AN ABSTRACT OF THE THESIS OF

Harry Henry Wagner (Name) for the Doctor of Philosophy (Degree)

in Fisheries (Major) presented on Dec. 2, 1970 (Date)

Title: THE PARR-SMOLT METAMORPHOSIS IN STEELHEAD TROUT AS AFFECTED BY PHOTOPERIOD AND TEMPERATURE

Abstract approved: Redacted for Privacy

Dr. Frank P. Conte (Thesis Professor)

Redacted for Privacy

Dr. James D. Hall (Major Professor)

The role of photoperiod and temperature in parr-smolt metamorphosis was studied at the behavioral, morphological, and physiological levels in steelhead trout (Salmo gairdneri).

In Experiment I (July 1965 to September 1966), the effects of constant photoperiods on metamorphosis were examined in relation to one constant temperature (12° C). Groups of fish reared in the absence of light and in continuous light were also included. Fish were introduced into the controlled environmental regimes as fry in July 1965 and as fingerlings in December 1965. In Experiment II (June 1967 to June 1968), the effects of rate of change in photoperiod and temperature cycles on metamorphosis were emphasized. In addition, the effects of monochromatic light were studied in several groups. Experimental fish were introduced as fry into controlled environments in June 1967.

The basic measurements made in the study were changes in migratory behavior, growth and coefficient of condition, sea-water adaptation, and thyroid activity.

Photoperiod was the main environmental factor controlling the onset of metamorphosis, but did not determine whether or not the event occurred. The primary measure of metamorphosis was taken to be migratory behavior and changes in coefficient of condition. Constant photoperiods of long duration ($\geq$ 16 hours in duration) appeared to inhibit migratory behavior whereas shorter photoperiods ($\leq$ 12 hours in duration) or continuous darkness did not. Fish reared under an accelerated photoperiod were migratory earlier than control fish regardless of the temperature cycle. Those receiving a decelerated photoperiod had a delayed and extended migratory period. Fish reared under the reverse photoperiod (decreasing daylength in the spring) were not migratory during the spring and lacked smolt characteristics. Metamorphic response was greatest in groups of fish reared under a natural photoperiod and temperature regime.

The data suggest that the rate at which the length of the daily photoperiod increases is the information most utilized by the fish for synchronizing the metamorphic response, rather than the length of the daily light or dark period *per se* or the accumulated number of hours of exposure. Migratory behavior and smolt characteristics were observed in some of the fish under constant photoperiod and temperature.

Therefore, metamorphosis appears to have an endogenous mechanism or possibly be synchronized through rhythmic geophysical factors other than light and temperature.

The parr-smolt metamorphosis appeared not to be affected by monochromatic spectra (peak wavelength of 450 mμ, 550 mμ and 662 mμ), intensity (11 to 2195 lux) or total radiant energy (12 to 896 μWcm^{-2}) of the light sources used.

Temperature had two measureable effects on metamorphosis. Fish reared in a variable temperature cycle moved downstream in greater numbers and more quickly than fish reared at constant temperature, regardless of photoperiod. Temperature also influenced the duration of the migratory period. For example, when the temperature cycle was out of phase but behind the photoperiod, the migratory period was extended.

There was no apparent difference in thyroid activity. Thyroid follicle cell heights among groups of fish reared under constant photoperiod and temperature were similar. Thyroid cell heights were not substantially different for fish reared under natural, accelerated, and decelerated photoperiod and temperature regimes. The development and control of the hypo-osmoregulatory mechanism was independent of the photoperiods tested.

The Parr-Smolt Metamorphosis in Steelhead Trout as Affected by Photoperiod and Temperature

by

Harry Henry Wagner

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1971

APPROVED:

Redacted for Privacy

Associate Professor of Zoology
in charge of thesis

Redacted for Privacy

Associate Professor of Fisheries
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 Dec. 2, 1970

Typed by Barbara Eby for Harry Henry Wagner

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to Dr. F. P. Conte, thesis advisor, for his guidance and encouragement during the study. The assistance of Dr. J. D. Hall, academic advisor, in the preparation of the manuscript and data analysis is greatfully acknowledged. Dr. W. S. Overton made substantial contributions to the experimental design.

This study was financed with Anadromous Fish Act (P. L. 89-304) funds through the Bureau of Sport Fisheries and Wildlife, and funds from the Salmon Research Account of the Oregon State Game Commission. I am deeply indebted to Dr. H. J. Rayner and H. J. Campbell of the Commission for their continued support.

Many people contributed ideas and technical assistance to the study. The following deserve special mention and thanks for their contributions: J. L. Fessler, F. E. Wieman, P. M. Iwanga, D. A. Williams, R. E. Rowland, J. Golden, J. L. Ehmke and C. Gnose.

Last but not least, I am most appreciative of the patience shown by my wife, Eleanor, and her continued encouragement. To my children, Jeffrey, Ann, and Karine, I apologize for not being able to give you the attention you deserved at various times during the course of the study.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

THE PARR-SMOLT METAMORPHOSIS IN STEELHEAD TROUT AS AFFECTED BY PHOTOPERIOD AND TEMPERATURE

INTRODUCTION

This study was undertaken to determine effects of photoperiod and temperature on the metamorphosis of juvenile steelhead trout (Salmo gairdneri) from a form adapted to life in freshwater to one capable of surviving in the marine environment. Past investigations have shown that changes in the environment serve as important sources of information for regulating the chronological sequence of certain biological activities in vertebrates. Among all the environmental factors showing a temporal rhythmicity, the most important appears to be photoperiod. Although temperature does show annual change which follows a pattern similar to photoperiod, temperature is generally considered an unreliable cue because of its unpredictable nature. There is a vast literature dealing with photoperiodically controlled or endogenous circadian and annual rhythms as related to behavior and function in animals (Withrow, 1959; Webb and Brown, 1959; Cold Springs Harbor Symposia on Quantitative Biology, 1960; Cloudsley-Thompson, 1961; Bünning, 1964; Farner, 1965). Photoperiodic regulation of annual reproductive and migratory cycles has been most extensively studied in birds and to a lesser degree in mammals (Hammond, 1954; Bullough, 1959; Farner, 1961, 1965; Wolfson, 1964a).

Temperature has a profound influence on the physiology of poikilotherms and complicates experimental assessment of photoperiodic effects. Teleost fishes have received the greatest attention among poikilotherms in regard to photoperiodic involvement in reproductive cycles. Photoperiod or temperature or both completely dominates either the entire reproductive cycle or part of it in different species of teleosts. In other species, a strong endogenous rhythm exists which appears to be only timed by environmental changes (Pickford and Atz, 1957; Harrington, 1959; Farner, 1961; Hoar, 1965b; Ahsan, 1966).

By comparison, the role of seasonal environmental factors in timing the migration of fishes has received little attention. One of the greatest difficulties in this type of study is the lack of appropriate criteria which would indicate whether or not migration has been induced (Baggerman, 1957). The seaward migration of juveniles of many anadromous salmonids is associated with a metamorphosis that transforms the cryptic colored, bottom dwelling fish (parr) in freshwater into a silvery pelagic form (smolt) adapted to the marine environment (Hoar, 1963). The smolts of steelhead trout and Atlantic salmon (Salmo salar) as well as those of some species of Pacific salmon (Oncorhynchus), which show the above morphological appearance, are similarly characterized by a number of biochemical, physiological, and behavioral changes (Hoar, 1953, 1963; Evropeitseva, 1957,

1962; Malikova, 1957; Barrington, 1961; Vanstone and Markert, 1968; Fessler and Wagner, 1969). Baggerman (1957) in her study of the timing of migration of the stickleback (Gasterosteus aculeatus) summarized the most important criteria used in the study of the migrations of fish and birds. Essentially these involve changes in behavior, osmotic regulation, salinity tolerance and preference, and fat reserves.

The index to parr-smolt metamorphosis most frequently referred to and used is the silveriness resulting from an increase in the levels of two purines, guanine and hypoxanthine, in the skin and on the scales. However, these changes in silvery appearance are not necessarily related to metamorphosis and migration, but may represent a gradual adaptation to photic conditions in experimental rearing tanks (Johnston and Eales, 1967, 1968).

Increased thyroid activity based on changes in the follicular cell height was noted over thirty years ago in Atlantic salmon smolts (Hoar, 1939a). Since that time increased thyroid activity has been documented histologically and radiochemically in a number of anadromous salmonids during the period of downstream migration (Robertson, 1948; Hoar and Bell, 1950; Fontaine, Leloup and Olivereau, 1952; Eales, 1963). The parr-smolt metamorphosis apparently involves an increased demand for thyroid hormone. A generalized function in metabolism, rather than a specific role in migration, is visualized as the reason for increased activity (Hoar, 1959, 1963).

The parr-smolt metamorphosis in several species of Salmo and Oncorhynchus is also characterized by a change in the coefficient of condition. A marked decrease in condition occurs for fish undergoing the metamorphosis, followed by rapid increase in condition at the time they revert to a non-migratory form (Hoar, 1939b; Kizevetter, 1948; Malikova, 1957; Akulin, 1966; Fessler and Wagner, 1969; Pinder and Eales, 1969). The lower coefficient of condition for the smolt reflects alterations in chemical composition of body constituents.

The developmental pattern of hypo-osmoregulation in several species of anadromous salmonids has been established. In species of Salmo and Oncorhynchus in which a parr-smolt metamorphosis occurs, sea-water adaptation appears to be related to size and not chronological age (Parry, 1958, 1960; Conte and Wagner, 1965; Conte et al., 1966; Wagner, Conte, and Fessler, 1969). Juvenile fish are capable of becoming euryhaline several months before migration, depending upon growth rate. The development and maturation of the mechanism for hypo-osmoregulation does not force an immediate change in migratory behavior. In steelhead, a loss of osmotic and ionic regulation was noted during and following the migratory period for fish in freshwater.

Many other features of the smolt have been described, but their relation to migratory behavior, endocrine control, and response to enviromental factors has been lacking in factual details. Hoar (1958a) has presented arguments against the idea that seaward migration is

purely fortituous and undirected and supports the theory that changes in internal motivation in response to external factors are important to migration of anadromous salmonids. The possible environmental factors involved in seaward migration of fishes have been tentatively divided into two groups, "primers" and "releasers" (Fontaine, 1954; Hoar, 1958b; Baggerman, 1960a). Priming factors prepare the animal for migration and result in a slow change in behavior, and might be external or internal or both in nature. Releasing factors are appropriate external stimuli that act over a short period of time and initiate migration once the preparatory phase is complete.

The importance of photoperiod and temperature in parr-smolt metamorphosis has been long suspected, but the exact functional relationship along with details of the mechanism remain to be determined. In part, the purpose of the thesis was to unravel the role that photoperiod and temperature play in the regulation of the metamorphosis at the behavioral, morphological and physiological levels.

METHODOLOGY

Biological Environment

Experimental Fish

Winter steelhead trout originating from Alsea River on the northern Oregon coast were used as experimental fish. The parr-smolt metamorphosis is markedly size dependent and seasonal in occurrence in these fish (Wagner, 1968). The mean size of downstream migrants is 16 cm in fork length and 43 g in weight (Wagner, Wallace, and Campbell, 1963). Juveniles spend one to four years, depending upon growth rate, in the natural stream before migrating seaward (Chapman, 1958), but under artificial propagation most fish reach the critical size of 14 to 16 cm in one year. The downstream migration of smolts occurs from April through May with the peak of migratory activity occurring some time between mid-April and mid-May (Wagner et al., 1963). Smolts prevented from migrating readapt to a fresh-water existence.

Fish Culture

Two year classes of experimental fish were hatched and reared at the Fishery Research Laboratory, Oregon State Game Commission, in Corvallis, Oregon. Fish used in Experiment I were brought into

the laboratory as eyed eggs and incubated under constant temperature (12° C). The mean hatching date was April 15, 1965. Fry were removed from the darkened incubator on May 17 upon absorption of the yolk sac and placed in a circular fiberglas rearing tank. Fish were reared under a natural photoperiod and constant temperature until the population was divided into six groups, each consisting of 750 of the larger fingerlings, and placed under controlled photoperiods on July 11. A seventh group of 2,000 fish was maintained on a natural photoperiod. In December 1965 1,000 fish were removed from this group and placed under controlled photoperiods. On May 6, 1965 an additional group of fertilized eggs was obtained to be reared in the absence of light. These fish hatched on June 6 and about 400 were placed in a rearing tank in the dark on June 28.

Fish used in Experiment II originated from recently fertilized eggs that were brought to the laboratory January 18 and 19, 1967. The incubation temperature increased from an initial 4° C to 6° C at the time of hatching on March 2, 1967. Fry were removed from the incubator on April 14, and by that time the temperature had been gradually increased to 12° C. Experimental fish were placed in individual rearing tanks under normal photoperiods or in darkness but at a constant temperature (12° C). The light source was either sunlight, fluorescent white light, or monochromatic light. On June 1, 1967 controlled photoperiods and temperature cycles were initiated. The

population was reduced to 500 of the larger fingerling in each tank receiving light and 400 fish in each tank without light on June 3.

Fish were fed a commercially prepared dry pellet (Clark's New Age Complete Trout Feed, J. R. Clark, Salt Lake City, Utah). Feeding rate and quantity varied depending upon size of fish and temperature. Fish up to about 10 cm in length were fed predetermined amounts with an automatic feeder. As fish grew larger, they were fed by hand, generally to repletion, from one to five times each day depending upon their size. The feeding period was between 8 A M and 5 P M, seven days a week. Fish reared in the absence of light in Experiment I were fed with automatic feeders periodically in the 24-hour day throughout the time they were in the laboratory. In Experiment II, fish reared in the dark were fed by hand after reaching about 10 cm in length, but were fed more frequently and given about 1.5 times as much food at each feeding as those reared in the light.

Mortalities were negligible in all environmental groups in both experiments and could usually be assigned to congenital abnormalities or handling. The water supply of the laboratory is believed to be free of fish pathogens. Fin nipping was prevalent, with secondary infection of common water-borne bacteria occurring in yearling fish. Treatment with malachite green was used to control the infection. Fish were subjected to a 1:500,000 solution of malachite green for one hour. Routine examination of the internal organs of fish killed for

biological data revealed the occasional presence of renal calculi (nephrolithiasis). No mortalities could be assigned to this condition.

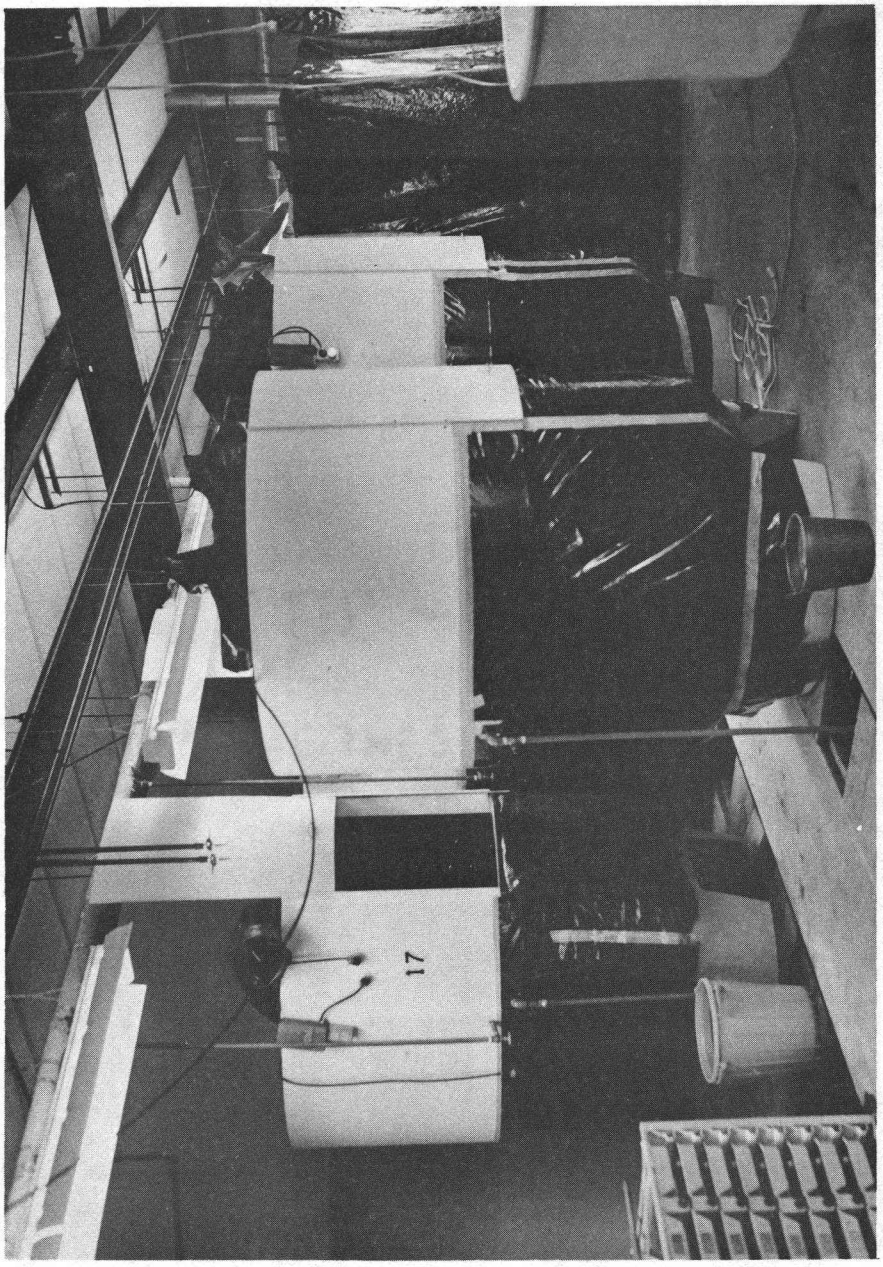
Physical Environment

Light

Rearing tanks were equipped with lightproof hoods to control the photoperiod (Figure 1). Illumination was provided by two 122 cm 40 W "Daylight" fluorescent lamps (General Electric F40D) and two 122 cm 40 W "Gro-Lux" fluorescent lamps (Sylvania F40/GRO). Distance from light source to water surface was 102 cm. Water depth was 53 cm. In tanks receiving blue, green or red light, four "Daylight" fluorescent lamps were provided with monochromatic filters (Powell Laboratories, Gladstone, Oregon). Distance from light source to water surface was 76 cm in this instance. An entrance compartment was provided to prevent any exposure to white light when hood doors were open.

Lights were controlled by timers which were routinely checked for accuracy. The timers were adjusted automatically for natural seasonal advancements in astronomical daylength for this latitude or were manually set for a constant photoperiod (Model 4005-OSZ-Astro Dial and Model 4001-0, Paragon Electric Company, Inc., Two Rivers, Wisc.). There were no daily periods of twilight. Depending on the

Figure 1. Rearing tanks and hoods.


17

light-intensity response threshold of the phenomenon, the biological daylength under a natural photoperiod because of the twilight periods might be longer than the astronomical daylength that was provided artifically in this study. Asynchronous phasing of the annual photoperiod cycle was achieved by either accelerating or decelerating the rate of change in the daily photoperiod (Figure 2). The accelerated and decelerated photoperiod cycles were controlled by manual adjustments of the automatic timers to produce a daily increment or decrement of approximately 6 minutes every 7 days (Appendix I). In the accelerated phase of the annual photoperiod cycle, the peak period of migration (mid-April to mid-May) as defined by photoperiod occurred from mid-February through early March. In the decelerated phase of the annual photoperiod cycle, it occurred from early June through mid-July. In the reverse photoperiod (complement of the natural), the cycle was normal in rate of change but six months out of phase. The photoperiod under which peak migration normally occurs was available to the fish from mid-October to mid-November.

Total radiant energy was measured with a spectroradiometer (Model SR, Instrumentation Specialities Co., 5624 Seward Ave., Lincoln, Nebr.). Spectral transmission curves for unfiltered and filtered light sources are shown in Figures 3 and 4, respectively. The blue filter transmitted light between the wavelengths of 400 mμ (millimicron) and 525 mμ with a peak in transmittance at 450 mμ. The

Figure 2. Photoperiod cycles used in Experiment II.

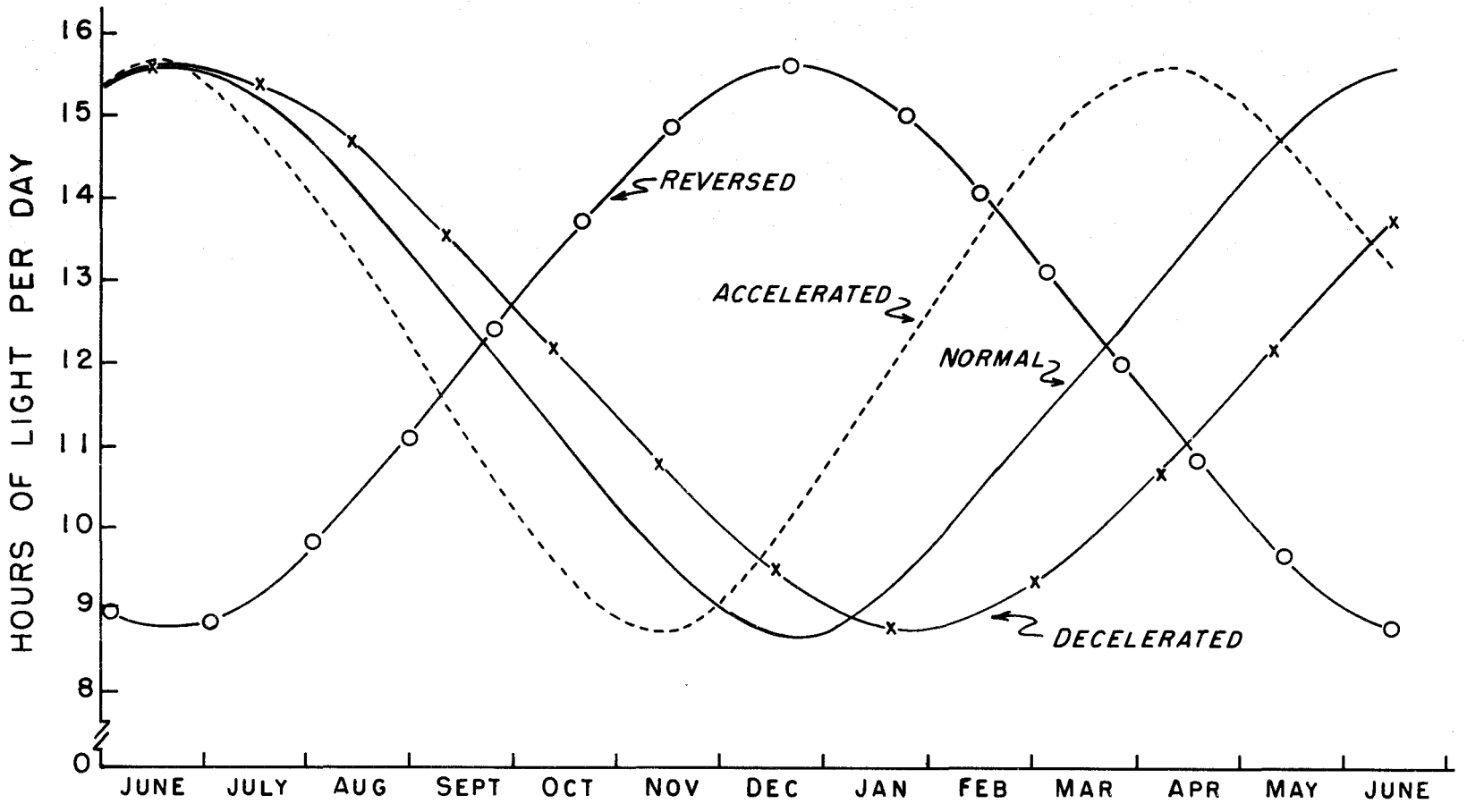
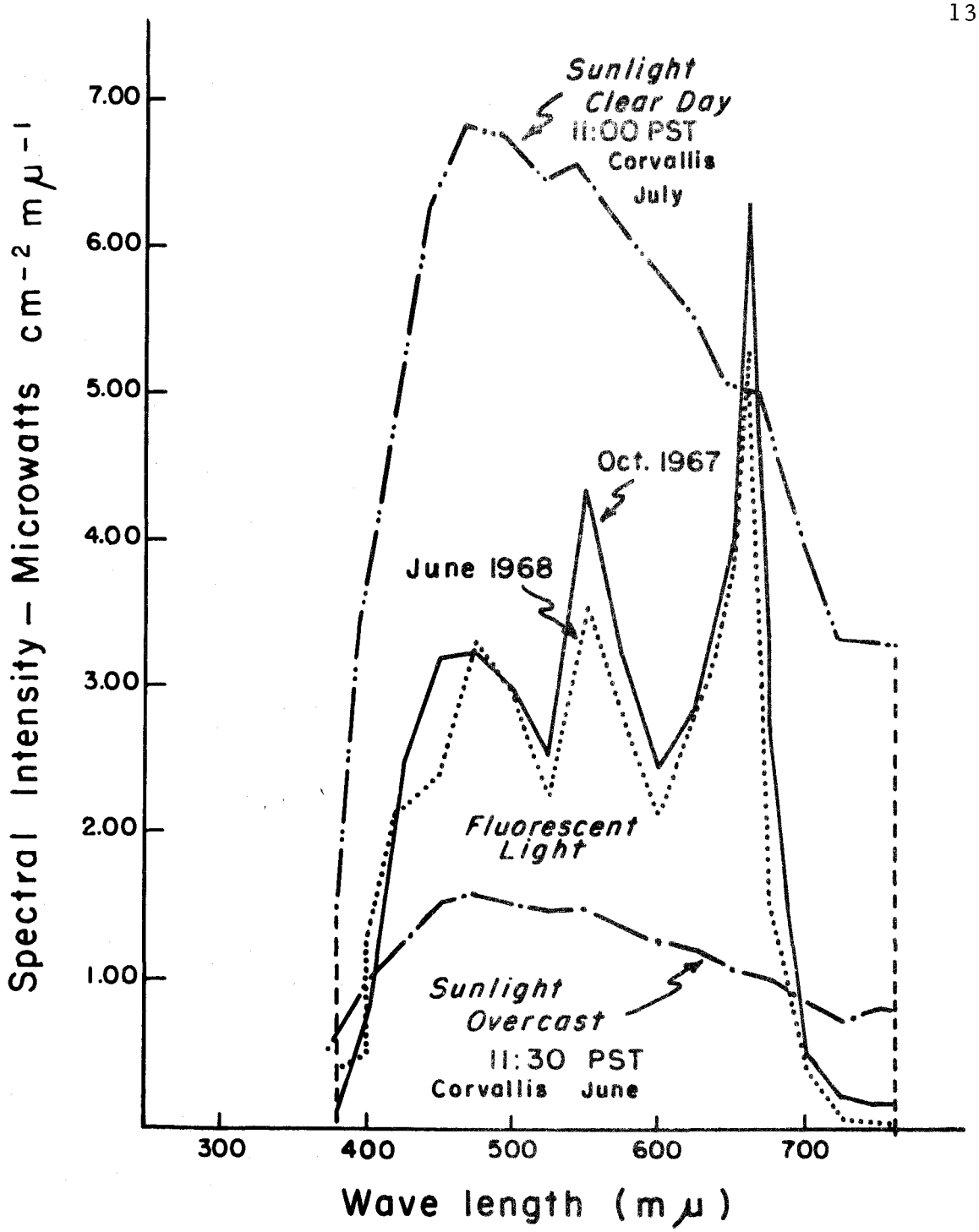

HOURS OF LIGHT PER DAY
16
15
14
13
12
11
10
9
8
0
REVERSED
ACCELERATED
NORMAL
DECELERATED
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUNE

Figure 3. Spectral transmission curves for fluorescent white light in comparison to natural sunlight. The spectral intensity of sunlight is obtained by multiplying the scale on the ordinate by 20 (1.00 microwatt cm^{-2} $m\mu^{-1}$ x 20).


Sunlight
Clear Day
11:00 PST
Corvallis
July
Oct. 1967
June 1968
Fluorescent
Light
Sunlight
Overcast
11:30 PST
Corvallis June
Spectral Intensity – Microwatts cm⁻² mμ⁻¹
7.00
6.00
5.00
4.00
3.00
2.00
1.00
300
400
500
600
700
Wave length (mμ)

transmittance for the green filter was between 500 mμ and 612 mμ with the peak at 550 mμ. The red filter transmitted light from 600 mμ into the infrared range (Figure 4). The peak in transmittance for the red filter was 662 mμ. Total radiant energy ($\mu W\ cm^{-2}$) and light intensity (lux) varied for the light sources (Table 1). Total radiant energy measurements are included because lux (lumens/m^2) and foot candles are photometric units of measure that are based on the spectral sensitivity of the human eye, rather than radiometric (physical energy) units (Beck, 1968; Whitney, 1969). The use of photometric units is consequently of doubtful value in a comparative context where the action spectrum of the animal under consideration might differ from the human eye (McInerney and Evans, 1970). Total radiant energy ranged from 896 $\mu W\ cm^{-2}$ for fluorescent white light to 11.8 $\mu W\ cm^{-2}$ for monochromatic green light. Light intensities ranged from 2195 lux for fluorescent white light to 11 lux for monochromatic red light. Computation of total radiant energy and light intensity were between the limits of 380 mμ to 760 mμ.

Fish reared in the absence of light were housed in a room constructed of double layers of black plastic sheeting. The room had a double door to prevent possible light exposure upon entering and leaving. Rearing tanks were covered with black plastic or wooden lids. An infrared light (Kodak No. 87C Wratten gelatin filter fitted to a Model A Kodak darkroom lamp supplied with a 15W bulb) and viewer

Figure 4. Spectral transmission curves for monochromatic filtered light. Measurements taken October 1967.

