

# Growth Rate and Body Composition of Fingerling Sockeye Salmon, *Oncorhynchus nerka*, in relation to Temperature and Ration Size

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The growth of young sockeye salmon (*Oncorhynchus nerka*) was studied at temperatures ranging from 1 to 24 C in relation to rations of 0, 1.5, 3, 4.5, and 6% of dry body weight per day, and at an "excess" ration. Optimum growth occurred at approximately 15 C for the two highest rations, shifting progressively to a lower temperature at each lower ration. The maximum growth rate for sockeye 5-7 months old was 2.6%/day; that for fish 7-12 months old was 1.6%/day. At 1 C a ration of 1.5%/day was sufficient to provide for a maximum growth rate of 0.23%/day. The maintenance ration was found to increase rapidly above 12 C, amounting to 2.6%/day at 20 C. No growth took place at approximately 23 C despite the presence of excess food.

Isopleths for gross and net food-conversion efficiencies were calculated. A maximum gross efficiency of 25% occurred in a small area with a center at 11.5 C and a ration of 4.0%/day; a maximum net efficiency of 40% occurred within a range of 8-10 C for rations of 1.5%/day down to 0.8%/day, the maintenance level.

Gross body constituents changed in response to the imposed conditions, varying in extreme from 86.9% water, 9.4% protein, and 1.0% fat for starved fish at 20 C to 71.3% water, 19.7% protein, and 7.6% fat on an excess ration at 15 C.

It is concluded on the basis of growth and food-conversion efficiency that temperatures from 5 to 17 C are most favorable for young sockeye, and that a general physiological optimum occurs in the vicinity of 15 C.

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## INTRODUCTION

THIS PAPER is the first of a series dealing with laboratory studies on the relation of environmental factors (abiotic and biotic) to the growth rate of young sockeye salmon, *Oncorhynchus nerka*. The aim is to obtain a broad understanding of the bioenergetics of this species throughout its life history. As such, the present work constitutes an extension of the research on metabolic rate and performance of sockeye salmon for which a considerable background of information concerning the effects of temperature, size, and swimming speed is available (Brett, 1964, 1965, 1967).

By relating food consumption, growth rate, and metabolic rate the energy budget can be determined, providing a measure of the efficiency of food conversion and of energy loss through metabolism and excretion (see Winberg,

1956; Warren and Davis, 1967). Studies of this sort can be expected to contribute to an improved understanding of the food requirements of natural populations as well as provide fundamental information for fish-cultural practices. Many of the methods and approaches to animal energetics, conducted for years on warm-blooded vertebrates (e.g., Brody, 1945; Kleiber, 1961; Blaxter, 1965), may be applied with profit to studies on fish energetics.

The present experiments deal with the combined effects of temperature and ration on growth rate. Temperature has been shown repeatedly to be one of the most influential environmental factors affecting the growth of fishes (Baldwin, 1957; Brown, 1957; Donaldson and Foster, 1940; Haskell et al., 1956; Paloheimo and Dickie, 1966a, b; Strawn, 1961; Swift, 1964; West, 1966). When food is present in abundance an optimum temperature for growth has been recorded, varying among species and in the case of the desert pupfish (*Cyprinodon macularius*) significantly influenced by salinity (Kinne, 1960). Quantity and quality of food under ambient temperature conditions have been studied intensively, especially for artificial culturing of fish (e.g., Brown, 1957; Halver and Shanks, 1960; Hatanaka and Takahashi, 1960; Phillips et al., 1966). Davis and Warren (1968) reported that young chinook salmon (*Oncorhynchus tshawytscha*) weighing 0.6 g would consume a ration as high as 20% of their dry body weight per day. However, the *interacting* effect of ration and temperature on the growth rate of fish does not appear to have been the object of critical study except where either maintenance or ad libitum rations were involved (Brown, 1946; Pentelow, 1939).

It was hypothesized that the optimum temperature for growth would drop as the ration decreased, accompanied by a reduction in conversion efficiency. This was based on the supposition that the decrease in maintenance metabolism that accompanies reduced temperature would permit comparatively better growth at lower temperatures when the source of energy was restricted. The assumption would apply only for a poikilotherm if the temperature-dependent activity of digestive enzymes and growth processes did not exert such a controlling influence that the potential shift was inhibited. The presence of sharp peaks in the activity of digestive enzymes in relation to temperature has been demonstrated for the brown bullhead (*Ictalurus nebulosus*) by Smit (1967). Hoar (1966) further confirms this as a general phenomenon among poikilotherms (see also Jennings, 1965).

#### MATERIALS AND METHODS

The program of study was conducted over a period of 3½ years during which time some change in methods was adopted. The initial phase, dealing with the effect of temperature (5, 10, 15, 20, and 24 C) using excessive ration, lasted for 7 months (June 2, 1964–January 12, 1965). This series served to establish the pattern of the growth curve, to provide an estimate of the maximum growth rate at each temperature, and to assess the methods employed. Subsequent experiments involving reduced rations were performed from November 1, 1965, to February 3, 1966, at temperatures of 5, 10, and 15 C, and from December 11, 1966, to March 5, 1967, at temperatures of 1 and 20 C. The methodology for the last two experiments was essentially similar. A distinction will be made only between the two series — *A group*, on excess ration, and *B group*, including restricted rations — whenever this is pertinent to the presentation.

## SOURCE AND CULTURING OF FISH

All fish were shipped as eyed eggs from Scully Creek, Lakelse Lake near Terrace, B.C. After hatching, the young were reared in circular or oval Fiberglas tanks at the Biological Station, Nanaimo, B.C. They were the progeny of a single cross in each of the 3 years. Subject to ambient water temperatures from a lake source, the fish were hand-fed on a diet of beef liver and Clark's pellet feed (J. R. Clark & Co., Salt Lake City, Utah) supplemented with a weekly supply of frozen brine shrimp. No history of epidemic disease, mortality in excess of 10%,<sup>1</sup> or poor growth was present in any of the stocks tested.

When transferred from the rearing tanks the fish were first screened for a fairly uniform, intermediate size (mean  $\pm 1$  SD) and then distributed by random numbers to the experimental tanks (see Table 1, 3). The order of tanks according to ration was also assigned by random numbers.

## EXPERIMENTAL TANKS

Twelve 197-liter (43-gal) oval tanks equipped with submerged jets to provide circulation and efficient water exchange were used (Fig. 1, 2; see also Alderdice et al., 1966). These were modified slightly by the addition of recirculating pumps and a gas-stripping column to supply approximately air-saturated water at each controlled temperature. In most instances a 12-inch, tubular air-breaker was provided as an additional source of oxygen, and served as an emergency stand-by. Water was flushed through the tanks at a rate of 240 liters/hr (53 gal/hr). At no time was the oxygen saturation found to exceed 106% or be less than 87%. The average was 95%. Cover was made available by a black coating over the center half of the Plexiglas top.

Water velocity within the tank ranged from 9 to 15 cm/sec (0.3–0.5 ft/sec) for most of the oval path; lower velocities occurred in the vicinity of the central drain. Fish were observed swimming mostly in the main flow away from the areas of reduced velocity. The application of a low velocity current was considered desirable not only for its cleaning action but also to facilitate food presentation and to maintain a greater uniformity of activity between tanks. Spontaneous activity is temperature-dependent in many fish including salmonids (Brown, 1957; Fisher, 1958). By inducing all fish to swim constantly reduction in this inherent variable was effected.

## TEMPERATURE AND LIGHT

By cross-mixing between temperature-controlled supply lines with hand valves, or by use of thermostatic valves, temperatures were maintained within  $\pm 0.3$  C (an average of  $\pm 2$  SD for all tanks, read from standardized thermographs — see Table 1). The extremes of experimental temperature (1 and 24 C) were chosen to be approximately 1 degree C above and below the respective lower and upper lethal temperatures for underyearling sockeye in fresh water (Brett, 1952).

The A-group fish were transferred from culture tanks at an ambient temperature of 7 C to their assigned growth tanks. The temperature was raised at a rate of 1 degree C/day, and length-weight measurements were taken as soon as the prescribed temperature for all tanks was reached (June 2). Since a growth "adjustment" period of the order of 2 weeks was observed in the initial experiments (see Fig. 3), the B-group fish were provided with this further introductory period. Their ambient temperature ranged from 10 to 12 C. The fish tested at 1 C were allowed an additional 2 weeks of acclimation at this low temperature after an intermediate 2 weeks at 5 C.

Fluorescent lighting illuminated the tanks with a minimum of 15 ft-c at the water surface. This was controlled by a time switch set for a 9-hr day (0800–1700 hr, PST). Natural light was reflected on the tanks from a louvre-shaded window providing normal photoperiod from spring to early fall.

<sup>1</sup>From physical damage, nipping, popeye, and accidental loss.

TABLE 1. Tank temperature and vital statistics of A-group sockeye fed on excess ration. Data for 1 C have been included from B group. Variability is recorded as  $\pm 2$  SE except for temperatures ( $\pm 2$  SD).

	Acclimation temperature (C)					
	1	5	10	15	20	24
Mean temp (C)	1.09 $\pm$ 0.16	4.80 $\pm$ 0.47	9.92 $\pm$ 0.16	14.91 $\pm$ 0.12	20.09 $\pm$ 0.28	23.68 $\pm$ 0.44
Test period (days)	83	219	219	220	224	44
Initial length (cm)	8.66 $\pm$ 0.11	5.41 $\pm$ 0.08	5.74 $\pm$ 0.14	5.65 $\pm$ 0.12	5.81 $\pm$ 0.05	5.67 $\pm$ 0.08
Initial wt (g)	6.04 $\pm$ 0.22	1.18 $\pm$ 0.06	1.43 $\pm$ 0.10	1.33 $\pm$ 0.09	1.40 $\pm$ 0.08	1.31 $\pm$ 0.06
Terminal length (cm)	9.20 $\pm$ 0.12	10.14 $\pm$ 0.68	16.78 $\pm$ 1.14	19.73 $\pm$ 0.86	16.85 $\pm$ 0.47	5.74 $\pm$ 0.20
Terminal wt (g)	7.69 $\pm$ 0.30	7.83 $\pm$ 1.76	46.40 $\pm$ 10.50	85.50 $\pm$ 12.70	51.70 $\pm$ 4.70	1.18 $\pm$ 0.22
Initial growth rate (%/day)	-	1.48 $\pm$ 0.57	2.97 $\pm$ 0.73	4.24 $\pm$ 0.57	5.05 $\pm$ 0.66	-0.34 $\pm$ 0.35
Intermediate growth rate (%/day)	-	0.99 $\pm$ 0.16	1.96 $\pm$ 0.17	2.60 $\pm$ 0.18	1.81 $\pm$ 0.17	-0.20 $\pm$ 0.66
Terminal growth rate (%/day)	0.23 $\pm$ 0.06	0.76 $\pm$ 0.11	1.35 $\pm$ 0.12	1.42 $\pm$ 0.11	1.21 $\pm$ 0.13	(50% dead)

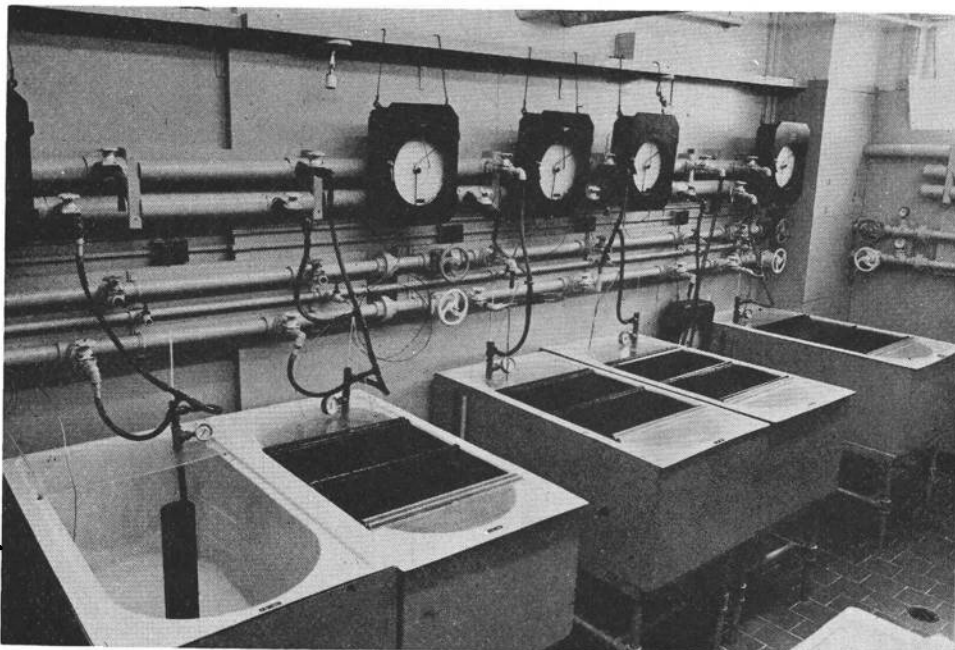


FIG. 1. Typical arrangement of tanks and services assembled for growth experiments.



