SOME ASPECTS OF TROPHIC RELATIONS

OF GIZZARD SHAD, DOROSOMA

CEPEDIANUM

by

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Thesis submitted to the Graduate Faculty of the

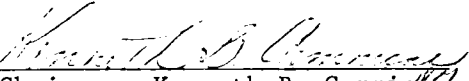Virginia Polytechnic Institute and State University
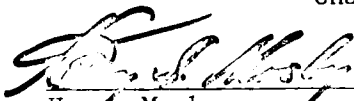
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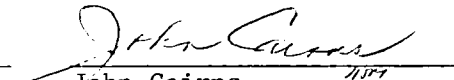
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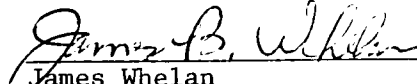WILDLIFE BIOLOGY

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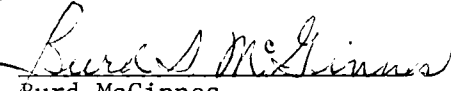Chairman, Kenneth B. Cummins

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Blacksburg, Virginia

TO JOE ANN AND CRYSTAL

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INTRODUCTION

Purpose and Scope of Study

One of the most desirable rough fish species in fresh waters is the
gizzard shad, _Dorosoma cepedianum_, which is sometimes called the "mud
shad" by sportsmen. Fishery biologists, in their endeavors to manage
lakes and reservoirs, have stocked gizzard shad as a forage base for
game fish, and this is with good reason for at least 17 game fish are
known to utilize this food resource. Miller (1960) and Jenkins (1957)
state that this particular clupeid provides one of the most direct links
in the food chains between the chlorophyllous primary producers and many
carnivorous fishes that can be established by current fishery management
practices.

The widespread success of gizzard shad introductions (natural or
otherwise) in lakes and reservoirs has, in recent years, led to many
investigations concerning the beneficial effect of this species on popu-
lations of game fishes and, when they become detrimentally over-abundant,
to methods of control of shad populations (Miller loc. cit.). Growth of
D. cepedianum young-of-the-year is very rapid. A size of five to seven
inches is attained in the first year. Beyong seven inches the shad is
no longer available as forage to many game species. The rapid growth
and high fecundity of this species lead, in some instances, to phe-
nomenal increases in population abundance. Madden (1951) reported that
the game fishes in Black Hawk Lake, Iowa, were suppressed by an increase

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in gizzard shad abundance. He also noted a decline in the bottom organisms with the progressive increase of shad. Kutkuhn (1958), in his study of plankton utilization by juvenile gizzard shad, intimated that populations of young shad may affect the condition and growth of young game fishes through competition for the microcrustacean food resource.

There have been several studies on the food of the gizzard shad (Smith 1963, Valesquez 1939, Tiffany 1921a and Kutkuhn 1958), but no recorded studies on the feeding behavior or metabolism of the gizzard shad. On the other hand many investigations have been conducted on the trophic relations of organisms which do not represent such direct links between sport fishes and the primary producers.

The importance of studies on the trophic relations of organisms was emphasized with the introduction of the concepts of trophic dynamics and trophic ecology (Lindeman 1942, Odum 1959 and Ivlev 1961). The knowledge of trophic relations (feeding ecology and energy transformations) of fishes is paramount in defining the flow of energy through aquatic ecosystems and equally valuable as a tool for better fishery management.

Review of the works of Ivlev (1945), Odum (1968), Slobodkin (1962), Winberg (1956) and Mann (1965) will show the key to understanding an organism's role in trophic ecology to be the description of particular organism's energy requirements. The energy requirements are usually studied from the standpoint of energy budgets, in which the main components are food energy intake, energy of egesta, energy of growth

(production) and energy of metabolism.

Since the gizzard shad is important in game fish management, an assessment of its energy requirements, and investigation of its food associations and feeding biology will aid in quantifying its role as a forage base for game fishes.

The objectives of this investigation were:

1. to describe feeding behavior,

2. to study food uptake and voidance,

3. to document aspects of respiratory metabolism, and

4. to estimate the energy requirements for shad.

The Study Organism

The gizzard shad, Dorosoma cepedianum (Le Sueur), of the subfamily Dorosomatinae, has become landlocked in freshwaters. It is a streamlined deep-bodied fish, characteristically silvery bluish grading to white below the lateral line, with a prominent black spot immediately above and posterior to the gill covers. The terminal rays of the dorsal fin form a long filament. There are generally 22-28 rays in the anal fin. Anterior to the anal fin, the abdomen is covered with a ridge of keeled bony scutes.

The shad, a filter feeder, has an elaborate filtering apparatus, and a unique digestive system. The gill rakers are abundant, fine and closely set, numbering more than 300 on the first gill arch for example. The rakers of Dorosoma are so numerous all underlying structures in the pharynx are completely veiled. A pair of phyryngeal pockets is connected

to the anterior opening of the esophagus. Bodola (1966) suggests that
this organ serves to force food materials into the esophagus. From the
espohagus, food enters a gizzard-like stomach. The intestine is long
and convoluted, often two to three times the body length.

The Study Area

Smith Mountain Reservoir is fed by the waters from the Blackwater
and Roanoke Rivers (Fig. 1). The hydroelectric facilities, located in
the gap of Smith Mountain, became operational in 1965. The design of
these facilities includes reversible pump-turbines, which are used in
periods of low power demands to recycle water from Leesville Reservoir
to Smith Mountain Reservoir.

The Roanoke River arm is 40 miles in length. The water quality of
this area is characterized by the inflow of domestic and industrial
waste water from the Roanoke and Vinton municipalities. The Blackwater
arm, 20 miles in length, receives very little, if any, waste from highly
populated areas. The quality of water in the basin results from flows
from the two river arms and water pumped back from the lower storage
reservoir, which has a major soft water input from the Pigg River.

Several studies on the reservoir have been completed to date. Of
these, one was conducted on primary productivity (Simmons 1968) and
another on the biology of gizzard shad (Schneider 1969). Simmons (loc.
cit.) classified Smith Mountain Reservoir as a mesotrophic impoundment.
The limnological aspects that reflect enrichment in the Roanoke River
arm are the average annual total alkalinity, 84 mg $CaCO_3/l$, and the
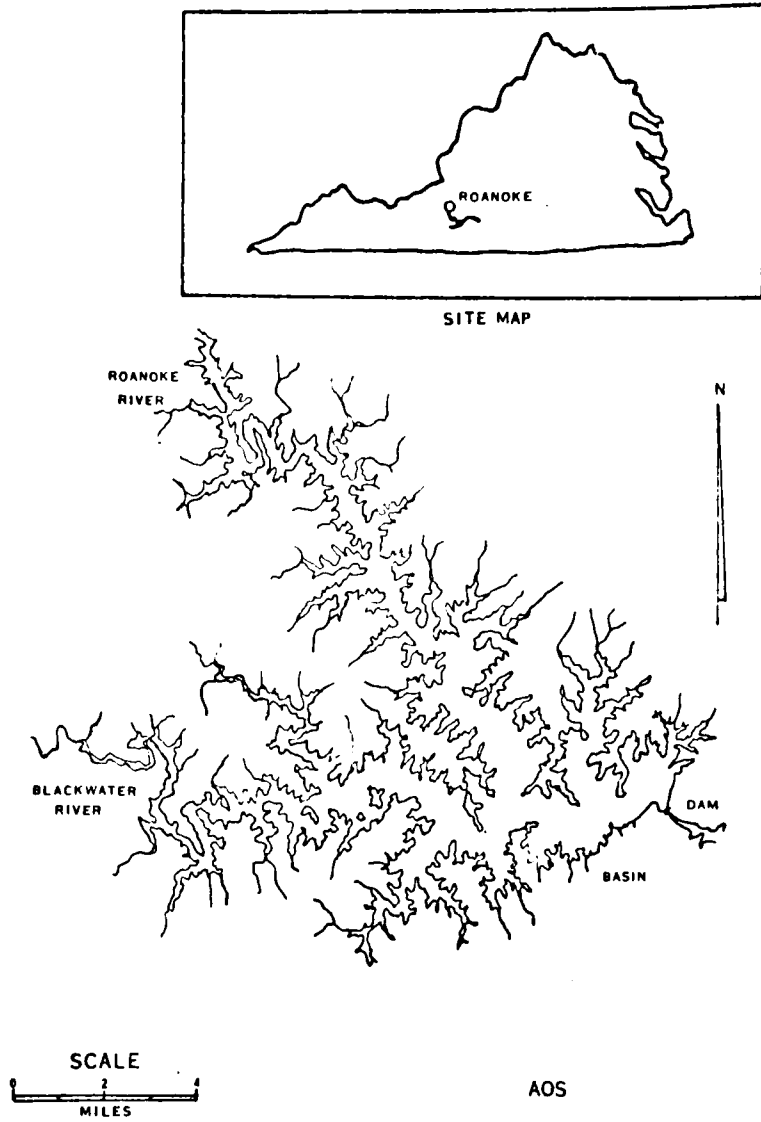
Fig. 1. Smith Mountain Reservoir, Virginia

average carbon assimilation, 171.1 mg $C/m^2/day$, compared to 74 mg $CaCO_3/l$ and 98.7 mg $C/m^3/day$, respectively, in the Blackwater River arm. Other limnological characteristics were generally similar throughout the reservoir, particularly during thermal stratification. From June to December surface temperatures range from 9 C to 22 C, pH from 7.1 to 8.1, and oxygen saturation levels from 90 to 127 per cent.

LITERATURE REVIEW

Habitat Associations and Foods

Nash (1960), in a study of the associations of fish species in
tributaries and shore waters of Western Lake Erie, found 71 per cent of
the total number of gizzard shad collected were taken from mud-bottom
waters and 29 per cent from hard-bottom lake shores. Other species
showing similar bottom associations were Carassius auratus, Morone
crysops, Pomoxis nigromaculatus and Micropterus salmoides. Nash main-
tains that the best indicator of fish habitat in shallow water is the
character of the bottom and that the composition of fish communities
reflects the nature of the bottoms over which they occur.

Bodola (1966) described the young-of-the-year shad habitat in
Western Lake Erie as the shallow, quieter waters along the shore where
the bottom is sandy or mucky.

Several studies have been conducted on the food of gizzard shad.
Tiffany (1921a, 1921b) identified 140 species of animal and plant foods
from the alimentary tracts of shad. His analyses showed 70 to 90 per
cent microalgae, 0 to 15 per cent microanimals, and 10 to 30 percent
mud in the diet of post larval shad.

Carmer and Marzolf (1970), Bodola (1966), Warner (1941), and
Miller (1960) found evidence that shad smaller than 20-30 mm in length
feed predominately on zooplankton, while larger fish feed mainly on
phytoplankton. Up to 90 per cent of the digestive tract contents was

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classified as mud and bottom debris.

Dalquest and Peters (1966) in a study of several rough fish species
from Lake Diversion, Texas, listed the food categories found in mature
gizzard shad diets. The shad above 50 mm in length contained mainly
sand, silt, diatoms, and ostracods; while those 25 to 50 mm in length
fed on copepods and clarocerans almost exclusively. In general, the
contents of mature shad were 80 to 90 per cent sand and debris, and
approximately 10 per cent diatoms. Kutkuhn (1957) also investigated
utilization of plankton by gizzard   ad. He found that minute plank-
ters, less than twenty microns in length, occurred consistently in the
digestive tracts. On a volume basis, phytoplankton constituted the
bulk of the post juvenile shad diet. Only in a few instances was the
total content of esophagus and "stomach" contents found to exceed 0.1
cc in volume. Kutkuhn concluded, as did Cramer and Marzolf (loc. cit.),
that green algae were apparently selected for and blue-green algae
selected against.

Bodola (loc. cit.) found the fish captured in open waters had fed
predominately on phytoplankton, those taken in areas of submerged
plants contained mainly cladocerans, copepods, and rotifers, while
those from turbid waters had large quantities of mud in their digestive
tracts. In some instances, sand particles too large (over 0.25 mm) to
have been in suspension were found among the foods, indicating that
shad secure materials directly from the bottom.

Feeding and Digestion

Valesquez (1939), from his study of the viability of algae obtained from serial segments of shad digestive tracts, concluded that the various amounts and kinds of alga in the segments reflect the activity of the fish and the variation of the algae in the environment at the time of feeding. Relatively full segments were taken as an indication of periods of rapid straining and swallowing of plankton. He described gizzard shad feeding as constant filtering of plankton as water passed over the gills. The food retained accumulates in the pharynx, is swallowed, and passed through the digestive tract by peristaltic movement. Tiffany (1920) was one of the first people to study the feeding habits of shad; he described them as "living tow nets."

