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Title: BIOENERGETICS AND SURVIVAL OF CHUM
(*ONCORHYNCHUS KETA*) AND PINK (*O. GORBUSCHA*)
SALMON IN HEATED SEAWATER

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The use of heated seawater for enhancing the culture of Pacific salmon was investigated. Food consumption rate, gross food conversion efficiency, growth rate, and survival of chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon fed to satiation were determined in relation to water temperature and body weight. Both species of salmon were raised at temperatures of 55°, 60°, 65°, and 70° F.

The highest food consumption rate, gross food conversion efficiency, growth rate, and survival of chum salmon occurred at temperatures of 65°, 55°, 55°-65°, and 55° F, respectively, while those of pink salmon occurred at 65°, 55°-65°, 60°-65°, and 55°-60° F, respectively. The response to all conditions measured was poorest for chum and pink salmon at 70° F. Pink salmon generally had a higher food consumption rate, gross food conversion efficiency, and growth rate than chum salmon.

Food consumption rate, gross food conversion efficiency, growth rate, and survival of chum and pink salmon decreased as body weight increased. As body weight increased, food consumption rate, gross food conversion efficiency, and growth rate generally decreased more at 60° -65° F than at 55° F for chum salmon, and more at 65° -70° F than at lower temperatures for pink salmon.

Survival was influenced by behavior and disease in addition to temperature. Diseases encountered were bacterial kidney disease and vibriosis, of which the former was most prevalent.

Chum and pink salmon can be cultured in heated seawater at temperatures not exceeding 65° F. Good growth (> 5% gain in body weight/day) and survival (60-100%) can be expected.

Bioenergetics and Survival of Chum (*Oncorhynchus keta*) and Pink (*O. gorbuscha*) Salmon in Heated Seawater

by

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BIOENERGETICS AND SURVIVAL OF CHUM (ONCORHYNCHUS KETA) AND PINK (O. GORBUSCHA) SALMON IN HEATED SEAWATER

INTRODUCTION

In the near future, thermal electric generating stations will probably become more common on rivers and coastal areas of the Pacific Northwest. A major by-product from thermal generating stations is the large volume of heated water (700,000 gpm or more for a 1 million kilowatt station).

Under certain circumstances, heated water can adversely affect aquatic life. Drastic changes in the diversity and abundance of fresh water and marine plant and animal species; outright mortality of phytoplankton, zooplankton, fish eggs and larvae; and abnormal copper accumulation in oysters (making them unfit for human consumption) have been attributed to heated water from thermal power stations (Adams, 1969; Allen, Boydstun, and Garcia, 1970; Anderson, 1969; Heinle, 1969; Marcy, 1973; Morgan and Stross, 1969; North and Adams, 1969; Roosenburg, 1969; Wood and Zieman, 1969).

On the other hand, there are apparent beneficial effects of heated water. Certain popular fresh water and marine sport fish which are attracted to warm water discharges, especially during the cold months of the year, provide year-around recreation (Allen et al., 1970; Elser, 1965; Gibbons, Hook, and Forney, 1972; Strawn, 1970). Heated water also appears to enhance the growth of certain commercially important fish and shellfish species, such as oysters, shrimp, catfish, flatfish, and salmon (Adams, 1969; Brett, Shelbourn, and Shoop, 1969; Brett, 1971; Gaucher, 1970; McNeil, 1970; Nash, 1969; Shelbourne, 1970; Strawn, 1970).

The seawater farming of salmon has recently received increased attention in the Pacific Northwest (Ledbetter, 1972; Mahnken, Novotny, and Joiner, 1970; Moring and Salo, 1972; Novotny, 1975). Although the technology for commercial salmon farming is still largely experimental, several corporations and Indian tribes have entered this farming activity on a commercial scale. Water temperature controls the metabolism, including growth, of salmon; hence, an ability to maintain a temperature regime which is optimum for growth would be of distinct advantage to salmon farming. The question arises: can heated discharge water from a coastal thermal power station be used effectively in salmon aquaculture?

The major objective of my research was to determine the temperature at which the highest growth rates of chum salmon, Oncorhynchus keta (Walbaum 1792), and pink salmon, O. gorbuscha (Walbaum 1792), occur when they are fed to satiation. Food consumption rate, gross food conversion efficiency, and survival of salmon raised at the experimental temperatures were also determined. The influence of body weight on food consumption rate, gross food conversion efficiency, and growth rate was examined.

Chum and pink salmon were selected as experimental fish because they acclimate readily to seawater as unfed fry and are fast-growing.

Four temperatures (55°, 60°, 65°, and 70° F) were selected to encompass the temperature range (55° - 70° F) in which the maximal growth rate of salmonids (Pacific salmon, Oncorhynchus spp.; trout, Salmo spp.; and char, Salvelinus spp.) occurs (Atherton and Aitken, 1970; Averett, 1969; Baldwin, 1957; Banks, Fowler, and Elliott, 1971; Brett et al., 1969; Haskell, Wolf, and Bouchard, 1956; Hokanson et al., 1973; Martin, 1966; McCormick, Hokanson, and Jones, 1972; Pentelow, 1939; Phillips, Livingston, and Dumas, 1960; Shelbourn, Brett, and Shirahata, 1973; Swift, 1955, 1961, 1964).

A satiation level of ration was necessary to attain maximal growth at each temperature (Averett, 1969; Brett et al., 1969; Shelbourn et al., 1973).

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Research was conducted at two Oregon State University facilities: the Marine Research Laboratory at Port Orford, Oregon, and the Marine Science Center at Newport, Oregon.

GENERAL METHODS

Experimental fish

Chum salmon

Chum salmon from two brood stocks were used in the experiments (Table 1). Chum salmon from Netarts Bay, Oregon (designated CI), were hatched at the Oregon State University Aquaculture Research Laboratory at Netarts Bay in January, 1971. Juveniles were then transported to the Oregon State University Marine Science Center at Newport, Oregon, and raised to a size of approximately 10 g per fish. When experimental facilities were ready, these fish were transported to the Oregon State University Marine Research Laboratory at Port Orford, Oregon, and were allowed to acclimate to conditions in the laboratory during September, 1971. In late September, three subgroups of fish were randomly selected and transferred to separate tanks. Each subgroup was acclimated to its particular rearing temperature for at least eight days prior to the initiation of Experiment CI (Table 2). This experiment was initiated on October 15th and terminated on November 15, 1971.

Chum salmon from Olsen Bay, Alaska (designated CII), were shipped as fertilized eggs from the National Marine Fisheries Service field station at Olsen Bay to the Oregon State Department of Fish and

Table 1. Experimental subgroups of chum and pink salmon.

Species of salmon	Experiment	Subgroup	Temperature (°F)	Origin of brood stock	Brood year	Initial number of fish	Experimental period (days)	Initial mean weight (g)
Chum	CI	CI55	55	Netarts Bay, Oregon	1970	20	30	17.30
		CI60	60					21.50
		CI65	65					16.06
	CIIa	CIIa55	55	Olsen Bay, Alaska	1971	250	70	1.40
		CIIa60	60					1.52
		CIIa65	65					1.46
		CIIa70	70					1.48
	CIIb	CIIb55	55			105	30	13.77
		CIIb60	60					14.64
		CIIb65	65					12.65
Pink	PIa	PIa55	55	Little Port Walter, Alaska	1970	29	40	47.08
		PIa60	60			29		46.53
		PIa65	65			27		47.98
	PIb	PIb65	65			19	30	111.72
		PIb70	70			17		92.12
	PIIa	PIIa55	55		1971	115	40	1.81
		PIIa60	60			120		1.80
		PIIa65$_1$	65			120		2.11
		PIIa65$_2$	65			120		1.77
	PIIb	PIIb55	55			62	50	9.76
		PIIb60	60			66		11.86
		PIIb65$_1$	65			57		17.54
	PIIc	PIIc55	55			59	40	16.16
		PIIc60	60			63		20.81
		PIIc65$_1$	65			62		27.60
		PIIc70	70			60		22.45

Table 2. Acclimation periods of chum and pink salmon to the experimental temperatures.

Species of salmon	Experiment	Temperature (°F)	Number of days allowed for acclimation to the following temperatures:			
			55°F	60°F	65°F	70°F
Chum	CI	55	18	--	--	--
		60	10	8	--	--
		65	10	--	8	--
	CIIa	55	23	--	--	--
		60	13	10	--	--
		65	13	--	10	--
		70	13	--	10	8
	CIIb	55	83	--	--	--
		60	13	70	--	--
		65	13	--	70	--
Pink	PIa	55	18	--	--	--
		60	10	8	--	--
		65	10	--	8	--
	PIb	65	10	40	8	--
		70	10	--	40	8
	PIIa	55	22	--	--	--
		60	10	10	--	--
		65_1	10	5	8	--
		65_2	10	5	8	--
	PIIb	55	62	--	--	--
		60	10	50	--	--
		65_1	10	5	48	--
	PIIc	55	82	--	--	--
		60	10	70	--	--
		65_1	10	5	70	--
		70	10	5	65	7

Wildlife Big Creek Hatchery at Knappa, Oregon. Eyed eggs were then shipped to the Marine Research Laboratory at Port Orford, Oregon, and hatched during September and October, 1971. Juveniles were raised at 55° F until they attained a weight of 1.4-1.5 g per fish. In November, these fish were randomly divided into four subgroups and acclimated to temperatures of 55°, 60°, 65° and 70° F (Table 2). This experiment, designated CIIa, was initiated on November 27, 1971. It was terminated on February 5, 1972 because of a temporary lack of water heaters and sufficient capacity for increased oxygen production. However, a second experiment, designated CIIb, was organized using some of the fish raised in Experiment CIIa at 55°, 60°, and 60° F. Each subgroup in Experiment CIIb was comprised of 105 of the largest fish retained from the subgroup raised at the same temperature in Experiment CIIa. Experiment CIIb was initiated on February 7th and terminated on March 12, 1972.

Pink salmon

Pink salmon from two brood years were used in the experiments (Table 1). Pink salmon from the 1970 brood year (designated PI) were shipped as eyed eggs from the National Marine Fisheries Service field station at Little Port Walter, Alaska to the Aquaculture Research Laboratory at Netarts Bay, Oregon in October, 1970. Juveniles were later transported to the Marine Science Center at Newport, Oregon, and raised to a size of 20-30 g per fish. When experimental facilities were ready, the fish were transported to the Marine Research Laboratory at Port Orford, Oregon. The fish were allowed to acclimate to conditions in the laboratory during part of September, 1971, and were then randomly divided into three subgroups and acclimated to temperatures of 55°, 60°, and 65° F (Table 2). This experiment, designated PIa, was initiated on October 5th, and terminated on November 15, 1971 because of high mortality in certain subgroups due to bacterial kidney disease. Inasmuch as a comparison of the growth rate of pink salmon at 70° F to that at some lower temperature was desirable, a second experiment, designated PIb, was organized using fish from Experiment PIa. The largest and healthiest-looking fish from Experiment PIa at 60° and 65° F were selected and acclimated to temperatures of 65° and 70° F, respectively (Table 2). Experiment PIa at 55° F was discontinued because of constantly increasing mortality. Experiment PIb was initiated on December 7, 1971 and terminated on January 6, 1972.

Pink salmon from the 1971 brood year (designated PII) were shipped as eyed eggs from Little Port Walter, Alaska to the National Marine Fisheries Service field station at Manchester, Washington. These eggs were later transported from Manchester to the Marine Research Laboratory at Port Orford, Oregon, where they hatched in October, 1971. Fingerlings were held at 55° F, and in February, 1972 they were randomly divided into four subgroups, of which two were acclimated to temperatures of 55° and 60° F, and the other two were acclimated to 65° F (65°_1 and 65°_2) (Table 2). This experiment, designated PIIa, was initiated on February 16th. It was terminated on March 27, 1972 because of concern over the effect of overcrowding (see Appendix 1, Table 1). A second experiment, designated PIIb, was organized using Experiment PIIa fish raised at each of the three temperatures. A certain number of the largest and healthiest-looking fish from a subgroup in Experiment PIIa were selected for the subgroup of the same temperature in Experiment PIIb (Table 1). Experiment PIIb was initiated on March 27th and terminated on May 18, 1972. A third experiment, designated PIIc, was also organized on March 27, 1972. In this experiment, the largest and healthiest-looking fish raised at 65° F in Experiment PIIa were acclimated to 70° F (Table 2). Experiment PIIc was initiated on April 18th and terminated on May 18, 1972. For statistical comparisons of food consumption rates, gross food conversion efficiencies and growth rates among the subgroups in an experiment, the mean weights of the subgroups should be as similar as possible and the experiment should be initiated at the same time for all subgroups. With this in mind, the food consumption rates, etc. of the Experiment PIIc fish at 70° F were compared with those of the Experiment PIIb fish raised at 55°, 60°, and 65° F during the same period (April 18th to May 18, 1972). Solely for comparative purposes with Subgroup PIIc70, Experiment PIIb fish raised at 55° , 60° , and 65° from April 18th to May 18, 1972 were given the Experiment PIIc subgroup designations of PIIc55, PIIc60, and PIIc65, respectively (Table 1).

Selection of fish for each temperature in an experiment

In Experiments CI, CIIa, PIa, and PIIa, subgroups for each experiment were randomly selected. After the selection process, fish were allowed to rest for about 24 hr, and were then acclimated from 55° F to the desired experimental temperature.

In Experiments CIIb, PIb, PIIb, and PIIc, subgroups for each experiment were chosen from the largest and healthiest-looking fish from subgroups in Experiments CIIa, PIa, PIIa, and PIIb, respectively. This non-random selection process was justified because it was necessary to select fish presumably having a high tendency to survive, in order to obtain accurate measurements of food consumption, food conversion, and growth. The largest fish appeared to be healthy and presumably could be expected to maintain good survival, while the smallest fish were in many cases diseased and probably incapable of surviving during the experimental period.

Acclimation of fish to elevated water temperature

Fish acclimate very rapidly (usually in five days) to increasing temperatures (Brett, 1946; Doudoroff, 1942, 1945, 1957; Tarzwell, 1970; Warren, 1971). Also, acclimation to increasing temperatures occurs at a faster rate at high temperatures than at low temperatures. Goldfish, Carassius auratus (Linnaeus 1758), raised at 68.0° F acclimated faster to 82.4° F than those raised at 39.2° F acclimated to 53.6° F (Brett, 1946).

All subgroups of salmon in my experiments were acclimated to their respective temperatures for at least seven days prior to experimentation. Acclimation to elevated temperatures was accomplished in stages by first exposing fish raised at ambient temperature (see Table 3) to 55° F. For most subgroups of fish raised at 60° or 65° F, the temperature was elevated directly from 55° F, while for Subgroups PIb65, PIIa65$_1$, and PIIa65$_2$, the temperature was elevated from 60° F. For all subgroups of fish raised at 70° F, the temperature was elevated from 65° F.

Table 3. Ambient seawater temperatures.

Experiment	Experimental period	Ambient seawater temperature (°F) Mean	Ambient seawater temperature (°F) Range
CI	Oct. 15-Nov. 15, 1971	50.2	47.8-52.5
CIIa	Nov. 27, 1971-Feb. 5, 1972	50.0	47.5-52.5
CIIb	Feb. 7-Mar. 12, 1972	51.6	48.9-53.8
PIa	Oct. 5-Nov. 15, 1971	50.2	47.8-52.5
PIb	Dec. 7, 1971-Jan. 6, 1972	48.2	46.4-50.5
PIIa	Feb. 16-Mar. 27, 1972	51.6	50.0-52.9
PIIb	Mar. 27-May 18, 1972	50.3	46.2-54.3
PIIc	Apr. 18-May 18, 1972	49.1	46.2-53.6

Fish rearing equipment and aquatic environment

All experiments were conducted in a vacated Coast Guard boathouse located adjacent to Nellie's Cove at Port Orford, Oregon. The boathouse was remodeled to provide laboratory facilities for raising fish at different temperatures and for conducting the food consumption, food conversion, and growth studies.

Rearing tanks

Salmon were raised in 100-gallon capacity, rectangular plywood tanks filled with seawater (salinity range = 26.5-33.4‰)(Figure 1). Interiors of all tanks were coated with fiberglass. Each tank was covered with a rigid, removable screen to prevent fish losses due to jumping.

Seawater was pumped from the bay into a 500-gallon capacity reservoir located in the attic of the laboratory. Water for each tank was obtained through a 0.5-inch (I.D.) polyvinyl chloride (PVC) pipe which connected the reservoir to the tank located on the floor of the laboratory. A PVC ball valve controlled water flow to each tank. Water drained from each tank through a screened 1.0-inch (I.D.) PVC pipe into the bay. Water flowing into each tank was at the ambient temperature of the bay (Table 3).