FIG. 2. Example of size difference in A-group fish after 3 months at 5 and 10 C, on excess ration. Note uniformity of size within tanks.

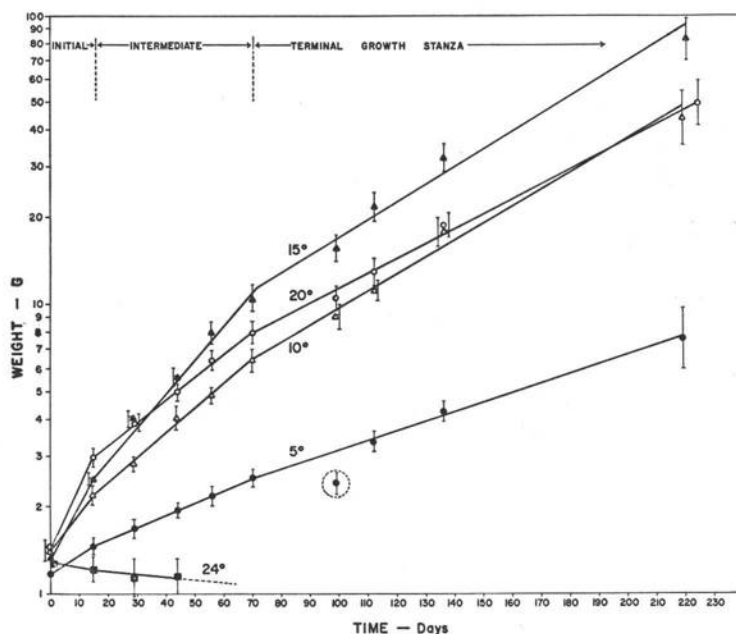


FIG. 3. Mean weights of samples ( $n=20$ ) of A-group fish held at five temperatures on excess rations. Experiments started on June 2. Limits are for  $\pm 2$  SE. Three stanzas of growth are indicated according to inflection of slopes. One point (circled) for fish at 5 C was discarded as being beyond the 95% confidence limit of the mean growth rate.

#### SAMPLING PROCEDURE

##### A GROUP

Samples of 20 fish were removed every 2 weeks from an initial stock of 250 fish per tank. On each occasion fish were herded into one end of the tank and caught by drawing a small dipnet vertically through the group. The fish were killed by anaesthetic (150 ppm M.S. 222), and rolled in a slightly damp cloth to remove surface moisture. Fork length and weight measurements were taken to the nearest 0.1 cm and 0.01 g. The fish were then placed into a deep freeze for later analysis of gross body constituents. The possibility of sampling bias was tested by measuring all the fish in a control tank in lots of 20, throughout the experimental period. No significant difference occurred between the sample and remaining population in seven such comparisons ( $P < 0.05$ , using the method of Hubbs and Hubbs, 1953).

##### B GROUP

To reduce chance differences between samples within each tank, later experiments were conducted with 25 fish only. These were lightly anaesthetized for measurements every 2 weeks and returned immediately to their respective tanks. Fish were not fed on weighing days.

To check on the possible effect of periodic handling and anaesthetic all the fish in a tank of 250 were subjected to "standard treatment" once a month and their weight relations compared with a control group. No significant difference was apparent over a 3-month period although the anaesthetized group grew 18% faster in the first 2 months, then slowed down slightly. Because of the rapid recovery of the fish and their excellent appetite, it was assumed that the effect of the biweekly treatment was unlikely to be different from the monthly check.

#### FOOD AND FEEDING

Although essentially the same ingredients were used (see Appendix A) the composition of the diet differed between the two groups (Table 2). The moisture content was purposefully

TABLE 2. Composition and calorific value of diet fed to the two groups of fish. Figures obtained from an average of 10 samples (A group) and 14 samples (B group).

	A group (1964-65)		B group (1965-67)	
	Wet (%)	Dry (%)	Wet (%)	Dry (%)
<b>Components</b>				
Water	51	—	63	—
Protein	25	50	22	60
Fat	13	27	6	16
Ash	4	8	3	8
Fiber <sup>a</sup>	1	2	1	2
Carbohydrate <sup>a</sup>	6	13	6	14
<b>Kcal/g</b>				
Bomb calorimeter	—	—	2.0	5.4
Calculated <sup>b</sup>	2.4	5.9	2.0	5.5

<sup>a</sup>Approximate fiber content determined from constituents (Anon., 1959) with carbohydrate estimated by difference.

<sup>b</sup>Calorific value calculated from proportion of dry constituents using values of 5.7 (protein), 9.5 (fat), and 4.0 (carbohydrate) kcal/g.

increased from an average of 51% for A group to 63% for B group, for which controlled rations were used, to facilitate dispensing. The reduction in fat was the result of differences between years in the composition of the major ingredients — canned salmon and commercial pelleted feed. New food was prepared every 2-3 weeks as required and stored at -10 C, the moisture content being checked on each occasion. Proximate analyses of frozen spot-samples were performed at the end of the test period. The methods used were the same as those for analysing fish, described in the next section.

The diet is one that has evolved over a number of years for use in culturing experimental fish in our laboratory. Obviously high in nutrient quality it has provided excellent growth, good condition, and no mortalities. Since the difference in diet composition occurred *between* A and B groups, and not *within* the B group for which restricted rations were used, the change did not result in any significant difference between the various excess feeding regimes, although there is a tendency for the A group to have somewhat higher mean growth rates (see Fig. 6).

For the A group, food was dispensed by shredding frozen cubes through a hand ricer. The fish were fed to satiation three times a day at 4-hr intervals, starting at 0830 hr. This was termed "excess." Depending on temperature, the daily amount presented during the terminal growth stanza ranged from 10 to 14% of the body weight on a dry weight basis.

The B group was fed with a small press that ejected a prescribed weight in the form of multiple short strings of unfrozen food. The restricted rations selected as a fraction of dry body weight were: 0, 1.5, 3, 4.5, and 6%, and excess. It was discovered that a single ration of 3%/day, dispensed in about 5 min, was sufficient to allow each fish to obtain a "fair share" of the food. The 1.5% daily ration was therefore presented as 3% every 2 days, and the 6% ration as 3% twice a day. In the case of excess ration the uneaten particles were washed out of the tank within 3-8 min from the time of introduction. For the B group the small wastage involved was assessed, providing an estimate of the maximum daily intake.

Sockeye are a naturally schooling fish. As underyearlings<sup>2</sup> they do not display obvious aggressive or territorial behaviour when food is evenly dispersed and general uniformity of conditions prevail within holding tanks. If food is *not* consumed proportionately amongst all fish, growth depensation occurs, resulting in an increased size-differential with time (Magnuson, 1962). The variance, as indicated in the growth relations of A-group fish (log weight  $\pm 2$  SE,  $n = 20$ , see Fig. 3), did not differ in extreme instances by more than 33% of the overall mean value, except at 24 C where growth was inhibited, and for the last weighing as a result of the smaller sample ( $n = 10$ ). Less difference occurred in the B-group experiments with the exception of three instances where there was a change in variance associated with the accidental loss of fish under anaesthetic, and one instance where maintenance ration was involved. In general, disparity in consumption of food among the members of each sample did not occur to any significant degree.

#### PROXIMATE ANALYSIS AND CALORIFIC VALUE

At the beginning and end of each experiment gross body constituents were determined from samples of 20–25<sup>3</sup> fish, starved for 24 hr. Subsamples of five fish were ground to a fine homogenate and weighed-fractions were used to determine water, fat, and protein content in duplicate by the following methods.

*Water* — Approximately half the subsample was oven-dried at 105 C for 24 hr. A correction for any moisture loss during deep-freezing was applied.

From the sum of all samples taken in the 1964 tests and those at the start of the 1965 tests a mean water content of  $74.4 \pm 1.2\%$  ( $\pm 2$  SE,  $n = 24$ ) was obtained. The B group alone averaged 74.9%. As a basis for calculating the ration in terms of fractions of dry body weight a general level of 25% dry material was applied throughout.

*Protein* — Nitrogen content was determined by the micro-Kjeldahl technique outlined by the Association of Official Analytical Chemists (1960). The value obtained was multiplied by 6.25 to obtain the average protein value.

*Nonprotein nitrogen* — The difference between the acid-soluble and the acid-insoluble nitrogen values (method of Association of Official Analytical Chemists, 1960) gave the nonprotein nitrogen content. It averaged 0.2% of dry weight (about 0.05% of wet weight) and varied from an undetectable amount to 1.2% of dry weight. The highest levels were associated with the highest temperatures, independent of ration except for starved fish, which contained consistently low levels. Since only major constituents were being examined these small values have been omitted from the compilation in Table 3.

*Fat* — Lipid analyses were first performed by the chloroform-methanol wet extraction technique of Folch et al. (1957). This was later changed to hexane extraction from dried material (see Appendix B). A slight difference in values was ascribed to the possible carry over of moisture by the wet extraction method. An appropriate correction was therefore applied to bring all results to a common basis for dry extraction.

*Carbohydrate* — No analysis of carbohydrate was conducted since this constituent does not amount to more than 0.5% of body weight (Vinogradov, 1953; Black, 1958). Highest concentration occurs in the liver where values from 3 to 4% have been obtained for normal feeding fish (Hochachka and Sinclair, 1962).

*Calorimetry* — Calorific values were determined with a Parr bomb calorimeter (methods prescribed by the American Society for Testing Materials, 1966).

When the calorific content was calculated from proximate analysis, values of 9.5 kcal/g for fat and 5.7 kcal/g for protein were applied (Brody, 1945; Kleiber, 1961).

#### DATA COMPILATION AND ANALYSIS

The quantitative laws governing growth have been treated as general concepts by such authors as Bertalanffy (1957) and Needham (1964), with more specific consideration of the process

<sup>2</sup>Aggressive behaviour has been observed in yearling fish, with intense periods occurring soon after feeding.

<sup>3</sup>Except in a few cases listed in Table 3.



TABLE 3. The effect of temperature and ration on the weight, growth rate, calorific value, and body constituents of sockeye fingerlings at the beginning ("cultured" fish) and end of each experiment.

