

AN ABSTRACT OF THE THESIS OF

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(Name of student) (Degree)

in FISHERIES presented on May 15, 1975
(Major) (Date)

Title: INFLUENCE OF DISSOLVED OXYGEN CONCENTRATION
AND SWIMMING VELOCITY ON FOOD CONSUMPTION AND
GROWTH OF JUVENILE COHO SALMON

Abstract approved: Redacted for Privacy
Dean L. Shumway

Laboratory studies were conducted on the food consumption, growth, and bioenergetics of juvenile coho salmon (Oncorhynchus kisutch) held at various swimming velocities and dissolved oxygen concentrations at 15 C. Food consumption and growth of salmon fed to repletion on housefly larvae (Mus domesticus) were reduced by increasing activity at and above 3 lengths per second (L/sec) and 2 L/sec, respectively. Food conversion efficiencies for growth decreased with increasing activity; efficiencies of converting food to growth and activity combined, however, increased with increasing activity. The logarithm of the rate of energy loss of unfed swimming salmon increased exponentially with increasing velocity.

The growth rates of salmon fed to repletion and held at 1.3 and 3.0 L/sec at an oxygen level of 3 mg/liter were reduced by 20 and 65

percent from that of control salmon held at respective velocities in air-saturated water. At the intermediate oxygen concentration of 5 mg/liter, growth rates of salmon were reduced by 0 and 15 percent over controls held at 1.3 and 3.0 L/sec, respectively.

The total respiration rate (TRR) of salmon fed to repletion and held at air saturation remained nearly constant over the range of activity levels tested (0 to 3.8 L/sec). At 1.3 L/sec the TRR of salmon increased with increasing food consumption, while at 3.7 L/sec increased food consumption did not alter the TRR. Reduction in oxygen concentration lowered the TRR of salmon, although growth was not reduced in every case.

The specific dynamic action of food (SDA), i. e., cost of food digestion and processing, ranged from 10 to 30 percent of the assimilated energy. The larger percentages were observed at high oxygen concentrations, generally at low food consumption rates, and at low velocities; and the lower percentages at low oxygen levels, high food consumption rates, and high velocities. The absolute value of SDA increased with increasing food consumption at 1.3 L/sec, but declined at 3.7 L/sec. In salmon fed to repletion, the SDA decreased with increased activity levels and reduced oxygen concentration.

Influence of Dissolved Oxygen Concentration and
Swimming Velocity on Food Consumption
and Growth of Juvenile Coho Salmon

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1974

APPROVED:

Redacted for Privacy

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Date thesis is presented

25 May 1973

Typed by Velda D. Mullins for Floyd Edward Hutchins

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation: to my major professor, Mr. Dean L. Shumway, Associate Professor of Fisheries, Oregon State University, for his support and advice, and especially for his time and constructive criticism during the preparation of this thesis; to Dr. C. E. Warren and Dr. Peter Doudoroff for helpful suggestions; to the staff and graduate students at the Oak Creek Laboratory for their help and advice; and to my wife, Anita, for her patience and perserverance during this study.

This research was supported by Public Health Service Training Grant Numbers 5T1-WP-52-02, 5T1-WP-52-03, and 5T1-WP-5-04.

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INFLUENCE OF DISSOLVED OXYGEN CONCENTRATION AND SWIMMING VELOCITY ON FOOD CONSUMPTION AND GROWTH OF JUVENILE COHO SALMON

INTRODUCTION

Many waters, especially those receiving putrescible organic matter from municipal and industrial effluents, have reduced dissolved oxygen concentrations. Even though not lethal, reduced levels of oxygen may seriously impair the growth processes of fish, and perhaps ultimately interfere with the survival of the population. Ellis (1937) in his classical study on the detection of stream pollution, concluded that in many regions of the United States dissolved oxygen concentration was an important factor limiting the abundance and distribution of many species of fish.

In order to be of economic value to man a fish population must not only survive and reproduce, but it must elaborate tissue (production) which can be utilized by man (yield). Since the production of a population is a function of the growth and numbers of individuals, reduced oxygen levels that adversely affect growth and survival can also reduce production and yield, thus reducing the value of that population as a resource to man.

Because of the difficulty in determining the influence of reduced oxygen concentrations on fish under complex natural conditions, much

of the understanding of the general problem of oxygen deficiency has come through laboratory studies. Summaries including many of these studies and discussions of their practical significance have been published by Fry (1960), Jones (1964), Doudoroff and Warren (1965) and Doudoroff and Shumway (1970). Many of these studies, although helpful in understanding the direct effects of oxygen on fish, contribute little to the knowledge of oxygen requirements of fish in their natural environment. Doudoroff and Shumway (1970) have reviewed the literature and summarized those studies they felt were useful in determining the oxygen requirements of fish.

Laboratory studies show that when temperature and food availability are sufficiently high, food consumption and growth of fish can be reduced by moderate reduction in the dissolved oxygen concentration below the air-saturation level. Studies at 18 and 20 C have shown food consumption and growth of repletion fed, juvenile coho salmon (Oncorhynchus kisutch) were impaired by any reduction in the oxygen concentration below air saturation (Herrmann et al., 1962; Fisher, 1963; and Trent, 1973). The growth of largemouth bass (Micropterus salmoides) fed to repletion was also reduced by any considerable reduction in oxygen concentration at 20 to 26 C (Stewart et al., 1967 and Trent, 1973).

At a much lower temperature of 10 C, however, food consumption and growth of bass and salmon were not restricted by oxygen levels as low as 3 mg/liter (Trent, 1973). When Fisher (1963)

restricted the food intake of salmon to the amount consumed at 3 mg/liter, growth rates were controlled by the level of food at oxygen concentrations above 3 mg/liter.

Salmon held at low oxygen levels in aquaria studies became generally lethargic (Herrmann et al., 1967; Fisher, 1963; and Trent, 1973). By such reduction in activity, fish were able to conserve energy, and thus reduce their need for oxygen. The reduced level of activity at low oxygen levels may have led to somewhat higher growth rates than would have occurred had activity not been altered. Lethargic fish in nature probably would not survive because they must compete for food and space, escape predation, etc., all requiring some degree of activity. Therefore, fish in nature may not be able to survive at oxygen concentrations that allowed some growth in the laboratory. Laboratory studies concerning the influence of oxygen on the growth of fish forced to spend energy at rates equal to those of fish in nature appear desirable.

Reduced dissolved oxygen concentration has been shown to influence the swimming performance of fish. In laboratory studies, the final swimming velocity of unfed juvenile salmon forced to swim against a gradually increasing water velocity was lowered by reduced oxygen concentrations (Davis et al., 1963 and Dahlberg et al., 1968). Oxygen consumption rates of unfed salmonids

swimming at near maximum levels were also lowered by reduced oxygen concentrations (Kutty, 1968 and Basu, 1959). Katz, et al. (1959) demonstrated, however, that unfed fish can maintain moderate swimming speeds for long periods of time at oxygen concentrations as low as 3 mg/liter. There is little reason to believe that the highest sustainable speed or the moderate speed which could be maintained for long periods of time without food are often required. Therefore, the practical significance of these studies is not known.

In the swimming studies above, the fish had not been recently fed, and therefore, they required no additional oxygen in order to digest and process food (Warren, 1971). Averett (1969) and Sethi (1969) have shown that the metabolic rate of slowly swimming fish approximately doubled for a number of hours following consumption of a large ration. Perhaps, if the fish had been recently fed in the study by Katz et al. (1959), the fish could not have maintained for long the moderate swimming velocities reported. Likewise, in the studies of Davis et al. (1963), Dahlberg et al. (1968), Kutty (1968), and Basu (1959), the final swimming velocity and the swimming velocity at any given respiration rate may have been reduced if food had been recently consumed. Since both activity and food processing do require oxygen, the question seems to be, would rapidly swimming salmon fed to repletion reduce their food consumption, level of activity, or both, when faced with a limited supply of oxygen?

Under natural conditions fish must expend energy in defending a territory, escaping predators, seeking and capturing food, reproducing, and for maintaining their body (standard metabolism). Energy is also required for digestion of food and for its resynthesis into fish tissue. When fish are faced with a limited supply of oxygen, one or more of these uses of energy may be impaired. It is important to know which of these uses of energy and to what they will be impaired by low oxygen concentrations, and how the impairment will affect the growth and production of fish. This interesting bioenergetic question is discussed by Warren and Davis (1968) and Warren (1971).

The study reported here is a segment of a comprehensive laboratory investigation on the dissolved oxygen requirements of freshwater fish. The principal objective of my study was to define the influences of dissolved oxygen concentration and level of activity (i. e., swimming velocity) on food consumption and growth rates of juvenile coho salmon.

MATERIALS AND METHODS

Experimental Apparatus

Nine units of experimental apparatus (enforced-activity troughs) were constructed and located in a constant-temperature room. Each enforced exercise trough was designed to subject eight fish to a rectilinear flow of water of controlled velocity, temperature, and dissolved oxygen content. The fish were held individually in screened compartments, and thus forced to swim against the water current. The apparatus employed is illustrated in Fig. 1, 2, and 3.

Each trough was constructed from 6-in. (19.7-cm) diameter aluminum pipe which had been split lengthwise. Two 8-ft (2.4-m) sections of the split pipe formed two parallel, round-bottom troughs about 40 cm apart. The ends of the troughs were connected with semi-circular sections of trough forming an elongate, annular trough in which water could circulate.

The water in the trough was circulated by two 16-in. (40-cm) diameter, aluminum paddle wheels. One paddle wheel was located at the head of each straight section of the annular trough. The outer edge of the paddle wheel blades were shaped to fit closely into the round-bottom trough (Fig. 1). Each paddle wheel was connected directly to a series-wound, gearhead motor by a rubber coupling. The speed of the motors could be regulated from 0 to 50 rpm

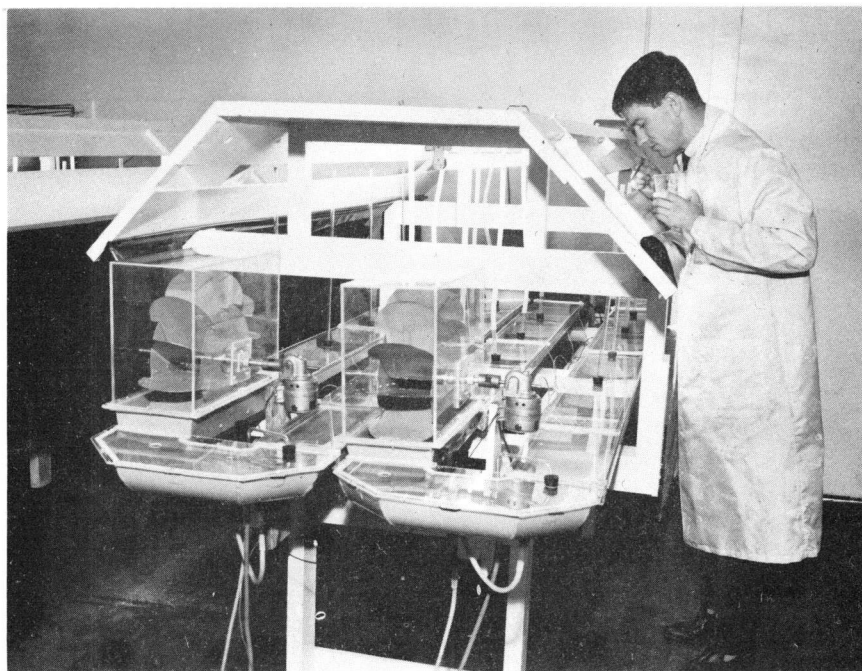


Figure 1. Photograph of two of the nine enforced activity troughs used in this study.

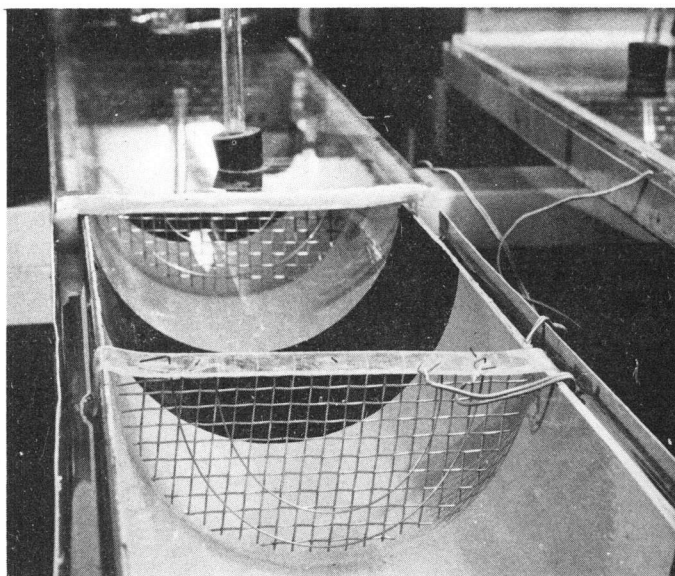


Figure 2. Photograph of a section of an enforced activity trough. Shown in the foreground is one of the electrified screens used to divide the trough into compartments. In the background, a glass tube through which food was introduced into each compartment can be seen passing through the plastic cover. Note the edges of the plastic covers fitted into the water filled channels along each side of the trough.