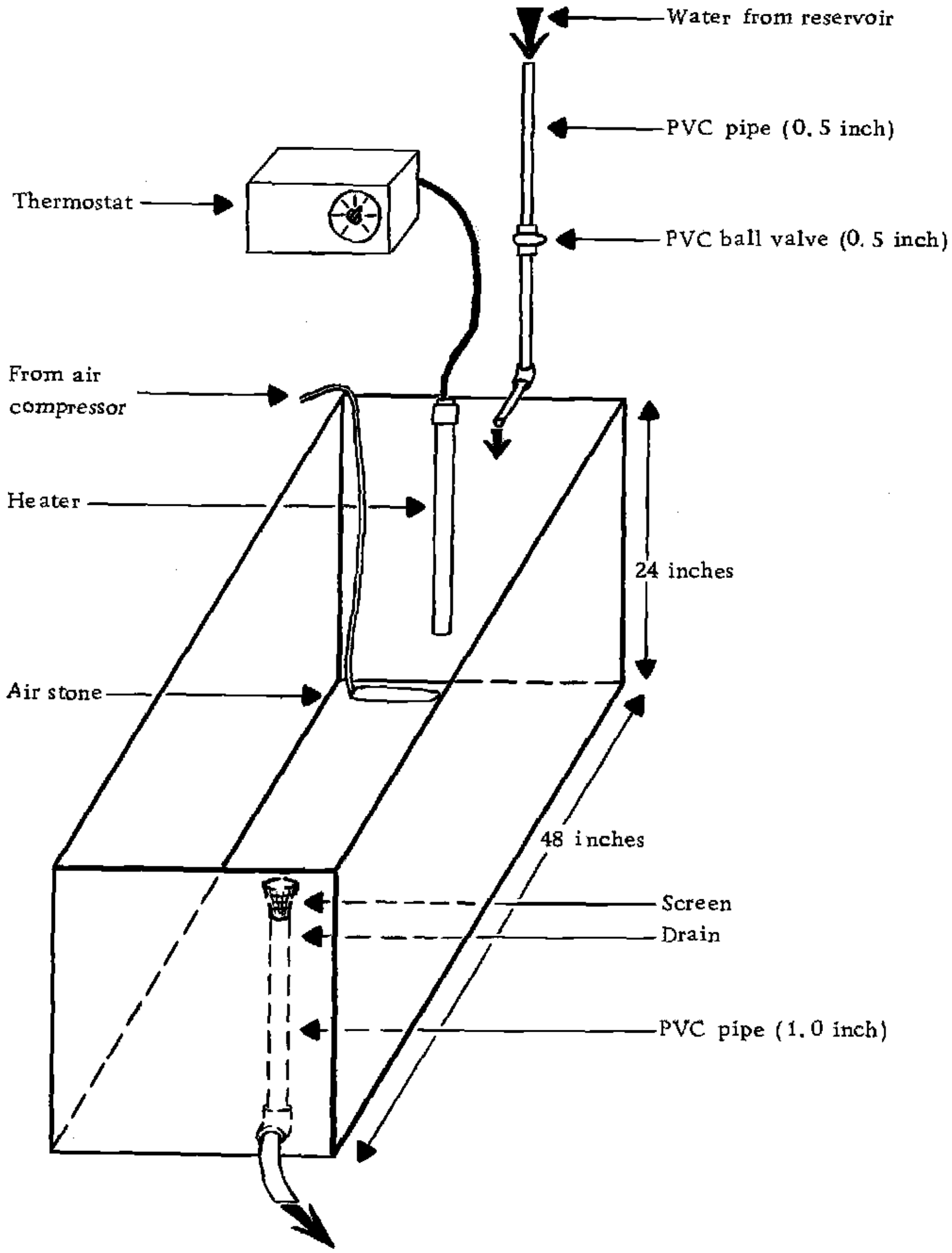

Figure 1. A typical 100-gallon rearing tank.

Maintenance of water temperature

Water in each tank was individually heated to the desired temperature by a 1500 watt Vycor immersion heater which was controlled by a NAPCO thermostat (Model 730-1).

Water temperatures were taken twice daily with a Fahrenheit thermometer calibrated at 0.2° F intervals. The temperature was taken at a depth of about five inches near the drain. Previous tests indicated that temperatures were identical at all locations in a tank. Temperature data for all experiments are depicted in Appendix 2, Table 1.

Tank water volume

Water volume in each tank was varied according to the total weight of fish in the tank. In Experiments CIIa and PIIa, total fish weight in each subgroup was less than 600 g at the beginning of an experiment, and a water volume of 50 gal per tank was used. This shallow water facilitated the initial feeding of small fish and the collection of food waste and dead fish. When the total fish weight per tank exceeded 600 g in any experiment, a system of determining the water volume for each tank was devised as follows. The subgroup having the highest total weight within an experiment was assigned a water volume of 85 gal, which was maintained throughout the experiment.

The water volume for each of the other subgroups within the experiment was calculated by solving the following equation:

$$V = 85 \cdot W_x / W_s$$

where W_s = total weight of fish in the subgroup having the highest total weight at any time,
W_x = total weight of fish in the subgroup for which water volume was to be determined, and
V = calculated water volume for the subgroup having the total fish weight of W_x.

The water volume in each tank was adjusted every 10th day when the fish were weighed.

Tank water flow and oxygen content

The water inflow rate for each tank was varied according to the total weight of fish in the tank. For each experiment, a standard water inflow rate of 0. 5 gpm was set for the subgroup having the highest total weight of fish. Water inflow rate for each of the other subgroups within an experiment was calculated by solving the following equation:

$$F = 0.5 \cdot W_x / W_s$$

where W_s = total weight of fish in the subgroup having the highest total weight at any time,
W_x = total weight of fish in the subgroup for which the water inflow rate was to be determined, and
F = calculated water inflow rate for the subgroup having the total weight of W_x.

The water inflow rate for each tank was checked and readjusted at least twice daily because of occasional blockage of the water inlet pipe by kelp, and was changed every 10th day when the fish were weighed.

A water inflow rate of 0.5 gpm was determined as a standard because this was the maximal water inflow rate that would allow a tank heater to maintain a water temperature of 70° F. For my experimental purposes, this water inflow rate was deemed adequate. According to the loading factor chart of Piper (1971), which allows one to calculate the total fish weight to stock (carrying capacity) per gpm inflow of water, over 2100 g of 10-inch salmon can be raised at temperatures of 55°, 60°, 65°, and 70° F when the water inflow rate is 0.5 gpm. The total fish weight per tank in all experiments and the carrying capacities recommended in Piper (1971) are depicted in Appendix 1, Table 1. The recommended carrying capacities were exceeded occasionally, but this was probably not harmful inasmuch as the incoming water was saturated with oxygen after being sprayed through screens, and the dissolved oxygen content at all temperatures was maintained in excess of 6.5 mg/l by forcing air through large air stones located in the tanks.

The dissolved oxygen content of the water for all subgroups in all experiments was maintained within 1.5 mg/l of saturation (Appendix 3, Table 1). Dissolved oxygen content in each tank was measured approximately every 10th day using the azide modification of the Winkler method (American Public Health Association, 1965). For a dissolved oxygen determination, a sample of water (standard D. O. bottle) was carefully collected by siphon hose at a mid-water depth adjacent to the drain. Previous tests indicated that dissolved oxygen content was identical at any location in a tank.

Tank hygiene

Tanks, water heaters, and air stones were cleaned and disinfected with malachite green every 10th day, when fish occupying the tank were weighed. A tank occasionally became dirty between regular cleaning days because of accumulated silt and bacterial growth, and was cleaned with an underwater siphoning device when necessary. Air stones were usually cleaned and backflushed twice between regular tank-cleaning days to insure their proper function.

Photoperiod

All fish were exposed to approximately 10 hr of light per day throughout the experimental period. Light was provided by fluorescent lamps suspended about 10 ft above the tanks.

Diet

All fish were fed the Oregon moist pellet (OMP) diet for four reasons. 1) This diet is nutritionally sound for the production of healthy salmon under various conditions, including different water temperatures (Hublou et al., 1959; Hublou, 1963). 2) OMP is easier to feed to salmon than a dry diet. Salmon have been observed to feed poorly on commercial dry pellet diets (Nielson and Mazuranich, 1959). Furthermore, salmon may reduce their food intake when a change is made from a smaller to a larger pellet size with a dry diet (Fowler and Burrows, 1971). 3) The OMP diet was relatively inexpensive ($0.16/lb.) during the experimental period (1970-72). 4) The OMP diet was easily obtained in most sizes throughout the year from either the Oregon manufacturer[1] or from an Oregon State Department of Fish and Wildlife hatchery.

The OMP diet was available in three formulations: OMP-I, OMP-II, and OMP-III. The OMP-II and OMP-III formulations promote faster salmon growth than the OMP-I formulation because of the higher amount of caloric energy, lipid, and high quality protein in the OMP-II and OMP-III formulations (Crawford, Law, and Babbitt, 1971a). Though OMP-III produces a slightly faster growth rate than OMP-II, the later formulation was selected as my experimental diet because of its availability in a wide range of pellet sizes.

Five sizes (diameter in inches) of Oregon moist pellets were fed to fish during the experiments: 0.045 (starter mash), 0.047,

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[1] Bioproducts, Inc., P.O. Box 429, Warrenton, Oregon 97146.

0. 062, 0. 094, and 0. 125. Starter mash was fed only to CII and PII fish prior to the initiation of any experiments.

In general, the pellet size fed was determined by fish size. However, all subgroups in an experiment were fed a uniform pellet size from the same bag at a feeding period despite differences in mean weight among the subgroups, in order to minimize any possible effect of pellet size as a variable affecting salmon growth. Different protein and lipid contents have been reported for batches (bags) of the OMP-II diet which were produced only a few days apart, but pellets of the same size from a single batch had similar protein and lipid contents (Crawford, Law, and Babbitt, 1971b). The pellet size selected for an experiment (see Appendix 4, Table 1) was the largest size which all fish in the subgroup having the smallest mean weight could easily ingest, according to the 1962 Oregon pellet feeding chart obtained from Bioproducts, Inc.

All fish were fed twice daily, six days a week. On the seventh day, the fish were fed either once or twice daily. The first and second feeding periods generally began at 0900 and 1700 hr, respectively. During each feeding period, fish in each subgroup were fed all they could consume in one hour, which insured that all fish were fed to satiation.

Disease treatment

Two diseases were encountered in chum and pink salmon: bacterial kidney disease (BKD) and vibriosis.

Treatment was attempted only for BKD because it was much more prevalent than vibriosis. When evidence of BKD was found in autopsied fish, all fish in the same subgroup as the diseased, autopsied fish were treated with oxytetracycline hydrochloride (Terramycin, TM-50D) in the diet at the rate of 36 g TM-50D/45.36 kg of fish per day for 10 days. Terramycin (TM-50D) is an effective antibiotic for preventing salmon deaths due to BKD, though it cannot eradicate the infection (Novotny, 1975; Snieszko and Griffin, 1955; Wood, 1968). When used at the correct treatment rate, Terramycin apparently does not affect the food consumption, food conversion, and growth of salmon (Snieszko and Griffin, 1955; Weber and Ridgway, 1967).

Erythromycin is more effective than Terramycin and other drugs (e. g., sulfonamides and nitrofuran compounds) in providing prolonged arrest of BKD well after treatment is discontinued (Bullock, Conroy, and Snieszko, 1971; Wolf and Dunbar, 1959). An attempt was made to treat BKD with erythromycin in the diet. However, chum and pink salmon, even when not fed for 24 hr, did not consume erythromycin in the diet, which was presumably due to the bitter taste of this antibiotic. Food consumption was only slightly better when the erythromycin-diet mixture was coated with brown sugar or chocolate syrup. Feeding of erythromycin was discontinued after two days to avoid substantial declines in gross food conversion efficiency and growth rate.

Measurement of food consumption rate

The food consumption rate of a subgroup is the amount of food consumed (wet weight, g)/mean total fish weight (wet, g) per day, which is more simply expressed as percent body weight/day. The food consumption rate of a subgroup was determined for each 10-day period between fish-weighings in the following manner. The total amount of food consumed by the fish during each feeding period was known because the amount of food remaining in the feed cup after feeding was subtracted from the amount of food at the beginning of the feeding period to obtain the amount of food presented to the fish, and the amount of uneaten food remaining in the tank was deducted from the amount of food presented to the fish. The weight of any uneaten pellets remaining in the tank was determined by counting the pellets siphoned from the tank, and then weighing an equal number of pellets which were randomly selected from the feed bag. Assuming no fish deaths, the mean total fish weight of a subgroup was obtained for the determination of food consumption rate by simply adding the total weights at the beginning and end of the 10-day period, and finding the mean value. If deaths occurred during the period, an adjustment was made to determine the mean total fish weight of a subgroup. Four assumptions were necessary to warrant this adjustment. 1) The mean weight of the dead fish presumably did not affect the mean weight of fish at the beginning ($\overline{W}_o$) and end ($\overline{W}_{10}$) of the 10-day period. This meant that fish destined to die presumably had a mean weight at the beginning of the 10-day period ($\overline{W}_{mo}$) equal to that of all fish at the beginning of the period ($\overline{W}_o$). 2) The number of deaths (N_m) did affect the number of fish at the end of the 10-day period and, therefore, the total fish weight. 3) Fish consumed some food and gained some weight prior to their death. The major cause of deaths at 55°, 60°, and 65° F was bacterial kidney disease (BKD), and at 70° F was presumably failure to adjust to the high temperature. Prior to their death, salmon with BKD or at 70° F consumed little or no food for 1 to 3 days. 4) In determining an adjusted mean total fish weight, I assumed that half of the fish destined to die ($N_m/2$) consumed some food and gained some weight during the first 5 days, and that the other half ($N_m/2$) consumed some food and gained some weight during the second 5 days of the period. The adjusted mean total fish weight was calculated in the following manner:

$$[\overline{W}_o (N_o-(N_m/2)) + \overline{W}_{10} (N_o-(N_m/2))] /2,$$

where N_o = number of fish at the beginning of the period. When both the amount of food consumed and the mean total (or adjusted mean total) weight were determined for the 10-day period, the food consumption rate was calculated as follows:

[food consumed/mean total (or adjusted mean total)weight· 0. 1]· 100%.

Measurement of gross food conversion efficiency

The gross food conversion efficiency of a subgroup is the gain in fish weight (wet, g)/amount of food consumed (wet weight, g) · 100%, which is more simply expressed as percent growth/food consumed.

Gross food conversion efficiency was determined for each 10-day period between fish-weighings in the following manner. The amount of food consumed was already measured for the determination of food consumption rate. If no fish died, the total fish weight at the beginning of the 10-day period was subtracted from that at the end of the period to obtain the gain in fish weight. If deaths occurred during the period, an adjustment was made to determine the gain in fish weight. The assumptions necessary to warrant this adjustment were already mentioned in the measurement of food consumption rate. The adjusted gain in fish weight was calculated in the following manner:

$$\overline{W}_{10}[N_o-(N_m/2)] - \overline{W}_o[N_o-(N_m/2)].$$

When both the amount of food consumed and the gain (or adjusted gain) in weight were determined for the 10-day period, the gross food conversion efficiency was calculated as follows:

[gain (or adjusted gain) in weight/amount of food consumed]· 100%.

Exponential growth equation

The growth in weight of fish and other vertebrates at an early age increases at any moment in proportion to the weight already attained (Brody, 1927, 1945; Parker and Larkin, 1959; Snedecor and Cochran, 1967). This type of growth is commonly called exponential growth. When growth is exponential, a plot of weight versus time yields an ascending curve increasing in slope as time increases. Mathematically, exponential growth can be represented by the differential equation

$$GW = \delta W/\delta t \tag{1}$$

which becomes

$$G = \frac{\delta W/\delta t}{W} \tag{2}$$

where W = weight,
t = time, and
G = growth rate relative to existing body weight, or simply relative growth rate.

The integration of equation 2 yields

$$W_t = W_o e^{Gt} \tag{3}$$

where W_o, W_t = weight when time is 0 and t, respectively. Written in logarithmic form, equation 3 yields the convenient equation for a straight line

$$\ln W_t = \ln W_o + Gt. \tag{4}$$

For a series of observations of weight at different times, then, the regression of the natural logarithm of weight on time would yield a straight line if growth was exponential. The growth rate, G, during the total time period is equal to the slope of the regression line. During any interval of time, $\Delta t = t_2 - t_1$, the growth rate can be calculated from the weights at the two times as follows:

$$G = \ln W_2 - \ln W_1 / t_2 - t_1. \tag{5}$$

The growth rate, G, is related to another growth term, h. The term h is familiar as the quarterly compounded interest rate on savings, and found in the expression

$$M_t = M_o\ (h+1)^t \tag{6}$$

where M_o, M_t = amount of money when time is 0 and t, respectively. Written in logarithmic form, equation 6 becomes the convenient equation for a straight line

$$\ln M_t = \ln M_o + \ln (h+1) \cdot t. \tag{7}$$

The regression of the natural logarithm of the amount of money on time yields a straight line because money grows exponentially.

If fish weight, W, is substituted for money, M, in equation 7, we obtain the equation

$$\ln W_t = \ln W_o + \ln (h+1) \cdot t. \tag{8}$$

Equation 8 is nothing more than equation 4 where ln (h+1) is substituted for G. The slope of the regression line, ln (h+1), like h, is the relative growth rate of the fish. During any interval of time, $\Delta t = t_2 - t_1$, the growth rate, h, can be calculated from the fish weights at the two times as follows:

$$h = \text{antilog } (\ln W_2 - \ln W_1 / t_2 - t_1) - 1. \tag{9}$$

Note that the growth rate, h, when multiplied by 100% is the % gain in body weight/day. In this thesis, h actually refers to 100% · h.

It is interesting to note that h and ln (h+1) are virtually identical. For values of h less than 6%/day (which was never exceeded in my experiments), ln (h+1) is similar to h. For example, when h = 5.13% or 0.0513/day, ln (h+1) = ln 1.0513 or 5.00%/day. This similarity can simplify the calculation of h from weight versus time data, inasmuch as when growth is exponential, h approximates the slope in equation 8. Also, during any time interval, $\Delta t = t_2 - t_1$, h approximates equation 5 so that equation 9 can be rewritten as

$$h \approx \ln W_2 - \ln W_1 / t_2 - t_1. \qquad (10)$$

The utility of the term h is apparent when one translates growth rate to absolute fish weight values. For example, if a fish grows at a rate of 2%/day, how long will it take for the fish to double its weight? The answer, 36 days, is found by a quick glance at a compound interest table, where the growth rate, h, is equal to the compound interest (Chemical Rubber Co., 1964). The time required for fish weight to increase at various growth rates is depicted in Appendix 5, Table 1.

Measurement of growth rate

The growth rate (h) of each subgroup was determined every 10th day. The mean weight of all fish in a subgroup at the beginning and end of the 10-day period was determined as follows. Fish were transferred in small numbers or singly, depending on size, from the tank, anesthetized in MS 222, placed on a dry towel to remove excess moisture, weighed to the nearest 0.01 g, and then placed in an auxiliary tank. After all fish had been weighed, they were transferred from the auxiliary tank to their rearing tank. Mean fish weight was calculated by dividing total weight by the number of fish. The mean weight was not adjusted if any fish died during the period for the following reason: fish destined to die presumably had a mean weight at the beginning of the period ($\overline{W}_{mo}$) equal to that of all fish at the beginning of the period ($\overline{W}_o$). When the mean weight of the subgroup at the beginning and end of the period had been calculated, growth rate was found by substituting $\overline{W}_o$ and $\overline{W}_{10}$ for W_1 and W_2, respectively, in equation 9 and solving for h as follows:

$$h = \text{antilog } (\ln \overline{W}_{10} - \ln \overline{W}_o / t_2 - t_1) - 1, \qquad (11)$$

where h = % gain in subgroup mean weight/day, or simply % gain in body weight/day, and
$t_2 - t_1 = 10$ days.