Temp (C)	Ration level (% dry wt)	No. fish (n)	Initial wet wt (g)	Terminal wet wt (g)	Growth rate (%/day)	Duration (days)	Duration (day- degrees)	Calories Kcal/g	Water (%)	Protein (%)	Fat (%)	Total <sup>a</sup> (%)
1	Cultured	25	6.01	—	—	Start	—	6.26 <sup>b</sup>	74.2	15.8	7.6	97.5
	0.0	25	5.62	4.96	-0.14±0.06	83	83	6.01 <sup>b</sup>	80.8	14.6	3.4	98.8
	1.48	25	6.19	7.19	0.17±0.08	83	83	6.54 <sup>b</sup>	77.2 <sup>c</sup>	14.9 <sup>c</sup>	6.6 <sup>c</sup>	98.7
	3.03 <sup>d</sup>	24	6.04	7.69	0.23±0.06	83	83	6.21 <sup>b</sup>	76.2	13.4	7.5	97.1
5	Cultured	25	5.52	—	—	Start	—	5.94	75.4	15.4	6.3	97.1
	0.0	25	5.62	5.16	-0.21±0.12	99	495	5.25	80.3	15.1	1.9	97.3
	1.78	24	5.43	7.26	0.38±0.11	99	495	6.16	75.4	14.2	7.4	97.0
	3.44	25	5.79	10.10	0.67±0.09	99	495	6.59	72.1	17.3	9.1	98.5
	3.59 <sup>d</sup>	24	6.30	10.65	0.64±0.09	99	495	6.63	72.6	16.3	9.5	98.4
	Excess	21	5.97	9.92	0.61±0.10	99	495	6.35	72.6	16.0	8.9	97.5
10	Cultured	25	6.02	—	—	Start	—	5.94	75.4	15.4	6.3	97.1
	0.0	19	5.24	3.83	-0.41±0.10	99	990	5.10	82.0	14.1	1.3	97.4
	1.77	23	6.14	8.04	0.31±0.10	99	990	5.95	77.3	14.0	5.9	97.2
	3.42	23	6.58	12.95	0.80±0.12	99	990	6.24	75.1	16.6	6.5	98.2
	4.99	20	7.36	20.04	1.17±0.14	99	990	6.23	72.9	19.0	6.6	98.5
	4.93 <sup>d</sup>	25	7.51	20.37	1.17±0.13	99	990	6.19	71.7	15.9	9.0	96.6
15	Cultured	25	6.51	—	—	Start	—	5.94	75.4	15.4	6.3	97.1
	0.0	14	5.61	3.30	-0.64±0.16	99	1485	4.62	83.2	13.2	0.6	97.0
	1.87	10	5.90	6.39	0.10±0.13	99	1485	5.42	75.7	16.0	4.4	96.1
	3.51	19	7.43	12.82	0.67±0.12	99	1485	5.96	74.9	18.6	5.2	98.7
	4.85	21	7.30	18.99	1.17±0.09	99	1485	6.24	72.2	20.0	6.0	98.2
	6.08	21	7.69	25.45	1.44±0.14	99	1485	6.33	71.8	17.3	8.5	97.6
	Excess	19	8.75	29.28	1.26±0.19	99	1485	6.37	71.3	19.7	7.6	97.6
20	Cultured	25	6.78	—	—	Start	—	6.26 <sup>b</sup>	74.2	15.8	7.6	97.5
	0.0	25	5.92	3.27	-0.50±0.08	85	1700	4.80 <sup>b</sup>	86.9	9.4	1.0	97.3
	1.52	24	6.30	5.09	-0.19±0.10	85	1700	5.53 <sup>b</sup>	81.6	12.7	3.1	97.4
	3.00	23	6.70	7.01	0.08±0.10	85	1700	5.81 <sup>b</sup>	79.2	13.2	4.8	97.2
	4.36	10	7.18	11.32	0.48±0.09	85	1700	6.47 <sup>b</sup>	77.2	14.7	6.7	98.6
	5.65	16	7.93	18.45	0.84±0.07	85	1700	6.39 <sup>b</sup>	75.1	13.6	8.6	97.3
24	Cultured	20	1.39	—	—	Start	—	6.10 <sup>b</sup>	76.5	16.5	5.2	97.2
	Excess	20	1.31	1.18	-0.19±0.35	44	1056	5.04 <sup>b</sup>	79.4	14.9	2.0	96.3

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<sup>a</sup>Ash was not determined. The mean amount by difference = 2% of the wet weight, allowing for a small percentage of carbohydrate and non-protein nitrogen.

<sup>b</sup>Calculated calorific content; otherwise obtained by bomb calorimetry.

<sup>c</sup>±2 SE for n = 25; water = ±0.70; protein = ±0.74; fat = ±0.51.

<sup>d</sup>A higher ration was prescribed but the fish did not accept more than recorded.

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in fish provided by Brown (1957), Taylor (1962), and Winberg (1956). Under conditions of environmental control and in the absence of limiting factors, growth is a multiplicative process, which, in the early stages of life, often follows an exponential curve. Under the influence of apparent inhibition with age its overall configuration tends to follow the sigmoid shape of a logistic curve. The instantaneous rate of gain in weight per unit weight (per cent change in weight/time, or specific growth rate) declines progressively with increasing size.

The general equation for exponential growth is  $w = be^{kt}$ , where  $w$  is size and  $t$  is time. When  $\log_e w$  is plotted against  $t$ , (Fig. 3) the slope  $k \times 100$  is equivalent to the specific growth rate (G). This was determined by taking length-weight measurements every 2 weeks, usually for a 10- to 12-week period. An estimate of the error of  $k$  was computed from the pooled data of all measurements ( $\pm 2$  SE). The restricted ration was adjusted at the *start* of each biweekly period according to the new mean weight obtained, on a dry weight basis. The *actual* proportion of the ration was subsequently calculated according to the observed mean weight achieved by the fish during the biweekly interval, e.g., as the fish grew the actual fraction became slightly less than the ration initially prescribed.

Because of the progressive change in growth rate that appears to occur in stanzas of decreasing slope (Fig. 3), a period of relatively stable growth from October to February (Fig. 5) was accepted as a suitable time for making comparisons between treatments, spread over a number of years.

## RESULTS

### TEMPERATURE $\times$ EXCESS RATION — A GROUP

As a result of the favorable change in density, diet, and feeding frequency that accompanied the transfer from culture to experimental conditions, all stocks showed a marked increase in growth rate, except those at 24 C (Fig. 3, Table 1). This surge declined after an initial 2 weeks "adjustment" (possibly less) and the growth rate remained constant for the next 8 weeks. At this time (August 10) a synchronous decrease in slope occurred in all stocks despite the difference in acclimation temperatures of 5–20 C. No further change was noted up to the time of terminating the experiment 21 weeks later (January 12). Such seasonal variations in growth rate have been observed by Swift (1955) for hatchery-reared brown trout (*Salmo trutta*) exposed to normal temperature and light. A reduced growth rate occurred in May and June despite increasing temperature and daylight. It is possible that changes in the production of growth hormone could account for such temperature-independent decreases in growth.

The maximum growth rate recorded in the initial period was 5.05%/day at 20 C, a doubling of weight in 2 weeks. The relation between temperature and maximum growth rate for the two subsequent stable periods ("intermediate" and "terminal" — Table 1) has been plotted in Fig. 4 including one instance where excess ration was fed in the B-group experiments (1 C, Table 3). At an age of 5–7 months, from the start of feeding, a pronounced optimum temperature for growth occurred at 15 C. Although still apparent for 7- to 12-month-old fish, the peaking of the relation is sufficiently reduced that no statistical difference exists between the growth rates at 10 and 15 C. With increasing age, growth continues to slow down so that optimum temperatures become progressively less apparent. The expression of maximum growth rate in relation

to acclimation temperature (Fig. 4) has been called the "scope for growth" by Warren and Davis (1967) by analogy with the "metabolic scope," which Fry (1947) used to describe the capacity to elevate metabolic rate above the maintenance or standard level at various temperatures.

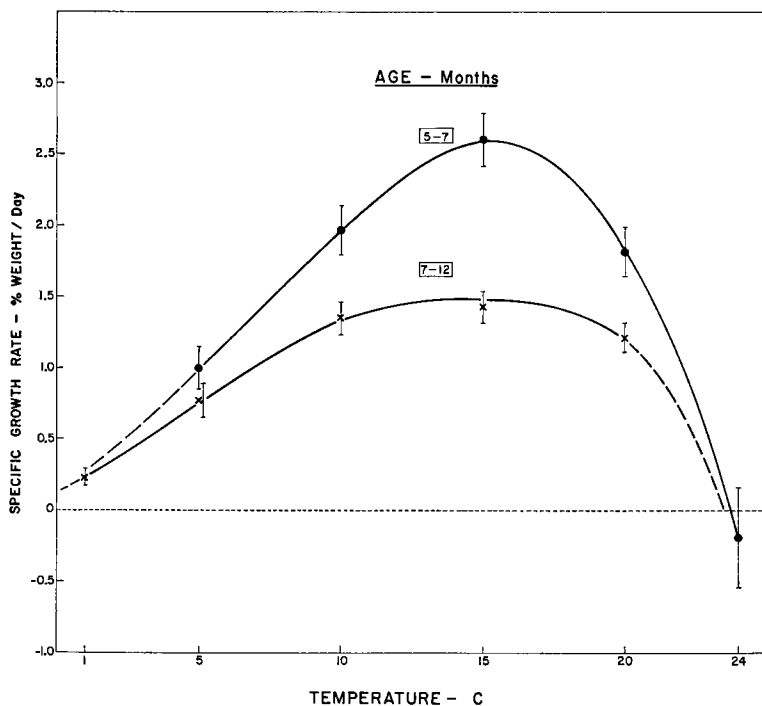


FIG. 4. Relation between temperature and growth rate ( $\pm 2$  SE) of young sockeye salmon fed on excess ration. Age is in months from start of feeding.

At 24 C some of the young salmon would not accept food. Mortalities commenced in the 1st week. The mean weight declined and the variance increased as a consequence of the variability in feeding response. Within 3 weeks one-third of the stock were "pin-heads," which died within the month. By the 44th day over 50% were dead, at which time the experiment was terminated.

Similar problems of feeding and subsequent mortality near the boundary of the upper tolerance limit for this species have been observed by Donaldson and Foster (1940) at 23 C, and were encountered by Brett (1952) when he attempted to acclimate 3-month-old sockeye to high temperatures, elevated by stages to 24 C.

