

AN ABSTRACT OF THE THESIS OF

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Title: INFLUENCE OF TEMPERATURE ON ENERGY AND  
MATERIAL UTILIZATION BY JUVENILE COHO SALMON

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The influence of temperature on energy and material utilization by young coho salmon (Oncorhynchus kisutch) was studied in the laboratory. Five experiments were conducted during the first year of life of the fish from early spring, 1967, to late winter, 1968. Housefly larvae (Musca domestica) were used as food. During each experiment, there were 5 temperatures at 3 C intervals.

Food consumption rate, growth rate, nonassimilation of food, specific dynamic action (SDA), standard metabolism, and activity were measured. The energy value of food consumed and that of growth were measured by oxygen bomb calorimetry. Energy expended as SDA and standard metabolism was determined by holding the fish in a respirometer and measuring their oxygen consumption. Food material not assimilated was measured by wet combustion. The energy cost of activity was estimated by summing the measured losses and uses of energy and materials and subtracting their sum from the energy

value of the food consumed.

The percentage of food that was not assimilated was a function of the consumption rate of the fish. It was approximately 15 percent between consumption rates of 10 to 110 cal/kcal salmon/day, but increased to about 27 percent at a consumption rate of 182 cal/kcal salmon/day. SDA was related to both temperature and consumption rate. At high temperatures and high consumption rates it accounted for up to 17 percent of the energy of the assimilated ration. The effect of SDA, regardless of the ration size, was generally complete within 24 hours after feeding. Standard metabolism exhibited the expected increase with increasing temperature, and the expected decrease with increasing fish size. With the small fish used in the early summer experiment, it accounted for up to 30 cal/kcal salmon/day at 20 C. Energy expended as activity by the fish was related to consumption rate, and was particularly high at high consumption rates, sometimes twice the energy cost of standard metabolism. Some of the energy cost of activity can be attributed to nitrogenous waste materials excreted by the fish but not measurable by the technique used in estimating waste products.

Energy budgets in the form of histograms are presented, illustrating the pattern of energy and material losses and uses by the coho at consumption rate intervals of 10 cal/kcal salmon/day. For any given season there were particular temperatures where growth

was most efficient. Growth rates of coho in nature suggest ration sizes in nature to be considerably smaller than the maximum rations fed in the laboratory, but in the range of the lower laboratory rations. The range of temperatures at which maximum efficiency of food utilization for growth occurs changes with season and depends upon the range of consumption rates being considered within a season. The most efficient growth, within consumption ranges occurring in nature, is at the temperatures of 5-14 C in early spring, 11-14 C in early summer, 14-17 C in late summer, 11-17 C in fall, and 5-8 C in late winter. Efficient food utilization for growth sometimes occurred at higher temperatures, but only at relatively high consumption rates, probably well beyond those usually existing in nature.

Influence of Temperature on Energy and  
Material Utilization by Juvenile  
Coho Salmon

by

Robert Craig Averett

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INFLUENCE OF TEMPERATURE ON  
ENERGY AND MATERIAL UTILIZATION  
BY JUVENILE COHO SALMON

INTRODUCTION

The success of any animal species ultimately depends upon its ability to obtain sufficient energy and materials to grow, reach maturity, and to reproduce. It is growth that has been given the greatest emphasis by man, especially in his husbandry of domestic animals. Yet, the energy and materials that an animal may use for growth are available only after all other metabolic costs have been satisfied. Energy must be available for maintaining the vital processes of the body even at rest, for movement, and for the breakdown of food materials and their transport throughout the body, as well as for synthesis. In addition, not all the food consumed by an animal is converted into useful energy and materials. Some is lost in the form of nitrogenous compounds (urea, uric acid, and ammonia), some is lost as feces, and some is lost through specific dynamic action.

The experiments described here were designed to determine the allocation of energy and materials by juvenile coho salmon (Oncorhynchus kisutch) fed rations of various levels and held at different temperatures. Temperature was studied as a physiological stress because of its importance to aquatic poikilotherms in controlling their food consumption and metabolism and because thermal

pollution is becoming an important water quality problem. There is a considerable literature concerning the effects of temperature on fish. Much of this literature is concerned with lethal temperatures (Brett, 1952, 1956), metabolic changes and preferenda (Fry, 1947, 1957, 1964 and Brett, 1964), and acclimation to changing temperatures (Doudoroff, 1942, Precht, 1958). Recently, Kennedy and Mihursky (1967) compiled a bibliography listing 1,220 references on relations between temperature and aquatic organisms.

In spite of the large amount of study on the influence of temperature on fish, little is known about sub-lethal effects on other than metabolic rate. With regard to growth alone, we speak of the optimum temperature without considering the consumption rate and the efficiency of food utilization. In many cases, no consideration is given to the size of the fish, season of the year, energy or materials in the diet, or to the previous nutritional history of the fish. Little is known about the total metabolic costs of fish\* and how these costs influence the amount of energy available for growth.

The most satisfactory initial approach to such problems is with laboratory experiments in which temperature can be controlled, rations determined accurately, and all major metabolic costs measured separately. Essentially, this is the bioenergetic approach. The approach is not new, and its roots are deep in the history of biology. Yet, it has received little attention from aquatic biologists.

Ivlev (1945) was probably the first to use the bioenergetic approach to study energy and material relationships between fish and their food supply. His energy budget for fish and his rationale for relating this budget to natural food resources paved the way for later studies. Although there are difficulties of definition and measurement in Ivlev's energy budget, his point of view still remains a milestone in our understanding of aquatic ecosystems. Brody's (1945) magnificent volume Bioenergetics and Growth provided a framework for more sophisticated studies.

Fry (1947) provided a very useful classification of environmental factors affecting animals. He defined these factors as being limiting, masking, lethal, directive, accessory, controlling, or some combination of these. Fry considered temperature to usually act as a controlling factor. He conceptualized "scope for activity" as the difference between energy expenditure for standard (basal) and active (maximum) metabolic rates of a fish under a given set of environmental conditions. Fry, Ivlev, and Brody all sought to measure the response of the whole animal to its environment. Such a framework was given additional impetus by Huntsman (1948) when he criticized descriptive biology and urged that studies be directed toward determining those environmental factors which ultimately determine whether or not an animal will be successful. Huntsman did not specify the bioenergetic approach, but his point of view lends it support. Almost

a decade later, Winberg (1956) summarized most of the information available on the bioenergetics of fish and suggested a balanced equation relating consumption, metabolism and growth.

Warren and Davis (1967) integrated the findings of Ivlev, Brody, Fry, and Winberg, as well as their own. They introduced the "scope for growth" concept and defined it as the difference between the energy of the food that an animal consumes and all other energy utilizations and losses under particular environmental conditions. They stressed that "scope for growth" is not the same as Fry's "scope for activity" because the food consumption rate of a fish will be influenced by and will influence the metabolic rate. Warren and Davis suggested an energy budget which is particularly useful because the terms are largely independent and can be measured. I employed their energy budget and suggested techniques in this study.

I conducted five experiments starting with newly emerged coho fry in April and ending with year-old coho the following February (1967-1968). The research was carried out at the Pacific Cooperative Water Pollution Laboratories, a division of the Department of Fisheries and Wildlife, Oregon State University.

## METHODS AND MATERIALS

Experimental Fish, Apparatus and Periods

The coho salmon used in all experiments were captured with a seine from the Yaquina River near Nashville, Oregon. Fish for the first three experiments were collected from the river when needed and brought directly to the laboratory where they were acclimated to the test temperatures for 21 days. Coho for the November-December and February-March experiments were captured from the river in late September and held in an earthen pond at the laboratory. When needed they were removed from the pond and brought into the laboratory to be acclimated for experiments. The mean weight of the fish used for each experiment corresponded, as nearly as possible, to that of the fish in the river at a particular season.

The experimental work was carried out in a constant temperature room (Figure 1). A nearby spring provided the water supply, the chemical characteristics of which have been reported by Doudoroff, Leduc and Schneider (1966). In the laboratory, the water was passed through five headboxes located above the experimental apparatus. Water temperatures in each headbox were maintained within  $\pm 0.2$  C of the test temperature with a stainless steel immersion cooler or with a 1,000 watt immersion heater connected to a control unit. Water from each headbox was distributed to one

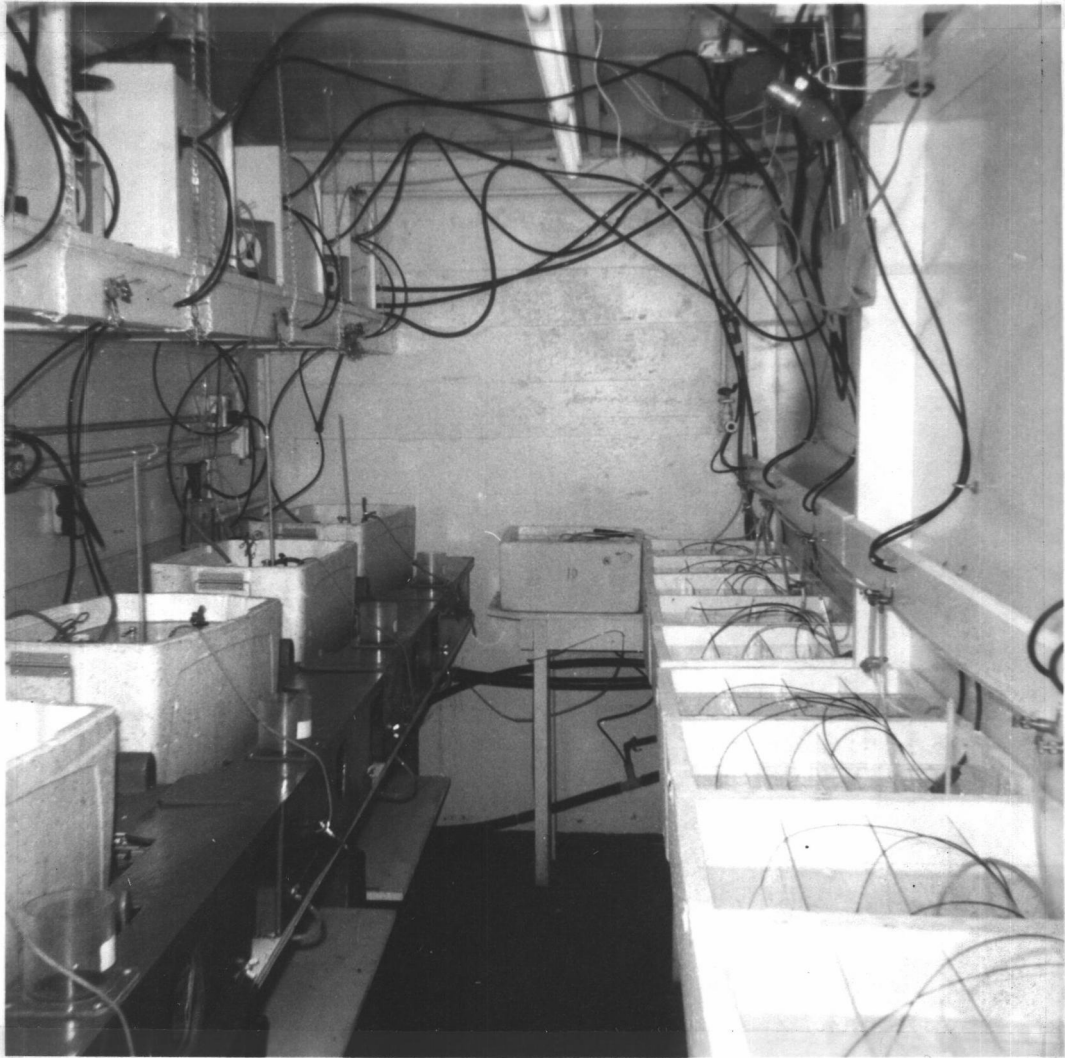


Figure 1. Some of the laboratory apparatus used in this study. Headboxes are at upper left. Styrofoam boxes at lower left contain respirometers. Aquaria are at lower right.



respirometer and two aquaria through black plastic lines of 0.5 cm inside diameter. Uniform temperature and air saturation levels of oxygen were maintained in each headbox water by aeration.

Ten styrofoam minnow-shipping cartons were used as aquaria. Each aquarium held 24.5 liters of water and was divided by 0.5 cm clear plexiglass into eight compartments holding 3 liters each. Two aquaria, providing separate compartments for 16 fish, were used for each test temperature. Temperature and exchange of the water in each aquarium were maintained by water flow from a headbox at a rate of 183 ml per minute. The water in each aquarium was aerated to further insure air saturation levels of oxygen.

One fish was placed into each compartment of the aquaria. At each temperature, eight fish were used in each growth experiment. The remaining eight were either sacrificed for determination of the caloric content of the fish before the growth experiment began, or were used in studies of standard metabolism, specific dynamic action, and nonassimilation of food.

Five respirometers, constructed of 0.5 cm clear plexiglass, were used for measuring oxygen consumption of fed and unfed fish at various swimming velocities (Figure 2). The swimming tube was 6.4 cm in diameter and 25 cm long. Stainless steel screens and plexiglass baffles provided an essentially rectilinear flow of water through the swimming tube. A fish entrance chamber measuring 10 cm on each

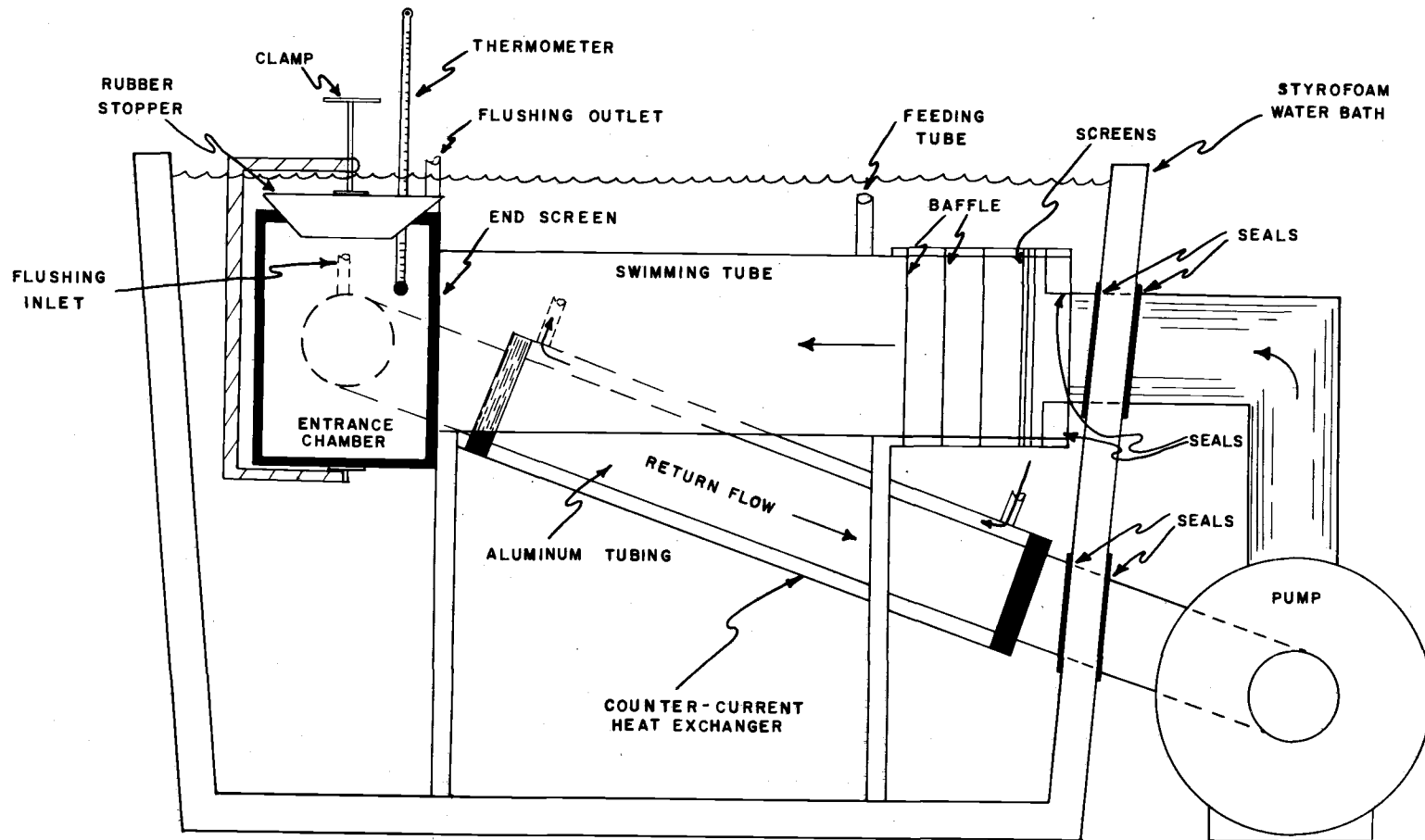


Figure 2. Schematic diagram of one of the five respirometers used to determine oxygen consumption of coho salmon. Left side of styrofoam container for water bath has been removed to show respirometer detail. Not shown is variable speed device used to change pump speed.

side was attached to the outlet end of the swimming tube. Leading from this chamber to the pump was a return line of aluminum tubing having an inside diameter of 2.5 cm. This line was enclosed in a plexiglass tube of 5 cm inside diameter which served as a counter-current heat exchanger. During operation of the respirometers, fluid friction tended to heat the water. Cooling water passing through the heat exchanger maintained water temperatures in the respirometers within  $\pm 0.3$  C. Each respirometer was mounted inside a styrofoam container filled with water which also assisted in maintaining a constant temperature. The water capacity of each respirometer, including the pump, was 3.26 l.