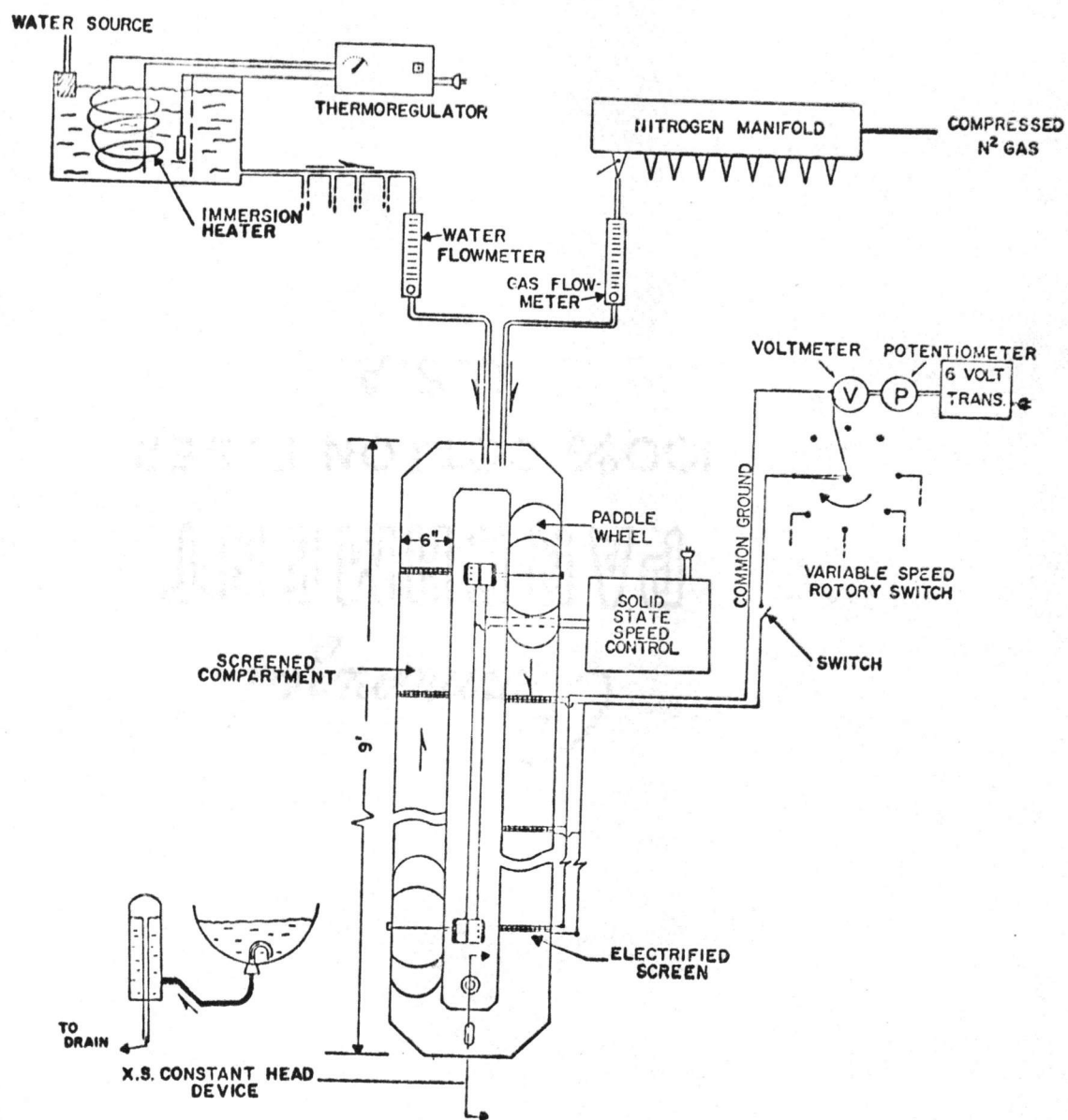


Figure 3. Schematic diagram of the experimental apparatus.

with a solid state speed control wired in parallel to both motors.

Water velocities up to 30 cm/sec could be attained.

To restrict the flow slightly and to remove the surface waves created by the paddle wheels, a piece of plastic was located immediately downstream from the paddle wheel. The upstream end of the plastic was positioned slightly above and the downstream end slightly below the water surface.

Stainless-steel screens (7 mm mesh size) were used to partition the straight sections of each trough into eight compartments. The screens were suspended from the top of the trough with plastic strips so that they did not touch the trough (Fig. 2). About 1 cm upstream from each screen, two stainless-steel wires were suspended from the plastic screen support. These wires were supplied with intermittent low voltage (4-6 volts) and low amperage (less than 1 milliamper) current via appropriate transformer, potentiometer, and variable speed, rotary switch. The electrical current provided a mild stimulus to fish that attempted to rest on the screens. To aid the fish in maintaining a position forward of the screens, a 5-in. black strip was painted across the trough in the center of each compartment.

The enforced-exercise trough and paddle wheels were covered with transparent acrylic plastic to essentially seal the atmosphere above the water from the surrounding atmosphere. The covers over

the paddle wheels and around the curved ends of the trough were fastened to the trough and sealed with foam plastic stripping. The plastic covers over the straight portions of the troughs were constructed with flanges that fit into water-filled channel along the outer edges of the troughs (Fig. 3).

Filtered, spring-fed creek water, or well water, was introduced into a head box which contained a thermostatically controlled, stainless-steel immersion heater, and heated to 15 C. The water was introduced into each trough at the rate of 500 ml/min via ball-displacement flowmeters. The water level in the troughs was regulated by withdrawing water from near the bottom of the troughs into a reservoir in which the water level was regulated by an adjustable standpipe (see constant-head device, Fig. 2). Since the water was removed from near the bottom of the trough, fecal matter and other debris were concurrently removed.

To control the dissolved oxygen content of the water, nitrogen or a mixture of nitrogen and air was introduced into the atmosphere above the water via ball-displacement flowmeters. The rate at which these gases was introduced governed the oxygen concentration in the water.

Canopies were placed over the enforced exercise troughs to isolate the fish from the movements of the operator (Fig. 1). Constant illumination of the troughs was provided by a single 50-watt,

fluorescent lamp attached to the underside of the canopy. Since the inside of the canopies were more brightly illuminated than the room, the salmon could be observed through a slit 3-in. (7.6-cm) wide located along each side of the canopies without frightening them.

To facilitate introduction of food, glass or tygon tubes extended through the canopy and plastic covers into the upstream end of each compartment. Each tube was fitted with a cork to prevent the loss of the controlled atmosphere.

Experimental Animals

The juvenile coho salmon used in this study were obtained from Oregon State Fish Commission's Fall Creek Salmon Hatchery, the upper Yaquina River, and Fall Creek, a tributary to the Alsea River. The salmon were obtained 7 to 14 days before the start of an experiment and held in 190-liter glass aquaria at 15 C. The aquaria were located indoors under constant illumination and were provided with a continuous flow of either filtered, spring-fed creek water, or well water. The salmon were fed daily on house-fly larvae (Mus domestica) and tubificid worms (Tubifex sp.). Tubificid worms were continuously available to the salmon.

Little or no difficulty was experienced in holding the salmon, except during August, when a few salmon were affected by a

bacterial disease of the fins. Malachite green was used to stop the spread of the disease. Five days after treatment, salmon that appeared free of the disease were selected for use.

In several experiments, a few salmon were lightly parasitized by small external parasites called "black grub" by Davis (1965). Several of the fish so infected appeared irritated by the parasites, and, occasionally rubbed their sides against the bottom of the trough.

Housefly larvae were used as food for the test fish during the experiments. The larvae were selected because they were rather uniform in size, and could be easily reared in the quantities needed. The fly larvae were grown at room temperature in a damp media consisting of three parts sawdust, two parts alfalfa meal, and one part grain meal. After the fly larvae attained a length of about 1 cm, they were held at 10 C to reduce further growth and postpone pupation. The larvae were used as food when they were 4 to 10 days old.

Experimental Procedures

Prior to the start of each experiment, the dial settings on the speed control was correlated to the water velocity. The water velocity was measured with a Gurely currentmeter.

Juvenile coho salmon that had been fasted 48 hr were sorted to approximately equal size, lightly narcotized with tricaine methanesulfonate (MS 222), measured, and weighed after removal

of excess water with a soft damp cloth. An initial sample of 8 or 16 fish was taken at random, killed in MS 222, and dried for 5 days at 70 C. The initial sample of fish was later used to estimate the initial dry weight and caloric content of salmon used in the experiment.

One salmon was placed in each compartment 8 hr prior to the start of an experiment. After the salmon were allowed several hours to adjust to their new environment, the water velocity was increased to a low level of 4 to 6 cm/sec and the electrical current applied to the screens to discourage the fish from resting on the screens. The electrical stimulant was rarely applied after the first day of the experiment.

At the beginning of an experiment, the water velocity was gradually increased over a 4-hr period from 4 to 6 cm to the desired level. In some experiments the oxygen concentration was gradually reduced over a 4- to 8-hr period from air saturation to about 5 and 3 mg/liter.

Salmon were either not fed, or they were fed specific rations every 12 hr. Salmon which were fed, were offered one fly larva in a downstream rotation until the desired ration had been consumed and in the case of the repletion rations, until each salmon had rejected at least two larvae. Rejected larvae passed downstream from one compartment to the next. This required continuous observation

during feeding to determine how many larvae each salmon consumed. A fine-mesh screen was placed in the trough prior to each feeding to collect uneaten larvae.

A sample of 25 larvae was taken each day, weighed, and dried for 5 days at 70 C. Once dried, the samples were weighed, and their caloric content determined with an oxygen bomb calorimeter. These samples of larvae were later used to estimate the mean dry weight and caloric content of the larvae fed each day.

Prior to removal from the troughs at the end of an experiment, salmon that received food during the experiment were held without food for 48 hr to insure elimination of fecal matter from their digestive track. During the first 24 hr of this period the salmon were held under experimental conditions of oxygen and velocity, after which the oxygen level was returned to air saturation and the velocity was reduced to zero. The salmon were held under these conditions for the remaining 24 hr. Salmon not receiving food were held under experimental conditions until they were removed at the termination of the experiment. Immediately after removal from the troughs, the salmon were killed in MS 222, weighed, measured, and placed in an oven and dried at 70 C for 5 days. The dried salmon were weighed, placed in a desiccator, and their caloric content was later determined with an oxygen bomb calorimeter.

The water velocity in each compartment was measured at the

termination of an experiment. This was necessary because algae and fecal matter often collected on the screens and slightly reduced the water velocity. The initial and final velocities for each compartment were used to calculate the mean swimming speed for the salmon held within that compartment.

Growth was considered to be the change in caloric content of the salmon during an experiment. The initial dry weights were estimated by multiplying the initial wet weight of each salmon by the percent dry weight of the sample of fish taken prior to the start of that experiment. The estimated dry weight of each salmon was multiplied by the calories-per-gram of dry tissue of the initial fish sample to determine the initial caloric content of each salmon. The final caloric content of each salmon was determined by multiplying the dry weight times the number of calories per gram of dry tissue. The number of calories per gram of dry fish tissue was determined for each salmon in Exp 1, 2, 4, and 5, and for a composite sample of all salmon in a trough in Exp 3, 6, and 7.

The number of calories in the food consumed was determined from the number and mean caloric content per larvae consumed each day. The mean caloric content was estimated from the sample of larvae taken each day. However, in Exp 3, 6, and 7, the daily samples of larvae were combined within each experiment before caloric determinations were made.

Food consumption and growth were computed as relative rates following Brody's (1945) formula for relative growth:

$$R = \frac{C}{\bar{C}} \div t \quad R = \text{relative rate of growth or food consumption in calories per mean kilcalorie of salmon per day (cal/kcal/day)}$$

C = growth (change in the caloric content of the fish) or food consumption in calories (cal)

\bar{C} = mean of initial and final caloric content of salmon in kilocalories (kcal)

t = days salmon received food, or were deprived of food.

Swimming velocities are given relative to the size of the fish as recommended by Brett (1964):

$$L/\text{sec} = \frac{\bar{V}}{\bar{L}} \quad L/\text{sec} = \text{relative velocity in fish lengths per second}$$

\bar{V} = mean of initial and final water velocities in centimeters per second

\bar{L} = average of initial and final fork lengths of salmon in centimeters.

Energy budgets for coho salmon were constructed for some experiments following the formulation of Warren and Davis (1967) who described growth in terms of apportionment of consumed energy:

$$Q_g = Q_c - (Q_s + Q_a + Q_w + Q_d)$$

When

Q_g = calories retained as growth

Q_c = calories consumed in food

Q_s = calories required for standard metabolism

Q_a = calories used for activity

Q_w = calories lost through excretions and fecal wastes

Q_d = calories used to digest and process the food consumed--
termed specific dynamic action (SDA) by Brody (1945).

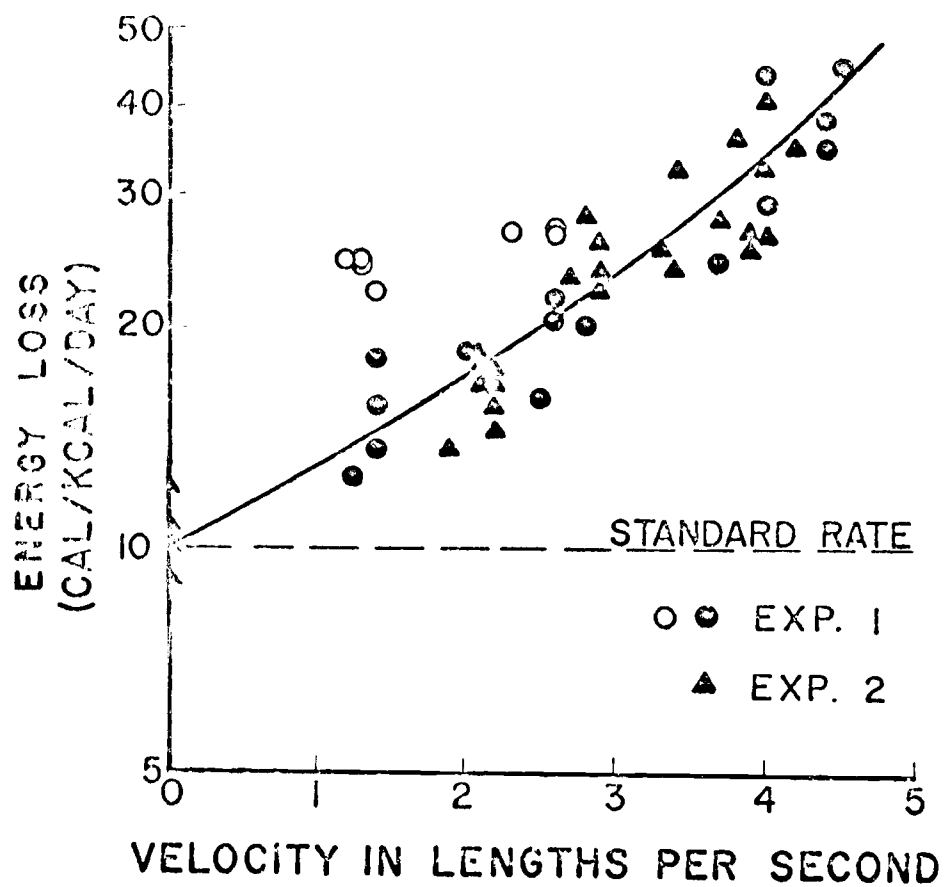
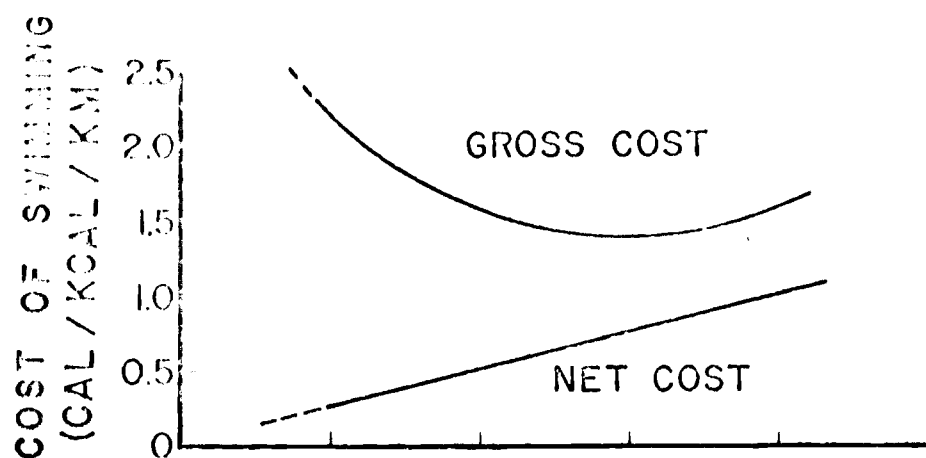
The energy consumed in food (Q_c) and that retained as growth (Q_g) were determined as previously described. Standard metabolic rate (Q_s) was considered to be the rate of caloric loss at zero swimming velocity. Active metabolic rates were the rates of caloric loss in swimming salmon. The cost of swimming activity (Q_a) was taken to be the difference between the standard and active metabolic rates. The amount of energy lost through excretions and fecal wastes (Q_w) was rather arbitrarily chosen to be 20% of the energy in the food consumed after examining available information. The energy in the food consumed that was not accounted for in other categories, was placed in the category SDA (Q_d).

