

AN ABSTRACT OF THE THESIS OF

ROBERT FRANK CARLINE for the M. S.

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GROWTH, AND ACTIVITY OF JUVENILE COHO SALMON

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Dr. James Hall

The food consumption and growth of juvenile coho salmon (Oncorhynchus kisutch) in an aquarium and an experimental stream were studied at different times of the year to gain an understanding of the influence of behavior and activity on these relationships.

Despite differences in the levels of activity between the stream and aquarium fish, there were no differences in the food and growth relationships. These differences in activity levels had no apparent effect on the efficiencies of food utilization. It was concluded that laboratory-derived food and growth relationships can be useful in estimating the food consumption of fish in nature.

In two of the experiments some of the fish in the stream were forced to swim constantly at a velocity of 7 cm/sec. The rates of weight loss for starved fish and the levels of the maintenance rations for the fish forced to swim were about double those of the fish not forced to swim. As the food consumption increased the effects of swimming activity on the utilization of food for growth decreased.

A 5°C rise in water temperature had the same effect on the maintenance ration and on the rates of weight loss for starved fish as did forcing the fish to swim.

Quantitative estimates of aggressive activity were made to examine its effects on the utilization and conversion of food. In only one experiment out of five was there a relationship between involvement in aggressive activity and efficiency of food utilization. The results of this experiment were further analyzed by examining the energy budgets for each fish. As the levels of aggressive involvement increased the energy expended for activity increased proportionately. High levels of aggressive involvement were associated with high food consumption and growth rates. Most of the dominant and subdominant fish consumed more food and grew more rapidly than did the subdominant fish. The effects of temperature, food abundance, and activity on growth are discussed in terms of behavioral adaptations for maximizing growth.

Laboratory Studies on the Food Consumption, Growth,
and Activity of Juvenile Coho Salmon

by

Robert Frank Carline

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APPROVED:

Redacted for privacy

Assistant Professor of Fisheries and Wildlife
in charge of major

Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

Date thesis is presented

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Typed by Marion F. Palmateer for Robert Frank Carline

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LABORATORY STUDIES ON THE FOOD CONSUMPTION, GROWTH, AND ACTIVITY OF JUVENILE COHO SALMON

INTRODUCTION

The evaluation of the productivity of aquatic ecosystems poses a problem of major importance in fisheries research. Davis and Warren (1967) point out that fish production studies, which have often been employed to evaluate the productivity of aquatic ecosystems, can be misleading if the population is little exploited and consists of many, large, slow-growing individuals. Such populations yield low estimates of production, yet the population's food consumption is high. Most of this food is used for the maintenance requirements of the population, and only a small portion of the food can be used for growth. In these instances an estimate of the food consumption of the population is a better measure of the system's capacity to produce fish than is an estimate of production.

Quantitative estimates of the food consumption for fish in nature can also be of value in laboratory studies. The results of laboratory experiments concerned with the physiology and performance of fish fed ad libitum rations may not be directly applicable to natural situations, as fish in nature rarely have an unlimited food supply available to them. If reliable estimates of the food consumption of fish in nature could be obtained, then fish in laboratory studies could be fed

appropriate rations and information more applicable to fish in nature could be obtained.

Davis and Warren (1967) reviewed the various methods that have been used to estimate the food consumption of fish. They believed the most reliable method was to conduct food consumption-growth rate studies in the laboratory at various times of the year; the growth rate of wild fish could then be used to estimate their food consumption from the laboratory-derived food consumption-growth rate relationships. This method is relatively simple, but its accuracy depends upon the assumption that the energy costs of activity for fish in aquaria and fish in nature are similar. Differences in the levels of activity could result in differences in the efficiencies of food utilization between the aquarium fish and wild fish. The accuracy of this method for estimating food consumption would decline as the differences in the efficiencies of food utilization became greater, because any change in the efficiencies of food utilization would affect the food consumption-growth rate relationship. Experiments were designed to compare the food consumption-growth rate relationships of juvenile coho salmon in aquaria and in an observation tank modified into an experimental stream. Juvenile coho salmon (Oncorhynchus kisutch) were chosen for this study, because they have a highly developed social organization. The observational facilities afforded an opportunity to study the effects of certain aspects of behavior on food

consumption-growth rate relationships.

Aggressive behavior and territorialism in juvenile coho salmon were first reported by Hoar (1951). Chapman (1962) showed the social status of the coho depended on their relative sizes. The dominant fish was usually the largest and they defended territories, while the subordinate fish formed loose hierarchies in the pools. Mason (1966) found that the size of coho fry upon emergence from the gravel influenced their subsequent social status. Earlier or larger emerging fry became the dominant fish and maintained faster growth rates than did the later or smaller emerging fry. These dominant fry often maintained and defended territories on the riffles. Chapman (1962) demonstrated that aggressive behavior was at least partly responsible for the downstream movement of coho fry. This emigration provided the remaining coho with additional space, which he suggested was necessary to obtain sufficient amounts of food for growth with a minimum of energy expenditure. It appears that the dominant fish have the highest food consumption rates, but to maintain these high rates of consumption they may have to take up positions in fast flowing waters and constantly defend these areas. High levels of activity by the dominant fish could affect their growth rates by causing a decrease in their efficiencies of food utilization.

The purpose of this study was to gain an understanding of the bioenergetic and behavioral relationships influencing the food

consumption and growth of coho salmon. More specifically the objectives were (1) to examine the effects of activity on the food consumption-growth rate relationships for fish in aquaria and in an experimental stream, and (2) to assess and interrelate the effects of aggressive behavior and constant swimming activity on the utilization and conversion of food by dominant and subordinate fish in an experimental stream.

METHODS AND MATERIALS

Description of Apparatus

The experiments were conducted in an outdoor observation tank (Figure 1) and in an adjacent aquarium at the Pacific Cooperative Water Pollution Laboratories, Oregon State University. The tank was divided in half by a partition with openings at the two ends, thus permitting a circular flow of water. Two paddlewheels propelled the water around the channels. Each half of the tank was divided into two sections, each consisting of a riffle, a glide, and a pool. The water velocity was 7 cm/sec on the riffles and decreased to less than 2.5 cm/sec in the pools. The stream sections were divided by 3 mm mesh screens, and a fiberglass screen cage was attached to the dividing screen of each pool to provide a refuge for any subordinated fish that might be driven out of the section. The bottoms of the sections were covered with washed gravel 2 to 5 cm in diameter. Well water was exchanged through the system at a rate of 4 liters/min. Each section had six glass tubes extending from the sides of the tank to the water surface for the introduction of food. The tank was designed so that the only food available to the fish were the fly larvae that I introduced daily. The entire structure was covered by fiberglass window screening to prevent food organisms from falling into the stream.

The initial aquarium experiments were conducted in a plywood structure

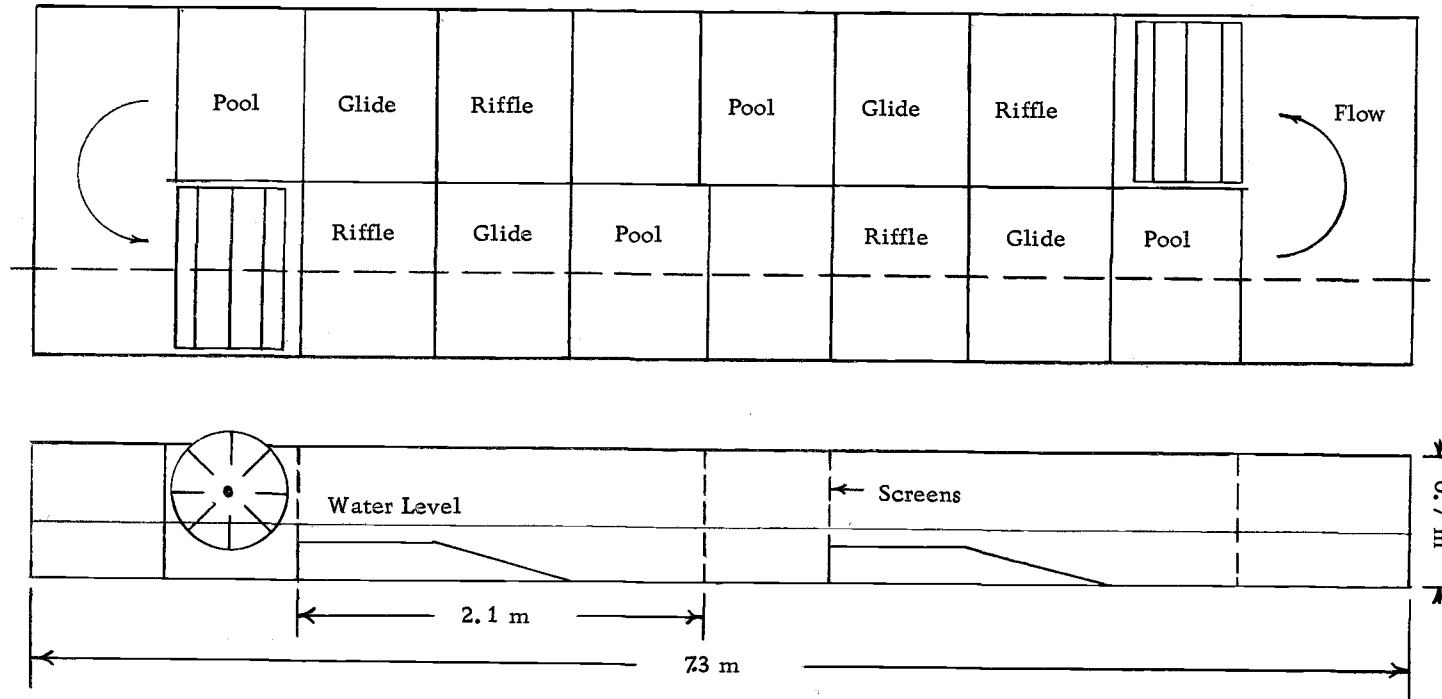


Figure 1. Top view and cut-away side view of the experimental stream. The windows on the sides of the tank are not shown.

divided into 14 compartments that were 27 cm long, 20 cm wide, and 25 cm high. The aquarium was coated with a white non-toxic paint. Exchange water from the observation tank was supplied to each compartment at 60 ml/min.

Experimental Procedures

Experiments I and II

The juvenile salmon were seined from nearby coastal streams. Each fish was marked with a cold-branding technique. Marking tools similar to those described by Groves and Novotny (1965) were immersed in a solution of dry ice and acetone. The fish were narcotized with MS-222 (Sandoz) and blotted dry; the cooled marking tool was applied for two seconds on the middle of each side of the fish below the dorsal fin. The fish were held in outdoor tanks and fed ad libitum a diet of housefly larvae and tubifex worms for two weeks prior to each experiment. The fish were then starved for 48 hours, narcotized, measured (fork length) to the nearest millimeter, blotted dry, weighed to the nearest 0.001 g on a Mettler top loading balance, and placed in the observation tank and in the aquarium.

Stream Experiments. Fly larvae, the only food organism fed to fish during the experiments, were generally introduced into the stream sections twice daily by washing them down the glass tubes.

Each fish could be identified by its distinctive mark. I estimated the food consumption rate of each fish by counting the number of larvae it consumed. Several samples of fly larvae were taken during each experiment to determine their percentage dry weight. Water temperatures were taken twice daily with a stem thermometer accurate to 0.5° C.

I observed the behavior of the fish for ten minutes prior to each feeding and during feeding. Each time an aggressive act was observed, the initiator of the act and the recipient of the act were noted. No distinction was made between threat displays, chases, or actual nips. If a threat display was followed by a nip, it was counted as a single aggressive act. The position of each fish in the stream was noted at each observation.

At the end of each experiment the fish were starved for 48 hours, weighed and measured, dried in an oven at 65° C from three to five days, and reweighed. Any fish showing signs of an external pathological condition was discarded.

Aquarium Experiments. One fish was placed in each of the 14 aquarium compartments. A predetermined number of fly larvae were fed to 11 of the fish once a day and three fish were starved. A different number of larvae were fed to the fish so as to attain a range of consumption rates from below the maintenance ration up to the maximum consumption rate. Uneaten larvae were removed from the

compartments the day after they had been fed to the fish and then more larvae were fed to the fish. Each aquarium experiment was conducted at the same time a stream experiment was conducted. The procedures for measuring and weighing the aquarium fish were identical to those described for the stream fish.

The dates, mean water temperatures, and other pertinent information about each stream and aquarium experiment are given in Table 1. Several changes were made in the experimental design as the research progressed; these changes are explained below.

Experiment III

To increase the amount of space available to the fish in Experiment III, the screens dividing Sections 1 and 2 and those dividing Sections 3 and 4 were removed, creating one large section in each half of the observation tank. The small screen cages attached to the ends of each section were not utilized by the subordinate fish in Experiments I and II, even though some of these fish were constantly intimidated; thus a larger screen cage 0.6 m square and 0.6 m high was attached to the downstream pool of each section to provide an exit from the sections. To hold starving fish in the stream a wire cage 0.4 m square and 0.6 m high was placed in the vacant area adjacent to one of the paddlewheels.

The wooden aquarium used in Experiments I and II was replaced

Table 1. The conditions under which each experiment was conducted.

Experiment	Date	Mean water temperature	Type of aquarium	Aquarium fish density (g/m ²)	No. of stream sections	No. of fish per stream section	Stream fish density (g/m ²)	No. of fish starved in stream	Ration fed to stream fish
I	8 October to 20 October 1966	9.0	wood	29.4	4	5	12.3	0	unrestricted
II	28 November to 12 December 1966	9.6	wood	42.1	4	5	19.8	0	unrestricted
III	19 February to 4 March 1967	5.9	Plexiglass	26.3	2	11	14.8	3	1 section restricted 1 section unrestricted
IV	24 March to 6 April 1967	7.2	Plexiglass ^a	4.17	4 riffles and 4 pools	4 per riffle 4 per pool	Riffles: 5.5 Pools: 4.5	4 on riffles 4 in pools	restricted to unrestricted
V	16 May to 2 June 1967	12.3	Plexiglass ^a	4.28	4 riffles and 3 pools	5 per riffle 6 per pool	Riffles: 3.2 Pools: 4.2	5 on riffles 5 in pools	restricted to unrestricted

^aWith and without cover

by a clear plexiglass aquarium so the fish could see each other. The aquarium was divided into 14 compartments that were 37 cm long, 23 cm wide, and 25 cm high. Well water was exchanged into each compartment at 60 ml/min and the aquarium was covered by fiberglass window screening.

Experiment IV

Adequate numbers of underyearling salmon could not be collected when this experiment was conducted. Consequently, several hundred sac fry of hatchery origin were obtained from the Oregon Game Commission Research Laboratory in Corvallis. These fish were held in an outdoor trough for several weeks and fed a diet of dry fish food and tubifex worms prior to the experiment. When the fry reached about 42 mm, they were cold branded, weighed, measured, and placed in the stream and in the aquarium.

Experiment IV was designed to compare the food consumption-growth rate relationships of fish in the pools and fish constantly swimming on the riffles. Screens were placed between each riffle and pool. Due to the limited amount of space, cages were not provided to allow movement out of the riffles or pools. The behavioral observations were omitted during feeding, because of the increased number of fish in the stream.

An additional objective of this experiment was to examine the

effect of cover on the food consumption-growth rate relationships of fish in the aquarium. Each aquarium compartment was divided in half with a piece of plexiglass, forming 28 compartments. Pieces of painted lead sheeting 8 cm long and 5 cm wide were bent into a U-shape and placed in the bottoms of 14 of the compartments along with enough stones to cover one-half of the bottom surfaces. Twenty-six fish were placed in separate aquarium compartments and three fish were starved in each of the remaining two compartments (one with cover and one without).

Experiment V

The objectives of this experiment were the same as those of Experiment IV. The only change in the stream design was to increase the number of fish on the riffles by converting one of the stream sections to one long riffle.

An attempt was made to increase the amount of cover available to fish in 14 of the aquarium compartments. The bottoms of the compartments were darkened by placing a sheet of black polyethylene underneath them and black plastic containers 15 cm square were placed in the compartments to provide overhead cover for the fish.