Ivlev (1961) studied the ecology of the feeding of fishes. He emphasized that feeding intensity must be the first consideration in trophic ecology. Evidence presented by Ivlev indicated that the rate of food intake was contingent on the size of the maximal ration of the fish, and the concentration and distribution of the food particles. The rate of food intake of Engraulis mordax, a filter feeder, was investigated by Leong and O'Connell (1969). Feeding trials with Artemia nauplii showed the food intake of northern anchovy can be expressed in terms of an equation:

$$n = 6.31 \ T^{0.97} \ W^{0.52} \ D^{0.59}, \tag{1}$$

where n is the number of nauplii consumed, T is time in minutes, W is

weight of fish, and D is density of food items.

A method of estimating the total daily food consumption of fishes was proposed by Bajkov (1935). He suggested use of the formula,

$$D = A \frac{24}{n} \tag{2}$$

where D is daily food consumption, A is the average amount of food in the stomachs at the time of examination, and n is the time required for all food to pass from the stomach into the intestine. This formulation is based on several assumptions:

1. that fish feed continuously,

2. that the rate of movement (digestion) of the meal is the same whether it is followed by more food or not, and

3. that capture and confinement of the fish do not affect the rate of digestion.

Dawes (1930a), however, demonstrated that the rate of food passage is affected by the degree of satiation of the fish.

The rates of food passage through the digestive tract, i.e., voidance, for 23 species of fingerling fish were reported by Lane and Jackson (1969). These authors demonstrated that the voidance rate is directly affected by changes in temperature.

<u>Growth</u> <u>and</u> <u>Metabolism</u>

<u>Growth</u>

Schneider (1969) calculated the annual growth of gizzard shad in

Smith Mountain Reservoir from scale annuli and standard length measure-
ments. Shad grew to 107.6, 172.6, and 214.7 mm in the first, second,
and third years, respectively. The length-weight relationship was de-
scribed by the equation:

$$\log W = -4.09229 + 2.71712 \log L, \tag{3}$$

where W is weight in grams, and L is length in millimeters.

During periods in which growth rates are constant, or nearly so,
the average daily weight increase equals the percentage of growth on
any of the days and is estimated by

$$C = \frac{2 \ (W - W_o)}{t \ (W + W_o)} \quad . \quad 100, \tag{4}$$

where C is the average daily weight increase, t - days, W_o - the ini-
tial weight, and W - the final weight. Winberg (1956) discussed the
details for use of estimates of daily weight gain increments and meta-
bolic rates in energy budgets.

Metabolism

The quantitative relation between metabolic rate and body size
(weight) has been discussed by von Bertalanffy (1951). He identified
several metabolic types. The first type is based on the surface rule,
where respiratory metabolism is proportional to the 2/3 power of
weight; the second is directly proportional to weight, in this case
the weight exponent is one; and the third is intermediate between the
other two and is characteristic of most fishes. This relation is

expressed by the allometric formula:

$$M = b \, W^a.\tag{5}$$

M is the metabolic rate, W is the body weight, and a and b are constants. Constant a represents the metabolic level for a body weight of one gram, whereas b is the weight coefficient representing the rate at which metabolism increases as body weight increases. Log-transformation of equation (5) yields the straight line formula:

$$\log M = \log b + a \log W\tag{6}$$

Winberg (1956, 1961) in a review of data of many authors concluded that standard oxygen consumption in fish is proportional to weight raised to a power of 0.8 and the standard metabolic level for a one gram fish equals 0.3. His version of equation (5) is

$$M = 0.3 \, W^{0.8}.\tag{7}$$

He also stated that the routine metabolic levels of fish in nature were at least double the levels measured for metabolism.

Routine and standard levels of metabolism have been investigated in many fish species. Beamish (1964a), Job (1957), Beamish and Mookhergii (1964) and Fry (1957) relate routine metabolism to the oxygen consumption of fish undergoing spontaneous physical activity. The standard metabolic rate is defined as the level of oxygen consumption in the absence of spontaneous activity.

Winberg (1956) and Beamish (1964b) discussed the concomitant increases in metabolic rates of fish with increases in temperature.

Respiration

Since the late 1930's, investigators of fish metabolic levels have used the rate of oxygen consumption as the basic tool of measurement. (Winberg 1960). The underlying assumption was that under most conditions all energy was released aerobically.

Kutty (1966), in a classic experiment on the respiratory quotients (R.Q.'s) of goldfish and trout, has shown fish metabolism is essentially aerobic at oxygen concentrations above 50 per cent saturation. He found both fish species exhibited R.Q.'s of unity at spontaneous activity levels. At levels of sustained activity the R.Q.'s were below unity.

Beamish (1964a) and Moss and Scott (1961), in their experiments on oxygen consumption levels of several fish species (white sucker, bluegill, largemouth bass and channel catfish), found no significant changes in levels of oxygen consumption after 48 hours of starvation. Such stabilization of metabolic levels reflect the reduction in oxygen requirements for food assimilation.

Energy Budgets

Estimates of energy utilization for growth and metabolism are primary considerations for computing energy budgets for aquatic organisms. The simplest energy budget is: food energy = energy of total metabolism + energy stored + energy given off as wastes. Variations

of this basic formula have been proposed by many investigators
(Ivlev 1960, Winberg 1956, Warren and Davis 1967, Mann 1965, and Davies
1964). Two of the most applicable energy budgets are those published
by Winberg (loc. cit.) and Warren and Davis (loc. cit.).

Winberg's equation is

$$pR = P + T \tag{8}$$

where R - energy of ration, P - energy of growth, T - energy of metabo-
lism, and pR - physiologically useful energy. After an extensive review
of published reports of food utilization in fishes, Winberg calculated
$p = 0.8$. Equation (8) then becomes

$$0.8\ R = P + T \tag{9}$$

Warren and Davis proposed use of the equation:

$$Q_c - Q_w = Q_g + Q_s + Q_d + Q_a \ . \tag{10}$$

Q_c is energy of ration, Q_w - the energy of waste products, Q_g - energy
of growth, Q_s - standard metabolism, Q_d - specific dynamic action,
and Q_a - energy of swimming activity.

PROCEDURES AND TECHNIQUES

Plankton Stock Determinations

Experimental Design

Using the findings of Simmons (1968) as a basis for dividing
Smith Mountain Reservoir into three unique study areas--basin, Roanoke
River arm and Blackwater River arm, emphasis was placed upon identify-
ing plankton stocks and ascertaining the degree of availability of the
plankton to fish in these areas.

Sampling stations were randomly chosen for each area from a grid-
coordinate map, using a table of random numbers. All sampling in the
Roanoke arm was restricted to the area downstream from Hales Ford
bridge which is located approximately 18 river miles from the dam site.
A sampling station, therefore, was a randomly chosen site within one
of the three areas listed above. At least one station in each area
was sampled each month over a 12-month period.

Plankton Sampling and Analysis

Plankton were collected three to five meters below the surface in
the areas selected. All plankton sampling was conducted with a Juday
Plankton Trap. The plankton bucket was constructed of #20 silk bolting
cloth (aperture size 0.076 mm). Generally the collections were made as
close to shore as possible.

The netseston was preserved in 10 per cent buffered formalin and later diluted to appropriate volumes, enumerated, and identified. A Sedgwick-Rafter cell was used for enumeration (Welch 1948). The counts were made along three random strips, one ocular field in width and 50 mm in length. Two such counts were made for each sample.

The plankton volumes were estimated by use of volume formulas for the geometric forms corresponding to the plankton form (Nalewajko 1966). The resulting volume estimates for each genus were summed over all genera for the estimate of total plankton volume in each sample.

Shad Food Analysis

Experimental Design

The sampling scheme for fish collections was the same as that for plankton analysis. Both collections were made on the same sampling day.

Collection Methods

Fish were collected for the food studies by electroshocking and gill nets. One gill net, 125 feet long and six feet deep was set at each sampling station. These nets were constructed of five 25-foot sections ranging from 3/4, 1, 1 1/4, 1 1/2 to 2 inches square measure. The smaller mesh sizes were set shoreward. The electroshocker was boat mounted and had six-foot dangling electrodes charged with three amps pulsating direct current. Most of the shad collected by these methods were in the second year of growth; few were over three years

of age. Age was determined from scale annuli formations and by comparisons of standard lengths with those given in a previous study on shad inhabiting this particular reservoir (Schneider 1969).

Analysis of Digestive Tract Contents

The food composition for each area and each season was determined from the materials washed from the esophagus, pharyngeal pockets, and stomach of the shad. It was assumed that this material represented foods eaten in the area of the lake from which the fish were taken. The contents of the above organs were stored in 10 per cent buffered formalin within 24 hours after the fish were harvested, and subsequently analyzed in the same manner as the plankton.

Laboratory Studies

Capture and Transport of Gizzard Shad

Gizzard shad used in the food uptake, voidance, and respiratory metabolism studies were collected by electroshocking in the Hardy Ford area of Smith Mountain Reservoir. These fish were placed in a 0.5 per cent salt solution for transport to the laboratory at Blacksburg. No anesthetic was used in transport.

Acclimation to Captivity

Acclimation to conditions in captivity was conducted in indoor

pools containing dechlorinated tap water. No attempt was made to control the water temperature and pool temperatures ranged from 9 C to 21 C annually. Generally the temperatures in the pools were within 2 C of the reservoir surface temperature at the time of fish transfer.

Daily rations of _Artemia salina_ nauplii and _Chlorella pyrenoidosa_ were provided as food. The shrimp were hatched at 80 F in a brine solution. An average weight of 1.54 g of shrimp eggs was added to six liters of solution. Ample aeration was provided to maintain the eggs in suspension. _Chlorella_ cultures were obtained from Dr. R. R. Schmidt, Biochemistry Department, Virginia Polytechnic Institute and State University. This diet was chosen because shad are plankton eaters and of the simplicity of culture techniques for the food organisms. In addition to food rations, two to three grams of silt were dispensed to the floors of the pools.

The fish were maintained as described for a minimum of 10 days prior to transfer to a holding tank in the laboratory. The fish were not fed _Chlorella_ in the laboratory holding tank. Gizzard shad that were used in one experiment, were not used in other experiments.

Food Uptake Determinations

Thirty-six sets of four fish each were used for determinations of the rate of food consumption by gizzard shad. The data collected from the four fish in each set were averaged and treated as single-fish data. This method was used to compensate for any variance in the time

of initial food intake. The rate of food consumption in this experiment was defined in relation to feeding duration, body size and food density.

Suspensions of <u>Artemia</u> nauplii were diluted to give final concentrations of 2, 5 and 15 nauplii/ml in 50 l of water in stainless steel-framed glass aquaria. The concentrations of food in the aquaria were determined by removing three 5 ml aliquots from each aquarium for counting. The coefficient of variation for the three food densities for all experimental sets was 25, 14 and 11 per cent, respectively. An air stone was located near the center of each aquarium to aid in the dispersion of the nauplii. The nauplii averaged 0.81 mm in length and 0.0123 mg wet weight.

Three size groups of fish were allowed to feed on the various food rations for time intervals of 5, 15, 30 and 90 minutes. The fish were removed, pithed, and preserved in 10 per cent buffered formalin for examinations at a later time. Prior to preservation each fish in a set was weighed and labeled. The bellies of the fish were slit longitudinally with the slit extending along the region of the air bladder from the anus to the opercular flap. The peritoneum was also slit.

Analysis of the effects of feeding duration, fish weight, and food density on the rate of food intake was conducted using the IBM System 360 computer and a multiple step-wise regression analysis package program (BMD02R). This program was prepared by the UCLA Medical Center for statistical and mathematical analysis in research problems. It is designed to produce a multiple linear regression equation by systematically selecting variables on the order of magnitude of the

partial correlations with the dependent variable.

Voidance Determinations

This study was conducted in two plans: (a) observations of void-
ing of foods consumed in a laboratory environment at 20 C, and (b) ob-
servations of voiding of foods consumed naturally in the reservoir at
21 C.

The objectives of the first plan were:

1. to establish the time interval from the onset of feeding to

    the entrance of food items into the intestine, and

2. to establish the time interval for food remains to pass

    through the intestine.

