

AN ABSTRACT OF THE THESIS OF

Raymond R. Boyce for the degree of Master of Science
in Fisheries and Wildlife presented on February 22, 1985

Title: EFFECTS OF FEEDING LEVEL, TEMPERATURE, AND
PHOTOPERIOD ON GROWTH AND SELECTED SCALE CHARACTERISTICS
OF JUVENILE STEELHEAD TROUT

Abstract approved: Redacted for Privacy

The main and interactive effects of feeding level (constant repletion and temporary decrease to maintenance), temperature (temporary extreme decrease: 18 to 6 to 18°C; constant: 12°C; temporary moderate increase: 12 to 18 to 12°C; and temporary extreme increase: 12 to 24 to 12°C), and photoperiod (natural and retarded by 3 months) on growth rate, circuli spacing and deposition rate, and formation of checks on scales of juvenile steelhead trout (Salmo gairdneri gairdneri) were evaluated. Additionally, the effects of growth rate and season on circuli spacing and body length-scale radius and body length-circuli number relationships were determined.

Feeding and temperature level were the primary environmental factors affecting formation of scale characteristics because of the pronounced effects of these factors on body growth. Photoperiod was a secondary factor because it affected growth to a lesser extent and its

effects could be overridden by feeding level and probably temperature. Checks were formed when growth rate decreased and appeared one to two months after body growth had increased. Distinct checks, which would be interpreted as annuli by scale analysts, were formed on nearly all scales after body growth was sharply reduced by maintenance ration, regardless of temperature or photoperiod, or by sharp decreases or increases in temperature, regardless of feeding level. Indistinct checks, which probably would not be interpreted as annuli, were formed on 63-93% of fish after growth was somewhat decreased by moderate increases in temperature or by decreased natural and retarded photoperiod.

Feeding and temperature level may be involved in annulus formation in natural populations but there is no evidence in the literature to clearly demonstrate this hypothesis. However, this study and field observations suggest that false annuli may be produced by seasonally elevated water temperature. Fishery biologists may be able to predict the timing and occurrence of false annuli based on measurements of water temperature and knowledge of temperature-growth relationships. The interaction of increased fish activity due to increased daylength and elevated temperature during summer combined with low food supply may also be important in false annulus production.

Growth rate and season appeared to have some effect on slopes and intercepts of body length-scale radius regressions. Variation in body length-scale radius relationships due to growth rate and season caused

errors of 10-14% in back-calculated fish lengths. Back-calculations would be most accurate by using actual intercepts of length-scale radius regressions calculated each year and perhaps each season. Errors in the back-calculations of lengths of juveniles from adult scales may be reduced by only using length-scale radius relationships of the fastest growing and largest juveniles which would have the highest probability of surviving to adulthood.

The spacing of circuli can be used to obtain reasonably accurate back-calculations of body growth as long as the time period corresponding to the circuli spacing is known. Seventy-five percent of variation in length increase for cumulative days to sampling dates was accounted for by average circuli spacing. Measurements of band width (4, 6, and 11 outer circuli) were less accurate (34-60% of variation accounted for in length increase over one and two months) because variation in circuli deposition caused band widths to be formed over different time periods than growth was measured.

Effects of Feeding Level, Temperature, and
Photoperiod on Growth and Selected Scale
Characteristics of Juvenile Steelhead Trout

by

Raymond Ronald Boyce

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed February 22, 1985

Commencement June 1986

APPROVED:

Redacted for Privacy

Professor of Fisheries and Wildlife
in charge of major

Redacted for Privacy

Head of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

Date thesis is presented February 22, 1985

Typed by Cheryl A. Boyce for Raymond R. Boyce

ACKNOWLEDGEMENTS

I would like to thank my major professor, Dr. Carl B. Schreck, for his strong guidance and support in all areas of this work. I want to thank Dr. Norbert Hartmann, Jr., Dr. Harry Wagner, and Jim Martin for their valuable assistance in design and analysis of the study, and Jim Lichatowich, Steve Cramer, Barry McPherson, and Mary Buckman for their excellent reviews of the manuscript.

Thanks to Dick Ewing and Jean McCrea for their help in obtaining eggs and setting up incubation, rearing, and experimental equipment.

Thanks to Pat Probst for preparing graphics and Bob Kuhn for photographic assistance.

Thanks to Lori Turner for typing the rough draft and Holly Ketter and staff for typing the final tables.

And, most of all, thanks to my patient, loving, and wonderful wife Cheri for typing the manuscript.

TABLE OF CONTENTS

INTRODUCTION.....	1
METHODS AND MATERIALS.....	4
Experimental Design.....	4
Source and Culturing of Fish.....	8
Physical Environment.....	9
Sampling and Scale Analysis.....	11
Body-Scale Relationships.....	16
RESULTS.....	18
Effects of Feeding Level, Temperature, and Photoperiod on Body and Scale Growth.....	18
Effects of Growth Rate and Season on Body-Scale Relationships.....	37
DISCUSSION.....	50
Effects of Feeding Level, Temperature, and Photoperiod on Body and Scale Growth.....	50
Factors Influencing Check Formation in Natural Populations....	53
Effects of Growth Rate and Season on Body-Scale Relationships.....	59
BIBLIOGRAPHY.....	66

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Types of checks formed on scales of juvenile steelhead and scale measurements made	13
2. Monthly changes in body and scale growth in relation to feeding level and photoperiod in Experiment I	24
3. Monthly changes in body and scale growth in relation to feeding level and temperature in Experiment II	29
4. Fish length-scale radius regressions calculated for October-January and February-April in Experiment I	40
5. Fish length-circuli number regressions calculated for October-January and February-April in Experiment I	41
6. Correlations of monthly change in scale radius and circuli number to body length in Experiments I and II	47
7. Correlation of average circuli spacing to rate of body length increase for cumulative days to each sampling date in Experiment I and II	48

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Factorial designs of Experiment I and II	5
2. Feeding and temperature schedules used in Experiments I and II	6
3. The main and interactive effect means and analysis of variances for each body and scale parameter between feeding levels and photoperiods in Experiment I	19
4. The main effect means and analysis of variances for each body and scale parameter between feeding levels and temperatures in Experiment II	22
5. Comparison of growth rates during October-January and February-April in Experiment I	38
6. Regressions of body length on scale radius and body length on circuli number during October-January and February-April in Experiment I	39
7. Analysis of covariances of slopes and intercepts of length-scale radius and length-circuli number regressions in Experiment I	42
8. Back-calculated body lengths of steelhead in Experiment I	44
9. Correlations of average changes in scale measurements to body length, weight, and condition factor in Experiments I and II	46

EFFECTS OF FEEDING LEVEL, TEMPERATURE, AND PHOTOPERIOD
ON GROWTH AND SELECTED SCALE CHARACTERISTICS,
OF JUVENILE STEELHEAD TROUT

INTRODUCTION

Interpreting fish scale patterns to determine various life history characteristics is a useful tool available to the fishery biologist. The determination of age and growth from scales is based on two critical assumptions, namely that in temperate climates the seasonal decrease in body growth of the fish during winter is recorded as an annual check (annulus) of thin and narrowly-spaced circuli on the scale and that the spacing between circuli or annuli accurately reflects body growth (Ottaway and Simkiss 1979). If these assumptions are valid, it is possible to age fish by counting the number of annuli and to back-calculate growth during previous years by the distance between annuli (Tesch 1968) or by the width of bands of circuli (Reimers 1973).

There are three problems which can affect the accuracy of age and growth rate data derived from these techniques. First is variation in time of annulus formation. The average time of annulus formation can vary (two to three months) over the geographical range of a species (Beckman 1943; Reiger 1962), and smaller but still significant variations (up to one month) in formation time can occur between years within localized populations (Hansen 1937; Cooper 1951; Gerking 1966).

Second is the production of accessory checks termed "false annuli." False annuli form due to a temporary suppression of body growth rather than as part of the seasonal growth cycle of a fish. The occurrence of false annuli in natural populations can be quite high: 65-90% of brook trout (Salvelinus fontinalis) examined from four Adirondack Lakes showed false annuli on their scales (Hatch 1957) and of 159 adult pink salmon (Oncorhynchus gorbuscha) recovered in commercial fisheries, about one-third showed a false annulus near the center of the scale (Bilton and Ricker 1965). The third problem is variation in body-scale relationships. Ottaway and Simkiss (1979) showed that the body length-scale radius relationship of juvenile bass (Dicentrarchus labrax) was different when fish experienced high growth in summer from when they exhibited low growth in the fall. They determined that errors of up to 20% in back-calculated length could be produced by not using length-scale relationship calculated separately for each season.

Knowledge of the role of environmental factors in causing such variation in check formation and body-scale relationships can be used to improve accuracy of scale analysis techniques to determine age and growth. Because of their influence on body growth, feeding level, temperature, and photoperiod are believed to be key environmental factors influencing formation of scale characteristics, however, the relative effects of these factors have yet to be clearly demonstrated under controlled laboratory conditions. Efforts to correlate these environmental factors to variation in time of annulus formation (Bhatia 1932; Lagler et al. 1962; Gerking 1966; Bilton 1974; Bulow and

Heitman 1978) and formation of false annuli (Beckman 1943; Cooper 1951; Hatch 1957; Van Oosten 1961; Coble 1970; Hoefstede 1974; Ottaway and Simkiss 1977) in natural populations have been unsuccessful due to inter-correlations between factors. Similarly, studies to determine the role of photoperiod in causing variation in body-scale relationships (Lindroth 1960; Ottaway and Simkiss 1979) have been inconclusive due to the close correlation between season and fish growth.

The objectives of my study relevant to steelhead trout were to:

- 1) Determine the main and interactive effects of feeding level, temperature, and photoperiod on body growth rate, circuli spacing and deposition rate, and formation of checks on scales.
- 2) Determine the effects of growth rate and season on body-scale relationships.

This study aims at providing a basis for assessing the timing and occurrence of true and false annuli and variations in spacing and deposition of circuli and body-scale relationships so that the accuracy of techniques to determine age and growth can be improved.

METHODS AND MATERIALS

Experimental Design to Determine Effects of Feeding Level,
Temperature, and Photoperiod

Juvenile steelhead were reared under different feeding level, temperature, and photoperiod regimes (Table 1). In Experiment I, two feeding levels (constant repletion and temporary decrease to maintenance) were studied in relation to two photoperiods (natural and retarded by three months). Fish were fed a repletion or maintenance ration according to the schedule given in Table 2. Fish fed repletion rations were given all the feed they could consume in two 10 minute feedings per day. Fish fed maintenance ration were fed 25% of the ration recommended for maximum growth of rainbow trout (Leitritz and Lewis 1976) divided into two daily feeding periods. Fish in constant feed regimes were fed to repletion throughout the study (October-April). Fish in temporary decrease to maintenance feed regimes were fed repletion ration in October, maintenance feed in November and December, and repletion feed January-April. Fish were reared under a natural or under a 3-month retarded photoperiod where the seasonal low in daylength occurred in March, three months after the natural seasonal low (December). Feeding levels and photoperiods were selected to simulate natural fluctuations in food supply and photoperiod which may be important in formation of winter checks (annuli). Experiment I was

Table 1. Factorial designs of Experiments I and II used to evaluate effects of feeding level, temperature, and photoperiod. Appearing in the boxes are the abbreviations used for treatments. See Table 2 for feeding and temperature schedules.

<u>Experiment I</u>	<u>Feeding Level</u>	
<u>Photoperiod</u>	<u>Constant</u>	<u>Temporary Decrease</u>
<u>Natural</u>	CF/NL	DF/NL
<u>Retarded</u>	CF/RL	DF/RL

<u>Equipment II</u>	<u>Feeding Level</u>	
<u>Temperature</u>	<u>Constant</u>	<u>Temporary Decrease</u>
<u>Temporary Extreme Decrease</u>	CF/6°C	DF/6°C
<u>Constant</u>	CF/12°C	DF/12°C
<u>Temporary Moderate Increase</u>	CF/18°C	DF/18°C
<u>Temporary Extreme Increase</u>	CF/24°C	DF/24°C

CF = Constant repletion feed DF = Temporary decrease to maintenance feed

6°C = Temporary extreme decrease temperature (18 to 6 to 18°C)

12°C = Constant temperature (12°C)

18°C = Temporary moderate increase temperature (12 to 18 to 12°C)

24°C = Temporary extreme increase temperature (12 to 24 to 12°C)

NL = Natural photoperiod

RL = 3-month retarded photoperiod

Table 2. Feeding and temperature schedules used in Experiments I and II.

Experiment I Feeding Schedule October 1978 to April 1979

<u>Treatment</u>	<u>Oct</u>	<u>Nov</u>	<u>Dec</u>	<u>Jan</u>	<u>Feb</u>	<u>Mar</u>	<u>Apr</u>
CF/NL and CF/RL	CF	CF	CF	CF	CF	CF	CF
DF/NL and DF/RL	CF	DF	DF	CF	CF	CF	CF

Experiment II Feeding and Temperature¹ Schedule June to September 1979

<u>Treatment</u>		<u>Jun</u>	<u>Jul</u>	<u>Aug</u>	<u>Sep</u>
CF/6°C	Feeding Level	CF	CF	CF	CF
	Temperature	18°C	6°C	18°C	18°C
DF/6°C	Feeding Level	CF	DF	CF	CF
	Temperature	18°C	6°C	18°C	18°C
CF/12°C	Feeding Level	CF	CF	CF	CF
	Temperature	12°C	12°C	12°C	12°C
DF/12°C	Feeding Level	CF	DF	CF	CF
	Temperature	12°C	12°C	12°C	12°C
CF/18°C	Feeding Level	CF	CF	CF	CF
	Temperature	12°C	18°C	12°C	12°C
DF/18°C	Feeding Level	CF	DF	CF	CF
	Temperature	12°C	18°C	12°C	12°C
CF/24°C	Feeding Level	CF	CF	CF	CF
	Temperature	12°C	24°C	12°C	12°C
DF/24°C	Feeding Level	CF	DF	CF	CF
	Temperature	12°C	24°C	12°C	12°C

CF = Constant repletion feed which was all the feed fish could consume in two 10-minute feedings per day.

DF = Temporary decrease to maintenance feed which was 25% of the ration recommended for maximum growth of rainbow trout (Leitritz and Lewis 1976) divided into two daily feeding periods.

¹ Fish were acclimated to temperatures at 2°C/d.

analyzed as a 2x2 factorial replicated once to determine the main and interactive effects of feeding level and photoperiod.

In Experiment II, two feeding levels (constant repletion and temporary decrease to maintenance) were examined in relation to four temperature regimes: temporary extreme decrease (18 to 6 to 18°C); constant (12°C); temporary moderate increase (12 to 18 to 12°C); and temporary extreme increase (12 to 24 to 12°C). Fish in constant repletion feed regimes were fed to repletion throughout the study (June–September) and fish in temporary decrease to maintenance feed regimes were fed repletion ration in June, maintenance ration in July, and repletion ration in August and September (Table 2). In the constant 12°C regime, temperature was held at 12°C June–September. In all fluctuating temperature regimes, starting temperatures were held constant in June, fluctuated in July, and returned to starting temperatures in August and held constant in September. Fish were acclimated to temperatures at 2°C/d. These feeding level and temperature regimes were selected to simulate natural fluctuations in food supply and temperature which may be important in formation of annuli and in formation of false annuli during summer. Experiment II was analyzed as a 2x4 factorial replicated once to determine the main and interactive effects of feeding level and temperature. The hypotheses tested were, there were no differences in body growth rate, circuli spacing and deposition rate, and number of checks originating from different feeding levels, temperatures, and photoperiods each month.