Measurement of survival

The survival of a subgroup is the percent of the initial number of fish that survived to the end of the experimental period. Dead fish were counted twice daily, and these daily counts were totaled at the end of the experiment to obtain the total number of dead fish, N_{mt}. Survival was then calculated by solving the following expression:

$$[(N_o - N_{mt})/N_o] \cdot 100\%.$$

Statistical methods

Covariance analysis

Covariance analysis was used in ascertaining the effect of temperature on food consumption rate and gross food conversion efficiency in all eight experiments, and growth rate in Experiments CI, PIb, PIIb, and PIIc.

An equal number of observations (N) of food consumption rate, gross food conversion efficiency, or growth rate were made at each temperature within each experiment. In an experiment, the food consumption rate, gross food conversion efficiency, or growth rate data (Y) formed a one-way classification for analysis of variance with the different temperatures being the classes. A typical analysis of variance model of a food consumption rate, or etc. value (Y_{ij}) of a subgroup for the $_j$th observation at the $_i$th temperature is

$$Y_{ij} = \mu_i + e_{ij} \tag{12}$$

where μ_i = population mean of the food consumption rates, or etc. obtained at the $_i$th temperature, and
e_{ij} = residuals.

In my experiments, analysis of variance alone was not precise enough because of the dependence of food consumption rate, gross food conversion efficiency, and growth rate on fish weight in addition to temperature. The different temperatures in an experiment generally resulted in different growth rates among subgroups, which meant that fish weight was generally different among subgroups during and at the termination of an experiment. Food consumption rate, gross food conversion efficiency, and growth rate are known to be inversely related to fish weight (Averett, 1969; Banks et al., 1971;

Brett et al., 1969; Brown, 1957; Haskell et al., 1956; Paloheimo and Dickie, 1966). This inverse relationship was demonstrated for my chum and pink salmon (Appendix 6, Table 1). The analysis of variance was rendered more precise to adjust for this negative linear relationship between food consumption rate, etc. and fish weight by the addition of a linear regression term to the analysis of variance model (equation 12) to set up the analysis of covariance model

$$Y_{ij} = \mu_1 + \beta\,(\overline{X}_{ij} - \overline{\overline{X}}) + \varepsilon_{ij} \tag{13}$$

where β = population regression coefficient of Y on X,
$\overline{X}_{ij}$ = subgroup mean weight value for the ${}_j$th observation at the ${}_i$th temperature,
$\overline{\overline{X}}$ = grand mean of all subgroup mean weights in an experiment, and
ε_{ij} = residuals which are generally smaller than e_{ij} (Snedecor and Cochran, 1967).

An estimate of μ_i which I designated $\overline{Y}a_i$ was obtained by solving

$$\overline{Y}a_i = \overline{Y}_i - b\,(\overline{X}_i - \overline{\overline{X}}) \tag{14}$$

where $\overline{Y}a_i$ = adjusted mean food consumption rate, or etc. for the subgroup raised at the ${}_i$th temperature,
$\overline{Y}_i$ = observed mean food consumption rate, or etc., and
b = sample estimator of β.

The adjusted mean food consumption rates, or etc. for the subgroups in an experiment were then statistically tested for any significant differences due to temperature. An F-test of the adjusted means ($\overline{Y}a$ values) was automatically provided on the covariance analysis program (for Monroe 1766 calculator). When the F-test detected differences among the $\overline{Y}a$ values in an experiment, a special "t" test was applied to determine statistical differences between individual $\overline{Y}a$ values in an experiment (Snedecor and Cochran, 1967). The calculated value of "t" is

$$t = \overline{Y}a_i - \overline{Y}a_j / \overline{S}_D$$

where $\overline{S}_D$ = standard error of the difference between $\overline{Y}a_i$ and $\overline{Y}a_j$.

Regression analysis

The effect of temperature on the growth rate of subgroups in Experiments CIIa, CIIb, PIa, and PIIa was determined by linear regression analysis. For each subgroup, the regression of ln mean weight on time was determined for the experimental period. The regression equation, which is similar to equation 8, is

$$\ln \overline{W}_t = \ln \overline{W}_o + \ln (\overline{h}+1) \cdot t \qquad (15)$$

where $\overline{W}_o$ = initial mean weight of the subgroup,
$\overline{W}_t$ = final mean weight of the subgroup,
$\overline{h}$ = mean growth rate of the subgroup, and
t = experimental period (days).

As mentioned previously, the growth rate, h, for all subgroups in all experiments was determined every 10th day. The mean growth rate, $\overline{h}$, for a subgroup was simply the mean of all the h values calculated throughout the experimental period. For subgroups in Experiments

CIIa, CIIb, PIa, and PIIa, $\bar{h}$ was simply calculated from the regression coefficient, ln $(\bar{h}+1)$, in equation 15.

Statistical differences between any two regression coefficients and, thus, between any two $\bar{h}$ values for any two subgroups in an experiment were determined by an F-test and a special "t" test (Bailey, 1959; Davies and Goldsmith, 1972). The calculated "t" value is

$$t = \bar{h}_1 - \bar{h}_2 / S_{e(\bar{h}_1 - \bar{h}_2)}$$

where $S_{e(\bar{h}_1 - \bar{h}_2)}$ = standard error of the difference between $\bar{h}_1$ and $\bar{h}_2$.

In the four experiments in which regression analysis was used, the initial mean weights of subgroups within any one experiment were generally similar (Appendix 7, Table 1). When the initial mean weights of subgroups in an experiment were not similar, as in the other four experiments (CI, PIb, PIIb, and PIIc), regression coefficients were not comparable because of the influence of body weight on growth rate; in this case the effect of temperature on growth rate was determined by covariance analysis as previously discussed.

RESULTS AND DISCUSSION

Food consumption rate

Effect of temperature

The food consumption rate of chum salmon was generally highest at 60° and 65° F, and higher at 55° F than at 70° F (Figure 2; Appendix 8, Table 1). The food consumption rate of pink salmon was generally highest at 65° F, higher at 60° F than at 55° F, and lowest at 70° F (Figure 2; Appendix 8, Table 1). The highest food consumption rate of pink salmon occurred at 65° F for small and medium-sized fish, and at three temperatures (55°, 60°, and 65° F) for large[2] fish (Figure 2). Food consumption rate was generally higher for pink salmon than for chum salmon of comparable body weight at each temperature, and it increased more for pink than for chum salmon as the temperature increased from 55° to 65° F (Table 4).

The observed effect of temperature on the food consumption rates of chum and pink salmon raised in seawater is generally consistent with results obtained for other salmonids, raised mostly in freshwater, by various workers. The food consumption rates of various salmonids, including my chum and pink salmon, increased

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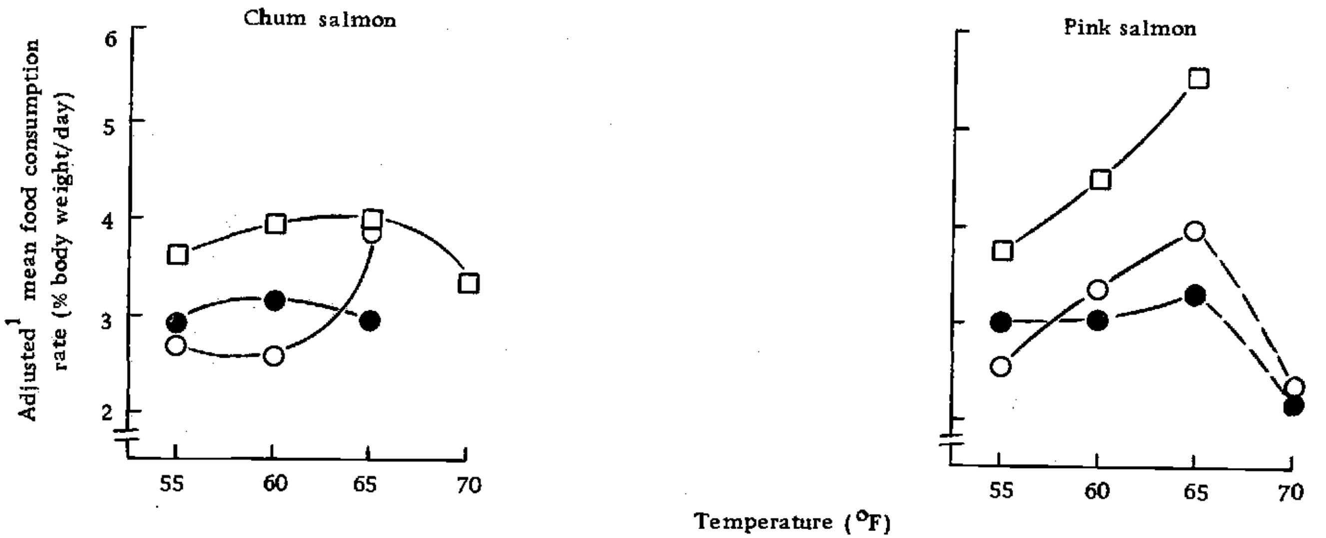
[2] In this and subsequent sections, "small," "medium," and "large" pink salmon were those which had mean weights of approximately 8.0 g, 27.7 g, and 69.7 g, respectively.



Experiment	Relative weight class	Experiment mean weight[2] (g)	Effect of temperature on food consumption rate
□ CIIa	small	5.9	$65 \overset{ns}{>} 60 \overset{*}{>} 55 \overset{*}{>} 70$
○ CIIb	medium	20.6	$65 \overset{**}{>} 55 \overset{n.s.}{>} 60$
● CI	medium	24.4	$60 \overset{n.s.}{>} 65 \overset{n.s.}{>} 55$

Experiment	Relative weight class	Experiment mean weight (g)	Effect of temperature on food consumption rate
□ PIIa	small	8.0	$65 \overset{*}{>} 60 \overset{**}{>} 55$
○ PIIb	medium	27.7	$65 \overset{*}{>} 60 \overset{**}{>} 55 \overset{n.s.}{>} 70^4$
● PIa	large	69.7	$65 \overset{n.s.}{>} 60 \overset{n.s.}{>} 55 \overset{ns}{>} 70^4$

Figure 2. Effect of temperature on the food consumption rates of chum and pink salmon.

[1] Adjusted by covariance analysis.

[2] The mean of all subgroup mean weights.

[3] The number (55, 60, 65 or 70) represents the adjusted mean food consumption rate at that temperature. Levels of significance above the "greater than" symbol (>) are: n.s. = not significant ($P > 0.05$), * = $P < 0.05$, and ** = $P < 0.01$.

[4] These food consumption rates at 70°F in Experiments PIIb and PIa were inferred from those in Experiments PIIc and PIb, respectively.

Table 4. Effect of temperature on the food consumption rates of chum and pink salmon of comparable size.

Experiments compared	Experiment mean weight (g)	Adjusted mean food consumption rate (% body weight/day) at the following temperatures:			Change in adjusted mean food consumption rate as temperature increased from 55° to 65°F
		55°F	60°F	65°F	
CIIa	5.9	3.61	3.93	3.98	10.2%
and					
PIIa	8.0	3.73	4.48	5.55	48.8%
CI	24.4	2.89	3.14	2.95	8.2%
and					
PIIb	27.7	2.55	3.35	3.97	55.7%

to a high value as temperature increased to a certain level, above which the rates declined (Figure 3). The highest food consumption rates of coho (Averett, 1969), chum (Rowan, 1975), and sockeye (Brett et al., 1969) salmon occurred at temperatures (62.6°-68.0° F) close to those of 60° and 65° F at which the highest food consumption rates of my chum and pink salmon occurred. The food consumption rates of two species of salmonids declined from a high value as the temperature increased to high levels (69.0°-73.4° F) which probably stressed the fish (Figure 3); this also occurred for my chum and pink salmon as temperature increased to a high level (70° F).

The changes in food consumption rates of chum and pink salmon as temperature increased can be explained by examining the destinies of the food consumed by a fish. Warren and Davis (1967) described these various destinies of consumed food in terms of relative rates (rate per unit of body mass per unit of time) in the following equation:

$$Ac - Aw = Ag + Ar \qquad (16)$$

where Ac = relative food consumption rate,
Aw = relative rate of food waste production as feces, urine, and as waste lost through gills and skin,
Ag = relative growth rate, and
Ar = relative total metabolic (respiration) rate.

The total metabolic rate (Ar) consists of three other destinies of consumed food as depicted in the following equation:

$$Ar = Aa + Ad + As \qquad (17)$$

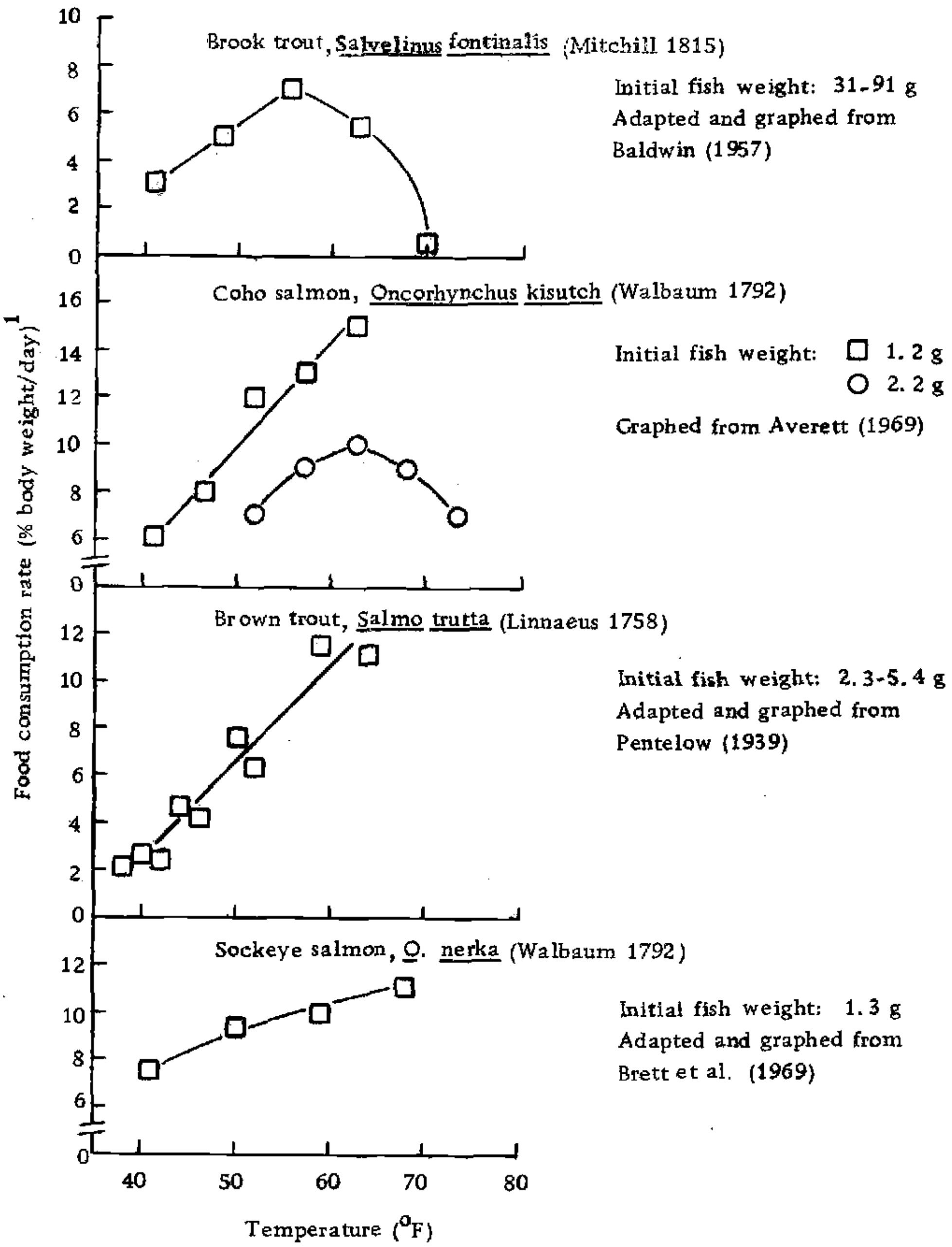


Figure 3. Food consumption rates of salmonids at different temperatures.

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[1] Food consumption rates are defined in terms of dry food and body weights for coho salmon, and in terms of wet weights for the other salmonids. Note: all plot lines were fitted by eye.

where Aa = relative rate of muscular activity in excess of that used for standard metabolism,
Ad = relative rate of food processing, i. e., the rate of digestion, assimilation, and storage of the food consumed, and
As = relative standard (basal) metabolic rate.

During the discussion of the effect of temperature on the food consumption rate of my salmon, I will frequently refer to Figure 4. Figure 4 depicts three graphs from three experiments for each species. Each graph depicts the change in food consumption rate (Ac) and destinies of consumed food (Ag, Aw, and Ar) as temperature increased. The A values are expressed as relative rates in terms of dry material weight:

Ai = grams material/100 g fish weight per day, or more simply,

% dry body weight/day

where i = c, g, w, and r.