Forty gizzard shad, averaging 41 g in weight, were starved for two days
and then allowed to feed on Artemia nauplii. Three fish each were
sampled at successive three-hour intervals, pithed, and examined immedi-
ately. The times of appearance of food particles in the first 5 mm of
the intestine and of food remains in the posterior 5 mm sections were
designated as the intestinal entrance and exit times, respectively.

In the second plan, 200 gizzard shad were collected from Smith
Mountain Reservoir, placed in a holding tank and sampled at specific
time intervals for the determination of voidance, which was considered
as the time necessary to completely empty the alimentary tract. Any
fecal materials or debris found in the tank were removed throughout
the test period to eliminate extraneous food uptake.

Ten fish were sacrificed and examined every four hours in the first 12-hour period and at two- to three-hour intervals thereafter. Intestinal lengths and linear measurements of the empty portions of the intestines were recorded.

Feeding Behavior Observations

Observations were made on gizzard shad feeding on Artemia nauplii to determine the behavioral pattern of silt uptake from the floor of aquaria and the effects of two food densities on feeding activity. The shad were held in 50 l of water in aquaria, each isolated such that no one fish was affected by the activity of others. Four fish were allowed to feed on rations of 100 nauplii/l and four fed on 1,500 nauplii/ l. The feeding activity was documented from visual observations. Attempts were made to calculate the frequency and duration of mouth openings during feeding from movie film.

Oxygen Uptake Determinations

Acclimation of gizzard shad to the desired test temperature, 10, 15 and 20 C, was accomplished in an aerated constant temperature tank. Acclimation was conducted over a 20-day period during which the maximum temperature change was 1 C per day.

The test fish were starved for 24 hours prior to transfer to the respirometer. Twenty-four additional hours were allowed for acclimation to confinement in the respirometer. The fish were not fed during

period to assure continued post absorptive metabolic levels and to eliminate the effects of specific dynamic action.

The initial experiments were conducted in a 12.3 l sealed respirometer submerged in an aerated constant temperature water bath (Fig. 2A). A siphon system was used for sampling and flushing the respirometer. The volume of water removed for dissolved oxygen analysis was replaced simultaneously with water drawn from the water bath. Approximately 3 l were siphoned in the course of filling two 300 mm B.O.D. bottles at the conclusion of each experiment. Flushing at the onset of each experiment was accomplished by siphoning enough water through the system to attain dissolved oxygen concentrations equal to that in the water bath.

This respirometer was later adapted to a flowing water system by adding a noncavitating submersible pump and a flow meter to one side of the siphon (Fig. 2B). Stable-flow rates and constant experimental conditions could then be maintained in the respirometer. The flow of water was controlled by valves (V_1 and V_2). Water from the constant temperature bath was pumped through the flow meter (FM) to the respirometer. Water samples for the determination of respiration levels were drawn from tubes IF and OF.

Dechlorinated tap water was aerated and maintained within $\pm$ 1 C of the desired test temperature in the water bath. The water bath was constructed with internal circulation, refrigeration, and an activated charcoal filtering system.

The standard Winkler procedure was used in dissolved oxygen
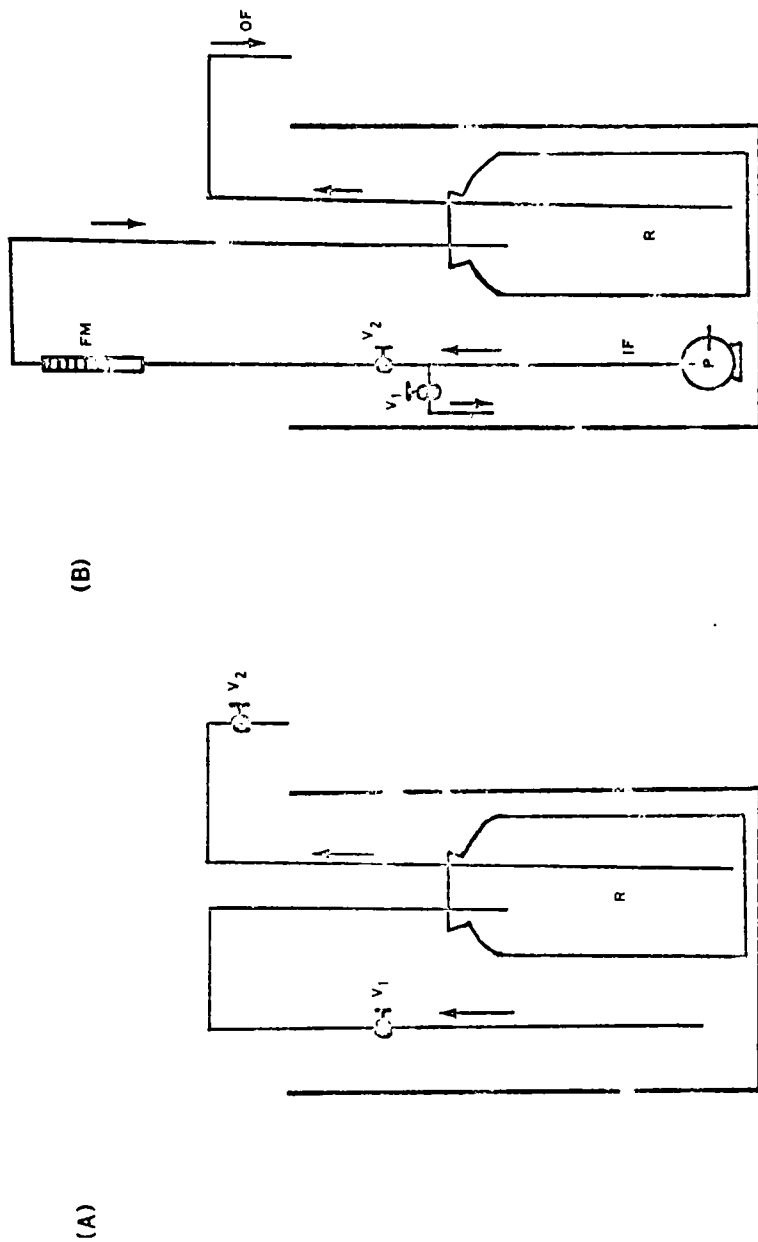
Fig. 2. Respirometers. (A) Sealed system. (B) Flowing water system.

analysis (American Public Health Association 1955). Titrations were made with a microburette and magnetic stirrer.

In the sealed respirometer, the initial experimental dissolved oxygen determinations were made after the system was thoroughly flushed. The final dissolved oxygen concentrations were determined for each experimental fish at the preset intervals of 15 and 30 minutes. These measurements were used to calculate the respiratory rates at each experimental temperature.

When respiratory rates were measured in the flowing water system, dissolved oxygen concentrations of the inflowing and discharge waters were determined simultaneously. The rate of flow in the system was maintained between 70 and 90 ml per minute for all experiments. This flow rate was sufficient to maintain a dissolved oxygen drop of 2-3 mg/l across the respirometer during the experiments. A series of oxygen uptake determinations were made at 20 C for each of 10 fish averaging 27.7 g in weight. The respiratory rates were calculated and expressed as milligrams of oxygen consumed per hour.

No attempts were made to measure the activity levels of the fish. Visual comparisons were made on the differences of activity between each test fish in the respirometers with the activity of fish in the acclimation tank. Experiments were rescheduled, if the activity of test fish appeared excessive or otherwise unusual.

The data assembled at each experimental temperature was subjected to regression analysis. The computer program used was the FRD 312-- Linear Regression of M. L. Dahlberg (1968), coded at the Fisheries

Research Institute, University of Washington.

Caloric Determinations

Caloric analyses were conducted on "stomach" contents and flesh samples of gizzard shad in a Parr Bomb Calorimeter (Parr 1960). Caloric content determinations were run on samples of the combined gizzard contents from 25 shad on two sample dates in 1969. Samples of flesh from the same fish used for a food analysis were also analyzed. All materials were weighed and dried at 60 C to a constant weight, ground, subsampled and combusted in the calorimeter. The caloric content was calculated and recorded as cal/g dry weight. These values were used to calculate the caloric equivalents of daily ration and production, i.e., the gram calorie value of food was multiplied by daily ration derived by equation (2) to obtain an estimate of daily caloric intake. The estimates of daily ration and production were used to construct an energy budget for gizzard shad.

RESULTS

Standing Crop

The October 1969 plankton samples from the three areas of Smith Mountain Reservoir were used to estimate the standing crops of the various net plankters (Table 1). The standing crop totals in the three areas were 26.8 x 10^7 cells/m^3 in the Roanoke River arm, 1.0 x 10^7 cells/m^3 in the Blackwater arm and 14.9 x 10^7 cells/m^3 in the basin area.

The basin contained the largest number of kinds of plankton, but the total numbers were less than that of the Roanoke area. Dinobryon and Centritracus were the dominant plankters in the Roanoke waters, compared to the predominance of Fragillaria and Centritracus in the basin. Centritracus was not identified in the Blackwater samples. Glenodinium, Bosmina, Fragillaria, Dinobryon, and copepod nauplii were distributed throughout the reservoir. Mougeotia Scenedesmus and Tabularia were found exclusively in the basin. Ankistodesmus was the only plankter occurring in the Roanoke River arm exclusively.

Foods and Feeding of Gizzard Shad

Food Spectra

Analysis of the seasonal abundance of shad foods in Smith Mountain Reservoir was made. The results presented in Table 2 show Dinobryon

26

Table 1. Plankton analyses from three areas of Smith Mountain Reservoir, October 1969

Organism	Cells x $10^7/m^3$		
	Roanoke arm	Blackwater arm	Basin
Glenodinium	0.46	0.08	0.76
Cyclops	-	-	0.41
Bosmina	1.49*	0.39*	1.06*
Mougeotia	-	-	0.16
Copepod nauplii	1.38	0.11	0.41
Fragillaria	1.51	0.11	7.10
Melosira	0.49	- .	0.32
Scenedesmus	-	-	0.11
Gymnodinium	0.11	-	0.60
Eudorina	-	0.11	0.09
Ankistodesmus	0.04	-	-
Dinobryon	3.58	0.20	1.44
Keratella	0.46	0.08	-
Centritracus	17.31	-	2.41
Tabularia	-	-	0.04
TOTALS	26.79	1.08	14.91

*Includes small numbers of other Cladocerans.

Table 2. Relative abundance of major food organisms of gizzard shad
         in Smith Mountain Reservoir, 1969

Item	Abundance[1]			
	Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.
Glenodinium	-	***	**	-
Diatoms	***	**	*	**
Pediastrum	-	*	*	-
Cladocera	*	**	*	-
Mougeotia	-	*	-	-
Copepod nauplii	*	**	*	-
Dinobryon	*	*	*	**
Keratella	-	**	**	*

[1] * = occasional, ** = common, and *** = abundant.

and various diatoms to be available throughout the year, with the diatoms predominating in the colder months. Glenodinium and Keratella were predominant in the warmer months. All organisms included in this analysis were in high concentrations from April to June.

Frequency of occurrence, a measure of dominance, was used to assess the degree of utilization of various plankton by shad. This emperical number was calculated by dividing the number of samples containing the organism by the total number of samples examined. The result was then expressed as a percentage. In 1969, gizzard shad were shown to have util.zed 10 of the 17 most frequently occurring net plankters in Smith Mountain Reservoir (Table 3). Of the types of organisms selected for analysis, seven occurred in greater frequency in the digestive tracts than in the plankton samples and seven identified as plankton were not present in the shad diets. During the period of sampling Centritracus, Dinobryon and Glenodinium were the most frequently occurring genera as plankton, whereas Glenodinium and Dinobryon were identified in the majority of the digestive tracts.

In terms of volume, Glenodinium and copepod nauplii predominated as food items (Table 4). The per cent relative volume is a measure of relative bulk of the various organisms in the food ration. To obtain these values, the sum of volumes of a particular item from all samples was divided by the total volume of all samples and the resulting number is expressed as a percentage. The volumes were probably overestimated due to the nature of the estimating procedure.