Source and Culturing of Fish

Summer steelhead trout returning to Cole Rivers Hatchery on the Rogue River, Oregon, were used. Brood fish were spawned on March 14, 1978 and green eggs were brought to the Oregon Department of Fish and Wildlife Research Laboratory in Corvallis, disinfected with a iodine solution (Wescodyne ®), and incubated in the dark in Heath incubators at 10°C. On May 11, when the yolk sac was completely absorbed, fry were transferred to each of eight tanks for use in Experiment I. Additional fry for use in Experiment II were transferred to tanks and reared for 12 months. Steelhead were 6 and 15 months old from hatching and averaged 11 and 17 cm when Experiments I and II began, respectively.

Fish were fed Oregon Moist Pellet according to the feeding level, feeding frequency, and pellet size recommended for maximum growth of rainbow trout (Leitritz and Lewis 1976). Feeding levels and feeding frequencies were adjusted to account for average weight per fish and temperature in each tank. Forty-five and 30 fish from each tank were weighed each month in Experiments I and II, respectively, to determine average weight per fish in each tank.

Nine steelhead matured as yearlings during February 1979 in Experiment I. These fish were identified by their dark coloration and were removed from the tanks and not used in the study. Internal inspection revealed that all were precocious males.

There was a 2.5% mortality among fish which were being reared for Experiment II during May in 1979. Dying fish developed pop-eye,

turned dark in color, and remained near the water surface. Fresh samples of dead fish were examined for disease by pathologists of the Oregon Department of Fish and Wildlife but no pathogens were detected externally or internally. Although cause of the mortality was not resolved, mortality subsided after one month of treatment with terramycin. Mortality was negligible ($<0.1\%$) and all fish appeared healthy in June when the experiment began.

Physical Environment

Circular fiberglass tanks used in Experiments I and II were 1.5 m in diameter except for two tanks in Experiment II (CF/12°C and DF/12°C) which were 1.8 m in diameter. Water volumes in each tank were generally maintained at 830 l, however it was necessary to increase volumes up to 1020 l in some tanks in Experiment I so that loading densities of fish in each tank did not exceed recommended levels by Westers (1970). Flow rates of 6 l/min were maintained in tanks receiving ambient (12°C) or chilled (6°C) water. Flow rates into tanks receiving heated water (18°C and 24°C temperature regimes) in Experiment II were less (5.3 - 5.6 l/min) due to limited heating capacity and output of the water heater used. Water turnover rates in tanks were approximately 0.5/hr. Water velocities were maintained at approximately 10-15 cm/sec in each tank to not only facilitate cleaning of tanks but to maintain uniform swimming activity of fish reared under different temperatures. It was necessary to insure a uniform swimming speed since Brett et al. (1969) has shown that spontaneous swimming activity is temperature-dependent in salmonids.

To alleviate problems with low dissolved oxygen and gas supersaturation (principally nitrogen) at elevated temperatures, inflow nozzles were fitted with caps drilled with fine holes to spray water into tanks. Dissolved oxygen, measured by titration using the Alsterberg modification of the Winkler method, ranged from 6.2 - 9.4 mg/l (63-89% saturation). Gas saturation was measured with a saturonometer and ranged from near saturation to 2% above saturation. These ranges of dissolved oxygen and gas saturation are considered to be non-limiting to growth of salmonids (Stewart et al. 1967; Dawley and Ebel 1975).

Water was heated with a 500,000 w water heater and chilled with a 25 hp chiller. Decreased and elevated temperatures were achieved by mixing ambient water with chilled or heated water. Temperature was regulated by contact thermometers (B. Braun Co.) installed on the tanks and relayed by super-sensitive relays (American Instrument Co.) to solenoids that added heated (35°C) or chilled (6°C) water as required. Mean temperatures achieved were within 0.10°C of targeted levels and 95% confidence intervals were less than 0.08°C.

To assess effects of photoperiod, fish in Experiment I were reared under a natural (NL) or a 3-month retarded (RL) photoperiod. Rearing tanks for the retarded photoperiod were equipped with light-proof hoods and illumination was provided by 122 cm 40 w Vita-lite fluorescent lamps that have spectral characteristics similar to natural sunlight. Distance to the water surface was approximately 90 cm. Under the natural photoperiod regime, illumination were

provided by overhead 244 cm fluorescent lamps (Vita-lite 40 w) in the laboratory and natural light entering through south-facing windows of the laboratory. Lamps were suspended approximately 150 cm above the water surface.

Photoperiods as provided by fluorescent lamps were controlled by astral timers (Sagamo Co.) which automatically adjusted for natural seasonal advancements in astronomical daylength. I adjusted timers so that the seasonal low in daylength in the retarded regimes occurred in March, three months after the natural seasonal low (December). Daily illumination was provided between sunrise and sunset (Corvallis time, U.S. Naval Observatory 1976) with no twilight in the morning and evening .

Sampling and Scale Analysis

Each month, 45 and 30 fish from each tank in Experiments I and II, respectively, were randomly selected, killed, weighed (wet weight) to the nearest 0.1 gram and measured in fork length to the nearest 0.1 cm. Only 30 fish were sampled in Experiment II due to a large number of tanks and a limited number of fish. Sample sizes of 45 produced estimates of the true value of length within 5% and weight within 10% at the 95% confidence level (Snedecor and Cochran 1967). Sample sizes of 30 produced estimates of the true value of length and weight within 10 and 15%, respectively, at the 95% level.

Sub-samples of 15 fish were sampled for scales and approximately 10 scales were scraped from a key scale area which was the area

between the dorsal and adipose fins two scale rows above the lateral line along a posteriorly directed diagonal from the posterior insertion of the dorsal fin (Clutter and Whitesel 1956). Three or four non-regenerated and regularly shaped scales were mounted per fish. In Experiment I, scales were mounted on glass slides using a mounting solution of 5% glycerin and 95% water glass (Clutter and Whitesel 1956). In Experiment II, scales were mounted on gummed cards and impressed on acetate at 100°C under 350 kg/cm^2 pressure for three minutes.

Two scales were read per fish. Scales were read at a magnification of 88X with a Microfiche Reader (Micro Design 4020) which was modified to project the scale image on a screen. Scale measurements and circuli counts were made on the screen at a 20° angle from the longitudinal midline of the scale along the longest side of the anterior region (Fig. 1). Radius of the nucleus, checks, the outer edge of the scale, and band widths of 4, 6, and 11 outer circuli were measured to the nearest 0.5 mm. Circuli were counted from the nucleus to the first thick circulus demarcating the check and to the edge of the scale. Band widths and average circuli spacing $[(\text{total scale radius} - \text{nucleus radius}) / (\text{total circuli number})]$ were the measures of circuli spacing and number of circuli deposited each month was the measure of circuli deposition rate.

Checks were identified by the presence of two to four circuli which were more narrowly spaced or thinner in diameter when compared to surrounding circuli. Checks were classified into two broad

Distinct Treatment Check

Indistinct Treatment Check

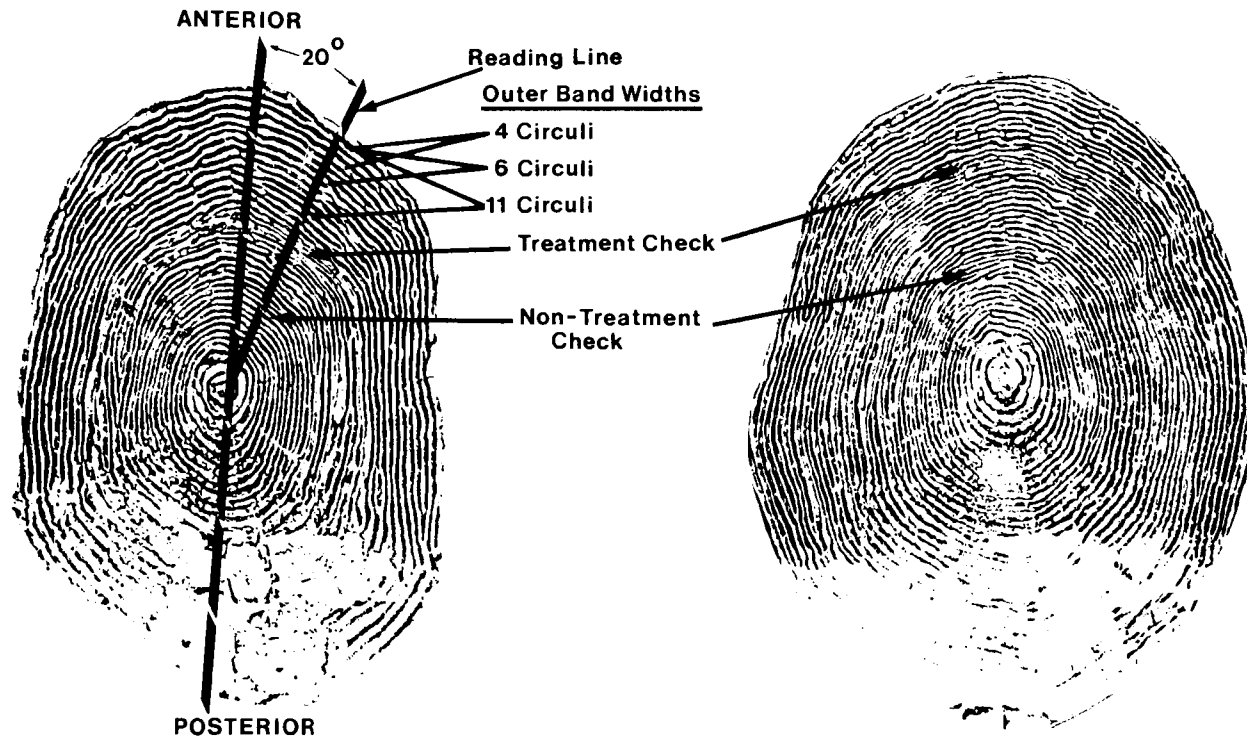


Fig. 1. Types of checks formed on scales of juvenile steelhead in the experiments. Scale at left is from a 22.2 cm fish sampled from DF/NL on 4/16/79 and scale at right is from a 23.4 cm fish sampled from CF/NL on 4/16/79. The 20° reading line used and band width measurements are shown.

categories, distinct or indistinct. Distinct checks were conspicuous marks on scales with "annulus-like" features: two to four thin, narrowly spaced, and irregular (broken, branched, clubbed, etc.) circuli followed by and often "crossed-over" by thicker, more widely spaced and regular circuli (Fig. 1). Indistinct checks were less conspicuous due to less contrast between circuli in checks and surrounding circuli (Fig. 1). Although circuli in these checks were incomplete and more narrowly-spaced, they were not always thinner in diameter or irregular when compared to surrounding circuli. These checks probably would not be interpreted as annuli by scale analysts.

I did not initiate experiments for at least six weeks after fish were transferred to allow adequate separation of "non-treatment" and "treatment" checks on scales. In addition to checks formed during the experiments, which I term "treatment" checks, most fish had other checks which were deposited prior to experimentation. These checks deposited prior to experimentation, which I term "non-treatment" checks, were commonly formed after fish were transferred from tanks used for rearing of fish to those used in the experiments. Soon after fish were transferred they began to feed and grow vigorously. From weekly inspections of scales I determined that it took about two weeks for the non-treatment checks to form. The checks may have been formed because fish were too crowded in the rearing tanks and consequently had decreased growth. Alternatively, the checks may have been caused by handling since handling has been shown to result in false annuli (Coble 1970; Bilton 1974).

Both myself and the person assisting me in analysis of scales used visual criteria (i.e., appearance of circuli) to identify checks. To determine differences between readers in check identification using visual criteria, we independently analysed a sample of scales in Experiment I for number of checks. We read scales from constant repletion feed (CF/RL and CF/NL) regimes February-April and temporary decrease to maintenance feed (DF/RL and DF/NL) regimes in April. Checks formed in CF (indistinct; Fig. 1) and DF (distinct; Fig. 1) feed regimes were representative of types of checks formed in the experiments. For DF regimes, we were in perfect (100%) agreement in number of checks formed (60 out of 60 scales examined). For CF regimes, I recorded 81 checks and the other analyst recorded 99 checks of 180 scales examined. A chi-square analysis revealed the difference (9%) was insignificant ($\chi^2 = 2.84$, 1 df, $P > 0.05$). On the basis of these comparisons, I feel reasonably certain that differences between readers were small and that the results of the study are comparable to those that would be obtained by other scale analysts using visual criteria.

We did not determine differences between readers in scale measurements and circuli counts. However, on the basis of comparisons of several scale readers using scales from steelhead from the Rogue River (unpublished data, Raymond R. Boyce, Oregon Department of Fish and Wildlife, Portland, Oregon), these differences should be insignificant.

Body-Scale Relationships

The effects of growth rate and season on body-scale relationships were determined from comparisons of regressions of body length-scale radius and body length-circuli number calculated for two time periods in Experiment I, October-January and February-April. Due to restricted ration, growth rates varied up to three-fold between treatments within time periods and between time periods within treatments.

To illustrate how effects of growth rate and season can cause errors in calculations of growth, I compared back-calculated fish lengths using 1) actual intercepts of body length-scale radius regressions calculated for each treatment during the October-January and the February-April period, and 2) a standard intercept (3.5) commonly used in growth studies of steelhead (Peterson 1978; Cramer and Martin 1978). Back-calculated lengths were determined with the Lee-Fraser formula (Tesch 1968):

$$L_n = \frac{S_n}{S} (L - C) + C$$

Where: L_n = length of fish at time n
 L = length of fish at sampling
 S_n = scale radius at time n
 S = scale radius at sampling
 C = intercept of body length-scale radius regression

Lengths were estimated at scale radii of 25, 50, and 100.

To determine relationships between incremental body and scale growth, I calculated correlations between changes in body growth (as measured by body length and weight and condition factor) and scale measurements used to estimate body growth (scale radius, circuli number, band width of 4, 6, and 11 outer circuli, and average circuli spacing) for each treatment in Experiments I and II. Changes in length, weight, circuli number, scale radius, and average condition factor were based on average differences between successive months. Because band widths represented spacing between circuli and hence body growth one to three months previous, I used length and weight change during one and two previous months and condition factor averaged for the month of sampling and the one and two previous months. There was insufficient data to calculate regressions of band widths on body growth during three previous months.

Since average circuli spacing is assumed to be a measure of average body growth during all previous months, I used average rate of increase in body length (cm/d) and weight (grams/d) from the estimated average date of formation of the first circulus (May 1, 1978¹) to each sampling date.

¹Determined from examination of scales during April and May, 1978.

