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THE EFFECT OF TEMPERATURE AND RATION ON GROWTH RATES, FOOD CONVERSION EFFICIENCIES AND THE FATE OF CARBON-14 LABELLED FOOD BY UNDERYEARLING SOCKEYE SALMON, ONCORHYNCHUS NERKA

by

Raymond Millo Biette

B.Sc., University of Manitoba, 1965
M.Sc., University of Manitoba, 1969

A THESIS SUBMITTED IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF
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in the Department
of
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The Effects of Temperature and Ration on Growth Rates, Food Conversion Efficiencies and the Fate of Carbon-14 Labelled Food by Underyearling Sockeye Salmon, *Oncorhynchus nerka*

(signature)

Raymond Millo Biette

(name)

June 28/78

(date)

ABSTRACT

One of the theories for the adaptive value of vertical migrations in thermally stratified waters is that migrants grow more rapidly and efficiently than non-migrants. Growth, growth efficiency, and the fate of ^{14}C labelled food of underyearling sockeye salmon (Oncorhynchus nerka) were studied to test this hypothesis.

Growth rates of underyearling sockeye fed rations of zooplankton of 14-84 cal/kcal sockeye/day, (1.3-7.8% of dry body wt) were determined at constant temperatures of 6.2, 11.3, 15.3, and 15.9 C, and under a cyclic temperature regime similar to that encountered by Babine Lake fish during their diel vertical migrations. At moderate rations (61 and 76 cal/kcal/day; 5.5 and 6.9% of dry body wt) growth was greater under cyclic temperatures than at constant temperatures. At a low ration (46 cal/kcal/day; 4.1% of dry body wt) growth under cyclic temperatures was not different from the constant low temperature. At the lowest and highest rations growth was greater, respectively, under the constant low temperature and the constant high temperature than under cyclic temperatures. Gross growth efficiency, ranging from < 1 to 31%, was affected by temperature and ration in much the same way as growth.

Underyearling sockeye fed ^{14}C labelled rations of 33.1 and 65.6 cal/kcal/day under constant temperatures of 5 and 15 C and cyclic temperatures permitted an assessment of the fate of ingested food. At the moderate ration (65.5 cal/kcal/day; 6.4%

of dry body wt) growth potential under cyclic temperatures was greater than at the constant low temperature but not different from the constant high temperature. At the low ration (33.1 cal/kcal/day; 3.4% of dry body wt) growth potential under cyclic temperatures was not different from constant temperatures.

At the moderate ration the enhancement of growth potential under cyclic temperatures relative to constant low temperatures resulted from a more efficient food incorporation and less food excreted as soluble organic products. At both low and moderate rations the lack of difference in growth potential between cyclic temperatures and the constant high temperature resulted from the savings in metabolic costs under cyclic temperatures being cancelled by a lower rate of food incorporation than at the constant high temperature. The discrepancy between observed growth and growth potential measured with ^{14}C was explained by a disproportionate low $^{14}CO_2$ respiration rate under the constant high temperature relative to cyclic temperatures and as a consequence growth potential at the constant high temperature was overestimated.

It is concluded that young sockeye ingesting moderate rations comparable to those probably available in the relatively warm surface layers of Babine Lake, and living under a thermal regime which involves twice daily migrations from deep cold waters to the surface and return, are likely to grow more rapidly and efficiently than fish maintained at constant temperatures. This suggests a possible selective value for vertical migrations in thermally stratified waters.

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It is a pleasure to express my sincerest appreciation to Dr. G.H. Geen, Chairman of my Research Supervisory Committee, who provided encouragement, patience and criticism during the course of this study.

I am grateful to Dr. D.W. Narver, a member of the Supervisory Committee, for proposing the research problem, and to his colleagues of the Department of Fisheries and the Environment, Pacific Biological Station, Nanaimo, for providing facilities, assistance and logistic support at the Field Station at Smithers Landing on the North Arm of Babine Lake. I thank other members of my Supervisory Committee, Drs. R.M. Sadleir, and B.A. McKeown for their advice, encouragement, discussion and critical review of the manuscript. I also thank Dr. A. van Overbeeke, originally on my Supervisory Committee. I acknowledge other members of the Department of Biological Sciences who have helped in several ways to make this work possible.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

Chapter 1

GROWTH RATES AND FOOD-CONVERSION EFFICIENCIES OF UNDERYEARLING SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, IN RELATION TO TEMPERATURE ~~AND RA~~TION

INTRODUCTION

In Babine Lake, British Columbia, underyearling sockeye salmon (Oncorhynchus nerka) undertake a diel vertical migration which takes them from the cold (5-9°C) hypolimnion at dusk to the warm (12-18°C) epilimnion where feeding occurs over a one to two-hour period (Narver, 1970). Following feeding, young sockeye descend to the upper stratum of the thermocline (12-15°C) and move into the epilimnion with dawn to feed briefly again, and then with daylight descend to the hypolimnion for the remainder of the day (Narver, 1970). By virtue of this diel vertical migration young sockeye may experience temperatures ranging between 5 and 18°C. This study examines the effect this cycling temperature regime has on growth and growth efficiency of underyearling sockeye salmon reared in outdoor tanks.

Many animals migrate to warmer waters where they feed for a limited time before returning to colder waters. The adaptive significance of this behaviour has been the subject of considerable speculation: escape from predators, energy gain, demographic effects, optimize food source, horizontal transport, social regulation of population size. A critical discussion of the proposed theories may be found in McLaren (1963), Swift (1976) and Enright (1977). One hypothesis, which this work was designed to examine, is that of McLaren (1963) who suggested that the reduced metabolic rate in the cooler, deeper water to which migrants descend when not feeding could leave more energy available for growth and reproduction. After reviewing the ecology of young sockeye in Babine Lake and relating it to his own metabolic and growth studies with young sockeye, Brett (1971a), concluded that whatever other value vertical migrations may have, McLaren's 'energy bonus' hypothesis could account for the sockeye behvaiour in this lake.

McLaren's hypothesis has been examined experimentally for stage III Pseudocalanus minutus (Lock and McLaren, 1970), 2-4 yr. Stizostedion vitreum vitreum (Kelso, 1972) and Chaoborus trivittatus larvae (Swift, 1976). Although Swift reported that at both high and low rations growth was greater under cyclic temperatures than a constant low temperature (5 °C), none of these workers observed a greater net gain in energy for growth under cyclic temperature regimes compared to constant high or intermediate temperatures. Consequently, they all concluded that McLaren's energetic hypothesis did not hold. However, Enright (1977) and Enright and Honegger (1977) demonstrated mathematically that migrant marine herbivores, Calanus helgolandicus (pacificus), feeding in the surface waters at night could gain more energy for growth and reproduction than non-migrants feeding continuously in warmer surface waters. McLaren (1974) revised his earlier explanation to emphasize demographic rather than energetic effects of vertical migration. His new model proposes that vertical migration, coupled with a seasonal environment and high juvenile mortality, permit migrants to develop more slowly and to grow large and be more fecund than non-migrants in surface waters. Empirical data on Pseudocalanus minutus support this theory.

Most growth and food conversion experiments with fishes have been conducted in the laboratory at relatively constant temperatures and with artificial diets (e.g. Donaldson and Foster, 1940; Brown, 1957; Brett et al., 1969). Thus, extrapolation to the natural situation is difficult. This study attempted to simulate in experimental tanks the ration and temperature conditions that young sockeye experience in nature, and to compare the resultant growth and food conversion efficiencies with those obtained under constant temperature and similar ration conditions.

The studies were conducted on the shores of the North Arm of Babine Lake at the Department of Fisheries and Environment Field Station at Smithers Landing. Located, in north-central British Columbia, Babine Lake is the largest (surface area 475 km^2) and most important sockeye salmon producing lake of the Skeena River system (Larkin and McDonald, 1968). The North Arm, including small Nilkitkwa Lake immediately downstream, currently serves as the major nursery area for young sockeye (McDonald, 1969). Babine Lake was chosen for the present study because of its importance as a sockeye nursery, background data, field facilities, and readily available supply of underyearling sockeye and their zooplankton foods. Experiments conducted at this site provided opportunity to compare results with those from natural populations.

MATERIALS AND METHODS

I conducted experiments during the summers of 1969 and 1970. The 1969 experiments were exploratory and established the relationship of growth to temperature and ration. The two sets of experiments conducted in 1970 (the first from June 23 to July 25, and the second from July 28 to August 29) will be referred to subsequently as Expt. 1 and Expt. 2. In both studies a factorial design was employed with three temperatures and five rations as the variables.

Underyearling sockeye salmon were obtained with a beach seine on the shores of Smokehouse Island of Nilkitkwa Lake for Expt. 1. Fish used in Expt. 2 were captured with a purse seine in the North Arm of Babine Lake in the basin 3 km north of Nine Mile Creek. Fish were transported to the field station at Smithers Landing, sorted to an average wet weight of 199 ± 60 mg (± 2 SE) in Expt. 1 and 966 ± 70 mg (± 2 SE) in Expt. 2 and randomly distributed to experimental tanks (36 fish per tank) where they were held for 2-4 days under the experimental temperature regime at which their growth was examined.

Fish were held in fifteen 197-litre oval, dark green fiberglass tanks housed in a shed with a white translucent roof and open sides. Each tank was fitted with a dark lit covering the entire tank to decrease light intensities during daylight and to provide cover for the fish. A continuous supply of lake-water was pumped from depths of 1 and 12 m and filtered through 80 _ nylon into two large storage tanks from which approximately

2-litre of water per minute was supplied to each experimental tank. The water was jetted into the side of each tank and discharged through a central standpipe.

The three temperatures used in Expt. 1 were 15.3 ± 1.8°C and 11.3 ± 1.0°C (± 2 SD) and a cyclic temperature regime (Fig. 1.1) which ranged from 4.5°C to 17.5°C. Temperatures were read daily from standardized thermographs. The cyclic temperature regime approximated those experienced by young sockeye during the course of their diel vertical migration (Fig. 1.2). In Expt. 2 the experimental temperatures were 15.9 ± 1.7°C and 6.2 ± 0.4°C (± 2 SD) and the cyclic temperature regime indicated in Fig. 1.1. Temperatures in the cyclic temperature tanks were altered by gradually changing the percentage of epilimnial and deeper water fed into the tanks. Incoming water from the deeper intake was cooled by two portable refrigeration units to achieve temperatures typical of the hypolimnion. By mixing water from the two supply lines with hand valves the intermediate constant temperature (11.3°C) and cyclic temperature regime were obtained.

Live zooplankton were collected daily from the surface of the North Arm of Babine Lake using 308 μ or 253 μ mesh size Nitex plankton nets and were strained gently through a series of sieves to obtain animals of fairly uniform size (< 1.5 mm; predominately *Diaptomus ashlandi*, *Cyclops scutifer*, and *Bosmina coregoni*). Species composition (by number) and moisture content of rations in both experiments were determined regularly. Different volumes of zooplankton were drawn from the catches,

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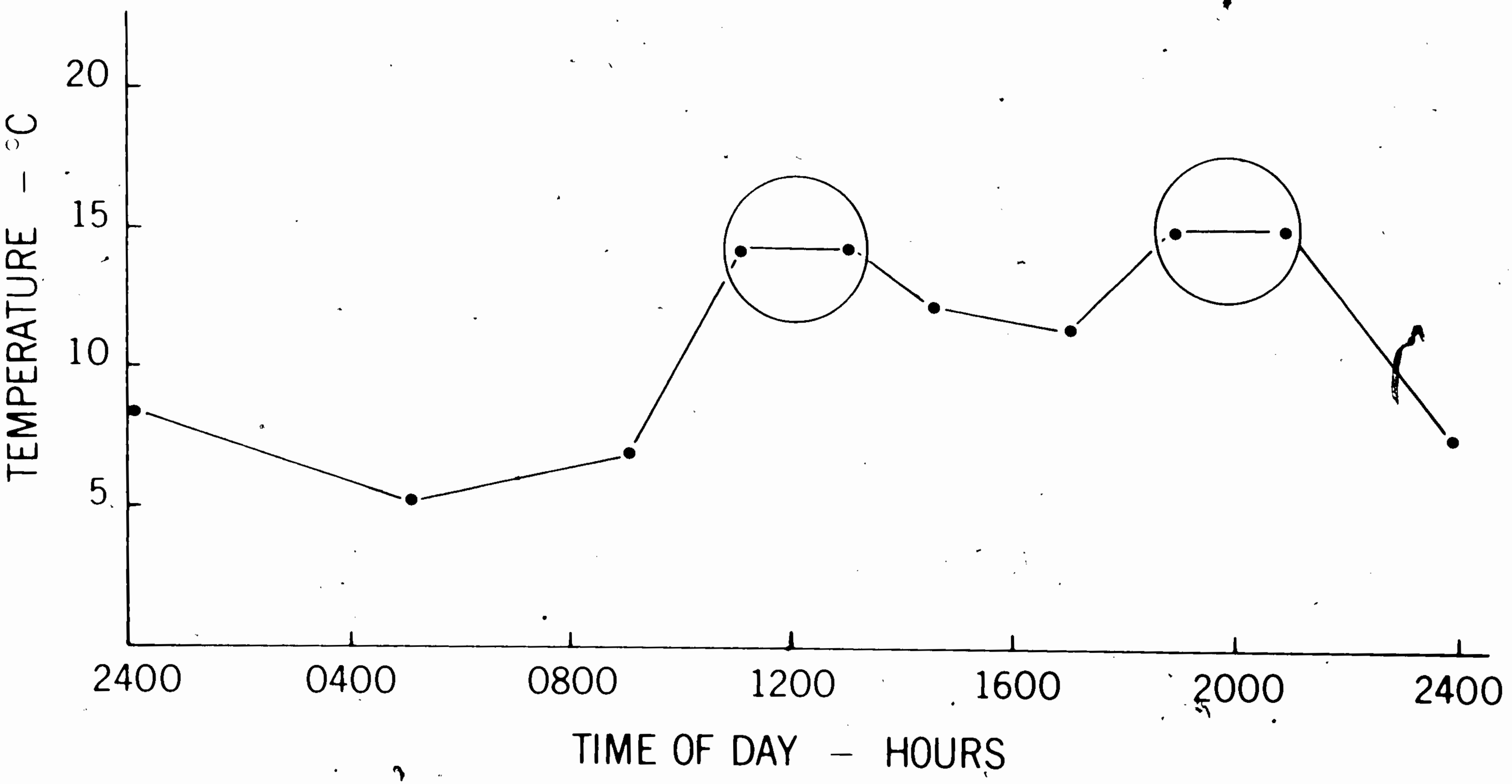
Figure 1.1 The cyclic temperature regime and the feeding times (indicated by circles) to which underyearling sockeye salmon were exposed in the outdoor tanks in both experiments.


TEMPERATURE – °C
20
15
10
5
2400
0400
0800
1200
1600
2000
2400
TIME OF DAY – HOURS

7b

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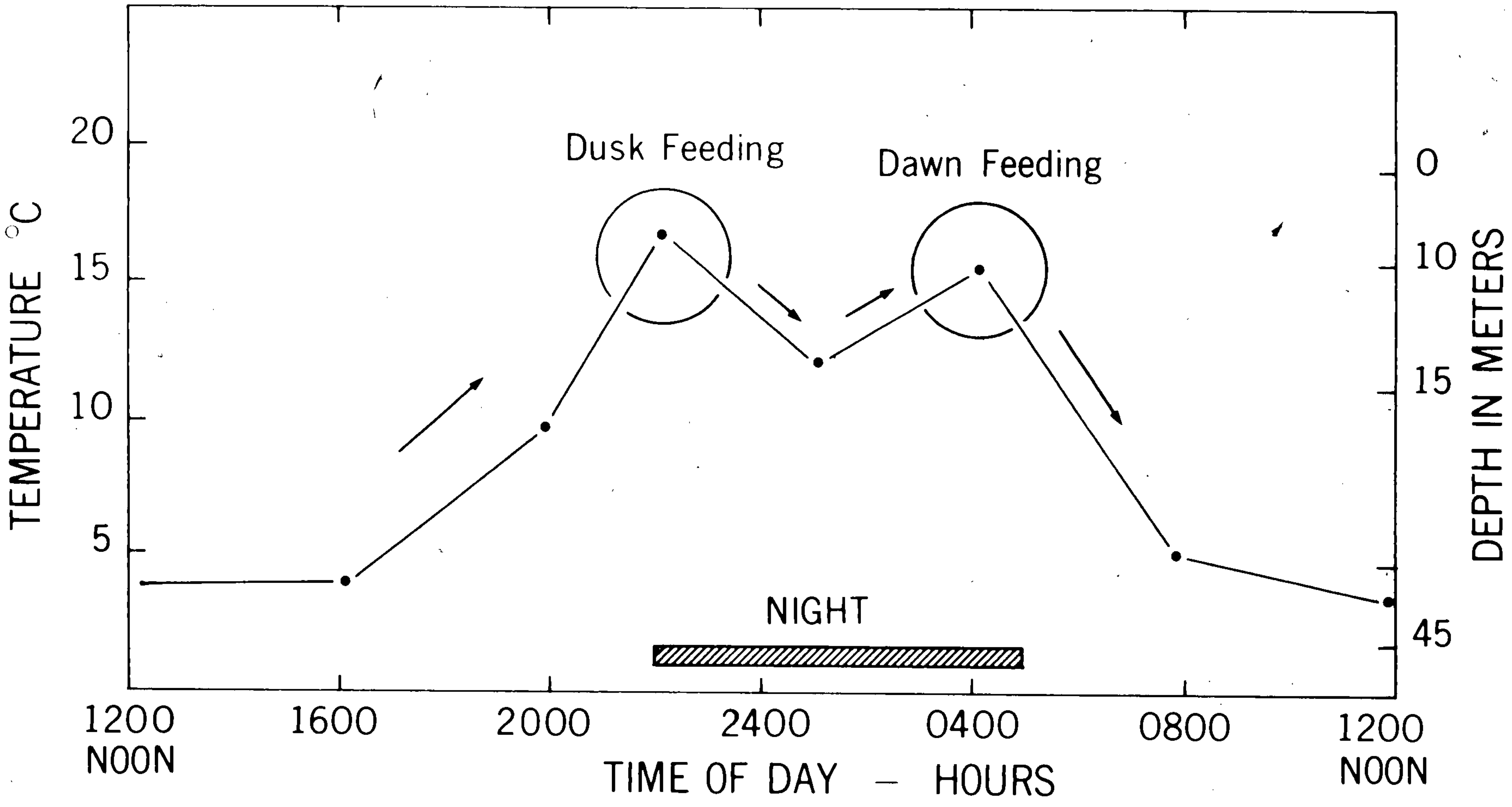
Figure 1.2 The pattern of diel vertical migration with corresponding temperatures and feeding periods (indicated by circles) of underyearling sockeye salmon in Babine Lake in mid-summer (Adapted from Brett, 1971a; McDonald, 1973).


Dusk Feeding
Dawn Feeding
NIGHT
TEMPERATURE °C
20
15
10
5
DEPTH IN METERS
0
10
15
45
1200 NOON
1600
2000
2400
0400
0800
1200 NOON
TIME OF DAY — HOURS

which were stirred to ensure a homogenous distribution, and added to each tank to provide a range of food quantity whose weight was a known percentage of the fish biomass in a given tank. Daily dry weight rations were 1.3, 4.0, 5.4, and 6.7% of dry body weight fish and excess (fed to satiation two times daily) in Expt. 1, and 1.4, 4.1, 5.5, and 6.9% of dry body weight fish, and excess in Expt. 2. One-half of the daily ration was provided at 1100 h and the remainder at 1900 h. The absolute quantity of food provided was adjusted at 10-day intervals in accordance with changes in fish weights. Tank covers were removed and water pumps turned off during each 2 h feeding period. The fish consumed all the food except in those tanks to which excess food had been added. Any excess food in the latter tanks was recovered 3 days each week, weighed and the % of fish dry weight consumed calculated. This ranged from 7.1-7.8%.

All fish were weighed to the nearest mg and fork length measured to the nearest mm at the beginning of the experiments and at 10-day intervals thereafter. Before measuring, the fish were lightly anaesthetized with 2-phenoxyethanol (0.26 mL/L) and blotted on paper towels to remove surface moisture. Following measuring, fish were returned to their tanks. To eliminate any variability in weight introduced by food in the gut, fish were not fed on weighing days which were not counted in the growth computations. After 33 days all fish were sacrificed, a sample drawn for dry weight measurements, the remainder quick frozen and stored for later caloric measurements.

Dry weights of fish sampled from the beginning and end of both experiments at each temperature and ration and representative samples of zooplankton were measured after oven drying samples at 60°C for 48 h. Wet weights of fish, including initial and final weights, averaged 5.46 (Expt. 1) and 5.24 (Expt. 2) times as great as dry weights. Zooplankton wet weights averaged 12.2 (Expt. 1) and 11.5 (Expt. 2) times dry weights.

Instantaneous growth rate was calculated with the equation $k = \frac{\ln w_1 - \ln w_o}{t_1 - t_o}$, where w_o is the initial dry weight w_1 is final dry weight, t is time in days, ln is natural logarithm, and k is instantaneous growth rate (Ricker 1958). By methods of least squares 'k' values were estimated. The slope 'k' x 100 is equivalent to the specific growth rate. Growth rate was also calculated on a caloric basis because of differences in energy content (cal/g) of the zooplankton and fish flesh. The caloric value of fish tissue at the beginning and end of both experiments at each temperature and ration and representative zooplankton samples were determined in a Phillipson micro-bomb calorimeter (Phillipson, 1964) standardized using benzoic acid (6318 cal/g). Ash content was determined by oxidizing samples of fish and zooplankton in a muffle furnace at 600°C. Ash values were subtracted from dry weights to calculate ash-free caloric values. Average relative growth rate, expressed as cal/kcal of fish/day, was calculated with the equation Growth rate $= \frac{w_1 - w_o}{0.5(w_o+w_1)t}$, where w_o is initial dry weight, w is final dry weight, t is time in days, and then converting this total dry weight increment $(w_1 - w_o)$ and the average dry weight of fish $(0.5 (w_o + w_1))$ to caloric equivalents.

Growth efficiency was determined by caloric comparison of the quantity of fish tissue elaborated as growth in relation to the amount of food ingested. Gross growth efficiency is defined as the ratio of growth to total food ingested and calculated as G/I, where G is average growth rate in cal/kcal of fish/day and I is ration in cal/kcal of fish/day. This value is also referred to in the literature as coefficient of growth of the first order or total growth efficiency (Warren, 1971). Net growth efficiency, also referred to as partial growth efficiency by Warren (1971), is the ratio of growth to food available for growth. Net growth efficiency is calculated from the expression $G/I-R_m$, where R_m is estimated maintenance ration when no growth occurs in cal/kcal of fish/day, $I - R_m$ is that portion of food eaten which is not immediately lost to metabolic and digestive costs (Macfadyen, 1963) and expressed as a %. Estimates of R_m were not determined directly.

RESULTS

Growth Rates

The change in wet weight of underyearling sockeye salmon measured at each of the three temperatures in relation to time at the five rations is shown in Appendix 1 for Expt. 1 and in Appendix 2 for Expt. 2. Noticeable temperature-dependent size differences were apparent within the first 10 days in both experiments. These differences were maintained and increased up to the termination of the experiment (33 days; Appendix 2).

Expt. 1 - Both temperature and ration produced significant differences in the specific growth rates (Table 1.1, Fig. 1.3). Specific growth rates at all except excess food rations were in decreasing order: cyclic temperature regime > 11.3 C > 15.3°C (Table 1.1). There was no significant difference between the 11.3°C and 15.3°C fish at 6.7% ration, nor between 11.3°C and the cyclic temperature regime at the excess ration (Table 1.1). At the lowest ration level (1.3% of dry body wt) positive growth was recorded only for fish grown under the cyclic temperature regime (Fig. 1.3). The lowest and highest growth rates occurred in fish grown at 15.3°C with rations of 1.3% and 7.8%/day, respectively (Fig. 1.3).

Expt. 2 - The growth measured in Expt. 2, as in Expt. 1 was affected by both temperature and ration (Table 1.2; Fig. 1.4). At the lowest ration (1.4% of dry body wt/day) growth rates were in descending order: 6.2°C > cyclic temperature regime > 15.9°C (Table 1.2; Fig. 1.4). At ration of 4.1% of dry body wt/day

Table 1.1 - Comparisons of temperature, ration and specific growth rates (dry body wt/day) in Experiment 1. Statistical comparisons of growth rates at various temperatures are also shown.

Ration % dry body wt/day	Cyclic temp. and 11.3 C					Cyclic temp. and 15.3 C					11.3 C and 15.3 C				
	Temp. comp. according to specific growth rates	Specific growth rates % dry body wt/day	t	df	Signif-icance	Temp. Comp. according to specific growth rates	Specific growth rates dry body wt/day	t	df	Signif-icance	Temp. Comp. according to specific growth rates	Specific growth rates / dry body wt/day	t	df	Signif-icance
1.3	Cyclic > 11.3	0.25 > -0.15	2.18	63	P < .05	Cyclic > 15.3	0.25 > -0.70	4.90	61	P < .01	11.3 > 15.3	-0.15 > -0.70	3.15	62	P < .01
4.0	Cyclic > 11.3	0.87 > 0.40	2.76	63	P < .01	Cyclic > 15.3	0.87 > 0.04	8.38	61	P < .01	11.3 > 15.3	0.40 > 0.04	2.56	62	P < .01
5.4	Cyclic > 11.3	1.43 > 1.01	4.04	65	P < .01	Cyclic > 15.3	1.43 > 0.57	6.76	64	P < .01	11.3 > 15.3	1.01 > 0.57	3.18	63	P < .01
6.7	Cyclic > 11.3	1.83 > 1.58	2.10	60	P < .05	Cyclic > 15.3	1.83 > 1.40	2.91	62	P < .01	11.3 > 15.3	1.58 > 1.40	1.56	62	NS
Excess[1]	11.3 > Cyclic	1.99 > 1.81	-1.57	63	NS	15.3 > Cyclic	2.50 > 1.81	6.34	63	P < .01	15.3 > 11.3	2.50 > 1.99	12.06	64	P < .01

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[1] Excess rations were 7.2, 7.7 and 7.8 of dry body wt at 11.3 C, cyclic temperature regime and 15.3 C, respectively.

