproductive costs, slow growth, and high adult natural mortality was investigated here.

INTRODUCTION

The history of Saginaw Bay can be characterized as one of change and disturbance. Fish species composition, benthic communities, water quality, exploitation levels, and fishing restrictions have all varied significantly since the turn of the century. These changes have been accompanied by fluctuations in both growth and abundance of yellow perch (Perca flavescens) (Hile 1954, El Zarka 1959, Eshenroder 1977). Previous studies have attempted to correlate numerous physical, biological, and human factors with yellow perch growth and abundance. El Zarka (1957) estimated that stock size had increased seven-fold between the periods 1929-30 and 1949-55. Concurrent with this increase there was a marked decline in the modal length of perch caught in trapnets. Eshenroder (1977) related increased perch growth in the late 1960's to intensified fishing effort and size limit removal. From 1970-85 trawl samples have shown a strong negative correlation between growth and density of perch in the Bay (Weber 1985). These results indicate that density dependent factors are important in determining perch growth. Other perch populations have also shown an inverse correlation between growth and abundance (Eschmeyer 1937, Tesch 1955, LeCren 1958, Rask 1983, Henderson 1985).

Since the early 1970's the trend for yellow perch in Saginaw Bay has been toward progressively slower growth and increased

densities (Weber 1985). Trawl collections for this period have yielded exceptional catches of 2 and 3-yr-old perch but considerably less older perch. Separate evaluations by Diana and Salz (1990) and Ledbetter (unpublished, Michigan Department of Natural Resources, Charlevoix) also indicated poor survival of perch past age three. Diana (unpublished, University of Michigan) related low incidence of older perch in gillnets to high natural mortality whereas Ledbetter identified fishing pressure as the main cause. Age composition in commercial trapnets shifted from a period of young perch (1968-75) to older perch (1975-83) (Weber 1985). These findings suggest that mortality rates declined during this period in response to reduced exploitation. Accurate mortality estimates are difficult to obtain in a large, complex system such as Saginaw Bay. Gear selectivity, migrations, and sampling variability are all potential biases. Studies on European perch (Perca fluviatilis) show that natural mortality can be highly variable between populations, year-classes, and sexes (Craig 1987).

At present the yellow perch population in Saginaw Bay consists predominantly of small, unharvestable fish with only a small percentage longer than the 8.5 inch minimum commercial size limit. Recent trawl data (1986-88) indicates both exceptional recruitment of yellow perch and growth rates that are well below the state average for this species (Haas, unpublished, Michigan Department of Natural Resources, Mt.

Clemens). Commercial catch and effort have declined steadily since the early 1970's while the sport fishery for yellow perch has expanded over this period (Keller et. al. 1987).

This study investigates growth and natural mortality of yellow perch in terms of energy allocation. According to Winberg's bioenergetics equation (Winberg 1956) , the difference between assimilated ration and metabolic dissipation is given as the surplus energy increment . Surplus energy can be further divided into 1) surplus reproductive energy and 2) surplus body energy. These two components are inversely related for a given level of total surplus energy. Therefore, growth and reproduction directly compete for a common limited resource (i.e. energy) (Calow 1985). Tradeoffs between surplus energy gained in the form of protein and lipid accumulation, and energy lost due to spawning, over-wintering, and parasitism affect growth and survival. Surplus body energy (without reproductive tissue) was studied here as a measure of the capacity for somatic growth and survival. Energy accumulation and depletion can vary with season, maturation state, sex, and age (Weatherly and Gill 1987). In addition, subpopulations may experience differential energy flux as a result of environmental differences (Diana and Salz 1990).

The energy indicators used here were percent water, dry weight, and condition factor. Percent water is inversely related to energy stored in the form of hydrophobic lipids (Iles and Wood

1965, Brett 1969, Niimi and Beamish 1974, Elliot 1976), and increases during starvation or depletion of other body constituents. While lipids make up only 2-12% of the total wet weight of fish (Weatherly and Gill 1987), as the main source of energy they are a critical component. Small changes in lipid content can significantly effect the health and longevity of a given fish. This is especially true for lean fish, such as yellow perch, that do not store much fat in their body tissue. Since perch store most of their fat in the visceral mass (Morawa 1956 from Thorpe 1977b), visceral percent water may be a better indicator of energy reserves than somatic percent water. Morawa (1956, from Thorpe 1977b) showed a strong inverse relationship between percent visceral water and percent visceral fat in European perch. Visceral and somatic percent water were examined separately for the present study. Dry weight provides a superior measure of growth than wet weight which can exhibit considerable short-term variability related to water uptake or loss (Love 1970, Weatherly and Gill 1983). Condition factor measures the variation in observed weight from expected weight for a given length. It is often used as an estimate of "fatness" or "well-being" in fish (Le Cren 1951). Parasite incidence was also analyzed to determine its impact on yellow perch energy content and survival. A previous study from Lake Erie has shown that parasites are widespread in Great

Lakes yellow perch and can result in considerable energy drain (Crites 1979).

The first specific objective of this study was to describe the change in surplus body energy of yellow perch due to gonad development and maturation. Gonado-somatic index (GSI), or the proportion of gonad weight to total body weight, is often used to estimate the relative cost of reproduction. The relationship between GSI and age can vary from population to population (Le Cren 1951, Brazo 1975) suggesting large variability in reproductive strategy among perch populations. Diana and Salz (1990) found that gonado-somatic index increased with age in yellow perch from Saginaw Bay . This indicated that as perch mature, proportionally more energy is spent on gonad growth with less available for somatic growth. Craig (1977) found that European perch from Windermere experienced a considerable body energy drain due to maturation and that older females had higher percent water content than younger females. Evidence for this shift in energy allocation as fish mature was investigated here. Seasonal trends in surplus body energy and condition related to reproductive costs were also investigated. Gonad production occurred mainly in August for male yellow perch from Saginaw Bay, while female gonad growth began in August and extended overwinter (Diana and Salz 1990). Yellow perch from Saginaw Bay spawned between late April and May (Diana and Salz 1990).

The second objective of this study was to describe differences between male and female yellow perch in terms of surplus body energy accumulation and energy loss due to reproductive costs. In general, male perch put less energy into reproduction than females although males mature at an earlier age (LeCren 1951,Tanasichuk 1978, Diana and Salz 1990). Despite greater reproductive costs, female perch often grow faster than males (Craig 1987, Thorpe 1977b). Differences in both somatic and gonadal growth between sexes are probably a function of differences in energy intake (Diana 1983) and food conversion efficiency (Malison et al. 1988). Thus, while female perch must accumulate more calories than males (Diana and Salz 1990), they also face greater energy demands. This tradeoff between energy accumulation and energy expenditure should be important in understanding differential natural mortality between sexes.

The third objective of this study was to compare subpopulations of yellow perch from different locations within Saginaw Bay. If differences in surplus body energy, condition or parasite load are found among sites it may be possible to correlate them with differences in prey size, water quality or perch density. Diana and Salz (1990) found that conditions for perch growth were more favorable in the less eutrophic outer Saginaw Bay than the highly eutrophic inner bay. Similar results were found in Lake Erie as perch from the mildly eutrophic

Central Basin grew faster than perch from the highly eutrophic Western Basin (Hayward and Margraf 1987). Other studies have found distinct growth-rate groups of perch within the same body of water (Schiemenz 1919, Roper 1936, Krasikova 1958; all from Thorpe 1977b). This occurence reflects the perch's ability to occupy more than one ecological niche (Thorpe 1977b). Comparing perch from different sites can provide a better understanding of the factors responsible for variable growth and mortality rates found in yellow perch.

The apparent high mortality of yellow perch past age four can be related to exploitation, natural mortality or a combination of both. Natural mortality due to energy depletion could result if food is limiting and the energy demands of reproduction, parasitism, and overwintering are not met. Yellow perch are physiologically intolerant of long periods of food deprivation and therefore susceptible to overwinter starvation mortality (Junk 1986).

The final objective of this study was to determine what type of size-selective mortality, if any, exists in the yellow perch population from Saginaw Bay. Evidence of size-selective mortality can often help distinguish natural mortality from fishing mortality. Fishing pressure can select against the largest fish from a given year-class causing positive size-selectivity . Natural mortality due to starvation or parasitism will often be greater in smaller individuals of a year-class

(Ricker 1969). This is known as negative size-selective mortality. Positive size-selective mortality would indicate that fishing pressure had a major effect on the total mortality of the population. If, however, only the largest fish from a cohort survived to age five or six (ie. negative size-selective mortality) it would support the idea that energy limitations are responsible for high mortality past age four. Large, fast growing individuals should have more surplus body energy than slow growers and , therefore, may be less prone to starvation or energy depletion mortality. Size-selective mortality can be identified using back-calculated lengths from scales. Back-calculated lengths also give yearly growth increments which may indicate a shift in growth rate due to maturation or diet switching.

The goal of this study was to test the hypothesis that energy limitations directly affect the growth, condition and survival of yellow perch in Saginaw Bay. The main objectives are summarized as follows :

1. To describe seasonal and age-related trends in surplus body energy, condition and parasite incidence of yellow perch from Saginaw Bay ;

2. To investigate differences in surplus body energy of male and female yellow perch from Saginaw Bay as evidence for differential mortality between sexes ;

3. To compare surplus body energy and parasite incidence of yellow perch among several locations in Saginaw Bay ;

4. To determine if mortality of yellow perch in Saginaw Bay is size-selective and, if so, what mechanism is responsible.

For this analysis comparisons were made both between groups of fish within a population (e.g. males versus females, mature versus immature) and across several perch populations from the literature. Much of the previous work on perch has been with the European species *Perca fluviatilis*. Yellow perch (*P. flavescens*) and European perch (*P. fluviatilis*) exhibit a high degree of biological and behavioral similarity (Thorpe 1977a), and are therefore directly comparable.

METHODS

Description of Site

Saginaw Bay is a shallow inlet of Lake Huron occupying a total area of 2,960 km^2 (Figure 1). The bay is divided into inner and outer bays based on geographical, physical, and biological distinctions. A line connecting Sand Pt. to Pt. Lookout (Figure 1) separates the shallow, nutrient enriched inner bay from the deeper, stratified outer bay. The inner bay has a mean depth of 15 feet and a maximum depth of 46 feet. It is greatly enriched with industrial, domestic, and agricultural inputs coming primarily from its main tributary, the Saginaw River. The inner bay experiences a relatively quick flushing rate (186 days) and frequent mixing of the water by the wind keeps oxygen levels sufficiently high for aquatic life. Conditions in the inner bay favor high productivity. This area has historically supported large biomasses of fish.

The outer bay has a mean depth of 48 feet, a maximum depth of 133 feet, and contains more than twice the volume of the inner bay (Beeton et al. 1967). Outer bay shorelands are, in general, less marshy than the inner bay. Extensive year-round mixing with Lake Huron proper keeps water quality high. Contaminant studies have shown that concentrations of
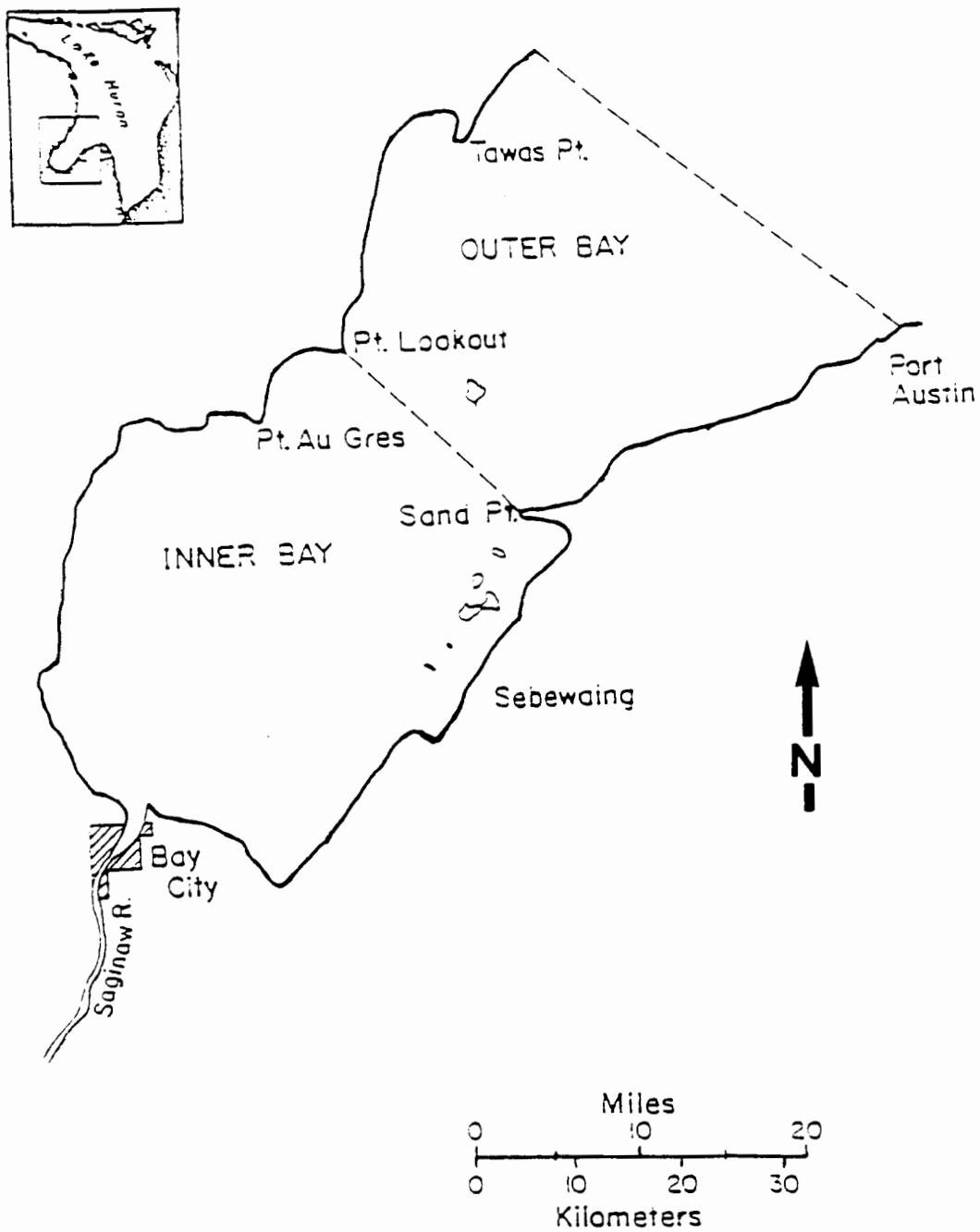
Figure 1.   The Saginaw Bay region of Lake Huron, Michigan.

polychlorinated biphenyls (PCBs) in yellow perch tend to decrease from inner to outer bay (Dolan et al. 1986). The outer bay stratifies during the summer months.

