To the Graduate Council:

I am submitting herewith a thesis written by Joseph W. Minton entitled "Bioenergetics of Sauger in Watts Bar Reservoir." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

J. L. Wilson, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

BIOENERGETICS OF SAUGER IN WATTS BAR RESERVOIR

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

This 17-month study describes the energy budget of sauger [Stizostedion canadense (Smith)] in Watts Bar Reservoir, Tennessee, in order to assess the effects of prey fluctuations on that major predator. Direct field determinations of consumption and laboratory determinations of metabolism are organized in the balanced energy equation of Winberg (1956) to predict the growth in energy value of typical sauger in two year classes. The Winberg equation is modified to include the energetic costs of specific dynamic action and the efficiency penalty of catabolizing body energy stores to realistically reflect energetics principles. Directly measured caloric growth and predicted growth over the growing season (March-October) agree within 5.0 to 13.2% for the two age classes modeled, thus verifying the model application. Predicted and observed gains over the winter were much more divergent, suggesting that the physiological assumptions of the balanced energy equation are invalid for describing the winter energetics of sauger. Further investigations of the growth efficiency of percids at low temperatures, or observations of field activity in the winter, or both are warranted.

Watts Bar sauger grew quickly in comparison to other populations. Modeling indicated that this rapid growth was the result of storing energy obtained by winter predation upon threadfin shad (Dorosoma petenense) and young-of-the-year gizzard shad (Dorosoma cepedianum), of heavy feeding upon shad in early summer, of prey switching to species

of equal or superior energy value, and of maintaining minimum levels of metabolic energy expenditures. In early summer sauger fed heavily on vulnerable shad which were concentrated in coves to spawn. Predation upon shad was again very heavy when winter cold stress rendered them vulnerable. Cold stressed shad are also susceptible to impingement upon powerplant intake screens and shad predation by sauger was correlated with impingement of shad at Kingston Steam Plant both winters of study.

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I. INTRODUCTION

This study characterizes the bioenergetic response of sauger (Stizostedion canadense) in Watts Bar Reservoir, Tennessee to fluctuations in the availability of their prey base. Populations of threadfin shad (Dorosoma petenense) and young-of-the-year gizzard shad (Dorosoma cepedianum), the principal prey of the Watts Bar sauger, are subject to seasonal crashes in numbers. The mechanism by which sauger adapt to these crashes was unknown.

Threadfin shad are near the northern edge of their range in Watts Bar Reservoir. They are native to warmer waters of the Gulf Coast drainage and are severely stressed by cold water temperatures. This cold stress renders them susceptible to predation and natural mortality. Sauger in Watts Bar are at the southeastern edge of their range and are not stressed by cold water temperatures. They feed heavily upon the vulnerable shad in winter until the combination of cold induced mortality, predation, and impingement at Kingston Steam Plant severely reduces the shad populations. Limited prey switching has been documented after this die-off, but whether the sauger maintain good condition and growth following the decline in prey numbers is unknown.

The specific objective of this study was to characterize the energy budget of Watts Bar Reservoir sauger over a 17-month period by (1) determining the metabolic expenditures of sauger in the reservoir, (2) monitoring the feeding rate and prey selection of sauger and the energy value of that prey, (3) monitoring the condition and caloric

growth of sauger through the period, and (4) incorporating these parameters into a realistic model of the sauger's bioenergetics, to assess the effect of the population fluctuations of the forage species.

II. RELATED LITERATURE

Sauger

The sauger, Stizostedion canadense (Smith), a successful top order piscivore in the family Percidae, occurs primarily throughout the Mississippi River drainage. East Tennessee is the southeastern border of its range; it is limited in further southeasterly distribution by geographical boundaries and by high summer temperatures (Collette et al. 1977).

The sauger is a temperate mesotherm, with a reported physiological optimum temperature of 22°C (Hokanson 1977). However, field distribution indicates the sauger's thermal preference is between 15 and 21°6 from May to August (Dendy 1945). The sauger is adapted for a riverine habitat and is often found in turbid, big river systems (Collette et al. 1977). Sauger seek a riverine habitat to spawn (Haslbauer and Mauges 1947, Nelson 1968), and in reservoir systems, spawning occurs in the tailwaters of dams (Nelson 1968).

Spawning occurs in spring and may extend over a month-long period (Haslbauer and Mauges 1947). A thorough investigation of the spawning and early life history of sauger has been compiled by Nelson (1968). Eggs are scattered randomly over rubble substrate, are fertilized externally as they fall, and are abandoned by the parents. The eggs hatch in 21 days at 8.3°C, and the yolk sac is absorbed 7 to 9 days later. The larval fish are planktivorous until they reach 70 to 110 mm, at which time fish become the major food item.

As adults, sauger become almost exclusively piscivorous, eating primarily the most abundant forage fish species of suitable size

(Wagner 1972, McGee et al. 1978). Loss of availability of preferred prey, whether by winter die-off or spatial separation due to differing temperature preferenda of the predator and prey, has been shown to severly affect the growth and production of Stizostedion species. Forney (1974) demonstrated a close positive correlation of the abundance of yellow perch (Perca flavenscens) as a forage species and the survival of one and two year old walleye (Stizostedion vitreum). Priegel (1969) considered the lack of sufficient forage fish to be the factor limiting growth of sauger in a Wisconsin lake.

The predator-prey interactions of sauger or walleye and shad (Dorosoma spp.) are particularly dynamic. Threadfin shad (D. petenense) are native to warm waters, but they and gizzard shad (D. cepedianum) often become the major diet item of coolwater Stizostedion species whenever the shad and sauger are sympatric (McGee et al. 1978). Introduction of threadfin shad has been shown to increase the growth rate of native walleye (Range 1973). However, both shad species are sensitive to cold stress, showing reduced swimming abilities at temperatures below 10°C (Neumann et al. 1977, Griffith 1978). Acute cold shock is fatal to gizzard shad (Cox and Coutant 1976) and threadfin shad (Hubbs 1951, Griffith 1978), and rapid temperature drops or sustained low temperatures have resulted in natural mass mortalities of shad (Hassler 1953, Parsons and Kimsey 1954, McLean et al. 1980). Thus, the clupeids may form an unstable forage base for piscivores (McGee et al. 1977). Reduction in growth rate and fecundity of Stizostedion spp. in northern systems has been attributed to the winter kill of shad (Forney 1965, Nelson 1969). The effect of winter kill of

shad on the growth of sauger has not been investigated in southern reservoirs.

Energetics

Studies of the nutrition and growth of fish have been based upon units of biomass (Swenson and Smith 1973, Popova and Sytina 1977), of protein (Gerking 1955, Birkett 1969), and of energy (Healey 1972, Kelso 1973). However, often there is no linear relationship between the biomass and energy value of a fish; the energy value of individuals of a given weight varies significantly over time for a variety of species (Beamish 1964, Illes and Wood 1965, Kelso 1972, Potapova and Tytova 1977). Also, the proximate composition of the fish's body in terms of protein, fat, and carbohydrate is labile, the components existing in a dynamic state (Baldwin 1952). Energy, however, serves as an integrator of all the components of the fish's diet and growth, (Warren and Davis 1967, Kelso 1973, Nimi and Beamish 1974, Kitchell et al. 1977, Webb 1978). Utilization of food for growth is governed by the energy requirements of an animal. This energy is obtained from the food through oxidation of all the biomass components: protein, fat, and carbohydrates (Kelso 1972). Thus, energy is the best common denominator of all nutrition and growth processes.

The relationship of energy intake to growth is described by the balanced energy equation as outlined by Ivlev (1939) and Winberg (1956):

$$P \cdot Q_R = Q_M + Q_G$$

where:

P = proportion of food consumed that is assimilated

Q_R = food consumed

Q_M = metabolism

Q_G = growth

The elaboration of this equation by Webb (1978) and Warren and Davis (1967) serves as the specific framework of growth models:

$$Q_R - (Q_F + Q_N) = Q_S + Q_L + Q_{SDA} + Q_G + Q_P$$

where:

Q_F = fecal loss

Q_N = excretion or nonfecal loss

Q_S = standard metabolism

Q_L = locomotor metabolic cost

Q_{SDA} = apparent specific dynamic action (the energy cost of food processing)

Q_P = gamete synthesis

Of primary concern in most energetics investigations is estimation of consumption (Q_R). Direct determination of Q_R for field populations is difficult; so it is most often estimated indirectly. Indirect estimates of consumption involve solving for the missing variable, consumption, in some variation of the balanced energy equation, given the known growth and thermal history of a population (MacKinnon 1973, Kitchell et al. 1977). Or they have proceeded by determining the feeding to growth relationship in the laboratory and projecting those results to known growth in the field (Allen 1951,

Hatanaka and Takahashi 1960, Gerking 1962, Warren et al. 1964). However, to interpret observed growth in terms of predator-prey relationships, as was the intent of this study, while avoiding teleological reasoning, requires that a direct estimate of consumption be made.

Digestion rates are used in the direct estimation of consumption. Mann (1978) reviewed and evaluated a variety of direct estimation methods. For a piscivore which feeds intermittently, such as sauger, he concluded that the weights of partially digested stomach contents should be adjusted to the original ingested weight to calculate consumption. Swenson and Smith (1973) and Popopa and Sytina (1977) used such a method for two Stizostedion species and Perca fluviatilis.

Not all of the food which is ingested is assimilated. Winberg (1956) first proposed that, in general, 15% of the food mass ingested by fish is lost in the feces (Q_F). Subsequently it has been shown that the assimilation efficiency for food of carnivorous fish expressed as weight, nitrogen, carbohydrates, etc., varies considerably (73-99%) (Webb 1978). In contrast, the assimilation efficiency for the energy value of the food, varies in a more narrow range (85-98%) (Beamish et al. 1975).

Some nitrogenous material that is assimilated is subsequently lost as urea and ammonia through the gills, kidneys, and skin of fish and thus is unavailable for metabolism (Smith 1929, Warren and Davis 1967). This loss (Q_N) amounts to 7.9-15% of the total diet energy (Forster and Goldstein 1969, Niimi and Beamish 1974).

The sum of the energy requirements of digesting, transporting, biochemically treating, and incorporating food are defined as the apparent specific dynamic action (Q_{SDA}). This component of the energy equation is estimated as the difference between the oxygen consumption rates of fed and unfed fish at a fixed temperature and activity level (Webb 1978). True specific dynamic action is limited to the energy cost of deaminating amino acids (Warren and Davis 1967), but its estimate is not easily separated from the other food processing costs. Therefore, all of these costs are commonly considered under the term "apparent specific dynamic action." The energy cost of apparent specific dynamic action is directly proportional to the energy value of the ration (Webb 1978, Brett and Groves 1979). Estimates of the cost of apparent specific dynamic action to fish ranged 12-16% in the most complete studies of this effect to date (Muir and Niimi 1972, Beamish 1974, Pierce and Wissing 1974).

Standard metabolism (Q_S) accounts for a significant portion of energy intake, particularly at low rations (Warren and Davis 1967). The metabolic rate of fish is estimated by determining the feeding rate which produces zero growth or by monitoring oxygen consumption rate of fish and translating this to calories released in oxidation. Metabolic rate is affected principally by temperature, body weight, activity, and feeding. The most standardized and repeatable rate estimate is that of standard metabolism, which controls feeding and activity level (Fry 1957, Webb 1978).

Growth (Q_G) and the energy cost of gamete synthesis (Q_P) result from the net energy (energy remaining after fecal, nonfecal, and SDA losses) that is in excess of the metabolic requirements. Growth in length of sauger has been studied for many populations (Hart 1928, Carlander 1949, Stroud 1949, Hassler 1953, Carufel 1963, Nelson 1969, Priegel 1969). Quantification of growth in length is useful in comparing the health of various populations, but is incomplete for application to the balanced energy equation which requires a knowledge of caloric gain. For instance, growth in length of sauger is known to stop when water temperatures are approximately 12°C or lower (Kelso 1972, Kelso and Ward 1972). However, development of energy-rich gonadal tissue occurs almost entirely in the winter months (Hokanson 1977, McLean et al. 1980), and sauger fat reserves also show an upward trend in this period (McLean et al. 1980).

Growth has been related to consumption for a variety of fish species, mainly in laboratory situations. Much of this literature has been reviewed by Paloheimo and Dickie (1965). However, to fully understand the relationship of consumption to growth of a fish requires synthesis of all the metabolsim and growth variables (Warren and Davis 1967, Kitchell et al. 1977). No such quantified bioenergetic description of a natural percid population has been completed to date. However, many aspects of period bioenergetics are well described. Perhpas only the family salmonidae has been more studied, making periods good candidates for energetics modeling.