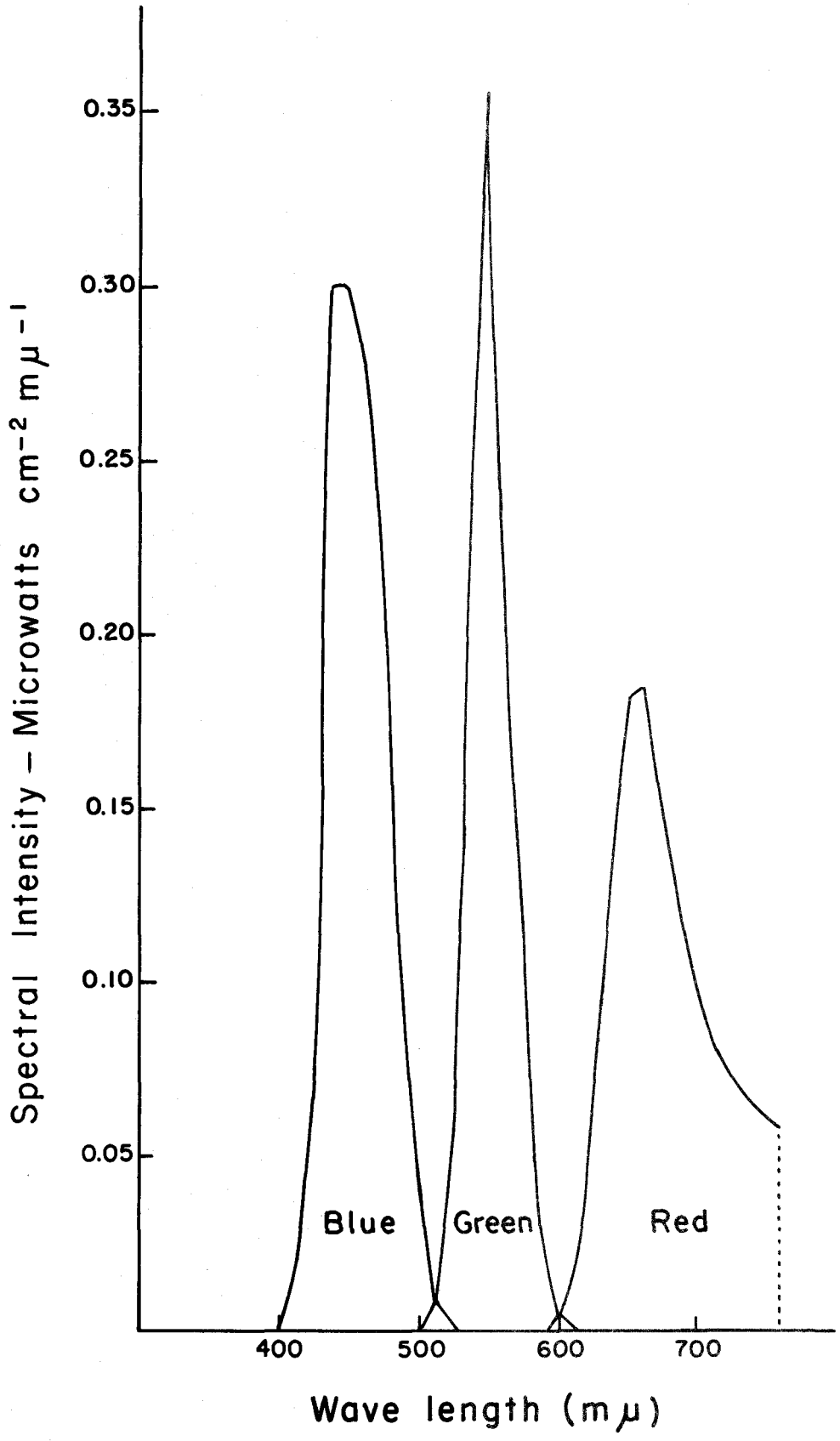

Spectral Intensity – Microwatts cm⁻² mμ⁻¹
0.35
0.30
0.25
0.20
0.15
0.10
0.05
Blue
Green
Red
400
500
600
700
Wave length (mμ)

Table 1. Total radiant energy and light intensity measurements.

Date	Light Source	Total energy[1] (μ Wcm^{-2})	Light intensity[1] (lux)
October 1967	Fluorescent white	958	2368
May 1968		835(833)[2]	2024(2067)[2]
Average		896	2195
October 1967	Monochromatic blue	16.7	18
May 1968		12.6	15
Average		14.6	17
October 1967	Monochromatic green	12.4	66
May 1968		11.1	58
Average		11.8	62
October 1967	Monochromatic red	15.8	11
May 1968		14.7	10
Average		15.2	11

[1] Measurements were made 24 inches above the water surface using a direct incident head.

[2] Measurements were made 3 inches above the water surface using a remote probe in mid-June showed that because of reflection the total energy and light intensity were similar whether measured near or 24 inches above the surface.

(Detectirscope Model 5500, Varo Optical, Inc., 5574 Northwest Hwy., Chicago, Ill.) were used as required for routine fish culture in both experiments and for taking growth measurements in Experiment II. Reactions (attraction, avoidance, orientation, and fright) of coho salmon (O. kisutch) fingerlings to infrared radiation were investigated by Duncan (1956). The experiments showed that coho could not perceive infrared radiation. Steelhead in this study were similar to coho in their response to this portion of the electromagnetic spectrum.

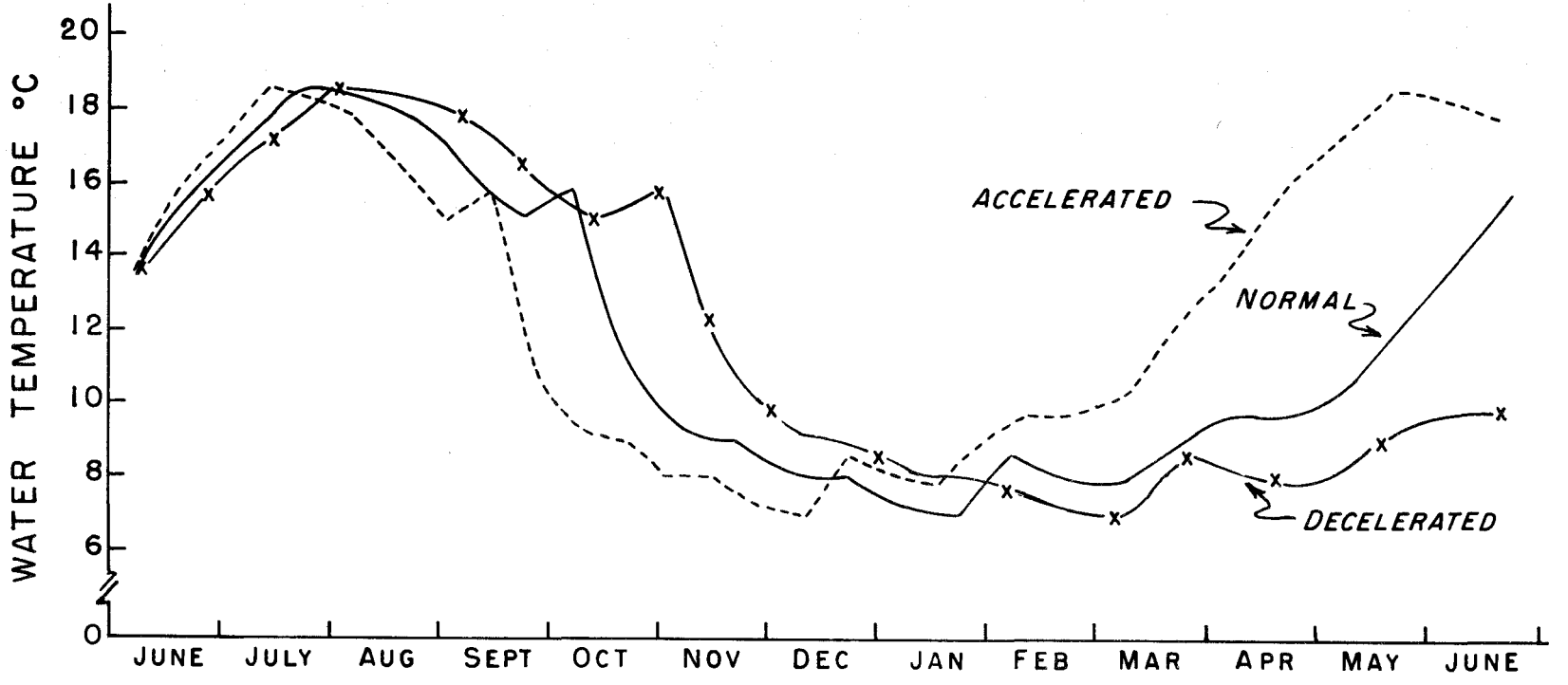
The problem of measuring the degree of darkness was not resolved. Ideally, an integrating photometer or very sensitive photometer for instantaneous measurements of light intensity would be used but none was available. During the study, film strips (Kodak Royal-X Pan; ASA 1250), portions of which were covered with an opaque black shield, were placed in the room for periods up to 10 days. No differences in negative density after development were noted between exposed and unexposed portions of the film. Films are normally used in an exposure of time of 1/10 to 1/1000 of a second and outside of this exposure range reciprocity failure is encountered (pers. comm. R. P. Michaelis). That is, the photographic effect of intensity times exposure is no longer a simple relation. It is impossible to derive any quantitative determinations with the present technique. However, this technique would indicate that the room illumination, if any, was extremely low.

Darkness is also difficult to define in terms of fish vision. Whitney (1969) suggested that in some fishes an operational definition of total darkness might be light intensities at which schooling ceased. I am not aware of any work for steelhead trout where the effects on behavior of low light intensity were studied. In juvenile Pacific salmon, schools disperse at an intensity of 0.001 lux, which is nearly equivalent to starlight (Ali, 1959). Light levels in the darkroom of the present study were less than starlight, based on my own observations.

Temperature

The ground water at the laboratory has a constant temperature of 12° C. Fluctuating temperatures were obtained with a commercial water heater and a cooling unit. The normal temperature cycle (6.9° to 18.6° C) simulated natural seasonal changes on the North Fork of the Alsea River based on a six year average (1958-1963). Temperatures were adjusted periodically to approximate seasonal cycles which were normal, accelerated, or decelerated in phase (Figure 5 and Appendix II). There was no measureable diurnal fluctuation in temperature in any regime except for the tank which received a constant temperature water supply outside the laboratory, where the exchange rate during Experiment II was insufficient to prevent heat loss or gain from ambient air. The diurnal fluctuation in temperature resulted in

Figure 5. Temperature cycles used in Experiment II. The normal temperature cycle simulated mean seasonal changes in the North Fork Alsea River for 1958-63.


WATER TEMPERATURE °C
20
18
16
14
12
10
8
6
0
JUNE
JULY
AUG
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUNE
ACCELERATED
NORMAL
DECELERATED

a 5° C seasonal change in the constant temperature regime (9.5° to 14.5°) in this tank.

Experimental Protocol

Experimental Design

In Experiment I, the effect of constant photoperiod on metamorphosis was examined in relation to one constant temperature of 12° C. Five groups of fish were exposed to constant photoperiods of different duration which ranged from continuous darkness to continuous light. Two groups were reared under seasonal photoperiod cycles; the light sources were sunlight and fluorescent white light. The controlled rearing period extended from July 11, 1965 to September 10, 1966. The following photoperiods were used:

1. Natural photoperiod (SL)[1, 2]
2. Normal photoperiod (NL)[3]
3. Winter solstice photoperiod; 8.5 hours (8.5L)
4. Equinox photoperiod; 12 hours (12L)
5. Summer solstice photoperiod; 16 hours (16L)

---

[1] Photoperiod (daylength) denotes the number of hours of exposure to light in a 24-hour day.

[2] Natural denotes no artificially controlled changes in an environmental factor (i.e. photoperiod or temperature).

[3] Normal denotes artificially controlled seasonal changes in an environmental factor to simulate a natural cycle.

6. Continuous light (LL)

7. Continuous darkness (DD)

Two lots of fish (A and B) were reared which differed in the time of introduction into the controlled photoperiods. Lot A was introduced on July 11, 1965 and Lot B on December 22, 1965. Fish in Lot B were reared under a normal photoperiod until the winter solstice. At that time they were marked by fin excision, and 200 were placed with the resident population in each of the following photoperiods: 8.5L, 12L, 16L, LL and NL.

The effect of rate of change in photoperiod and temperature cycles on the metamorphosis were investigated in Experiment II. To my knowledge, this is the first experimental design for studying the photoperiodic control of migration in fish employing rate of change rather than constant photoperiod of different duration. A few studies of reproductive cycles have employed photoperiods in which rate of change varied but they involved photoperiods which were longer or shorter than natural for the latitudes where the studies were conducted (Hoover and Hubbard, 1937; Hazard and Eddy, 1951; Corson, 1955; Henderson, 1963). The spectral transmission of the light source was controlled for several groups in the present study to determine if a wavelength dependency existed.

Temperatures in previous studies were held constant or allowed to vary naturally. No experiments have been noted where the seasonal

temperature cycle was varied in conjunction with photoperiod.

Fish were reared under 16 different controlled environmental regimes at the laboratory from June 1, 1967 to June 20, 1968. A group of fish reared at Alsea Trout Hatchery under natural conditions of photoperiod (SL) and temperature (ST) was used as an additional control. The following combinations of photoperiod and temperature cycles were used at the laboratory.

1. Natural photoperiod (SL) - Normal temperature cycle (NT).
2. Natural photoperiod (SL) - Constant temperature of 12° C (CT).
3. Normal photoperiod (NL) - Normal temperature cycle (NT).
4. Normal photoperiod (NL) - Constant temperature (CT).
5. Normal photoperiod (NL) - Accelerated temperature cycle (AT).
6. Normal photoperiod (NL) - Decelerated temperature cycle (DT).
7. Accelerated photoperiod (AL) - Normal temperature cycle (NT).
8. Accelerated photoperiod (AL) - Accelerated temperature (AT).
9. Decelerated photoperiod (DL) - Normal temperature (NT).
10. Decelerated photoperiod (DL) - Decelerated temperature (DT).

11. Normal photoperiod; monochromatic blue light (NLB) - Constant temperature (CT).

12. Normal photoperiod; monochromatic green light (NLG) - Constant temperature (CT).

13. Normal photoperiod; monochromatic red light (NLR) - Constant temperature (CT).

14. Reverse photoperiod (RL) - Constant temperature (CT).

15. Continuous darkness (DD) - Normal temperature (NT).

16. Continuous darkness (DD) - Constant temperature (CT).

In Experiment I, the continuous light regime was interrupted several times by power failures that provided a dark period lasting from several minutes up to one hour. In addition, small numbers of fish reared in continuous darkness were exposed to light while being weighed and measured each month in Experiment I. Fish reared in continuous darkness were exposed to dim indirect light once momentarily during an emergency in Experiment II.

Analytical Procedures

The basic analytical assays made were changes in migratory behavior, growth, sea-water adaptation, and thyroid activity.

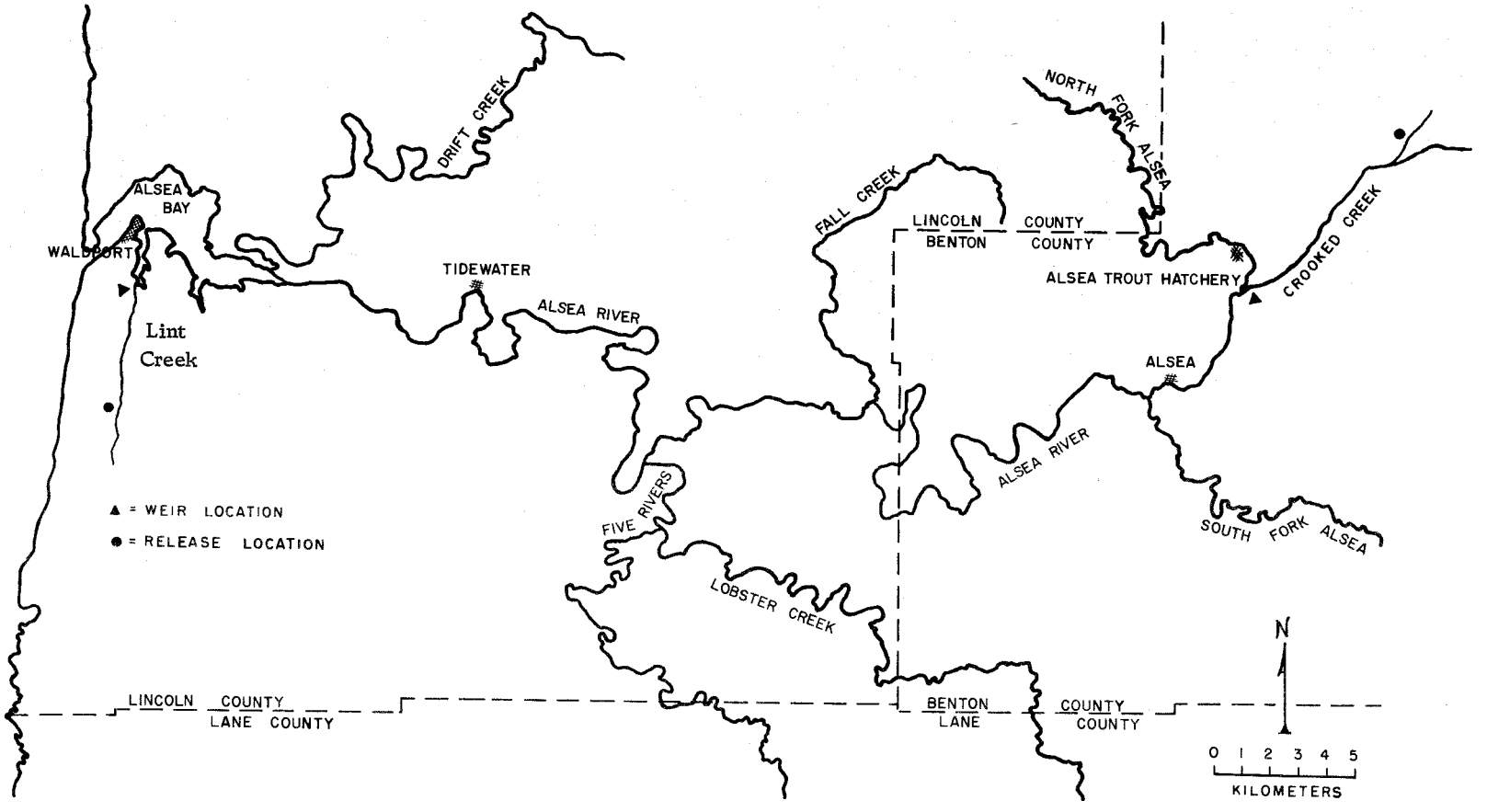
Migratory tendencies were assessed by periodic releases of experimental fish into natural streams and observation of the numbers of downstream migrants from each release group. Sexually immature

fish $\geq$ 16 cm in length were selected for release because smolting and precocious sexual development are believed to be incompatible biological processes (Evropeitseva, 1960). The size dependency of parr-smolt metamorphosis has been established and was the basis for size selection.

In Experiment I, a single release of 50 fish from each group in Lot A was made. No fish from Lot B were released. Fish were weighed, measured and marked by fin excision prior to stocking on March 25, 1966. On April 13, 1966, 50 fish were stocked from Alsea Trout Hatchery. Releases were made at a point approximately 4.8 km upstream from a weir on Lint Creek, a tributary to Alsea Bay (Figure 6). The primary purpose of the single release in 1966 was to determine the feasibility of using Lint Creek as a test stream, but some information on the migratory behavior of the fish was provided. Ideally, releases should have occurred each month as migrant-sized fish became available in various experimental groups.

In Experiment II, releases of fish were made from each experimental group from February through July 1968. Fish were identified by branding (Stott, 1968) and fin excision as to experimental treatment and month of release. Fish were stocked in Lint Creek in February, March, and April. Because of low streamflow in Lint Creek beginning in April, all subsequent releases were made in Crooked Creek, a tributary to the North Fork Alsea River (Figure 6). A temporary weir

Figure 6. Alsea River system showing release and recovery sites.


DRIFT CREEK
ALSEA BAY
WALDPORT
TIDEWATER
ALSEA RIVER
Lint Creek
▲ = WEIR LOCATION
● = RELEASE LOCATION
FIVE RIVERS
LOBSTER CREEK
LINCOLN COUNTY
LANE COUNTY
FALL CREEK
LINCOLN COUNTY
BENTON COUNTY
NORTH FORK ALSEA
ALSEA TROUT HATCHERY
CROOKED CREEK
ALSEA
ALSEA RIVER
SOUTH FORK ALSEA
BENTON COUNTY
LANE COUNTY
N
0 1 2 3 4 5
KILOMETERS

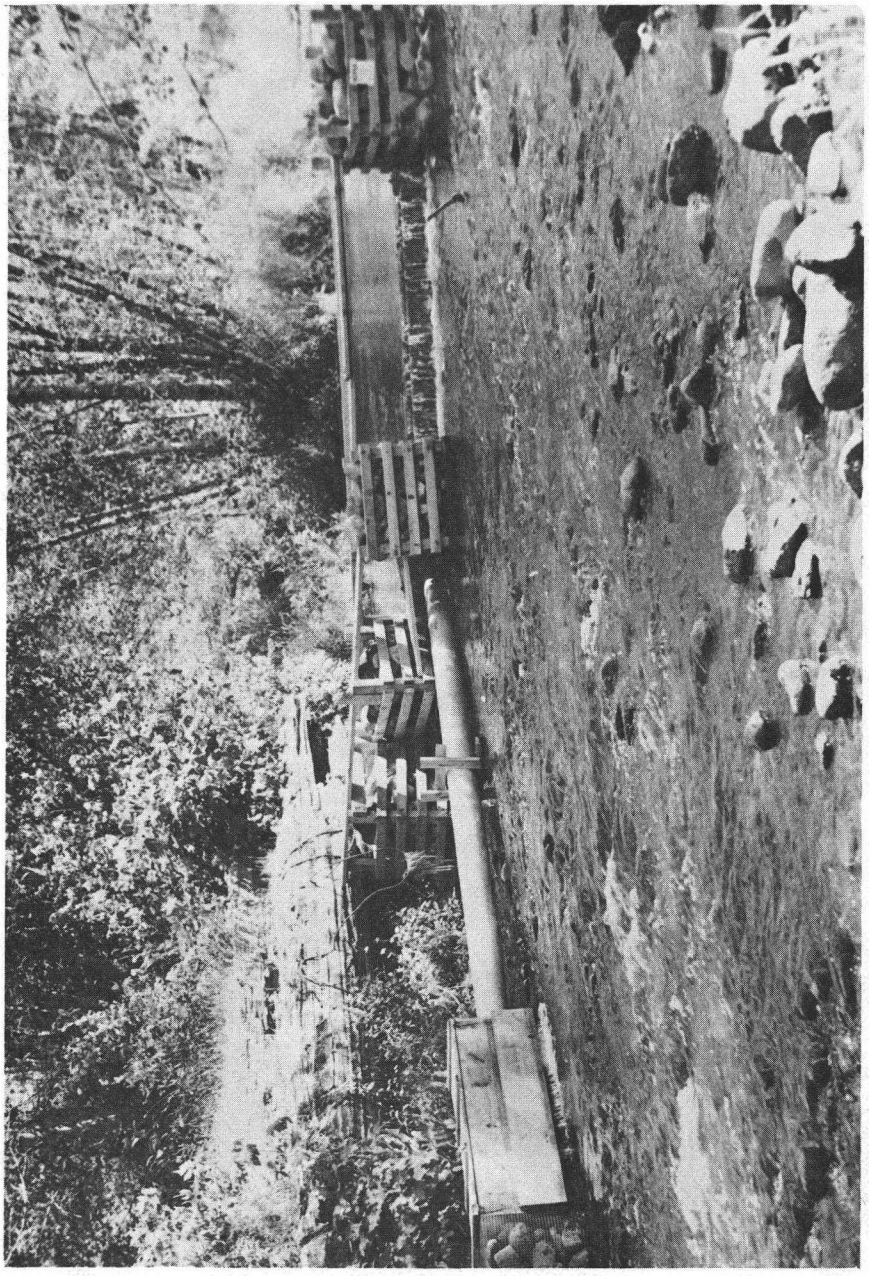
and trap were constructed on Crooked Creek about 6.4 km below the release site (Figure 7).

Trapping was terminated in late July in 1966 and 1968. Streams were sampled by electrofishing at selected points in late spring and summer to determine the distribution and abundance of released fish which were not recovered at the weirs.

There are no stream gauging stations on the test streams. Lint Creek watershed is about 6.3 km^2 in area and its flow closely reflects rainfall. An index to streamflow on Lint Creek was obtained from discharge records for nearby Deer Creek which has a watershed of 1.9 km^2. Visual inspection of the streamflow records for Deer Creek and precipitation records for Lint Creek indicated that rainfall pattern was similar for the two watersheds. Lint Creek flow was estimated by expanding Deer Creek flow by a factor of three (Appendices III and IV). A gauging station is present on the North Fork of the Alsea River and discharge records can be used as an index to flow changes on Crooked Creek. The flow for Crooked Creek equals about 20 percent of the North Fork discharge based on watershed area (Appendix V). Temperatures for Lint Creek and Crooked Creek are included with the flow records.

A random sample of between 50-100 fish was weighed and measured from each group monthly in Experiment I and semi-monthly in Experiment II. Individual fish ($\geq$ 10 cm) were weighed to 0.1 g and

Figure 7. Weir used to capture downstream migrants on Crooked Creek in Experiment II. Pipe leads from weir fence downstream to livebox. Photograph taken in late June 1968.



smaller fish to 0.01 g on Mettler K-7T and P-120 balances, respectively. Fork length was determined to 0.1 cm. All fish were anesthetized in tricane methanesulfonate (MS-222) prior to processing (Bell, 1964).

The coefficient of condition (K) was determined for each fish in the sample using the formula $K = 100\ W/L^3$, where W denotes weight in grams and L denotes fork length in centimeters (Hoar, 1939b). The mean coefficient of condition ($\overline{K}$) is the average of individual values.

Instantaneous daily growth rates in weight and length were estimated from the relationship

$$g = \frac{LnX_t - LnX_0}{t}$$

where g denotes the instantaneous growth rate in weight or length during the time t in days (LeBrasseur and Parker, 1964). The symbol X denotes weight in grams or length in centimeters. The abbreviation Ln denotes the natural logarithm of the specified term.

Monthly in Experiment I, fish were exposed to sea water (30 °/oo) by immediate transition from freshwater. Survival provided a gross measurement of the osmoregulatory ability of test fish. Test procedures were previously described by Conte and Wagner, 1965. The seawater exposure period was from 15 to 28 days in duration. A random sample of 10 to 50 fish of Lots A and B were removed from the

controlled environments and placed in either 3.5 liter glass jars, or in 20-liter or 80-liter plexiglass aquaria. Temperature was maintained at 12° C to 13° C, and the room provided with a normal photoperiod (NL). Following a three day acclimation, the freshwater was replaced with sea water. All experiments were conducted under static water conditions with individual aquaria aerated with compressed air. Water was changed daily about one hour after feeding to prevent the accumulation of metabolic wastes. Fish to about 9 cm in length were fed frozen brine shrimp (Artemia sp.) and tubifex worms (Tubifex sp.), while larger fish were fed the standard rearing diet.

From April 1966 to September 1966 survivors of the sea-water exposure period were killed to determine the osmotic and ionic properties of their blood. Analytical procedures were reported earlier (Conte and Wagner, 1965). Blood was obtained by severence of the caudal peduncle. Blood flowing from the caudal artery was dropped onto small pieces of paraffin film and immediately transferred via polyethylene tubing into small polyethylene micro-centrifuge tubes and centrifuged (Beckman Microfuge, Beckman Instruments, Palo Alto, Calif.) at 5500 g for 1 min. The supernatant plasma was removed and frozen until such time as the analytical measurements could be made. Sodium concentrations in plasma were measured by flame photometry utilizing a Beckman B flame spectrophotometer and using standard solutions for comparison and calibration. Plasma chloride

concentrations were measured by microtitration using the modified method of Schales and Schales (1941). The osmotic concentration of the blood was measured through the use of a vapor pressure osmometer (Mechro-Lab, Inc., Mountain View, Calif.) which had been calibrated with standard solutions of mannitol and sodium chloride.

Thyroid activity was assayed by killing a sample of 5 to 10 fish monthly in Experiment I or semi-monthly in Experiment II. The tissues were fixed for 24 hours in Bouin-Hollande-sublimate then rinsed in distilled water and transferred to 70 % isopropyl alcohol for storage. After removal from storage, the tissues were prepared for histological study by routine methods. The thyroid tissue was sectioned at 7 to 10μ and stained in Harris's haematoxylin (Humason, 1962, p. 125) and eosin.

A random sample of 20 unbroken thyroid follicles was measured for cell height for each fish. Ten follicles were measured on each of two slides prepared from tissue taken around the second branchial arch. A distance of 150μ of tissue was allowed between slides to avoid repetitive measurements of follicles. Each follicle was measured at four different points (90° coordinates). The average of 80 measurements (20 follicles x 4 measurements/follicle) represented the index of cell height for any given fish. The cell height for a group of fish was determined from averaging the individual means. In the thesis, the term activity when used in reference to thyroid refers to cell

height or radioiodide metabolism and not to function.

A record of the number of fish observed with maturing gonads was kept. A reference to the stage of gonadal development was given by the gonosomatic index (GSI) which is estimated from the relationship

$$\text{Mean GSI} = \frac{\sum\left(\frac{\text{wt. of gonad}}{\text{total wt. of fish}} \times 100\right)}{N}$$

where wt denotes weight in grams and N denotes number of fish in the sample (Wiebe, 1968).