This experiment was planned for three weeks to see if an additional week of experimentation would yield results different from those obtained in Experiment IV. However, the experiment was

terminated after only 16 days, because of a sparse accumulation of filamentous green algae and a few tiny chironomid larvae that could have provided food for the fish. During the final 48 hours of the experiment, a drift net was placed in the stream to detect the possible presence of drifting organisms. A single dipteran larva was the only organism found in the net.

Food Consumption and Growth Rates

An average relative growth rate expressed in terms of dry weight was computed for each fish. To compute the average relative growth rate, the change in dry weight was divided by the mean of the initial and final dry weight of the fish and the quotient was divided by the number of days in the interval. To estimate the initial dry weight of each fed fish, its initial wet weight was multiplied by its final percentage dry weight. This method assumed there was no change in percentage dry weight of the fish during the experiment. To estimate the initial dry weight of the starved fish, the mean percentage dry weight of the growing fish in the experiment was multiplied by the initial wet weight of the starved fish. The final percentage dry weight of the starved fish was not used, because the percentage dry weight of starved fish decreases with time (Phillips et al., 1960).

An average relative consumption rate was also computed for each fish. The number of fly larvae consumed was multiplied by the

mean dry weight per larva. The total dry weight of larvae consumed was divided by the mean dry weight of the fish and the quotient was divided by the number of days in the interval.

The curves for the food consumption-growth rate relationships have been fitted by the method of regression analysis. A linear relationship was assumed unless a statistically significant reduction in the residual sum of squares resulted from a curvilinear relationship. The equations and correlation coefficients for each relationship are given in Table 2.

Compilation of Behavioral Data

Each fish was assigned to one of four different social groups. The dominant fish were placed in Group I. The fish that defended a territory often violated by the dominant fish, but rarely by the other subordinates, were placed in Group II. The fish that did not have territories and were frequently attacked by Groups I and II were classified as Group III fish. The most subordinate fish, which were intimidated by all the other fish, were placed in Group IV. The aggressive behavior of each fish is reported (Appendix) in number of acts initiated per minute and in number of acts received per minute; the sum of these two terms is referred to as the total aggressive involvement per minute.

Field Observations

To obtain an estimate of the water velocities in which juvenile coho are found, I observed fish in Needle Branch, a small headwater stream in the Alsea River drainage. Low water levels and excellent visibility provided ideal conditions for observations. Four sites, each having a riffle and a pool, were randomly chosen. The position of each fish was noted and the water velocity was measured at each of these positions with a Stevens Midget Current Meter. This current meter was not accurate at velocities less than 4 cm/sec, and it was difficult to find the exact position of each fish in the stream, so the velocities should be viewed merely as approximations.

RESULTS

Effects of Activity on Food Consumption-Growth Rate Relationships of Stream and Aquarium Fish

The relationships between the food consumed and growth achieved for fish held in an aquarium and in an experimental stream can be compared to determine the utility of aquarium-derived relationships for estimating the food consumption of fish in nature. The fish in the aquarium were isolated and received very few external stimuli. In contrast, the fish in the experimental stream were subjected to constant stimulation from the current and from social contacts. Differences between the food consumption-growth rate relationships may be attributed to the greater levels of activity by stream fish or to some possible effect of confinement on the aquarium fish.

To help clarify the physiological bases for the shapes of the food consumption-growth rate relationships, I have included graphs of the gross and net efficiencies plotted against food consumption. These efficiencies have been calculated directly from the fitted food and growth curves rather than from the food consumption and growth of each fish. Gross efficiency (growth divided by consumption) is the fraction of the total food consumed that is laid down as growth. As the growth rate increases with an increasing food consumption rate, the gross efficiencies will increase and approach a maximum value.

When the gross efficiencies increase asymptotically to a maximum, the food and growth relationship is linear. A decrease in the gross efficiencies after having reached a maximum results in a curvilinear food and growth relationship. As the maintenance ration increases the food consumption rate at which the gross efficiency is maximum will increase. Net efficiency (growth divided by consumption in excess of the maintenance ration) is a measure of the efficiency of food utilization for growth above the maintenance ration. The magnitudes of the net efficiencies influence the slope of the food consumption and growth relationship; the higher the net efficiencies are, the greater the slope. When the net efficiencies remain constant over the range of consumption rates, the food and growth relationship will be linear. If the net efficiencies decline, the relationship will be curvilinear.

Since the following discussion will be primarily concerned with the activity of the fish, we should recognize that there are many types of activity. This activity may be categorized into four components: aggressive, exploratory, feeding, and that associated with maintaining a position in the stream by swimming against the current. The present discussion will consider the total activity of the fish. A few components of the total activity will be examined in a following section.

Experiment I

The wooden aquarium provided complete visual isolation for the fish; the only time they were disturbed was during the once-a-day feeding. It was difficult to observe the fish in the aquarium without disturbing them, but the few times I did see them, they appeared to be lethargic. In contrast, the stream fish were quite active. There was much aggressive activity among the fish and they often swam around the pools in what appeared to be exploratory behavior.

The food consumption-growth rate relationship for the aquarium fish was curvilinear and the relationship for the stream fish was linear (Figure 2), although the difference between them was slight. The aquarium fish had a maintenance ration (where the fitted curve crossed the zero growth line) less than one-half the maintenance ration for the stream fish, yet both groups of fish attained their highest growth rates at nearly the same consumption rate. The gross efficiencies of the aquarium fish rose to a maximum at 30 mg/g per day of consumption and then declined; the gross efficiencies for the stream fish continued to increase to their highest consumption rates. The stream fish reached a maximum gross efficiency at a higher food consumption rate than the aquarium fish, because the stream fish had a greater maintenance ration. The rise and subsequent decline of the gross efficiencies for the aquarium fish is reflected in

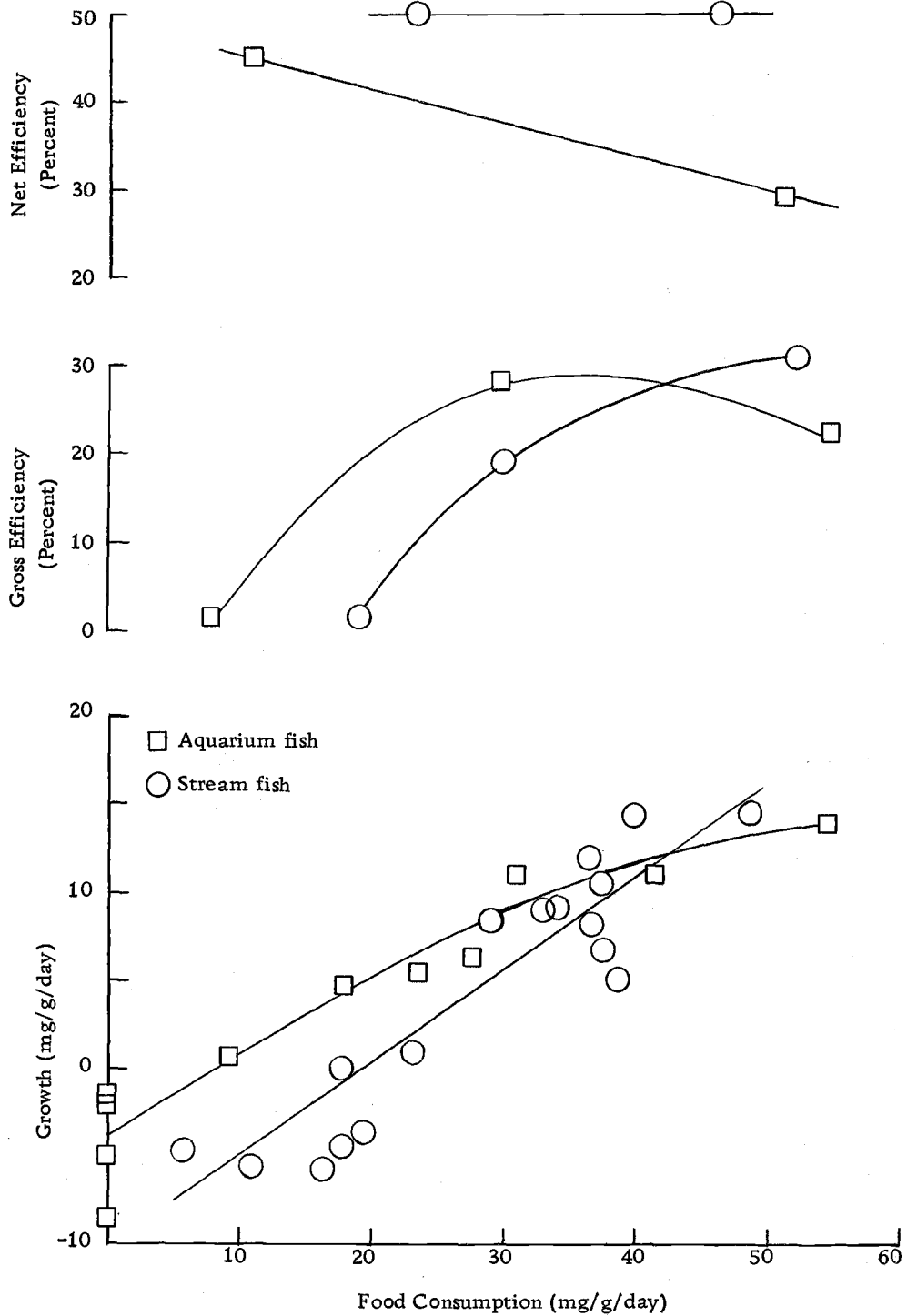


Figure 2. Relationships between food consumption and growth, consumption and gross efficiency, and consumption and net efficiency for Experiment I.

Table 2. Formulas and correlation coefficients for the food consumption-growth rate relationships of Experiments I through V.

Experiment I		
Stream Fish	$y = -9.91 + 0.52x$	$r = 0.94^*$
Aquarium Fish	$y = -4.05 + 0.54x - 0.004x^2$	$R = 0.96^*$
Experiment II		
Stream Fish	$y = -8.98 + 0.56x$	$r = 0.94^*$
Aquarium Fish	$y = -5.41 + 0.34x$	$r = 0.93^*$
Experiment III		
Stream and Aquarium Fish	$y = -13.60 + 1.11x - 0.011x^2$	$R = 0.93^*$
Experiment IV		
Stream (pools) and Aquarium Fish	$y = -6.29 + 0.58x - 0.004x^2$	$R = 0.93^*$
Pool Fish	$y = -3.58 + 0.46x - 0.002x^2$	$R = 0.92^*$
Riffle Fish	$y = -11.61 + 0.77x - 0.007x^2$	$R = 0.94^*$
Experiment V		
Stream (pools) and Aquarium Fish	$y = -17.43 + 0.69x - 0.003x^2$	$R = 0.93^*$
Pool Fish	$y = -18.22 + 0.91x - 0.006x^2$	$R = 0.96^*$
Riffle Fish	$y = -30.48 + 0.61x$	$r = 0.94^*$

* Significant at 1% level.

the constant decline of the net efficiencies. The aquarium fish were progressively less efficient in utilizing the food above the maintenance ration. Although the stream fish had a higher maintenance ration than the aquarium fish, the net efficiencies of the stream fish remained constant, enabling them to attain a maximum growth rate comparable to that of the aquarium fish.

The high levels of activity by the stream fish compared to the aquarium fish had the most pronounced effect on growth at low consumption rates. This effect is shown by the difference in the maintenance rations. However, above the maintenance ration the stream fish were more efficient than the aquarium fish in utilizing their food; thus the effect of activity diminished as food consumption increased. It appears that under conditions of this experiment, aquarium-derived food and growth relationships may not be used to estimate the food consumption of fish in nature.

Experiment II

To confirm the findings of Experiment I, I conducted another experiment under similar conditions. The numbers of fly larvae fed to the stream fish were increased so that the fish received as much food as they would eat. The same numbers of fish were used, but the fish in this experiment were larger, therefore, the fish densities (g/m^2) in the stream and aquarium were higher than in Experiment I.

Although this experiment was conducted in early December, more than a month after the previous one, the mean water temperature was slightly higher (0.6°C) than in Experiment I. As in the previous experiment the aquarium fish were lethargic and the stream fish were active.

The lack of points between 0 and 20 mg/g per day of consumption for both the stream and aquarium fish precludes a complete analysis of the food consumption-growth rate relationships (Figure 3). The relationship for the aquarium fish could have been curvilinear as in Experiment I. The only portions of the relationships that can be compared are between 33 and 45 mg/g per day of consumption. In this region most of the stream fish had higher growth rates than the aquarium fish; the gross efficiencies of the stream fish were higher than those of the aquarium fish. I have not included a graph of the net efficiencies, because the maintenance rations could not be accurately determined. The increase in food supply allowed each stream fish to consume enough food to gain weight. The highest consumption rates for the stream and aquarium fish in this experiment were greater than those in Experiment I.

The lack of a well defined food consumption-growth rate relationship over the entire range of rations prevents me from making any conclusions about the effects of activity on these relationships. The stream fish had higher growth rates than the aquarium fish in

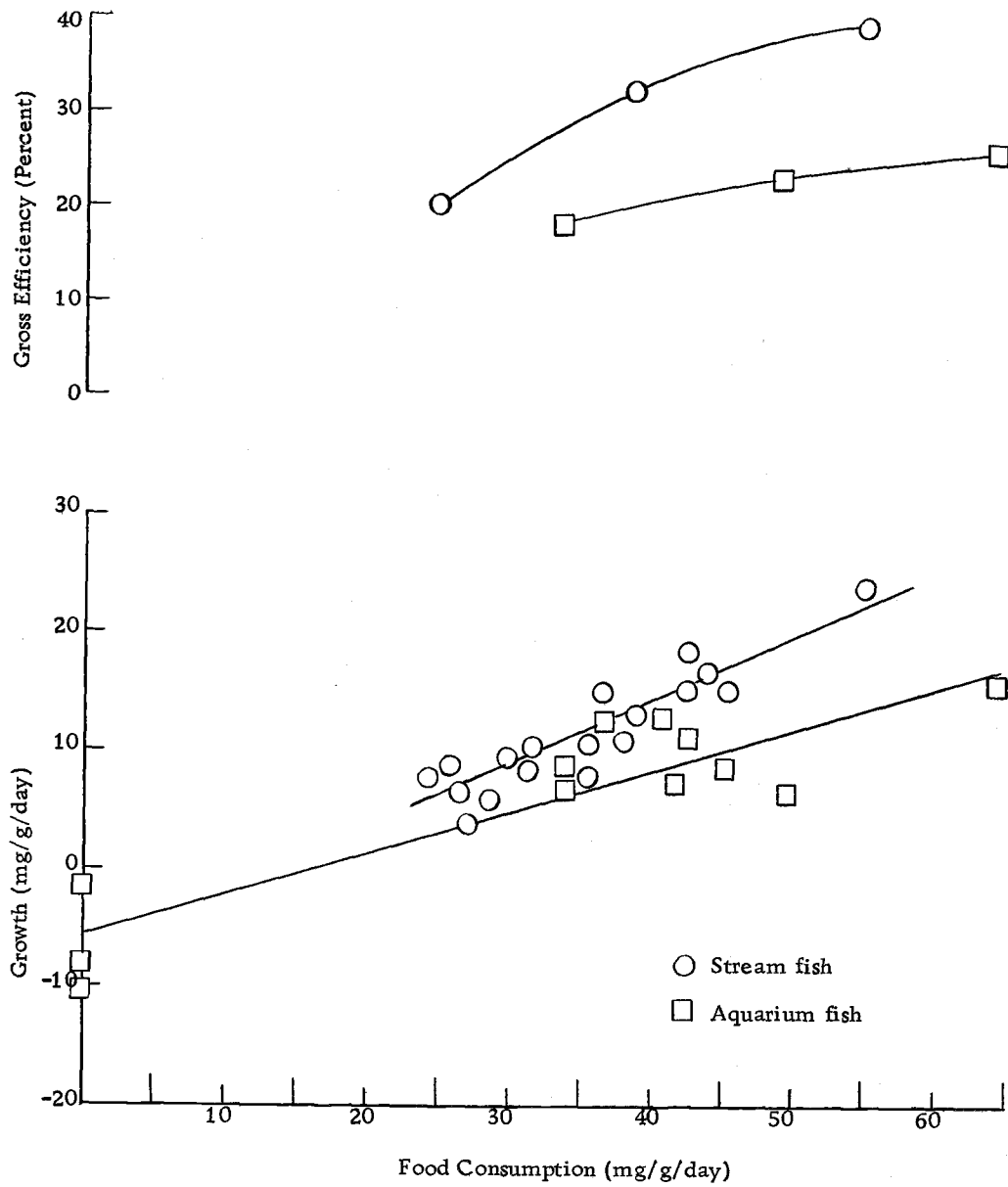


Figure 3. Relationships between food consumption and growth, and consumption and gross efficiency in Experiment II.

this experiment and the reverse was true for Experiment I. This discrepancy may have been due to the visual isolation of the fish. The aquarium fish in Experiment II had the highest density per unit area compared to the aquarium fish in the other Experiments (Table 1). The differences in growth rates between the stream and aquarium fish may have been the result of a lack of sufficient space for the aquarium fish. Comfort (1956) found that female guppies (Lebistes) grew faster in large containers than in small containers. Yamagishi (1962) has shown that decreasing available space while maintaining the same fish density resulted in lower growth rates. Neither investigator accurately measured the food consumption of the fish; therefore, it is impossible to determine whether these decreases in growth rates were due to a decrease in efficiency of food utilization or to a decrease in food consumption.