Food consumption rates (Ac) and growth rates (Ag) at 55°, 60°, and 65° F were derived from actual experimental data. Ac and Ag values in Experiment CIIa at 70° F were derived from actual data, but Ac and Ag values in Experiments CIIb and CI at 70° F were inferred from the data of Subgroup CIIa70, while Ac and Ag values for pink salmon at 70° F in all three experiments were inferred from the data of Subgroups PIIc70 and PIb70. Waste production rates (Aw) were theoretical values inferred from the data of Averett (1969) for coho salmon. Inasmuch as waste production rate (Aw) is a direct function of food

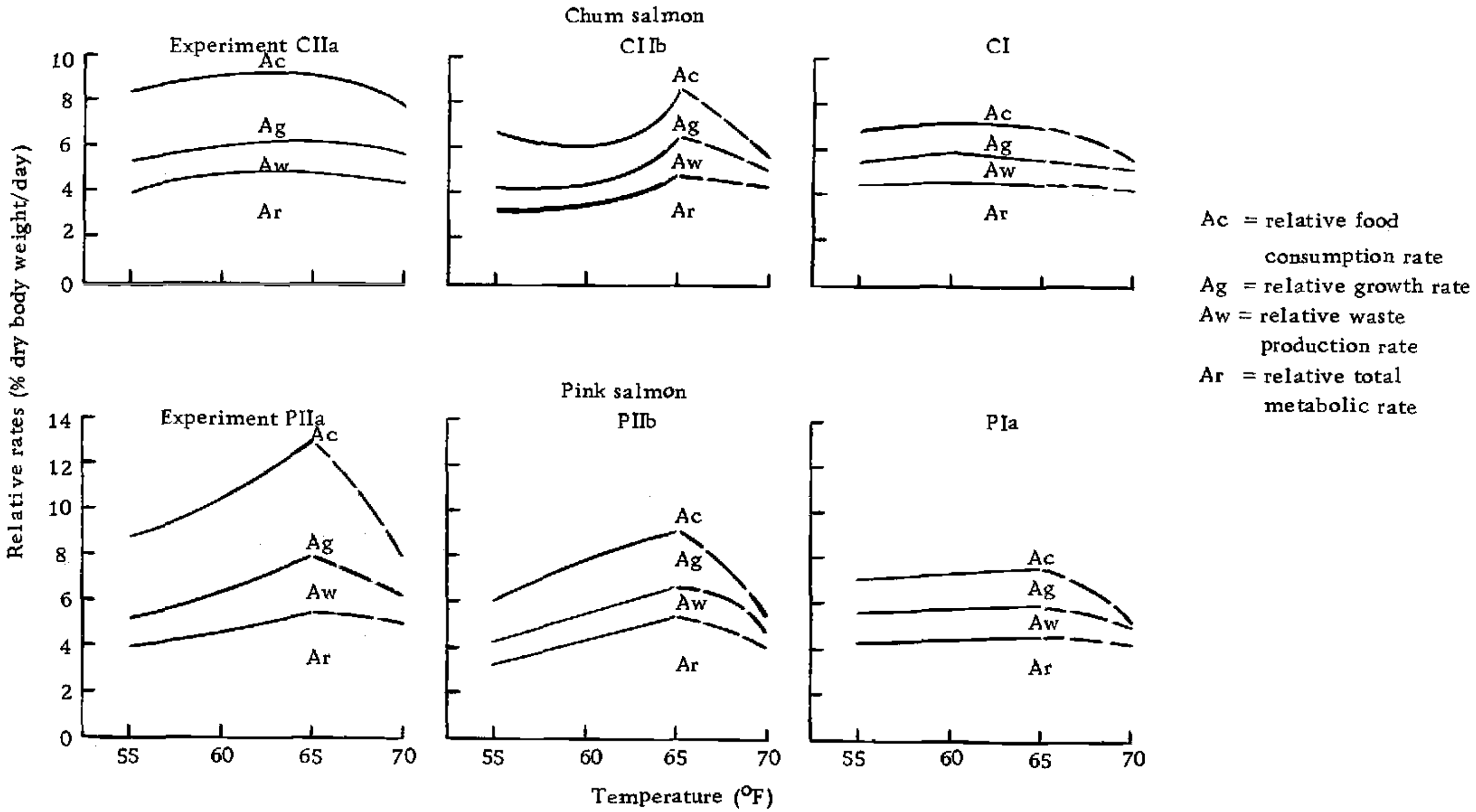

Figure 4. Food consumption rates (Ac) and destinies of consumed food (Ag, Aw, and Ar) for chum and pink salmon at various temperatures.

consumption rate, theoretical Aw values were calculated by solving the following equation:

$$Aw = Ac \cdot (Aw_c / Ac_c)$$

where Aw = calculated theoretical waste production rate for my experimental fish,
Ac = actual food consumption rate of my experimental fish,
Aw_c = waste production rate for Averett's (1969) coho salmon, and
Ac_c = food consumption rate of Averett's (1969) coho salmon.

Values for total metabolic or respiration rates (Ar) were calculated from equation 16, where

$$Ar = Ac - Ag - Aw.$$

The influence of temperature on the metabolic rate of most chum and pink salmon apparently accounted for the increased food consumption rate as temperature increased from 55° to 65° F. Temperature is a major factor influencing the metabolic rate of poikilotherms. Fry (1947) stated that temperature acts as a controlling factor on the metabolism of fish, i. e., it controls both the standard and active metabolic rates by influencing the activation level of the metabolites. It is well known that the standard metabolic rate (As) of salmonids increases as temperature increases to the lethal level (Averett, 1969; Fry, 1947, 1957, 1971; Job, 1955). The total metabolic rate (Ar) of salmonids can also increase as temperature increases due mainly to increases in standard metabolic rate (As) as well as apparent increases in the rates of both muscular activity (Aa) and food processing (Ad) (Averett, 1969; Molnár and Tölg, 1962; Shrable, Tiemeier, and Deyoe, 1969; Smit, 1967; Warren, 1971). The food consumption rate of salmonids is apparently a direct function of metabolic rate (As and Ar). The data of Averett (1969) indicated that the food consumption rate of coho salmon increased linearly (r=0.943) up to temperatures of 62.6° or 68.0° F as the standard and total metabolic rates (As and Ar) increased. The standard and total metabolic rates of most of my chum and pink salmon increased as temperature increased from 55° to 65° F, and their food consumption rates increased in response to the increased energy cost of metabolism.

The food consumption rate of the largest pink salmon (Experiment PIa), unlike that of smaller pink salmon, did not increase significantly as temperature increased from 55° to 65° F. The highest food consumption rate tended to occur at a high temperature for smaller pink salmon, and over a broad temperature range for large pink salmon. The total metabolic rate (Ar) of these larger salmon, unlike that of the smaller salmon, apparently did not increase as temperature increased from 55° to 65° F. Inasmuch as the standard metabolic rate (As) must have increased, the rate of activity (Aa) must have decreased as temperature increased from 55° to 65° F. The rate of food processing (Ad) apparently did not increase, of course, because food consumption rate did not increase.

An interaction between oxygen consumption rate and high temperature may account for the reduction in food consumption rate of my chum and pink salmon as temperature increased from 65° to 70° F. The standard metabolic rate (As) of my salmon was higher at 70° F than at lower temperatures, because the standard metabolic rate of salmonids increases as temperature increases up to the lethal temperature, which usually exceeds 70° F (Brett, 1964; Fry, 1957, 1971). However, the total metabolic rate (Ar) of my salmon might have decreased as temperature increased from 65° to 70° F (Figure 4). My salmon were much more sluggish at 70° F than at lower temperatures. This reduced activity (Aa) at 70° F would account for a reduction in total metabolic rate (Ar) and, subsequently, food consumption rate as temperature increased from 65° to 70° F. This contradicted the apparent increase in total metabolic rate (Ar) for most of my salmon as temperature increased from 55° to 65° F (Figure 4). Averett (1969) observed a similar response to temperature with coho salmon, and found that total metabolic rate (Ar) increased as temperature increased from 51.8° to 68.0° F, and then declined as temperature continued rising to 73.4° F. The activity (Aa) of Averett's (1969) coho salmon decreased by 200% as temperature increased from 68.0° to 73.4° F, which accounted for the reduction in total metabolic rate (Ar). Averett (1969) found also that the food consumption rate of coho salmon was higher at 68.0° F than at

73.4°, which agrees with my observations on chum and pink salmon.

The reduction in total metabolic rate (Ar) and, of course, food consumption rate of my chum and pink salmon as temperature increased from 65° to 70° F was caused by either a reduced or unchanged oxygen consumption rate. As temperature increased from 65° to 70° F, the increased standard metabolic rate (As) required more oxygen. A limited (i. e., reduced or unchanged) oxygen consumption rate at 70° F would not have provided enough oxygen to support as high a total metabolic rate (Ar) and food consumption rate as occurred at 65° F, because of the higher oxygen requirement for standard metabolism at 70° F than at 65° F. A reduction in the active oxygen consumption rate (active metabolic rate)[3] of other salmonids as temperature increased has been observed by other workers. The active oxygen consumption rate of lake trout, Salvelinus namaycush (Walbaum 1792), decreased as temperature increased from 65° to 70° F (Gibson and Fry, 1954), and that of sockeye salmon decreased as temperature increased from 59° to 68° F (Brett, 1964). Some of my salmon,

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[3] The active oxygen consumption rate is the oxygen consumption rate that occurs at the highest sustained level of activity. The active metabolic rate is equivalent to the active oxygen consumption rate.

particularly chum salmon, apparently experienced difficulty in controlling their oxygen consumption rate at 70° F, and acquired an oxygen debt (oxygen use rate > oxygen consumption rate), which probably caused the higher mortality for chum salmon at 70° F (35. 6%) than at lower temperatures (3. 2-7. 6%).

The oxygen consumption rate of my salmon at 70° F was limited either by dissolved oxygen content or by certain structural features of the fish or both. The active oxygen consumption rate, total metabolic rate (Ar), and food consumption rate of salmonids are all generally dependent on dissolved oxygen content up to levels of 7-8 mg/l. Job (1955) observed that the active metabolic rate of brook trout raised in the temperature range of 50° -68° F increased rapidly as dissolved oxygen content increased from 2 to 8 mg/l. The total metabolic rate and food consumption rate of coho salmon at 59° F increased rapidly as dissolved oxygen content increased from 3 to 7 mg/l (Hutchins, 1974). Fisher (1963) observed that the food consumption rate of coho salmon at 65° F increased rapidly as dissolved oxygen content increased from 2. 5 to about 8. 0 mg/l. The active metabolic rate of sockeye salmon increased as the temperature increased from 59° to 68° F only when dissolved oxygen content was increased from 10. 1 to 14. 0 mg/l, whereas it actually decreased when dissolved oxygen content remained at 9. 1-10. 1 mg/l (Brett, 1964). There was a possibility, then, that oxygen consumption rate and, hence, food consumption rate of my chum and pink salmon at 70° F were limited by dissolved oxygen content, even though it exceeded 7 mg/l (Appendix 3, Table 1). The dissolved oxygen content at 70° F was possibly too low for an effective transfer of oxygen from the water through the gills to the blood in spite of a presumably high cardiac output and ventilation rate (Randall, 1971a, b).

The oxygen consumption rate of my salmon at 70° F was perhaps limited by certain structural features of the fish, and was independent of dissolved oxygen content. There is evidence that the active oxygen consumption rate, total metabolic rate, and food consumption rate of salmonids raised at 59° F or higher are essentially independent of dissolved oxygen content at levels exceeding 7-8 mg/l. Job (1955) observed that an increase in dissolved oxygen content from about 8 to 20 mg/l resulted in a negligible increase, if any, in the active metabolic (oxygen consumption) rate of brook trout. For coho salmon, an increase in dissolved oxygen content from 7 to 10 mg/l resulted in a negligible increase, if any, in total metabolic rate and food consumption rate (Hutchins, 1974). Fisher (1963) found that an increase in dissolved oxygen content from 7. 0 to 9. 5 mg/l resulted in no change in the food consumption rate of coho salmon. The oxygen consumption rate and, hence, food consumption rate of my salmon at 70° F were probably independent, then, of dissolved oxygen contents above 7 mg/l, and limited instead by two structural features of the fish, namely: gill surface area and oxygen carrying capacity of the blood. Gill surface area could have restricted any increase in oxygen consumption rate as the temperature increased from 65° to 70° F. Oxygen carrying capacity of the blood, more than gill surface area, probably limited the oxygen consumption rate at 70° F. The oxygen carrying capacity of the blood of salmonids decreases as temperature increases (Fry, 1957; Hochachka and Somero, 1971), in spite of an increased efficiency of oxygen-uptake due to an increased number of erythrocytes, a higher hemoglobin level, and the decreased volume of each erythrocyte (Randall, 1971b). Reduced oxygen carrying capacity of blood at high temperatures results from the high partial pressure of oxygen in the blood, which weakens the hemoglobin-oxygen bond (Hochachka and Somero, 1971). The increased partial pressure of CO_2 in the blood at high temperatures possibly caused a decrease in pH, which reduced both the affinity of hemoglobin for oxygen (Bohr effect) and the oxygen carrying capacity of the blood (Root effect) (Fry, 1957; Randall, 1971b).

Differences between chum and pink salmon regarding the effect of temperature on food consumption rate are now discussed. The generally higher food consumption rate of pink salmon than of chum salmon of comparable weight at a particular temperature probably resulted from higher metabolic rates (As and Ar) for pink than for chum salmon. When both species of salmon were unfed and resting (standard metabolism condition), pink salmon tended to school and swim around the tank, while chum salmon remained more solitary and tended to maintain station. At feeding time, when both species were very active (total metabolism condition), pink salmon were noticeably more active than chum salmon. Therefore, pink salmon generally consumed more food than chum salmon to provide energy for their higher metabolic rates.

The greater increase in the food consumption rate of pink salmon over that of chum salmon of comparable body weight as temperature increased from 55° to 65° F was probably due to a differential response in total metabolic rate. There is no evidence to my knowledge that the standard metabolic rate (As) of any salmonid having a naturally high As value would increase more than that of another closely related salmonid having a naturally lower As value as temperature increases. In fact, evidence suggests the opposite (Averett, 1969; Fry, 1957; Job, 1955). On the other hand, there is evidence that the total metabolic rate (Ar) of a salmonid having a naturally high Ar value could increase more than that of another closely related salmonid having a naturally lower Ar value as temperature increases. The active metabolic rates of some salmonids which have naturally high active metabolic rates increased more than those of related salmonids which have naturally lower active metabolic rates as temperature increased from 50° to 68° F (Table 5). Total metabolic rate (Ar) is generally a direct function of active metabolic rate as temperature increases to 68° F according to the data of Averett (1969). Active metabolic rate and total metabolic rate can be similar at the same temperature. Investigations of active metabolic rates of salmonids reported in most of the papers reviewed involved unfed fish, so that this rate is comprised only of the rates of muscular activity (Aa) and standard metabolism (As) because $Ad \approx 0$. On the other hand, investigations of total metabolic rate generally use fed fish, so that this rate is comprised of Aa, As, and Ad because $Ad > 0$. If total metabolic rate (Ar) is measured when fish are unfed and activity (Aa) is high, Ar would approximate the active metabolic rate.

Effect of body weight

The food consumption rates of both chum and pink salmon decreased as the body weight increased, but the decrease appeared to be greater for pink than for chum salmon in the experiments in which body weight increased comparably (Table 6).

Temperature influenced the effect of body weight on food consumption rate. The food consumption rates of both chum and pink salmon decreased more at 65° F than at lower temperatures as body weight increased, with the following exception: the food consumption

Table 5. Effect of temperature on the active metabolic rates of salmonids.

Species of salmonid	Active metabolic rate (ml O_2/kg body weight/hr) at 50°F	Change in active metabolic rate as temperature increased from 50° to 68°F	Source of data
Coho salmon	420	+140%	Averett (1969)
Brown trout	175	+ 86%	Data of J. M. Graham in Fry (1957)
Lake trout	160	+ 69%	Gibson and Fry (1954)
Brook trout	110	+ 59%	Job (1955)

Table 6. Effect of body weight on the food consumption rates of chum and pink salmon.

Species of salmon	Food consumption rate and body weight data were compared between the following two experiments having low and high mean weights:	Increase in experiment mean weight going from an experiment having a low weight to one having a higher weight	Change in adjusted mean food consumption rate[1] (% body weight/day)
Chum	CIIa and CIIb	250%	-20.9%
	CIIa and CI	300%	-21.8%
Pink	PIIb and PIa	150%	- 4.0%
	PIIa and PIIb	250%	-27.9%
	PIIa and PIa	770%	-29.7%

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[1] This food consumption rate in each of the two experiments compared is the mean value of the adjusted mean food consumption rates at all temperatures.

rate of chum salmon decreased more at low temperatures (55° and 60° F) than at 65° F as body weight increased 250% (Table 7). The food consumption rate of pink salmon decreased more at 70° F than at 65° F as body weight increased.

The decrease in food consumption rate as body weight increased as seen for my chum and pink salmon, has been observed for other salmonids (Averett, 1969; Brown, 1957), and apparently resulted from a decrease in the standard and total metabolic rates (As and Ar). As mentioned previously, food consumption rate is generally a direct function of standard and total metabolic rates (As and Ar), so that a decrease in food consumption rate reflects a decrease in metabolic rate. The decrease in metabolic rate as body weight increases has been shown in other studies. Brett (1970) found that the metabolic rate of salmonids and other fish decreases as body weight increases. The standard metabolic rate of brook trout (Job, 1955), and both the standard and total metabolic rates of coho salmon (Averett, 1969) decreased as body weight increased. The maintenance ration of brown trout decreased as body weight increased, which surely reflected a decrease in total metabolism inasmuch as the energy from a maintenance ration is used exclusively for total metabolism (Brown, 1957).

The greater decrease in the food consumption rate of pink than of chum salmon as body weight increased probably reflected a greater

Table 7. Effect of temperature on the relationship between food consumption rate and body weight for chum and pink salmon.

Species of salmon	Food consumption rate and body weight data were compared between the following two experiments having low and high mean weights:	Increase in experiment mean weight going from an experiment having a low weight to one having a higher weight	Change in adjusted mean food consumption rate (% body weight/day) at the following temperatures:			
			55°F	60°F	65°F	70°F
Chum	CIIa and CIIb	250%	-25.9%	-34.1%	-2.8%	--
	CIIa and CI	300%	-19.9%	-19.8%	-25.7%	--
Pink	PIIb and PIa	150%	+15.4%	-6.5%	-16.5%	--
	PIIc and PIb	240%	--	--	-17.0%	-26.2%
	PIIa and PIIb	250%	-25.9%	-24.8%	-32.9%	--
	PIIa and PIa	770%	-19.1%	-30.0%	-40.1%	--

decrease in the metabolic rates (As and Ar) of pink than of chum salmon. The body weight of large pink salmon (Experiment PIa) was 150% greater than that of medium-sized chum salmon (Experiment CI). Interestingly, the food consumption rates of these chum and pink salmon were similar (Figure 4), which apparently resulted from similar metabolic rates (As and Ar) for these chum and pink salmon. This supports the hypothesis that metabolic rates (As and Ar) were higher for pink than for chum salmon of comparable weight.