Water was circulated through the respirometers with a centrifugal pump having a capacity of 40 l per minute at zero head. The housing and impellers of the pump were made of polyethylene. Each pump was driven by a one-half horsepower electric motor rated at 3,500 rpm. A system of variable diameter pulleys and V-belts permitted pump speeds to be varied between 500 and 3,500 rpm.

Water velocities in the swimming tubes were measured with a Leupold and Stevens midget current meter. The velocities were graphically related to the rpm of the pump shaft, which was measured with a portable tachometer. With this relationship known, a given water velocity in the swimming tube could be established simply by adjusting the rpm of the pump shaft to correspond to the desired

water velocity.

The fish were introduced into the respirometers through openings at the top of the entrance chambers. Stainless steel screens of 0.5 cm mesh were then inserted to keep the fish within the swimming tubes. During operation of the respirometers, the openings in the top of the entrance chambers were sealed by rubber stoppers through which thermometers accurate to 0.1 C were inserted.

Water from the headboxes entered the respirometers through the flushing inlets and passed through the pumps and swimming tubes before leaving through the flushing outlets. Pieces of latex tubing of 0.3 cm inside diameter and 45 cm in length were attached to the outlets. Water was removed from the respirometers through these tubes for measurement of dissolved oxygen concentrations. The flushing rate of each respirometer was 473 milliliters per minute. Food for the fish was introduced through tubes located near the swimming tube baffles. The outlet tubes and the feeding tubes were closed during operation of the respirometers.

The oxygen consumption of an individual fish inside a respirometer was determined by the difference in oxygen concentration between an initial and terminal water sample drawn into a 100 ml glass stoppered bottle. The bottle was allowed to overflow its volume once, resulting in the removal of 200 ml of water from the respirometer. The inlet line from the headbox was left open at all times to insure

that no air became trapped in the respirometer. After the initial water sample was collected, the outlet tube was clamped, thus stopping the flushing flow and sealing the respirometer. After an hour had elapsed, the terminal water sample was removed in the same manner. The difference in dissolved oxygen content between the initial and terminal samples was attributed to consumption by the fish. A number of tests were conducted on the oxygen content of water from the respirometers in the absence of fish, and the difference between these initial and terminal samples never exceeded 0.02 mg of oxygen. The introduction of 200 ml of replacement water made no measurable difference in the dissolved oxygen content.

Between oxygen consumption determinations, the respirometers were flushed for 30 minutes. During this period the water in the respirometers was exchanged 4.35 times, returning the oxygen concentration in the respirometers to levels near air saturation.

All oxygen determinations were made using the Azide modification of the Winkler method (American Public Health Association, 1965). The sodium thiosulfate used as a titrant was 0.025 N and was regularly standardized with 0.025 N potassium bi-iodate.

Oxygen consumption values were converted to calories with an oxycaloric coefficient of 3.42 calories per milligram of oxygen (Brody, 1945, Winberg, 1956). Winberg mentions that regardless of whether the animal is oxidizing fat, carbohydrates, or proteins, the

oxycalorific coefficient will not vary more than 1.5 percent. Ivlev (1934) on the basis of a potassium dichromate oxidation method has presented oxycalorific coefficients for a number of aquatic animals. His values ranged from 3.332 to 3.494.

Table 1 summarizes the experimental periods and conditions. It generally took two months for preparation and completion of a single experiment, but the length of a single growth experiment was 14 days. The temperature of each experiment was adjusted to include that range which would occur in nature as well as higher temperatures. In each experiment, five temperatures, at 3 C intervals, were tested. The initial wet weight and corresponding caloric values per gram (dry weight) of fish at the beginning of each growth experiment are also given in Table 1. Upon completion of a growth experiment, weight and caloric content of the fish varied greatly depending upon ration size and test temperature. The mean calories per gram (dry weight) of fly larvae ranged from 5,502 to 6,040.

Illumination in the laboratory was provided by four fluorescent lights of 40 watts each. The lights were mounted in a single row 1.2 m above the aquaria and were controlled by a timer. At each experimental season the timer was set to turn the lights on at sunrise and off at sunset.

Table 1. Experimental periods, temperatures, hours of illumination, mean initial weights and mean caloric content of fish, and mean caloric content of fly larvae.

Experiment	Period of growth experiment	Temperature range tested (C)	Mean illumination period (hours)	Mean initial wet weight of fish (grams)	Mean initial calories per gram of fish (dry weight)	Mean calories per gram of fly larvae (dry weight)
April-May	23 Apr-6 May	5-17	14.0	1.209	5,303	5,502
June-July	23 Jun-6 July	8-20	15.5	1.859	5,527	6,040
August-September	19 Aug-1 Sept	11-23	13.5	2.215	5,371	5,354
November-December	17 Nov-30 Nov	8-20	9.0	4.596	5,044	5,463
February-March	3 Feb-16 Feb	5-17	10.0	6.445	5,504	5,572

Bioenergetic Equations and Growth Efficiencies

The bioenergetic equation proposed by Warren and Davis (1967) and used in this study has the following form:

$$Q_c = Q_g + Q_w + Q_s + Q_d + Q_a$$

where

$Q_c$  = energy value of food consumed,

$Q_g$  = total change in energy value of materials of body (growth),

$Q_w$  = energy value of waste products in feces, in urine, and lost through gills and skin,

$Q_s$  = energy equivalent to that released in the course of metabolism of unfed and resting fish (standard metabolism),

$Q_d$  = additional energy released in the course of digestion, assimilation, and storage of materials consumed (SDA),  
and

$Q_a$  = additional energy released in the course of swimming activity.

The energy cost of activity ( $Q_a$ ) was the only component of the formula which was not directly measured. It was estimated as the residual after all other costs had been subtracted from the energy value of the food consumed.



The above formula is in terms of total energy assimilation and loss by a single fish over a given time period. Warren and Davis (1967) discussed the need for a rate equation and suggested the substitution of the terms  $A_i$  for  $Q_i$  in the above equation where

$$A_i = \frac{Q_i}{W^x t}$$

where

$W$  = mean body weight or energy value,

$t$  = time in days (always 14 in the case of the growth experiments),

$x$  = some mean power of  $W$ , and

$i$  = c, w, g, s, d, or a.

The equation that I employed in this study used the terms  $A_i$ . For  $W^x$ , I used the mean energy value of the body of the fish (kilocalories) to the first power ( $W^1$ ). All rate values were per day. The units of each term were thus calories/kilocalorie salmon/day (cal/kcal salmon/day).

Gross and net growth efficiencies were also computed:

$$\text{Gross efficiency} = \frac{G}{C}; \text{ and}$$

$$\text{Net efficiency} = \frac{G}{C-M}$$

where

$G$  = growth rate in cal/kcal salmon/day,

C = food consumption rate in cal/kcal salmon/day, and

M = maintenance ration in cal/kcal salmon/day.

The efficiency values were multiplied by 100 and expressed as percentages.

### Food Consumption and Growth

Live housefly larvae (Musca domestica) were used as the food. There was no indication that the larvae were deficient in any essential nutrient component. Three fish were fed from September through May on the larvae, and during this period they grew well and appeared to be in a healthy condition. Before being fed to the fish, the larvae were cleaned of debris and given sufficient time to empty their intestinal tracts. Samples of the larvae were dried and caloric determinations made to use in determining the energy value of the food consumed (Table 1).

Eight fish were tested at each experimental temperature. One fish was starved, one was fed a 1 percent ration (based upon initial live weight), one was fed a ration of 2.5 percent, and two were fed 4 percent rations. The remaining three fish were fed to repletion twice each day, once in the morning and once in late afternoon. By using this array of rations, it was possible to obtain a growth curve which expressed the energy cost of starvation and maintenance and which defined growth at low, intermediate and repletion rations.

Each ration for each fish was weighed to the nearest milligram.

Each growth experiment had a duration of 14 days. The fish were acclimated to their respective test temperatures for a period of 21 days. They were placed directly into water of the desired test temperature. Those that died were replaced, and all fish were acclimated until the minimum acclimation period was at least 21 days. Mortality during the acclimation period was usually less than 10 percent and was generally complete within the first five days. During the acclimation period, each fish received a ration approximating four percent of its body weight.

Following the acclimation period, the fish were fasted for 48 hours. They were then anaesthetized with tricaine methanesulfonate (MS-222), blotted dry, and weighed to the nearest milligram, after which they were returned to their respective aquarium compartments. The next day, 72 hours after the last feeding, the growth experiment was initiated. During the initial weighing period, three fish from each experimental temperature were sacrificed to determine initial percentages of dry weight and caloric values.

After being dried for 4 days at 70 C, the fish were ground to a fine powder and caloric determinations were made on their bodies. An oxygen bomb calorimeter (Parr Model 1411 semi-micro) was used for all caloric determinations. The instructions given in Parr manuals 128 and 130 were followed. The average dry weight of

sample for caloric determination was about 0.1 gram. Usually three caloric determinations were made for each fish, and the results were averaged. With the small fish used in the spring and summer experiments, it was possible to make only one, or sometimes two, determinations.

At the conclusion of a growth experiment, the fish that had been starved were removed from the aquaria, weighed, and placed in the drying oven. The remaining fish, those which had received food, were fasted an additional 72 hours before being removed from the aquaria. Caloric determinations were made on all fish at the conclusion of an experiment.

#### Nonassimilation of Food

That portion of the food consumed that was not assimilated by the fish and was passed as feces was collected by keeping individual fish in containers holding a liter of water and feeding the fish a known ration. The fish were not fed for 96 hours prior to an experiment, and were left in the containers 96 hours after feeding. Desired water temperatures were maintained by immersing the containers in water baths. To avoid excessive bacterial oxidation at the higher temperatures, much of the fecal material was removed daily by means of a pipette. In the earlier experiments this was the only method used to remove feces from the water in the containers. The

water picked up with the feces was separated by centrifugation. In later experiments, the entire liter of water was filtered through glass wool.

Thirty milliliters of distilled water were added to the fecal material and this solution was then oxidized using the chemical oxygen demand test (American Public Health Association, 1965). When the glass wool filter method was used, the entire filter was placed in the oxidizing flask, as the glass wool was found to have no oxygen demand.

Some fecal material remained in solution. To measure this, material contained in 30 milliliter aliquots of water from the holding containers was also oxidized. The values for dissolved materials were added to the values for suspended and settled materials.

The chemical oxygen demand method involves the use of potassium dichromate as an oxidizing agent and concentrated sulfuric acid as a digesting agent. In practice, an excess of dichromate is used and the remainder is back-titrated after refluxing for two hours. Ferrous ammonia sulfate is used as the titrant, with ferroin as the indicator. The titration endpoint is dark red and easy to identify. The chemical oxygen demand method gives, as a final result, milligrams of oxygen required to oxidize the organic matter. The oxygen values were converted to calories with the oxycalorific coefficient of 3.42. This method is quite precise. Three 0.025 gram samples of fly larvae which ranged from 5,325 to 5,747 cal/gram dry weight

based upon calorimetry, gave a narrower range of 5,338 to 5,534 cal/gram dry weight with the chemical oxidation method.

It must be emphasized that the method described measured fecal matter, and is thus a measure of nonassimilation. It does not, however, measure total waste because most nitrogenous wastes are not oxidized by the method. Consequently, the data do not completely satisfy the term  $Q_w$  of the bioenergetic equation.

### Specific Dynamic Action

Specific dynamic action (SDA) was determined by measuring the difference in oxygen consumption between a fish which had consumed a known amount of food, and that of the same fish in the post-absorptive condition. The activity of the fish was maintained constant by forcing it to swim at a fixed low velocity. The fish were placed in the respirometers several days before the SDA experiments began and were trained to swim at the fixed low velocity and to consume fly larvae introduced through the feeding tubes. Fish that did not swim well or take food were replaced. After this initial period, the fish were fasted for 24 hours, removed for weighing, and returned to the respirometers. After another 12 hours, 36 hours since their last meal, they were fed and an SDA experiment was begun.

During an SDA experiment, oxygen consumption measurements were generally made every two hours for 28 to 40 hours after the

initial feeding. The oxygen consumption values determined for the fed fish and for the same fish in the post-absorptive condition were plotted against time on coordinate paper, and the area between the two curves, when plotted one beneath the other, was determined with a compensating polar planimeter. It is this area that I took to be the SDA for the ration consumed. The results were converted from milligrams of oxygen consumed into caloric units with the oxycalorific coefficient of 3.42.

The components of the energy budget proposed by Warren and Davis (1967) are assumed to be independent of one another. This, however, is not strictly true in the case of SDA and activity, because if the activity of a fed fish is increased the energy expenditure measured as SDA will be decreased. It is possible that some of the energy available from protein deamination can be utilized by the fish for activity. It is for this reason that in determining SDA, the fish must be forced to swim at the lowest possible fixed velocity that will eliminate random activity.

#### Standard Metabolism

Standard metabolism is the metabolic rate of a fish in the post-absorptive condition whose activity has been projected to zero on a graph relating its metabolic rate and activity level (Brett, 1964, Warren and Davis, 1967). Individual fish which had not eaten for 24

hours were weighed and placed in the respirometers. They were forced to perform for a period of 12 hours at a water velocity of 6.5 cm per second before oxygen consumption determinations were made. Thus the fish had fasted for 36 hours, and this insured that there was no increased oxygen consumption as a result of SDA. Generally, three oxygen determinations were made at a given swimming speed and then the water velocity was increased. The respirometers were flushed for one-half hour between oxygen determinations.

After each velocity increase, 3 to 6 hours were required before the metabolic rate characteristic of that velocity became established. The fish displayed a temporary increase in metabolic rate over and above the increase necessary to sustain the increased swimming performance. Such an effect was also found by Wells (1932) and Mann (1965).

The water velocities were increased stepwise until the fish could no longer maintain themselves against the current and would begin to rest against the end screen. Measurements made while the fish were darting into the current after resting against the end screen, were discarded. Such erratic swimming was common at the highest velocities and sometimes it was possible to obtain only one valid measurement of oxygen uptake at these velocities.

Because of the time involved in preparing for standard metabolism measurements, it was often necessary to feed the fish after



oxygen determinations had been made at several velocities. A period of 36 hours was again allowed to elapse before measurements were resumed. It generally took 7 to 10 days to establish the relationship between temperature and standard metabolism.

The metabolic rate of a fish increases in a logarithmic manner with increasing activity. To obtain straight line relationships, the results were plotted on 5-cycle semi-logarithmic paper. The line is drawn through the lowermost points because such points are indicative of the least amount of oxygen required for that level of activity (Brett, 1964). All standard metabolic rates were converted to caloric units using the oxycalorific coefficient of 3.42.

