Stomach Capacity, Digestion Rate, and 24-Hour Consumption Rate for the Bear Lake Sculpin (Cottus Extensus)

Joseph H. Williamson

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STOMACH CAPACITY, DIGESTION RATE, AND 24-HOUR
CONSUMPTION RATE FOR THE BEAR LAKE SCULPIN

(COTTUS EXTENSUS)

by

Joseph H. Williamson

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Fishery Biology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah
1970
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Joseph H. Williamson
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ABSTRACT

Stomach Capacity, Digestion Rate, and 24-Hour Consumption Rate for the Bear Lake Sculpin (Cottus Extensus)

by

Joseph H. Williamson, Master of Science

Utah State University, 1970

Major Professor: Dr. William T. Helm
Department: Wildlife Resources

A curvilinear regression model was used to determine an expected stomach capacity for any size Bear Lake sculpin with a standard length between 4-9.5 centimeters. Stomach contents were then expressed as a percent fullness and the change in percent fullness with time intervals was used to compute an instantaneous digestion rate. The instantaneous consumption rate was computed by the formula \( C = \log P_1 - \log P_0 + d \), where \( C \) = instantaneous consumption rate. The amount of food consumed during a time interval was computed from the formula \( I_t = C_t \delta_t \), where \( I_t \) = amount of food ingested during a time interval expressed in percent fullness of stomach. The 24 hour consumption rate was computed by summing the consumption rates for 4 consecutive time intervals of 6 hours each.

Studies in September, December, and May give instantaneous digestion rates of -.424, -.214, and -.235 and total food consumption
rates of 22.2, 10.2, and 6.1 percent of stomach capacity for each individual fish in the population.
CHAPTER I
INTRODUCTION

The rate at which energy can move through the food web is in part determined by the productivity of the aquatic habitat. Productivity in turn can be measured indirectly by age and growth studies on the fish populations present. However in higher organisms such as fish the production of biomass may not be an accurate measurement of the energy entering into that link of the food web. It has been pointed out by Davis and Warren (1965) that in years of high population density the production of biomass may be nonexistent but the energy consumed and metabolized may be high. Lakes with overcrowded stunted populations would be good examples of this condition. It must be remembered that high population density is a relative thing; a more descriptive way of expressing population density would be calories of available energy per individual.

To manage a fish population with the highest growth rate possible one needs to know at what rate energy is being passed through the population. With a rate on the passage of food through a fish, its food equated to calories, and a rate at which that energy is produced in the environment an estimate of the best population level for maximum growth can be made.

The passage of food, which can be equated with energy, through the Bear Lake sculpin (*Cottus extensus*) is as important as a growth
study of the sculpin. To estimate the passage of energy through sculpin the digestive rate as well as the consumption rate must be measured.

The sculpin is an important link in the food web of Bear Lake. The sculpin feeds on chironomids and cladocerans and occasional other small invertebrates as opportunity permits. The sculpin in turn constitutes an important food item in the diet of lake trout (Salvelinus namaycush), cutthroat trout (Salmo clarki), rainbow trout (Salmo gairdneri irideus), and the Bonneville whitefish (Prosopium spilonotus) as reported by McConnell, Clark, and Sigler (1957).

One of the problems in determining the amount of food passing through a fish population is the different sizes of fish in that population. Hathaway (1927) states that a small fish eats less than a large fish, but a small fish eats more per unit body weight than a large fish. Ignoring this problem and treating all fish as equal can lead to a biased sample, especially where the number of individuals comprising a sample is small. A sample consisting of small individuals would underestimate food consumption and a sample of large individuals would overestimate consumption. A large sample of mixed sizes gives the best estimate. However there is still the problem of equating different amounts of food in different size fish if any comparison on an individual basis is to be made.

This problem was handled by Kimball (1970) for brown trout (Salmo trutta) and the rocky mountain whitefish (Prosopium williamsoni)
by determining the stomach capacity and then expressing the contents as a percent of what the stomach could contain.

With both the brown trout and whitefish a non linear regression model was used to express a relationship between length of fish and stomach capacity. This eliminated the need of measuring each individual stomach in future samples. The expected stomach capacity for any fish (which fit this relationship) could be obtained by measuring the fish and solving the following formula:

\[ Y = b_1 x^2 + b_2 + b_3 \]

where \( Y \) is the expected stomach capacity, 
\( b_1, b_2, b_3 \) are regression coefficients, 
\( x \) is the fish's standard length in centimeters.

Kimball (1970) computed the instantaneous digestion rate from the slope of the linear regression line between the independent time intervals and the dependent natural log of the percent fullness of the sample. The instantaneous consumption rate was calculated from the formula, \( C = \log P_1 - \log P_0 + d \)

where \( C \) = instantaneous consumption rate
\( \log P_1 \) = natural log of the percent fullness measurement at end of time interval
\( \log P_0 \) = natural log of the percent fullness measurement at start of time interval
\( d \) = digestion rate.

The amount of food ingested during a time interval was computed by the formula, \( I_t = C_t S_t \)
where

\[ I_t = \text{amount of food ingested during a time interval expressed in percent fullness of stomach} \]
\[ C_t = \text{instantaneous consumption rate during the time interval} \]
\[ S_t = \text{geometric average of percent fullness of stomach during time interval} \]

The 24-hour consumption rate was calculated by summing the amounts of food ingested during the 4 consecutive time intervals of 6 hours each.
Statement of Thesis Problem

Bear Lake, a large oligotrophic lake, contains four endemic species of fish: the Bonneville cisco (Prosopium gemifer), the Bonneville whitefish (Prosopium spilonotus), the Bear Lake whitefish (Prosopium abyssicola) and the Bear Lake sculpin (Cottus extensus). This alone makes the management of Bear Lake a critical situation. Fish have been introduced in the past to improve the fishing without regard to their impact on the native endemics. Part of this problem has no doubt been due to the lack of information present on the endemic species. This study will provide more information on the Bear Lake sculpin.