The generally greater decrease in the food consumption rates of chum and pink salmon at higher temperatures (65° or 70° F) as body weight increased probably resulted from a correspondingly greater decrease in metabolic rates (As and Ar). This hypothesis is supported by appropriate data from the literature. Averett (1969) found that both the total metabolic rate and food consumption rate of coho salmon decreased more at 62.2° F than at 51.8° F as body weight increased. The standard metabolic rate of brook trout decreased more at 68° F than at both 60° and 50° F as body weight increased (Job, 1955).

The greater decrease in the food consumption rate of chum salmon at both 55° and 60° F than at 65° F as the body weight increased 250% could have occurred for two reasons: 1), the decrease at 55° and 60° F was possibly overestimated because of disease problems at these temperatures and high mortality at 60° F in Experiment

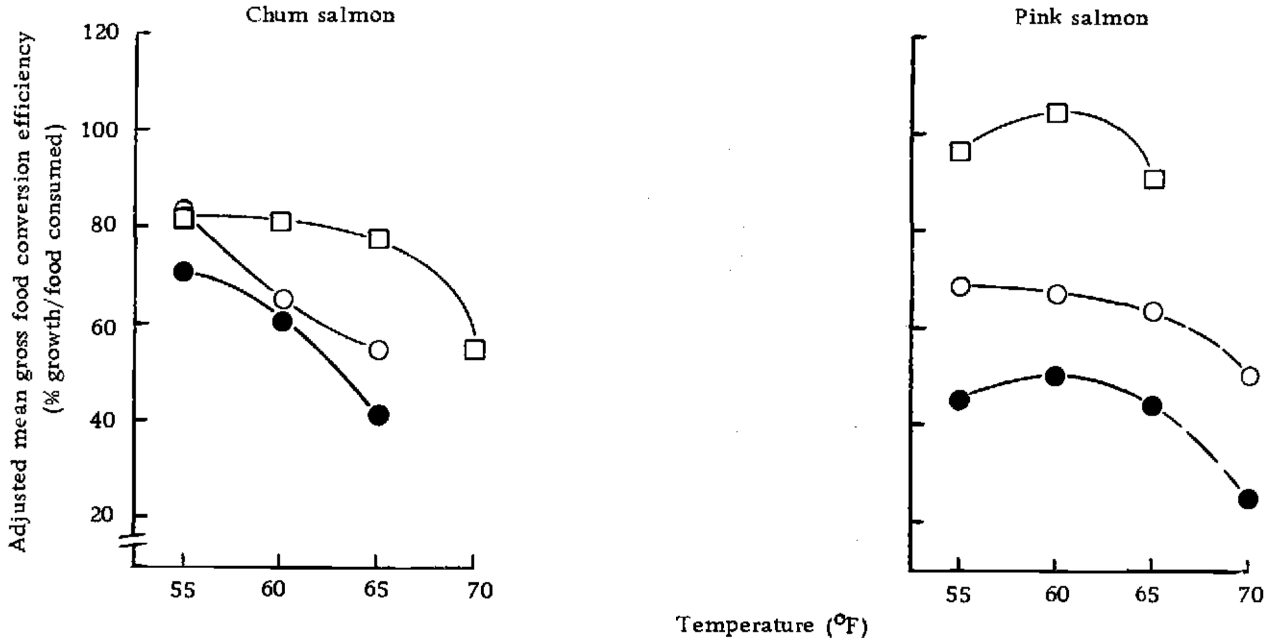
CIIb, which caused a severe restriction in food consumption, and 2), the decrease at 65° F was possibly underestimated because the selection of salmon for this temperature in Experiment CIIb was biased towards fish having a higher than "normal" food consumption rate.

Gross food conversion efficiency

Effect of temperature

The gross food conversion efficiency of chum salmon was generally highest at 55° F, slightly higher at 60° F than at 65° F, and lowest at 70° F (Figure 5; Appendix 8, Table 2). The gross food conversion efficiency of pink salmon was generally similar at 55°, 60°, and 65° F (Figure 5; Appendix 8, Table 2). In Experiment PIIc, gross food conversion efficiency was significantly higher ($0.10 > P > 0.05$) at both 60° and 65° F than at 70° F. Gross food conversion efficiency was generally higher for pink than for chum salmon of comparable body weight at each temperature (Table 8).

The observed effect of temperature on the gross food conversion efficiencies of chum and pink salmon is generally consistent with results obtained for other salmonids by various workers. The gross food conversion efficiencies for various salmonids have been reported to increase to a high value as the temperature increased to a certain level, above which the efficiencies declined (Figure 6). The highest



Experiment	Relative weight class	Experiment mean weight (g)	Effect of temperature on gross food conversion efficiency
□ CIIa	small	5. 9	$55 \overset{n.s.}{>} 60 \overset{n.s.}{>} 65 \overset{*}{>} 70$
○ CIIb	medium	20. 6	$55 \overset{*}{>} 60 \overset{n.s.}{>} 65$
● CI	medium	24. 4	$55 \overset{n.s.}{>} 60 \overset{n.s}{>} 65$; $55 \overset{*}{>} 65$

Experiment	Relative weight class	Experiment mean weight (g)	Effect of temperature on gross food conversion efficiency
□ PIIa	small	8. 0	$60 \overset{n.s.}{>} 55 \overset{n.s.}{>} 65$
○ PIIb	medium	27. 7	$55 \overset{n.s.}{>} 60 \overset{n.s.}{>} 65 \overset{n.s.}{>} 70$[1]
● PIa	large	69. 7	$60 \overset{n.s.}{>} 55 \overset{n.s.}{>} 65 \overset{n.s.}{>} 70$[1]

Figure 5. Effect of temperature on the gross food conversion efficiencies of chum and pink salmon.

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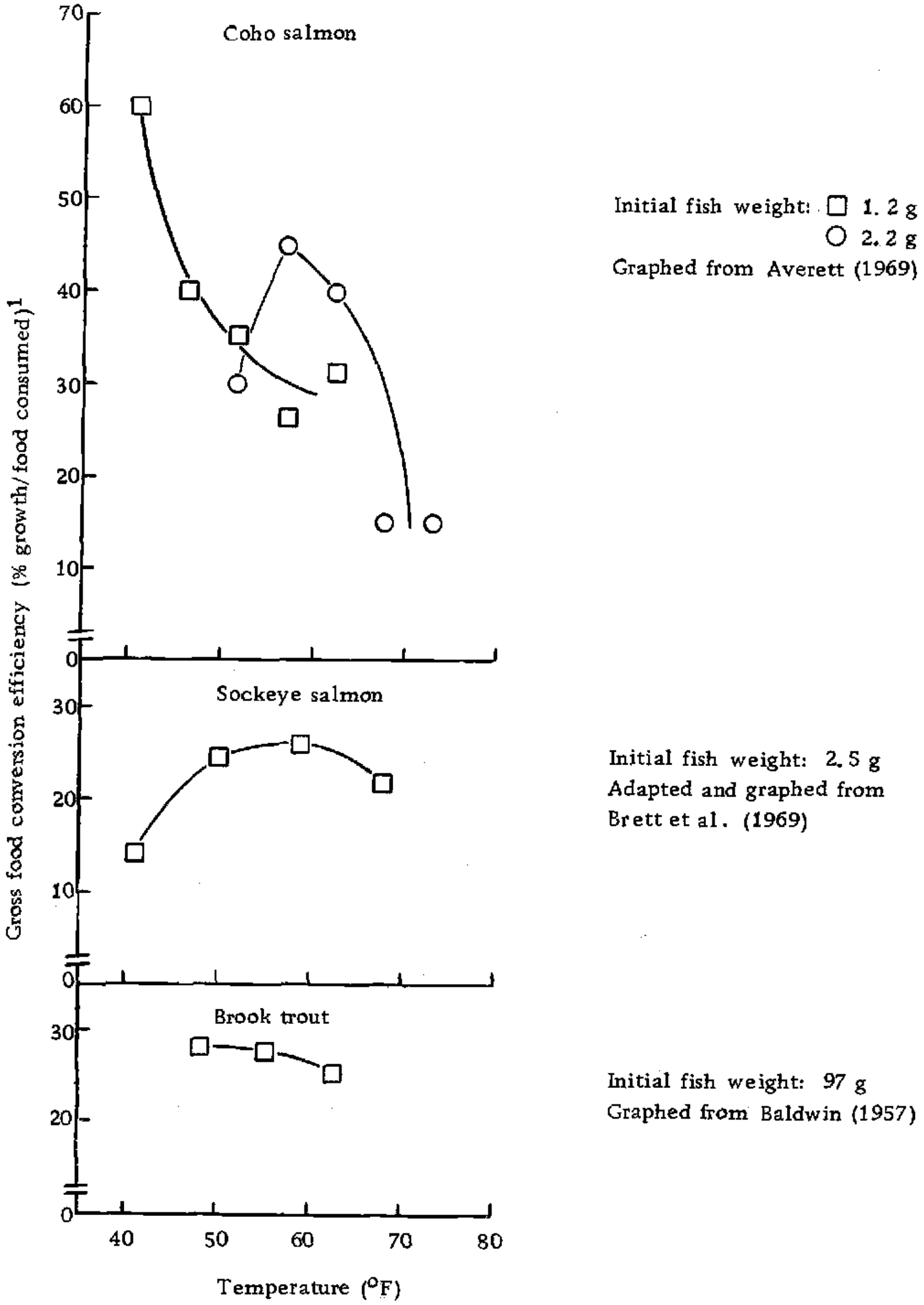
[1] These gross food conversion efficiencies at 70°F in Experiments PIIb and PIa were inferred from those in Experiments PIIc and PIb, respectively.

Table 8. Effect of temperature on the gross food conversion efficiencies of chum and pink salmon of comparable size.

Experiments compared	Experiment mean weight (g)	Adjusted mean gross food conversion efficiency (% growth/food consumed) at the following temperatures:		
		55°F	60°F	65°F
CIIa	5.9	82.6	81.9	77.9
and				
PIIa	8.0	96.7	104.6	91.0
CI	24.4	71.3	60.9	41.3
and				
PIIb	27.7	68.5	66.8	63.2



Graphed from Averett (1969)

Adapted and graphed from Brett et al. (1969)

Graphed from Baldwin (1957)

Figure 6. Gross food conversion efficiencies of salmonids at different temperatures.

[1] Gross food conversion efficiencies are defined in terms of dry food and body weights for coho salmon, and in terms of wet weights for the other salmonids. Note: all plot lines were fitted by eye.

gross food conversion efficiencies of coho (Averett, 1969), chum (Rowan, 1975), and sockeye (Brett et al., 1969) salmon occurred at temperatures (56.3° -59.0° F) which were close to those of 55° and 55° -65° F at which the highest gross food conversion efficiencies of my chum and pink salmon, respectively, occurred. The lowest gross food conversion efficiencies at temperatures exceeding 55° F occurred at high temperatures for coho and sockeye salmon (68.0° -73.4° F) (Figure 6) and for my chum and pink salmon (70° F).

The effect of temperature on the gross food conversion efficiency of my salmon may be explained in terms of the destinies of the food consumed by a fish as described by Warren and Davis (1967). In Experiment CIIb, food consumption rate (Ac) increased as temperature increased from 55° to 65° F in response to increased metabolic rates (As and Ar). The waste production rate (Aw) and ratio of Aw to Ac (Aw/Ac) both apparently increased as the food consumption rates of chum and pink salmon increased. This conclusion was based on Averett's (1969) observation that the percent nonassimilation (≈Aw/Ac) increased rapidly at high Ac values as food consumption rate increased. Therefore, the decrease in gross food conversion efficiency for these chum salmon (Experiment CIIb) apparently resulted from an increase in the Aw/Ac ratio as the temperature increased from 55° to 65° F. As the Aw/Ac ratio increased, the percentage of assimilated food (Ac-Aw/Ac) available for growth (Ag) decreased. The ratio of food consumption rate to total metabolic rate (Ac/Ar) could have either increased, remained unchanged, or decreased in this experiment (CIIb), because the Aw/Ac ratio increased and the growth rate (Ag) was somewhat similar at 55° and 65° F. In this same experiment, however, the decrease in gross food conversion efficiency as the temperature increased from 55° to 60° F resulted from a decrease in the Ac/Ar ratio because the Aw/Ac ratio probably remained unchanged and the growth rate (Ag) decreased. In this case, a greater percentage of consumed food (Ac) was metabolized (Ar) at 60° F than at 55° F, so that a lower percentage of Ac was available for growth (Ag).

In Experiment CIIa, the food consumption rate increased as temperature increased from 55° to 65° F. The gross food conversion efficiency must have decreased, though not significantly according to the data, because growth rate remained constant as temperature increased. This decrease in gross food conversion efficiency resulted from an increase in the Aw/Ac ratio, and subsequent decrease in the percentage of assimilated food (Ac-Aw/Ac) available for growth. The Ac/Ar ratio could have either increased, remained unchanged, or decreased in this experiment, because the Aw/Ac ratio increased, and the growth rate was equivalent at 55°, 60°, and 65° F.

In Experiment CI, food consumption rate and growth rate did not significantly change as the temperature increased from 55° to

65° F. This was impossible, however, because gross food conversion efficiency seemed to decrease. If the food consumption rate had increased and the growth rate had remained constant or decreased as the temperature increased from 55° to 65° F, the decrease in gross food conversion efficiency would have resulted from an increase in the Aw/Ac ratio. If the food consumption rate had remained unchanged and the growth rate had decreased as the temperature increased from 55° to 65° F, the decrease in gross food conversion efficiency would have resulted from a decrease in the Ac/Ar ratio.

The gross food conversion efficiency of pink salmon remained somewhat constant as the temperature increased from 55° to 65° F. The food consumption rate (Ac) and waste production rate (Aw) for pink salmon in Experiments PIIa and PIIb increased as the temperature increased from 55° to 65° F, and the Aw/Ac ratio presumably increased because food consumption rate increased. The Ac/Ar ratio also must have increased for these pink salmon because the growth rate (Ag) increased. The increased food consumption rate covered the increased energy cost of total metabolism (Ar) and provided enhanced growth (Ag), even though the percent assimilation (Ac-Aw/Ac) decreased.

The gross food conversion efficiency as well as both the food consumption rate and growth rate of pink salmon in Experiment PIa apparently remained somewhat constant as the temperature increased from 55° to 65° F. These pink salmon probably restricted their total metabolic rate (Ar), which resulted in no significant change in the Ar and Aw values, and Aw/Ac and Ac/Ar ratios as the temperature increased from 55° to 65° F.

The decrease in the gross food conversion efficiencies of chum and pink salmon as temperature increased from 65° to 70° F apparently resulted from a decrease in the Ac/Ar ratio. Food consumption rate (Ac) and waste production rate (Aw) apparently decreased as temperature increased from 65° to 70° F due to a limited oxygen consumption rate at 70° F, and the resultant need to conserve oxygen for the high standard metabolic rate (As) at 70° F. The Aw/Ac ratio presumably decreased as temperature increased from 65° to 70° F.

The generally higher gross food conversion efficiency of pink salmon over chum salmon of comparable body weight at each temperature was due to a higher Ac/Ar ratio for pink than for chum salmon. This occurred in spite of the presumably higher Aw/Ac ratio for pink salmon due to their higher food consumption rate. Fish with a high metabolism (pink salmon) apparently can have a higher food consumption rate and gross food conversion efficiency than closely-related fish with a lower metabolism (chum salmon).

Effect of body weight

The gross food conversion efficiencies of chum and pink salmon decreased as body weight increased (Table 9). Gross food conversion efficiency apparently decreased more for pink salmon than for chum salmon as body weight increased 250%.

For chum salmon, gross food conversion efficiency decreased most at 65° F, and more at 60° F than at 55° F as body weight increased (Table 10). The gross food conversion efficiency of pink salmon decreased at all temperatures as body weight increased, but the decrease was apparently not greater at one temperature than at another due to the inconsistency of the data; an exception was that the gross food conversion efficiency decreased much more at 70° F than at 65° F (Table 10).

The decrease in gross food conversion efficiency as body weight increased has been observed for other salmonids (Averett, 1969; Paloheimo and Dickie, 1966; Warren, 1971).

The decrease in the gross food conversion efficiencies of my chum and pink salmon was due to a decrease in the Ac/Ar ratio as body weight increased. The Aw/Ac ratio presumably decreased, however, as body weight increased because food consumption rate decreased. This implies that for small chum and pink salmon, a relatively low percentage of consumed food was metabolized (Ar), while a high percentage was available for growth as evidenced by a high gross food conversion efficiency. For larger chum and pink salmon, a relatively high percentage of consumed food was apparently

Table 9. Effect of body weight on the gross food conversion efficiencies of chum and pink salmon.

Species of salmon	Gross food conversion efficiency and body weight data were compared between the following two experiments having low and high mean weights:	Increase in experiment mean weight going from an experiment having a low weight to one having a higher weight	Change in adjusted mean gross food conversion efficiency[1] (% growth/food consumed)
Chum	CIIa and CIIb	250%	-17.2%
	CIIa and CI	300%	-39.7%
Pink	PIIb and PIa	150%	-29.5%
	PIIa and PIIb	250%	-32.1%
	PIIa and PIa	770%	-52.1%

---

[1] This gross food conversion efficiency in each of the two experiments compared is the mean value of the adjusted mean gross food conversion efficiencies at all temperatures.

Table 10. Effect of temperature on the relationship between gross food conversion efficiency and body weights for chum and pink salmon.

Species of salmon	Gross food conversion efficiency and body weight data were compared between the following two experiments having low and high mean weights:	Increase in experiment mean weight going from an experiment having a low weight to one having a higher weight	Change in adjusted mean gross food conversion efficiency (% growth/food consumed) at the following temperatures:			
			55°F	60°F	65°F	70°F
Chum	CIIa and CIIb	250%	+ 0.6%	-20.9%	-30.0%	--
	CIIa and CI	300%	-13.7%	-25.6%	-46.9%	--
Pink	PIIb and PIa	150%	-33.4%	-24.7%	-30.3%	--
	PIIc and PIb	240%	--	--	-28.6%	-62.4%
	PIIa and PIIb	250%	-25.1%	-35.5%	-35.5%	--
	PIIa and PIa	770%	-52.8%	-51.9%	-51.6%	--

metabolized, while a low percentage was available for growth as evidenced by a low gross food conversion efficiency.