#### TEMPERATURE $\times$ PRESCRIBED RATION — B GROUP

An example of the effect of ration level on growth rate at a given temperature is illustrated in Fig. 5. It was characteristic of most of the data to exhibit

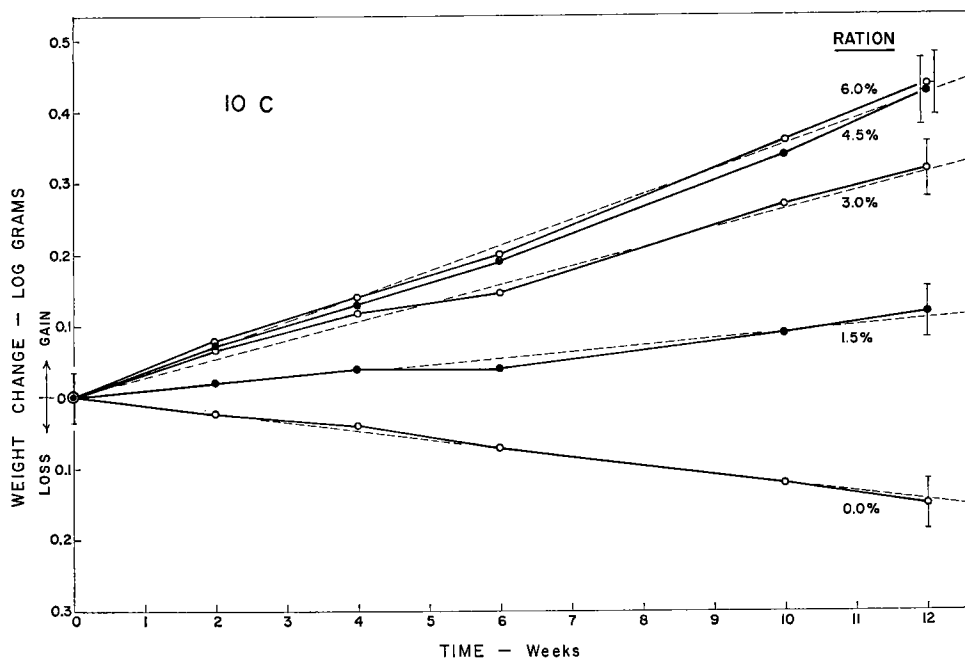
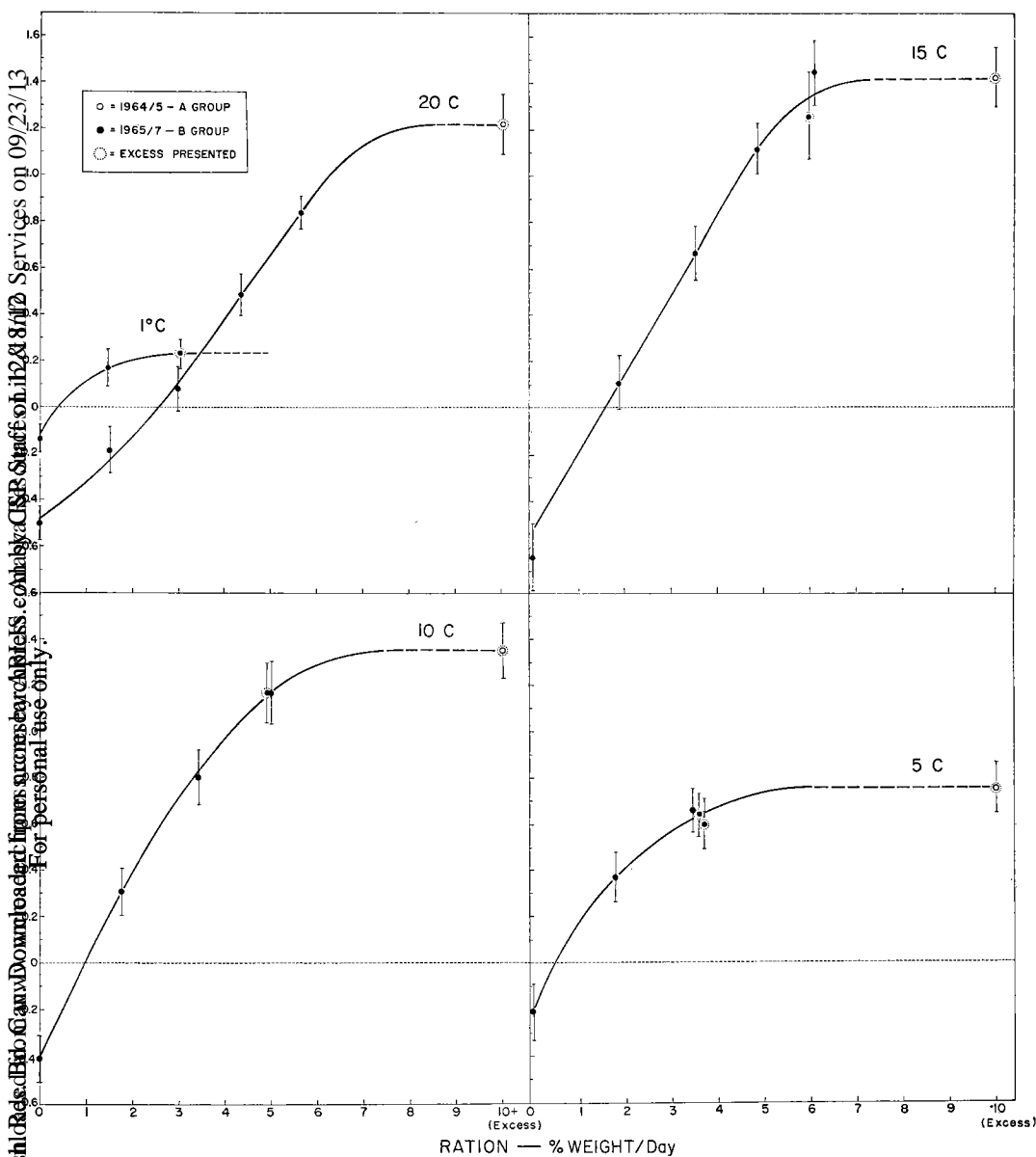


FIG. 5. The effect of ration on growth rate of fingerling sockeye at 10 C. For ease in comparing rates (slopes) a common origin for all stocks has been used. Solid lines link each mean weight ( $n=25$ ; limits =  $\pm 2$  SE). Broken lines represent the computed slopes for all data at each ration. Prescribed rations are indicated; actual consumed rations are presented in Table 3. Note that the statistical separation of the fish on 3% ration was not possible in less than 6 weeks.

deviations along the path of exponential growth, and these deviations, together with the difference in weight within each lot of 25 fish, contributed to the variance in slope (specific growth rate, Table 3). At high feeding rates, approaching the maximum intake, it is apparent that the time required to demonstrate a significant difference in growth rate between two levels of ration was of the order of 6–8 weeks (e.g., 3 and 4.5% ration at 10 C, Fig. 5).

When growth rate was plotted against ration for each temperature a series of curves was obtained, which change in form from a "logistic shape" at 20 C to a "geometric shape" at lower temperatures (Fig. 6). In the absence of a generally suitable transformation a smooth curve has been fitted by eye to pass through the means  $\pm 2$  SE. Since various growth parameters can be obtained by interpolation all the computed points are presented graphically for inspection in Fig. 6.

The parameters of particular interest were: (1) the maintenance ration, i.e., that ration that just maintains the fish without any weight change; (2) the optimum ration, i.e., that ration that provides for the greatest growth for least intake (most efficient); and (3) the maximum ration, i.e., that ration that just provides for the maximum growth rate.



6. Relation of growth rate to ration at five temperatures. Points for A-group fish (○) have been fed for an average ration of 10%, presented as excess. Where B-group fish were satiated by the prescribed ration, or fed a measured excess, the points have been circled.

These may be derived geometrically (Fig. 7) (cf. Thompson, 1941). The fact that the optimum ration can be determined by drawing the tangent to the curve from the origin may be proven by calculating the ratio of *growth rate* to *ration* for a series of rations. The parameter most difficult to determine

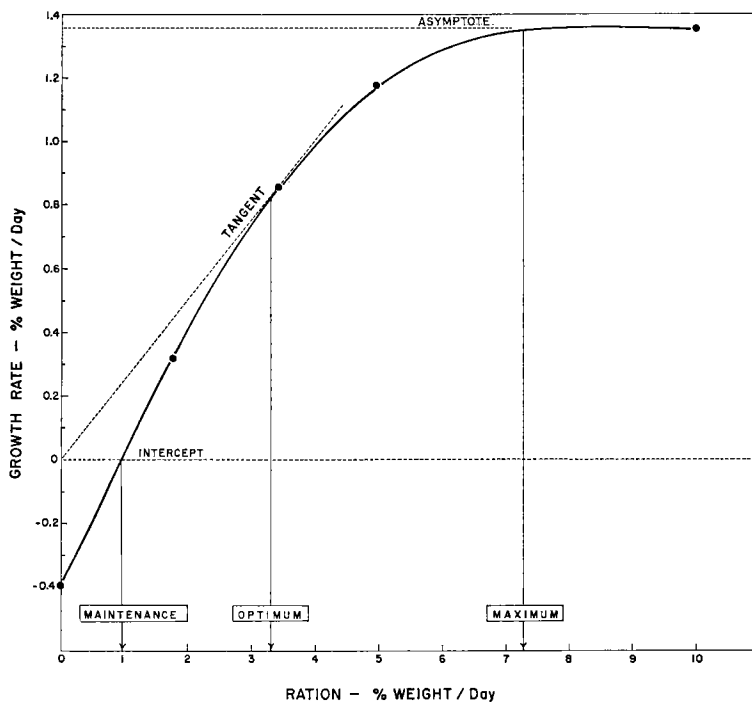


FIG. 7. Geometric derivation of various parameters of growth with accompanying ration, using the data for fish at 10 C as an example.

accurately was the maximum ration, involving the asymptote for maximum growth rate, the values for which were subject to greater variability than most of the other rates.

With increasing temperature there was a large increase in the ration required to meet the defined growth parameters (Fig. 8). The maintenance ration at 20 C was seven times that at 1 C; the optimum was five times greater for the same temperature difference; and the maximum just under three times greater. The maximum food intake per day was approximately 8% of the dry body weight at 20 C. The temperature  $\times$  ration relations could be made linear (Fig. 8, equations), improving the basis for estimated values and providing for extrapolation to the extremes of temperature at which food was still accepted. Above 23.3 C loss of appetite and inefficiency of food conversion were responsible for the breakdown in the overall relation, and the ultimate death of the fish.

#### GROSS BODY CONSTITUENTS

Both ration level and temperature had a considerable effect on all body constituents (Table 3). They ranged from 86.9% water, 9.4% protein, and 1.0% fat at 20 C for fish starved for 83 days, to 71.3% water, 19.7% protein, and 7.6% fat for fish on an excess ration for 99 days at 15 C — the optimum

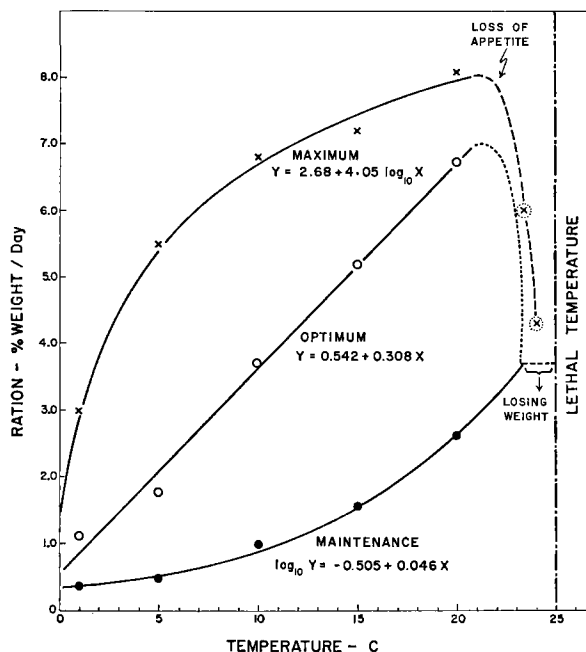


FIG. 8. Relation of maintenance, optimum, and maximum ratios to temperature. Points were determined as outlined in text, except the two circled points, which were derived by inspection from Fig. 11.

temperature for growth. This dynamic and variable state of body constituents is apparent for all stocks and is represented by the progressive change in moisture content depicted in Fig. 9. At all temperatures a lower water fraction occurred with increasing ration, reaching a minimum of about 72% by the termination of the experiments.

Among the starved fish the moisture content varied according to temperature, with the exception of the fish held at 1 C. Since the rate of change in composition will be dependent on some function of temperature and time, it would be expected that changes would proceed very slowly at 1 C. Comparison between experiments of equal duration cannot be made on common physiological grounds unless a static state of body composition has been reached. This is suggested by including a column in Table 3 for day-degrees, as one indication of physiological time. It may be seen that on this basis the experiments ranged from 83 to 1700 day-degrees. In addition it was an inevitable outcome that considerable difference in size would characterize the various groups at the terminal stage. Size has been shown to influence body composition of young pink salmon, *Oncorhynchus gorbuscha* (Parker and Vanstone, 1966).