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Figure 1.3 Relation of growth rate to ration for underyearling sockeye salmon held at constant temperatures of 15.3°C (○), and 11.3°C (●) and a diel cyclic temperature pattern (△). Limits $\bar{x}$ ± 2 SE.

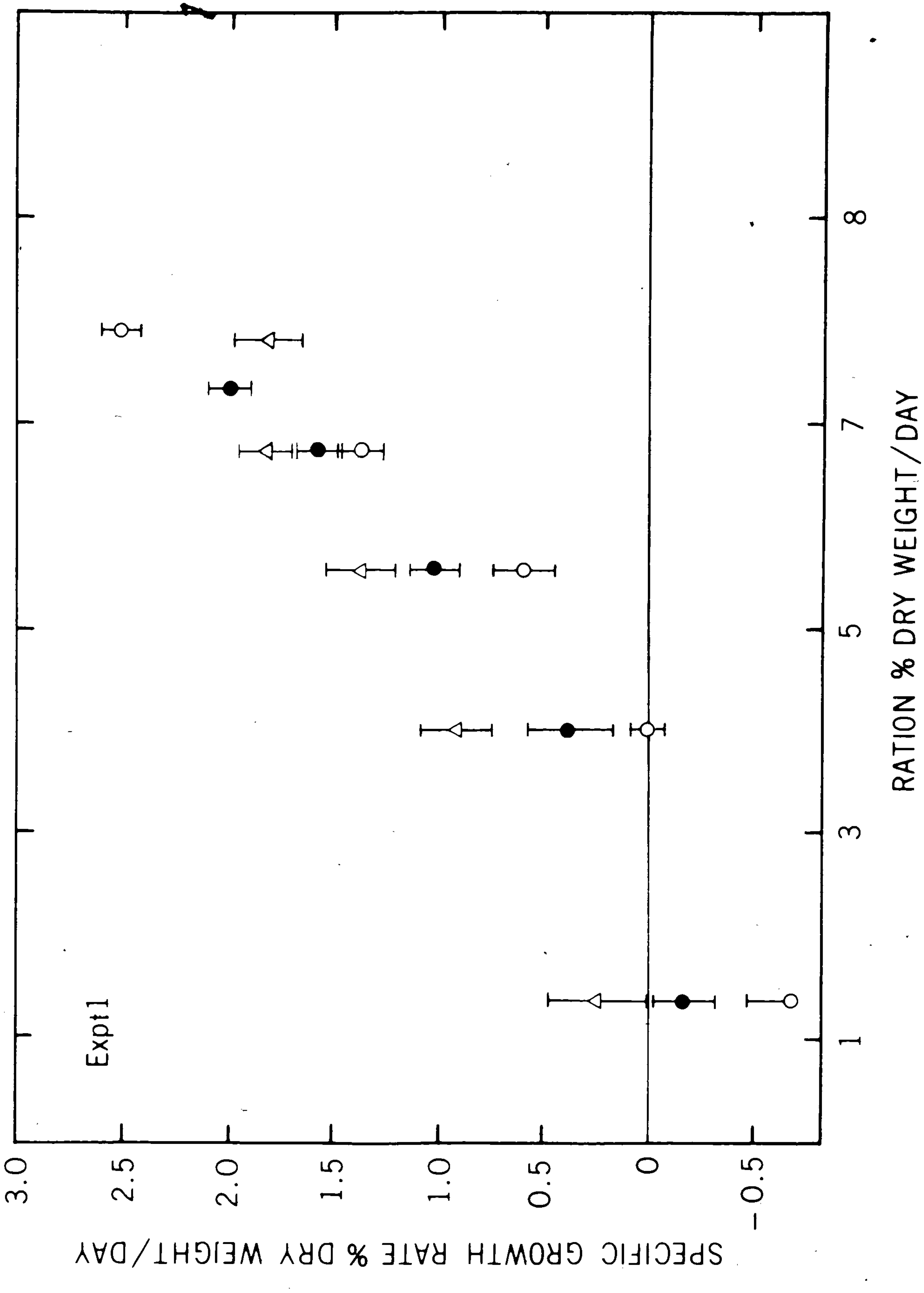
Expt 1
SPECIFIC GROWTH RATE % DRY WEIGHT/DAY
3.0
2.5
2.0
1.5
1.0
0.5
0
−0.5
RATION % DRY WEIGHT/DAY
1
3
5
7
8

Table 1.2 Comparisons of temperature, ration and specific growth rates (dry body wt/day) in Experiment 2. Statistical comparisons of growth rates at various temperatures are also shown.

Ration dry body wt/day	Cyclic temp. and 6.2 C					Cyclic temp. and 15.9 C					6.2 C and 15.9 C				
	Temp. comp. according to specific growth rates	Specific growth rates dry body wt/day	t	df	Signif-icance	Temp. comp. according to specific growth rates	Specific growth rates dry body wt/day	t	df	Signif-icance	Temp. Comp. according to specific growth rates	Specific growth rates % dry body wt/day	t	df	Signif-icance
1.4	6.2 > Cyclic	-0.17 > -0.37	-2.86	68	P < .01	Cyclic > 15.9	-0.33 > -0.89	5.68	64	P < .01	6.2 > 15.9	-0.17 > -0.89	8.00	64	P < .01
4.1	6.2 > Cyclic	0.33 > 0.30	-0.47	68	NS	Cyclic > 15.9	0.30 > -0.77	12.05	65	P < .01	6.2 > 15.9	0.33 > -0.77	12.30	67	P < .01
5.5	Cyclic > 6.2	0.83 > 0.61	3.72	68	P < .01	Cyclic > 15.9	0.83 > 0.23	8.17	68	P < .01	6.2 > 15.9	0.61 > 0.23	5.13	68	P < .01
6.9	Cyclic > 6.2	1.20 > 0.58	7.36	68	P < .01	Cyclic > 15.9	1.20 > 0.88	3.70	65	P < .01	15.9 > 6.2	0.88 > 0.58	3.10	65	P < .01
Excess[1]	Cyclic > 6.2	1.23 > 0.80	4.56	56	P < .01	15.9 > Cyclic	1.62 > 1.23	-4.21	63	P < .01	15.9 > 6.2	1.62 > 0.80	8.25	55	P < .01

[1] Excess rations were 7.1, 7.6 and 7.6 of dry body wt at 6.2 C, cyclic temperature regime and 15.9 C, respectively.

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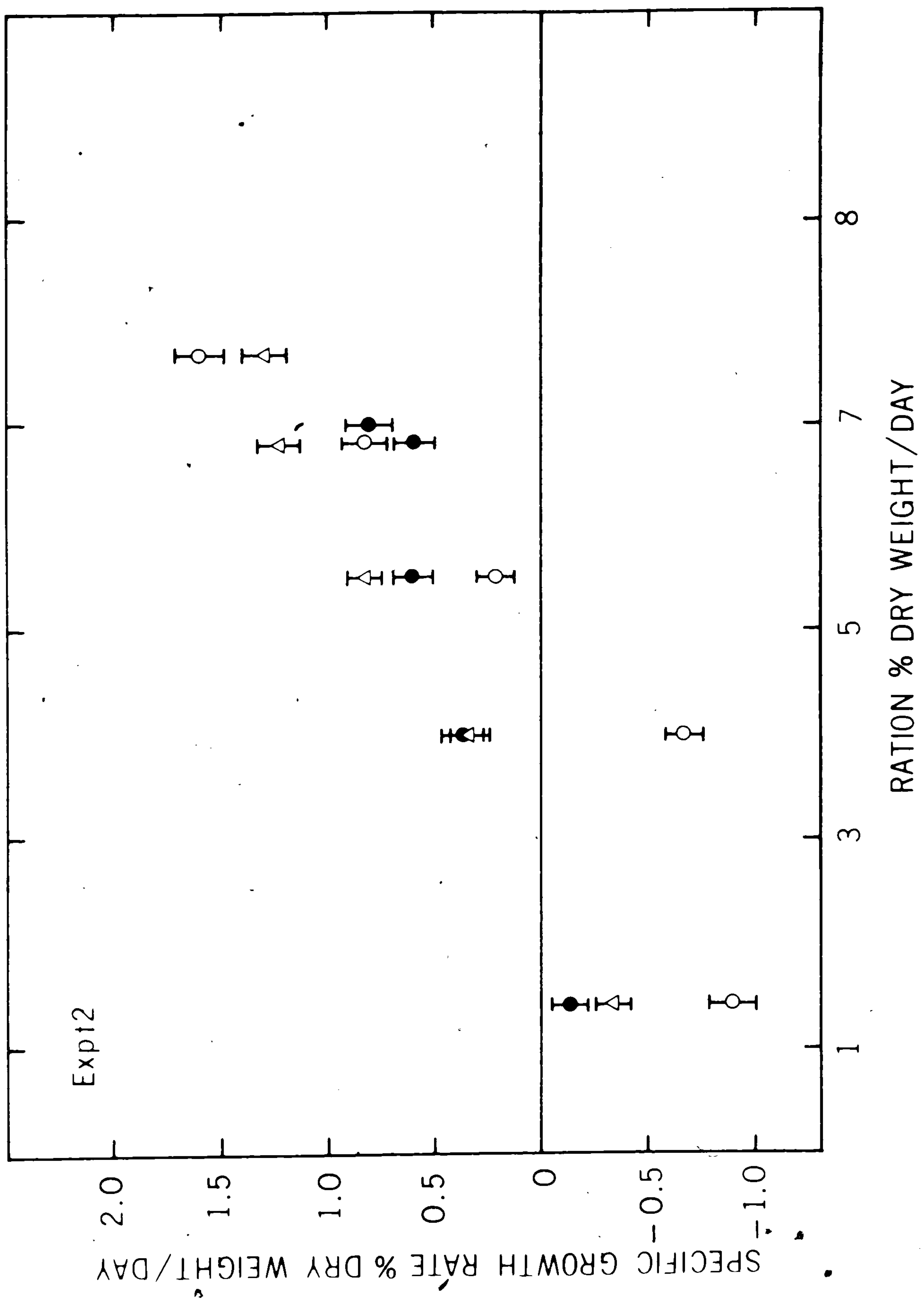
Figure 1.4 Relation of growth rate to ration for underyearling sockeye salmon held at constant temperatures of 15.9°C (O) and 6.2 C (●) and a diel cyclic temperature pattern ([illegible]). Limits $\bar{x}$ ± 2 SE.


Expt2
SPECIFIC GROWTH RATE % DRY WEIGHT/DAY
2.0
1.5
1.0
0.5
0
-0.5
-1.0
RATION % DRY WEIGHT/DAY
1
3
5
7
8

growth rates were in the following order: 6.2°C = cyclic temperature regime > 15.9°C (Table 1.2, Fig. 1.4). At moderate rations (5.5 and 6.9% of dry body wt/day) growth under the cyclic temperature regime was greater than that under either constant temperature (Table 1.2, Fig. 1.4). At excess ration growth rates were in the following order: 15.9°C > cyclic temperature regime > 6.2°C. As in Expt. 1 the minimum and maximum growth rates were recorded in those fish kept at the constant high temperature and lowest and highest rations respectively (Fig. 1.3, 1.4). In general, growth rates in Expt. 2 (Table 1.2, Fig. 1.4) were less than those in Expt. 1 (Table 1.1, Fig. 1.3); an expected result in view of the differences in initial size.

Caloric Equivalents

There was no significant difference ($P \geq 0.05$) per unit weight in the energy content of samples of fish, excluding contents of the gastrointestinal tract, at each temperature and ration measured at the beginning and end of each experiment. The mean caloric values were 6.02 (Expt. 1) and 6.14 (Expt. 2) kcal/g ash free dry wt (Table 1.3). Average caloric value of the zooplankton, as determined on representative samples of the ration fed to underyearling sockeye, were 6.33 and 6.79 kcal/g ash free dry wt in Expt. 1 and 2, respectively (Table 1.3). In Expt. 1 <u>Diaptomus ashlandi</u> and <u>D. pribilofensis</u> made up 60% or more of the total number of zooplankton present in the ration.

Table 1.3 - Caloric value for underyearling sockeye salmon and rations determined by micro-bomb calorimetry.

Species[c]	Expt.	No. Determ.	Ash/free[b] kcal/g	Ash[d] %
Oncorhynchus nerka	1	80[a]	6.02	1.8
Oncorhynchus nerka	2	80	6.14	2.0
67% *Diaptomus ashlandi* & *D. pribilofensis* 24% *Bosmina coregoni* 8% *Cyclops scutifer* 1% *Daphnia longispina*	1	5	6.43	6.3
62% *Diaptomus ashlandi* & *D. pribilofensis* 25% *Cyclops scutifer* 13% *Bosmina coregoni*	1	6	6.23	6.0
64% *Bosmina coregoni* 33% *Diaptomus ashlandi* & *D. pribilofensis* 3% *Daphnia longispina*	2	6	6.90	7.2
43% *Diaptomus ashlandi* & *D. pribilofensis* 33% *Cyclops scutifer* 20% *Bosmina coregoni* 4% *Daphnia longispina*	2	6	6.68	6.9

[a] Five determinations were made on samples at the beginning of the experiment and five determinations were made on samples at the end of the experiments for each of the three temperatures and five rations (5 + 5x3x5 = 80).

[b] Mean of all measurements.

[c] Species composition of a ration provided on a particular day is by number.

[d] Obtained by oxidizing samples in a muffle furnace.

In Expt. 2 Bosmina coregoni made up 50% or more of the total number of zooplankton present in the ration during the first 10 days of the experiment, than D. ashlandi and D. pribilofensis made up 70% or more of the total number during the remaining period.

The relationship of average relative growth rates (cal increment/kcal of fish/day) to ration size (cal plankton/kcal of fish/day) are shown in Fig. 1.5, 1.6. The same general trends were evident when either dry weights or caloric contents were used for comparison (Fig. 1.3, 1.4, 1.5 and 1.6).

The ration at which zero growth occurs was defined as the R_m (Fig. 1.3, 1.4, 1.5, 1.6). It is assumed that the zero growth maintenance ration is the same when growth is greater or less than zero. The R_m values were determined at the intersection of a smooth curve, fitted by eye to pass through the growth means, and the zero growth line (Fig. 1.5, 1.6). Extrapolation was necessary only in one case (Fig. 1.5, cyclic temperature). The R_m values, expressed as cal/kcal fish/day are as follows:

Experiment 1		Experiment 2	
Cyclic regime	6	Cyclic regime	34
11.3°C	20	6.2°C	25
15.3°C	42	15.9°C	58

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Figure 1.5 Relation of growth rate to ration for underyearling sockeye salmon held at constant temperatures of 15.3°C (○) and 11.3°C (●) and under a diel cyclic temperature pattern (△). Limits $\bar{x}$ ± 2 SE.

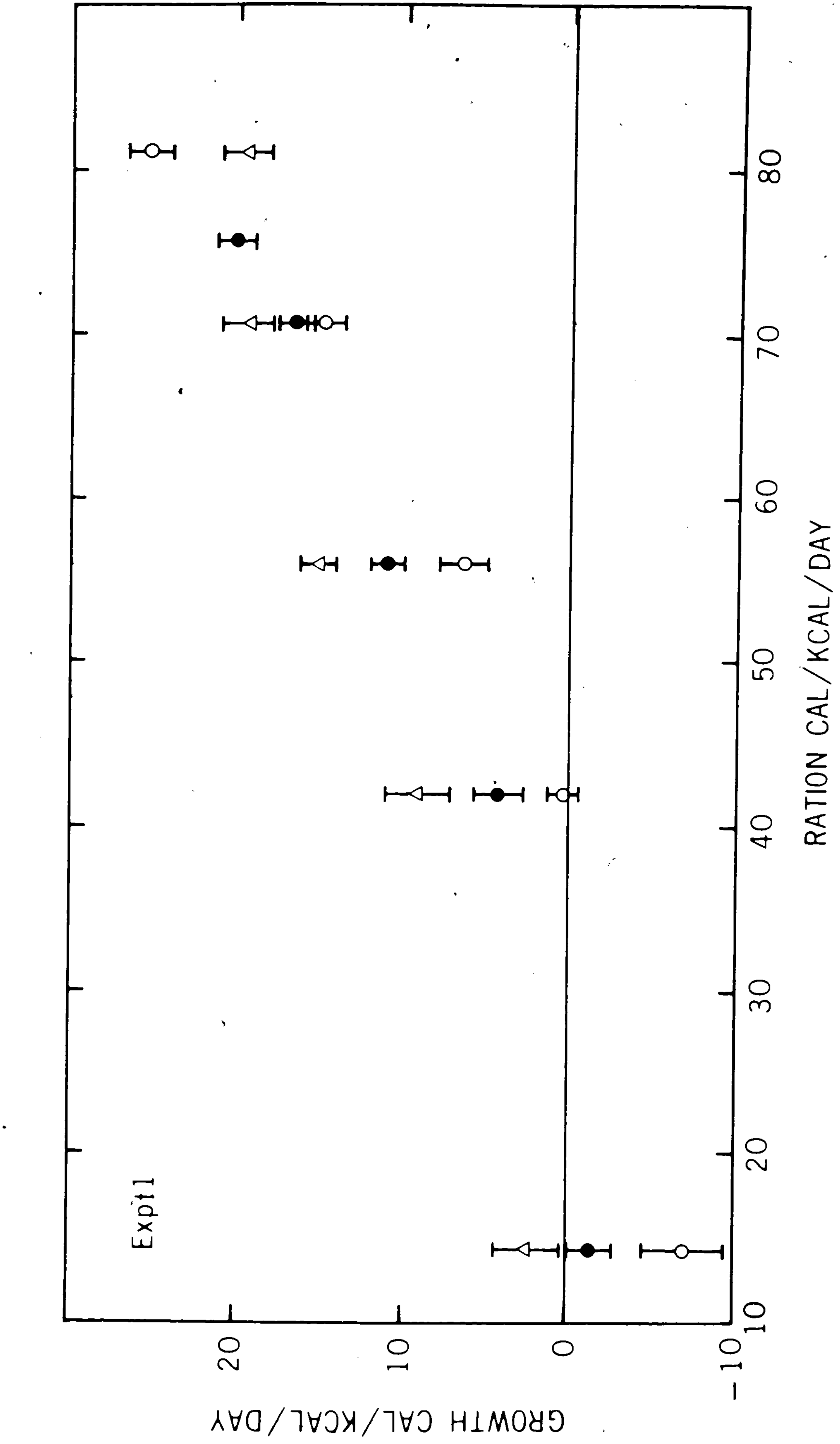
Exptl
GROWTH CAL/KCAL/DAY
20
10
0
−10
RATION CAL/KCAL/DAY
10
20
30
40
50
60
70
80

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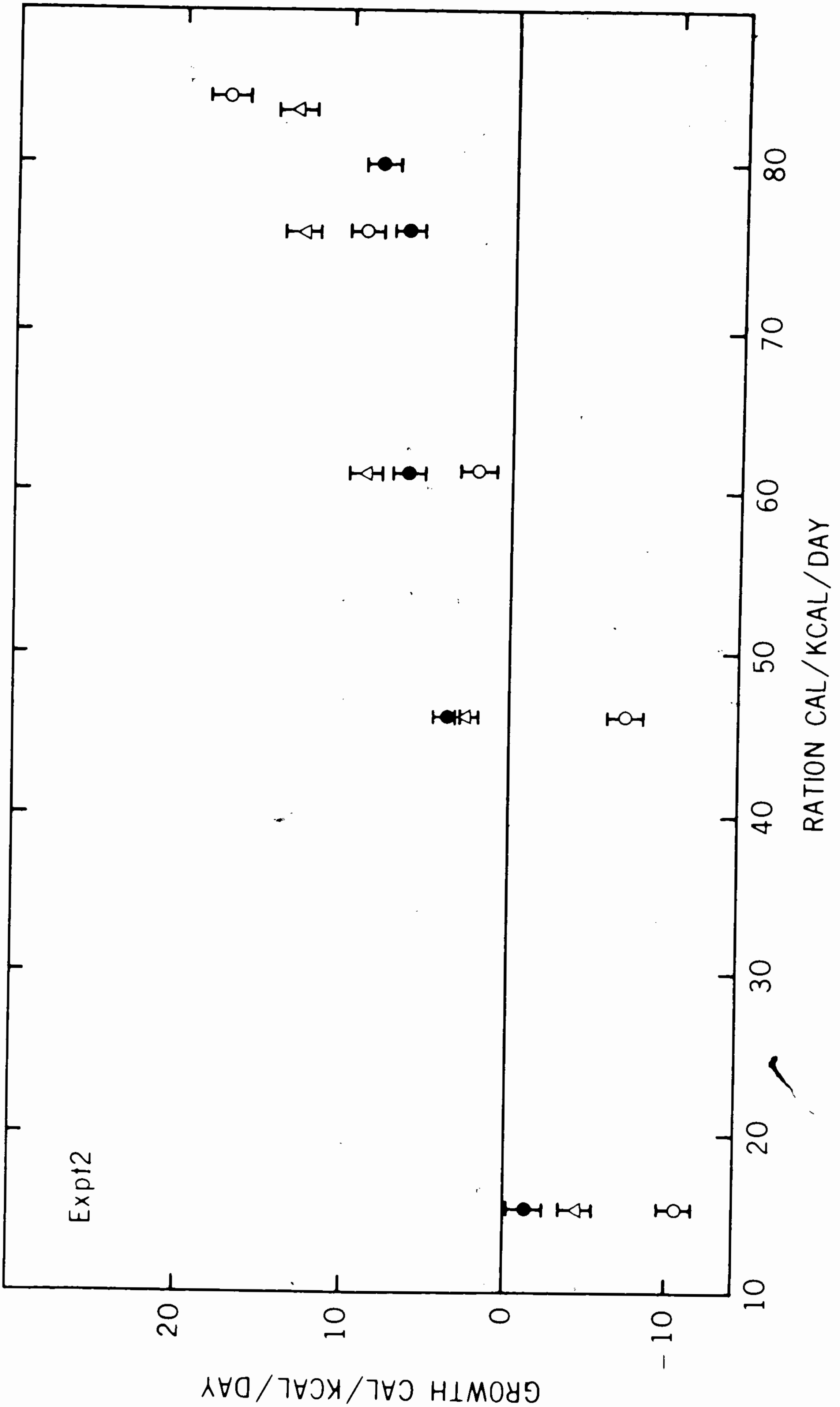
Figure 1.6 Relation of growth rate to ration for underyearling sockeye salmon held at constant temperatures of 15.9°C (○) and 6.2°C (●) and a diel cyclic temperature regime (△). Limits $\bar{x}$ ± 2 SE.


Expt2
GROWTH CAL/KCAL/DAY
20
10
0
-10
RATION CAL/KCAL/DAY
10
20
30
40
50
60
70
80

Growth Efficiencies

The gross growth efficiencies calculated from the data in Expt. 1 are compared in Fig. 1.7. Minimum and maximum gross growth efficiencies in Expt. 1 were obtained at 15.3°C and were 0.43% at a ration of 43 cal/kcal fish/day and 31% at a ration of 82 cal/kcal fish/day, respectively (Fig. 1.7). Gross growth efficiency was affected by both temperature and ration (Fig. 1.7). At constant temperatures of 11.3°C and 15.3°C an increase in ration increased conversion efficiency. Under cyclic temperatures gross conversion efficiency reached a plateau and then declined slightly at excess rations. Temperature influenced the gross growth conversion efficiencies in much the same way as the growth rates (Fig. 1.5, 1.7).

The net growth efficiency in Expt. 1 in relation to temperature and ration is shown in Fig. 1.8. Net conversion efficiencies were greater at 15.3°C than 11.3°C or the cyclic temperature.

The gross efficiency of food conversion in Expt. 2 under the three temperatures is presented in Fig. 1.9. Gross conversion efficiencies were influenced by temperature in much the same way as growth rates (Fig. 1.6). At a ration of 46 cal/kcal fish/day gross growth efficiency under cyclic temperatures was not significantly different from the constant low temperature. At moderate rations (61 and 76 cal/kcal fish/day) the gross efficiency was greatest under cyclic temperatures. At excess rations gross growth conversion efficiencies were highest (20%)

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Figure 1.7 Gross efficiency of food conversion in relation to ration at constant temperatures of 15.3°C and 11.3°C and under the cyclic temperature regime.

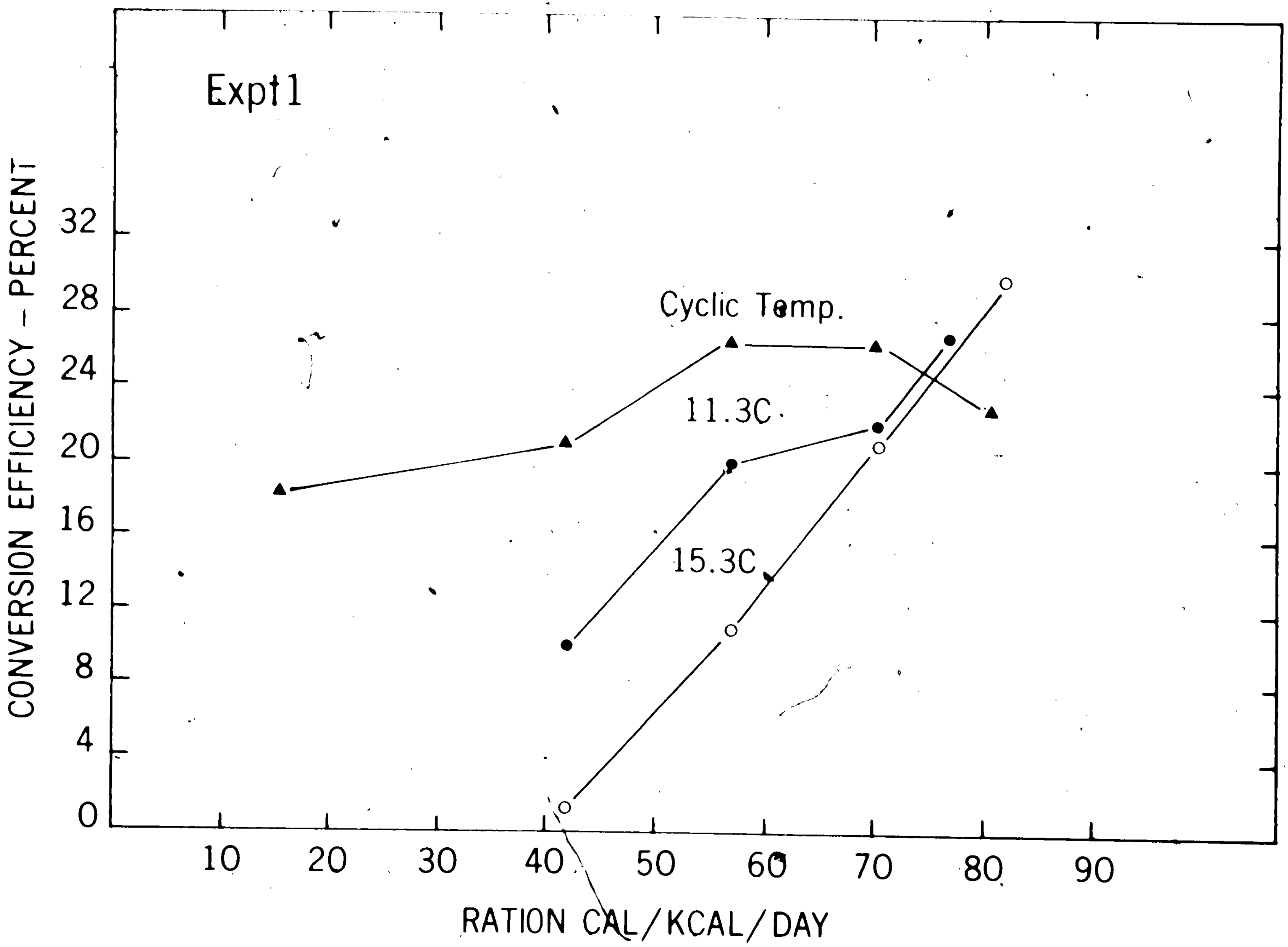
Exptl
Cyclic Temp.
11.3C
15.3C
CONVERSION EFFICIENCY – PERCENT
0
4
8
12
16
20
24
28
32
10
20
30
40
50
60
70
80
90
RATION CAL/KCAL/DAY

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Figure 1.8 Net efficiency of food conversion in relation to ration at constant temperatures of 15.3°C and 11.3°C and under the cyclic temperature regime.