Experiment III

In this experiment the stream and aquarium were altered in an attempt to increase the level of activity in the aquarium fish and to decrease the levels of activity in the stream fish. The clear plexiglass aquarium allowed the fish to see each other, and the compartments were enlarged to provide more space for the aquarium fish. Conversion of the four stream sections into two resulted in a greater amount of space than was available in the first two experiments. The

wire cages also permitted volitional movement out of the stream sections, thus reducing the likelihood of constant intimidation of the most subdominant fish.

The fish in the aquarium remained extremely lethargic; the only time they became active was when they were fed. The stream fish were more active than the aquarium fish, but less active than the stream fish in the previous experiments. The stream fish in this experiment exhibited little exploratory behavior; most of their activity was confined to aggressive behavior. Despite the differences in the levels of activity between the stream and aquarium fish, there appears to be no difference between the food-consumption-growth rate relationships (Figure 4). The net efficiencies continually declined with increasing rations and the gross efficiencies rose to a maximum and also declined. This reduction in the efficiency of food utilization caused a rapid decrease in the slope of the food consumption and growth relationship at the higher consumption rates.

These results indicate that the greater activity of the stream fish compared to aquarium fish did not affect the utilization of food for growth. The lower levels of activity of stream fish as compared to the levels of activity of the fish in previous experiments may have been due to the low water temperatures (Table 1). There was also a substantial reduction in the variability of the food consumption and growth relationship in this experiment compared to the previous ones.

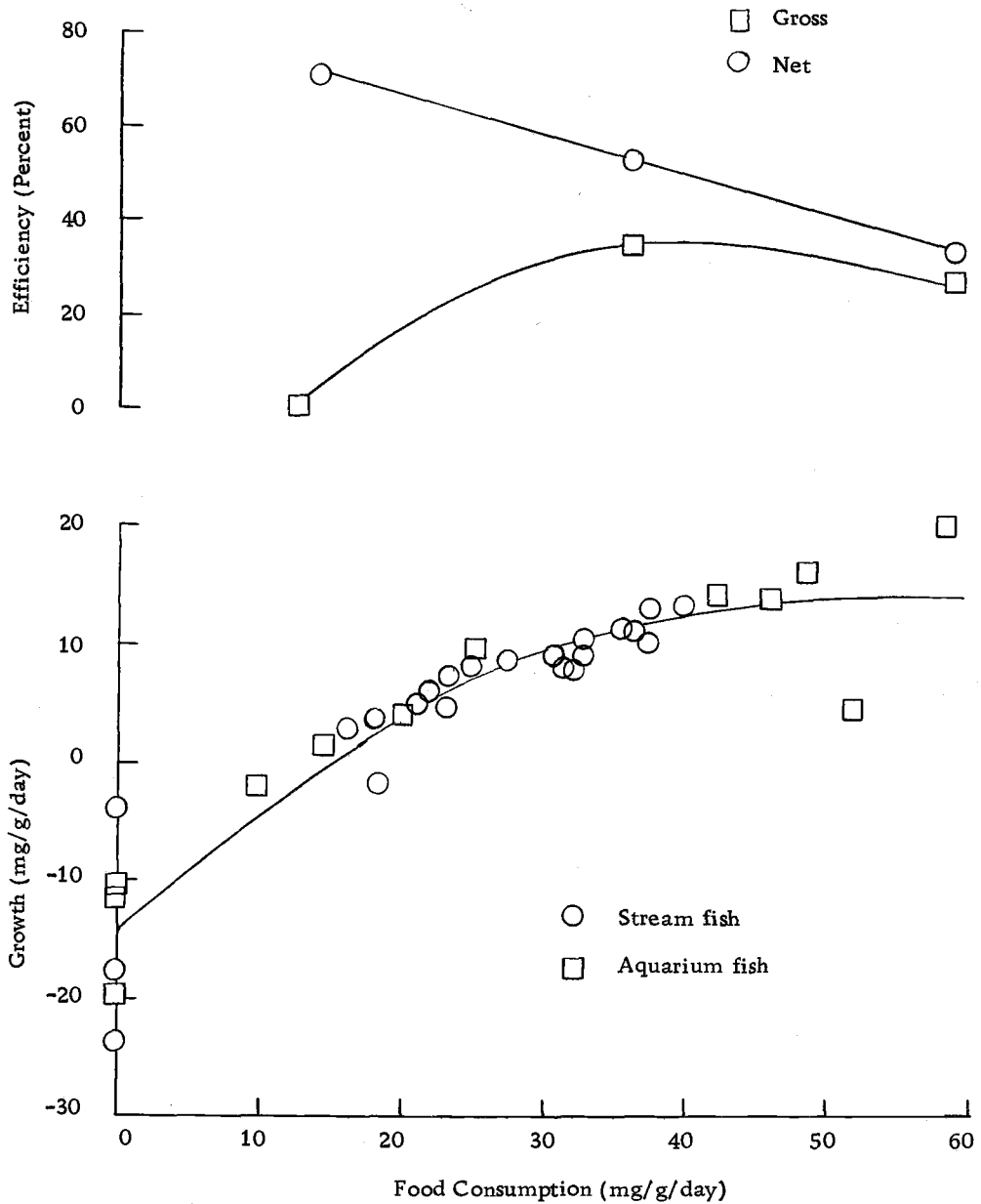


Figure 4. Relationship between food consumption and growth, consumption and gross efficiency, and consumption and net efficiency in Experiment III.

The relationship between food consumption and growth for fish in aquaria under the conditions of this experiment would be useful in estimating the food consumption of fish in nature.

Experiment IV

In addition to determining the effects of activity on the food consumption-growth rate relationships of stream and aquarium fish, this experiment had two other objectives. The first was to see if providing cover for the aquarium fish had any effect on their food consumption-growth rate relationships. The second objective was to determine the effect of constant swimming on the food and growth relationship of fish confined to the riffles of the stream. The results of the experiment pertaining to the latter objective will be discussed in a following section.

The fish in the experiment had been recently hatched and were younger than the fish in the first three experiments. These fish weighed about 1 g, whereas the fish in the previous experiments weighed from 3 to 8 g. These smaller fish were much more active in the stream than the larger fish had been; not only was there more aggressive activity among these small fish, but there was also more exploratory behavior. The fish in the aquarium were lethargic, as were the larger fish in the previous experiments. Despite the differences in activity between the stream and aquarium fish, there are

no apparent differences between the food-consumption-growth rate relationships for the two groups of fish (Figure 5). The fish in the aquarium compartments with cover were rarely seen lying beneath the U-shaped pieces of lead. Their food consumption-growth rate relationship is not distinguishable from that of the other aquarium and stream fish; consequently, a single curve was fitted to the points representing the stream and aquarium fish. The maximum consumption rates attained by the aquarium fish were higher than those attained by the stream fish, because a few fish in the aquarium always had food available, whereas the stream fish were fed only twice a day. The fish in this experiment had higher maximum consumption rates than did the fish in the first three experiments, because small fish can consume more food relative to their body weight than can large fish. The gross efficiencies reached a maximum at 40 mg/g per day of consumption (Figure 6); the net efficiencies also declined beyond 40 mg/g per day of consumption. Due to this reduction in efficiency of food utilization, the slope of the food consumption-growth relationship declined rapidly beyond 40 mg/g per day of consumption. These results show that the differences in the levels of activity between the stream and aquarium fish had no apparent effect on the food consumption and growth relationships.

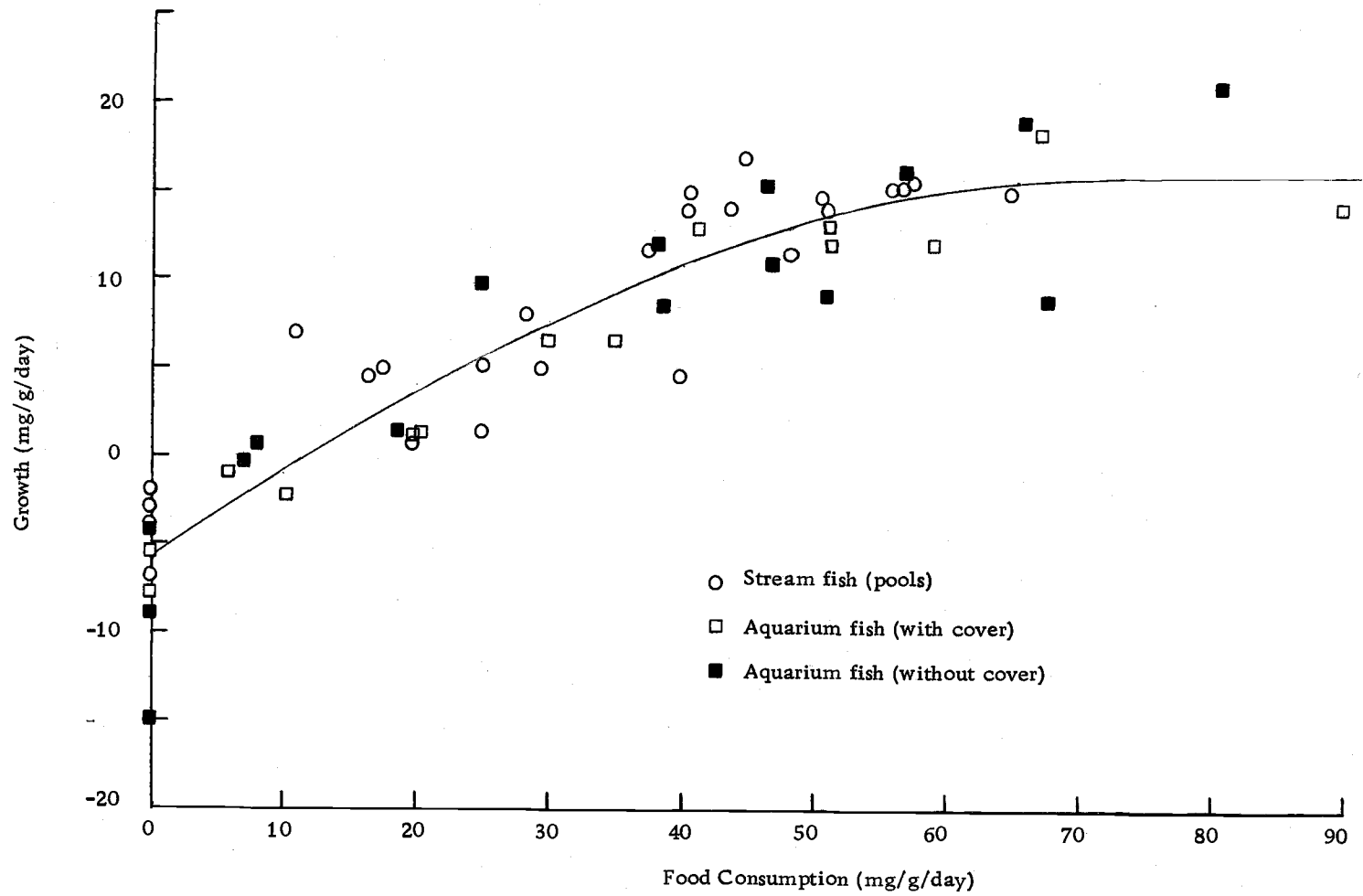


Figure 5. Relationship between growth and food consumption in Experiment IV.

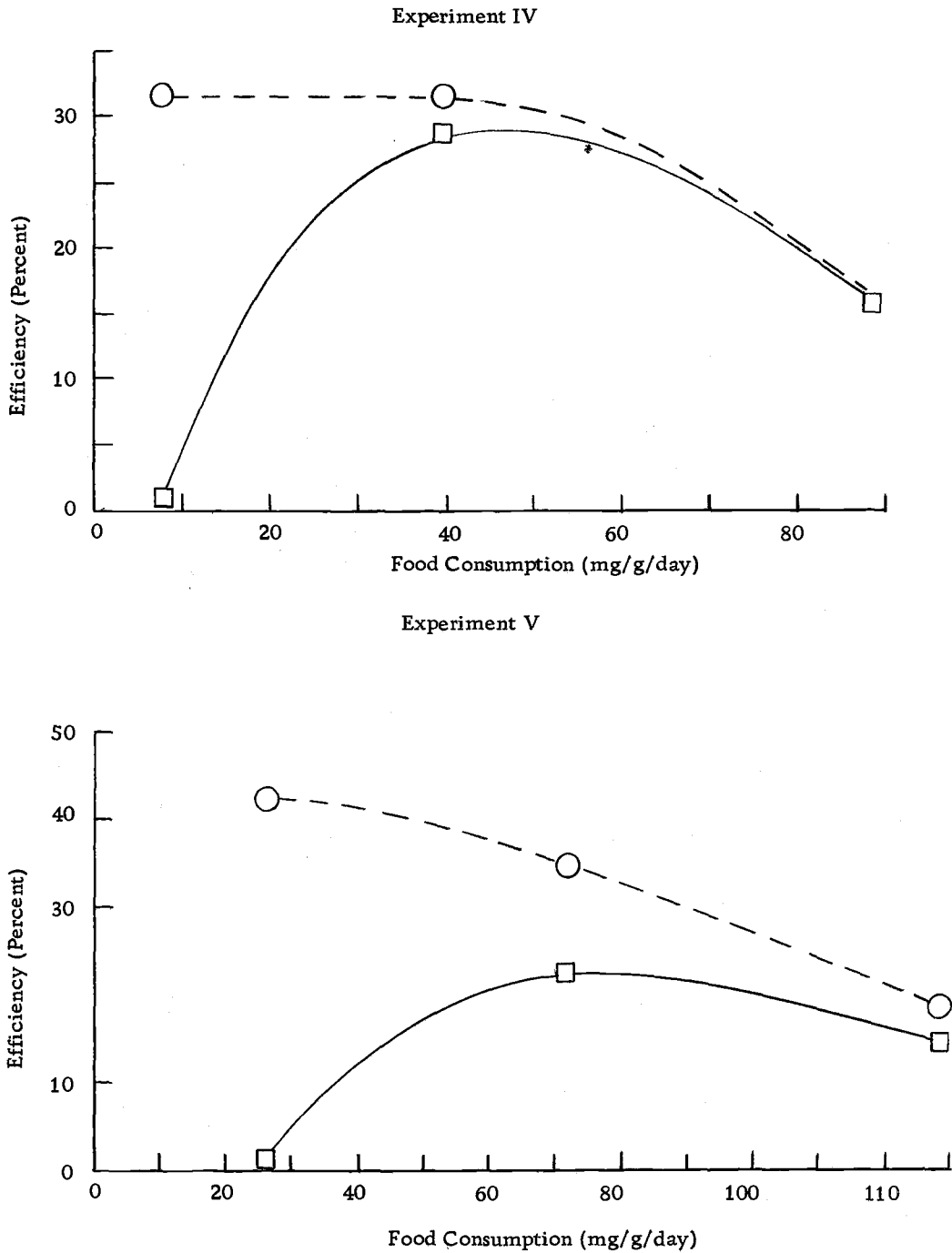


Figure 6. Relationships between food consumption and gross efficiency (solid line), and consumption and net efficiency (dotted line) for Experiments IV and V. Combined data for fish in stream pools and aquarium.