As water content increased, both fat and protein decreased.<sup>4</sup> In the light of this highly significant negative correlation (fat = -0.89,  $P < 0.01$ ; protein = -0.80,  $P < 0.01$ ) it was possible to derive simple equations with appropriate

<sup>4</sup>Above the maintenance ration any decrease in protein is strictly relative; however, fat may show some absolute changes.

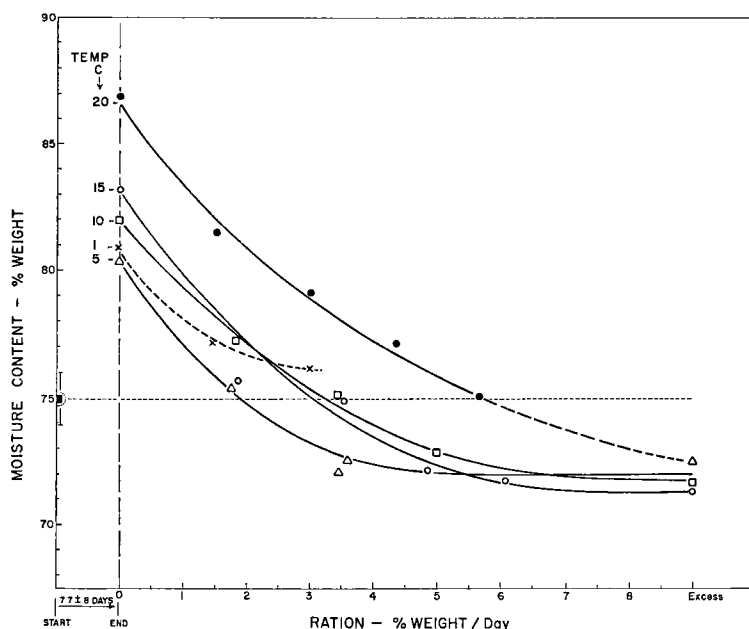


FIG. 9. Moisture content of fish at the start (single circled point with  $\pm 2$  SE) and end of growth experiments. Each "eyed" curve represents the final percentage of body water in relation to daily ration for a given temperature. With the exception of 1 C, it is likely that these represent equilibrium states for any ration and temperature.

confidence limits relating water content to corresponding fat and protein levels (Fig. 10). Contributing to the variability in composition between samples of fish are the direct and interacting effects of temperature, ration, size, growth rate, and conversion efficiency, coupled with a degree of curvilinearity produced by approaching threshold levels of these major constituents. No attempt has been made to sort these out. It is apparent, however, that by determining the moisture content *only* the total gross body constituents can be estimated fairly accurately from the above relations, assuming an average ash of 2% of wet weight (Table 3).

## DISCUSSION

### SOURCES OF ERROR

The experiments were designed to provide statistical sensitivity for determining the difference *between* treatments (temperature and ration) by reducing the variability *within* lots (tanks of fish). Reduction in genetic variability was achieved by selecting a limited size range from the progeny of one female. Although this was undoubtedly an effective approach in any one year, it did not anticipate the subsequent need for comparison between years, as well as the desirable feature of obtaining a wider representation of the population. The limited gene pool can be expected to be one of the factors



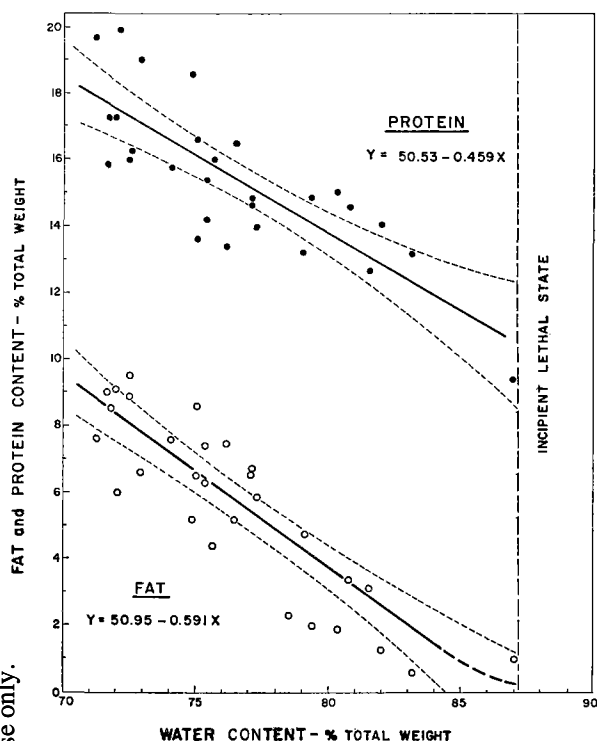


FIG. 10. Relation of protein and fat content to water content of young sockeye. Points represent pooled data from all temperatures and rations. Lines of best fit determined by least squares, with 68% confidence limits (broken lines).

contributing to the differences in maximum growth rate between years, as exemplified by the various stocks of fish on excess ration at any one temperature (Fig. 6). Yet it can be seen that the dissimilarity was not great, amounting, for example, to a difference in specific growth rate of about 0.2%/day for stocks at 15 C. Since some change in diet occurred between A and B groups (Table 2), and it was decided to present excess food twice a day rather than three times a day in later experiments, the question of maximum growth rate for the species at this age and size remains undetermined though probably not seriously underestimated. Indeed, with advances in nutrition and in making environmental conditions optimal, it is doubtful if the full potential for growth of any species including man has yet been assessed.

It is apparent from the change in body constituents that accompanied the different treatments that the presentation of restricted rations on the basis of the initial moisture content would apply throughout the experimental period only to those instances that did not deviate significantly from the original state (signified by the points close to the dotted line for 75% moisture in Fig. 9). Except for starving and excess-fed fish an error progressively creeps in for all other instances, reaching a maximum at the end of the test time. The extremes occur at low temperature on high ration, and at high temperature on low ration. For example, the fish held at 5 C on 3.5% ration had a terminal

average moisture content of 72.5%. On the final day the prescribed ration of 3.5% was actually 3.2% of the existing dry weight. Lacking knowledge of the rate at which the constituents changed, coupled with the fact that it would apply in varying degrees up to the sort of error indicated, no correction was possible.

The basis of conducting exacting experiments on bioenergetics and growth in fish is treated with insight by Warren and Davis (1967). From a bioenergetic point of view the conversion of food should be based on calorific rather than dry weight values because of the differences in the fat/protein ratio. When considering growth only, there is justification for calculations based on nitrogen content such as Gerking (1962) used in studies on food conversion of the bluegill, *Lepomis macrochirus*. Since the protein fraction of the dry weight varied somewhat less than the fat fraction (Fig. 10), the inherent error indicated above would be reduced accordingly. It is worth stating here that subsequent experiments are being conducted by increasing the number of fish to allow for biweekly subsamples to be withdrawn for appropriate analysis.

With the above limitations set forth it is possible to examine the combined effects of temperature and ration on the specific growth rate, and to proceed to a consideration of the efficiency of food conversion.

#### TEMPERATURE-RATION RELATIONS

From the relation between ration and growth rate for each temperature (Fig. 6), the form of the growth  $\times$  temperature curves for each prescribed ration may be determined (Fig. 11). The temperature for optimum growth shifts progressively to the left as the ration is reduced, moving from 15 C on excess ration to approximately 5 C for a ration of 1.5%/day. The outer curve is the same as that describing the scope for growth for 7- to 12-month-old sockeye presented previously (terminal growth rate, Table 1, Fig. 4). With the exception of the relation for starved fish, each of the remaining domed curves represents the scope for growth characterizing each reduced level of available food. As the fish grow older there would be a corresponding flattening of this fleet of curves, approaching the ultimate minimum growth rate for aged fish.

The shunt in optimum temperature supports the hypothesis that, for acclimated fish, digestion and growth can still proceed effectively at low temperatures. It suggests that either the enzymes involved are relatively temperature-independent (wide spectrum), that a fleet of enzymes is present with a wide range of temperature reactivity, or that rapid changes in the metabolic system occur to meet the new situation. The marked increase in energy requirements for maintenance that accompanies rising temperature (Fig. 8) accounts for the decreasing scope for growth, to the point of losing weight at low rations (Fig. 11).

Fish feeding on a limited ration in nature would achieve better growth by moving along the temperature axis, towards the appropriate optimum.

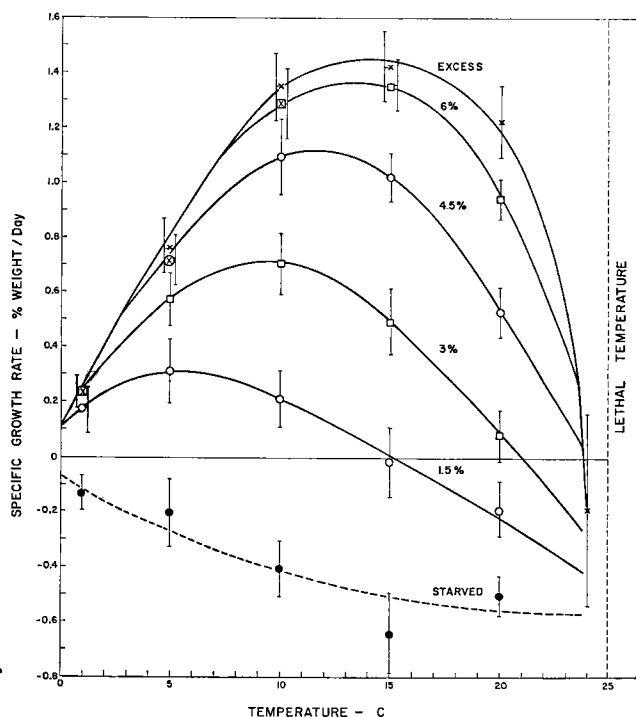


FIG. 11. Effect of reduced ration on the relation between growth rate ( $\pm 2$  SE) and temperature, for 7- to 12-month-old sockeye. Points for excess ration or where a prescribed ration turned out to be excessive are marked with an X. The broken line for starved fish is a provisional interpretation.

Thus, at 15 C on a ration of 1.5%/day no growth would occur, whereas for the same ration at 5 C a size increase of 0.3%/day would be possible. The daily vertical movements of young sockeye observed during the summer in Babine Lake (Narver, MS, 1967) involved changes of 10 C, from near-surface feeding at dusk followed by a gradual retreat to depths of 100 ft or more shortly after dawn. This could be conceived as a mechanism evolved to improve growth in the presence of a limited food supply. Since yearling migrants frequently average no more than 6 g (Johnson, 1965), whereas experimentally fed young sockeye under optimum conditions may weigh as much as 80 g 4 months prior to the smolt phase, it is not hard to conceive that food is a limiting factor for this species in many lakes.

The predictive value associated with established food requirements is best illustrated by calculating the growth-rate isopleths (Fig. 12). The food ration necessary to provide for any given growth rate at any particular temperature may be ascertained readily by checking the appropriate combination. Since this applies to only one growth stanza, or age, it is possible to see that by a series of such experiments, conducted at selected intervals throughout the life history, a method of computing the total food requirements would be obtained.