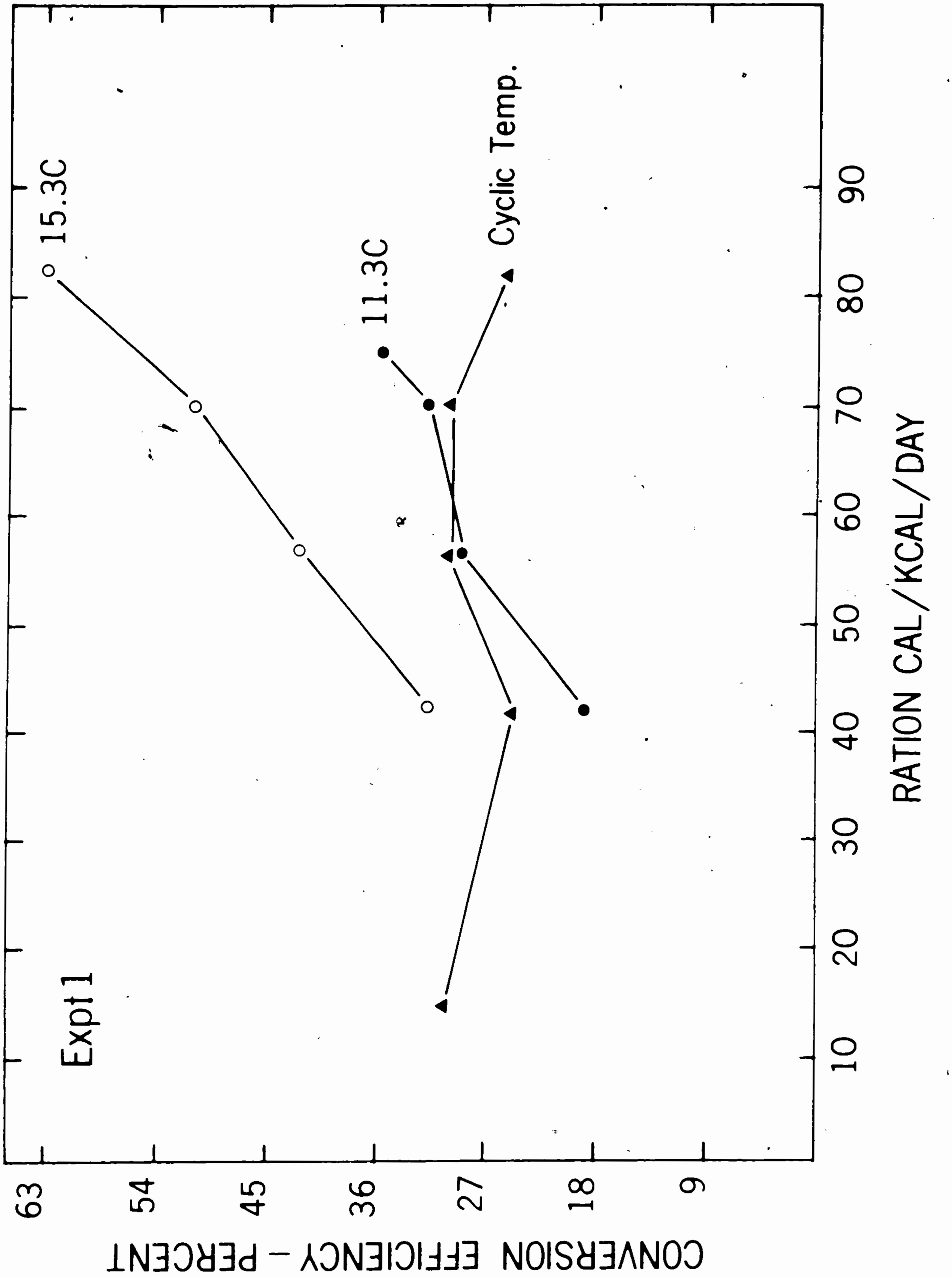
Expt 1
15.3C
11.3C
Cyclic Temp.
CONVERSION EFFICIENCY – PERCENT
63
54
45
36
27
18
9
RATION CAL/KCAL/DAY
10
20
30
40
50
60
70
80
90

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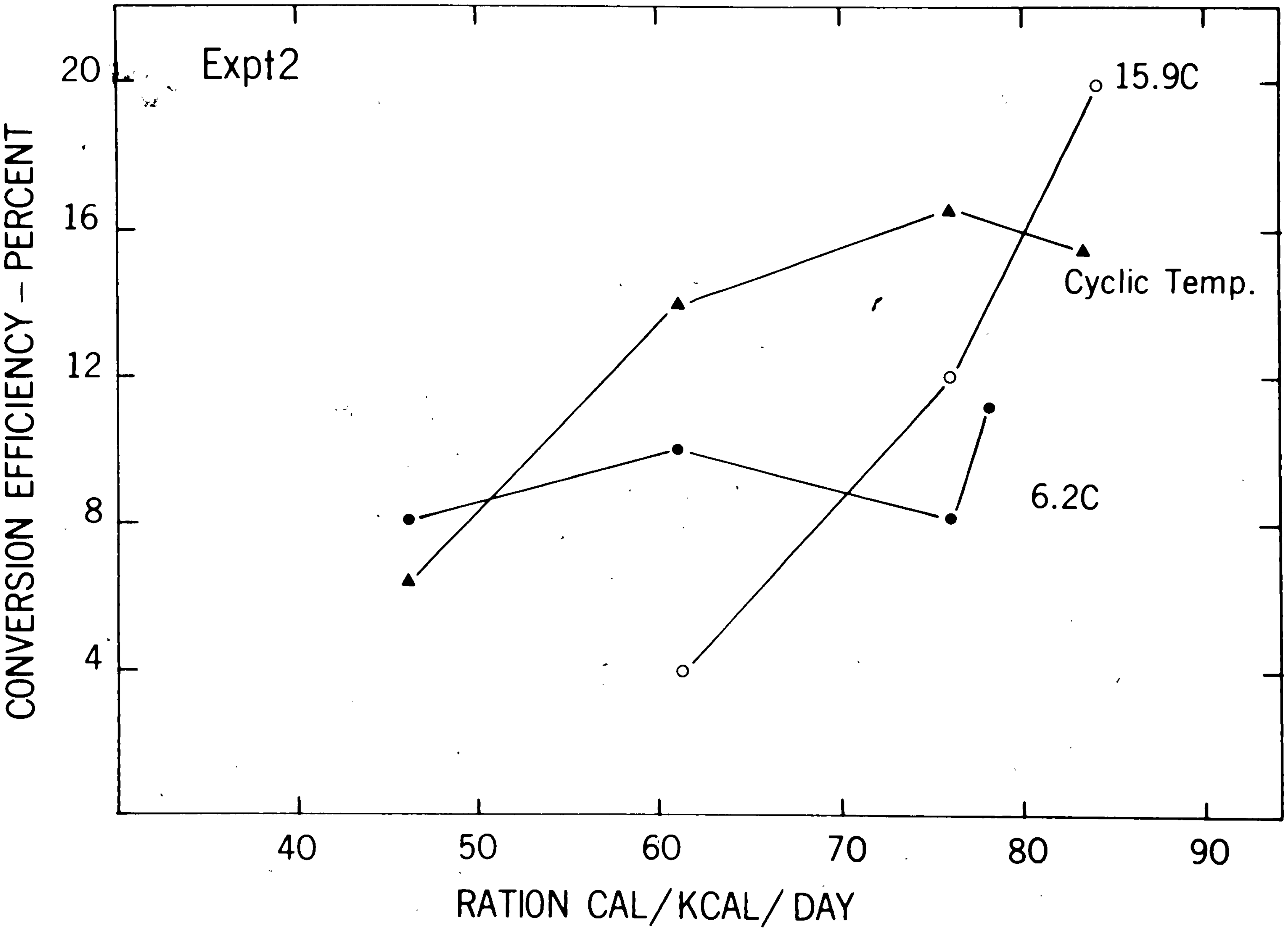
Figure 1.9 Gross efficiency of food conversion in relation to ration at constant temperatures of 15.9°C and 6.2°C and under the cyclic temperature regime.


Expt2
15.9C
Cyclic Temp.
6.2C
CONVERSION EFFICIENCY – PERCENT
20
16
12
8
4
40
50
60
70
80
90
RATION CAL/KCAL/ DAY

at 15.9°C (Fig. 1.9). Net conversion efficiencies in Expt. 2 were in the following order at all ration levels: 15.9°C > cyclic temperatures > 6.2°C (Fig. 1.10).

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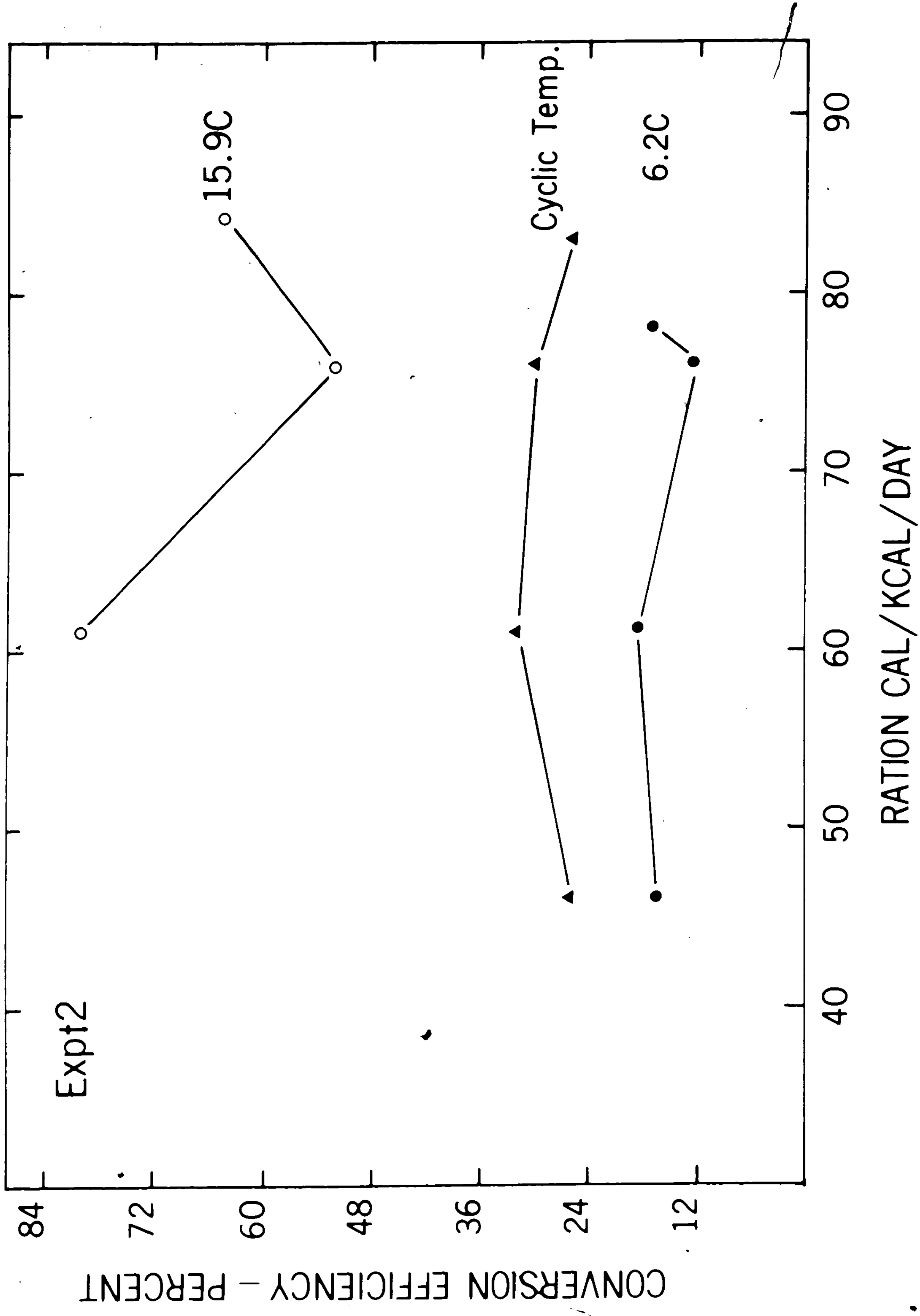
Figure 1.10 Net efficiency of food conversion in relation to ration at constant temperatures of 15.9 °C and 6.2 °C and under the cyclic temperature regime.


Expt2
15.9C
Cyclic Temp.
6.2C
84
72
60
48
36
24
12
CONVERSION EFFICIENCY – PERCENT
40
50
60
70
80
90
RATION CAL/KCAL/DAY

DISCUSSION

The hypothesis central to this study is that the diel vertical migration of underyearling sockeye salmon, Oncorhynchus nerka, which result in daily body temperature fluctuations, combined with periodic feeding in warmer water is related to the most efficient conversion of the available food into growth. This hypothesis was tested by comparing growth rates of young sockeye fed known rations and held under a diel cyclic temperature regime with those fed similar rations and held under constant temperatures.

Growth rates of young sockeye reared in experimental tanks supported the hypothesis. At all rations except excess, growth was greater under the cyclic temperature regime than at the constant high and intermediate temperatures (Fig. 1.3, 1.4, 1.5, 1.6). At rations of 61 cal/kcal of fish/day (5.5% of dry body wt/day) and at excess ration growth was greater under the cyclic temperature regime than at the constant low temperature (Fig. 1.6, Table 1.2). At ration of 46 cal/kcal fish/day (4.1% dry body wt/day) growth under cyclic temperatures was not different from the constant low temperature. At the lowest ration of 15 cal/kcal fish/day (1.4% dry body wt/day) growth was greater under the low temperature than the cyclic temperature regime (Fig. 1.6, Table 1.2). The maximum growth rate occurred at constant high temperatures and excess rations (Fig. 1.3, 1.4, 1.5, 1.6).

Growth rates at the two constant high temperatures (15.3°C and 15.9°C) and under the cyclic temperature regimes averaged 5.3 and 2.4 times greater, respectively, in Expt. 1 (July) than Expt. 2 (Fig. 1.3, 1.4). The slight temperature and ration differences do not account for these differences. The initial weight of fish used in Expt. 1 was one-fifth that in Expt. 2 (Appendix 1, 2). It seems likely that the higher maintenance costs of the larger fish in Expt. 2 accounted for the lower growth rates. Other workers (e.g. Shelbourn et al., 1973; McDonald, 1973) have reported a decrease in growth rates with increasing weight of young sockeye salmon.

Brett et al. (1969) reported the effect of constant temperatures and rations (artificial diet) on the growth of young sockeye reared under laboratory conditions. Their work is the most comparable to this study. In Table 1.4 I have compared the growth rates I measured at constant temperatures with those of Brett et al. (1969). Both studies revealed an increase in growth with increasing rations. Further, both studies showed that at high rations growth rates were greater at 15°C than 6°C, whereas at low rations growth rates were greater at 6°C than at 15°C (Table 1.4). However, my growth rates at 15°C and 11°C did not tend to level off under excess ration as did those measured by Brett et al. (1969). This difference is probably attributable to the higher excess ration (10-14% of dry body wt/day) provided by these workers. Growth rates in my experimental fish were consistently less than those by Brett et al. (1969), except under excess rations (Table 1.4). This could be attributable to

Table 1.4 - Comparison of specific growth rates from Fig. 1.3 and 1.4 in this study at constant temperatures 15, 11 and 6 °C with those from other sources. Differences in the initial size of fish (wet weight) and diet are also shown.

Fish average initial wet wt. g	Expt. 1 or 2 or Source paper	Diet	Ration % dry body wt/day	Specific growth rates at constant temp. °C % body wt/day[a]		
				15	11	6
0.2	Expt. 1 (Fig. 1.3)	freshwater zooplankton (freshly caught)	1.3	-0.70	-0.15	
			4.0	0.04	0.40	
			5.4	0.57	1.01	
			6.7	1.40	1.58	
			Excess[b]	2.50	1.99	
1	Expt. 2 (Fig. 1.4)	freshwater zooplankton (freshly caught)	1.4	-0.89		-0.17
			4.1	-0.77		0.33
			5.5	0.23		0.61
			6.9	0.88		0.58
			Excess[b]	1.62		0.80
6	Fig. 11, Brett et al. (1969)	artificial (commercial sockeye	1.5	0	0.1	0.25
			3.0	0.5	0.75	0.6
			4.5	1.0	1.1	0.8
			6.0	1.4	1.2	0.9
			Excess[c]	1.5	1.3	0.9
26	Fig. 2, Brett (1971b)	marine zooplankton (frozen)	1.4	-1.0		
			4.1	-0.4		
			5.5	-0.1		
			6.9	0.2		
			7.8	0.4		
0.4	Fig. 2 Shelbourn et al. (1973)	artificial (Clark's)	Excess[c]	6.5	5.5	2.4

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[a] Expt. 1, Expt. 2 and Brett (1971b) data are growth rates as dry weight. Other data are growth rates as wet weight.

[b] Fed to satiation twice daily.

[c] Fed to satiation three times a day.

the differences in diet quality. Brett (1971b) reported higher growth rates in young sockeye fed commercially prepared diets than those fed frozen marine zooplankton. The growth of the young sockeye fed marine zooplankton at about 15°C was the most comparable at the lower rations to that I obtained in young sockeye fed live zooplankton and maintained at 15.9°C (Table 1.4). Further, Shelbourn et al. (1973) have reported higher growth rates at the excess ration in young sockeye of similar size to my experimental fish and fed a commercially prepared diet than those of this investigation (Table 1.4).

Gross growth efficiencies, which I calculated, were also enhanced under cyclically varying temperatures and in much the same way as growth (Fig. 1.7, 1.9). Thus, gross growth efficiencies at the rations examined ranging from 14-76 cal/kcal fish/day were greater under the cyclic temperature regime than those under constant high and intermediate temperatures. At rations of 61 and 76 cal/kcal fish/day gross growth efficiencies were greater under the cyclic temperatures than the constant low temperature. However, at a ration of 46 cal/kcal fish/day, gross conversion efficiency under cyclic temperatures was not significantly different ($P > 0.05$) from that at the constant low temperature.

My data on gross growth efficiencies are not in agreement with those of Brett et al. (1969) who reported a relatively constant gross growth efficiency (~20%) over a temperature range of 5-17°C. I obtained higher gross conversion efficiencies at constant high temperatures and excess ration and lower conversion efficiencies at constant low temperatures and low rations. Differences in diet quality, size of fish, and maintenance ration may account for these differences between my study and that of Brett et al. (1969). Higher maintenance rations and the zooplankton diet could account for the lower conversion efficiencies I observed at constant low temperature. However, neither diet quality nor higher maintenance ration could explain the higher conversion efficiency I observed relative to that of Brett et al. (1969) under conditions of constant high temperatures and excess ration. The smaller size of fish I used might explain the differences. Kelso (1972) reported that assimilation efficiency decreased with increasing size of walleye (Stizostedion vitreum vitreum).

My results do not agree with those of Paloheimo and Dickie (1966a), Le Brasseur (1969), and Kerr (1971) who have found that increasing rations are associated with decreased gross growth efficiency. Only under cyclic temperatures was there a tendency for gross growth efficiencies to decrease at the higher rations (Fig. 1.7, 1.9). It is possible that in young sockeye the position of the maximum growth efficiency may only occur at rations higher than rations of 76-84 cal/kcal/day provided in my experiments.

Although net growth efficiency, a ratio of growth to food available for growth ($G/I-R_m$), has no meaning to the organism, it was calculated in an attempt to explain the ration and temperature dependent differences in gross growth efficiency. The net efficiency was greatest at constant high temperatures

(15.3°C, 15.9°C) and greater under cyclic temperatures than the constant low temperature (6.2°C) irrespective of ration. Net efficiency was equal at cyclic temperatures and constant temperature 11.3°C, except at the excess ration where net efficiency was greater at 11.3°C (Fig. 1.8, 1.10). In general, regardless of ration size, net growth efficiency increased with increasing temperature. The net efficiency demonstrated that all rations except excess, the lower maintenance ration under cyclic temperatures relative to the constant high and intermediate temperatures accounted for at least part of the enhanced gross efficiency. However, gross efficiency was enhanced under cyclic temperatures over the constant low temperature despite increased maintenance costs under cyclic temperatures. Similarly, the maximum gross efficiency could not be predicted from the size of the maintenance ration because it occurred at the highest maintenance ration. Hence, other differences in expenditure of energy accounted for this efficient growth.

Support for the hypothesis that growth efficiency would be enhanced under cyclic temperatures relative to constant temperatures depended partly on a saving in maintenance costs over constant high and intermediate temperatures and on a more efficient use of the energy ingested than at the constant low temperature. For the enhancement of gross growth conversion efficiency under cyclic temperatures over constant high and intermediate temperatures rations ranging from 14-76 cal/kcal fish/day were required. Further, for the enhancement of gross growth conversion efficiency under cyclic temperatures over constant low temperatures rations greater than 61 cal/kcal fish/day were required. This suggests that under cyclic temperatures and rations greater than 76 cal/kcal fish/day and less than 61 cal/kcal fish/day more energy is expended on respiration, lost as fecal production, or excreted in relation to the constant temperatures than at moderate rations. Hence, the assumption that the maintenance ration is constant over the range of rations tested is probably only partly valid. Other workers (e.g. Brown, 1957; Paloheimo and Dickie, 1966b) have indicated that the maintenance ration was affected by the available ration. My data do not permit an explanation of the differences under cyclic temperatures and moderate rations from those at rations greater than 76 cal/kcal fish/day or less than 61 cal/kcal fish/day.

My results that at all rations except excess, growth for underyearling sockeye salmon was greater under cyclic temperatures than at constant high temperatures is in general agreement with Enright (1977) and Enright and Honegger (1977). Calculations by Enright demonstrated that under certain conditions migrants, such as _Calanus helgolandicus_ (_pacificus_), feeding at night in the warmer surface waters accumulated a greater net energy gain than non-migrants feeding continuously in the surface waters. Conditions pertinent to my study are: that migrants can reduce their metabolic costs during non-feeding hours; that food is limited (i.e., the model is inapplicable at excess food); that feeding is nocturnal; that the optimum timing for the onset of feeding is 1-2 h prior to dusk; and that periodic feeding evokes an increase in the initial rate of feeding. The first condition is implicit in my test. The second condition supports my conclusion; McLaren's proposal did not hold for young sockeye fed high rations. The assumption of nocturnal feeding is related to field obse[illegible]ns on the daily timing of vertical migrations for marine herbivores and is different from the feeding times in my experiments (dusk and dawn, Fig. 1.2). However, this difference may be relatively unimportant. Underlying the condition of time of feeding is the additional condition that feeding is periodic. The condition that feeding occurs in the warmer surface waters and that non-feeding occurs in the cooler waters may override the importance of differences in daily timing of feeding. Although the last two conditions do not match my experimental ones they have a direct bearing on my study for two reasons. First, migrants present in the surface waters prior to dusk, begin feeding before photosynthesis ends and are therefore exposed to more food per hour than at dusk or night; assuming that ingestion by grazers is proportional to phytoplankton biomass. Further, a high initial feeding rate permits migrants, present in the surface waters at this time, to consume the higher food concentrations. This feeding strategy for grazers implies that the optimum growth advantage for migrants over non-migrants (surface waters) occurs at higher food levels than at lower levels. This is contrary to my data which indicated that the greater difference in growth between cyclic temperatures and constant high or intermediate temperatures occurred at lower rations than at higher rations (Fig. 1.5, 1.6). However, food levels provided in my study may have been higher than those inferred in Enright's calculations. Second, Enright and Honegger (1977) used the observation that migrants which feed before dusk when the surface waters are still illuminated to reject the predator-avoidance explanation for vertical migration and consequently they concluded that, at least for certain life history stages of C. helgolandicus, the 'energy bonus' explanation for vertical migration was the most favourable one. This conclusion is in accord with Brett's (1971a) view for under-yearling sockeye salmon in Babine Lake.

My results are also in partial agreement with Swift (1976) who examined the effect of a cyclically varying temperature (5-20°C) on growth for fourth-instar of Chaoborus trivittatus larvae. In accord with my results, he reported that at high rations growth was less under cyclic temperatures than at a constant high temperature (20°C) and growth was greater under cyclic temperatures than at a constant low temperature (5°C). Contrary to my results, Swift noted that at low rations growth was also less under cyclic temperatures than the constant high temperature. Also contrary, he showed that for the lowest ration growth was greater under cyclic temperatures than at the constant low temperature. These differences in growth may be explained by differences in food concentrations. Swift observed that under cyclic temperatures and the constant low temperature larval growth was not different at high and low rations, suggesting that at the low ration larvae held at either of these two temperatures were feeding at their maximum rate. Although Swift concluded that McLaren's hypothesis does not hold for C. trivittatus larvae in

Eunice Lake, British Columbia, lower food concentrations could lead to different conclusions.