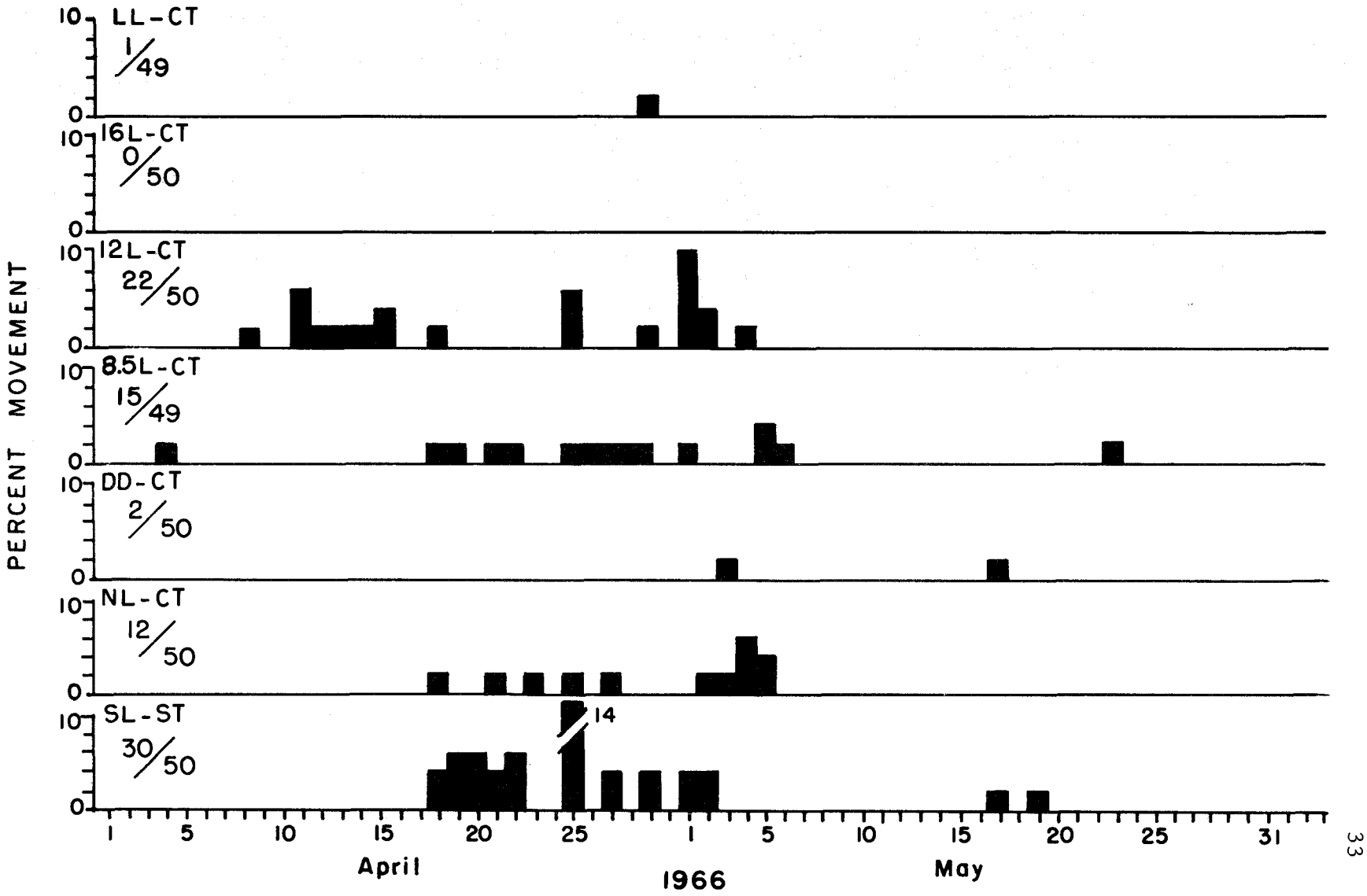
RESULTS

Migratory Behavior

Substantial differences were found in the numbers of fish that migrated downstream from groups released in late March in Experiment I (Figure 8). Fish reared in 8.5L, 12L, NL, and SL photoperiods possessed the greatest migratory tendencies as evidenced by their movements. Fish from NL and 8.5L photoperiods were similar in that 24% and 30% of the fish were recovered migrating downstream, respectively. The 12L fish showed the greatest number of migrants (44%) of groups released from the laboratory. No SL fish from the laboratory were released because of insufficient numbers. A 60% recovery was obtained from a group of SL-ST fish from Alsea Trout Hatchery released on April 13. No movement occurred in 16L fish and only 2% and 4% of those released were recovered from the continuous light (LL) and darkness (DD) groups, respectively. Lack of movement from the DD group might be accounted for on the basis of size, as all fish were smaller than 15 cm.

Even though the number of fish migrating downstream varied among groups, the period of movement was similar. Most fish were captured from mid-April to mid-May, with the exception of a slightly earlier movement of 12L fish (Figure 8). A small freshet began on April 9 and might have had an influence on the movement of all groups

Figure 8. Pattern and magnitude of downstream migration of juvenile steelhead released in Lint Creek, March 25, 1966. See abbreviations on pages 20-21; SL-ST group from Alsea Hatchery released on April 13, 1966; Ratios are the number of fish captured to number of fish released for a particular group.


PERCENT MOVEMENT
LL-CT
1/49
16L-CT
0/50
12L-CT
22/50
8.5L-CT
15/49
DD-CT
2/50
NL-CT
12/50
SL-ST
30/50
14
10
0
1
5
10
15
20
25
1
5
10
15
20
25
31
April
1966
May

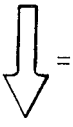
(Appendix III).

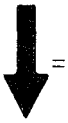
Fate of fish not captured at the weir is unknown. No fish were recovered in the isolated pools in 1.2 km of stream below the release site when it was electrofished in June. Earlier movement upstream was prevented by a barrier. Fish which might have moved downstream at later dates were probably prevented by low stream flow but the number of fish residing in the impounded water behind the weir is not known. Natural mortality is believed to be high for fish released in Lint Creek because of avian and mammalian predation.

In Experiment II, substantial differences were observed in the timing and magnitude of movement from February to July 1968 for groups reared under different photoperiod and temperature cycles (Table 2 and Figures 9 and 10).

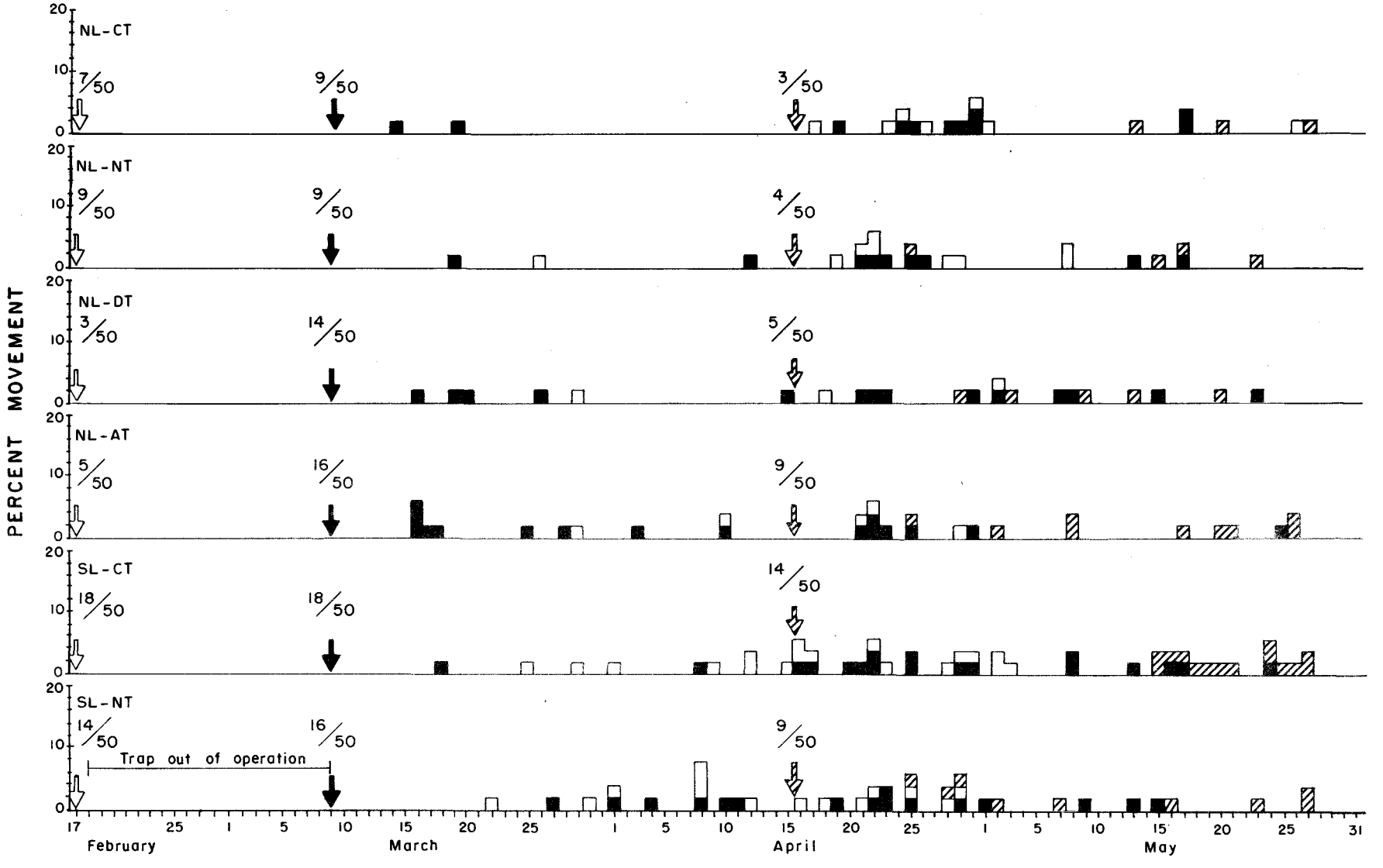
The first release into Lint Creek was made in mid-February. Unfortunately, the weir and trap became inoperable from February 18 through March 9 because of high stream flow (Appendix IV). The number of fish which migrated downstream during this time and escaped capture are not known. Despite these opportunities for movement, most of the experimental groups apparently remained in the stream until April and May (Figure 9). The SL-CT fish showed highest recoveries (36%) during this time while no fish were captured from the RL group.

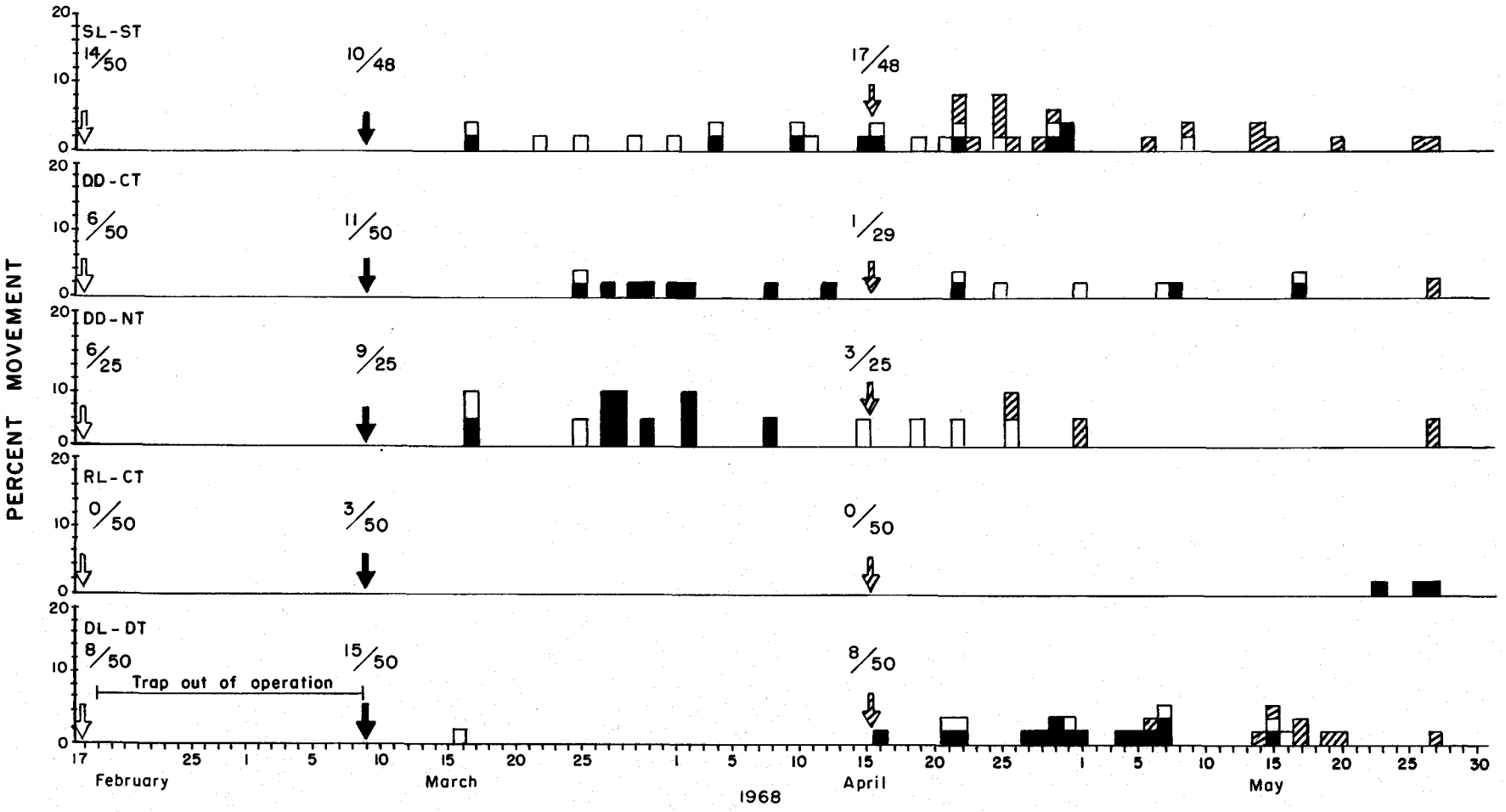
Figure 9. Pattern and magnitude of the downstream migration of juvenile steelhead released in Lint Creek in 1968. See abbreviations on pages 22-23; Total area of each histogram is proportional to percentage of fish that migrated from that release; Ratios above arrows (date of release) are the number of fish captured to number of fish released for a particular group.

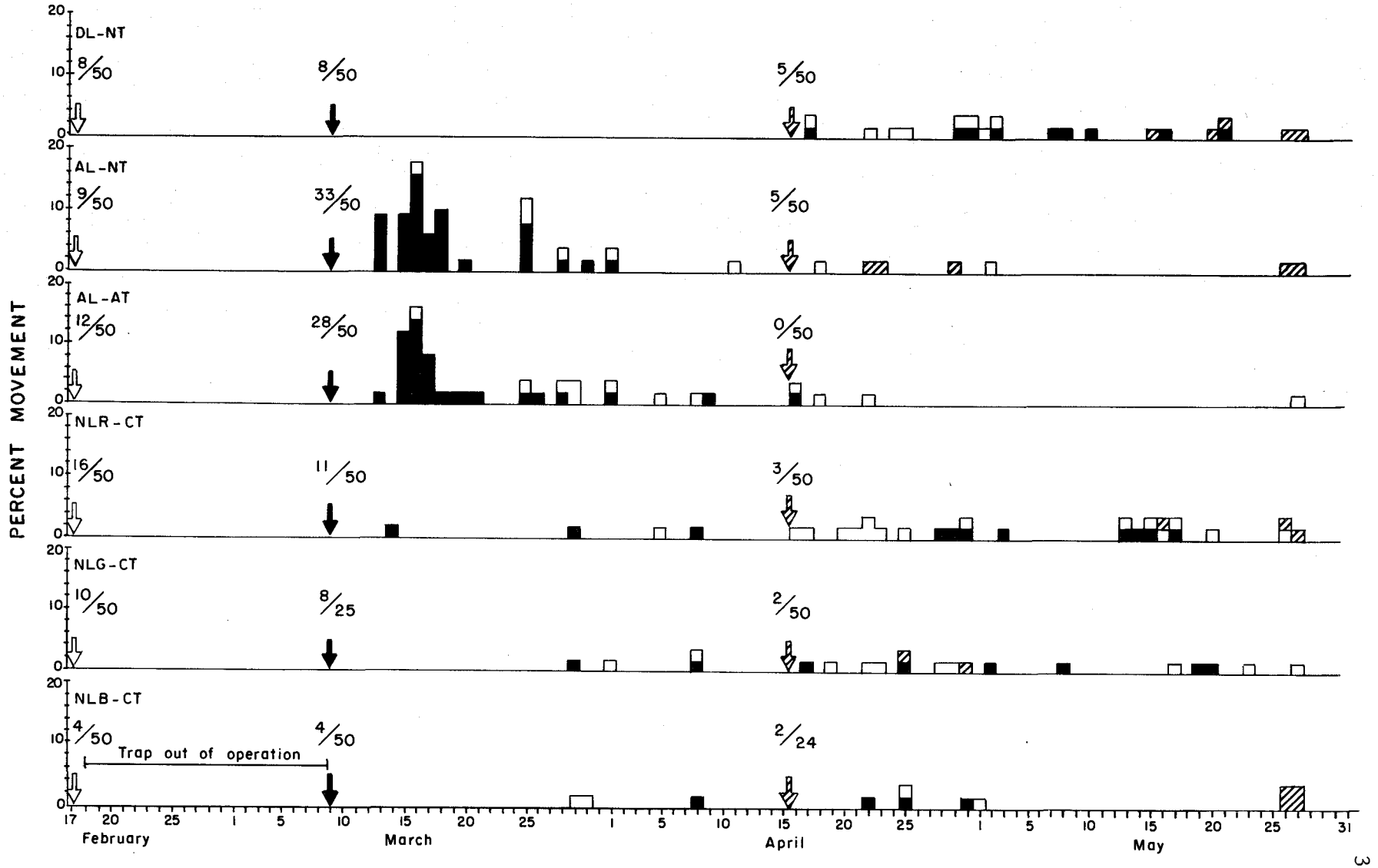

= February 17 release


= March 9 release


= April 15-16 release


PERCENT MOVEMENT
NL-CT
7/50
9/50
3/50
NL-NT
9/50
9/50
4/50
NL-DT
3/50
14/50
5/50
NL-AT
5/50
16/50
9/50
SL-CT
18/50
18/50
14/50
SL-NT
14/50
16/50
9/50
Trap out of operation
0
10
20
17
25
1
5
10
15
20
25
1
5
10
15
20
25
1
5
10
15
20
25
31
February
March
April
May


PERCENT MOVEMENT
SL-ST
14/50
10/48
17/48
QD-CT
6/50
11/50
1/29
DD-NT
6/25
9/25
3/25
RL-CT
0/50
3/50
0/50
DL-DT
8/50
15/50
8/50
Trap out of operation
17 February 25 1 5 10 15 20 25 March 1 5 10 15 20 25 April 1 5 10 15 20 25 30 May
1968


PERCENT MOVEMENT
DL-NT
8/50
8/50
5/50
AL-NT
9/50
33/50
5/50
AL-AT
12/50
28/50
0/50
NLR-CT
16/50
11/50
3/50
NLG-CT
10/50
8/25
2/50
NLB-CT
4/50
4/50
2/24
Trap out of operation
17 20 25 1 5 10 15 20 25 1 5 10 15 20 25 1 5 10 15 20 25 31
February
March
April
May

A second release was made in Lint Creek in early March to gather information on the migratory behavior of the various experimental groups prior to the normal period of downstream movement. Water conditions were optimal for movement as a result of a series of freshets which occurred after the fish were released (Appendix IV). The two accelerated photoperiod groups (AL) showed an immediate and substantial downstream movement. The AL-AT recovery was 44% and AL-NT was 52% in the first 15 days after release (Table 2). Recovery of fish from the other 15 groups ranged from 0 to 8%. In the first 30 days after release, greatest recoveries, omitting the AL groups, were for fish reared in the absence of light (DD-NT = 36%; DD-CT = 14%). Other experimental groups in the second release were captured in greatest numbers over one month later with recoveries ranging from 8% to 36%. Only 6% of the RL fish were recovered by the end of July.

Experimental fish were released for the third time in Lint Creek in mid-April, but as a result of low stream flow preceding and following release, I believe downstream movement was restricted (Appendix IV). Less than 20% of the fish were recovered from any given release group with the notable exceptions of SL-CT and SL-ST groups where 28% and 35% of the fish were recovered, respectively (Table 2). The movement that did occur was in the latter part of May when stream flows again increased (Figure 9).

Table 2. The number of fish released and captured migrating downstream from February 17, 1968 through July 31, 1968[a].

Treatment[b]	Feb. 17		Mar. 9		April 15-16		May 1		June 13	
	First 15 days	Total[c]	First 15 days	Total[c]	First 15 days	Total[c]	First 15 days	Total[d]	First 15 days	Total[e]
SL-ST	No	14/50(28)[f]	1/48(2)	10/48(21)	9/48(18)	17/48(35)	95/100(95)	99/100(99)	23/100(23)	23/100(23)
SL-NT	Data	14/50(28)	0/50(0)	16/50(32)	3/50(6)	9/50(18)	29/35(83)	31/35(88)	39/67(58)	39/67(58)
SL-CT		18/50(36)	1/50(2)	18/50(36)	0/50(0)	14/50(28)	18/25(72)	21/25(84)	17/71(24)	17/71(24)
NL-NT		9/50(18)	1/50(2)	11/50(22)	1/50(2)	4/50(8)	26/35(74)	29/35(83)	18/73(24)	18/73(24)
NL-AT		5/50(10)	5/50(10)	16/50(32)	1/50(2)	9/50(18)	38/50(76)	46/50(92)	10/82(12)	10/82(12)
NL-DT		3/50(6)	3/50(6)	14/50(28)	1/50(2)	5/50(10)	31/35(88)	32/35(91)	38/75(51)	38/75(51)
NL-CT		7/50(14)	2/50(4)	9/50(18)	0/50(0)	3/50(6)	25/50(50)	33/50(66)	17/68(25)	17/68(25)
NLB-CT		4/50(8)	0/50(0)	4/50(8)	0/24(0)	2/24(8)	13/25(52)	19/25(76)	9/66(13)	9/66(13)
NLG-CT		10/50(20)	0/50(0)	8/50(16)	2/50(4)	2/50(4)	21/50(42)	31/50(62)	12/65(18)	12/65(18)
NLR-CT		16/50(32)	1/50(2)	11/50(22)	0/50(0)	3/50(6)	19/35(54)	26/35(74)	12/76(15)	12/76(15)
AL-AT		12/50(24)	22/50(44)	28/50(56)	0/50(0)	0/50(0)	5/50(10)	9/50(18)	0/61(0)	0/61(0)
AL-NT		9/50(18)	26/50(52)	33/50(66)	3/50(6)	5/50(10)	29/50(58)	35/50(70)	0/67(0)	0/67(0)
DL-DT		8/50(16)	0/50(0)	15/50(30)	0/50(0)	8/50(16)	9/35(25)	31/35(89)	41/66(68)	41/66(68)
DL-NT		8/50(16)	0/50(0)	9/50(18)	0/50(0)	5/50(10)	8/25(32)	23/25(92)	39/70(56)	41/70(59)
RL-CT		0/50(0)	0/50(0)	3/50(6)	0/50(0)	0/50(0)	0/35(0)	1/35(3)		
DD-NT		6/25(24)	1/25(4)	9/25(36)	1/25(4)	3/25(12)	10/25(40)	18/25(72)	3/8(37)	3/8(37)
DD-CT		6/50(12)	0/50(0)	11/50(22)	0/29(0)	1/29(3)	5/25(20)	13/25(52)	4/50(8)	8/50(16)

[a] Fish released May 20, 1968 and July 3, 1968 from Alsea Trout Hatchery are not included.

[b] See abbreviations on pages 22-23.

[c] No movement observed after May 31, 1968.

[d] Trap out of operation May 26 through June 12 because of high water.

[e] No movement observed after July 11, 1968.

[f] No. captured/no. released (percent).

The fourth release was made in the larger Crooked Creek instead of Lint Creek during the peak period of natural downstream migration. On the first of May, fish were released about 6.4 km above a temporary weir. Flows in the stream were adequate for movement as indicated by the capture of wild smolts (Appendix VI). In addition, a stream survey showed no obvious obstructions over the migration route. Both the magnitude and pattern of movement differed for various experimental groups. Recoveries ranged from 0% to 95% in the first 15 days after release (Figure 10). Fish reared under a normal (NL) or natural (SL) photoperiod and a variable temperature (ST, NT, AT, or DT) were captured in greatest numbers (Table 2), with recoveries ranging from 74% to 95%. The next highest recoveries were from groups of fish reared under a normal photoperiod (NL), regardless of light quality (NL, NLB, NLG, or NLR), and at constant temperature (CT). Recoveries ranged from 42% to 54% of the fish released. In the first 15 days after release, 72% of the SL-CT fish were recovered. The greater migratory tendencies of this group in comparison to other CT groups (NL, NLB, NLG, and NLR) might be related to the unscheduled seasonal temperature variation that occurred during the rearing period at the laboratory.

Recoveries of fish reared under accelerated photoperiods (AL) were strikingly different for the May release. Fish reared at a normal temperature cycle (NT) were apparently migratory, as 58% of the

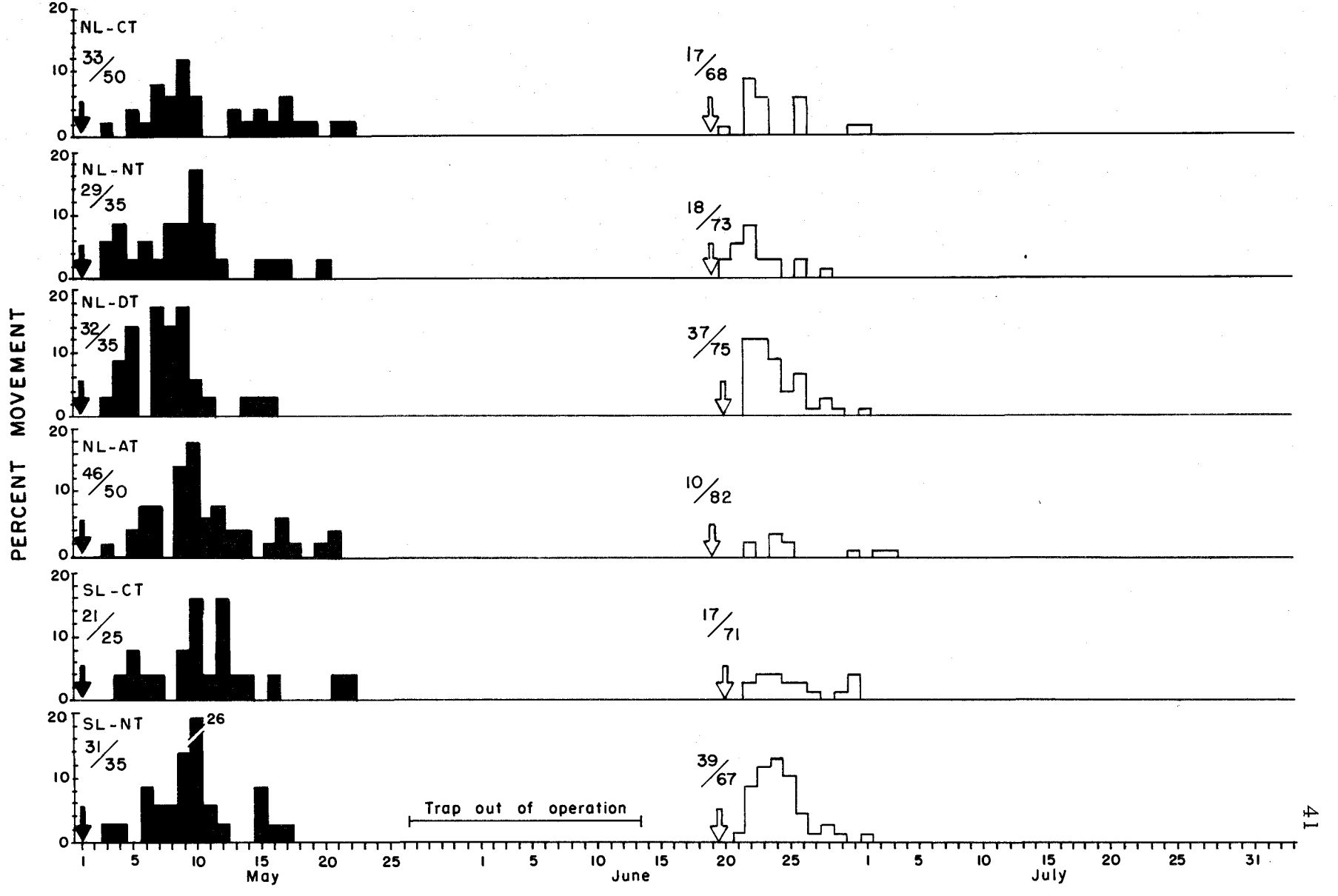
Figure 10. Pattern and magnitude of the downstream migration of steelhead released on Crooked Creek in 1968. See abbreviations on pages 22-23; Total area of each histogram is proportional to percentage of fish that migrated from that release; Ratios above the arrows (date of release) are the number of fish captured to number of fish released for a particular group.