RESULTS AND INTERPRETATION

To estimate the energy juvenile coho salmon expend for swimming activity, unfed salmon were forced to swim for 10 to 12 days at several constant velocities. The caloric loss represents the energy required for standard metabolism and swimming activity. The relationship between the rate of energy loss in juvenile salmon and swimming speed is presented in Fig. 4. The rate of energy expenditure increased exponentially with increasing velocity. The rate of energy loss at zero velocity represents the energy expenditure for standard metabolism. Energy expenditures above this rate can be directly associated with increased activity (i. e., swimming).

Also presented in Fig. 4 are the relationships of swimming velocity to average gross and net costs per kilometer swam. Gross cost is defined as the total energy expended divided by the distance swam in kilometers. Net cost is defined as that portion of the total energy expended which was used for swimming activity divided by the distance swam in kilometers. The net cost of swimming increased with increasing velocity, while the gross cost declined to a minimum value at a velocity of 3 L/sec, and then increased with further decreases in velocity. The curved relationship between gross cost of swimming and swimming velocity is the result of the

Figure 4. Influence of swimming velocity on the rate of energy loss from the resulting swimming efficiencies of unfed juvenile coho salmon held at 15 C for 10 to 12 days during Exp 1 and 2. The open circles represent data which may be in error as evidenced by unusual relationships between the wet and dry weights of the fish and have been disregarded in plotting the relationship. The swimming efficiency is presented as the caloric cost (loss) per kilocalorie of salmon per kilometer swam. Data plotted at zero velocity are for unfed salmon held under darkened conditions with no appreciable water current.

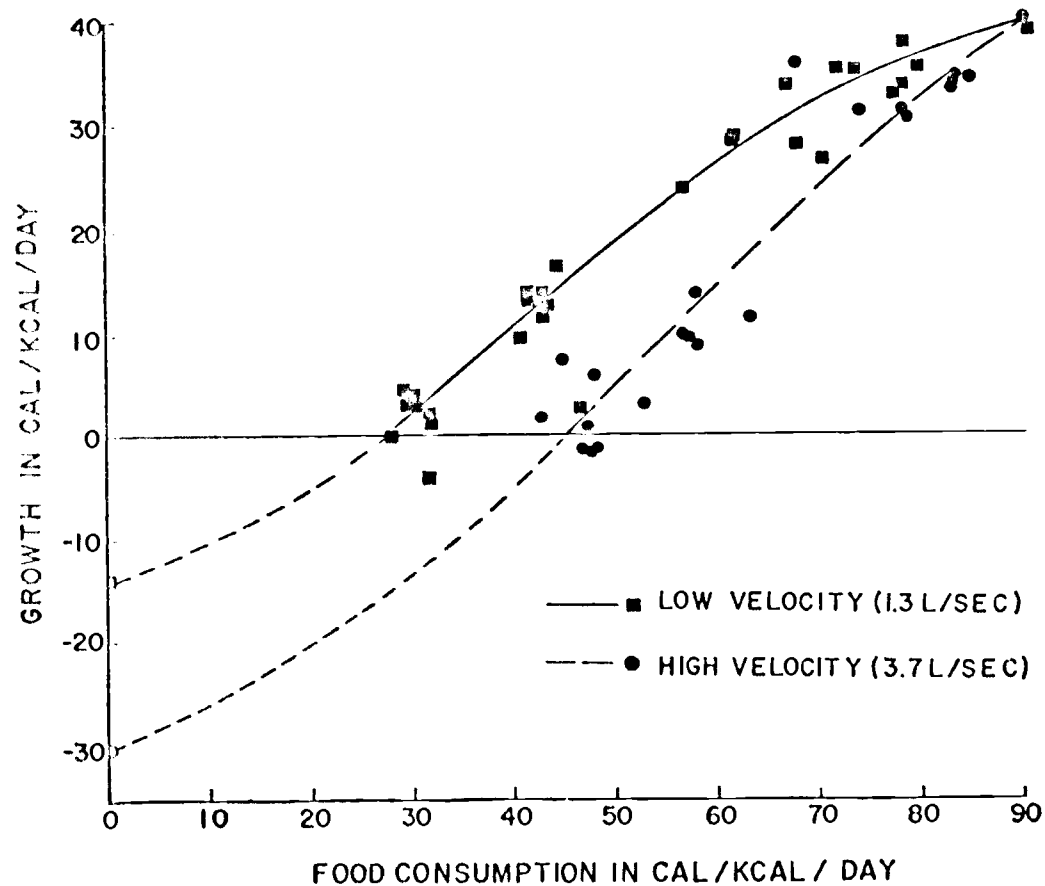
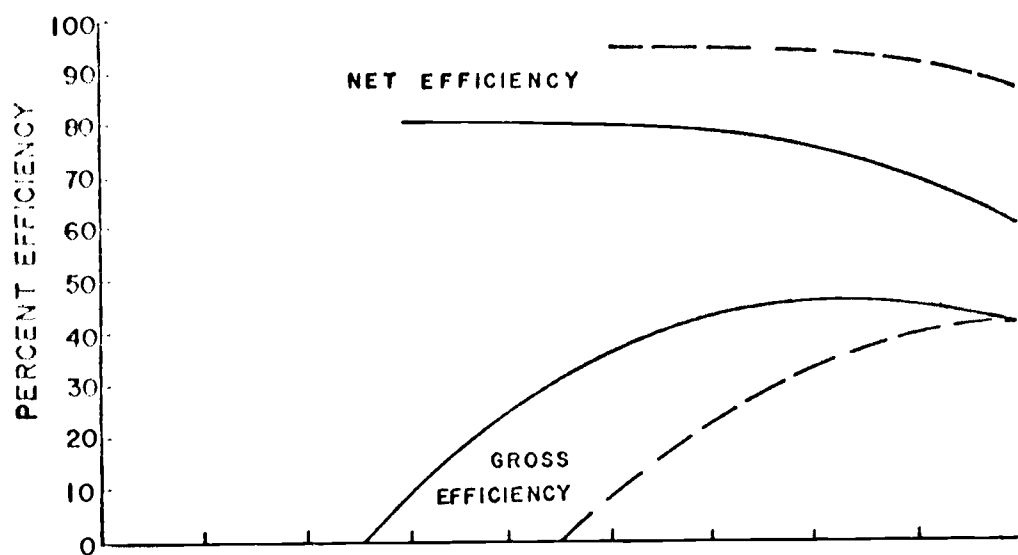


constant standard metabolic cost and the linear, increasing net swimming cost of swimming as velocity increased. The most efficient swimming speed occurs where the gross cost is the lowest, i.e., at this velocity (3 L/sec), the swimming speed to energy expended is optimal.

Figure 5 presents the relationship between growth rate and food consumption rate of coho salmon swimming at 1.3 and 3.7 L/sec. That portion of the food consumption-growth rate curve above the zero growth line is curvilinear for salmon swimming at 1.3 L/sec; whereas, the curve at 3.7 L/sec is nearly linear. The curve for salmon swimming at 3.7 L/sec is displaced to the right of the curve for salmon swimming at 1.3 L/sec. The two curves intersect at food consumption and growth rates of about 90 and 40 cal/kcal/day, respectively.

Also presented in Fig. 5 are the relationships of food consumption rate to gross and net percent efficiencies of food utilization for growth. Gross percent efficiency is the percent of the total caloric intake that was stored as growth. The gross efficiency of salmon held at a velocity of 1.3 L/sec reached a maximum value of 46% at a consumption rate of 70 cal/kcal/day, and then declined slightly with further increases in food consumption. At the higher velocity of 3.7 L/sec, the gross efficiency increased with food consumption, reaching a maximum value of 43% at the highest food

Figure 5. Relationships of growth rate and efficiency of food utilization for growth to food consumption rate in juvenile coho salmon held at 15 C and forced to swim at a low velocity (1.3 L/sec) and a high velocity (3.7 L/sec) during Exp 3. Both gross and net efficiency were estimated with the aid of the food consumption-growth rate curve rather than from data of individual fish.



consumption rate (90 cal/kcal/day). Gross efficiency was higher for salmon swimming at 1.3 L/sec than for salmon swimming at 3.7 L/sec for all consumption rates except at the highest rate where they were the same.

Net efficiency of food utilization for growth is the percent of the energy intake above the maintenance level that occurred as growth. At all food consumption rates tested, the net efficiency of salmon swimming at 3.7 L/sec was higher than that of salmon at 1.3 L/sec. At both levels of activity, the net efficiency curves noticeably declined only at rather high food consumption rates.

Juvenile coho salmon were held at several water velocities and dissolved oxygen concentrations and fed to repletion twice daily. Food consumption and growth rates were determined for individual salmon and the mean rates for each set of experimental conditions are listed in Table 1. The mean values listed are calculated using only data for the five salmon with the highest food consumption rates and exhibiting normal behavior. Data for salmon which ate little or no food and those which exhibited abnormal behavior (resting or excessively active) more than five times were excluded. This was done to prevent unduly biased mean food consumption and growth rates. Data for all salmon are given in App 4 through 7.

Figure 6 presents the relationships of swimming velocity to mean food consumption and growth rates of salmon held at an

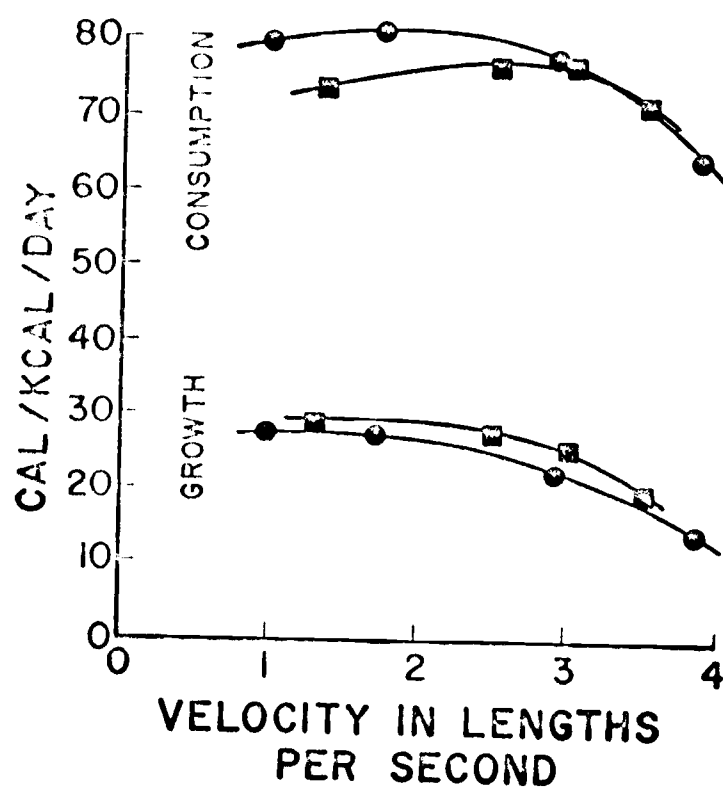
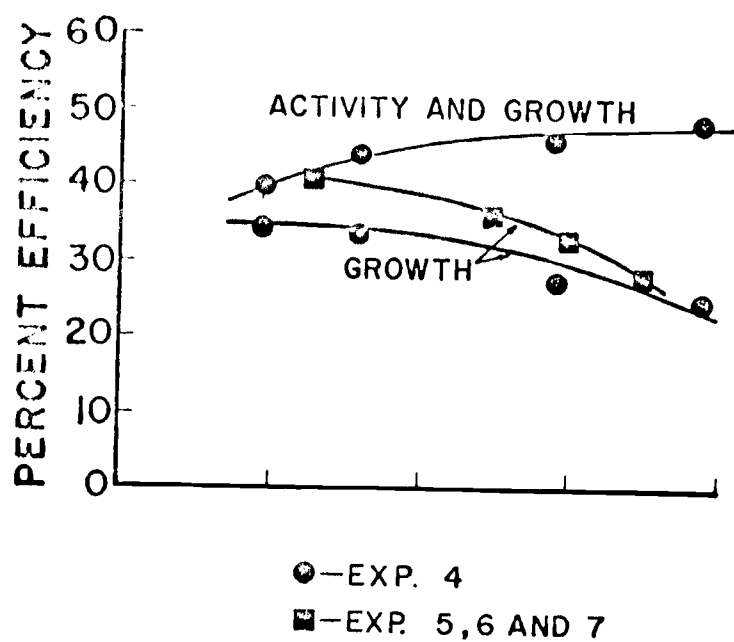
Table 1. Fork lengths, food consumption rates, and growth rates of juvenile coho salmon held at various oxygen concentrations and water velocities for 10 to 12 days. The salmon were fed housefly larvae to repletion twice daily. All values are means based on the five fish with the highest food consumption rates under each set of experimental conditions (see text).

Expr. No. . date and duration	Dissolved oxygen ^{1/} (mg/liter)	Water velocity (L/sec)	Fork length (mm)	Growth (cal/kcal/day)	Food consumption (cal/kcal/day)
Expr. 4	9.5	1.0	62	27.5	80.0
7/13/67	9.5	1.8	63	30.9	82.0
10 days	9.5	2.9	63	23.1	81.9
	9.5	3.8	63	14.9	67.0
Expr. 5	9.5	1.3	62	21.0	55.7
8/11/67	9.5	2.6	63	24.1	59.9
10 days	9.5	3.5	63	12.7	55.0
	5.0	1.6	62	24.6	59.2
	5.3	2.4	61	22.4	59.1
	--- ^{2/}	3.4	64	2.4	34.5
	3.3	1.4	62	22.1	47.3
	3.2	2.8	62	14.4	43.0
Expr. 6	9.5	1.4	67	32.9	72.5
10/2/67	9.5	2.7	67	34.2	84.8
11 days	9.5	3.4	66	21.8	63.8
	4.9	1.3	69	32.9	69.3
	5.0	2.7	67	32.3	70.4
	5.0	3.6	68	29.6	74.7
	3.1	1.3	67	28.7	61.7
	3.6	2.8	66	19.2	56.8
Expr. 7	9.5	1.2	73	37.1	91.8
12/21/67	9.5	2.2	73	26.6	74.1
10 days	9.5	2.9	73	31.2	94.7
	5.3	1.3	75	34.3	84.9
	5.0	2.4	74	29.2	91.4
	5.4	3.3	73	31.3	86.9
	3.2	1.0	74	22.8	62.3
	3.1	1.9	73	18.0	64.3
	3.4	3.1	73	6.6	53.7

^{1/} Oxygen concentrations are time integrated means.