My results, however, are not in agreement with those of Lock and McLaren (1970) and Kelso (1972). Lock and McLaren (1970) reported no difference in mean lengths of stage III Pseudocalanus minutus copepodites reared under a cyclic temperature regime (12 h 8°C, 12 h 12°C) with those at a constant intermediate temperature of 10°C. Difference in results may be explained by higher food concentrations provided in their study. Since copepods were constantly exposed to food, they may have been feeding at high food concentrations where there is likely no advantage to exposure to fluctuating temperatures. In addition, McLaren's proposal is based on the condition that feeding only occurs when near the surface in the warmer waters. Lower food concentrations, coupled with periodic feeding, could lead to different conclusions. Kelso (1972) reported that gross growth efficiency in 2-4 yr walleye (Stizostedion vitreum vitreum) was less under a cyclic temperature (14 h 16°C, 10 h 8°C) than at constant temperatures of 12, 16 or 20°C. However, Kelso's investigation may not be comparable to this one as energy is probably not apportioned in the same way by older migrants as by younger ones. It is conceivable that in the larger walleye migrations through thermally stratified waters might be related to fecundity and not growth.

My study was designed to permit comparison of growth and growth efficiency for young sockeye reared in tanks under cyclic temperatures and fed natural food with those in nature. The temperatures associated with feeding and catabolism, length of time between the two daily feeding periods, and diet quality were comparable to those in nature.

The growth and ration estimates of McDonald (1973) for wild Babine Lake sockeye provided the basis of comparison of my results with those in nature. McDonald calculated growth between July 5 and August 24 as 2.9% of dry body weight. This calculation was based on initial and final wet weights of 0.390 g and 1.678 g, respectively, and a moisture content of 80%. He also reported that the daily intake ration was 14 mg or 4.2% of dry body weight. For purposes of comparison, I converted McDonald's values to cal/kcal/day by assuming that the average caloric values I obtained for fish (6.08 kcal/g) and for zooplankton (6.56 kcal/g) apply to his data. On this basis, the daily growth and ration for fish in nature were 29 and 45 cal/kcal, respectively, and the gross growth efficiency was 64%. At a ration of 45 cal/kcal/day, the experimental growth rates, interpolated from Fig. 1.5, 1.6 (cyclic temperature regime), were 10 cal/kcal/day (Expt. 1) and 3 cal/kcal/day (Expt. 2). The corresponding experimental gross growth efficiencies were 22% (Expt. 1; Fig. 1.7) and 7% (Expt. 2; Fig. 1.9). This 3 to 9-fold discrepancy could be attributed to the following factors: the ration in nature is an underestimate; the growth rate for wild fish is an overestimate; or the experiments do not simulate natural conditions.

Although there is little information available on rates of food intake in nature, it seems unlikely that the ration in nature has been underestimated. Experimental fish provided with unlimited food for 2-h periods twice a day consumed maximum daily rations of 7.1-7.8% of dry body wt (Fig. 1.3, 1.4) or 76-84 cal/kcal (Fig. 1.5, 1.6). In addition, the maximum daily ration measured by Brett et al. (1969) for young sockeye provided unlimited food three times a day at 4-h intervals was 10-14% of dry body wt. Since it is unlikely that the high rations provided in these experiments are available in nature, a daily ration of 45 cal/kcal or 4.2% of dry body wt seems reasonable.

The growth rate for wild sockeye is, however, possibly an overestimate. Parker (1971) pointed out that growth for wild O. gorbuscha and O. keta could be overestimated by 0.30-0.5% of body length/day because of predator selectivity for smaller individuals. McDonald (1973) calculated growth in length for O. nerka in Babine Lake during July 5 and August 24 as approximately 0.9% of dry length/day. Thus, it is possible that as much as 55% of the growth calculated for wild fish may be due to the effect described by Parker and may account, in part, for the difference in growth rates between experimental and wild fish.

Studies of Paloheimo and Dickie (1966b), Kerr (1971), have shown that tank studies of fish growth are not comparable to those in nature because of the many artificial constraints imposed on fish. Factors such as the cost of searching for prey and cost of vertical migration could influence growth and are not accounted for in experimental tanks. However, the cost of searching for prey may be insignificant in Babine Lake because sockeye feed in the surface waters where the zooplankters are concentrated. The cost of vertical migration, as discussed in Chapter 2, may also be negligible. One possible source of error, however, is the effect of sustained swimming of sockeye in the tanks. Although a uniformity of activity between tanks was maintained by subjecting sockeye to a constant water current, sustained swimming would also have the overall effect of increasing metabolic costs and consequently could account for lower growth rates relative to field conditions.

The estimated daily ration of wild Babine Lake fish (45 cal/kcal/day) falls within the ration range where the differences between cyclic and constant high and intermediate temperatures were significant, but insignificant between cyclic and the constant low temperature. This lack of difference between cyclic temperatures and the constant low temperature at the ration 45 cal/kcal/day might not have any ecological significance. In nature, any fish living constantly in the hypolimnion would be unlikely to obtain the same ration as provided in the tank studies. Or, there might be a greater energetic cost involved in the collection of the sparsely distributed zooplankton. Therefore, in nature food conversion might be more efficient under cyclic temperatures relative to constant low temperatures. Thus, at rations comparable to those that are probably available in the warmer surface waters at Babine Lake the hypothesis that the diel vertical movements of young sockeye results in the most efficient conversion of the available food into growth is supported. This suggests a selective advantage for vertical migrations in thermally stratified waters.

Chapter 2

The Fate of Carbon-14 Labelled Food By Underyearling Sockeye Salmon, *Oncorhynchus nerka*, In Relation To Temperature and Ration

INTRODUCTION

Chapter 1 described growth and gross conversion efficiencies of underyearling sockeye salmon, Oncorhynchus nerka. At moderate rations (61 and 76 cal/kcal sockeye/day) of natural zooplankton, but not at low (15 and 45 cal/kcal sockeye/day) or excess rations, growth and gross conversion efficiencies was greater under cyclically varying temperatures than at constant temperatures. The work described in this chapter was undertaken to examine the short-term fate of food consumed in an attempt to explain these ration and temperature-dependent differences in growth.

Warren and Davis (1967) and Warren (1971) pointed out that growth can be examined by studying the energy flow of the organism. Growth can then be viewed as the difference between the energy of the food an organism consumes and all other energy uses and losses; i.e., P = C-R-F-U (Ricker, 1958) where P is growth, C is consumption, R is respiration, F is feces, and U is excreted material. Warren and Davis (1967), Warren (1971) and Brett (1976) defined this concept as 'scope for growth" and discussed how environmental factors affect growth through their influence on the rate of food consumption and expenditure of energy. Using the scope for growth concept these authors, among others, examined the relationship between temperature, ration and growth. They demonstrated that a greater percentage of the ingested ration is converted to tissue in fish exposed to intermediate temperatures than extremes. Growth is apparently suppressed at high temperatures because of a disproportionate increase in maintenance costs. Food intake, which decreases with decreasing temperatures, appears to limit growth at low temperatures. Brett et al. (1969), among others, have also shown that as rations increase above maintenance the specific growth rate increases at a decreasing rate to a maximum level. The reasons behind growth rate decreases at high rations are uncertain. Kerr (1971) contends that there is a disproportionate increase in spontaneous activity, as rations increase. Warren (1971) suggests a disproportionate increase in waste products, specific dynamic action and activity. All of these studies have considered the fate of food consumed by fish in terms of either growth, food conversion or respiratory metabolism. This study examines the short-term fate of ingested food under different temperature regimes using an isotopic tracer as suggested by Sorokin (1966).

Radioactive tags have been used by several workers (Sorokin, 1966; Schindler, 1968; Hargrave, 1970; Bell and Ward, 1970 and Swift, 1976) to study the fate of ingested food by aquatic invertebrates, but they have seldom been applied to fish, except for the work of Sorokin and Panov (1966) with bream larvae (Abramis brama) and of Gunn et al. (1977) with brown bullhead (Ictalurus nebulosus).

I designed experiments to compare the fate of ingested food in fish fed low or moderate rations and held under constant temperatures or cyclically varying temperatures corresponding to those encountered by young sockeye during their diel vertical migration in Babine Lake, B.C. (Chapter 1). Following ingestion of a ^{14}C labelled ration of Daphnia pulex, radiactivity present in the gastrointestinal tract, in the fish tissue, respired, egested or excreted over 72 or 84 h was determined.

MATERIALS AND METHODS

From July 1970 to January 1972, three sets of experiments, referred to as experiments 1, 2 and 3, were conducted.

Expt. 1 (Low Ration; duration 24 h) - Sockeye fry (0.7 - 2.9 g) obtained near smokehouse Island of Nilkitkwa Lake (Chapter 1), were placed in each of three 45-litre fiberglass tanks housed in the shed described in Chapter 1 and supplied with filtered Babine Lake water. Each tank was fitted with a dark lid covering the entire tank to decrease light intensities. One tank of fish was maintained under a diel cyclic temperature regime ranging from 4.3 to 17.2°C that approximated the temperatures experienced by young sockeye in Babine Lake during the course of their diel vertical migration while water in the other two tanks was held at constant temperatures of 5.5 ± 1.4°C and 15.8 ± 1.8°C (± 2 SD). Temperature control was obtained as described in Chapter 1.

Daphnia pulex, a species similar to one of the natural food items (*D. longispina*) of young sockeye in Babine Lake, was supplied as the food organism. They were taken in plankton nets, strained through sieves to obtain animals of 1.0-1.5 mm in size, quick frozen and offered to the young sockeye after thawing. Labelled food was prepared by placing freshly caught *D. pulex* in ^{14}C labelled axenic log phase cultures of *Chlamydomonas reinhardtii* at concentrations of 3.4×10^5 cells/mL and allowing to feed for 4 h. They were then removed from the algal culture, rinsed and quick frozen.

A mean ration of 3.4% of dry body wt (33.1 ± 2.8 cal/kcal of fish; ± 2 SE) was provided once daily at 1100 h (Fig. 2.1).

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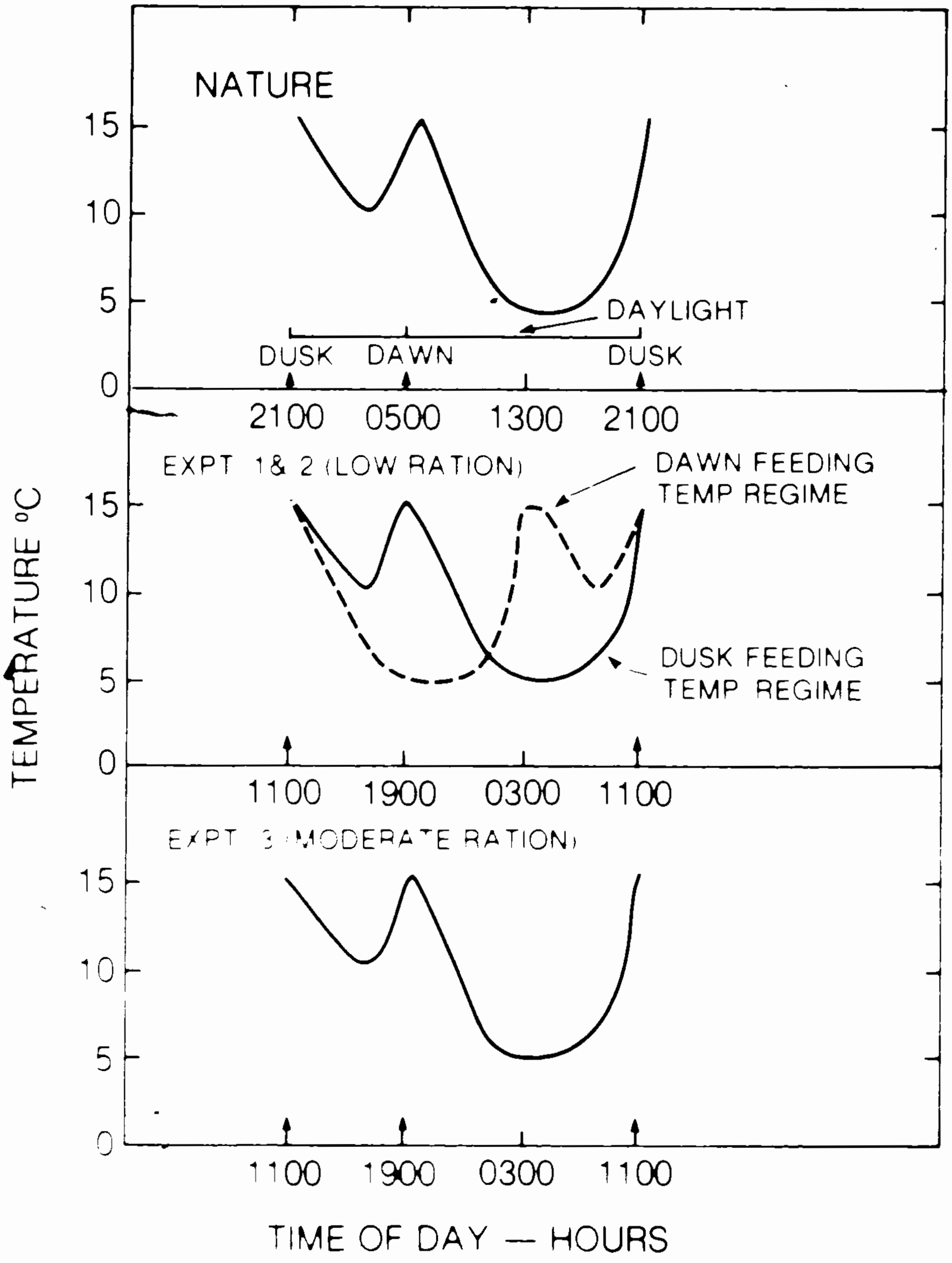
Figure 2.1 The patterns of the diel cyclic temperature regimes to which fish were exposed in the three experiments and that encountered by Babine Lake fish during their vertical migration (nature) in relation to time of day. In nature fish feed at dusk and dawn. In Expt. 1 and 2 fish were fed a low ration of 33.1 cal/kcal sockeye/day (3.4% dry body wt) at 1100 h. In Expt. 3 fish were fed a moderate ration of 65.6 cal/kcal sockeye/day (6.4% dry body wt), one-half at 1100 h and the remainder at 1900 h. In Expt. 1 and 2 two cyclic temperature regimes were employed; one corresponding to a dwan feeding in nature and the other to a dusk feeding. Arrows on the abscissa indicate feeding times.


NATURE
15
10
5
0
DAYLIGHT
DUSK
DAWN
DUSK
2100
0500
1300
2100
EXPT 1& 2 (LOW RATION)
DAWN FEEDING TEMP REGIME
DUSK FEEDING TEMP REGIME
1100
1900
0300
1100
EXPT 3 (MODERATE RATION)
TEMPERATURE °C
TIME OF DAY — HOURS

Ration size was determined by volume measurement as described in Chapter 1. In the cyclic temperature experiments food was presented when fish were exposed to one daily temperature maxima which corresponded to the position on the temperature regime of the dawn or dusk feeding in nature (Fig. 2.1). Following feeding, the tank covers were replaced and fish were held both at lower temperatures, corresponding to day or night depths in nature, and at the second daily maxima temperature as experienced in nature at the surface (Fig. 2.1). In the constant temperature experiments fish were fed and held at the same temperature.

Fish were held for 5 days under the experimental temperature and food regime after which the experiment was started. Groups of 3 fish from each tank (except at 15°C where 2 fish were used) were weighed (mean wet wt of 2.6 ± 0.69; ± 2 SE), washed in an antibiotic solution (50 mg/L of Penicillin G,100 mg/L of Streptomycin sulfate), placed in 3.8 litre wide-mouth polypropylene containers filled with Millipore (HA 0.45 μ) filtered water at the test temperature and provided with the ration of known radioactivity of *D. pulex*. Fish consumed all the food offered within 15-20 min and were then transferred to a 'clean' set of containers. Antibiotics were added to these containers to reduce microbial activity. The lid of each container was lined with a glass-fibre filter soaked with 2-6 mL of hyamine hydroxide, a CO_2 absorbent, and sealed. The holding vessels were then suspended at the appropriate depth in Babine Lake to maintain the temperature regimes in the tanks. Cyclic temperature regimes encountered in the tanks (Fig. 2.1) were achieved by gradually changing the depth at which the vessels were suspended. Holding vessels were covered with black tape to ensure that the fish were maintained under constant light conditions. At 12 h after ^{14}C feeding, fish were transferred quickly to a 'clean' set of vessels containing water at the test temperature to maintain oxygen levels in the holding vessels above 5 mg/L. The containers were then returned to the lake at the appropriate depth.

Fish were removed from the holding vessels, rinsed and killed at 0.1, 2, 4, 6, 8, 12, 15, 18, 22 and 24 h intervals after ingestion of the labelled ration. All water and glass fiber filters were removed from the container when the fish were removed. The stomach and intestine of each fish were opened separately and their contents washed out and collected. It was not possible to remove the contents from the pyloric caeca. Thus, the pyloric caeca were included with the contents of the intestine since absorption occurs at both sites. At each interval radioactivity present in the contents of the stomach, of the intestine and pyloric caeca, the fish tissue as well as that lost as particulate and soluble materials were determined. At each interval all fish at any one temperature were pooled before ^{14}C activity was measured. Seven replicates were conducted at each interval for any one temperature. Thus, a total of 280 tests (10 intervals x 7 replicates x 4 temperature regimes) were conducted involving 770 fish; 2 fish/replicate at 15 C and 3 fish/replicate at the other temperatures.

Expt. 2 (Low Ration; duration 72 h) - This experiment was conducted at Simon Fraser University using sockeye fry (mean wet wt of 1.2 ± 0.7 g; ± 2 SE) obtained from the Weaver Creek spawning channel operated by the International Pacific Salmon Fisheries Commission. This experiment was similar to Expt. 1 except for the following modifications. Temperature and photoperiod control were achieved with an environmental chamber. Constant temperatures of 14.9 ± 0.2°C and 4.8 ± 0.5°C (± 2 SD) and a diel cyclic temperature regime ranging from 4.7 to 15.8°C (Fig. 2.1) were employed. Fluorescent lighting illuminated the holding vessels with a light intensity of 150-200 ergs/cm^2/sec and 25-50 ergs/cm^2/sec during feeding and non-feeding periods, respectively. This approximated the light intensities experienced by young sockeye in Babine Lake. The test period was extended to 72 h following ^{14}C feeding. The 72 h duration was selected after a preliminary experiment demonstrated that approximately 48 h were required to clear the gastrointestinal tract of food at 5°C. The clearance time was less at the higher test temperatures, but for comparison the length of the experiment was the same for all temperatures. After 48 h all ingested food was either absorbed, egested or regurgitated. Thus, at 24 and 48 h following ^{14}C feeding, fish were transferred to fresh water and fed unlabelled food at the prescribed ration and time (Fig. 2.1). Following feeding fish were returned to 'clean' holding vessels and held for the remainder of the day under the test temperature. At each of the intervals used in Expt. 1 and at 36, 48, 60 and 72 h after ^{14}C feeding, all fish were treated identically to those in Expt. 1.

Expt. 3 (Moderate Ration; duration 84 h) - Experiment 2 conditions were modified to approximate the feeding pattern of young sockeye in Babine Lake. Food was provided twice a day (Fig. 2.1) and a ration of 6.4% of dry body wt (65.6 ± 4.2 cal/kcal sockeye/day) was employed because it was not possible to divide the lower ration between two feedings and have sufficient radioactivity for measurement following a feeding. One-half of the daily ration was provided at 1100 h and the remainder at 1900 h. In the cyclic temperature experiment fish were fed at the twice daily temperature maxima (Fig. 2.1). The duration of the experiment was extended to 84 h following ^{14}C ingestion as the larger ration increased by 12 h the time to clear the gastro-intestinal tract of food at 5°C. Fish (mean wet wt of 3.2 ± 0.2 g; 2 SE) were treated identically to those in Expt. 2 and sampled at 0.1, 4, 8, 12, 15, 18, 24, 36, 48, 60, 72 and 84 h.

Fish tissue ^{14}C activity was determined as follows. The fish, including the emptied stomach and intestine, were homogenized and the homogenate transferred to glass beakers containing Soluene$^{\text{TM}}$-100, a solublizing agent (2 mL/100 mg wet tissue). Beakers were covered with tin foil, heated for 24 h at 50°C, cooled and a freshly prepared benzyl peroxide solution was added (200 ml/L of Soluene) to decolorize the digest. The decolorizing agent was prepared by heating 1 g reagent grade benzyl peroxide in 5 ml toluene to 60°C, followed by cooling to room temperature and filtering. The digest (0.5 mL) was added to liquid scintillation vials containing 12 mL of a fluor composed of 6 g PPO and 75 mg POPOP per litre of scintillation grade toluene and assayed for radioactivity with a liquid scintillation counter.

The ^{14}C activity of D. pulex, as well as ^{14}C activity of the contents of the stomach and of the intestine including pyloric caeca was determined by digesting in Soluene and treating as above.

Total particulate labelled material (feces and regurgitated D. pulex remains) was collected in two ways. Visible feces and regurgitated food were removed with forceps, rinsed in distilled water, dissolved in Soluene and treated in the same manner as the fish tissue. Second, particulate material was collected on Millipore filters (HA 0.45 μ). The filters were then placed into vials containing a fluor (modified Bray's) composed of 4 g PPO, 60 g POPOP, 60 g napthalene monomethyl ether made up to 1 litre with dioxane and the radioactive material retained on the filters determined. Total particulate labelled material was the sum of radioactivity retained on the filters and digested in Soluene.

The soluble labelled fraction was determined from the radioactivity retained on the glass-fibre filters from vessel caps and in 1 mL aliquots of filtered water samples. Both the glass-fibre filters and the 1 mL aliquots were placed directly into vials of modified Bray's scintillation fluor. The soluble inorganic fraction ($^{14}CO_2$) was removed from the ^{14}C soluble organic fraction by acidifying the filtered water to pH 3 and aerating vigorously for 3 h by which time less than 1% of the $^{14}CO_2$ remains (Thomas, 1971). After bubbling, 2 mL aliquots were assayed for radioactivity, corrected for total volume of the container water and used to provide an estimate of excretion of soluble organic material. The inorganic soluble ^{14}C fraction was taken as the difference in radioactivity of the samples before and after acidification and bubbling and the total, based on the volume of the container water was added to the radioactivity retained on the glass-fibre filters to provide an estimate of total ^{14}C respired.

The activity in all vials was corrected for quenching, counting efficiency, background, and volume. Separate quench standards were prepared for the various homogenates, filter and filter samples. The channels ratio method of quench correction was employed (Peng, 1966). A minimum of 10 replicates was counted for the various fractions at each interval of time for any one temperature.

For any one temperature data were compiled as the percentage of ^{14}C present in the various fractions to ^{14}C ingested. Percentage data, binominally distributed, were transformed to a normal distribution by the square-root transformation. Then, at each temperature the means for the various fractions and intervals of time were compared by analysis of variance and Duncan's multiple range test (Steel and Torrie, 1960). Following a logarithmic transformation, regression coefficients from computed equations at each temperature were tested for homogeneity by analysis of covariance.

RESULTS

The total ^{14}C activity in the fish as a result of ingesting labelled D. pulex in experiments 1 and 2 was 3.10 ± 0.04 (±2 SD) x 10^5 cpm/g wet wt sockeye and for experiment 3 was 3.87 ± 0.02 (± 2 SD) x 10^5 cpm/g wet wt sockeye. Since fish consumed all radioactive food offered, theoretically the radioactivity provided in the labelled food should equal the sum of activity recovered in the fish tissue, gastrointestinal tract, particulate and soluble material fractions. In these experiments an average of 90.9% of the ^{14}C activity provided was accounted for (Appendix 3). Neither temperature, ration nor duration of the experiment had an apparent effect on percentage recovery.

Since at any one temperature the means of ^{14}C activity at each time interval after ^{14}C feeding in the various fractions for Expt. 1 (Babine Lake fish) were not significantly different ($P > 0.05$) from the same intervals in Expt. 2 (Weaver Creek fish), the values from both sets of experiments in each fraction were pooled. Subsequently, Expt. 1 and 2 will be referred to as the low ration experiment and Expt. 3 will be referred to as the moderate ration experiment. Further, under the cyclic temperature regime in the low ration experiment there was not a significant difference ($P > 0.05$) between means at each interval in the various fractions for fish fed at what corresponded to dusk or dawn. Hence, data from both feeding periods were combined and a single value shown for the cyclic temperature regime.

^{14}C in Stomach Contents

At any one temperature, percentage of the ingested ^{14}C activity remaining in the stomach contents decreased exponentially with time after ^{14}C feeding (Fig. 2.2). This relationship was expressed with the equation $\ln Y_t = \ln Y_o - kt$ where Y_t is % ^{14}C remaining in the stomach, Y_o is initial ^{14}C ingested (100%), t is time after feeding (h), ln is natural logarithm and k (slope) is the instantaneous rate of gastric evacuation (movement of food from the stomach) estimated by least squares regression. Since the equation does not allow a Y_t value of 0, 1% of ^{14}C activity remaining in the stomach was considered the end point. The equations for the calculated regressions at the low and moderate ration experiments for each temperature are shown in Table 2.1. Gastric evacuation rates at both low and moderate rations were dependent on temperature and for both rations were in the following order: 15°C > cyclic temperature regime > 5°C (Fig. 2.2; Table 2.2). There was no significant difference ($P > 0.05$) in gastric evacuation rates at any one temperature between those fish fed low and moderate rations. However, the time to empty the stomach of radioactive food increased with the larger ration (Fig. 2.2).

^{14}C in Contents of Intestine and Pyloric Caeca (including Pyloric Caeca).

Mean percentages of ^{14}C recovered from the contents of

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Figure 2.2 Comparison of the rate of decrease of ^{14}C labelled food in the stomach contents of underyearling sockeye salmon in relation to time after ^{14}C feeding at 15°C ((O), 5°C (●) and the cyclic temperature regime (Δ). In A, fish were fed a low ration of 33.1 cal/kcal sockeye/day. In B, fish were fed a moderate ration of 65.6 cal/kcal sockeye/day. Arrows indicate the time ^{14}C labelled food presented.