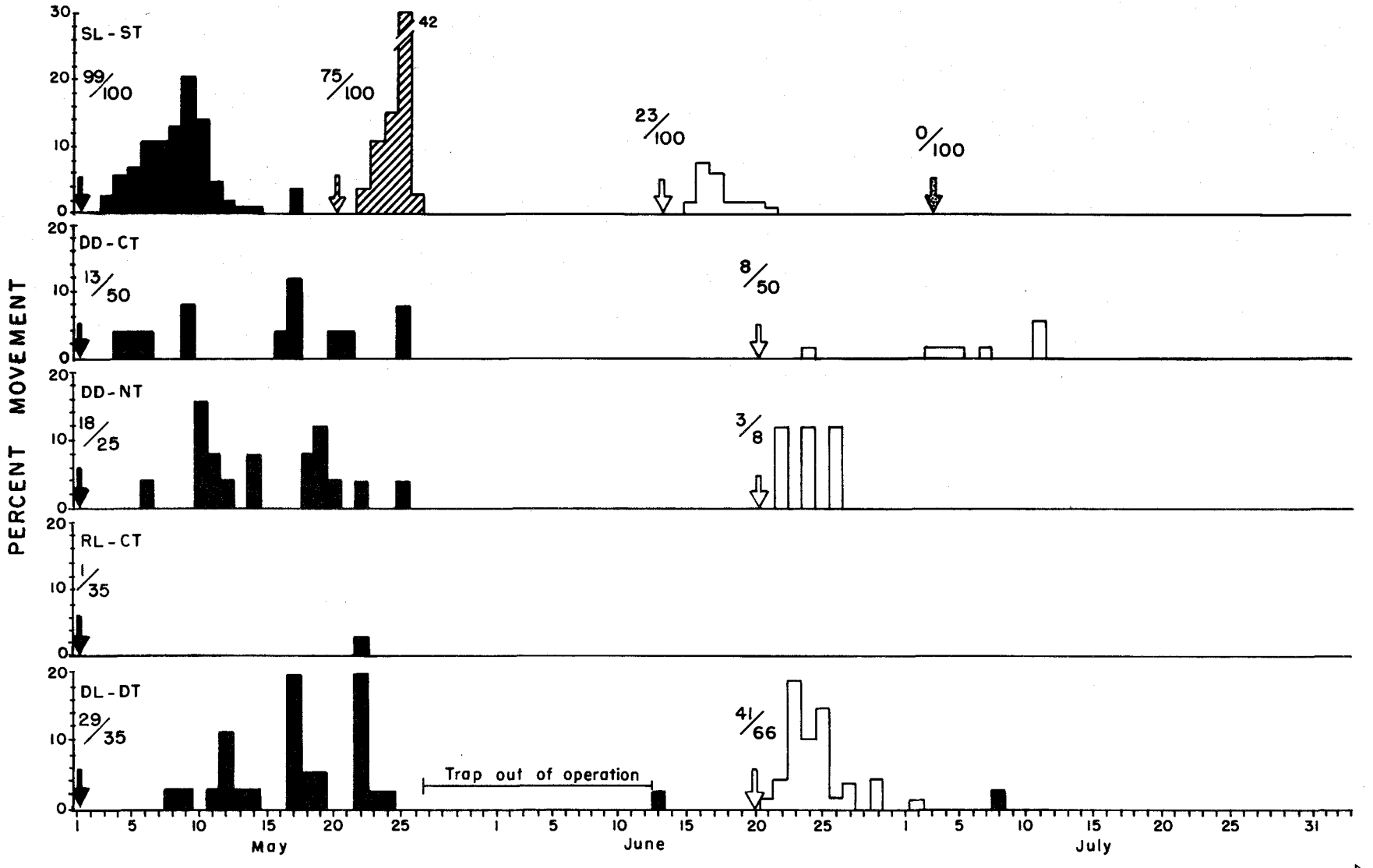

= May 1 release

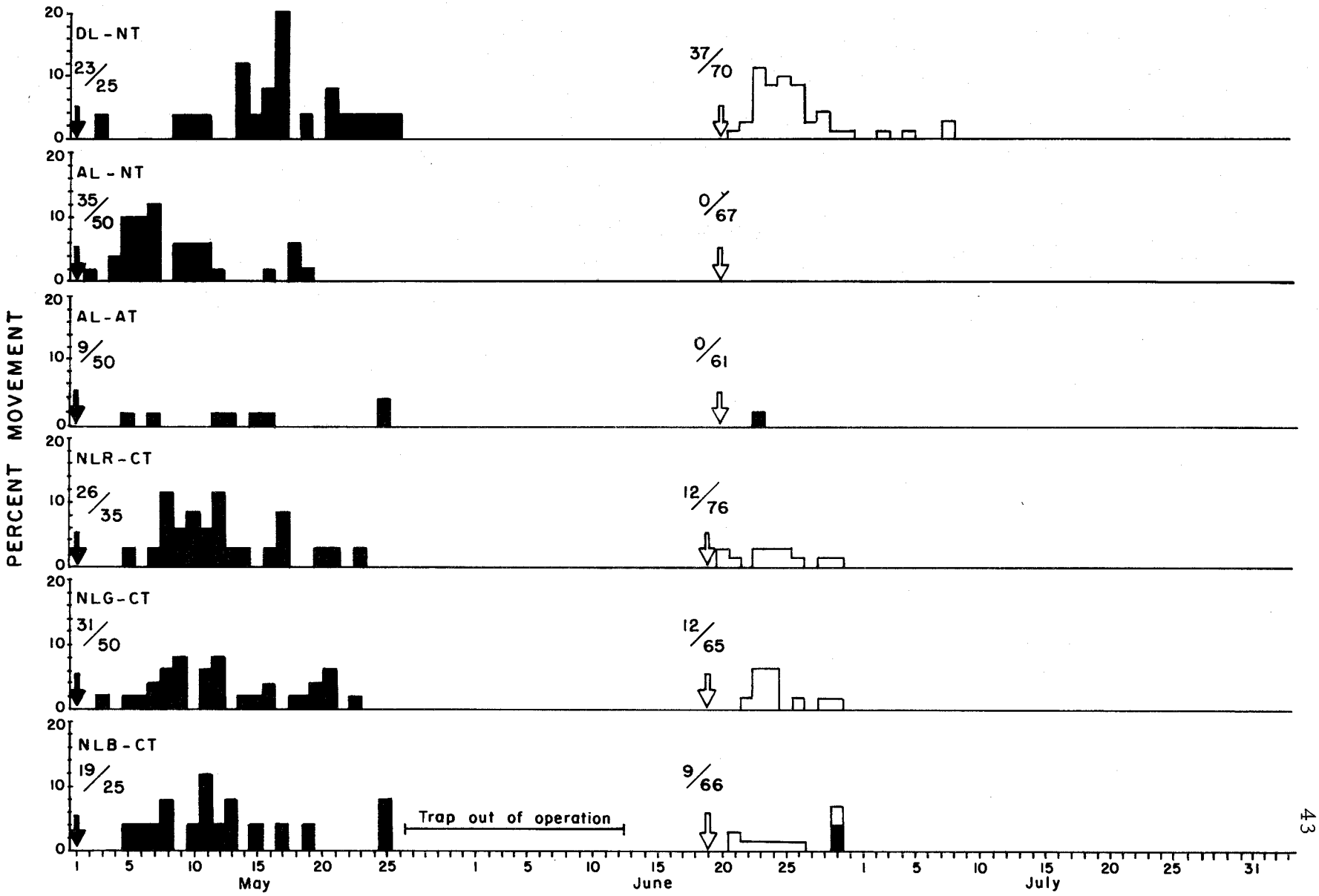

= May 20 release


= June 13, and 19-20 releases


= July 3 release


PERCENT MOVEMENT
NL-CT
33/50
17/68
NL-NT
29/35
18/73
NL-DT
32/35
37/75
NL-AT
46/50
10/82
SL-CT
21/25
17/71
SL-NT
31/35
26
39/67
Trap out of operation
May
June
July


PERCENT MOVEMENT
SL - ST
99/100
75/100
42
23/100
0/100
DD - CT
13/50
8/50
DD - NT
18/25
3/8
RL - CT
1/35
DL - DT
29/35
41/66
Trap out of operation
May
June
July


PERCENT MOVEMENT
DL - NT
23/25
37/70
AL - NT
35/50
0/67
AL - AT
9/50
0/61
NLR - CT
26/35
12/76
NLG - CT
31/50
12/65
NLB - CT
19/25
9/66
Trap out of operation
May
June
July

fish released were recovered. Those reared under an accelerated temperature cycle (AT) were much less migratory as contrasted by the 10% recovery.

The two groups of fish reared under a decelerated photoperiod (DL) and either a decelerated (DT) or normal temperature (NT) cycle showed less immediate movement than those reared under a NL or SL photoperiod. In the first 15 days after being released in May, only 25% and 32% were recovered respectively, from the DL-DT and DL-NT groups (Table 2). After 25 days the accumulative recovery rose to 83% and 92%, respectively. Thus, while the pattern of movement differed in being later, the magnitude was comparable to that observed for NL and SL groups reared on variable temperature cycles (Figure 10). Only one fish (3%) was captured from the RL group by July.

Fish reared in the absence of light and on a CT or NT temperature cycle differed markedly in migration tendencies in May. Forty percent of the fish released were captured from the DD-NT group in the first 15 days after release but only 20% from the DD-CT group. The difference between groups was not as great 25 days after release. At this time, 72% and 52% of the fish had been recovered respectively, for the DD-NT and DD-CT groups. The results again indicate a marked difference in migratory behavior between fish reared on constant and variable temperature.

On May 20, a single group of SL-ST fish from Alsea Trout Hatchery was released in Crooked Creek. In a period of 6 days, 75% of the fish released were recovered at the trap (Figure 10). Trapping operations were discontinued from May 26 to June 12 because of high water. The pattern of movement suggests that most of the SL-ST fish which were migratory had left the area prior to termination of trapping.

The fifth release of fish occurred in mid-June. Flows in Crooked Creek at the time were comparable to those existing the first of May (Appendix V). The proportion of fish that migrated downstream in the first 15 days after release decreased in all groups with the exception of those reared on a decelerated photoperiod. The recoveries were 56% and 68% respectively, for DL-NT and DL-DT groups. Recoveries of fish from the NL or SL photoperiods regardless of temperature ranged from 12% to 25% with the exception of fish from the SL-NT and NL-DT groups which had recoveries of 58% and 51%, respectively. No fish were recovered from the two AL groups released in June. Fish from the DD-CT group were less migratory than before as evidenced by the fact that only 8% were recovered. There were not sufficient fish available to measure the migratory tendencies of the DD-NT group. No fish were released from the RL group. No recoveries were made for the SL-ST fish released July 3 from Alsea Trout Hatchery.

The release site on Crooked Creek was sampled by electrofishing in mid-May to capture fish released earlier which were not recovered at the weir. A sample of 40 fish was captured within 0.4 km of the release site. The release site was electrofished again in mid-July. Of the 238 experimental fish recovered, 31 were from the May release and 207 fish were from the June release. The fish observed in the greatest numbers at the release site were from groups which showed the lowest recovery at the weir (Table 3). In late July, portions of Crooked Creek were sampled from the weir upstream to within 0.8 km of the release site. Only 2 fish from the release in June were recovered. The sampling provided further evidence that fish which were not captured at the weir stayed near the release site. The condition of fish which remained in the stream was generally good with the coefficient of condition $\geq$ 1.0 (Appendix VII).

Electrofishing on the lower and upper segments of Lint Creek produced only two recoveries in June. Both fish had been released in mid-April and originated from the reverse photoperiod. In late September, the impounded water behind the weir was drained and one RL fish from the March release was recovered.

Table 3. The ratio of the number of fish recovered to those stocked as determined by electrofishing on Crooked Creek on May 15 and July 12, 1968.

Treatment[a]	May 15, 1968		July 12, 1968			
	May 1 release		May 1 release		June 12 release	
SL-ST[b]	0/100	(0)[c]	0/100	(0)	12/100	(12)
SL-NT	0/35	(0)	0/35	(0)	7/67	(10)
SL-CT	0/25	(0)	0/25	(0)	18/71	(25)
NL-NT	0/35	(0)	0/35	(0)	9/73	(12)
NL-AT	1/50	(2)	1/50	(2)	19/82	(23)
NL-DT	0/35	(0)	0/35	(0)	6/75	(8)
NL-CT	1/50	(2)	4/50	(8)	14/68	(20)
NLB-CT	2/25	(8)	2/25	(8)	18/66	(27)
NLG-CT	2/50	(4)	1/50	(2)	20/65	(30)
NLR-CT	3/35	(8)	0/35	(0)	22/76	(29)
AL-AT	14/50	(28)	6/50	(12)	30/61	(50)
AL-NT	1/50	(2)	6/50	(12)	21/67	(31)
DL-DT	2/35	(5)	0/35	(0)	1/66	(2)
DL-NT	4/25	(16)	0/35	(0)	1/70	(1)
RL-CT	7/35	(20)	9/35	(25)		
DD-NT	0/25	(0)	0/25	(0)	0/8	(0)
DD-CT	3/25	(12)	2/25	(8)	9/50	(18)

[a] See abbreviations on pages 22-23.

[b] No fish were recovered from the SL-ST group stocked on May 20, 1968, but a 42% recovery was made of fish released July 3, 1968.

[c] Percent.

Growth

The parr-smolt metamorphosis in juvenile winter steelhead trout is dependent upon growth as evidenced by the age and size of smolts migrating seaward in Pacific coast streams (Gudjonsson, 1946; Shapovalov and Taft, 1954; Cartwright, 1960; Wagner et al., 1963). Atlantic salmon parr must be approximately 10 cm in length in the fall to become smolts the following spring (Elson, 1957). No established guide has been given for steelhead trout but observations made on fish reared in the hatchery and the natural environment indicate that 14 to 15 cm in length is the minimum size of most smolts (Wagner, unpublished). Presumably they might be smaller at the time metamorphic changes began.

Therefore, if one were to judge on the basis of size alone, it would be March 1966 before any number of smolts would be expected in Experiment I regardless of environmental conditions (Appendices VIII and IX). In Experiment II, it would be mid-November to mid-December 1967 before large numbers of smolts would be present in the constant and variable temperature groups (Appendix X).

Somatic Growth

These experiments were not designed expressly as a study of growth in relation to photoperiod and temperature, but some references

to growth seem appropriate, first, to describe how the animals grew under markedly different environments and secondly, to assist in the interpretation of changes in coefficient of condition.

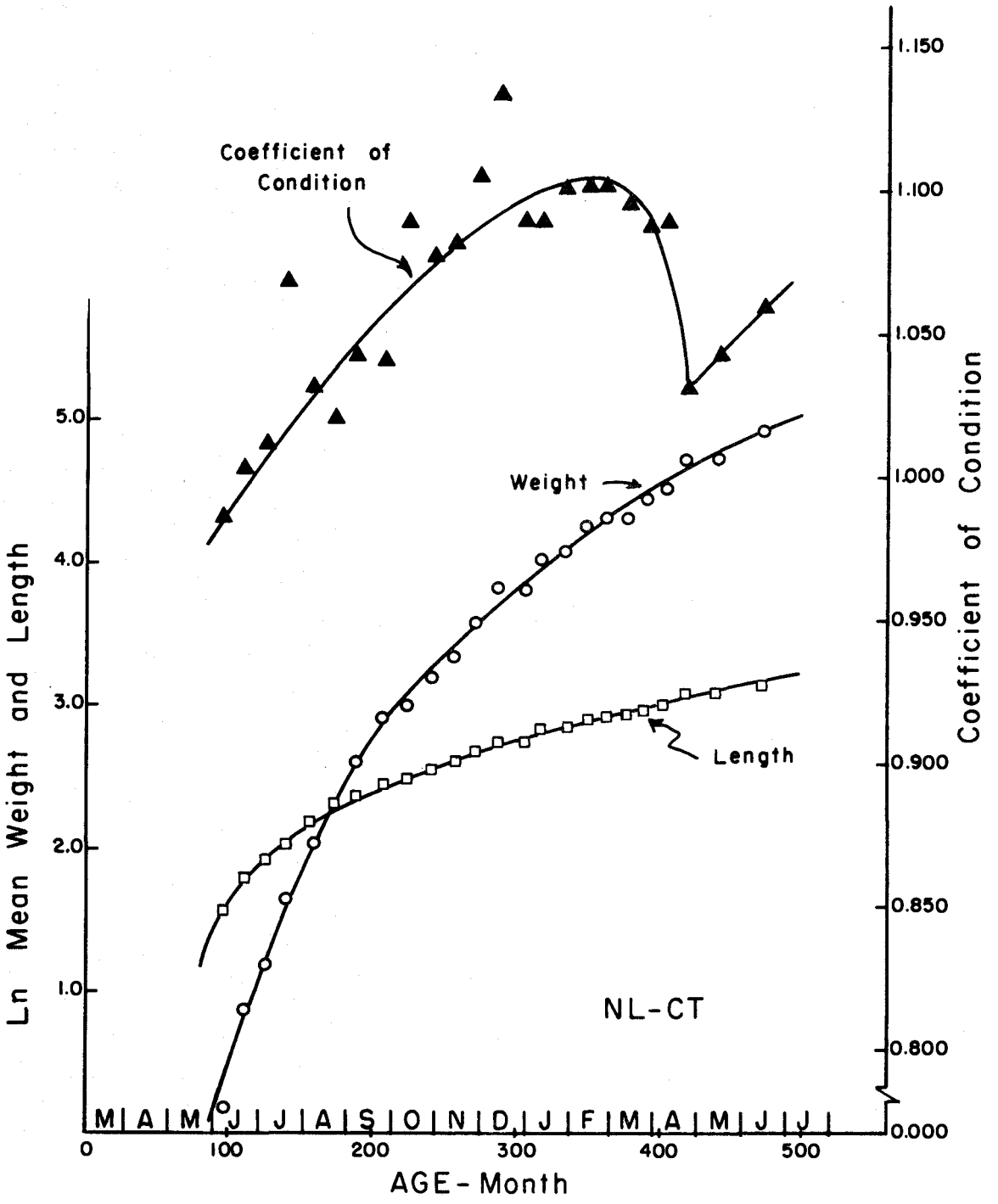
An increase in size can result from an enlargement or multiplication of cells, or accumulation of material (e. g. adipose tissue or water) which does not contribute further to the growth of the organism (von Bertalanffy, 1960; Laird, 1966). Changes in weight can result from one or both of the above causes while length increases result usually from material which is capable of further growth. For the interpretation of the coefficient of condition data, increases and decreases in weight are more meaningful than increase in length. Also, changes in growth are more readily apparent in terms of body mass than length so that results are presented primarily in terms of weight in the thesis. Examination of semi-logarthmic plots of mean weight and length against age for each experimental group in Experiment I and II was made. It was not thought desirable to present and discuss all the growth curves but to select representative examples typifying the growth curves of most groups.

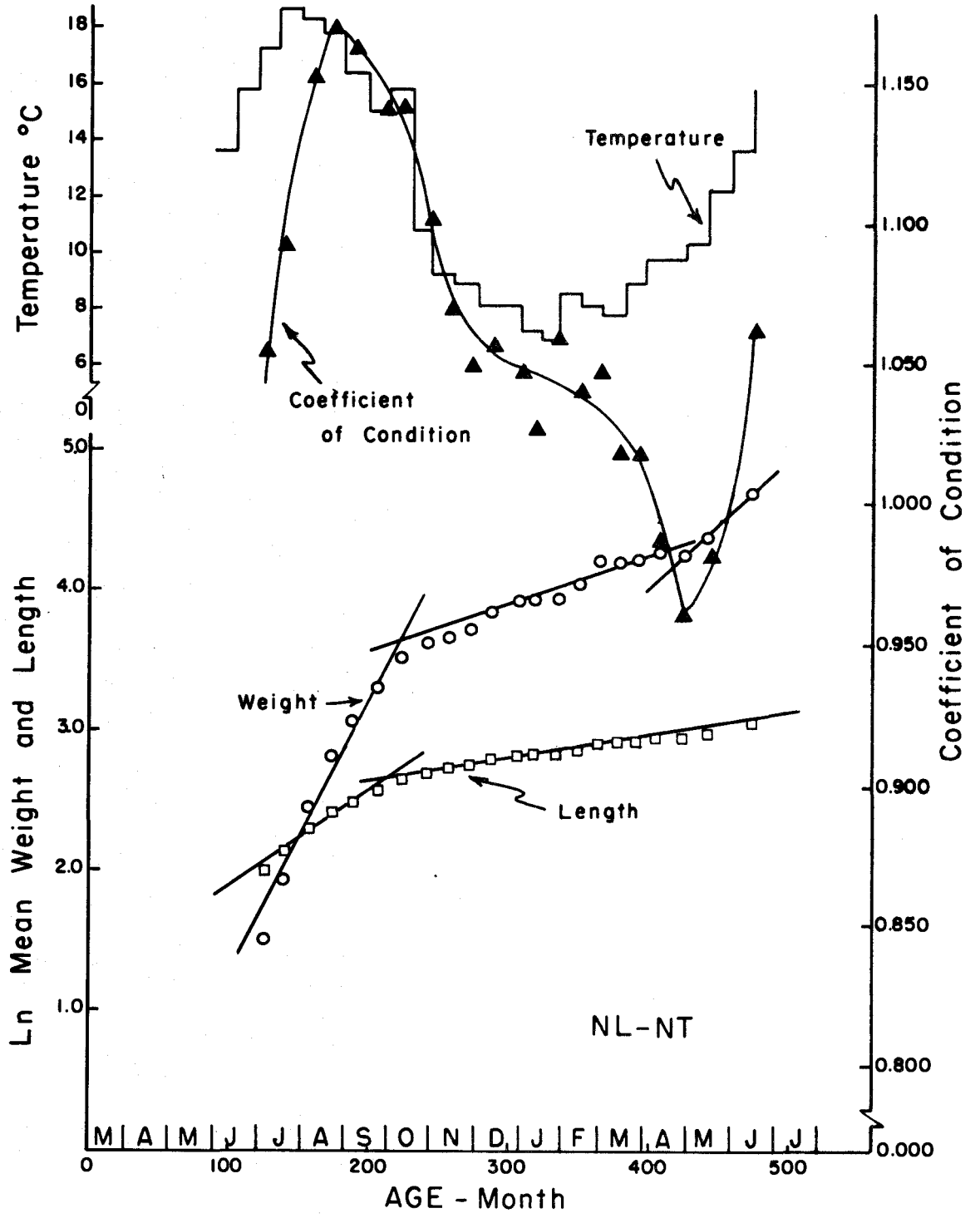
Marked differences between patterns of growth existed for fish reared under constant or variable temperature cycles. Fish reared under a normal photoperiod (NL) and at constant temperature (CT) had a growth rate that decelerated continuously with an increase in size (Figure 11A). Fish reared under a normal photoperiod (NL) and

Figure 11. Changes in mean length, weight, and coefficient of condition for two groups of fish in Experiment II. Ln = natural logarithm; Age is days post-hatching. Lines are fitted by eye and are highly subjective but are useful for purposes of interpretation.

A. Fish reared under a normal photoperiod (NL) and constant temperature (CT).

B. Fish reared under a normal photoperiod (NL) and normal temperature (NT).


Coefficient of Condition
Weight
Length
NL-CT
Ln Mean Weight and Length
Coefficient of Condition
AGE - Month
M A M J J A S O N D J F M A M J J
0
100
200
300
400
500
1.0
2.0
3.0
4.0
5.0
0.000
0.800
0.850
0.900
0.950
1.000
1.050
1.100
1.150


Temperature °C
Ln Mean Weight and Length
Coefficient of Condition
Temperature
Coefficient
of Condition
Weight
Length
NL-NT
AGE - Month
M A M J J A S O N D J F M A M J J
0
100
200
300
400
500
18
16
14
12
10
8
6
0
5.0
4.0
3.0
2.0
1.0
1.150
1.100
1.050
1.000
0.950
0.900
0.850
0.800
0.000

temperature cycle (NT) demonstrated more or less distinct inflection points[4] that could be used to delineate growth stanzas[5] characterized by a quasi-constant rate of growth (Figure 11B). Changes in slope were depicted as sharp breaks to facilitate interpretation. Growth tended to be exponential over any given stanza. In Figure 11B, there were two inflections with the first occurring in the fall, and the second appearing in the spring which seemed to be associated with the parr-smolt metamorphosis. Smolting usually involved a temporary weight loss or little or no growth in both temperature regimes. At other times a weight loss or little or no growth was observed in a given group, but these weight changes were not associated with a marked decline in the coefficient of condition (Figure 11B).

In Experiment I, most environmental groups reared on constant temperature had growth curves similar to that depicted in Figure 11A. Fish introduced in December 1965 into constant photoperiods (8.5L, 12L, 16L, and LL) grew at a faster rate than those in residence since July 1965 as evidenced by their final weights (Table 4). The 12L and LL fish had, respectively the highest and lowest growth rates for both the July and December introductions. The differences must be related to photoperiod as light intensity, feeding procedures, population

[4]Inflection point denotes a more or less sudden change in growth rate which delimits the different growth stanzas.

[5]Growth stanza denotes a portion of the growth curve where the rate of change tends to be constant between inflection points.

Table 4. Growth rates, initial and final weights, and chronology of inflection points for groups of fish in Experiment I.

Treatment[a]	Initial weight (g)	Final weight (g)	Mean growth rate (daily)	Stanza growth rate and chronology of inflection points		
Lot A						
SL	1.5	197.1	.0124			
NL	1.7	167.6	.0116	.0144 (mid-April)	.0013 (late June)	.0095
DD[b]	0.6	77.2	.0124			
8.5L	1.5	135.5	.0115			
12L	1.4	161.4	.0121			
16L	1.6	127.1	.0111			
LL	1.4	106.9	.0110	.0166 (early March)	.0044	
Lot B						
NL	18.2[c]	167.6	.0091			
8.5L	18.2	167.7	.0091			
12L	18.2	184.5	.0095			
16L	18.2	147.4	.0086			
LL	18.2	126.5	.0080	.0179 (late March)	.0044	

[a] See abbreviations on pages 20-21.

[b] Fish reared in the absence of light were 52 days younger than the other groups.

[c] Initial weight equals mean weight on December 30, 1965 of fish reared on a natural photoperiod (SL), which served as the stock for the introductions. The mean weight of fish in other experimental groups of Lot A in December 1965 was as follows: NL = 24.9g, 8.5L = 22.1g, 12L = 18.4g, 16L = 21.1g, and LL = 20.9g.

density, oxygen content of the water, and temperature were comparable The SL fish had the greatest overall growth rate (0.012). Fish reared in the absence of light were not comparable to any other experimental group because of a later hatching date but they grew well as evidenced by a growth rate of 0.012 (Table 4).

Most groups reared on constant or variable temperature cycles in Experiment II had growth curves which resemble these in Figure 11A or B, respectively. However, growth curves were altered with respect to the timing of inflection points by the rate of change of the temperature and photoperiod cycles. For example, SL-NT, AL-AT, and DL-DT groups were respectively, similar, accelerated, and decelereated to the NL-NT in the occurrence of the two inflection points (Table 5).

Mean weights ranged from 108 g for the SL-NT group to 153 g for the NL-AT group at the termination of the experiment. Instantaneous daily growth rates ranged from a low of 0.009 to a high of 0.011 for July 1967 to June 1968 (Table 5).

Growth curves for length tended to parallel those for weight for fish in constant temperature (Figure 11A). Whereas in a variable temperature three distinct growth stanzas are apparent for weight, there were no substantial changes in the length curve after the initial inflection (Figure 11B). The first inflection on the growth curve for NL-NT group (Figure 11B) occurred in mid-October when the

Table 5. Growth rates, initial and final weights, and chronology of inflection points for groups of fish in Experiment II.

Treatment[a]	Initial weight (g)	Final weight (g)	Mean growth rate (daily)	Stanza growth rate and chronology of inflection points		
SL-NT	4.3	108	.0093	.0204 (mid-Oct)	.0049 (early May)	.0088
NL-NT	4.5	109	.0092	.0216 (mid-Oct)	.0042 (mid-Apr)	.0087
NL-AT	4.5	153	.0102	.0250 (mid-Sept)	.0055 (mid-Apr)	.0097
NL-DT	3.6	114	.0100			
AL-AT	4.6	148	.0100	.0204 (late Sept)	.0038 (early Mar)	.0100
AL-NT	4.4	120	.0095	.0216 (late Sept)	.0056 (mid-Mar)	.0062
DL-DT	4.1	105	.0093	.0213 (mid-Nov)	.0040	
DL-NT	3.9	118	.0098	.0223 (mid-Oct)	.0047 (early May)	.0095
DD-NT	3.3	111	.0101			
SL-CT	4.0	118	.0098			
NL-CT	3.3	137	.0107			
NLB-CT	3.4	138	.0108			
NLG-CT	4.0	144	.0103			
NLR-CT	4.0	127	.0100			
RL-CT[b]	3.6	110	.0114			
DD-CT	3.1	142	.0110			

[a] See abbreviations on pages 22-23.

[b] The time period is July 20, 1967 to May 16, 1968 as opposed to July 6, 1967 to June 17, 1968 for the other groups.

instantaneous growth rates decreased from 0.022 to 0.004 for weight but proportionately less for length, from 0.007 to 0.002. The second inflection in June resulted in an increase in growth rate to 0.009 for weight but little or no change for length.

The data indicate that the decline in $\overline{K}$ during the winter was a result of proportionately greater reduction in rate of growth in weight than in length. An actual weight loss in some individuals during the parr-smolt metamorphosis contributed further to the decline in $\overline{K}$. Following the parr-smolt metamorphosis growth rate in weight was proportionately greater than length and $\overline{K}$ increased markedly.

Temperature is apparently of major importance in the autumnal inflection as evidenced by the absence of a detectable inflection when fish were reared under a constant temperature (Figure 11A and B). The autumnal inflection in Experiment II is, in part, an artifact of the temperature cycle (Figure 5 and Appendix II) where a change of 5^{o} C occurred between October 15 and November 1 for fish on a normal temperature cycle (NT). Although photoperiod seemed to be of major importance in the timing of the second or vernal inflection as a result of the metabolic requirements of the metamorphosis, temperature again became a major factor in determining growth rate following the metamorphosis (Table 5).

Coefficient of Condition

Steelhead trout (SL-ST) undergoing the parr-smolt metamorphosis evidence a marked decline in coefficient of condition (K) followed by an increase in condition upon reverting to a non-migratory form (Fessler and Wagner, 1969). This pattern did not occur for fish reared under constant photoperiod (DD, 8.5L, 12L, 16L, and LL) and temperature in Experiment I regardless of date of introduction (Figure 12A and B). Generally, there was a gradual and continuous increase in $\overline{K}$ from August 1965 through February 1966. From February to September $\overline{K}$ remained relatively constant with the exception of a slight decline in condition in June for 8.5L and 12L fish in Lots A and B.

The only group of fish in Experiment I which showed a marked change in $\overline{K}$ was reared under a normal photoperiod (NL) in Lots A and B (Figure 12A-B). The pattern was similar to that depicted in Figure 11A. The vernal (June) minimum $\overline{K}$ of 0.99 was substantially greater in magnitude than that observed in April for fish of this stock ($\overline{K}$ = 0.89 to 0.96) reared under a natural photoperiod and temperature cycle (Wagner, 1968, 1969). The $\overline{K}$ for SL-CT fish in the present study did not decline substantially in April and May but did demonstrate a marked increase during the June-August period. The reason for the different $\overline{K}$ pattern exhibited between the NL-CT

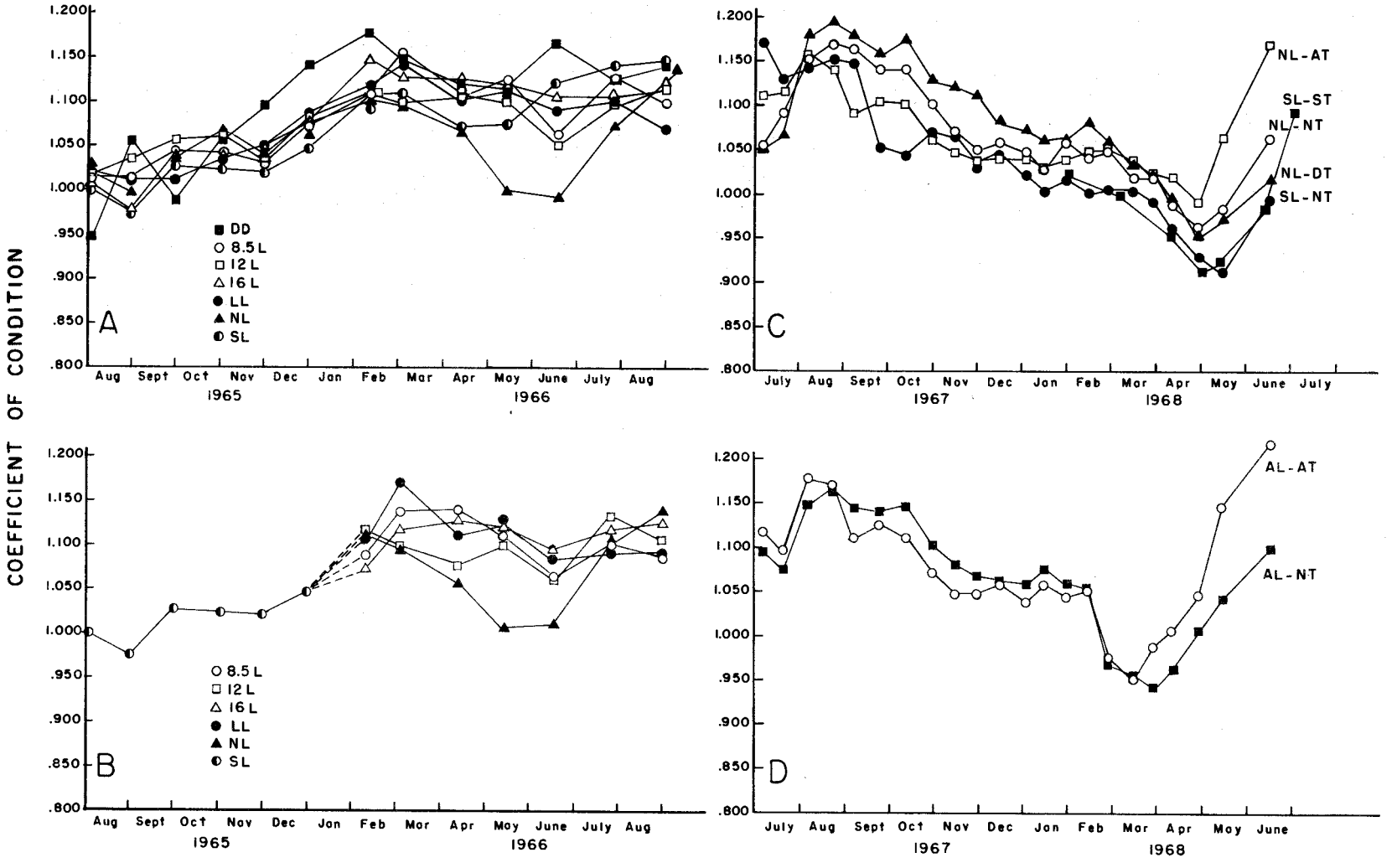
and the SL-CT groups is not known.