RESULTS

Effects of Feeding Level, Temperature, and Photoperiod on Growth Rate, Circuli Spacing and Deposition Rate, and Formation of Checks

Feeding level and temperature were the primary environmental factors affecting formation of scale characteristics in juvenile steelhead largely due to the effects of these factors on body growth. These results on effects of feeding level, temperature, and photoperiod are shown in two ways. First, Tables 3 and 4 show the main and interactive means and analysis of variances for each body and scale parameter by treatment in Experiments I and II. Secondly, to illustrate relationships between feeding level, temperature, and photoperiod and incremental body and scale growth, monthly changes (Δ) in length, condition factor, scale radius, circuli number, and band width of 4 outer circuli, and percentage of checks formed are shown for selected treatments (Figs. 2 and 3).

In both experiments when ration was decreased to maintenance, steelhead showed little monthly gain in length, weight, scale radius, and circuli number, and showed low condition factor and narrow band widths regardless of photoperiod (Tables 3 and 4; Figs. 2A and 2B). Changes in average circuli spacing were generally insignificant. After ration had been increased to repletion for one month, fish showed sharp increases in body and scale growth and distinct "annulus-like" checks appeared on 93-100% of fish.

Table 3. Analysis of variances of length, weight, condition factor, scale radius, circuli number, band width, average circuli spacing, and checks between feeding levels and photoperiods in Experiment I.

		Main Effects Means ^{1 2}						Standard Error of FL & Means
		Feeding Level			Photoperiod			
	Month	CF	DF	F Diff. ³	RL	NL	F Diff. ³	
Length (cm)	Oct.	11.01	10.79	7.37	11.05	10.76	12.83*	0.06
	Nov.	12.39	12.35	0.11	12.58	12.16	1.54	0.24
	Dec.	14.35	12.72	14.08*	14.08	12.98	6.44	0.31
	Jan.	16.87	13.45	1548.05**	15.74	14.57	181.50**	0.06
	Feb.	18.10	15.56	40.17**	16.78	16.87	0.05	0.03
	Mar.	19.58	17.27	123.87**	18.05	18.80	12.98*	0.15
	Apr.	22.11	20.55	18.96**	20.52	22.14	20.63*	0.25
Weight (g)	Oct.	16.00	16.30	0.04	17.00	15.30	1.16	1.10
	Nov.	24.15	24.70	0.09	26.05	22.80	3.15	1.27
	Dec.	40.65	24.15	40.68**	35.45	29.35	5.75	1.78
	Jan.	58.15	26.65	96.56**	46.05	38.75	5.93	2.15
	Feb.	78.70	45.65	58.13**	66.05	58.30	3.39	2.96
	Mar.	96.35	68.15	25.37*	79.05	85.05	1.05	3.84
	Apr.	135.10	101.45	24.07*	112.00	124.55	3.50	4.70
Condition Factor	Oct.	1.278	1.251	0.97	1.269	1.260	0.11	0.019
	Nov.	1.254	1.263	0.26	1.255	1.262	0.18	0.013
	Dec.	1.254	1.123	14.57*	1.186	1.191	0.02	0.025
	Jan.	1.210	1.096	63.88**	1.149	1.157	0.03	0.010
	Feb.	1.235	1.215	0.66	1.243	1.207	2.18	0.018
	Mar.	1.204	1.240	1.30	1.215	1.228	0.16	0.022
	Apr.	1.235	1.222	0.32	1.252	1.205	4.50	0.016
Scale Radius (mm x 88)	Oct.	43.61	43.61	0.00	44.16	43.06	7.04	0.29
	Nov.	52.06	52.82	1.09	53.31	51.56	5.88	0.51
	Dec.	60.48	53.95	27.15*	60.51	53.92	27.67*	0.89
	Jan.	73.18	58.44	469.74**	68.53	63.09	63.96**	0.48
	Feb.	79.04	68.07	26.03*	73.23	73.88	0.09	1.52
	Mar.	86.93	77.31	35.72*	79.27	84.97	12.48*	1.13
	Apr.	99.22	93.81	12.31*	91.66	101.38	39.68**	1.09
Circuli Number	Oct.	19.05	19.58	2.93	19.32	19.32	0.00	0.22
	Nov.	23.82	24.38	1.50	24.33	23.87	1.02	0.33
	Dec.	28.08	25.38	128.65**	27.62	25.85	55.08**	0.17
	Jan.	31.62	25.87	250.23**	29.65	27.83	24.98*	0.25
	Feb.	33.47	29.37	36.28**	31.37	31.47	0.02	0.48
	Mar.	35.60	33.48	6.12	33.78	35.30	3.14	0.60
	Apr.	40.88	38.78	12.74*	38.78	40.88	12.74*	0.42

Table 3. cont.

		Main Effects Means ^{1 2}						Standard Error of FL & Means
		Feeding Level			Photoperiod			
	Month	CF	DF	F Diff. ³	RL	NL	F Diff. ³	
Band Width	Oct.	6.15	5.82	2.68	6.36	5.62	13.31*	0.14
of 4 Outer	Nov.	6.01	6.15	0.47	6.42	5.75	10.63*	0.14
Circuli	Dec.	6.19	5.29	18.29*	6.32	5.15	30.86*	0.15
(mm x 88)	Jan.	6.17	4.82	55.33**	5.81	5.17	12.65*	0.12
	Feb.	6.47	6.64	0.71	6.19	6.92	12.74*	0.14
	Mar.	6.83	7.49	10.86*	6.28	8.04	77.69**	0.14
	Apr.	7.31	7.68	4.49	7.11	7.88	19.30*	0.12
Band Width	Oct.	9.55	9.18	2.69	9.50	9.23	1.38	0.16
of 6 Outer	Nov.	9.33	9.70	5.22	9.59	9.44	0.91	0.11
Circuli	Dec.	10.51	9.42	12.24*	10.62	9.32	17.42*	0.22
(mm x 88)	Jan.	11.05	10.01	19.74*	11.03	10.04	18.02*	0.17
	Feb.	10.97	9.95	74.29*	9.98	10.94	67.18*	0.08
	Mar.	11.80	11.97	0.31	10.83	12.94	47.72*	0.22
	Apr.	12.28	13.10	6.63	11.81	13.58	30.97*	0.22
Band Width	Oct.	19.12	18.44	2.92	18.97	18.60	0.86	0.28
of 11 Outer	Nov.	18.16	18.59	5.10	18.54	18.20	3.32	0.14
Circuli	Dec.	19.81	18.65	8.33	20.19	18.27	22.49*	0.29
(mm x 88)	Jan.	21.96	19.74	31.52*	21.64	20.07	15.65*	0.28
	Feb.	22.27	19.61	19.29*	21.10	20.78	2.78	0.43
	Mar.	23.10	21.66	5.36	21.01	23.76	19.53*	0.44
	Apr.	23.87	25.28	8.42	22.59	26.57	62.04*	0.34
Average	Oct.	2.03	1.99	0.79	2.04	1.99	1.48	0.03
Circuli	Nov.	1.95	1.96	0.03	1.97	1.94	0.99	0.02
Spacing	Dec.	1.97	1.93	1.84	2.01	1.90	11.55*	0.02
(mm x 88)	Jan.	2.16	2.07	5.07	2.14	2.09	2.32	0.03
	Feb.	2.20	2.15	1.76	2.16	2.19	0.47	0.03
	Mar.	2.29	2.17	6.78	2.17	2.28	4.95	0.03
	Apr.	2.33	2.31	0.26	2.26	2.38	26.72*	0.02
Checks	Oct.	1.00	1.00	0.00	1.00	1.00	0.00	0.00
($\sqrt{x + 1.0}$)	Nov.	1.00	1.00	0.00	1.00	1.00	0.00	0.00
	Dec.	1.00	1.00	0.00	1.00	1.00	0.00	0.00
	Jan.	1.00	1.00	0.00	1.00	1.00	0.00	0.00
	Feb.	1.17	1.41	334.09**	1.22	1.35	98.45**	0.01
	Mar.	1.14	1.41	169.00**	1.22	1.34	32.11*	0.01
	Apr.	1.28	1.41	98.45**	1.34	1.36	2.44	0.01

Table 3. cont.

		<u>Interactive Means</u> ^{1 4}				<u>Standard Error of</u>	
		<u>CF/RL</u>	<u>CF/NL</u>	<u>DF/RL</u>	<u>DF/NL</u>	<u>F Inter.</u> ³	<u>Treatment Means</u>
Condition							
Factor	Jan.	1.239	1.181	1.059	1.133	21.05*	0.014

¹ Means are averaged from replicates (n=60). There were no significant differences ($P > 0.05$) between replicates.

² No significant ($P > 0.05$) feeding level and photoperiod interaction.

³ Degrees of freedom = 1,3.

⁴ Significant ($P < 0.05$) feeding level and photoperiod interaction.

** Indicates significance at $P < 0.01$.

* Indicates significance at $P < 0.05$.

CF = Constant feed DF = Temporary decrease to maintenance feed

RL = 3-month retarded photoperiod NL = Natural photoperiod

FL = Feeding level P = Photoperiod

Table 4. Analysis of variances of length, weight, condition factor, scale radius, circuli number, band width, average circuli spacing, and checks between feeding levels and temperatures in Experiment II.

		Main Effects Means ^{1 2}									
	Month	Feeding Level		F Diff. ³	Standard Error	Temperature				F Diff. ⁴	Standard Error
		CF	DF			6°C	12°C	18°C	24°C		
Length (cm)	Jul.	18.80	19.08	1.97	0.14	18.60	19.34	19.06	18.74	2.74	0.20
	Aug.	19.87	19.40	7.00*	0.13	19.08	20.52	19.95	19.00	16.81**	0.18
	Sept.	22.05	21.27	79.26**	0.06	20.89	22.46	22.68	20.60	148.40**	0.09
Weight (g)	Jul.	80.22	83.23	1.86	1.58	78.23	86.08	83.10	79.47	2.53	2.24
	Aug.	99.44	82.76	28.46**	2.21	82.81	108.60	99.59	73.40	25.91**	3.13
	Sept.	142.96	125.50	50.62**	1.74	121.27	152.69	156.65	106.31	99.14**	2.45
Condition Factor	Jul.	1.192	1.185	0.46	0.08	1.200	1.177	1.188	1.188	0.83	0.011
	Aug.	1.226	1.116	101.52**	0.08	1.173	1.228	1.232	1.052	59.52**	0.011
	Sept.	1.282	1.279	0.07	0.08	1.305	1.306	1.317	1.194	26.00**	0.011
Scale Radius (mm x 88)	Jul.	81.41	83.52	3.84	0.76	83.42	82.36	82.35	81.73	0.42	1.07
	Aug.	87.24	86.23	0.46	1.07	83.02	90.36	89.76	83.81	6.54*	1.51
	Sept.	98.53	93.03	32.21**	0.69	93.97	99.41	99.62	90.14	22.33**	0.97
Circuli Number	Jul.	41.25	41.28	0.00	0.28	41.50	41.53	40.45	41.60	1.97	0.39
	Aug.	44.03	43.38	2.13	0.32	42.22	45.17	45.33	42.10	15.68**	0.45
	Sept.	49.24	46.52	27.27**	0.37	47.17	48.73	49.65	45.97	9.83**	0.52
Band Width of 4 Outer Circuli (mm x 88)	Jul.	6.19	6.28	0.68	0.08	6.13	6.37	6.28	6.18	0.96	0.10
	Aug.	5.74	5.14	27.56**	0.08	5.14	5.98	5.46	5.18	12.04**	0.11
	Sept.	6.58	6.56	0.03	0.08	7.14	6.66	6.25	6.14	16.87**	0.11
Band Width of 6 Outer Circuli (mm x 88)	Jul.	9.46	9.72	1.88	0.14	9.62	9.52	9.88	9.33	1.48	0.19
	Aug.	9.81	9.65	0.84	0.12	9.22	10.40	9.57	9.73	8.26*	0.17
	Sept.	10.38	9.80	10.41*	0.13	9.91	11.06	10.19	9.20	17.62**	0.18

Table 4. cont.

	Month	Main Effects Means ^{1 2}									
		Feeding Level		F Diff. ³	Standard Error	Temperature				F Diff. ⁴	Standard Error
		CF	DF			6°C	12°C	18°C	24°C		
Band Width	Jul.	19.29	19.92	2.65	0.28	19.66	19.41	19.98	19.36	0.53	0.39
of 11 Outer	Aug.	19.86	19.50	1.12	0.24	19.16	20.47	19.27	19.82	3.13	0.34
Circuli	Sept.	20.27	19.31	11.10*	0.20	19.31	21.46	19.77	18.60	17.96**	0.29
Average	Jul.	1.81	1.86	5.18	0.02	1.84	1.82	1.87	1.81	1.51	0.03
Circuli	Aug.	1.82	1.83	0.02	0.02	1.80	1.85	1.83	1.81	1.28	0.03
Spacing	Sept.	1.85	1.85	0.01	0.02	1.83	1.90	1.86	1.80	2.87	0.04
(mm x 88)											
Checks	Jul.	1.00	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	0.00
($\sqrt{x + 1.0}$)	Aug.	1.00	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	0.00
	Sept.	1.30	1.41	198.39**	0.01	1.41	1.21	1.40	1.39	167.01**	0.01

¹ Means are averages from replicates (n = 60). There were no significant differences (P > 0.05) between replicates.

² No significant (P > 0.05) feeding level and temperature interaction.

³ Degrees of freedom = 1,7.

⁴ Degrees of freedom = 3,7.

** Indicates significance at P < 0.01.

* Indicates significance at P < 0.05.

CF = Constant repletion feed.

DF = Temporary decrease to maintenance feed.

6°C = Temporary extreme decrease temperature (18 to 6 to 18°C).

12°C = Constant temperature (12°C).

18°C = Temporary moderate increase temperature (12 to 18 to 12°C).

24°C = Temporary extreme increase temperature (12 to 24 to 12°C).

Fig. 2. Monthly changes (Δ) in body length, scale radius, circuli number, and condition factor and band width of 4 outer circuli, and percentage of checks formed in relation to feeding level and photoperiod in Experiment I. Increments in body length, scale radius, and circuli number could not be calculated for the first month of sampling (October). Sample sizes: $n = 90$ (length and condition factor) and $n = 60$ (all scale measurements).