^{2/} Oxygen concentration fell below 2 mg/liter for several hours. Only two fish survived.

Figure 6. Influence of swimming velocity on food consumption rate, growth rate, and food utilization efficiency in juvenile coho salmon held at 15 C in air-saturated water and fed to repletion twice daily. Efficiency for "activity and growth" is the percent of the consumed energy used for growth and activity. The energy cost of activity was estimated from the curve presented in Fig. 5. Circles represent mean value for Exp 4. Squares represent the mean of values (interpolated as described in text) for salmon held in air-saturated water during Exp 5, 6, and 7.



oxygen concentration near the air-saturation level (9.5 mg/liter) and fed to repletion twice daily. Both growth and consumption rates of salmon changed very little with increasing velocity to about 3 L/sec, but declined rather sharply with further increases in velocity.

Also presented in Fig. 6 is the relationships of swimming velocity to the percent gross efficiency of utilization food for growth, and for growth and activity combined. The efficiency for growth decreased with increasing swimming velocity. The efficiency of food utilization for growth and activity appeared to increase slightly with increasing velocity.

The influence of reduced oxygen on the food consumption and growth rates of salmon can be seen in Table 1, Exp 5, 6, and 7. In general, food consumption and growth rates of salmon were reduced by oxygen concentrations below 5 mg/liter. In some cases, food consumption and growth rates were reduced at oxygen concentrations above 5 mg/liter. The greatest reductions occurred at the higher swimming velocities.

As shown in Table 1, each level of oxygen and velocity normally varied with each experiment as well as among the three experiments (Exp 5, 6, and 7). This made it necessary to slightly adjust the food consumption and growth rates before meaningful two-dimensional graphs depicting the influence of oxygen on the good

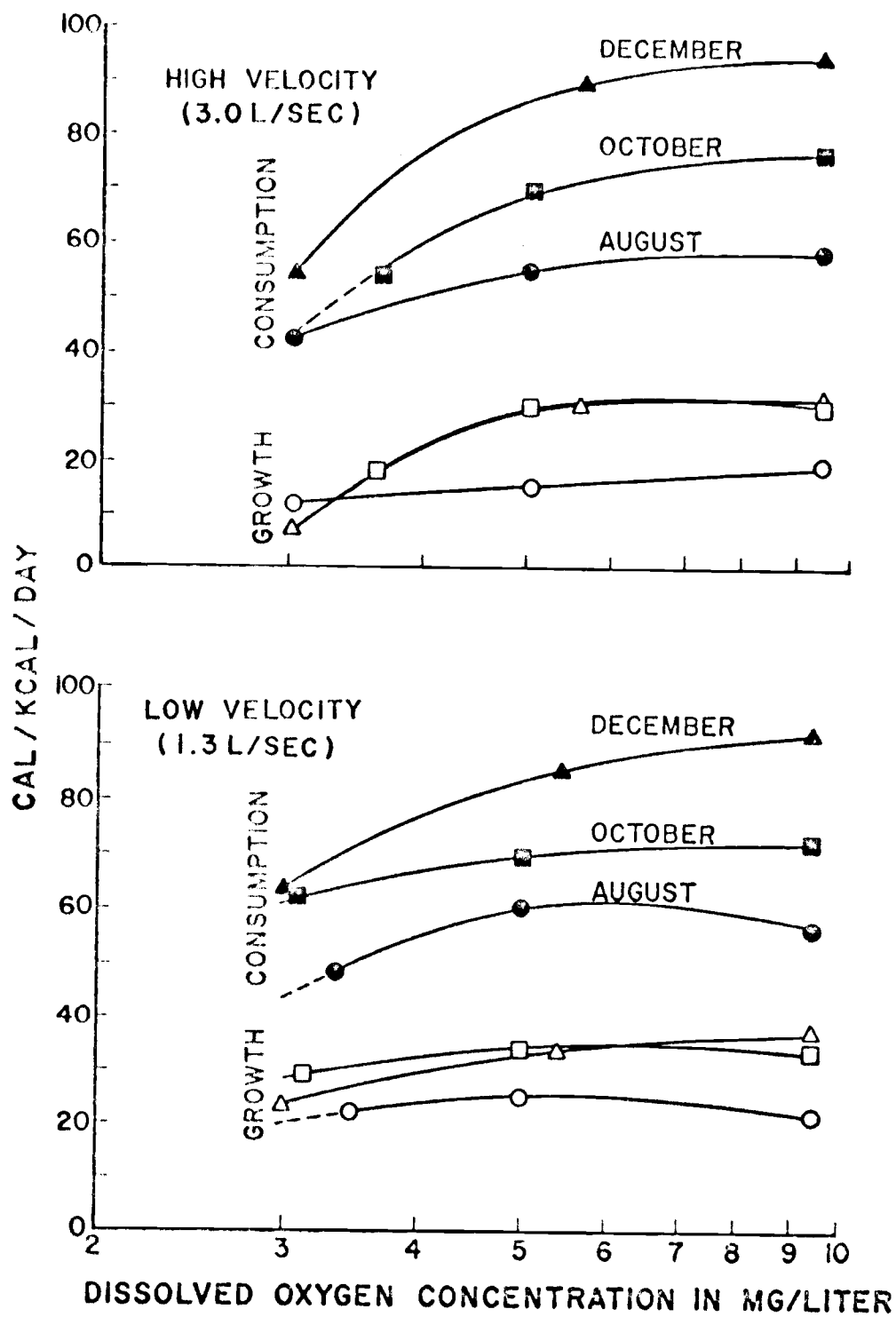
consumption and growth rates could be constructed. The adjustments were made by fitting smooth curves to the mean food consumption and growth rates given in Table 1 for Exp 5, 6, and 7. From these curves, food consumption and growth rates were interpolated at selected velocities.

Food consumption and growth rates obtained as described above for salmon swimming 1.3 and 3.0 L/sec are presented in Fig. 7. The food consumption rates increased substantially at nearly all oxygen concentrations at both velocities as season progressed. The increase in food consumption was more pronounced at high oxygen concentrations than at low concentrations.

Growth rates exhibited less seasonal response to changes in experimental conditions than did the food consumption rates. Growth rates were generally lowest in August as were food consumption rates. Growth rates of salmon in the October and December experiments were nearly the same; whereas, the food consumption rate at all oxygen concentrations was considerably higher in December than it was in October.

Food consumption and growth rates were lowered by reduced oxygen concentrations at both velocities. At oxygen concentrations above 5 mg/liter, swimming velocity had little influence on food consumption and growth rates, except during August when growth at all oxygen concentrations was lowered by elevated activity. At

Figure 7. Influence of oxygen concentration and two selected swimming velocities on the food consumption and growth rates of juvenile coho salmon held at 15 C and fed to repletion twice daily during Exp 5 (August), 6 (October), and 7 (December).



oxygen concentration below 5 mg/liter, growth rates were reduced considerably more at the higher velocity (3.0 L/sec) than at the lower velocity (1.3 L/sec).

Figure 8 presents the influence of oxygen concentration on the mean percent reductions in the food consumption and growth rates of salmon held at two velocities (1.3 and 3.0 L/sec). The values used to calculate the mean percent reductions were extracted from Fig. 7 at 3, 5, and 9.5 mg/liter. For salmon swimming at the lower velocity (1.3 L/sec), the percent that food consumption and growth were reduced was dependent on oxygen concentration only below 5 mg/liter. At this low velocity, the food consumption and growth rates of salmon held at 3 mg/liter were reduced 24 and 19%, respectively. For salmon swimming at the higher velocity (3.0 L/sec), the percent that food consumption and growth rates were reduced was dependent on oxygen concentration near the air-saturation level. Food consumption and growth rates were reduced 8 and 13%, respectively, at 5 mg/liter; and 34 and 63%, respectively at 3 mg/liter.

Swimming velocity had little influence on the relationship between the percent reduction in food consumption and oxygen concentration, but had considerable effect on the relationship between the percent reduction in growth and oxygen concentration.

Figure 9 presents an energy budget for coho salmon fed to

Figure 8. Influence of oxygen concentration on the mean percent reduction in food consumption and growth rate from rates achieved by juvenile coho salmon swimming at similar velocities in 15 C, air-saturated water. Values used to calculate percent reductions were interpolated from Figure 7.

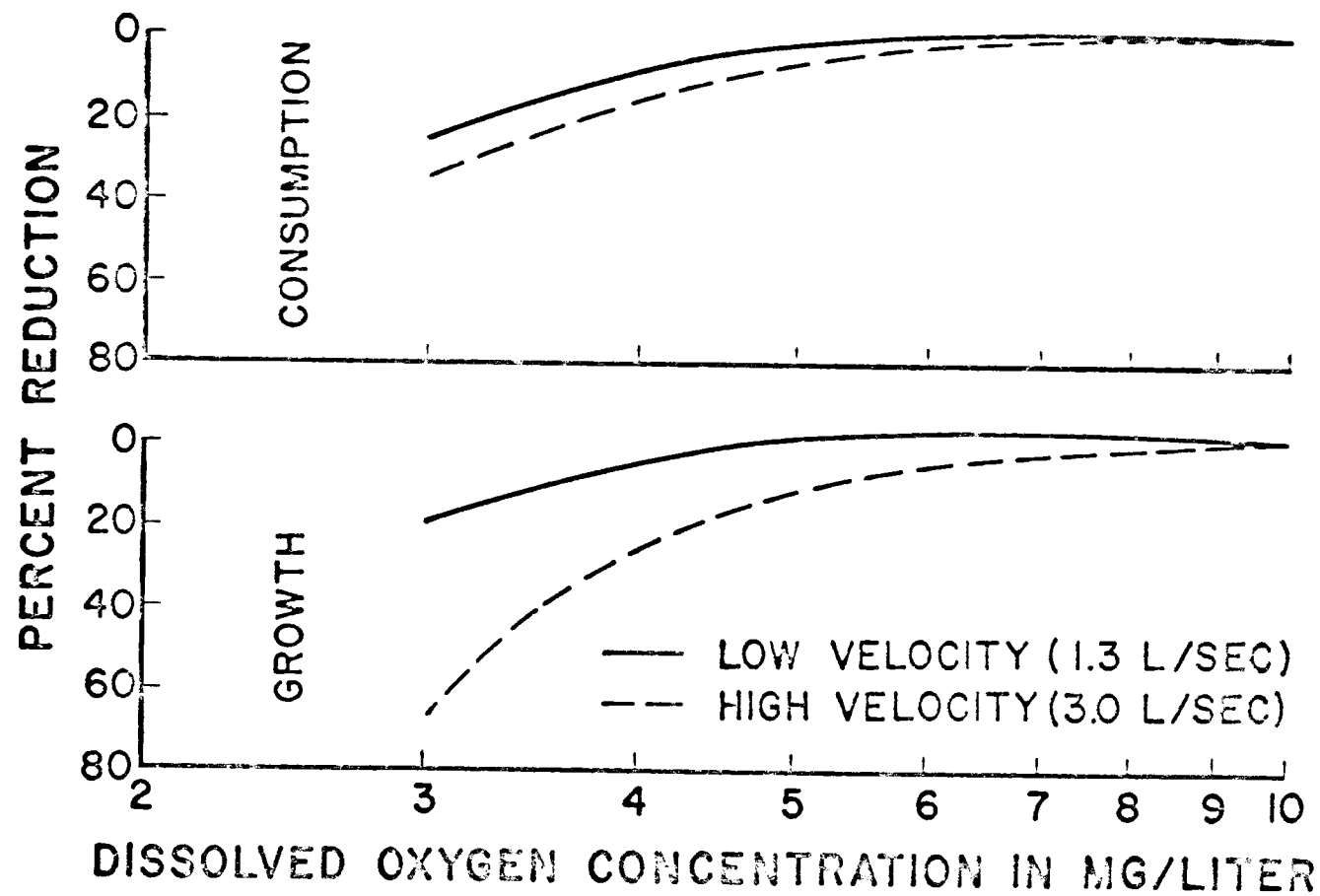
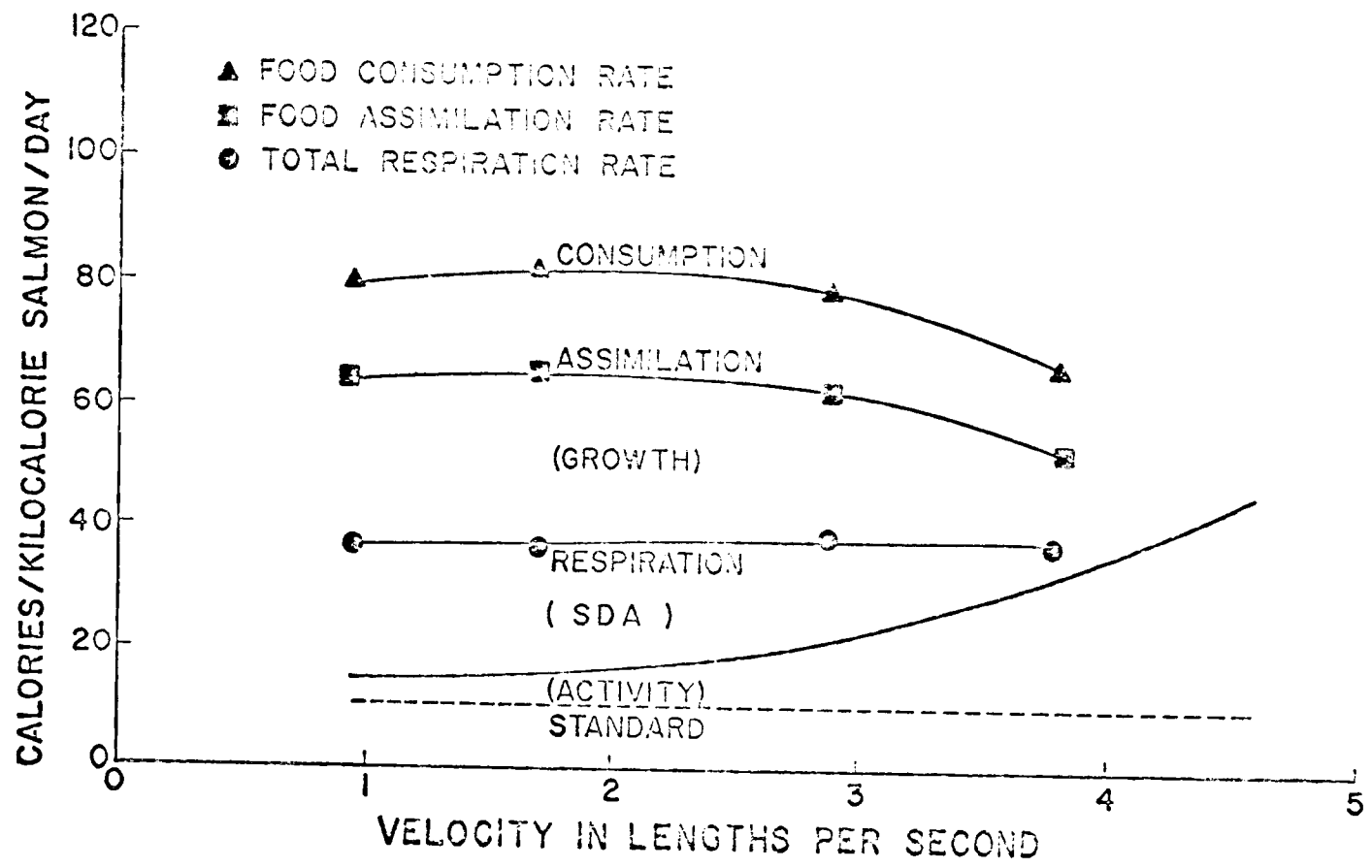