Our study was designed to accomplish this bioenergetic description, utilizing an energetics model which expressed the basic

framework of the balanced energy equation. All of the bioenergetic parameters important to the growth of Watts Bar Reservoir sauger were determined in the laboratory and field and were incorporated in the model. In applying the model, the parameter interactions can be illustrated, and the ecological significance of the interactions can be demonstrated.

III. MATERIALS AND METHODS

Field Sampling

Watts Bar Reservoir is a 13,300 hectare impoundment created in 1942 by the construction of a Tennessee Valley Authority dam at Tennessee River Mile 529.9. The reservoir is characterized by broad reaches and shallow flats about the main channel and by narrow riverine topography in two of three tributaries. It is a mesotrophic system with a diversity of native and introduced fish species (TVA unpublished manuscript 1974).

To quantify the energetic parameters of the sauger population, sauger were captured from the reservoir for analysis over a 17-month period. Sauger were caught in five 38-m experimental gill nets consisting of five panels with 13-, 19-, 26-, 32- and 38-mm mesh sizes. The nets were placed in five locations in the reservoir for 24 h biweekly for the period November 1978 to March 1980. Surface and bottom water temperature, dissolved oxygen, and visibility measured with a secchi disc were recorded at each sampling for all stations. All fish captured were analyzed in the laboratory within three h or were frozen for analysis at a later date.

On seven selected dates over the 17-month study sauger were captured in a special sampling procedure for consumption rate analysis. Nets were placed in various sites in the reservoir and fished for two h, so that the time of capture of sauger would be known within one h. These fish were immediately frozen on dry ice for

transport to the laboratory. Water quality parameters were recorded at these times as in the biweekly sampling operation.

Consumption

In the dissection of the specimens specially sampled for consumption analysis, the length, weight, and identity of any stomach contents were recorded. Partially digested fish found in the sauger stomachs were identified to genus or species if possible, by identification of taxa-specific structures resistant to digestion such as gizzards, otoliths, and spines. If the entire fish, including head and tail, was intact, the total length was measured. If the head was undigested but the tail damaged or missing, the standard length was measured. If the head was digested, the backbone was excised and its length recorded. Given the identity of the prey eaten and one of the length measurements, the undigested weight of the prey was estimated by length to weight regressions determined from prey captured in the gill nets.

The average individual daily ration of the sauger population was then estimated by the equation of Popova and Sytina (1977):

$$R = \sum_{i=1}^{V} \frac{S_i \div n_i}{V} \cdot \frac{n}{N}$$

where:

R = daily ration of the population, g prey/g predator

V = number of days required for digestion to reach 90% completion

S_i = original undigested weight of prey items eaten on day i expressed in g prey/g predator

n_i = number of fish which contained food eaten on day i

n = number of fish in the sample which contained food

N = number of fish in the sample

When time required for digestion to reach 90% completion equalled 24 h, the equation simplified to : $R = S_i/N$. Digestion rate was determined as a function of water temperature by regressing the time required for digestion to reach 90% completion (Swenson and Smith 1973, McGee et al. 1978) over temperatures ranging from 5-20°C. This regression yielded the equation:

$$y = 66.83 - 2.50\ T$$

where:

y = time required for digestion to reach 90% completion

T = water temperature °C

The coefficient of determination for this regression equation was 0.92. The 90% digestion period was utilized because the length of the final digestion phase, the residual phase, is quite variable (Windell 1966). Digestion time was calculated for meals of 35 mg/g because this was the mean meal size of Watts Bar sauger, and over 90% of the meals consumed fell in the narrow 20 to 60 mg/g range.

To avoid any possible bias associated with nonregular feeding patterns (Darnell and Meirrotto 1962), blocks of 24 h were considered in determining consumption rates. For instance, if the water temperature resulted in a 90% digestion period of more than 48 h, only stomach contents less than or equal to 48 h old were included in the

analysis. If the digestion period was 24 to 48 h, only stomach contents less than or equal to 24 h old were included in the analysis. If the 90% digestion period was less than 24 h, two gill net samples were collected 12 h apart, and only stomach contents which were less than or equal to 12 h old were included in the analysis of each half of the day's feeding estimate. Because digestion progresses linearly with time in sauger (Swenson and Smith 1973, McGee et al. 1978), the degree of digestion of food items equalled the proportion of the 90% digestion period that food items had been in the stomach. Thus, time of ingestion was calculated as the sample time minus the time since ingestion. Times of ingestion were used to determine the major feeding periods of sauger.

For the samples in which the complete digestion time was at least 24 or 48 h, numbers of feeding incidents were summed over four six-h periods which roughly corresponded to a dawn, day, dusk, and night cycle. These were 0200 to 0800, 0800 to 1400, 1400 to 2000, 2000 to 0200. The distribution of sums was analyzed by the Chi-square statistic to check for periodicity of feeding.

The weight of fish eaten by sauger was converted to energy for the purposes of the energetics modeling. This conversion was accomplished through determination of the energy value per unit weight of forage species caught from Watts Bar. The specimens were first dried to a constant weight in an oven at 70°C. They were then ground into a homogeneous powder either in a Waring blender or a Wiley mill. Then two 0.5 to 1.0 g aliquots of each sample were analyzed calorimetrically in a Parr Adiabatic Bomb Calorimeter, which was standardized each day

of operation by oxidation of benzoic acid crystals of known caloric value. The ash content of the samples was also determined by burning duplicate 1 to 3 g aliquots at 500°C for 12 h. These analyses were conducted in cooperation with S. M. Adams (unpublished data).

Further consumption estimates were derived from gut content data of sauger caught in the 24-h net sets. These data could not be used to directly calculate daily ration, because the time of capture within the 24-h net set was unknown, and digestion of stomach contents continued after the fish were caught. However, it was hoped that these data would serve as a relative index of feeding which could be correlated with daily ration. The percent of the fish caught in 24-h net sets which contained food (feeding index) was adjusted for the effects of temperature on stomach emptying rates by the formula:

$$AFI = FI \bullet 24/HT,$$

where:

AFI = adjusted feeding index

FI = feeding index

HT = number of h to 90% completion of digestion of a 35-mg/g meal at the ambient temperature.

The daily ration determinations were then regressed as a function of the adjusted feeding indices of paired 24-h samples caught on the same or consecutive dates to determine how daily ration could be inferred from the 24-h samples.

Weights of sauger livers were also monitored as a potential index of feeding rates in the field. Heidinger and Crawford (1977)

demonstrated a positive correlation of feeding rate and liver weights in largemouth bass held in the laboratory. The liver weight increase was perhaps due to storage of fat (Bailey 1952) or glycogen as an energy source (Hoar 1957).

Metabolism

The relationship of the sauger metabolic rate to temperature was determined in the laboratory using two groups of sauger taken from Watts Bar Reservoir. On May 15, 1979, four sauger (356-406 g, $\bar{X}$ = 393 g) were caught in gill nets, carefully removed, and transported immediately to a holding tank at ambient water temperature in the laboratory. Another group of four (384-414 g, $\bar{X}$ = 397 g) was caught on July 5, 1979 and was placed in an identical tank. Both groups received a prophylactic treatment of 1-ppm malachite green following introduction to the tanks. The 780-l circular fiberglass tanks were supplied constantly with well water in which the temperature was controlled by computer. The tanks were aerated and maintained at low light intensity by covering with a 0.1-mm black polyethylene sheet. The fish were given a week to acclimate to the laboratory, during which time they accepted live fathead minnows (Pimephales promelas) as food.

Before respiration was measured with the two groups, the sauger were allowed to digest all food, and all uneaten food was removed from the tank. The drainpipe was closed, and the water level was allowed to rise to the top of the tank. Aeration was discontinued; a stirring motor was switched on to prevent stratification; and probes for a YSI telethermometer and YSI printing dissolved oxygen meter were

introduced. Duplicate water samples were siphoned off for Winkler dissolved oxygen analysis (American Public Health Association et al. 1971), and the polyethylene sheet was adjusted to lie on the water surface, sealing the tank and preventing air exchange. The holding tank was thus converted into a respirometry chamber without stress to the fish, a significant bias in certain respirometry techniques (Black et al. 1939, Edwards et al. 1972).

The dissolved oxygen meter was monitored so that the chamber's dissolved oxygen was never allowed to drop below 4 ppm, below which point the fish may have been stressed. Automatic photography revealed that the fish were quiescent in darkened chambers; however, the dissolved oxygen record was checked for irregular decline rates to verify that only standard metabolism was occurring (Fry 1957). At the end of the experimentation period, between 8 and 30 h later, water samples were again siphoned off for Winker analysis.

Oxygen consumption of the May fish was determined from 15 to 25°C at approximately 2°C intervals. The July group was tested from 17.4 to 5°C at the same intervals. Tank temperature was adjusted at 1°C per day to avoid thermally stressing the fish.

A trial was conducted to assure that oxygen did not permeate through the polyethylene sheet. The fish were removed from the chamber while dissolved oxygen was well below saturation, and the chamber was resealed. Dissolved oxygen levels remained constant for at least 48 h. Periodic empty chamber runs at saturated oxygen levels also indicated that biochemical oxygen demand did not significantly influence oxygen decline rates.

The relationship of metabolism to both temperature and body weight was estimated by deriving a multiple regression equation which combined the empirically determined metabolism-temperature relationship with the general teleost metabolism-weight relationship. The standard metabolic rate of fish is proportional to approximately the 0.85 power of weight at all temperatures (Winberg 1956, Ricker 1973). Kelso (1972) calculated that the exponent of walleye (Stizostedion vitreum) was actually 0.84.

Growth

Quantification of growth completed the energetic description of the population. The various aspects of growth, i.e., length, weight, energy, and body components, were monitored independently so that their roles in the energetics of the sauger could be studied.

Beginning in October 1979, scale samples were removed from all sauger dissected. Four or five scales were extracted from the left side of the fish, just beyond the tip of the posteriorly extended pectoral fin. These scales were analyzed by the method by Tesch (1971) to determine the fishes' ages and to determine the radius to each annulus. The geometric means regression analysis of Ricker (1973) was used to estimate their total length at each annulus formation.

When sauger were dissected, total length, wet weight, sex, gonad developmental stage, gonad weight, and visceral fat weight were recorded. Beginning in October 1979 sauger livers were also weighed. The visceral fat, which occurred in a discrete mass suspended from the viscera, the gonads, and liver were completely excised by hand for weighing.

Caloric analysis was performed on at least two representatives of adult sauger of both sexes randomly selected monthly or bimonthly. Visceral fat, gonads, and the remaining carcass were analyzed independently if they amounted to more than 1% of body weight. The total energy value of individuals of the monthly sample was estimated as the sum of the products of the body component weights and the mean caloric values per gram of the subsamples. The monthly energy equivalent per gram of body mass considered in the analyses was estimated as the monthly mean of the energy values of the individuals divided by their weights.

Those growth parameters of the sauger which analysis of variance disclosed to vary significantly with the size class of fish were estimated independently for the two dominant cohorts in the samples. To estimate the age of those fish whose scales were not analyzed, the mean total lengths of the two year classes at annulus formation were predicted by the scale analysis. Annulus formation was assumed to have occurred in mid-March in 1979, when the water temperature was the same as in mid-March 1980, when annulus formation was observed. Sauger captured in March 1979 or any prior month in the winter, no-growth period, whose total length fell within $\pm$ one standard deviation of the mean predicted length of a year class, were assumed to be of that year class. The mean and standard deviations of the lengths of the year classes in October 1979, when scale samples were first analyzed, were also determined. The ranges of standard deviations between March and October were then interpolated for the intervening months to designate the size ranges of the year classes in that period.

Total caloric growth over a period was determined as the difference between the observed final and initial mean energy values of individuals of a year class. The initial individual energy value of the growing season was calculated as the product of the mean energy equivalent per gram of the predicted size range of a year class at annulus formation and the mean predicted weight of the year class at that time. This body weight was estimated by applying the mean predicted length of a year class to a regression equation relating weight to length of all sauger caught in the month of annulus formation. In calculating growth through the spring and summer, the gonadal tissue energy value was omitted in the calculated initial value, as this store is lost to the fish upon spawning. The growth estimate was divided by the consumption estimate to determine the gross efficiency of the transfer of intake energy to growth. To determine total ration for an average individual within a year class, each mean monthly caloric ration per gram of sauger of a year class was multiplied by the mean individual weight of the year class for each month.

Energetics Model

The energetics parameters were incorporated in the predictive energetic growth model to illustrate their interactions and evaluate the ecological significance of those interactions. The model calculated the growth of a population of fish given their feeding and metabolic rates and an assumed efficiency of food utilization.