- A. Temporary decrease to maintenance feed/Natural photoperiod (DF/NL)
- B. Temporary decrease to maintenance feed/Retarded photoperiod (DF/RL)
- C. Constant repletion feed/Natural photoperiod (CF/NL)
- D. Constant repletion feed/Retarded photoperiod (CF/RL)

DF/NL

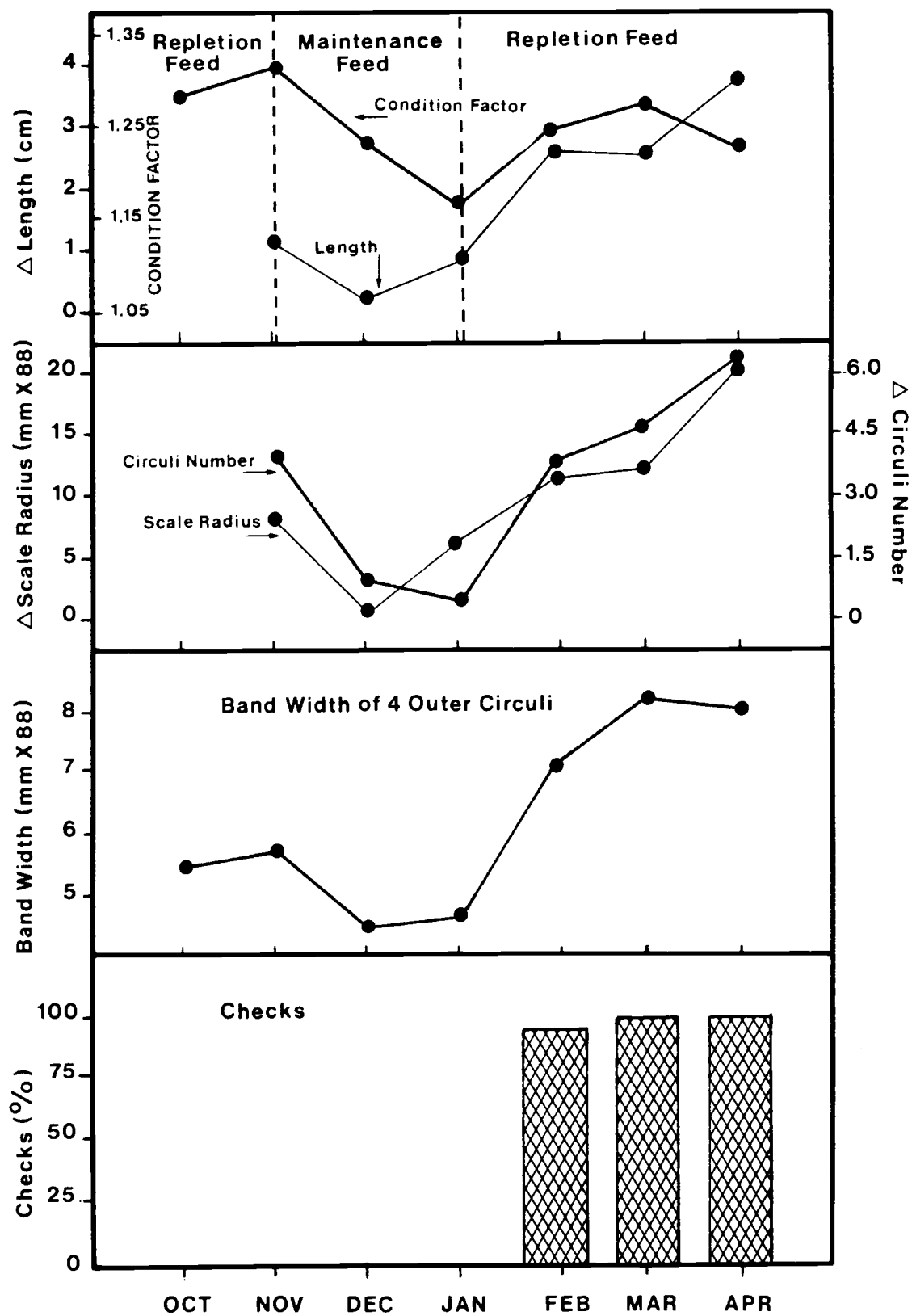


Fig. 2A.

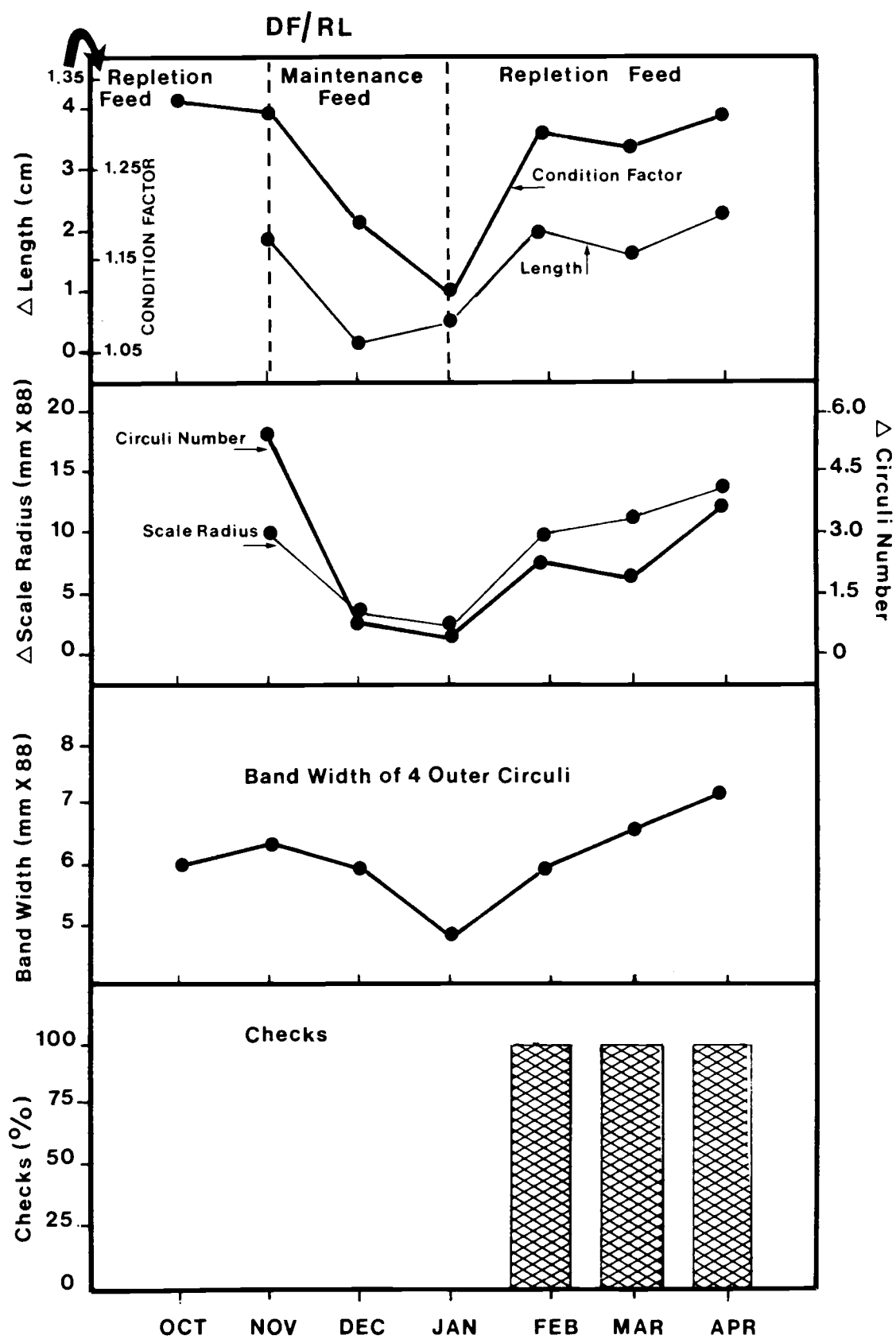


Fig. 2B.

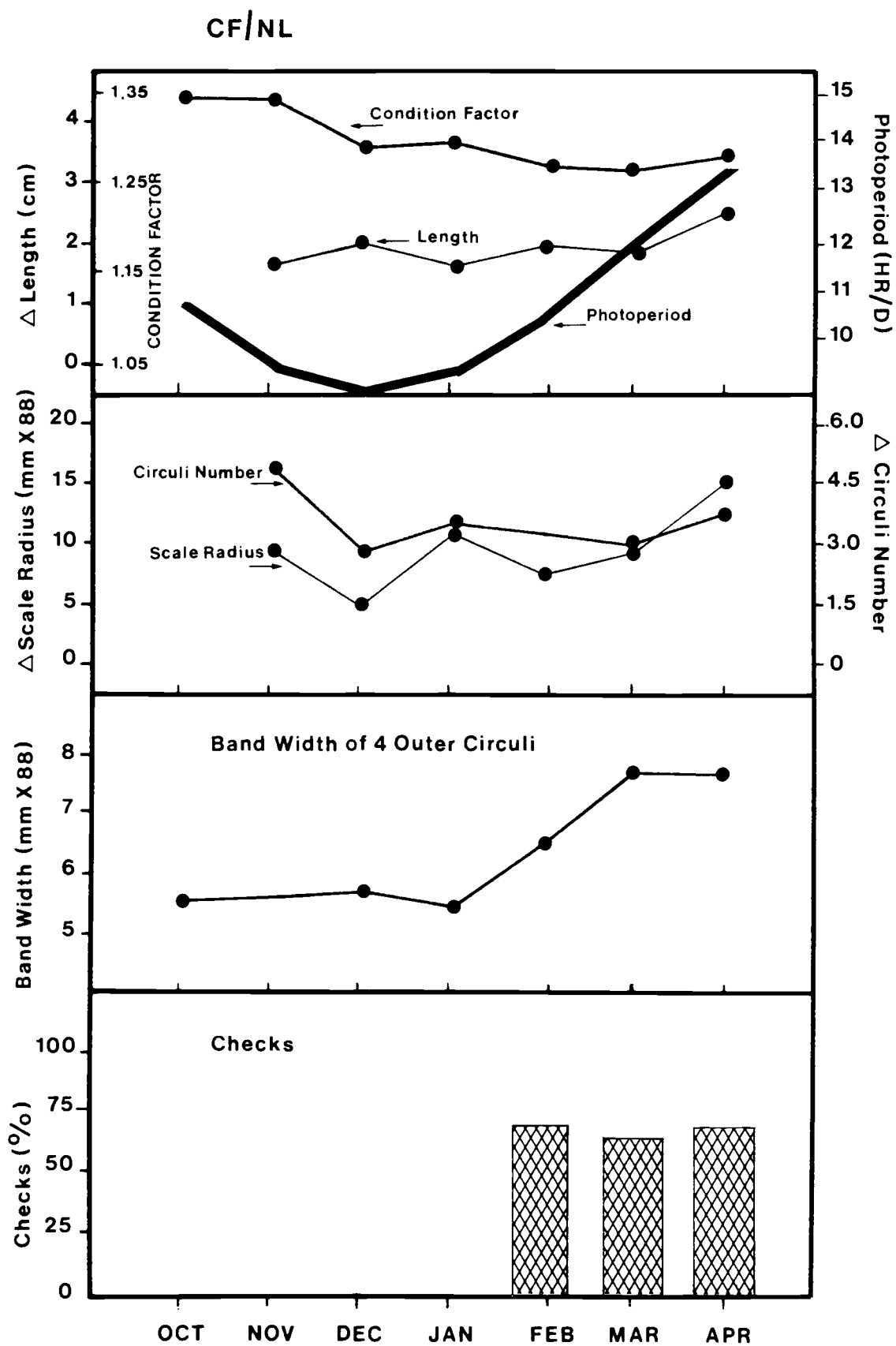


Fig. 2C.

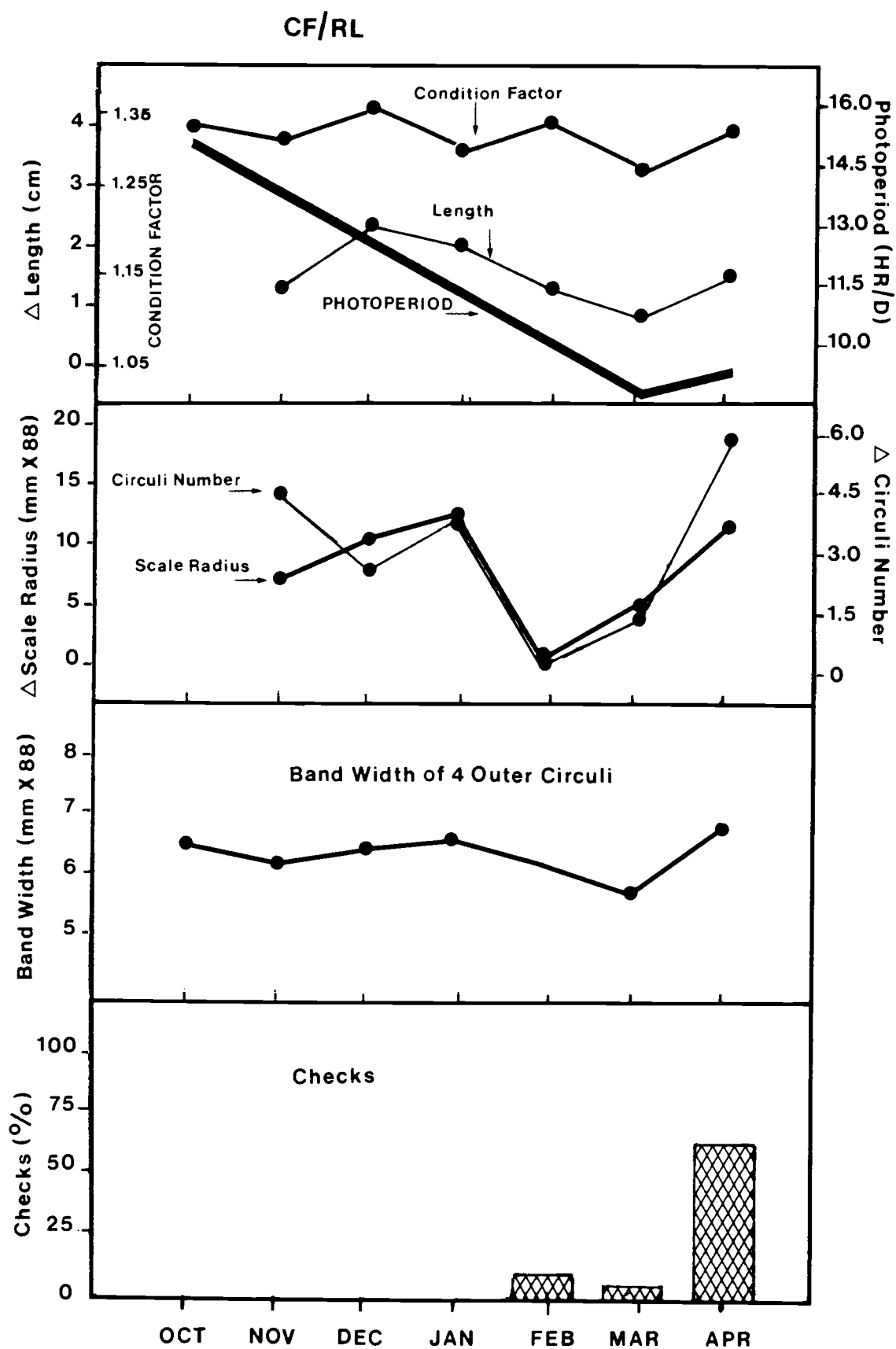


Fig. 2D.

Fig. 3. Monthly changes (Δ) in body length, scale radius, circuli number and condition factor, band width of 4 outer circuli, and percentage of checks formed in relation to feeding level and temperature in Experiment II. Sample sizes: $n = 90$ (length and condition factor) and $n = 60$ (all scale measurements).