All perch analyzed for growth and energy content were collected from the inner bay, except for the back-calculation analysis which included fish from the outer bay (Tawas and Port Austin, Figure 1). Within the inner bay there exists a high degree of heterogeneity among sites. Differences between inner bay localities involve not only depth but also water quality, bottom types and other physical and chemical factors. Comparisons of inner bay sites were made between the index stations: North Island, Wildfowl Bay, Blackhole, and Au Gres (Figure 2). Wildfowl Bay is a very shallow, productive sub-bay which provides ideal nursery grounds for many fish species. North Island, located just west of Wildfowl Bay, is slightly deeper and less protected than the sub-bay itself. The Blackhole, is considerably deeper than either Wildfowl Bay or North Island and produces a highly organic sediment which supports an abundance of benthic invertebrates. Of the four index stations, Blackhole is the closest to the mouth of the Saginaw River. The Au Gres station is located near the outer bay and has a mean depth close to 30 feet. This station should more closely resemble the less polluted, well mixed outer bay.
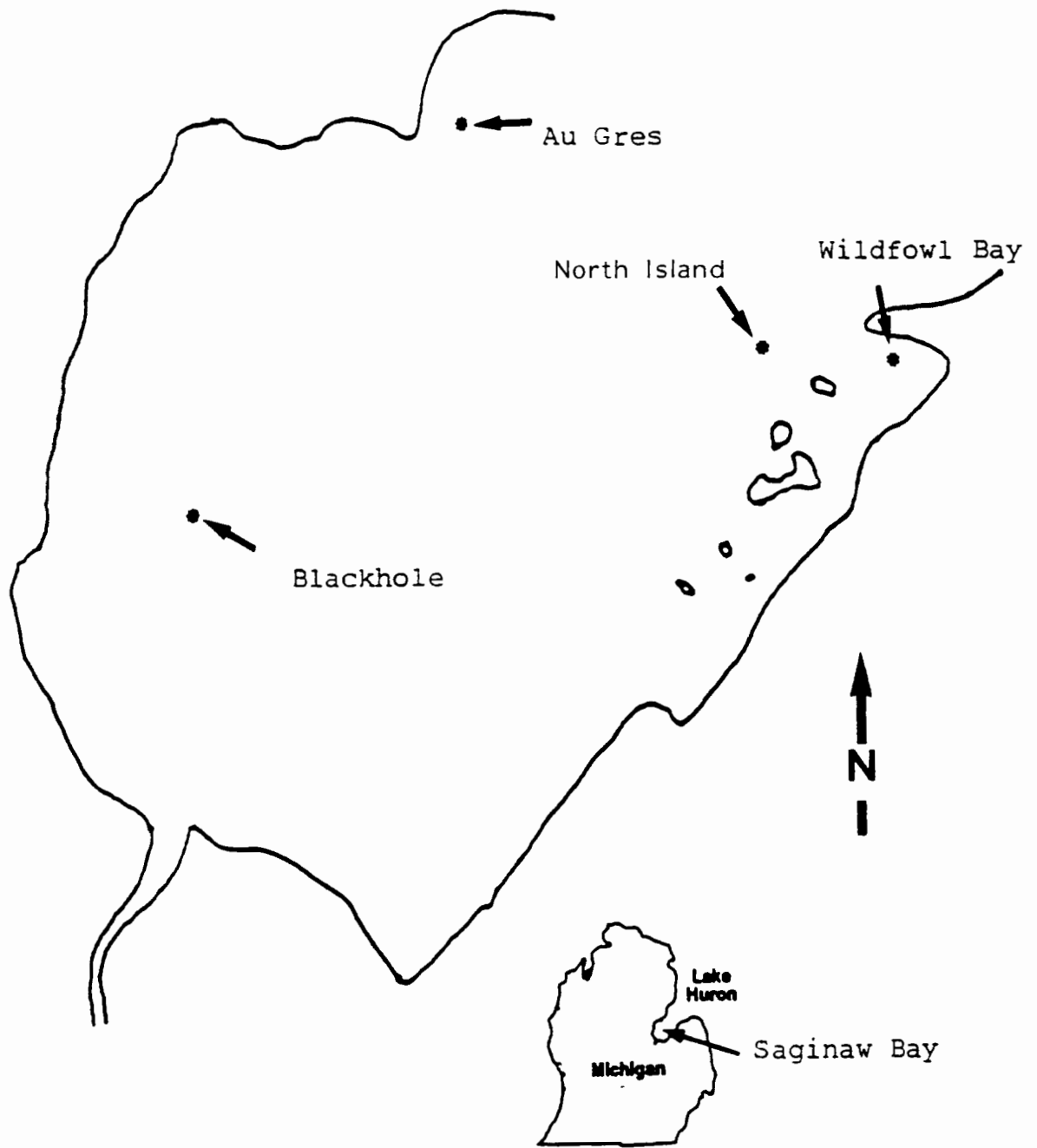
Figure 2.   Inner Saginaw Bay with index stations used for
yellow perch collections.

Eshenroder (1977) summarizes the physical and chemical data for Saginaw Bay, while Khallaf (1982) and Keller et al. (1987) provide more detailed descriptions of the study area.

Field Methods

Field collections were made from Michigan Department of Natural Resources research vessel CHANNEL CAT. The survey was conducted during the field season May through October in 1986 and 1987. Individual monthly cruises lasted between 8 to 10 days and were generally held around the middle of each month when weather permitted. Yellow perch were sampled at various locations throughout inner Saginaw Bay, Lake Huron (Figure 2). North Island, Wildfowl Bay, Blackhole, and Au Gres were chosen as fixed index stations and collections from these sites accounted for over 90% of the 11,563 perch used in this study. Collections were made between 6 AM and 6 PM at the index stations, while diel (24- hour) sampling was also conducted in Wildfowl Bay and North Island. A 9.75 meter otter-board bottom trawl was the predominant gear used to collect perch. Trawls were towed for ten minutes at an average speed of two knots. A smaller proportion of the perch analyzed were caught using floating and sinking experimental gillnets with mesh sizes ranging from 1.9 to 10.2 cm stretch. Gillnets were set for six hours. In general, gillnetting was far less effective at

collecting perch samples than trawling. A subsample of 62 perch (52 adults, 10 yearling) from each trawl or gillnet was frozen in liquid nitrogen for further processing and measurement in the lab. Adults were subsampled randomly but some selection was made to include a wide range of sizes.

Laboratory Methods

Frozen yellow perch were partially thawed in the lab. Total length (mm) and wet weight (to 0.01g) were recorded. Fish were cut open from anus to gills, sexed, and checked for redworm (Eustrongylides tubifex) infestation (i.e. presence or absence). Visceral wet weight including gonads but minus stomach was recorded (to 0.01g). Somatic wet weight (whole fish minus viscera) was also recorded. Scale samples from each fish were taken below the lateral line and posterior to the tip of the pelvic fin. Both the viscera and body were refrozen in separate plastic bags with individual sample codes for each fish.

At a later date viscera and body were again thawed, removed from the bags and placed inside aluminum containers. Visceral and somatic wet weights recorded after the second thaw were considerably smaller than those taken after the first thaw. Fish had lost water weight as a result of dessication in the freezer. In general, smaller perch lost a greater proportion

of their wet weight when frozen than large perch as a result of their greater relative surface area. For this analysis, percent water content was calculated using the initial wet weights taken after the first thaw. The aluminum weigh boats were placed in a drying oven for 72 hours at 74 C (166 F). Samples were then removed and dry weights were recorded (to 0.0001g). Percent water was calculated for the viscera and body separately by :

% Water=((wet weight - dry weight)/wet weight) X 100

Yellow perch from the 1986 survey were aged from scales. Scale impressions of four to eight scales were made on accetate for each fish. Annuli were identified by crowding, crossing over, or discontinuity of circuli (Ricker 1971). Ages were not available for fish collected in 1987 and therefore analysis of these fish utilized length groups only rather than age-groups.

Back-calculation Methods

Scales were taken from yellow perch collected by the University of Michigan between April and August, 1983-84 (see Diana and Salz 1990 for details). Fish were caught with experimental gillnets in three localities of Saginaw Bay; Port Austin (June 1983), Tawas Pt. (July-August 1983), and Sebewaing (April 1984) (Figure 1). In all, 195 yellow perch

between ages 1 and 6 were used for the back-calculation analysis. This represents a subsample of the total number of perch available from the 1983-84 sampling. Sample sizes for individual age-classes were determined based on time considerations and availability. Certain age-classes (ages 1, 5 and 6) were poorly represented in gillnets and smaller sample sizes had to be used.

The Whitney and Carlander (1956) back-calculation technique was used to calculate individual fish lengths at each successive annulus. The first step was to compute a simple linear regression of fish length versus scale diameter for all fish from a given location. The equation is as follows:

$$Length= a + slope(scale\ diameter)$$

The intercept, a, represents the length of the fish when the scale was first formed (diameter=0). This value was used in the following formula:

$$L_i = a + (L_c-a)S_i/S_c$$

where L_i is the length of fish at age i, S_i is the scale diameter at age i, L_c is the length of fish at capture, and S_c is the scale diameter at capture. When using the Whitney and Carlander (1956) equation for back-calculated length at age, it is important to determine a valid intercept from the body-scale regression. The choice of intercept used can greatly affect

growth estimates. Furthermore, the intercept can vary significantly depending on the age structure chosen for the body-scale regression. Intercepts from several body-scale regressions were compared for differences between sites, within sites and with other perch populations. Carlander (1982) suggests 30.0mm as a standard intercept for the body-scale regression of yellow perch. This standard value is simply the average intercept taken from the literature of other perch back-calculation studies. While Carlander emphasizes good representation of the younger age groups for an accurate intercept, he does not specify what proportion of each age-class should be used. Previous study has shown that the location where the scales are removed from and what age fish are used have a greater effect on the body-scale regression than do location or month of sampling (Carlander 1982).

As indicated earlier, the criteria used to identify annuli were crossing over, discontinuity of circuli and crowding of circuli (Ricker 1971). A subsample of the scales were read by several persons for verification and the results were similar to my own. Scales were read using a Realist micrographic viewer and measurements were taken directly off the screen to the nearest millimeter. Brief inspection of a few slides indicated that scale diameter varied greatly between scales taken from the same fish. While it is a reasonable assumption that the ratio of the distance to each annulus and the scale diameter

should be the same for each scale from the same fish, exceptions may occur (Whitney 1956). To check for scale variability, the ratios of S1/Sc and S2/Sc were compared for several scales from each of five 2-yr-old perch.

Statistical Methods

Differences between male and female lengths and weights were tested using one-way analysis of variance (ANOVA) for individual ages and months. An analysis of covariance (ANCOVA) was used to test differences in size at age between sites. The regression of length on julian date was computed for each site and the slopes and adjusted means were compared between sites. Log transformations of weight and length were done to linearize the weight-length relationship. ANCOVA's were also used to compare the regression equations of log (weight) on log (length) for different sexes, sites and year-classes. To compare the relative condition of groups of fish the slopes and intercepts of the log transformed data must first be examined. Only if the slopes are statistically not different can the relative condition factor, K, be compared (Le Cren 1951). Condition was determined by:

$$K = W/\hat{W}$$

where W is the weight of fish and $\hat{W}$ is the expected weight based on the derived relationship $W=aL^b$. Seasonal changes in K were tested by ANOVA.

ANOVA was also used to test seasonal, sex, site and size differences in visceral and somatic percent water.

Chi-square tests were performed to look at differences in redworm occurrence across sites, sexes, ages and years. ANOVA's were used to test differences in percent water between perch with redworm infestation and those without the parasite.

For the back-calculation analysis, several ANCOVA's were computed to validate the body-scale regression equation used in determining the intercept, a. Back-calculated first year growth was correlated with age at capture using regression and an ANCOVA was done to test this relationship among the three sites. Differences in back-calculated lengths between cohorts were tested by ANOVA.

All statistics were done using MIDAS (Fox and Guire 1976), with alpha set at 0.05. When ANOVA's involved comparison of more than two strata, Scheffe's (1964) pairwise tests were run for direct comparisons of two strata means at a time. Ninety-five percent confidence intervals were calculated by MIDAS.

RESULTS

Percent Water

Both somatic and visceral percent water varied
significantly with sex, age, season, and sample location. Mature
female perch had higher somatic percent water than mature
males but no difference was found between sexes of immature
fish. For yellow perch between 125-175mm, females had a
significantly higher somatic percent water than males during
the individual months June through October (ANOVA); (Figure 3).
Female percent water was also greater than male percent water
in May but not statistically significant (ANOVA). There was no
difference in somatic percent water between males and females
in the size range 75-125mm for four out of six months. Females
did have greater somatic percent water than males in July and
October in this size range. There was no difference in somatic
percent water between age one males and age one females for
all six months examined. After maturation female yellow perch
appeared to be less fit than similar sized male yellow perch.
Groups of fish (e.g. males and females) were often compared by
length-groups rather than age-groups as shown in Figure 3.
Although several months are shown on the horizontal axis, these

Figure 3.   Mean somatic percent water (with 95% confidence

intervals) of 125-175 mm male and female yellow perch

collected May through October from Saginaw Bay.

graphs do not represent seasonal trends since individual fish may grow out of length-groups from May to October.

Visceral percent water differed between sexes and this relationship changed seasonally as a result of gonad development. Visceral percent water of males was greater than that of females in the months when mature gonads were present in the viscera. Mature male perch (125-175mm) had a greater visceral percent water than similar sized females in May, females had a greater percent water from June through August, and males were greater again in September and October (Figure 4). For immature (age one) yellow perch, there was no difference in visceral percent water between the sexes for months June through September. Age 1 males had a greater visceral percent water than females in October. For months when gonads were mature, differences in visceral percent water between sexes might be due to differences in gonadosomatic index, water content of testes versus ovaries, or age at maturation. Visceral percent water for these months may be less indicative of surplus body energy since a large proportion of the visceral fat is contained in the gonads. Visceral percent water was greater in females than in males for months without gonads (June-August), indicating less lipid reserves in females after spawning.