Table 3. Per cent frequency occurrence of selected organisms in the plankton and shad digestive tract samples, Smith Mountain Reservoir, 1969

Organism	Per cent frequency occurrence	
	Plankton	Digestive tracts
Glenodinium	23.3	69.6
Tabularia	0.1	-
Mougeotia	0.6	5.3
Cyclops	1.7	-
Copepod nauplii	6.3	2.9
Bosmina	13.2	17.0
Pediastrum	3.2	-
Fragillaria	13.8	7.7
Melosira	16.1	15.1
Eudorina	2.5	8.5
Ankistodesmus	4.8	9.2
Ceriodaphnia	4.0	-
Dinobryon	27.0	57.0
Scenedesmus	4.8	-
Keratella	4.5	5.3
Gymnodinium	6.3	-
Centritracus	38.6	-

Table 4. Relative volumes of food organisms in gizzard shad diets in
Smith Mountain Reservoir, June-December 1969

Organism	Per cent relative volume
Glenodinium	87.6
Mougeotia	1.2
Copepod nauplii	73.9
Bosmina	13.2
Fragillaria	1.9
Melosira	11.6
Eudorina	0.1
Ankistodesmus	0.6
Dinobryon	47.8
Keratella	6.9

Feeding Cycles

Of the 701 shad digestive tracts examined for seasonal patterns of feeding, only 4.4 per cent were empty (Table 5). One-fifth of the 21 shad examined during the colder months were completely void. Although the results were biased by the low catch of shad during the colder months, there was a definite increase in the occurrence of empty digestive tracts during the colder months.

In a study to determine the daily feeding patterns of shad, the intestines of most of the fish were full. Only 30 of the 600 intestines collected over a 24-hour period were less than 100 per cent full (Table 6). Seven of the 30 were less than 70 per cent full. Shad apparently do not exhibit diurnal patterns of feeding activity.

Feeding Behavior

Shad feeding on various densities of Artemia nauplii in laboratory studies displayed two patterns of behavior: feeding near the substratum at high food densities and feeding randomly at all levels at low food densities. At the highest food density, 15 nauplii/ml, the fish fed near the bottom of the tank. This feeding pattern was characterized by the fish swimming close to the substratum, frequently touching and scraping the bottom with its boney scutes (Fig. 3). If sand or other particulate matter was present on the substratum, the lighter particles were brought into suspension by the scraping action

Table 5. The monthly percentage of gizzard shad which had empty
digestive tracts, 1969

Month	Number fish caught	Number fish sampled	Number empty tracts	Per cent empty
January	0	0	0	0
February	3	3	1	33.3
March	4	4	0	0
April	30	30	2	6.6
May	51	30	0	0
June	157	60	1	1.7
July	345	166	14	8.4
August	174	140	0	0
September	207	140	7	5.0
October	114	114	3	2.6
November	8	8	0	0
December	6	6	3	50.0
TOTAL	1,099	701	31	4.4

Table 6. Per cent emptiness of shad intestines as a function of time
of day at Smith Mountain Reservoir, May 22-23, 1970

Time of collection	Number fish examined	Number of intestines showing measurable emptiness*		
		10-30% void	31-60% void	61-100% void
0800	50	1	1	1
1000	50	8	-	-
1200	50	-	-	-
1400	50	-	-	-
1600	50	1	-	1
1800	50	3	-	-
2000	50	-	1	-
2200	50	-	-	-
2400	50	7	-	-
0200	50	-	-	2
0400	50	1	-	-
0600	50	2	-	1

*Per cent void = $\dfrac{\text{length of intestine containing no food}}{\text{total length of intestine}}$ x 100

Fig. 3. Gizzard shad feeding over the substratum.

and by "fanning" from the caudal fin as the fish swam past. Fish swimming through the suspension invariably consumed some of the bottom matter. The shad also appeared to intentionally seek particulate material. Infrequently shad displayed the "directed activity" of shoveling along the bottom, the lower jaw extended, for a distance of 1-2 cm.

At low food concentrations (100 to 200 nauplii/l), the fish swam randomly about the tank, infrequently touching the substratum. The fish did not appear to maintain any particular distance from either the substratum or the water's surface.

Most of the fish used in the feeding behavior studies were starved for 24 hours prior to introduction of food. The fish which were not starved did not display behavioral patterns very much different from those described above. Thus, starved fish do not exhibit a pronounced feeding frenzy when food becomes available.

The attempts to quantitate swimming speed and rate of mouth openings, before and after food introduction, from filmed recordings were not completely successful. The experimental conditions were not conducive to measuring swimming speed in cm/sec as originally planned; however, the swimming speed was estimated to increase from 1.5 to 2 body lengths/sec aft r introduction of food (Fig. 4). No measurements of the rate of mouth openings were obtained.

Food Uptake

Gizzard shad of various weights were allowed to feed on three
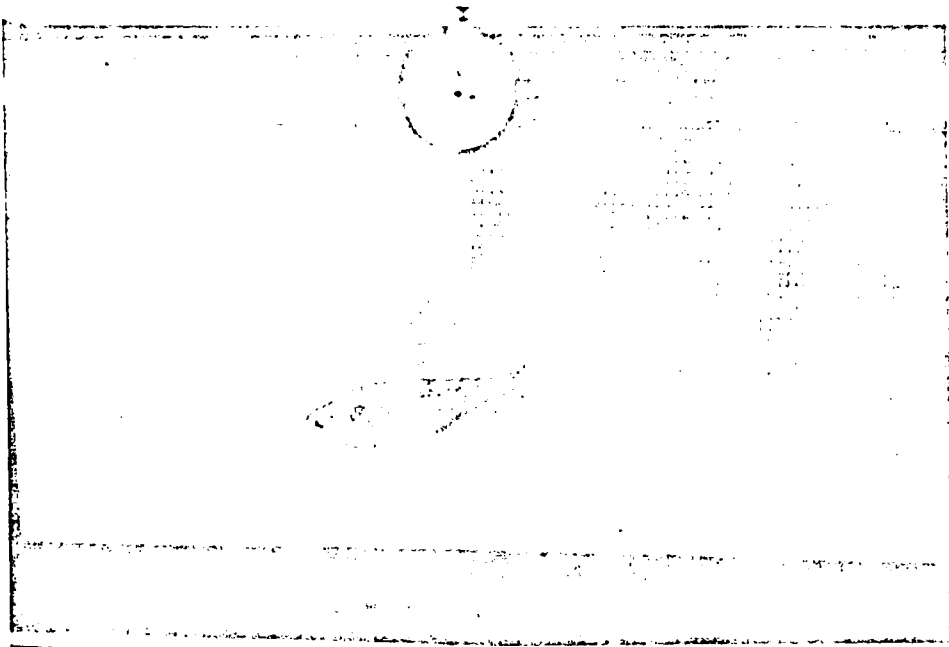
Fig. 4.   Equipment used in making observations of
          swimming speed.

densities of <u>Artemia</u> nauplii (2, 5, and 15 nauplii/ml) for periods of 5, 15, 30 and 90 minutes (Tables 7 and 8). Visual inspection of the tabulated results reveals high correlation between feeding duration and the actual number of nauplii consumed. Multiple step-wise regression analysis was used to evaluate the significance of fish weight and food density effects on the rates of food consumption. The BMDO2R packaged program used for this analysis is designed to produce a multiple linear regression equation by systematically selecting variables on the order of magnitude of the partial correlation with the dependent variable. The results of regression analysis of the log-transformed data are shown in Table 9. The partial correlation coefficients for the weight and food density variables were 0.76 and 0.19, respectively, after removal of feeding duration effects. The results indicate that weight of the fish (size) exerted a stronger influence on the food intake rates than did the food densities.

The regression equation relating the variables to the rate of food intake was

$$n/T = K \ T^{(a-1)} \ W^b \ D^c \tag{11}$$

or

$$n/T = 1.363 \ T^{0.2266} \ W^{0.4588} \ D^{0.0945} \tag{12}$$

n/T is the number of nauplii consumed per unit of time, K - the regression constant, T - the feeding time in minutes, W - the weight of fish in grams, and D - the density of food particles. The exponents of the variables are a, b, and c, respectively. Table 10 shows the coefficients.

Table 7. The variates for gizzard shad feeding on _Artemia_ nauplii
for 5- and 15-minute intervals

Duration of feeding (min)	Density (nauplii/ ml)	Fish wt. (g)	No. nauplii consumed	Expected No. nauplii consumed
5	15	49.1	457	305
	15	28.2	279	236
	15	6.9	117	124
5	5	48.9	424	274
	5	21.4	229	188
	5	7.3	105	114
5	2	39.0	364	227
	2	19.4	200	164
	2	7.3	74	105
15	15	43.5	992	1112
	15	21.0	520	796
	15	7.5	331	496
15	5	45.7	895	1025
	5	30.6	494	852
	5	8.0	418	460
15	2	56.6	917	1037
	2	21.1	393	659
	2	7.3	397	405

Table 8. The variates for gizzard shad feeding on Artemia nauplii for 30- and 90-minute intervals

Duration of feeding (min)	Density (nauplii/ ml)	Fish wt. (g)	No. nauplii consumed	Expected No. nauplii consumed
30	15	45.6	2114	2660
	15	19.4	2816	1796
	15	7.7	1405	1175
30	5	39.6	2039	2247
	5	20.3	1236	1653
	5	8.4	1117	1102
30	2	44.3	2922	2169
	2	26.1	1224	1701
	2	6.7	1187	911
90	15	44.7	8727	8184
	15	28.0	7073	10146
	15	7.9	7195	4579
90	5	49.0	9766	9537
	5	23.5	8355	6807
	5	7.9	4489	4127
90	2	35.7	7117	7563
	2	19.4	5583	5715
	2	8.5	5503	3914

Table 9. Partial correlation coefficients for fish weight and food
density after taking in account the feeding duration effects

Variable name	Units of measurement	Variable range	Partial correlation coefficient*
Weight	grams	6.7-56.6	0.7614
Food density	no./ml.	2-15	0.1961

*Residual degree of freedom = 32. Partial correlation coefficient
must be 0.339 to be significant at the 0.95 per cent level
(Snedecor 1956:147).

Table 10. Variables influencing food intake of gizzard shad

Variable	Coefficient	Std. error	F
Weight (g)	0.4588	0.0670	46.83**
Feeding duration (min.)	0.2266	0.0473	67.61**
Food density (no./ml.)	0.0945	0.0603	2.45*

**Indicates significance at 0.01 per cent level.

*Indicates significance at 0.10 per cent level.

of regression (variable exponents) and the statistical significance
levels. The density coefficient was not significant at the preselected
0.95 per cent confidence level. Although weight appears as an influ-
encing factor affecting food consumption, it actually represents the
influences of other physical parameters such as area of mouth opening
(volume of buccal cavity) and swimming speed at the time of food intake.

Since food density, D, is in terms of organisms/ml, the inverse,
1/D, represents the volume of water containing one nauplii. Applying
this to equation (11), the food density coefficient, c, becomes c-1,
or -0.9055. This in effect is a measurement of the filtering rate of
the shad. The negative sign denotes a decrese in the filtering rate
with increaing tim. and with increasing body weight of fish.

Evacuation

Passage of Foods

Starved gizzard shad, averaging 43 grams in weight, were fed
Artemia nauplii at a concentration of 200 organisms/1 in a 50 1 volume
for each fish tested. It was assumed that each fish began feeding
immediately upon introduction of food. The criteria for assessing food
passage was based on the presence of identifiable food remains in the
first 5 mm of the intestine and in the posterior 5 mm section. The
elapsed time (since onset of feeding) of the first sample in which all
fish met the aforementioned criteria was designated as time of intes-
tinal entrance or time of intestinal exit. The intestinal entrance

time, time for food to pass from the mouth into the intestine, was nine hours, and the intestinal exit time, time for food particles to pass through the intestine, was also nine hours (Table 11). It appears that the time required for food remains to enter the intestine equals the time required for food to pass through the intestine.

Voidance

Two hundred gizzard shad were collected from Smith Mountain Reservoir for investigation of voidance of natural foods. This assessment of voidance, the time required for complete emptying of the digestive tract, was made by determini the degree of intestinal emptiness at regular intervals after capture. It was assumed that the shad were actively feeding at the time of capture and food consumption was nil under the conditions of observation.