### Activity

The energetic cost of swimming activity was measured as a residual by summing all the measured energy costs and subtracting them from the energy value of the food consumed. Activity, as estimated in this manner, should reflect the energy expended to capture food and for random swimming in the aquaria. However, activity was related to consumption rate and, as will be discussed later, the activity estimate probably includes caloric values of nitrogenous waste materials such as urea and ammonia. In other words, activity costs, being determined as a residual, will include non-measured categories and error values.

### Experimental Temperatures

During each season I shifted the experimental temperature range to correspond with seasonal water temperature ranges that occur in nature (Table 2). Needle Branch and Flynn Creek are two small Oregon coastal streams which have coho salmon populations, and their 1965 water temperatures were used in establishing the temperatures for the laboratory experiments. In general, the temperatures used in the laboratory experiments include the ranges found in Needle Branch Creek and Flynn Creek. However, not all coho streams have spring and summer temperatures as low as these two streams. Tobe Creek, another Oregon coho stream which will be discussed in a later section, has a spring and summer water temperature range of 12 to 24 C, considerably higher than that in Needle Branch Creek and Flynn Creek. In this regard then, the seasonal temperature ranges employed in the laboratory experiments should encompass those water temperatures that coho in nature are subjected to.

At each season, the temperatures of 11, 14 and 17 C were tested along with higher or lower temperatures. This made it possible to compare the energy losses and uses at these three temperatures between seasons.

Table 2. Temperature means and ranges for Needle Branch and Flynn Creek,<sup>1/</sup> and test temperatures used in the laboratory experiments during different seasons.

Season	Temperature means and ranges		Laboratory temperatures (C)
	Needle Branch	Flynn Creek	
April-May	8.0 (6.5-10.3)	8.4 (5.5-10.5)	5, 8, 11, 14, 17
June-July	10.8 (8.9-13.9)	10.5 (8.1-13.9)	8, 11, 14, 17, 20
August-September	11.4 (9.9-13.9)	11.4 (8.9-14.3)	11, 14, 17, 20, 23
November-December	8.4 (4.5-10.0)	8.6 (5.0-8.9)	8, 11, 14, 17, 20
February-March	6.8 (4.5-7.1)	7.5 (5.0-9.8)	5, 8, 11, 14, 17

<sup>1/</sup> Data from U. S. Geological Survey, Water Resources Data for Oregon, Part 2, Water Quality Records, 1965.

## RESULTS AND INTERPRETATION

Food Consumption, Growth, and Growth Efficiency

Curves relating growth and growth efficiency to food consumption at different temperatures during the five seasonal experiments are shown in Figures 3-7. The calculation of gross and net growth efficiencies has been explained, but additional discussion will clarify the forms efficiency curves can assume. If food assimilation efficiency decreases, or the proportion of food energy lost through SDA increases, the net efficiency will decline with increasing ration and gross efficiency will reach a maximum at some intermediate consumption rate. In this case, the food consumption rate-growth rate relationship will be curvilinear. If assimilation efficiency and the proportion of food going to SDA and activity are constant over the range of consumption rates tested, net efficiency will remain constant with increasing ration and gross efficiency will asymptotically approach a maximum at the maximum consumption rate. In this case, the food consumption rate-growth rate relationship will be linear (Warren and Davis, 1967). At consumption rates near the maintenance ration, some of the computed net efficiency values exceeded 100 percent. Such values are not realistic and are the result of errors in measurement. They are not shown graphically.

The highest food consumption rates during the five experiments

were obtained with the small fish used during the April-May and June-July experiments. These fish had initial weights of less than two grams, and consumed nearly twice as much food on a rate basis as did the larger fish used in the other three experiments.

At 5 and 8 C during the April-May experiment, consumption rates were relatively low, but the consumption rate-growth rate curves are steep (Figure 3). The net efficiencies for these two experiments are high at low consumption rates, but decline steeply with increasing consumption, in part because of an increased energy cost of SDA, but probably also because of increased activity at higher consumption rates, a problem to be considered later. At 11, 14, and 17 C, the consumption rate-growth rate curves are shifted successively to the right, in part because of an increase in standard metabolism. Higher consumption rates were attained at the higher temperatures. Although growth increased with increasing consumption rates at these temperatures, the rate of increase in growth per unit of food consumed declined as higher consumption rates were attained. This was to be expected, because increasing ration, SDA and nonassimilation increased; matters that will be considered in later sections. In addition, there was an increase in activity associated with increased ration. The maintenance ration, the consumption rate where there is no increase or decrease in the caloric content of the fish, was lowest at 5 C and highest at 17 C, primarily because of an increase in the

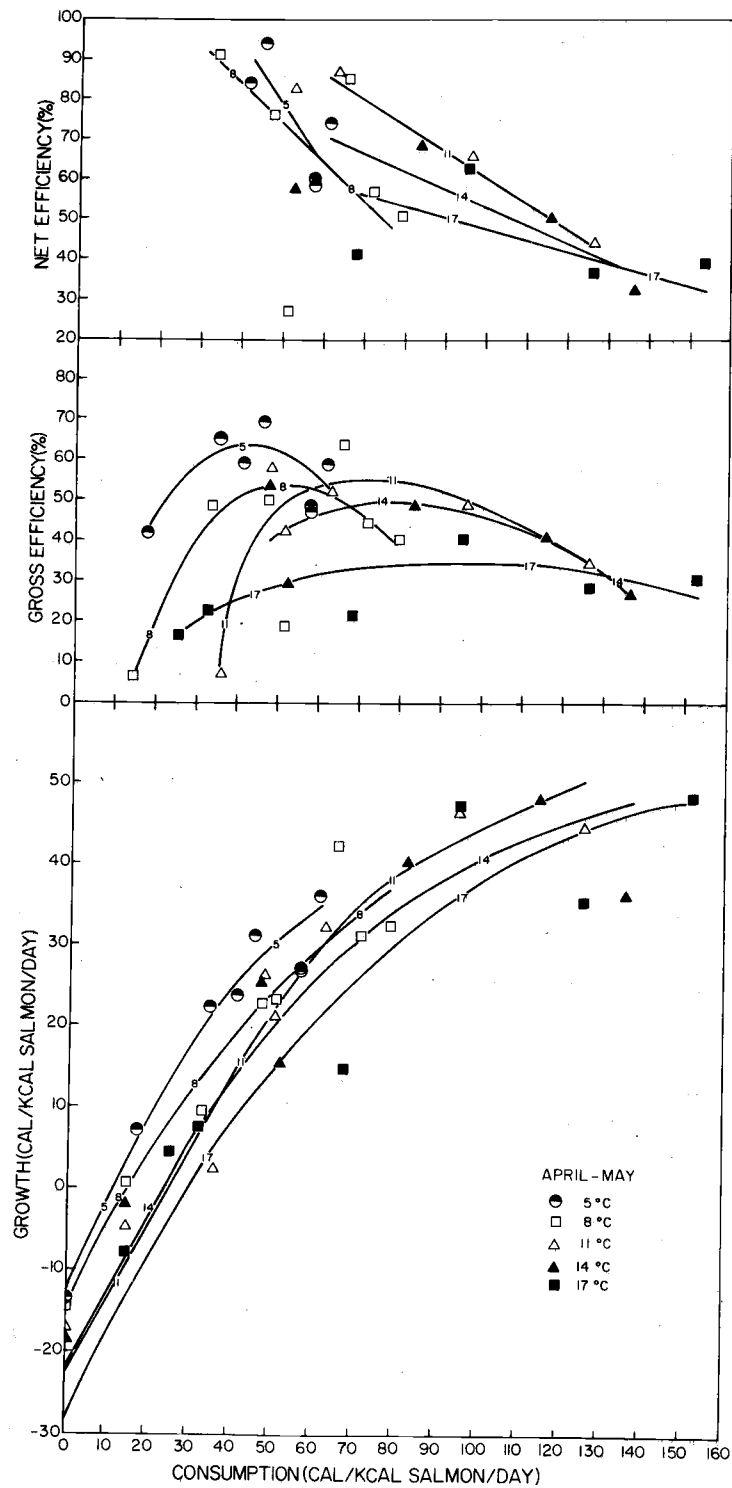


Figure 3. Relationships between consumption rate, growth rate, growth efficiencies and temperature for coho salmon in the April-May experiment.

standard metabolic rate with an increase in temperature. The gross efficiency curves at all temperatures are curvilinear and reach maxima at intermediate rations. This must occur when net efficiencies decline with increasing rations. Net efficiencies tended to decline more rapidly at low than at high temperatures. This tended to offset any advantage fish at low temperatures would have gained by any appreciable increase in consumption rate. It is thus very interesting that fish at the lower temperatures severely limited their maximum consumption rates.

The consumption rate-growth rate curves during the June-July experiment fall into two distinct groups (Figure 4). The curves for 17 and 20 C are displaced to the right of those for the lower temperatures. This is reflected in a marked increase in the maintenance ration between 14 and 17 C. Increases in standard metabolism and SDA at temperatures above 14 C were important causal factors.

Maximum consumption rates at all temperatures were lower with the larger fish used in the August-September experiment (Figure 5). As in the June-July experiment, the consumption rate-growth rate curves for the two higher temperatures are displaced markedly towards the right from those for the lower temperatures. Net efficiencies did not decline much with increasing ration at any temperature, but they are much lower at 20 and 23 C than at 14 and 17 C, with those for 11 C being intermediate. Thus, very little growth occurred

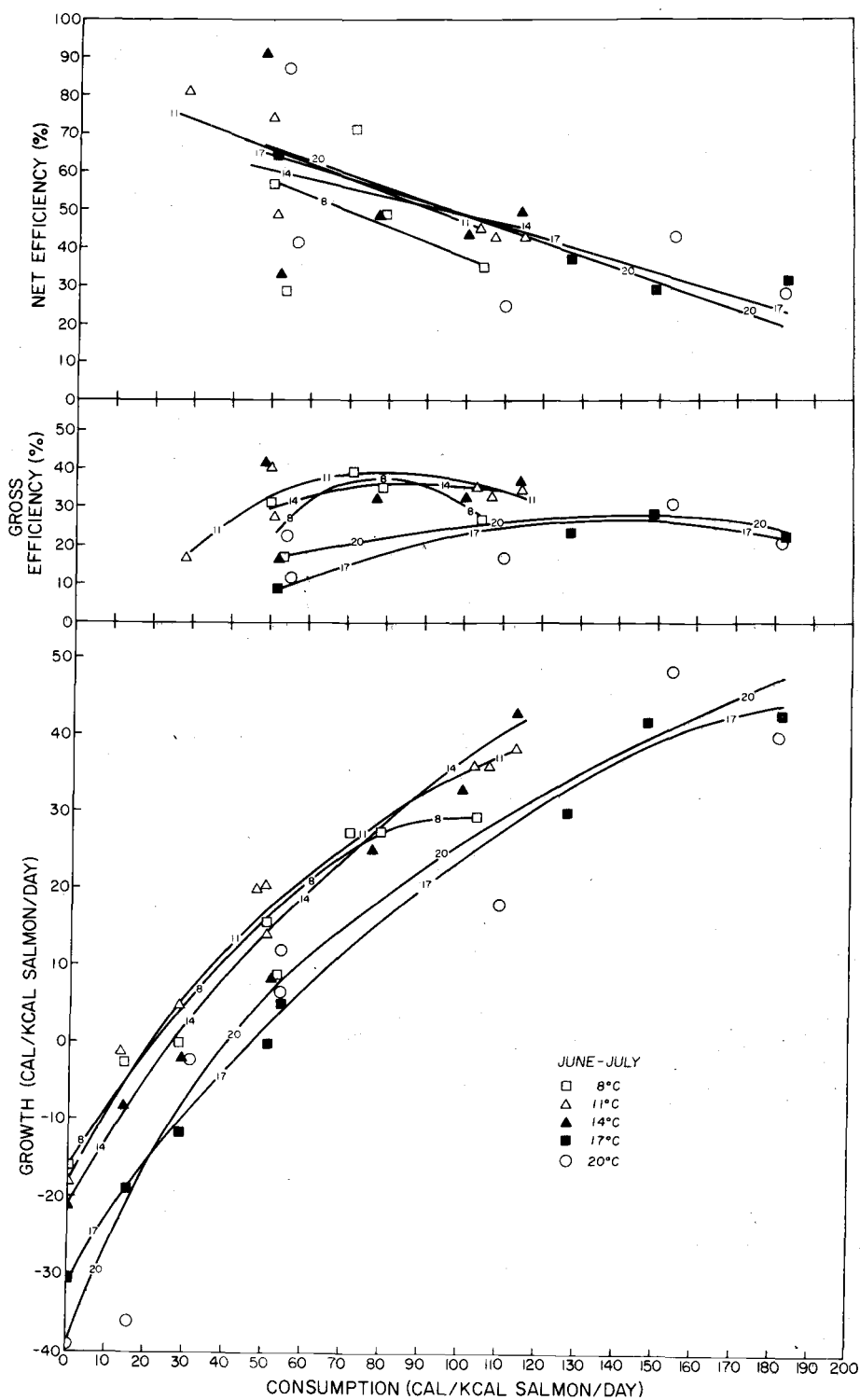


Figure 4. Relationships between consumption rate, growth rate, growth efficiencies and temperature for coho salmon in the June-July experiment.



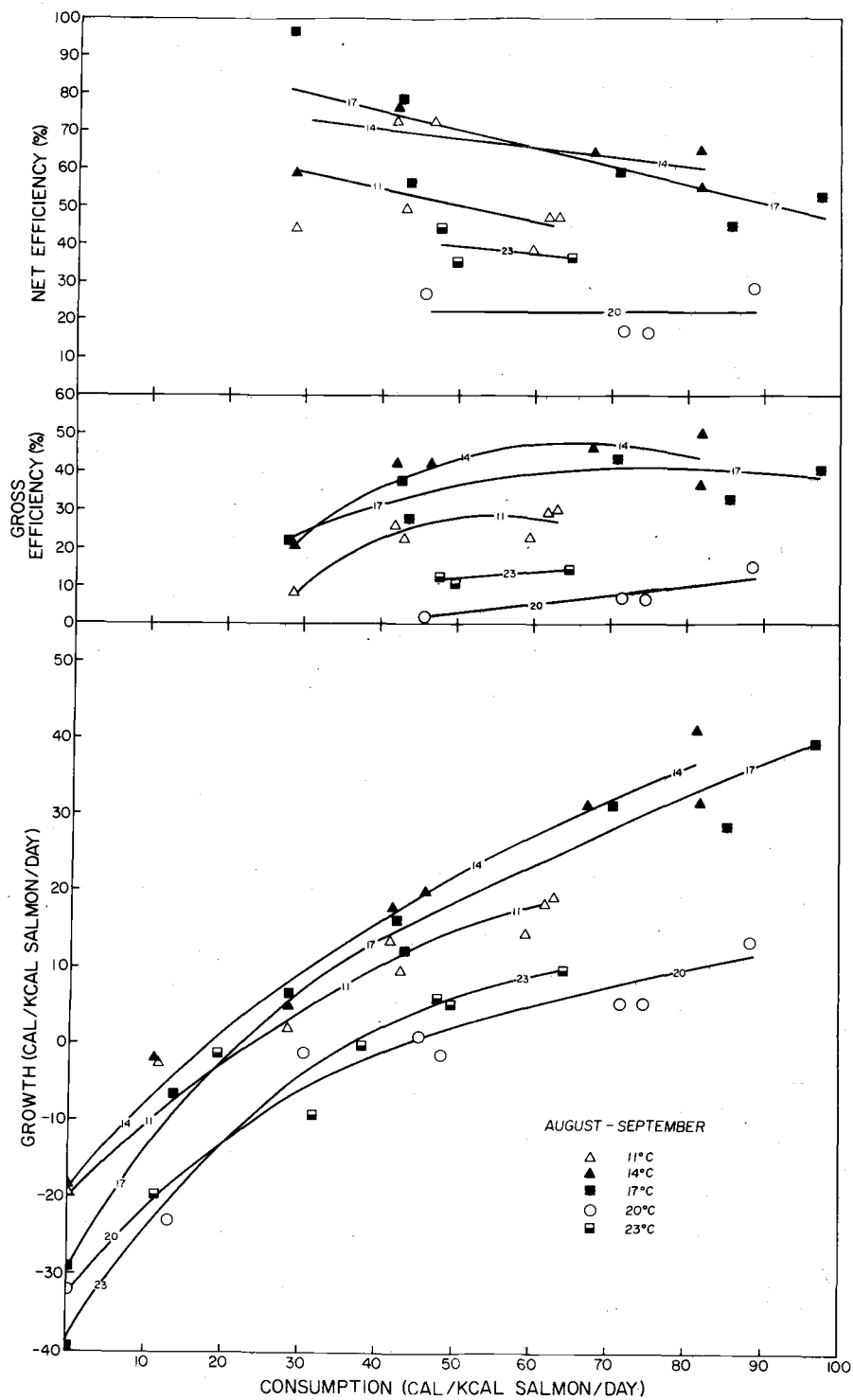


Figure 5. Relationships between consumption rate, growth rate, growth efficiencies and temperature for coho salmon in the August-September experiment.

at any ration when temperatures were 20 and 23 C, and gross efficiencies are very low. There was a marked decrease in the consumption rate at 23 C as compared to 20 C. Maximum consumption rates were lower at 11 and 23 C than at the intermediate temperatures, perhaps suggesting these to be extreme temperatures for this season. The upper incipient lethal level for juvenile coho salmon is near 25 C (Brett, 1956).