Gross food conversion efficiency appeared to decrease more for pink salmon than for chum salmon as the body weight increased comparably. This probably resulted from a greater decrease in the Ac/Ar ratio for pink than for chum salmon as body weight increased. Therefore, a higher percentage of consumed food was metabolized by pink than by chum salmon as body weight increased. The food consumption rate and presumably the Aw/Ac ratio also decreased more for pink than for chum salmon as body weight increased.

The gross food conversion efficiency of chum salmon decreased most at 65° F, and more at 60° F than at 55° F as body weight increased, which probably resulted from a greater decrease in the Ac/Ar ratio at 65° F than at 60° F, and at 60° F than at 55° F.

The decrease in gross food conversion efficiency of pink salmon as body weight increased was not generally influenced by temperature at temperatures of 55°, 60°, and 65° F because the Ac/Ar as well as Aw/Ac ratios apparently decreased similarly at these temperatures. However, the gross food conversion efficiency apparently decreased much more at 70° F than at 65° F and possibly at any lower temperature as body weight increased (see Table 10). This apparently resulted from a greater decrease in the Ac/Ar ratio at 70° F than at lower temperatures. Thus, a higher percentage of consumed food was metabolized at 70° F than at lower temperatures as body weight increased.

Growth rate

Exponential growth

The growth of chum and pink salmon was apparently exponential. For exponential growth, a plot of ln weight on time must describe a straight line, and the correlation between ln weight and time must be high. The regression of ln mean weight on time was linear for chum and pink salmon at all temperatures, and the correlation between ln mean weight and time was very high (> 0.96) (Table 11).

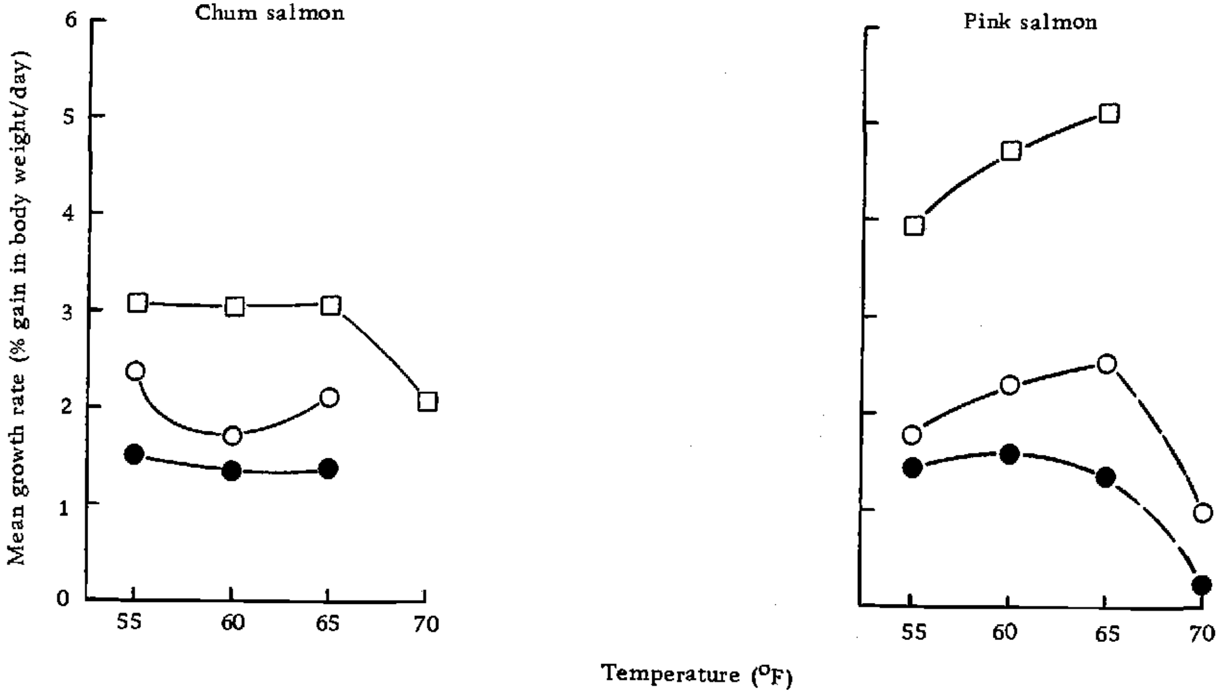
Effect of temperature

The growth rate of chum salmon was generally similar at 55°, 60°, and 65° F, and lowest at 70° F (Figure 7; Appendix 8, Table 3). However, in Experiment CIIb, growth rate was higher at both 55° and 65° F than at 60° F.

The growth rate of pink salmon was generally highest at 60° and 65° F, and higher at 55° F than at 70° F (Figure 7; Appendix 8, Table 3). The highest growth rate occurred at 65° F for medium-sized pink salmon, and at three temperatures (55°, 60°, and 65° F) for large pink salmon (Figure 7). Pink salmon grew faster than chum salmon

Table 11. Correlation between ln mean weight and time for chum and pink salmon.

Experiment	Temperature (°F)	Correlation coefficient between ln mean weight and time (r)
CI	55	0.996
	60	0.999
	65	0.999
CIIa	55	0.995
	60	0.994
	65	0.996
	70	0.996
CIIb	55	0.999
	60	0.997
	65	0.995
PIa	55	0.992
	60	0.991
	65	0.998
PIb	65	0.999
	70	0.965
PIIa	55	0.999
	60	0.999
	65_1	0.998
	65_2	0.998
PIIb	55	0.996
	60	0.994
	65_1	0.989
PIIc	55	0.999
	60	0.997
	65_1	0.972
	70	0.984



Experiment	Relative weight class	Experiment mean weight (g)	Effect of temperature on growth rate
☐ CIIa	small	5.9	$55 \overset{n.s.}{>} 65 \overset{n.s.}{>} 60 \overset{**}{>} 70$
○ CIIb	medium	20.6	$55 \overset{n.s.}{>} 65 \overset{*}{>} 60$
● CI	medium	24.4	$55 \overset{n.s.}{>} 65 \overset{n.s.}{>} 60$

Experiment	Relative weight class	Experiment mean weight (g)	Effect of temperature on growth rate
☐ PIIa	small	8.0	$65 \overset{n.s.}{>} 60 \overset{*}{>} 55$
○ PIIb	medium	27.7	$65 \overset{*}{>} 60 \overset{**}{>} 55 \overset{*}{>} 70$[1]
● PIa	large	69.7	$60 \overset{n.s.}{>} 55 \overset{n.s.}{>} 65 \overset{**}{>} 70$[1]

Figure 7. Effect of temperature on the growth rates of chum and pink salmon.

[1] These growth rates at 70°F in Experiments PIIb and PIa were inferred from those in Experiments PIIc and PIb, respectively.

of comparable body weight at each temperature (Table 12).

The observed effect of temperature on the growth rates of chum and pink salmon is generally consistent with experimental results obtained for other salmonids by various authors. The growth rates reported for various salmonids increased to a high value as temperature increased to a certain level, above which the rates declined (Figures 8 through 10). In my experiments, the growth rate of pink salmon increased to a high value as temperature increased to 60° or 65° F, and then declined as temperature continued rising to 70° F, while the growth rate of chum salmon decreased as temperature increased from 65° to 70° F. The highest growth rates of various salmonids occurred in the temperature range of 53.1° - 65.0°F (Figures 8 through 10),which includes the temperature ranges of 55° -65° and 60° -65° F in which the highest growth rates of my chum and pink salmon, respectively, occurred. The growth rates of various salmonids were lower at high temperatures (68° -75° F) than at 55° F (Figures 8 and 10), and the growth rates of my chum and pink salmon were also lower at a high temperature (70° F) than at 55° F.

The effect of temperature on the growth rates of chum and pink salmon may be explained in terms of food consumption rate, gross food conversion efficiency, and the destinies of the food consumed by a fish as described by Warren and Davis (1967). The growth rate

Table 12. Effect of temperature on the growth rates of chum and pink salmon of comparable size.

Experiments compared	Experiment mean weight (g)	Mean growth rate (% gain in body weight/day) at the following temperatures:		
		55°F	60°F	65°F
CIIa	5.9	3.08	3.03	3.07
and				
PIIa	8.0	3.95	4.74	5.13
CI	24.4	1.50	1.35	1.37
and				
PIIb	27.7	1.77	2.30	2.55

of chum salmon in Experiment CIIa remained essentially constant (see Figure 7) as temperature increased from 55° to 65° F, which occurred in spite of an apparent increase in food consumption rate. However, as temperature increased, any potential for enhanced growth from increased food consumption was unrealized because gross food conversion efficiency decreased. Food consumption rate apparently increased just enough to cover the increased waste production (Aw) and metabolic (Ar) rates.

The growth rate of chum salmon in Experiment CIIb was significantly higher at 55° and 65° F than at 60° F as previously mentioned. The higher growth rate at 55° F than at 60° F was due to a much higher gross food conversion efficiency at 55° F than at 60° F inasmuch as food consumption rates were equivalent at both temperatures. The higher growth rate at 65° F than at 60° F resulted from the much higher food consumption rate at 65° F than at 60° F, even though gross food conversion efficiency was somewhat higher at 60° F than at 65° F.

The growth rate of chum salmon in Experiment CI decreased slightly as the temperature increased from 55° to 65° F, because food consumption rate essentially remained constant and gross food conversion efficiency decreased.

Growth rates of most pink salmon (Experiments PIIa and PIIb) generally increased as temperature increased from 55° to 65° F,

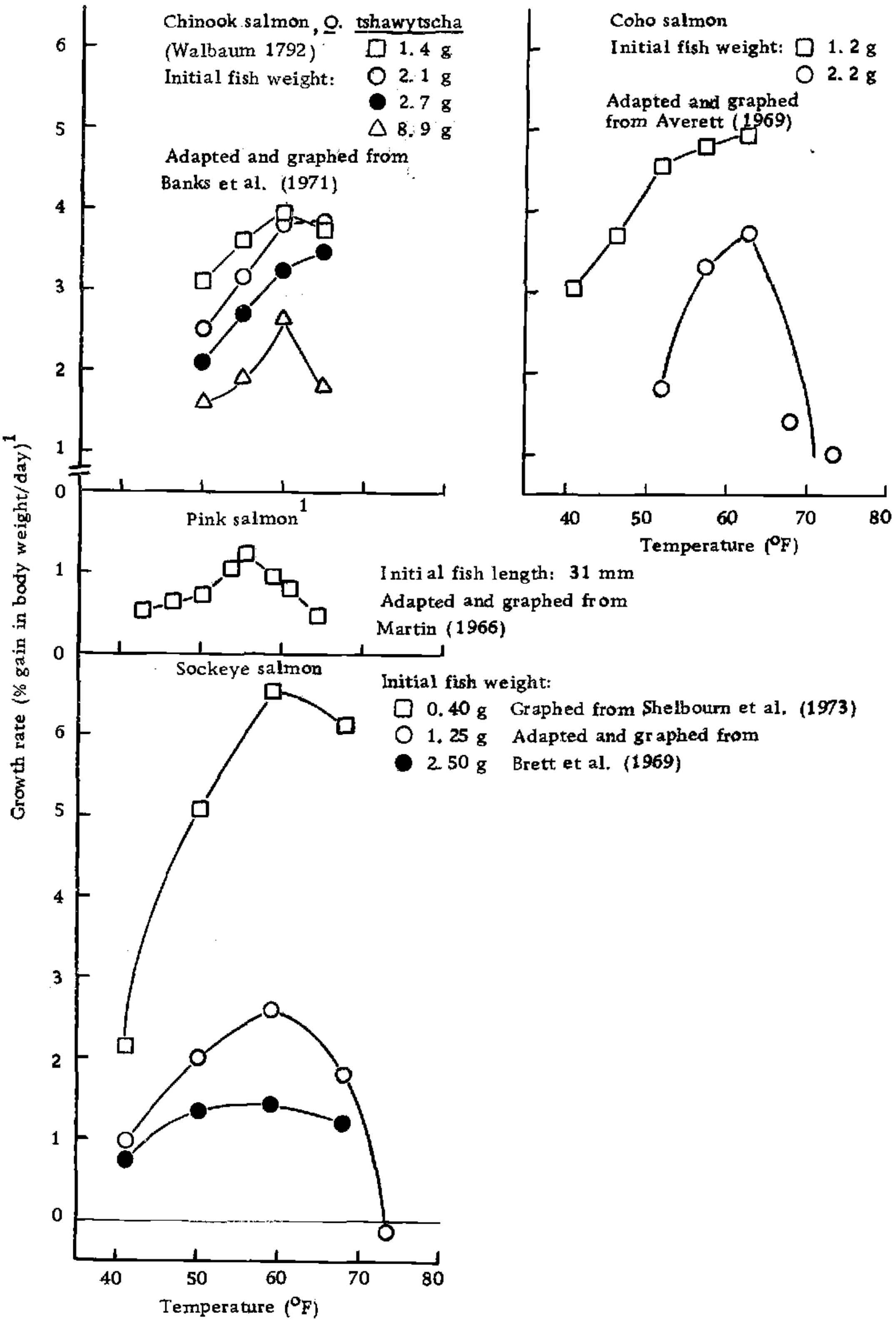
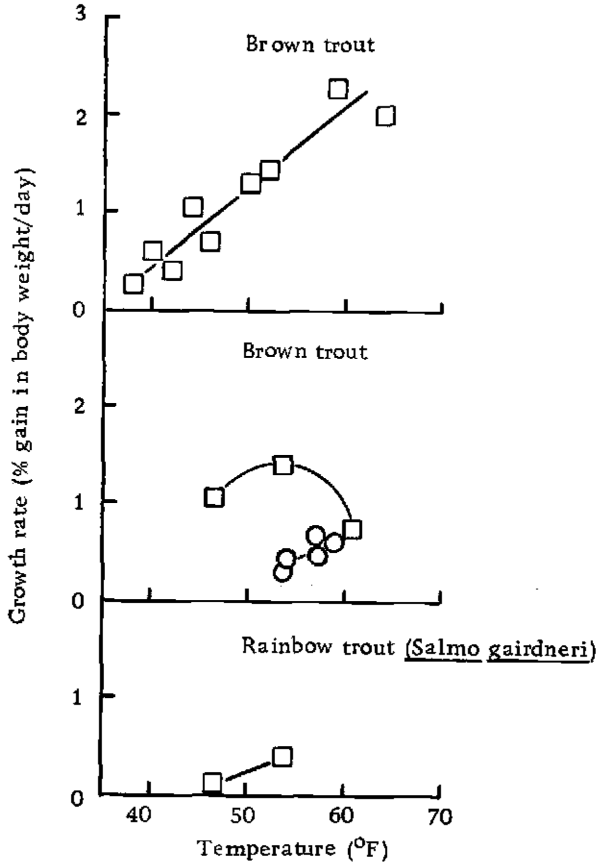


Figure 8. Growth rates of Pacific salmon at different temperatures.

[1] Growth rate of pink salmon is % gain in body length/day. Note: all plot lines were fitted by eye.



Initial fish weight: 2.3-5.4 g
Adapted and graphed from
Pentelow (1939)

Initial age:
□ 1 year Adapted and graphed from Swift (1961)
○ 3 years Adapted and graphed from Swift (1955)

Initial fish weight: 41 g
Adapted and graphed from
Atherton and Aitken (1970)

Figure 9. Growth rates of trout at different temperatures.[1]

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[1] Note: all plot lines were fitted by eye.

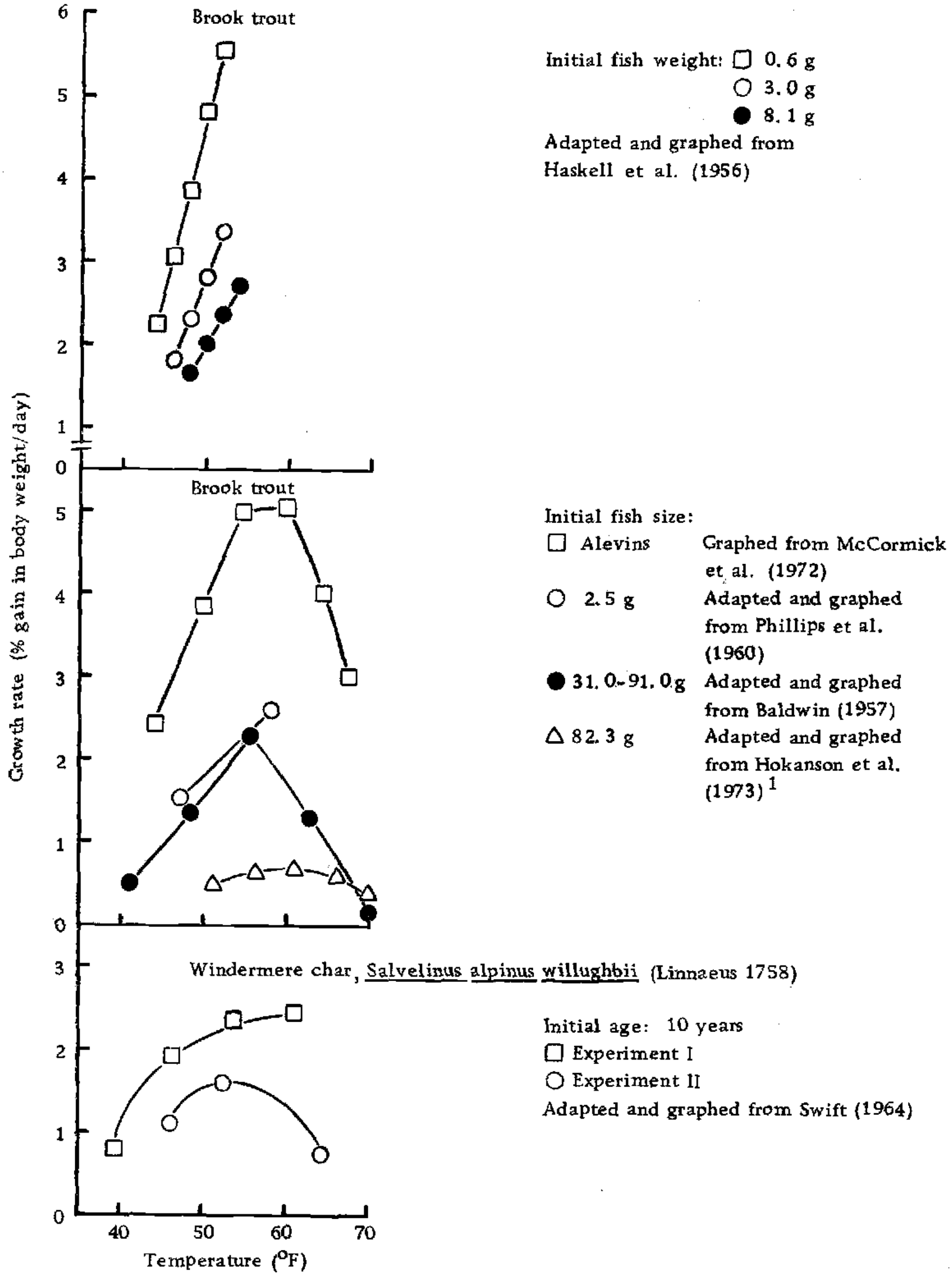

Figure 10. Growth rates of char at different temperatures.