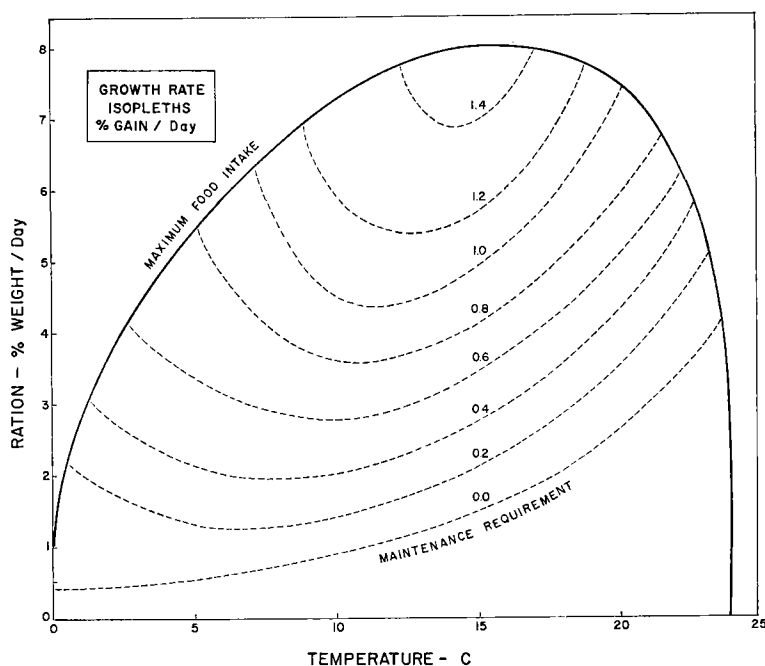


FIG. 12. Growth rate isopleths for yearling fingerling sockeye, showing the percentage gain in weight per day that would be expected for any combination of ration and temperature.

#### STARVATION EFFECT

The rate of loss of body weight for starved fish in relation to temperature was difficult to interpret since the mean rate for 15 C ( $-0.64\%/day$ ) was unexpectedly greater than the mean for the 20 C ( $-0.50\%/day$ ). These bordered on being statistically different ( $P = 0.04$ ). A provisional line was drawn in Fig. 11 to represent the most likely relation for increased temperature.

The experiments for temperatures of 1 and 20 C were conducted a year later than those for 5, 10, and 15 C. Aside from a difference in the origin of stocks it was conceivable that spontaneous activity might have been highest at 15 C resulting in a generally higher metabolic rate than for the stock at 20 C. It should be noted, however, that the fish at 20 C had a terminal moisture content of 86.9%, whereas the fish at 15 C were 83.2% water (Table 3). A check on the provisional interpretation was made by conducting a comparable experiment at temperatures of 5, 10, 15, and 20 C for 12 weeks in 1967-68. At this time only fish of approximately twice the weight were available ( $12.0 \pm 0.3$  g). The results gave confirmation for the rate of loss of weight at 5 and 20 C but not for the intermediate points (Fig. 13).

It must be concluded that greater variability is either natural or somehow induced during starvation experiments. The sample size should therefore be increased and the conditions governing excitation should be rigidly controlled,

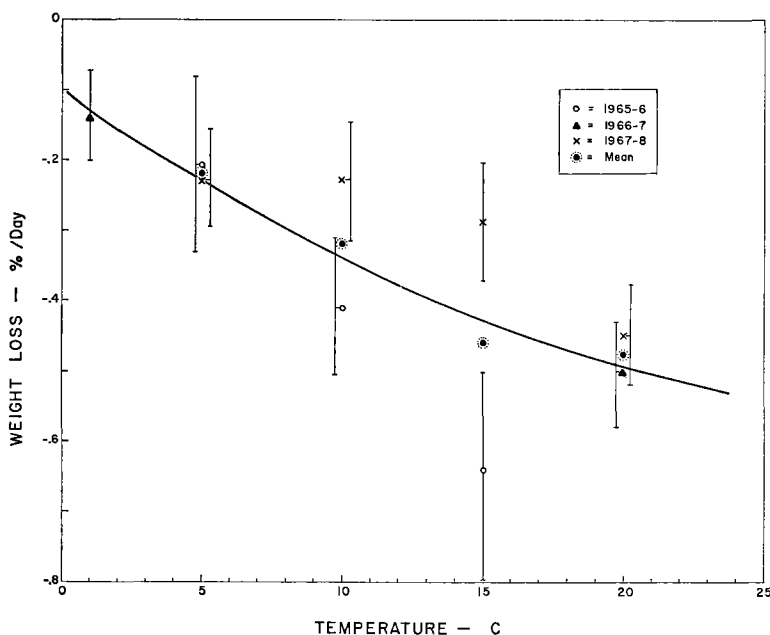


FIG. 13. Rate of loss of weight for starved fish in relation to temperature. Experiments conducted with three groups of fish in separate years. Initial mean weight of fish for experiments in 1965-67 was 6.5 g; that for 1967-68 was 12.0 g.

particularly regarding disturbances that may result inadvertently from the feeding of adjacent tanks. The mean for all data has been used in Fig. 13 as the best representation of the general temperature relation.

## CONVERSION EFFICIENCIES

### GROSS EFFICIENCY

Few studies of growth relations in fish have been performed with sufficient accounting of food consumed and flesh produced to permit determining conversion efficiencies (Kinne, 1960). With a common unit of dry weight, nitrogen content, or calorific value, the gross efficiency ( $E_g$ ) may be calculated as the

ratio of output to input by the formula  $E_g = \frac{G}{I} \times 100\%$ , where  $G$  = growth,

and  $I$  = food intake. This simple index provides one of the most revealing aspects in analyzing growth phenomena, not only by indicating the circumstances under which the animal is most effective but also by providing a measure of the most economical use of food.

In addition to the factors of temperature and salinity, gross efficiency has been shown to depend on the type of diet, the feeding interval, and the size or age of the fish (Paloheimo and Dickie, 1966b; Pandian, 1967a, b). Conversion values range from 8% for omnivorous adult carp feeding on detritus

and algae (Kevern, 1966) to 44% for carnivorous young *Ophiocephalus striatus* feeding on a diet of prawns and chopped fish (Pandian, 1967a). Ivlev (1945) considered 35% to be a maximum for young fish on a high ration. Under-yearling cutthroat trout, *Salmo clarki*, showed an individual variation of 13–37% in ability to convert a diet of housefly larvae and adults at a mean temperature of 8.5 C (Warren and Davis, 1967).

The combined effect of temperature and ration provided a small maximum area of 25% efficiency for fingerling sockeye, with a graphically determined center at 11.5 C and ration of 4.0%/day (Fig. 14).<sup>5</sup> The mapped isopleths for

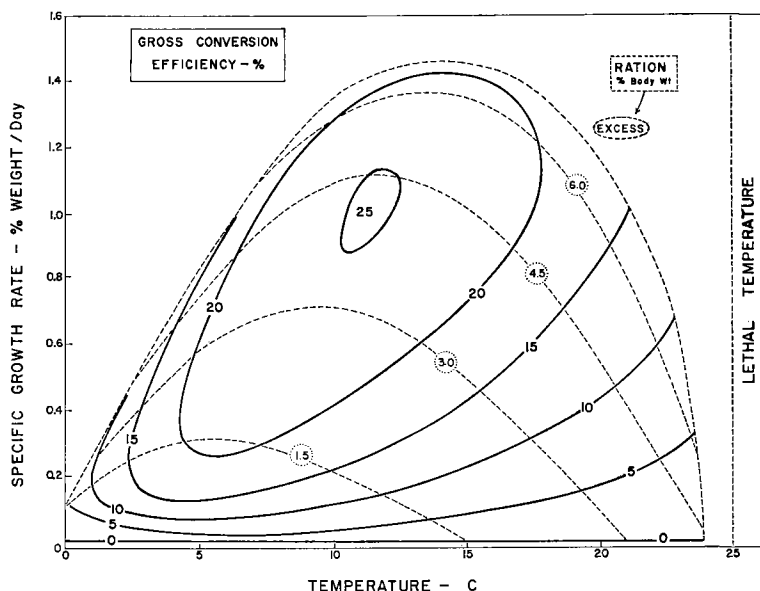


FIG. 14. Gross efficiency of food conversion in relation to temperature and ration, drawn as isopleths overlying the growth curves of Fig. 11 (broken lines).

decreasing efficiencies radiate outwards, with a “favourable axis” passing from the lower left corner diagonally upwards through the various growth optima for each prescribed ration. In line with this axis a large oval area is encompassed by the 20% conversion contour.

It is apparent that temperature may have as much effect as ration on conversion efficiency when the full ranges of both are considered. The conclusion of Winberg (1956) that temperature has virtually no effect appears to result from a lack of available evidence for temperatures *above* the optimum. When food is present in abundance (ad libitum, or excess rations), temperatures

<sup>5</sup>As an aid to interpreting this graph it is worth pointing out that by following a vertical line at any one temperature, say 10 C, the conversion efficiency increases from zero at a maintenance ration, passes through a maximum value at an intermediate ration, and then decreases reflecting some wasteful gorging at high rations (cf. Fig. 7).

below the optimum are associated with reduced food intake resulting in a fairly constant conversion efficiency, such as that along the "favourable axis" of Fig. 14. This interaction produces an apparent temperature independence, which proves to be circumstantial when the whole phenomenon is examined.

A similar sort of limitation appears to apply to the analyses of Paloheimo and Dickie (1966b) who concluded that at a given temperature increasing ration results in a decreasing conversion efficiency. Because of the paucity of available data on restricted rations the majority of instances cited by these authors relate to supraoptimum rations, which inevitably result in lowered efficiency. The full range of response is clearly demonstrated in the case of young sockeye by applying the method of analysis of Paloheimo and Dickie (1966b) who determined that the logarithm of the gross growth efficiency ( $\log K_1$ ) decreased linearly with increasing ration. Evidence to support such an hypothesis could come only from rations that were sufficiently above the maintenance level to provide for "excessive feeding." Efficiency of food assimilation increased from 71.5% to 86.5% for goldfish fed restricted rations near the maintenance level, at 21.5 C (Davies, 1963). Assuming a moisture content of 75% for the adult goldfish the respective rations ranged from about 0.5%/day to 2%/day on a dry weight basis. It is possible that in some species the position of maximum growth efficiency may occur at comparatively low rations, particularly under experimental conditions where the work associated with food-finding is minimal. As is indicated for young sockeye (Fig. 15) the inflection of  $\log K_1$  to a negative slope occurred at progressively higher rations with increasing temperature. An optimum ration was not even reached at 20 C. The latter circumstance prevails because fish would not accept a sufficiently high ration at this temperature to surpass the point of maximum conversion.

The small size of most yearling sockeye at the time of migration makes it highly unlikely that supraoptimum food conditions characterize this phase of life so that the use of  $\log K_1$  as developed by Paloheimo and Dickie would not be applicable during freshwater growth.

#### NET EFFICIENCY

If the maintenance ration is known a further calculation may be made of the net efficiency ( $E_n$ ) by subtracting the fraction of the total ration that is involved in maintenance (M), thereby deriving the efficiency of utilization

of the fraction of food available for growth. In this instance  $E_n = \frac{G}{I-M} \times 100\%$ .