The primary objectives of this study were:

1. To determine the relationship between standard length and stomach capacity.
2. To determine the digestion rate at different seasons. No attempt was made to correlate the difference with charges in temperature, photoperiod, or metabolic changes in the fish's physiology.
3. To determine the consumption rate during a 24-hour period.
Bear Lake: Setting for the Study

The following statistical information was taken from McConnell, Clark and Sigler (1957) and Smart (1958).

Bear Lake, situated on the Utah-Idaho border, is a large oligotrophic lake occupying an area of 284.9 square kilometers. The long axis is 32.2 kilometers north to south, and the width varies between 6.4 to 12.9 kilometers. The deepest spot, over 61 meters, is on the east side and the lake becomes shallower as one proceeds west. More than half of the lake is deeper than 30.5 meters. Water is diverted to the lake from the Bear River in the spring and pumped out as needed for irrigation during the summer. Although it is possible to lower the lake 6.4 meters by pumping, the annual fluctuation is usually only .9 to 1.2 meters.

The bottom types found in the lake change with depth. Out to 3 meters the bottom is rocks except along the north, northwest, and south shores which are sandy beaches. Between 3 to 8 meters is found sand, from 8 to 23 meters silt and marl, and over 23 meters the bottom is composed of fine gray silt marl.

Surface temperatures in summer reach 21 C. and a thermocline develops at about 15 meters. Water temperature below 46 meters seldom exceeds 6.7 C.

Rooted aquatics include cattail (Typha sp), bulrush (Scirpus sp), and pondweed (Potamogeton sp). A dense growth of Ranunculus sp is
found in a sheltered cove at the mouth of Swan Creek.

Invertebrate organisms found in the lake change in abundance according to the bottom types. Gammarus, aquatic mites, midge larvae, and crayfish can be found in the rocky areas. Sandy areas are inhabited by mites and diptera larvae. Rooted aquatics are occupied by midge larvae, gammarus, mites, Mayfly, dragonfly, and damselfly nymphs. The sand-silt-marl mixture maintains the maximum density of midge larvae along with some aquatic oligochaets and an ostracod found on or just above the surface. Below 23 meters where the bottom is fine silt marl oligochaets reach their maximum density and some ostracods are also present.
CHAPTER II

REVIEW OF LITERATURE

Need for Digestion and Consumption Rates

Pearse (1924) stated the need for quantitative measurements on the amounts of food a fish consumes from his environment so that the fish manager will have some idea of the population levels which will provide the greatest growth. Surber (1930) emphasized the importance of determining a fish's daily meal, the daily meal being the amount of food ingested per day. Ricker (1946) and Seaburg and Moyle (1964) saw the need to distinguish between the daily meal and the daily ration. The daily ration being the grams of food ingested per day gram of fish weight. The estimation of a daily ration or a daily meal necessitates the estimation of a digestion rate and a consumption rate.

Digestion Rate

Methods of determining

Digestion rates have been measured in different ways over the years. Bajkov (1935) collected a large sample of fish at one time and used part to determine the average amount of food in the stomach at time of capture and the others were placed in food free containers in the lake so that the temperature did not change. A small number of fish were then examined every few hours and it was possible to
determine the rate of digestion by the change in average volume of the stomach contents.

Molnar and Tolg (1962a, 1962b) used X-rays to follow the digestion of a piscivorous force-fed fish.

Darnell and Meierotto (1962) determined the stages of digestion of a "standard food item" (Hyalella azteca) in the laboratory for black bullheads (Ictalurus melas).

Hunt (1960) and Seaburg and Moyle (1964) determined digestion rates by feeding a known volume of food and measuring by water displacement that remaining in the stomach after a period of time.

Windell (1967) determined the percent organic matter of food organisms, and after feeding fish in the laboratory a known meal, recorded the rate at which the digestible organic matter disappeared from the stomach.

Factors affecting digestion rate

Numerous factors have been reported as or suspected of affecting the rate of digestion. Some of the factors affecting digestion rate are: temperature, size of fish, composition of food, amount of food, handling, starvation, season or photoperiod, and mechanical effects of gastric function.

Temperature. Molnar and Tolg (1962a) reported a change in the rate of digestion of 50 percent between 5 and 10 °C. for largemouth bass, (Micropterus salmoides Lacepede). The change in the digestion
rate between successive 5 degree changes was not as large as the change between 5 to 10 C. Pomazovskaya (1962) reported that for perch and the ruffe the rate of digestion depended upon the water temperature.

**Size of fish.** Seaburg and Moyle (1964) reported a faster digestion rate for bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*) and black crapple (*Pomoxis Nogromaculatus*) than for larger game fish but digestion rates for the same kinds of food in different sizes of panfishes were similar. Hunt (1960) reported a slower digestion rate for larger gar than smaller ones although digestion rates varied greatly among the same size of fish.

**Composition of food.** Seaburg and Moyle (1964) reported that the digestion rate of plants was slower than the digestion rate of animal foods. Pegel, Remorov, and Eroshenko (1966) state that the digestion rate is influenced by the type of food eaten. Windell (1967) reported no difference in digestion rate for seven food organisms differing in percent of chitin. He postulated that the slower digestion rate associated with mealworms was due to the high fat content. Windell and Norris (1969) reported a difference in the digestion rates for meals of oligochaetes, pellets, and mealworms. Twelve hours after ingestion 70 percent of the meal of oligochaetes was digested compared to 29.4 percent for the mealworms and only 27.9 percent for the pellets.

**Amount of food.** Hunt (1960) reported that the rate of digestion in the gar (*Lepisosteus platyrhincus*) is related to the amount of food
present. Increasing the size of the meal by a factor of three caused the digestion rate to slightly more than double. Pomazovskaya (1962) reported that for perch the digestion rate slowed down after 50 percent of the stomach volume was digested in 4 to 5 hours at 10 C. Seaburg and Moyle (1964) reported that with panfishes at 17.7 to 23.3 C., 50 percent of the stomach volume was digested in 4 to 5 hours and 75 percent in 12 hours. This indicated a slowing down of the digestion rate after the first 5 hours. Windell and Norris (1969) reported that for Salmo gairdneri gastric digestion proceeded rapidly until 75 percent of the stomach contents were removed and then slowed down.