Percent water of yellow perch in Saginaw Bay was inversely related to size over the range 25-150mm. Somatic
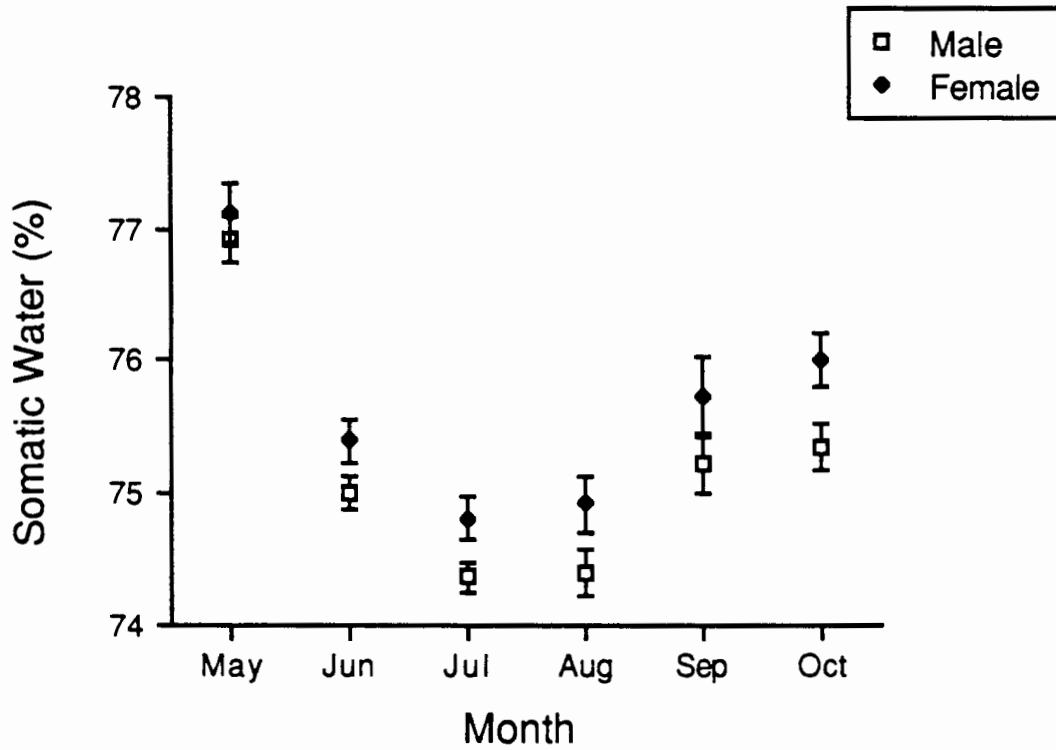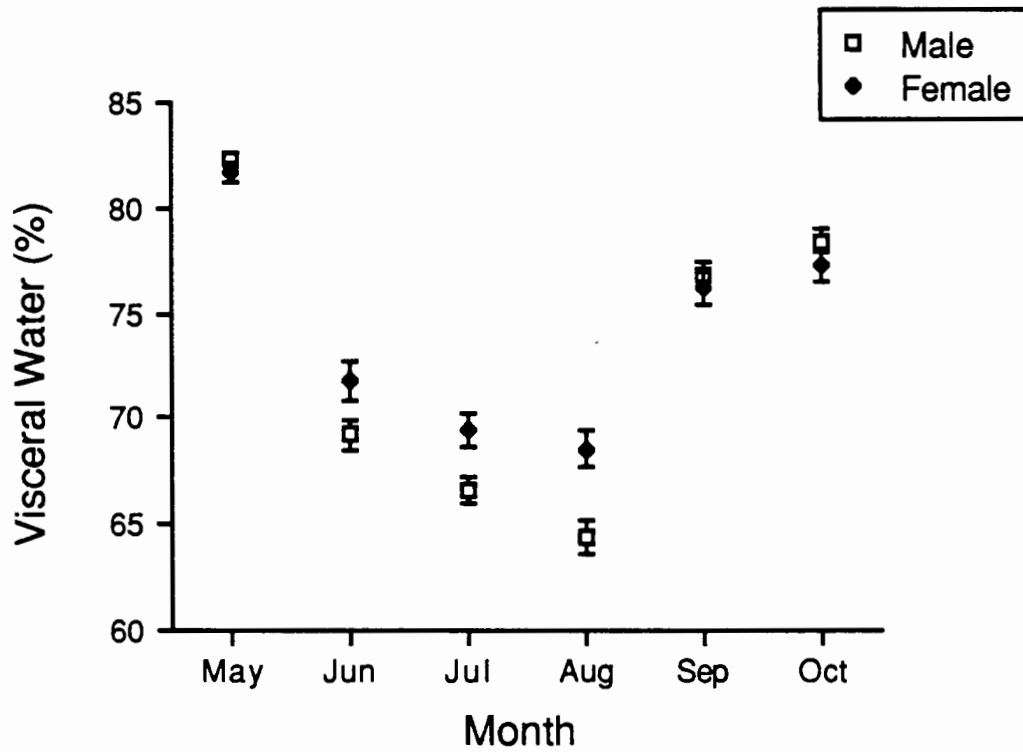
Figure 4.   Mean visceral percent water (with 95%

confidence intervals) of 125-175 mm male and female

yellow perch collected May through October from

Saginaw Bay. (Confidence intervals smaller than symbol

when not visible)

percent water declined with size until 150mm where it stabilized (Figure 5). This trend was found for all months and both sexes examined separately. Somatic percent water declined with age until age two (Figure 6). Visceral percent water also showed a downward trend (Figure 5) with size up to 150mm. After 150mm visceral percent water increased significantly until 200mm (ANOVA). This trend held for all months and sexes examined separately. Visceral percent water decreased from age 1 to 2 and then increased from age 2 to 5 (Figure 6). Increase in visceral percent water with age is likely related to the utilization of proportionally more visceral lipids to meet increasing reproductive costs.

Percent water was higher in late spring than early fall for both sexes and all ages analyzed . Somatic percent water declined significantly from June through August (Figure 7). Somatic percent water increased from August to September and then decreased to October, although this trend varied by age and sex (Figure 7). The overall change in somatic percent water from August-October was slight compared to the sharp decline from June-July. Yellow perch visceral percent water was high after spawning (June), dropped sharply until August and then increased significantly from August to October (Figure 8). The seasonal trend in visceral percent water represents storage of visceral fat in early summer followed by utilization of these lipids after August. Immature 1-yr-old females did not show a
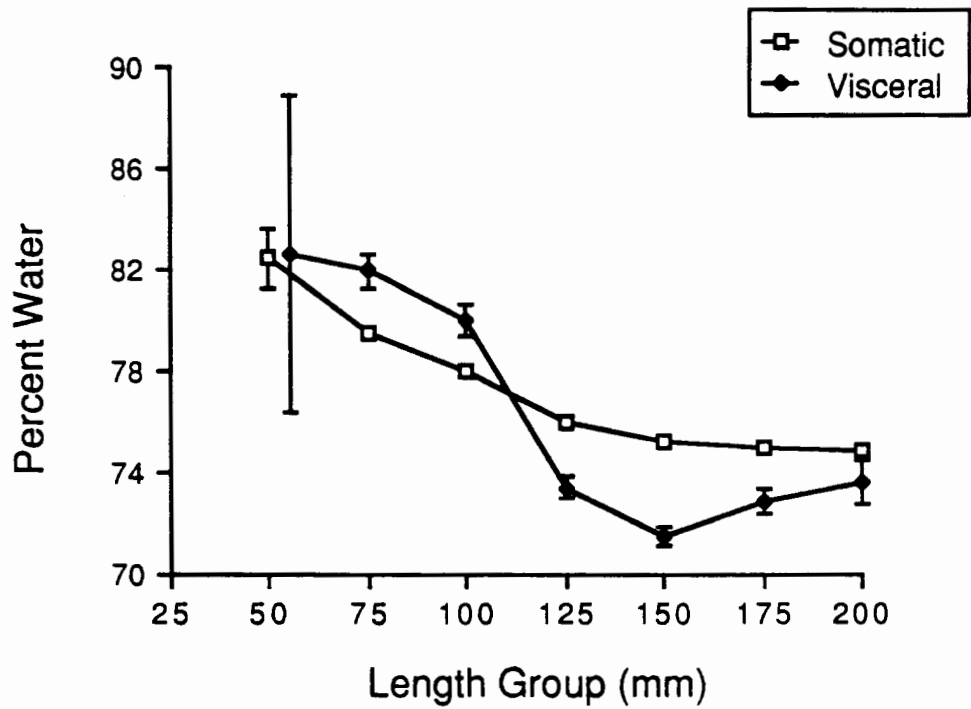
Figure 5.   Mean somatic and visceral percent water (with 95%

confidence intervals) of yellow perch by 25 mm length group

(eg. 50mm= 26-50mm) with sexes and months pooled.

(Confidence intervals smaller than symbol when not visible)
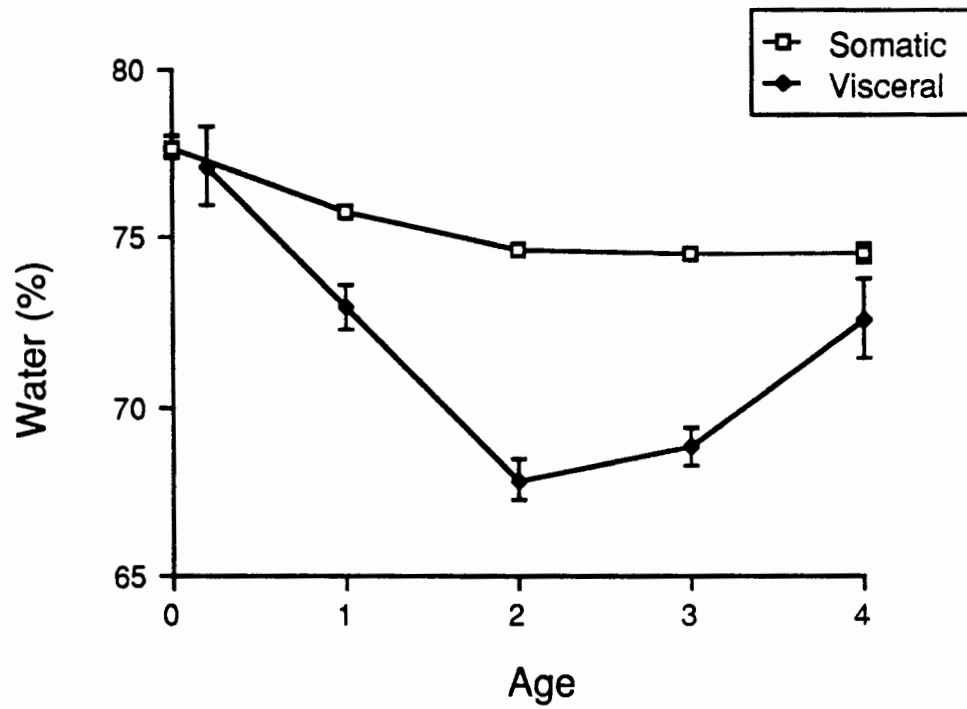
Figure 6.   Mean somatic and visceral percent water (with 95%

confidence intervals) of yellow perch by age group with

sexes and months pooled. (Confidence intervals smaller

than symbol when not visible)
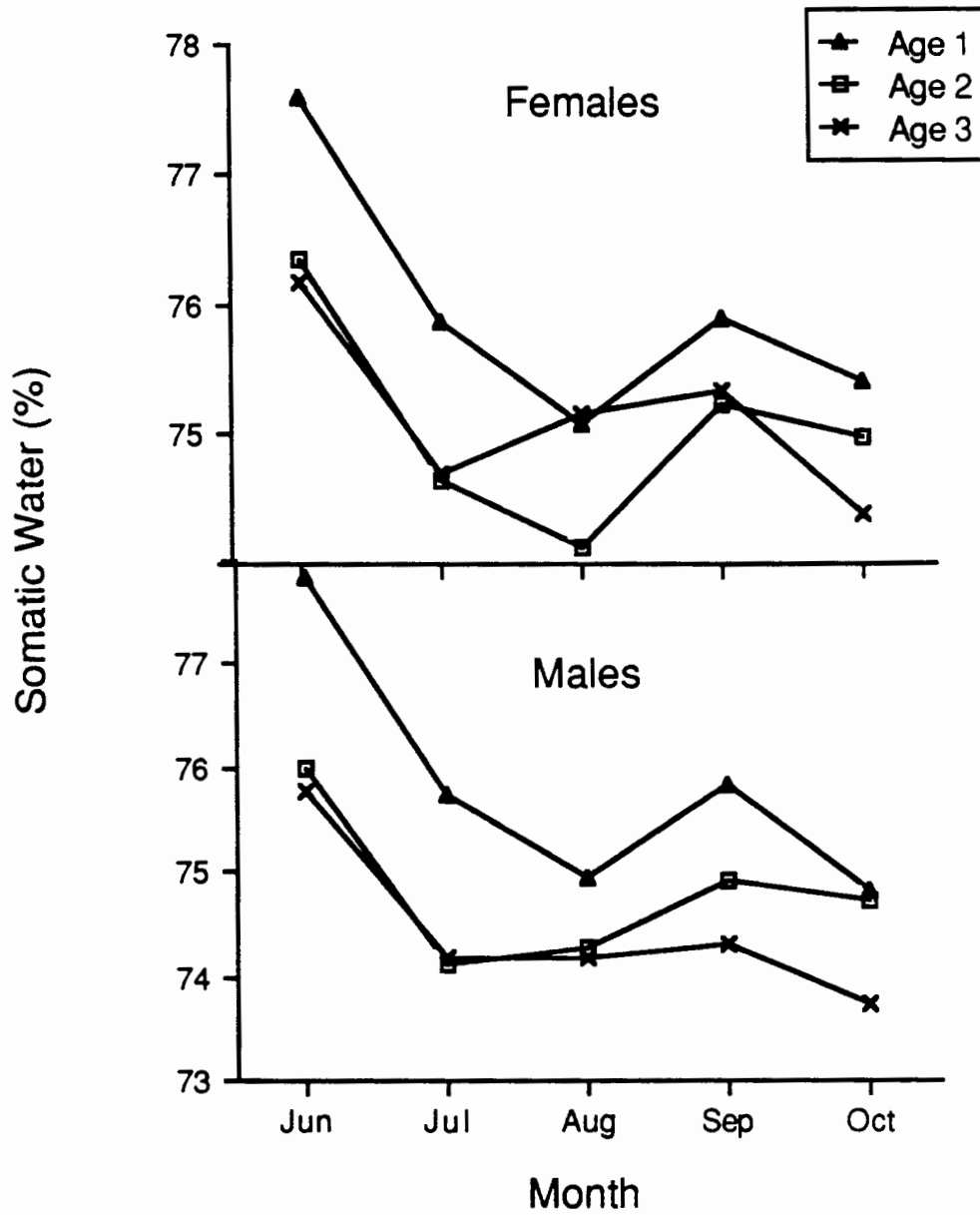
Figure 7.   Seasonal trend (June through October) in mean somatic