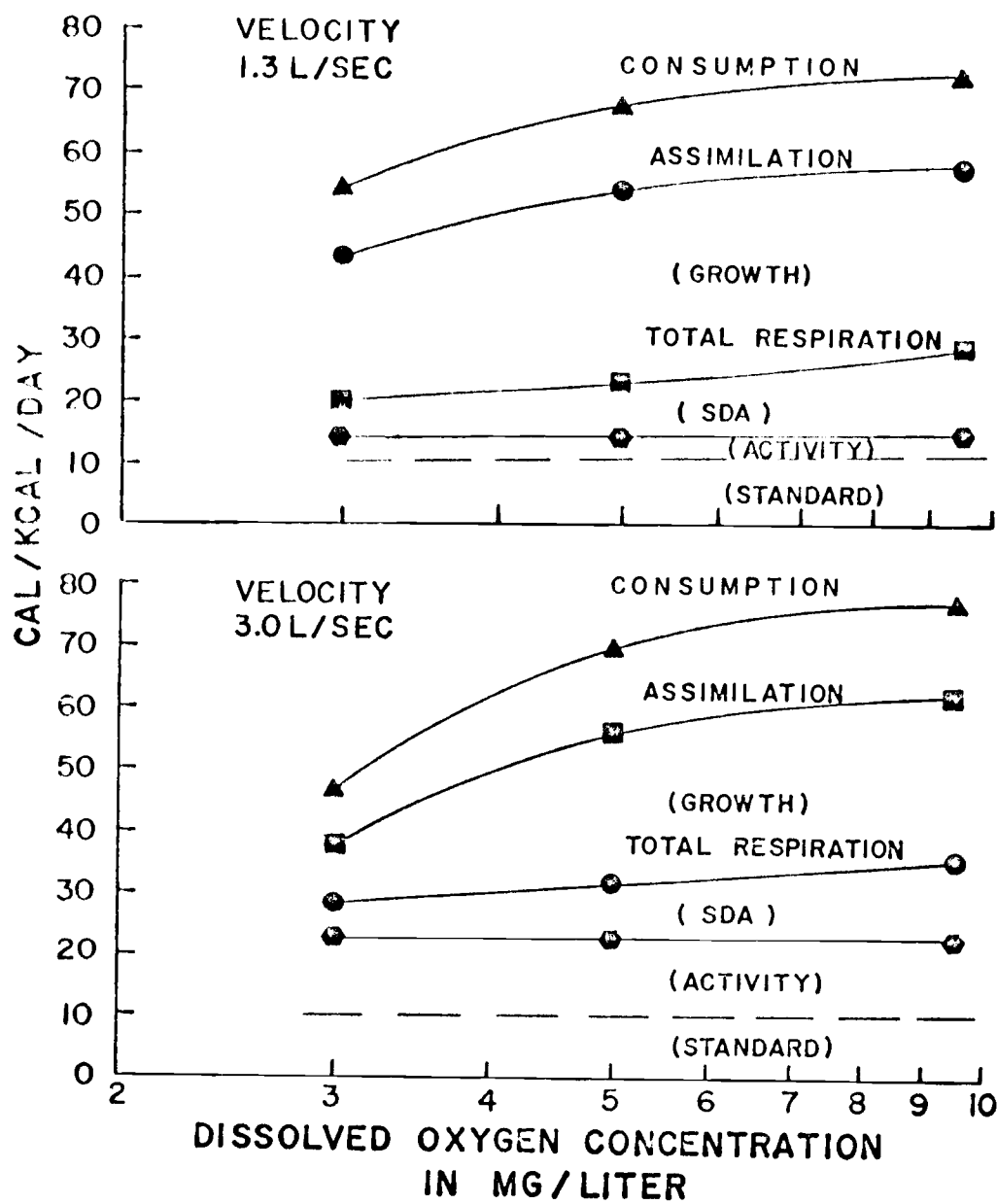
Figure 9. Relationships of swimming velocity to food consumption, losses and uses of energy, and growth of juvenile coho salmon. The salmon were held at 15 C in air-saturated water and fed to repletion twice daily (Exp 4).



repletion twice daily and forced to swim at several constant velocities when the oxygen concentration was near the air-saturation level. The energy assimilated was assumed to be 80% of the energy intake. Energy for standard metabolism and for activity was estimated from Exp 1 and 2, Figure 4. The amount of energy in the category SDA was estimated as that portion of the energy intake (food consumption) not accounted for in other categories. The sum of the energy categories, standard metabolism, activity, and SDA has been termed total respiration rate (TRR) since all of these energy uses ultimately require oxygen.

The remarkable feature of this energy budget is that the TRR of 38 cal/kcal/day was maintained over the range of swimming velocities tested even though the cost of swimming was increased with increasing velocity. The consistency of the TRR appeared to be possible because the increasing cost of swimming was offset by decreases in the SDA. Part of the decrease in SDA can be attributed to a reduced food consumption rate at velocities above 3 L/sec. Much of the decline in SDA appears to be some function of activity level since SDA decreased from 26% of the energy intake at 1 L/sec to only 7% at 3.7 L/sec.

Figure 10. Relationships of dissolved oxygen concentration to food consumption, losses and uses of energy, and growth of juvenile coho salmon at two selected swimming velocities (1.3 and 3.0 L/sec). Salmon were held at 15 C and fed to repletion twice daily (Exp 5, 6, and 7).



DISCUSSION

Oxygen consumption rates were measured by Averett (1969) and Brett (1964) for young salmon of similar size and held at temperatures similar to those used in this study. Comparison of rates they reported with the metabolic rates determined here were made possible by conversions ^{1/} of the metabolic rates expressed in cal/kcal/day to equivalent oxygen consumption rates (mg/kg/hr). In general, standard and active metabolic rates reported by Averett and Brett were greater than those rates reported here for juvenile coho salmon. They reported standard metabolic rates (SMR) of 350 and 230 mg/kg/hr for coho and sockeye salmon (Oncorhynchus nerka); whereas, I observed a SMR of 130 mg/kg/hr for coho salmon. The metabolic rate of salmon swimming 30 cm/sec reported by Averett (900 mg/kg/hr) was much higher than comparable rates reported here (540 mg/kg/hr) and reported by Brett (550 mg/kg/hr).

The difference in the standard metabolic rates may be attributed, in part, to the duration fish were held under experimental conditions. Salmon in my study were held under test conditions for

^{1/} An oxy-calorific coefficient of 3.4 and the appropriate number of calories-per-gram for each salmon were used to make the conversions.

10 to 12 days; whereas, Averett and Brett held their salmon only a few hours at each velocity. The longer period of adjustment may have reduced random (or nervous) activity and, thereby, lowered the standard metabolic rate. Beamish (1964) has shown that about 3 days were required for the SMR of brook trout (Salvelinus fontinalis) to reach a minimum level. He also reported the routine metabolic rate declined for about 10 days, indicating random activity also declined for that period.

The logarithm of the energy loss rate (metabolic rate) of unfed, juvenile coho salmon increased at an exponential rate with increased swimming speed. However, Averett (1969) and Brett (1965) reported the logarithm of oxygen consumption rate (metabolic rate) increased at a linear rate with increased swimming speed. Brett reported that Hatanka found the relationship between the logarithm of the percent decrease in weight and swimming velocity was also linear.

The methods used in calculating the metabolic rates of swimming fish may explain, in part, the differences observed in the relationships between metabolic rates and swimming velocity. Brett, Averett, and Hatanka used the initial weight of the fish in their calculations; whereas, I used the mean caloric content of the salmon present over the experimental period. In my study, salmon swimming at higher velocities used up more of their stored energy reserves than did those swimming at lower velocities. Since both

the weight and the calories per gram of fish declined with increasing activity, the mean caloric content of faster swimming salmon was considerably lower than that of less active salmon. Use of the mean rather than the initial caloric content raised the calculated metabolic rate of faster swimming salmon somewhat more than in slower swimming salmon. The mean caloric content is probably a better estimate of the average metabolically active tissue present over the experimental period than is the initial caloric content. However, when initial caloric content was used to calculate the metabolic rates, the relationship between the logarithm of the metabolic rate and swimming velocity was still somewhat curvilinear.

The curvilinear relationship between the logarithm of the metabolic rate (caloric loss rate) and swimming speed may, in part, be the result of the manner in which the rates were measured. Salmon held at higher velocities swam greater distances, used more of their stored energy, and derived more of that energy used from protein catabolism than did less active salmon. Salmon held at high velocities used most of their stored energy as evidenced by caloric values as low as 4200 cal/g at the termination of the experiment (App. 1 and 2). Thus, the more active salmon apparently were forced to use materials such as proteins that were rather inefficient suppliers of energy. Winberg (1956) states that the physiologically useful energy in protein is about 20% less than the caloric value as

determined by calorimeter. This inefficient mobilization of stored energy in very active salmon could account, in part, for the curvilinear relation between the logarithm of energy loss and swimming velocity.

The greater use of protein in faster swimming fish may have been more a function of the percent of the body tissues catabolized in the salmon than of swimming speed. I do not know if the oxygen consumption rates reported by Averett and Brett for salmon during the first few hours of swimming would be the same after many additional hours of swimming. In this respect direct comparisons of the metabolic rates reported here to those reported by Averett (1969) and Brett (1964) may not be justified.

The energy value of materials not assimilated, i. e., wastes (Q_w), was not measured in this study. The value applied to Q_w (20% of the energy intake) was rather arbitrarily chosen after reviewing the values presented in the literature. Brocksen et al. (1968) reported energy voided as wastes by cutthroat trout fed moderate rations was about 15% of the energy intake. Averett (1969) reported non-assimilated energy was 12 to 30% of the energy value of consumed food in juvenile coho salmon fed housefly larvae at the rate of 60 to 100 cal/kcal/day. In a preliminary study not reported here, I found that 14 and 17% of the energy intake of juvenile coho salmon was lost as waste when fed housefly larvae

for 5 consecutive days at the rate of 50 and 60 cal/kcal/day.

The value of 20% used for the category Q_w in this study was slightly higher than values most often reported. The 20% value was chosen primarily because the wet combustion technique employed does not completely oxidize some nitrogenous compounds. The error caused by incomplete oxidation of these nitrogenous compounds probably would not exceed 5% of the energy intake (Winberg, 1956).

Estimates of assimilation efficiency were not available for all experimental conditions tested. The influence of activity on assimilation efficiency is unknown. It is possible, however, that food assimilation efficiency may increase somewhat with increased activity particularly at high food consumption rates (Florey, 1966). Thatcher (1973) has shown that dissolved oxygen concentration had little or no influence on assimilation efficiency. Since total respiration rate (TRR) and the cost of digestion and processing of food (SDA) were estimated by difference, error in estimating Q_w would result in erroneous values for TRR and SDA.

The energy lost through SDA (Q_d) has been associated mainly with deamination of amino acids, and its magnitude related to the amounts and kinds of amino acids injected as well as their fates in the body. I found that SDA in salmon ranged from 10 to 30% of the assimilated energy. The higher value was found for salmon

fed at high food consumption rates and held at low velocities. Some of the variation in SDA appeared to be the result of seasonal change. SDA values of similar magnitude were reported by Averett (1969) who determined SDA values directly by measuring the increase in oxygen consumption following food intake. He detected no consistent relationship between SDA and season.

From the results obtained in this study, SDA appears to be a function of food consumption rate and activity level. At high food consumption rates (more than 50 cal/kcal/day), SDA declined with increasing swimming velocity (Exp 4). At low food consumption rates, SDA was nearly the same for salmon swimming at 1.3 and 3.7 L/sec. However, when food consumption of salmon was increased, SDA increased at 1.3 L/sec but remained rather constant at 3.7 L/sec (Exp 3). Averett (1968), Sethi (1969), and Lee (1969) also reported SDA increased with increasing food consumption in fish that were not very active. To my knowledge, SDA values have not been reported for very active fish.

Well fed fish swimming at high velocities can utilize food energy more efficiently than do fish swimming at low velocities. The improved efficiency may be due to improved assimilation or to reduced SDA, or to both. Although the influence of activity on the assimilation efficiency of fish is not known, there are reasons to believe that efficiency may improve with increased activity

(Florey, 1966). However, in my study, even if assimilation improved to near 100% at the highest velocity tested (Exp 4), SDA still would have been lower than that of salmon held at lower velocities.

The reason SDA is influenced by activity at high, but not at low, food consumption levels, is not known. Perhaps in highly active fish, energy from assimilated food is utilized nearly as fast as it is digested, largely negating the necessity to convert this energy into a storable form such as fat. If the rate of digestion is slowed by increased activity, a rather steady supply of energy could be provided directly from the digested food.

The TRR of salmon in this study was estimated by the energy budget technique as previously described. The TRR is analogous to the total metabolic rate (TMR) used by Lee (1969) and Brake (1972), and was determined by the same techniques. The TRR and TMR may also be estimated by oxygen consumption rate.

The TRR of juvenile coho salmon swimming at a relative low velocity (1.3 L/sec) increased more rapidly as food consumption rate increased. Similar relationships between TMR and food consumption have been reported by Lee (1969) for bass held in aquaria. Brocksen et al. (1968) also reported that the TRR of young cutthroat trout (Salmo clarkii) increased as food availability and presumably food consumption increased. They attributed the

increase in TRR primarily to the increased cost of handling and processing food (SDA) as food consumption increased.

The TRR of coho salmon swimming at a relatively high velocity (3.7 L/sec), remained rather constant over most of the food consumption levels tested. The TRR remained constant because SDA did not increase with increased food consumption as expected. The lack of increase in SDA as food consumption increased cannot be attributed entirely to erroneous estimates of assimilation efficiencies, since an efficiency of nearly 100% would still not yield the high SDA value observed for salmon swimming at a low velocity and fed at the same levels.

When coho salmon were fed to repletion, their TRR was nearly constant as swimming velocity increased over the range tested. The SDA appeared to decline at about the same rate as the cost of swimming increased, thus allowing the TRR to remain unchanged. One possible reason why SDA may have declined with increased swimming velocity has already been given, and there are undoubtedly others. The important fact is that TRR of the salmon was found to be rather constant over a variety of experimental conditions tested, suggesting that fish have the ability to maintain some degree of respiratory homeostasis.