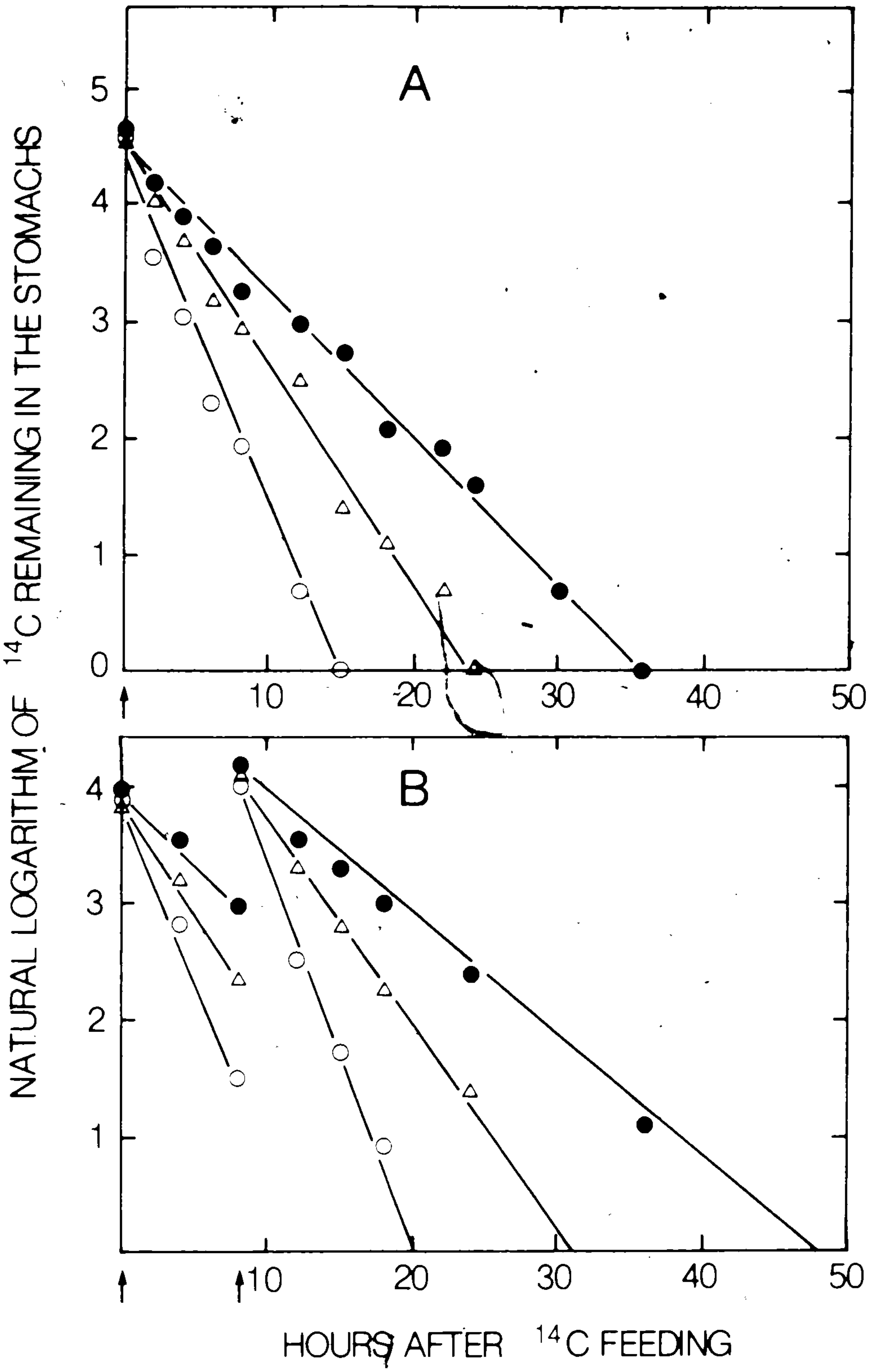
A
B
NATURAL LOGARITHM OF ¹⁴C REMAINING IN THE STOMACHS
HOURS AFTER ¹⁴C FEEDING
0
1
2
3
4
5
10
20
30
40
50

Table 2.1 - Summary of time dependent change of ^{14}C percentage data measured in each fraction. Equations for the calculated regression lines or the average percentage of ingested ^{14}C present over the duration of experiment for the various fractions at the three temperatures and two ration levels are shown. Asymptotic or maximal observed values for some fractions are also shown.

^{14}C Fraction	Time dependent change of ^{14}C	Temp $^{\circ}C$	Equations: Low Ration (Expt. 1 & 2)	Equations: Moderate Ration (Expt. 3)	Asymptotic value[1] (% of ^{14}C ingested): Low	Asymptotic value[1] (% of ^{14}C ingested): Mod. Ration
Stomach Contents (Fig. 2.2)	Exponential decrease of ^{14}C	15 Cyclic 5	$\ln Y = \ln 4.278 - 0.295t$ $\ln Y = \ln 4.426 - 0.182t$ $\ln Y = \ln 4.422 - 0.122t$	$\ln Y = \ln 3.937 - 0.300t$[2] $\ln Y = \ln 3.925 - 0.194t$ $\ln Y = \ln 3.923 - 0.113t$		
Incorporated (Fig. 2.4, 2.5)	Exponential increase of ^{14}C towards an asymptote	15 Cyclic 5	$\ln(Yasymp-Y) = \ln 4.404 - 0.317t$ $\ln(Yasymp-Y) = \ln 4.121 - 0.177t$ $\ln(Yasymp-Y) = \ln 4.387 - 0.122t$	$\ln(Yasymp-Y) = \ln 4.734 - 0.281t$ $\ln(Yasymp-Y) = \ln 4.771 - 0.157t$ $\ln(Yasymp-Y) = \ln 4.072 - 0.082t$	67 63 67	64 67 51
Respired (Fig. 2.7, 2.8)	Exponential increase of ^{14}C towards an asymptote	15 Cyclic 5	$\ln(Yasymp-Y) = \ln 3.408 - 0.052t$ $\ln(Yasymp-Y) = \ln 2.734 - 0.038t$ $\ln(Yasymp-Y) = \ln 2.562 - 0.036t$	$\ln(Yasymp-Y) = \ln 2.500 - 0.042t$ $\ln(Yasymp-Y) = \ln 2.917 - 0.028t$ $\ln(Yasymp-Y) = \ln 2.431 - 0.026t$	28 20 17	23 19 12
Soluble Organics (Fig. 2.9, 2.10)	Exponential increase of ^{14}C towards an asymptote	15 Cyclic 5	$\ln(Yasymp-Y) = \ln 2.397 - 0.036t$ $\ln(Yasymp-Y) = \ln 2.609 - 0.038t$ $\ln(Yasymp-Y) = \ln 2.862 - 0.027t$	$\ln(Yasymp-Y) = \ln 2.638 - 0.032t$ $\ln(Yasymp-Y) = \ln 3.040 - 0.036t$ $\ln(Yasymp-Y) = \ln 3.485 - 0.040t$	17 17 20	19 21 28
Particulates (Fig. 2.11)	Linear increase of ^{14}C to a maximum	15 Cyclic 5	$Y = -8.728 + 1.327t$ $Y = -3.061 + 0.573t$ $Y = -3.661 + 0.455t$	$Y = -3.097 + 0.656t$ $Y = -3.855 + 0.528t$ $Y = -7.701 + 0.685t$	24 21 20	26 21 33

			Average Percentage of Ingested ^{14}C present in the fraction[3]: Low Ration (Expt. 1 & 2)	Average Percentage of Ingested ^{14}C present in the fraction[3]: Moderate Ration (Expt. 3)
Intestine and Pyloric Caeca Contents[4] (Fig. 2.3)	Increase of ^{14}C to a maximum and then decrease	15 Cyclic 5	14.7 15.8 19.0	10.8 10.7 19.2
Fish Tissue (Fig. 2.6)	Increase of ^{14}C to a maximum and then decrease	15 Cyclic 5	28.7 31.5 33.8	31.5 29.9 16.3

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[1] Except for particulate matter fraction where maximal observed values are presented.

[2] Equations for 1st ^{14}C meal are shown. Equations for 2nd ^{14}C meal are: 15 C, $\ln Y = + \ln 6.387 - 0.309t$ Cyclic, $\ln Y = \ln 5.382 - 0.170t$; 5 C, $\ln Y = \ln 4.870 - 0.103t$.

[3] Average percentage was calculated by measuring the area under the ^{14}C activity (%) vs. time curves in Fig. 2&3, 2.6 and then dividing by time.

[4] Including pyloric caeca

Table 2.2 - Temperature comparisons at the two ration levels and ration comparison of the three temperatures according to regression coefficients, asymptotic values, maximal observed values or average values shown in Table 2.1 for the various ^{14}C fractions.

^{14}C Fraction	Temperature Comparison			Ration Comparison		
	Regression Coefficient					
	Ration Size	Order of	Significance	Temp. °C	Order of	Significance
Stomach Contents	Low	15 > cyclic > 5	$P < 0.05$	15	Mod. > Low	NS
				Cyclic	Mod. > Low	NS
	Mod.	15 > cyclic > 5	$P < 0.05$	5	Low > Mod.	NS
Incorporated	Low	15 > cyclic > 5	$P < 0.05$	15	Low > Mod.	NS
				Cyclic	Low > Mod.	NS
	Mod.	15 > cyclic > 5	$P < 0.05$	5	Low > Mod.	NS
Respired	Low	15 > cyclic > 5	$P < 0.05$[1]	15	Low > Mod.	NS
				Cyclic	Low > Mod.	NS
	Mod.	15 > cyclic > 5	$P < 0.05$[1]	5	Low > Mod.	NS
Particulate Matter	Low	15 > cyclic > 5	$P < 0.05$[1]	15	Low > Mod.	$P < 0.05$
				Cyclic	Low > Mod.	NS
	Mod.	5 > 15 > cyclic	$P < 0.05$	5	Mod. > Low	$P < 0.05$
Soluble Organic Matter	Low	15 > cyclic > 5	NS	15	Low > Mod.	NS
				Cyclic	Low > Mod.	NS
	Mod.	5 > cyclic >15	NS	5	Mod. > Low	$P < 0.05$

^{14}C Fraction	Asymptotic value (% of ingested ^{14}C)					
	Ration Size	Order of	Significance	Temp. °C	Order of	Significance
Incorporated	Low	15 > 5 > cyclic	NS	15	Low > Mod.	NS
	Mod.	15 > cyclic > 5	$P < 0.05$[1]	cyclic	Low > Mod.	NS
				5	Low > Mod.	$P < 0.05$
Respired	Low	15 > cyclic > 5	$P < 0.05$[1]	15	Low > Mod.	NS
	Mod.	15 > cyclic > 5	$P < 0.05$[1]	cyclic	Low > Mod.	NS
				5	Low > Mod.	NS
Soluble Organic Matter	Low	5 > cyclic = 15	NS	15	Mod. > Low	NS
	Mod.	5 > cyclic > 15	$P < 0.05$[1]	cyclic	Mod. > Low	NS
				5	Mod. > Low	$P < 0.05$
	Maximal observed value (% of ingested ^{14}C)					
	Ration Size	Order of	Significance	Temp. °C	Order of	Significance
Particulate Matter	Low	15 > cyclic > 5	NS	15	Mod. > Low	NS
	Mod.	5 > 15 > cyclic	$P < 0.05$[1]	cyclic	Low = Mod.	
				5	Mod. Low	$P < 0.05$

^{14}C Fraction	Average percentage of ingested ^{14}C present in the fraction[2]					
	Ration Size	Order of	Significance	Temp. °C	Order of	Significance
Intestine and Pyloric Caeca Contents (including pyloric caeca)	Low	5 > cyclic > 15	NS	15	Mod. > Low	$P < 0.05$
	Mod.	5 > cyclic > 15	$P < 0.05$[1]	cyclic	Mod. > Low	$P < 0.05$
				5	Mod. > Low	$P < 0.05$
Fish Tissues	Low	5 > cyclic > 15	NS	15	Mod. > Low	$P < 0.05$
	Mod.	15 > cyclic > 5	$P < 0.05$[1]	cyclic	Mod. > Low	$P < 0.05$
				5	Mod. > Low	NS

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[1] Temperatures underscored are not significantly different.

[2] Calculated as the area under the ^{14}C activity (%) vs. time curves in Figs. 2.3, 2.6 and then dividing the area by time.

the intestine and pyloric caeca (including the pyloric caeca) in relation to temperature and time after ^{14}C feeding are shown in Fig. 2.3. For both levels of rations at each temperature the mean percentages of ^{14}C activity rose to a maximum and then decreased. For the low ration experiments it reached a maximum of 27-30% by 6, 8 and 12 h under 15°C, cyclic and 5°C temperature regimes, respectively, was reduced to half that by 18, 30 and 36 h at the respective temperatures above and reduced to 2% by 30, 36 and 48 h at respective temperatures above (Fig. 2.3A). For the moderate ration, mean percentages of ^{14}C at 15°C and cyclic temperature regime reached a maximum of 22-23% at 15 h, was reduced to half that 9 h later and contained 2% by 36 h at 15°C and by 48 h under cyclic temperature regime (Fig. 2.3B). On the other hand, at 5°C mean percentages of ^{14}C reached a maximum of 32% at 24 h, was reduced to half that at 48 h and reduced to 2% by 60 h (Fig. 2.3B).

To compare the trends in the curves (Fig. 2.3), an average percentage of ingested ^{14}C recovered from this fraction was calculated for each temperature at the two ration levels by measuring the area under the curves using a planimeter and then dividing the area by the time required to empty the intestine and pyloric caeca of radioactive food. In these experiments evacuation was considered complete at 2% of ingested ^{14}C activity remaining. The calculated average percentages are shown in **Table** 2.1 and were independent of temperature at the low ration (**Table** 2.2). However, at the moderate ration the average percentage was significantly greater ($P < 0.05$) at 5°C then at

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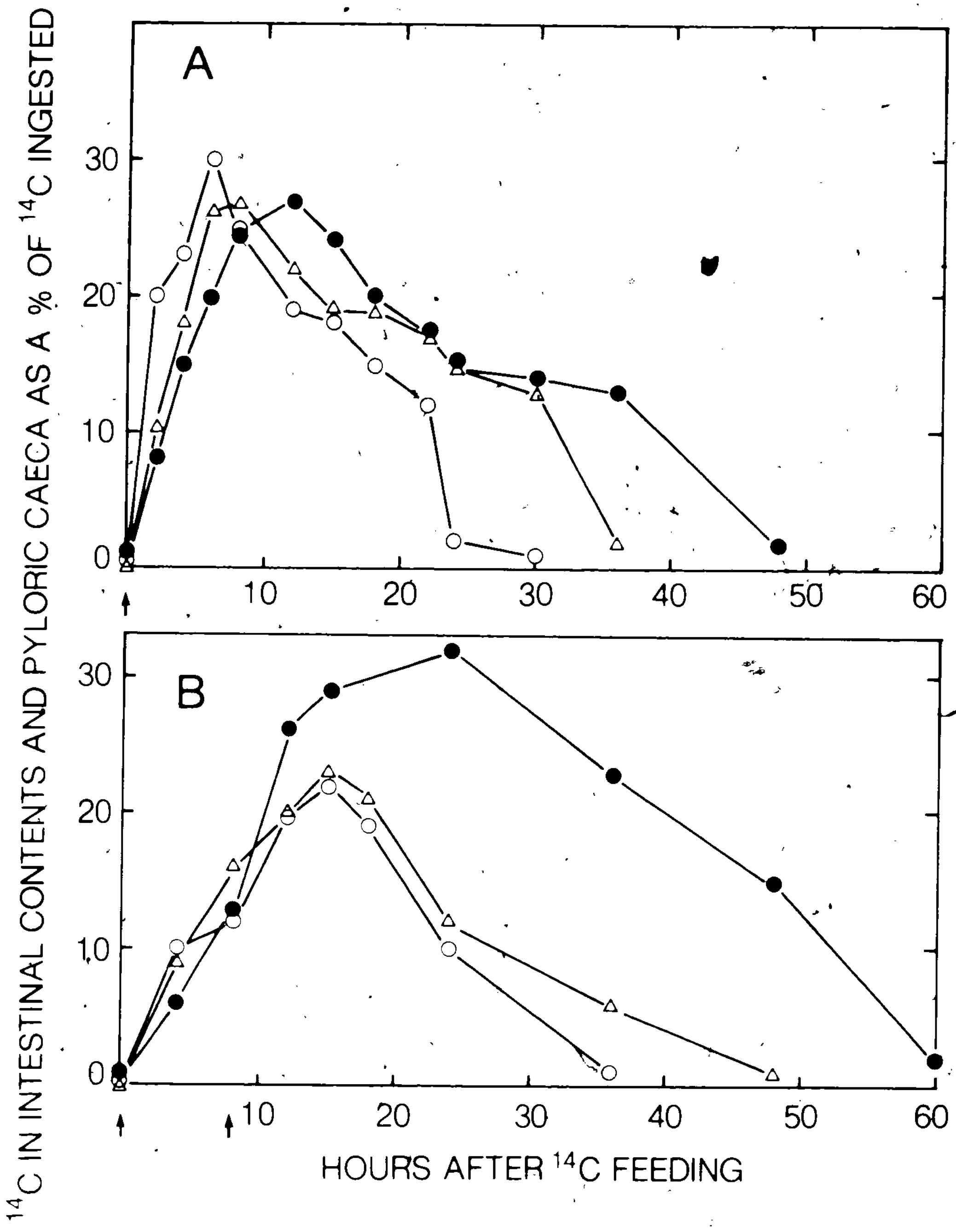
Figure 2.3 Comparison of ^{14}C labelled food in the contents of intestine and pyloric caeca (including the pyloric caeca) of underyearling sockeye salmon in relation to time after ^{14}C feeding at 15°C (○), 5°C (●) and the cyclic temperature regime (△). In A, fish were fed a low ration of 33.1 cal/kcal sockeye/day. In B, fish were fed a moderate ration of 65.6 cal/kcal sockeye/day. Arrows indicate the time ^{14}C labelled food was presented.


A
B
30
20
10
0
10
20
30
40
50
60
^{14}C IN INTESTINAL CONTENTS AND PYLORIC CAECA AS A % OF ^{14}C INGESTED
HOURS AFTER ^{14}C FEEDING

15°C and under the cyclic temperature regime. Differences between the latter two temperatures were not significant (Table 2.2). However, at the moderate ration the average percentage was significantly greater ($P < 0.05$) at 5°C than at 15°C and under the cyclic temperature regime. Differences between the latter two temperatures were not significant (Table 2.2). Although the absolute value at all temperatures was greater at the moderate than low ration, the percentage value at 15°C and under the cyclic temperature regime was less at the larger ration.

^{14}C Incorporated

Since respiratory and soluble organic material loss of ^{14}C activity began within 2 h of consumption of the labelled meal, ^{14}C activity present in sockeye tissue represented net uptake rather than actual incorporation. Thus, incorporation was assumed to be the sum of ^{14}C activity present in the tissue, as $^{14}CO_2$, and as soluble organic material.

At both ration levels percentages of ^{14}C incorporated in relation to temperature and duration of the experiment are presented in Fig. 2.4A, 2.5A. At each temperature percentages increased exponentially with time after ^{14}C feeding at a progressively decreasing rate. This relationship for each temperature was expressed in linear form as $\ln(Y_{asymp.t} - Y_t) = \ln(Y_{asymp.o} - Y_o) - kt$, where Y_t is % ^{14}C incorporated at time t, Y_o is % ^{14}C incorporated at time 0,

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Figure 2.4 Comparison of ^{14}C incorporated by underyearling sockeye salmon in relation to time after ^{14}C feeding at a low ration of 33.1 cal/kcal sockeye/day and at $15^{\circ}C$ (○), $5^{\circ}C$ (●) and the cyclic temperature regime (Δ). Arrows indicate the time ^{14}C labelled food was presented. Linear regression lines in C have been calculated from the percentage data in A expressed as natural logarithm of the difference between observed percentage values at each time interval and the asymptote. The regression terminated for the first time interval where more than 95% of the asymptotic value was present. Equations for the regression lines are shown in Table 2.1. B shows, as an example, the estimated asymptote for under the cyclic temperature regime and points out that it is the difference between observed percentage values (Y) and the asymptote which is decreasing exponentially, so that if for each point the value of Y is subtracted from the asymptote, the series of differences fall on a straight line when plotted on a logarithmic scale against time (C).

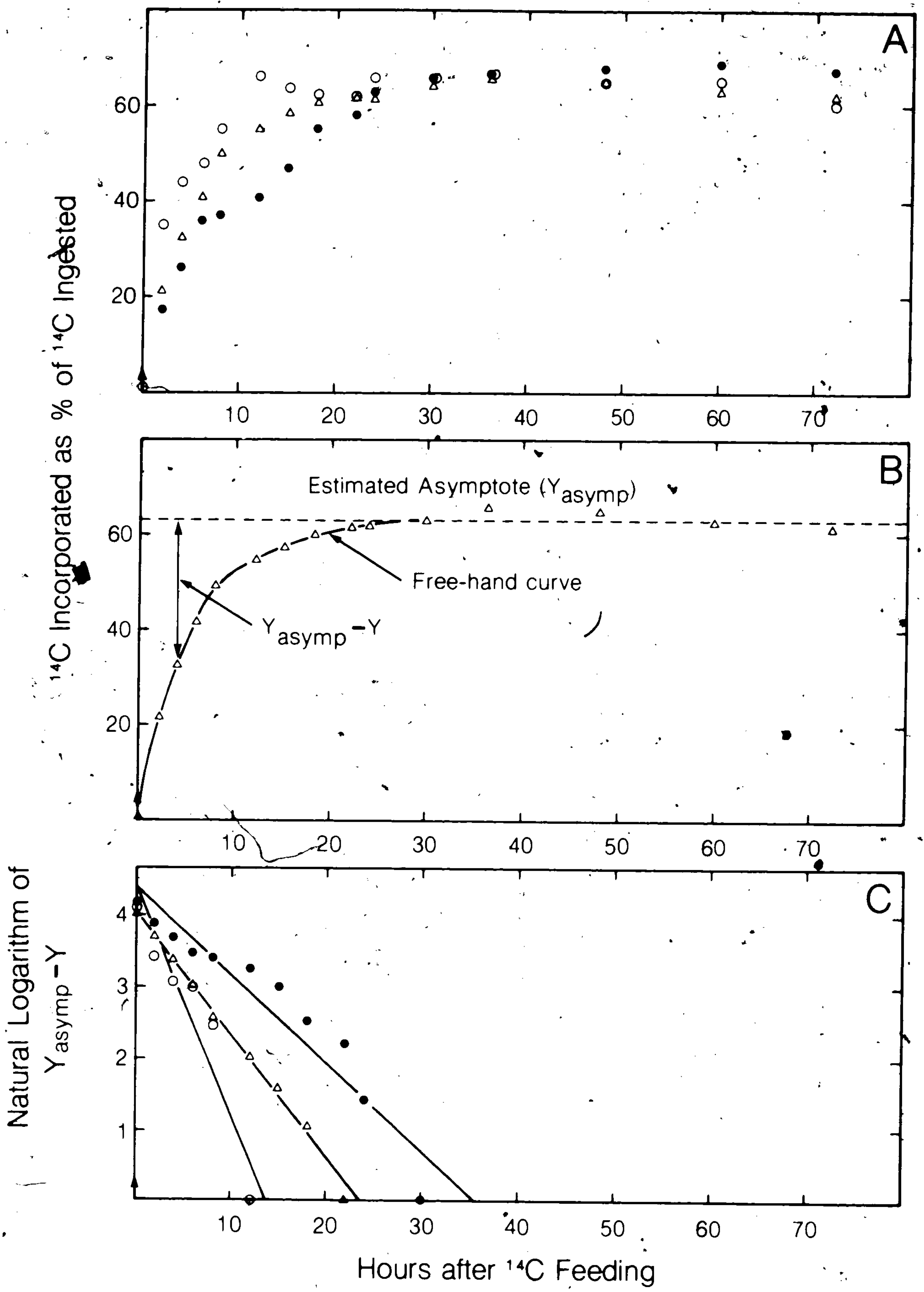
A
B
C
Estimated Asymptote (Y_{asymp})
Free-hand curve
$Y_{asymp} - Y$
^{14}C Incorporated as % of ^{14}C Ingested
Natural Logarithm of $Y_{asymp} - Y$
Hours after ^{14}C Feeding
20
40
60
1
2
3
4
10
20
30
40
50
60
70

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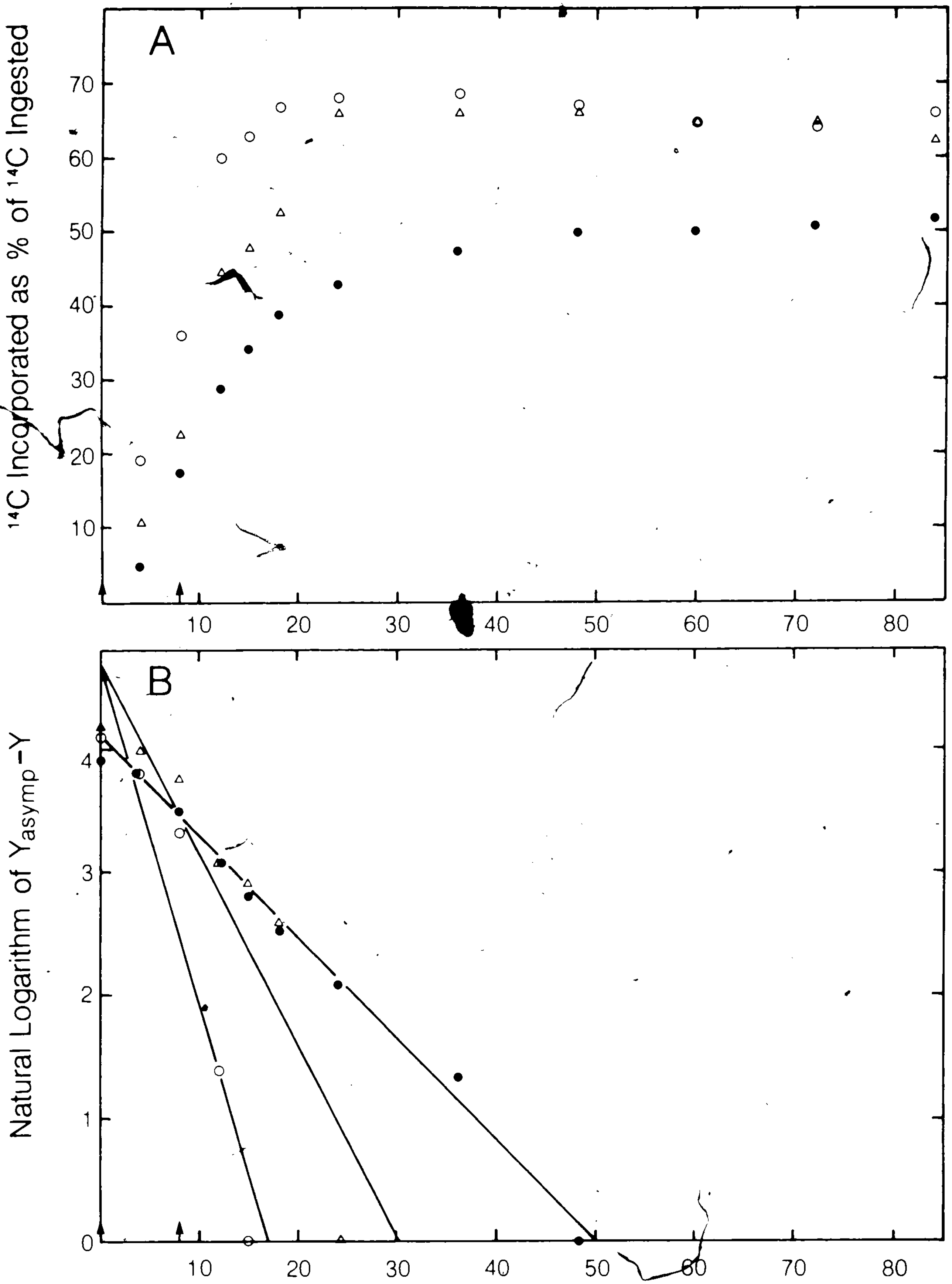
Figure 2.5 Comparison of ^{14}C incorporated by underyearling sockeye salmon in relation to time after ^{14}C feeding at a moderate ration of 65.6 cal/kcal sockeye/day (6.4% dry body wt) and at 15 °C (O), 5 °C (●) and the cyclic temperature regime (Δ). Arrows indicate the time ^{14}C labelled food presented. Linear regression lines in B have been calculated from the percentage data in A expressed as natural logarithm of the difference between observed percentage values at each time interval and the asymptote. Regression terminated for the first time interval where more than 95% of the asymptotic value was present. Equations for the regression lines are shown in Table 2.1.