percent water of female and male yellow perch
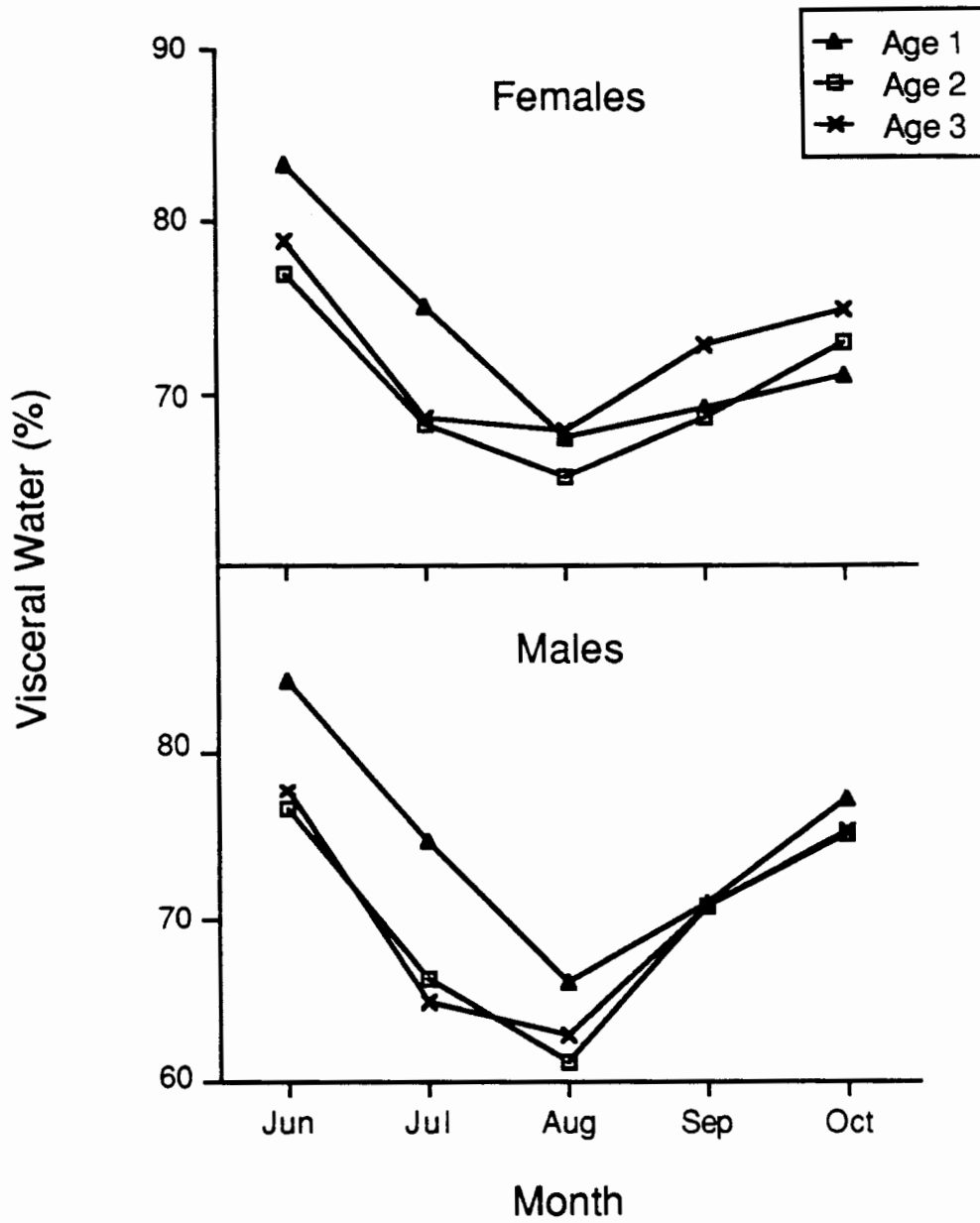
ages 1-3.

Figure 8.   Seasonal trend (June through October) in mean visceral

percent water of female and male yellow perch

ages 1-3.

significant increase in visceral percent water from August to October but 1-yr-old males did.

The previous analyses indicated that percent water in yellow perch was highly variable between sexes, months, and size/age groups. Among sites, perch from Wildfowl Bay had significantly higher somatic percent water than perch from Blackhole or Au Gres (Figure 9) . This trend held for perch greater than 125mm but was not found in immature perch (75-125mm). There was no difference in somatic percent water between perch from Blackhole and perch from Au Gres. Visceral percent water was also consistently greater in perch from Wildfowl Bay than from the other locations. Visceral percent water was significantly greater in perch from Wildfowl Bay than Blackhole for 17 out of the 18 (6 months x 3 sites) ANOVA's tested (Figure 10). Likewise, visceral percent water was greater in perch from Wildfowl Bay than from Au Gres for 16 out of the 18 comparisons of means. Visceral percent water in perch from Au Gres was significantly greater than perch from Blackhole for 5 out of the 18 tests but for the other 13 ANOVA's no difference was found. With all sizes pooled, visceral percent water was significantly greater in perch from Wildfowl Bay than the other two sites for each month examined (Figure 11). Differences in percent water among sample locations suggest differential energy storage and utilization due to environmental heterogeneity or different population structures.
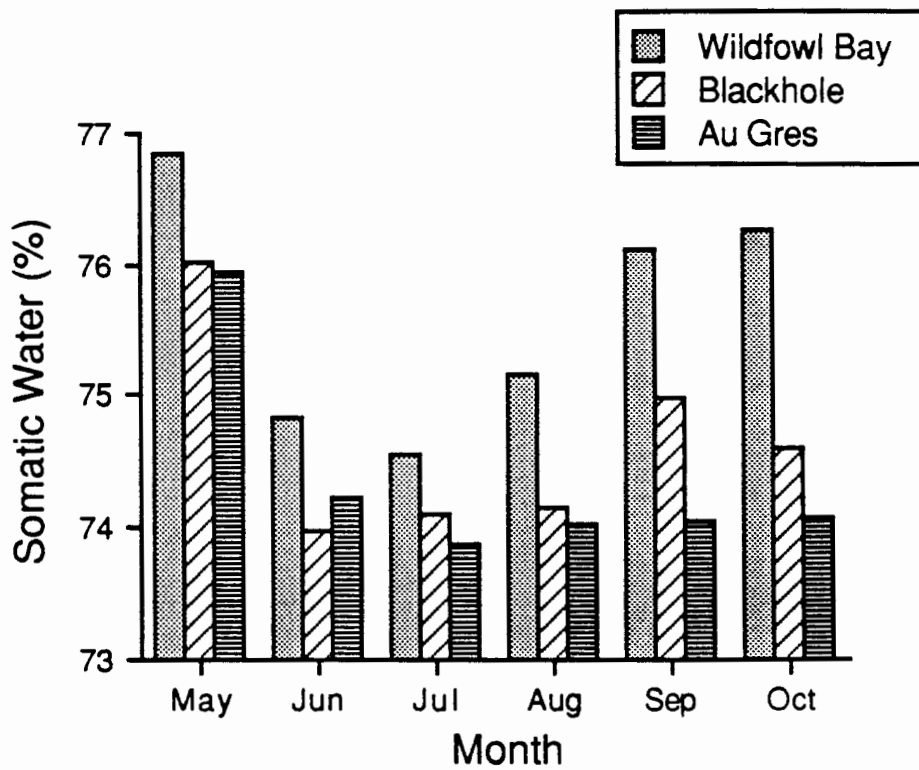
Figure 9.   Mean somatic percent water of 150-175 mm yellow perch

from three sample locations in inner Saginaw Bay,

(Wildfowl Bay, Blackhole, and Au Gres), for months May

through October.
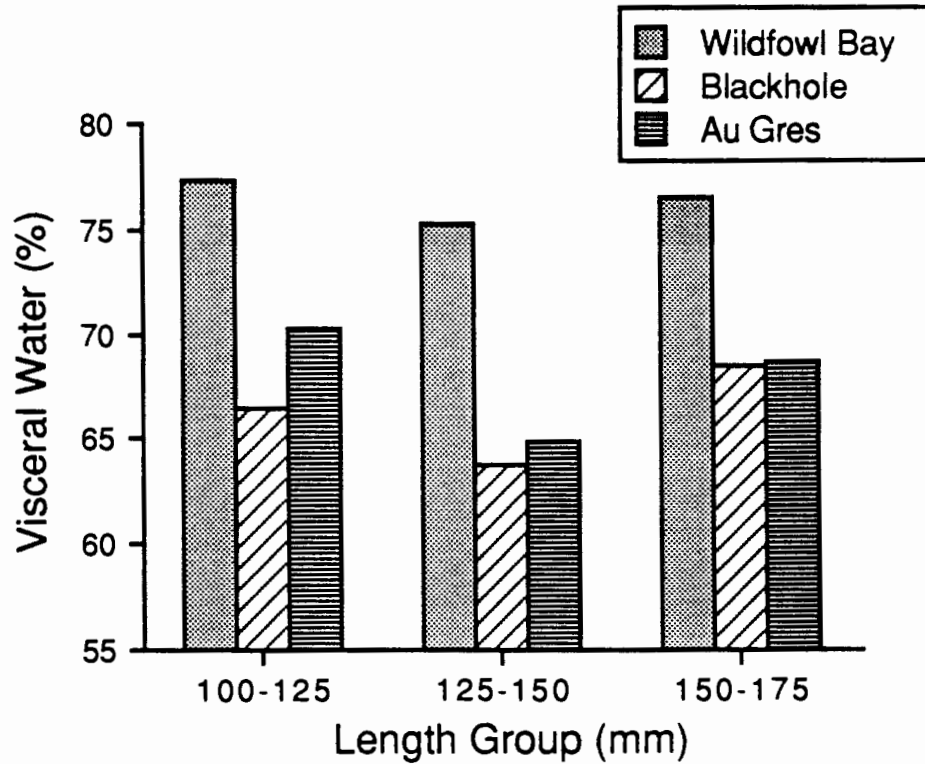
Figure 10.   Mean visceral percent water of yellow perch

from three sample locations in inner Saginaw Bay,

(Wildfowl Bay, Blackhole, and Au Gres), by 25 mm length

group with all months pooled.
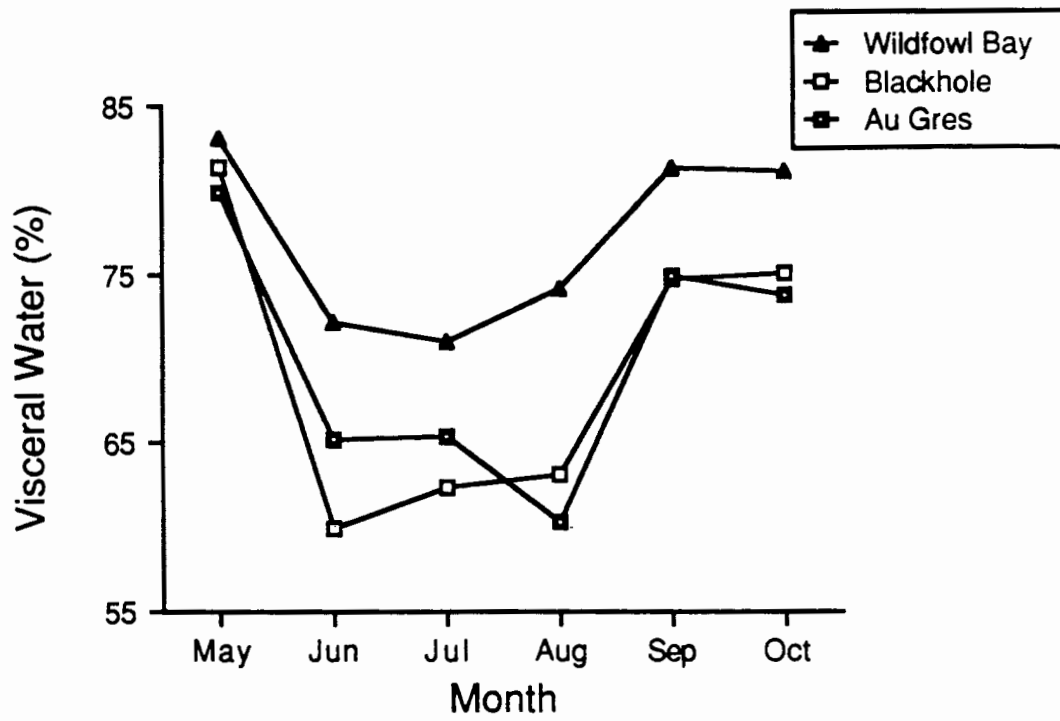
Figure 11.   Seasonal trend (May through October) in mean visceral

percent water of yellow perch from 3 sample sites,

(Wildfowl Bay, Blackhole, and Au Gres),with all sizes pooled

Growth in Length and Weight

Length at age was similar for immature males and females, but after age 1 females were consistently longer (ANOVA) (Figure 12). Growth in length for both sexes was added predominantly between June and August (Figure 13).

Ages of yellow perch from Wildfowl Bay were not available for the analyses of length at age and condition (next section). Site comparisons were made using the North Island station in place of Wildfowl Bay. These two subpopulations should exhibit similar growth due to geographic proximity (Figure 2). Length at age was greater in perch sampled from Blackhole than from North Island or Au Gres. Growth was compared for these three sites using ANCOVA with length the dependent variable and julian date the independent variable. No differences in either regression slopes or adjusted means were found between North Island and Au Gres for ages 2-4. Blackhole and North Island had equal slopes but Blackhole showed significantly larger adjusted mean lengths for each age group. Blackhole also had larger adjusted mean lengths than Au Gres for yellow perch ages 2 and 3.