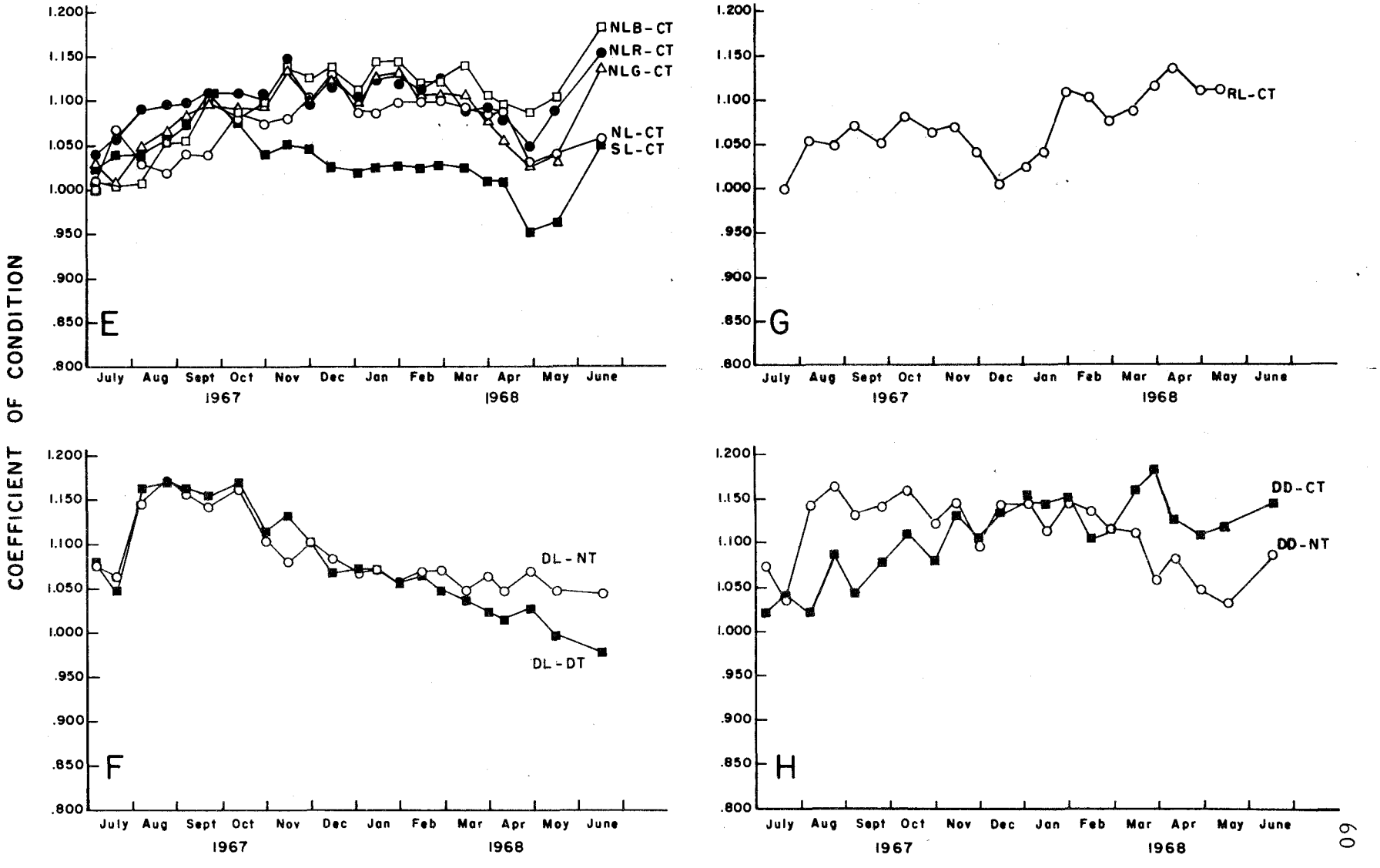
Marked differences existed in the $\overline{K}$ curves for groups of fish in Experiment II (Figure 12C-H). Groups receiving a normal (NL) or natural (SL) photoperiod and a variable temperature cycle (ST, NT, AT, or DT) demonstrated seasonal changes in $\overline{K}$ similar to the pattern reported by Fessler and Wagner (1969). One typical curve is shown in Figure 11B. The nadir of all curves was reached the first week of May with the exception of the one for the SL-NT group which occurred in mid-May. A marked increase in condition occurred in all groups following the nadir. Although the general patterns were similar among the five groups, the magnitude of individual values differed (Figure 12C). The differences in magnitude appeared to be, in part, a function of temperature.

For experimental fish reared in an accelerated photoperiod (AL) with an accelerated (AT) or normal temperature (NT) cycle, the nadir of the curves was reached in mid-March and early April, respectively (Figure 12D). The group receiving an accelerated temperature cycle had the most rapid rate of increase in coefficient of condition after the vernal nadir.

Under a decelerated photoperiod (DL) and a normal or decelerated temperature (DT) cycle, $\overline{K}$ declined continuously from August 1967 to June 1968. At the time the experiment was terminated in June 1968, the coefficient of condition was still declining (Figure 12F). From

Figure 12. Changes in the mean coefficient of condition for experimental steelhead reared in Experiment I (Figure 12A and B) and Experiment II (Figure 12C-H). See abbreviations on pages 20-23; Figure 12A fish introduced July 11, 1965 and Figure 12B fish introduced December 22, 1965. Standard errors are not shown but are $\leq$ 1.5% of the mean, or less than symbol height.


COEFFICIENT OF CONDITION
1.200
1.150
1.100
1.050
1.000
.950
.900
.850
.800
A
DD
8.5 L
12 L
16 L
LL
NL
SL
Aug Sept Oct Nov Dec Jan Feb Mar Apr May June July Aug
1965
1966
B
8.5 L
12 L
16 L
LL
NL
SL
C
NL-AT
SL-ST
NL-NT
NL-DT
SL-NT
July Aug Sept Oct Nov Dec Jan Feb Mar Apr May June July
1967
1968
D
AL-AT
AL-NT
July Aug Sept Oct Nov Dec Jan Feb Mar Apr May June
1967
1968


COEFFICIENT OF CONDITION
1.200
1.150
1.100
1.050
1.000
.950
.900
.850
.800
NLB-CT
NLR-CT
NLG-CT
NL-CT
SL-CT
E
July Aug Sept Oct Nov Dec Jan Feb Mar Apr May June
1967
1968
RL-CT
G
DL-NT
DL-DT
F
DD-CT
DD-NT
H

February through June, the group of fish reared at a normal temperature cycle had a higher $\overline{K}$ than fish reared where the temperature cycle was synchronous with the photoperiod.

Seasonal changes in $\overline{K}$ for groups of fish reared under normal, accelerated, and decelerated photoperiods were similar from July 1967 to February 1968 (Figure 12C, D, and F). It is only after mid-February that differences become apparent.

Fish reared at a constant temperature of 12° C and under a normal (NL) photoperiod showed similar patterns of change in $\overline{K}$ regardless of the spectrum and intensity of the light. The pattern (Figure 12E) was similar to that observed for fish reared under constant photoperiods and temperature in Experiment I (Figure 12A and B) with the exception of the occurrence of a marked decline in condition in May (Figure 12E).

Although the general pattern of $\overline{K}$ was markedly different over most of the year between groups of fish reared at constant and variable temperature, comparison of Figures 12C and E shows similar characteristics in the chronology of the vernal nadir in the $\overline{K}$ curve and the average decrease in condition. From February to May, fish at constant temperature declined 0.073 units in coefficient of condition while those groups with a variable temperature cycle declined on the average 0.077 units.

The group of fish reared under a natural photoperiod (SL) and constant temperature (CT) had a $\overline{K}$ pattern which tended to resemble that of groups reared in variable temperature cycles (Figure 12C). The pattern was probably a result of uncontrolled seasonal diurnal temperature fluctuations that occurred in this rearing tank.

In the reverse photoperiod (RL), the fluctuation in the pattern of change of $\overline{K}$ was greater than in other photoperiod groups (Figure 12G). A nadir in the curve occurred in December at which time the fish were receiving a June photoperiod. Based on growth it would be mid-December (calendar month) before many smolt-sized fish would be expected. An examination of $\overline{K}$ on the basis of size revealed that for fish $\geq$ 15 cm in length, $\overline{K}$ = 0.99 (n=37), but for fish $\leq$ 14.9 cm in length, $\overline{K}$ = 1.05 (n=12). The latter value is comparable to $\overline{K}$ observed for the NL-CT group at that time. The nadir was followed by an increase in $\overline{K}$ which reached a high in early February (August photoperiod). The pattern through the remainder of the rearing period showed no consistent trend with $\overline{K}$ increasing and decreasing but never declining below 1.05.

The annual changes in $\overline{K}$ for DD-CT and DD-NT groups, while more variable than that found in other groups (Figure 12H), tended to resemble the patterns observed for fish reared under normal photoperiods on constant or normal temperature cycles, respectively (Figure 11E and 12C). Two nadirs occurred in the $\overline{K}$ curve for fish reared at constant temperature, one in mid-February and again in early

May. The nadir of the $\overline{K}$ curve occurred in mid-May for fish reared under a normal temperature cycle.

The effects of temperature on early changes in $\overline{K}$ as mediated by growth rate can be seen in Figure 11A and B. At a constant temperature of 12° C there was a gradual increase in condition until February when metamorphic changes began to exert an effect on $\overline{K}$ (Figure 11A). In a normal temperature cycle, $\overline{K}$ increased and decreased rapidly with seasonal changes in temperature until February when metamorphic changes apparently had an influence. The $\overline{K}$ continued to decline until completion of the metamorphosis in May (Figure 11B).

The above interpretation with respect to metamorphic affects agrees with the coefficient of condition data presented by Fessler and Wagner (1969). In that study, changes in $\overline{K}$ were followed in two size groups of juvenile steelhead, migrant-sized fish $\geq$ 14.0 cm and non-migrant-sized fish $\leq$ 13.9 cm in length. Non-migrants declined in condition during the winter but their condition remained relatively stable after February, whereas the larger fish continued to lose condition until May (Fessler and Wagner, 1969; Figure 2; p. 2829).

In summary, seasonal changes in $\overline{K}$ have as a basis alterations in the rate of growth in length and weight that result primarily from temperature changes and the metabolic demands of the metamorphosis. The coefficient of condition appears to be a more sensitive indicator of the metamorphosis than changes in growth curves.

Seawater Adaptation

The parr-smolt metamorphosis has been depicted as being associated with developmental changes in the osmotic and ionic regulatory mechanism of juvenile fish. The rationale upon which this premise is based is that survival in a marine environment requires a fully developed and functional hypo-osmoregulatory mechanism. The development of halophilic behavior and a predisposition toward its physiological development in juvenile fish has been investigated in a number of salmonids (Parry, 1958, 1960, 1961; Houston, 1959, 1960, 1961; Baggerman, 1960b; McInerney, 1961, 1964; Houston and Threadgold, 1963; Conte and Wagner, 1965; Conte et al., 1966; Weisbart, 1968; Wagner et al., 1969 ; Otto and McInerney, 1970). The purpose of this segment of the study was to determine if photoperiod played a key role in the timing of the genesis of the hypo-osmoregulatory system.

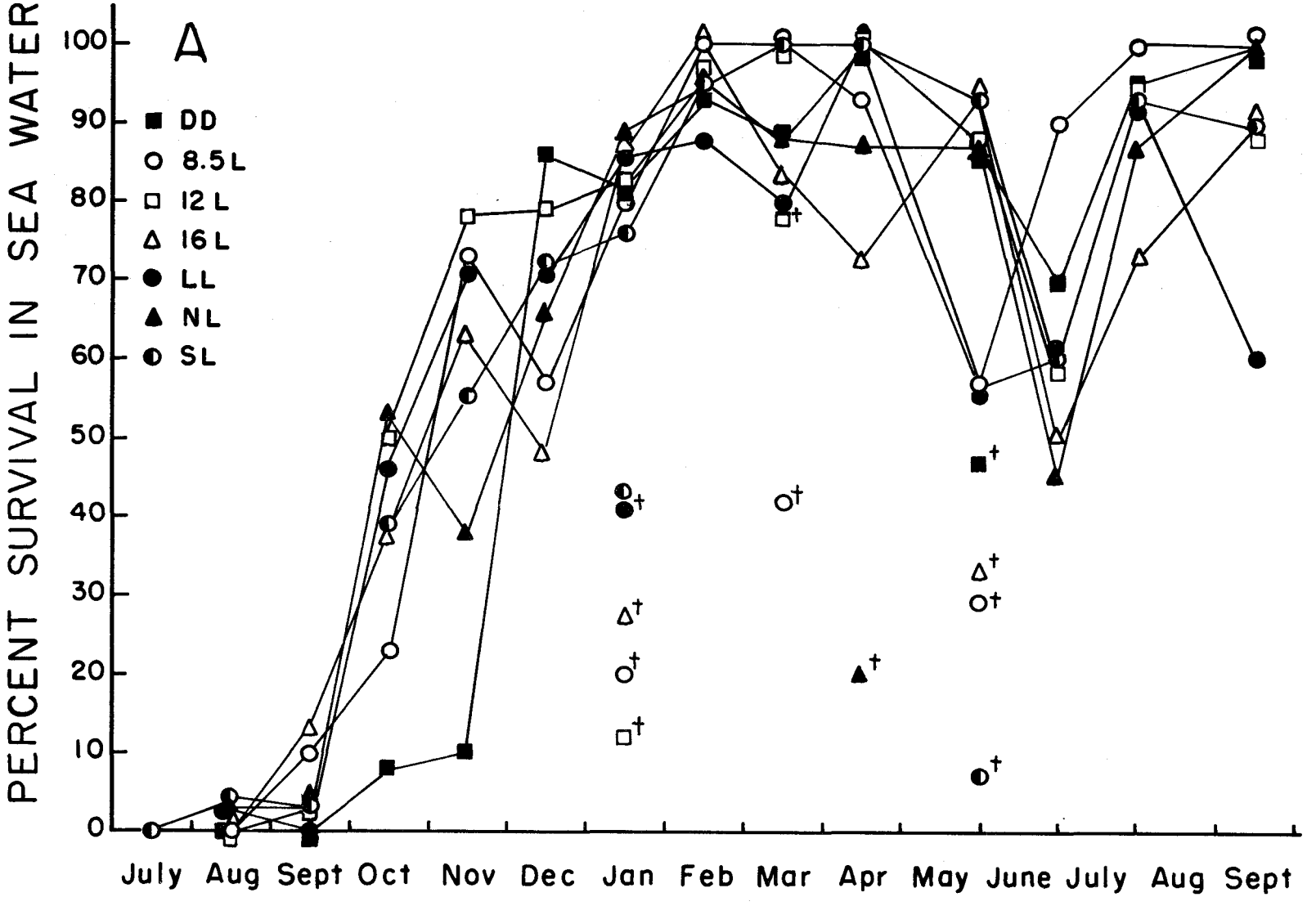
The sea-water survival curves appear to be similar for all groups in Lot A of Experiment I regardless of photoperiod (Figure 13A and Appendix XI). Survival increased as the fish grew larger, which agrees with earlier results reported in other studies (Parry, 1958, 1960; Houston, 1961; Conte and Wagner, 1965; Conte et al., 1966; Weisbart, 1968; Wagner et al., 1969). In July 1965, fish were obligatory freshwater but achieved facultative status, that is euryhalinity

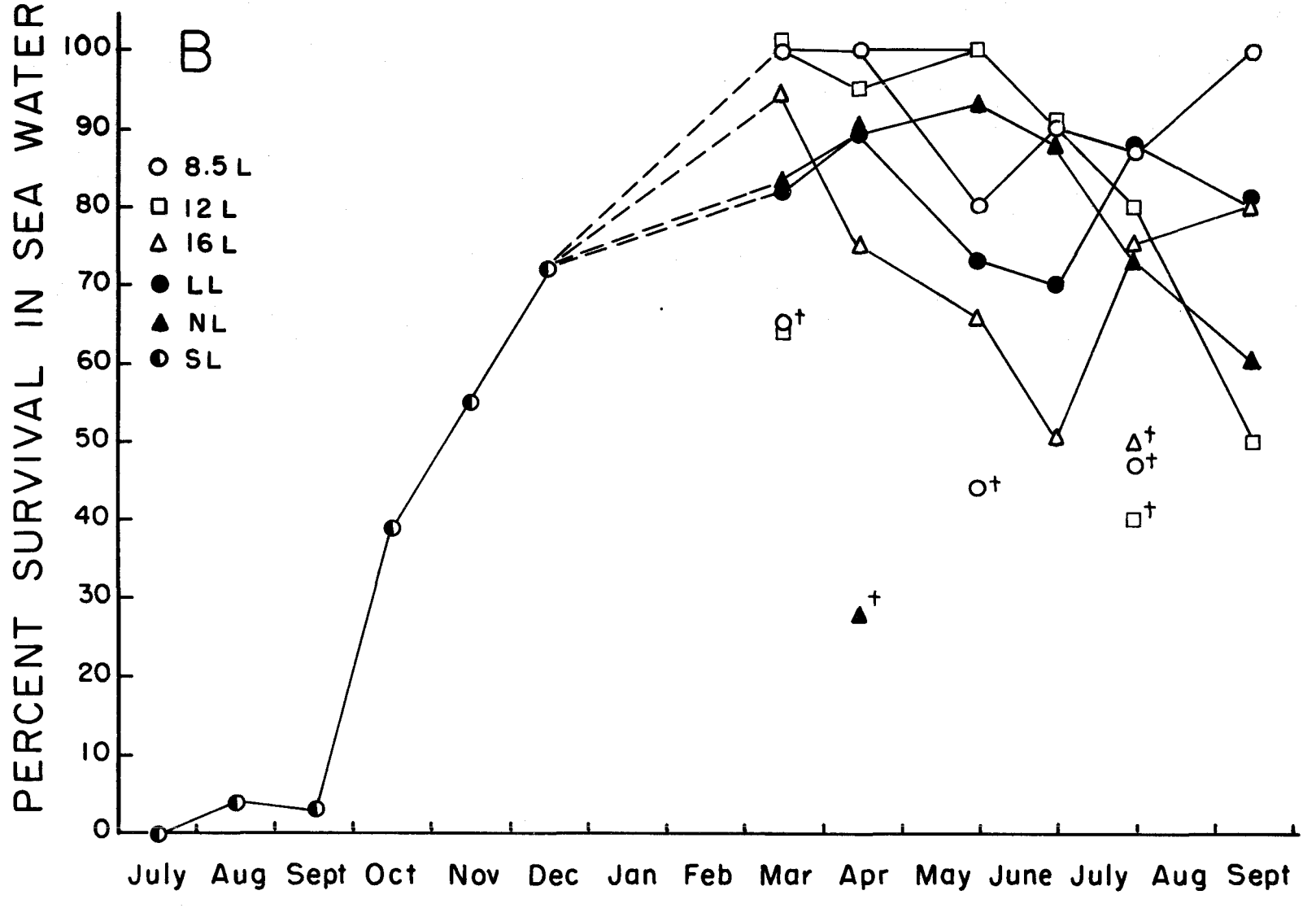
Figure 13. Chronological development of sea-water adaptation by juvenile steelhead trout reared under controlled photoperiods and at constant temperature (12° C) in Experiment I.

A. Fish held under controlled photoperiods from July 11, 1965 to September 10, 1966.

B. Fish held under controlled photoperiods from December 22, 1965 to September 10, 1966.

+ = Mortalities occurred late in the exposure period and are believed to be artifacts.


A
PERCENT SURVIVAL IN SEA WATER
100
90
80
70
60
50
40
30
20
10
0
DD
8.5L
12 L
16 L
LL
NL
SL
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept


B
PERCENT SURVIVAL IN SEA WATER
100
90
80
70
60
50
40
30
20
10
0
8.5 L
12 L
16 L
LL
NL
SL
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept

(survival $\geq$ 80%), by February 1966. A partial deactivation of the hypo-osmoregulatory mechanism began during April reducing survival to the 50% level in June-July of 1966. The hypo-osmoregulatory mechanism became fully functional again in September.

Most of the juvenile steelhead were euryhaline at a size of 12 to 13 cm in length and 20 to 30 g in weight (266 to 292 days post-hatching) However, fish reared in the absence of light were euryhaline at a size of about 8 cm and 6 g and were younger than the light-reared fish (181 days post-hatching). No explanation can be given for the earlier development of the hypo-osmoregulatory mechanism in fish reared in the absence of light. Two tests were conducted in the dark during January and February to determine the effects of light exposure on sea-water survival of dark reared fish. Survival was comparable for fish tested in the light and dark.

Survival curves of fish reared under constant photoperiod and temperature are strikingly similar to the developmental pattern of sea-water adaptation reported earlier for juvenile steelhead trout of the same genetic stock reared under natural photoperiod and temperature cycles (Conte and Wagner, 1965). The major difference is that the deactivation of the hypo-osmoregulatory mechanism was not complete for fish in the present study and euryhalinity occurred at a smaller size (12-13 cm) as opposed to a larger size (14-15 cm) in the earlier study.

Fish introduced into the controlled photoperiods in December 1965 (Figure 13B and Appendix XII) showed some differences in survival curves in comparison to fish introduced in July 1965 (Figure 13A) in the extent and timing of the regression during the April-September period. However, in view of the similarity between fish of Lot A and B with respect to plasma osmolarity and ionic values (Figure 14 and Appendix XIII and XIV) I do not consider the development or regression in sea-water adaptation to be significantly different for the two groups.

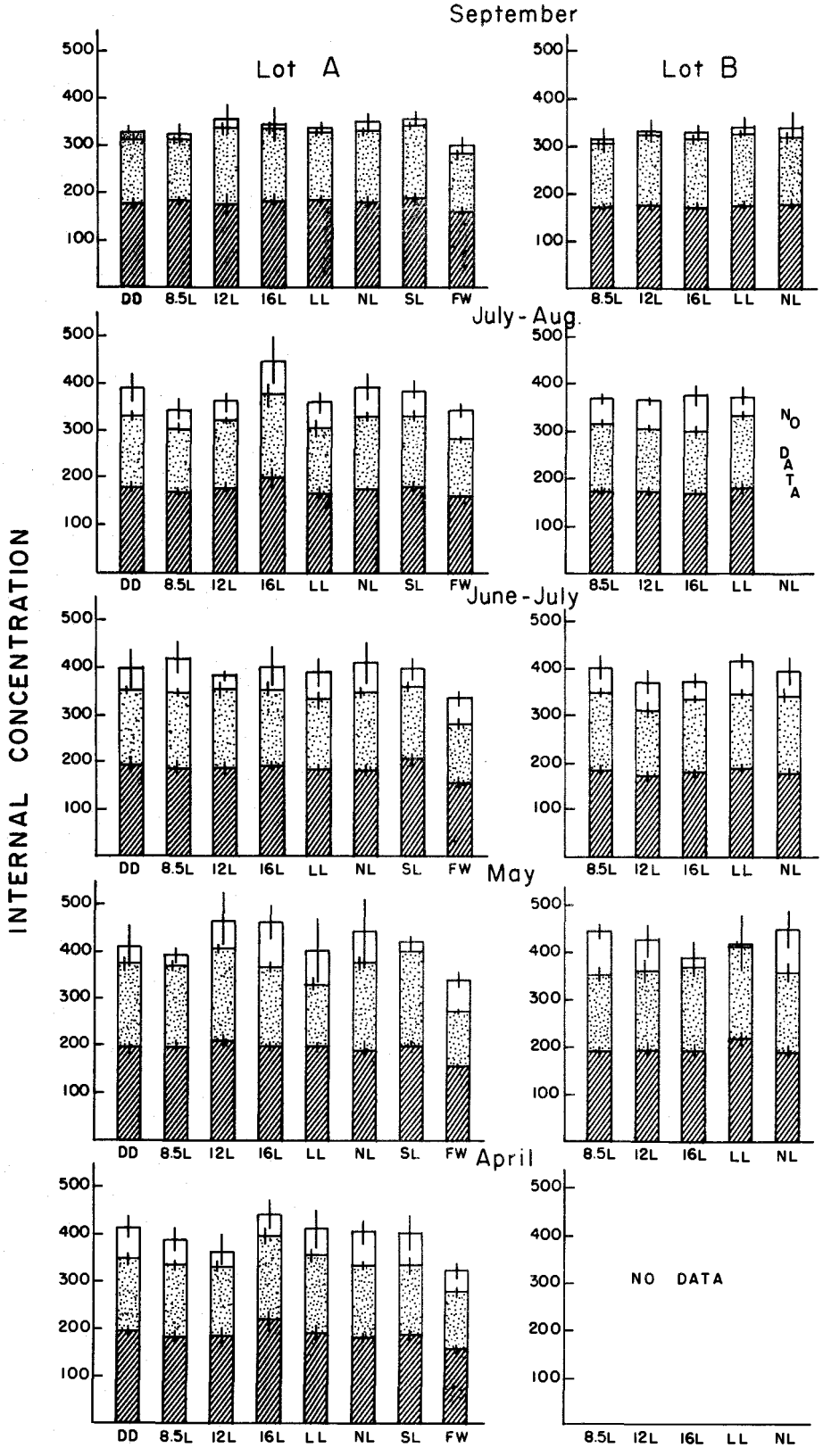
No significant differences ($P = 0.01$) were found for plasma osmolarity and electrolyte values between groups of fish with respect to photoperiod exposure or date of introduction but a significant difference occurred between months (Appendix XV). The sea-water survivors for the months of April through August experienced difficulty in maintaining homeostasis of the interne milieu as evidenced by the average plasma osmotic concentration of 403 ± 35 m-osmol./ℓ with sodium and chloride ion levels of 190 ± 13 m-equiv./ℓ and 160 ± 15 m-equiv./ℓ, respectively. The survivors of the September test had an average plasma osmotic concentration of 338 ± 25 m-osmol./ℓ with sodium and chloride ion levels of 180 ± 12 m-equiv./ℓ and 146 ± 12 m-equiv./ℓ, respectively. Generally, reduced regulatory ability was apparent even in the survivors during the regression period (April-

Figure 14. Plasma osmotic and ionic concentrations for juvenile steelhead surviving 20-28 days of exposure to sea water in the months of April through September 1966. FW denotes the freshwater control fish which were a composite of all experimental groups. Total height of column represents osmotic concentration (m-osmol./ℓ) of plasma ± 1 standard error. See abbreviations on pages 20-21.


chloride concentration (m-equiv./ℓ) ± 1 standard error


sodium concentration (m-equiv./ℓ) ± 1 standard error


other substances


September
Lot A
Lot B
July - Aug.
June - July
May
April
INTERNAL CONCENTRATION
500
400
300
200
100
DD
8.5L
12L
16L
LL
NL
SL
FW
NO DATA
NO DATA

August), and reduced osmotic pressure corresponded to the higher survival observed in September.

Endocrine Activity

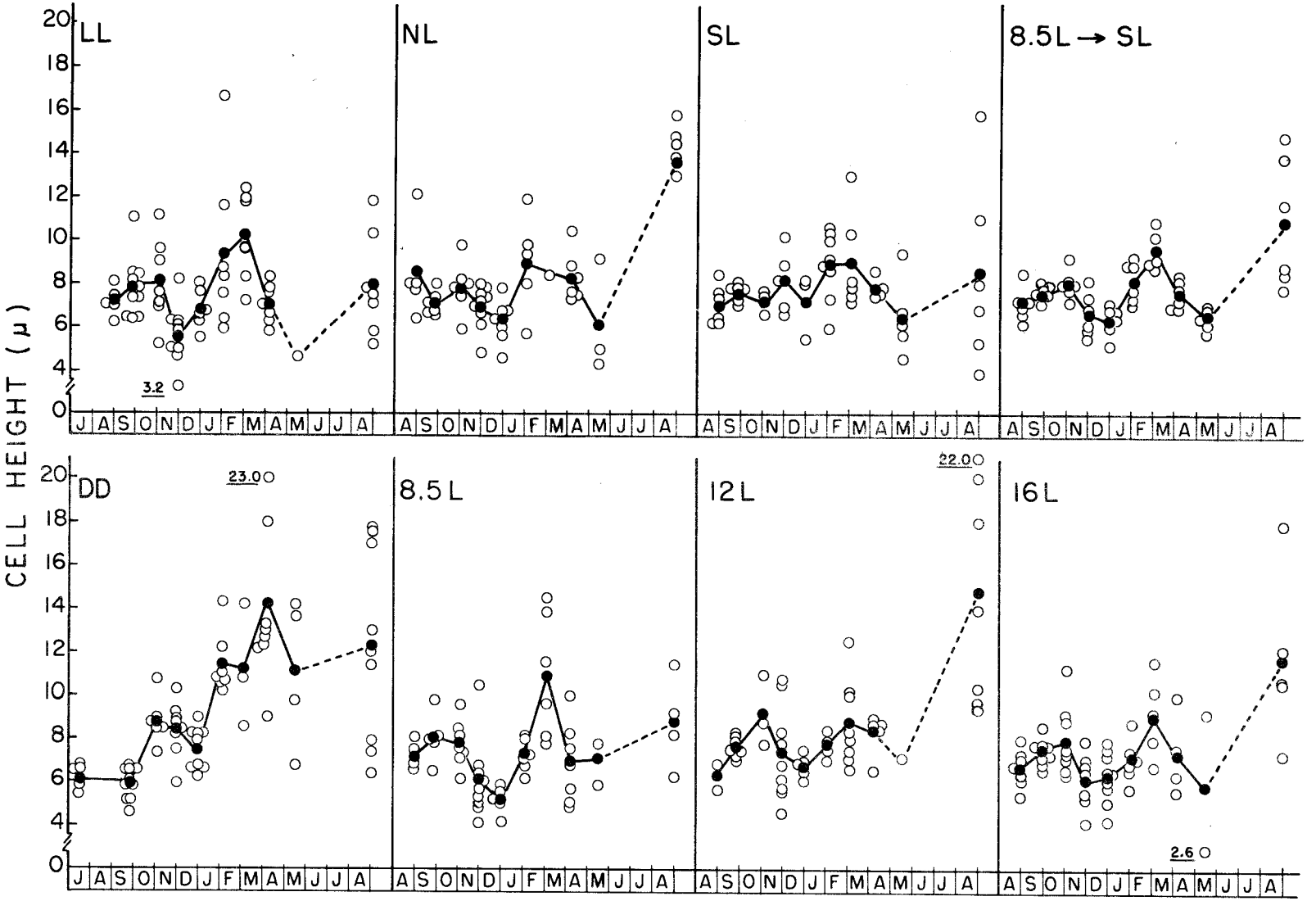
Thyroid Cytology

Fish reared in Experiment I (Lot A) under constant photoperiods (8.5L, 12L, 16L, and LL) had similar seasonal changes in follicular cell height (Figure 15). The curves of cell heights reflect changes over a 12-month period and tend to be bimodal in shape. The cell heights were higher in early fall and spring but lower in early winter and summer. A statistical test (Duncan, 1957) showed that generally only the lowest and highest means in a given experimental group were significantly different ($P = 0.05$) (Appendix XVI).