A
^{14}C Incorporated as % of ^{14}C Ingested
10
20
30
40
50
60
70
10
20
30
40
50
60
70
80
B
Natural Logarithm of Y_{asymp}−Y
0
1
2
3
4
0
10
20
30
40
50
60
70
80
Hours after ^{14}C Feeding

$Y_{asymp.t}$ is asymptote at time t, $Y_{asymp.o}$ is asymptote at time 0, k is instantaneous rate constant estimated by regression analysis, t is time after ^{14}C feeding (h), and ln is natural logarithm (Fig. 2.4C, 2.5B). Rate relations transformed in this way were linear over most of the time scale, except where the incorporated values were at or close to the maximum value. The regression calculations included data from the first time interval where more than 95% of the calculated asymptotic value was present. Fig. 2.4B shows, as an example, how the parameters of this equation under the cyclic temperature regime at the low ration level were determined. First an asymptote was estimated, illustrated by the broken line. The natural logarithm of the difference between Y_t and the asymptote ($\ln(Y_{asymp.t} - Y_t)$) was plotted against time and a linear regression line was calculated. The estimate of the asymptote was revised until one was found that gave the least mean square error for regression. The slope (k) of this line gives the rate of change at which $Y_{asymp.t} - Y_t$ is decreasing exponentially towards the asymptote and the intercept on the Y - axis gives $Y_{asymp.o} - Y_o$, i.e. total change which Y will undergo in time.

The regression equations and the asymptotic values for each temperature at the low and moderate ration experiments are shown in Table 2.1. At both low and moderate rations regression coefficients (k values) were 15°C > cyclic temperature regime > 5°C ($P < 0.05$) but there was no significant difference in regression coefficients at any one temperature between the two levels of ration (Table 2.2). Thus, the absolute rate of incorporation (^{14}C concentration/h) was more rapid for the larger than smaller ration. Also, the time required for complete incorporation (intercept on x - axis) increased with the larger ration (Fig. 2.4C, 2.5B).

Incorporation efficiencies, calculated as the proportion of total ^{14}C incorporated (asymptotic value) relative to total ^{14}C ingested, are shown for both ration ~~levels~~ for the three temperatures in Table 2.3. At low rations incorporation efficiency was not affected by temperature ($P > 0.05$); at moderate rations incorporation efficiency was less ($P < 0.05$) at 5°C than at 15°C and cyclic temperature regime. Also, incorporation efficiency at 5°C was less ($P < 0.05$) at the larger than smaller ration. There was no significant difference ($P > 0.05$) in incorporation efficiency at 15°C and cyclic temperature regime between fish fed low and moderate rations.

^{14}C in Fish Tissue

Percentages of ingested ^{14}C activity present in sockeye tissue at the various temperatures and times after ^{14}C feeding are presented in Fig. 2.6. For both levels of rations at each temperature percentages of ^{14}C increased to a maximum and then decreased. Uptake of radioactivity by tissues was very rapid. For the low ration within 2 h of ^{14}C feeding 25%, 15% and 11% of ^{14}C ingested was present in the tissue under 15°C, cyclic and 5°C temperature regimes, respectively (Fig. 2.6A). For the low ration the mean percentages reached a maximum value of

Table 2.3 - Comparison of ^{14}C incorporation efficiencies of underyearling sockeye salmon held at 15°C, 5°C and a cyclic temperature regime and fed low and moderate rations of 33.1 cal/kcal sockeye/day (3.4% dry body wt) and 65.6 cal/kcal sockeye/day (6.4% dry body wt), respectively.

Temperature °C	Incorporation Efficiency %	
	Low Ration (Expt. 1 & 2)	Moderate Ration (Expt. 3)
15	67	64
Cyclic regime	63	67
5	67	51

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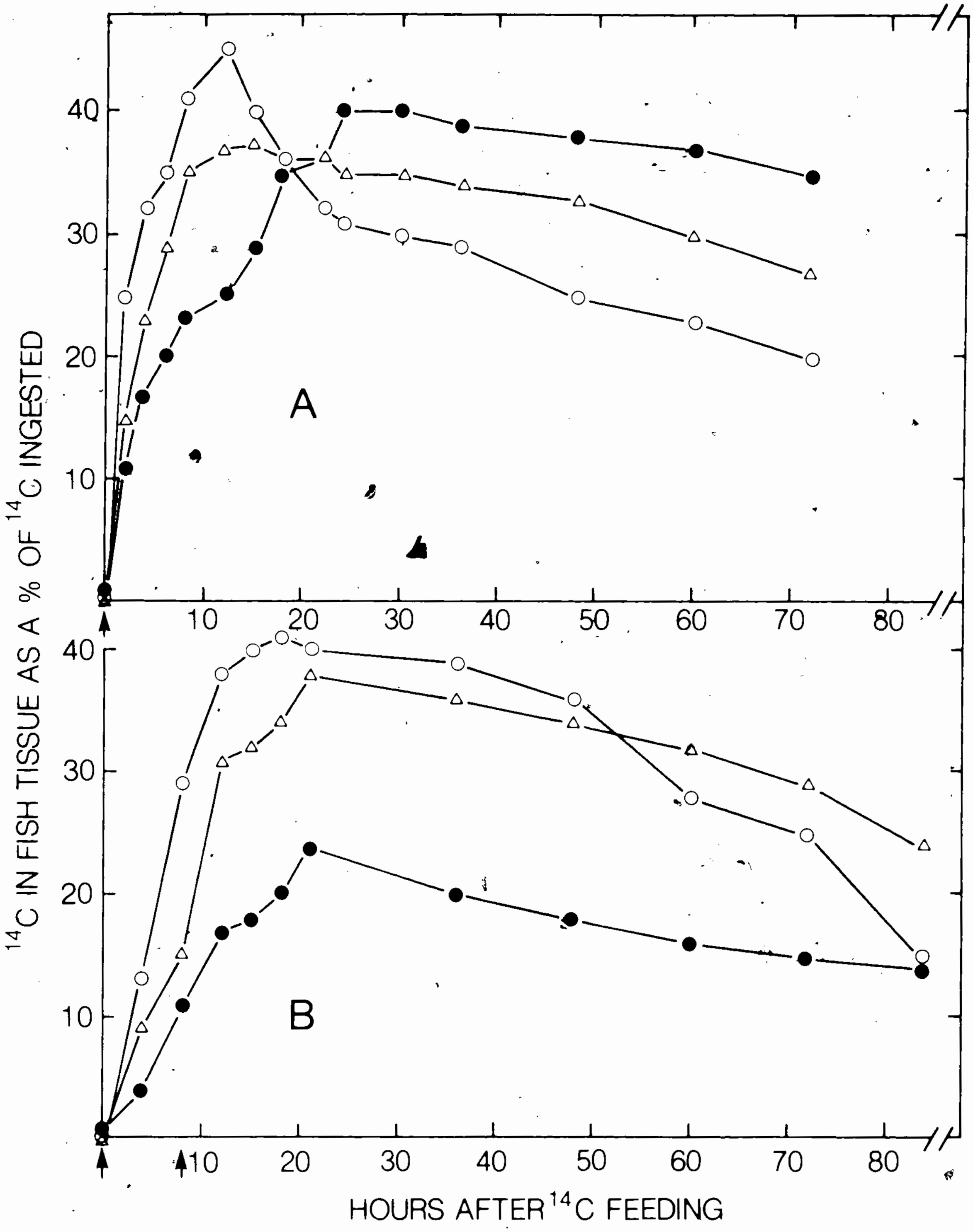
Figure 2.6 Comparison of ^{14}C in underyearling sockeye salmon tissue in relation to time after ^{14}C feeding at 15°C (O), 5°C (●) and the cyclic temperature regime (Δ). In A, fish were fed a low ration of 33.1 cal/kcal sockeye/day. In B, fish were fed a moderate ration of 65.6 cal/kcal sockeye/day. Arrows indicate the time ^{14}C labelled food presented.


A
B
^{14}C IN FISH TISSUE AS A % OF ^{14}C INGESTED
HOURS AFTER ^{14}C FEEDING
10
20
30
40
10
20
30
40
50
60
70
80

37-45% by 12, 15 and 24 h under 15 °C, cyclic and 5 °C temperature regimes, respectively and was reduced to 20%, 27% and 35% under the same respective temperatures by 72 h (Fig. 2.6A). A similar trend was observed in the moderate ration experiments except that at 5 °C the maximum value observed was approximately one-half that for the other temperatures (Fig. 2.6B). Under the 5 °C, 15 °C and cyclic temperature regimes, respectively there was 14%, 15%, and 24% of ^{14}C ingested present in fish tissues by 84 h (Fig. 2.6B).

For each temperature at the two ration levels the average percentage of ingested ^{14}C recovered in fish tissue was calculated as the area under the curves in Fig. 2.6 divided by the duration of the experiment. These calculated values represent the proportion of the ration available for growth and respiration (growth potential) averaged over the duration of the experiment. The calculated average values ranging from 16-34% of the ration are given in Table 2.1. Average percentages were independent of temperature ($P > 0.05$) at the low ration (Table 2.2). However, at the moderate ration, the average percentage was less at 5 °C than at 15 °C and cyclic temperature regime. Differences between the latter two temperatures were not significant (Table 2.2). At 15 °C and cyclic temperature regime there was no difference in average values between the two ration levels. At 5 °C, however, the average percentage was approximately 2 times greater at the smaller than at the larger ration (Table 2.2).

^{14}C Respired

At both low and moderate rations, mean percentage of ingested ^{14}C respired as $^{14}CO_2$ at any one temperature increased exponentially with time after ^{14}C feeding towards an asymptote except for the last 15°C value (Fig. 2.7A, 2.8A). This exponential change, excluding the last 15°C value, was expressed in linear from in the manner described above (Fig. 2.7B, 2.8B). The equations and asymptotic values (%) for the rate of $^{14}CO_2$ respired for each temperature at the low and moderate ration experiments are shown in Table 2.1. At both levels of rations regression coefficients were significantly greater at 15°C than under the cyclic temperature and 5°C (Table 2.2). Differences between the latter two temperatures were not significant ($P > 0.05$), but the regression coefficients indicated a trend to greater values under the cyclic temperature compared to 5°C. Asymptotic values, representing the total loss of respired $^{14}CO_2$, were also greater at 15°C than the other temperatures at the low ration but not at the moderate ration where they were greater at 15°C than at 5°C (Table 2.2). Regression coefficients and percentage asymptotic values irrespective of temperature, were independent of ration size (Table 2.2), although for each temperature the absolute value of maximal respiration was greater at the larger ration.

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Figure 2.7 Comparison of ^{14}C respired by underyearling sockeye salmon in relation to time after ^{14}C feeding at a low ration of 33.1 cal/kcal sockeye/day (3.4% dry body wt) and at 15°C (O), 5°C (●) and the cyclic temperature regime (Δ). Arrows indicate the time ^{14}C labelled food presented. Linear regression lines in B have been calculated from the percentage data in A expressed as natural logarithm of the difference between observed percentage values at each time interval and the asymptote. The regression did not include the last 15°C value. Equations for the regression lines are shown in Table 2.1.

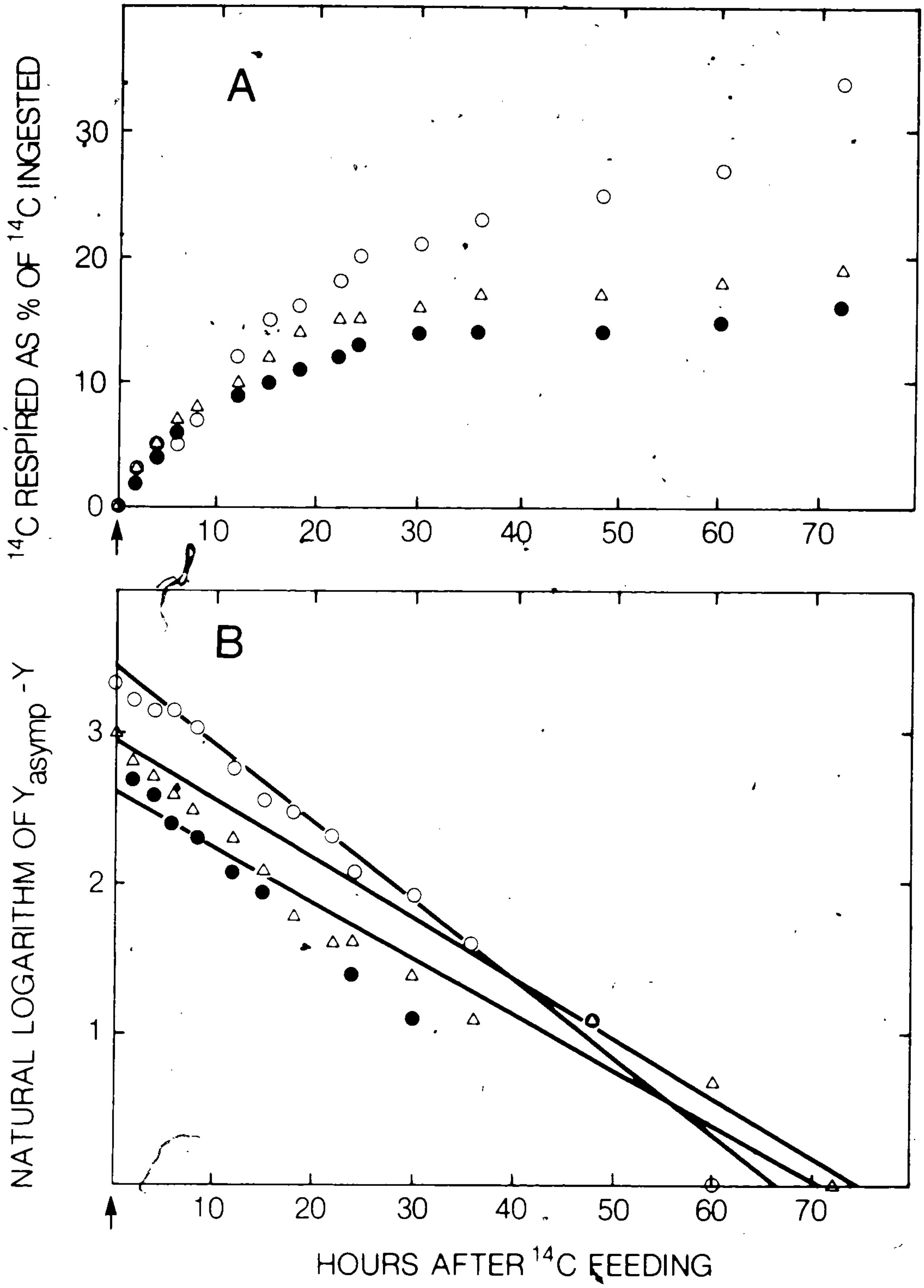
A
B
^{14}C RESPIRED AS % OF ^{14}C INGESTED
0
10
20
30
NATURAL LOGARITHM OF Y_{asymp} -Y
1
2
3
10
20
30
40
50
60
70
HOURS AFTER ^{14}C FEEDING

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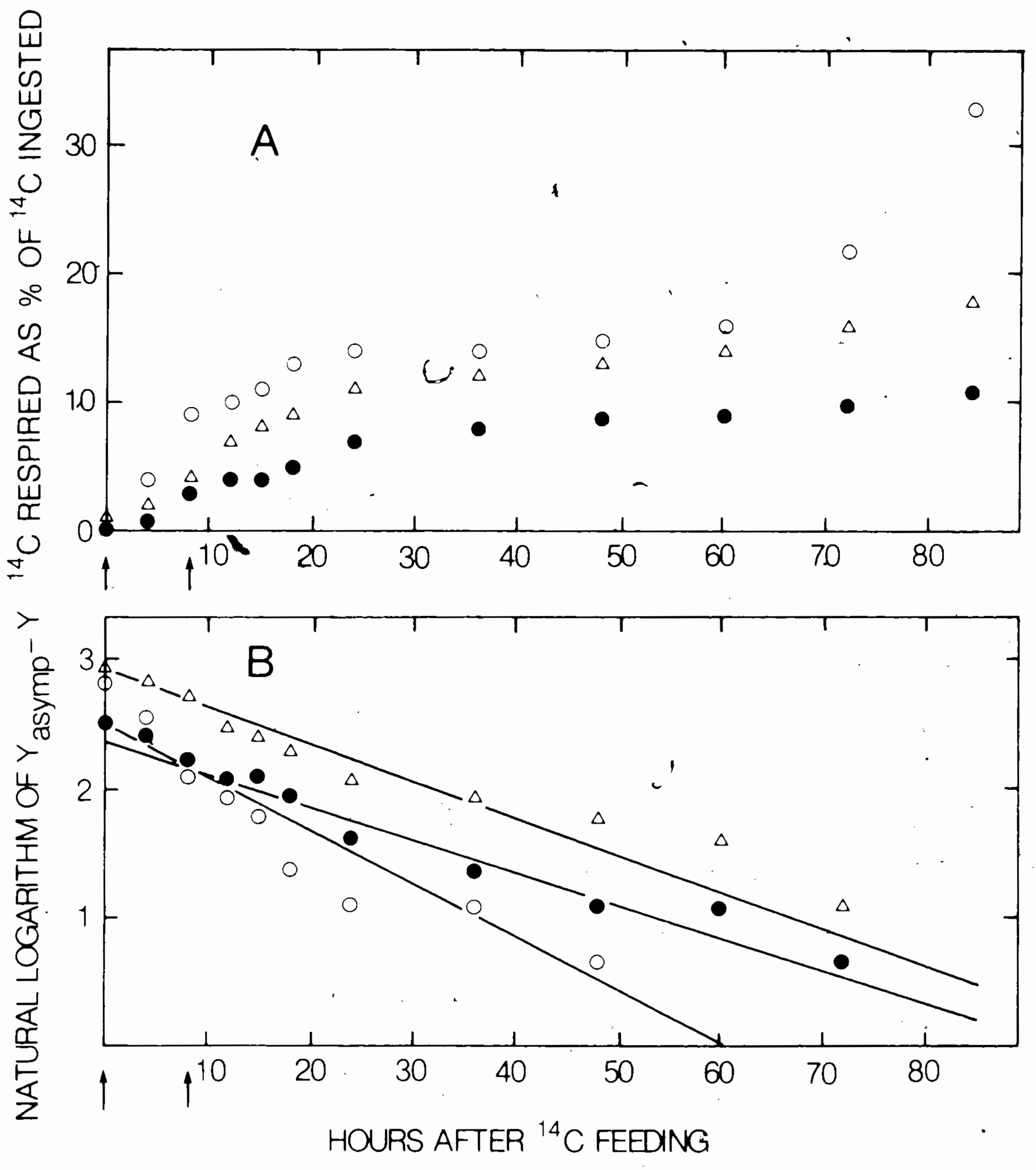
Figure 2.8 Comparison of ^{14}C respired by underyearling sockeye salmon in relation to time after ^{14}C feeding at a moderate ration of 65.6 cal/kcal sockeye/day (6.4% dry body wt) and at 15°C (O), 5°C (●) and the cyclic temperature regime (Δ). Arrows indicate the time ^{14}C labelled food presented. Linear regression lines in B have been calculated from the percentage data in A expressed as natural logarithm of the difference between observed percentage values at each time interval and the asymptote. The regression did not include the last 15°C value. Equations for the regression lines are shown in Table 2.1.


A
B
^{14}C RESPIRED AS % OF ^{14}C INGESTED
NATURAL LOGARITHM OF $Y_{asymp} - Y$
0
10
20
30
1
2
3
10
20
30
40
50
60
70
80
HOURS AFTER ^{14}C FEEDING

^{14}C Soluble Organic Material

At any one temperature percentage of ingested ^{14}C activity recovered in the water as soluble organic material increased exponentially with time after ^{14}C feeding towards an asymptote (Fig. 2.9A, 10A). This exponential change was expressed in the manner described above (Fig. 2.9B, 10B). The linear equations and asymptotic values for each temperature at the low and moderate ration experiments are shown in Table 2.1. At both ration levels the regression coefficients were not significantly related to temperature (Table 2.2). However, the regression coefficients at 5°C were significantly greater at the larger than smaller ration. There were no significant differences in regression coefficients at the other two temperatures between those fish fed low and moderate rations (Table 2.2).

Asymptotic values, representing the total loss of soluble excretory products, at the moderate ration were greater at 5°C than at 15°C and under the cyclic temperature regime (Table 2.2). Differences between the latter two temperatures were not significant. For each temperature the absolute amount of the asymptotic value observed was greater at the moderate than low ration. However, the percentage value at 15°C and under the cyclic temperature regime was not significantly different between low and moderate rations (Table 2.2). In contrast, at 5°C the asymptotic percentage value was significantly ($P < 0.05$) greater at the larger ration size.

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Figure 2.9 Comparison of ^{14}C soluble organic material released by underyearling sockeye salmon in relation to time after ^{14}C feeding at a low ration of 33.1 cal/kcal sockeye/day (3.4% dry body wt) and at 15°C (O), 5°C (●) and the cyclic temperature regime (△). Arrows indicate the time ^{14}C labelled food presented. Linear regression lines in B have been calculated from the percentage data in A expressed as natural logarithm of the difference between observed percentage values at each time interval and the asymptote. Equations for the regression lines are shown in Table 2.1.