Visceral dry weight (including gonads) was not significantly different between sexes for the months June-October. For 18 of the 20 comparisons (4 ages-groups x 5
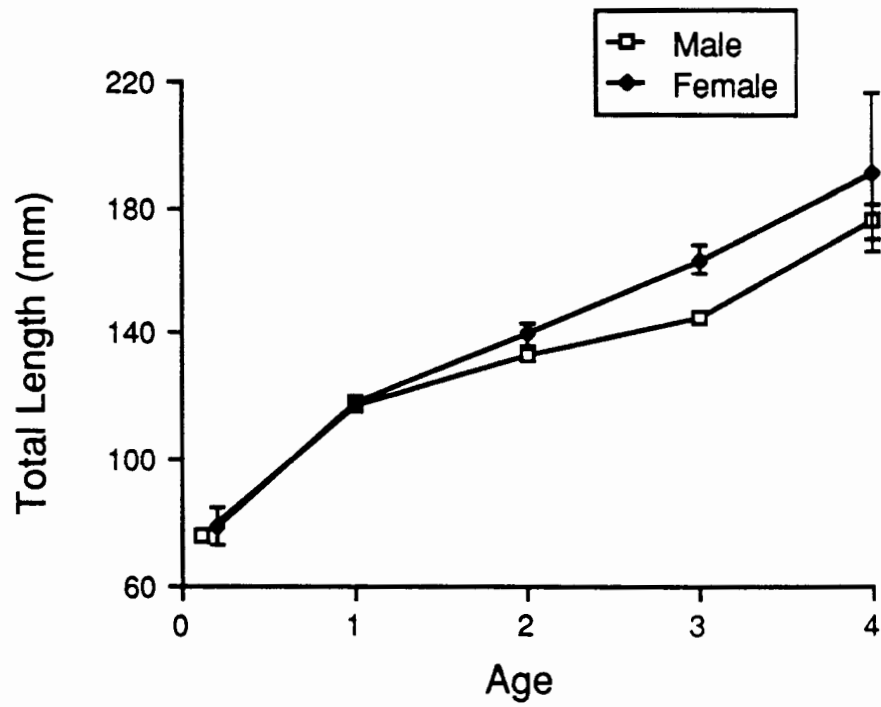
Figure 12. Mean length (with 95% confidence intervals) at age of
male and female yellow perch collected in October
1986-87 from inner Saginaw Bay, Lake Huron.
(Confidence intervals smaller than symbol when not visible)
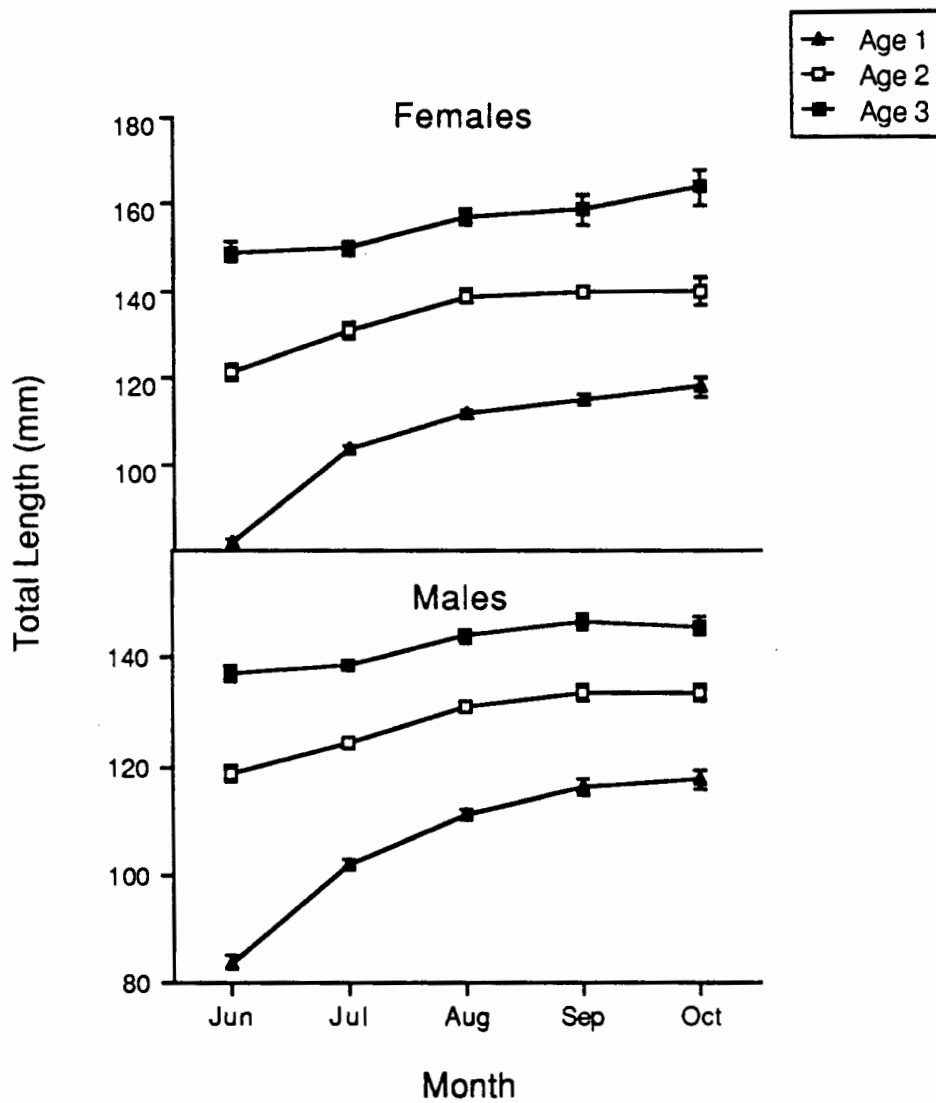
Figure 13.   Seasonal trend (June through October) in mean length
(with 95% confidence intervals) of female and male
yellow perch ages 1-3 from Saginaw Bay. (Confidence
intervals smaller than symbol when not visible)

months ; ANOVA) there was no difference in visceral dry weight between males and females. Mean dried viscera of age one males was heavier than age one females in September and October. This difference was probably due to gonad weight since males mature earlier than females. Sexes were pooled to examine seasonal trends in visceral dry weight. The greatest proportion of visceral dry weight was added between June and July for age 1, 2 and 3 perch (Figure 14).

Somatic dry weight was greater in females than in males past age one (Figure 15). The seasonal trend in somatic dry weight was similar to that for length with most growth occurring between June and August (Figure 16). Yellow perch from Saginaw Bay appear to have a very short growing season. Little or no somatic tissue is added from the onset of gonad production in late August until spawning in May.

Condition Factor

The slopes of the log wet weight (gm) versus log length (mm) regressions varied among age groups and therefore all fish could not be pooled into one length-weight relationship. Three year-old perch were selected to examine seasonal change in condition associated with gonad production. All male and most female perch (72%) reach maturation by age three in Saginaw Bay (Diana and Salz 1990). Females had a significantly different
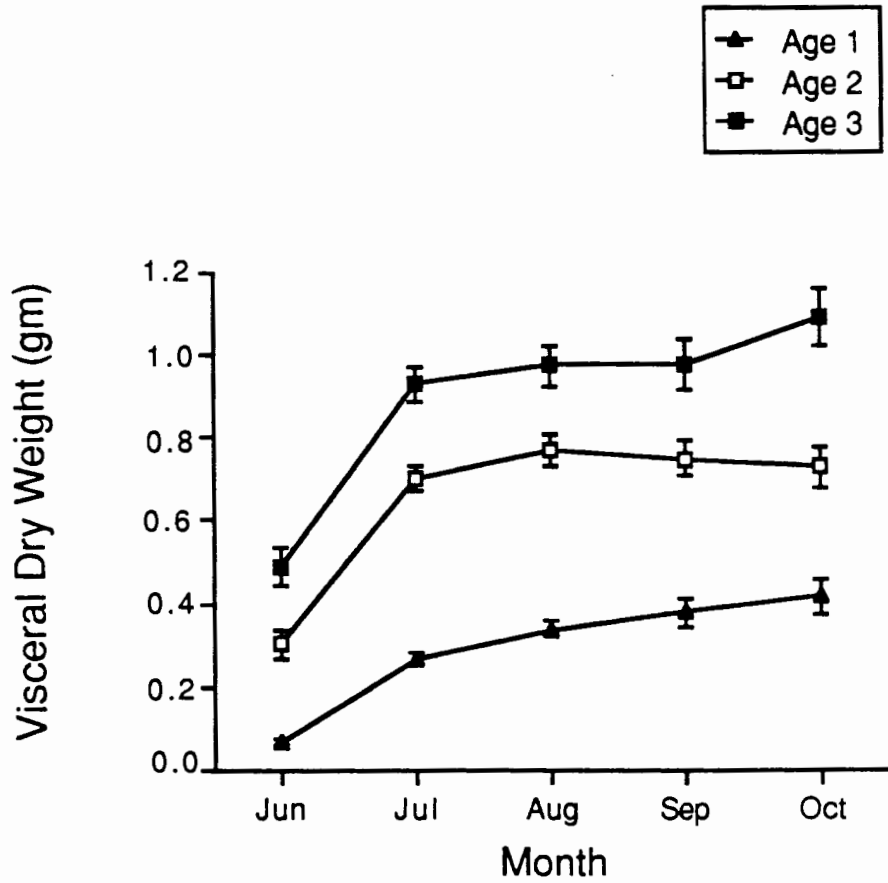
Figure 14.   Seasonal trend (June through October) in mean visceral dry

weight (with 95% confidence intervals) of yellow perch

ages 1-3 with sexes pooled.
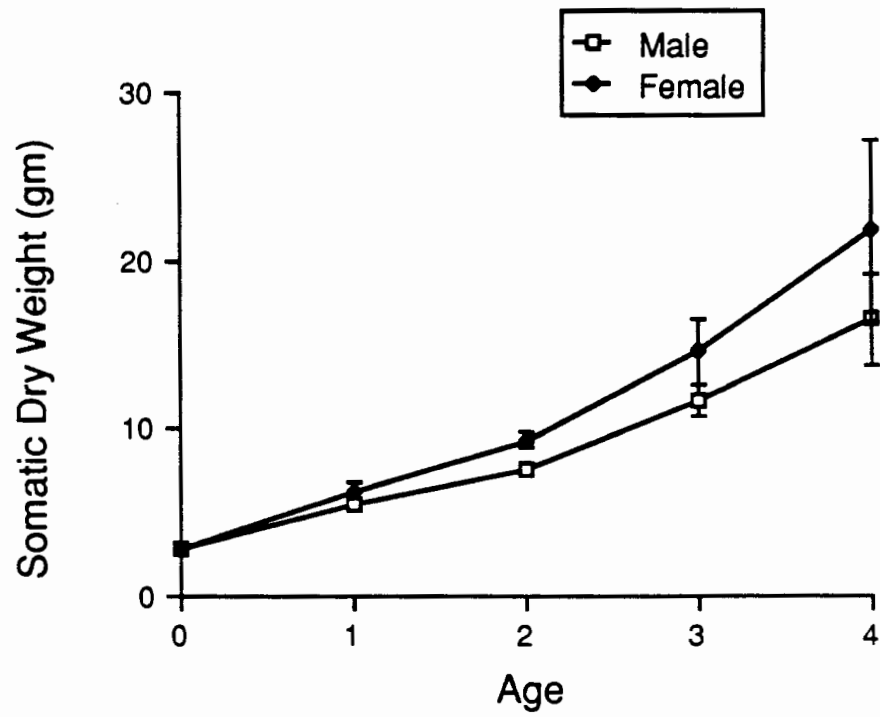
Figure 15.   Mean somatic dry weight (with 95% confidence intervals) by

age of male and female yellow perch collected in July.

(Confidence intervals smaller than symbol when not visible)
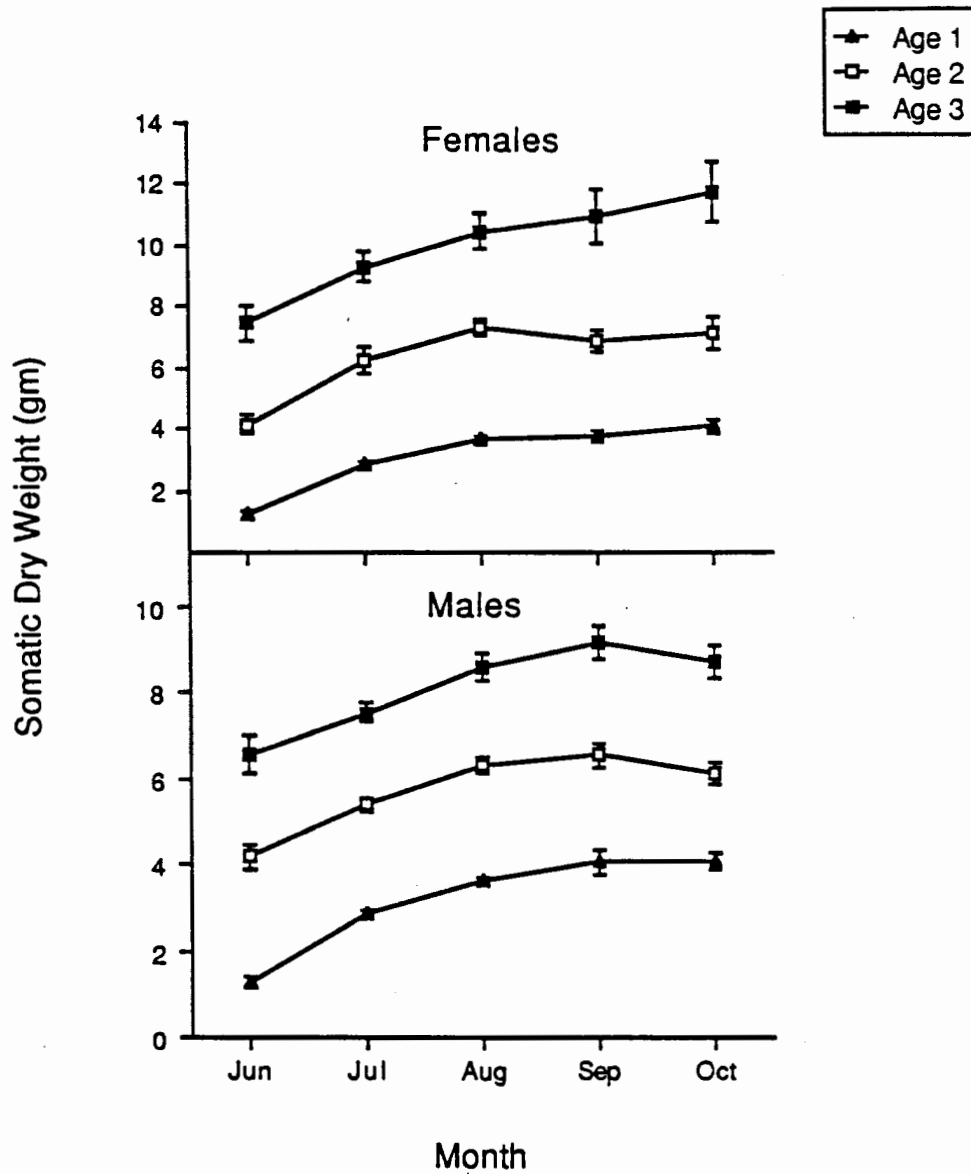
Figure 16.   Seasonal trend (June through October) in mean somatic
              dry weight (with 95% confidence intervals) of female
              and male yellow perch ages 1-3. (Confidence intervals
              smaller than symbol when not visible)

length-weight relationship than males (ANCOVA), and sexes were treated separately. The equations used to predict weight were:

$$\hat{W} = 1.82 \times 10^{-5} (Length)^{2.9156}$$

and

$$\hat{W} = 9.6 \times 10^{-6} (Length)^{3.0394}$$

for 3-yr-old male and female yellow perch, respectively.

Condition increased significantly from June through August for both male and female yellow perch (ANOVA; Figure 17). Female condition declined significantly from August through October whereas male condition did not change during the same period. The drop in female condition coincided with gonad production. Female condition factor, K, decreased sharply despite the added weight of the ovaries in the calculation of $W/\hat{W}$.