Lee (1969) reported a nearly constant TMR for largemouth bass in artificial ponds. The results of his experiments suggests that as prey density increased, the cost of food capture (activity)

declined even though food consumption increased. The increased food consumption raised SDA by an amount equal to the decrease in the cost of activity, resulting in a rather constant TMR. If such respiratory homeostasis is characteristic of largemouth bass under natural conditions, the problem of determining their oxygen requirements may be greatly simplified.

The nearly constant TMR or TRR of bass and salmon reported above is not a maximum rate. The TRR (35 to 38 cal/kcal/day) maintained by juvenile coho salmon in my study is well below the metabolic rate (45 cal/kcal/day) observed in unfed coho salmon swimming at 4.5 L/sec in Exp 1 and 2. Averett (1969) has shown that unfed juvenile coho salmon were capable of respiration rates several times greater than the TRR reported here. Krueger, et al. (1968) observed metabolic rates of 270 cal/kcal/day for unfed juvenile coho salmon swimming 7.2 L/sec for several hours. However, such a high rate must have been achieved in part through anaerobic respiration and, therefore, could not have been maintained for long periods. The constant TMR of largemouth bass (27 cal/kcal/day) foraging in artificial ponds was also well below the maximum rates for rapidly swimming bass in a respirometer (Lee, 1969). Lee (1969) and Brake (1972) suggested that the TMR of bass in the artificial ponds may be regulated by temperature, but limited by the dissolved oxygen concentration.

The TRR may be reduced by any oxygen concentration below the air-saturation level. Lee (1969) examined benchnotes of N. E. Steward and R. J. Fisher (Dept. of Fisheries and Wildlife, Oregon State University, Corvallis) and found oxygen uptake rates of largemouth bass and salmon fed to repletion declined with any reduction of dissolved oxygen below the air-saturation level. Brake (1972), using energy budgets, found the TMR largemouth bass foraging in artificial ponds declined whenever reduced oxygen levels restricted food consumption and growth. These reductions only occurred at temperatures above 13.5 C. Trent (1973) found oxygen consumption of abundantly fed bass held at 10, 15, and 20 C in aquaria, decreased with decreasing oxygen concentration over the entire range of oxygen concentrations tested. Growth and food consumption rates were not, however, reduced in tests at 10 and 15 C, except at the lowest concentration tested (2.4 mg/liter). In the study reported here, TRR also declined with any reduction in oxygen concentration below air saturation, even though growth was not reduced in every case.

A decline in the TRR without a corresponding reduction in growth might be attributed, in part, to lower random activity at reduced oxygen levels. Herrmann et al. (1962), Fisher (1963), and Trent (1973) reported that salmon became lethargic at low oxygen concentrations 2 to 3 mg/liter). Fish in nature may not be able

to reduce activity levels without sacrificing some unknown competitive advantage they possess. Thus, a depression of the TRR may be a sensitive measure of the oxygen requirements of fish.

The swimming performance of salmon fed to repletion appeared to be unaffected by oxygen levels as low as 3 mg/liter, even at the highest velocity tested (3.1 L/sec). Since the TRR of salmon was lowered by reduced oxygen levels and the activity levels unaffected, apparently, SDA was reduced by the limited supply of oxygen. The limited amount of oxygen available for digestion and food processing (SDA) may be responsible for the lowered food consumption rates observed at reduced oxygen levels.

Food consumption and growth rates, particularly at high oxygen concentrations were generally lower in my study than those reported by other investigators (Herrmann, et al., 1962; Fisher, 1963, and Trent, 1973). The percent by which food consumption and growth rates were reduced by low oxygen concentration was also generally lower in my study. These differences may have been due, in part, to the types of food offered and the manner of its presentation. Herrmann fed his salmon beach amphipods, and Fisher and Trent fed their salmon tubificid worms. Part of these differences may also have been due to the higher test temperatures used by Herrmann and Fisher.

The housefly larvae which I used may not have been as palatable

to salmon as were the amphipods and tubificid worms, and therefore, may have limited food consumption and growth, especially at high oxygen concentrations. Brocksen and Seim (unpublished data, Dept. of Fisheries and Wildlife, Oregon State University, Corvallis) have demonstrated that food consumption and growth of cutthroat trout were greater when fed to repletion on tubificid worms or chironomid larvae than when fed housefly larvae. Restriction of food consumption rates at high oxygen levels by the palatability of the housefly larvae might explain, in part, why the food consumption and growth rates as well as the percent these rates were reduced by lowered oxygen levels were generally less in my study than in those reported by Herrmann, Fisher, and Trent.

The oxygen concentration at which food consumption and growth rates of salmon in laboratory studies become dependent on oxygen appears to increase with increases in temperature, food availability, and activity, because increases in these factors tend to raise the TRR (Trent, 1973; Fisher, 1963; and Herrmann et al., 1962). Trent (1973) has shown that food consumption and growth rates of salmon fed to repletion can be lowered by any reduction of the oxygen concentration below air saturation at 20 C, but only below 3 mg/liter at 10 C.

In studies by Fisher (1963) at 18 C, oxygen concentrations as low as 3 mg/liter had no effect on food consumption and growth of

salmon that were fed restricted rations; yet when food was plentiful, oxygen concentrations only slightly below air saturation reduced growth. Since the TRR increases with increasing food consumption as indicated in my study at low velocities, the TRR of salmon on restricted rations was probably at or below the TRR limited by oxygen.

When fish were forced to swim at a high velocity in air-saturated water, the TRR did not increase as expected with increased food consumption rate. Since the TRR was rather constant and was relatively high, it may have been limited by oxygen. Perhaps if oxygen had been moderately reduced in this particular study, the TRR of salmon might have been reduced even at low food consumption levels. For salmon swimming at a low velocity, the growth of salmon fed to repletion was dependent of oxygen concentrations near 5 mg/liter, but at a high velocity growth was dependent on oxygen concentrations near the air saturation.

As shown in this, as well as other studies, activity or swimming level of fish can greatly influence their oxygen requirements under laboratory conditions (Doudoroff and Shumway, 1971). However, the activity levels of fish in nature are largely unknown. It is unlikely, however, that fish perform at their maximum ability for long periods. We do know that they must be active to maintain position in streams, defend a territory, escape predation, seek

out and capture food, migrate, and reproduce. It is difficult to relate these diverse activities to the constant swimming of the salmon in my study, and therefore, difficult to predict how these diverse activities influence the oxygen requirements of salmon under natural conditions. Forcing fish to swim at constant velocities is not without merit, however, as it is a useful technique to regulate the energy and oxygen demands of the fish in laboratory studies. From casual observations of juvenile coho salmon in natural and artificial streams, I would assume their average energy expenditure for activity is not more than that of salmon swimming constantly at 3 L/sec and usually less than 2 L/sec.

The ability to predict oxygen concentrations that limit growth of fish under natural conditions, may to a large extent, be influenced by the manner in which fish react to changes in food density under natural conditions. Largemouth bass are active predators and spend considerable energy seeking and capturing food. In artificial ponds, largemouth bass react to decreased prey density by exerting more effort to capture food, but are less successful so they consume less (Lee, 1968). Since the increase in activity associated with food capture just compensated for the decrease in SDA, the TMR remained unchanged over the range of prey densities tested.

As opposed to foraging bass, most young salmonids feed

rather passively on organisms drifting near them, and therefore feeding activity is influenced very little by increased density of food, even though food consumption may increase (Brocksen, 1968). The increase in SDA associated with the increases in food consumption tends to raise the TRR as food density increases.

Brake (1972) has shown that the rather constant total metabolic rate of bass in the ponds was limited by oxygen concentration at moderate to high temperatures. At these temperatures, it appears that any reduction in oxygen concentration will reduce the growth of foraging bass regardless of the prey density. This appears true because bass tend to vary activity and food consumption with changes in food density, thus keeping their TRR near the level limited by oxygen.

In a study not reported here, I found growth rates of salmon which were feeding rather naturally on drifting organisms in artificial streams were dependent on oxygen concentrations only at high food densities and presumably at high food consumption levels. These results are similar to those obtained by Fisher (1963) in aquaria studies, and therefore, the TRR appears to have been regulated by food availability rather than oxygen except when salmon were feeding near repletion levels.

The estimation of oxygen levels that limit growth of bass under natural conditions appears not too difficult because the TRR of

foraging bass apparently remains constant over normal levels of food densities and this TRR is similar at the same temperature to that of repletion fed bass in aquaria. Thus, the oxygen requirements of bass under natural conditions can be predicted from the oxygen requirements of bass fed to repletion in aquaria studies.

In salmonids estimation of oxygen concentrations that limit growth under natural conditions is not so readily accomplished. Laboratory studies are useful to predict oxygen concentrations that will not limit growth in nature if the TRR of the salmonids are near those in nature. Since most young salmonids seldom have the opportunity to consume all the food they desire, they do not appear to utilize the potential TRR limited by oxygen concentration as do the bass. Thus, the TRR of salmonids varies with the food supply. The TRR of salmonids under natural conditions could be estimated with an energy budget, but this would necessitate determining their food consumption rates--a most difficult task. However until we know something about the level of their TRR or the food consumption rates of salmonids, accurate predictions of oxygen concentrations that will restrict their growth rates under natural conditions cannot be made.

The growth of most young salmonids is probably limited by the food supply in their natural environment (Brocksen, 1968). Chapman (1965) reported that the growth of juvenile coho salmon in

some coastal streams of Oregon seldom reach 1% of their body weight per day. Much of the year, growth rates were well below this level. Based on the study reported here and other laboratory studies, such low growth rates probably would not be further reduced by oxygen concentration as low as 3 mg/liter.

Since these growth rates reported by Chapman were measured over two or more week periods, they do not show short term changes in food consumption and growth rates. There are undoubtedly times, when the food supply and, therefore, food consumption is high (during hatches of certain insects, etc.). Fish may make much of their annual growth during such periods. If food consumption is restricted by reduced oxygen at these times, considerable reduction in growth may occur.

The growth rates reported by Chapman (1965) were averages of a considerable number of individuals. Some dominant individuals may have had growth rates much in excess of 1% per day, and therefore, their growth rates might have been restricted at oxygen concentrations above 3 mg/liter.

Reduced growth of fish would most likely lead to lowered production of the population. Since the sustained yield to man can only come from production, any loss in fish production makes the population less valuable as a resource. In fact, since the growth rates of most young salmonids in their natural environment appear

to be very low, any reduction in their growth may seriously interfere with the survival of the population.

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APPENDICES

Appendix 1. Swimming velocity, fork length, weights, caloric content, and rate of caloric loss for individual coho salmon held at 15 C in air-saturated water without food for 12 days. Experiment 1, June 1, 1967.

Swimming velocity (L/sec)	Fork length (mm)	Initial ^{1/}	Final				Loss in calories (cal/kcal/day)
		Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories (cal)	Calories per gram (dry)	
4.1	65	2.71	2.21	.366	1632	4460	43.8
4.5	63	2.53	2.00	.366	1632	4460	38.3
4.3	66	2.75	2.28	.425	1841	4332	35.3
4.5	65	2.65	2.05	.366	1574	4301	44.8
3.8	67	2.75	2.32	.445	2074	4672	24.7
4.1	64	2.50	1.97	.354	1517	4285	44.3
4.3	64	2.53	2.13	.405	1871	4620	29.1
4.0	65	2.65	2.23	.424	1881	4437	29.4
2.7	65	2.73	2.42	.473	2246	4749	18.7
3.0	63	2.30	1.99	.372	1724	4631	26.1
2.9	65	2.55	2.29	.437	2054	4770	20.4
3.1	63	2.55	2.30	.435	2062	4741	20.2
2.4	65	2.89	2.53	.499	2448	4906	16.1
2.8	65	2.70	2.43	.471	2141	4546	22.2
2.9	64	2.50	2.13	.398	1847	4637	27.8
3.1	64	2.49	2.20	.403	1842	4572	27.4

Appendix 1. Continued.

Swimming velocity (L/sec)	Fork length (mm)	Initial ^{1/}	Final				Loss in calories (cal/kcal/day)
		Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories (cal)	Calories per gram (dry)	
1.4	63	2.50	2.25	.432	1967	4554	22.5
1.4	66	2.94	2.69	.546	2673	4897	10.5
1.4	65	2.65	2.42	.473	2265	4790	15.6
1.3	63	2.49	2.25	.428	1911	4465	24.5
1.3	65	2.70	2.42	.487	2394	4916	12.6
1.3	62	2.38	2.10	.403	1823	4525	24.7
1.2	67	2.90	2.61	.490	2211	4513	24.9
1.4	63	2.50	2.23	.429	2072	4828	18.1

^{1/} The percent dry weight (20.1) and the calories per gram of dry tissue (5154) were determined for an initial sample of eight salmon. These values can be used to determine the initial dry weights and caloric content of the test fish.

Appendix 2. Swimming velocity, fork length, weights, caloric content, and rate of caloric loss for individual coho salmon held at 15 C in air-saturated water without food for 11 days. Experiment 2, June 17, 1967.

Swimming velocity (L/sec)	Fork length (mm)	Initial ^{1/}	Final				Loss in calories (cal/kcal/day)
		Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Calories per ^{3/} gram (dry)	
3.9	64	2.81	2.35	.471	2237	4750	25.3
4.0	63	2.71	2.39	.448	2128	4750	26.7
4.2	62	2.64	2.26	.401	1905	4750	34.9
4.0	65	2.84	2.29	.438	2081	4750	33.4
3.8	65	2.76	2.28	.414	1976	4750	36.1
3.7	67	3.04	2.62	.494	2346	4750	28.3
3.9	63	2.65	2.28	.436	2071	4750	27.1
4.0	62	2.62	2.21	.375	1781	4750	40.8
2.9	62	2.41	2.01	.390	1877	4814	26.3
2.9	62	3.07	2.68	.536	2580	4814	22.6
3.4	63	2.61	2.10	.399	1921	4814	33.0
3.4	63	2.55	2.22	.426	2051	4814	24.3
2.7	67	3.28	2.90	.551	2652	4814	23.8
2.8	65	2.74	2.31	.438	2108	4814	28.6
2.9	67	3.10	2.69	.518	2494	4814	24.3
3.3	62	2.41	2.11	.398	1916	4814	25.4
2.1	63	2.67	2.40	.455	2278	5007	18.4
2.2	65	2.76	2.52	.483	2418	5007	15.8
2.2	65	2.99	2.61	.529	2649	5007	14.7
2.2	67	3.02	2.73	.518	2594	5007	17.7

Appendix 2. Continued.