Handling. Hunt (1960) concluded that force feeding of warmouth (Chaenobryttus gulosus) did not alter the digestion rate since the digestion rate for fish force fed did not differ from controls which consumed the meal voluntarily. Molnar and Toig (1962a) concluded that the digestion rate of largemouth bass was not affected by being narcotized in a 2 methylchinoline (Quinaldin) solution since the digestion rate did not differ from controls. Windell (1967) pointed out the need for careful handling of fish used in digestion studies and cited evidence from recent studies that handling produces stress in fish.

Starvation. Windell (1967) showed that as the period of starvation increased the rate of gastric digestion decreased for bluegill sunfish, (Lepomis macrochirus).
Season or photoperiod. Windell and Norris (1969), by eliminating temperature as a variable, showed that the digestion rate was not affected by changes in the photoperiod for rainbow trout, (Salmo gairdneri).

Mechanical effects of gastric function. Molnar, Tamassy, and Tolg (1967) suggested that an important influence on the digestion rate would be the different ways in which food is moved through the stomach.

Consumption Rate

Methods of determining

Measurements of consumption rates can be classified as direct or indirect.

Direct methods. Bajkov (1935) calculated the daily food consumption of fish by using the formula $D = A \frac{24}{n}$ where

$D$=the daily consumption,

$A$=the average amount of food in the stomach,

$n$=number of hours necessary for passing all the food from the stomach into the intestine (rate of digestion).

The digestion rate was obtained by a digestion study at the time of the experiment and the average amount of food in the stomach was calculated from successive collections during a twenty-four hour period.

Davis and Warren (1968) reported that Fortunatova was able to tell for pike (Scorpaena porcus L.) on which of the three previous days a food item was consumed. The size of the food item was reconstructed by tables using the length of the mandibles or size of the otoliths of the
food organism. With this data consumption rates were calculated. This method was only useful for fish which fed infrequently and consumed large food items when they did eat.

Darnell and Meierotto (1962) established a time interval for the digestion by black bullheads of a standard food item. By assuming that the standard food item was representative of the other stomach contents it was possible to calculate the amount of food ingested during a time interval. By sampling at three-hour time intervals a daily consumption was determined.

Welch and Ball (1966) estimated benthos consumption by comparing the benthic biomass inside and outside of wire fish exclosures in the presence and absence of fish predators.

**Indirect methods.** Various indirect methods have been suggested for determining the consumption of fishes. Davis and Warren (1968) reported that Winberg assumed that fish digest 85 percent of the food they eat and lose 3 percent of the energy value through excretion of nitrogenous waste. Thus the metabolizable portion of the ration is assumed to be 80 percent of the total ration. Winberg further assumed that the metabolic rate of fish in nature is twice that of their routine metabolic rate in the laboratory. Winberg was then able to compute the consumption rate with the formula:

\[
C = 1.25 (R + B) \text{ where}
\]

- \( C \) = consumption rate,
- \( R \) = total energy of metabolism,
- \( B \) = total change in energy value of materials of body (growth).
Davis and Warren (1968) explained the nitrogen balance method of estimating consumption which has been used by Soviet fishery scientists. In this method the rate of nitrogen intake was estimated by summing the rate at which nitrogen accumulated in growth and the rate at which nitrogen was lost through defication and excretion by the kidneys and gills. Knowing the rate of nitrogen intake the food consumption rate was estimated from the ratio of the nitrogen content to wet weight of the food organism.

Davis and Warren (1968) gave a method for determining a consumption rate from an estimated growth rate. The growth rate of fish in the laboratory fed a known amount of food or on a known consumption rate was determined. The growth rate of the wild fish was then used to compute their consumption rate.

Factors affecting consumption rate

Some of the factors which have been suspected of affecting the consumption rates of fish are temperature, size of fish, season or photoperiod, and density of food organisms.

Temperature. Hathaway (1927) found that food consumption increased with increase of temperature. Surber (1930) stated that the amount of food consumed per unit of time was dependent on temperature. Brown (1946) stated that an increase in temperature increased the amount of food required for maintenance and increased the amount eaten by the fish.
Size of fish. Pearse (1924) reported that the amounts of food consumed were proportional to the size of the fish, but in relation to their volume smaller fish eat more than larger fish. Hathaway (1927) showed that smaller fish in proportion to their body weight consumed more than larger individuals of the same species. Surber (1930) stated that the amount of food eaten by a fish per unit of time was dependent on the size or age of that fish. Seaburg and Moyle (1964) reported that the average stomach volume of food found in small fish was less than large fish.

Season or photoperiod. Hathaway (1927) tested bass (Micropterus salmoides) to see if photoperiod influenced food consumption. There seemed to be no definite correlation between photoperiod and the quantity of food eaten. Kogan (1963) reported that for a bream (Abramis brama L.) depending on vision to find its food on the bottom the minimum and maximum amounts of food consumed depended on the length of the photoperiod.

Density of food organisms. Warren and Davis (1967) point out the relationship between food density and consumption and the energy cost of obtaining food.
CHAPTER III

METHODS OF PROCEDURE

Capturing Fish

The fish used for this study were all captured using an eight meter semi-balloon bottom trawl. A small mesh liner in the cod end of the net prevented the escape of small fish. The trawl was fished from a large research platform, and was set and retrieved with the aid of a small winch. Towing speed was approximately 5 kilometers per hour. Fish were collected at different depths and areas of the lake during the study.

Procedure for Determining the Relationship of Standard Length to Stomach Capacity

A 1,000 liter cattle trough on the platform was used as a holding tank to keep fish alive. When fish were captured below the thermocline water was obtained from below the thermocline by using a gasoline driven water pump and an appropriate length of garden hose. This prevented loss of fish due to temperature shock. Fish not used immediately were maintained at the laboratory in a circular metal tank kept cold and oxygenated by the addition of unchlorinated city water.