Experiment V

The objectives of this experiment were the same as those of Experiment IV. The only changes were an increase in the number of fish on the riffles and an increase in the amount of cover for one-half of the fish in the aquarium. The fish in this experiment were the same size as those in Experiment IV, and these fish were equally as active as the fish in the previous experiment.

The points representing the food consumption and growth rates for the stream and both groups of aquarium fish are thoroughly interspersed (Figure 7), and a single curve has been fitted to these points. As in Experiment IV the cover provided for the aquarium fish seems to have had no effect on their food consumption-growth rate relationship, even though the fish were often seen inside the plastic containers. The fish in the compartments without available cover were more active than those having cover available, yet both groups of aquarium fish were relatively inactive compared to the fish in the stream pools. Although there were consumptions as high as 128 mg/g per day, at consumptions above 80 mg/g per day the fish could utilize only a small fraction of the food for growth. This decrease in efficiency of food utilization is illustrated by the decline of both the gross and net efficiencies at the high rations (Figure 6). The higher water temperatures (12.3° C) in this experiment compared to

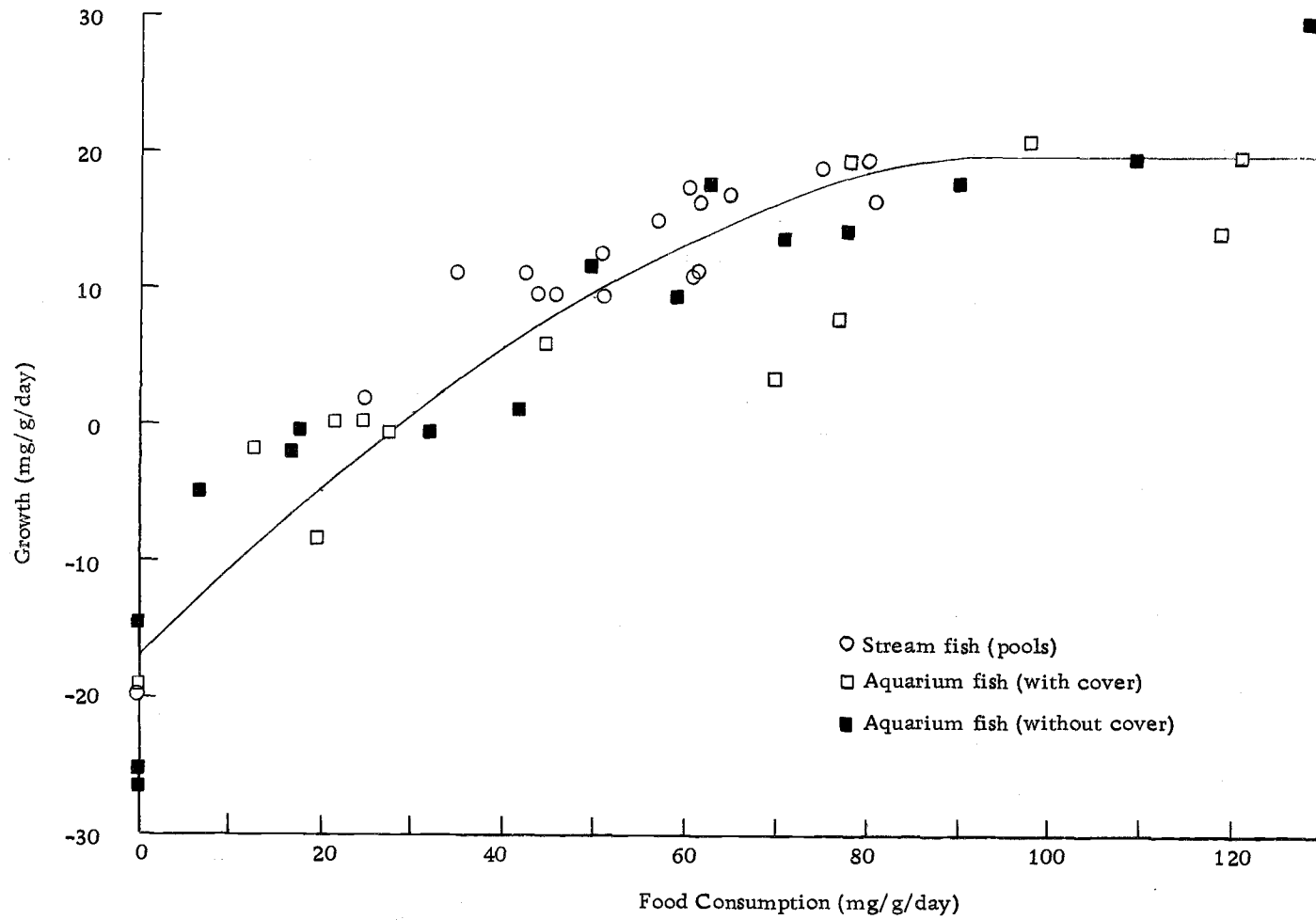


Figure 7. Relationship between growth and food consumption in Experiment V.

the previous one (7.2°C) were probably the reason for the increase in the maximum consumption rates and the maximum growth rates; the maximum consumption rates increased from 90 to 128 mg/g per day, and the maximum growth rates increased from 21 to 29 mg/g per day. The results of this experiment confirmed the findings of Experiments III and IV; differences in activity between the stream and aquarium fish had no apparent effect on the food consumption and growth relationships.

Efficiency of Food Utilization for Growth

The maximum gross efficiencies occurred at different consumption rates in each of the five experiments. Despite the differences in the size of the fish and the water temperatures among the experiments, the gross efficiencies were maximum at consumption rates that corresponded to growth rates between 10 and 15 mg/g per day. Beyond these consumption rates the efficiencies of food utilization declined.

Warren and Davis (1967) suggest that a decline in gross efficiencies is caused by the increasing metabolic cost of specific dynamic action or to a decrease in efficiency of assimilation at high rations. The causes for the decrease in gross efficiency with increasing rations are of theoretical interest, but they may not be of any practical importance. Studies on the growth and production of

populations of juvenile coho salmon by Chapman (1965) and Iverson (1967) have shown that the growth rate of coho for most of the year was less than 10 mg/g per day. These growth rates correspond to low food consumption rates, compared to the consumption rates of the experimental fish. The decline of the gross efficiencies at the higher rations suggests that coho have not evolved the physiological capacity to efficiently utilize large amounts of food.

Estimation of Food Consumption

The results of Experiments I and II were contradictory, which may have been caused by inadequate aquarium facilities. The results of Experiments III, IV, and V suggested that the energy used for activity by the stream fish did not affect the efficiencies of food utilization. However, there is another possible explanation for the similarity in food consumption-growth rate relationships between the stream and aquarium fish; the energy used for activity by the stream fish could have been a significant portion of the total energy intake and had a pronounced effect on the relationship between food and growth. The aquarium fish could have been under some type of stress that resulted in a higher than normal metabolic rate. Thus the energy used for activity by the stream fish might have been nearly equal to the energy utilized for maintaining the abnormally high metabolic rate of the fish in the aquarium. Rasquin and

Rosenbloom (1954) have shown that stress induced by prolonged darkness increased the level of ACTH in the blood of Astyanax. Hane et al. (1966) found that the stress resulting from confinement was responsible for a four-fold increase in the plasma concentration of a particular adrenocortical secretion in immature chinook salmon (Oncorhynchus tshawytscha). Efforts to provide cover for the fish in the aquarium and reduce any possible stress had no apparent effect on the food consumption-growth rate relationships. Other factors such as increasing available space or holding several fish in a single compartment might have reduced the stress resulting from confinement. Although I cannot adequately explain the similarities in the food consumption-growth rate relationships of the stream and aquarium fish, the method of estimating the food consumption of fish in nature from laboratory-derived relationships seems reliable. Factors such as fish size and age, season, food types, and temperature should be considered to obtain the most useful relationships (Davis and Warren, 1967).

Effects of Constant Swimming on the Food Consumption-Growth Rate Relationships of Stream Fish

Some of the stream fish in Experiments IV and V were forced to swim continuously on the riffles so that their levels of activity could be more easily estimated. Much of the activity of the fish in the

pools was exploratory, but the fish on the riffles exhibited very little exploratory behavior, and their levels of aggressive behavior were less than those of the pool fish. The fish on the riffles confined their aggressive activity to brief encounters; they rarely chased and nipped at each other for extended periods, as the pool fish often did. Aside from their aggressive activity, the riffle fish spent practically all of their time heading upstream and swimming against the current, maintaining a stationary position.

Experiment IV

The most pronounced effects of forcing the fish to swim were on the rates of weight loss for the starved fish and the levels of the maintenance rations (Figure 8). The maintenance ration of the riffle fish was about double that of the pool fish. The mean rate of weight loss for the fish starved on the riffles was also double the rate of weight loss for the fish starved in the wire cage. The pool fish had higher growth rates than the riffle fish at comparable consumptions; this is reflected in the higher gross efficiencies of the pool fish. Despite the difference between the maintenance rations, the highest growth rates of the riffle fish approached those of pool fish, because the riffle fish had higher net efficiencies than the pool fish at most levels of consumption.

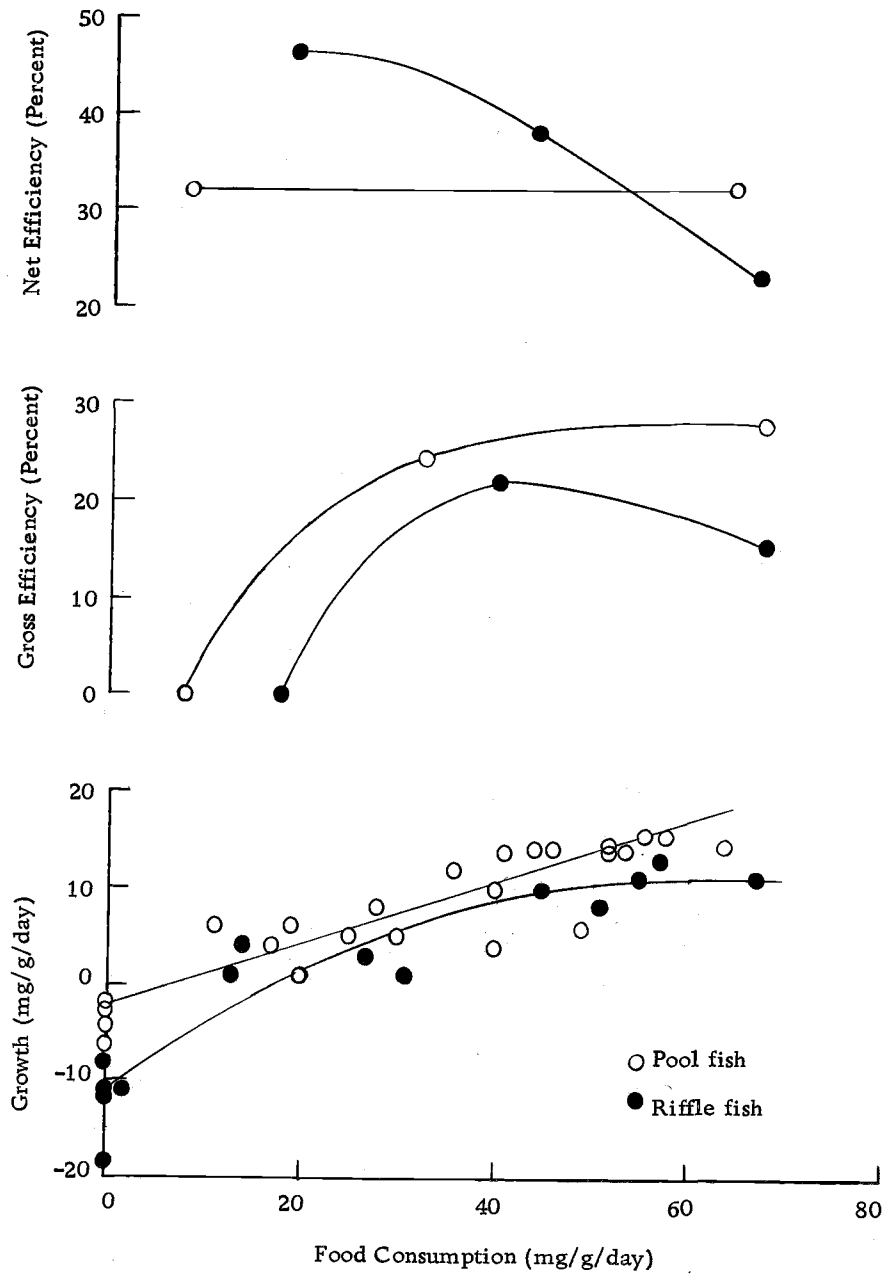


Figure 8. Relationships between food consumption and growth, consumption and gross efficiency, and consumption and net efficiency in Experiment IV.

Experiment V

The food consumption-growth rate relationships of the pool and riffle fish were widely separated at the low consumption rates and then converged at the highest consumption rates (Figure 9). Three of the starving fish on the riffles were rarely visible; they hid among the rocks. Two of the fish were always visible and they had the highest rates of weight loss. The mean rate of weight loss for the starving fish on the riffles is probably an underestimate. The maintenance ration of the riffle fish was about double the maintenance ration of the pool fish. The gross efficiencies of the pool fish reached a maximum at a consumption rate of 50 mg/g per day and then declined. The riffle fish had their highest gross efficiency at the highest consumption. The decrease in efficiency of food utilization by the pool fish is shown by their declining net efficiencies. The riffle fish maintained a constant net efficiency that was higher than the net efficiencies of the pool fish. The curves for the food consumption-growth rate relationships intersect, because the riffle fish had consumed and efficiently utilized enough food to approach their maximum growth rate. Thus the effect of constant swimming was most pronounced at low rations and continually diminished as the food consumption increased.