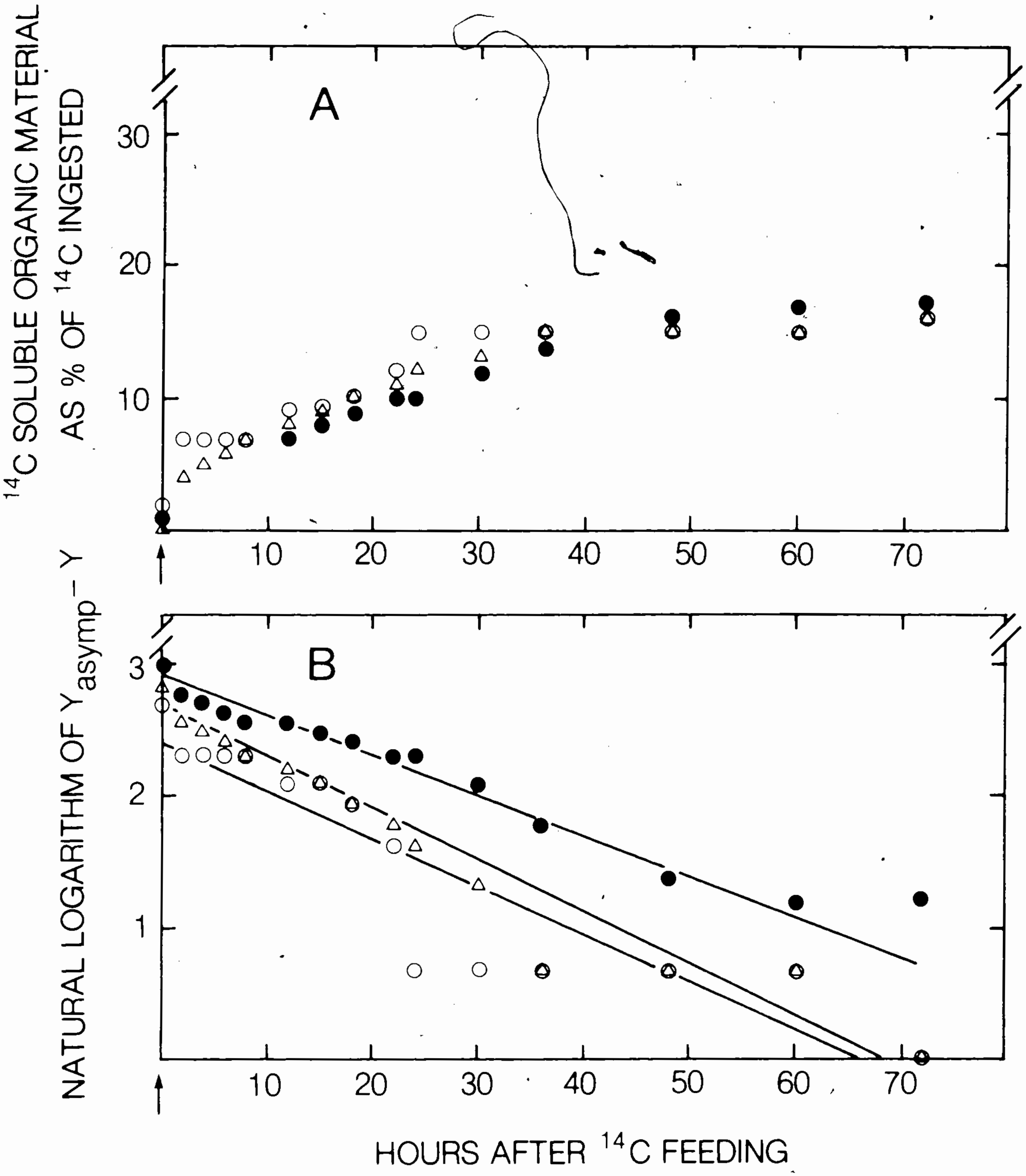
A
B
^{14}C SOLUBLE ORGANIC MATERIAL AS % OF ^{14}C INGESTED
10
20
30
NATURAL LOGARITHM OF Y$_{asymp}$ − Y
1
2
3
10
20
30
40
50
60
70
HOURS AFTER ^{14}C FEEDING

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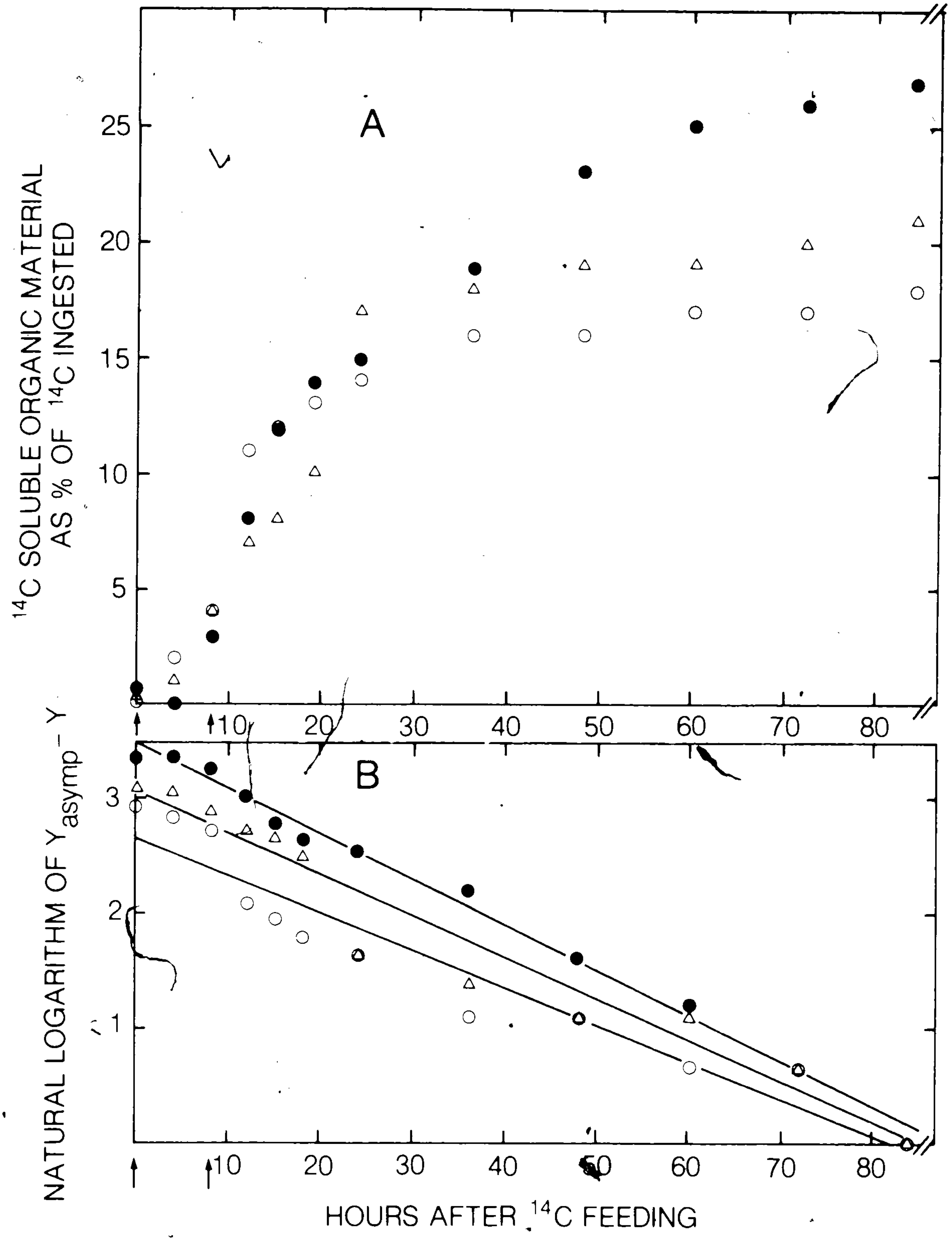
Figure 2.10 Comparison of ^{14}C soluble organic material released by underyearling sockeye salmon in relation to time after ^{14}C feeding at a moderate ration of 65.6 cal/kcal sockeye/day (6.4% dry body wt) at 15°C (O), 5°C (●) and the cyclic temperature regime (△). Arrows indicate the time ^{14}C labelled food presented. Linear regression lines in B have been calculated from the percentage data in A expressed as natural logarithm of the difference between observed percentage values at each time interval and the asymptote. Equations for the regression lines are shown in Table 2.1.


A
B
^{14}C SOLUBLE ORGANIC MATERIAL AS % OF ^{14}C INGESTED
NATURAL LOGARITHM OF $Y_{asymp} - Y$
HOURS AFTER ^{14}C FEEDING
5
10
15
20
25
1
2
3
10
20
30
40
50
60
70
80

^{14}C Particulate Material

Percentages of ingested ^{14}C recovered as particulate material at the various temperatures and times at the low and moderate ration experiments are presented in Fig. 2.11. No detectable ^{14}C activity was present in the particulate fraction within 6 h of ^{14}C feeding regardless of temperature. At 8 or 12 h, the percentage of ^{14}C particulate material increased linearly with time until reaching a plateau, a reflection of cessation of defecation and regurgitation of food. The linear increase of ^{14}C activity was expressed with the equation $Y = a + kt$. The equations and maximal values (%) for each temperature at the low and moderate ration experiments are shown in Table 2.1. Both the regression coefficients and maximal values were influenced by temperature and ration (Table 2.2). In the low ration experiments, regression coefficients were significantly greater at 15°C than under cyclic temperature regime and at 5°C. At the larger ration regression coefficients were greater ($P < 0.05$) at 5°C than under the cyclic temperature regime (Table 2.2). Regression coefficients at 15°C were greater ($P < 0.05$) at the smaller ration size; regression coefficients at 5°C were greater at the larger ration. Maximal values, representing total loss of particulate matter, at the moderate ration were significantly greater at 5°C than at the other two temperatures (Table 2.2). Also, maximal values at 5°C were greater at the larger than smaller ration size (Table 2.2). Differences between the two ration sizes at the other

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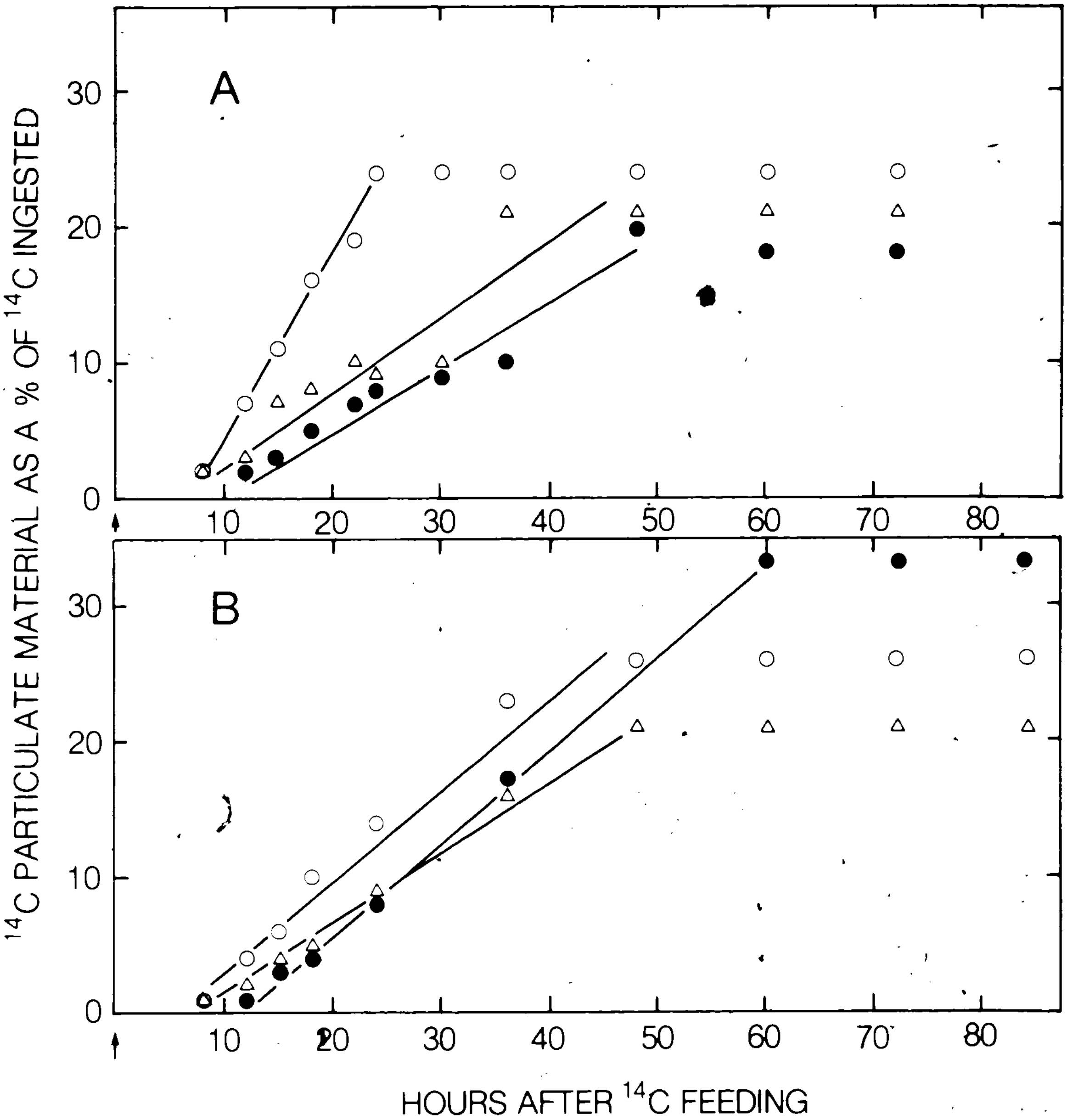
Figure 2.11 Comparison of ^{14}C particulate material released by underyearling sockeye salmon in relation to time after ^{14}C feeding at 15°C (O), 5°C (●) and the cyclic temperature regime (Δ). In A, fish were fed a low ration of 33.1 cal/kcal sockeye/day. In B, fish were fed a moderate ration of 65.5 cal/kcal sockeye/day. Arrows indicate the time ^{14}C labelled food presented. The linear regression lines for each temperature and ration have been calculated from the time period when percentage data increased with time after ^{14}C feeding. No detectable ^{14}C activity was present prior to 8 or 12 h after feeding. Equations for the regression line are shown in Table 2.1.


A
B
^{14}C PARTICULATE MATERIAL AS A % OF ^{14}C INGESTED
HOURS AFTER ^{14}C FEEDING
0
10
20
30
10
20
30
40
50
60
70
80

temperatures or between the other temperatures at the two rations were not significant ($P > 0.05$).

DISCUSSION

McLaren (1963) hypothesized that diel migrations of organisms from warm water, where feeding occurs, to colder water, where most of metabolism (catabolism) occurs, yields an 'energy bonus' which results in more rapid growth under a cyclic temperature regime than constant temperatures. This hypothesis was supported for underyearling Babine Lake sockeye salmon reared in tanks and fed moderate rations (61-76 cal/kcal sockeye/day; 5.5-6.9% of dry body wt) of natural zooplankton (Chapter 1). However, my results did not support the hypothesis for underyearling sockeye salmon fed low (15-45 cal/kcal sockeye/day; 1.4-4.1% of dry body wt) or excess rations (Chapter 1). The studies reported in this Chapter using ^{14}C labelled food were designed to compare the short-term fate of ingested food by underyearling sockeye salmon fed low (33.1 cal/kcal/day) and moderate (65.5 cal/kcal/day) rations and held under a diel cyclic temperature regime or under constant temperatures.

If McLaren's hypothesis holds, it would follow that over the duration of the experiment growth potential (the proportion of the ration retained in the tissues of young sockeye salmon and available for growth and respiration) would be greater under the cyclic temperature regime than at the constant temperatures. This was not the case for underyearling sockeye salmon provided a low ration (3.4% of dry body wt), although there was some support for the hypothesis in sockeye fed a moderate ration (6.4% of dry body wt). At low rations, growth potential of young sockeye under the cyclic temperature and constant temperature regimes (5°C and 15°C) were not statistically different (Table 2.2). When fed moderate rations growth potential of sockeye under the cyclic temperature and constant high temperature (15°C) was also not statistically different (Table 2.2). However, at the moderate ration growth potential of sockeye was significantly greater under the cyclic temperature than the constant low temperature (5°C). This observation lends support to the McLaren hypothesis.

Since the dynamics of uptake of labelled food into the fish tissues and its subsequent loss from the tissues change not only with temperature but also with the duration of the experiment (Fig. 2.6), different experimental periods might have altered my conclusion. To examine the effect of the length of the experiment on my results, I compared the calculated growth potential for 72 or 84 h experiments with those calculated for shorter (12, 24, 36, 48, 60 h) and longer (4 to 13 days) experiments. The growth potentials for the longer experiments were calculated by the method described above except that the ^{14}C measurements in the tissue were obtained by extrapolating the rate of carbon loss from the tissue; rate estimated from slope of the least square regression line (lnY = lnY - kt) fitted to the data from the time period when percentage data shown in Fig. 2.6 decreased with time. The temperature comparisons according to these calculated growth potentials are shown in Table 2.4. At both rations the results of 24, 36, 48 or 60 h experiments indicated the same effect of temperature on growth potential as I reported for the 72 h or 84 h experiment. On

Table 2.4 – Temperature comparisons at the two ration levels according to the calculated growth potential[1] as affected by the duration of the experiment.

Duration of Expt. (day)	Low Ration (Expt. 1 & 2) Order of Growth Potential	Low Ration (Expt. 1 & 2) Significance	Moderate Ration (Expt. 3) Order of Growth Potential	Moderate Ration (Expt. 3) Significance
0.5 (12 h)	15 > cyclic > 5	$P < 0.05$[2]	15 > cyclic > 5	$P < 0.05$[2]
1 (24 h)	15 > cyclic > 5	NS	15 > cyclic > 5	$P < 0.05$[2]
1.5 (36 h)	15 > cyclic > 5	NS	15 > cyclic > 5	$P < 0.05$[2]
2 (48 h)	cyclic > 5 > 15	NS	15 > cyclic > 5	$P < 0.05$[2]
2.5 (60 h)	5 > cyclic > 15	NS	15 > cyclic > 5	$P < 0.05$[2]
3 (72 h)	5 > cyclic > 15	NS	15 > cyclic > 5	$P < 0.05$[2]
3.5 (84 h)			15 > cyclic > 5	$P < 0.05$[2]
4	5 > cyclic > 15	NS	cyclic > 15 > 5	$P < 0.05$[2]
5	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$[2]
6	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$[2]
7	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$[2]
8	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$[2]
9	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$[2]
10	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$
11	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$
12	5 > cyclic > 15	$P < 0.05$[2]	cyclic > 15 > 5	$P < 0.05$
13	5 > cyclic > 15	$P < 0.05$	cyclic > 5	$P < 0.05$

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[1] Growth potential was calculated by measuring the area under the ^{14}C activity vs. time curves (Fig. 2.6) and then dividing the area by the duration of the experiment.

[2] Temperatures underscored are not significantly different.

the other hand, a 12 h experiment would have altered the results and shown that at the low ration growth potential was less at 5°C than at the other temperatures and at the moderate ration growth potential was less at 5°C and the cyclic temperature 15°C (Table 2.4). A 12 h experiment, however, is too short to assess growth potential. At 12 h ultimate incorporation is underestimated at the lower temperatures because of the slower incorporation rates associated at these temperatures (Table 2.2). Further, at the low ration a 4, 5 or 6 day experiment showed results similar to my 72 h one (Table 2.4). Similarly, at moderate rations a 4 to 9 day experiment indicated the same results (15°C = Cyclic temperature > 5°C) as the 84 h one (Table 2.4). On the other hand, a 7-day experiment at the low ration or a 10-day experiment at the moderate ration would have altered the conclusion. At the moderate ration the extrapolation for 10-13 day experiments showed that growth potential was greater under cyclic temperatures than at the constant temperature. At the low ration the extrapolation for 7-13 day experiments showed that at first growth potential was greater under 5°C and cyclic temperatures than at 15°C and then greatest under 5°C (Table 2.4). However, labelled compounds available for respiration will decrease as the length of the experiment increases (Conover and Francis, 1973). Consequently, experiments longer than 3 or 4 days will likely overestimate growth and therefore are too long to assess growth potential. Therefore, the length of the experiment that was adopted had little influence on the results.

The results reported in this study may have been affected by the two different feeding regimes employed in the low and moderate ration experiments. In the low ration experiments (Expt. 1 and 2), fish were fed once daily and in the moderate ration experiment (Expt. 3) fish were fed twice daily (Fig. 2.1). However, ration size had little influence on the fate of consumed food except for incorporation efficiency and the excretion of soluble organic products and then only at 5°C (Table 2.3). Hence, there is little evidence that feeding regimes affected the results.

Support for the hypothesis that growth potential would be enhanced under cyclic temperatures and moderate ration depended on a more efficient food incorporation and on a lower excretion of soluble organic products in relation to the constant low temperature than at low rations. At the constant low temperature incorporation efficiency decreased from 67 to 51% with the increasing ration from 33.1 to 65.6 cal/kcal/day (Table 2.3). In contrast, under the cyclic temperature regime incorporation efficiency averaged 65% and did not vary appreciably with ration size. Hence, the conditions of moderate ration and constant low temperature reduced the amount of labelled food incorporated.

The loss of soluble excretory products was also affected by temperature and ration and in much the same way as incorporation efficiency. At the constant low temperature the loss of soluble organic products increased from 17 to 28% of the total food intake with the increasing ration (Table 2.1; Fig. 2.9, 2.10). On the other hand, under the constant high and cyclic temperature regimes loss of soluble organic products averaged 18% of the intake and did not vary appreciably with ration size. Thus, under conditions of moderate ration and constant low temperature not only was less food incorporated, but also more food was lost through subsequent requirements for excretion. Consequently, the enhancement of the growth potential under cyclic temperatures relative to the constant low temperature required the moderate ration.

The way in which temperature and ration size affect incorporation efficiency is not clear. When fish were fed the larger ration, more ^{14}C accumulated in the intestine and pyloric caeca at the constant low temperature than at the other temperatures (Fig. 2.3), suggesting that absorption may be affected under the combination of low temperature and moderate ration. It may be that gastric enzymes become saturated under these conditions as stated by Norris et al. (1973). This could result in undigested food passing into the intestine and pyloric caeca and being subsequently voided. This suggests superfluous feeding similar to that suggested by Beklemishev (1962) for marine zooplankton. This situation may not have any ecological significance. In nature, young sockeye living in the low temperature hypolimnion are unlikely to obtain rations comparable to the moderate ration provided in this study.

The literature on the effect of ration and temperature on incorporation efficiency in fish is contradictory. Most workers (e.g., Dawes, 1930; Brown, 1946; Kinne, 1960; Ursin, 1967; Averett, 1969) suggest that incorporation efficiency decreases with increasing ration. On the other hand Ivlev (1939), Gerking (1955) and Kelso (1972) report that incorporation efficiency is not influenced by ration. Many workers, such as Menzel (1960); Kevern (1966); Pandian (1967); Kelso (1972) report that incorporation efficiency is independent of temperature. However, Brocksen and Bugge (1974) report that incorporation efficiencies in rainbow trout (Salmo gairdneri) provided a ration of 5% body weight/day increased from 71.8% to 84.8% as temperatures increased from 5°C to 20°C. The contradictory reports may result from a lack of observations on fish fed varying rations in relation to temperature.

Efficiencies of incorporation I determined ranged from 51-67% which is lower than the 85-98% for most carnivorous fish species reported by Beamish et al. (1975). The lower values I obtained are partially explained since 6-11% of the ration was not recovered (Appendix 3). Also, other workers have not measured incorporation directly but as the difference between consumption and fecal production. When my data are treated in a similar fashion, the efficiencies of incorporation were 67-80%; still lower than those reported by Beamish et al. However, the lower values in this study could be attributable to the differences in diet since the values reported by Beamish et al. are not for zooplankton diets.

There is no information in the literature on the effect of temperature on excretion by fish. However, excretion measured in this study, accounting for 17-27% of the total food intake, was higher than that reported by other workers using different methods. Although the amount excreted in this study would depend on the extent to which the ^{14}C label appears in urea, Winberg (1956) reported that soluble excretory products for fish account for less than 2% of the total food intake and more recently both Niimi and Beamish (1974) and Brett (1976) reported that normal nitrogenous wastes in the form of ammonia and urea account for less than 10% of total food intake.

There is no possibility that any of the soluble organic products measured in this study came from the food through mechanical damage during its seizure and manipulation as suggested by Conover (1966) and Dagg (1974) since fish were transferred to clean water immediately after feeding. It is also unlikely that soluble organic products were derived by leaching from feces as the loss of these products decreased rapidly when defecation was completed (Figs. 2.9, 2.10, 2.11). However, possibly some of the soluble organic material may be attributed to the digestive process. Soluble organic products could have arisen through solublization of ingested food during digestion as suggested by Hargrave (1971) and Johannes and Webb (1970) for a variety of aquatic invertebrates. In addition, soluble organic products could arise during regurgitation of food or from ^{14}C exchange between discarded <u>D. pulex</u> remains and the water. Since there was a similarity between the loss of soluble excretory products and fecal production (Fig. 2.9, 2.10, 2.11), there is some evidence for this possibility. Both the loss of soluble organic products and fecal production decreased rapidly as the gut emptied. Also, at 5°C both the loss of fecal and soluble organic material increased with the larger ration. Consequently, if soluble organic products were derived from the digestive process, the loss of excretory products measured in this study was overestimated and may explain my apparently higher values. However, regardless of the origin of soluble excretory products, it is material that is not available for potential growth.

Most of the unincorporated food was accounted for as fecal production. Fecal production accounted for 20-26% of the ration except at conditions of moderate ration and constant low temperature where it accounted for 33% (Tables 2.1, 2.2; Fig. 2.11). Fecal production was estimated from the particulate material fraction. However, particulate material was not derived entirely from defecation. Underyearling sockeye salmon consume *D. pulex* whole, retain it for a period of time and then regurgitate the emptied carapace intact and other *D. pulex* remains. Regurgitation occurred throughout the period when the stomach contained food. Since fecal pellets also contained *D. pulex* remains and since fecal pellets decomposed in the water with time, it was not possible to separate fecal material from regurgitated food. Thus, fecal production may have been overestimated. On the other hand, there may have been a loss of fecal material through leaching. However, if leaching occurred, it was only early in the experiment as the percent in the particulate fraction remained constant following the completion of defecation.

Information in the literature on the effect of different temperatures on defecation by fish fed known rations is lacking. However, the effect of ration size on the length of time to complete defecation has been the subject of some study. Although it was not possible to separate fecal material from regurgitated food, defecation probably required longer to complete. Hence, in this study defecation was completed at 24-48 h after feeding at low rations and required 12 or 24 h longer at the larger ration (Fig. 2.11). Beamish (1972) reported that an increased ration size from less than 4% to 6-8% of dry body wt/day increased the time to complete defecation from 48 to 72 h after feeding in a 91 g largemouth bass (Micropterus salmoides) held at 15°C. The longer time for bass to complete defecation compared to young sockeye is probably related to the larger size of the bass. This view is supported by Beamish (1972) who reported that a 91 g bass required 12 h longer to complete defecation than a smaller bass (7 g).

The isotopic experiments failed to demonstrate a significant difference in growth potential between cyclic temperatures and the constant high temperature at both low and moderate rations and between cyclic temperatures and the constant low temperature at the low ration (Table 2.1, 2.2). In both cases, this lack of difference between cyclic temperatures and constant temperatures resulted from the cancellation of the effect of temperature on the rate of respiration by the effect of temperature on the rate at which food was incorporated. At both rations $^{14}CO_2$ respiration rate was significantly lower under cyclic temperatures than the constant high temperature

(Fig. 2.7, 2.8; Table 2.2). This demonstrated that young sockeye could reduce their metabolic costs under cyclic temperatures relative to constant high temperatures. The k-values of $^{14}CO_2$ respiration rate at the respective low and moderate rations were 40 and 50% lower under cyclic temperatures than at the constant high temperature. These savings in metabolic costs under cyclic temperatures could represent an 'energy bonus' available for more rapid growth. However, in this study this 'energy bonus' did not result in a greater growth potential. During the experimental period the rate at which food was incorporated cancelled out these savings in metabolic costs. Similarly, the trend in savings in metabolic costs under the constant low temperature compared to cyclic temperatures (Fig. 2.7, 2.8; Table 2.2) was cancelled by the effect of temperature on the rate of food incorporation.