The model is a sequential operation of the basic energy equation of Winberg (1956):

$$Q_{G_i} = P \cdot Q_{R_i} - Q_{S_i}$$

where:

Q_{G_i} = somatic and gonadal caloric growth over a time interval, i

P = proportional constant representing fecal, nonfecal, and apparent specific dynamic action (SDA) energy loss

Q_{R_i} = total energy ration over a time interval, i

Q_{S_i} = total energy requirement of standard metabolism over an interval, i

The model's calculation was performed independently on the two most abundant year classes. The model integrated monthly intervals and based each calculation on the preceding month's predicted energy gain. The weight of an average individual was estimated from its predicted energy value by the observed mean monthly weight-energy equivalent for the year class. The mean monthly caloric ration per gram was multiplied by the individual's predicted weight to determine its total monthly ration. The proportionality constant P reduced total intake energy by the sum of all fecal, nonfecal and apparent specific dynamic action energy loss. Fecal and nonfecal energy losses combined were assumed to account for a constant 20% of the total caloric ration, the average value observed for most piscivorous fish (Brett and Groves 1979). Apparent specific dynamic action was assumed to consume a constant 15% of the total diet energy, the accepted general approximation of apparent specific dynamic action in teleosts (Webb 1978, Brett and Groves 1979). The adjustment of the total ration by the proportionality constant was thus 0.65 [1- (0.20 + 0.15)].

The energy consumption of standard metabolism (Q_S) was estimated by a submodel which related metabolism to body weight and the mean monthly water temperature. Locomotor metabolic cost was assumed to be minimal in sauger (Kitchell et al. 1977), even though it may be significant during spawning and was not included in the predicting model.

The total ration was reduced by the proportionality constant and then by the cost of standard metabolism to predict the energy gain over a month. This gain was added to the initial individual energy value of the month to predict the initial energy value of the next month. Whenever the model predicted a negative energy balance for a period, an additional energy loss of 7.5% of that balance was assessed to reflect the physiological cost of utilizing stored energy for metabolic requirements (Niimi and Beamish 1974, Kleiber 1961).

The model was manipulated to predict the effects of an altered energy balance on the sauger population. The effect on the population of failing to gain energy value in the winter was simulated by setting the adult cohort's initial energy value of the growing season to the level of the previous November. Two different scenarios of production over the growing season were then simulated with the model. In one, the final energy value of the cohort at the end of the growing season was predicted given its observed weight-specific consumption rate. In another, the cohort's consumption rate was increased by a constant to determine how much extra food would have to be consumed for the cohort to achieve its observed year-end energy value without the winter energy gain.

IV. RESULTS

Consumption

Daily ration, as determined on the seven special sampling dates, ranged from 0 mg/g (0 cal/g) in March 1980 to 36.7 mg/g (42.9 cal/g) in December 1979 (Table 1). The prey species' length to weight to energy value relationships which were employed in the ration determination are presented in Table 2.

Regression analysis of paired observations of the daily ration of the special samples and the adjusted feeding indicies of the 24-h samples indicated a highly significant relationship of the two ($P < 0.001$) (Figure 1). Based in this relationship and the fact that the seven daily ration determinations spanned most of the time period of the study and nearly the entire range of feeding rates observed, daily ration was estimated from the adjusted feeding indicies of the 24-h samples for the entire study period (Figure 2). The total sample size of these netting operations was 788.

The chi-square analyis of feeding periodicity of the daily ration sample showed the population's feeding to be regularly distributed over 24 h ($P < 0.05$). Thus the adjusted feeding index of the 24-h sample was unbiased with respect to feeding periodicity. It was hypothesized that the strength of the correlation of daily ration and the adjusted feeding index was due to the ration being influenced principally by the population's feeding frequency (percent of any sample containing food varied 0-100) and not by the size of the meals consumed (meal size varied only 20-60 mg/g).

Table 1. Estimated daily ration (mg/g/day) of the sauger population for the dates on which special sampling was conducted

Date	Daily Ration (mg/g/day)	Sample Size
1979		
March 7	18.0	11
April 14	0.0	15
May 2	3.0	10
July 22	10.8	16
August 8	15.7	36
December 6	36.4	10
1980		
March 7	16.8	11

Table 2. Regression equations relating the weight of a fish to its length for the major prey species and energy values for those prey

Species	Regression equation[a]	r^2	N[b]	Energy value[c,d]	N[e]
Bluegill (*Lepomis macrochirus*)	log W = 3.0366 · log BL - 1.2144	0.89	22	1.06	29
	log W = 3.5241 · log SL - 2.0948	0.96			
	log W = 3.6144 · log TL - 2.5271	0.95			
Drum (*Aplodinotus grunniens*)	log W = 3.3241 · log BL - 1.6266	0.87	34	1.25	7
	log W = 3.2962 · log SL - 1.9127	0.94			
	log W = 2.6661 · log TL - 1.6055	0.94			
Logperch (*Percina caprodes*)	log W = 1.7380 · log BL - 0.3482	0.70	26	1.30	7
	log W = 2.5708 · log SL - 1.3928	0.82			
	log W = 2.6146 · log TL - 1.6197	0.83			
Shad (*Dorosoma cepedianum* and *D. petenense*)	log W = 2.3854 · log BL - 5.9438	0.92	71	1.17	66
	log W = 2.9665 · log SL - 1.6982	0.96			
	log W = 3.0027 · log TL - 2.0652	0.96			

[a] W = total wet weight in grams.
BL = backbone length in centimeters.
SL = standard length in centimeters.
TL = total length in centimeters.

[b] Sample size of regression analysis.

[c] kcal/g wet weight.

[d] Data taken in conjunction with S. M. Adams (unpublished data).

[e] Sample size of caloric analysis.

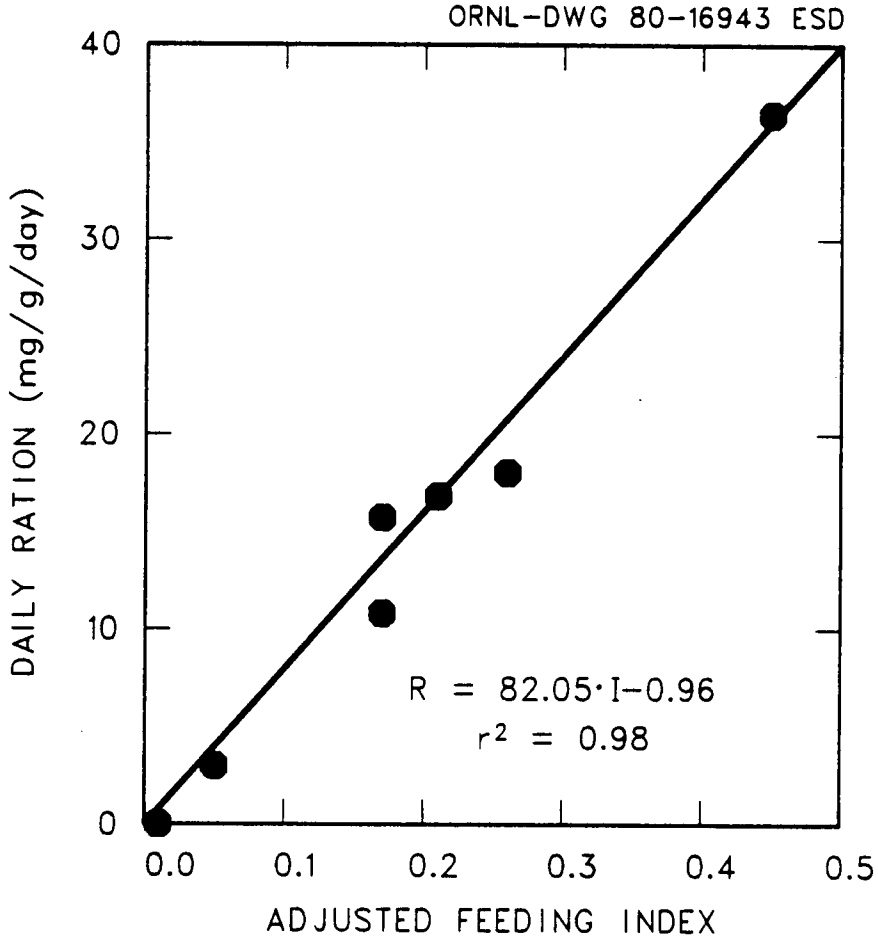


Figure 1. The relationship between paired observations of the adjusted feeding index of sauger caught in the 24-h net sets and the daily ration (mg/g/day) of sauger caught in the seven special netting efforts.

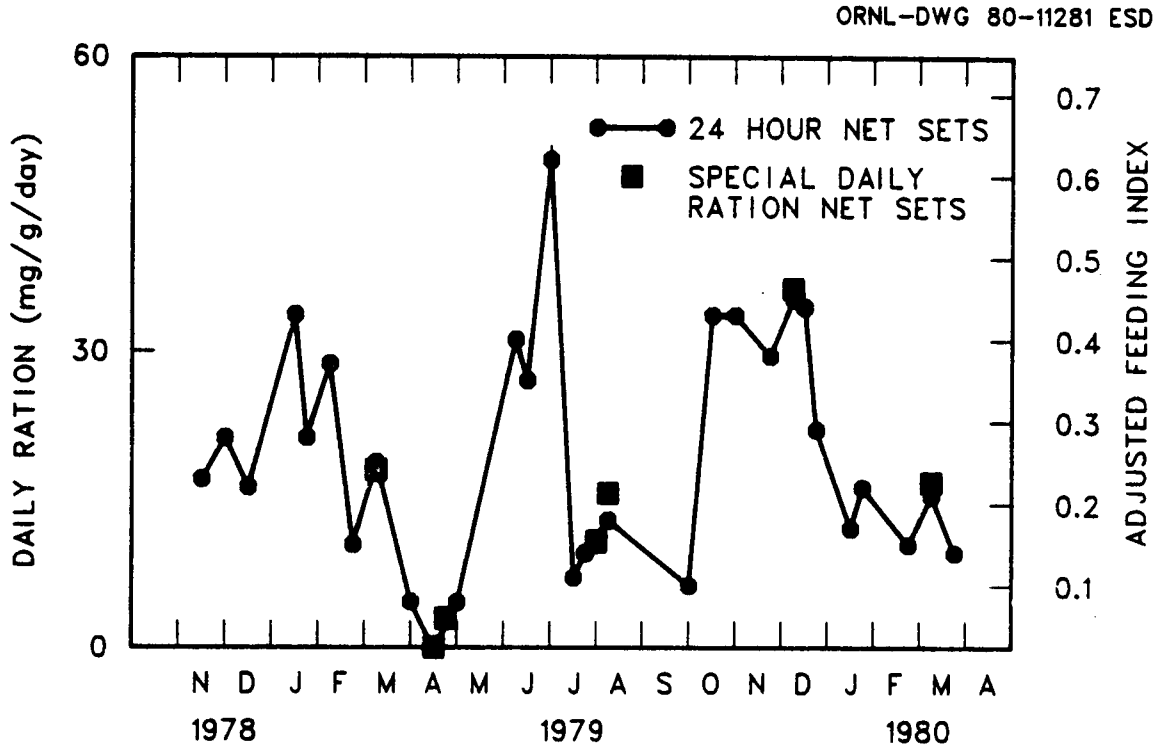


Figure 2. Comparison of daily ration and adjusted feeding index. Squares represent the daily ration (mg/g/day) of the sauger caught in the seven special netting efforts. Circles represent the adjusted feeding index of sauger caught in the 24-h net sets.

Since the prey weight to sauger weight ratio did not vary significantly with the various prey species (one-way ANOVA, $P > 0.05$) multiplication of the monthly mean ration by the percent composition of clupeid and non-clupeid species in the diet each month, indicated the importance of the two species groups as forage (Figure 3). Shad comprised over 90% of the identifiable diet in the winter, heavy-feeding months of November 1978 through February 1979 and over 78% from October 1979 to February 1980. Non-shad prey species did not contribute nearly as large a proportion of the annual intake as did shad, but they were the major food source in all periods of very low feeding.

Feeding rate was reflected by changes in liver weight. The proportion of the total body weight that was liver (liver index) varied significantly over time ($P < 0.0001$) but not with sexes, year classes, or interaction effects ($P > 0.05$) in the limited period for which such data was gathered (three-way ANOVA). However, no significant correlation existed between the mean liver index and the ration for the respective months. A weak positive correlation was established ($r = 0.36$, $P < 0.01$), however, when monthly mean liver indices were paired with the rations of each previous month. This suggests that liver weight was somewhat responsive to feeding rate after a delay period, as noticed by Heidinger and Crawford (1977).