The slopes of the regression equations (log weight on log length) for North Island and Blackhole were statistically equivalent for both sexes (age 3) ; (ANOVA). This allowed direct comparison of the two sites for K. Mean condition factor was consistently higher in perch from Blackhole than perch from North Island (Figure 18). Perch from Au Gres showed a significantly different log-log regression than from the other sites and therefore could not be used in comparisons of condition.
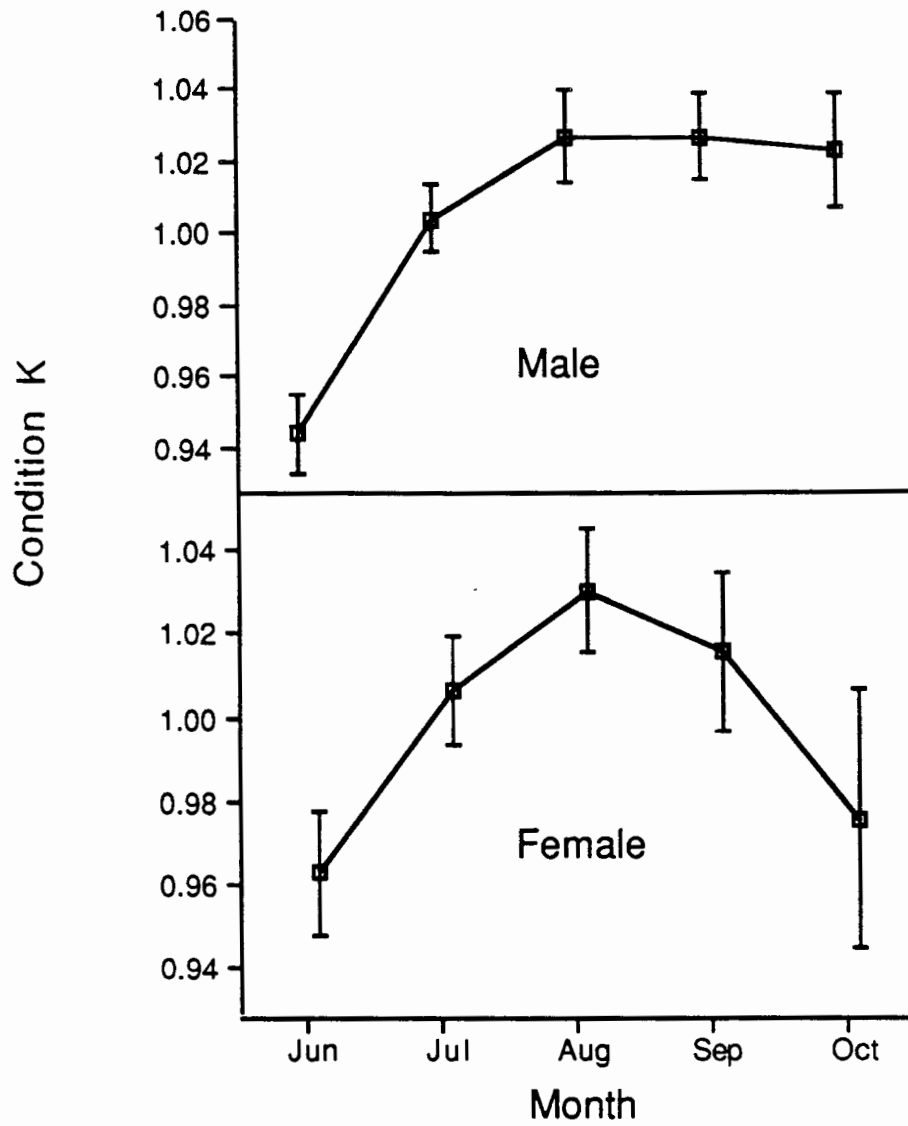
Figure 17.   Seasonal trend (June-October) in mean condition factor,

K, (with 95% confidence intervals) of 3-yr-old male

and female yellow perch.
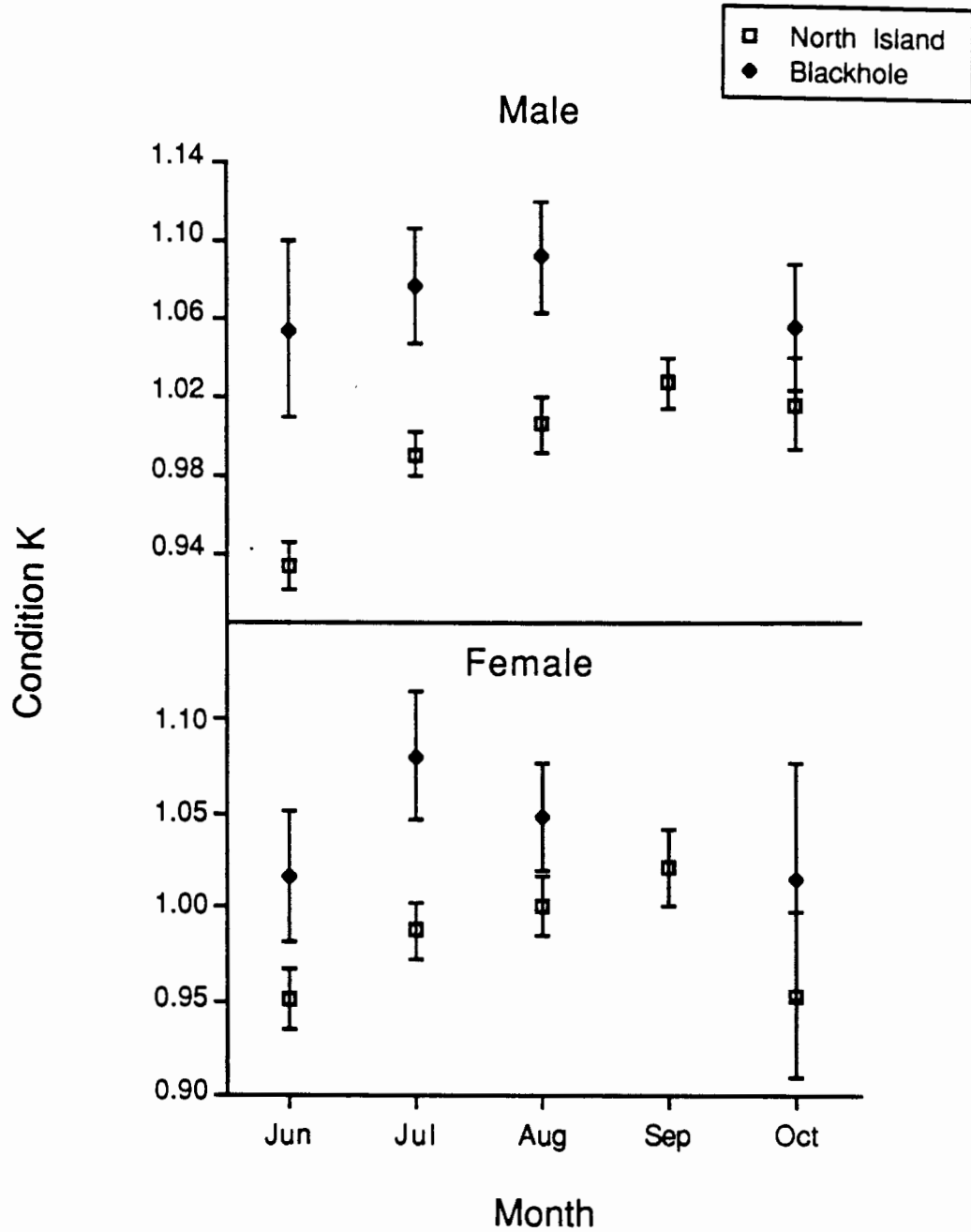
Figure 18.   Mean condition factor, K, (with 95% confidence intervals)
of 3-yr-old male and female yellow perch collected from
North Island and Blackhole.

Redworm Infestation

A large proportion of the yellow perch from Saginaw Bay were infected with the parasitic redworm (Eustrongylides tubifex). Redworm incidence was rare in young-of-year perch and increased with age up to age three (Table 1). No difference in the percent infected with redworm was found between 3, 4 and 5-yr-old perch (Chi-square). Incidence increased with size until 125mm after which it stabilized. Redworm incidence was greater in 1987 than 1986 at North Island (Chi-square, four out of five months) (Figure 19). This difference was most noticeable in June and July. No difference in redworm incidence was detected between males and females.

Redworm incidence was at a minimum in early summer and greatest in October (Table 1). Differences in redworm occurence between locations were also found (Figure 20). A smaller percentage of perch collected from the Au Gres station had redworm than from Wildfowl Bay (Chi-square, 5 out of 6 months significant) or Blackhole (Chi-square, 4 out of 6 months). Comparing Wildfowl Bay with Balckhole there was no statistical difference in redworm percentage for 5 out of 6 months.

Percent water was analyzed to measure the effect redworm had on the energy reserves of its host. Visceral percent water was significantly greater in perch (125-200mm)

Table 1. Percent of yellow perch from Saginaw Bay with redworm by age and month.

Month

Age	June	July	Aug	Sep	Oct	Total
0	----	----	0.0	1.0	0.0	0.5
1	10.0	6.9	24.3	23.5	40.0	16.7
2	13.3	31.7	57.9	59.4	65.2	47.1
3	28.0	48.4	65.2	64.0	71.3	55.8
4	31.0	48.1	65.7	73.3	52.0	52.0
5	20.0	39.6	66.7	75.0	----	45.7
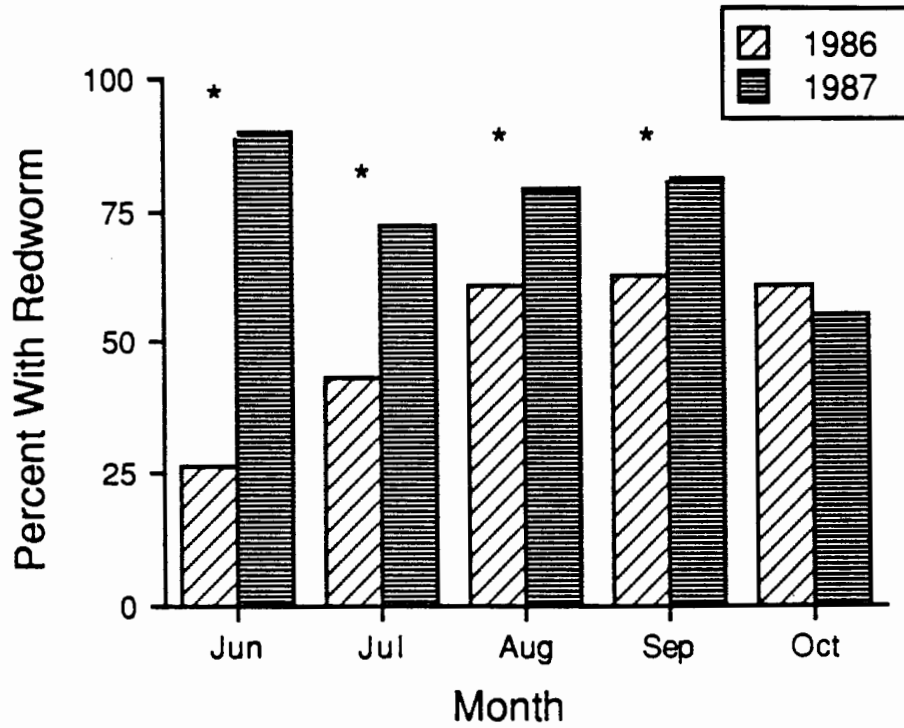
Figure 19. Percent of 125-200 mm yellow perch from North Island

infected with redworm by sample year (1986-87) for the

months June-October. (* indicates significant difference

between years; Chi-square, p < 0.05)
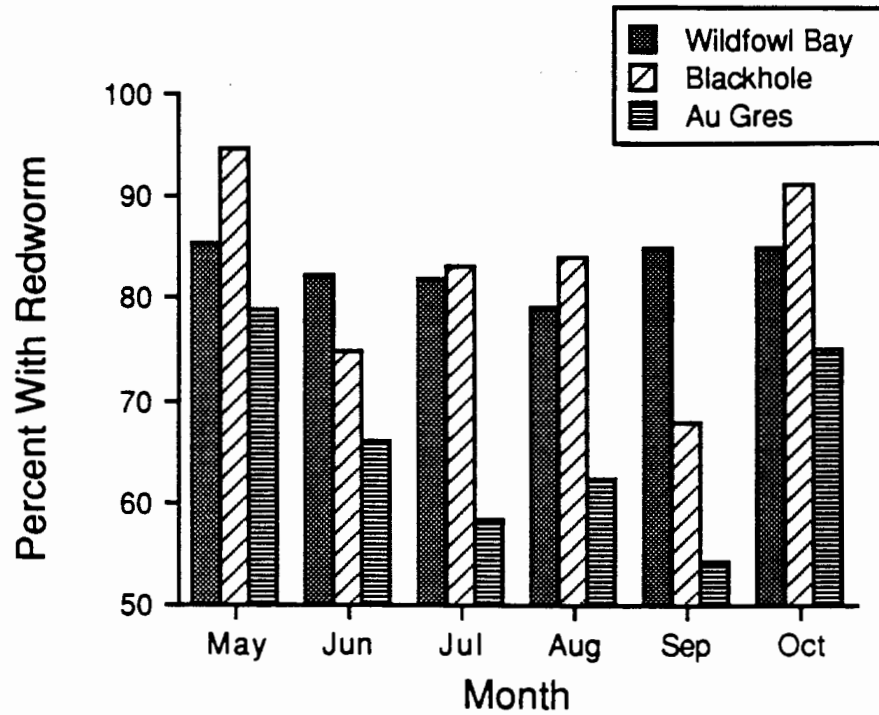
Figure 20.   Percent redworm incidence in 125-200 mm yellow perch

from three sample locations within inner Saginaw Bay,

(Wildfowl Bay, Blackhole, and Au Gres) for the months

May-October.

with redworm than those without redworm for all months examined except May (all sites pooled) ; (Figure 21). This trend held for perch from Wildfowl Bay examined separately (4 out of 6 months significant) and, therefore, was not simply a function of site differences. Since perch from Wildfowl Bay and Blackhole showed no difference in redworm incidence (Chi-square) these sites were pooled. Again, infected perch consistently had greater visceral percent water than perch without redworm (ANOVA, 5 out of 6 months significant). No difference in somatic percent water was detected between perch with redworm and perch without redworm for each site checked.

Back-calculation Analysis

Comparisons of the ratios of Si/Sc for several scales from the same fish supported the use of just one scale per fish for back-calculations. Five 2-yr-olds were examined for differences in this ratio for both annuli (S1 and S2). For the ten comparisons in total the greatest difference [(Si/Sc)max-(Si/Sc)min] within a single fish was less than 5 percent (n=5 scales) while most differences were closer to 3 percent. These slight differences should not greatly influence back-calculated lengths. The residuals from the linear regression of length and
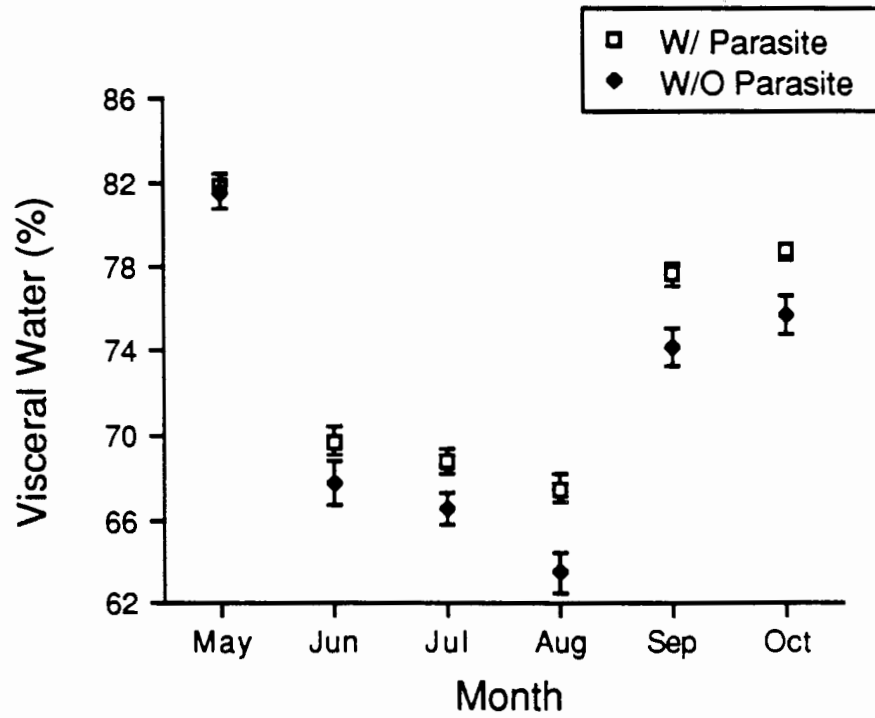
Figure 21.   Mean visceral percent water (with 95% confidence intervals)

of 125-200 mm yellow perch with redworm and perch without

the parasite for months May through October.

scale diameter were tested for homogeneity and normality. Both of these assumptions were met.