- A. Constant repletion feed/Temporary extreme increase temperature (CF/24°C)
- B. Constant repletion feed/Temporary extreme decrease temperature (CF/6°C)
- C. Constant repletion feed/Temporary moderate increase temperature (CF/18°C)
- D. Constant repletion feed/Constant temperature (CF/12°C)

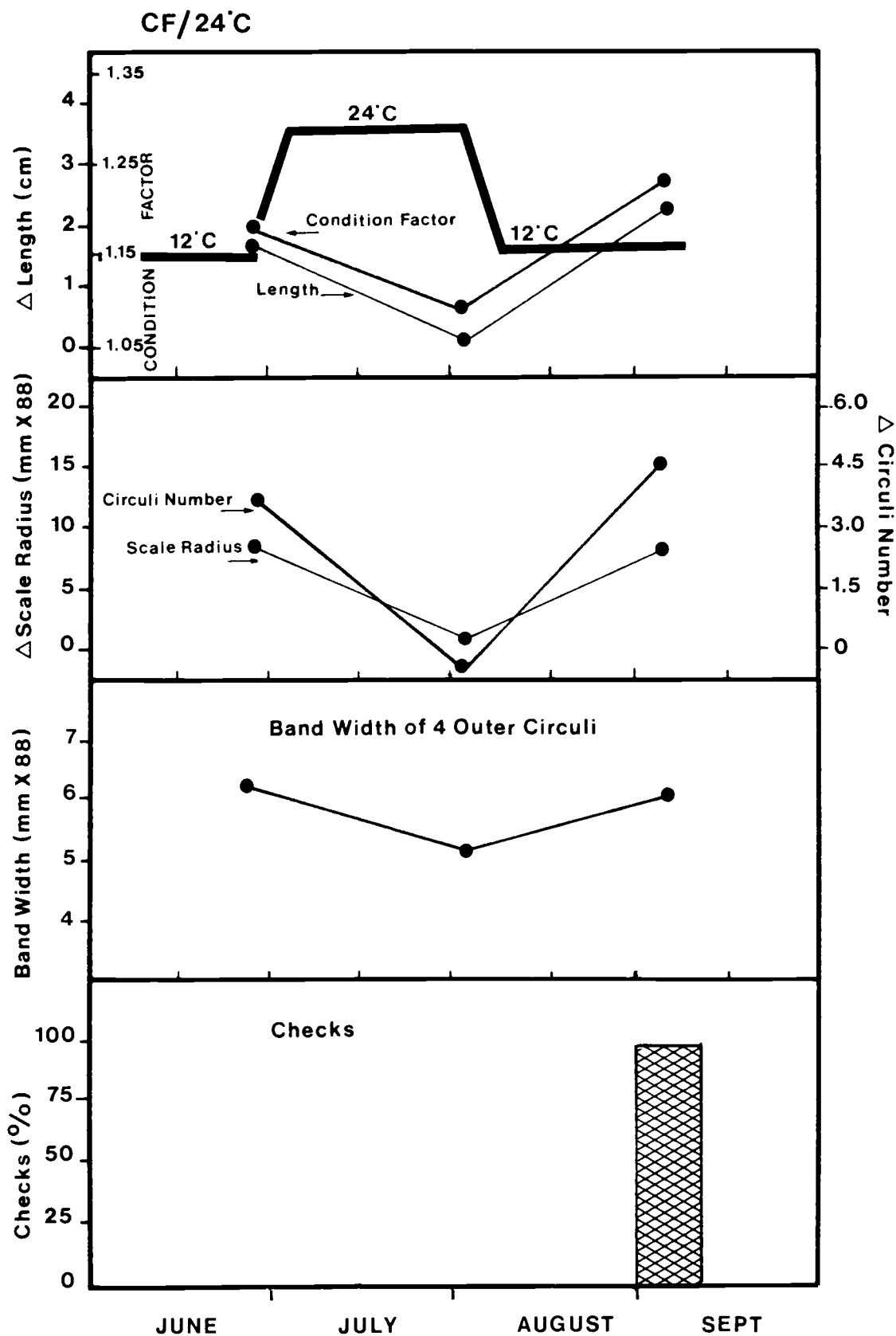


Fig. 3A.

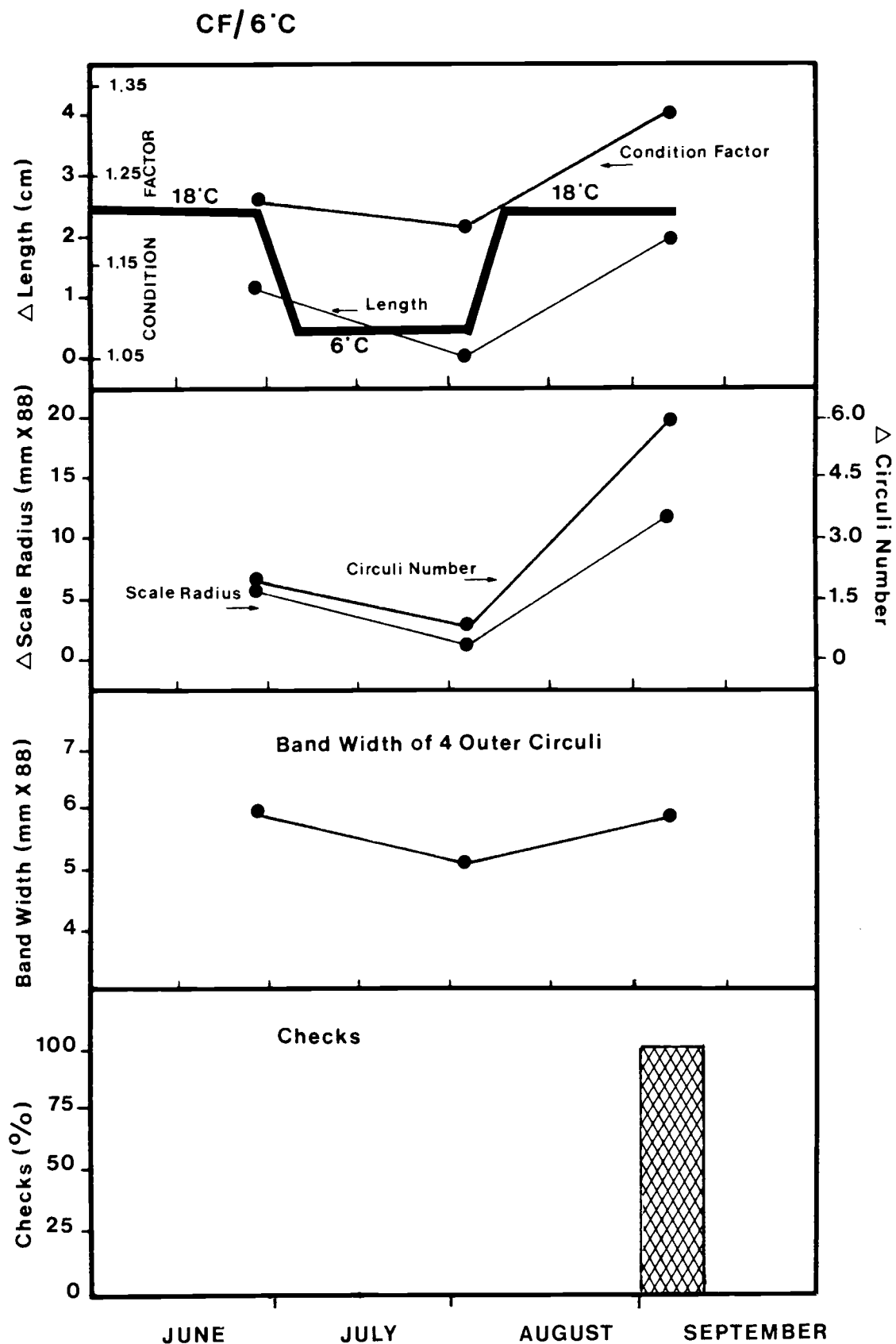


Fig. 3B.

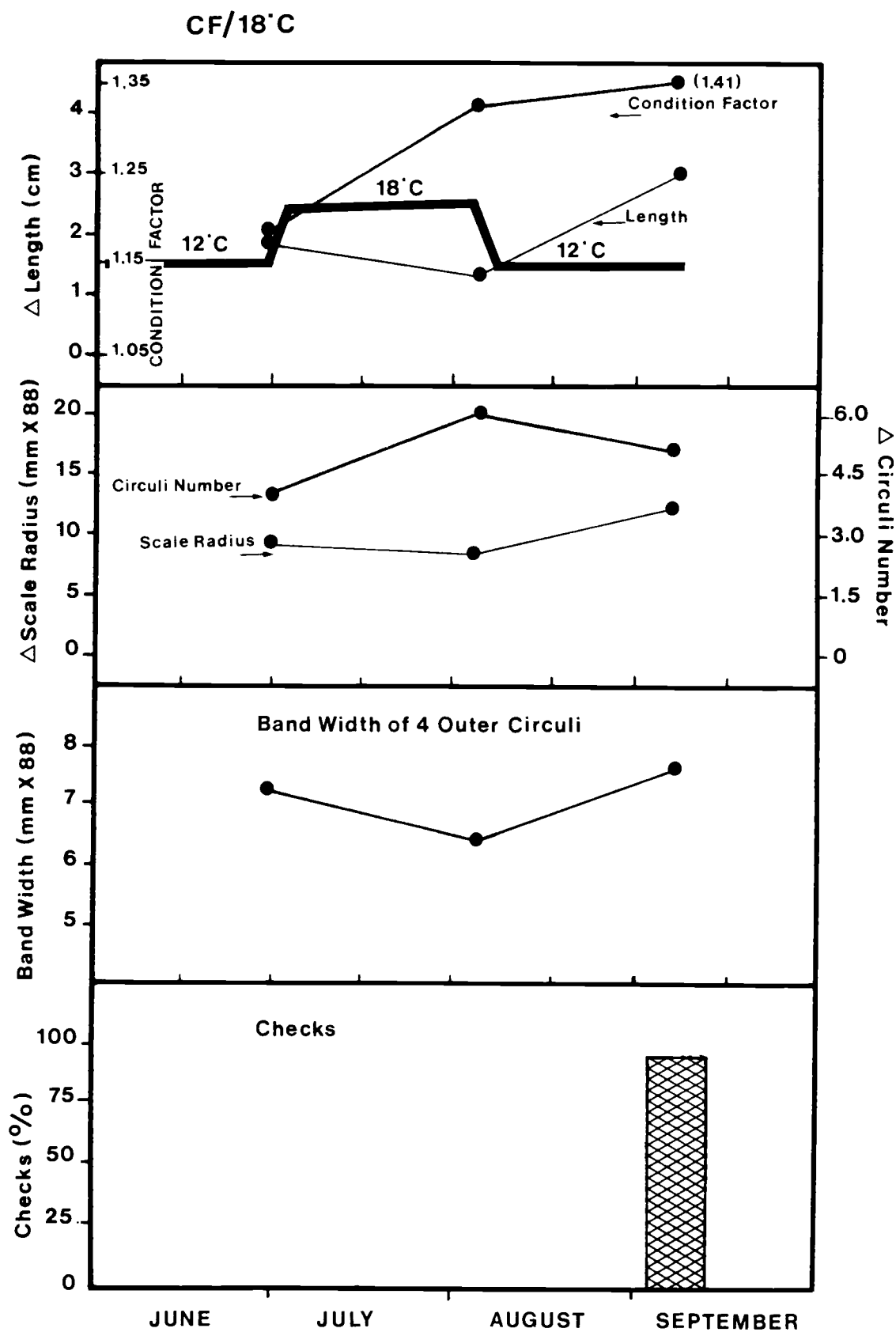


Fig. 3C.

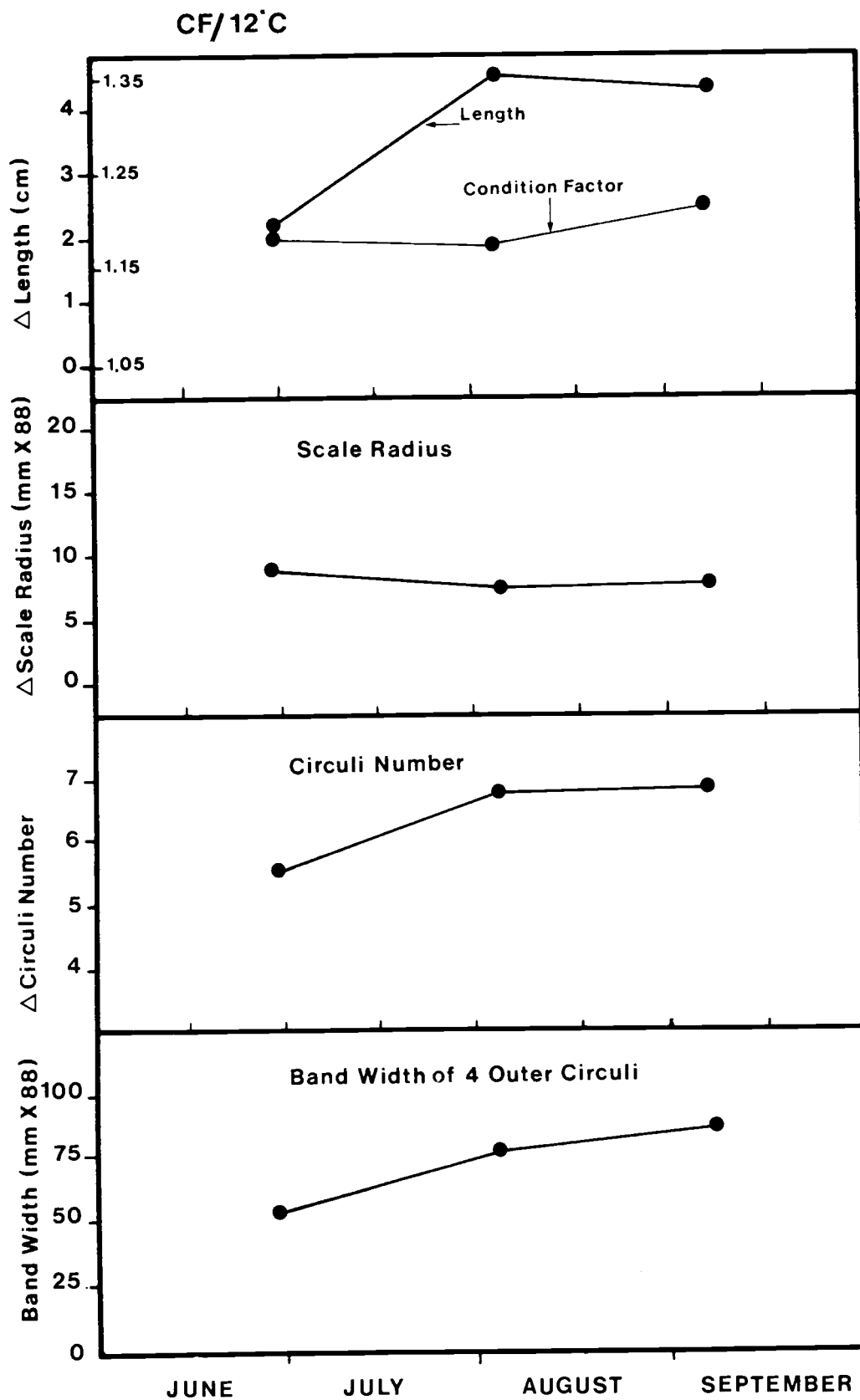


Fig. 3D.

Effects of temporary extreme increase (12 to 24 to 12°C) and decrease (18 to 6 to 18°C) temperatures on body and scale growth were similar to temporary decrease to maintenance feeding. Elevation in temperature to 24°C had the greatest effect on body and scale growth of steelhead of any treatment in the study. When temperature was elevated from 12° to 24°C with the constant feed (CF/24°C), steelhead fed sparingly and body and scale growth sharply decreased (Table 4; Fig. 3A). Shortly after temperature was reduced from 24 to 12°C, fish resumed feeding. In September, one month after temperature had been decreased, fish showed sharp gains in body and scale growth and 93-97% of fish showed distinct "annulus-like" checks on their scales.