Metabolism

Dissolved oxygen concentrations declined linearly in all metabolism determinations. There were no initial periods of elevated oxygen consumption due to stress, nor effects due to activity, diel

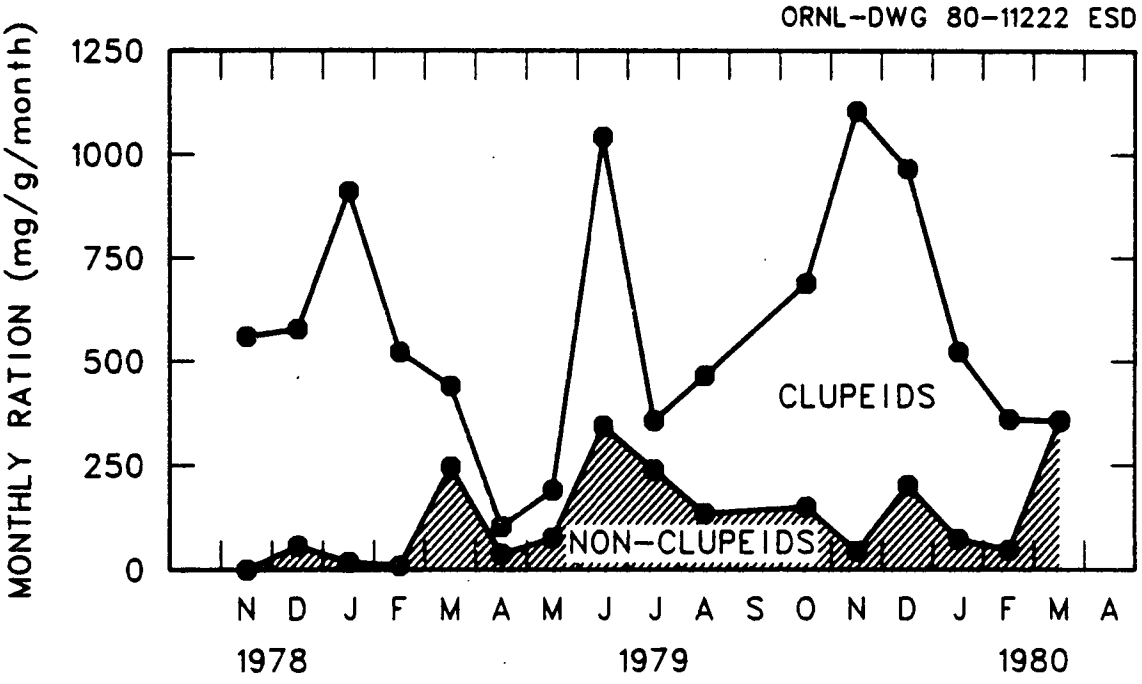


Figure 3. The monthly ration of sauger (mg/g/month). The upper line represents the total ration of all species consumed, the lower line represents that part of ration consisting of non-clupeid species, and the difference between the lines represents that ration consisting of clupeid species.

metabolic periodicity, rising carbon dioxide tension, or declining dissolved oxygen tension.

The relationship between the standard oxygen consumption rate of sauger and temperature (Figure 4) was best described ($r^2 = 0.91$) by the regression equation:

$$Q'_s(mg_2O/h/g) = 0.0233 \cdot 10^{0.03T} ,$$

where:

T = temperature in degrees Celcius.

Given the metabolism-weight relationship, the form of the complete metabolism equation is:

$$Q_s(mg_2O/h) = X \cdot 10^{0.03T} \cdot W^{0.85} ,$$

where:

W = weight in grams.

X = unknown regression coefficient.

Because the metabolic rate of a 395 g sauger (the mean weight of our experimental animals) was predicted by our weight specific metabolism regression times 395, we solved for the coefficient of the complete regression required to balance the equation.

The metabolic rate of a 395 g sauger at 20°C (standard temperature of metabolism investigations) predicted by the empirical equation is:

$$Q_s(mg\ O_2/h/g) \cdot g = 0.0233 \cdot 10^{0.03(20)} \cdot 395 = 36.64 .$$

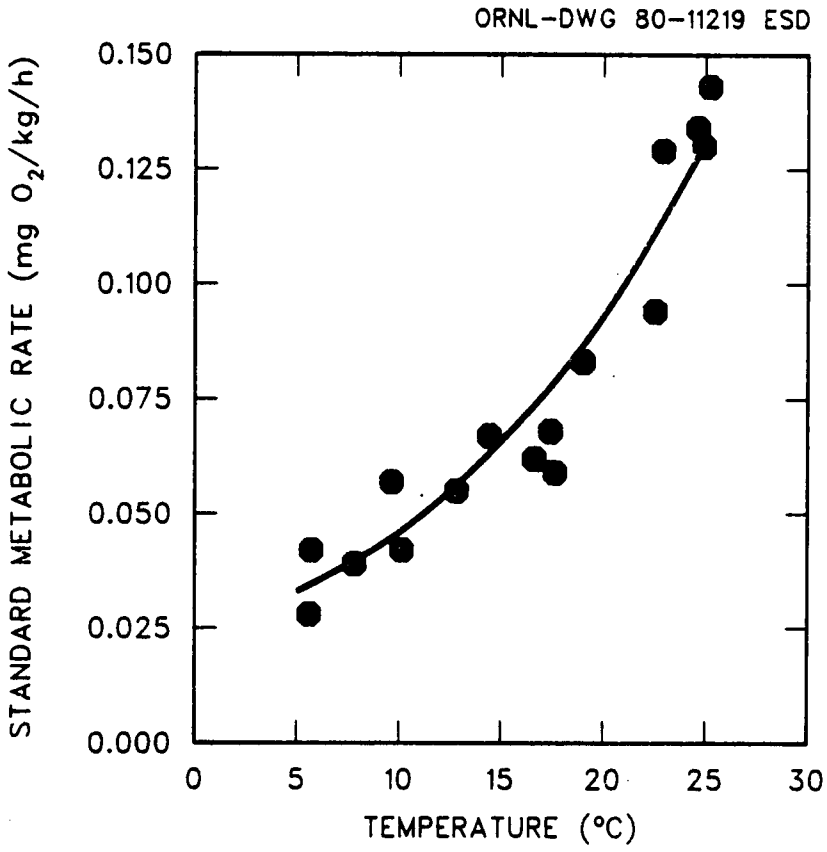


Figure 4. The observed standard metabolic rate of sauger at various temperatures in milligrams of oxygen consumed per gram of fish per hour. The curve represents the log-transformed regression curve fitted to the data by the method of least squares.

We then solved for the multiple regression coefficient:

$$Q_s(mgO_2/h) = 36.64 = X \cdot 10^{0.03(20)} \cdot 395^{0.85}$$

$$X = 0.057 \quad .$$

Therefore the complete regression equation is:

$$Q_s(mgO_2/h) = 0.057 \cdot 10^{0.03T} \cdot W^{0.85}$$

Respiration metabolism was converted to energetic metabolism, for the purposes of the energetics model, using the relationship of calories of food energy released per milligram of oxygen consumed. For a carnivorous diet such as the sauger's, this equals 3.36 (Phillipson 1966). The standard energetic metabolism equation was then expressed as:

$$Q_s(cal/h) = 0.192 \cdot 10^{0.03T} \cdot W^{0.85} \quad .$$

Growth

The parameters which determined the energy value of sauger were length, body weight per unit length, gonad weight, fat weight, and the weight-specific energy values of the body components (gonads, fat, and body minus gonads and fat).

Analysis of 179 scales for age and growth in length of the population showed that one specimen was of the 1979 year class (was spawned in the past year), 122 were of the 1978, 47 were of the 1977,

and 7 were of the 1976. No year class grew significantly in length over the winter from October 1979 to February 1980 (one-way ANOVA, $P > 0.05$).

The relationship of the total length of sauger to the scale radius was best described by a linear geometric means regression equation. Lengths back calculated from this relationship compared closely to the actual measured lengths of the fish, verifying the validity of the scale radius to length relationship.

	Year Class			
	1979	1978	1977	1976
Mean calculated length (mm)	259	347	420	489
Mean measured length (mm)	259	349	421	489
Sample size	1	123	47	7

The lengths of the various year classes at previous annulus formations were then calculated (Table 3). The mean size at any given age declined with successive year classes; however, only the 1976 and 1977 year classes at age three differed significantly (one way ANOVA, $P < 0.05$).

Gonad weight strongly influenced the total body weight (W) per unit length (L) or condition factor K ($K = 100 \bullet W/L^3$) (Tesch 1971). The condition factor showed significant variation due to time, year class, sex, and all interaction effects (three-way ANOVA, $P < 0.01$). To realistically monitor the true somatic tissue weight, we calculated an adjusted condition factor in which gonad weight (G) was subtracted

Table 3. Mean and standard deviation of the calculated total lengths (mm) of sauger after each year of growth

Year Class	Calculated total length at age (mm)				n
	1	2	3	4	
1976	290 ± 34	385 ± 31	447 ± 18	489 ± 07	7
1977	272 ± 22	366 ± 27	420 ± 27		47
1978	260 ± 28	347 ± 36			123
1979	259				1

from body weight and in which the exponent of length was changed from the standard of 3.0 to 3.4. This modified exponent was the coefficient of the regression relating the logs of the somatic weights of all sauger to the logs of their lengths. The adjusted condition factor ($ACF = 100 \bullet (W-G)/L^{3.4}$), did not vary significantly with sex, year class or interaction effects but only with time (three-way ANOVA, $P < 0.0001$). Because most of the other physical growth parameters varied with size of the fish, they and ACF were analyzed independently for the two most abundant year classes, the 1977 and 1978 year classes. These two cohorts accounted for 458 of the total 897 sauger caught. The ACF was highest for both year classes in the winter of 1979 and was lowest that year in October (Figure 5). The range of variation was not negligible; the seasonal range in condition factor of the 1977 year class represents a 134 g range in weight for a 40 cm sauger.

Gonad development began in October or November in 1979 for both sexes of both year classes (Figure 6). Beginning in the fall the gonad somatic ratio (gonad weight divided by the total body weight less the gonad weight) of both sexes and year classes increased regularly and significantly (one-way ANOVA, $P < 0.0001$). When sampling began in November 1978, gonad weights of the 1977 year class were already elevated over the basal, post-spawning level. The younger year class was not mature and did not develop gonads. The index of the 1977 year class dropped sharply following spawning to a basal level in June 1979.

The fat somatic ratio of sauger (fat weight divided by total weight less gonad weight) varied significantly between year classes

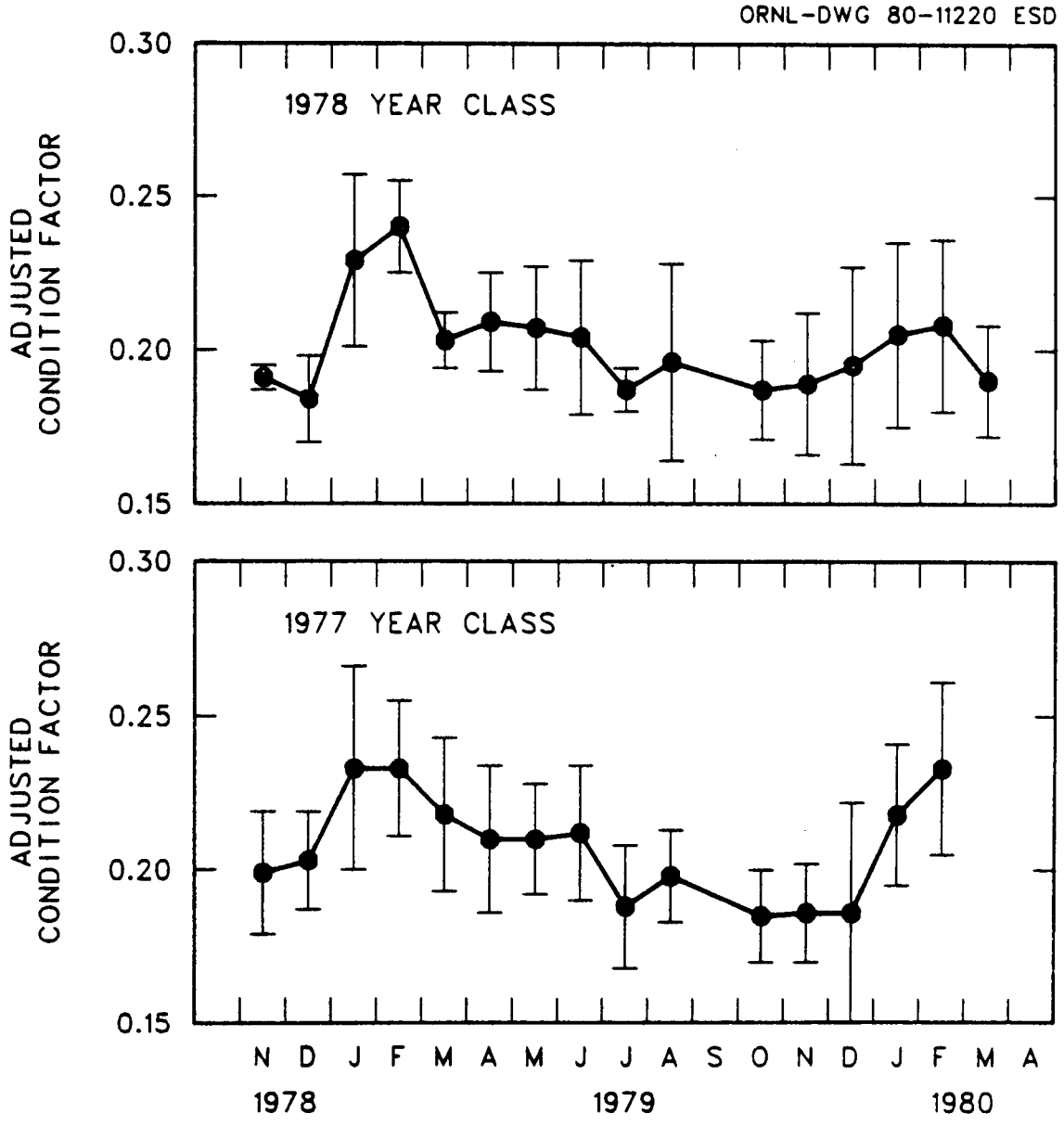


Figure 5. Calculated monthly means and standard deviations of the adjusted condition factor ($100(W-G)/L^{3.4}$) of individuals of the 1978 year class (upper graph) and 1977 year class (lower graph).