The intercept, a, calculated from the regression of length on scale diameter varied significantly by site. Scale annulus distances were measured from perch collected at three sample locations in Saginaw Bay: Port Austin, Tawas, Sebewaing (Figure 1). Separate body-scale regressions were done for yellow perch collected from each site and an analysis of covariance was computed to compare the three. The slopes of these regressions were significantly different and there was also considerable variation in intercepts: a=19.5 (Port Austin), 32.3 (Sebewaing), 25.6 (Tawas). The proportion (%) of fish from each age-class used for these three regressions is given in Table 2A. While it is possible that the differences found here are a function of subpopulations of perch at different sites, it is more likely that they are related to differences in regression design.

To further investigate this, four validation sets were designed for body-scale regressions (2 from Port Austin fish, 2 from Tawas). Each validation set consisted of 49 scales in total and each set contained the same proportional age structure (Table 2B). The scales were taken from June through August at Port Austin and July through August at Tawas. No difference was found in the body-scale regressions (slopes or intercepts) within each site (ANCOVA). These results indicate

Table 2.   Age structure (by percent) used and regression intercepts, a,
             calculated for A) the body-scale regressions of Saginaw Bay
             yellow perch from 3 sites and, B) the validation body-scale
             regressions based on proportional representation of each age group.

A)   Initial Body-Scale Regressions

| | | | | AGE | | | | | |
Site	0	1	2	3	4	5	6+	n	a
Port Austin	0	16	4	33	31	6	10	49	19.5
Sebewaing	0	0	28	25	28	8	12	65	32.2
Tawas Pt.	5	7	32	17	17	10	11	81	25.6
3 Sites Pooled	2	7	23	24	24	8	11	195	24.6

B)   Validation Body-Scale Regressions

| | | | | AGE | | | | | |
Site	0	1	2	3	4	5	6+	n	a
Tawas I	0	20	27	29	14	4	6	49	38.3
Tawas II	0	20	27	29	14	4	6	49	39.9
Tawas I & II	0	20	27	29	14	4	6	98	39.1
Port Austin I	0	20	27	29	14	4	6	49	32.8
Port Austin II	0	20	27	29	14	4	6	49	36.9
Pt. Aus. I& II	0	20	27	29	14	4	6	98	34.6
Tawas & Port Austin	0	20	27	29	14	4	6	196	36.6

that there was little variation in the intercept between two samples of fish taken from the same location. This would support the use of a relatively small set of scales (<200) for the body-scale relationship given that all ages are well represented. The two validation sets from each site were pooled in order to compare regressions between the sites. There was no statistical difference in the body-scale regression equations between perch from Tawas and Port Austin.

Most of the variation found in the body-scale regression for yellow perch can be explained by the age-structure used. In general there was a positive relationship between intercept and the proportion of younger fish in the regression design. The exception to this was Sebewaing which had a relatively large intercept (Table 2A) but no young-of-year or 1-yr-olds in the scale sample. The combined intercept from the four validation sets was comparatively larger than the combined original regression intercept for the three sites (Table 2). The age-class structures from the pooled regressions further exhibited the trend of increasing "a" with increasing percentages of young fish. The pooled validation regression intercept (36.6mm) was similar to Carlander's (1982) suggested standard intercept of 30.0mm for yellow perch . Length at age was back-calculated for six year-classes using this computed intercept. An important assumption when using the Whitney-Carlander back-

calculation technique is that there exists a linear relationship between fish length and scale diameter. This relationship was apparent after plotting the data (Figure 22) but should not be assumed for all populations. The accuracy of back-calculated lengths from scales is questionable if this assumption is not met (Whitney and Carlander 1956).

Differences in mean back-calculated lengths were found among age groups of yellow perch from Tawas. Older perch consistently showed greater back-calculated lengths than younger perch at each annulus (Table 3A). This is known as reverse Lee's phenomenon. First-year growth of age 5 and 6 fish was significantly greater than in ages 1-4 for all simple pairwise comparisons (ANOVA). Age 5 and 6 fish were not significantly different from each other in first-year growth. The regression of first-year growth with age at capture was highly significant (Figure 23, Tawas Point) and both assumptions of normality and homogeneity were met. Growth increments from mean length at age showed that there was little difference in growth rates among the six year-classes after the first year (Table 3B).

To increase the sample size males and females were pooled for the back-calculation analysis. Since females grew faster than males after the first year, comparisons of mean back-calculated lengths among year-classes can be biased if the sex ratios of the fish examined differ between year-classes. If a

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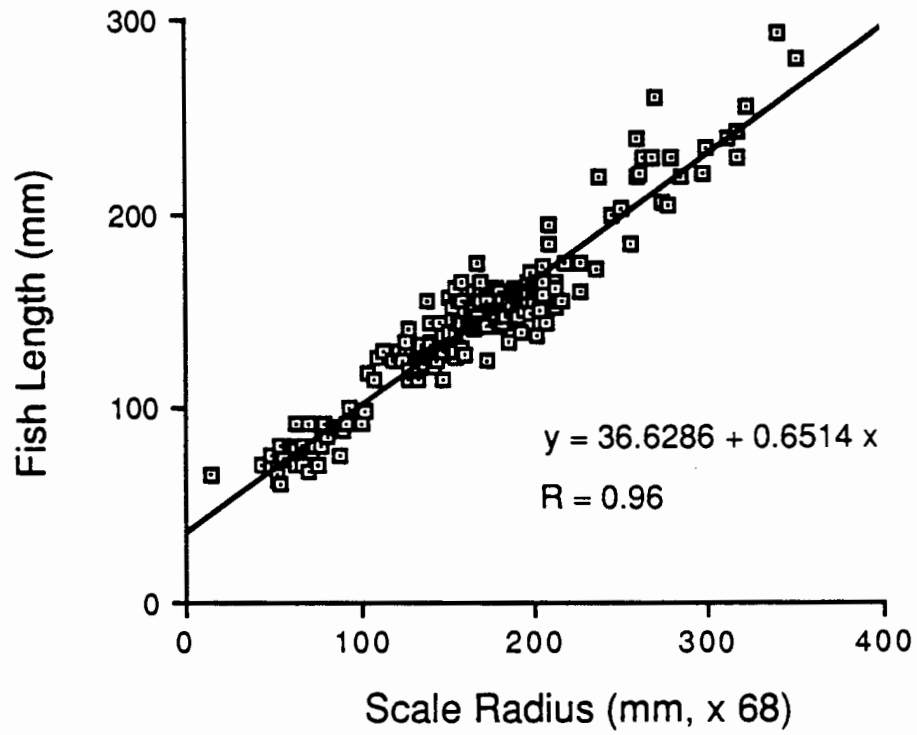
Figure 22.   Relation between body length and scale length of

Saginaw Bay yellow perch.

Table 3. A) Mean back-calculated lengths (mm) at age of yellow perch from
Tawas Pt., Saginaw Bay using the calculated intercept,
a=36.6 mm. Number of males (m) and females (f) used for each
year-class also given. (Means in parentheses refer only to samples
sizes, n, in parentheses)
    B) Increments from mean length (mm) at age of yellow perch
from Tawas Point, Saginaw Bay (1977-82). Based on
differences in back-calculated mean lengths at successive annuli
from Table 3A.

A)

Year-class	m	f	1	2	3	4	5	6
					Length (mm) at end of year			
1982	0	6	64					
1981	7	20	70	105				
1980	6	8	73	107	127			
1979	1 (2)	5 (11)	(74)	107	130	151		
1978	3	5	85	120	140	161	183	
1977	1 (1)	2 (7)	(86)	124	144	168	189	204

B)

Year-class	0-1	1-2	2-3	3-4	4-5	5-6
1982	64	35	20	21	22	15
1981	70	34	23	21	21	----
1980	73	33	20	24	----	----
1979	(74)	35	20	----	----	----
1978	85	38	---	----	----	----
1977	(86)	---	---	----	----	----
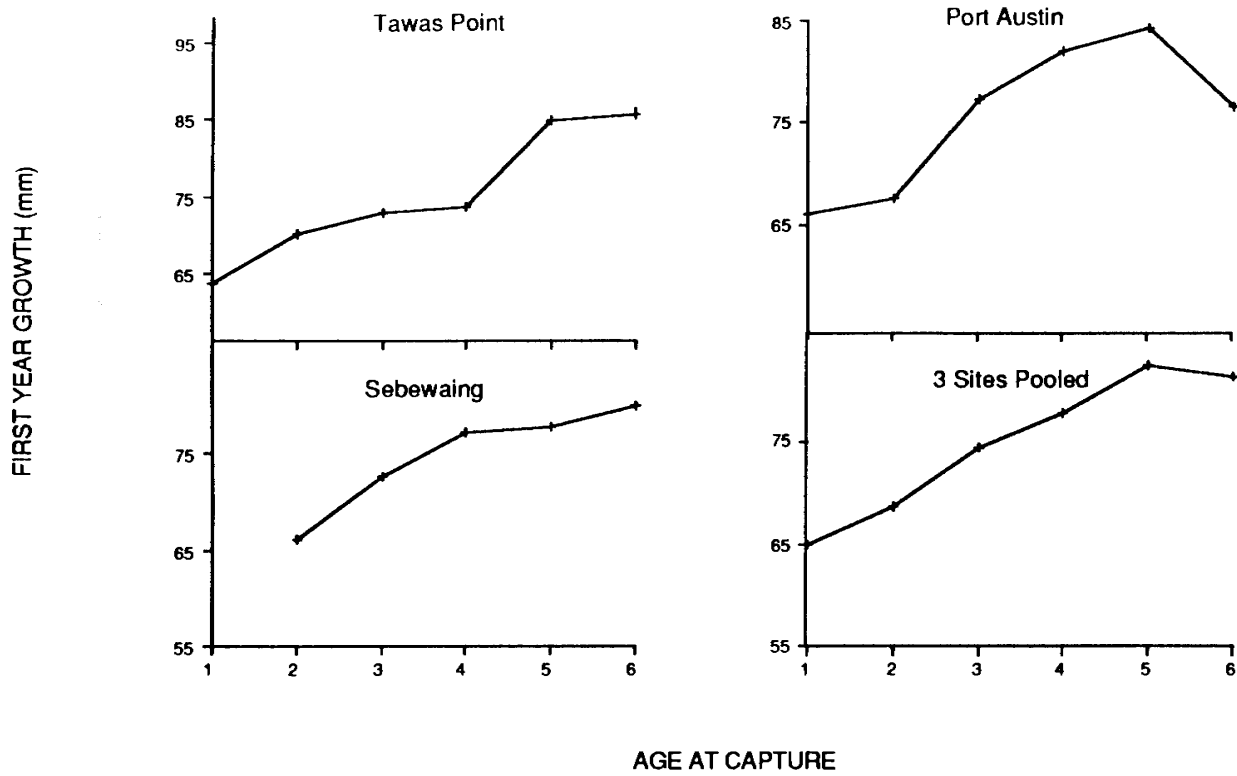
Figure 23. Back-calculated first year growth (mm) versus age at capture

of Saginaw Bay yellow perch collected between 1983-84 from

Tawas Point, Sebewaing, Port Austin, and 3 sites pooled.

greater proportion of the 5 and 6-yr-olds used were female than in the younger fish (ages 1-4), the observed differences in back-calculated lengths could be a function of differential growth between sexes. However, the actual sex ratios used (Table 3A) indicated that, in general, a greater percentage of the younger fish analyzed were female than the older fish. Thus, reverse Lee's phenomenon may actually be stronger than these results show. No difference in back-calculated first-year growth was found between sexes within each individual year-class. Therefore, the sex ratio used for each year-class should not affect mean back-calculated first-year lengths.

A positive relationship between back-calculated first-year growth and age was also found in perch collected from Sebewaing and Port Austin (Figure 23). First-year growth was back-calculated for an additional 114 fish collected from Sebewaing in April, 1984 and Port Austin in June, 1983. The regression for Sebewaing showed a highly significant relationship between first-year growth and age at capture. This relationship was not as strong for the Port Austin sample but the general trend was similar.

To support pooling all three sites for a larger sample size, an analysis of covariance was computed testing for differences in the regression lines from each site. The slopes of the lines were not significantly different although the intercepts were. This indicated that the trend of increasing first-year growth

with age was similar for all sites but the actual lengths at each age varied by site. Combining all three sites yielded a highly significant regression equation (Figure 23).

For the pairwise comparisons with all sites pooled, older fish generally had greater first-year back-calculated lengths than younger fish. The exceptions here were pairwise comparisons between age 1 and 2 fish and between age 5 and 6 fish where no differences in first-year growth were found.

DISCUSSION

Large energetic costs associated with maturation and gonad production can negatively affect body growth (Craig 1989) and survivability (Calow and Sibley 1983). The results presented here support this idea for yellow perch from Saginaw Bay. Seasonal trends in somatic growth, percent water content, and condition showed significant shifts with the start of gonad maturation in August. Nearly all somatic growth and lipid storage occurred during the short interval between spawning (May) and onset of gonad production (August). Both visceral and somatic percent water declined and condition factor increased significantly over this period. Yellow perch condition declined in females and stabilized in males from August-October as gametes were produced. Dry weight, length and somatic percent water showed only slight changes from August to October. These results suggest that after August accumulated energy was channeled mainly into metabolism and reproduction with little available for somatic addition of proteins and lipids (June-August). Craig (1977) found that even with the added weight of the gonads perch condition (both male and female) continued to decline from September throughout the winter. Similar to the results presented here, condition increased from May-August in that population.

Makarova (1973) found that perch feeding activity and lipid storage were greatest from June through August. However, Diana and Salz (1990) found no change in body calorific equivalent over these same months for yellow perch from Saginaw Bay. If perch from Saginaw Bay are storing lipids over summer this should result in the subsequent increase in body calorific equivalent. The decline in percent water and increase in visceral dry weight from June through August found in the present study suggest that some lipid storage does occur, but is probably not as significant as found for other perch populations. Morowa (1956, from Thorpe 1977b) found a seven-fold increase in visceral fat content from May to August in perch from Grosser Ploner See.