Maximum consumption rates at all temperatures were relatively low during the November-December experiment except at 20 C (Figure 6). The food consumption rate-growth rate curve at 20 C is markedly displaced to the right from the curves at the lower temperatures. Higher standard metabolic rate, SDA, and activity are all involved and are reflected in the much higher maintenance ration. Net efficiencies tended to decline not only with increasing ration, but with decreasing temperature. Except at 8 C, gross efficiencies at any temperature are markedly constant over the range of rations the fish would consume.

The coho used in the February-March experiment (Figure 7) were one year old and were the largest used in any of the experiments. Consumption rates, as in the November-December experiment, were low. At 5 C, the maximum consumption rate was very low, but it increased with increasing temperature. The data at all temperatures were highly variable, and any detailed analysis of the various curves

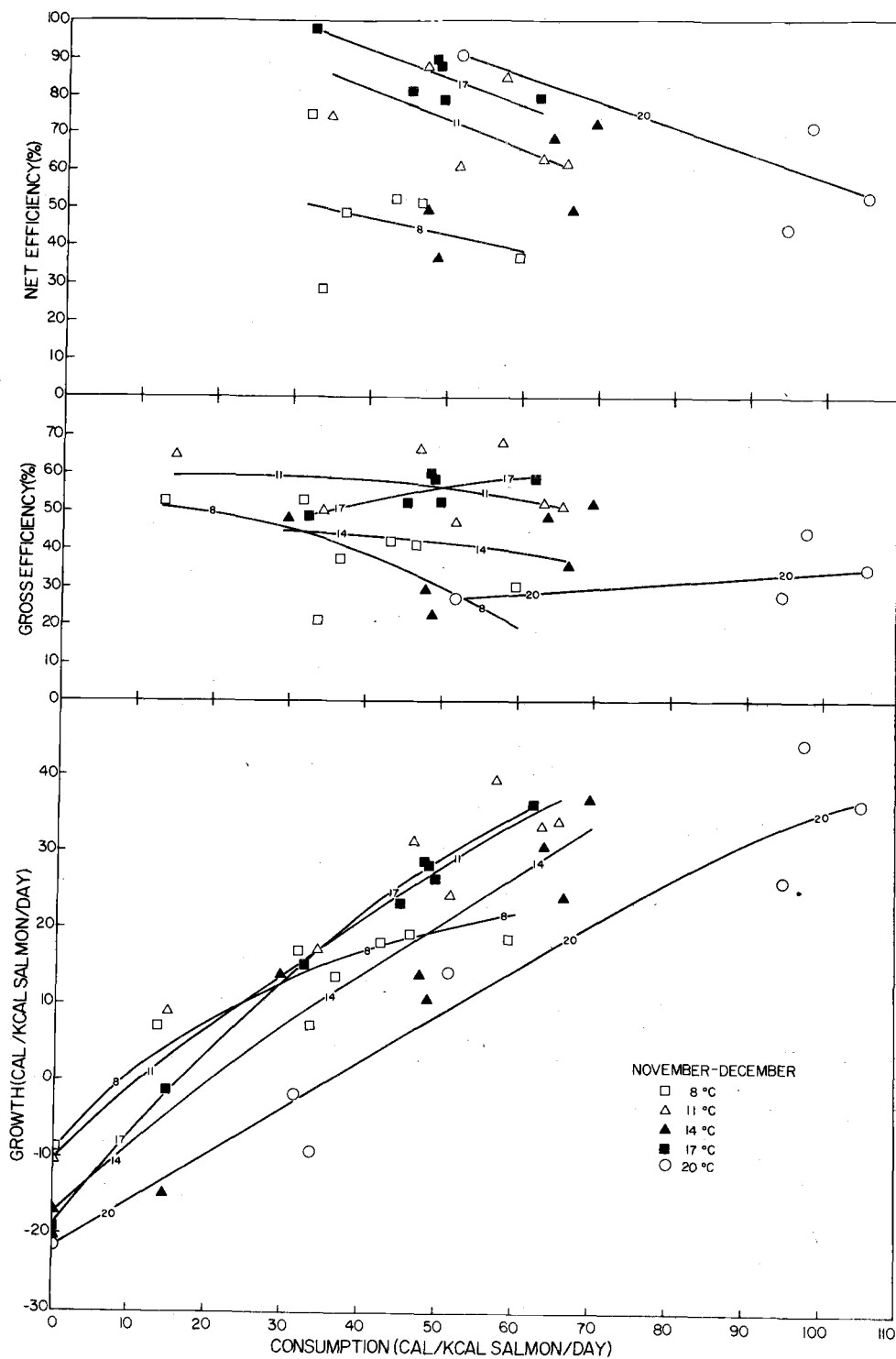


Figure 6. Relationships between consumption rate, growth rate, growth efficiencies and temperature for coho salmon in the November-December experiment.

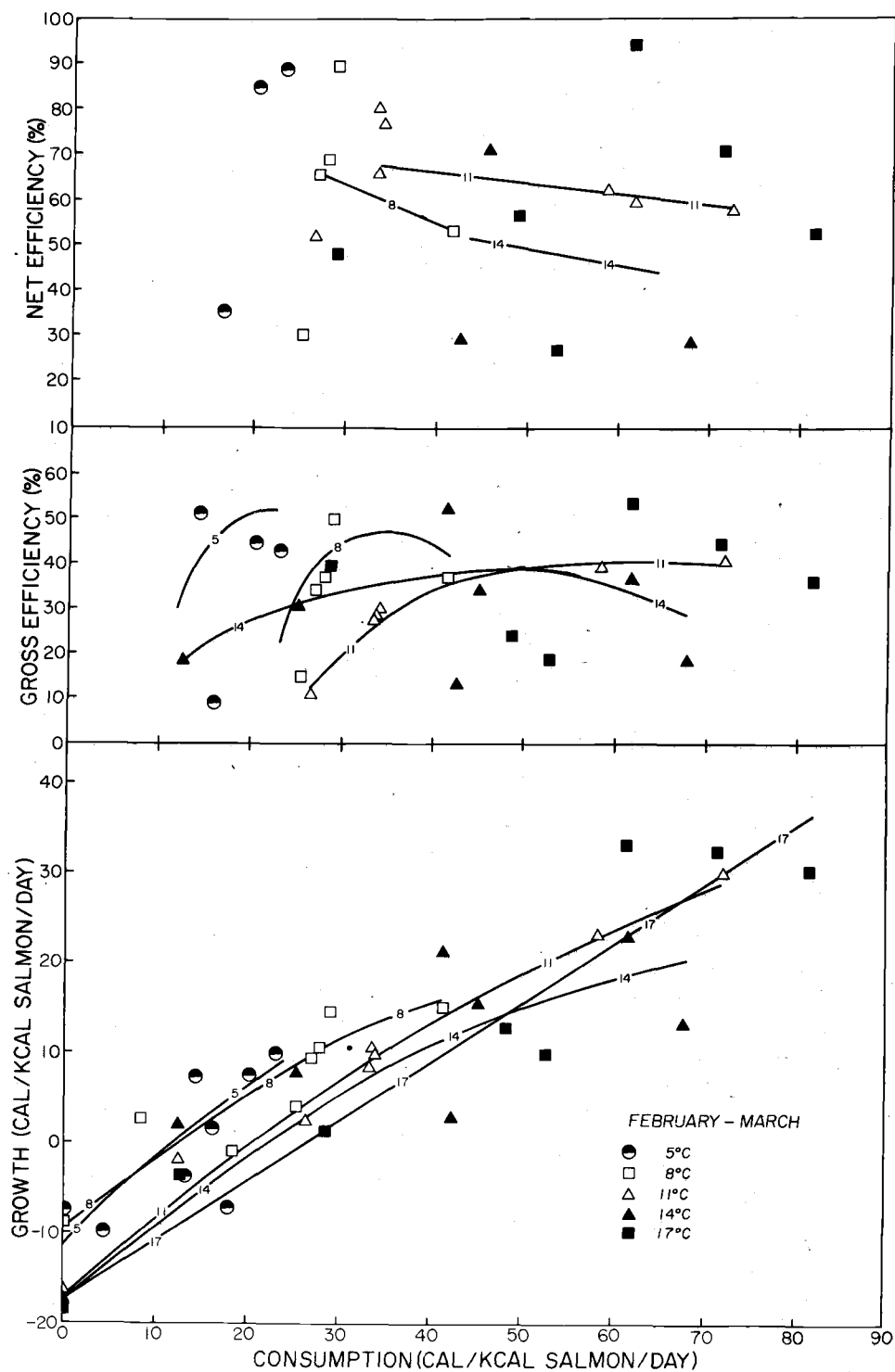


Figure 7. Relationships between consumption rate, growth rate, growth efficiencies and temperature for coho salmon in the February-March experiment.

would not be fruitful. As would be expected with increasing temperature, the consumption rate-growth rate curves tend to be displaced toward the right; and the higher consumption rates at higher temperatures permitted greater growth.

Generally, then, it is apparent from the results that at each season there were temperatures where growth was efficient, as well as temperatures where it was not. Efficient growth is associated with lower metabolic costs resulting from either lower consumption or temperature. The effect of elevated temperature is generally to increase the rate of food consumption, and increase the energy cost of standard metabolism and SDA. But, when the consumption rate is increased beyond a certain level, there is a corresponding increase in the energy loss due to nonassimilation. These metabolic costs and activity all tend to depress the growth rate and the efficiency of growth with increasing temperature. In spite of these negative effects, higher consumption rates at intermediate to high temperatures permit some of the highest growth rates when food is relatively unlimited. It remains now to consider the metabolic costs separately, and to assess their relationships to temperature, food consumption rate, and season.

#### Nonassimilation of Food

The percentage of food materials not assimilated showed no clear trend with season or temperature. Consequently, the results

for all experiments were combined to obtain a curve relating consumption rate to nonassimilation (Figure 8). Between the consumption rates of 10 and 110 cal/kcal salmon/day, nonassimilation is close to 15 percent, this indicating that within this consumption range the fish assimilated their food with efficiencies of about 85 percent.

Winberg (1956) assumed that the digestibility of natural foods would average about 85 percent with consumption rates occurring in nature. Brocksen, Davis and Warren (1968), using a wet combustion method which employed potassium iodate and the oxidizing agent, found that young cutthroat trout (Salmo clarki) had a mean food assimilation efficiency of about 85 percent. With young sculpins (Cottus perplexus) it averaged 82 percent (Davis and Warren, 1965).

The percentages of nonassimilation rose sharply with consumption rates beyond 110 cal/kcal salmon/day, the efficiency of food assimilation at high consumption rates dropping rapidly. Though in agreement with the findings of Brown (1946) and Kinne (1960), my findings contrast with those of Davies (1964), who found that food assimilation efficiency in the goldfish (Carassius auratus) increased with increasing consumption. Davies fed his fish whiteworms (Enchytraeus albidus), but he did not remove the fecal matter from the test chamber until 7 to 23 days had passed. He held his fish at 12 and 21.5 C, and it is probable that bacteria oxidized much of the fecal material before he collected it for analysis.

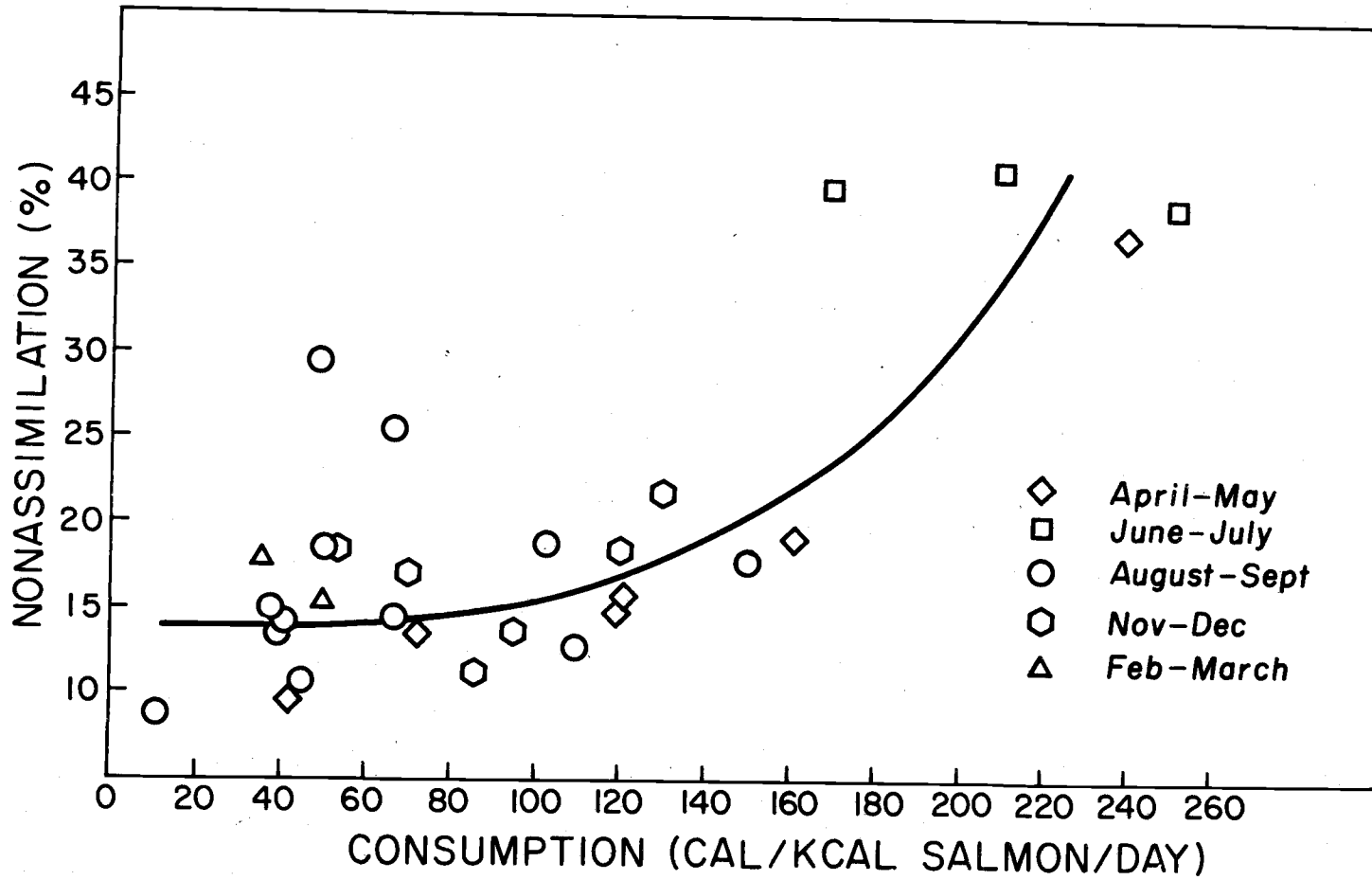


Figure 8. Relationship between consumption rate and percentage of nonassimilation of food for coho salmon.