These experiments show how the abundance of food and the position a fish takes up in the stream will affect the growth rate of that

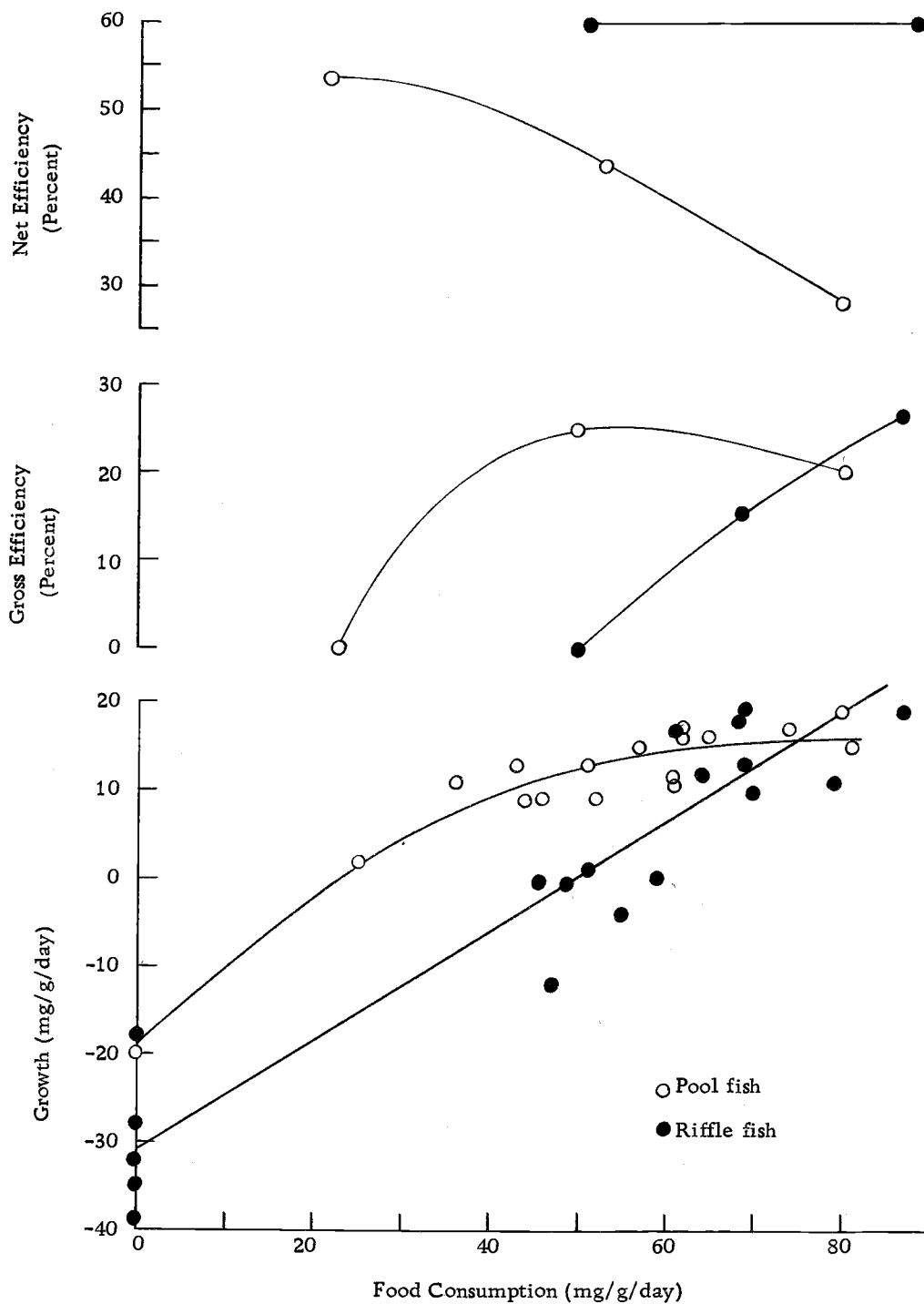


Figure 9. Relationships between food consumption and growth, and consumption and net efficiency in Experiment V.

fish. When food is limiting, a fish holding a position adjacent to food-bearing currents will have a distinct advantage over another fish that has taken up a position directly in the current, if both fish are equally efficient in exploiting the food resource. The low growth rates reported by Chapman (1965) and Iverson (1967) suggest either that food is limiting or that the fish are maintaining positions directly in the current and they are utilizing a significant portion of their total energy intake for swimming.

Field Observations

The riffles of the stream sections in which I observed the coho were composed of a uniform-sized rubble with a few obstructions. Only a few fish were observed on the riffles and these fish were generally near or behind an obstruction. About two-thirds of the observed coho were found in water velocities less than 4 cm/sec (Table 3) and 84 percent of the observed fish were found in water velocities less than the water velocities on the riffles of the experimental stream (7 cm/sec).

Table 3. Water velocities at locations where juvenile coho were observed in Needle Branch, June 8, 1967.

Range in Water Velocity (cm/sec)	Number of Fish Observed
0 - 4	95
5 - 7	24
8 - 10	17
> 10	5

These observations were made in June during the period of low stream flows. The seasonal changes in the relative abundance of aquatic and terrestrial organisms may have some effect on the distribution of the fish. Chapman (1966a) reported that terrestrial insects were a more important part of the coho diet during the summer months than at other times of the year. From other personal observations, I believe that fish in pools are more efficient at capturing insects off the surface than are fish in faster flowing waters. The problem of seasonal distribution of coho in streams requires further study, but at least for the summer months it seems that food is limiting and that most of the coho take up positions at which they are not required to actively perform.

Effects of Temperature on the Maintenance Ration and
the Rates of Weight Loss for Starved Fish

Temperature has often been cited as one of the most important physical factors affecting the metabolism of poikilotherms. The rate of weight loss for starved fish and the maintenance ration are indicative of the metabolic rate and may be utilized to examine the effects of temperature on the metabolic rate of juvenile coho in these experiments, even though there were differences in the levels of activity.

The mean maintenance ration for stream (pools) and aquarium

fish remained constant between 6° and 9° C and then doubled at 12.3° C (Figure 10). The maintenance ration of the riffle fish more than doubled with the rise in temperature from 7.2° to 12.3° C. Brown (1946) found a sigmoid relationship between the maintenance requirement and temperature in two-year-old brown trout (Salmo trutta). The maintenance ration increased slightly from 4° to 8° C, rose abruptly beyond 11° C, then increased gradually above 14° C. The relationship for the stream (pools) and aquarium fish is similar to that reported by Brown (1946).

With increasing temperature the mean rates of weight loss for the starved fish in the stream and aquarium and the levels of the maintenance rations followed similar trends. The mean rate of weight loss for the starved fish at 5.9° C was higher than one might expect. Lawrence (1941) and Pentelow (1939) have shown that the rates of weight loss for starving rainbow (Salmo gairdneri) and brown trout increased with rising water temperatures. In Experiments IV and V the mean rate of weight loss for the starving fish on the riffles doubled when the temperature increased from 7.2° to 12.3° C. Job (1955) also found that the standard metabolism of brook trout (Salvelinus fontinalis) doubled with a 5.0° C rise in temperature.

The effects of forcing the fish to swim and raising the water temperature 5° C were found to be additive for the riffle and pool fish of Experiments IV and V; the maintenance rations increased four-fold,

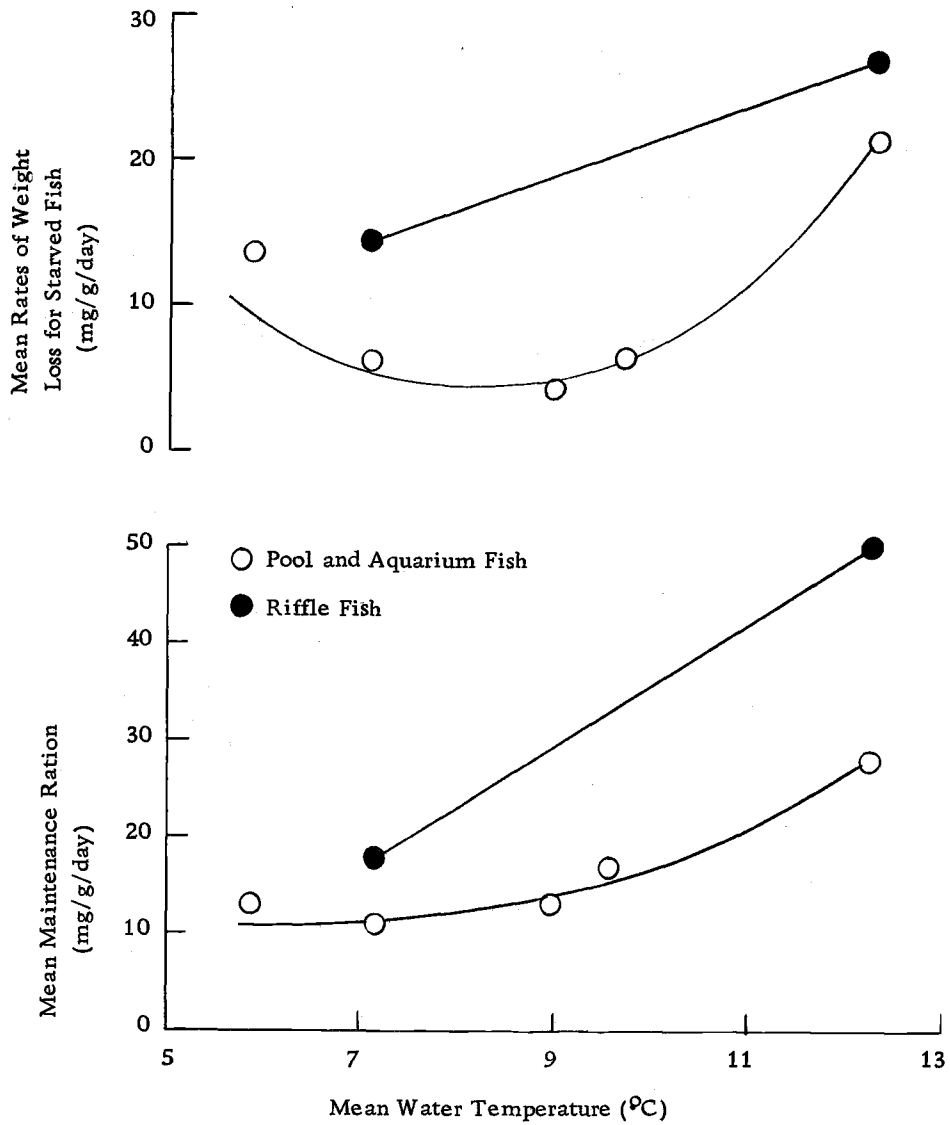


Figure 10. Relationships between mean water temperature and mean maintenance ration, and temperature and mean rate of weight loss for starved fish in the five experiments.

as did the rates of weight loss for the starving fish. These results indicate that even moderate activity can be equally as important as temperature in affecting the metabolic rate of juvenile coho.

Effects of Aggression and Social Status on the
Efficiency of Food Utilization

A few days after the coho were introduced into the sections, a hierarchy became established. The dominant fish, usually the largest fish, took up a position between the riffle and pool and actively defended this area. The dominant fish would often swim around the pool, threatening and chasing any nearby subordinate fish. The aggressiveness of the dominant fish varied considerably. The more aggressive the dominant fish was, the more stable the resulting hierarchy. Oftentimes a subordinate fish would take up a position 15 to 30 cm downstream from the dominant fish. These subordinate fish (Group II) defended this area against the remaining subordinates. The remaining subordinate fish spent most of their time in the lower parts of the pools to avoid the dominant and Group II fish. Generally one of the subordinates in the pool was more aggressive than the other subordinates and often attacked the less aggressive fish. The most intimidated fish (Group IV) favored the corners of the pools and were reluctant to leave these areas. All of the fish avoided the riffles and seemed to prefer areas of slow water velocity.

The fly larvae were introduced evenly throughout the section, yet the dominant fish consumed much of the food. At unrestricted rations the subordinate fish consumed more food than at the restricted rations, because the dominant fish became satiated and consequently less aggressive. There was an obvious reluctance among many of the subordinate fish to seize a drifting larva near the dominant fish. Occasionally a subordinate fish would pick detritus off the rocks and spit it out when the dominant fish consumed a larva. This reaction of the subordinates appears to be displacement activity as defined by Tinbergen (1952).

To examine the effects of aggressive activity on the efficiency of food utilization for the stream fish, I have plotted the deviations from the food consumption-growth rate regression curves for each fish against that individual's total aggressive involvement per minute. These deviations may be viewed as a measure of the fish's relative efficiency of food utilization. Fish with positive deviations, i. e. lying above the fitted food consumption-growth rate curve, would have higher relative efficiencies than the fish with negative deviations. In this analysis I have used the prefeeding aggression data, because aggressive activity declined during the feeding; I felt the estimates for aggressive activity during feeding were not representative of the activity throughout the entire day.

Only in Experiment II was there an apparent relationship

between relative efficiencies and total aggressive involvement. The dominant fish were the most aggressive and their points lie about the zero deviation line (Figure 11). Four of the five fish in Group II had levels of aggression much less than the dominants, and these Group II fish had the highest relative efficiencies of all the fish. Group III fish had levels of aggression comparable to Group II, but Group III was less efficient than Group II. The most subordinate fish (Group IV) had slightly higher levels of aggression than other subordinates, and three of the fish in Group IV had relative efficiencies lower than all of the other fish. Among the subordinate fish a high social ranking was associated with a high relative efficiency of food utilization.

The relationship between total aggression and relative efficiency in Experiment II (Figure 11) suggests that the efficiency of food utilization was affected by aggressive activity and social status. The decrease in relative efficiency between Groups I and II may have been due to the greater activity of the dominant fish. The decrease in relative efficiency among the subordinate fish may have been the result either of a stress from being intimidated or of unrecorded activity.

In Experiment II the dominant fish were very aggressive and their levels of aggression were higher than most of the dominant fish in the other experiments. The hierarchies that developed were quite stable, which may have been the reason for the distinct grouping of

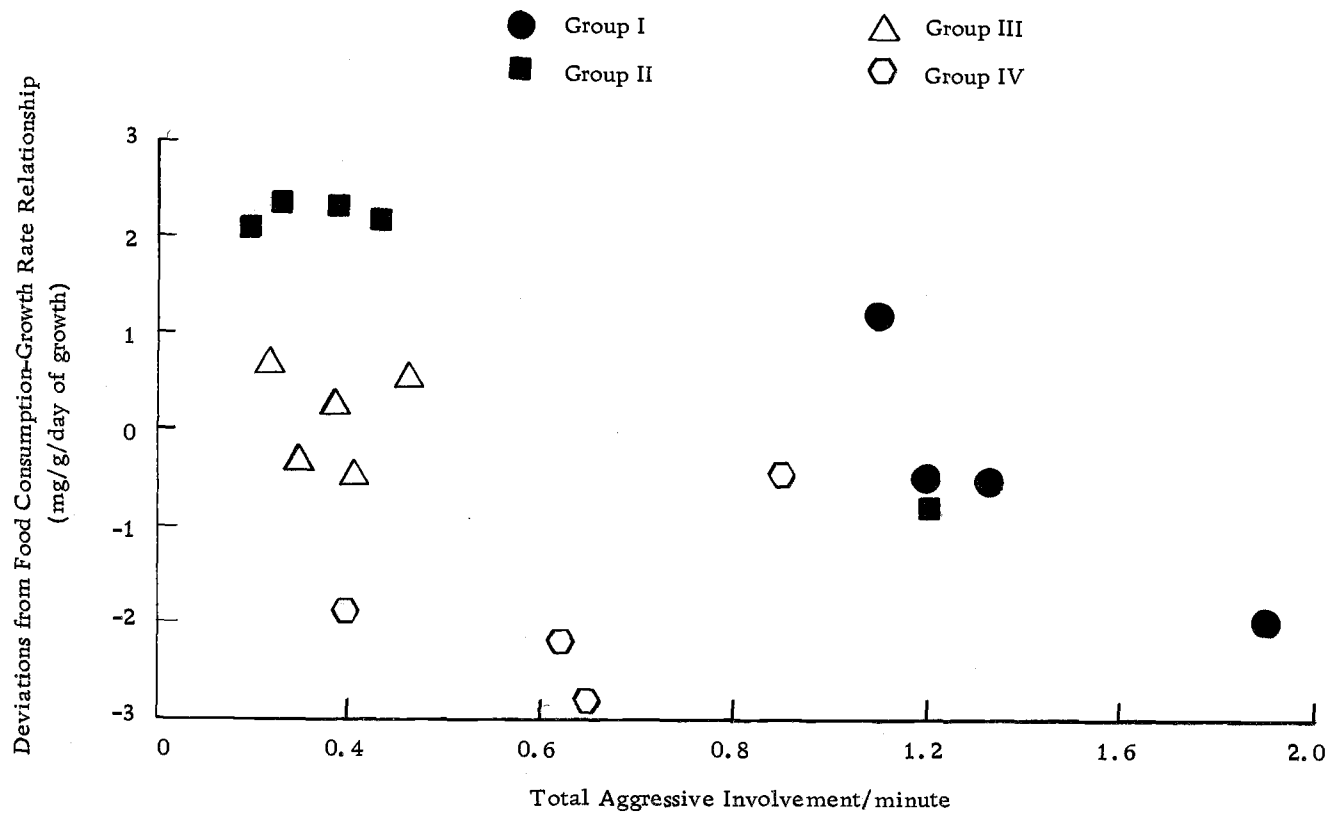


Figure 11. Relationship between the deviations from the food consumption-growth rate relationship and the total aggressive involvement in Experiment II.

the fish in relation to their relative efficiencies and total aggressive involvement (Figure 11). The lack of adequate facilities for volitional movement contributed to the high levels of aggressive activity, because the subordinate fish could not leave the sections. Had the subordinate fish been able to leave the sections, the relationship between the relative efficiencies and the total aggressive involvement might not have been evident.