Diana and Salz (1990) also found that in perch from Saginaw Bay most somatic growth occurred between spring and early summer. The present perch population may experience a shorter period of somatic addition than historical yellow perch populations from Saginaw Bay. Hile and Jobes (1940) found that 77% of the total yellow perch production in Saginaw Bay (1936-38) took place between September and December. In other perch populations somatic growth occurred from May or June to September or October (Langford and Martin 1940, Le Cren 1947, Jobes 1952, Ney and Smith 1975).

Visceral percent water increased with age after maturation. This could be the direct result of increasing

reproductive costs with age. Somatic percent water declined to age two but remained constant with increasing age after maturation. Body water content generally continues to decline with age in all higher animals (Shul'man 1974). This "drying up" is caused by the weakening hydrophilic properties of the tissues and the increasing mass of metaplasmic substances (Shul'man 1974). Contrary to this, Craig (1977) found that in female European perch percent body water was positively related to age. Craig (1977) concluded that older female perch had lower energy contents than young ones due to the energy drain associated with sexual maturation. Somatic growth was very slow in old perch from that population due to the increasing energy demand of reproduction with increasing age (Craig 1977). The yellow perch population from Saginaw Bay exhibits early age at maturation and high, increasing reproductive costs with age (Diana and Salz 1990). Both of these are characteristic of slow growing populations.

In addition to the body energy drain associated with reproduction, many yellow perch were heavily parasitized with redworm. _Eustrongylides tubifex_ capsules are formed in the mesenteries, liver, gonads and body wall of yellow perch (Crites 1979). Redworm incidence increased with age only up to age three. Percentages of older perch with redworm may be artificially low as a result of selective mortality of infected fish. Visceral percent water was consistently greater in perch

with the parasite than those without. This suggests that redworm drains the lipid reserves in their host. The condition or fat content of the fish host may influence its susceptibility to infection (Craig 1987). Perch that are in poor condition to begin with may be less resistant to redworm infection than healthier perch. Visceral percent water increased from August to October. This trend did not represent the transfer of lipids from viscera into gonads since gonad weight was included in the measurement of visceral percent water. Instead this may represent the loss of visceral lipids related to other factors such as prey availability, temperature, or parasitism. Parasite incidence did increase seasonally (May-October) and this increase was most noticeable in August. Histopathological study of E. tubifex capsules has shown that they are true cancerous granulomas which can enlarge and result in mortality of the host organism (Crites 1979). Both the nematode and the tumorous capsules utilize energy that would otherwise be channeled into fish growth (Crites 1979).

The results presented here show that parasitism is less of a factor towards the deeper, less eutrophic outer Bay than it is in Wildfowl Bay. This may partially explain the low energy content found in perch from Wildfowl Bay as compared to other locations. However, redworm was as common in perch from Blackhole as in Wildfowl Bay. This was suprising since Blackhole perch were faster growing than the less parasitized

perch from Au Gres. In 1979, the U.S. Department of Commerce conducted an extensive study on the impact of redworm in yellow perch from Lake Erie. Yellow perch from the hypereutrophic Western Basin had more parasites, were smaller, and had worse condition factors than perch from the mildly eutrophic central basin. The Lake Erie study also identified the nematode _Philometra cylindracea_ and the tapeworm _Triaenophorus nodulosus_ as common parasites in perch. Redworm presents a problem not only in terms of perch growth and survival but also in terms of discouraging fishing or consumption.

Significant differences were found among sample sites for the energy indicators investigated. Perch from Wildfowl Bay had consistently greater visceral and somatic percent water than perch from Blackhole or the Au Gres station. This trend held for all months and sizes. Differences in percent water reflect differences in fat content and overall well being. Grove (1970) noted that in salmon, lipid content was a function of the nutritional history of the fish while the other body constituents (protein, water, ash) were predictable from fish size. Yellow perch from Blackhole showed faster growth than perch from North Island or Au Gres, and condition was also greater in perch from Blackhole than from North Island. Growth and condition in Wildfowl Bay, (not available for this study), are expected to be at least as poor as found at North Island

(Robert Haas, personal communication, Michigan Department of Natural Resources, Mt. Clemens). Yellow perch from the Blackhole appeared to have more surplus body energy than perch from Wildfowl Bay despite being as heavily parasitized.

Differences between sites within the inner bay may be due to differences in perch abundance, prey availability, and water quality. Diana and Salz (1990) found that outer bay perch accumulated more total calories than inner bay perch. No differences were found in length at age or percent water (whole fish) between inner and outer bay sites (Diana and Salz 1990). In Lake Erie, Hayward and Margraf (1987) found that food limitation in the Western Basin was related to a reduced size structure of benthic prey. In the Central Basin benthic animals were larger and yellow perch consumption rates were higher. Stresses such as starvation and parasitism (Craig 1987) in fish are often associated with density dependence. If intraspecific competition is causing reduced surplus body energy, one would expect to find higher densities of perch in Wildfowl Bay than the other sites. Trawl densities from 1988 give no indication of this (Robert Haas, unpublished, Michigan Department of Natural Resources, Mt. Clemens) and , in fact, suggest that greater numbers of perch are located outside Au Gres rather than Wildfowl Bay. These results are tenuous due to small sample sizes, large catch variability, and potential gear bias related to trawling depth. It is possible, however, that prey

size is as important in determining perch growth as prey abundance. If so, slow growth may be a function of both low energy prey items and competition for a limited resource. The effect of interspecific competition on perch growth must also be considered.

The back-calculated length analysis indicated that either first-year growth became progressively worse from 1978-84 or that negative size-selective mortality was a factor in this population. Growth rates for Saginaw Bay yellow perch have, in general, declined since the 1970's (Weber 1985). However, it is questionable whether first-year growth declined by 25% between 1978 and 1984, as shown from the calculated lengths. First-year growth estimates from empirical lengths for the years 1978-84 were not available for comparison with back-calculated estimates. The positive relationship between first-year growth and age at capture is likely due to a combination of the factors, 1) reduced growth rate from 1978-84 and 2) size-selective mortality. This second factor would be negative size-selective mortality where fast growing individuals of a given year-class have a survival advantage. If so, the 5 and 6-yr-olds captured in 1983 were the largest fish of their year-classes in 1977-78. El Zarka (1959) did not find reverse Lee's phenomenon in back-calculated lengths of yellow perch from Saginaw Bay in the 1950's. Rather, his results suggested some degree of selective mortality against the more rapidly growing

individuals of the population. El Zarka noted that this phenomenon could have been related to sampling bias or size-selection by the commercial fishery.

For all three sites investigated there was strong evidence for negative size-selective mortality. Negative size-selective mortality can be related to one of several mechanisms in a population. Predation could be a factor whereby smaller individuals are susceptible to predators for a longer period of time. Walleye (Stizostedion vitreum), channel catfish (Ictalurus punctatus) and large perch can all prey on young perch, but piscivores are sparse compared to forage fish in this system (Keller 1987). Size-selective predation and size-selective overwinter starvation mortality have been identified as mechanisms limiting survival of young-of-year perch (Post 1988). However, back-calculated lengths indicate size-selective mortality in all ages of perch. Reverse Lee's phenomenon is most strongly suggested at age four when perch are too large for size-selective predation to be a factor.

A more likely explanation is that only the largest perch have enough energy reserves to meet the demands of reproduction, overwintering, and parasitism. Perch have been known to abruptly switch to larger prey items at a given size (Ricker 1969). Larger perch within a year-class will switch earlier and this switch may enhance survival (Ricker 1969). Saginaw Bay supports a high abundance of small forage fish

(e.g. Alosa pseudoharengus, Notropis hudsonius, Percopsis omniscomaycus) which have diets similar to young perch. Switching to larger prey may reduce competition. In addition, perch that can utilize these forage fish as prey should have easy access to this abundant, high energy food source. Perch have been shown to become piscivorous at around 175 mm. This is also the size at which size-selective mortality was most strongly suggested (age 5). Shentyakova (1959 from Thorpe 1977b) found distinct groups of fast and slow growing perch from the same population. He related this difference to diet with the fast growers specializing on fish and the slow growers utilizing a wide range of invertebrate prey. If perch are switching to a higher energy diet at this size, one would expect to find an increase in growth rate with increasing age. Length increments do not increase but level off after age two (Table 3B). However, an increase in growth rate after the second year is more likely to show up as added weight rather than length.

When using back-calculated information to make inferences about year-classes, several types of bias must be considered. Ricker (1969) identified these as falling into one of three categories: 1) technical, 2) biased sampling, and 3) selective mortality. The first involves the use of the wrong regression equation for back-calculations. Biased sampling can occur if the sampling gear is more effective at catching larger or

smaller fish from a cohort. Whereas 1 and 2 are related to technique, selective mortality is a property of the fish population (Ricker 1969). The body-scale relationship used here yielded an intercept (36.6mm) that was close to the standard intercept suggested for yellow perch (30.0mm; Carlander 1982). Changing the intercept would affect the actual back-calculated lengths more so than the difference between year classes. El Zarka (1959) found a linear relationship between standard length and scale radius only for perch longer than 75mm (intercept=30.5mm). For back-calculated lengths less than 75mm he used a correction factor. This was not necessary for the present study since the body-scale regression fit well over all portions of the graph. Sampling bias was probably not the cause since the gear used was very effective at catching small perch. The difference in size between the largest and the smallest individuals of a given year-class is probably too small to cause sampling bias related to trawling gear. Ricker (1969) noted that biased sampling almost always results in positive Lee's phenomenon and can act to supress evidence of negative size-selective mortality.

If mortality is size-selective, differential mortality between sexes might be expected. Differential mortality between sexes of perch can vary from population to population and should be closely linked to differences in reproductive strategy and growth rate. In Saginaw Bay females grew faster

than males after maturation. This is found in many perch populations (Thorpe 1977b, Craig 1987). While length and weight at age were consistently greater in females, females also had higher percent water values (both somatic and visceral without mature gonads) indicating less surplus body energy in females. Therefore, while mature females were larger than males, at least some of this difference was related to additional water uptake in females. However, comparing dry weights, females had more somatic dry tissue than males of the same age. This additional body energy was needed for gonad production in females which was a far more costly event than for males. Female perch from Lac. Ste. Anne utilized both body protein and visceral fat in gonad development whereas males only used visceral fat (Tanasichuk 1978).

The ratio of male to female yellow perch from recent trawl collections in Saginaw Bay is nearly 2 to 1 (Robert Haas, personal communication, Michigan Department of Natural Resources, Mt. Clemens). This suggests that mortality rates may be greater in females than males. Observations on gravid female perch suggest that during winter months they were incapable of taking food due to occlusion of the intestine by the ovary (Newsome and Leduc 1975). Newsome and Leduc (1975) found that male perch from Laurentian lakes in Quebec contained more body fat reserves and had lower winter mortality than females. They related these differences to the large energy

drain associated with female ovogenesis. Prior to spawning most of the lipid content of mature female perch was deposited in the ovaries and subsequently not available for maintenance requirements (Newsome and Leduc 1975). Khallaf (1982) reported greater mortality in male yellow perch from Saginaw Bay than females in 1980. In many perch populations, males are reported as having a higher natural mortality rate than females (Craig 1987).

Size-selective mortality could potentially influence the analysis of surplus body energy. The seasonal trends in growth and condition described here could be overestimates if small individuals from each year-class were selectively eliminated over the months analyzed. Seasonal change in percent water and redworm infestation could also be biased since both are size correlated. However, the effect of size-selective mortality may be much greater in the winter than for the months described here (June-October) due to the susceptability of yellow perch to overwinter starvation (Newsome and Leduc 1975, Junk 1986). Size-selective mortality could also affect comparisons of these fish with other perch populations.

Another factor that could bias these results is movement or mass migrations of yellow perch. The seasonal trends described here rely on the assumption that the same fish population is being sampled each month. Large perch are thought to move from the outer bay to the inner bay to spawn each spring

(Diana and Salz 1990). Predominantly small perch (50-200mm) were analyzed for this study. The full extent of movement by yellow perch in this size range is not known but warrants further investigation.

The cumulative effect of increasing industrial and agricultural nutrient loading into lakes is often termed cultural eutrophication. Cultural eutrophication has progressed rapidly in the sheltered bays and shallow waters of the Great Lakes (e.g. Saginaw Bay, Green Bay, Western Basin of Lake Erie). Previous studies have adressed the effect of eutrophication on fish communities and, in particular, on yellow perch. Moderate nutrient enrichment can initially trigger increased production and growth. Hayward and Margraf (1987) found that yellow perch growth increased (1970-1983) with nutrient loading into the mildly eutrophic Central Basin of Lake Erie. However, at some point on the trophic continuum nutrient loading can become deleterious (Leach et al. 1977). As conditions proceed toward hypereutrophy part of the nutrient load may be channeled through unharvestable food chains (Leach et al. 1977). Perch growth in the hypereutrophic Western Basin of Lake Erie declined due to food limitations (Hayward and Margraf 1987). Hayward and Margraf (1987) found that food limitations were more serious for larger perch than small ones.

Conditions in Saginaw Bay are typical of those found in slow growing perch populations. The inner Bay is shallow,

highly eutrophic, and very abundant with perch and other forage species. Yellow perch feed predominantly on small plankton and benthic invertebrates (e.g. chironomidae) and may be energy limited in their diets. High energy allocation into reproduction and parasitism also negatively affects somatic growth.

Factors which cause slow somatic growth may also lead to high natural mortality. A stunted fish just narrowly meets the energetic costs associated with reproduction, maintenance and survival, with no energy left for body growth. At some critical age the increasing energy demands of reproduction (Craig 1977, Diana and Salz 1990) and parasitism can become so great that even maintenance costs are not met. In yellow perch from Saginaw Bay this critical age appears to be four or five. Orton's theory (Orton 1929) of "over-reproduction" leading to death states that the allocation of energy for reproduction increases with age at the expense of the soma. In direct support of this theory, Craig (1989) found that goldeye (Hiodon alosoides) channelled energy into reproduction at the expense of the soma. Orton's theory is considered more applicable to slow growing perch populations than fast growing populations (Verlagsbuchhandlung 1978). If adult mortality is high due to starvation or parasitism, there may be favorable selection for early maturation and large reproductive allocation. Thus, large reproductive costs, slow growth, and high natural mortality can be interrelated. In Saginaw Bay there is strong evidence for all

three. Slow growing populations of fish may have a greater life expectancy than fast growing populations (Craig 1987). However, this difference appears largely to be a function of temperature in comparisons between northern and southern populations or between year-classes that experience different climatic conditions (Miller and Kennedy 1948, Thorpe 1977b). Comparing two populations with the same thermal experience, or groups of fish from the same year-class may yield an inverse relationship between body growth and natural mortality. Here slow growth is a function of energy limitations which when taken to the extreme can accelerate natural mortality.

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