Data gleaned from the fish, which had been feeding on natural foods, show that shad, 19 to 56 g in weight, completed voiding in 15 to 22 hours (Table 12). The relation of the mean length of the intestines containing food for all fish in a sample and the elapse time since capture is shown in Fig. 5. The terminus of an eye fitted line shows voiding to be completed in 21 hours. In gizzard shad, the length of the intestine appears to be a determinant of the length of time a particle of food is retained in the digi tive tract. The intestine lengths of a group of fish similar in size structure to those used in this study ranged from 1.3 to 2.8 times the body length (Appendix Table I)

Table 11. Number of fish with food in the first and last sections of intestine after being fed on _Artemia_ nauplii at 20 C-- August 1969 as a function of time since feeding

| Elapsed time (hrs) | Av. fish wt. (g) | No. fish sampled | No. fish exhibiting | |
			Intestinal* entrance	Intestinal** exit
0	39.0	3	0	0
3	38.5	3	0	0
6	38.9	3	1	0
9	35.9	3	3	0
12	52.1	3	3	0
15	41.7	3	2	2
18	44.1	3	3	3
21	52.4	3	3	3
24	39.2	15	15	11

*Food remains appearing in anterior 5 mm of intestine

**Food remains appearing in posterior 5 mm of intestine

Table 12. Voidance data for gizzard shad at 21 C

Item measured		Elapsed time in hours							
		0	3	6	9	12	16	20	22
1. Fish* weight (g)	Mean	39.0	32.0	33.1	29.8	32.5	32.8	32.5	29.7
	S.D.	14.8	11.6	10.8	12.6	11.6	11.8	13.8	7.9
	C.V.	37.8	36.5	32.5	42.3	33.6	36.6	42.5	26.7
2. Fish length (mm)	Mean	158.5	144.8	146.2	143.2	146.7	150.5	146.0	144.7
	S.D.	22.9	20.0	18.9	27.6	25.1	26.1	23.5	14.6
	C.V.	14.4	13.9	12.9	19.3	17.1	17.3	16.1	10.1
3. Length of intestine containing food (mm)	Mean	247.0	224.3	284.1	158.2	131.0	47.0	14.7	7.3
	S.D.	102.1	81.7	64.1	65.9	29.6	28.0	10.6	15.0
	C.V.	41.3	33.4	22.5	41.6	22.6	59.5	72.2	203.0
4. Length of intestine (mm)	Mean	269.2	254.5	310.5	250.0	302.8	280.6	246.2	275.2
	S.D.	56.2	72.1	56.8	50.7	61.2	71.4	77.2	53.2
	C.V.	20.8	28.3	18.2	20.2	20.2	25.4	31.3	19.3
5. Ratio of times 3 and 4 (%)	Mean	90.0	95.6	91.3	63.0	43.0	18.3	6.0	2.7
	S.D.	31.6	10.3	12.9	23.0	7.0	13.5	4.4	5.7
	C.V.	35.1	10.7	14.1	33.5	16.2	73.5	72.6	205.3

*Samples of ten fish.
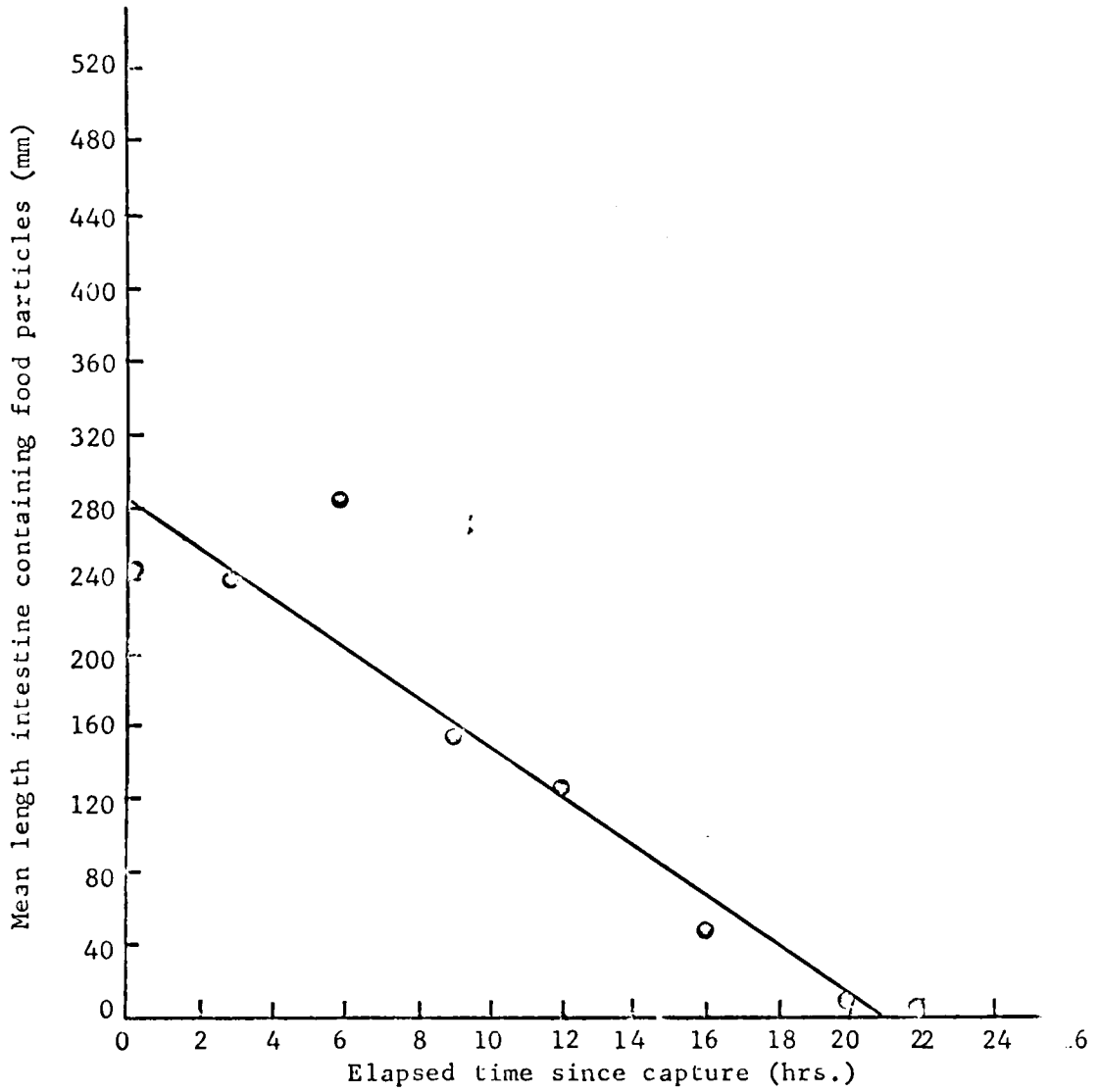
Fig. 5. Mean length of intestine containing food particles in relation
to elapsed time since capture.

Respiratory Metabolism

Several series of measurements of routine oxygen consumption of gizzard shad at three temperatures (10, 15 and 20 C) were made in a sealed respirometer. A flowing water respirometer was also used to measure oxygen consumption at 20 C. The data obtained are listed in Appendix Tables II-V. No attempt was made to measure the activity levels of the shad.

The mathematical relationship between body size and metabolic rate is shown in equation (5). The linearized model (equation 6) was used to derive the regression equations listed in Table 13.

It is quite evident that respiratory metabolism increases with increasing body size (Fig. 6).

At each experimental temperature the slope, or weight coefficient, was less than unity. The derived coefficient were 0.848, 0.841 and 0.937 at 10, 15 and 20 C, respectively, in the sealed respirometer experiments, and 0.813 at 20 C in the flowing water system. The difference between the weight coefficient derived from experiments in the two respirometers at 20 C is attributed to experimental error. The correlation coefficients for the two sets of data at 20 C were 0.94 (sealed system) and 0.90 (flowing system).

The metabolic levels for gizzard shad were -0.717, -0.544 and -0.413 at 10, 15 and 20 C, respectively, for the sealed respirometer analyses (Table 13). By log-transformation these become 0.192, 0.286 and 0.387 mg O_2/g body weight. The relative magnitudes of these values

Table 13. Regression equations for routine oxygen consumption of gizzard shad at three temperatures

Acclimation temperature (C)	Regression equation	Standard deviation of slope	Calculation O_2 consumption for 100 g - fish (mg/hr)
10*	log M = -0.717 + 0.848 log W	0.0388	9.52
15*	log M = -0.544 + 0.841 log W	0.0665	13.72
20*	log M = -0.413 + 0.937 log W	0.0698	29.03
20**	log M = -0.203 + 0.813 log W	0.0391	26.54

*Sealed respiromete..

**Flowing water respirometer.
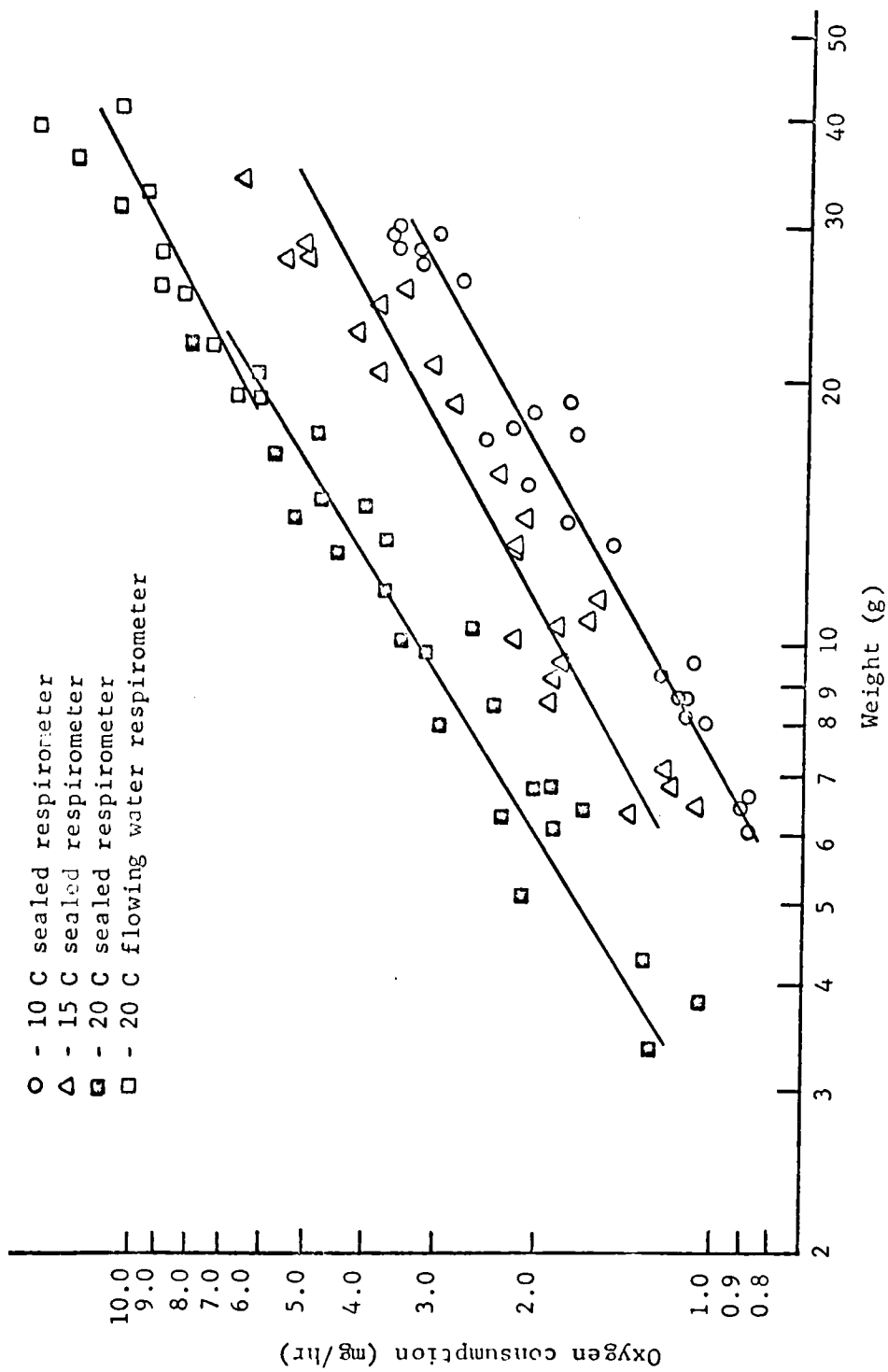
Fig. 6. Oxygen consumption of gizzard shad in relation to weight.

indicate that metabolic levels per unit weight of fish increased with increases in temperature. Fig. 7 graphically shows the respiration rates for a 100 gram fish as they relate to the respective acclimation temperature. The fitted line shows how metabolic rate increases as temperature increases.