The patterns of change in cell height after December 1965 for fish reared under seasonal photoperiods (NL and SL) were similar to those of constant photoperiod groups but prior to that time the pattern was more variable. In the absence of light, fish showed seasonal changes in cell heights that were similar to the other groups but were substantially higher for DD fish after December 1965.

All groups, except those reared in the absence of light, showed a remarkable degree of similarity in thyroid cytology as evidenced graphically for combined groups (Figure 15). There was less variation between fish in a given group from July to December 1965 than there was during the remainder of the rearing period. Mean follicular cell height for individual fish ranged from about 5 to 8μ.

Figure 15. Changes in thyroid follicular cell height for fish reared under different photoperiods and at constant temperature from July 11, 1965 to September 16, 1966 in Experiment I. ○ = mean cell height for individual fish, ● = mean cell height for a given group; 8L → SL = all groups combined omitting DD, ○ = mean cell height for a given group and ● = grand mean; See abbreviations on pages 20-21.


LL
NL
SL
8.5L → SL
DD
8.5 L
12L
16L
CELL HEIGHT (μ)
20
18
16
14
12
10
8
6
4
0
3.2
23.0
22.0
2.6
J A S O N D J F M A M J J A

Greatest variation in cell height for any particular group occurred in the early spring and again late in the second summer. Cell heights in excess of 15μ were observed and in such cases the follicles appeared to be undergoing hypertrophy.

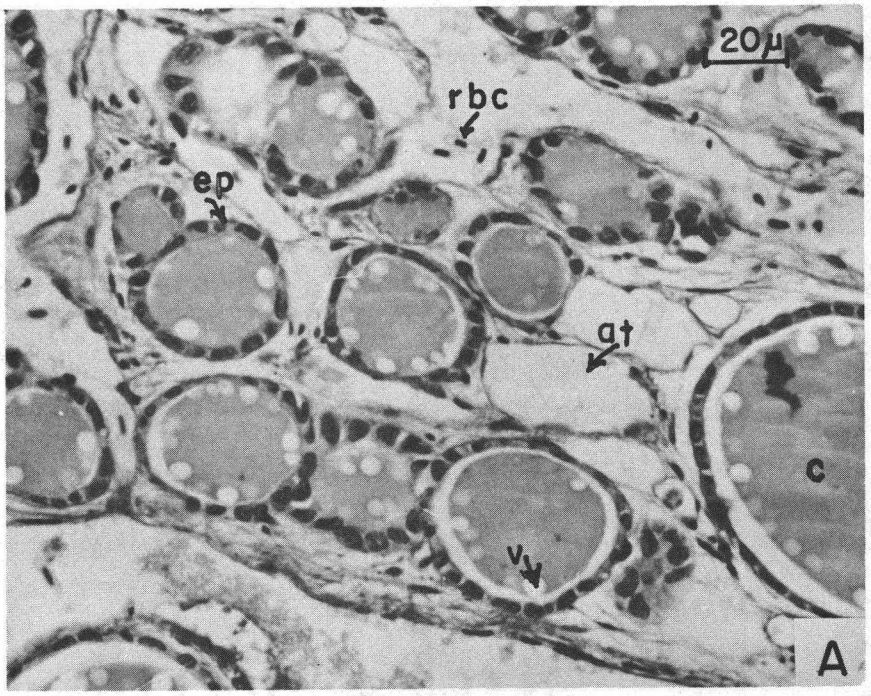
The following groups from Experiment II were examined for changes in thyroid cytology: NL-NT; NL-CT; AL-AT; DL-DT; RL-CT; DD-NT; DD-CT. A photomicrograph (Figure 16) gives evidence of the extreme differences that could be seen in cell height during the study. The changes in cell height were not substantially different for NL-NT, AL-AT and DL-DT groups (Figure 17). Generally, cell height tended to be higher in the fall and spring months and lower during the winter. In comparison to the fish reared on constant photoperiod and temperature in Experiment I, the first summer-fall decrease in cell height for the NL-NT, AL-AT, and DL-DT groups tended to occur earlier and the spring increase tended to occur later. The DD-NT group tended to reflect similar changes in thyroid cytology except for greater variation during the spring. For fish receiving a reverse photoperiod (RL) and constant temperature, cell heights tended to increase in the fall and then reached a plateau for several months during which individual fish variation was greater. Cell heights became small as the photoperiod shortened.

The NL-CT and DD-CT groups demonstrated similar patterns in thyroid cell cytology except for greater variation in the latter group in

Figure 16. Photomicrographs of transverse section of the thyroid follicles from steelhead trout showing gross differences in epithelial cell height. Hematoxylin and eosin. Legend for all plates: at, adipose tissue; bm, basement membrane; c, colloid; ep, follicular epithelium; rbc, erythrocycte; v, peripheral vacule.

A. Fish reared in decelerated photoperiod and temperature cycle; sampled 1/30/68; length = 16.9 cm and weight 53.3 g.

B. Fish reared in darkness on normal temperature cycle; sampled 1/30/68; length = 17.8 cm and weight 59.6 g.


20μ
rbc
ep
at
c
v
A

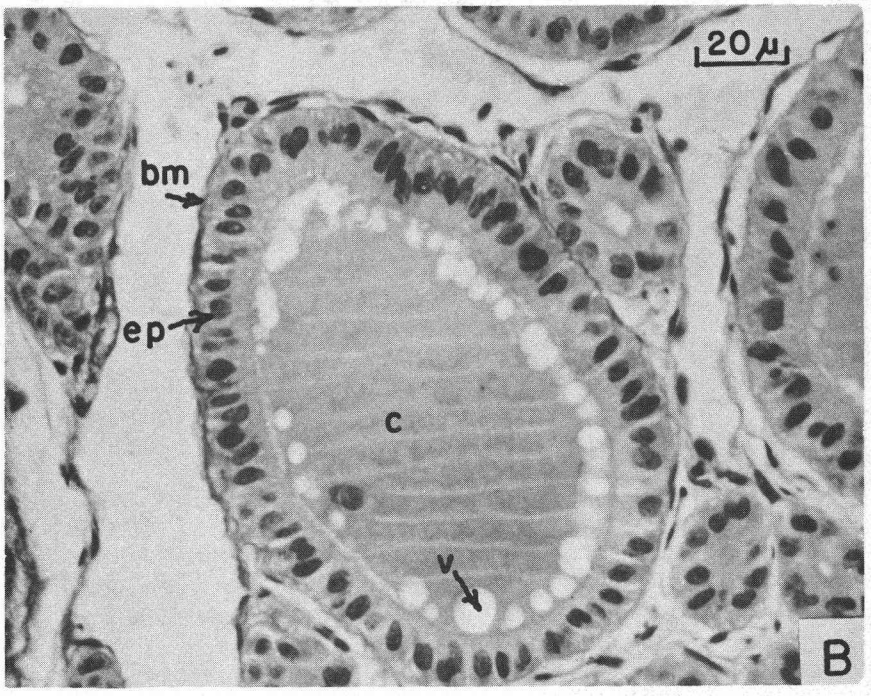
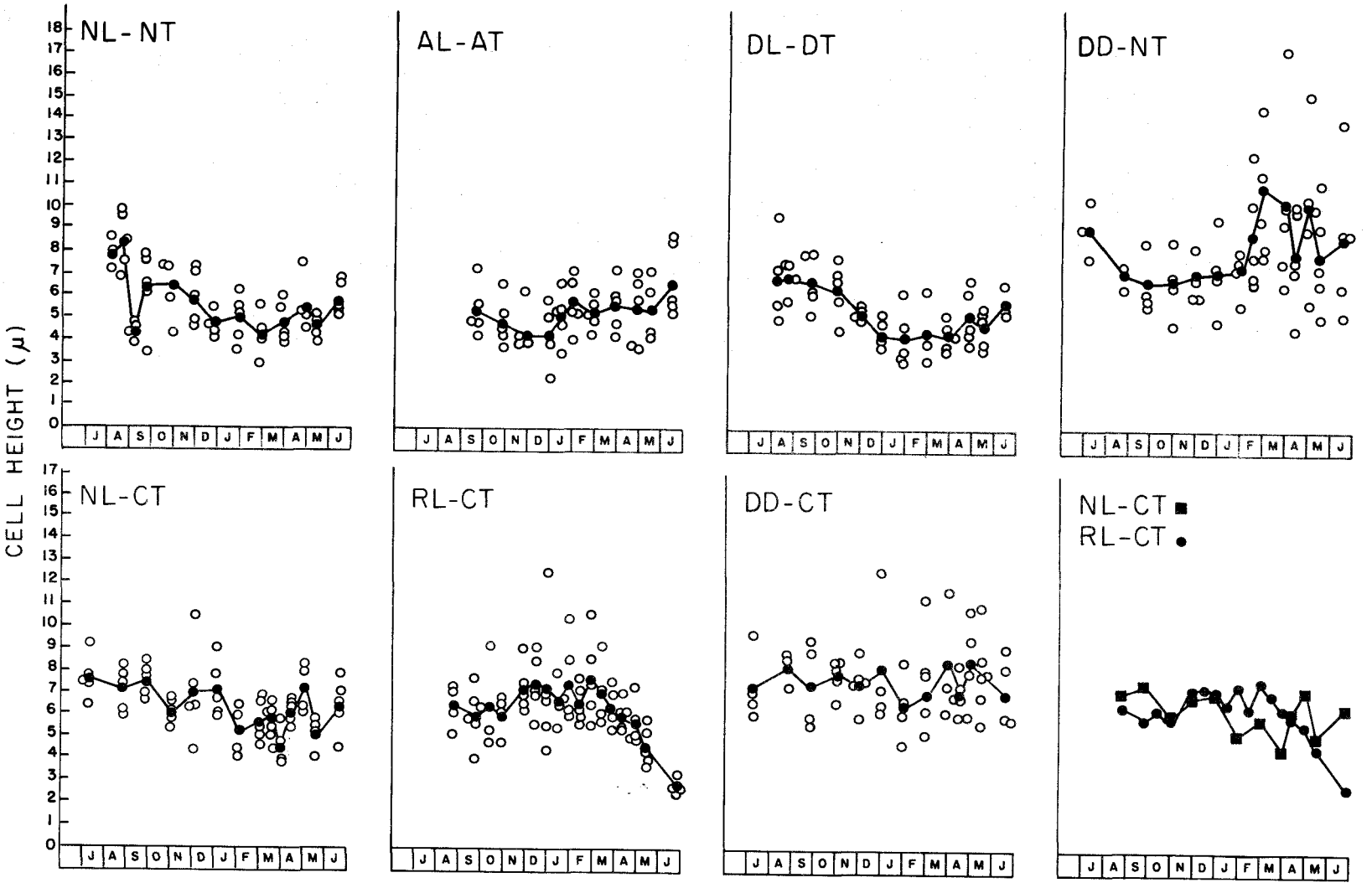

20μ
bm
ep
c
v
B

Figure 17. Seasonal changes in thyroid follicular cell height for fish reared under different photoperiod and temperature cycles in Experiment II; ○ = mean cell height for individual fish; ● or ■ = mean cell height for given group; See abbreviations on pages 22-23.

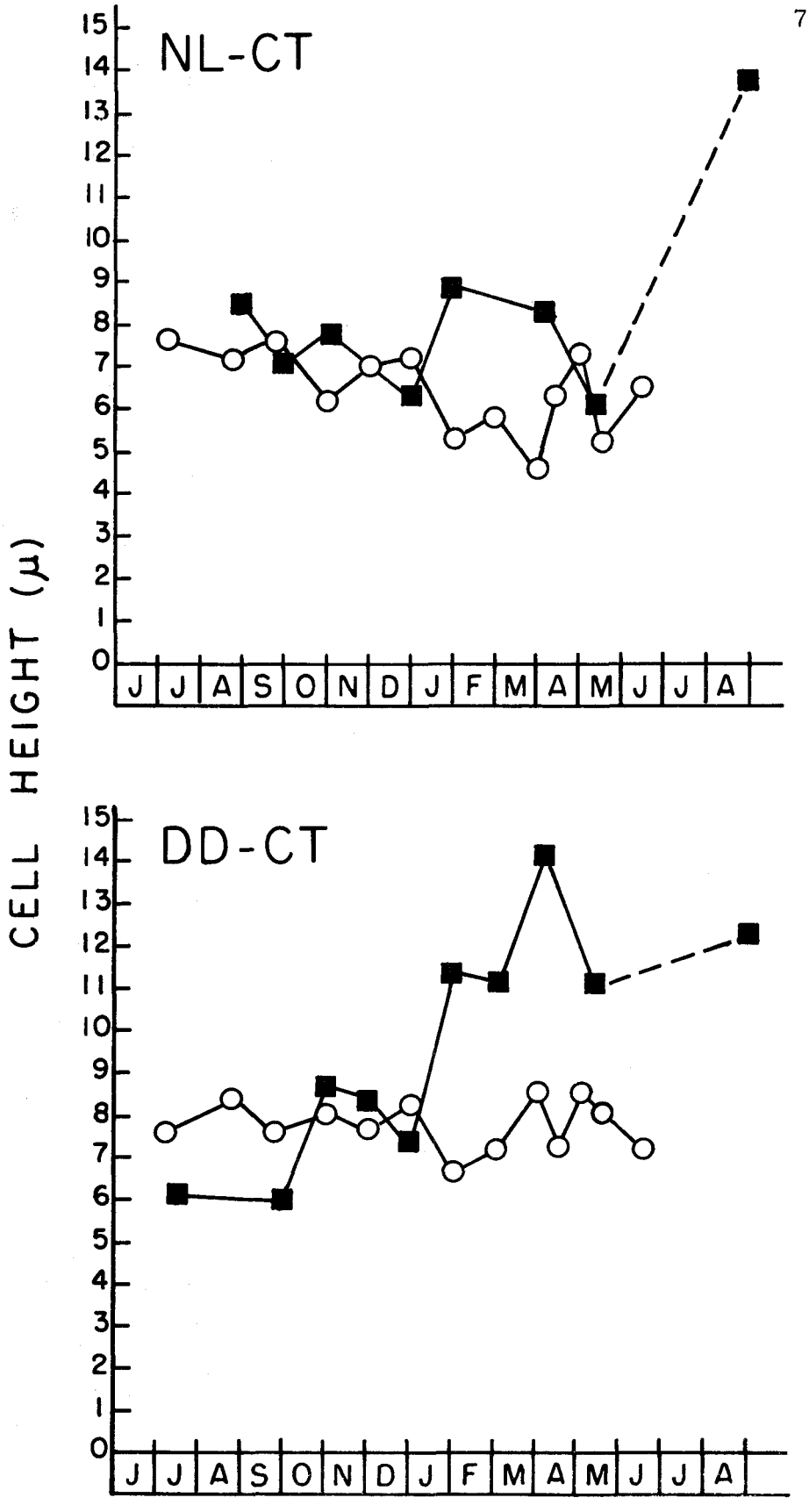

CELL HEIGHT (μ)
NL-NT
AL-AT
DL-DT
DD-NT
NL-CT
RL-CT
DD-CT
NL-CT ■
RL-CT ●
J A S O N D J F M A M J

Experiment II. Seasonal patterns were not the same as those obtained in Experiment I for these two experimental groups (Figure 18). The causal relationship between fluctuations of cell height for groups of fish reared under identical temperature and photoperiod regimes is not revealed. A number of extrinsic factors such as nutrition, locomotor activity, fish size, mineral content of water and sexual maturation as well as photoperiod and temperature have been shown to influence thyroid activity (Dodd and Matty, 1954; Pickford and Atz, 1957; Leloup and Fontaine, 1960; Matty, 1960; Barr, 1965; Eales, 1965). Of these mentioned, food (e. g., amount of iodine in the diet) and weight might account for part of the differences between experiments. The amount of iodine in the diet is unknown and it is possible that some changes in the formula occurred between experiments. The NL-CT groups in both experiments were more comparable in size than fish in the DD-CT groups (Appendices VIII and X). However, I do not feel that size was of major importance because differences in cell heights were apparent only after January.

Gonadal Activity

Precocial gonadal development has been observed in underyearling male steelhead parr in the late winter and early spring (Eales, 1965; Wagner, unpublished). In addition, some yearling fish (mostly males with an occasional female greater than 17 cm in length) that

Figure 18. Comparison thyroid follicular cell heights for the same environmental groups in Experiment I (■) and II (○). See abbreviations on pages 20-23.


NL-CT
DD-CT
CELL HEIGHT (μ)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
J J A S O N D J F M A M J J A

are retained in the hatchery beyond the normal period of seaward migration begin early gonadal maturation in the late summer months (Appendix XVII). I believe that these fish represent the precocial males or females which are found returning to the river after growth of only one summer in the ocean. However, in Atlantic salmon, which are similar in life history to steelhead trout, precocial male parr are common in nature but sexual development at the post-smolt stage occurs infrequently and is perhaps confined mainly to fish artificially reared (Saunders and Henderson, 1965). Because smolting and precocious sexual development are believed to be incompatible biological processes (Evropeitseva, 1960), I wished to determine if photoperiod and temperature used in the experiments influenced these early sexual cycles.

In Experiment I, from July to September 1966 incidental observations were made on the number of maturing fish from Lot A. The following ratios of maturing males to total immature fish (sex ratios unknown) were observed for the indicated photoperiods: DD = 1/50, 8.5L = 1/35, 12L = 1/35, 16L = 1/35, LL = 0/35, NL = 4/34, and SL = 4/34. It is apparent from these preliminary data that long term exposure to photoperiods of different but constant duration did not have a stimulatory effect on early gonadal development in comparison to control groups (NL and SL). No data are available for fish of Lot B.

In Experiment II some groups appeared to have had disproportionately more mature or maturing fish than others (Appendix XVIII). The exact number of male fish maturing for any group was not determined. Undoubtedly those fish in the early stages of sexual maturation might have been placed unknowingly into the release groups for assessment of migratory behavior. The data do suggest that there were more maturing fish in the reverse (RL) and accelerated (AL) photoperiods and perhaps in groups of fish receiving a normal photoperiod of monochromatic light than in other environments. The gonosomatic index for maturing or mature fish at the time that the experiment was terminated in June 1968 provides a reference to the stage of gonadal development (Appendix XVIII).

Many (30%) of the males in the reverse photoperiod reached functional maturity in that free flowing sperm were present in the gonoduct. Under an accelerated photoperiod about 35% of the males possessed enlarged gonads but did not have free flowing sperm. Males in natural (SL or NL) or decelerated photoperiods showed a much lower incidence (0 to 1.5%) of precocial sexual development. One mature fish was observed in the groups reared in the absence of light. The number of precocial males in the tanks receiving monochromatic light was not well documented either to number or stage of development. Results, therefore, cannot be presented as to the possible effects that wavelength and light intensity have on this biological activity.

The mean GSI for immature males was 0.040 (n = 125) while for maturing males it ranged from 0.438 (n = 2) for the DL groups to 7.693 (n = 12) for the AL-NT group in June 1968 (Appendix XVIII).

Gradual and abrupt lengthening of the photoperiod have induced altered maturation in fishes (Harrington, 1959). The data from this thesis suggest that steelhead trout can readily utilize rate changes as well as phase shifts in photoperiod as a stimulus toward altering the cycle of sexual maturation. The temperature alterations appeared not to affect precocial males.

Coloration

At the time of sampling experimental fish for length and weight measurements, individuals were assigned to a category of parr, intermediate, or smolt based on body coloration. The coloration criteria used were similar to those employed by Evropeitseva (1957).

Parr: No apparent silvering, body color yellowish-brown, belly dark, parr marks dark and clearly delineated; ventral and anal fins orange colored with tinge of white on edge.

Intermediate: Moderate degree of silvering confined to the anterior of the body, parr marks light in color and more or less indistinct.

Smolt: Moderate to heavy silvering, belly light in color, parr marks absent or just visible under oblique light, back an iridescent blue or greenish blue, caudal fin commonly with a black band on posterior edge.

A photographic record of these differences was made of fish from the various photoperiod and temperature groups from February through June 1968. Fish reared under fluorescent white light showed a gradual fading of parr marks and spotting until at the end of four or five months, parr marks and in some cases spots on the dorsal surface were indistinct. Most of the fish appeared silvery when viewed in the lateral plane but in others the skin color appeared to be

deficient in color pigments. A dorsal view showed the backs of most fish to be gray or brownish gray with iridescence, while in others, the back appeared as a iridescent blue or bluish gray. Generally, fish in Experiment I were lighter in coloration than fish in Experiment II. Fish in the first experiment were held on a light green background whereas in the second experiment a darker green background was used.

Fish in Experiment I were classified as "intermediates" throughout most of the rearing period. Additional changes in body coloration might have occurred but without a photographic record valid comparisons cannot be made.

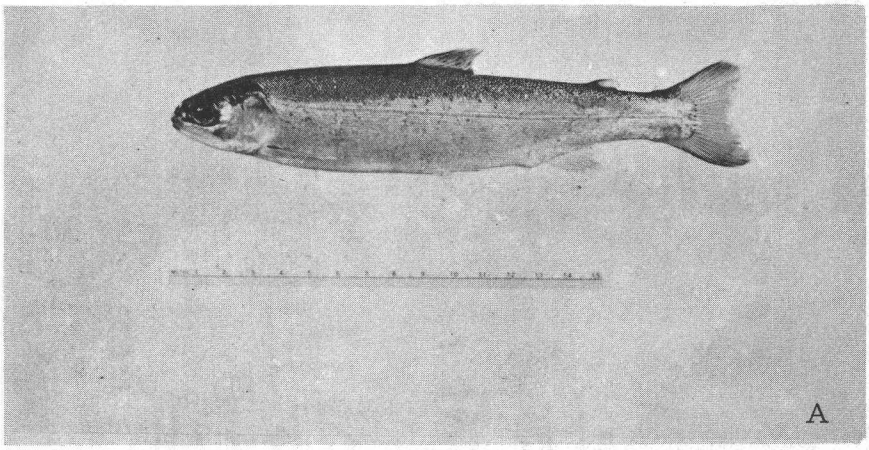
Fish cultured in Experiment II under white light were more silvery in late April than in February regardless of photoperiod. In addition, there was less individual variation within a given group of fish in April as compared to February. Fish reared under accelerated or decelerated photoperiods did not look substantially different from those reared under a normal photoperiod in the degree of silveriness. Although some scale loss had been observed throughout the study, the loss of scales became noticeably heavier in June particularly for those groups on a normal photoperiod. Fish reared in the reverse photoperiod were generally darker and less silvery than the other groups from February to June.

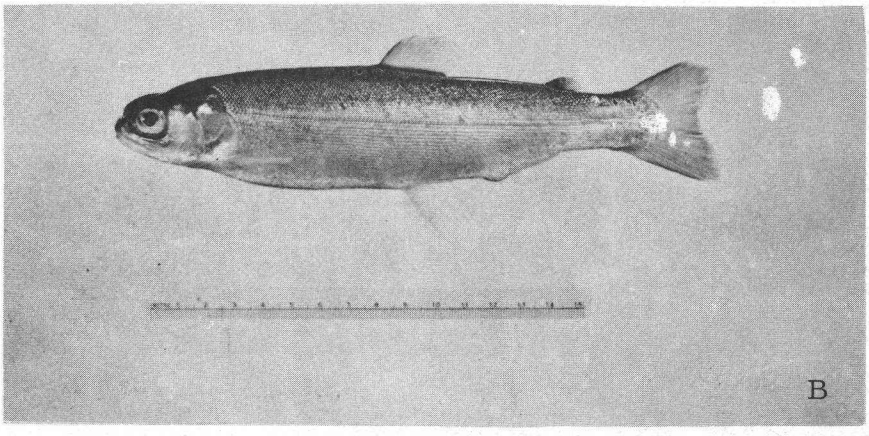
Fish reared in the absence of light in both experiments became silvery. In Experiment II, the fish were completely silvered by late

April while in Experiment I silvering did not occur until July. Fish prior to becoming silvery resembled the cryptic colored parr. Fish reared in the absence of light (DD) or a normal photoperiod (NL) were similar in silvery coloration in April in Experiment II (Figure 19).

Marked differences in body coloration appeared in groups of fish reared under different light spectra. Many fish that were reared under blue or green light had reduced pigmentation on their dorsal surface and variable purine depositions on their sides after 4 to 5 months of exposure. By late April most fish reared under blue or green lights were uniformly silvered with some variation in dorsal coloration. Fish reared under red light resembled the cryptic colored parr reared in the absence of light. But, from late April to June about half of these fish became silvery with a dark blue back. The remainder were yellowish brown with indistinct parr marks.

Figure 19. Comparison of the degree of silveriness between a juvenile steelhead trout reared under a normal photoperiod (A), and one reared in the absence of light (B) on April 23, 1968. Note the similar degree of silvery coloration in the two fish. Scale in centimeters.


A


B

DISCUSSION

Light and Temperature Regulation of the Parr-Smolt Metamorphosis

Most organisms are found in natural environments which fluctuate rhymthically. Survival of the species often depends upon the precise timing of certain biological activities to proper environmental conditions, especially when such important aspects of the life cycle as reproduction and migration are involved. Since biological processes require considerable time to complete, it is advantageous for the organism to anticipate and prepare for changes in the environment (Webb and Brown, 1959). In this study both photoperiod and temperature were observed to have an effect on the temporal orientation of parr-smolt metamorphosis.

The alternate roles of photoperiod in the timing of biological processes appear as follows: (1) it keeps an endogenous rhythm in daily synchrony or in a periodicity with the annual season; or (2) it controls the frequency as well as the phasing of the endogenous rhythm; or (3) it controls the periodicity completely so that without a photoperiod cycle the biological process disappears (Farner, 1961; Wolfson, 1964a). The role of photoperiod in separate aspects of the cyclic biological process has been defined as (1) an all or none reaction determining the occurrence of an event or (2) a chronometric

reaction governing the rate of development and duration of a response (Wolfson, 1964a). In addition, various responses appear to utilize different aspects of the daily photoperiod. There is a well-defined relation between length of the daily photoperiod per se and the response. But there is additional evidence that emphasizes the change in the length of the daily photoperiod as a basis for timing a biological process (Harrington, 1959; Farner, 1961; Wurtman, 1967).

While specific photoperiodic requirements have been identified, only very broad generalizations can be made for the role of temperature in the temporal orientation of biological processes. Homeotherms appear to be largely independent of thermal periodicities (Hammond, 1954). In poikilotherms, temperature is well documented as one of the main modifiers of metabolic processes and activity (Brown, 1957) and thus can be expected to have a modifying effect on cyclic biological processes. Less is known about thermoperiodicities in poikilotherms. In the reproduction of some fishes temperature appears to be more than a modifier and actually controls cyclical changes in the gonads (Pickford and Atz, 1957; Ahsan, 1966).

Cyclic Photoperiods

In this study, photoperiod appeared to be the major factor controlling the onset of metamorphosis but did not determine whether or not the event occurred. The data suggest that the rate at which the

length of the daily photoperiod increases is the information most readily utilized by the fish for synchronizing the response, rather than the length of the light or dark period per se or accumulated number of hours of exposure.

Fish reared under an accelerated photoperiod metamorphosed earlier than did those under a natural photoperiod. Those receiving a decelerated photoperiod demonstrated a delayed and extended metamorphic period in comparison to the control fish as directly evidenced by migratory behavior (Figure 10 and Table 2) and indirectly by changes in the coefficient of condition (Figure 12). There was no additive effect, as total hours of light exposure were comparable among the NL, AL, and DL groups at the time markedly different migratory behavior and coefficient of condition patterns were observed (Table 6).

Additional evidence of photoperiodic influence over parr-smolt metamorphosis was obtained from those fish reared under a reverse photoperiod in Experiment II. The cycle maintained a normal frequency but was six months out of phase to the natural photoperiod. The larger fish ($\geq$ 15 cm) receiving this light regime might have been migratory as early as December (June photoperiod) if one based parr-smolt metamorphosis on changes in coefficient of condition (Figure 12). The RL fish released in the spring months when migration naturally occurs did not migrate (Figure 10 and Table 2). These observations

Table 6. Total light exposure in hours from June 1, 1967 to various calendar dates in Experiment II.

Calendar date[1]	Photoperiod		
	Normal	Accelerated	Decelerated
February 26, 1968	3205	3231	3274
May 1, 1968	4014	3892	3952
June 27, 1968	4894	4720	4685

[1] The normal migration period is from April through May with the peak period of movement occurring from mid-April to mid-May for this stock reared under natural conditions (Wagner et al., 1963). The peak period of migratory activity is assumed to be May 1. Fish reared under an accelerated or decelerated photoperiod reached the May 1 photoperiod on February 26 and June 27, respectively.

on RL fish are in agreement with the findings on Atlantic salmon which were subjected to a reverse photoperiod (Saunders and Henderson, 1970). Their fish were silvery in appearance in the spring but unlike smolts had a higher coefficient of condition while in freshwater. When transferred to sea water, they ate less and had lower efficiencies of food conversion than those reared in a natural photoperiod.

Photoperiodic control of the timing of metamorphosis did not appear to be complete, as evidenced by migratory behavior and coefficient of condition patterns in the AL, DL, and RL groups. Migratory response was less intense than predicted on the basis of photoperiod alone and might have occurred later in AL groups than expected as evidenced by the 56% to 66% movement of fish released in early March under freshet conditions. The extension of the migratory period into May for the AL-NT group is believed to be a function of temperature and will be discussed later. The DL groups showed greater movement than expected when released in early May, but less than expected movement when released in mid-June (Figure 10 and Table 2).

In the interpretation of movement data, it must be considered that in some instances fish were reared in one type of photoperiodic environment and then released into an entirely different photoperiod. Not only was there this difference but temperature and many other biological and physical factors had changed. The migration of

experimental groups might have been greater or less if the fish had been tested under the rearing environments. The fact that the groups of fish responded in a predictable manner does indicate that the changes which prepare juvenile steelhead for migration or terminate migration do not occur suddenly but once completed will sustain the behavior pattern for at least 15 to 30 days and perhaps longer.