The foregoing analysis of aggressive activity and efficiency of food utilization has helped to explain how aggressive activity and social status have contributed to some of the variability in food consumption-growth rate relationships. However, these relative efficiencies do not show what portion of the total food consumption was used for aggressive activity. In fact, the relative efficiencies suggests the dominant fish do not have an advantage over the subordinate fish. To show the relationships between aggression, food consumption, and growth it would be helpful if the experiments were viewed in terms of a bioenergetic framework in which the various metabolic activities of the fish are expressed in energy equivalents.

DISCUSSION

The Bioenergetics of Aggression

The food consumed by an animal is oxidized, stored, and excreted through a variety of metabolic processes. To help in understanding the fates of the energy available from the food consumed, these processes must first be categorized into a few measurable entities. The rates and end products of these processes may then be determined to account for all of the energy in the food. Warren and Davis (1967) have suggested a scheme in which each entity, expressed in calories, can be experimentally measured. One form of their energy budget is:

$$pQ_c = Q_s + Q_d + Q_g + Q_a$$

where,

p = efficiency of assimilation,

Q_c = energy value of food consumed,

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

Q_d = energy released in the course of digestion, assimilation, and storage of materials consumed (specific dynamic action),

Q_g = energy value of materials accumulated as growth, and

Q_a = energy released in the course of activity.

To further analyze the effects of aggressive activity on the utilization

of food by fish in Experiment II, I have estimated the components of the above energy budget. The manner by which each value has been calculated and the source of the information necessary to make these calculations are given in Table 4. The values for each fish are given in the Appendix.

Table 4. The methods for calculating the components of the energy budget and the sources of information necessary to make these calculations.

Component	Source	Calculation
Efficiency of food assimilation	Brocksen <u>et al.</u> , (1968)	$p = 0.85$
Caloric content of fly larvae	Brocksen <u>et al.</u> , (1968)	$Q_c = 6110 \text{ cal/g} \times \text{dry weight of food consumed}$
Standard metabolism	Averett (1967) ^a	$Q_s = 170 \text{ cal/g} \times \text{mean weight of fish}$
Specific dynamic action	Averett (1967) ^a	$Q_d = 124 \text{ cal/g} \times \text{wet weight of food consumed}^b$
Caloric content of elaborated tissue	Fisher (1963)	$Q_g = 5773 \text{ cal/g} \times \text{dry weight increase of fish}$
Activity	---	$Q_a = pQ_c - (Q_s + Q_d + Q_g)$

^aMethods described by Warren and Davis (1967, p. 180-181).

^bPreliminary determination based on a single food consumption rate.

I have graphically presented an energy budget for the average of all fish in each social group in Experiment II (Figure 12). Each component of the energy budget is also given as a percentage of the

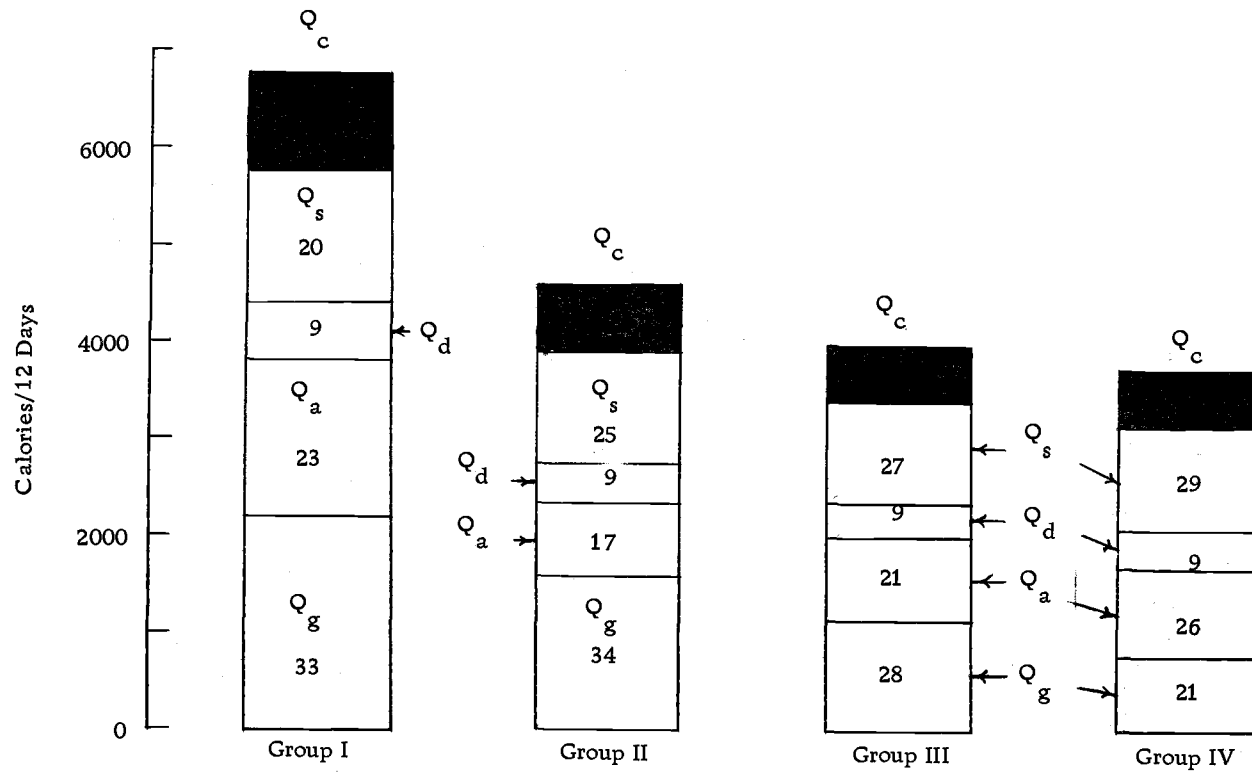


Figure 12. Graphical presentation of the energy budgets for each social group in Experiment II. The shaded portions represent the unassimilated energy. Each component of the energy budget is also expressed as a percentage of the total consumption.

total energy intake for each group of fish. The dominant fish had the greatest energy intake and grew most rapidly. The second most important use of energy-rich compounds in the dominant fish was activity, but the energy utilized for standard metabolism was nearly as important. The energy used for specific dynamic action was the least important, even less than the unassimilated energy, although sufficient data were not available to calculate the specific dynamic action at each food consumption rate. The total energy intake decreased from Groups II to IV, as did the energy accumulated as growth. The energy used for activity increased slightly from Groups II to IV. Among the Group II fish the energy accumulated as growth was the most important item, and standard metabolism was next in importance. The energy expended for standard metabolism remained nearly constant in each group, because standard metabolism is simply a function of the fish size. As the total energy intake decreased from Groups I to IV, the proportion of this energy used for standard metabolism increased.

In Experiment II the food was unlimited, although strictly speaking it was only unlimited for the dominant fish, since they often prevented the subordinant fish from consuming some of the available food. If the food supply had been decreased and the energy costs for each social group remained in the same relative proportions, then the energy accumulated as growth would have decreased. A

substantial reduction in the food supply would first result in a weight loss for the Group IV fish; with a further reduction Group III fish, and then Group II fish, would lose weight. The dominant fish utilized a greater amount of energy for activity than the subordinate fish did, yet the dominant fish more than compensated for the increased cost of activity by their increased energy intake. By viewing the energy budgets in this manner the advantage that the dominant fish have over the subordinate fish becomes apparent.

There was a positive correlation between the energy expended for activity and the total aggressive involvement in Experiment II (Figure 13). The dominant fish had the highest levels of aggression and utilized more energy for activity than did most of the subordinate fish. The existence of this relationship does not necessarily imply that the energy utilized for aggressive activity was a major part of the energy expended for the various types of activity. The level of aggressive involvement could simply have been a good index of the total activity. From the available data there is no way of knowing which is the case.

Based on the points for the dominant and subordinate fish, the relationship between activity and food consumption was nearly linear (Figure 14); an increase in consumption was associated with an increase in activity. However, the most growth was attained by the dominant fish that had an intermediate level of activity (Figure 15).

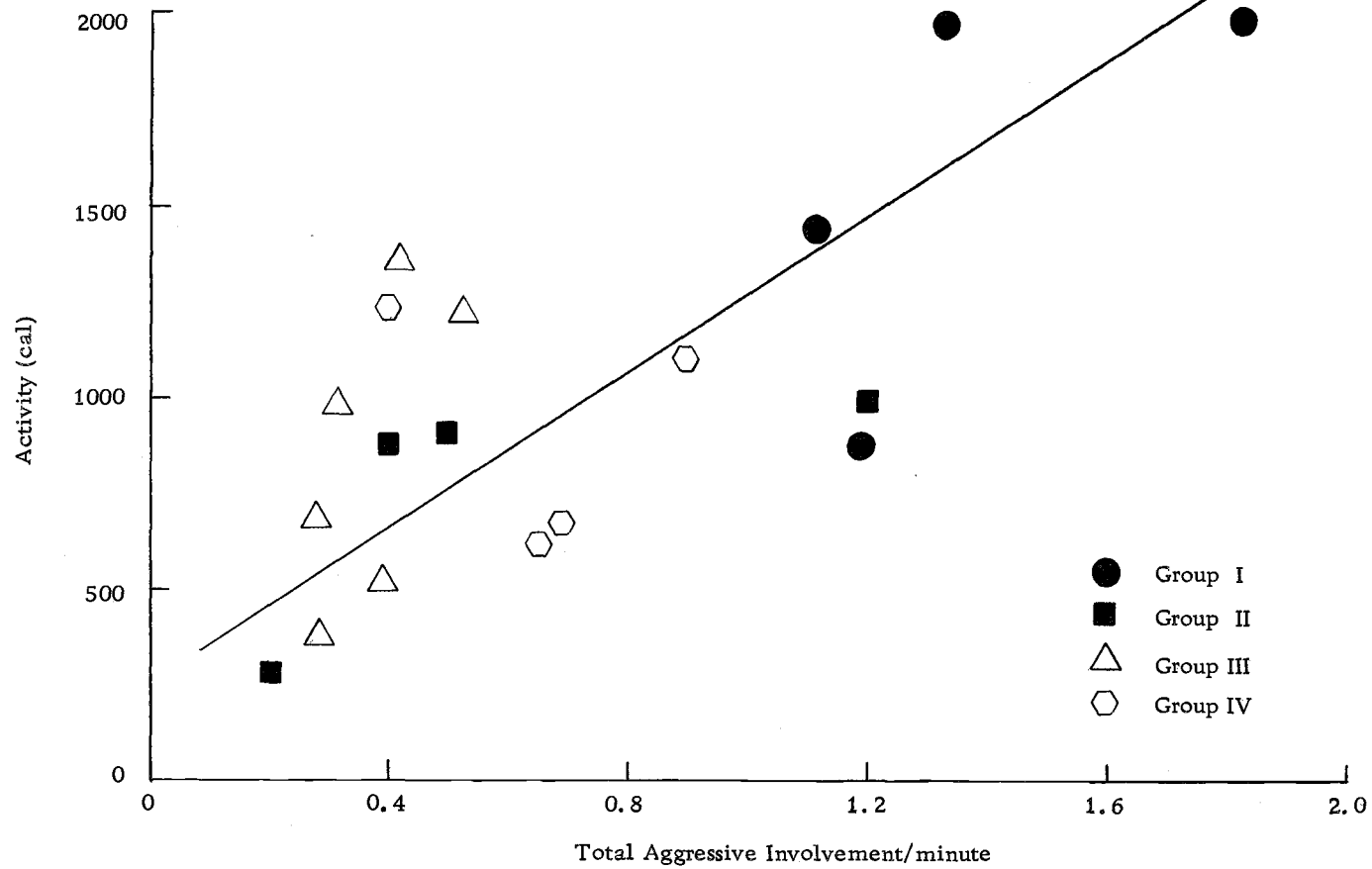


Figure 13. Relationship between the energy used for activity and the total aggressive involvement in Experiment II. Line fitted by inspection.

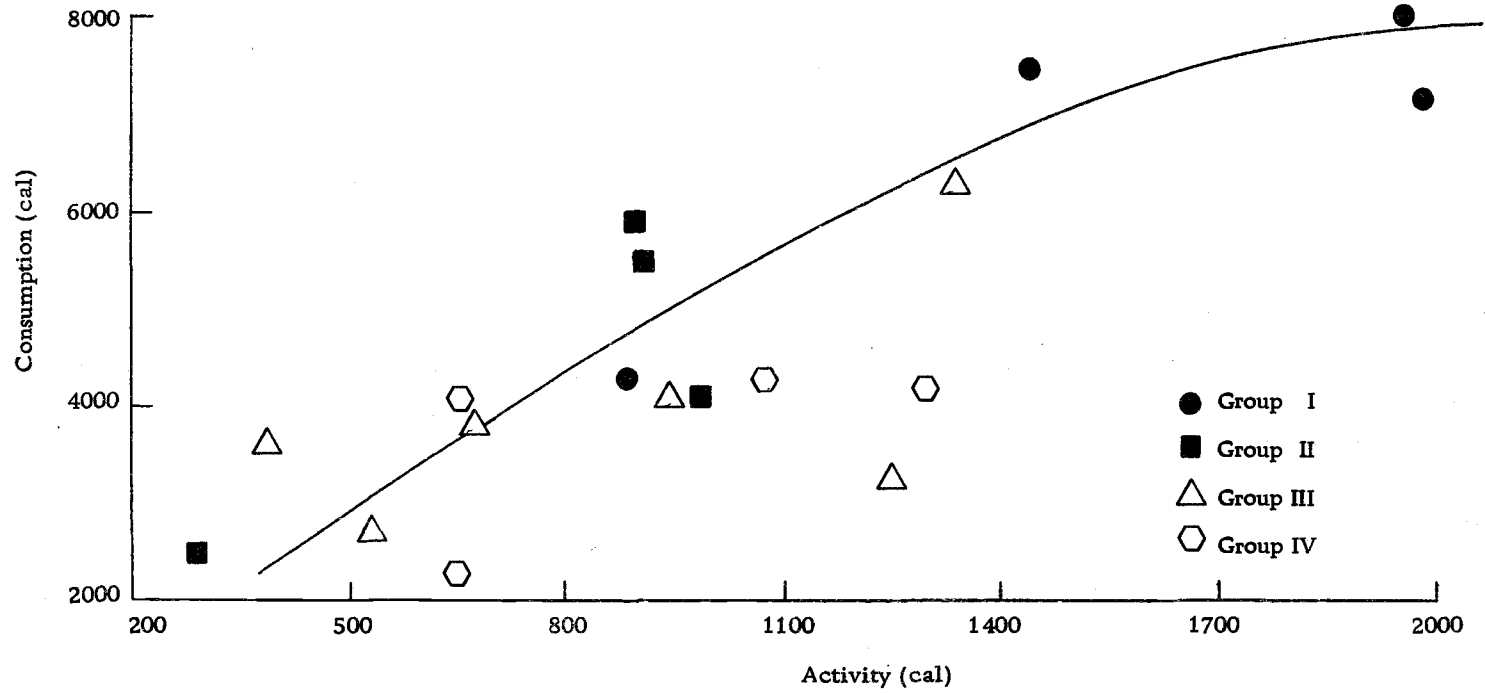


Figure 14. Relationship between the energy of food consumed and the energy used for activity in Experiment II. Curve fitted by inspection.