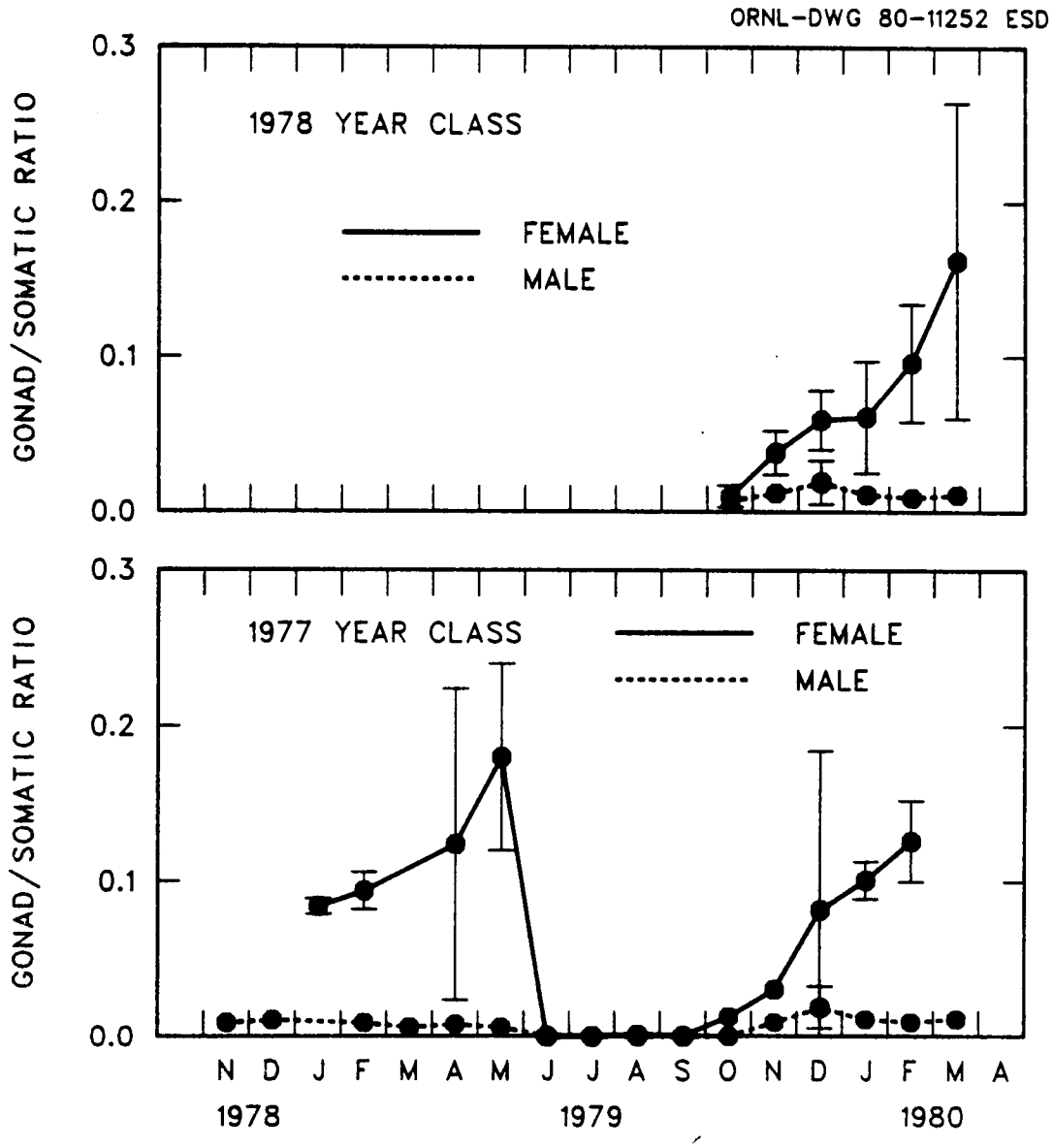


Figure 6. Calculated monthly means and standard deviations of the ratios of gonad weight to somatic weight for individuals of the 1978 year class (upper graph) and 1977 year class (lower graph).

(three-way ANOVA, $P < 0.0001$) and, therefore, was analyzed independently by year class. The fat somatic ratio of the 1977 year class varied significantly over time alone (two-way ANOVA, $P < 0.01$). No significant variation in the fat somatic ratio of the 1978 year class occurred with sex, time, or interaction effects (two-way ANOVA, $P > 0.05$). However, the pattern of variation over time was similar for the two year classes, with the older year class (1977) maintaining a higher ratio (Figure 7). Both year classes developed fat stores in the winter months and lost them relative to body weight in the summer.

The energy value per gram ash-free dry weight (AFDW) of the sauger carcass, with fat and gonadal tissue removed, varied significantly over time ($P < 0.05$) but not with sexes, year classes, or interaction effects (three-way ANOVA, $P > 0.05$). The value peaked in the winter months (Figure 8). The energy values per gram of the fat and gonadal tissues did not vary significantly with time, sex, year class, or interaction (three-way ANOVA, $P > 0.05$).

The calculated energy value per gram of the whole body was strongly influenced by the high caloric value of the fat and gonads. The overall mean values for fat, gonads, and carcass were 7.7 kcal/g wet weight (9.1 kcal/g AFDW), 4.2 kcal/g wet weight (6.8 kcal/g AFDW), and 1.4 kcal/g wet weight (6.1 kcal/g AFDW), respectively. The energy value per gram of the 1977 year class was consistently higher than that of the 1978 year class. For both year classes, this energy value peaked in the early spring (Figure 9). For both this variation over time was significant ($P < 0.05$), but the sexes were not significantly different (two-way ANOVA, $P > 0.05$).

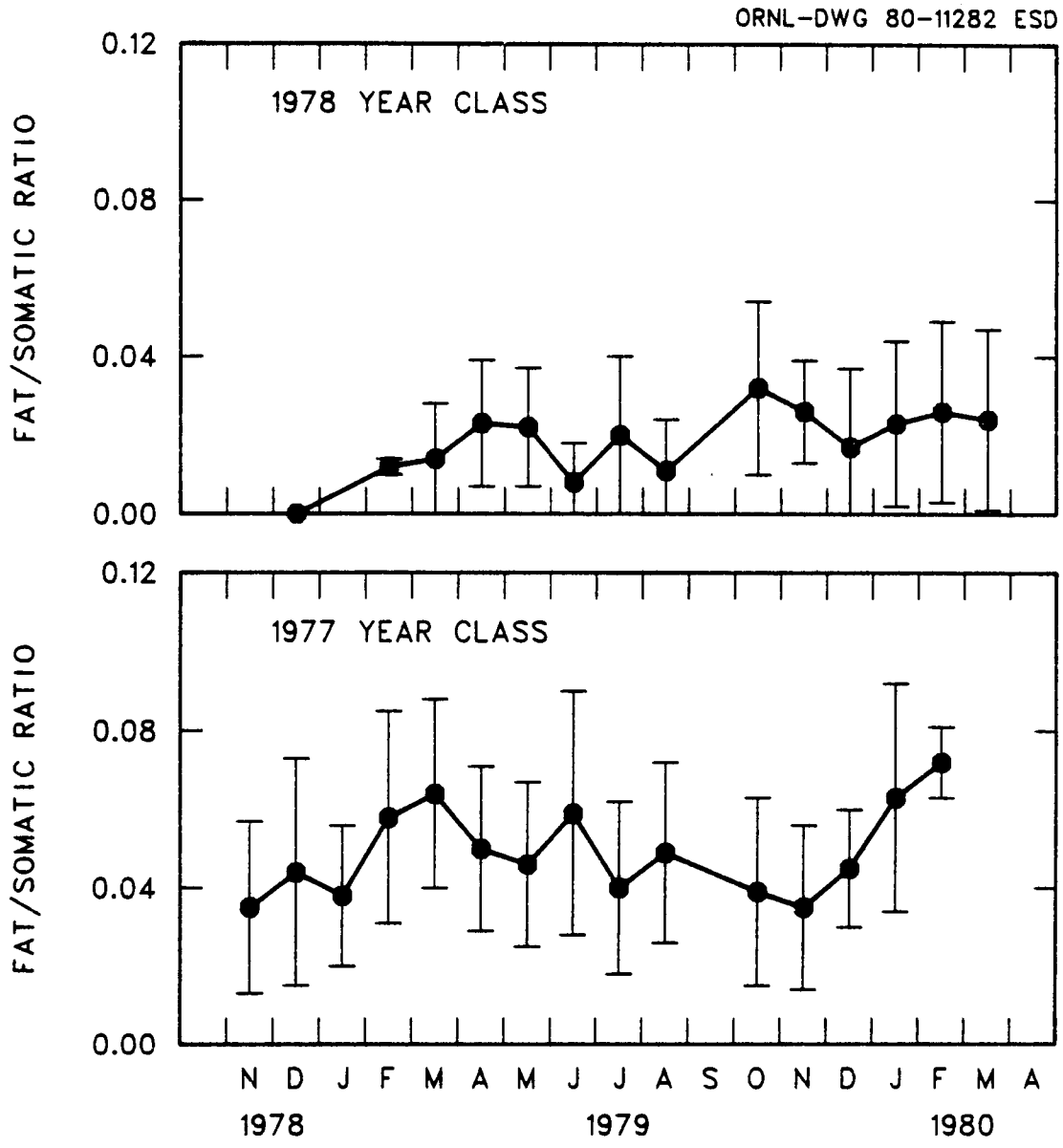


Figure 7. Calculated monthly means and standard deviations of the ratios of fat weight to somatic weight for individuals of the 1978 year class (upper graph) and 1977 year class (lower graph).

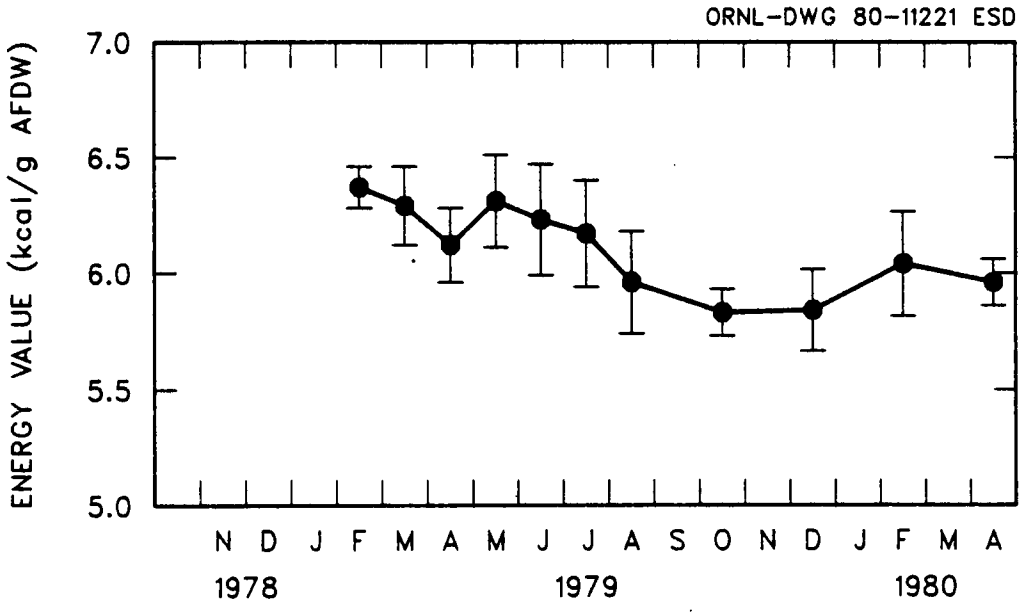


Figure 8. Monthly means and standard deviations of the energy values of sauger carcasses with fat and gonads removed (kcal/g AFDW).