Groups of 5 to 10 sculpin were taken from the holding tank and anesthetized with MS-222. Each fish was measured to a hundredth of
a centimeter with a vernier caliper and given an identification number. Because of the small size of most of the stomachs, under one cubic centimeter, a method other than the water injection technique of Kimball was used. An undetected loss of water during the injection of such a small stomach would constitute a large percentage error.

To eliminate this problem red liquid latex was substituted for water as the injection medium. A leak in the stomach wall became immediately apparent. To accomplish the injection the fish was cut open along the ventral midline, a lateral cut was made behind the pectorals, and the sides were pinned back to expose the abdominal cavity. The stomach was tied off with light cord at the pyloric sphincter and a blunt nosed needle was inserted down the esophagus into the stomach proper. A string was tied around the esophagus at the juncture of the stomach and held tight while the injection proceeded. Latex from a plastic syringe was injected into the stomach until just prior to the bursting of the stomach. This bursting pressure was learned by trial and error. The needle was then withdrawn maintaining the constant pressure so that the volume vacated by the needle was filled with latex. The string on the upper esophagus was pulled tight and tied when the needle was completely withdrawn. Fish with detected leaks were discarded. Fish with stomachs free from leaks and with an identifying number attached were placed in a liter of 10 percent formaldehyde solution with 10 milliliters of 2 percent acetic acid added until the latex hardened in 24 to 48 hours. The stomach along with the stomach wall was then dissected out of the fish.
and a volumetric measurement was made using graduated cylinders, to one twentieth of a cubic centimeter. The stomach wall was not removed to prevent the loss of any unhardened liquid in the stomach.

A sample of 157 fish 4 to 9.5 centimeters in length was injected in this manner and volumetric measurements determined. Mathematical and statistical analyses were then performed to determine if a relationship between standard length and stomach capacity for the Bear Lake sculpin existed.
Digestion Study Procedure

Fish captured for the digestion study were retained in the holding tank on the platform until placed in the individual digestion cages and lowered to the appropriate depth. Fish captured below a thermocline were returned below the thermocline so the digestion rate was not affected by a temperature change during the digestion period. When the lake was not stratified the cages were not lowered to any great depth.

The cylindrical digestion cages were constructed from 0.6 cm hardware screen which allowed free circulation of water at all times. Because sculpin are bottom feeding fish and their principal food items, chironomids and cladocerans, are bottom associating it was not thought necessary to prevent water from fully circulating through the cages. Since Bear Lake is an oligotrophic lake the open water was free from food organisms of a sufficient size for the sculpin to feed on and care was taken to insure that the cages were well off the bottom.

During the injection of the stomachs it was noticed that the time for the complete emptying of the stomach was greater than 24 hours, so the sampling times for the digestion study were set 6 hours apart. In the September study 10 fish were used as a sample. Since 86 sculpin were captured 8 digestion cages were used, the eighth cage containing only 6 sculpin. This allowed 48 hours for the digestion study. In the December collection 20 fish were placed in each digestion
cage and only 4 cages were used. The digestion study was 24 hours long. The initial sample to determine the percent fullness of the population was taken immediately in both cases.

In the May digestion study a change in the procedure was made. Both of the previous digestion studies had been conducted before the length to stomach capacity relationship had been fully determined and therefore no idea of the variance encountered in the percent fullness for individuals comprising one sample was known. Prior to the May collection the fish length to stomach capacity relationship was used to evaluate the previous two digestion studies. It was found from tables in Ostel (1963) that a sample size of 99 fish was needed to determine if a difference of 2 percent in the percent fullness of stomachs was significant at the .05 level with a Beta level at 0.5. This meant that larger samples would be needed to more accurately estimate the digestion rate. Since 500 fish were needed for the sample and it was unlikely that 500 would be captured in one trawl, a change in the digestion study procedure was necessary. Four trawls were made over a 4 hour time period and the fish combined to make one large sample. Fish captured during the first three trawls were kept alive in a large plastic garbage pail. The last trawl was divided between the 4 digestion cages and the initial sample. Space limitations prevented the keeping of all trawls separate. It was not possible to launch the research platform and the trawling was done with a small boat.
Because the theoretical capacity of a known length fish was available, the stomach from each fish was expressed in terms of percent fullness. This allowed recognition of individual differences and determination of average percent fullness for the population at that time. The instantaneous digestion rate was obtained from the slope of the linear regression line between the independent time interval and the dependent natural log of the percent fullness of the sample.

**Food Consumption Rate Procedure**

The food consumption study was conducted as soon after the digestion study as possible for September and December and before the digestion study for the May collection. In September and December a sample size of 20 fish was used, whereas in the May collection a sample size of 100 fish was desired. Immediately upon capture the fish were anesthetized with MS-222, measured, cut open, and preserved in 10 percent formaldehyde. Individual measurements of percent fullness were made as well as an estimate of percent fullness of the population. The instantaneous consumption rate was obtained from the formula, 
\[
C = \log P_1 - \log P_0 + d,
\]
and the amount of food consumed during a time interval was calculated from the formula, 
\[
I_t = C_t S_t.
\]
The amount of food consumed during a 24 hour period was calculated by summing the amount of food consumed during 4 consecutive time intervals of 6 hours each.
Measuring Stomach Contents

The stomach contents were measured by water displacement using a tuberculin syringe calibrated in 100th of a cubic centimeter. Measurements less than 100th of a cubic centimeter were not readable. To distinguish between completely empty stomachs and those with an unmeasurably small amount of food the latter were automatically given a stomach contents measurement of 0.005 cubic centimeter.