### Specific Dynamic Action

It has long been known that there is an increase in oxygen uptake by animals following food consumption. This effect is commonly referred to as specific dynamic action or SDA (Brody, 1945). I am aware of no recent literature on SDA although Cohn (1963) touched upon it in relation to feeding frequency studies with rats, and Warren and Davis (1967) discussed it in relation to energy utilization of fish. The most comprehensive experimentation concerning SDA appears to have been done with mammals (Brody, 1934, 1945, Borsook, 1936, and Sadhu, 1947).

An indication of the level of metabolic expenditure required by fish during the digestion of a meal is revealed in a reference by Fry (1957) to a single experiment conducted by Job (1954). Job fed two yearling speckled trout (Salvelinus fontinalis) to repletion with minnows and found that they required a rate of oxygen consumption equivalent to their active oxygen consumption as determined in a laboratory swimming apparatus.

I conducted over 75 individual experiments in an effort to quantify the energy expenditure of SDA. Its effects, regardless of the amount of food consumed, were generally complete within 24 hours after feeding. The amount of oxygen consumed as a result of feeding varied with temperature, ration size, and season, as shown in the examples given in Figure 9. In general, the baseline did not



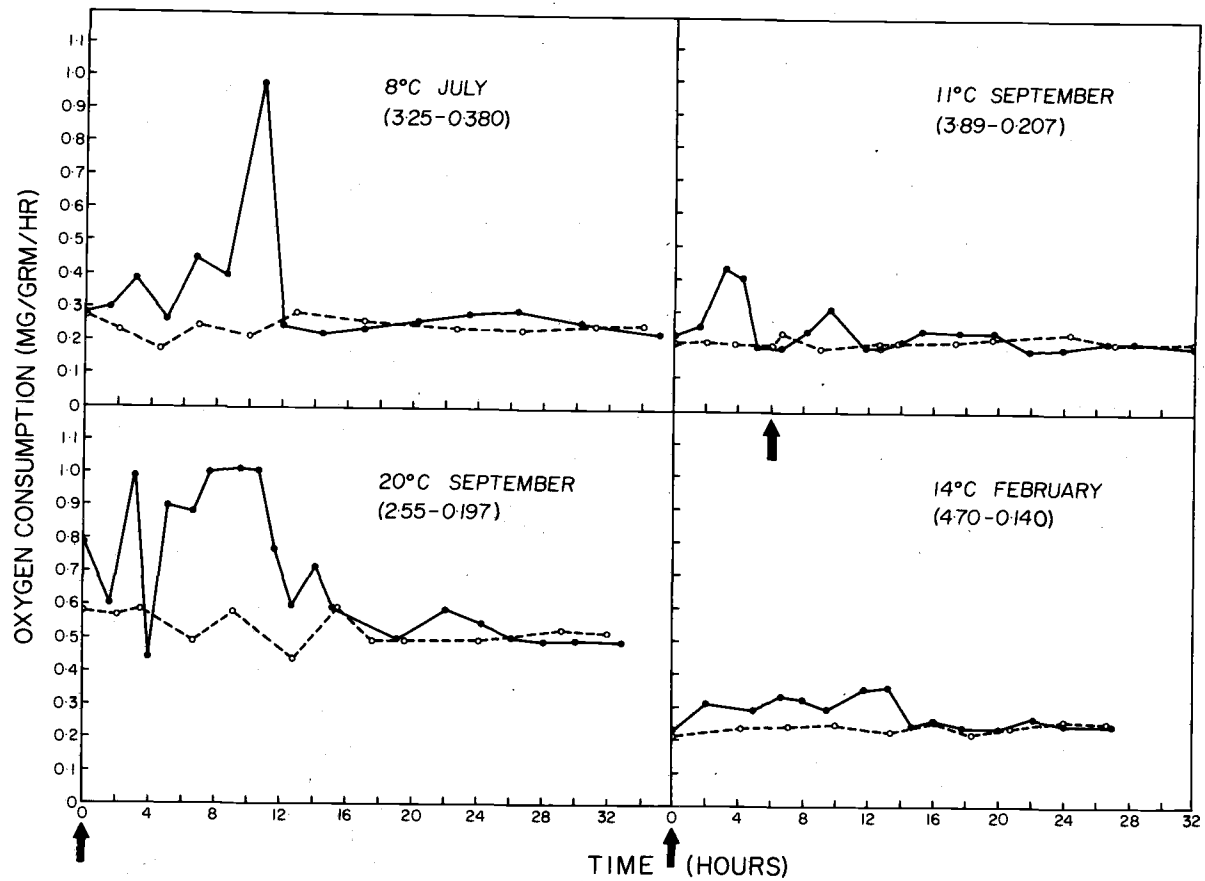


Figure 9. Examples of oxygen consumption of coho salmon as a result of specific dynamic action. Solid lines are oxygen consumption of fed fish, broken lines are oxygen consumption of same fish in post-absorptive condition. First number in parentheses is wet weight of fish; second number is wet weight of food fed. Arrows denote hour of feeding.

fluctuate greatly, and in many cases remained flat over relatively long periods of time. The greatest fluctuations in oxygen consumption in both the baseline and the SDA curves occurred at higher temperatures.

The highest SDA peak was recorded during the July experiment at 8 C (Figure 9). The ratio between oxygen consumption at the peak and that at the baseline is 4.1, which corresponds to many of the active-standard metabolic rate ratios to be discussed later. I attempted to determine if the energy cost of SDA was reduced when the fish were fed two equal rations separated by a time interval of six hours. The example at 11 C during September (Figure 9) illustrates one such effect of feeding two rations. In this example the peaks are clearly separated. However, in all other instances superimposition occurred and it was impossible to separate the SDA effect of one ration from another. Not enough data were obtained to determine whether or not SDA is reduced when the fish were fed the same total ration in two parts, separated by a time interval. However, even when two rations were fed at six hour intervals, the effects of SDA were always complete within 24 hours of the first feeding. I concluded from the SDA experiments that the shapes of the curves could not be predicted, but that the area under the curve, relating to the amount of oxygen consumed by the fish as a result of consuming a given quantity of food, could be determined with surprising precision.

Curves relating the energy cost of SDA to consumption rate at different temperatures and seasons are shown in Figure 10. SDA values were not obtained over a wide range of consumption rates in some cases, and it was necessary to extrapolate the curves to obtain SDA values for all consumption rates occurring in the growth experiments. The energy cost of SDA never reached zero even at consumption rates as low as 10 cal/kcal salmon/day, 1 percent of the body per day. It appears then that fish receiving even a sub-maintenance ration have a cost of food handling.

The energy cost of SDA increased with increasing ration and was generally greatest at the highest temperature tested. However, it was sometimes highest at the next lower temperature. At high consumption rates and at high temperatures, SDA ranged from 10.7 to 17.3 percent of the energy value of the food assimilated. At low rations it was usually less. A notable exception occurred at the 10 calorie consumption rate at 17 C during the February-March experiment. The curve relating SDA to consumption rate at 17 C is higher than those for the other temperatures, and SDA accounted for 40.7 percent of the energy value of the food consumed at the lowest ration. This is an exceptionally high SDA cost, but there is no indication that the result is an error in measurement.

The SDA values were surprisingly similar for fish held at the same temperature and fed the same amount of food. In the April-May

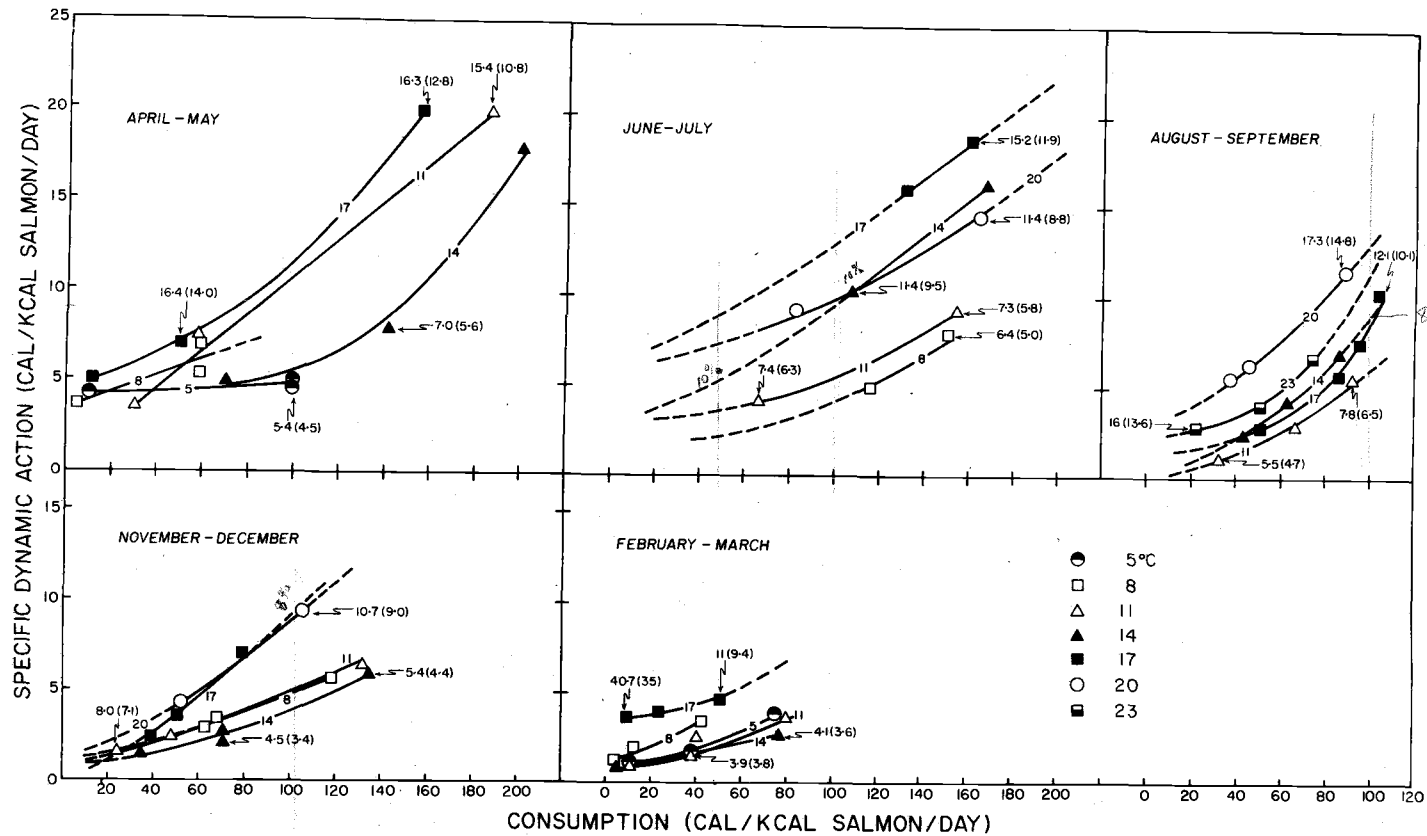


Figure 10. Relationships between consumption rate, specific dynamic action and temperature for coho salmon for the five experiments. Numbers with arrows refer to percent specific dynamic action of assimilated ration (outside parentheses) and percent of total ration (inside parentheses). Broken lines refer to extrapolated values.

experiment, for example, at 8 C and a consumption rate of 58 cal/kcal salmon/day, the difference in SDA values in replicate tests was only 1.5 cal/kcal salmon/day. In the November-December experiment at 14 C and a consumption rate of 70 cal/kcal salmon/day, the difference between replicates was only 1 cal/kcal salmon/day.

It is clearly evident from Figure 10 that at some temperatures during each season the increase in SDA with increasing ration is abrupt. It is at these temperatures that the decline in net growth efficiency, due to increasing SDA with increasing ration, is most apparent.

The primary energy cost of SDA is generally attributed to the oxidative deamination of proteins and to a lesser extent to comparable changes in carbohydrates and fats (Brody, 1945). However, Warren and Davis (1967) noted that a part of the energy cost of SDA is due to the transport and deposition of food materials throughout the body. Energy is required for these processes, and one cannot separate them from energy losses due to deamination of proteins by measuring oxygen consumption of the whole animal.

#### Standard Metabolism

Standard metabolism is independent of consumption rate because it is an estimate of the metabolic rate of a quiescent fish in the post-absorptive condition. It is clearly a function of temperature and of

body size (Fry, 1957; Brett, 1964). However, other factors which my experiments were not designed to distinguish may be involved.

Roberts (1961) found that the metabolic rate of carp (Carassius carassius) increased with increasing photoperiod. Recently, Beamish (1964) has shown that in mature trout the standard metabolic rate increased as the fish approached the spawning period.

Total metabolic rates at different temperatures and seasons as a function of swimming speed are shown in Figure 11. Extrapolation of these curves to zero activity was done to obtain estimates of the standard metabolic rates. The determination of active metabolic rates was not a primary objective of this study but was necessary to determine standard metabolic rates. As noted in the materials and methods section, the extrapolated lines are drawn according to the method of Brett (1964) through the lower points at low swimming velocities. Random activity by the fish causes oxygen consumption rates at the lower velocities to be above those required for the measured swimming performance.

The small fish used in the April-May experiment could not swim against a water velocity in excess of 22.5 cm per second. The slightly larger fish used in the June-July experiment all swam against velocities of 32.5 cm per second, and the fish at 14 C swam against a water velocity of 40 cm per second. With the coho used in the August-September experiment, only the fish held at 17 C attained a

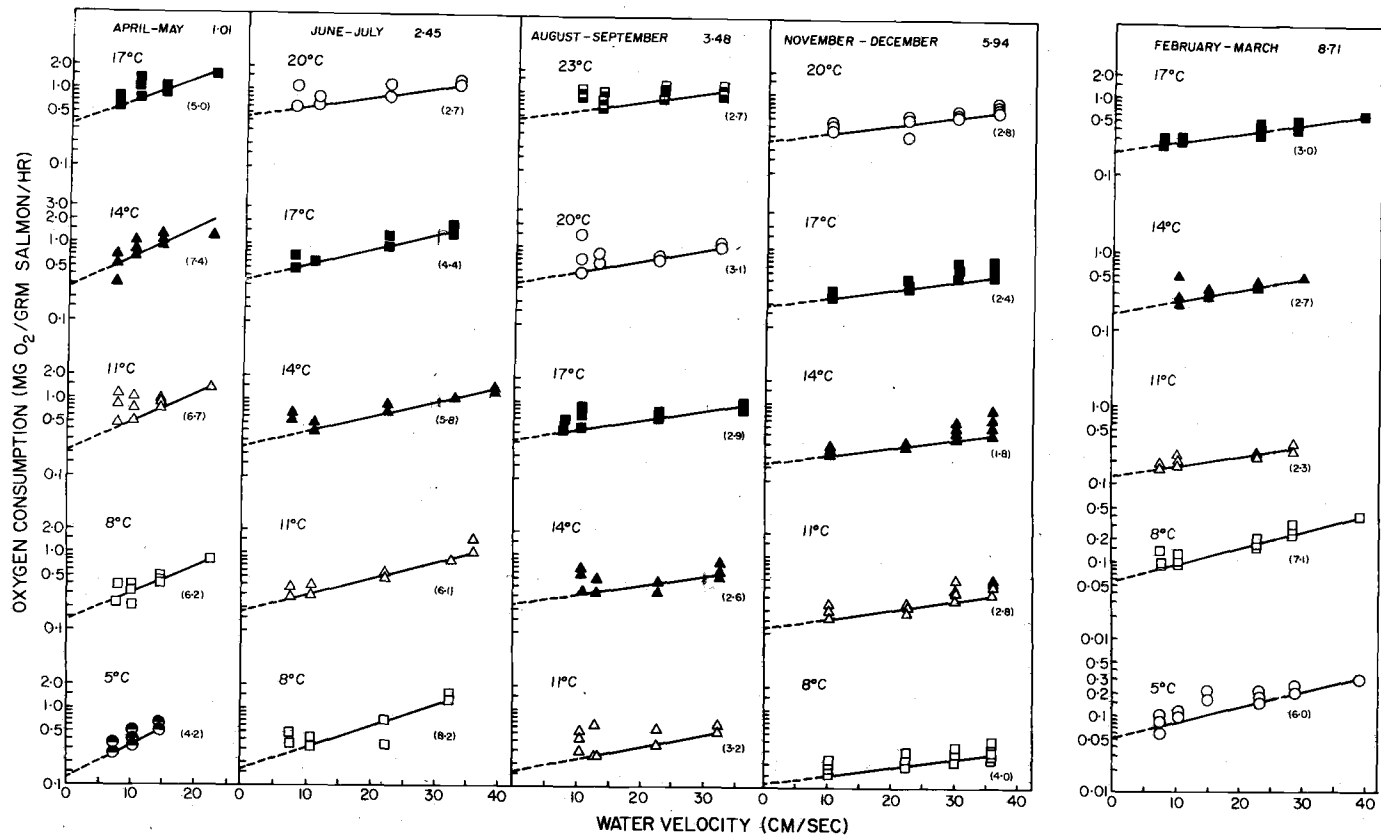


Figure 11. Relationships between swimming speed (water velocity) and oxygen consumption by coho salmon at different temperatures during the five experiments. Broken lines extrapolated to zero water velocity denote standard metabolism. Numbers in parentheses denote ratio of active to standard metabolism. Numbers by date are mean wet weights of fish.

swimming speed of 35 cm per second, but none was able to exceed this velocity. The results of the February-March experiment were variable. At the temperatures of 5, 8, and 17 C, the coho were able to swim at velocities up to 40 cm per second. In contrast, those held at 11 and 14 C could not exceed 30 cm per second.