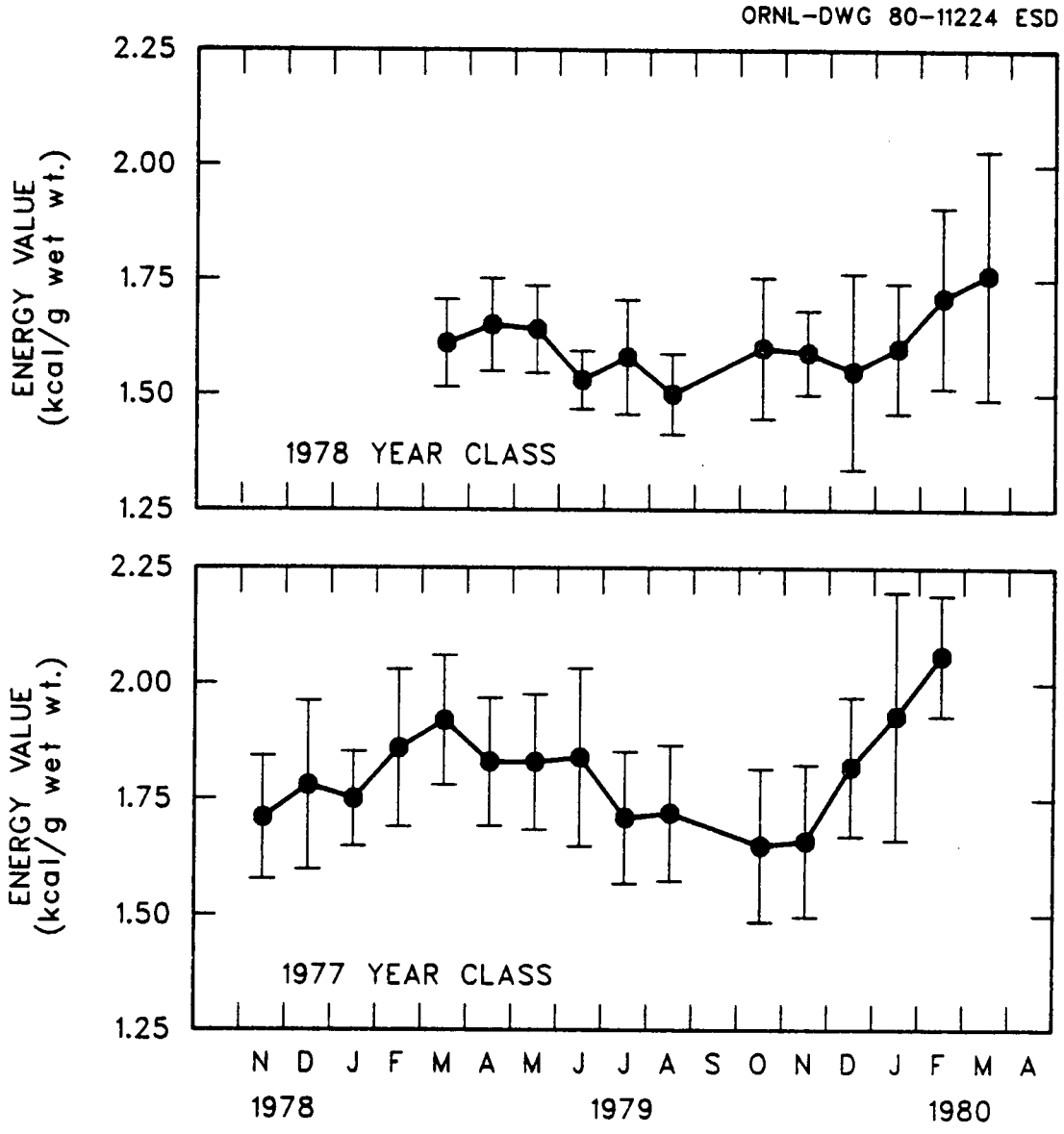


Figure 9. Calculated monthly means and standard deviations of the energy values of individuals of the 1978 year class (upper graph) and 1977 year class (lower graph) (kcal/g).

Average total energy values of individuals of a year class were determined to calculate growth over a defined period (Table 4). During the 1979 growing season, mid-March to mid-October, the average individual of the 1978 year class had an initial energy value of 226.2 kcal and a final value of 584.1 kcal representing a gain of 357.9 kcal. The average 1977 year class sauger gained 392.3 kcal in this period, not including gonad growth subsequently lost in spawning. This gonad energy loss averaged 75.3 kcal for females and 0.0 kcal for males. Because no significant differences between males and females could be detected between the sexes in gonad-free initial or final energy values (least-squares-means procedure, $P > 0.05$) or in consumption rates (one-way ANOVA, $P > 0.05$), this energy loss was disregarded. This simplification will result in a slight underestimate of the amount of growth displayed by individuals in the 1977 year class.

Sauger of both year classes gained energy value in the winter due to fat and gonad storage, despite their failure to grow in body length. From mid-November 1978 to mid-March 1979, the average individual of the 1977 year class gained 225.1 kcal. From mid-October 1979 to mid-March 1980, the average 1978 year class sauger gained 157.1 kcal. Low sample size of the 1977 year class prevented an accurate estimate of growth in the latter period.

The gross efficiency for the observed growth in energy value of the sauger was calculated to be 24.4% for the 1978 year class in the growing season, 8.0% in the winter of 1979-80, and 18.1% for the 1977 year class in the growing season.

Table 4. Calculated caloric values of average individuals of the 1978 and 1977 year classes of sauger at critical times in the study period

Date	Caloric value (kcal)	
	1978 Year Class	1977 Year Class
November 15, 1978	224.0	644.4
March 15, 1979	226.2	869.5 (826.3)[a]
October 15, 1979	584.1	1218.6
March 15, 1980	741.2	b

[a]Energy value not including gonads.

[b]Insufficient sample size for accurate estimate.

Energetic Model

The predictive growth model ($Q_G = P \bullet Q_R - Q_S$) synthesized the parameters of the sauger population's energetic dynamics. The predicted energy gain over the summer growth period was close to the observed gain for both age classes of sauger (Table 5). The model equation, in which the variables refer to columns of parameters in Tables 5 and 6, was:

$$G = 0.65(A \bullet D \bullet E) - (A \bullet 0.0046 \bullet 10^{0.03(F)} \bullet D^{0.85})$$

where:

$$D = B/C$$

$$B_{i+1} = B_i + G.$$

The model disclosed monthly periods of negative as well as positive energy balance (Table 5). Although the exact values are not thought to be precise determinations of the energetic balance for the periods, the monthly balances do serve as a gross index of a cohort's energy dynamics.

The model predicted that in mid-October 1979, that the 1978 year class would have a mean caloric value of 566.0 kcal, representing a 339.8 kcal energy gain since March 15, 1979. This predicted growth was 5.0% lower than the observed growth of 357.9 kcal. The calculation for the 1977 sauger year class predicted a final value of 1270.6 kcal, a 444.3 kcal energy gain over the period, 13.2% higher than the observed 392.3 kcal gain.

The predicted energy surplus over the winter period for the 1978 sauger year class was quite high (Table 6); the model predicted a

Table 5. Calculated results of the bioenergetics model for the period March 15, 1979 to October 15, 1979, for the 1978 and 1977 year classes

1978 Year Class

Column	A	B	C	D	E	F	G
Initial date of interval	Days in interval	Predicted body caloric value (kcal)	Observed body energy equivalent (kcal/g)	Predicted body weight (g)	Observed caloric ration (kcal/g/day)	Observed mean monthly temperature (°C)	Predicted caloric growth in interval (kcal)
March 15, 1979	16	226.2	1.660	136.3	.00697	5.7	3.2
April 1	30	229.4	1.593	143.4	.00087	11.3	-19.5
May 1	31	209.9	1.537	136.3	.02948	16.6	52.5
June 1	30	262.4	1.457	180.1	.05900	19.6	162.9
July 1	31	425.3	1.492	285.4	.02539	19.6	80.6
August 1	31	505.9	1.488	339.5	.01106	21.3	-10.5
September 1	30	495.4	1.530	323.8	.01833	23.0	23.4
October 1	15	518.9	1.574	329.6	.02587	19.2	47.1
October 15	0	566.0	1.574	359.6			

1977 Year Class

Column	A	B	C	D	E	F	G
Initial date of interval	Days in interval	Predicted body caloric value (kcal)	Observed body energy equivalent (kcal/g)	Predicted body weight (g)	Observed caloric ration (kcal/g/day)	Observed mean monthly temperature (°C)	Predicted caloric growth in interval (kcal)
March 15, 1979	16	826.3	1.816	455.0	.00720	5.7	15.4
April 1	30	841.7	1.791	470.2	.00633	11.3	1.6
May 1	31	843.3	1.755	480.5	.00045	16.6	-84.5
June 1	30	758.8	1.756	427.3	.02663	19.6	129.3
July 1	31	888.1	1.610	551.6	.02448	19.6	157.4
August 1	31	1045.4	1.728	604.3	.01106	21.3	-6.6
September 1	30	1038.9	1.760	590.3	.02200	23.9	99.5
October 1	15	1138.4	1.788	636.0	.03481	19.2	132.2
October 15	0	1270.6	1.788	709.8			

Table 6. Calculated results of the bioenergetics model for the period October 15, 1979 to March 15, 1980, for the 1978 year class

1978 Year Class							
Column	A	B	C	D	E	F	G
Initial date of interval	Days in interval	Predicted body caloric value (kcal)	Observed body energy equivalent (kcal/g)	Predicted body weight (g)	Observed caloric ration (kcal/g/day)	Observed mean monthly temperature (°C)	Predicted caloric growth in interval (kcal)
October 15,1979	16	584.1	1.633	357.6	.02425	19.2	51.6
November 1	30	635.7	1.603	390.0	.03787	14.7	227.0
December 1	31	862.7	1.605	537.5	.04790	8.6	466.4
January 1, 1980	31	1329.1	1.646	807.5	.00903	7.0	80.5
February 1	29	1409.6	1.773	795.0	.02276	4.9	284.4
March 1	15	1694.0	1.869	906.4	.03347	9.4	257.5
March 15	0	1946.5	1.869	1041.4			

1362.4 kcal surplus for growth, while known growth was only 157.1 kcal. We consider this one order of magnitude discrepancy in observed and predicted caloric growth to be much greater than the margins of error in the modeling parameters' estimated values. Therefore, it is likely that the energetic principles of the model are invalid for the winter no-growth period. The winter period energetics of the 1977 year class were not modeled due to inadequate sample sizes in this period.

The model simulation indicated that if the 1977 year class had not stored energy reserves in the winter (initial energy value of 644.4 kcal), then its individuals would grow to a mean energy value of only 920.1 kcal by October 15, 1979. This final energy value is 24.0% less than the observed mean October 15 energy value of 1218.6 kcal. If the cohort was to adjust its feeding rate, the model predicted the cohort would require 13.0% more food energy than it was observed to consume in the growing season if it was to reach the observed energy value in October.

V. DISCUSSION

This study presents one of the few models of growth of individuals in a natural fish population which has been verified by comparing independent predicted and observed energetic parameter values. The approach was an extension of the basic energy equation; however, our model incorporates two variables recently recognized as significant to the energy balance of fish: (1) specific dynamic action and (2) self-catabolism efficiency. Previous verified modeling applications have failed to include specific adjustments for the effects of these two variables. However, it is now known that specific dynamic action significantly affects the efficiency of growth, because it consumes around 15% of intake energy (Brett and Groves 1979). Furthermore, through analysis of observed weight losses of starving animals Kleiber (1961) described the efficiency penalty of utilizing stored energy which is characteristic of all biochemical transformations. Niimi and Beamish (1974) quantified this efficiency as 92.5% in starved largemouth bass. Thus, in modeling, if energy intake drops below a maintenance level, energetic losses should be increased by 7.5%.

In our modeling effort, growth of the average population member and all the major input parameters thought to be critical to that growth have been directly determined. The model's growth prediction is relatively close to that observed (within 14% of the observed growth of both age classes). Thus the study represents a closely verified model of the bioenergetics of a fish population, and the model reinforces the

accuracy of the current techniques we employed for estimating bioenergetic parameters and the validity of the current modeling assumptions.