Calculating Percent Fullness

The percent fullness of an individual stomach was calculated using the following formula:

\[
\text{Percent fullness} = \frac{\text{Measured stomach contents}}{\text{Calculated stomach capacity}}
\]

The percent fullness for the population was estimated using the following formula:

\[
\text{Percent fullness} = \frac{\text{Summation of the individual percent fullness values expressed as a decimal}}{\text{Number of individuals in the sample}}
\]
CHAPTER IV

ANALYSIS OF DATA

Length to Stomach Capacity Relationship

Non-linear regression model

Standard length and actual stomach capacity measurements were obtained for 157 fish. A computer program using the non-linear regression model, $Y = b_1 x b_2 x^2 b_3$, was tested on the data. A coefficient of determination ($r^2$) value of .700 was obtained. The curve generated for expected stomach capacities was below most of the actual stomach capacities for small fish and only for the larger fish did the curve fall between the points on the scatter diagram in Figure 1.

Linear regression model

A plain regression model, $Y = b_0 + b_1 X$, was tested on the data and although the $r^2$ value obtained was slightly better (.707) the model was judged biologically inappropriate since fish less than 4.5 centimeters were given a negative stomach capacity (Figure 1).

Means of length interval classes

A third approach of obtaining an expected stomach capacity was to divide the sample into length intervals of 1/2 centimeter and determine a mean stomach capacity for that interval (Table 1). When this was done it graphically displayed the inappropriateness of the
Figure 1. Length to stomach capacity relationship for the Bear Lake sculpin by non-linear and linear regression. Each dot represents an individually measured stomach capacity. The broken horizontal lines are the means of the stomach capacities for 1/2 centimeter intervals. The continuous curved line gives the expected stomach capacity by non-linear regression. The continuous straight line gives the expected stomach capacity by linear regression.

Non linear regression
\[ Y = b_1 b_2 x^2 \]
\[ Y = (0.003049083)(348.1846)x^{2} (2, 396671)x^{2} \]
\[ r^2 = .700 \]
\[ r = .837 \]

Linear regression
\[ Y = b_0 + b_1 x \]
\[ Y = -.926267 - 2.033478x \]
\[ r^2 = .707 \]
\[ r = .841 \]
Table 1. Means of actual stomach capacity measurements for class intervals of 1/2 centimeters.

<table>
<thead>
<tr>
<th>Class Interval (centimeters)</th>
<th>Sample Size (n)</th>
<th>Mean (Y) (milliliters)</th>
<th>Variance</th>
<th>Confidence Intervals .05 level</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.0-X 4.5</td>
<td>13</td>
<td>.063</td>
<td>.0003731</td>
<td>.051-Y-.075</td>
</tr>
<tr>
<td>4.5-X 5.0</td>
<td>22</td>
<td>.091</td>
<td>.0007800</td>
<td>.079-Y-.103</td>
</tr>
<tr>
<td>5.0-X 5.5</td>
<td>23</td>
<td>.129</td>
<td>.0007901</td>
<td>.117-Y-.141</td>
</tr>
<tr>
<td>5.5-X 6.0</td>
<td>20</td>
<td>.194</td>
<td>.0090263</td>
<td>.150-Y-.238</td>
</tr>
<tr>
<td>6.0-X 6.5</td>
<td>20</td>
<td>.238</td>
<td>.0038874</td>
<td>.209-Y-.267</td>
</tr>
<tr>
<td>6.5-X 7.0</td>
<td>24</td>
<td>.366</td>
<td>.0127280</td>
<td>.318-Y-.414</td>
</tr>
<tr>
<td>7.0-X 7.5</td>
<td>27</td>
<td>.469</td>
<td>.0105918</td>
<td>.428-Y-.510</td>
</tr>
<tr>
<td>7.5-X 8.0</td>
<td>20</td>
<td>.609</td>
<td>.0405295</td>
<td>.515-Y-.703</td>
</tr>
<tr>
<td>8.0-X 8.5</td>
<td>22</td>
<td>.820</td>
<td>.0012347</td>
<td>.804-Y-.836</td>
</tr>
<tr>
<td>8.5-X 9.0</td>
<td>16</td>
<td>.928</td>
<td>.1436105</td>
<td>.726-Y-.113</td>
</tr>
<tr>
<td>9.0-X-9.5</td>
<td>10</td>
<td>1.120</td>
<td>.1373333</td>
<td>.812-Y-1.43</td>
</tr>
</tbody>
</table>
previous two models (Figure 1).

Curvilinear regression model

A final attempt to fit a mathematical model to the data was made using the quadratic formula $Y=b_0 + b_1 X + b_2 X^2$. An $r$ squared value of .763 was obtained and the generated curvilinear regression line closely followed the means of the length interval classes as seen in Figure 2. The last mathematical model was used to determine the expected stomach capacity of any fish between 4-9.5 centimeters. For convenience a computer program was run to obtain the expected stomach capacity of any fish between 4-9.5 centimeters in increments of 100th of a centimeter.

Digestion studies

During the September digestion study the lake had a thermocline. Fish for the study were captured at a depth of 27 meters where the water temperature was 5.5°C and lowered to 27 meters in 35 meters of water. The instantaneous digestion rate was computed to be -.424 with a correlation coefficient ($r$) value of .92 and an $r^2$ value of .85 (Figure 3)

During the December digestion study the lake was isothermal and the water temperature was 4°C. Fish for the digestion study were captured in 55 meters of water. In this study the initial sample determining the percent fullness of the population at the
Curvilinear regression

\[ Y = b_0 + b_1 X + b_2 X^2 \]

\[ Y = 0.9697233 + (-4.002909)X + 4.535401X^2 \]

\[ r^2 = 0.763 \]

\[ r = 0.873 \]

**Figure 2.** Length to stomach capacity relationship for Bear Lake sculpin by curvilinear regression. Each dot represents an individually measured stomach capacity. The broken horizontal lines are the means of the stomach capacities for 1/2 centimeter intervals. The continuous curved line gives the expected stomach capacity for curvilinear regression.
Figure 3. Digestion study of Bear Lake sculpin conducted on Sept. 11 and 12, 1969. Solid sloping line represents the instantaneous digestion rate. Each horizontal line represents the mean percent fullness of the sample. The vertical lines represent the 95% confidence interval on the mean. Broken line represents a theoretical digestion rate.
at the start of the digestion study was eliminated. An error in the selection of fish resulted in the mean size of fish in this sample being 7.2 centimeters (6.5 percent fullness) compared to 6.08 centimeters (9.4 percent fullness) for the second sample.