Decrease in temperature to 6°C with the constant feed (CF/6°) had less but still significant effects on body and scale growth of steelhead. When temperature was decreased from 18° to 6°C, fish showed moderate decreases in length, scale radius and circuli number increments, and in condition factor and band width of 4 outer circuli (Table 4; Fig. 3B). Similar to the CF/24°C treatment, feeding of fish at 6°C was minimal. When temperature was elevated from 6 to 18°C, feeding and body and scale growth of fish increased and distinct "annulus-like" checks were formed on 100% of fish. Although fish growth in this treatment was reduced less, the checks formed were similar in appearance to other treatments in which distinct checks were formed.

Elevation in temperature to 18°C had small effects on body and scale growth of steelhead. When temperature was increased from 12 to

18°C with the constant feed (CF/18°C), a small depression was seen in increments of length and scale radius and in band width of 4 outer circuli (Fig. 3C). Weights of fish and condition factor, however, had increased. The increase in temperature appeared to have little effect on feeding of fish. In September when temperature was decreased from 18 to 12°C, increments in length and scale radius and band width of 4 outer circuli increased and indistinct checks were formed on 93% of fish.

With the constant feed, constant temperature (CF/12°C), no checks were formed as body and scale growth increased or remained high (Table 4, Fig. 3D).

Photoperiod had less effect than feeding level and temperature on body and scale growth of steelhead. The effect of photoperiod was most evident in the constant feed treatments although the effect was small. Except for band width of 4 outer circuli, changes in monthly increments in body and scale growth were generally insignificant in the constant feed, natural photoperiod treatment (CF/NL) as photoperiod fluctuated from 10.9 hr/d on the sampling date in October to the seasonal low in December (8.8 hr/d) to 13.5 hr/d in April (Fig. 2C). Band width of 4 outer circuli generally followed the photoperiod cycle, decreasing to a minimum in January, one month after the photoperiod had decreased to the nadir, and increasing February-April as photoperiod increased. A slight depression in length increment also occurred in January. In February, two months after photoperiod had increased from the seasonal low, indistinct checks were formed on 70% of fish coincident with increased length increment and band width.

Effects of photoperiod were greater with the constant feed, 3-month retarded photoperiod treatment (CF/RL). In this treatment, photoperiod decreased from 15.2 hr/d in October (equivalent to July in a natural photoperiod cycle) to 8.8 hr/d in March (equivalent to December photoperiod), and increased to 9.2 hr/d in April (equivalent to January photoperiod). There was a trend for increased body and scale growth at the higher but decreasing photoperiods November-January (Fig. 2D). Further decreases in photoperiod, however, had an inhibitory effect on body and scale growth as photoperiod decreased nearer and to the nadir. Increments in body length and band width were lowest in March when photoperiod was lowest, but the lowest increments in scale radius and circuli number occurred one month earlier. In April, one month after photoperiod had increased from the nadir, body and scale growth increased and indistinct checks were formed on 63% of fish.

The interaction of feeding level and photoperiod on condition factor in Experiment I was significant ($P < 0.05$) in January, two months following maintenance feeding in temporary decrease to maintenance feed regimes (Table 3). A similar trend was observed in December but the interaction was not significant at $P < 0.05$. The interaction occurred because the effects of feeding level on condition factor were not equal between photoperiods. For steelhead fed constant repletion feed, condition factor was higher in the retarded photoperiod, conversely, for fish fed maintenance feed, condition factor was lower in the retarded photoperiod. During November and

December, the average daylength was longer in the retarded (13.4 hr/d) than the natural (9.2 hr/d) photoperiod. There were no other significant ($P > 0.05$) interactions between feeding levels and photoperiods in Experiment I. Additionally, there were no significant ($P > 0.05$) interactions between feeding levels and temperatures for each body and scale measurement each month in Experiment II (Table 4).

Effects of Growth Rate and Season on Body-Scale Relationships

Growth rate appeared to effect the slope and intercept of body length-scale radius and body length-circuli number regressions. Feeding regimes supplying constant repletion levels (CF/RL and CF/NL), which resulted in about 50% greater fish growth rates than regimes that temporarily decreased rations to maintenance levels (DF/RL and DF/NL) October-January (Table 5), also had higher slopes and lower intercepts of length-scale radius and length-circuli regressions during this time period (Table 6; Figs. 4 and 5). The difference between feeding levels was not significant at $P < 0.05$ for slopes but was significant at $P < 0.05$ for intercepts (Table 7). Other differences in slopes and intercepts occurred between treatments February-April and between time periods within treatments, but these differences were not consistently related to differences in growth rate.

Slopes and intercepts of length-scale radius regressions changed seasonally independent of change in growth rate. In both natural photoperiod regimes (CF/NL and DF/NL) slopes were lower and intercepts were higher February-April than October-January, significant at

Table 5. Comparison of growth rates during October-January and February-April in Experiment I

Time Period/ Treatment	Growth Rate ¹ (cm/d \pm 95% CI)
<u>October- January</u>	
CF/RL	0.074 \pm 0.009
CF/NL	0.068 \pm 0.007
DF/RL	0.035 \pm 0.007
DF/NL	0.030 \pm 0.007
<u>February- April</u>	
CF/RL	0.059 \pm 0.013
CF/NL	0.074 \pm 0.014
DF/RL	0.070 \pm 0.010
DF/NL	0.098 \pm 0.010

¹ Calculated by the equation:
$$\frac{\text{Length } i - \text{Average Length } i}{\text{Number of days in period}}$$

Length i - length (cm) of individual fish at the end of the period in treatment i.

Average length i - average length (cm) of all fish at the beginning of the period in treatment i.

CF/RL = Constant repletion feed/Retarded photoperiod

CF/NL = Constant repletion feed/Natural photoperiod

DF/RL = Temporary decrease to maintenance feed/Retarded photoperiod

DF/NL = Temporary decrease to maintenance feed/Retarded photoperiod

Table 6. Regressions of body length on scale radius and body length on circuli number during October-January and February-April in Experiment I.

Length - scale radius regressions

<u>Period and Treatment</u> ²	<u>Regression Equation</u>	<u>n</u>	<u>R²</u>	<u>t¹</u>
<u>October-January</u>				
CF/RL	$y = 0.1941x + 2.5791$	120	0.881	29.62
CF/NL	$y = 0.1906x + 2.6615$	120	0.871	28.25
DF/RL	$y = 0.1693x + 3.4950$	120	0.797	21.49
DF/NL	$y = 0.1814x + 2.8733$	120	0.778	20.35
<u>February-April</u>				
CF/RL	$y = 0.1822x + 3.9428$	90	0.801	18.81
CF/NL	$y = 0.1644x + 5.1235$	90	0.755	16.48
DF/RL	$y = 0.1872x + 2.9151$	90	0.840	21.45
DF/NL	$y = 0.1632x + 4.8068$	90	0.829	20.65

Length - circuli number regressions

<u>October-January</u>				
CF/RL	$y = 0.4704x + 1.8019$	120	0.806	22.11
CF/NL	$y = 0.4520x + 1.8421$	120	0.762	19.43
DF/RL	$y = 0.4057x + 2.7565$	120	0.658	15.06
DF/NL	$y = 0.3991x + 2.7363$	120	0.613	13.66
<u>February-April</u>				
CF/RL	$y = 0.4967x + 1.6503$	90	0.700	14.33
CF/NL	$y = 0.4852x + 2.0838$	90	0.629	12.22
DF/RL	$y = 0.5140x + 0.1181$	90	0.740	15.83
DF/NL	$y = 0.4458x + 2.9916$	90	0.712	14.76

¹ All were significant at $P < 0.01$

² See Table 5 for explanation of treatment abbreviations.

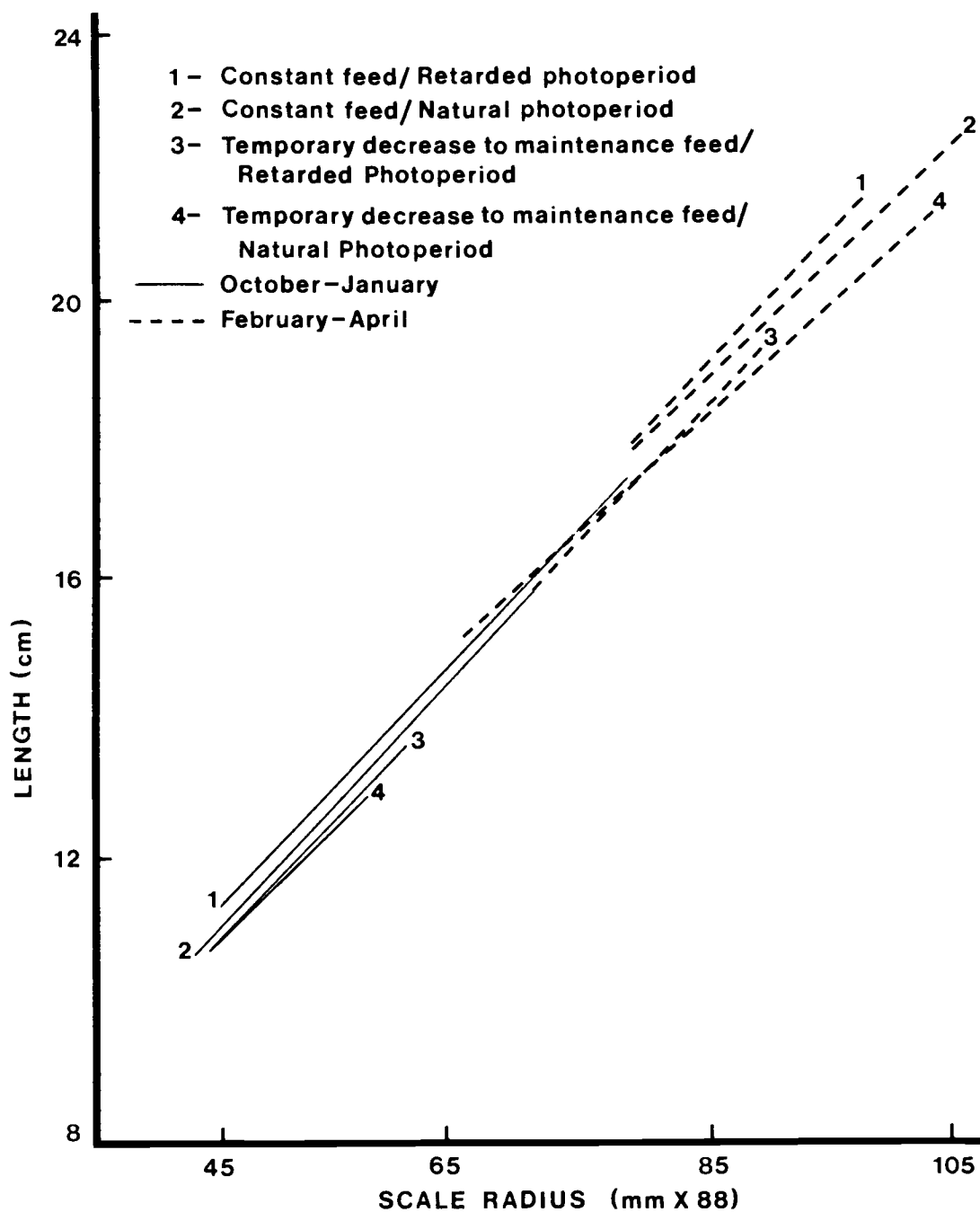


Fig. 4. Fish length-scale radius regressions calculated for October-January and February-April in Experiment I.

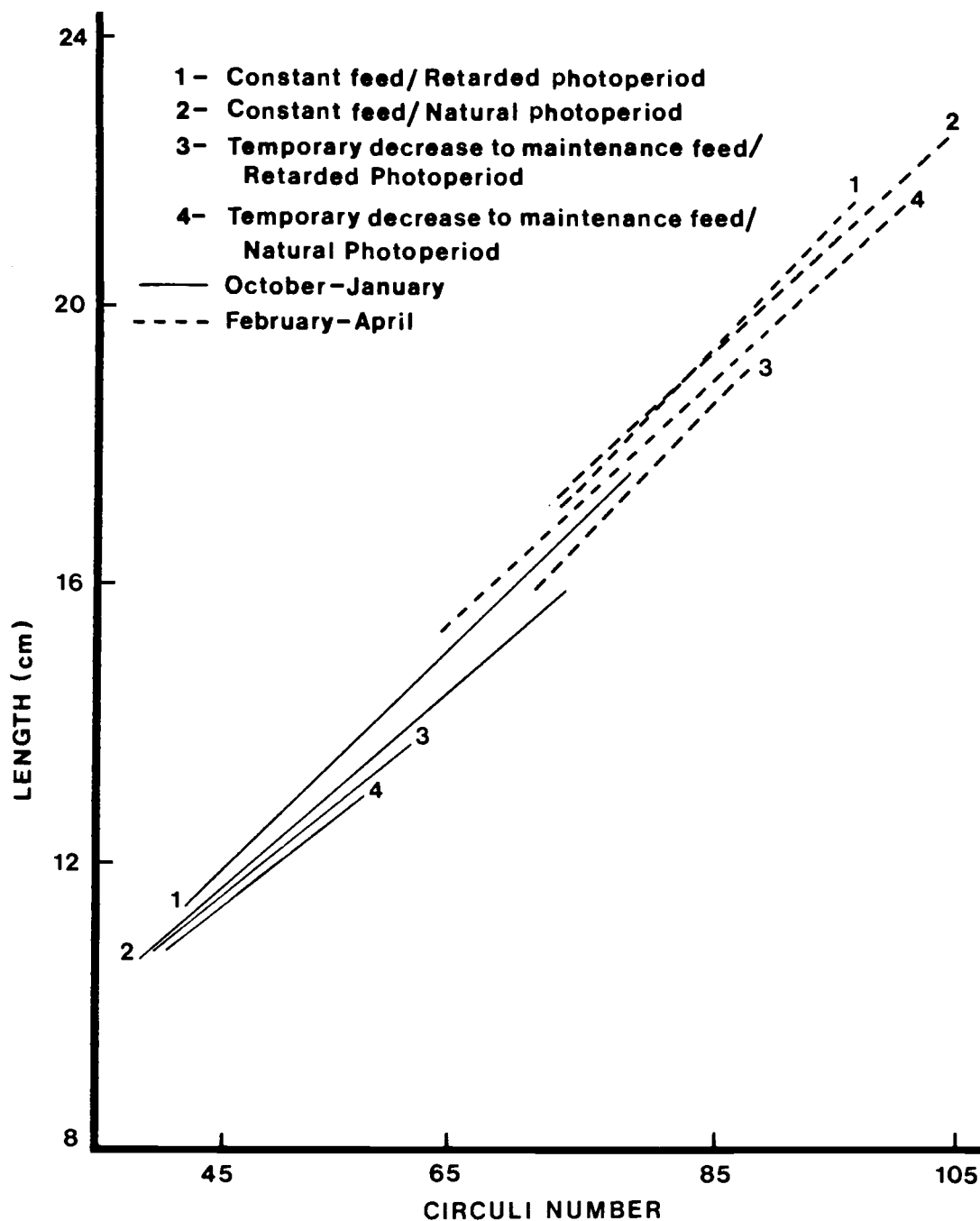


Fig. 5. Fish length-circuli number regressions calculated for October-January and February-April in Experiment I.