Because Brown (1957) reported that the maintenance ration was difficult to determine directly, since the fish kept adapting their growth rate to compensate for reduced rations, Pandian (1967a) dismissed the value of determining net efficiency. Paloheimo and Dickie (1966b) also considered that the difficulties of obtaining satisfactory maintenance estimates precluded useful application of net efficiencies. However, since it has been shown that where stable growth

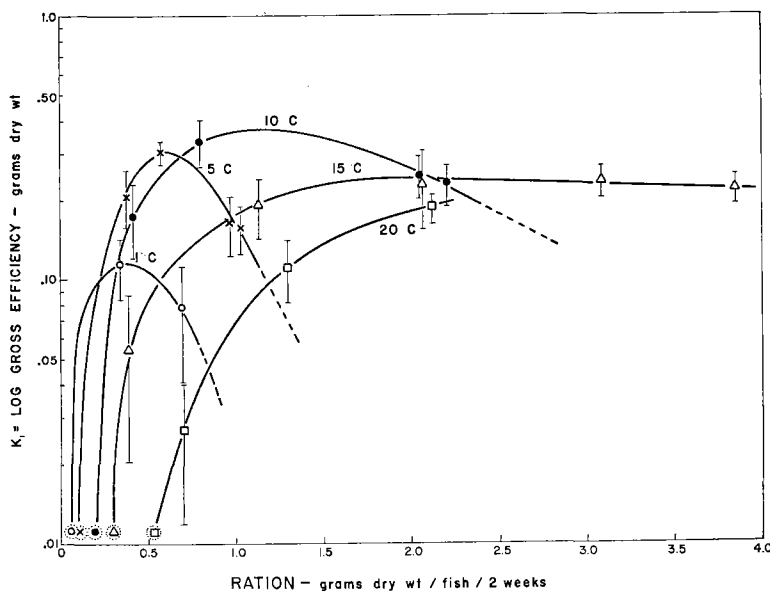


FIG. 15. Relation between logarithm of gross growth efficiency and ration at five different temperatures. Circled points were calculated from interpolated values (Fig. 6). The efficiency,  $K_1$ , was determined in the manner of Paloheimo and Dickie (1966b) using the daily gain in dry weight/daily dry ration. Straight line projections beyond the optimum suggest the relation determined by these authors.

Each point was calculated from the total growth during a 10- or 12-week period. Variability within tanks is indicated as  $\pm 1$  SD of the biweekly  $K_1$  values, which did not show any consistent trend in relation to increasing ration. Variance increases as  $K_1$  approaches zero.

rates have been established the maintenance ration can be determined quite accurately by interpolation (see Fig. 6 and 8; also Warren and Davis, 1967), the case for net efficiency is worth further consideration.

Brody (1945) recounts that net values were used primarily to compare the efficiencies of farm produce (such as milk and eggs) without the maintenance costs for the different domestic animals being involved. Since it is a matter of producing flesh or converting energy in fish that is of concern it might seem reasonable to dismiss the net efficiency. However, it is important wherever possible to partition the energy relations to distinguish the relative contributions when comparing produce, species, rations, ages, or the effects of environmental factors.

Since the estimated maintenance portion of the ration is subtracted from the total ration, it is obvious that the net efficiency will always be greater than the gross efficiency. This difference is least at maximum growth rate on a high ration and greatest approaching the maintenance level, i.e., the utilization of that small fraction of the ration in excess of maintenance tends to be very efficient. By using actual and interpolated values from the curves relating growth rate and ration (Fig. 6) a set of isopleths were constructed for net



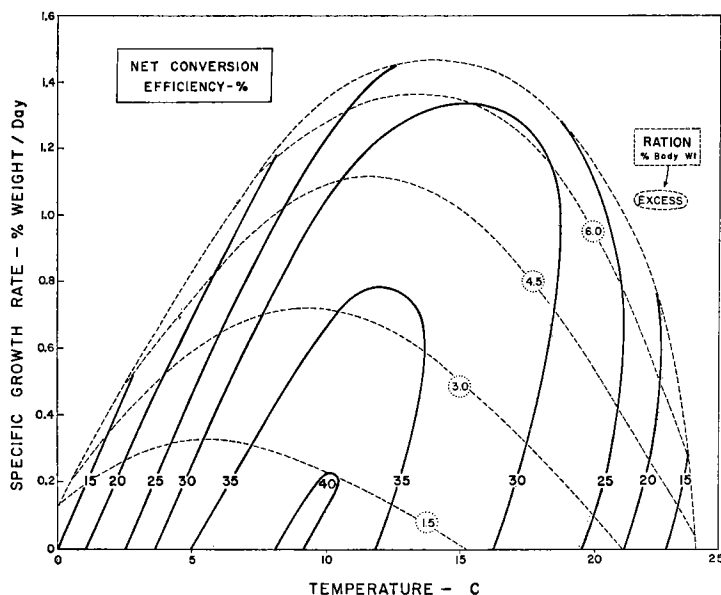


FIG. 16. Net efficiency of food conversion in relation to temperature and ration, drawn as in Fig. 14.

efficiency (Fig. 16). A maximum net efficiency, just bordering on 40%, occurred between 8 and 10 C for rations of 1.5%/day down to 0.8%/day, the maintenance level. Minimum efficiency of 15% occurred at low temperatures 1–3 C) at all accepted rations, and at  $23 \pm 0.5$  C for rations in excess of 4%/day.

The net efficiency isopleths form a pattern opposite to those for gross efficiency, net efficiency *decreasing* with increasing growth rate (cf. Fig. 14 and 16). The “favourable axis” has a center in the same temperature region (9–10 C) but is rotated anticlockwise in a more vertical position with relation to the temperature axis. The advantage of low temperature for gross efficiency conversion is not present for net efficiency demonstrating that the process of growth, when separated from the interwoven complex of the energy requirements and food turnover associated with maintenance, has a narrower, different focal area in relation to temperature.

The combined evidence from growth rates and conversion efficiencies indicates that temperatures between 5 and 17 C provide young sockeye with the best environmental circumstance for elaborating cells and storing energy.

#### BODY COMPOSITION

Many factors have been shown to influence body composition (Love, 1957). In addition to quantity of food and environmental temperature, Parker and Vanstone (1966) reported that young pink salmon (*O. gorbuscha*) showed changes in composition with size, age, diet, and at particular stages of life (ontogenesis). Slight but significant changes in moisture content even occurred

diurnally. Various investigators noted that starvation is accompanied by an early decrease in fat followed by gradual protein depletion; loss of body weight is partially offset by an increase in the proportion of water (Idler and Clemens, 1959; Phillips et al., 1966).

At any one stage in life it can be expected that the balance of body constituents will be governed by the level of food intake and the rate of expenditure of energy. To a large extent energy expenditure is governed by activity and temperature. Since metabolic rate appears to be closely correlated to feeding rate (Paloheimo and Dickie, 1966a), it may be deduced that temperature will act as a *major* independent variable. It is therefore of interest to examine further some of the interrelations between food intake and temperature as they affect the body composition of young sockeye in an effort to distinguish the respective roles.

#### FAT PROPORTION

At all temperatures the most responsive constituent to food intake was fat, which varied from a low of 0.6% to a high of 9.5% (Table 3). If the percentage composition of fat is considered in relation to ration (Fig. 17A) there is a direct proportionality at each level of temperature, with very little distinction between the fish held at 20 C and those at 15 C. At lower temper-

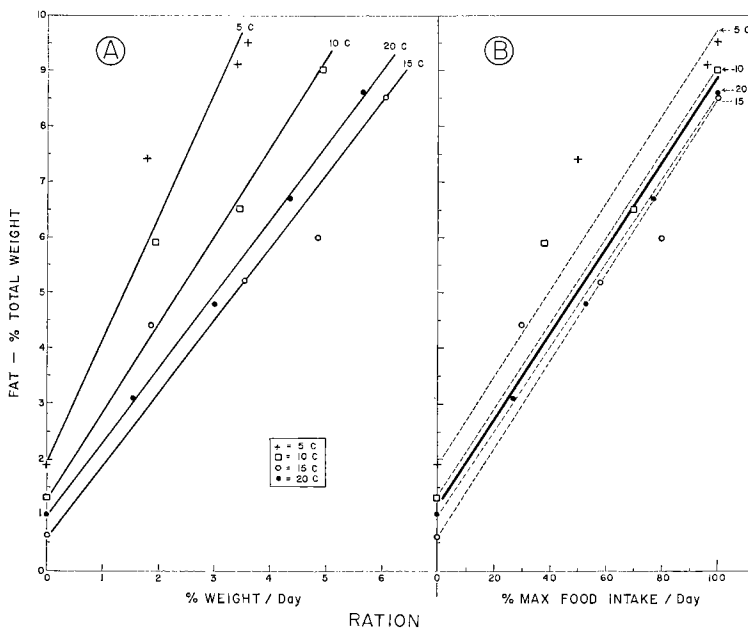


FIG. 17. Relation of body fat to daily ration expressed as a fraction of dry body weight (A) and of the maximum food intake (B), showing the relative influence of temperature. Trend lines for each temperature have been drawn by eye in A. The solid line in B has been drawn for all points, with broken lines representing the constrained effect of temperature when body fat is related to percent maximum food intake.

atures high fat fractions of about 9% occur at lower levels of daily ration, as might be expected from the reduction in maintenance associated with reduced temperature.

A refinement of the above relation may be made by expressing the ration as a fraction of the maximum daily food intake. Since the latter is exponentially temperature-dependent (see Fig. 8) a large proportion of the temperature influence is removed (Fig. 17B). Only at 5 C does there appear to be sufficient difference to warrant separate representation of the data. It is quite possible that the fish at 5 C had not reached a static balance of their body constituents at each ration, and that in time they would have been inseparable from the rest.

Aside from demonstrating the dominant role that ration plays in defining the proportion of body constituents, it is apparent that a simple determination of the fat fraction is likely to reveal at what sort of level the fish is feeding in relation to its capacity, without particular concern for temperatures. As long as some stage of metamorphosis such as smolt-transformation is not in progress the fat assessment should be of value to the ecologist as a means of assessing the general feeding level of any particular population.

Since protein tends to be the most stable component of the gross body constituents it might be thought that the fat/protein ratio (or fat to fat-free dry material) would provide a better indicator of feeding intensity. However, it will be recalled (Fig. 10) that both fat and protein respond in a similar manner to reduced ration so that with the exception of the lowest rations and highest temperatures the fat/protein ratio does not provide a useful index of the relative feeding rate.

#### WATER CONTENT

The starved and excess-fed fish provide examples of extremes of water content that can occur for a given species, age, and diet (71–86.9%, Table 3). Love (1957) records values for fish ranging from 53 to 89.3%, but warns that determinations are not strictly comparable because of different analytical techniques.

Despite this wide variation (which is temperature dependent on a *fixed* ration), when food is present at either the maintenance level or sufficient for maximum growth the body composition was found to be remarkably constant at all temperatures. Under maintenance conditions the water content ranged from 78.3 to 79.7%; on a maximum ration the values ranged from 72.0 to 73.0%. This demonstrates the sort of balance that is struck when particular feeding rations are considered.

#### CONCLUDING COMMENTS

The prime purpose was to determine how temperature affects the growth and efficiency of food conversion of young sockeye salmon at various levels of feeding intensity. The hypothesis that the optimum temperature for growth would shift to a lower temperature with a decrease in ration was supported.

A change in the optimum from 15 to 5 C occurred when the ration was reduced from 6 to 1.5%/day.

The support for the hypothesis depended on maintaining a favorable balance between reduced maintenance costs and efficiency of growth processes (including digestion and transformation) associated with lower temperatures. The fact that a gross conversion efficiency of 20% occurred at 5 C on a reduced ration lends confirmation to the conclusion that the saving in maintenance costs that low temperature affords is the main contributor to sustained efficiency. This is further resolved and supported by examining net efficiency, which indicates some interaction between temperature and food transformation in favor of sustained efficiency at reduced temperature, but not to the same extent as is the case for gross efficiency. This suggests that distinct relations exist between temperature and each of maintenance, metabolism, digestion, and transformation. Although not defined with precision, it is apparent from the high gross efficiency between 5 and 17 C that the enzymatic process of digestion is relatively temperature-independent.