Initially it was thought that by converting the amount of food to a percent fullness measurement it would be possible to use smaller samples because the amount eaten by larger fish would be better equated with the amount eaten by smaller fish. The sample taken on December 18, 1969, at 1450 is a good example. A linear regression between the length of fish and absolute quantity of food eaten gave a correlation coefficient of .68. By converting this to percent fullness the correlation coefficient was reduced to -.12. (Figure 4). However upon examination of other samples it was found that larger fish do not always contain an appreciably greater amount than smaller fish, and on a percent fullness basis smaller fish influence a sample more than larger fish. The sample taken on September 18, 1969, at 2040 hours is a good example. A linear regression between length of fish and quantity of food in the stomach gave a correlation coefficient value of -.13. This can for all practical purposes be considered no correlation at all. When the contents of the stomach were converted to a percent fullness measurement the correlation coefficient was -.67. Although it is not a good correlation there is quite a difference between the two as seen in Figure 5.

Table 2 provides a comparison between the stomach contents
Table 2. Comparison between the stomach contents treated on an absolute quantity basis and converted to a percent fullness measurement.

<table>
<thead>
<tr>
<th>Sept. 17, 18, 1969</th>
<th>Mean Length of fish</th>
<th>Mean % full</th>
<th>.95 Confidence interval on mean percent full</th>
<th>Mean stomach contents in cubic centimeters</th>
</tr>
</thead>
<tbody>
<tr>
<td>2115</td>
<td>6.11</td>
<td>12.2</td>
<td>.069-X-.175</td>
<td>.023</td>
</tr>
<tr>
<td>0330</td>
<td>6.20</td>
<td>7.8</td>
<td>.049-X-.107</td>
<td>.018</td>
</tr>
<tr>
<td>0922</td>
<td>6.79</td>
<td>13.0</td>
<td>.056-X-.204</td>
<td>.036</td>
</tr>
<tr>
<td>1640</td>
<td>7.56</td>
<td>19.9</td>
<td>.155-X-.243</td>
<td>.103</td>
</tr>
<tr>
<td>2040</td>
<td>6.23</td>
<td>12.6</td>
<td>.074-X-.178</td>
<td>.025</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sept. 17, 18, 1969</th>
<th>.95 confidence interval on stomach contents in cc</th>
<th>.95 conf. int. on mean % full converted to cubic centimeters. Stomach cap. for mean length of fish used</th>
<th>r value for linear regression between length and % full</th>
<th>r value for linear regression between length and absolute quantity</th>
</tr>
</thead>
</table>
Table 2. Continued

<table>
<thead>
<tr>
<th>Dec. 18, 19, 1969</th>
<th>Mean Length of fish</th>
<th>Mean % full</th>
<th>.95 Confidence interval on mean percent full</th>
<th>Mean stomach contents in cubic centimeters</th>
</tr>
</thead>
<tbody>
<tr>
<td>0935</td>
<td>6.85</td>
<td>10.2</td>
<td>.069-X-.135</td>
<td>.036</td>
</tr>
<tr>
<td>1450</td>
<td>6.94</td>
<td>16.1</td>
<td>.122-X-.200</td>
<td>.067</td>
</tr>
<tr>
<td>2100</td>
<td>6.73</td>
<td>7.3</td>
<td>.047-X-.099</td>
<td>.026</td>
</tr>
<tr>
<td>0335</td>
<td>7.29</td>
<td>6.0</td>
<td>.036-X-.084</td>
<td>.025</td>
</tr>
<tr>
<td>0953</td>
<td>6.75</td>
<td>12.0</td>
<td>.089-X-.151</td>
<td>.037</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Dec. 18, 19, 1969</th>
<th>.95 confidence interval on stomach contents in cc</th>
<th>.95 conf. int. on mean % full converted to cubic centimeters. Stomach cap. for mean length of fish used</th>
<th>r value for linear regression between length and % full</th>
<th>r value for linear regression between length and absolute quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td>0935</td>
<td>.025-X-.047</td>
<td>.024-X-.048</td>
<td>-.29</td>
<td>.32</td>
</tr>
<tr>
<td>1450</td>
<td>.046-X-.088</td>
<td>.046-X-.075</td>
<td>-.12</td>
<td>.68</td>
</tr>
<tr>
<td>2100</td>
<td>.016-X-.036</td>
<td>.016-X-.033</td>
<td>-.32</td>
<td>.20</td>
</tr>
<tr>
<td>0335</td>
<td>.018-X-.032</td>
<td>.017-X-.039</td>
<td>-.45</td>
<td>.26</td>
</tr>
<tr>
<td>0953</td>
<td>.029-X-.045</td>
<td>.030-X-.050</td>
<td>-.65</td>
<td>.04</td>
</tr>
</tbody>
</table>
treated on an absolute quantity basis and converted to a percent fullness measurement along with the correlation coefficients for the linear regressions for collections in September and December. It should be noticed that in all cases by converting to a percent fullness basis the slope of the regression line switched from positive to negative which means that more weight was given to the amount of food in smaller fish than to the amount of food in larger fish.

Including the initial December sample in the calculations gave an instantaneous digestion rate of -0.097 with an $r^2$ value of .36. With the initial sample eliminated the instantaneous digestion rate was -0.214 with an $r$ value of .94 and an $r^2$ value of .88 (Figure 6). The latter instantaneous digestion rate was used to compute the consumption rates for December.

During the May digestion study the lake was isothermal at a temperature of 4°C. Fish for this study were captured between 55 and 61 meters. The instantaneous digestion rate was computed to be -0.236 with an $r$ value of .95 and an $r^2$ value of .90 (Figure 7). It should be noted that the instantaneous digestion rates are almost the same for both December and May with the same water temperature.

For a comparison of the three digestion studies attention is called to Table 3.