Caloric Analysis

Analysis of the caloric content of fish flesh and foods contained in the gizzard were made in a Parr Bomb Calorimeter. The fish were of various sizes, ranging 20 to 50 g in weight. The average food content in the gizzards was 0.076 g dry weight and the caloric content was 6100 cal/g (Table 14). Approximately 30 per cent of the food volume was botto debris. Flesh samples taken from the area just below the anterior portion of the dorsal fin yielded 6090 cal/g dry wt.

Energy Budget for Shad

The average weight of all fish used in the preceding investigations was 34 g. Therefore it was deemed appropriate to estimate the energy requirements and transformations for a fish of this size.

The metabolic energy requirement was calculated by the regression equation derived from the flowing water respirometer experiment. This equation was $\log M = -0.203 + 0.813 \log W$. Reasons for using this particular equation will be given in the next section. At 20 C, the shad consumes 264 mg O_2/day (Appendi). This transforms to 905 cal/day
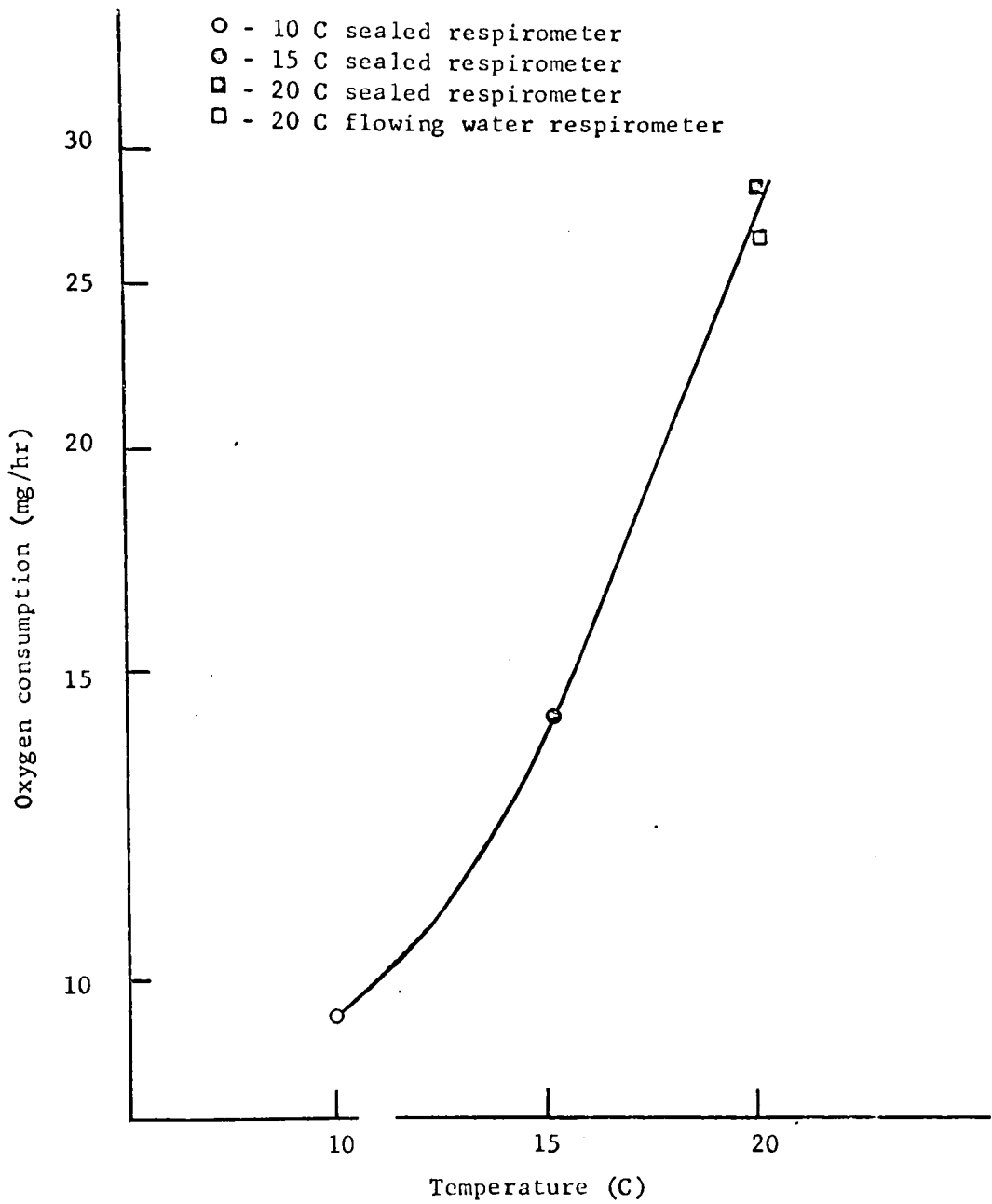
Fig. 7. Rate of oxygen consumption of a 100-g gizzard shad in relation to temperature.

Table 14. Caloric analysis of gizzard shad flesh and gut contents for two days in 1969

Date	Type sample	No. fish sampled*	Dry wt/ fish (g)	Water content (%)	cal/g dry wt/fish (cal)
26 June	gut	10	0.082	65	5531
"	"	10	0.074	74	5977
"	"	10	0.068	78	6716
"	dorsal muscle	1	0.510	92	5693
"	" "	1	0.470	88	5978
"	" "	1	0.630	89	5443
10 October	gut	10	0.078	79	5682
"	"	10	0.074	81	6716
"	dorsal muscle	1	0.530	94	6301
"	" "	1	0.341	88	7026

*The fish sizes ranged from 20 to 50 grams in weight.

by applying the oxy-calorific coefficient of 3.42 cal/mg O_2 consumed (Brody 1945, Winberg 1956).

Schneider (1969) estimated the gizzard shad in Smith Mountain Reservoir grew to lengths of 107.6 and 172.6 mm in the first and second years of life, respectively. The corresponding weights, 25.13 g and 100.15 g, were calculated with the regression equation log W = -4.09 + 2.717 log L. Substituting these weights in equation (4), the average daily growth rate of 0.57 per cent was calculated. This translates to an average daily gain of 0.19 g or 118 calories for a 34 g shad. The energetic expenditures of a 34 g gizzard shad for routine metabolism and growth amounts to about 1023 cal/day.

Following the premise that gizzard shad feed continuously, and the rate of movement of food from the gizzard into the intestine is the same at all times of the day, Bajkov's (1935) formula, $D = A \frac{24}{n}$, equation (2), was used to calculate the caloric equivalent of the daily food ration. A 34 g shad consumes 1204 cal/day. The time required for all food to pass from the gizzard into the intestine was estimated to be nine hours (see section on food passage).

An energy budget for gizzard shad of approximately 34 g in weight is given in Fig. 8. The caloric values derived from the food intake, oxygen consumption, and growth estimates are shown in this simple scheme. The direction of this investigation did not lead to estimates of the energy of waste products or the energy utilized for Specific Dynamic Action (SDA).

Following Winberg's thesis, the daily energy requirement was
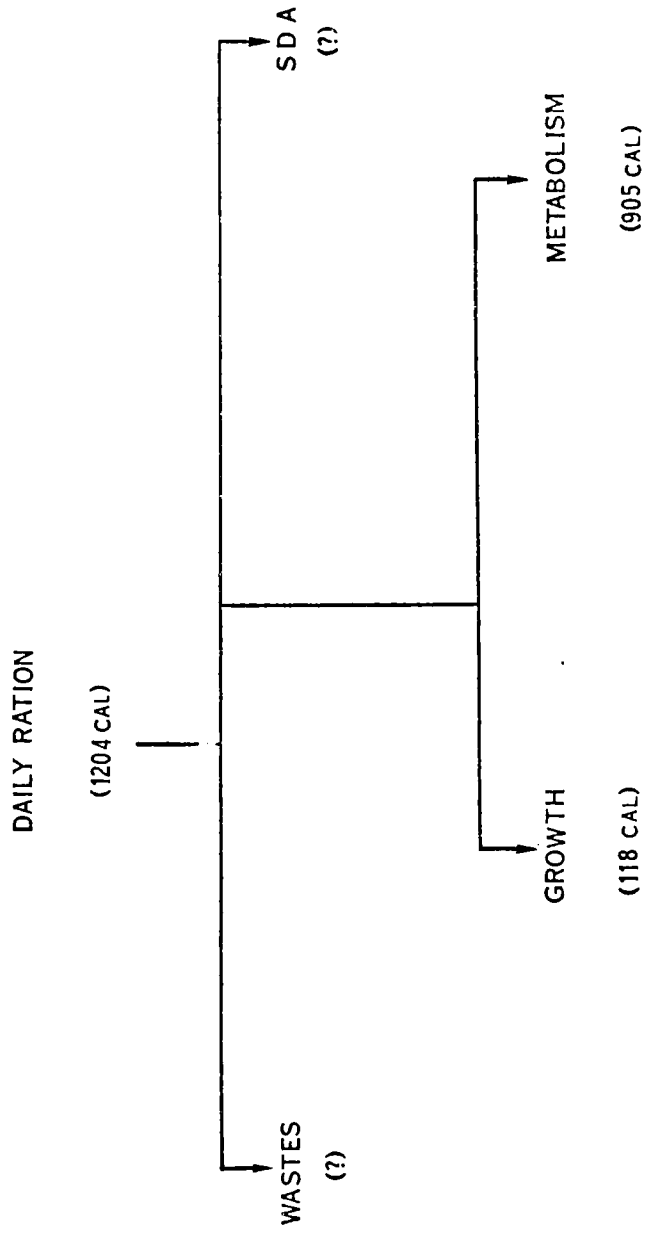
Fig. 8. Energy budget for a 34-g gizzard shad at 20 C.

recalculated by $0.8R = P + T$, equation (8). This estimate is 1278

calories per day. Comparatively this is 6.1 per cent over the 1204

cal previously calculated.

DISCUSSION

Except for the region of the Roanoke River arm above Hales Ford
Bridge, there are small differences in the limnological characteristics
measured in the three study areas of Smith Mountain Reservoir (Appendix
Table VI). The standing crops of the various plankters in the study
areas revealed differences in the quantity and types of plankton en-
countered in the study areas.

Simmons (1968:195) found the Roanoke water to be more productive
at the primary level than other areas of the lake. The Blackwater area
was the least productive. His measurements showed the carbon assimila-
tion rate in the Roanoke River arm exceeded those of the Blackwater
arm by 72.4 $C/m^2/day$ in winter, by 435.0 $C/m^2/day$ in spring, and by
only 21.8 $C/m^2/day$ in summer. Generally, the productivity levels in
the basin area were intermediate to the other areas. Although carbon
assimilation rates are not necessarily directly correlated with stand-
ing crops of net phytoplankton, the results of Simmons' analysis do
reflect the levels of nutrient enrichment in the various areas of the
lake. Simmons and Neff (1969:33) estimate the annual standing crop in
the reservoir varied between 10^4 to 10^7 cells/m^3. They found _Fragil-
laria crotonensis_ Kitt, and _Melosira granulata_ (Ehr.) to be the domi-
nant net plankters occurring annually. In October 1969, the basin
area of the reservoir contained the largest number of kinds of plankton,
but the estimated total numbers of plankters were less than that for

the enriched Roanoke arm. Dinobryon was found to be in the highest

concentration of all plankton in the basin area, while Centritracus was

dominant in the Roanoke arm and Bosmina was dominant in the Blackwater

arm. In each area of the reservoir, the highest concentrations of

plankton occurred on the leeward side of the lake. This appeared to be

the trend throughout the 12-month sampling period.

Apparently the gizzard shad is able to utilize most of the micro-

forms of plankton during some stage of its life. This fish feeds pre-

dominately on zooplankton in its initial growth period, and at sizes

above 50 mm the shad's diet consists mainly of phytoplankton. The

actual composition of the diet depends upon the plankton populations

in the environment and the particular area in which any particular fish

feeds, i.e., in open water, among submerged vegetation, or on shoals.

Many of the known foods of gizzard shad are listed in Appendix Tables

VII-X.

Seldom is any food item found in the digestive tract that exceeds

300 microns in length. Filamentous algae do not appear to be common

in the shad diet. Tiffany (1921b:116) and Dalquest and Peters (1966:

14), however, noted the occurrence of Oscillatoria, a filamentous alga,

in their shad food habit studies.