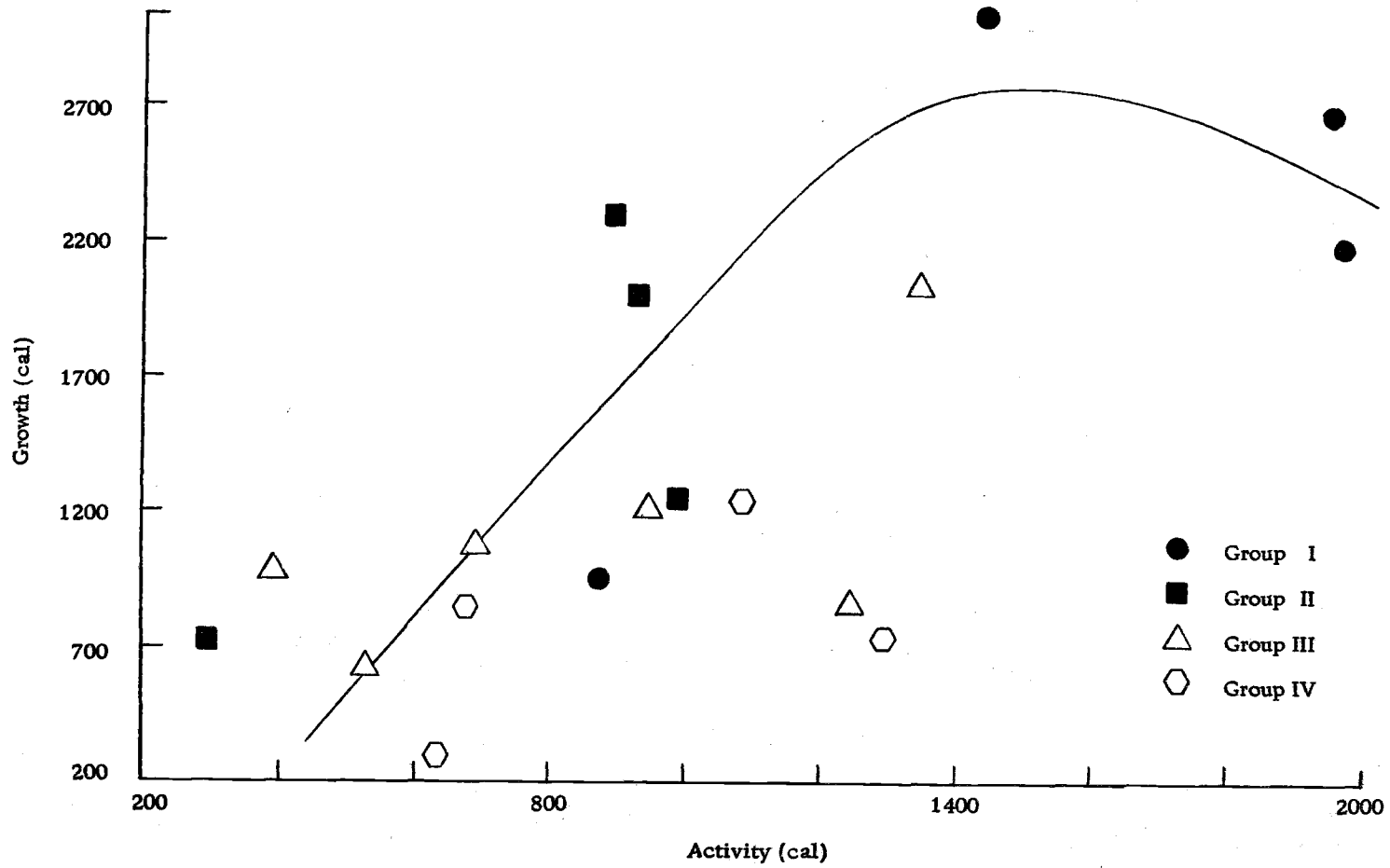


Figure 15. Relationship between the energy accumulated as growth and the energy expended for activity in Experiment II. Curve fitted by inspection.

The energy expended for aggressive activity by the subordinate fish was used mostly for fleeing from the dominant fish, whereas the energy expended by the dominant fish was used for maintaining their social status and keeping the subordinate fish confined to a small area in the pools. By maintaining their social status the dominant fish were able to suppress the subordinate fish. Therefore, the relationships between activity and food consumption were slightly different for the dominant and subordinate fish (Figure 14), as were the relationships between activity and growth (Figure 15).

Energy budgets were also calculated for the fish in other experiments, but no relationships similar to those found in Experiment II were evident. The relationships found in Experiment II may have been an artifact resulting from the particular conditions under which the experiment was conducted. Experiment II was distinguished by a very stable hierarchy, an unrestricted food supply, a high biomass of fish, and high levels of aggressive activity. Despite the fact that the relationships found in Experiment II may not be directly applicable to natural situations, the methods used to analyze the significance of aggressive behavior can be of value in other similar studies. Although the requirement of precise measurements of food consumption limits the use of energy budgets to laboratory studies at the present time, the approach offers a means of assessing the energy costs of various behavioral activities.

Behavior and Its Adaptions

The function of behavior is to place an animal in the best possible relationship with its environment. The ultimate test of the adaptiveness of behavior is whether or not the animal can successfully reproduce and perpetuate the population. Therefore, the animal must not only survive, but it must grow so that it can reach sexual maturity. Growth can then serve as some measure of the adaptiveness of behavior.

The observations of coho in streams showed that most of the fish were in the slow-moving waters of the pools. Only a small percentage of the fish were in positions where they might have had to actively swim against the current. John McIntyre (1967) found that most of the juvenile coho and cutthroat trout (Salmo clarki clarki) he observed from an observation tank were in the pools. The coho on the riffles remained in front of large rocks; because of the low frequency of their tailbeats, McIntyre felt the current velocities in which the fish were swimming were much lower than the current velocities above and alongside these rocks. It appears that juvenile coho in most instances do not take up positions in the stream where they must maintain high levels of activity, thereby reducing the likelihood of utilizing a significant portion of their total energy intake for swimming.

The results of Experiment II indicated that aggressive activity can be an important energy requirement under certain conditions. The problem now is to determine what are the levels of aggressive activity in nature. Chapman (1962) observed juvenile coho in a stream and counted the number of nips made by the fish. The mean number of nips per minute he observed was 0.19, considerably lower than the mean number of acts initiated in Experiment II (0.32/min). However, the relative importance of the energy requirements for activity will depend upon the total energy intake. If the fish observed by Chapman (1962) had low food consumption rates, then the energy expended for activity could have been a major portion of the total energy intake. It seems unlikely that fish in nature would be so aggressive that they would not be utilizing the available food to the best of their advantage, particularly if food is limiting. Chapman (1962) has suggested that the downstream migration of subordinate fish would allow the population to be evenly dispersed and would insure against extremely high levels of aggressive activity. Thus the coho have incorporated into their behavior a mechanism that would enable them to exploit their energy resources more efficiently than if the subordinate fish did not emigrate.

I think it is obvious that the abundance and availability of food is a critical factor determining the growth of coho. As the food availability decreases the food consumption decreases along with

gross efficiency. As the activity of the fish increases, the problem becomes more acute, because the maintenance requirement increases and gross efficiency decreases even further. An increase in water temperature will also cause an increase in the metabolic rate of the fish, which would result in an even higher maintenance requirement. Thus the activity of the fish and the water temperature have a significant role in determining the amount of food a fish must consume to maintain itself. The fish can only grow if the available food supply is sufficient for it to obtain more than the maintenance requirements. It would seem then that the behavior of the coho must in some way be related to the abundance and availability of food.

Mason (1966) provided evidence showing that the social behavior of coho was food-linked. In a recent paper Chapman (1966) discussed the problem of food and space as regulators of the population density. He felt that instead of directly competing for food, coho compete for space. Territoriality and the emigration of subordinated fish are outcomes of this competition for space. The inter-relationships between the behavior of coho and the environment may be best summed up in Chapman's (1966b) own words:

The spatial requirements of territorial fish should be determined not only by food supply and an innate minimum spatial demand but also by efficient energy utilization (this latter would be expressed via the defended area). There must be a compromise between space defended and

efficient metabolism. Selection would favor the fish maximizing growth rate, doing so with minimal wastage of energy used for unnecessarily extended aggressive forays.

The effects of various environmental factors on the physiology of fish have been extensively studied, and there has also been much research on the behavior of fish. However, little has been done to interrelate these two areas of study. The environment will exert its effect on the physiology of the fish and the fish will in turn adjust to the environment through its behavior. We can easily study the effects of temperature and oxygen, for instance, on the physiology of fish, with the variety of apparatus now available, but it is much more difficult to study the effects of these factors on the behavior of fish. Nevertheless, if we hope to properly evaluate the effects of changing environmental conditions on fish life, we must not only consider the physiology of the fish, but also its behavior, in relation to the food supply.

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APPENDIX

Appendix Table 1. The lengths, weights, food consumed and behavioral data for the fish in Experiment I.

Fish No. Stream	Initial	Initial	Final	Final	Final	Food	Food	Growth	Deviation from	No. of acts	No. of acts	Social
	wet wt. (g)	fork length (mm)	wet wt. (g)	fork length (mm)	dry wt. (g)	consumption dry wt. (mg)	consumption rate mg/g/day		growth rate mg/g/day			
1	4.290	72	4.769	77	1.079	417	33.9	8.8	0.94	0.36	0.00	I
2	5.259	77	5.223	80	1.208	245	16.8	-0.5	0.60	0.03	0.19	III
3	2.781	61	3.072	65	0.741	312	36.8	8.3	-1.08	0.10	0.08	II
4	4.269	71	4.118	74	0.975	220	18.5	-3.0	-2.79	0.00	0.11	III
5	3.270	67	3.087	69	0.603	47	6.3	-4.7	1.91	0.01	0.10	III
6	2.781	64	2.779	66	0.578	115	16.6	0.0	1.21	0.18	0.12	III
7	4.057	72	4.504	76	1.007	378	32.9	8.7	1.36	0.19	0.14	II
8	6.280	82	6.699	86	1.503	668	38.0	5.3	-4.71	0.36	0.12	I
9	3.207	66	3.068	68	0.732	141	15.7	-3.7	-2.02	0.00	0.25	IV
10	4.930	73	4.600	74	1.105	147	10.7	-5.7	-1.40	0.00	0.08	III
11	4.377	73	5.219	78	1.157	626	49.1	14.7	-1.13	0.31	0.02	I
12	4.810	77	5.464	80	1.222	516	37.4	10.6	0.90	0.06	0.07	II
13	3.480	69	4.042	73	0.847	346	36.6	12.5	3.22	0.16	0.66	III
14	4.479	74	4.849	78	1.066	457	37.1	6.6	-2.94	1.28	0.26	II
15	3.984	75	4.240	77	0.960	424	40.0	14.3	3.24	0.66	0.09	I
16	3.273	66	3.625	69	0.856	281	28.7	8.5	3.36	0.12	0.29	III
17	3.939	72	3.995	74	0.927	248	22.5	1.2	-0.69	0.07	0.98	IV
<u>Aquarium</u>												
1	2.798	67	2.999	69	0.586	158	23.2	5.7				
2	6.509	86	6.289	88	1.355	0	00.0	-1.8				
3	3.727	68	3.220	70	0.727	0	00.0	-5.0				
4	5.420	81	5.818	85	1.312	414	27.2	5.9				
5	3.295	67	3.502	69	0.784	166	18.1	4.8				
6	2.429	62	2.776	65	0.579	245	31.5	10.7				
7	3.291	68	3.319	69	0.665	72	9.0	0.8				
8	2.922	63	2.790	65	0.552	0	00.0	-8.0				
9	4.592	75	4.338	76	0.937	0	00.0	-1.6				
10	3.338	68	3.788	70	0.778	371	42.2	10.6				
11	2.038	59	2.391	60	0.485	292	54.1	13.0				

Appendix Table 2. The lengths, weights, food consumed, and behavioral data for the fish in Experiment II.

Fish No.	Initial	Initial	Final	Final	Final	Food	Food	Growth	Deviation from	No. of acts	No. of acts	Social Group
	wet wt. (g)	fork length (mm)	wet wt. (g)	fork length (mm)	dry wt. (g)	consumption dry wt. (mg)	consumption rate mg/g/day	rate mg/g/day	food consumption growth rate curve (mg/g/day growth)	initiated/ min	received/ min	
1	6.358	83	8.675	91	1.978	1239	55.6	23.7	1.34	1.06	0.02	I
2	7.008	86	8.811	91	1.949	976	43.0	17.6	2.34	0.13	0.26	II
3	4.997	75	5.828	79	1.481	668	37.4	11.8	-0.30	0.05	0.25	III
4	5.380	73	5.924	80	1.347	422	25.3	7.4	2.12	0.10	0.10	II
5	6.531	85	7.416	87	1.661	647	31.9	9.7	0.70	0.05	0.20	III
6	5.250	78	6.002	81	1.444	538	30.2	8.5	0.46	0.01	0.52	III
7	6.962	87	7.760	90	1.781	687	31.3	8.3	-0.36	1.12	0.08	I
8	7.003	85	8.393	89	2.087	908	36.5	13.8	2.21	0.21	0.26	II
9	5.532	79	5.974	81	1.397	454	26.0	5.9	0.23	0.03	0.36	III
10	5.771	80	6.395	83	1.517	663	35.3	7.9	-3.02	0.03	0.66	IV
11	7.077	87	8.627	91	1.970	1020	43.7	15.2	-0.45	0.25	0.17	III
12	6.923	85	7.404	88	1.944	697	28.5	5.2	-1.88	0.05	0.36	IV
13	7.026	82	8.480	87	2.210	1180	44.9	14.4	-1.93	1.78	0.07	I
14	5.940	82	6.840	85	1.647	713	35.6	10.8	-0.29	0	0.90	IV
15	8.333	86	10.087	91	2.613	1323	42.7	14.7	-0.39	1.34	0.01	I
16	5.050	75	5.948	78	1.436	683	39.6	12.6	-0.74	0.80	0.41	II
17	4.690	74	4.917	75	1.119	380	26.7	3.7	-2.37	0.03	0.64	IV
18	7.698	90	8.440	92	1.954	592	24.4	7.1	2.33	0	0.25	III
<u>Aquarium</u>												
1	6.550	84	7.216	86	1.685	864	41.3	7.5				
2	4.375	74	4.128	74	0.892	0	0	-7.9				
3	3.671	69	3.466	69	0.727	0	0	-10.1				
4	3.350	68	4.073	70	0.911	709	65.7	15.0				
5	4.175	76	4.913	77	1.049	512	40.6	12.5				
6	5.419	80	6.361	83	1.422	627	36.6	12.3				
7	5.627	80	5.443	79	1.246	0	0	-1.6				
8	4.973	75	5.504	77	1.312	540	33.3	7.8				
9	3.520	69	4.056	70	0.927	487	43.3	10.9				
10	5.002	78	5.419	79	1.266	524	33.1	6.2				
11	4.235	73	4.609	73	1.011	627	49.7	6.5				
12	7.084	90	7.979	91	1.766	994	45.9	9.1				

Appendix Table 3. The lengths, weights, food consumed, and behavioral data for the fish in Experiment III.