**Food consumption rate studies**

The total food consumption for a 24 hour period was calculated
Figure 6. Digestion study of the Bear Lake sculpin conducted on December 6 and 7, 1969. Line A represents the instantaneous digestion rate with all samples included. Line B represents the instantaneous digestion rate with the initial sample eliminated. The horizontal lines represent the mean percent fullness of the sample. The vertical lines represent the .95 confidence interval on the mean.
Digestion study of the Bear Lake Sculpin conducted on May 8 and 9, 1970. The horizontal lines represent the mean percent fullness of the sample. The vertical lines represent the .95 confidence interval on the mean. The slanting line is the instantaneous digestion rate.
to be 22.2 percent of stomach capacity in September, 10.2 percent in December, and 6.14 percent in May. Table 4 gives a comparison of the calculated consumption rates during consecutive samples. A negative consumption rate was generated whenever the computed instantaneous digestion rate was not sufficient to account for the difference between the percent fullness at the beginning of a time period and a lower percent fullness at the end of the time period. The population did not appear to be feeding and the digestion rate was not sufficiently high to account for the difference in percent fullness between two consecutive samples. When the sample at the end of a time period was larger than the sample at the beginning of the time period a negative consumption rate was not computed.

Feeding chronology

From the data available it appears that the Bear Lake sculpin feeds during daylight, reaches a peak in percent fullness in late afternoon and does not feed during darkness. Figure 8 gives the percent fullness measurements for the three 24-hour collections used to measure the food consumption rates. Negative food consumptions developed during periods of darkness or during periods encompassing decreasing light intensities.
Table 3. Results of digestion studies conducted on Sept. 11 and 12, 1969 (S); Dec. 6 and 7, 1969 (D); and May 8 and 9, 1970 (M).

<table>
<thead>
<tr>
<th>Time Interval</th>
<th>Mean Length of Fish</th>
<th>Mean Percent Fullness</th>
<th>Range of Percent Fullness in Sample</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S</td>
<td>D</td>
<td>M</td>
</tr>
<tr>
<td>1</td>
<td>6.38</td>
<td>7.20</td>
<td>5.07</td>
</tr>
<tr>
<td>2</td>
<td>6.94</td>
<td>6.08</td>
<td>5.06</td>
</tr>
<tr>
<td>3</td>
<td>6.20</td>
<td>6.73</td>
<td>5.11</td>
</tr>
<tr>
<td>4</td>
<td>7.01</td>
<td>6.52</td>
<td>5.26</td>
</tr>
<tr>
<td>5</td>
<td>7.46</td>
<td>6.51</td>
<td>5.06</td>
</tr>
<tr>
<td>6</td>
<td>6.42</td>
<td></td>
<td>2.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Interval</th>
<th>.95 Confidence Interval on the Mean Percent Fullness</th>
<th>Number of fish in Sample</th>
<th>Number of fish with empty stomachs</th>
<th>% of sample with empty stomachs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S</td>
<td>D</td>
<td>M</td>
<td>S</td>
</tr>
<tr>
<td>1</td>
<td>14.8-X-22.8</td>
<td>4.3-X-8.7</td>
<td>4.6-X-8.4</td>
<td>10</td>
</tr>
<tr>
<td>2</td>
<td>13.1-X-26.1</td>
<td>6.2-X-12.6</td>
<td>2.6-X-7.6</td>
<td>10</td>
</tr>
<tr>
<td>3</td>
<td>8.4-X-27.6</td>
<td>4.5-X-9.7</td>
<td>3.0-X-7.1</td>
<td>10</td>
</tr>
<tr>
<td>4</td>
<td>3.5-X-9.3</td>
<td>4.9-X-9.3</td>
<td>1.7-X-5.3</td>
<td>10</td>
</tr>
<tr>
<td>5</td>
<td>2.4-X-10.6</td>
<td>2.6-X-6.6</td>
<td>1.3-X-3.8</td>
<td>9</td>
</tr>
<tr>
<td>6</td>
<td>-1.1-X-5.7</td>
<td></td>
<td></td>
<td>10</td>
</tr>
</tbody>
</table>
Table 3. Continued

<table>
<thead>
<tr>
<th>Time Interval</th>
<th>No. of fish with less than .01 cc in stomach</th>
<th>% of fish with less than .01 cc in stomach</th>
<th>% of fish with empty stomachs or less than .01 in stomach</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S</td>
<td>D</td>
<td>M</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td></td>
<td>10</td>
</tr>
</tbody>
</table>
Table 4. 24-hour Consumption Rate Study of the Bear Lake Sculpin.

<table>
<thead>
<tr>
<th>September 17 and 18, 1969</th>
<th>December 18 and 19, 1969</th>
<th>May 2 and 3, 1970</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>2115</td>
<td>12.2</td>
<td>7.023</td>
</tr>
<tr>
<td>0330</td>
<td>7.8</td>
<td>9.35</td>
</tr>
<tr>
<td>0922</td>
<td>13.0</td>
<td>.850</td>
</tr>
<tr>
<td>1640</td>
<td>19.9</td>
<td>7.033</td>
</tr>
<tr>
<td>2040</td>
<td>12.6</td>
<td>1008</td>
</tr>
</tbody>
</table>

A = Time sample was taken  
B = Mean percent fullness of stomachs of sample  
C = instantaneous consumption rate between consecutive samples  
D = Amount of food consumed (in percent fullness of stomachs) during consecutive samples.
Figure 8. 24-hour Percent fullness of stomach values of the Bear Lake sculpin used to measure the food consumption rates. Each dot represents the mean percent fullness of stomach for a sample of fish. Number in parenthesis represents number of fish in sample.
CHAPTER V

DISCUSSION

Effect on handling on digestion rate

Fish used in the digestion studies were captured at 27 meters in September and between 55 and 61 meters in December and May using a bottom trawl. It is not known whether there was any effect on the digestion rate because of the change in pressure caused by bringing the fish to the surface. During the September and December digestion studies there was little mortality but during the May digestion study mortality was heavy. In May there was more crowding in the holding container for a longer period of time since 4 trawls were necessary to increase the sample size. Sculpin secrete a slime which might interfere with respiration by coating the gills. Handling does not appear to have much effect on sculpin since larger sculpin were feeding on small sculpin in the holding tank and had to be eliminated from some samples.