The veracity of the model's assumptions and parameter estimates have each been considered independently and are believed to represent a valid application of fish energetics principles.

The technique of the consumption estimation was a variation of those of Swenson and Smith (1973) and Popova and Sytina (1977). In his extensive review of techniques for determining consumption, Mann (1978) endorsed this technique, regretting that its difficulty required the Swenson and Smith study to be limited to one year class of fish for one season of the year.

We did not adjust the digestion rate for every size meal consumed by sauger as did Swenson and Smith (1973). The relatively conservative range in meal sizes of Watts Bar sauger (20-60 mg/g) would result in a maximum range of estimates of digestion rates of about 10%. The added complexity of the separate calculations was judged to be unwarranted.

The consumption estimate of our study relied in part on Swenson and Smith's determination of the digestion rate of sauger. Their data was readily applicable to the Watts Bar sauger population because they determined that there was no significant difference in the digestion rate between neighboring sauger populations or even between sauger and walleye.

We were able to estimate the consumption rate over a 17-month period by correlating the relatively limited daily ration data with the extensive feeding data from the 24-h net sets. The relationship of the

two consumption indices is promising, because the 24-h sample feeding index is considerably easier to determine than the direct daily ration. Though this relationship may hold only for populations which exhibit continuous diel feeding, this feeding mode may be fairly common for predator populations in the numerous turbid riverine and reservoir systems (Ryder 1977). Lack of crepuscularity in feeding of Watts Bar sauger is attributable to the perennial turbidity of this system; the mean secchi disk visibility over the study period was 93.8 $\pm$ 34.8 cm. Swenson and Smith (1973) noted continuous feeding of walleye in one month of their study in Lake of the Woods, Minnesota.

The regression equation relating the sauger's standard caloric metabolism to temperature was parallel to that relating maintenance metabolism to temperature for walleye of unspecified weight determined by Kelso (1972) by controlled feeding. The two regression equations are:

$$\text{LOG } Q_S = 1.120 + 0.0297T,$$

(sauger standard metabolism (cal/g/week))

$$\text{LOG } Q_m = 1.286 + 0.0290T,$$

(walleye maintenance metabolism (cal/g/week)).

The coefficients of determination of the two regressions are 0.91 and 0.96, respectively. That these relationships of the two closely related species were so nearly parallel reinforces the validity of our estimates.

The model assumes that activity metabolism was not an important parameter governing the growth of sauger. This is perhaps the least

substantiated assumption employed. Winberg (1956) proposed that in general a fish's field metabolism was two times its routine metabolic rate (Winberg II) because of the extra energetic cost of activity, but this has not been accepted as applicable to all species. Warren and Davis (1967) suggested that activity metabolism was a negligible portion of a moderately active fish's total field metabolism including specific dynamic action. Evidence suggests the field metabolism of sauger is less than Winberg II, because the sauger is inactive much of the time in the field and laboratory (Craig Harned, Tennessee Valley Authority, personal communication; Minton, unpublished data). Following ultrasonic telemetry studies of the field activity of another cold tolerant piscivore, northern pike (Esox lucius), Diana (1979 a,b) concluded that the field metabolism of that predator approximated standard metabolism. In their energetics model, Kitchell et al. (1977) assumed that the field metabolism of walleye was the same as the standard metabolism. However, their assumption was untestable due to the hypothetical nature of their input parameters.

Our model application closely predicted the observed summer growth of sauger without adjustment for activity metabolism. Margins of error in the modeling parameter estimates prohibit concluding that sauger exhibit no activity metabolic costs in the growing season. Nonetheless, the closeness of the growth prediction indicates that activity metabolism is not of primary importance in influencing the growth of sauger in the summer.

The assumption that fecal, non-fecal, and apparent specific dynamic action losses account for a constant 35% of energy intake is

supported by current research. The portion attributed to apparent specific dynamic action is consistently within 12 to 16% of energy intake within natural ranges of feeding rates and temperatures. The carefully controlled studies of apparent specific dynamic action in largemouth bass (Micropterus salmoides) (Beamish 1974), aholehole (Kulia sandvicensis) (Muir and Niimi 1972), and bluegill (Lepomis macrochirus) (Pierce and Wissing 1974) all estimated values of apparent specific dynamic action of around 15% of diet energy.

Elliot (1976) determined that proportional fecal and nonfecal losses of brown trout (Salmo trutta) varied with ration and temperature changes. However, the two effects were antagonistic, resulting in only conservative variation in the total energy loss. Other investigations with a variety of fish species demonstrated that the fecal and nonfecal energy losses represented a relatively constant proportion of the energy ration over a range of temperatures and ration levels. Combined fecal and nonfecal losses of most piscivorous fish studied average around 20% of intake energy (Brett and Groves 1979).

Kelso (1972) reported a very high energy assimilation efficiency in walleye fed a diet of fish (around 97%); however, he made no concurrent measure of nonfecal energy losses. Solomon and Brafield (1972) monitored both the fecal and nonfecal losses of another percid, the perch (Perca fluviatilis), which was fed a diet of amphipods. Total fecal and nonfecal energy losses of the perch averaged 24.2% of intake energy. The losses of piscivorous percids are probably lower, because the efficiency of assimilating hard exoskeletal invertebrates

is generally less than the efficiency of assimilating a diet of fish (Brett and Groves 1979).

As a verified delineation of the dynamics of production of sauger, the bioenergetic model serves several functions: (1) It constitutes a framework which interrelates the associated processes of energetics. (2) The model functions as a working simulator of the energetic dynamics of sauger by which the effects on sauger of system perturbations may be predicted. (3) The model helps identify the critical parameters regulating growth, thus directing the priority of further research.

Framework of energetic processes

The model's mean monthly energy balances indicate how metabolism and consumption interact in determining growth. For example, the consumption rate of the 1977 year class sauger in August 1979 was 75% higher than in April while the metabolic rate in August resulted in a net energy loss for the month of 6.6 kcal; whereas, in April the sauger gained 1.6 kcal. This phenomenon gives insight into the mechanisms which cause reduced growth of Stizostedion species subjected to elevated summer thermal regimes (Wrenn et al. 1979).

The heavy feeding in early summer fueled the first major positive energy balance of the growing season for both year classes (Table 5). The feeding rate of the 1977 year class was very low in April and May due to migration to spawning habitats which had very low prey density, as evidenced by the gill net catches. The feeding rate of the smaller sauger, of the 1978 year class was also very low in April. Perhaps

this was due to the lack of young-of-the-year forage species of suitable size. However, in June and July 1979, shad concentrated in certain coves to spawn in shallow water where they may have become easy prey for sauger to capture (Johnson 1969). The ration of both year classes increased dramatically in this period and resulted in the major positive energy balance of the growing season.

Sauger energy intake substantially exceeded their metabolic requirements during one other period of the year, late fall and winter. This surplus occurred at the time when extra energy was required for the sauger's gonad development and spawning migration. The surplus was the result of very heavy feeding upon shad.

It was hypothesized that the increased feeding rate on shad was due to the vulnerability to predation of the shad due to cold stress. Impingement of shad on the cooling water intake screens of power facilities has been correlated with cold stress (McLean et al. 1980). Thus, it was thought that sauger predation on shad might be correlated with shad impingement by virtue of the hypothesized common cause. In fact, the monthly ration of the sauger population was highly correlated ($r = 0.76$, $P < 0.05$) with the monthly percent of the total seasonal impingement count on the intake screens of the Tennessee Valley Authority's Kingston Steam Plant power generating facility on Watts Bar Reservoir in the winters of 1978-79 and 1979-80 (McLean, unpublished data) (Figure 10). However, predation on the clupeids was not significantly correlated with the actual numbers of clupeids impinged over the two years, ($P > 0.05$). Many more shad were impinged per month in the winter of 1978-79 than in the winter of 1979-80, while

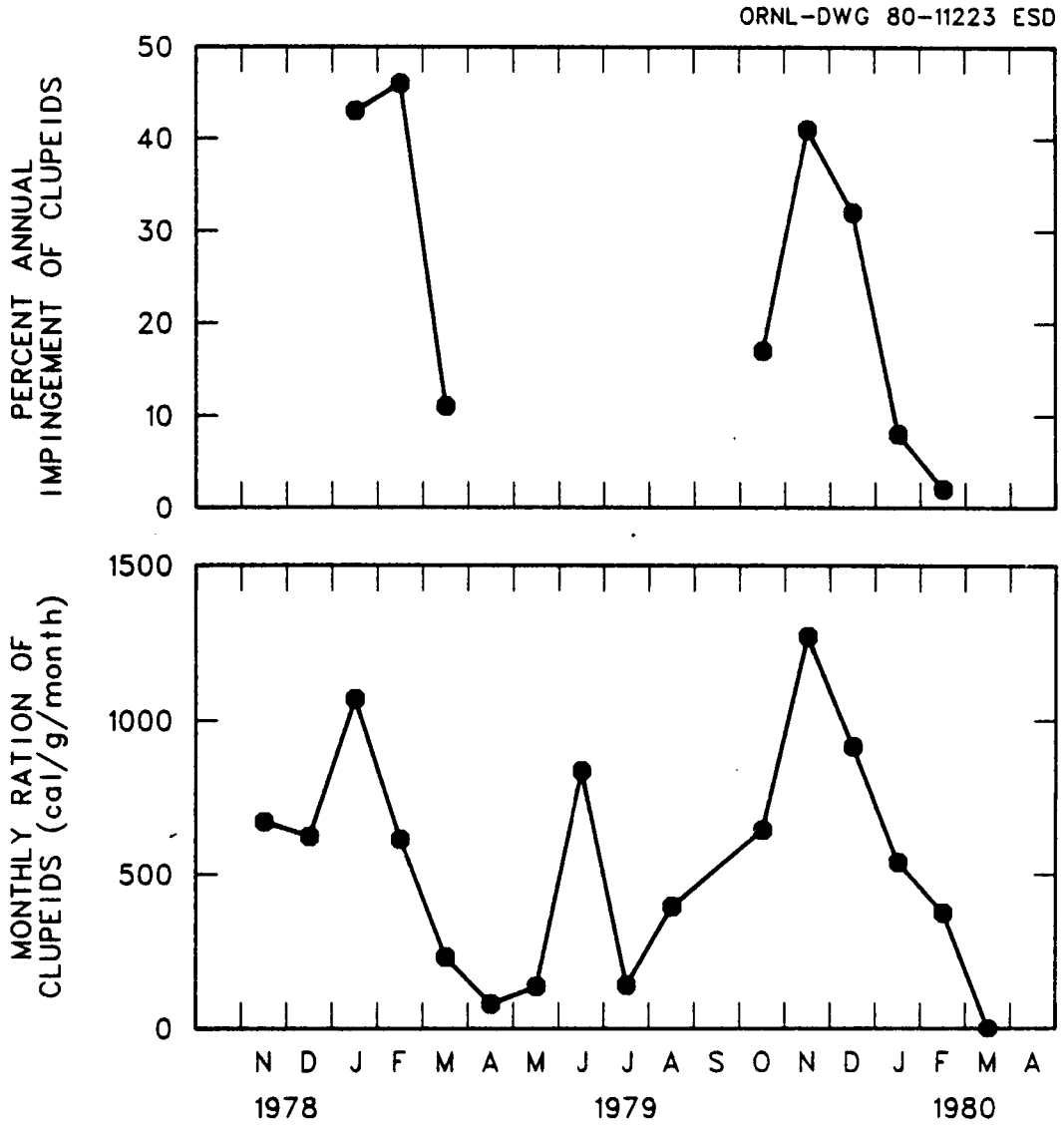


Figure 10. Upper graph: monthly percentage of the total annual count of clupeid species impinged at Kingston Steam Plant. Lower graph: sauger's monthly ration in energy value of clupeid species (cal/g/month).

slightly less shad were consumed in 1978-79. This suggested that in neither year were the sauger prey limited and that predation was actually a function of the relative vulnerability of the prey, not its density.

In both years, the sauger's ration of clupeids peaked at or near the time of their greatest impingement rate and then declined proportionally to impingement. The impingement peak likely represented the time of the first severe cold stress of the shad populations. The decline thereafter probably represented a decline in shad population numbers due to cold kill, predation, impingement, and the increasing restriction of the population to a few thermal refuges. These refuges are areas of water warmer than ambient in winter and are predominantly located in coves which have inflowing springs of moderate water temperatures. The hypothesized retreat to these refuges is supported by the order of magnitude increase of the biweekly gill net catches of clupeids in both winters in the two thermally affected sampling stations (McLean et al. 1980).