A decrease in the maximum growth rate with age supports the general concept that growth rate is size-specific at any given temperature. That this is not entirely so is indicated by the duration of the growth stanzas. Thus, at 15 C on excess ration sockeye showed a relatively stable growth rate of 1.7%/day from August to January although changing in weight from 10 to 80 g. Since a variety of mathematical transformations have been applied to the growth process, it may be that use of the simple exponential equation is inadequate for a consideration of the effect of size. It is apparent from the sockeye data that the temperature optimum becomes broader with age, so that the significance of temperature to growth, in the presence of unrestricted food, is greatest in the very early stages. Additional significance may be attached to the high efficiency potential that occurs between 5 and 17 C. This temperature range characterizes much of the lacustrine distribution of the species in its early freshwater life. Experimentally, the determination of food-conversion efficiency may well offer one of the greatest sources of insight concerning what governs the success of an organism in nature.

The presence of an optimum for growth at 15 C (when fed to excess) coincides with optimum metabolic scope, greatest tolerance to oxygen-debt, and maximum sustained speed (Brett, 1964). It is apparent that a general physiological optimum occurs at this temperature in fresh water.

The potential for increasing returns in the culturing of fish is self-evident by the presence of such a wide range of efficiency. By determining the particular combination of temperature and ration that produces maximum growth a gross efficiency of 25% is predictable.

Finally, the insight gained by conducting growth  $\times$  ration  $\times$  temperature experiments, accompanied by determinations of body constituents, obviously offers a great deal to the general problem of interpreting ecological relations.

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## REFERENCES

- ALDERDICE, D. F., J. R. BRETT, AND D. B. SUTHERLAND. 1966. Design of small holding tank for fish. J. Fish. Res. Bd. Canada 23: 1447-1450.
- AMERICAN SOCIETY FOR TESTING MATERIALS. 1966. Method D.271, for Parr bomb calorimeter. Am. Soc. Testing Materials 19: 42-46.
- ANON. 1959. The Heinz handbook of nutrition. McGraw-Hill Book Co., New York. 439 p.
- ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1960. Methods of analysis. 9th ed. Assoc. Offic. Anal. Chemists, Washington, D.C.
- BALDWIN, N. S. 1957. Food consumption and growth of brook trout at different temperatures. Trans. Am. Fish. Soc. 86: 323-328.
- BERTALANFFY, L. VON. 1957. Quantitative laws in metabolism and growth. Quart. Rev. Biol. 32: 217-231.
- BLACK, E. C. 1958. Energy stores and metabolism in relation to muscular activity in fishes, p. 51-67. In P. A. Larkin [ed.] The investigation of fish-power problems. H. R. MacMillan lectures in fisheries, Univ. of British Columbia, Vancouver, B.C.
- BLAXTER, K. L. [ed.] 1965. Energy metabolism. Academic Press Inc., New York. 450 p.
- BRETT, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Bd. Canada 9: 265-323.
1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Canada 21: 1183-1226.
1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada 22: 1491-1501.
1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. J. Fish. Res. Bd. Canada 24: 1731-1741.
- BRODY, S. 1945. Bioenergetics and growth. Reinhold Publishing Corp., New York. 1023 p.
- BROWN, M. E. 1946. The growth of brown trout (*Salmo trutta* Linn.). II. Growth of two-year-old trout at a constant temperature of 11.5°C. J. Exptl. Biol. 22: 130-144.
1957. Experimental studies of growth, p. 361-400. In M. E. Brown [ed.] Physiology of fishes, Vol. 1. Academic Press, Inc., New York.
- DAVIES, P. M. C. 1963. Food input and energy extraction efficiency in *Carassius auratus*. Nature 4881: 707.
- DAVIS, G. E., AND C. E. WARREN. 1968. Estimation of food consumption rates, p. 204-225. In W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. Intern. Biol. Programme Handbook 3. Blackwell Scientific Publications, Oxford and Edinburgh.
- DONALDSON, L. R., AND F. J. FOSTER. 1940. Experimental study of the effect of various water temperatures on the growth, food utilization, and mortality rates of fingerling sockeye salmon. Trans. Am. Fish. Soc. 70: 339-346.
- FISHER, K. C. 1958. An approach to the organ and cellular physiology of adaptation to temperature in fish and small mammals, p. 3-39. In C. L. Prosser [ed.] Physiological adaptation. Am. Physiol. Soc., Washington, D.C.
- FOLCH, J., M. LEE, AND G. H. S. STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226: 497-509.

- FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Studies, Biol. Ser. 55, Publ. Ont. Fish. Res. Lab. 68: 1-62.
- GERKING, S. D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monographs 32: 31-78.
- HALVER, J. E., AND W. E. SHANKS. 1960. Nutrition of salmonoid fishes. VIII. Indispensable amino acids for sockeye salmon. J. Nutr. 72: 340-346.
- HASKELL, D. C., L. E. WOLF, AND L. BOUCHARD. 1956. The effect of temperature on the growth of brook trout. New York Fish Game J. 3: 108-113.
- HATANAKA, A., AND MASAO TAKAHASHI. 1960. Studies on the amounts of the anchovy consumed by the mackerel. Tohoku J. Agr. Res. 11: 83-100.
- HOAR, W. S. 1966. General and comparative physiology. Prentice-Hall, Inc., New Jersey. 815 p.
- HOCHACHKA, P. W., AND A. C. SINCLAIR. 1962. Glycogen stores in trout tissues before and after stream planting. J. Fish. Res. Bd. Canada 19: 127-136.
- HUBBS, C. L., AND C. HUBBS. 1953. An improved graphical analysis and comparison of series of samples. Systematic Zool. 2: 49-56.
- IDLER, D. R., AND W. A. CLEMENS. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. Intern. Pacific Salmon Fish. Comm. Progr. Rept. 80 p.
- IVLEV, V. S. 1945. [The biological productivity of waters.] Usp. Sovrem. Biol. 19: 98-100. (In Russian; Transl. in J. Fish. Res. Bd. Canada 23: 1727-1759.)
- JENNINGS, J. B. 1965. Feeding, digestion and assimilation in animals. Pergamon Press, London and New York. 228 p.
- JOHNSON, W. E. 1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Intern. Ver. Limnol. 13: 66-87.
- KEVERN, N. R. 1966. Feeding rate of carp estimated by a radioisotopic method. Trans. Am. Fish. Soc. 95: 363-371.
- KINNE, O. 1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. Physiol. Zool. 33: 288-317.
- KLEIBER, M. 1961. The fire of life. An introduction to animal energetics. John Wiley & Sons, Inc., New York. 454 p.
- LOVE, R. M. 1957. The biochemical composition of fish, p. 401-418. In M. E. Brown [ed.] Physiology of fishes, Vol. 1. Academic Press, Inc., New York.
- MAGNUSON, J. J. 1962. An analysis of aggressive behavior, growth and competition for food and space in medaka, *Oryzias latipes* (Pisces, Cyprinodontidae). Canadian J. Zool. 40: 313-363.
- NARVER, D. W. MS, 1967. Diel vertical movement of pelagial sockeye salmon juveniles. Fish. Res. Bd. Canada, MS Rept. Ser. 949: 24-28.
- NEEDHAM, A. E. 1964. The growth process in animals. Sir Isaac Pitnam and Sons Ltd., London. 522 p.
- PALOHEIMO, J. E., AND L. M. DICKIE. 1966a. Food and growth of fishes. II. Effects of food and temperatures on the relation between metabolism and body weight. J. Fish. Res. Bd. Canada 23: 869-908.
- 1966b. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Bd. Canada 23: 1209-1248.
- PANDIAN, T. J. 1967a. Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprionides* and *Ophioccephalus striatus*. Marine Biol. 1: 16-32.
- 1967b. Transformation of food in the fish *Megalops cyprionides*. I. Influence of quality of food. Marine Biol. 1: 60-64.
- PARKER, R., AND W. E. VANSTONE. 1966. Changes in chemical composition of central British Columbia pink salmon during early sea life. J. Fish. Res. Bd. Canada 23: 1353-1384.

- PENTELOW, F. T. K. 1939. The relation between growth and food consumption in the brown trout (*Salmo trutta*). J. Exptl. Biol. 16: 446-473.
- PHILLIPS, A. M., JR., D. L. LIVINGSTON, AND H. A. POSTON. 1966. The effect of changes in protein quality, calorie sources and calorie levels upon the growth and chemical composition of brook trout. N. Y. State Dept. Conserv. Fish. Res. Bull. 29: 6-7.
- SMIT, H. 1967. Influence of temperature on the rate of gastric juice secretion in the brown bullhead (*Ictalurus nebulosus*). Comp. Biochem. Physiol. 21: 125-132.
- STRAWN, K. 1961. Growth of largemouth bass at various temperatures. Trans. Am. Fish. Soc. 90: 334-335.
- SWIFT, D. R. 1955. Seasonal variations in the growth rate, thyroid gland activity and food reserves of brown trout (*Salmo trutta* Linn.). J. Exptl. Biol. 32: 751-764.
1964. The effect of temperature and oxygen on the growth rate of the Windermere char, *Salvelinus alpinus* (Willughbii). Comp. Biochem. Physiol. 12: 179-183.
- TAYLOR, C. 1962. Growth equations with metabolic parameters. J. Conseil, Conseil Perm. Intern. Exploration Mer 27: 270-286.
- THOMPSON, D. H. 1941. The fish production of inland streams and lakes. Symp. Hydrobiol., Univ. Wisconsin Press, Madison, Wis. p. 206-217.
- VINOGRADOV, A. P. 1953. The elementary chemical composition of marine organisms. Efron and Setlow [translators]. Yale Univ. Press, New Haven, Conn. p. 463-566.
- WARREN, C. E., AND G. E. DAVIS. 1967. Laboratory studies on the feeding, bioenergetics and growth of fish, p. 175-214. In S. D. Gerking [ed.] The biological basis for freshwater fish production. Blackwell Scientific Publications, Oxford.
- WEST, B. W. 1966. Growth rates at various temperatures of the orange-throat darter *Etheostoma spectabilis*. Arkansas Acad. Sci. Proc. 20: 50-53.
- WINBERG, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian State Univ., Minsk. 251 p. (Fish. Res. Bd. Canada Transl. Ser. 194.)

(Appendices A-B follow)

## APPENDIX A.

INGREDIENTS AND PERCENTAGE COMPOSITION BY WEIGHT OF DIET  
USED IN SOCKEYE GROWTH EXPERIMENTS, 1964-67.

	%	
Water	37.2	
Drained, canned salmon	29.7	
Clark's pellet feed	11.1	(J. R. Clark & Co., Salt Lake City, Utah)
Fresh beef liver	10.0	
Yeast	3.7	
Pabulum mixed cereal	2.2	(Edward Dalton Co., Toronto, Ont.)
Cod-liver oil	2.2	
Vitamin pack	1.5	(Nutritional Biochemicals Corp., Cleveland, Ohio)
Gelatin	1.5	
Iodized salt	0.9	

## APPENDIX B.

PROCEDURE FOR DRY EXTRACTION OF FAT<sup>6</sup>

Frozen fish were sliced longitudinally and their abdominal cavities cut open. The fish were then placed on tared aluminum foil trays and dried to constant weight in a forced air oven at 80 C. The fish were not left in the oven any longer than necessary in order to minimize fat oxidation.

The dried fish were crushed and transferred, along with the aluminum foil, to a 500-ml Erlenmeyer fitted with an aluminum foil-wrapped stopper. The material in the flask was extracted with 200 ml of *n*-hexane. The foil was then removed and the sample was further extracted with three successive 100-ml portions of hexane. Each extraction proceeded with occasional shaking for 24 hr. After each extraction the hexane was poured off through a small tared filter paper to prevent loss of suspended particulate material. Final traces of hexane were removed from the fish in a vacuum oven at 40 C.

Subsequent ash (predominantly as oxides) and total protein determinations carried out on the fat-extracted material accounted for 99.5% of the sample.

<sup>6</sup>Method used by Dr T. D. D. Groves, Department of Biochemistry, University of Victoria, Victoria, B.C.