Brett, Hollands and Alderdice (1958) appear to be the only other workers to have measured the swimming performance and active metabolic rates of juvenile coho salmon. At a temperature of 15 C, they found fish having a mean weight of 1.72 grams were able to attain maximum swimming speeds up to 24.4 cm per second, whereas at the same temperature the maximum swimming speed of coho weighing 8.06 grams was 37.5 cm per second. These findings are in close agreement with mine. Young sockeye salmon (Oncorhynchus nerka) apparently can swim against greater water velocities than can coho salmon. Brett (1965) reports that a 3.38 gram sockeye can swim against a water velocity of 51.5 cm per second at 15 C.

The ratios of the active to standard metabolic rates ranged from a low of 1.8 to a high of 8.2 (Figure 11). Fry (1957) found that the active metabolic rate of fish is restricted to a few multiples of the standard, usually about 4. His information is for the lake trout (Salvelinus namaycush), brown trout (Salmo fario), bullheads (Ameiurus nebulosus), and goldfish. The experiments discussed by Fry were conducted in a rotating chamber respirometer and it is



possible that the fish did not attain their maximum swimming speed. Brett (1964), using a tunnel respirometer, has obtained ratios up to 10 with yearling sockeye salmon, but with the smaller sockeye discussed earlier, the ratio was 4.

The standard metabolic rates of the juvenile coho salmon tested during the different seasonal experiments are shown as functions of temperature in Figure 12. Standard metabolic rate clearly increases with increasing temperature during all seasons of the year. With successive experiments beginning in April and ending in March, the standard metabolic rates at any one temperature decrease. The size of the fish tested increased through the successive experiments and it is generally accepted that the metabolic rates of animals decrease with increasing body size. That other factors associated with the age of the fish or the season of year may have been involved cannot be discounted on the basis of my experiments.

### Activity

In the growth experiments, energy utilization for activity appears generally to have been low when food consumption rates were below 40 cal/kcal salmon/day (Figure 13). Beyond this feeding level, energy utilization for activity appears to have increased rapidly. Only at low rations was it independent of consumption rate. The highest expenditure of energy for activity occurred during the June-July

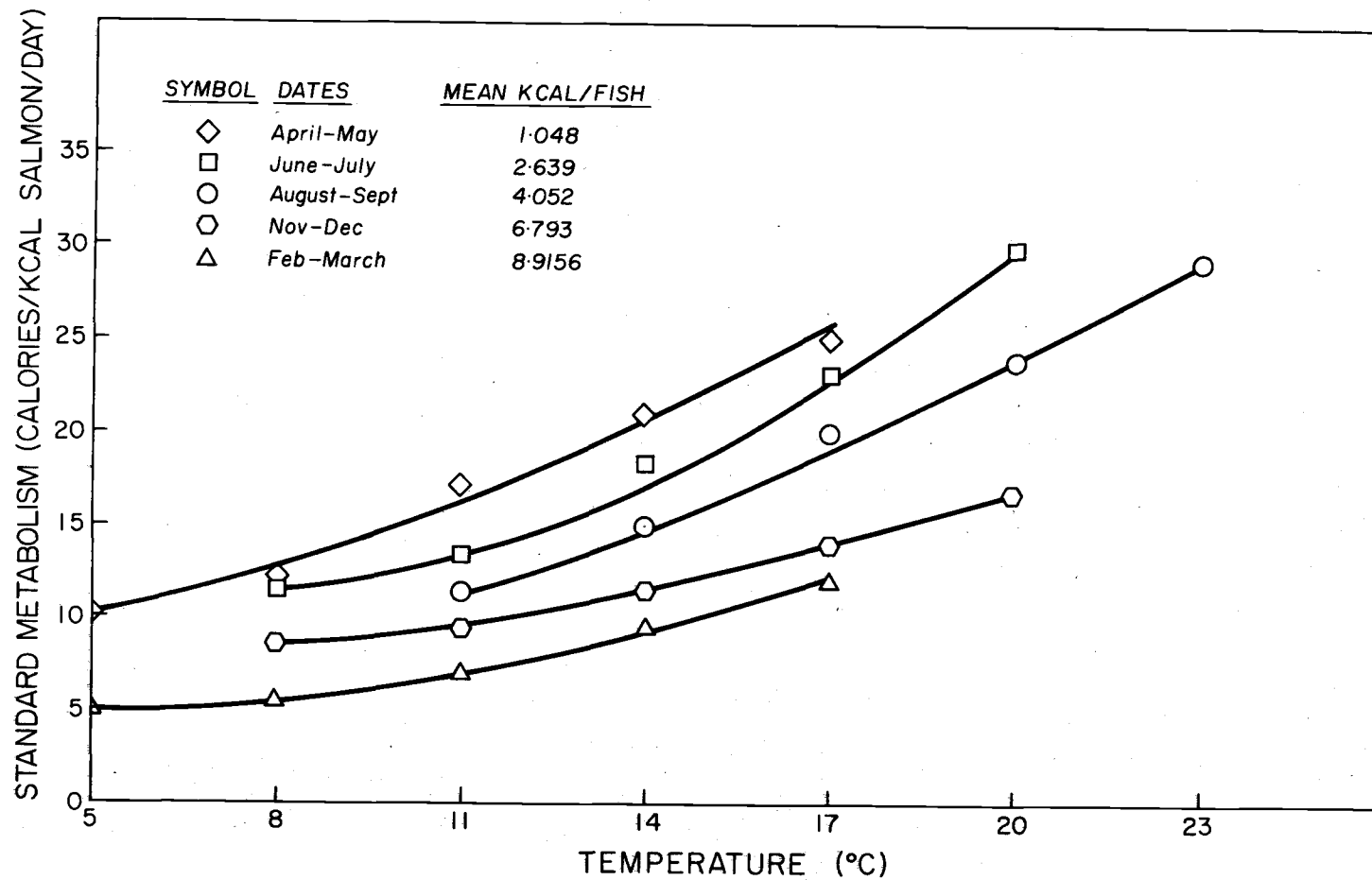


Figure 12. Relationship between temperature and standard metabolism of coho salmon during the five experiments.

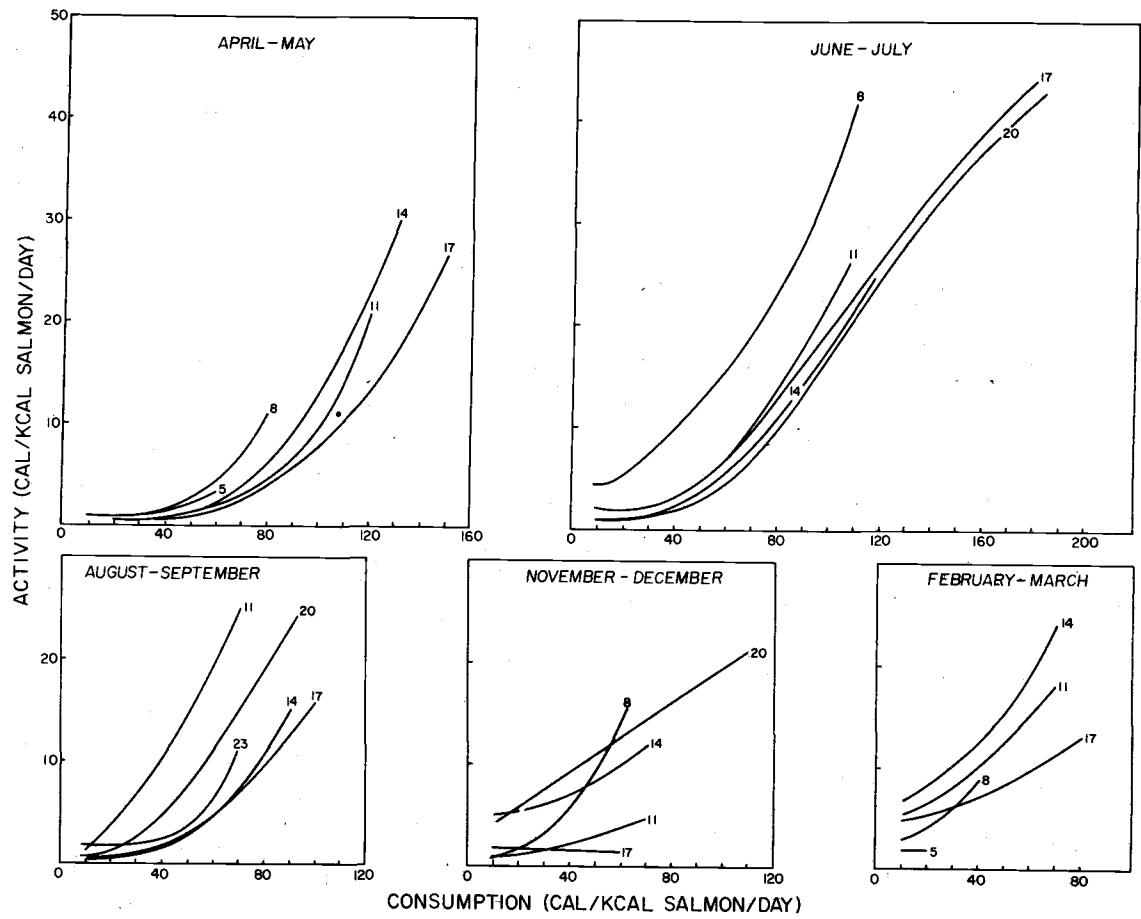


Figure 13. Relationships between consumption rate and activity at different temperatures for coho salmon during the five experiments.

growth experiment at the high consumption rates. These high values were approximately twice those for standard metabolism at the same temperatures.

The energy cost of activity was determined as a residual, and, as a consequence, includes errors made in measuring the other terms in the energy formula. One such possible error occurs in the waste product term ( $Q_w$ ). It is doubtful that much of the nitrogenous waste excreted through the gills and kidneys was oxidized by the method employed. Winberg (1956) states that in the case where 50 percent of the nitrogen excreted occurs in the form of ammonia, the energy loss would be about 3 percent of the energy value of the food consumed if 85 percent of the food were assimilated.

The high increase in energy utilized for activity with increasing food consumption appears to have resulted from the feeding behavior of the fish. It could present a serious problem of interpretation if fish in nature were to consume food at high rates, unless costs of activity were similarly related to consumption in nature. The five fish receiving sub-repletion rations at each temperature were fed only once each day, in the morning. Usually it took less than a minute for them to consume their allotted ration. In contrast, the three fish fed to repletion were fed twice each day, once in the morning and once in late afternoon. Usually it took in excess of one hour and sometimes up to two hours to insure each had consumed all the food it desired.

When a repletion fed fish was nearing satiation, it would hold the fly larvae in its mouth and exhibit vigorous swallowing movements. Often the larvae would be ejected from the fish's mouth, drift to the bottom of the aquaria, and be picked up again; the swallowing activity then being resumed. Fish were observed to repeat this procedure for periods up to 20 minutes. Because such activity took place twice each day it is probably a contributing factor in the relationship between consumption and activity. It is clearly not the only factor, however, for even at intermediate rations the cost of activity is relatively high at some temperatures, especially during the June-July experiment. During the November-December experiment, the activity curve for 17 C declines with increasing consumption. Some error in the measurement of the other metabolic costs may be involved here, but it is probably not too great, for at 17 C during this experiment, the fish displayed exceptionally high growth at a relatively low consumption rate (Figure 6).

In general, the cost of activity was usually greatest at intermediate temperatures. Fish exhibit preferences for different temperatures, and these preferences change with season. In this regard, they are often most active within their preferred temperature range (Sullivan and Fisher, 1953, Fry, 1957).

### Energy Budgets

We can now bring together in overall energy budgets, for each temperature and consumption rate, the various uses and losses of energy and materials contained in the food consumed (Figures 14-18). From a bioenergetic point of view, these budgets most usefully describe the changes occurring in the fish with changes in season as well as food consumption rate and temperature.

The energy budgets were developed by plotting individually the measured values of growth, standard metabolism, SDA, and non-assimilation as functions of food consumption rate. A smooth curve was then fitted to the measured values, and for each 10 cal/kcal salmon/day consumption interval the corresponding energy or material use or loss value was taken from the curve. The energy cost of activity was estimated as a residual by summing all other measured energy or material uses and losses and subtracting them from the consumption rate at the given 10 cal/kcal salmon/day interval. The budgets are shown as histogram bars. The top of each histogram bar refers to the total energy consumed by the fish. Lines connecting the centers of the tops of the histogram bars would have slopes of 1. It is helpful to visualize similar lines through the growth levels of the histogram bars at each temperature to see how food utilization for growth changes with increasing food consumption. Changes in metabolic costs and energy and material losses with changing food

consumption rates can be similarly evaluated. Only at maximum food consumption rates, where the fish were fed to repletion, did food not limit the possible growth. The effects of temperature on material and energy utilization depend greatly on the food consumption rate. Temperatures favoring growth at high consumption rates may be entirely unsatisfactory for growth at lower consumption rates, such as might occur in nature, where food may be severely limiting. Thus, proper interpretation of my findings depends upon a knowledge of food availability, a question I will return to in the Discussion.

The small coho used during the April-May experiment displayed efficient utilization of food for growth at 5 and 8 C up to the maximum amount they would consume (Figure 14). Though the fish at 11 and 14 C consumed much higher maximum rations, poorer assimilation and increased metabolic costs prevented much increase in growth with increasing rations. At the much higher consumption rates at 17 C, growth was no greater than at the lower maximum consumption rates at 11 and 14 C. At low consumption rates, growth was considerably less at 17 C than it was at 11 and 14 C. Nonassimilation, SDA, and activity at a consumption rate of 60 cal/kcal salmon/day (the maximum at 5 C) were not greatly different for the various temperatures. However, standard metabolism increased with temperature increases, and this decreased the proportion of food available for growth.