Analysis of the relative abundance of the major food organisms

available to shad in Smith Mountain Reservoir showed Dinobryon and

various diatoms to be available throughout the year and predominant in

the winter months and Glenodinium and Keratella predominant in the

summer months.

Although statistical analysis probably would indicate that gizzard shad exhibit some degree of selectivity in feeding, it is believed by this investigator that shad feed opportunistically relative to the spatial and temporal fluctuations of plankton abundance. Gizzard shad were reported to have fed upon 189 of the 236 species and varieties of phytoplankton and 71 of the 122 species of zooplankton in North Twin Lake, Iowa (Kutkuhn 1958:86). Kutkuhn observed that increases of a given taxa of plankton in the environment generally resulted in greater utilization by this fish.

Bodola (1966:421) concluded that shad do not exhibit selectivity of foods. He attributes all differences of occurrence among food items and various plankton forms in the environment to differences in the relative abundance of the various plankters at different times and different places.

In 1969, gizzard shad utilized 10 of the 17 most frequently occurring net plankters in Smith Mountain Reservoir. During the period of sampling, Centritracus, Dinobryon, and Glenodinium were the most frequently occurring genera in the plankton samples, whereas Glenodinium and Dinobryon occurred in the majority of the digestive tract samples.

Gizzard shad are thought to be continuous feeders. In a study to determine the daily feeding patterns of shad, the intestines of most of the fish examined were full. Only 30 of the 600 intestines examined over a 24-hour period were less than 100 per cent full. Seven of the above 30 were less than 70 per cent full. There was no evidence of a diurnal feeding pattern.

The gizzard shad, being a pelagic fish, can be seen schooling throughout the reservoir in the summer and fall months. From August through October, giz' rd shad are located around most of the shoals and protected areas from dusk to just before dawn. Characteristically, the highest concentrations of shad were located on the windward side of the reservoir. This is contrary to the findings on location of the highest plankton concentrations. Nash (1960:562), in a study of fish species associations, found 71 per cent of the total numbers of gizzard shad collected, were located in mud-bottom shallow waters. Other species showing similar bottom associations as the shad were Carassius auratus, Morone crysops, Pomoxis nigromaculatus and Micropterus salmoides.

Laboratory studies revealed that shad feeding on food concentrations in the magnitude of 10^7 organisms per cubic meter (15 nauplii/ml) fed near the substratum and invariably consumed some bottom matter which was brought into suspension as a result of the feeding activity. The fish were also observed scraping the substratum with its lower jaw. This action explains the occurrence of considerable amounts of mud and bottom debris in the digestive tracts of wild shad. It also accounts for the presence of sand particles too large to have been in suspension (Bodola 1966:421).

Laboratory investigations of shad feeding on Artemia nauplii in concentrations similar in magnitude as the plankton concentrations of 10^4 and 10^7 cells/m^3 reported by Simmons and Neff (1969:38) revealed that fish size (weight) and food density were important determinants

of food intake rates. Leong and O'Connell (1969:573) reported similar
findings in their study of Engralis mordax food intake rates. Statis-
tical analysis showed that body-size effects were more significant than
food-density effects. It is not likely that the derived formula,
equation (12), showing the relationship of these variables is applicable
to wild shad feeding on natural foods.

Moore (1941:91), in commenting on the application of findings
from laboratory fish to studies of wild fish, noted that such applica-
tion is biased as a result of the effects of confinement of experimental
animals, the use of unnatural foods and regulation of environmental con-
ditions in the laboratory.

Darnell and Meieretto (1962:318) reviewed the factors affecting
the rate of evacuation in fish. The rate is affected by temperature,
character of the diet, and time of last feeding. Dawes (1930a) demon-
strated that the rate of food passage is related to the amount of re-
cently consumed foods. Movement of foods in the alimentary tract, as
is generally known, is dependent upon peristaltic waves of the intesti-
nal musculature. Lagler, et al. (1962:156) state that there is some
voluntary control of food passage in digestive tracts of fishes. Such
control is exercised through the skeletal muscles in the walls of the
anterior region of the alimentary tract. To what extent this voluntary
action influences the rate of food passage in the gizzard shad is not
known.

The passage of foods in gizzard shad were studied in two plans:
one in which food was continuously available for consumption and the

other in which continued food consumption was nil. In the first study
gizzard shad required 18 hours for food to pass through the alimentary
canal; in the second study the time required for passage was 21 hours.
The evacuation rates for gizzard shad derived from the two analyses
are in general agreement. It must be emphasized that under the condi-
tions of the first study food was available for continuous feeding, and
in the second study no food was available to the fish during the periods
of observation.

Oxygen uptake has been studied in relation to various levels of
fish activity. The standard metabolic rate is described by Fry (1957:
24) as a minimum rate which is the minimum consistent with the continued
existence of the animal. This minimum is interprested to be the rate
of respiration in the absence of spontaneous activity. Active metabo-
lism is measured at sustained swimming speeds, while routine metabolism
encompasses the levels between these extremes and is not specifically
defined as to the degree of spontaneous activity of the organism in
question. The gizzard shad is a pelagic species and is not known to
maintain stationary positions; because of this, the metabolic levels
referred to in this report are considered routine.

Oxygen consumption has been shown to increase in relation to body
size raised to a power (von Bertalanffy 1957, Brody 1945, and Kleiber
1947). This mathematical relationship is expressed in equation (5).
The weight exponents derived in the respiratory metabolism studies were
0.848, 0.841 and 0.937 at 10, 15 and 20 C, respectively in the sealed
respirometer and 0.813 at 20 C in the flowing water system.

The weight exponents given above are within the 0.8-0.9 range that Beamish (1964:181) assigns to standard levels of metabolism of various fishes and are comparable to the 0.7-0.9 values of routine metabolism of several fish species reported by Hickman (1959:1011).

Winberg (1956:105) reviewed the oxygen consumption data of many authors and concluded that the average expected metabolism at 20 C for each fish weight can be calculated by $M = 0.3 \ W^{0.8}$. Paloheimo and Dickie (1966:875) reviewed the factors affecting the estimation of the weight exponent and concluded that Winberg's weight exponent, 0.80, holds true at both standard and routine levels of metabolism in fish.

The metabolic levels for gizzard shad were -0.717, -0.544, and -0.413 at 10, 15 and 20 C, respectively, for the sealed respirometer analysis (Table 13). By log-transformation these become 0.192, 0.286, and 0.387 mg O_2/g body weight. These values indicate that metabolic levels per unit weight of fish increased with increases in temperature. The overall effect of temperature on metabolic level is shown by comparison of the relative positions of the regression lines in Fig. 6. Correspondingly, seasonal variation in temperature is one of the influencing factors of metabolic levels in nature.

The study of production in fishes from the standpoint of energy transformations is a relatively new development. Investigations of the conversion of food energy to fish flesh have been conducted by Mann (1964), Brocksen, et al. (1968), Pandian (1967), and Davis and Warren (1965).

Winberg (1956) apparently was the first to project the theoretical

bases for the study of energetics of natural fish populations. He reviewed the interdependency of food intake, growth and metabolism as presented in the published works of many investigators, and concluded that the two equations given below can be used to estimate the energy budgets of fish.

Winberg's generalized equation, $M = 0.3 \ W^{0.8}$, equation (7), can be employed to estim te the energy expenditure for metabolism by converting the calculated oxygen consumption to its caloric equivalent. The second equation, $pR = P + T$, equation (8) in this report, is used to estimate the physiologically useful energy derived from the food ration. Following reexamination of the nitrogen balance data of Ivlev (1939) and data from other investigators, Winberg suggested that metabolic levels under natural conditions are at least twice those measured as routine metabolism in the laboratory. Equations (7 and 8), therefore, become $M = 0.6 \ W^{0.8}$ and $pR = P + 2T$, respectively. This factor of two is in line with Mann's (1965, 1967) findings from reanalysis of Pentalow's (1939) trout data and Johnson's (1960) data on pike. It is Mann's (1967) conjecture that confidence limits of ± 25 per cent can be placed on the estimation of wild fish rations using Winberg's equations.

Following Winberg's thesis, the energy requirement for a 34-g gizzard shad was calculated using the regression equation derived from the flowing water respirometer experiment. The regression equation, $\log M = -0.203 + 0.813 \log W$ (Table 12), in allometric form is $M = 0.627 \ W^{0.813}$. This particular equation approximates Winberg's

$$M = 0.6 \ W^{0.8}.$$

Using the data gleaned from the metabolism studies and caloric determinations a simple energy budget was derived for gizzard shad. The caloric equivalent of the daily food ration for a 34 gram shad was 1204 calories of which approximately 118 calories was used in production of new flesh and 905 calories for routine maintenance. Following Winberg's thesis, equation (8), the caloric intake was estimated to be 1278 cal/day.

These estimates compare favorably to the 996 cal for Megalops and 1044 cal for Ophiocephalus extrapolated for a 34-g fish from Pandian's (1967:25) analysis of food intake and conversion in these fish. Wissing (1969:124) reported young-of-the-year white bass feeding on zooplankton consumes approximately 940 cal/day.

The investigations on the trophic relations of gizzard shad as they are reported herein are truly exploratory in nature. They demonstrate however that assessment of the role of gizzard shad in the trophic ecology of fresh waters is possible. They also demonstrate the lack of knowledge of (1) growth curves of gizzard shad, (2) the influence of satiation on food intake rates, (3) the effects of spatial and temporal fluctuations of the food resource components on the energy content of the daily ration, (4) the energetic expenditure for Specific Dynamic Action, and (5) the energy lost in waste products. As additional knowledge of growth curves, the degree of utilization by other fishes, and the abundance and structure of shad populations in various waters is amassed, full understanding of the role of gizzard shad in the

trophic relations of the aquatic ecosytem becomes possible. As these

relations are further resolved and quantitated, fishery biologists will

perhaps begin to view the gizzard shad not only as a unique pelagic

species, but also as a dynamic pool of energy to be managed for optimum

transfer of that energy to higher trophic levels.

CONCLUSIONS

1. The composition of the gizzard shad's diet is affected by the spatial and temporal distributions of both plankters and shad. The bulk of the diet consists of Glenodinium, Dinobryon, and copepod nauplii. Gizzard shad utilize 10 of the 17 most frequently occurring plankters in Smith Mountain Reservoir.

2. Gizzard shad do not exhibit pronounced diurnal feeding patterns, but show some decrease in food intake during the colder months.

3. Shad complete voiding in 18 to 21 hours. Evacuation rates are influenced by the amounts of food available and duration of continuous feeding.

4. In the presence of high food concentrations, 10^7 organisms per cubic meter, shad feed near the substratum, infrequently consuming material directly from the substratum.

5. The rate of food consumption is influenced by duration of feeding, weight of fish and food density, in that order. The filtering rate is inversely related to both feeding duration and size of fish.

6. Metabolic levels per unit weight of fish are directly proportional to temperature levels. Shad, one gram in weight, consumes 0.452, 0.659 and 0.769 mg O_2/hr at 10, 15 and 20 C, respectively.

7. The metabolic energy requirements of a hypothetical 34-g fish is 905 cal/day and the daily energy intake is in the magnitude of 1204 cal.

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<u>APPENDIX</u>

Appendix Table I. Ratio of intestine length to fish length

Weight (g)	Body Length (mm)	Intestinal Length (mm)	Ratio*
39	157	348	2.2
55	181	283	1.5
56	183	247	1.3
54	179	324	1.8
46	168	320	1.9
48	175	361	2.0
41	169	286	1.6
22	133	261	1.9
25	135	222	1.6
20	127	189	1.4
24	135	200	1.4
48	169	376	2.2
47	171	319	1.8
45	166	241	1.4
28	137	229	1.6
30	149	278	1.8
22	133	199	1.5
21	124	182	1.5
19	123	197	1.6
21	120	176	1.5
46	165	363	2.2
48	178	373	2.1
39	162	405	2.5
28	141	289	2.0
23	129	271	2.1
37	156	320	2.1
44	149	299	2.0
25	136	313	2.3
20	125	248	2.0
21	121	225	1.9
42	192	340	1.8
41	171	282	1.6

*Intestine length divided by body length.