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[1] In the growth equation for these brook trout, fish weight is total weight - gonad weight. Note: all plot lines were fitted by eye.

because food consumption rate increased rapidly and gross food conversion efficiency remained somewhat constant. Food consumption rate increased enough to cover increased waste production (Aw) and metabolic (Ar) rates, and still provide for enhanced growth (Ag).

The growth rate of pink salmon in Experiment PIa remained essentially constant as temperature increased from 55° to 65° F, because food consumption rate and gross food conversion efficiency remained somewhat constant.

The increase in growth rate of small (Experiment PIIa) and medium-sized (Experiment PIIb) pink salmon as temperature increased from 55° to 65° F resulted from increased food consumption rate, while the growth rate of large pink salmon (Experiment PIa) remained somewhat constant because food consumption rate was apparently similar at 55°, 60°, and 65° F. This trend for the highest growth rate to occur at a high temperature for smaller pink salmon and over a broader temperature range for large pink salmon is similar to a trend observed for sockeye salmon by Brett et al. (1969).

Growth rates of chum and pink salmon decreased to a very low level as temperature increased from 65° to 70° F due to the decline in both food consumption rate and gross food conversion efficiency to low levels. The higher percentage of consumed food (Ac) and assimilated food (Ac-Aw/Ac) required for metabolism (Ar) at 70° F than at 65° F resulted in low growth at 70° F.

The higher growth rate of pink salmon than of chum salmon of comparable body weight at each temperature was due to both the generally higher food consumption rate and gross food conversion efficiency of pink salmon. Though the waste production (Aw) and metabolic (Ar) rates were apparently higher for pink than for chum salmon, the higher food consumption rate of pink salmon resulted in a higher growth rate (Ag).

The highest growth rate and food consumption rate occurred at the same temperature for most pink salmon (Experiments PIIa and PIIb). Similar observations have been made for other salmonids (Averett, 1969; Baldwin, 1957; Pentelow, 1939). The highest growth rate and gross food conversion efficiency could not have occurred at the same temperature because the percentage of food energy used in total metabolism (Ar) and waste production (Aw) was highest at this temperature.

Effect of body weight

The growth rates of chum and pink salmon decreased as body weight increased (Table 13). Growth rate decreased more for pink than for chum salmon as body weight increased 250% (Table 13).

The growth rate of chum salmon decreased more at 60° and 65° F than at 55° F as body weight increased, while that of pink

Table 13. Effect of body weight on the growth rates of chum and pink salmon.

Species of salmon	Growth rate and body weight data were compared between the following two experiments having low and high mean weights:	Increase in experiment mean weight going from an experiment having a low weight to one having a higher weight	Change in mean growth rate[1] (% gain in body weight/day)
Chum	CIIa and CIIb	250%	-33.1%
	CIIa and CI	300%	-54.1%
Pink	PIIb and PIa	150%	-33.5%
	PIIa and PIIb	250%	-51.5%
	PIIa and PIa	770%	-68.1%

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[1] This growth rate in each of the two experiments compared is the mean value of the mean growth rates at all temperatures.

salmon decreased most at 70° F, more at 65° F than at 60° F, and more at 60° F than at 55° F as body weight increased (Table 14).

The decrease in growth rates of my chum and pink salmon as body weight increased has been observed for other salmonids (Averett, 1969; Banks et al., 1971; Brett et al., 1969; Haskell et al., 1956).

This decrease in growth rate of my salmon was due to the decrease in both food consumption rate and gross food conversion efficiency as body weight increased. An increased percentage of consumed food (Ac) was apparently metabolized (Ar) as body weight increased, which resulted in a decrease of high magnitude in growth. Therefore, the ratio of growth rate to total metabolic rate (Ag/Ar) apparently decreased as body weight increased, as was observed by Brett (1970) for salmonids and other fish species.

The greater decrease in the growth rate of pink than of chum salmon as body weight increased resulted from the greater decrease in food consumption rate and gross food conversion efficiency for pink than for chum salmon. Therefore, the Ag/Ar ratio apparently decreased more for pink than for chum salmon as body weight increased.

The greater decrease in the growth rates of chum and pink salmon at high temperatures than at lower temperatures as body weight increased has been observed for other salmonids by other workers (Table 15). In my experiments, the greater decrease in the growth rate of chum salmon at both 60° and 65° F than at 55° as

Table 14. Effect of temperature on the relationship between growth rate and body weight for chum and pink salmon.

Species of salmon	Growth rate and body weight data were compared between the following two experiments having low and high mean weights:	Increase in experiment mean weight going from an experiment having a low weight to one having a higher weight	Change in mean growth rate (% gain in body weight/day) at the following temperatures:			
			55°F	60°F	65°F	70°F
Chum	CIIa and CIIb	250%	-23.4%	-43.9%	-31.9%	--
	CIIa and CI	300%	-51.1%	-55.9%	-55.3%	--
Pink	PIIb and PIa	150%	-17.8%	-30.6%	-46.6%	--
	PIIc and PIb	240%	--	--	-53.4%	-79.8%
	PIIa and PIIb	250%	-44.9%	-50.3%	-59.3%	--
	PIIa and PIa	770%	-63.3%	-66.2%	-73.5%	--

Table 15. Change in growth rates of salmonids at various temperatures as body weight increases.

Species of salmonid	Increase in body weight	Temperature of highest growth rate (^{o}F)	Change in growth rate (% gain in body weight/day) at the following temperatures (^{o}F):							Source of data
			46	48	50	52	55	60	65	
Chinook salmon	430%	65	--	--	--	--	-39.7%	-31.8%	-53.4%	Banks et al. (1971)
Sockeye salmon	330%	60	--	--	-31.1%	--	-42.0%	-45.4%	--	Brett et al. (1969)
Brook trout	400%	52	-36.7%	-37.4%	-37.9%	-38.5%	--	--	--	Haskell et al. (1956)

body weight increased, partially resulted from a greater decrease in gross food conversion efficiency at both 60° and 65° F than at 55° F. This also resulted from a greater decrease in food consumption rate at 60° and 65° F than at 55° F as body weight increased 250% and 300%, respectively. The Ag/Ar ratio apparently decreased more at both 60° and 65° F than at 55° F as body weight increased.

The growth rate of pink salmon decreased most at 70° F, more at 65° F than at 60° F, and more at 60° F than at 55° F as body weight increased. This resulted from the tendency for both food consumption rate and gross food conversion efficiency to decrease most at 70° F, and for food consumption rate alone to decrease more at 65° F than at 60° F, and more at 60° F than at 55° F as body weight increased. As a result, the Ag/Ar ratio apparently decreased most at 70° F, more at 65° F than at 60° F, and more at 60° F than at 55° F as body weight increased.

Survival

Influence of behavior

Some losses of pink salmon and, to a lesser extent, chum salmon resulted from jumping. These losses occurred at all temperatures except 70° F at which activity was reduced. Unfortunately, losses occurred during the feeding period when fish were most active and tank screens were removed.

Effect of temperature

The lowest survival of chum and pink salmon in an experiment occurred at 70° F (Table 16). High temperature was probably the major cause of losses at 70° F, even though 70° F is apparently not considered to be a lethal temperature for salmon by various investigators such as Averett, (1969); Brett, (1964); and Brett et al., (1969).

Salmon death at 70° F possibly resulted from oxygen debt, as I mentioned previously, or from a loss of control in the circulatory, nervous, osmoregulatory, and respiratory systems (Fry, 1957; Warren, 1971). At the cellular level, death possibly resulted from enzyme inactivation and/or changes in intracellular and membrane proteins and lipids (Giese, 1962; Hochachka and Somero, 1971; Warren, 1971).

Disease was presumably not the primary cause of losses at 70° F inasmuch as no evidence of vibriosis and little evidence of bacterial kidney disease (BKD) were found in autopsied fish. BKD does not develop well in salmon at 70° F according to Sanders (1972).

Effect of disease

Disease was the primary cause of salmon death at 55°, 60°, and 65° F. BKD was much more prevalent than vibriosis, and was

Table 16. Survival of chum and pink salmon.

Species of salmon	Experiment	Temperature (°F)	Experimental period (days)	Initial mean weight (g)	Initial number of fish	Survival (% of initial number of fish that survived to the end of the experimental period
Chum	CI	55	30	17.30	20	50.0
		60		21.50		70.0
		65		16.06		85.0
	CIIa	55	70	1.40	250	96.8
		60		1.52		94.8
		65		1.46		92.4
		70		1.48		64.4
	CIIb	55	30	13.77	105	90.5
		60		14.64		61.9
		65		12.65		87.6
Pink	PIa	55	40	47.08	29	93.1
		60		46.53	29	84.0
		65		47.98	27	85.2
	PIb	65	30	111.72	19	84.2
		70		92.12	17	82.4
	PIIa	55	40	1.81	115	95.7
		60		1.80	120	96.7
		65_1		2.11	120	91.7
		65_2		1.77	120	90.0
	PIIb	55	50	9.76	62	90.3
		60		11.86	66	92.4
		65_1		17.54	57	86.0
	PIIc	55	40	16.16	59	93.2
		60		20.81	63	93.7
		65_1		27.60	62	100.0
		70		22.45	60	90.0

positively identified in autopsied fish by Mr. Richard Holt.[4] Evidence of vibriosis was found in only five or six individual chum and pink salmon.

Survival was generally higher in experiments with small salmon (CIIa and PIIa) than in those with larger salmon (CI, CIIb, PIa, PIb, and PIIb) (Table 16), which probably reflected delayed mortality due to the chronic nature of BKD.

Survival in experiments which contained BKD-infected fish was somewhat related to water temperature. The survival of some chum and pink salmon increased as temperature increased from 55° to 60° or 65° F (Table 16), which agreed with observations by Sanders (1972) on coho salmon infected with BKD. For other chum and pink salmon, survival was lower at 65° F than at 55° F (Table 16) for one or more of the following reasons. 1) The experimental period was possibly not long enough to depict the true total mortality, because, according to Sanders (1972), salmon death rate over a short term is apparently higher at 65° F than at 55° F, even though total mortality over an infinite period of time should be higher at 55° F than at 65° F. 2) Chum and pink salmon were perhaps more vulnerable to BKD at higher temperatures than the coho salmon of Sanders (1972). 3) The immune response of these chum and pink salmon to BKD was possibly more

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effective at 55° F than at 65° F. 4) A strain of *Corynebacterium* (the etiological agent of BKD) which developed better at 65° F than at 55° F was perhaps present.

POSSIBLE SOURCES OF ERROR

Diversity in brood stock and brood year

Characteristics which typify a species of salmon can vary considerably among individual fish. This variance results from genotypic as well as environmental variation. Populations of salmon derived from different brood stocks or from different brood years in the same geographic location can be genotypically different.

Diversity in brood stock and brood year did not influence any intraexperimental comparisons regarding the effect of temperature on food consumption rate, gross food conversion efficiency, and growth rate. However, interexperimental comparisons, whether intra or interspecific, regarding the influence of temperature or body weight on food consumption rate, etc. were possibly influenced by diversity in brood stock or brood year.

Size differences among fish

Results concerning the effect of temperature on food consumption rate, gross food conversion efficiency, and growth rate were probably influenced by body weight in Experiments CIIb, PIb, PIIb, and PIIc, because mean body weights at the beginning of an experiment were generally not similar among subgroups in each of these experiments (Appendix 7, Table 1). However, the influence of body weight on the effect of temperature on food consumption rate, etc. in each experiment was presumably minimized by covariance analysis.

Diseases

In addition to causing fish losses, BKD affected the food consumption rate, gross food conversion efficiency, and growth rate data in another way. The food consumption rate and, hence, gross food conversion efficiency and growth rate of infected chum and pink salmon decreased, which has been observed for other salmonids (Novotny, 1975; Mr. Jim Sanders,[5] personal communication, 1975; Snieszko and Griffin, 1955).

The decrease in food consumption rate, etc. of infected salmon was not surprising, considering the pathology of BKD. Total hematocrit and total plasma protein of infected fish are reduced because BKD attacks the kidney (Bullock et al., 1971; Hunn, 1964). In this anemic condition, infected salmon probably had a reduced oxygen consumption rate, and any oxygen obtained was used primarily for metabolism and the disease-combating processes. Thus, a reduced amount of oxygen was available for food consumption, food conversion, and growth.

The extent of any errors in the food consumption rate, etc. data caused by the effect of BKD on infected fish was impossible to ascertain. Subgroups which had the highest mortality presumably had the

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highest number of infected fish, and hence, the highest amount of error associated with food consumption rate, etc. data.

Other important diseases of chum and pink salmon, namely furunculosis and vibriosis, probably also affect food consumption rate, gross food conversion efficiency, and growth rate. Furunculosis is generally encountered by chum and pink salmon during their residence in freshwater, though it is transmittable in seawater (Novotny, 1975). Drug therapy, using antibiotics, nalidixic acid, and furinase compounds, effectively controls this disease (Novotny, 1975; Wood, 1968). Bacteria causing furunculosis can be eliminated from the incoming freshwater by filtration and UV irradiation.

Chum and pink salmon are exposed to vibriosis throughout their residence in seawater. Vibriosis can be controlled by vaccination and drug therapy. The oral vaccination of salmon in freshwater with vibrio vaccine as described by Fryer, Nelson, and Garrison (1972) for chinook salmon may prevent vibriosis in salmon while they are in seawater. Vibriosis is effectively controlled by oral administration of antibiotics, sulfonamides, and nitrofuran compounds (Anderson and Conroy, 1970; Fryer et al., 1972; Novotny, 1975; Wood, 1968).

Mortality

Mortality probably affected calculations of food consumption rate, gross food conversion efficiency, and growth rate. Food consumption rate and gross food conversion efficiency were underestimated or overestimated depending on the actual amount of food consumed and weight gained by dead fish prior to their death. Growth rate and also food consumption rate and gross food conversion efficiency were underestimated or overestimated if the mean weight of fish destined to die during a 10-day period was at the beginning of the period ($\overline{W}_{mo}$) equal to that of all fish at the beginning of the period ($\overline{W}_{o}$).

Food consumption rate and gross food conversion efficiency would have been underestimated and overestimated, respectively, if dead fish had consumed no food and gained no weight prior to their death. However, if dead fish had consumed as much food and gained as much weight prior to their death as the surviving fish, food consumption rate and gross food conversion efficiency would have been overestimated and underestimated, respectively. If $\overline{W}_{mo}$ had actually been larger or smaller than $\overline{W}_{o}$, food consumption rate, gross food conversion efficiency, and growth rate would have been underestimated or overestimated, respectively.

CONCLUSION

Chum and pink salmon are suited for culture in heated seawater. The growth rate of chum salmon is similar at 55°, 60°, and 65° F, but the gross food conversion efficiency decreases as temperature increases. Pink salmon grow rapidly at 60° and 65° F, though growth is related to size: small salmon (2-50 g per fish) grow fastest at 65° F, while larger salmon (> 50 g per fish) grow fastest at 60° and even 55° F. Also, pink salmon grow faster than chum salmon. Good survival for both species (60-100%) occurs at all temperatures except 70° F. High temperatures such as 70° F are not conducive to the growth or survival of chum and pink salmon.

The major biological problem in raising salmon in heated seawater is disease. In my experiments, chum and pink salmon were especially vulnerable to bacterial kidney disease. These salmon are exposed to BKD during the short period of their residence in freshwater.

Recommendations for successful heated seawater culture of salmon are as follows. I recommend that chum salmon be raised at 55° F. Pink salmon should be raised at 65° F when small (2-50 g per fish) and at lower temperatures (55° or 60° F) when larger (50 g per fish). Other recommendations generally well-known by fish culturists include the following. 1) Salmon should come from fast-growing, disease-resistant stocks. 2) Good water quality such as high dissolved oxygen content and low ammonia content enhances survival and growth of salmon. 3) A high quality diet enhances fish health and growth. 4) Rapid diagnosis and treatment of diseases are necessary for stock survival.

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APPENDICES

Appendix 1 Table 1. Total weight of salmon in each tank and water inflow rates.