Swimming velocity (L/sec)	Fork length (mm)	Initial ^{1/}	Total				Loss in calories (cal/kcal/day)
		Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Calories per ^{3/} gram (dry)	
1.9	66 3116	3.02 .607	2.74	.539	2698	5007	13.9
2.1	63	2.67	2.36	.463	2318	5007	16.8
2.2	62	2.70	2.43	.479	2398	5007	14.5
2.1	63	2.51	2.21	.430	2153	5007	17.9
0	66 3219	3.12 .627	2.85	.551	2832	5140	12.3
0	67	3.18	3.00	.597	3068	5140	06.2
0	65	3.04	2.80	.548	2817	5140	10.2
0	65	2.37	2.18	.432	2220	5140	9.2
0	62	2.39	2.20	.428	2200	5140	10.9
0	66	3.09	2.83	.555	2853	5140	10.6

^{1/} The percent dry weight (20.1) and the calories per gram of dry tissue (5134) were determined for an initial sample of eight salmon. These values can be used to determine the initial dry weights and caloric content of the test fish.

^{2/} Final calories were calculated by multiplying a salmon's final dry weight by the calories per gram of dry fish tissue.

^{3/} Final calories per gram of dry fish tissue was determined on a composite sample consisting of the eight salmon in each trough.

Appendix 3. Experimental conditions, mean fork length, weights, caloric content, growth rate, and food consumption rates for coho salmon held in air-saturated water at 15 C and fed prescribed rations of fly larvae twice daily for 11 days. Experiment 3, November 16, 1967.

Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/} wet weight (g)	Final			Growth rate (cal/kcal/day)	Food consumption rate	
			Wet weight (g)	Dry weight (g)	Calories (cal)		Dry (mg/g/day)	Calories (cal/kcal/day)
1.2	73 ^{2/}	3.99	4.00	.830	4152	4.7	26.5	29.6
1.2	74	4.12	4.14	.845	4227	3.4	25.7	29.9
1.3	72	3.33	3.32	.665	3328	1.1	27.2	32.0
1.4	68	3.37	3.35	.697	3489	4.3	26.1	30.4
1.2	68	3.36	3.29	.686	3434	3.1	26.4	30.7
1.4	68	3.24	3.07	.639	3199	0.0	24.6	28.8
1.5	70	3.49	3.44	.709	3548	2.6	27.1	31.7
1.7	70	3.72	3.62	.765	3829	-3.9	26.5	30.9
1.3	74	3.92	4.04	.879	4524	14.1	35.9	41.3
1.3	72	3.58	3.75	.791	4070	12.8	38.1	43.7
1.2	74	4.32	4.46	.963	4960	13.7	37.5	43.1
1.2	72	3.92	4.08	.871	4484	13.3	36.1	41.4
1.1	72	3.65	3.77	.795	4095	11.6	37.5	43.2
1.1	71	3.67	3.54	.729	3754	3.2	40.7	46.8
1.1	74	3.73	3.87	.860	4428	16.7	38.6	44.3
1.1	70	8.04	4.19	.871	4486	9.8	35.1	40.7
1.3	73	4.07	4.47	.993	5247	24.1	50.3	56.9
1.3	70	3.39	4.37	.980	5178	39.0	81.1	91.4
1.3	73	3.72	4.24	1.028	5432	35.3	60.9	68.6
1.4	70	3.65	4.50	1.011	5342	35.3	66.5	74.9
1.4	69	3.45	3.93	.866	4576	26.6	62.6	70.7
1.4	72	3.60	4.15	.924	4882	28.6	55.1	62.2
1.4	74	4.29	5.10	1.135	5997	37.3	68.3	77.2
2.2	70	3.40	4.40	1.007	5307	40.9	80.8	91.1
2.3	70	3.25	3.94	0.940	4999	39.6	74.7	84.3
2.6	67 ^{3/}	3.01	3.12	0.635	3348	10.8	40.5	46.0
2.6	70	3.10	3.34	0.922	4858	41.3	72.1	81.3
2.4	71	3.49	4.12	0.920	4848	30.7	71.9	81.3
2.3	72	3.65	4.20	0.945	4981	29.1	64.9	69.6
2.4	72	3.71	3.97	0.946	4459	17.8	48.4	54.8
2.3	76	4.31	5.09	1.177	6204	34.0	67.4	76.2

Appendix 3. Continued.

Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/} wet weight (g)	Final			Growth rate (cal/kcal/day)	Food consumption	
			Wet weight (g)	Dry weight (g)	Calories (cal)		Dry (mg/g/day)	Calories (cal/kcal/day)
3.4	74	4.60	4.32	0.924	4609	1.8	36.8	42.9
3.8	69	3.23	3.20	0.647	3226	1.0	40.5	47.3
3.9	69	3.11	3.09	0.605	3016	-1.6	41.4	48.4
3.8	72	3.73	3.66	0.726	3619	-1.7	41.4	48.4
3.9	70	3.43	3.28	0.668	3331	-1.5	40.4	46.9
4.0	67	3.17	3.11	0.586	2922	-12.4	41.1	48.0
3.5	74 ^{3/}	4.01	4.04	0.865	4311	7.7	39.9	45.1
3.6	73	3.91	3.96	0.827	4122	5.9	39.9	48.3
3.8	71	4.18	4.42	0.961	4799	13.7	49.8	58.3
3.6	73	3.90	4.02	0.861	4298	9.9	48.9	57.2
3.8	67	3.52	3.60	0.720	3593	3.0	45.5	53.0
3.2	73	3.80	4.04	0.856	4272	12.8	54.5	63.6
3.5	70 ^{4/}	3.55	3.80	0.760	3796	7.2	41.8	44.3
3.5	72 ^{3/}	3.98	4.10	0.865	4320	8.4	48.8	51.7
3.7	74	3.76	3.99	0.815	4071	8.4	50.1	58.3
3.2	77 ^{3, 4/}	4.57	5.28	1.216	6607	34.2	80.3	83.4
3.5	73	4.31	4.87	1.106	6008	31.0	70.3	78.1
3.7	71	3.66	4.45	1.034	5619	39.5	81.8	90.7
3.7	75	4.00	4.80	1.107	6015	37.7	75.3	83.4
3.2	73	3.87	4.51	0.987	5366	30.5	70.5	78.3
3.3	75	4.20	4.78	1.138	6182	35.8	61.3	68.8
3.3	75	4.21	4.79	1.079	5864	31.0	66.4	73.8
3.7	69	3.47	4.01	0.919	4997	33.9	76.9	85.4
1.4	70	3.13	3.84	0.856	4493	33.6	73.1	82.8
1.3	69	3.19	3.86	0.910	4779	37.4	69.5	78.6
1.2	70	3.34	4.07	0.927	4867	34.9	63.6	72.1
1.8	72	3.44	4.07	0.941	4939	33.6	69.2	78.3
1.2	72	3.56	4.10	0.974	5114	33.7	62.7	66.7
1.3	71	3.93	4.35	0.856	4492	28.1	60.3	68.3
1.3	69	3.30	3.80	0.917	4815	19.5	65.7	74.6
1.2	74 ^{3/}	4.06	4.34	0.826	4334	7.1	44.1	50.1

^{1/} The percent dry weight (20.0) and the calories per gram of dry tissue (4938) were determined for an initial sample of eight salmon. These values can be used to determine the initial dry weights and caloric content of the test fish.

^{2/} Replacement fish--held at experimental conditions for eight days.

^{3/} Salmon was observed resting on compartment screens more than five times.

^{4/} Replacement fish--held at experimental conditions for ten days.

Appendix 4. Experimental conditions, mean fork length, weights, caloric content, growth rate, and food consumption rates for coho salmon held at 15 C and fed to repletion on fly larvae twice daily for 10 days. Experiment 4, July 13, 1967.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final			Growth rate (cal/kcal/day)	Food Consumption	
			Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories (cal)		Dry (mg/g/day)	Calories (cal/kcal/day)
9.5	1.0	61	2.56	2.88	.699	3980	30.3	76.9	77.3
	1.0	62	2.51	3.00	.710	4055	34.0	86.4	86.5
	0.9	62	2.51	2.91	.659	3577	21.7	80.0	82.6
	0.9	63	2.81	3.18	.748	4194	20.6	77.0	80.2
	1.0	63	2.75	3.22	.759	4298	30.8	73.0	73.5
	1.0	61 ^{2/}	2.61	3.17	.745	4025	29.6	66.5	69.3
	0.9	62	2.51	2.86	.676	3604	22.4	60.4	56.2
	1.0	63	2.72	3.03	.699	3929	23.0	58.5	59.3
9.5	1.8	64	2.96	3.41	.848	4924	36.9	77.4	77.2
	1.6	63	3.03	3.32	.800	4525	26.4	72.5	77.3
	1.6	64	3.83	3.11	.758	4336	28.9	76.2	82.5
	1.8	63	2.93	3.47	.837	4689	33.1	79.1	95.4
	1.8	61	2.55	2.83	.677	3916	29.1	77.4	77.8
	1.8	61	2.50	2.80	.660	3648	23.9	69.9	71.7
	1.8	64	3.00	3.37	.805	4626	26.6	65.4	65.8
	2.0	63	2.95	3.26	.750	4088	19.0	70.1	71.1
9.5	2.8	63	2.69	2.90	.683	3796	20.8	75.8	77.6
	2.9	64	2.89	3.25	.713	3490	22.4	75.3	79.1
	2.9	63	2.80	2.98	.743	4142	24.2	85.3	87.6
	2.8	62	2.57	2.93	.692	3953	29.2	91.5	92.4
	3.2	63	2.66	2.82	.650	3616	18.8	74.8	72.8
	3.2	62	2.49	2.37	.545	2940	-8.5	43.2	52.3
	2.4	65	3.03	3.11	.723	3962	13.3	50.9	61.2
	3.1	63	2.71	2.88	.708	3932	23.4	67.8	72.5
9.5	3.7	62	2.50	2.66	.612	3343	15.3	67.5	72.7
	3.8	62	2.55	2.67	.607	3391	14.9	68.0	69.6
	3.9	64	3.01	3.08	.751	4114	17.4	65.3	64.9
	3.8	63	2.88	2.94	.696	3882	16.3	63.0	61.3
	3.7	62	2.57	2.64	.605	3285	10.8	64.2	66.6
	3.9	62 ^{2/}	2.65	2.99	.673	3687	19.3	73.6	75.5
	3.7	63 ^{2/}	2.88	2.64	.570	3073	-6.9	25.3	26.5
	3.8	62 ^{2/}	2.72	2.57	.595	3232	3.6	45.7	47.5

^{1/} The percent dry weight (21.5) and the calories per gram of dry tissue (5328) were determined for an initial sample of 16 salmon. These values can be used to determine the initial dry weights and caloric content of the test fish.

^{2/} Salmon observed resting on compartment screens more than five times.

Appendix 5. Experimental conditions, mean fork length, weights, caloric content, growth rates, and food consumption rates of coho salmon held at 15 C and fed to repletion with fly larvae twice daily for 10 days. Experiment 5, August 11, 1967.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final			Growth rate		Food consumption rate	
			Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Dry (mg/g/day)	Caloric (cal/kcal/day)	Dry (mg/g/day)	Caloric (cal/kcal/day)
9.5	1.2	62	2.40	2.72	.589	3109	12.3	13.9	49.7	57.5
	1.3	64	2.85	3.18	.783	4115	23.6	23.3	51.1	52.5
	1.4	62	2.35	2.75	.609	3249	17.7	18.7	58.1	61.1
	1.5	63	2.48	2.78	.633	3480	16.2	20.2	47.4	48.5
	1.3	61	2.27	2.60	.601	3243	19.7	21.9	55.3	58.9
	1.3	63	2.45	2.65	.591		10.6		47.2	
	1.5	60	2.28	2.33	.503		1.6		31.4	
9.5	2.1	65	2.83	3.04	.718	3958	15.6	19.9	55.2	56.5
	2.7	61	2.35	2.75	.640	3503	22.6	26.1	65.4	61.9
	2.8	62	2.40	2.75	.616	3347	16.7	19.5	54.2	55.4
	2.6	61	2.50	2.78	.645	3578	17.2	22.1	58.3	56.9
	2.6	65	2.80	3.15	.758	4282	22.0	33.0	59.5	59.6
	2.3	60	2.27	2.33	.524		6.1		35.6	
	2.5	60	2.34	2.51	.582		13.6		44.7	
	2.6	64 ^{2/}	2.70	3.05	.697		17.3		50.7	
9.5	3.5	63	2.65	2.78	.631	3463	9.3	13.1	53.2	55.7
	3.8	61	2.42	2.54	.577	3113	9.4	11.6	48.6	58.7
	3.3	65	2.82	2.96	.685	3694	11.2	13.4	46.0	52.1
	3.8	61	2.45	2.16	.481		-10.1		10.0	
	3.7	60	2.30	1.85	.352		-34.6		0.0 ^{4/}	
	3.8	60	2.33	1.85	.397		-31.6		0.0 ^{4/}	
5.0	1.4	65	3.00	3.33	.819	4614	24.0	29.1	59.4	57.8
	1.6	61	2.39	2.89	.674	3699	26.0	29.8	71.5	73.7
	1.6	62	2.45	2.83	.673	3766	14.8	29.1	55.0	58.3
	1.7	61	2.49	2.70	.634	3475	16.0	19.7	58.6	55.7
	1.6	63	2.54	2.70	.628	3399	13.1	15.5	51.6	53.7
	1.5	65	2.85	3.20	.751		19.4		51.3	
	1.4	65	2.84	3.09	.696		12.2		48.5	
	1.5	63	2.71	2.93	.677		14.0		35.8	
5.3	2.4	64	2.52	2.91	.692	3874	23.6	29.3	63.0	63.5
	2.5	63	2.40	2.69	.616	3325	16.7	18.9	58.5	61.7
	2.2	60	2.29	2.59	.604	3268	19.5	21.5	62.0	63.8
	2.3	60	2.25	2.47	.592	3260	19.3	23.4	55.3	57.1
	2.4	60	2.28	2.51	.579	3251	15.6	18.7	56.5	57.5
	2.3	60	2.25	2.28	.520		6.4		39.6	
	2.4	61	2.34	2.33	.510		0.0		27.1	

Appendix 5. Continued.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final			Growth rate		Food consumption rate	
			Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Dry (mg/g/day)	Caloric (cal/kcal/day)	Dry (mg/g/day)	Caloric (cal/kcal/day)
5.0 ^{5/}	3.5	63	2.69	2.62	.612	3332	4.85	7.9	34.2	36.3
	3.4	65	2.74	2.62	.581	3042	-2.38	-3.2	34.8	36.4
3.3	1.4	60	2.29	2.47	.594	3322	17.8	23.5	45.6	45.5
	1.4	65	2.86	3.20	.768	4256	21.2	25.9	46.8	48.0
	1.4	62	2.49	2.60	.600	3206	10.5	11.7	48.4	50.7
	1.5	61	2.48	2.74	.638	3513	17.0	21.2	51.2	48.7
	1.4	65	2.74	3.07	.739	4167	21.6	28.1	48.1	44.4
	1.4	65 ^{3/}	2.84	2.98	.706		13.6		39.5	
3.2	2.8	62	2.68	2.71	.610	3428	4.7	9.9	39.4	40.8
	2.6	64	2.85	3.01	.702	3923	12.7	18.4	48.0	49.8
	2.9	60	2.31	2.35	.516	2766	2.9	4.5	32.0	43.3
	2.5	62	2.48	2.68	.626	3417	15.1	18.4	47.1	39.9
	3.2	60	2.29	2.57	.583	3238	15.9	20.9	53.0	55.1
	2.5	62	2.45	2.66	.674		17.6		38.0	
	2.7	62 ^{3/}	2.92	2.98	.604		6.1		34.0	
	2.8	64 ^{3/}	2.79	2.71	.583		-0.2		29.2	

^{1/} The percent dry weight (21.8) and the calories per gram of dry tissue (5281) were determined for an initial sample of 16 salmon. These values can be used to determine the initial dry weight and caloric content of the test fish.