Under the RL photoperiod the nadir of the $\overline{K}$ curve for the larger fish occurred in early December (calendar month), or about two or three weeks later than expected. A possible factor in this delay might have been rate of growth. In mid-October there were few, if any, fish 15 cm in length.

There are probably a number of factors other than photoperiod involved in changing the timing of migration. Advancement or delay of migration might be the result of "releasing" factors in the natural stream, variation in the metamorphosis based on growth, the presence of an endogenous rhythm, and the modifying effects of other physical environmental factors.

The parr-smolt metamorphosis appears to have an endogenous mechanism or possibly be synchronized through rhythmic geophysical factors other than light and temperature. Migratory behavior and smolt characteristics were observed in some fish under constant photoperiod and temperature. Fish reared in the absence of light on constant temperature in Experiment II demonstrated maximum migratory

activity in May (Figure 10 Table 2). This period of increased activity was associated with a decline in coefficient of condition (Figure 12H), and an increase in thyroid activity or cell height variability (Figures 15 and 17) and purine deposition (Figure 19). Steelhead trout apparently will undergo parr-smolt metamorphosis under conditions of constant light and temperature but if provided with a photoperiod cycle will utilize the periodicity to entrain what appears to be an endogenous rhythm. The metamorphic response was greatest in fish reared under a natural photoperiod and temperature regime and least for fish reared in the absence of light at a constant temperature. Changes in the external environment perhaps cause an enhancement of physiological changes at parr-smolt metamorphosis or simply act to synchronize behavior and endocrine rhythms among individuals so that metamorphosis occurs more or less simultaneously.

Constant Photoperiod

There are many difficulties associated with substituting an artificial "square wave" for the "sine wave" of the natural photoperiod. One of the most obvious is that the biological process might have a requirement for a light or dark period of a specific length and that this requirement might also vary for different developmental stages of the process. Thus, the efficacy of the constant photoperiod selected might be quite low depending on the developmental stage of the organism

as well as its previous photic exposure. For example recent experiments have shown that a constant photoperiod of 13.5L-NT begun in January was stimulatory to parr-smolt metamorphosis from March until early May whereas a 16L-NT appeared to be inhibitory (Wagner, unpublished).

The effects of constant photoperiods (8.5L, 12L, 16L and LL) on the metamorphosis are difficult to interpret in my study. Fish reared on constant photoperiods of 8.5L or 12L from July 1965 to March 1966 demonstrated a migratory response comparable to control fish (NL) while those exposed to 16L or continuous light (LL) did not migrate when released (Figure 8).

The slightly earlier movement of fish from the 12L group in comparison to the 8.5L and NL groups might be a result of the 12L fish being in a greater state of preparedness at the time of release. A daily photoperiod of 12 hours is about 2.25 hours away from the May 1 photoperiod of 14.25 hours when migration normally peaks whereas there is a 5.75 hour difference between 8.5L and the May 1 photoperiod. Exposure to the natural environment might have hastened the changes leading to migration in 8.5L and 12L fish which were in a receptive developmental stage at the time of release. Saunders and Henderson (1970) found that a 13L photoperiod was neither stimulatory nor inhibitory to smolting in Atlantic salmon as evidenced by coefficient of condition changes, and growth rate in sea water. However, the

exposure was begun in the spring and the results might have been different if it had started earlier.

No marked changes in $\overline{K}$ occurred in any of the groups on constant photoperiods. However, some suggestive changes did occur in the 8.5L and 12L groups. Minimum $\overline{K}$ occurred in mid-June for both groups and was followed by an increase in condition. I attach significance to this pattern of change because of the migration data and feel that the experimental population held in the laboratory demonstrated a metamorphic response under 8.5L and 12L photoperiods late in the spring of 1966. It is possible that the metamorphosis as indicated by $\overline{K}$ might be quite subtle under constant photoperiod and temperature, or perhaps eliminated entirely. Webb and Brown (1959) point out that it is necessary to distinguish between rhythmicity of an indicator and the stable rhythmicity in a basic system which persists after modification of the indicator.

Previous exposure to a photoperiod decreasing at a natural rate had no influence on future $\overline{K}$ patterns when the fish were placed under constant photoperiods of different duration (Figure 11B). If long photoperiods of constant duration were stimulatory with respect to parr-smolt metamorphosis, I anticipated a marked decrease in $\overline{K}$ in migrant-sized fish when transferred from a December to a 16L photoperiod, but it did not occur. At the time of the transfer, fish were not all migrant-sized and using $\overline{K}$ as an indicator might be misleading.

Individual fish as they reached the critical size in the 16L photoperiod could undergo the metamorphosis and revert to the non-migratory form without a corresponding decrease and increase in $\overline{K}$ for the group. However, no relation was shown between fish size and K in any given month in Experiment I.

The migratory behavior contrasted with the pattern for $\overline{K}$ indicates that an extensive regime of 16L photoperiods acts to terminate migration. This response is perhaps analogous to the refractory period observed in birds and some fish during which they can no longer be stimulated by long daily photoperiods into a reproductive state without experiencing an interruption by a sequence of short photoperiods (Harrington, 1959; Farner, 1961; Wolfson, 1964a). The absence of a response in fish reared under continuous light is also probably a long photoperiod effect but might indicate the requirement of some critical physiological function in the metamorphosis for an interrupted light period. In contrast, short photoperiods (8.5L or 12L) or continuous darkness allow for expression of the endogenous rhythm.

Regardless of photoperiod in Experiment I, with the possible exception of those reared in the absence of light, thyroid activity, seawater adaptation, and purine deposition appeared to be similar for all groups. The association of these parameters to the metamorphosis will be discussed later. It suffices at this point to say that while the different photoperiod groups generally appeared to be similar with

respect to the above parameters, there were differences in migratory behavior.

The interpretations of the findings in the present study on the effects of constant photoperiod on the parr-smolt metamorphosis are not entirely in agreement with the findings of other investigators who have studied the effects of environmental factors on one or more indicator processes and extrapolated these findings to the metamorphosis as an entity.

Two-year-old "potential" smolts of steelhead trout held from January to May under four controlled photoperiod and temperature regimes (8L-5^{o} C; 8L-NT; NL-5^{o} C; NL-NT) all underwent the parr-smolt metamorphosis in the spring based on visual appearance (Eales, 1965). The coefficient of condition (0.74 to 0.76) was comparable in all groups from April to early June (pers. comm. J. G. Eales). However, thyroid morphological and radiochemical measurements on the same fish revealed increased thyroid activity to be influenced by the environments. Eales (1965) did not reconcile the differences between the independence of parr-smolt metamorphosis upon photo- and thermal-periodicity as based on silveriness and the dependency of the metamorphosis as indicated by thyroid activity. Later Johnston and Eales (1968) placed greater emphasis on the thyroid activity as a smolting characteristic when referring to the same data. Although in steelhead trout the initiation of silvering was not affected by a short photoperiod,

rate or extent of silvering appeared to be correlated with lengthening photoperiod or thyroid activity or both (Eales, 1965). Atlantic salmon show neither a complete dependency upon photoperiod or temperature for a change in silvery appearance, but purine levels were greater under a normal temperature cycle than at constant temperature regardless of photoperiod (8L or NL) (Johnston and Eales, 1968). A pronounced decrease in the coefficient of condition also occurred for fish reared in the NT regimes. In a later study, it was demonstrated that regardless of size of fish (< 10 cm, 10-12 cm and > 12 cm), there was a marked effect of temperature on silvering and coefficient of condition in this species (Johnston and Eales, 1970). Their data also showed that the larger the fish the more rapid is the development of the silvery appearance. It is apparent from these studies that interpretations of the effects of environmental factors on the metamorphosis as expressed by degree of "silveriness" must be made with caution. Apparent also is the fact that the various species or different stocks of the same species can respond differently to photoperiod and temperature in relation to parr-smolt metamorphosis as indexed by silveriness and coefficient of condition.

Litchtenheld (1966) studied the effects of photoperiod and temperature on spontaneous locomotor activity and silveriness of steelhead trout. Fish ranged from 17.5 to 20.7 cm in length and were exposed to either 18 hour (18L), natural (SL) or 6 hour (6L) daily photoperiods

and a seasonal temperature cycle beginning in mid-January. Past investigations have shown that increased locomotor activity and alertness to sensory stimuli are characteristic of smolts (Hoar, 1951b; Hoar, Keenleyside, and Goodall, 1957; Pinhorn and Andrews, 1965).

In Lichtenheld's experiments, fish reared in a natural photoperiod exhibited an annual bimodal pattern of locomotor activity with heightened activity appearing in spring and late fall. Vernal activity was correlated with increased purine deposition, and peak smolt numbers based on silveriness occurred in late May. The 18L and 6L groups displayed unimodal patterns of locomotor activity with maximal responses occurring in the summer for the 18L and the winter for 6L groups. Increased activity for the 18L and 6L groups was shifted to temperature levels that the given photoperiod was normally associated with in nature. Lichtenheld stated that peak smolt numbers of 6L fish occurred from mid-September to mid-October or about six months later than NL fish whereas the 18L fish showed peak smolt numbers in late April or about one month earlier than control fish. However, various degrees of silveriness were present in both 18L and 6L prior to and after the peak smolt period. Silvering fish were most numerous during periods of least locomotor activity for the 18L and 6L groups in contrast to what would be expected from earlier findings. I calculated coefficient of condition values for the various groups from growth data given by Lichtenheld (Appendix XIX). The vernal nadir

in the curves occurred in late April and May for fish in the 18L and NL groups, respectively and was related to peak numbers of smolts based on silveriness. There was no marked change in $\overline{K}$ for the 6L fish. Based on $\overline{K}$ and purine deposition, smolting occurred in April and May for the 18L and NL groups, respectively, but was not associated with increased locomotor activity for the 18L groups. The metamorphosis might not have occurred in the 6L group.

Changes in salinity preference and behavior (schooling, aggressiveness, and general activity) have been studied in downstream migrants of Pacific salmon. Under natural photoperiods yearling coho and sockeye (O. nerka) salmon prefer hypertonic seawater during the period of seaward migration (Baggerman, 1960; McInerney, 1961). At this time the fish are characterized by a high level of activity, strong schooling behavior and depressed aggressive behavior (McInerney, 1961). A short photoperiod (8L) had an inhibiting or delaying effect on the change in preference for hypertonic seawater and in behavior, whereas a long photoperiod (16L) induced an earlier change than under natural or short photoperiods.

I find it difficult to arrive at any firm conclusions concerning the effects of artificial constant photoperiods on parr-smolt metamorphosis based on data from my thesis and that of other investigations. Experimental conditions which were employed have been diverse with respect to species, photic history, and developmental stages of the experimental fish, temperature regimes, and nutritional state of the fish. However, there is substantial evidence that a number of physiological processes associated with the metamorphosis can be altered by exposing fish to short or long constant photoperiods in conjunction with constant or variable temperature cycles. However, the fact that light and temperature manipulation result in a change in one or two parameters does not mean that a metamorphosis has been effected with the expected change in migratory behavior.

Photospectrum and Intensity

The parr-smolt metamorphosis was not affected by the spectrum and intensity of the light regimes in the present study. Fish reared for a year under blue (peak transmittance at 450 mμ), green (550 mμ), and red (662 mμ) light compared favorably to control fish (NL-CT) in time and magnitude of migration (Table 2 and Figure 10), coefficient of condition pattern (Figure 11E), and growth (Table 5). There are few other studies with which to compare these findings.

The effects of monochromatic light on the growth of young salmon were investigated by Crawford (1930). Growth rates were slowest and mortality greatest in blue light, while growth in red light was similar to that observed for fish reared in total darkness. Green and yellow light were optimal for growth. He felt that differences were probably related to uncontrolled temperature differences more than to light. No information is available on the species of salmon used or the properties of the filters; as well, no quantitative data are presented. Although the paper has been referenced by other investigators with respect to the effects of light on vertebrate development, I believe the author's intention was only to emphasize the need for control of extraneous variables.

Spectral effects on growth and endocrine histology were studied in the fish Astyanax mexicanus by Cahn (1952). There were no substantial differences among the experimental groups in growth and maintenance of the essential intregrity of endocrine systems. Some differences in thyroid cell heights were observed between control fish and some of those reared under red, yellow, green, and blue light but the spectra were not discrete.

Exposure to longer wavelengths (approximately 560-720 mμ) retarded the maturation of the gonad in the ayu (Plecoglossus altivelis), whereas shorter wavelengths (approximately 400-560 mμ) accelerated gonadal maturation (Shiraishi, 1965a). In contrast, sticklebacks

exposed to discrete segments of the visible spectrum (388-468, 455-518, 513-583 and 585-653 mμ) showed no substantial differences in seasonal rates of gonad maturation (McInerney and Evans, 1970).

The retinae of salmon and trout are a mixture of two visual pigments with peaks in absorption spectra at 503 mμ and 527 mμ (Muntz and Beatty, 1965). I would expect, if visual pigments made up the first link in the chain of events controlled by a photoperiodic mechanism, that the action spectra would be near the absorption spectra for the visual pigments. In a study on the effects of photoperiod and temperature on daily pattern of locomotor activity in juvenile sockeye salmon, the eyes were the primary sensory receptors mediating photoperiodic information (Byrne, 1968). However, the transfer of information was not by optic nerve pathways. Byrne suggests that chemical agents (melatonin and serotonin) produced by the retinae or pineal or both might control the degree of locomotor activity in the light and dark.

The number of studies concerned with the action spectra of photoperiodic responses in vertebrates is limited, but there appears to be less dependency on the wavelength properties of visible light than in plants and possibly in invertebrates (Hammond, 1954; Withrow, 1959; Farner, 1961; Beck, 1968). Fish appear to be less selective than birds with respect to light quality but this apparent difference might be a result of the more numerous studies on birds. In birds

the maximum sensitivity is in the range of about 600 mμ to 750 mμ for gonadal stimulation (Farner, 1959). The action spectra tend to be farther to the red than that for photopic vision but still suggests the involvement of carotenoid compounds. It has been demonstrated by Benoit (1938) as cited in Farner (1959) that visual receptors are not necessary for the photoperiodic process. The entire visual spectrum can act directly on the hypothalamic centers of ducks to stimulate gonadal development. Two pathways are apparently present, a visual one with a wavelength dependency and a nonocular one which is not wavelength dependent.

The pineal organ of fishes is a recognized photoreceptor (Breder and Rasquin, 1950; Hoar, 1957) and might be of some significance in photoperiodic responses. The transparent dorsal covering of the brain in the region of the pineal in juvenile salmonids and other fishes, for instance, makes both the nervous tissue and pineal subject to direct light stimulation. The above might explain the lack of wavelength dependency for photoperiodicities in some fish. Turner (1966) has suggested that the mammalian pineal gland serves as a transducer in the mediation of environmental stimuli; it might play an even greater role in fish. Shiraishi (1965b) demonstrated that ophthalmectomized ayu (P. altivelis) responded to short and long photoperiods with respect to the timing of sexual maturation, as did intact fish. However, because of the heavy skull structure in the threespine stickleback (G.

aculeatus), McInerney and Evans (1970) felt that it was unlikely that the broad spectrum response was a result of stimulation of encephalic receptors. The authors suggest that another interpretation for the wide action spectrum is that fish show a primitive pattern of retinal connections, with most optic fibers passing to the thalamus and optic lobe regions of the brain. Whereas in birds and terrestrial vertebrates optic fibers pass indirectly to the forebrain and that this alteration might have included the loss of certain shorter wavelength receptors.

The photoperiodic mechanism of the parr-smolt metamorphosis in steelhead trout also showed a wide tolerance to light intensity and radiant energy levels in the present study. The intensity of the light sources varied from 11 lux for red light to 2195 lux for the fluorescent white light (Table 1). Radiant energy level varied from 11.8 $\mu W\ cm^{-2}$ (118 ergs $sec^{-1}\ cm^{-2}$) for monochromatic green to 896 $\mu W\ cm^{-2}$ (8960 ergs $sec^{-1}\ cm^{-2}$) for fluorescent white light. All the above experimental groups appear to have responded similarily with respect to parr-smolt metamorphosis.

Henderson (1963) found no influence on the reproductive cycle in brook trout, Salvelinus fontinalis, at light intensities ranging from 86 lux to 678 lux. In stickleback, G. aculeatus, gonad development was comparable at light intensities ranging between 269-323 lux and 3229 lux. The response time was greater, however, at a lower

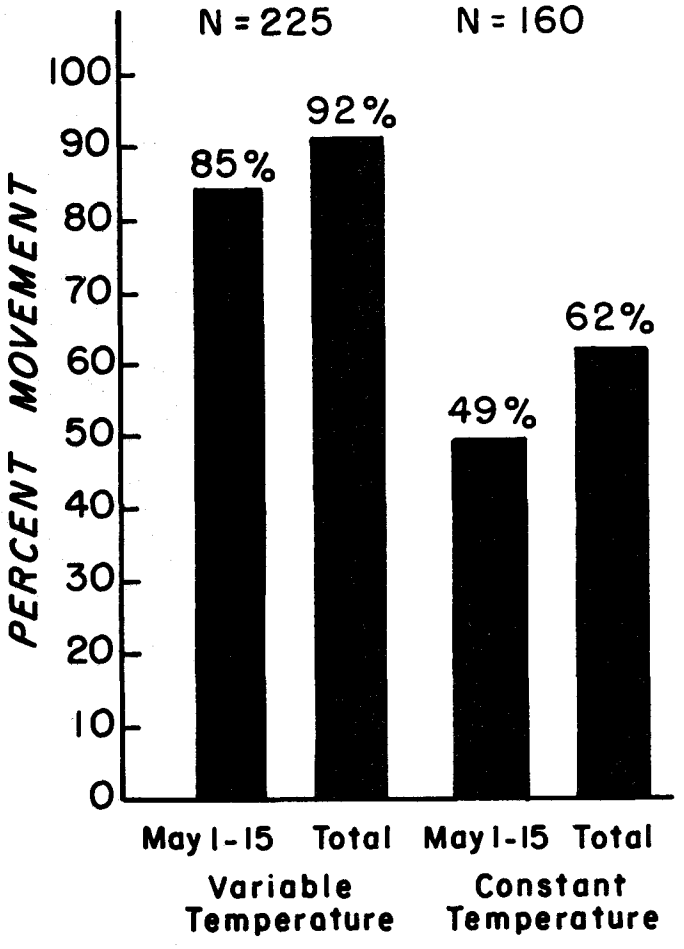
intensity of 161 lux than at 269-323 lux (Baggerman, 1957).

McInerney and Evans (1970) maintained the level of light energy relatively low (< 37 μWcm^{-2} or < 370 ergs sec^{-1} cm^{-2}) on each group of sticleback reared under monochromatic light. Illuminance levels were in the approximate range of 5 lux (purple light) to 330 lux (green light). These levels had no effect on gonad maturation.

The sensitivity of the photoperiodic mechanism in the fishes studied is low and in this respect the mechanism appears similar to that found in insects and vertebrates (McInerney and Evans, 1970). However, in a number of birds, the rate of photoperiodic response in gonad development is a positive function of light intensity up to about 160 lux or less (Farner, 1959, 1961).

Temperature as a Modifier of Photoperiod Effects

Temperature had two measureable effects on the metamorphosis as indexed by seaward migration and changes in coefficient of condition. First there was the difference in migratory activity between fish reared at constant and variable temperature. Fish from a normal or natural photoperiod cycle showed their greatest migratory activity in the May release. At this time, fish reared in a variable temperature cycle, including ST, NT, AT, and DT cycles, moved downstream not only in greater numbers but more quickly than fish reared at constant temperature (Figure 20). This temperature effect is also apparent in


N = 225
N = 160
100
90
80
70
60
50
40
30
20
10
0
PERCENT MOVEMENT
85%
92%
49%
62%
May 1-15
Total
May 1-15
Total
Variable Temperature
Constant Temperature

fish reared in the absence of light (Table 2). It should be noted, however that from May 26 to June 12 the weir was inoperable and any movement during this time would have gone undetected. The numbers of fish that migrated from the CT groups could have been larger. However, the recovery of fish at the release site by electrofishing on May 15 and again on July 12 indicated about the same numbers of CT fish in residence (Table 3).

Second, the data indicate that temperature has an effect on the duration of the migratory period. When the temperature cycle was out of phase but behind the photoperiod (e. g. AL-NT or NL-DT), the migratory period was extended. In contrast, when the temperature cycle was out of phase but in advance of the photoperiod (e. g. NL-AT), the migration period tended to be shortened in comparison to when temperature and photoperiod were in phase (Table 2).

Temperature variations, including diurnal as well as seasonal, might act to sensitize the organism with respect to releasing factors (Fontaine, 1954; Hoar, 1958b). In addition, the seasonal changes in growth which appear to a large extent to be dependent on temperature variation might be essential to the smolting process (Figure 11).

Temperature modification of the duration of the smolt period might be a function of increased reaction rates of biochemical processes involved in the metamorphosis so that fish on an accelerated temperature (warmer) cycle complete the physiological changes sooner

than those on a normal or decelerated (cooler) cycle. The data do not indicate an earlier or later beginning for the smolting process, for example see the $\overline{K}$ patterns for AL-NT and AL-AT groups (Figure 12D), but only an influence on the length of time that the fish were migratory. Under natural conditions, photoperiod and temperature probably reinforce one another and the maximum response will be obtained when the two are in phase.

In comparison to the vast literature on photoperiod effects on migration, there is little information on the effects of temperature with which to compare my data. Baggerman (1960a) in her excellent review of the factors in the diadromous migrations of fish cites only two papers with respect to temperature influences. Stickleback migrate to freshwater earlier when temperatures are warmer (Baggerman, 1957). The timing of the seaward migration of sockeye salmon from a lentic environment was dependent upon the temperature in January, February, and March which precede migration (Foerster, 1937). However, Hartman, Heard, and Drucker (1967) believed that photoperiod plays an important role in timing the migration of smolts of this species. Fontaine (1954) states that smolting and migration were earlier for Atlantic salmon if the average water temperatures were higher in the preceding months. Recent evidence for Oncorhynchus masou indicates that the smolting process is accelerated at higher temperatures (Kubo, 1959, 1965). A temperature range of 10° to 14° C advanced parr-smolt

metamorphosis in comparison to 4 to 7° C regimes. Pinder and Eales (1969) noted that seasonal changes in buoyancy in Atlantic salmon smolts (smolts being more buoyant than parr) were hastened by an increase in temperature but did not seem to be affected by photoperiod. Temperature also increased the incidence of silvering in these same fish (Johnston and Eales, 1968). It is apparent that water temperature is an important factor influencing physiological changes at the time of the metamorphosis in some species.

Chemical and Nervous Regulation of the Parr-Smolt Metamorphosis

Thyroid Activity

It has been shown that morphological and radiochemical analyses of thyroid activity do not always agree (Swift, 1959; Eales, 1963, 1964, 1965; Drury and Eales, 1968). Thyroid activity as indexed by radiochemical methods increases with increasing temperature while histological criteria, principally cell height, indicate decreased activity. The possibility that thyroid gland can respond directly to increases in ambient temperature in terms of its iodine metabolism and hormone synthesis without an increase in cell height has been proposed by Eales (1964), suggesting that control by the pituitary through thyroid stimulating hormone (TSH) is shunted.

A basic annual cycle of thyroid activity occurring in a number of temperate fishes including trout has been described by Swift (1960). A greater activity occurs during the winter and spring and lesser activity during the summer. The thyroid has been implicated in many physiological processes but its precise function and mode of action remain obscure (Lynn and Wachowski, 1951; Pickford and Atz, 1957; Hickman, 1959; Gorbman, 1959; Matty, 1960; Barrington, 1961; Barr, 1965). Lack of statistical significance in the present study between means in a given group makes the thyroid data difficult to interpret, particularly its role in parr-smolt metamorphosis. There appears to be no difference in thyroid follicle cell heights among groups reared at constant temperature under 8.5L, 12L, 16L, LL or natural photoperiods (Figure 15). These findings are partially in agreement with those of Eales (1965) for steelhead parr where some factor other than temperature and photoperiod appeared to be involved in cell height changes occurring in the spring. Fish reared in the absence of light showed greatest cell heights or variability of any group during the spring in both of my experiments, perhaps indicating a greater demand for thyroid hormone or a malfunction in the feedback mechanism in the absence of light.

It is of interest that under a reverse photoperiod (RL) and at constant temperature thyroid cell height pattern tended to be different from all groups (Figure 17) whereas with constant photoperiods varying

from no light through continuous light (Figure 15) the cell heights were similar. This suggests that the control over thyroid morphology will be greater if some type of environmental stimulus is changing. Constancy in photoperiod or temperature or both for extended periods of time might allow for expression of an endogenous rhythm which normally is entrained by the seasonal change of environmental factors.

Finally, groups of fish with apparently similar thyroid cell heights had markedly different patterns of migration and coefficients of condition. Kalleberg reports (cited in Hoar, 1963; pers. comm.) that Atlantic salmon smolted (criteria not specified) after destruction of the thyroid gland with radioiodine in the parr stage. The findings along with those in this study cast additional doubt on the role of the thyroid in parr-smolt metamorphosis.

Neuroendocrine System

There are several topics which I would like to review briefly with respect to the parr-smolt metamorphosis under the heading of the neuroendocrine system. They are the role of the neuroendocrine system, the pathway of the photoperiodic response, the size dependency aspect of the metamorphosis and the termination of migratory behavior.

The parr-smolt metamorphosis is generally belived to be under the control of the endocrine system, with changes in the thyroid, adrenal

tissue and pituitary documented to various degrees (Hoar, 1953, 1957, 1959, 1963, 1965a; Fontaine, 1954; Baggerman, 1960a). It should be noted that whereas seasonal changes have been demonstrated in endocrine activity, there have been no pituitary studies under controlled photoperiods. Two modes of hormonal action have been theorized (Hoar, 1963). A general permissive role is theorized where seasonal activation of the neuroendocrine system elevates metabolic processes and increases the organism's excitability and subsequent response to stimuli. These changes could lead to migratory behavior in the presence of appropriate "releasing" factors. In contrast, a specific role for various hormones in different segments of the migratory sequence of events could exist. However, while hormones serve as the chemical link between the fish and the environment, there is little evidence that any specific hormone controls any particular reaction (Hoar, 1963, 1965a).

The hypothalamo-pituitary neuroendocrine system has been most studied in mammals and birds with perhaps more experimentation in birds with respect to photoperiodic pathways (Benoit, 1962; Wolfson, 1964a, b; Farner and Follett, 1966). There is increasing evidence that external environmental control over reproductive and migration cycles is integrated through this system but much detail of the mechanism is still obscure.

The following theorized sequence of events is proposed for the photoperiodic control of parr-smolt metamorphosis. Changes in the photoperiod are detected by receptors which might be ocular or encephalic or both. These effectors transmit in some unknown way to integration centers in the diencephalon or directly to the neurosecretory sites in the hypothalamus. Neurosecretions which control the production of trophic hormones from the adenohypophysis are activated. The trophic hormones then regulate body processes directly or through other endocrine glands. Circulating hormones provide the feedback mechanism which might be by way of interceptors in the nervous system or which might act direcly on the pituitary.

What evidence is there for such a system in terms of structure and function? These secretory neurons in fish are composed of the nucleus preopticus and the nucleus lateralis tuberis. The secretions from the two types have different staining properties (Stahl and Leray, 1962; Dodd, 1963; Dodd and Kerr, 1963). Honma and Tamura (1965) studied the neurosecretory system of the salmonid (Salvelinus leucomaenis pluvius). The axons of the nucleus preopticus and nucleus lateralis tuberis enter the pituitary stalk and penetrate into the extensive ramifications of the neurohypophysis in different areas and to different degrees. In other teleosts, the fibers filled with neurosecretory

material from the nucleus preopticus penetrate between the cells of the adenohypophysis (Stahl and Leray, 1962). It is apparent from these studies that neurosecretions are directed and have a close spatial relationship to the pituitary.

Although there is considerable evidence to indicate that the hypothalamic centers mediate environmental influences on the pituitary (Scharrer, 1959), there is meager experimentation under controlled environmental conditions. In the brook lamprey, neurosecretory material is more abundant in the neurohypophysis prior to the metamorphosis than during or after (Kamer and Schreurs, 1959). Recently Honma and Suzuki (1968) demonstrated photoperiodic control over the neurosecretory system. They indicated that the gonadotrophic activity was related to secretions by the nucleus lateralis tuberis and that the nucleus preopticus was perhaps involved with osmoregulation and ovulation. However, a lack of correlation between the neurosecretory and pituitary cytological changes in goldfish receiving X-irradiation has been observed (Sathyanesan and Chavin, 1966). The radiodestruction of the preoptic nucleus did not alter the pituitary cytology. This suggests that the stainable neurosecretory material might not be related to the pituitary releasing factors.

Where in this tentative control mechanism does the somatic growth of the organism play a part? Growth can probably be translated into physiological age in terms of development of some part of

the control mechanism. The neurosecretory centers apparently develop morphologically and functionally in terms of secretory products in Salmo shortly after hatching (Klein, 1966; Honma and Tamura, 1967). In addition, trophic hormones from the pituitary are functional, and target organs and tissues are apparently capable of responding in young fish ($\leq$ 15 cm) because seasonal cycles of endocrine activity, growth, and locomotor activity are observed. Perhaps the parr-smolt metamorphosis is, in part, simply a more intense expression of an annual physiological cycle as a result of a change in tissue sensitivity or hormonal level.

Exposure to long photoperiods for extensive duration appears to terminate migration. These fish may enter a refractory period similar to that observed in reproductive cycles of some birds and fish. Evidence indicates that during the refractory period in birds neurosecretions are stored. A similar mechanism might exist in fish which demonstrate a distinct parr-smolt metamorphosis. At any rate, smaller fish which have reached the critical size by late spring have been "over-exposed" with respect to the refractory "link" and the sequence of events is stopped at that point.

While photoperiod has been identified as the major environmental factor monitoring the timing of parr-smolt metamorphosis and subsequent seaward migration, the pathway of the photoperiodic response and the nature of the neuroendocrine regulation are not well understood.

If an endogenous rhythm exists it is probably linked to the neuroendocrine system.

Sea-Water Adaptation and the Parr-Smolt Metamorphosis

Hoar (1965a) states that salmonid fishes are genetically endowed with a physiological cycle that changes temporally in the juvenile by favoring life in a marine rather than a freshwater environment. In his hypothesis there are three postulates (1965a; p. 178):

1. In all salmonids, the physiology of osmotic and ionic regulation changes seasonally;
2. The cycle is an endogenous one, which is adjusted by photoperiod; and
3. The evolution of the many migratory species of salmon has depended on modification of this basic cycle.