The June-July season can probably be considered the end of the

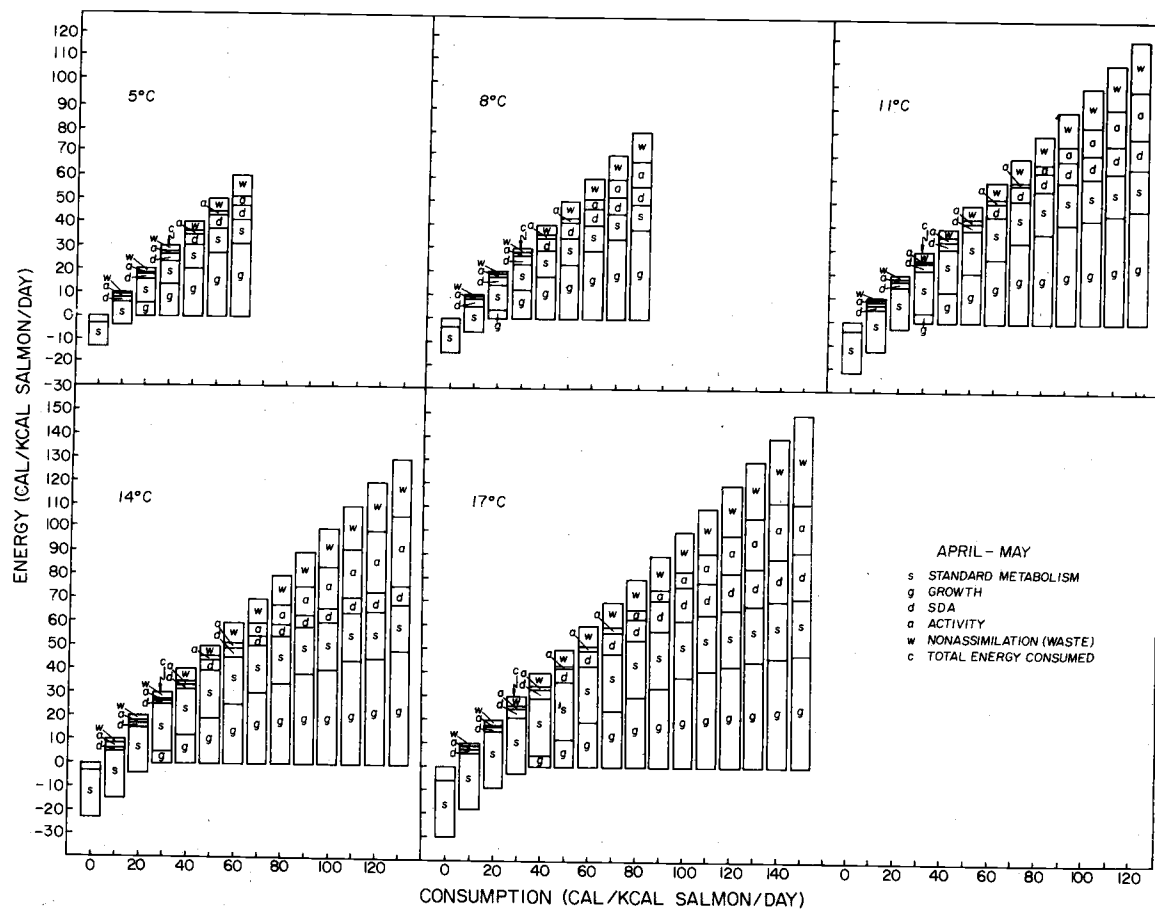


Figure 14. Relationships between consumption rate, energy and material uses and losses, and temperature for coho salmon during the April-May experiment.



good growth period for young coho in nature. At 11 and 14 C, the utilization of food for growth was good at all consumption rates (Figure 15). At 8 C, it was poor at the higher consumption rates. Food utilization for growth was poor at all consumption rates at 17 and 20 C. Between 11 and 14 C, there was little difference in growth, or in the energy values for standard metabolism, SDA, activity and nonassimilation. However, when a comparison is made between energy and material utilization between these two temperatures and those at 8, 17, and 20 C at comparable consumption rates, the reasons for the poorer growth at the lower and higher temperatures are apparent. At 8 C, poor food utilization for growth was mainly because of increased activity; whereas at 17 and 20 C it was because of increases in all other fates of the food consumed.

During August and September, the maximum rations the coho would consume at 11, 14, 17, and 20 C were considerably less than they consumed at the same temperatures during the June-July experiment (Figure 16). Over the range of rations the fish did consume during the August-September experiment, food utilization for growth was quite good at 11, 14, and 17 C. Low consumption rates and energy utilization and losses for activity, standard metabolism, and SDA permitted little growth at 20 and 23 during the August-September experiment.

Maximum food consumption rates were low at 8, 11, 14, and 17

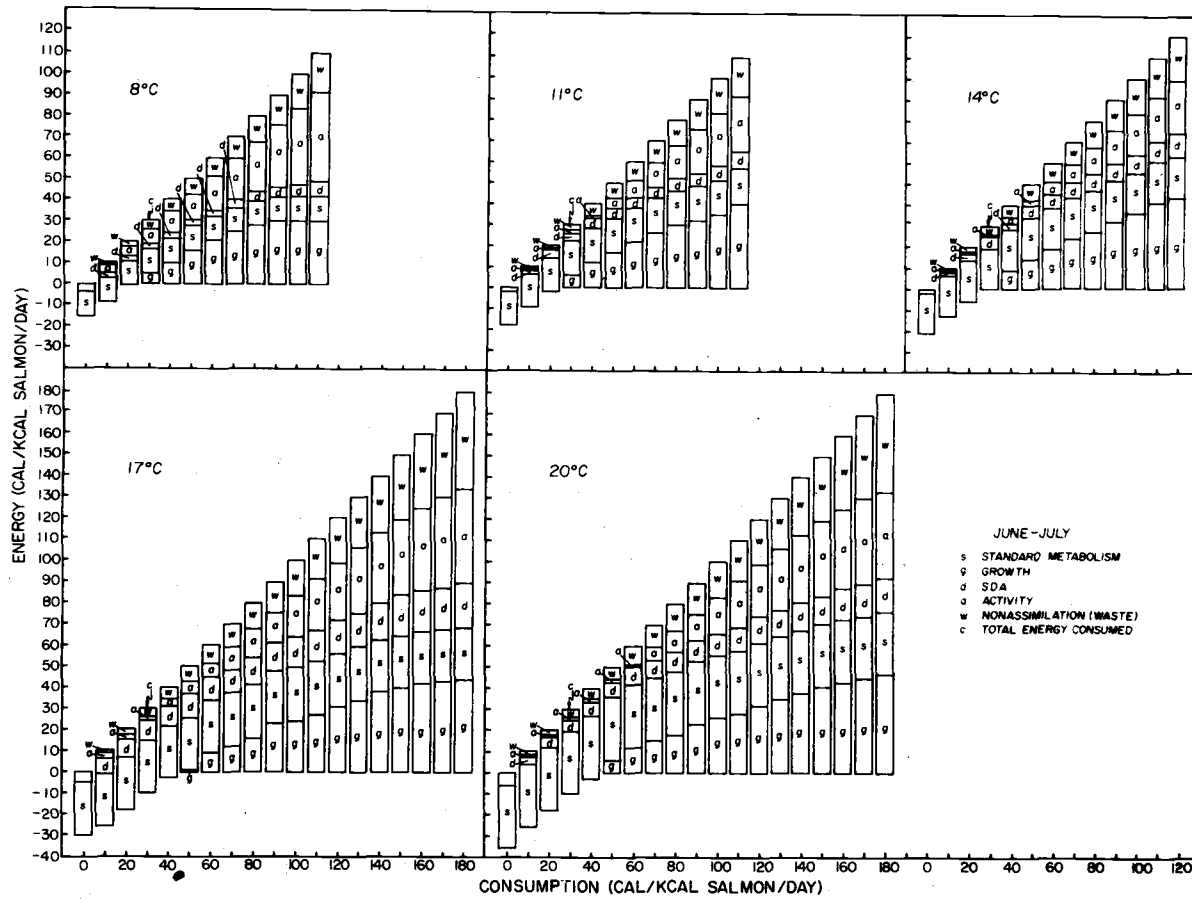


Figure 15. Relationships between consumption rate, energy and material uses and losses and temperature for coho salmon during the June-July experiment.

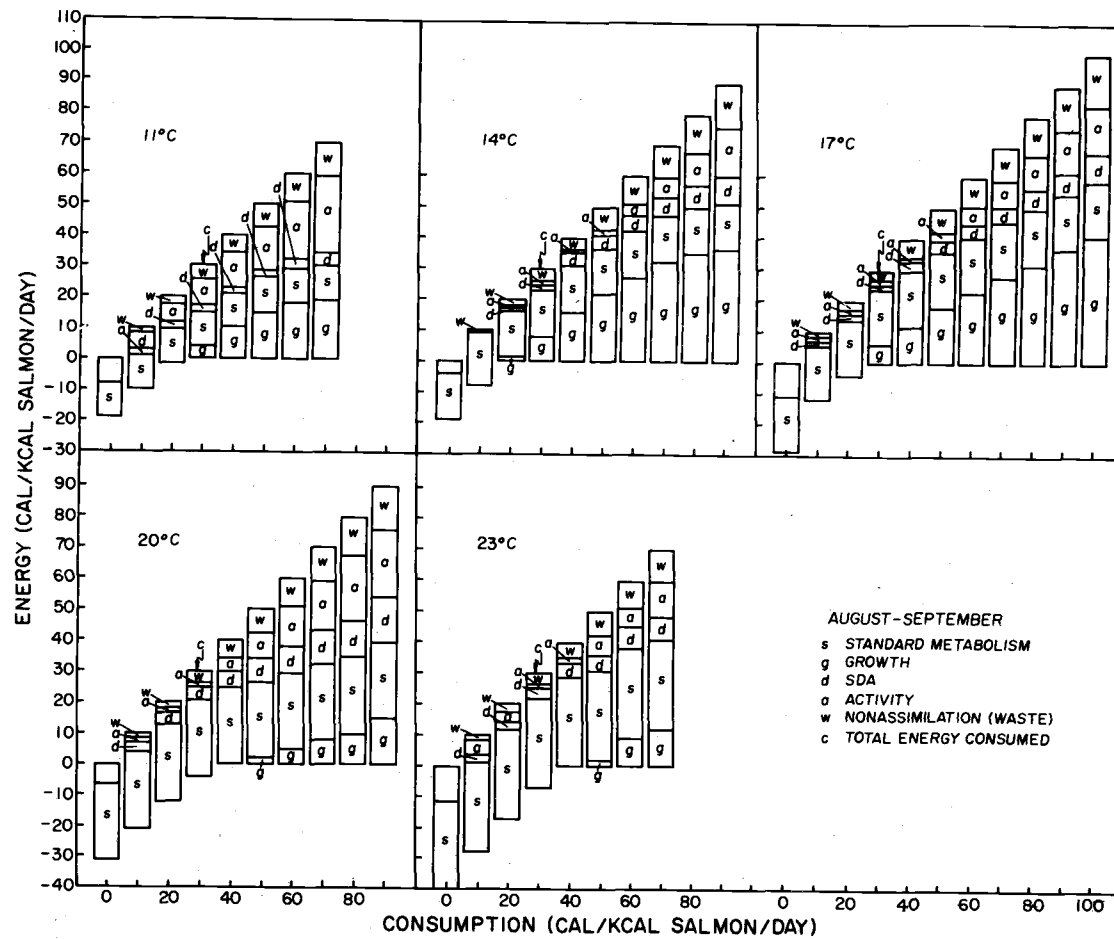


Figure 16. Relationships between consumption rate, energy and material uses and losses and temperature for coho salmon during the August-September experiment.

C during the November-December experiment, but growth was quite efficient at all temperatures because other uses and losses of energy and materials were relatively low (Figure 17). Food utilization for growth was somewhat less efficient at 8 and 14 C than at 11 and 17 C, primarily because energy utilization for activity was greatest at 8 and 14 C. Maximum consumption rates were much higher at 20 C than at other temperatures, but food utilization for growth was poor. The energy uses and losses for standard metabolism, activity, and SDA were great at 20 C, and permitted little growth at low consumption rates.

Maximum food consumption rates were extremely low at 5 C, and quite low at 8 C during the February-March experiment (Figure 18). However, food utilization for growth was quite good at both temperatures. Maximum food consumption rates were much higher at 11, 14, and 17 C, but food utilization for growth was less efficient primarily because of greater energy utilization for standard metabolism and activity. At higher consumption rates, growth was less efficient at 14 C than at 11 and 17 C, apparently because of greater energy utilization for activity.

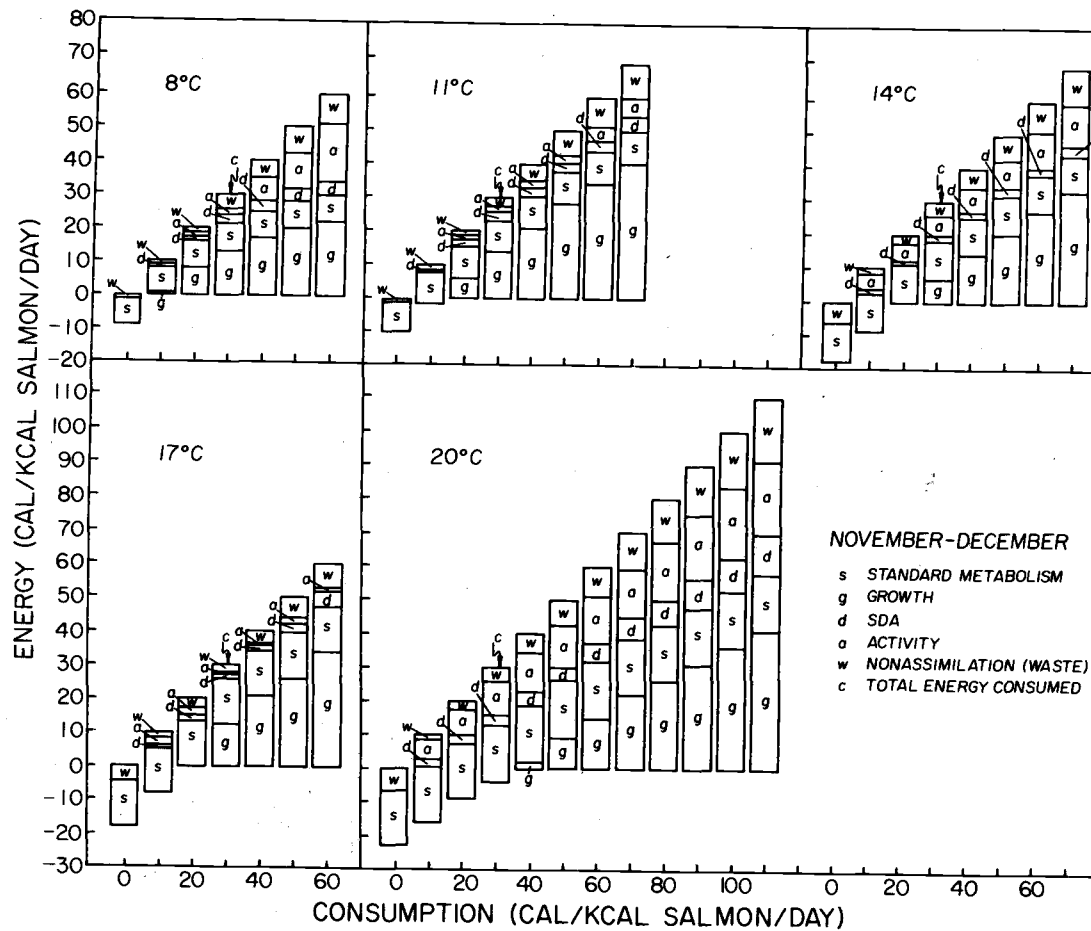


Figure 17. Relationships between consumption rate, energy and material uses and losses and temperature for coho salmon during the November-December experiment.