Table 7. Analysis of covariances of slopes and intercepts of length-scale radius and length-circuli number regressions in Experiment I. See Table 5 for explanation of treatment abbreviations.

		<u>Slopes</u>	<u>Intercepts</u>
<u>Length - scale radius</u>			
I.	Between treatments, October-January	NS	CF/RL < DF/RL (**) CF/RL < DF/NL (*) CF/NL < DF/RL (**) CF/NL < DF/NL (**)
II.	Between treatments, February-April	DF/RL > DF/NL (*)	CF/RL > DF/RL (**) CF/RL < DF/NL (**) CF/NL > DF/RL (*) CF/NL < DF/NL (**)
III.	Between time periods within treatments		
	CF/RL	NS	Oct-Jan < Feb-Apr (*)
	CF/NL	Oct-Jan > Feb-Apr (*)	Oct-Jan < Feb-Apr (**)
	DF/RL	NS	Oct-Jan > Feb-Apr (**)
	DF/NL	NS	Oct-Jan < Feb-Apr (**)
<u>Length - circuli number</u>			
I.	Between treatments, October-January	NS	CF/RL < DF/RL (**) CF/RL < DF/NL (**) CF/NL < DF/RL (**) CF/NL < DF/NL (**)
II.	Between treatments, February-April		
	CF/RL	DF/RL > DF/NL (**)	CF/RL > DF/RL (**)
	CF/NL	DF/RL > DF/NL (**)	CF/RL < DF/NL (**)
	DF/RL	DF/RL > DF/NL (**)	CF/NL > DF/RL (**)
	DF/NL		CF/NL < DF/NL (**)
III.	Between time periods within treatments		
	CF/RL	NS	Oct-Jan > Feb-Apr (*)
	CF/NL	NS	Oct-Jan < Feb-Apr (**)
	DF/RL	Oct-Jan < Feb-Apr (*)	NS
	DF/NL	Oct-Jan < Feb-Apr (**)	Oct-Jan < Feb-Apr (**)

** - Indicates significance at $P < 0.01$

* - Indicates significance at $P < 0.05$

NS - Indicates no significant difference at $P < 0.05$

$P < 0.05$ for slopes of CF/NL, and $P < 0.01$ for intercepts of CF/NL and DF/NL. This change in slopes and intercepts occurred coincidentally with a seasonal shift in photoperiod; photoperiod in the natural photoperiod was generally decreasing from October to January but was increasing from February through April. No such trend in slopes and intercepts occurred in retarded photoperiod regimes (CF/RL and DF/RL) where photoperiod was decreasing in both time periods except for the last month in the October-January time period. The shift in slopes and intercepts in NL regimes appeared not to be related to differences in growth rate between time periods since growth rate had not changed in CF/NL and had increased over three-fold during February-April in DF/NL. Similar effects of photoperiod were not apparent on slopes and intercepts of length-circuli regressions.

The use of a standard intercept in back-calculations resulted in substantial errors in estimates of growth. Compared to back-calculations using actual intercepts of regressions calculated for the October-January period, body lengths of fish would be over-estimated in three of four treatments by using the standard intercept (Table 8). Constant repletion feed regimes had low intercepts during October-January (2.6 - 2.7) (Table 6) which I attributed to the high growth rates of fish. Lengths in constant repletion feed regimes would be over-estimated (indicated by positive differences) up to 10% at 25 mm (8.0 cm fish), 3.7% at 50 mm (12.5 cm), and 0.8% at 100 mm (21.0 cm). In contrast, compared to back-calculations using actual intercepts of regressions calculated for the February-April period,

Table 8. Back-calculated body lengths of steelhead in Experiment I.

Time Period/ Treatment ¹	Back-Calculated Length (cm)								
	Using Actual Intercept of Regression			Using Standard Intercept of 3.5			Difference from Actual %		
	Scale radius (mm)			Scale radius (mm)			Scale radius (mm)		
	25	50	100	25	50	100	25	50	100
<u>October-January</u>									
CF/RL	7.43	12.28	21.99	8.17	12.74	22.17	+10.0	+3.7	+0.8
CF/NL	7.43	12.19	21.72	8.10	12.61	21.88	+ 9.0	+3.4	+0.7
DF/RL	7.72	11.96	20.42	7.72	11.96	20.42	0.0	0.0	0.0
DF/NL	7.40	11.94	21.01	7.91	12.26	21.14	+ 6.9	+2.7	0.6
<u>February-April</u>									
CF/RL	8.49	13.03	22.16	8.14	12.83	22.07	- 4.1	-1.5	-0.4
CF/NL	9.28	13.44	21.76	7.98	12.63	21.44	-14.0	-6.0	-1.5
DF/RL	7.60	12.28	21.04	8.06	12.57	21.75	+ 6.0	+2.4	0.5
DF/NL	8.89	12.97	21.13	7.84	12.31	20.87	-11.8	-5.1	-1.2

¹ See Table 5 for explanation of treatment abbreviations.

lengths would be under-estimated in three of four treatments by using the standard intercept. Intercepts in natural photoperiod regimes during February-April were high (4.8 - 5.1) which I hypothesized was due to a seasonal shift in photoperiod. Lengths in natural photoperiod regimes would be under-estimated up to 14.0% at 25 mm, 6.0% at 50mm, and 1.5% at 100 mm.

Monthly increments in scale radius was most correlated to body length ($r = 0.907$) (Table 9; Fig. 6). Scale radius, generally like other scale measurements, was most correlated to length, less correlated to weight, and least correlated to condition factor. Circuli number was less correlated to length ($r = 0.755$). For a given length increase, steelhead deposited widely variable number of circuli (Fig. 6). Variation in circuli deposition appeared not to be related to differences between treatments, fish size or growth rate pattern, or whether samples were from months before, during, or after check formation.

The correlation of average circuli spacing to rate of length increase was highest ($r = 0.867$) of any circuli spacing-length correlation. Steelhead generally had narrow average circuli spacing when rate of length increase was low and wide average circuli spacing when rate of length increase was high (Fig. 7). Correlations of band widths to length change over one and two previous months were lower ($r = 0.587$ to 0.773) than the average circuli spacing-length correlation. Band width of 4 outer circuli was more correlated to length change over one ($r = 0.773$) than two ($r = 0.691$) previous months. Conversely, band

Table 9. Correlations of average changes in scale measurements to body length, weight, and condition factor in Experiments I and II.

Scale Measurement	Time Period	n	r value		Condition Factor
			Length	Weight	
Circuli Number	1 month	36	0.755**	0.794**	0.637**
Scale Radius	1 month	36	0.907**	0.751**	0.532**
Band Widths					
4 outer circuli	1 month	36	0.773**	0.700**	0.537**
	2 months	18	0.691**	0.656**	0.533*
6 outer circuli	1 month	36	0.665**	0.451**	0.232
	2 months	18	0.716**	0.350	0.415
11 outer circuli	1 month	36	0.587**	0.387*	0.164
	2 months	18	0.683**	0.293	0.409
Average circuli spacing	Cumulative days to sampling date ¹	48	0.867**	0.385**	--2

¹ See text for explanation.

² Not calculated.

** Indicates significance at $P < 0.01$.

* Indicates significance at $P < 0.05$.

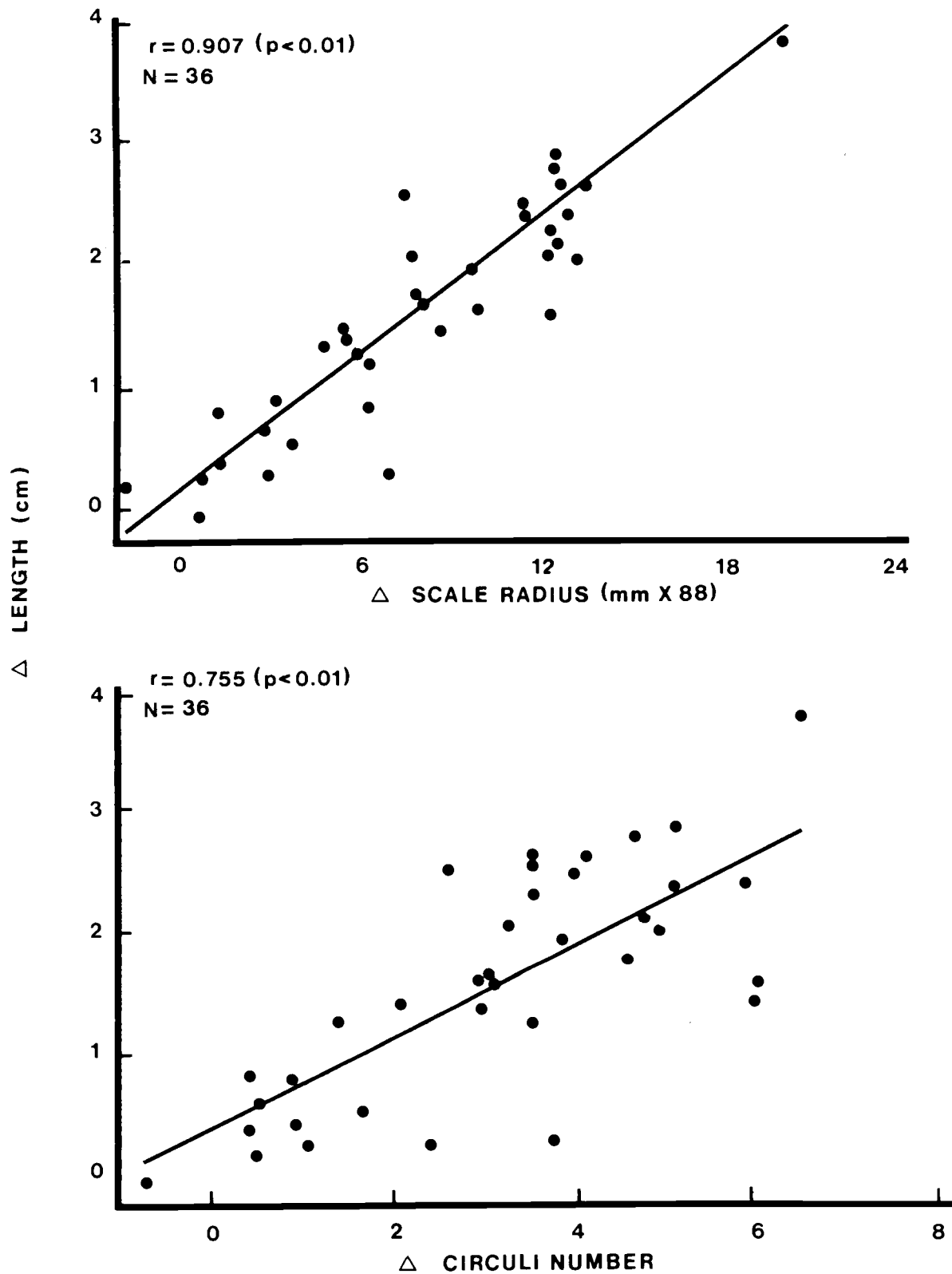


Fig. 6. Correlations of average monthly change (Δ) in scale radius and circuli number to body length in Experiments I and II.

width of 6 and 11 outer circuli were more correlated to length change over two than one previous month ($r = 0.665$ and 0.587 , respectively).

DISCUSSION

Effects of Feeding Level, Temperature, and Photoperiod on Growth Rate, Circuli Spacing and Deposition Rate, and Formation of Checks

Feeding level and temperature were the primary environmental factors influencing body and scale growth of steelhead. Sharp decreases in growth and formation of distinct "annulus-like" checks were produced by restricting ration for one to two months and increasing feed for one month. In both experiments when ration was decreased to maintenance, fish experienced sharply decreased increments in body and scale growth, regardless of temperature or photoperiod. Starvation followed by feeding (two months of starvation followed by one to three months of feeding; one to three months of feeding followed by two months of starvation; constant feed) with young sockeye salmon (Oncorhynchus nerka) of four different races and young kokanee (O. nerka kennerlyi), coho (O. kisutch), and chinook salmon (O. tshawytscha) (Bilton 1974) yielded results similar to mine.

Sharp decreases in body and scale growth and formation of distinct checks were also produced by extreme temperature fluctuation to low (18 to 6 to 18°C) or high (12 to 24 to 12°C) temperature for one month. With intermediate temperature fluctuation (12 to 18 to 12°C), small decreases in body and scale growth and formation of indistinct checks were produced. At a constant temperature (12°C), no checks were formed as body and scale growth remained high. At 6 and 24°C steelhead ate sparingly because these temperatures were

apparently well below and above, respectively, the optimal temperature for growth of the experimental fish. Most fish species show a typical rapid increase in growth rate as temperature rises reaching a peak at the optimum temperature and usually falling at an increasingly rapid rate as high temperatures become adverse (Brown 1957; Brett 1979).

My results and those of Cutler (1918), Dannevig (1956) and Hopson (1965) suggest that the spacing and deposition of circuli are dependent on temperature with greater spacing and rate of deposition at moderate than either extremely low or high temperature. In goldfish (Carassius auratus), Ouchi (1969) showed that increments of scale radius and circuli number increased with temperature (12.5, 17.5, 22.5, and 27.5°C) but spacing of circuli remained constant. This lack of difference in circuli spacing between temperatures is difficult to explain but it is possible that circuli spacing in goldfish is altered only at more extreme temperatures than at those tested in Ouchi's experiments.

Photoperiod was a secondary factor affecting body and scale growth of steelhead. At constant repletion feeding level, slight decreases in growth and formation of indistinct checks could be produced by cycling photoperiod through the seasonal low. Growth generally decreased as photoperiod decreased and increased as photoperiod increased. These results were similar for both a natural photoperiod and a 3-month retarded photoperiod where the seasonal minimum in photoperiod occurred in March, three months after the natural low

of December. Similar effects of photoperiod on body and scale growth have been shown by Bilton and Robbins (1971a; 1971b). They showed that young sockeye reared in continuous or in 12 hr/d light increased more in body size and scale growth than those reared in continuous darkness suggesting the lack of light was inhibiting to growth.

In my study, response to photoperiod was greater in the retarded than natural photoperiod. Body and scale growth were depressed more and there was no lag period between changes in body growth and photoperiod in the retarded photoperiod. Although not measured, light intensity was obviously greater in the covered tanks of the retarded photoperiod. This greater intensity may have enhanced growth since evidence by Eisler (1957) and Kwain (1975) indicates that fish growth is greater at higher light intensity.

For steelhead fed at repletion levels, I found that condition factor was higher for fish reared under retarded photoperiod, conversely, for steelhead fed maintenance feed, condition factor was lower for fish reared under retarded photoperiod. The higher condition factor of steelhead fed repletion feed and reared under retarded photoperiod can be attributed to greater feeding rates of fish under the longer daylengths of the retarded photoperiod. The reason for the lower condition factor of steelhead fed maintenance feed and reared under retarded photoperiod is unknown but it is possible that because of longer photoperiods in the retarded regime, fish were more active and spent more energy in search of food which reduced growth. The predominance of day-active patterns in swimming activity has been

documented for several salmonids including steelhead (Hoar 1942; Lichtenheld 1966; Richardson and McCleave 1974; Godin 1981).