Fish No.	Initial	Initial	Final	Final	Final	Food	Food	Growth	Deviation from	No. of acts	No. of acts	Social Group
	wet wt. (g)	fork length (mm)	wet wt. (g)	fork length (mm)	dry wt. (g)	consumption dry wt. (mg)	consumption rate mg/g/day	rate mg/g/day	food consumption growth rate curve (mg/g/day growth)	initiated/ min	received/ min	
<u>Stream</u>												
1	5.356	80	5.989	82	1.358	513	33.2	9.3	-1.01	0.77	0.09	I
2	4.550	73	5.020	76	1.108	416	32.8	8.2	-1.96	0.01	0.08	IV
3	4.789	75	5.057	77	1.148	284	21.2	4.5	0.20	0.02	0.07	III
4	3.782	71	4.089	73	0.871	229	22.8	6.6	1.32	0	0.16	IV
5	5.576	78	6.310	80	1.377	584	37.5	10.3	-1.41	0.03	0.29	III
6	6.040	82	6.979	86	1.608	650	36.1	12.0	0.70	0.61	0.07	I
7	5.479	80	6.501	84	1.481	665	40.6	14.2	1.73	0.07	0.10	III
8	5.410	80	6.345	84	1.421	594	37.6	13.3	1.56	0.13	0.29	II
9	6.285	80	7.128	82	1.664	630	33.5	10.5	0.07	0.03	0.21	III
10	4.257	72	4.747	75	1.072	386	31.6	9.1	-0.59	0.06	0.25	III
11	4.999	75	5.258	78	1.162	320	23.5	4.2	-1.49	1.11	0.40	I
12	4.102	73	4.046	74	0.855	173	17.3	-1.2	-2.86	0	0.20	III
13	4.617	75	4.927	77	1.076	274	21.9	5.4	0.67	0.20	0.33	III
14	4.730	76	5.227	78	1.134	361	27.9	8.3	0.26	0.23	0.64	III
15	4.348	72	4.824	75	1.058	406	32.1	8.3	-1.59	0.06	0.50	IV
16	4.284	74	4.430	75	0.952	173	15.4	2.7	2.40	0.04	0.54	IV
17	6.509	84	7.471	88	1.655	686	36.9	11.5	-0.04	0.77	0.08	I
18	5.553	80	6.079	83	1.308	355	23.6	7.5	1.75	0.89	0.33	II
19	4.915	75	5.097	78	1.077	229	18.0	3.0	0.84	0.10	0.15	III
20	6.353	81	5.480	81	1.072	0	0	-22.5				
21	5.779	80	5.433	79	1.226	0	0	-3.5				
22	5.101	80	4.729	80	0.926	0	0	-16.5				

Appendix Table 3. Continued.

Fish No.	Initial wet wt. (g)	Initial fork length (mm)	Final wet wt. (g)	Final fork length (mm)	Final dry wt. (g)	Food consumption dry wt. (mg)	Food consumption rate (mg/g/day)	Growth rate (mg/g/day)
<u>Aquarium</u>								
1	5.532	80	5.641	81	1.235	198	13.5	1.6
2	5.408	80	6.021	82	1.366	818	52.5	8.9
3	7.383	85	9.325	91	2.154	1326	57.3	19.4
4	4.588	73	5.577	76	1.242	594	43.7	16.2
5	4.369	73	4.037	74	0.847	0	0	-11.0
6	6.610	84	7.301	87	1.605	437	23.8	8.3
7	4.976	76	4.805	77	1.033	122	9.7	-2.9
8	3.943	73	4.782	76	1.044	538	47.0	16.0
9	4.689	77	4.345	76	0.825	0	0	19.1
10	5.175	76	5.440	79	1.175	284	20.6	4.1
11	6.519	83	6.097	83	1.275	0	0	-10.3
12	4.437	74	5.501	77	1.256	665	48.8	17.8

Appendix Table 4. The lengths, weights, food consumed, and behavioral data for the fish in Experiment IV.

Fish No.	Initial	Initial	Final	Final	Final	Food	Food	Growth	Deviation from		No. of acts	No. of acts	Social
	wet wt.	fork length	wet wt.	fork length	dry wt.	consumption	consumption		food consumption	growth rate curve			
	(mg)	(mm)	(mg)	(mm)	(mg)	(mg)	mg/g/day	mg/g/day	(mg/g/day growth)	min	min	Group	
<u>Stream(Pools)</u>													
1	851	45	1007	47	174	103	53.4	14.0	-0.46	0.23	0.91	II	
2	740	43	887	45	156	71	41.3	15.1	3.60	0.02	0.30	III	
3	798	44	913	45	160	88	48.8	11.1	-2.31	0.08	0.77	IV	
4	770	43	927	45	152	93	55.7	15.5	0.55	2.33	0.07	I	
5	659	42	817	44	139	69	45.8	17.9	5.22	0	0.60	IV	
6	682	42	719	43	113	53	40.1	4.5	-6.67	0.02	0.53	IV	
7	899	46	1061	47	187	91	43.9	14.0	1.81	0.40	0.48	II	
8	846	45	1016	46	177	111	57.0	15.4	0.18	0.59	0.68	II	
9	704	42	841	43	141	99	63.7	14.8	-1.66	0.17	0.42	III	
10	962	46	1147	47	203	117	52.2	14.7	0.50	1.28	0.26	I	
11	1040	47	1229	49	215	125	52.4	13.8	-0.44	2.85	0.02	I	
12	900	45	974	46	165	21	11.0	6.8	5.61	0.23	0.58	II	
13	669	43	630	43	97	30	25.0	5.0	-1.47	0	0.46	IV	
14	950	46	1122	48	197	88	40.2	13.7	2.50	0.17	1.27	II	
15	741	43	750	44	127	30	19.8	1.3	-3.31	0.01	0.50	IV	
16	847	45	932	46	158	52	28.7	8.3	0.58	0.21	0.61	III	
17	869	45	933	45	163	36	19.0	5.8	1.48	0.13	0.72	III	
18	1010	47	1165	49	200	81	36.1	12.0	1.97	2.25	0.02	I	
19	651	41	690	42	117	40	29.3	5.1	-2.81	0.04	0.62	IV	
20	585	41	598	41	97	28	24.3	1.7	-4.53	0	0.86	IV	
21	705	43	746	44	129	26	17.2	4.6	0.96	0.25	0.45	II	
22	943	45	887	45	149	0	0	-6.9					
23	702	42	668	42	118	0	0	-2.0					
24	980	46	929	46	161	0	0	-4.0					
25	887	46	828	46	148	0	0	-2.7					

Appendix Table 4. Continued.

Fish No.	Initial wet wt. (mg)	Initial fork length (mm)	Final wet wt. (mg)	Final fork length (mm)	Final dry wt. (mg)	Food consumption dry wt. (mg)	Food consumption rate mg/g/day	Growth rate mg/g/day	Deviation from food consumption growth rate curve (mg/g/day growth)	No. of acts initiated/ min	No. of acts received/ min	Social Group
<u>Stream (Riffles)</u>												
1	760	43	688	43	115	1	0.6	-10.8				
2	691	43	601	42	95	1	0.7	-18.6				
3	838	44	778	44	131	1	0.6	-7.8				
4	712	42	649	42	108	1	0.7	-10.8				
5	873	45	965	45	173	100	50.6	8.6	-1.96	0.18	0.65	III
6	852	45	966	45	170	129	67.2	10.4	-0.17	0.18	0.54	III
7	655	41	741	42	123	76	55.0	10.8	-0.11	0.02	0.54	IV
8	832	44	986	46	169	107	57.1	13.8	2.81	1.44	0.05	I
9	805	44	726	43	120	3	1.8	-11.2	-0.95	0.01	0.01	III
10	790	44	797	44	132	49	31.0	0.6	-5.33	0	0.03	III
11	1200	49	1358	51	254	129	44.9	10.4	0.67	0.02	0	III
12	980	46	992	46	179	27	12.6	0.9	3.87	0.01	0.92	IV
13	1507	51	1582	53	303	50	14.0	3.9	6.04	0.85	0.10	I
14	966	46	1006	47	178	58	27.6	3.3	-1.32	0.62	0.47	II

Appendix Table 4. Continued.

Fish No.	Initial wet wt. (mg)	Initial fork length (mm)	Final wet wt. (mg)	Final fork length (mm)	Final dry wt. (mg)	Food consumption dry wt. (mg)	Food consumption rate (mg/g/day)	Growth rate (mg/g/day)
<u>Aquarium (without cover)</u>								
1	1061	47	1050	48	182	15	6.8	-0.9
2	638	42	616	41	100	15	12.3	-2.4
3	1134	48	1326	48	244	114	41.9	12.8
4	843	45	984	45	172	101	52.7	13.0
5	684	42	695	41	110	28	21.4	1.5
6	732	44	717	43	115	28	20.1	1.4
7	871	46	941	47	156	55	30.5	6.6
8	700	42	757	42	125	51	35.4	6.9
9	665	43	763	43	129	77	53.2	11.7
10	849	45	1024	45	177	110	56.5	15.4
11	1253	49	1512	51	275	179	59.3	12.2
12	1027	48	1272	50	220	159	66.7	18.0
13	759	44	889	45	152	154	91.0	13.0
14	869	46	794	45	135	0	0	-8.7
15	893	45	794	44	140	0	0	-7.9
16	859	45	800	43	138	0	0	-5.8
<u>Aquarium (with cover)</u>								
1	775	43	771	43	130	15	9.5	-0.6
2	740	44	740	42	121	15	10.3	0.6
3	710	42	792	43	130	56	37.7	8.7
4	890	46	1086	47	196	123	57.4	16.3
5	812	45	830	44	139	31	18.7	1.8
6	637	41	718	40	116	31	23.5	9.8
7	632	41	764	42	123	63	46.6	15.5
8	610	41	706	41	116	48	37.0	12.3
9	1213	51	1383	51	252	135	47.5	10.9
10	859	44	965	45	174	104	52.6	9.6
11	888	46	1118	47	199	139	64.8	19.1
12	905	45	1012	47	182	139	67.1	9.1
13	719	43	924	45	166	145	81.9	20.9
14	838	43	716	43	120	0	0	-15.1
15	990	48	963	47	162	0	0	-4.0
16	773	43	731	43	124	0	0	-9.0

Appendix Table 5. The lengths, weights, food consumed, and behavioral data for the fish in Experiment V.

Fish No.	Initial	Initial	Final	Final	Final	Food	Food	Growth	Deviation from		No. of acts	No. of acts	Social
	wet wt.	fork length	wet wt.	fork length	dry wt.	consumption	consumption		food consumption	growth rate curve			
Stream (Pools)	(mg)	(mm)	(mg)	(mm)	(mg)	(mg)	mg/g/day	mg/g/day	(mg/g/day growth)	min	min		
1	707	42	897	45	157	182	81.0	14.8	-1.17	0.04	0.94	III	
2	1151	51	1529	53	299	310	73.9	17.6	1.43	1.09	0.34	II	
3	612	43	740	42	126	115	62.4	11.8	-3.39	0.05	0.13	III	
4	1170	50	1598	53	312	344	79.5	19.3	3.23	1.00	0.04	I	
5	759	45	996	46	182	157	61.2	16.9	1.90	0	0.22	III	
6	760	42	965	46	168	138	57.4	14.9	0.63	0.18	0.64	III	
7	1418	53	1477	54	272	108	25.3	2.5	1.45	0.27	0.57	III	
8	1025	49	1325	51	246	229	65.6	15.9	0.27	1.44	0.39	II	
9	671	41	830	45	151	112	51.2	13.2	0.51	0.01	0.51	III	
10	600	41	698	42	115	89	52.0	9.4	-3.52	0.08	0.62	IV	
11	1421	52	1834	55	352	308	61.6	15.8	0.73	0.79	0.04	I	
12	669	41	805	44	145	92	43.3	11.5	1.49	0.05	1.06	IV	
13	679	43	792	45	135	93	46.3	9.6	-1.51	1.27	0.21	II	
14	647	42	767	43	135	123	61.7	10.6	-4.48	0.35	0.92	II	
15	1161	50	1344	52	241	158	43.9	9.1	-1.14	0.99	0.04	I	
16	1009	48	1219	50	210	110	35.8	11.8	5.05	0.25	0.68	III	
17	1480	53	1187	52	196	0	0	-19.7	0	0	0	0	

Appendix Table 5. Continued.

Fish No.	Initial	Initial	Final	Final	Final	Food	Food	Growth	Deviation from		No. of acts initiated/ min	No. of acts received/ min	Social Group
	wet wt. (mg)	fork length (mm)	wet wt. (mg)	fork length (mm)	dry wt. (mg)	consumption dry wt. (mg)	consumption rate mg/g/day		food consumption rate curve (mg/g/day growth)	growth rate			
<u>Stream (Riffles)</u>													
1	670	42	491	41	72	0	0	-32.2					
2	893	45	651	44	104	0	0	-27.5					
3	1087	48	921	48	149	0	0	-17.6					
4	683	43	457	43	65	0	0	-38.8					
5	847	45	577	44	87	0	0	-34.9					
6	1450	52	1963	56	400	386	69.3	18.8	7.29	1.51	0.13	I	
7	823	45	1078	48	200	172	60.9	16.8	10.38	0.20	0.32	III	
8	1057	48	1429	52	267	323	86.9	18.7	-3.47	1.07	0.48	II	
9	801	46	965	47	181	208	78.5	11.6	-5.48	0.21	0.64	III	
10	999	48	1164	48	210	219	70.1	9.5	-2.49	0.45	0.82	III	
11	730	43	892	45	155	146	64.7	12.5	3.78	0.17	0.36	III	
12	732	44	598	43	93	78	47.1	-12.5	-10.55	0	0.02	III	
13	870	46	812	46	141	128	54.7	-4.2	-6.86	0	0.13	III	
14	820	45	1001	48	180	180	68.7	12.4	1.25	0.28	0.01	I	
15	630	42	630	42	108	102	59.0	0.1	-5.17	0.02	0.14	III	
16	870	45	1158	49	230	216	67.0	17.7	7.59	0.43	0.01	I	
17	641	43	622	43	104	83	49.1	-1.8	-1.07	0	0.15	III	
18	752	44	751	44	128	94	45.8	-0.1	2.63	0.02	0.14	III	
19	751	44	778	44	135	112	52.7	2.2	0.75	0.03	0.19	III	

Appendix Table 5. Continued.

Fish No.	Initial	Initial	Final	Final	Final	Food	Food	Growth rate
	wet wt. (mg)	fork length (mm)	wet wt. (mg)	fork length (mm)	dry wt. (mg)	consumption dry wt. (mg)	consumption rate (mg/g/day)	
<u>Aquarium (without cover)</u>								
1	841	44	731	42	123	43	20.3	-8.6
2	706	41	713	44	122	43	22.1	0
3	1145	48	1146	49	205	81	24.7	0
4	769	42	751	44	128	58	27.9	-1.4
5	1043	49	1147	49	205	141	45.0	5.9
6	646	43	679	43	111	120	69.5	3.1
7	594	42	667	42	120	144	77.7	7.2
8	728	43	903	45	160	275	118.9	13.4
9	921	45	1255	48	247	268	78.2	19.2
10	628	40	596	40	99	21	12.9	-3.2
11	792	44	1080	46	206	346	121.1	19.2
12	1092	47	1544	50	304	412	99.2	21.4
13	1213	49	1008	48	163	0	0	-18.9
<u>Aquarium (with cover)</u>								
1	910	44	873	45	146	44	18.4	-2.5
2	1011	47	920	46	152	44	17.2	-5.8
3	611	41	625	41	102	68	42.1	1.4
4	801	45	766	45	129	68	32.2	-2.7
5	649	41	787	42	145	107	50.5	12.0
6	835	44	951	46	171	151	58.7	8.1
7	709	41	933	43	165	148	63.7	17.0
8	762	43	941	45	179	183	70.6	13.1
9	921	44	1242	47	245	376	110.1	18.5
10	1152	50	1442	51	271	305	78.2	14.0
11	806	46	1302	49	248	412	128.3	29.4
12	963	47	888	46	139	16	6.9	-5.0
13	1010	48	1341	49	255	329	92.0	17.6
14	1055	47	833	46	149	0	0	-15.7
15	759	42	597	41	90	0	0	-26.3
16	1129	50	946	50	133	0	0	-26.6

Appendix Table 6. Calculated values of the energy budget for the stream fish in Experiment II. Each value is expressed in calories.

Fish No.	$p Q_c$	Q_s	Q_d	Q_g	Q_a
1	6434	1279	665	3048	1442
2	5071	1345	522	2303	901
3	3470	921	369	1218	962
4	2193	961	228	716	288
5	3361	1186	351	1143	681
6	2792	957	289	872	1243
7	3568	1252	395	1056	865
8	4717	1309	487	1992	928
9	2358	979	242	600	530
10	3440	1035	358	854	669
11	5297	1336	549	2043	1369
12	3617	1218	373	733	1293
13	6128	1319	640	2188	1981
14	3703	1087	383	1253	1080
15	6868	1567	714	2627	1960
16	3550	935	366	1253	996
17	1973	817	214	300	642
18	3073	1373	312	993	395