At both rations incorporation rates measured in this study were also greatest at the constant high temperature and were greater under the cyclic temperature regime than at the constant low temperature (Fig. 2.4, 2.5; Tables 2.1, 2.2). Further, at both rations for each temperature the gastric evacuation rate and the incorporation rate were statistically not different ($P > 0.05$). Hence, at both rations labelled food was incorporated at the same rate at which the stomach moved the digested food into the intestine and pyloric and caeca; $15^{\circ}C$ > cyclic temperature regime > $5^{\circ}C$ (Fig. 2.2, 2.4, 2.5). Therefore, since both the rate of uptake of labelled food into fish tissues and its subsequent rate of loss from the tissues through respiration were in the same order with temperature, the net effect of temperature on growth potential through its influence on rates of incorporation and respiration was zero. Consequently, at both rations and at the low ration growth potential under cyclic temperatures was not different, respectively, from the constant high temperature and from the constant low temperature. Different duration of experimental periods might have changed this balance between uptake and loss and as a result altered my findings. However, as discussed above, only experimental periods that were too short (12 h) or too long (7 or 10 days) to assess growth potential would have altered my results (Table 2.4).

Gastric evacuation rates measured in this study were consistent with the results obtained by other workers using different methods and a variety of fish species fed pellets or small invertebrates (e.g., Kitchell and Windell, 1968; Windell et al. 1969; Tyler, 1970; Brett and Higgs, 1970; Elliott, 1972) who all reported that gastric evacuation rate is proportional to the stomach contents. In other studies (Hunt, 1960; Pandian, 1967; and Beamish, 1972), where fish were fed a few large organisms, the gastric evacuation rate was negligible for the first few hours after which the rate was constant. Further, gastric evacuation rates reported in this study exhibited the same relation to temperature and ration (i.e., increase with increasing temperatures and independent of ration size) as those reported in other studies (such as Molnár et al., 1967; Brett and Higgs, 1970; Tyler, 1970). However, the gastric evacuation rates that I measured were 1.7 and 1.5 times greater at 5°C and 15°C than those determined by Brett and Higgs (1970) on yearling sockeye (30-40 g) held at comparable temperatures and fed moist "1/8" Abernathy pellets. Since gastric evacuation rates are independent of fish size (Windell, 1966; Hunt, 1960; Tyler, 1970; Beamish, 1972; Elliott, 1972), these differences may be related to the higher ~~fat~~ content of the pelleted food. This view is supported by Elliott (1972) who studied the gastric evacuation in brown trout (_Salmo_ _trutta_) fed a variety of natural food organisms. His results were comparable to mine when the fish were fed _Gammarus_, chironomid or oligochaetes. However, he found a lower evacuation rate when the fish were fed _Hydropsyche_ which has a high fat content. This reduced rate was similar to those observed by Brett and Higgs (1970) for pelleted food.

The only previous data on directly measured incorporation by fish are those of Sorokin and Panov (1966). Their 49 mg bream larvae (_Abramis_ _brama_) feeding on ^{14}C labelled _Bosmina longirostris_ over a range of ration sizes incorporated 2.62-62.8 ug C/individual/2 h. To facilitate comparison I transformed incorporation results we both obtained to mgC/g/h. Using a carbon content of 3.95 mgC/g and 7.89 mgC/g wet wt fish for the low and moderate rations, respectively, I converted the total radioactivity incorporated (asymptotic values, Table 2.1) to carbon based on the assumption that radioactivity incorporated is proportional to carbon of the food ingested. Incorporation rates for bream larvae increased from 0.027 to 0.641 mgC/g/h with increasing rations from 15 to 1000 Bosmina/L. Incorporation rates for salmon averaged 0.141 mgC/g/h at the low ration and 0.225 mgC/g/h at the moderate ration. Assuming that Bosmina weigh one-fifth that of Daphnia, then at comparable rations incorporation rates for salmon are approximately 3 times lower than those for bream larvae. Although the temperature prevailing during their study is not stated, the larger size of the salmon could account for the lower values.

Other workers, such as Bourne (1959), Bell and Ward (1970), Hargrave (1970) used ^{14}C to directly measure incorporation of carbon in small aquatic invertebrates under varying experimental conditions. Despite considerable differences in test organisms, a brief comparison of results is useful. My results were expressed as calories incorporated as a per cent of total body calories of young sockeye. Monakov (1972) refers to this value as the index of assimilation. This transformation was based on a caloric content of 33.1 and 65.6 cal/kcal sockeye/day for the two rations, a caloric content of 6.05 kcal/g dry wt for sockeye and the assumption that radioactivity incorporated is proportional to caloric content of the food ingested. My results ranged from 2-4% and were less than values reported for invertebrates. Invertebrate values ranged from 7.1% for Hyalella azteca (Hargrave, 1970) to 30% for Daphnia magna (Schindler, 1968). Monakov (1972) reports that this index in most invertebrates feeding on natural food organisms at optimum concentrations varies widely but rarely exceeds 50%.

The ^{14}C experiments were designed to permit comparison of growth potential with observed growth reported in Chapter 1.

Growth Expt. 2 will be used for this comparison. The temperatures and fish size employed in this experiment are most comparable to those in the ^{14}C experiments. For purposes of comparison I converted the radioactivity measured for growth potential averaged over the duration of the experiment to calories assuming that radioactivity for growth potential is proportional to the calories of the labelled food ingested. At comparable temperatures and rations observed growth and growth potential, expressed in cal/kcal of fish per day, are shown in Fig. 2.12. In general, growth potential was greater than observed growth. The difference between observed and potential growth was greater at comparable low rations than at moderate rations and greater at the constant high temperatures than at the other temperatures. Further, growth potential and observed growth under cyclic and constant low temperature regimes, but not under cyclic and constant high temperature regimes, showed the same trends with temperature (Fig. 2.12). That is, at low rations both observed and potential growth under cyclic temperatures were not different from the constant low temperatures. At moderate rations both observed and potential growth were greater under cyclic temperatures than at the constant low temperatures. In contrast, at both rations potential growth under cyclic temperatures was not different from the constant high temperatures whereas observed growth was greater under cyclic temperatures than at the constant high temperature.

The discrepancies between observed growth and growth

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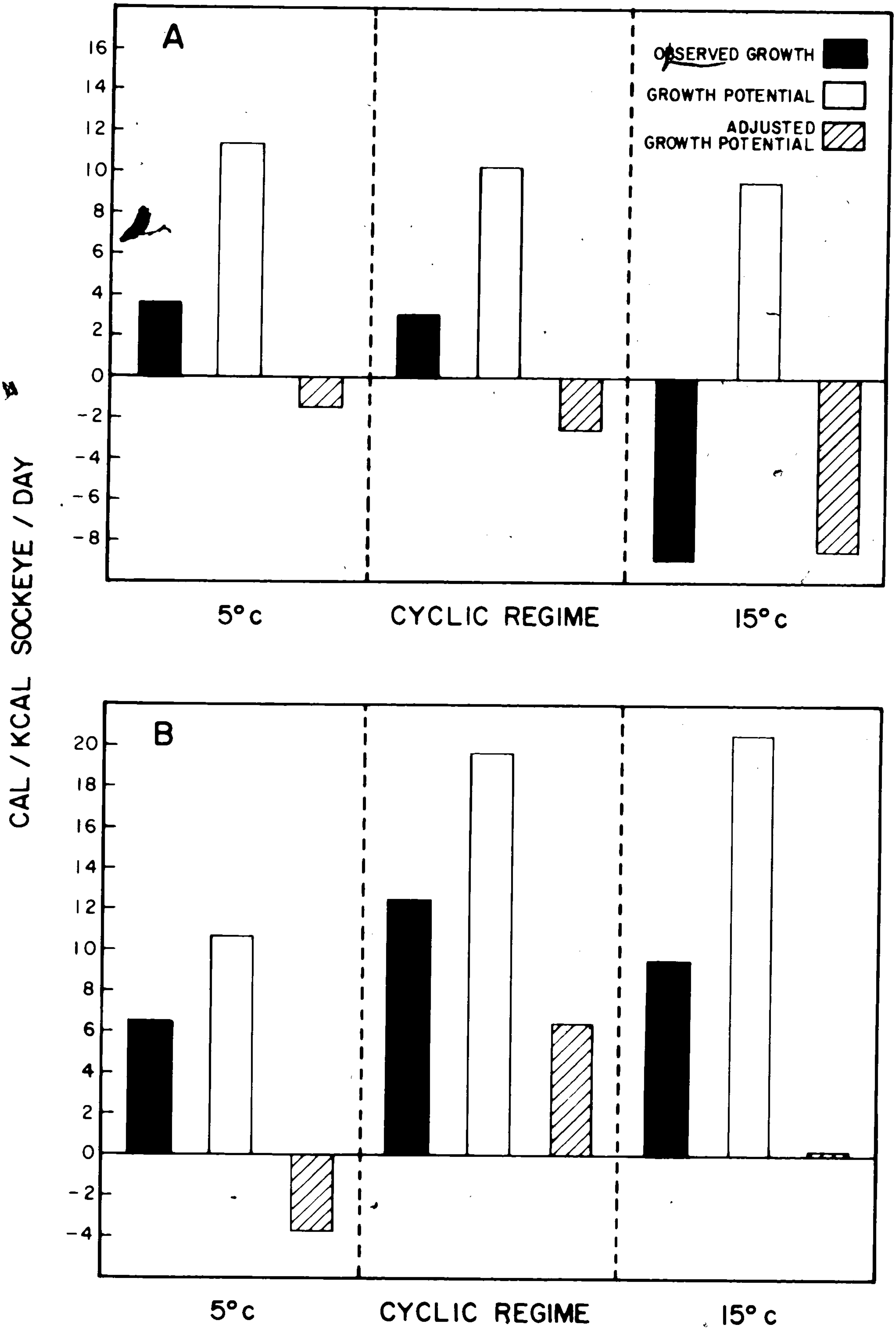
Figure 2.12 Growth potential converted to calories compared with observed growth rates reported in Chapter 1 as a function of temperature employed in the ^{14}C experiments. Comparable temperatures for growth experiment 2 (Chapter 1) were 6.2, 15.9°C and cyclic temperature regime. In A, fish were fed low rations of 33.1 cal/kcal sockeye/day (growth potential) and 46 cal/kcal/day (observed growth). In B, fish were fed moderate rations of 65.5 cal/kcal/day (growth potential) and 61 cal/kcal/day (observed growth). Adjusted growth potential, corrected for the low ^{14}C estimates of respiration, for each temperature and ration size is also shown.


A
OBSERVED GROWTH ■
GROWTH POTENTIAL □
ADJUSTED GROWTH POTENTIAL ▨
16
14
12
10
8
6
4
2
0
-2
-4
-6
-8
5°c
CYCLIC REGIME
15°c
CAL / KCAL SOCKEYE / DAY
B
20
18
16
14
12
10
8
6
4
2
0
-2
-4
5°c
CYCLIC REGIME
15°c

potential may have resulted from the limitation of the ^{14}C method to estimate metabolic costs (Conover and Francis, 1973). Organisms respire both labelled and unlabelled compounds simultaneously. Since fish were fed unlabelled food on days 2 and 3, labelled compounds available for respiration were reduced over the experimental period. The exponential curves shown in Fig. 2.4 and 2.5 reflect this time dependent decrease in ^{14}C respired values. Further, respiratory substrates may have been largely unlabelled since fish were fed unlabelled food during the pretreatment. To compare estimates of metabolic costs using ^{14}C with oxygen consumption data reported for 2 g sockeye salmon by Brett and Glass (1973), I converted the ^{14}C values to $mgO_2/kg/h$. Assuming that radioactivity respired is proportional to the carbon content of the food ingested, I converted for each temperature at the two ration levels the hourly mean ^{14}C respired value to carbon using a carbon content of 3.95 and 7.89 mgC/g wet wt fish for the respective low and moderate rations. The hourly mean ^{14}C value was calculated as the total ^{14}C respired during the experimental period divided by the duration of the experiment. Then, assuming a respiratory quotient of 1, I applied an oxygen-carbon equivalent of $1\ mgO_2 = 0.375\ mgC$ (Sorokin and Panov, 1966). The ^{14}C metabolic costs in $mgO_2/kg/h$ for the respective low and moderate rations were 50 and 83 at 15°C, 28 and 45 under the cyclic temperature regime and 23 and 28 at 5°C. At the two constant temperatures the ^{14}C metabolic rates were 1.5 to 2.6 times lower than the standard metabolic rates reported for these temperatures by Brett and

Glass (1973). Under the cyclic temperature regime, the $^{14}CO_2$ respiration rates were 4 to 6 times lower than the daily mean metabolic rate of 170 mgO_2/kg/h estimated for 2 g sockeye salmon exposed to comparable cyclic temperatures by Brett (1971a) and Brett and Glass (1973). Furthermore, since <u>D. pulex</u> probably contains a relatively high protein content (Brett 1971b), the respiratory quotient is probably less than 1, resulting in even lower ^{14}C respiration rates. Therefore, it seems likely that the ^{14}C method grossly underestimated metabolic costs.

To correct for the low $^{14}CO_2$ respiration rate, I estimated metabolic costs for each temperature from the daily mean metabolic rate of 170 mgO_2/kg/h reported for 2 g sockeye salmon under cyclic temperatures by Brett (1971a) and Brett and Glass (1973). I used this value directly for the cyclic temperature regime and adjusted it on the basis of the k-values of the $^{14}CO_2$ respiration rates (Table 2.1) for the constant temperatures. Thus, I estimated a daily mean metabolic rate for 15°C at low and moderate rations by increasing 170 mgO_2/kg/h by 40% for the low ration and 50% for the moderate rate. I estimated a daily mean metabolic rate for 5°C at low and moderate rations by decreasing 170 mgO_2/kg/h by 5% and 7%, respectively. The increase was based on the difference in the k-values at each ration between cyclic and the constant high temperature and the decrease was based on the difference in the k-values at each ration between cyclic and the constant low temperature. The daily mean metabolic rates in mgO_2/kg/h for the respective low and moderate rations were 238 and 255 at 15°C, 170 and 170 under cyclic temperatures and 161 and 158 at 5°C.

The corrected metabolic rates were used to calculate an adjusted growth potential. The daily mean metabolic rates were first converted to cal/kcal of fish per h by applying an oxycalorific equivalent of 3.36 cal/mgO_2 (Brett, 1976), a caloric value of 6.05 kcal/g dry wt fish and moisture content of 80% I obtained for experimental fish. Since growth potential is expressed in terms of an average for the experimental period, I then used the daily mean metabolic cost (cal/kcal of fish per h) to compute an average metabolic expenditure for the experimental period. This is, I calculated for each temperature at the two rations the metabolic cost which accumulated over the experimental period, measured the area under the curves and then divided by the duration of the experiment. An adjusted growth potential, in cal/kcal of fish per day, was then calculated for each temperature at the two ration levels as the growth potential minus the difference in metabolic expenditure between the corrected respiration rate (cal/kcal/day) and the $^{14}CO_2$ respiration (cal/kcal/day) which was obtained by compilations similar to those for the corrected respiration. The adjusted growth potential is compared with potential and observed growth on Fig. 2.12. For both rations at the three temperatures adjusted growth potential was less than observed growth except under conditions of low ration and 15°C. Thus, respiration may be overcorrected. However, both adjusted growth potential and observed growth showed the same order with temperature at low and moderate rations, respectively, 5 °C = cyclic temperature regime > 15 °C and cyclic temperature regime > 15 °C > 5 °C (Fig. 2.12). Hence, the lack of difference in growth potential between cyclic and the constant high temperature regimes may have resulted from a disproportionate low ^{14}C respiration rate at the constant high temperature. Therefore, growth potential, corrected for the low ^{14}C respiration rate, is in agreement with observed growth reported in Chapter 1.

To summarize the fates of consumed food described in this study, I calculated an energy budget using the equation $C = P+R+F+U$ (Ricker, 1958), where C is isotopic ration ingested, P is adjusted growth potential, R is corrected metabolic rate, F is fecal production and U is excretion. The budget, expressed in cal/kcal/day, for both rations at each temperature is shown in Table 2.5. Of the ration ingested 20 to 26% was lost through fecal production (F) and 17 to 20% was excreted (U) except at conditions of moderate ration and constant low temperature where 33% was lost through fecal production and 28% excreted (Table 2.5). Possibly both F and U may be overestimated because regurgitated food may be included. However, even if this were the case, it would not alter the proportion of food available for growth and respiration. Thus, 55-62% (C-F+U) of the ration was available for growth and respiration except at conditions of moderate ration and constant low temperature where it was 39%. Respiration accounted for 50 to 73% of intake at the low ration and 29 to

Table 2.5 - An energy budget for underyearling sockeye salmon fed low and moderate rations of ^{14}C labelled D. pulex and held under 15 ^{0}C, 5 ^{0}C and a diel cyclic temperature regime. The parameters of the budget are expressed in cal/kcal/day and as a percentage of ingested food (in brackets).

Temperature ^{0}C	Consumption C	Growth Potential Adjusted P	Respiration Corrected R	Fecal Production F	Excretion Release of soluble organic products U	Unaccounted for
Low Ration (Expts. 1 and 2)						
15	33.1	-8.6 (-26%)	24.2 (73%)	7.9 (24%)	5.6 (17%)	4.0 (12%)
Cyclic regime	33.1	-2.6 (- 7%)	17.3 (52%)	7.0 (21%)	5.6 (17%)	5.8 (17%)
5	33.1	-1.5 (- 4%)	16.4 (50%)	6.6 (20%)	6.6 (20%)	5.0 (14%)
Moderate Ration (Expt. 3)						
15	65.6	0.1 (< 1%)	30.1 (46%)	17.1 (26%)	12.5 (19%)	5.9 (9%)
Cyclic regime	65.6	6.5 (10%)	20.1 (31%)	13.8 (21%)	13.8 (21%)	11.4 (17%)
5	65.6	-3.5 (- 5%)	18.7 (29%)	21.6 (33%)	18.4 (28%)	10.4 (15%)

46% at the moderate ration. In addition, 9 to 17% of intake was unaccounted for. Therefore, at low rations the sum of R+F+U is greater than C (intake) and negative growth results. Similarly, fish fed moderate rations and held at 5°C results in negative growth. On the other hand, fish fed moderate rations and held under 15°C and cyclic temperatures accumulate < 1 to 10% of the ration as growth since all other uses and losses (R+F+U) are less than intake. Temperature affects growth through its influence on respiration (R). At the low ration R is greatest at 15°C and least at 5°C and as a consequence negative growth is greatest at 15°C and least at 5°C (Table 2.5). Similarly, at moderate rations 46% of the ration was used on respiration at 15°C leaving < 1% for growth, under cyclic temperatures 31% was expended on respiration leaving 10% for growth. In addition, both temperature and ration size affect growth through their influence on incorporation efficiency and excretion. Thus, at 5°C although only 29% of intake was expended on respiration, negative growth results as 61% was lost as fecal and soluble organic products and 15% was unaccounted for (Table 2.5).

The energy expended by underyearling sockeye salmon in the process of vertical migration has been neglected in the above calculations. Alexander (1972) estimated that the metabolic cost required to maintain a negatively buoyant fish at its daytime depth may be 25 $cm^3 O_2$/kg/h. As argued by Alexander, a swimbladder provides fifh with neutral buoyancy at the surface so that downward migration simply represents sinking (swimbladder becomes compressed) and upward migration represents rising. Then, at the daytime depth to avoid sinking fish must compensate hydrodynamically. Assuming that young sockeye remain 8 h at the daytime depth and then converting Alexander's estimate to cal/kcal/day, the cost of vertical migration for sockeye is 0.81 cal/kcal/day which is less than 5% of the daily metabolic rate and less than 3% of intake. This calculation agrees well with those of Vlymen (1970), Foulds and Roff (1976) and Swift (1976) which suggest negligible energy cost of vertical migration for zooplankton. Therefore, it is highly unlikely that the cost of vertical migration would cancel out the savings in respiration costs under cyclic temperatures compared to the constant high temperatures demonstrated in this study.

Growth experiments described in Chapter 1 showed that at moderate rations, but not at low or high rations, McLaren's (1963) 'energy bonus' concept for the adaptive value of vertical migration holds for underyearling sockeye salmon in Babine Lake. The isotopic experiments, corrected for low ^{14}C respiration costs, also supported at moderate rations, but not at low rations, McLaren's 'energy bonus' concept. Support for the hypothesis that growth is enhanced under cyclic temperatures and moderate rations depended partly on more energy incorporated and less energy excreted in relation to the constant low temperature than at low rations. However, an explanation for enhanced growth under cyclic temperatures over the constant high temperatures remain tenuous until more reliable data on respiration rates are available. The ration that is available for young sockeye in Babine Lake is probably in the order of 45 cal/kcal/day which is less than the moderate ration (Chapter 1). The lack of difference at the smaller ration probably has no significance in nature. Hence, the enhancement of growth under cyclic temperatures compared to constant temperatures described in this study give strong evidence that support McLaren's 'energy bonus' hypothesis and may explain the adaptive value of vertical migration of underyearling sockeye salmon in Babine Lake.

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Appendix 1

The change in wet weight of underyearling sockeye salmon held at constant temperatures of 15.3 °C, 11.3 °C and under a cyclic temperature regime in relation to time at rations of 1.3, 4.0, 5.4, 6.7% of dry body wt/day and excess.

Experiment 1

Time	Temperature °C		
Days	15.3	11.3	Cyclic regime
		Ration 1.3%	
0	199 mg	199	199
11	182	197	201
22	168	193	209
33	158	189	215
		Ration 4.0%	
0	199	199	199
11	197	207	218
22	201	217	245
33	200	226	263
		Ration 5.4%	
0	199	199	199
11	204	222	226
22	222	245	243
33	240	279	316
		Ration 6.7%	
0	199	199	199
11	233	245	243
22	274	302	266
33	313	331	363
		Excess Ration	
0	199	199	199
11	250	253	248
22	331	331	271
33	440	375	363

Appendix 2

The change in wet weight of underyearling sockeye salmon held at constant temperatures of 15.9°C, 6.2°C and under a cyclic temperature regime in relation to time at rations of 1.4, 5.5, 6.9% of dry body wt/day and excess.

Experiment 2

Time	Temperature °C		
Days	15.9	Cyclic regime	6.2
		Ration 1.4%	
0	966 mg	966	966
11	855	898	944
22	789	881	907
33	712	847	913
		Ration 4.1%	
0	966	966	966
11	898	1100	983
22	838	1100	1100
33	742	1060	1080
		Ration 5.5%	
0	966	966	966
11	973	1115	1100
22	1007	1213	1100
33	1041	1263	1180
		Ration 6.9%	
0	966	966	966
11	1110	1122	1109
22	1231	1334	1111
33	1291	1421	1171
		Excess Ration	
0	966	966	966
11	1210	1121	1120
22	1423	1320	1232
33	1647	1436	1263

Appendix 3

The distribution of ^{14}C, expressed as a percentage of ^{14}C ingested, among the various fractions after different times following ^{14}C feeding at 15°C, 5°C, or the cyclic temperature regime at the two rations. Each value represents the mean of seven measurements. The total ^{14}C recovered is shown as the sum of the mean percentage recovered among the various fractions after different periods of ^{14}C feeding at 15°C, 5°C, or the cyclic temperature regime. The overall mean percentage of ^{14}C recovered for each temperature is shown as well.

A. LOW RATION

Time h	Stomach Contents			Intest. Pyloric Caeca Contents			Particulate			Soluble Organic			Soluble Inorganic			Fish Tissue			Accounted For		
	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5
0.1	95	96	94	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	97	96	94
2	34	57	65	20	10	8	-	-	-	7	4	4	3	3	2	25	15	11	89	89	90
4	21	40	49	23	18	15	-	-	-	7	5	5	5	5	4	32	23	17	88	91	90
6	10	24	38	30	26	20	-	-	-	7	6	6	5	7	6	35	29	20	87	92	90
8	7	19	26	25	27	25	2	2	-	7	7	7	7	8	7	41	35	23	89	98	88
12	2	12	20	19	22	27	7	3	2	9	8	7	12	10	9	45	37	25	94	92	90
15	1	4	15	18	19	24	11	7	3	9	9	8	15	12	10	40	37	29	94	88	89
18	-	3	8	15	19	20	16	8	5	10	10	9	16	14	11	36	36	35	93	90	88
22	-	2	7	12	17	17	19	10	7	12	11	10	18	15	12	32	36	36	93	91	89
24	-	1	5	2	15	15	24	9	8	15	12	10	20	15	13	31	35	40	92	87	91
30	-	-	2	1	13	14	24	10	9	15	13	12	21	16	14	30	35	40	91	87	91
36	-	-	1	-	2	13	24	21	10	15	15	14	23	17	14	29	34	39	91	89	91
48	-	-	-	-	-	2	24	21	20	15	15	16	25	17	14	25	33	38	89	86	90
60	-	-	-	-	-	-	24	21	20	15	15	17	27	18	15	23	30	37	89	84	89
72	-	-	-	-	-	-	24	21	20	16	16	17	34	19	16	20	27	35	94	83	88
																		x	91.3	89.5	89.8

Appendix 3 (continued)

B. MODERATE RATION

Time h	Stomach Contents			Intest. Pyloric Caeca Contents			Particulate			Soluble Organic			Soluble Inorganic			Fish Tissue			Accounted For		
	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5	15	Cy	5
0.1	98	98	98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	98	98	98
4	34	48	68	20	18	10	-	-	-	5	3	1	7	4	3	27	20	9	93	93	91
8.1	51	50	65	12	16	13	1	1	-	4	4	3	9	4	3	29	15	11	106	90	95
12	12	26	35	20	20	26	4	2	1	11	7	8	10	7	4	39	31	17	96	93	91
15	3	15	27	22	23	29	6	4	3	12	8	12	11	8	4	40	32	18	94	90	93
18	2	9	20	19	21	30	10	5	4	13	10	14	13	9	5	41	34	20	98	88	93
24	-	4	11	10	12	32	14	9	8	14	17	15	14	11	7	40	38	21	92	91	94
36	-	-	3	1	6	23	23	16	17	16	18	19	14	12	8	39	36	20	93	88	90
48	-	-	1	-	1	15	26	21	26	16	19	23	15	13	9	36	34	18	93	88	92
60	-	-	-	-	-	2	26	21	33	17	19	25	16	14	9	28	32	16	87	86	85
72	-	-	-	-	-	-	26	21	33	17	20	26	22	16	10	25	29	15	90	86	84
84	-	-	-	-	-	-	26	21	33	18	21	27	33	18	11	15	24	14	93	84	85
																		x	94.3	89.5	90.9

- below detectable limits

Cy refers to the cyclic temperature regime