^{2/} Final calories were calculated by multiplying the salmon's final dry weight times the calories per gram of dry fish tissue determined for a composite sample. For each trough, the sample consisted of the five fish exhibiting the highest food consumption rates and normal behavior (see footnote 3).

^{3/} Salmon observed resting on compartment screens more than five times, or exhibiting other abnormal behavior as described in the results section.

^{4/} Salmon was deprived of food.

^{5/} Dissolved oxygen content fell below 2 mg/liter and only two salmon survived.

Appendix 6. Experimental conditions and mean fork length, weights, caloric content, growth rates, and food consumption rates of coho salmon held at 15 C and fed to repletion with fly larvae twice daily for 12 days. Experiment 6, October 2, 1967.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final			Growth rate		Food consumption rate	
			Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Dry (mg/g/day)	Caloric (cal/kcal/day)	Dry (mg/g/day)	Caloric (cal/kcal/day)
9.5	1.4	67	3.07	3.56	0.836	4661	23.3	30.3	64.6	69.7
	1.4	67	2.91	3.70	0.875	4873	31.2	38.2	71.4	77.0
	1.4	68	3.30	3.78	0.890	4959	22.5	29.6	64.4	69.0
	1.4	65	2.86	3.35	0.779	4349	23.4	30.4	66.1	71.3
	1.3	69	3.19	3.95	0.933	5198	29.1	36.1	68.6	74.3
	1.3	68	3.42	3.76	0.862		16.9		55.6	
	1.4	67	3.40	3.57	0.849		16.2		44.6	
	1.5	67	3.28	3.68	0.858		19.1		54.4	
9.5	2.7	66	2.99	3.74	0.861	4728	27.8	33.7	75.4	82.1
	2.6	68	3.09	3.97	0.934	5125	31.7	34.7	73.4	82.5
	2.7	69	3.23	4.38	1.029	5648	35.7	41.6	89.7	97.4
	2.6	69	3.31	3.88	0.896	4920	22.8	28.7	74.1	80.4
	2.7	66	3.09	3.66	0.874	4797	26.3	32.2	65.6	71.4
	2.7	69	3.57	4.19	0.990		24.7		60.9	
	3.0	64	2.73	3.26	0.769		20.6		66.6	
	2.8	66	2.83	3.20	0.706		16.1		69.3	
9.5	3.5	66	3.07	3.44	0.802	4377	19.8	25.3	60.7	66.4
	3.2	70	3.59	3.99	0.938	5122	19.8	25.3	50.9	57.5
	3.6	64	2.82	3.00	0.650	3548	9.5	15.0	61.4	67.4
	3.0	67 ^{3/}	3.30	2.79	0.554		-16.7		4.4	
	3.5	65 ^{3/}	3.17	2.77	0.954		-7.7		19.2	
	3.7	62 ^{3/}	2.59	2.59	0.565		-0.3		27.2	
5.0	1.4	68	3.17	3.82	0.865	4846	23.4	30.9	62.5	67.3
	1.2	70	3.60	4.22	0.971	5441	22.5	30.0	60.1	64.7
	1.2	68	3.15	3.82	0.880	4931	27.3	32.8	64.1	68.9
	1.2	67	3.13	3.86	0.929	5205	30.2	37.7	66.4	71.3
	1.4	70	3.22	3.95	0.906	5077	25.9	33.4	69.9	74.3
	1.6	64	2.81	2.92	0.657		10.7		57.1	
	1.7	62 ^{3/}	2.87	2.87	0.654		8.6		39.7	
	1.6	69	2.28	3.68	0.852		20.7		56.1	
5.0	2.7	68	3.18	3.83	0.934	5193	29.4	36.2	66.6	71.9
	2.8	66	2.82	3.49	0.814	4527	25.0	34.8	66.8	72.4
	2.6	64	2.92	3.53	0.813	4519	25.0	31.9	68.9	74.3
	2.6	69	3.47	4.00	0.940	5202	22.6	29.2	59.5	64.3
	2.8	67	3.12	3.55	0.843	4686	22.5	29.5	64.6	69.1
	2.9	65	2.85	3.07	0.702		15.0		51.6	
	2.8	66	2.86	3.09	0.681		12.0		53.6	
	2.8	66	2.65	2.89	0.666		15.3		51.1	

Appendix 6. Continued.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final		Calories ^{2/} (cal)	Growth rate		Food consumption rate	
			Wet weight (g)	Wet weight (g)	Dry weight (g)		Dry (mg/g/day)	Caloric (cal/kcal/day)	Dry (mg/g/day)	Caloric (cal/kcal/day)
5.0	3.4	71	3.48	4.33	0.991	5580	26.9	34.7	73.2	78.6
	3.8	65	2.95	3.34	0.760	4278	18.7	26.7	65.2	70.2
	3.7	69	3.21	3.56	0.813	4580	17.4	25.1	64.0	73.7
	3.4	69	3.30	4.08	0.942	5300	29.6	35.9	77.5	80.8
	3.5	68	3.22	3.55	0.817	4609	17.6	25.4	65.4	70.0
	3.7	66	3.06	3.32	0.730		14.5		61.1	
	2.8	66	2.92	3.15	0.699		12.7		62.3	
	3.5	70	3.53	3.77	0.867		13.7		59.5	
3.1	1.3	69	3.50	3.96	0.949	5321	22.9	30.5	56.4	60.7
	1.4	66	2.87	3.37	0.757	4242	20.6	28.2	65.6	70.6
	1.4	68	3.19	3.69	0.866	4857	23.0	30.7	54.1	57.8
	1.2	69	3.47	4.04	0.932	5226	21.4	29.7	58.1	62.0
	1.3	65	2.71	3.12	0.710	3807	20.0	24.1	51.9	57.4
	1.5	67	3.41	3.73	0.846		15.6		48.2	
	1.3	65	2.67	3.06	0.679		13.7		48.1	
	1.3	65 ^{3/}	2.80	3.06	0.659		15.1		49.9	
3.6	2.9	66	3.22	3.47	0.771	4148	12.6	17.0	50.1	55.4
	2.9	64	2.79	3.00	0.687	3697	15.0	18.1	56.1	62.2
	2.3	72	3.59	3.83	0.885	4760	15.6	19.8	58.9	65.2
	2.8	64	2.64	2.84	0.635	3416	13.0	17.3	48.1	53.0
	2.9	65	2.97	3.19	0.724	3894	19.3	23.6	43.6	48.2
	2.6	67 ^{3/}	3.13	3.25	0.733		11.0		38.1	
	2.7	62 ^{3/}	2.63	2.60	0.538		-0.9		27.7	

^{1/} The percent dry weight (20.6) and the calories per gram of dry tissue (5107) were determined for an initial sample of 16 salmon. These values can be used to determine the initial dry weight and caloric content of the test fish.

^{2/} Final calories was calculated by multiplying the salmon's final dry weight times the calories per gram of dry fish tissue determined for a composite sample. For each trough the sample consisted of the five fish exhibiting the highest food consumption rates and normal behavior (see footnote 3).

^{3/} Salmon observed resting on compartment screens more than five times, or exhibiting other abnormal behavior as described in the results section.

Appendix 7. Experimental conditions, mean fork length, weights, caloric content, growth rates, and food consumption rates of coho salmon held at 15 C and fed to repletion with fly larvae twice daily for 12 days.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final			Growth rate		Food consumption rate	
			Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Dry (mg/g/day)	Caloric (cal/kcal/day)	Dry (mg/g/day)	Caloric (cal/kcal/day)
9.5	1.2	71	3.58	4.22	0.913	4823	24.2	31.9	73.2	88.0
	1.2	72	3.74	4.36	0.948	5010	23.7	31.4	79.4	87.2
	1.2	77	4.07	5.55	1.165	6157	34.5	41.9	96.6	109.7
	1.3	74	3.85	4.79	1.070	5653	31.9	39.4	81.4	92.6
	1.3	71	3.42	4.29	0.924	4884	29.4	40.7	72.0	82.0
	1.2	73 3/4	3.62	4.13	0.872		19.1		73.5	
	1.2	75 3/4	4.23	4.26	0.808		-2.1		35.9	
	1.2	72	3.48	3.91	0.852		20.5		63.5	
9.5	2.3	75	3.96	4.83	1.058	5451	28.3	33.6	71.0	82.0
	2.2	72	3.57	3.85	0.848	4371	17.9	23.8	54.5	63.0
	2.1	76	3.64	4.31	0.898	4609	20.8	26.4	61.7	71.4
	2.3	72	3.61	4.01	0.901	4648	22.2	27.9	69.2	80.1
	2.9	70	3.58	3.88	0.814	7198	11.6	21.5	57.5	66.6
	2.5	72 3/4	3.55	3.57	0.717		3.2		46.8	
	2.5	72 3/4	3.70	3.10	0.533		-18.9		10.5	
	2.4	72 3/4	3.61	3.73	0.734		3.8		41.4	
9.5	2.8	73	3.51	4.03	0.848	4512	19.4	27.8	74.8	85.0
	2.8	75	4.01	5.03	1.123	5979	32.5	40.7	85.9	97.3
	2.9	75	3.76	4.55	1.004	5342	28.3	36.5	93.2	105.6
	2.9	72	3.53	3.89	0.715	3804	14.5	23.1	79.0	95.3
	3.2	72	3.93	4.50	0.950	5057	19.5	27.8	79.7	90.5
	2.7	70	3.11	4.54	0.718		15.4		70.8	
	3.0	70	2.57	3.35	0.721		11.1		64.6	
	3.3	72	3.34	3.67	0.762		14.3		68.5	
5.3	1.2	75	3.75	4.37	0.943	4962	23.0	30.4	69.7	79.7
	1.4	72	3.35	4.14	0.909	4785	29.8	37.4	79.9	91.3
	1.5	74	3.72	4.29	0.936	4923	23.1	30.4	69.0	78.7
	1.3	76	4.10	5.07	1.114	5862	32.4	40.9	78.4	89.4
	1.1	76	4.24	5.11	0.827	5759	25.4	32.6	74.6	85.2
	1.4	72	3.75	4.16	0.872		16.0		58.1	
	1.2	73	3.92	4.32	0.903		14.9		61.6	
	1.2	74	3.70	4.24	0.827		18.7		50.4	
5.0	2.5	71	3.64	4.33	0.978	4844	28.9	30.8	79.0	93.9
	2.5	76	4.11	4.79	1.006	4982	20.6	22.5	68.0	80.4
	2.2	73	3.70	4.37	0.951	4709	24.9	26.8	72.8	86.1
	2.3	74	3.85	4.59	1.018	5043	27.5	29.4	76.3	90.2
	2.6	75	3.99	5.08	1.141	5652	34.4	36.3	89.9	106.2
	2.6	70 3/4	3.55	3.00	0.522		-12.0		12.0	
	2.6	73	3.66	3.90	0.809		11.2		58.9	

Appendix 7. Continued.

Dissolved oxygen (mg/liter)	Swimming velocity (L/sec)	Mean fork length (mm)	Initial ^{1/}	Final			Growth rate		Food consumption rate	
			Wet weight (g)	Wet weight (g)	Dry weight (g)	Calories ^{2/} (cal)	Dry (mg/g/day)	Caloric (cal/kcal/day)	Dry (mg/g/day)	Caloric (cal/kcal/day)
5.4	3.6	76	4.47	4.86	1.075	5731	21.0	31.3	73.9	84.0
	3.2	71	3.44	3.94	0.834	4446	19.5	28.2	77.2	87.5
	3.4	74	3.83	4.38	0.954	5085	22.1	30.5	78.5	89.1
	3.1	71	3.47	4.10	0.901	4803	27.1	34.2	82.5	88.2
	3.2	74	3.65	4.34	0.930	4957	24.2	32.5	75.7	85.8
	3.2	76	4.15	4.46	0.905		11.2		59.7	
	2.9	71	3.19	3.53	0.747		16.6		64.8	
	2.9	72 ^{3/}	3.43	3.61	0.735		6.0		67.4	
3.2	0.9	75	4.05	4.75	0.998	5254	21.1	28.5	59.7	66.9
	1.0	75	3.92	4.46	0.937	4934	18.4	25.9	62.1	71.0
	1.0	75	4.09	4.83	1.031	5427	23.1	30.5	60.9	69.6
	0.8	73	3.53	3.61	0.712	3747	3.1	10.6	48.7	55.9
	1.1	72	3.40	3.57	0.748	3939	10.9	18.5	50.6	57.9
	1.1	72	3.63	3.56	0.711		0.1		44.5	
	1.0	73	3.71	3.83	0.818		11.2		44.6	
3.1	1.8	72	3.57	3.76	0.766	4003	8.7	15.5	50.5	58.1
	1.9	74	4.04	4.15	0.850	4406	6.8	12.9	47.5	54.6
	1.7	73	3.77	4.21	0.906	4737	18.9	26.8	75.2	86.4
	2.0	70	3.41	3.71	0.726	3795	7.9	14.2	44.0	50.6
	2.2	75	3.83	4.09	0.871	4553	13.9	20.7	62.5	71.9
3.4	3.5	74	4.00	4.19	0.848	4251	7.6	10.7	45.9	54.0
	3.3	73	3.82	3.98	0.817	4096	8.3	11.3	54.8	69.6
	3.2	73	3.67	3.76	0.750	3760	4.6	8.0	40.2	47.3
	2.8	72	3.53	3.53	0.678	3399	-1.5	-1.9	43.9	51.7
	2.9	72	3.66	3.68	0.750	3760	4.5	5.1	43.5	50.7
	2.8	73 ^{3/}	3.96	3.86	0.706		-8.1		9.8	

^{1/} The percent dry weight (19.5) and the calories per gram of dry tissue (4850) were determined for an initial sample of 16 salmon. These values can be used to determine the initial dry weight and caloric content of the test fish.

^{2/} Final calories was calculated by multiplying the salmon's final dry weight times the calories per gram of dry fish tissue determined for a composite sample. For each trough, the sample consisted of the five fish exhibiting the highest food consumption rates and normal behavior (see footnote 3).

^{3/} Salmon observed resting on compartment screens more than five times, or exhibiting other abnormal behavior as described in the results section.