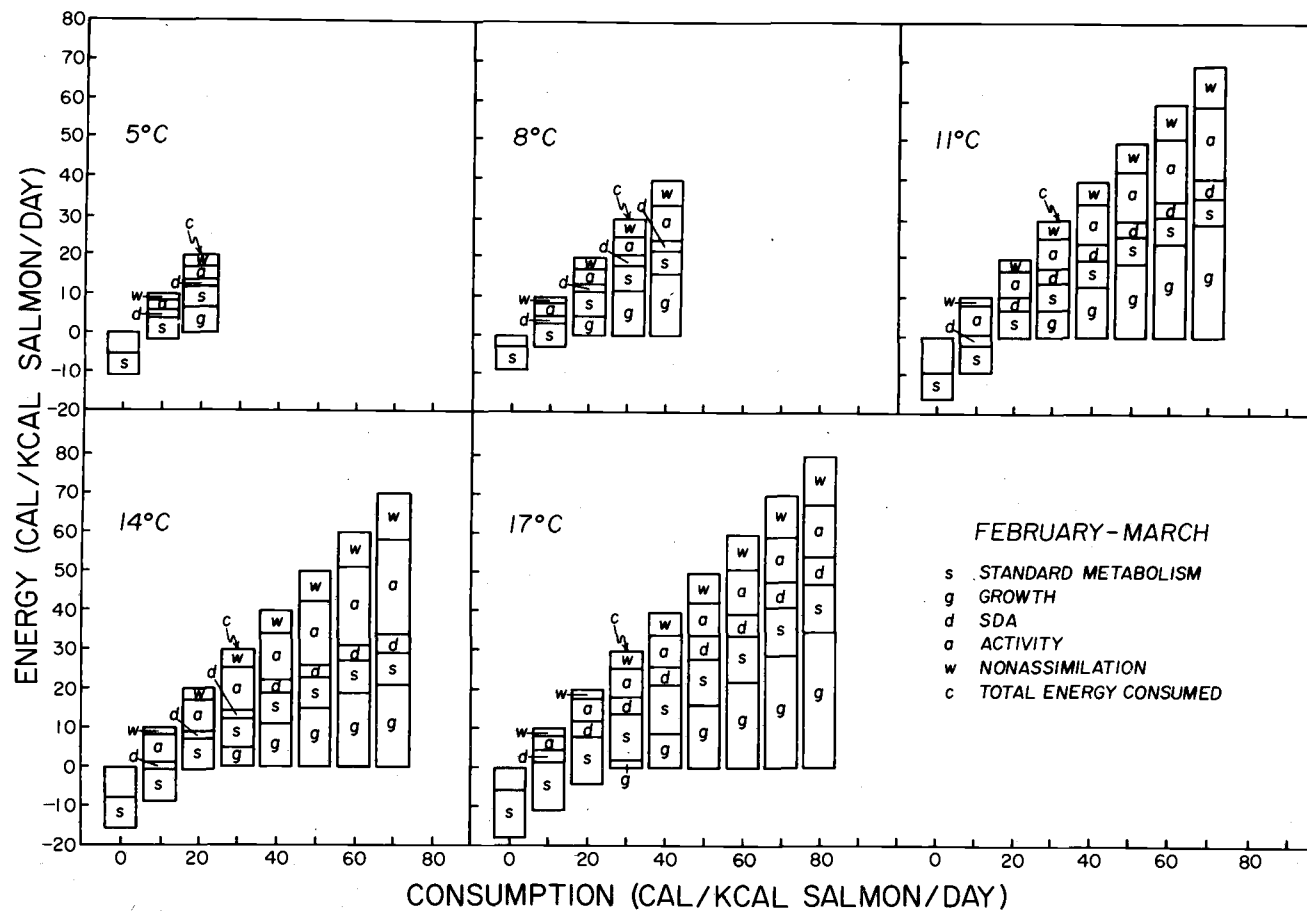


Figure 18. Relationships between consumption rate, energy and material uses and losses and temperature for coho salmon during the February-March experiment.

## DISCUSSION

The growth of an animal depends upon the energy and materials which it obtains in its food and their apportionment between growth and non-growth uses and losses. Temperature influences not only the amount of food a fish will consume, but also the non-growth uses and losses, and in these ways determines growth. In my laboratory studies, growth at rations from below maintenance levels to all the fish would consume was measured. In nature, food usually appears to be limiting (Brocksen, Davis, and Warren, 1968). It becomes, then, very important to know something about how much food fish are able to obtain in nature, if we are to draw any conclusions from our laboratory studies as to the temperature ranges in nature which are suitable for growth during different seasons. It also becomes important to know whether the growth of coho salmon at particular rations in the laboratory approximates that of those consuming nearly the same ration in nature.

Carline (1968) studied the bioenergetics and growth of juvenile coho salmon under rather natural conditions in laboratory streams as well as in aquaria. His findings suggest that food utilization for growth in nature is not very different from that which might be obtained under aquarium conditions similar to those I employed. Carline's experiments were conducted in an artificial stream equipped with glass sides for observation and having pools and riffles

formed by the arrangement of gravel and rubble on the bottom. The fish were fed with fly larvae introduced to the surface of the stream through glass tubes. As the fish were individually marked, Carline was able to observe and record the number of larvae captured by each fish, and convert the data to weight of food consumed. He was also able to identify the dominant fish from those that were sub-dominant in the hierarchal social structure that developed.

The fish used by Carline were similar in weight, at all seasons, to those that I used. His mean water temperatures were 12.3 C in the spring, and 9.6 C in the fall. From information obtained in his November-December experiment, he developed energy budgets for the groups of fish having different social status. Carline found that the relationship between aggression per unit time, and energy expenditure for activity was positive and linear. The energy of activity was expended in both the capturing of food and the defense of territory. The energy expended for activity by the fish ranged from 26 percent of the energy value of the food consumed by his Group IV sub-dominant fish, down to 17 percent for his Group II sub-dominant fish. His dominant fish, Group I, expended 23 percent of their energy for activity. I have divided the energy expended as activity by consumption rate from my findings in the laboratory (Figure 13), and found that all but a few of the activity values were within the 17 to 26 percent range reported by Carline. In addition, Carline found that his consumption rate-



growth rate data from both laboratory stream and aquarium experiments could be well defined by the same curve. It would appear, then, that there may be little difference between the efficiency of food utilization for growth in nature and under aquarium conditions similar to the ones which Carline and I employed.

Now, we can consider the growth rates and the probable ranges of food consumption of juvenile coho salmon in at least one natural stream. Mr. Ronald Iverson has kindly permitted me to use some unpublished growth rates obtained from coho salmon in Tobe Creek, Oregon, a small coastal stream with a minimum flow near 0.3 cfs. He studied the growth of juvenile coho at 4 collection sites. Sites I and II were in a virgin coniferous forest and were heavily shaded. Afternoon water temperatures at these sites ranged from 12 to 17 C from May to October. Sites III and IV were in an open area where the forest had been removed by logging. Here, the afternoon water temperatures ranged from 12 to 24 C, and thus these fish were subjected to warmer water than were those at Sites I and II.

Iverson found two distinct size groups of coho fry in Tobe Creek, and he designated them as small fry and large fry. His weight information shows that the large fry were very similar in size, at any given season, to those that I used. I have plotted the growth rates for both sizes of fry (Figure 19); but, in the analysis to follow, only the growth rates for the large fry will be used. The growth rates for

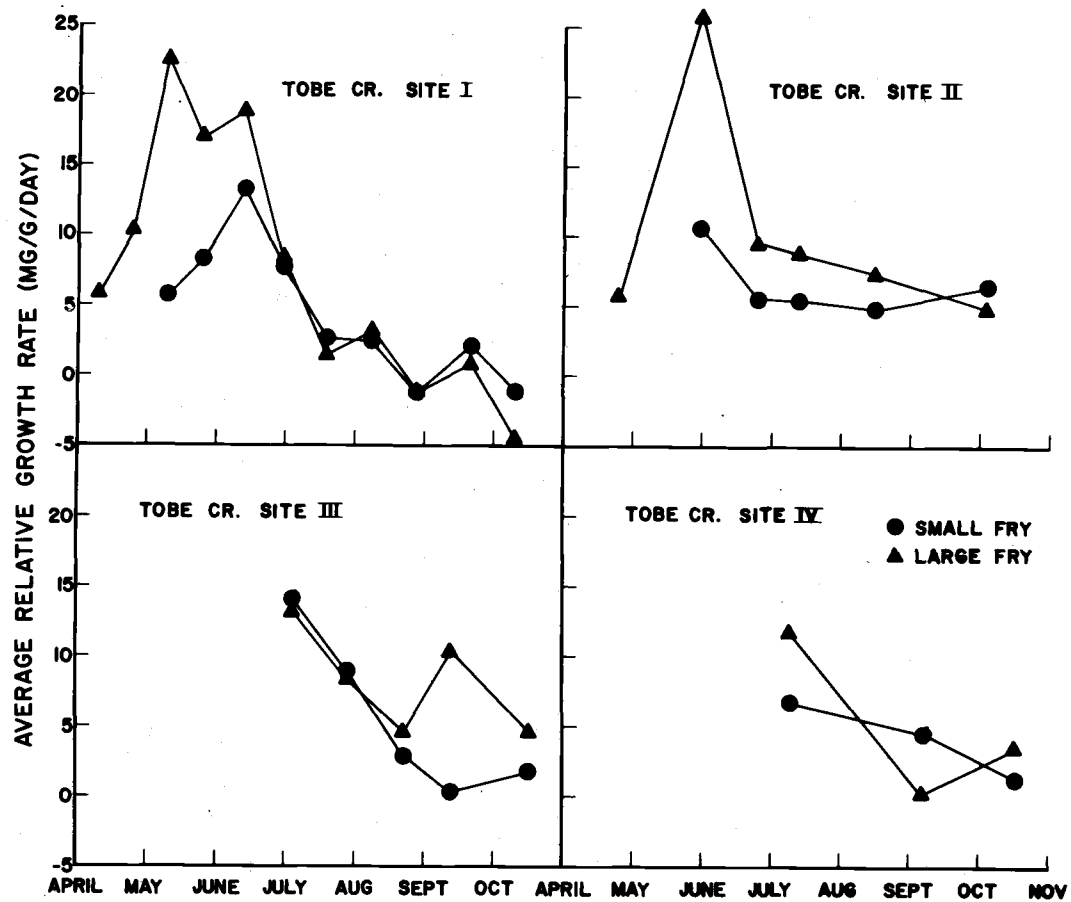


Figure 19. Relationship between month of year and growth rates of coho salmon in Tobe Creek, Oregon. See text for explanation of site locations (data of Iverson).

Tobe Creek salmon are in mg/gram/day. One milligram of wet fish weight is approximately equivalent to one calorie, and the Tobe Creek growth rates in milligrams can be considered as growth rates in calories without significant error.

In using the growth rates from Tobe Creek, I must make an arbitrary distinction to compare stream and laboratory temperatures. I have considered temperatures up to and including 14 C in my study to be comparable to those in Tobe Creek at Sites I and II, and temperatures above 14 C to be comparable to those at Sites III and IV. Growth rates of coho salmon in Tobe Creek were not determined over the entire year, and thus no direct comparisons can be made with the experiments I conducted during November-December or February-March.

I have taken the mean growth rate of the large fry in Tobe Creek for a particular season and the maximum growth rate attained by the fish in the same season and located these growth rates on my curves relating growth rates to food consumption rates (Figures 3-7). The consumption rates corresponding to those growth rates were then graphically determined (Table 3). This was done for each of the temperatures tested during the April-May, June-July, and August-September experiments. The findings clearly suggest that consumption rates in nature are little above the maintenance rations determined in the laboratory experiments, and are not near the maximum

Table 3. Growth rates of Tobe Creek coho and corresponding ranges of consumption rates in aquaria experiments.

Season	Mean and maximum growth rates in cal/kcal salmon/day from Tobe Creek. <u>1/</u>		Mean and maximum consumption rates in cal/kcal/salmon/day from aquaria studies (Figures 3-7) obtained from Tobe Creek growth data. <u>2/</u>							
	<u>Sites</u>		<u>Temperature (C)</u>							
	I and II	III and IV	5	8	11	14	17	20	23	
April-May	11-23	<u>3/</u>	30-40 (60)	30-50 (80)	30-50 (120)	40-50 (130)	<u>3/</u>			
June-July	12-26	11-13		40-70 (110)	40-70 (110)	40-80 (120)	70-80 (180)	60-80 (180)		
August-September	4-7	5-10			30-30 (70)	20-30 (90)	30-30 (100)	60-80 (90)	50-60 (70)	

1/ First number refers to mean growth rate in Tobe Creek during the two month period. Second number is maximum growth rate in Tobe Creek during the same period.

2/ The food consumption rates were obtained by matching Tobe Creek growth rates to the same growth rates obtained in the aquaria studies. The first number refers to the consumption rate at the mean Tobe Creek growth rate. The second number refers to the consumption rate at the maximum Tobe Creek growth rate. Number in parentheses refers to maximum consumption rates obtained in laboratory studies.

3/ No growth rates were obtained from Tobe Creek coho at these two sites for this season.

rations consumed by the fish in the laboratory.

All the growth rates (mean and maximum) attained by the coho in Tobe Creek appear to be within the consumption range where net growth efficiency was relatively high. This is because at low consumption rates assimilation is high and the energy cost of SDA is low. This does not mean that gross efficiencies of growth in nature are high or similar at all temperatures, for it has been shown in this research that metabolic energy costs vary with temperature and season. Thus, it is apparent that in attempting to determine the effects of temperature on the growth of young salmon in nature, on the basis of laboratory experiments, it is growth at the lower part of the range of consumption values studied in the laboratory that is pertinent. It appears that the low growth rates of fish in nature from April through October are primarily determined by food availability, rather than by temperature or other seasonal effects. This is apparent from my laboratory experiments, because the maximum consumption rates were much higher in the laboratory than those attained by the fish in Tobe Creek.

From my laboratory findings, the range of temperatures at which maximum efficiency of food utilization for growth occurs changes with season, and depends upon the range of consumption rates being considered within a season. In the spring (April-May, Figure 14), newly emerged coho fry had relatively high growth and

utilized food for growth effectively at consumption rates up to 80 cal/kcal salmon/day in the temperature range of 5-14 C. An increase in the consumption rate beyond 80 cal/kcal salmon/day at temperatures from 11 to 17 C contributed little to growth.

During early summer (June-July, Figure 15), food utilization for growth was fairly efficient at consumption rates up to 110 cal/kcal salmon/day in the temperature range of 11 to 14 C. It was somewhat less efficient at 8 C and considerably less at 17 and 20 C. Higher consumption rates were obtained at 17 and 20 C, but these led to little increase in growth.

In late summer (August-September, Figure 16), at consumption rates up to 70 cal/kcal salmon/day, food utilization for growth was quite efficient at the temperatures of 14 and 17 C. At 11 C it was less so, and at 20 and 23 C much less efficient.

During the fall (November-December, Figure 17), at consumption rates up to 60 cal/kcal salmon/day, food utilization for growth was more efficient in the temperature range of 11-17 C than at 8 or 20 C. A consumption rate of 110 cal/kcal salmon/day was necessary at 20 C to yield the same growth as 70 cal/kcal salmon/day yielded at 11 C.

One-year-old coho in the winter (February-March, Figure 18), at low consumption rates, in general utilized food for growth more effectively in the temperature range of 5-8 C than at 14 and 17 C.

Nevertheless, food utilization for growth was relatively good at 17 C at high consumption rates.

It would appear, then, that with the levels of food availability that probably exist in nature, coho salmon would be most able to grow in the spring (April-May) at temperatures ranging from 5 to 14 C. In early summer (June-July), temperatures ranging from 11 to 14 C would be most suitable. Late summer (August-September) temperatures ranging from 14 to 17 C would appear to be satisfactory. Having no growth rate information from Tobe Creek for fall and winter, I cannot estimate natural food consumption rates for these seasons. Assuming that, relative to consumption rates, food is as abundant during these seasons as during spring and summer, tentative conclusions can be drawn from my laboratory studies. During the fall (November-December), temperatures ranging from 11 to 17 C could be satisfactory. And, during the winter (February-March), temperatures ranging from 5 to 11 C might be suitable for growth of juvenile coho salmon in nature.

It would appear that temperatures either above or below these ranges for the different seasons would be inimical to the growth of coho salmon in nature, with the levels of food availability that appear to exist in natural streams. At lower temperatures, food consumption would decrease, regardless of food availability, and efficiency of food utilization for growth also would decrease. At higher

temperatures, assuming food availability did not increase, increases in standard metabolism and SDA would depress severely the energy and materials available for growth, and decrease growth itself. Considering the low rates of growth maintained in nature, this could have serious effects on the success of salmon populations.

Man's ultimate interest is not with animals in the laboratory, but in predicting the response of animals to changes in their natural environment. In nature, fish are seldom subjected to constant environmental temperatures, and the food supply varies with season. But, for any given season the environmental temperature and food supply will lie within a given narrow range of values. If this range of values is known, then the metabolic energy costs to the fish and their efficiency of growth can be estimated. Thus, the bioenergetic approach provides a way of determining the response of the whole animal to changes in its environment, as well as providing a framework for predicting the effects of environmental disturbances resulting from the activities of man.



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