Appendi. Table II.   Variates of oxygen consumption analyses of one-fish
                     trials in a sealed respirator at 10 C, November-
                     December 1969

Fish weight (g)	O_2 consumption (mg/1)	Expected O_2 consumption (mg/hr)	% deviation
6.0	0.91	0.87	- 4.3
6.3	0.94	0.91	- 3.1
6.7	0.96	0.96	0.0
8.0	1.14	1.11	- 2.6
8.2	1.26	1.13	- 10.3
8.8	1.14	1.21	+ 6.1
9.3	1.10	1.27	+ 15.4
9.6	1.14	1.30	+ 14.0
9.7	1.32	1.31	- 0.7
14.1	1.44	1.80	+ 25.0
14.7	1.92	1.87	- 2.6
16.5	2.32	2.06	- 11.2
16.6	1.98	2.07	+ 4.5
17.4	2.02	2.16	+ 6.9
17.7	1.79	2.19	+ 22.3
17.9	2.50	2.21	- 11.6
18.9	2.44	2.31	- 5.3
24.7	3.52	2.90	- 17.6
28.2	3.11	3.24	+ 4.1
28.4	3.47	3.27	- 5.7
28.6	3.13	3.29	+ 5.1
28.6	3.20	3.29	+ 2.8
28.6	3.18	3.29	+ 3.4
30.7	3.67	3.49	- 4.9

Appendix Table III. Variates of oxygen consumption of one-fish trials
in a sealed respirometer at 15 C, September-
October 1969

Fish weight (g)	O_2 consumption (mg/1)	Expected O_2 consumption (mg/hr)	% deviation
6.5	1.63	1.37	- 15.9
6.6	1.48	1.39	- 6.0
6.7	1.16	1.41	+ 21.5
6.8	1.35	1.43	+ 5.9
8.2	2.09	1.67	- 20.0
8.6	2.09	1.74	- 35.0
9.1	1.90	1.82	- 4.2
10.1	3.03	1.99	- 34.3
10.9	1.81	2.13	+ 17.6
11.2	1.50	2.17	+ 44.6
12.2	2.16	2.34	+ 8.3
14.7	2.50	2.73	+ 9.2
15.3	2.42	2.83	+ 16.9
16.4	2.64	3.00	+ 13.6
19.8	2.84	3.51	+ 23.5
21.6	3.34	3.78	+ 13.1
22.2	4.16	3.87	- 6.9
25.1	4.69	4.29	- 8.5
26.8	4.32	4.50	+ 4.1
27.3	4.04	4.61	+ 14.1
29.1	5.58	4.86	- 12.9
29.6	6.05	4.93	- 18.5
30.9	5.58	5.11	- 8.4
34.9	6.24	5.67	- 9.1

Appendix Table IV.   Variates of oxygen consumption of one-fish trials
in a sealed respirometer at 20 C, June-August 1969

Fish weight (g)	O_2 consumption (mg/l)	Expected O_2 consumption (mg/hr)	% deviation
3.4	1.30	1.21	- 6.9
4.0	1.16	1.41	+ 21.5
4.6	1.73	1.61	- 6.9
5.5	2.49	1.91	- 23.2
6.0	2.02	2.07	+ 2.4
6.4	2.79	2.20	- 21.1
6.7	1.62	2.30	+ 41.9
6.7	2.43	2.30	- 5.3
6.8	2.22	2.33	+ 4.9
8.3	3.72	2.81	- 24.4
9.7	3.56	3.25	- 8.7
9.7	2.32	3.25	+ 40.0
10.2	2.56	3.42	+ 33.5
10.8	4.01	3.60	- 10.2
12.7	4.19	4.19	0.0
14.1	4.41	4.62	+ 4.7
14.7	3.79	4.80	+ 26.6
15.0	5.61	4.90	- 12.6
16.5	6.50	5.35	- 17.6
17.7	5.50	5.72	+ 4.0
17.8	5.12	5.75	+ 12.3
18.1	5.89	5.74	- 2.5
20.3	7.61	6.50	- 14.4
25.1	8.14	7.94	- 2.4

Appendix Table V.   Variates of oxygen consumption of one-fish trials
in a flowing water respirometer at 20 C, June-
July 1970

Date	No. of trials	Weight (g)	Av. O_2 consumption (mg/hr)	Std. dev. of O_2 consumption (mg/hr)	Expected av. O_2 consumption (mg/hr)
June 22-24	10	20.5	7.33	0.627	7.30
20	10	26.4	9.30	0.272	8.97
26	10	30.5	10.00	0.462	10.09
28	10	25.8	8.65	0.606	8.81
30	10	39.9	12.60	0.496	12.56
July 4	10	36.4	11.51	0.758	11.66
2-3	10	28.3	9.56	0.985	9.50
6	10	23.2	8.38	1.146	8.08
14	10	20.7	7.20	0.926	7.36
16	10	31.9	10.45	0.818	10.47

Appendix Table VI.   Surface water analysis data from Smith Mounatin
                     Reservoir, 1969

Date	Area	Secchi disk (cm)	Dissolved oxygen (ppm)	pH	Surface temperature (C)
28.vi	RR*	137	9	7.6	18
	BR**	170	10	7.3	20
	Basin	204	10	7.9	19
11.vii	RR	216	11	7.2	19
	BR	137	10	7.4	20
	Basin	212	11	7.2	19
16.viii	RR	185	9	7.5	19
	BR	115	6	7.4	21
	Basin	107	10	7.2	21
28.ix	RR	133	9	7.2	21
	BR	144	7	7.1	20
	Basin	201	7	7.3	18
20.x	RR	217	7	7.4	15
	BR	296	8	8.1	19
	Basin	325	7	7.3	22
18.xi	RR	329	6	7.6	13
	BR	340	7	7.6	9
	Basin	267	7	7.5	13
17.xii	RR	256	9	7.2	10
	BR	333	8	7.4	10
	Basin	303	10	7.6	9

*Roanoke River arm.
**Blackwater River arm.

Appendix Table VII.   Some of the major food types of the gizzard shad
                      as determined by Tiffany (1921a)

Merismopedia

Microcystis

Euglena

Peridinium

Melosira

Navicula

Synedra

Arthrodesmus

Staurastrum

Closterium

Cosmarium

Euastrum

Pandorina

Eudorina

Pediastrum

Tetraedon

Kirchneriella

Scenedesmus

Colaestrum

Appendix Table VIII. Types of algae found in the digestive tracts of gizzard shad (Smith 1963)

Euglena

Diatoms

Phacus

Gymnodinium

Chroococcus

Lyngbya

Merismopedia

Microcystis

Closterium

Coelastrum

Cosmarium

Crucigenia

Eudorina

Oedogonium

Oocysystis

Pandorina

Pediast· m

Platydorina

Scenedesmus

Spirogyra

Staurastrum

Appendix Table IX. Some of the food categories of the gizzard shad as
                    given by Dalquest and Peters (1966)

Diatoms:	Navicula,* Cymbella,* Cystopleura, Cyrosigma, Gomphonema, and Surirella
Green algae:	Desmids, Cladophora, and Spirogyra
Protozoa:	Difflugia,* and Volvox*
Cladocera:	Bosmina
Copepoda	
Ostracoda	
Blue-green algae:	Oscillatoria, Nostoc, and Merismopedia

*Dominant types

Appendix Table X. A list of zooplankton found in gizzard shad (Cramer
                   and Marzolf 1970)

Diaptomus

Cyclops (adults and copopids)

Copepod nauplii

Daphnia

Bosmina

Keratella

Asplanshna

Brachionus

Diaphanosoma

Hexartha

Polyarthra

Appendix Table XI. The effects of temperature on voidance time for
fish (Lane and Jackson 1969)

Species	Temperature (C)	Average weight (g)	Time to void (hrs)
Goldfish	12	0.8	48
Goldfish	12	2.5	36
Goldfish	20	1.5	72
Goldfish	20	1.2	60
Goldfish	25	0.8	60
Fathead minnow	12	1.7	36
Fathead minnow	20	0.9	12
Bluegill	12	1.1	60
Bluegill	12	1.2	84
Bluegill	12	1.3	36
Bluegill	20	1.2	36
Bluegill	20	1.6	48
Bluegill	20	1.6	60
Bluegill	25	0.5	36
Bluegill	22	0.6	36
Bluegill	17	0.6	48
Bluegill	12	0.6	84

Calculations

Estimated daily ration for 34 g fish (% day^{-1})

$$D = A \frac{24}{n}$$

$$A = 0.076 \text{ g} \times 6100 \text{ cal g}^{-1}$$

$$D = 1204.1 \text{ cal day}^{-1}$$

$$n = 9 \text{ hrs}$$

Average daily growth rate (% day^{-1})

$$C_m = \frac{2}{t} \frac{(W_1 - W_0)}{(W_1 + W_0)} \; 100$$

$$W_0 = 25.13 \text{ g}$$

$$W_1 = 100.15 \text{ g}$$

$$C_m = 0.57\% \text{ day}^{-1}$$

$$t = 210 \text{ days above } 13 \text{ C}$$

Production for 34 g fish (cal day^{-1})

$$P = W \cdot C_m \cdot Q_f$$

$$W = 34 \text{ g}$$

$$P = 118 \text{ cal day}^{-1}$$

$$C_m = 0.0057$$

$$Q_f = 608.9$$

$$\text{cal g}^{-1} \text{ (wet weight of shad)}$$

Metabolic expenditure for 34 g fish at 20 C (cal day^{-1})

$$M_Q = Q \cdot t \cdot aW^b$$

$$\log M_Q = \log Q + \log t + \log a + b \log W$$

$$\log M_Q = 2.95633$$

$$Q = 3.42 \text{ cal mg}^{-1} \text{ O}_2$$

$$M_Q = 904.9 \text{ cal day}^{-1}$$

$$t = 24 \text{ hrs} \qquad W = 34 \text{ g}$$

$$b = 0.813 \qquad a = 0.626$$

Estimated food value - Winberg's equation (cal day^{-1})

$$pR = P + T \qquad\qquad p = 0.8$$

$$R = 1277.8 \text{ cal day}^{-1} \qquad\qquad P = 118 \text{ cal day}^{-1}$$

$$T = M_Q = 904.9 \text{ cal day}^{-1}$$

VITA

The author, son of Ruby F. and Frank E. Smith, was born January 25, 1935, in Richmond, Virginia. He received his elementary and secondary education in the Richmond Public School System, graduating from Armstrong High School in 1953.

He enjoyed a tour of duty in the U. S. Army and afterward worked for a photographic firm. He entered Virginia State College in the fall of 1958, and received the Bachelor of Science and Master of Science degrees in Biology from that institution, June 1962 and June 1964, respectively.

He held positions with the State of Virginia Health Department and Virginia State College prior to beginning work for the doctorate in the Division of Forestry and Wildlife Sciences at Virginia Polytechnic Institute, Blacksburg, Virginia, in 1967.

In 1960, he married the former Joe Ann Sanders of Alexandria, Virginia. They have a daughter, Crystal LaVerne.

Alphonso O. Smith

SOME ASPECTS OF TROPHIC RELATIONS
OF GIZZARD SHAD, DOROSOMA
CEPEDIANUM

Alphonso Oscar Smith

Abstract

Foods, feeding, voidance, and bioenergetics of gizzard shad were
investigated. Ten of the 17 most frequently occurring plankters in
Smith Mountain Reservoir were utilized as food: the bulk of the diet
consisted of Glenodinium, Dinobryon, and copepod nauplii. The feeding
behavior of shad was described. Shad were observed to demonstrate the
directed activity of seeking particulate materials from the substratum.
It was concluded that shad are continuous feeders, but show seasonal
variation in food intake. Evacuation of the alimentary tract re-
quired 18 to 21 hours and was related to continuous feeding activity.
Feeding trials with Artemia nauplii yielded the equation: $\frac{n}{T} = 1.36$
$T^{0.23} W^{0.46} D^{0.09}$. Filtration rates were shown to be inversely related
to feeding duration and body size. Oxygen consumption was measured at
three temperatures. Routine metabolism-weight relations were shown to
be $M = 0.452 W^{0.848}$ at 10 C, $M = 0.659 W^{0.841}$ at 15 C and $M = 0.769$
$W^{0.937}$ at 20 C in a siphon-equipped respirometer. At 20 C this rela-
tionship was $M = 0.627 W^{0.813}$ in a flowing water system. A typical
yearling gizzard shad, 34 g in weight, required a dietary equivalent
of 1204 cal/day of which 905 cal were spent for respiratory metabolism.