The power facility intake appeared to act as a predator, taking clupeids in numbers proportional to their vulnerability. It is unlikely, however, that the power facility offered severe competition to the sauger for shad, because the numbers of shad impinged are far short of the numbers killed by natural cold stress (McLean et al. 1980). Furthermore, in the final weeks of the cold stress season, when the clupeid populations are greatly reduced, potential competition between the facility and sauger is minimized by the spawning migration of the adult sauger out of the winter habitats of the shad. However, the relationship of the consumption of prey by a predator and the

impingement of that prey is potentially very important. The extensive nationwide impingement data base perhaps could serve as a valuable index of prey availability during winter months in the various systems.

The observed model parameters suggest that sauger may be uniquely adapted for utilizing sporadically available forage. During periods of low principal prey availability sauger prey switched to alternate species of energy values comparable to shad. Sauger also minimized metabolic expenditures by inactivity and a relatively low thermal preference (Dendy 1945; Minton, unpublished data). During periods of high prey availability the ration of the sauger far exceeded metabolic requirements, thus maximizing energy gain. The sauger is particularly adapted for utilizing cold-stressed prey, because it is cold tolerant (Collette et al. 1977) and is able to digest food relatively rapidly at low temperatures (McGee et al. 1977). Furthermore, gonad development, fat storage, and increases in somatic tissue energy value per gram all occurred primarily in winter, utilizing increased energy intake. Winter energy storage, particularly building fat reserves, occurs widely among cold tolerant species (Wilkins 1967, Brett et al. 1969, Groves 1970, Love 1970).

As a result of their successful adaptation to fluctuations in prey availability, the sauger exhibited rapid growth in length. The Watts Bar Reservoir population grew at a faster rate than that reported for Northern sauger and faster than one of three Southern populations studied (Table 7).

Because previously published studies of sauger growth calculated the scale radius to total length relationship by

Table 7. Comparison of sauger growth in different waters

Location	Mean Calculated Total Length of sauger of each age group (mm)					Reference
	1	2	3	4	5	
Lake Nipigon, Ontario			239	264	312	Hart 1928
Lake of the Woods, MN	126	185	235	276	313	Carlander 1949
Lewis & Clark Lake, SD	188	324	404	466	514	Nelson 1969
Garrison Reservoir, ND	125	219	305	378	457	Carufel 1963
Lake Winnibago, WI	130	246	309	357	377	Priegel 1969
Cherokee Reservoir, TN	236	373	439			Stroud 1949
Douglas Reservoir, TN	251	396				Stroud 1949
Norris Reservoir, TN	213	337	396	437	472	Hassler 1957
Watts Bar Reservoir, TN	238	337	398	418		McGee Unpublished data
Watts Bar Reservoir, TN	281	363	418	468		a
	270	366	434	489		b

[a]As calculated by least squares regression analysis (Tesch 1971).

[b]As calculated by geometric means regression analysis (Ricker 1973).

least-squares-regression analysis (Tesch 1971), we also performed growth analysis by that method in addition to the geometric means regression analysis (Ricker 1973) for comparison. Results of both analyses on our data are reported in Table 7. The least-squares technique calculated greater mean lengths for age one sauger and lesser mean lengths for age four than did the geometric-means technique. The geometric-means technique more closely predicted the actual measured lengths of sauger.

Growth was consistently good over the four years disclosed by this study, indicating the sauger could adjust to varying degrees of severity of cold stress and winter kill of principal prey over the period (McLean, unpublished data).

Model simulation

The results of the model's simulation of sauger growth without winter energy gains emphasized the importance to adult sauger of winter energy gain. Growth of the mature year class would be substantially less if the winter feeding and energy gain did not occur. This facet of the energetics of sauger was examined because of its importance in defining the niche of sauger in Watts Bar and other southeastern reservoirs where their predation strategy is similar (Stroud 1949, Hassler 1953).

In these systems the largemouth bass (Micropterus salmoides) is frequently the dominant predator. In Watts Bar the largemouth does not appear to capitalize on winter shad vulnerability (S. M. Adams, personal communication). However, Adams determined that largemouth grow rapidly in Watts Bar. Good growth of both predators is likely the

result of niche partitioning such that largemouth utilize forage throughout the growing season but not beyond, and sauger maximize the utilization of cold stressed shad, many of which are destined to die naturally (McLean et al. 1980). The simulation indicated that for sauger to maintain good growth in spite of a failure to gain energy in the winter, feeding in summer would have to increase significantly, thus potentially increasing competition with the largemouth.

Prioritizing future research

The discrepancy in predicted and observed winter energy gains of the 1978 year class demonstrates that the balanced energy equation does not adequately describe the winter energetics of sauger. Factors contributing to the discrepancy in predicted and observed growth include errors in the modeling parameter estimates and inaccurate modeling assumptions (Table 8). Since the reasonable accuracy of the parameter estimates is well established and was verified for the summer season by the agreement of predicted and observed energetic growth, the bulk of this large error must be due to inaccurate assumptions for low temperature energetics modeling.

Reduced growth efficiency in winter has been noted for other species (Warren and Davis 1967), and may be due to excretion of food energy sources or activity. Brett et al. (1969) determined that the growth rate of sockeye salmon (Oncorhynchus nerka) fed fixed ration levels in the laboratory reached a maximum at some temperature between 5 and 15°C, depending on the ration level, and declined with increasing and decreasing temperatures around the optimal one. For instance,

Table 8. Potential sources of error in energetics modeling

Potential Sources of Error	Evaluation Criteria	Evaluation
Energetic Parameter Estimates:		
Consumption	-digestion rate determination specific to sauger -strong correlation of adjusted feeding index and daily ration -relatively large sample size sampled over diverse habitats	likely subject to a small margin of error
Metabolism	-standard metabolism-temperature relationship well estalished and parallel to maintenance metabolism of walleye (Kelso 1972) -metabolism-weight relationship inferred from related species -accurate field temperature data	likely very close to true standard metabolism
Growth	-measured in energy units for integration of all growth parameters -relatively large standard deviations of mean energy values of a year class -initial energy value of growing season based on predicted length at assumed time of annulus formation	likely subject to a small margin of error
Modeling Assumptions:		
Fecal and Nonfecal Losses	-assumed to consume a constant proportion of energy intake - though may increase with low temperatures	likely accurate at moderate temperatures but may underestimate losses at low temperatures
Field Metabolism	-assumed to equal standard metabolism based on field and laboratory observation of sauger -spawning migration of late winter unaccounted for	likely somewhat greater than standard year-round; significant difference occurring during the spawning run

growth occurred twice as rapidly at 10°C as at 5°C on a fixed 45 mg/g daily ration. The growth rate declined above the optimum temperature because of high metabolic costs associated with high temperatures, as predicted by the balanced energy equation. The decline in growth rate below optimum temperatures may have been due to increasing fecal and nonfecal intake energy losses with decreasing temperature, an effect noted in brown trout (Salmo trutta) by Elliot (1976). However, the proportional fecal and nonfecal losses of other species examined did not vary significantly with temperature (Brett and Groves 1979).

Paloheimo and Dickie (1966) noted that the gross growth efficiency of a number of fish species decreased as ration increased. This decrease may be explained by the observation of Kerr (1971) that spontaneous activity and energetic demands of fish increase with increasing consumption. The spawning migration of sauger would account for additional increases in activity during the heavy feeding period of winter. This activity could significantly decrease the sauger's energy surplus for growth. Brett and Groves (1979) determined that the metabolic rate of migrating sockeye salmon was 8.5 times their standard metabolic rate.

Combined assimilation efficiency declines and activity costs, as noted in the salmonids, would more than account for the discrepancy in predicted and observed winter caloric gain of Watts Bar sauger. However, complete characterization of the sauger's catabolic processes at low temperatures and the energetics of its activity will be required to describe its winter energetics. This would also require observation of the activity of the sauger in the field.

The validity of this model as a predictor of growth of sauger would be enhanced by comparison to further annual and within-year growth determinations. As the model is offered now, however, it predicts growth of sauger very closely to that observed for one season. This validates the basic structure and assumptions of the model. Thus, the model is clearly a valuable tool which serves as a framework for the energetic processes, simulates the effects of perturbations, and prioritizes future research.

VI. SUMMARY

The purpose of this study was to characterize the bioenergetic response of sauger to fluctuations in the availability of their principal prey, threadfin shad and young-of-the-year gizzard shad, which are subject to seasonal population crashes. The response of the sauger population was assessed by quantifying key energetic parameters and incorporating them into a model of the sauger's energetics. The results of the 17-month study are as follows:

1. This study presents one of the few models of growth of individuals in a natural fish population which has been verified by comparing predicted and observed energetic parameter values. Energetic parameters specific to the Watts Bar Reservoir sauger population, i.e., consumption, metabolism, and growth, were quantified by direct empirical determination. Other modeling assumptions were derived from published studies of related species. The model predicts the growth in energy value of average individuals of two year classes of sauger over one growing season. The predicted growth falls within 14% of the observed growth of the two year classes. The model is unique in that it incorporates apparent specific dynamic action and efficiency of catabolizing body energy stores, whose effects on growth were only recently evaluated.

2. The model's growth calculation is based upon direct determinations of the consumption and standard metabolism of Watts Bar sauger. The quantification of the consumption rate of two year classes of sauger over a 17-month period represents one of the most extensive studies of predation by piscivores to date. The determination was

facilitated by correlation of the daily ration of fish caught in two-hour net sets and feeding indices of fish caught in 24-hour sets. This relationship offers promise as a labor-saving technique for estimating the consumption rate of populations which feed regularly over 24 hours, as did the sauger.

The metabolic rate of sauger in the reservoir was determined as a function of water temperature and body weight. The relationship of weight-specific metabolism (Q_s) to temperature (T) (Q_S(mg O_2/kg/h) = 0.023 • $10^{0.03T}$) was empirically determined. The effect of body weight on metabolism was estimated by application of the results of studies on related species.

3. As a verified description of the energetic dynamics of sauger, our growth model serves to: (1) interrelate associated energetic processes, illustrating their function in determining the growth of sauger, (2) simulate growth dynamics of sauger, predicting the effect of perturbation to the population, and (3) identify critical energetic parameters, prioritizing future research efforts.

4. The sauger appeared to be uniquely adapted to utilizing the fluctuating prey base provided by threadfin shad and young-of-the-year gizzard shad. The cold tolerant sauger fed heavily on sluggish, cold-stressed shad in both winters of the study. Cold-stressed shad are also vulnerable to impingement. Sauger predation on shad and impingement of shad at Kingston Steam Plant were correlated in both winters by virtue of their common cause, cold stress. Sauger consumed large numbers of shad also in June, 1979, when the shad were concentrated in coves to spawn and were vulnerable to predation.

The sauger maximized utilization of peaks in predation by storing energy. Both dominant year classes stored significant amounts of energy in fat and gonads in the winters when growth in length did not occur. When shad availability declined, sauger prey switched to a limited degree. The sauger also minimized metabolic energy expenditures in the growing season through their low thermal preference and inactivity. Model simulation indicated that the energetic costs of field metabolism, including activity costs, were not significantly different from standard metabolism.

5. Model simulation also indicated the significance of the storage of energy reserves by sauger in winter, no-growth periods. If the sexually mature two-year-old sauger had failed to store energy in the winter of 1978-79, whether due to unavailability of prey or the physiological inability to utilize or store that diet energy, the total energy values of individuals of the year class at the end of the growing season would have averaged 24% lower than that observed.

6. Comparison of the growth of the Watts Bar Reservoir sauger population with other populations which had available a variety of prey bases, indicated that the adaptation of the Watts Bar population to its niche is quite successful. The Watts Bar population grew faster than any northern sauger population studied, and its growth was well within the range of the observed growth rates of other southern sauger populations.

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VITA

Joseph Walker Minton was born in Knoxville, Tennessee, on January 14, 1956. He attended Holston High School in Knoxville and graduated as valedictorian of his class in 1974. He entered The University of Tennessee, Knoxville in the fall of 1974. For one semester in the fall of 1977, Mr. Minton studied biology at Nottingham University, Nottingham, England. He received a Bachelor of Arts degree in biology from The University of Tennessee in the spring of 1978, graduating summa cum laude. While at The University of Tennessee, Mr. Minton was awarded a high school valedictorian scholarship and three academic merit scholarships.

Mr. Minton entered a Master of Science degree program in ecology at The University of Tennessee in the fall of 1978. In the winter of 1979 he accepted a research assistantship at Oak Ridge National Laboratory, where he conducted his thesis research. He received a Master of Science degree in March of 1981. Mr. Minton has accepted a Ph.D. assistantship in biological sciences at Florida State University. He will enter that program after graduation.

He is married to the former Susan Wymer of Oak Ridge, Tennessee. Mr. Minton is a member of the American Fisheries Society.