Factors Influencing Check Formation in Natural Populations

Annuli may be caused by seasonally decreased water temperature or food supply. Distinct "annulus-like" checks were formed in the temperature regime simulating seasonally decreased water temperature (18 to 6 to 18°C) regardless of feeding level, and in all temporarily decreased to maintenance feeding regimes (repletion to maintenance to repletion), regardless of temperature or photoperiod. Annuli would form in spring when temperature and feeding level became non-limiting to growth. There is however, no conclusive evidence to clearly demonstrate that hypothesis. The annulus of Pacific sardines (Sardinops caerulea) formed during winter months when water temperatures were minimal (Kimura and Sakagawa 1972). Similarly, Beckman (1943) showed the timing of annulus formation of bluegill (Lepomis macrochirus) was correlated with a minimum threshold temperature during spring. No annuli were observed before mean daily water temperatures exceeded 10°C and all had formed annuli when temperatures reached 15°C. The timing of annulus formation was also shown to be progressively later from southern to northern Michigan owing to earlier warming in southern lakes. However, for bluegill living in northern Indiana lakes, Gerking (1966) could find no relationship between length of the growing season, assumed to commence with annulus formation, and water temperature during two years of study. Similarly, I (unpublished data, Raymond R.

Boyce, Oregon Department of Fish and Wildlife, Portland, Oregon) failed to find any correlation between timing of annulus formation of juvenile steelhead in the Rogue River, Oregon during 1976-81 and minimum and maximum water temperature averaged over several time periods. These insignificant correlations may be due to interannual variation in food supply which may vary independently of water temperature. Clearly, additional research is needed to understand the role of temperature, food abundance and availability in annulus formation.

Results of my study also suggest that the seasonal decrease in photoperiod alone is probably not responsible for annulus formation. I showed that slight decreases in body growth and the formation of indistinct checks could be produced by cycling photoperiod through the seasonal low. These results were duplicated in a natural and 3-month retarded photoperiod. The checks were faint and lacked scale characteristics normally associated with annuli. Photoperiod therefore is probably a secondary factor to temperature and food supply in formation of annuli.

Photoperiod, however, may affect timing of annulus formation. My results, as well others (Swift 1961; Gross et al. 1965; Knutsson and Grav 1976), indicate that increasing photoperiod is stimulating to growth. The formation of annuli in spring may be due to the interactive effects of increasing photoperiod, food supply, and temperature.

In contrast to my findings, Hogman (1968) showed a significant influence of photoperiod on body and scale growth. He concluded that

photoperiod was the primary environmental factor governing seasonal growth and annulus formation in the four species of coregonids in his study. He showed that the seasonal decrease in body growth and formation of annuli were more correlated to photoperiod than partially regulated water temperature. The seasonal decrease in body growth closely followed changes in photoperiod with minimum growth occurring one month after the nadir in photoperiod; no such correlation occurred in relation to water temperature. Annuli formed in March and April coincident with increased photoperiod but constant water temperature. The water temperature during winter ($10.0 \pm 0.2^{\circ}\text{C}$) did not arrest metabolic activity and fish were fed all the feed they could consume, thereby eliminating food availability as a factor in annulus formation. I cannot explain why Hogman demonstrated a much larger effect of photoperiod than observed in mine and others' experiments. However, since his results have not been corroborated by any other data, I suggest that further experimentation needs to be done with coregonids and other species to understand the role of photoperiod in influencing seasonal growth and annulus formation of fish.

The hormonal cycle may indirectly affect annulus formation. The influence of hormones on fish growth has been well established (Donaldson et al. 1979), and there is at least one study showing that circuli deposition is affected by hormones (Ball 1969). Swift and Pickford (1965) showed that the seasonal body growth cycle and circuli spacing of perch (Perca fluviatilis) was paralleled by a suspected cycle in pituitary growth hormone and temperature. Body and scale growth were

low in winter when hormone content in the gland was low and temperature was below 14°C. Growth commenced in spring when hormone level increased and temperature exceeded 14°C. Rising temperature in spring may stimulate hormone production since responsiveness of fish to growth hormone has been shown to be temperature related (Pickford and Atz 1957). Photoperiod, food supply, temperature, as well as production of growth hormone may influence seasonal body growth and formation of annuli.

My study indicates that false annuli can be produced in natural populations by seasonally elevated water temperature. Distinct "annulus-like" checks were formed in my temperature regime simulating seasonally elevated water temperature during summer (12 to 24 to 12°C) even though fish were fed to repletion. Appearance of false annuli have been correlated with extreme summer temperature in populations of brook trout (Cooper 1951; Hatch 1957) and dace (Leuciscus leuciscus) (Hoefstede 1974). The high correlation of summer growth depression and summer temperatures found by Le Cren (1958), Swift (1961), and Cech and Wohlschlag (1975) also is an indication that elevated summer temperature is important in production of false annuli. Swift (1961) found that growth of wild brown trout (Salmo trutta) increased in spring with increasing temperature reaching a maximum in early summer when temperature reached 13°C. Growth steadily declined in summer as temperature rose to 20°C but increased again in fall as temperature decreased. Growth continued to increase in fall until temperature dropped below 13°C. Similar to

the way Swift was able to monitor trout growth based on water temperature, fishery biologists may be able to predict the timing and occurrence of false annuli based on measurements of water temperature during summer and fall and knowledge of temperature-growth relationships of the fish specie.

False annuli may also be caused by a temporary reduction in food abundance or availability. The correlation of mid-summer growth depression and low food availability found for populations of juvenile chinook in the Sixes Estuary (Bottom et al. 1982) is indicative that food availability may be important in formation of false annuli. Low food abundance or availability as well as elevated temperature during summer may cause false annulus formation. The detrimental effects of elevated temperatures at low food abundances on fish growth has been well documented (Brown 1957; Wurtsbaugh and Davis 1977; Brett 1979). Wurtsbaugh and Davis (1977) showed that at rations near maintenance, elevated temperatures decreased growth of rainbow trout and as feeding rate was increased the detrimental effects of temperature on growth was reduced. Low food abundance or availability combined with elevated summer temperature could thus decrease growth and cause false annuli to be formed.

Elevated summer temperature may also affect growth by altering the quantity of benthic organisms upon which the fish prey. Iverson (1972) reported a 50% reduction in insect production in model streams experiencing a temperature increase from 17 to 22°C.

The interaction of increased activity during longer days during summer combined with low food supply and high temperature may also be important in summer growth depression and false annulus production. I found that at maintenance ration, steelhead growth was lower in a treatment where photoperiod was greater and hypothesized that the growth reduction was caused by increased energy spent in search of food under the longer photoperiod. Other studies have shown that fish activity is greater at higher temperatures. Brett et al. (1969) and Elliott (1975) found that the shape of the growth rate-ration curve shifted from a simple geometric shape at low temperature to a logistic shape at high temperatures; fish that were fed low ration at high temperatures (e.g., 20°C) exhibited a great deal of searching which compounded the expenditure of energy in the lower end of the growth-ration curve causing the convex rise.

Finally, the effect of photoperiod on the reproductive cycle of fish may affect false annulus production. The reproductive cycle of fish, as well as other animals, has been shown to be related to photoperiod (Combs et al. 1959; Henderson 1963). False annuli have been attributed to spawning checks (Cragg-Hine and Jones 1969) but many cannot be associated with spawning for they occur in immature fish (Bennett et al. 1940; Sprugel 1954; Swift 1955; Hogman 1968; Payne 1976). Payne (1976) reported that check formation in the cyprinid (Barbus liberiensis) takes place in two stages; first resorption of scale material which occurs during April and coincides with the most rapid phase of gonad development and second, the establishment of

the mark itself during July by which time gonad maturation is complete but spawning has not yet taken place. Simkiss (1974) suggested that these types of checks, referred to as "maturation checks," may be the result of calcium metabolism in the reproduction cycle. Simkiss felt that resorption of scales during gonad development probably reflects an increased demand for calcium by the gonads which requires a net removal of calcium from the scales. This observation is consistent with Garrod and Newell (1958) who showed a fall in the calcium content of the scales associated with the development of the ovary in Tilapia. Once reproduction has occurred, the calcium requirement probably declines allowing resumption of scale growth and formation of checks. Sexual maturation was not a factor in check formation of steelhead in my study since less than 0.3% of fish matured (all precocious males) as subyearlings and yearlings during the experiments and scales from these fish were not used in the study.

Effects of Growth Rate and Season on Body-Scale Relationships

Growth rate appeared to have some effect on slopes and intercepts of body length-scale radius and body length-circuli number regressions. Regression slopes tended to be higher and intercepts tended to be lower in treatments with higher growth rates indicating that when steelhead are growing fast they deposit fewer radii and circuli per length increment than at lower growth rates. These findings are consistent with other studies. For populations of juvenile sockeye, kokanee, coho, and chinook, Bilton (1974) found that slopes

of length-scale radius and length-circuli number regressions were higher in constant feed regimes which had greater growth rates than decreased feed regimes. Lindroth (1960) found that adult Atlantic salmon (Salmo salar) captured in the Baltic Sea tended to have higher slopes of length-scale radius regressions in autumn when growth rate was comparatively fast than in winter when growth was slow. Similarly, Ottaway and Simkiss (1979) reported that juvenile bass (Dicentrarchus labrax) had higher slopes and lower intercepts of length-scale radius regressions in July during a period of fast body growth, and lower slopes and higher intercepts in September during a period of slow body growth.

I also found that length-scale radius regressions varied seasonally independent of change in body growth rate. Fish reared under natural photoperiods (CF/NL and DF/NL) had lower slopes and higher intercepts during the February-April period than during October-January indicating steelhead were depositing scale radii at a greater rate per length increment in the later time period. This change occurred coincidentally with a seasonal shift in photoperiod which was generally decreasing October-January but increasing February-April. No such trend was observed for fish reared under retarded photoperiod where daylength was decreasing in both time periods except for the last month in the second time period. The change in slopes and intercepts did not appear to be due to differences in growth rate between time periods since growth rate had not changed in CF/NL and had increased over three-fold in DF/NL. Thus, the change appears to have been

caused by the shift in photoperiod from decreasing to increasing daylength. Although body length-scale radius relationships have been shown to vary seasonally due to change in growth rate (Ottaway and Simkiss 1979), to my knowledge this is the first demonstration that they can vary seasonally independent of change in growth rate. I also found that similar effects of photoperiod were not apparent in length-circuli number regressions which suggests that seasonal change in photoperiod affects body-scale diameter but not body-circuli number relationships.

Variation in length-scale radius relationships due to fish growth rate or season caused errors up to 10-14% in back-calculated lengths of steelhead at a fish size of 8 cm by using a standard intercept in the Lee-Fraser equation rather than the actual intercepts of length-scale radius regressions. The percentage error in back-calculations was less at larger fish sizes. In comparison, Ottaway and Simkiss (1979) calculated that errors up to 20% in back-calculations could be produced from seasonal variation in length-scale relationships of 8.5 cm bass. The precept of using standard intercepts in back-calculations is that length-scale radius relationships are constant for a given population and observed seasonal and annual variation is due to errors in sampling and measurement (Carlander 1982). My results suggest that the relationships are not constant but may vary due to fish growth and season. Back-calculations would thus be most accurate by using actual intercepts of length-scale radius regressions calculated for each year and perhaps each season. The

relationship between body length and scale radius was shown to vary between fall to winter and spring months in my study, but it may also vary between summer and fall months when photoperiod shifts from increasing to decreasing daylength.

There is evidence that faster growing juveniles survive better to adulthood than slower growing juveniles as shown by the positive correlations between size at release of juveniles and survival to maturity demonstrated for coho, chinook, and steelhead (Wagner et al. 1963; Reisenbichler et al. 1981; Bilton et al. 1982; Johnson 1982; Wade and Buchanan 1983). Because of greater growth rates, my results indicate that the length-scale radius regression of surviving adults would have a higher slope and a lower intercept than the one of juveniles. This would cause lengths of juveniles back-calculated from adult scales to be over-estimated especially at small fish sizes. These errors may be reduced by only using length-scale radius relationships of the fastest growing and largest juveniles which would have the highest probability of surviving to adulthood.

Correlation of monthly increments of scale radius to body length was high ($r = 0.907$) but lower for circuli number ($r = 0.741$). For a given length increase, steelhead deposited a fairly constant amount of scale radius but widely variable number of circuli. Variation in circuli deposition appeared not to be related to differences between treatments or pattern of growth. Fisher (unpublished data, Department of Oceanography, Oregon State University, Corvallis, Oregon) also found a

fairly low correlation ($r = 0.713$) of rate of circuli deposition and rate of length increase of individually marked coho in a two month study.

I found a reasonably good correlation ($r = 0.867$) between average circuli spacing and body length increase for cumulative days to each sampling date, similar to the correlation Fisher found for coho in his experiment ($r = 0.812$). In my study, correlations of band width of 4, 6, and 11 outer circuli to length increase over one and two previous months were lower ($r = 0.587$ to 0.773). One factor causing variation in circuli spacing-length relationships was variation in circuli deposition. For a given length increase, the amount of scale radius deposited was fairly uniform but the number of circuli deposited was widely variable which would cause variation in circuli spacing-length relationships. Another factor causing variation in band widths-length relationships was methodological: failure to measure spacing of circuli deposited in the same time period that length change was measured. I measured length change over the previous one and two months, however, because number of circuli deposited by fish was variable (-0.7 to 6.5 circuli/mo average) dependent on growth rate, measurements of circuli spacing using standard bands of 4, 6, and 11 outer circuli reflected more than two months of growth for slow growing fish. Band width of 4 outer circuli was most correlated to length change over one month because fish deposited an average three to four circuli/mo in the experiments. This would also explain why band width of 6 and 11 outer circuli were more correlated to length change over two rather than one month. Average circuli

spacing showed high correlation to length increase for cumulative days to each sampling date because the body measurement corresponded to the same time period as the scale measurement.

These results suggest that the spacing of circuli can be used to obtain reasonably accurate estimates of growth as long as the time period corresponding to the circuli spacing is known. I was able to account for over 75% of variation in length increase for cumulative days to sampling dates using average circuli spacing. A danger with using standard band widths of circuli in back-calculations (Reimers 1973; Cramer and Martin 1978) is that variation in circuli deposition rates can cause band widths to be formed over different time periods. In my study I was able to account for only 34-60% of variation in length increase over one and two months using band width of 4, 6, and 11 outer circuli. This level of accuracy is probably unacceptable for most growth studies which raises question about their use. Accuracy of growth estimates could be increased by adjusting time periods by monitoring circuli deposition rates. This, however, is usually not practical in most studies.

Bilton (1975) was first to point out that errors in back-calculations of growth using body-scale relationships can occur during periods of low growth. My data and his indicate that fish do not form circuli and increase their scale radius when growth is very low (Fig. 6). If a fish undergoes a prolonged period of little or no growth, there will be no record on the scale to indicate growth had decreased during the period the fish was not growing. Back-calculations of

growth made during a low growth period will therefore be a measure of growth previous to the low growth period. Caution should be taken when interpreting growth measurements from scales during winter or other months when fish may not be growing.

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