Value of percent fullness

An r value of 0.87 was obtained in the program selected for expressing the relationship between standard length and stomach capacity. Because it is doubtful that a fish would feed until just prior to the bursting of its stomach the estimated stomach capacity measurement in itself has no value. The expected stomach capacity is merely used to compare the amount of food in fish regardless of size, by converting
the absolute quantity to a percent fullness measurement. Initially it was thought that larger fish eat more than smaller fish. Converting the absolute amount of food to a percent fullness measurement would make it possible to use smaller samples since different size fish would be put on a more comparable basis. However (Table 2) larger sculpin do not always contain enough food to justify converting values to a percent fullness basis, since this reverses the situation and gives more weight to the amount of food in small fish. If sample size is sufficiently large and care is taken to insure that fish of all lengths are included, there would be an advantage in using percent fullness since this would enable comparisons with other species of fish. It is possible that there was not enough size difference between the largest and smallest sculpin used in the study to make the statement "that larger fish eat more than smaller fish" valid. Another possibility would be that since Bear Lake is rather unproductive and the size of the food organisms is small, larger fish do not have enough time to accumulate larger amounts.

Validity of digestion rates

Because the instantaneous consumption rate is calculated using the instantaneous digestion rate it is critical that an accurate estimate of the instantaneous digestion rate be obtained. By computing a linear regression line of the mean percent fullness of the samples through time, slight differences in the digestion rate between the samples
can be averaged out over the whole time period. However the $r$ value obtained when this is done does not give an estimate of how close the estimated digestion rate approximates the actual digestion rate, but only how well the regression line fits the estimated percent fullness measurements. How close the estimated percent fullness measurements reflect the actual percent fullness of the population, and how a change in the estimated percent fullness would effect the computation of the instantaneous digestion rate and ultimately the 24-hour consumption rate remains unanswered.

In the September digestion study the mean percent fullness of the population was computed by sampling at six time intervals and a .95 confidence interval placed on the means. However the slope of the linear regression line could be different if other percent fullness measurements had been obtained, even though these measurements were in the .95 confidence interval. To see how much the digestion rate would be altered by different percent fullness measurements, six different points representing the mean percent fullness of the population were chosen. These points were within the .95 confidence interval of the original mean percent fullness measurements obtained by sampling. This produced an $r$ value of .99 and an $r^2$ value of .99 (Figure 3). Even though this represents a perfect fit it is not a more valid estimate of the instantaneous digestion rate than that computed. Because the confidence interval on the sample means is large the regression line can assume many positions and the computed
instantaneous digestion rate may not be identical to the actual instantaneous digestion rate.

The instantaneous digestion rate calculated with the observed percent fullness measurements was -0.424 compared to -0.273 calculated by the theoretical percent fullness measurements. The observed 24-hour consumption rate was calculated to be 22.2 percent of stomach capacity for every fish in the population compared to 14.4 percent of stomach capacity for the theoretical percent fullness measurements. The difference of 7.8 percent of stomach capacity for each individual fish in the population would account for a large difference in the amount of food consumed.

Including empty stomachs in digestion study

During the May digestion study the population appeared to be feeding very little (Table 3), but it does not seem that this would effect the computed instantaneous digestion rate. By including empty stomachs the initial value of percent fullness if lowered. If it is assumed that, initially approximately the same percentage of empty stomachs was included in each sample, then the change in the percent fullness was due to digestion, and a change in the percent of empty stomachs with time was due to an emptying by digestion. Since there appears to be a gradual increase in the percent of empty stomachs with each sample this seems a valid assumption. When the fish with
less than .01 cubic centimeter of food in the stomach and the fish
with empty stomachs are combined the relationship is even stronger
(Table 3).

Value of study

Although there is too large a variance in estimating the percent
fullness of a sample for fine measurements on the population, it
does appear that this method can be used to point out trends in feeding
intensity. Unless larger fish in other situations eat considerably
more than smaller fish, the variance associated with estimating
the percent fullness of a sample and the size of the sample required
to give an accurate estimate will limit the usefulness of this technique.
CHAPTER VI

SUMMARY

The primary objectives of the study were to first; determine the relationship between standard length and stomach capacity, second; determine the instantaneous digestion rate at different seasons, and third; to determine the food consumption rate during a 24 hour period.

A curvilinear regression model $Y=b_0+b_1X+b_2X^2$ was used to determine an expected stomach capacity for any size Bear Lake sculpin between 4-9.5 centimeters. Stomach contents were then converted to a percent fullness basis. The change in percent fullness with time was used to compute an instantaneous digestion rate by plotting a linear regression between the natural log of the percent fullness and time intervals between samples. The instantaneous consumption rate was computed by the formula $C=log P_1-log P_0+d$, and the amount of food consumed during a time interval was computed from the formula $I_t=CtS_t$. The 24 hour consumption rate was determined by summing the consumption rates of 4 consecutive time intervals of 6 hours each.

Studies in September, December, and May gave instantaneous digestion rates of -.424, -.214, and -.236; and total food consumption rates of 22.2, 10.2 and 6.1 percent of stomach capacity for each individual fish in the population.


Pomazovskaya, I. V. 1962. On the rate of digestion in perch and ruffe. (Oskorost. perevarivaniy a pishchi okunem i ershom.) In: Gidrobiologicheskie issledovaniya (Hydrobiological studies.) Tartu. 3:201-205. (Original not seen; abstracted in Biological Abstracts 45 (4): Abst. No. 13949. 1964.)


VITA

Joseph Harold Williamson

Candidate for the Degree of

Master of Science

Thesis: Stomach Capacity, Digestion Rate, and 24-Hour Consumption Rate for the Bear Lake Sculpin (Cottus Extensus)

Major Field: Fishery Biology

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Professional Experience: Four years service in the United States Air Force. Served in Berlin, Germany and Trabzon, Turkey.