Experiment	Temperature (°F)	Initiation of experiments: Total weight of fish (g)	Initiation of experiments: Total weight of fish to stock as recommended in Piper (1971) (g)	Initiation of experiments: Water inflow rate (gpm)	Termination of experiments: Total weight of fish (g)	Termination of experiments: Total weight of fish to stock as recommended in Piper (1971) (g)	Termination of experiments: Water inflow rate (gpm)
CI	55	346	1090	0. 40	244	851	0. 25
	60	430	1171	0. 50	435	1318	0. 45
	65	321	931	0. 37	493	1258	0. 50
CIIa	55	140	460	0. 46	570	1124	0. 48
	60	152	440	0. 50	590	1171	0. 50
	65	146	362	0. 48	576	987	0. 49
	70	148	310	0. 48	293	350	0. 25
CIIb	55	1446	1280	0. 47	2619	2213	0. 65
	60	1537	1171	0. 50	1458	1025	0. 35
	65	1328	870	0. 43	2030	1258	0. 50
PIa	55	942	2043	0. 50	1658	2724	0. 50
	60	931	1961	0. 48	1624	2670	0. 49
	65	960	2043	0. 50	1657	2724	0. 50
PIb	65	2123	2014	0. 50	2456	2928	0. 50
	70	1566	1490	0. 37	1418	1757	0. 30
PIIa	55	208	410	0. 41	872	735	0. 27
	60	215	370	0. 42	1236	937	0. 40
	65_1	254	377	0. 50	1602	1007	0. 50
	65_2	212	317	0. 42	1188	745	0. 37
PIIb	55	605	817	0. 30	1488	1430	0. 35
	60	783	937	0. 40	2051	1651	0. 47
	65_1	1000	1007	0. 50	2198	1510	0. 50
PIIc	55	953	1124	0. 33	1488	1430	0. 35
	60	1312	1318	0. 45	2051	1651	0. 47
	65_1	1447	1258	0. 50	2198	1510	0. 50
	70	1347	971	0. 45	1407	828	0. 32

Appendix 2 Table 1. Experimental temperatures.

Experiment	Temperature (°F) Planned	Temperature (°F) Observed (Mean ± 95% confidence interval)	Number of observations
CI	55	55.43 ± 0.20	60
	60	60.08 ± 0.11	
	65	65.08 ± 0.19	
CIIa	55	55.11 ± 0.10	140
	60	60.08 ± 0.17	
	65	64.99 ± 0.15	
	70	69.94 ± 0.24	
CIIb	55	54.95 ± 0.12	60
	60	59.84 ± 0.38	
	65	64.95 ± 0.14	
PIa	55	55.05 ± 0.18	80
	60	60.12 ± 0.23	
	65	65.14 ± 0.20	
PIb	65	65.14 ± 0.21	60
	70	70.29 ± 0.18	
PIIa	55	55.14 ± 0.11	80
	60	60.05 ± 0.13	
	65_1	65.06 ± 0.11	
	65_2	65.02 ± 0.23	
PIIb	55	55.03 ± 0.19	100
	60	60.07 ± 0.20	
	65_1	64.83 ± 0.14	
PIIc	55	54.97 ± 0.25	60
	60	59.89 ± 0.27	
	65_1	64.78 ± 0.20	
	70	69.90 ± 0.23	

Appendix 3 Table 1. Dissolved oxygen content of water in each tank.

Experiment	Temperature (°F)	Dissolved oxygen content of water during the experimental period (mg/l)		Saturated dissolved oxygen content of water based on measurements of salinity and temperature[1]	
		Mean	Range	Mean salinity[2] (‰)	Estimated saturated dissolved oxygen content (mg/l)
CI	55	8.7	8.2-9.0	32.9	8.6
	60	8.2	8.0-8.6		8.1
	65	7.9	7.8-8.0		7.7
CIIa	55	7.8	7.4-9.0	31.6	8.7
	60	7.2	7.0-8.4		8.2
	65	7.6	7.2-8.0		7.8
	70	7.5	7.2-7.8		7.4
CIIb	55	7.4	7.3-7.4	28.8	8.8
	60	7.7	7.7		8.3
	65	8.0	8.0		7.9
PIa	55	7.6	7.0-8.4	32.9	8.6
	60	7.2	6.8-7.4		8.1
	65	7.5	7.4-7.6		7.7
PIb	65	7.1	6.8-7.6	31.5	7.8
	70	7.2	6.6-7.4		7.4
PIIa	55	8.5	8.2-8.9	29.8	8.8
	60	8.2	7.9-8.3		8.3
	65_1	7.7	7.1-8.0		7.9
	65_2	7.6	7.2-8.0		7.9
PIIb	55	7.7	7.4-8.1	31.5	8.7
	60	7.2	7.2		8.2
	65_1	7.7	7.6-7.8		7.8
PIIc	55	7.7	7.4-8.1	32.3	8.7
	60	7.2	7.2		8.2
	65_1	7.7	7.6-7.8		7.8
	70	7.1	7.0-7.2		7.4

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[1] Saturated dissolved oxygen content was calculated from Carpenter's oxygen solubility tables in Gilbert, Pawley, and Park (1968).

[2] Mean salinity was determined from tables in Wyatt and Gilbert (1972) and Gilbert (1973).

Appendix 4 Table 1. Sizes of Oregon moist pellets selected for each experiment.

Experiment	Mean weight range among subgroups (g)	Pellet size actually fed (diameter in inches)	Pellet size recommended in 1962 Oregon pellet feeding chart (diameter in inches)
CI	15.52- 19.25	0.125	0.125
CIIa	1.40- 1.52	0.047	0.047
	2.48- 4.23	0.062	0.094
	4.06- 7.04	0.094	0.094 & 0.125
CIIb	12.65- 14.64	0.094	0.125
	18.39- 21.88	0.125	0.125
PIa	46.53- 47.98	0.125	0.125
PIb	92.12-111.72	0.125	0.125
PIIa	1.77- 2.11	0.062	0.062
	5.83- 10.27	0.094	0.125
PIIb	9.76- 17.54	0.125	0.125
	16.16- 27.60	0.125	0.125
PIIc	16.16- 27.60	0.125	0.125

Appendix 5 Table 1. Conversion of growth rate values to time required for fish weight to increase.

Growth rate (% gain in body weight/day)	Days required for fish weight to increase		
	100%	200%	300%
1. 0	70	111	140
1. 5	48	75	94
2. 0	36	57	71
2. 5	29	46	57
3. 0	25	38	48
3. 5	21	33	41
4. 0	19	29	36
4. 5	17	26	33
5. 0	15	26	30
5. 5	14	24	27
6. 0	13	20	25

Appendix 6 Table 1. Linear relationship of food consumption rate, *gross food conversion efficiency*, and growth rate of chum and pink salmon to body weight: regression and correlation data.[1]

Rate or efficiency	Temperature (°F)	CHUM SALMON Regression coefficient of rate or efficiency *on* body weight *(b)*	Correlation coefficient (r)	Degrees of freedom for table value of "t"	Results of "t" test for significance of r	PINK SALMON Regression coefficient of rate *or efficiency on* body weight *(b)*	Correlation coefficient (r)	Degrees of freedom for table value of "t"	Results of "t" test for significance of r
Food consumption rate	55	-0.004	-0.712	10	P <0.01	-0.001	-0.483	8	P <0.06
	60	-0.005	-0.809	10	P <0.01	-0.002	-0.679	8	P <0.01
	65	-0.003	-0.387	10	n. s.[2]	-0.003	-0.763	8	P <0.01
Gross conversion efficiency	55	-0.501	-0.325	10	n. s.	-0.566	-0.814	8	P <0.01
	60	-1.522	-0.946	10	P <0.01	-0.724	-0.820	8	P <0.01
	65	-1.735	-0.798	10	P <0.01	-0.727	-0.714	8	P <0.01
Growth rate[3]	55	-0.648	-0.653	12	P <0.01	-0.640	-0.765	11	P <0.01
	60	-0.869	-0.801	12	P <0.01	-0.876	-0.871	11	P <0.01
	65	-0.862	-0.748	12	P <0.01	-1.375	-0.929	11	P <0.01

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[1] Food consumption rate, gross food conversion efficiency, growth rate, and body weight data were obtained for each temperature from Experiments CI, CIIa, and CIIb for chum salmon, and from Experiments PIa, PIIa, and PIIb for pink salmon.

[2] Defined as not statistically significant (P > 0.05).

[3] Growth rate was regressed on ln body weight.

Appendix 7 Table 1. Differences among initial mean weights of subgroups in each experiment.

Experiment	Temperature (°F)	Initial mean weight (g)	Range of differences among initial mean weights
CI	55	17.30	7.17-25.30%
	60	21.50	
	65	16.06	
CIIa	55	1.40	1.40- 7.90%
	60	1.52	
	65	1.46	
	70	1.48	
CIIb	55	27.87	5.90- 8.10%
	60	24.31	
	65	23.34	
PIa	55	47.08	1.17- 3.02%
	60	46.53	
	65	47.98	
PIb	65	111.72	17.54%
	70	92.12	
PIIa	55	1.81	0.05-16.10%
	60	1.80	
	65_1	2.11	
	65_2	1.77	
PIIb	55	9.76	17.71-44.36%
	60	11.86	
	65_1	17.54	
PIIc	55	16.16	7.31-41.45%
	60	20.81	
	65_1	27.60	
	70	22.45	

Appendix 8 Table 1. Effect of temperature on the food consumption rates of chum and pink salmon: covariance data.

Experiment	Temperature ($^{\circ}$F)	Number of observations of food consumption rate	Mean food consumption rate (% body weight/day) ($\overline{Y}$)	Subgroup mean weight (g) ($\overline{X}$)	Common regression coefficient of Y on X (/)	Adjusted mean food consumption rate (% body weight/day) ($\overline{Y}$a)	F test for acceptance of null hypothesis that all μ_i are equal	Degrees of freedom for table value of "t"	Results of "t" tests for significant differences between $\overline{Y}$a values in an experiment[1]
CI	55	3	2.92	23.90	-0.066	2.89	Accepted	5	$60 \overset{n.s.}{>} 65 \overset{n.s.}{>} 55$
	60		2.91	27.86		3.14			
	65		3.14	21.43		2.95			
CIIa	55	6	3.55	6.30	-0.148	3.61	Rejected	19	$65 \overset{n.s.}{>} 60 \overset{*}{>} 55 \overset{*}{>} 70$
	60		3.78	6.84		3.92			
	65		3.86	6.69		3.98			
	70		3.67	3.67		3.34			
CIIb	55	3	2.84	22.45	+0.089	2.67	Rejected	5	$65 \overset{**}{>} 55 \overset{n.s.}{>} 60$
	60		2.58	20.53		2.58			
	65		3.71	18.79		3.87			
PIa	55	4	3.02	69.46	-0.006	3.02	Accepted	8	$65 \overset{n.s.}{>} 60 \overset{n.s.}{>} 55$
	60		3.12	71.84		3.14			
	65		3.33	67.79		3.32			
PIb	65	3	2.38	138.95	-0.008	2.54	Accepted	3	$65 \overset{n.s.}{>} 70$
	70		1.67	99.43		1.67			
PIIa	55	3	4.07	6.00	-0.173	3.73	Rejected	7	$65_1 \overset{*}{>} 65_2 \overset{*}{>} 60 \overset{**}{>} 55$
	60		4.55	7.52		4.48			
	65_1		5.11	10.46		5.54			
	65_2		4.93	7.89		4.92			
PIIb	55	5	3.02	20.35	-0.063	2.55	Rejected	11	$65_1 \overset{*}{>} 60 \overset{**}{>} 55$
	60		3.43	26.56		3.35			
	65_1		3.43	36.24		3.97			
PIIc	55	3	2.57	24.22	-0.007	2.52	Rejected	7	$65_1, 60 \overset{*}{>} 70$ $55 \overset{n.s.}{>} 70$
	60		2.99	31.87		2.99			
	65_1		2.98	43.34		3.06			
	70		2.29	27.95		2.26			

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[1] The number (55, 60, 65, or 70) represents the $\overline{Y}_a$ value at that temperature. Levels of significance above the "greater than" symbol (>) are: n.s. = not significant ($P > 0.05$), * = $P < 0.05$, and ** = $P < 0.01$.

Appendix 8 Table 2. Effect of temperature on the gross food conversion efficiencies of chum and pink salmon: covariance data.

Experiment	Temperature (°F)	Number of observations of gross food conversion efficiency	Mean gross food conversion efficiency (% growth/food consumed) ($\bar{Y}$)	Subgroup mean weight (g) ($\bar{X}$)	Common regression coefficient of Y on X (b)	Adjusted mean gross food conversion efficiency (% growth/food consumed) ($\bar{Y}a$)	F test for acceptance of null hypothesis that all μ_i are equal	Degrees of freedom for table value of "t"	Results of "t" tests for significant differences between $\bar{Y}a$ values in an experiment
CI	55	3	72.2	23.90	-1.774	71.3	Rejected	5	$55 \overset{*}{>} 65$ $55 \overset{n.s.}{>} 60 \overset{n.s.}{>} 65$
	60		54.8	27.86		60.9			
	65		46.6	21.43		41.3			
CIIa	55	6	82.2	6.30	-1.148	82.6	Rejected	19	$55 \overset{n.s.}{>} 60 \overset{n.s.}{>} 65 \overset{*}{>} 70$ $55, 60 \overset{**}{>} 70$
	60		80.8	6.84		81.9			
	65		77.0	6.69		77.9			
	70		58.1	3.67		55.5			
CIIb	55	3	82.6	22.45	-0.281	83.1	Rejected	5	$55 \overset{*}{>} 60 \overset{n.s.}{>} 65$ $55 \overset{**}{>} 65$
	60		64.8	20.53		64.8			
	65		55.1	18.79		54.6			
PIa	55	4	45.8	69.46	-0.651	45.7	Accepted	8	$60 \overset{n.s.}{>} 55 \overset{n.s.}{>} 65$
	60		48.9	71.84		50.3			
	65		45.3	67.79		44.0			
PIb	65	3	44.6	138.95	-0.082	46.2	Accepted	3	$65 \overset{n.s.}{>} 70$
	70		18.0	99.43		16.3			
PIIa	55	3	95.7	6.00	+0.521	96.7	Accepted	7	$60 \overset{n.s.}{>} 55 \overset{n.s.}{>} 65_1 \overset{n.s.}{>} 65_2$
	60		104.4	7.52		104.6			
	65_1		92.3	10.46		91.0			
	65_2		90.9	7.89		90.9			
PIIb	55	5	71.7	20.35	-0.423	68.6	Accepted	11	$55 \overset{n.s.}{>} 60 \overset{n.s.}{>} 65_1$
	60		67.3	26.56		66.8			
	65_1		59.6	36.24		63.2			
PIIc	55	3	74.3	24.22	-2.098	58.3	Rejected	7	$65_1, 60 \overset{1}{>} 70$ $55 \overset{n.s.}{>} 70$
	60		66.8	31.87		66.9			
	65_1		62.4	43.34		86.5			
	70		47.8	27.95		39.7			

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[1] $0.10 > P > 0.05$.

Appendix 8 Table 3. Effect of temperature on the growth rates of chum and pink salmon: covariance and regression data.

		COVARIANCE DATA							
Experiment	Temperature (°F)	Number of observations of growth rate	Mean growth rate $(\overline{h})$[1] $(\overline{Y})$	Log_e subgroup mean weight (g) $(\overline{X})$	Common regression coefficient of Y on X (β)	Adjusted mean growth rate $(\overline{ha})(\overline{Ya})$	F test for acceptance of null hypothesis that all μ_i are equal	Degrees of freedom for table value of "t"	Results of "t" tests for significant differences between $\overline{Y}a$ values in an experiment
CI	55	4	1.52	3.02	-0.65	1.50	Accepted	8	$55 \overset{ns.}{>} 65 \overset{ns.}{>} 60$
	60		1.25	3.20		1.35			
	65		1.45	2.91		1.36			
PIb	65	3	1.07	4.82	-1.04	1.21	Rejected	3	$65 \overset{**}{>} 70$
	70		0.32	4.57		0.19			
PIIb	55	5	2.18	2.76	-1.48	1.76	Rejected	11	$65_1 \overset{*}{>} 60 \overset{**}{>} 55$
	60		2.35	3.00		2.30			
	65_1		2.09	3.35		2.55			
PIIc	55	3	1.92	3.18	-1.94	1.43	Rejected	7	$55 \overset{*}{>} 70$ $65_1,\ 60 \overset{**}{>} 70$
	60		2.01	3.45		2.05			
	65_1		1.94	3.76		2.59			
	70		1.12	3.33		0.92			

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[1] Defined as % gain in body weight/day.

Appendix 8 Table 3. (Continued)

REGRESSION DATA

Experiment	Temperature (°F)	Subgroup mean weight (g)		Experimental period (days)	Regression coefficient of subgroup mean weight on time $[\ln(\bar{h}+1)]$	Mean growth rate ($\bar{h}$)	95% confidence interval of $\bar{h}$	Degrees of freedom for table value of "t"	Results of "t" tests for significant differences between $\ln(\bar{h}+1)$, hence $\bar{h}$ values in an experiment
		Initial	Final						
CIIa	55	1. 40	11. 40	70	0. 030	3. 08	±0. 32	14	$55 \overset{n.s.}{>} 65 \overset{n.s.}{>} 60 \overset{**}{>} 70$
	60	1. 52	11. 81		0. 030	3. 03	±0. 34		
	65	1. 46	11. 53		0. 030	3. 07	±0. 30		
	70	1. 48	5. 85		0. 020	2. 08	±0. 22		
CIIb	55	13. 77	27. 87	30	0. 023	2. 36	±0. 17	4	$55 \overset{n.s.}{>} 65 \overset{*}{>} 60$ $55 \overset{**}{>} 60$
	60	14. 64	24. 31		0. 016	1. 70	±0. 38		
	65	12. 65	23. 34		0. 021	2. 09	±0. 70		
PIa	55	47. 08	82. 90	40	0. 014	1. 45	±0. 34	6	$60 \overset{n.s.}{>} 55 \overset{n.s.}{>} 65$
	60	46. 53	85. 48		0. 016	1. 60	±0. 39		
	65	47. 98	82. 85		0. 013	1. 36	±0. 15		
PIIa	55	1. 81	8. 23	40	0. 038	3. 95	±0. 28	6	$65_1 \overset{n.s.}{>} 65_2 \overset{n.s.}{>} 60 \overset{*}{>} 55$ $65_1, 65_2 \overset{**}{>} 55$
	60	1. 80	11. 23		0. 046	4. 74	±0. 32		
	65_1	2. 11	14. 97		0. 050	5. 13	±0. 63		
	65_2	1. 77	11. 20		0. 047	4. 80	±0. 47		