My study provides some data that modify the second postulate.

Constant photoperiods of different duration did not alter the developmental pattern of salinity tolerance of juvenile steelhead trout reared at constant temperature in the present study (Figures 13 and 14). The rhythmic nature of the hypo-osmoregulatory mechanism appears to be independent of the photoperiods tested. The limited observations on migratory behavior and growth suggest that changes in osmoregulatory ability do not necessarily reflect parr-smolt

metamorphosis. If sea-water adaptation is a better indicator of metamorphosis than the available observations on migratory behavior and changes in coefficient of condition for fish reared on constant photoperiods, then all groups in Experiment I demonstrated a similar chronology of metamorphosis. This interpretation disagrees with one based on migratory behavior and coefficient of condition only for fish in the 16L, LL and DD groups. Other studies have indicated that metamorphosis and sea-water adaptation are separate phenomenon in Oncorhynchus (Conte et al., 1966; Wagner et al., 1969). Atlantic salmon exposed to a reverse photoperiod (RL) did not grow as well as fish reared in a NL or 13L photoperiod when placed in sea water (30 $^{o}/_{oo}$) in the spring (Saunders and Henderson, 1970). The authors suggest that photoperiod acted through the endocrine system to affect growth patterns during and after smolting as well as certain aspects of the smolting process itself. However, there were no differences in osmotic and ionic regulatory ability among the groups.

The differences between the results in this thesis and those reported by Conte and Wagner (1965) on the extent of the regression might be related to the nutritional status of the fish. The complete regression in sea water survival might have been a result of the depletion of lipid reserves required for metamorphoic adjustments followed subsequently by catabolism of body proteins for caloric requirements of salt secretion. This energy demand may be too high to be met by

the artificial diet and feeding regimes.

For example, juvenile steelhead reared under natural temperature changes have a lower coefficient of condition than fish reared on constant temperature and show a complete loss of sea-water tolerance (Conte and Wagner, 1965). The reoccurrence of euryhalinity in the fall is associated with improved condition. In contrast, fish reared on constant temperature in Experiment I had a higher $\overline{K}$ throughout the spring regardless of photoperiod and therefore suffered only a partial regression in tolerance. During the sea-water exposure period, fish were fed the standard rearing diet once a day. It was apparent from observations that feeding activity in the aquaria was reduced. Food intake was below that required for maintenance metabolism in most cases as evidenced by the fact that there was a decrease in $\overline{K}$ during the 15-28 day test period in both fresh-water and sea water. Thus, fish entering the test period with reduced energy stores would be at a disadvantage in comparison to fish with greater lipid reserves.

More than nutrition is probably involved in the loss of sea-water tolerance as indicated by the regression in non-migrant-sized ($\leq$ 15 cm in length) fish as shown by Conte and Wagner (1965). These fish showed neither a vernal decline in condition nor changes in body constituents, if the findings of Fessler and Wagner (1969) can be applied to winter steelhead from the Alsea River. Seasonal changes in endocrine

function have been implicated in water and electrolyte regulation and might be a factor in the present study, but the picture which has emerged is far from clear (Hoar, 1951a, 1959; Fontaine, 1956; Smith, 1956; Pickford and Atz, 1957; Barr, 1965; Parry, 1966).

In summary, the development, regression, and redevelopment of the hypo-osmoregulatory mechanism was independent of the photoperiods tested. The development appears to be largely size and perhaps growth rate dependent. The regression and reactivation of the hypo-osmoregulatory mechanism might be controlled by an innate hormonal rhythm which is reinforced by the smolting process.

BIBLIOGRAPHY

Ahsan, S. N. 1966. Effects of temperature and light on the cyclical changes in the spermatogenetic activity of the Lake chub, Couesius plumbeus (Agassiz). Can. J. Zool. 44:161-171.

Akulin, V. N. 1966. Izmeneniya zhirnosti molodi krasnoi i svyaz' ikh so skatom. (Changes in fatness of young sockeye as related to their downstream migration.) Rybn. Khozy. 42(8):11-12. (FRB Transl. Ser. 716).

Ali, M. A. 1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Can. J. Zool. 37:965-996.

Baggerman, B. 1957. An experimental study of the timing of breeding and migration in the three-spined stickleback (Gasterosteus aculeatus L.). Arch. Neer. Zool. 12:105-317.

_____. 1960a. Factors in the diadromous migrations of fish. Symp. Zool. Soc. (London), 1:33-60.

_____. 1960b. Salinity preference, thyroid activity and the seaward migration of four species of Pacific salmon (Oncorhynchus). J. Fish. Res. Bd. Can. 17:295-322.

Barr, W. A. 1965. The endocrine physiology of fishes. Oceanog. and Marine Bio. Ann. Rev. 3:257-298.

Barrington, E. J. W. 1961. Metamorphic processes in fishes and lampreys. Am. Zool. 1:97-106.

Beck, S. D. 1968. Insect photoperiodism. Academic Press, Inc., New York. 288 p.

Bell, G. R. 1964. A guide to the properties, characteristics, and uses of some general anaesthetics for fish. Fish. Res. Bd. Can. Bull. 148, 4 p.

Benoit, J. 1938. Action de divers éclairements localisés dans la region orbitaire sur la gonadostimulation chez le canard mâle impubère. Croissance testiculaire provoquée par l'éclairement direct de la région hypophysaire. Compl. rend. soc. biol. 127:909-14. (Cited in: Farner, D. S. 1959. Photoperiodic

control of annual gonadal cycles in birds, p. 717-750. In R. B. Withrow [ed.] Photoperiodism and Related Phenomena in Plants and Animals. Am. Ass. Advance. Sci., Wash., D. C.

Benoit, J. 1962. Hypothalamo-hypophyseal control of the sexual activity in birds. Gen. Comp. Endocrinol., Suppl. 1:254-274.

Bertalanffy, L. von. 1960. Principles and theory of growth, p. 137-259. In W. W. Nowinski [ed.] Fundamental aspects of normal and malignant growth. Elsevier Publishing Co., New York.

Breder, C. M., and P. Rasquin. 1950. A preliminary report on the role of the pineal organ in the control of pigment cells and light reactions in recent teleost fishes Science 111:10-12.

Brown, M. E. 1957. Experimental studies on growth, p. 361-400. In M. E. Brown [ed.] The Physiology of Fishes. Vol. 1. Academic Press, Inc., New York.

Bullough, W. S. 1959. Vertebrate photostimulation, p. 641-649. In R. W. Withrow [ed.] Photoperiodism and Related Phenomena in Plants and Animals. Am. Asso. Advance. Sci., Wash., D. C.

Bünning, E. 1964. The physiologic clock. Springer-Verlag, Berlin. 145 p.

Byrne, J. E. 1968. The effects of photoperiod and temperature on the daily pattern of locomotor activity in juvenile sockeye salmon, Oncorhynchus nerka (Walbaum). Ph. D. thesis, Univ. of British Columbia. 125 p.

Cahn, P. H. 1952. Spectral effects on the growth rate and endocrine histology of the teleost, Astyanax mexicanus. Zoologica 37:33-42.

Cartwright, J. W. 1960. Steelhead propagation in British Columbia, 1954-1959. Fish and Game Branch, Dept. Rec. and Conserv., Victoria, B. C., 13 p.

Chapman, D. W. 1958. Studies on the life history of Alsea River steelhead. J. Wildl. Manage. 22:123-134.

Cloudsley-Thompson, J. L. 1961. Rhythmic activity in animal physiology and behavior. Academic Press., Inc., New York. 236 p.

Cold Spring Harbor Symposia on Quantitative Biology. 1960. Biological clocks. Vol. 25. 524 p.

Conte, F. P., and H. H. Wagner. 1965. Developement of osmotic and ionic regulation in juvenile steelhead trout Salmo gairdneri. Comp. Biochem. Physiol. 14:603-620.

Conte, F. P., H. H. Wagner, J. Fessler, and C. Gnose. 1966. Development of osmotic and ionic regulation in juvenile coho salmon Oncorhynchus kisutch. Comp. Biochem. Physiol. 18:1-15.

Corson, B. W. 1955. Four years' progress in the use of artificially controlled light to induce early spawning in brook trout. Prog. Fish-Cult. 17:99-103.

Crawford, D. R. 1930. Some considerations in the study of the effects of heat and light on fishes. Copeia (173):89-92.

Dodd, J. M. 1963. The pituitary complex, p. 161-185. In P. Eckstein and F. Knowles [ed.] Techniques in Endocrine Research. Academic Press, Inc., New York.

Dodd, J. M., and A. J. Matty. 1954. Comparative aspects of thyroid function, p. 303-356. In R. Pitt-Rivers and W. R. Trotter [ed.] The thyroid gland. Buttersworths, London, Vol. 1.

Dodd, J. M., and T. Kerr. 1963. Comparative morphology and histology of the hypothalamo-neurohypophysial system. Symp. Zool. Soc. (London), 9:5-27.

Drury, D. E., and J. G. Eales. 1968. The influence of temperature on histological and radiochemical measurements of thyroid activity in the eatern brook trout, Salvelinus fontinalis Mitchell. Can. J. Zool. 46:1-9.

Duncan, D. B. 1957. Multiple range tests for correlated and heteroscedastic means. Biometrics 13:164-176.

Duncan, R. E. 1956. Use of infrared radiation in the study of fish behavior. U. S. Fish Wildl. Serv., Spec. Sci. Rep-Fish. 170,16p.

Eales, J. G. 1963. A comparative study of thyroid function in migrant juvenile salmon. Can. J. Zool. 41:811-824.

Eales, J. G. 1964. The influence of temperature on thyroid histology and radioiodine metabolism of yearling steelhead trout, Salmo gairdneri. Can. J. Zool. 42:829-841.

_____. 1965. Factors influencing seasonal changes in thyroid activity in juvenile steelhead trout, Salmo gairdneri. Can. J. Zool. 43:719-729.

Elson, P. F. 1957. The importance of size in the change from parr to smolt in Atlantic salmon. Can. Fish-Cult. 21:1-6.

Evropeitseva, N. V. 1957. Perekhod v pokatnoe sostoianie i skat molodi lososei. (Transformation to smolt stage and downstream migration of young salmon.) Uch. Zap. Leningr. Gos. Univ. Ser. Biol. Nauk 44(228 of main Ser.):117-154. (FRB Transl. Ser, 234).

_____. 1960. Sootnoshenie protsessov rannego razvitiia gonad i perekhod v pokatnoe sostoianie u samtsov Baltiiskoyo lososia (Salmo salar L.) v prudovykh usloviiakh. (Correlation between the processes of early gonad ripening, and transformation to the seaward-migrating stage, among male Baltic salmon (Salmo salar L.) held in ponds.) Zool. Zhur., 39(5):777-779 (FRB Translation Series No. 430).

_____. 1962. Sravnitelnyi analiz protsessa desmoltifikatsii u molodi raznykh ekologicheskikh form Atlanticheskogo lososia. (Comparative analysis of the desmoltification process among the young of different ecological forms of Atlantic salmon.) Uchenye Zapiski Leningradskogo Gosudarstvennogo Universiteta, No. 311, p. 46-73. (FRB Translation Series No. 431).

Farner, D. S. 1959. Photoperiodic control of annual gonadal cycles in birds, p. 715-750. In R. B. Withrow [ed.] Photoperiodism and Related Phenomena in Plants and Animals. Am. Assoc. Advance. Sci. Wash., D. C.

_____. 1961. Comparative physiology: photoperiodicity. Ann. Rev. Physiol. 23:71-96.

_____. 1965. Circadian systems in the photoperiodic responses of vertebrates, p. 357-369. In J. Aschoff [ed.] Circadian Clocks. Proc. Feldafing Summer School. North-Holland Publishing Company, Amsterdam.

Farner, D. S., and B. K. Follett. 1966. Light and other environmental factors affecting avian reproduction. J. Anim. Sci., Suppl. 25:90-118.

Fessler, J. L., and H. H. Wagner. 1969. Some morphological and biochemical changes in steelhead trout during the parr-smolt transformation. J. Fish. Res. Bd. Can. 26:2823-2841.

Foerster, R. E. 1937. The relation of temperature to the seaward migration of young sockeye salmon (Oncorhynchus nerka). J. Biol. Bd. Can. 3:421-438.

Fontaine, M. 1954. Du determinisme physiologique des migrations. Biol. Rev. 29:390-418.

_____. 1956. The hormonal control of water and salt-electrolyte metabolism in fish. Mem. Soc. Endocrinol. 5:69-82.

Fontaine, M., J. Leloup, and M. Olivereau. 1952. La fonction thyroïdienne du jeune saumon, Salmo salar L (parr et smolt) et son intervention possible dans da migration d'avalaison. Arch. Sci. Physiol. 6:83-104.

Gorbman, A. 1959. Problems in the comparative morphology and physiology of the vertebrate thyroid gland, p. 266-282. In A. Gorbman [ed.] Comparative Endocrinology. John Wiley and Son, Inc., New York.

Gudjonsson, T. W. 1946. Age and body length at the time of seaward migration of immature steelhead trout (Salmo gairdneri Richardson) in Minter Creek Washington. M. S. Thesis, Univ. Wash., 52 p.

Hammond, J., Jr. 1954. Light regulation of hormone secretion. p. 157-206. In R. S. Harris, G. F. Marrian and K. T. Thimann [ed.] Vitamins and Hormones, Vol. 12. Academic Press, Inc., New York.

Harrington, R. W., Jr. 1959. Photoperiodism in fishes in relation to the annual sexual cycle, p. 651-667. In R. B. Withrow [ed.] Photoperiodism and related phenomena in plants and animals. Am. Assoc. Advance. Sci., Wash., D. C.

Hartman, W. L., W. R. Heard, and B. Drucker. 1967. Migratory behavior of sockeye salmon fry and smolts. J. Fish. Res. Bd. Can. 24:2069-2099.

Hazard, T. P., and R. E. Eddy. 1951. Modifications of the sexual cycle in brook trout (Salvelinus fontinalis) by control of light. Trans. Am. Fish. Soc. 80:158-162.

Henderson, N. E. 1963. Influence of light and temperature on the reproductive cycle of the eastern brook trout, Salvelinus fontinalis (Mitchell). J. Fish. Res. Bd. Can. 20:859-897.

Hickman, C. P., Jr. 1959. The osmoregulatory role of the thyroid gland in the starry flounder, Platichthys stellatus. Can. J. Zool. 37:997-1060.

Hoar, W. S. 1939a. The thyroid gland of the Atlantic salmon. J. Morph. 65:257-295.

_____. 1939b. The weight-length relationship of the Atlantic salmon. J. Fish. Res. Bd. Can. 4:441-460.

_____. 1951a. Hormones in fish. Univ. Toronto Stud., Biol. Ser. 59. 51 p.

_____. 1951b. The behavior of chum, pink and coho salmon in relation to their seaward migration. J. Fish. Res. Bd. Can. 8:241-263.

_____. 1953. Control and timing of fish migration. Biol. Rev. 28:437-452.

_____. 1957. Endocrine organs, p. 245-285. In M. E. Brown [ed.] The Physiology of Fishes. Vol. 1 Academic Press, Inc., New York.

_____. 1958a. The evolution of migratory behavior among juvenile salmon of the genus Oncorhynchus. J. Fish. Res. Bd. Can. 15:391-428.

_____. 1958b. The analysis of behaviour of fish, p. 99-111. In P. A. Larkin [ed.] The Investigation of Fish-Power Problems. H. R. MacMillian Lectures in Fisheries, Univ. of British Columbia.

_____. 1959. Endocrine factors in the ecological adaptation of fishes, p. 1-23. In A. Gorbman [ed.] Comparative Endocrinology. John Wiley and Son, Inc., New York.

Hoar, W. S. 1963. The endocrine regulation of migratory behaviour in anadromous teleosts. Proc. XVI Int. Congr. Zool. 3:14-20.

_____. 1965a. The endocrine system as a chemical link between the organism and its environment. Trans. Roy. Soc. Can. Ser. 4, Sec. III, 3:175-200.

_____. 1965b. Comparative physiology: hormones and reproduction in fishes. Ann. Rev. Physiol. 27:51-70.

Hoar, W. S., and G. M. Bell. 1950. The thyroid gland in relation to the seaward migration of Pacific salmon. Can. J. Res. 28: 126-136.

Hoar, W. S., M. H. A. Keenleyside, and R. G. Goodall. 1957. Reactions of juvenile Pacific salmon to light. J. Fish. Res. Bd. Can. 14:815-830.

Honma, Y., and E. Tamura. 1965. Studies on the Japanese chars, the iwana (Genus Salvelinus). II. The hypothalamic neurosecretory system of the Nikkô-iwana, Salvelinus leucomaenis pluvius (Hilgendorf). Bull. Jap. Soc. Sci. Fish. 31:878-887.

_____. 1967. Studies on Japanese chars of the Genus Salvelinus. IV. The caudal neurosecretory system of the nikkô-iwana, Salvelinus leucomaenis pluvius (Hilgendorf). Gen. Comp. Endocrinol. 9:1-9.

Honma, Y., and A. Suzuki. 1968. Studies on the endocrine glands of the salmonid fish, the ayu, Plecoglossus altivelis Temminck et Schlegel - VII. The hypothalamic neurosecretory system of the Koayu exposed to the artificial photoperiods. Jap. J. Icthy. 15:11-27.

Hoover, E. E., and H. E. Hubbard. 1937. Modification of the sexual cycle in trout by control of light. Copeia 4:206-210.

Houston, A. H. 1959. Osmoregulatory adaptation of steelhead trout (Salmo gairdneri Richardson) to sea water. Can. J. Zool. 37: 729-748.

_____. 1960. Variations in the plasma-level of chloride in hatchery-reared yearling Atlantic salmon during parr-smolt transformation and following transfer into sea-water. Nature 185:632-633.

Houston, A. H. 1961. Influence of size upon the adaptation of steelhead trout (Salmo gairdneri) and chum salmon (Oncorhynchus keta) to sea water. J. Fish. Res. Bd. Can. 18:401-415.

Houston, A. H., and L. T. Threadgold. 1963. Body fluid regulation in smolting Atlantic salmon. J. Fish. Res. Bd. Can. 20:1355-1369.

Humason, G. L. 1962. Animal tissue techniques. W. H. Freeman and Co., San Francisco. 468 p.

Johnston, C. E., and J. G. Eales. 1967. Purines in the integument of the Atlantic salmon (Salmo salar) during parr-smolt transformation. J. Fish. Res. Bd. Can. 24:955-964.

_____. 1968. Influence of temperature and photoperiod on guanine and hypoxanthine levels in skin and scales of Atlantic salmon (Salmo salar) during parr-smolt transformation. J. Fish. Res. Bd. Can. 25:1901-1909.

_____. 1970. Influence of body size on silvering of Atlantic salmon (Salmo salar) at parr-smolt transformation. J. Fish. Res. Bd. Can. 27:983-987.

Kizevetter, I. V. 1948. Ob zmeneniyakh khimicheskogo sostava tela krasnoi (nerki). (Changes in chemical composition of the body of red (sockeye) salmon.) Izv. Tikhookeans. Nauchn. Issled. Inst. Rybn. Khoz. i Okeanogr. 27:29-42. (Transl. in Pacific salmon. Office Tech. Serv. 60-51139, U. S. Dept. Commerce, Washington, D. C. p. 86-100).

Kramer, J. van de, and A. F. Schreurs. 1959. The pituitary gland of the brook lamprey (Lampetra planeri) before, during and after metamorphosis (a preliminary, qualitative investigation). Z. Zellforsch. mikrosk. Anat. 49:605-630.

Klein, C. 1967. Etude du développement du système hypothalamo-hypophysaire chez le Saumon Salmo salar L. Gen. and Comp. Endocrinol. 8:368-377. (in French, English abstr.)

Kubo, T. 1959. A preliminary study of the effects of environmental factors upon the attainment of the smolt stage in juvenile Masu salmon. Sci. Rep. Hokkaido Salmon Hatchery, 14:15-19. (in Japanese, English abstr.)

Kubo, T. 1965. On the influence of temperature upon the acceleration of smolt-transformation in juvenile Masu salmon (Oncorhynchus masou). Sci. Rep. Hokkaido Salmon Hatchery. 19:25-32. (in Japanese, English abstr.)

Laird, A. K. 1966. Postnatal growth of birds and mammals. Growth 30:349-363.

LeBrasseur, R. J., and R. R. Parker. 1964. Growth rate of central British Columbia pink salmon (Oncorhynchus gorbuscha). J. Fish. Res. Bd. Can. 21:1101-1128.

Leloup J., and M. Fontaine. 1960. Iodine metabolism in lower vertebrates. Ann. N. Y. Acad. Sci. 86:316-353.

Lichtenheld, R. W. 1966. Effect of light, temperature and gamma radiation on the locomotor activity of juvenile steelhead trout (Salmo gairdneri). Ph. D. thesis, Univ. Wash., 237 p.

Lynn, W. G., and H. E. Wachowski. 1951. The thyroid gland and its functions in cold-blooded vertebrates. Quart. Rev. Biol. 26: 123-168.

Malikova, E. M. 1957. Biokhimicheskaia otsenka molodi lososia pri perekhode v sostoianie, blizkoe k pokatnomu, i pri zadershke serebrianok v presnoi vode. (Biochemical analysis of young salmon at the time of their transformation to a condition close to the smolt stage, and during retention of smolts in freshwater.) Tr. Latv. Otd. VNIRO 2:241-255. (FRB Transl. Ser. 232).

Matty, A. J. 1960. Thyroid cycles in fish. Symp. Zool. Soc. (London), 2:1-15.

McInerney, J. E. 1961. An experimental study of salinity preference and related migratory behavior of juvenile Pacific salmon. M. S. thesis, Univ. of British Columbia. 73 p.

_____. 1964. Salinity preference: an orientation mechanism in salmon migration. J. Fish. Res. Bd. Can. 21:995-1018.

McInerney, J. E. and D. O. Evans. 1970. Action spectrum of the photoperiod mechanism controlling sexual maturation in the threespine stickleback, Gasterosteus aculeatus. J. Fish. Res. Bd. Can. 27:749-763.

Munz, F. W., and D. D. Beatty. 1965. A critical analysis of the visual pigments of salmon and trout. Vision Res. 5:1-17.

Otto, R. G., and J. E. McInerney. 1970. Development of salinity preference in pre-smolt coho salmon, Oncorhynchus kisutch. J. Fish. Res. Bd. Can. 27:793-800.

Parry, G. 1958. Size and osmoregulation in salmonid fishes. Nature 181:1218-1219.

_____. 1960. The developement of salinity tolerance in the salmon, Salmo salar (L.) and some related species. J. Exp. Biol. 37:425-34.

_____. 1961. Osmotic and ionic changes in blood and muscle of migrating salmonids. J. Exp. Biol. 38:411-427.

_____. 1966. Osmotic adaptation in fishes. Biol. Rev. 41:392-444.

Pickford, G. E., and J. W. Atz. 1957. The physiology of the pituitary gland of fishes. N. Y. Zool. Soc., New York. 613 p.

Pinder, L. J., and J. G. Eales. 1969. Seasonal buoyancy changes in Atlantic salmon (Salmo salar) parr and smolt. J. Fish. Res. Bd. Can. 26:2093-2100.

Pinhorn, A. T., and C. W. Andrews. 1965. Effects of photoperiods on the behavior of juvenile Atlantic salmon (Salmo salar L.) in vertical and horizontal light gradients. J. Fish. Res. Bd. Can. 22:369-383.

Robertson, O. H. 1948. The occurrence of increased activity of the thyroid gland in rainbow trout at the time of transformation from parr to silvery smolt. Physiol. Zool. 21:282-295.

Sathyanesan, A. G., and W. Chavin. 1966. Effect of whole-body irradiation on the preotico-hypophyseal neurosecretory system and hypophysis of the goldfish Carassius auratus L. Radiat. Res. 29:100-113.

Saunders, R. L., and E. B. Henderson. 1965. Precocious sexual development in male post-smolt Atlantic salmon reared in the laboratory. J. Fish. Res. Bd. Can. 22:1567-1570.

Saunders, R. L., and E. B. Henderson. 1970. Influence of photoperiod on smolt development and growth of Atlantic salmon (Salmo salar). J. Fish. Res. Bd. Can. 27:1295-1311.

Schales, O., and S. S. Schales. 1941. A simple and accurate method for the determination of chloride in biological fluids. J. Biol. Chem. 140:879-884.

Scharrer, B. 1959. The role of neurosecretion in neuroendocrine integration, p. 134-148. In A. Gorbman [ed.] Comparative Endocrinology. John Wiley and Son, Inc., New York.

Shapovalov, L., and A. C. Taft. 1954. The life history of the steelhead rainbow trout, Salmo gairdneri gairdneri, and silver salmon, Oncorhynchus kisutch, with special reference to Waddel Creek, California and recommendations regarding their management. Calif. Dept. Fish and Game, Fish Bull. 98. 375 p.

Shiraishi, Y. 1965a. The influence of photoperiodicity on the maturation of ayu-fish, Plecoglossus altivelis. IV. The effect of wave length and of conversion of darkness and light on the maturation [in Japanese, English summary]. Bull. Freshwater Fish. Res. Lab. 15:77-84.

_____. 1965b. The influence of photoperiodicity on the maturation of ayu-fish, Plecoglossus altivelis V. The effect of removal of eye on the maturation [in Japanese, English summary]. Bull. Freshwater Fish. Res. Lab. 15:85-90.

Smith, D. C. W. 1956. The role of the endocrine organs in the salinity tolerance of trout. Mem. Soc. Endocrinol. 5:83-101.

Stahl, A., and C. Leray. 1962. The relation between diencephalic neurosecretion and the adenohypophysis in teleost fishes, p. 149-163. In H. Heller and R. B. Clark [ed.] Neurosecretion. Academic Press, Inc., New York.

Stott, B. 1968. Marking and tagging, p. 78-92. In W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.

Swift, D. R. 1959 Seasonal variations in the activity of the thyroid gland of yearling brown trout (Salmo trutta Linn.). J. Exp. Biol. 36:120-125.

Swift, D. R. 1960. Cyclical activity of the thyroid gland of fish in relation to environmental changes. Symp. Zool. Soc. (London), 2:17-27.

Turner, C. 1966. General Endocrinology (4th ed.). W. B. Saunders Co. Philadelphia. 579 p.

Vanstone, W. E., and J. R. Markert. 1968. Some morphological and biochemical changes in coho salmon Oncorhynchus kisutch, during parr-smolt transformation. J. Fish. Res. Bd. Can. 25:2403-2418.

Wagner, H. H. 1968. Effect of stocking time on survival of steelhead trout, Salmo gairdnerii, in Oregon. Trans. Amer. Fish. Soc. 97:374-379.

_____ 1969. Effect of stocking location of juvenile steelhead trout, Salmo gairdnerii, on adult catch. Trans. Amer. Fish. Soc. 98:27-34.

Wagner, H. H., R. L Wallace, and H. J. Campbell. 1963. The seaward migration and return of hatchery-reared steelhead trout, Salmo gairdneri Richardson in the Alsea River, Oregon. Trans. Amer. Fish. Soc. 92:202-210.

Wagner, H. H , F. P. Conte, and J L. Fessler. 1969. Development of osmotic and ionic regulation in two races of chinook salmon Oncorhynchus tshawytscha. Comp. Biochem. Physiol. 29:325-341.

Webb, H. M., and F. A. Brown, Jr. 1959. Timing long-cycle physiological rhythms. Physiol. Rev. 39:127-161.

Weisbart, M. 1968. Osmotic and ionic regulation in embryos, alevins, and fry of the five species of Pacific salmon. Can. J. Zool. 46:385-397.

Whitney, R. R. 1969. Schooling of fishes relative to available light. Trans. Amer. Fish. Soc. 98:497-504.

Wiebe, J. P. 1968. The effects of temperature and daylength on the reproductive physiology of the viviparous seaperch, Cymatogaster aggregata Gibbons. Can. J. Zool. 46:1207-1219.

Withrow, R. B. 1959. A kinetic analysis of photoperiodism, p. 439-471. In R. B. Withrow [ed.] Photoperiodism and related phenomena in plants and animals. Amer. Assoc. Advance. Sci., Wash., D. C.

Wolfson, A. 1964a. Animal photoperiodism, p. 1-49. In A. C. Giese [ed.] Photophysiology. Vol. 2. Action of light on animals and microorganisms; Photobiochemical mechanisms; Bioluminescence. Academic Press, Inc., New York.

_____. 1964b. Role of day length and the hypothalamo-hypophysial system in the regulation of annual reproductive cycles. Proc. 2d Int. Congr. Endocrinol. (London). Excerpta Medica Found. Int. Congr. Series 83, Part I:183-187.

Wurtman, R. J. 1967. Effects of light and visual stimuli on endocrine function, p. 19-59. In L. Martini and W. F. Ganong [ed.] Neuroendocrinology. Vol. II. Academic Press, Inc., New York.

APPENDICES

APPENDIX I.

Schedule for manual adjustments for automatic timers (Model 4005-0SZ-Astro Dial) for accelerated and decelerated photoperiods used in Experiment II.

On this date	Accelerated timer should read	Decelerated timer should read
June 2 (1967)	June 4	June 2
June 9	June 13	June 8
June 16	June 21	June 14
June 23	June 30	June 20
June 30	July 9	June 26
July 7	July 17	July 2
July 14	July 26	July 8
July 21	August 4	July 14
July 28	August 12	July 20
August 4	August 21	July 26
August 11	August 30	August 1
August 18	September 7	August 7
August 25	September 16	August 13
September 1	September 25	August 19
September 8	October 3	August 25
September 15	October 12	August 31
September 22	October 21	September 6
September 29	October 29	September 12
October 6	November 7	September 18
October 13	November 16	September 24
October 20	November 24	September 30
October 27	December 3	October 6
November 3	December 12	October 12
November 10	December 20	October 18
November 17	December 29	October 24
November 24	January 6	October 30
December 1	January 15	November 5
December 8	January 23	November 11
December 15	February 1	November 17
December 22	February 9	November 23
December 29	February 18	November 28
January 5 (1968)	February 27	December 4
January 12	March 7	December 10
January 19	March 16	December 16
January 26	March 25	December 22
February 2	April 2	December 27
February 9	April 11	January 2
February 16	April 20	January 8
February 23	April 28	January 14
March 1	May 5	January 20
March 8	May 14	January 26
March 15	May 23	February 1

Appendix I continued

On this date	Accelerated timer should read	Decelerated timer should read
March 22 (1968)	May 31	February 7
March 29	June 9	February 13
April 5	June 18	February 19
April 12	June 26	February 25
April 19	July 4	March 3
April 26	July 13	March 9
May 3	July 21	March 15
May 10	July 30	March 21
May 17	August 6	March 27
May 24	August 13	April 2
May 31	August 20	April 8
June 7	August 27	April 14
June 14	September 3	April 20
June 21	September 10	April 26
June 27	September 17	May 1

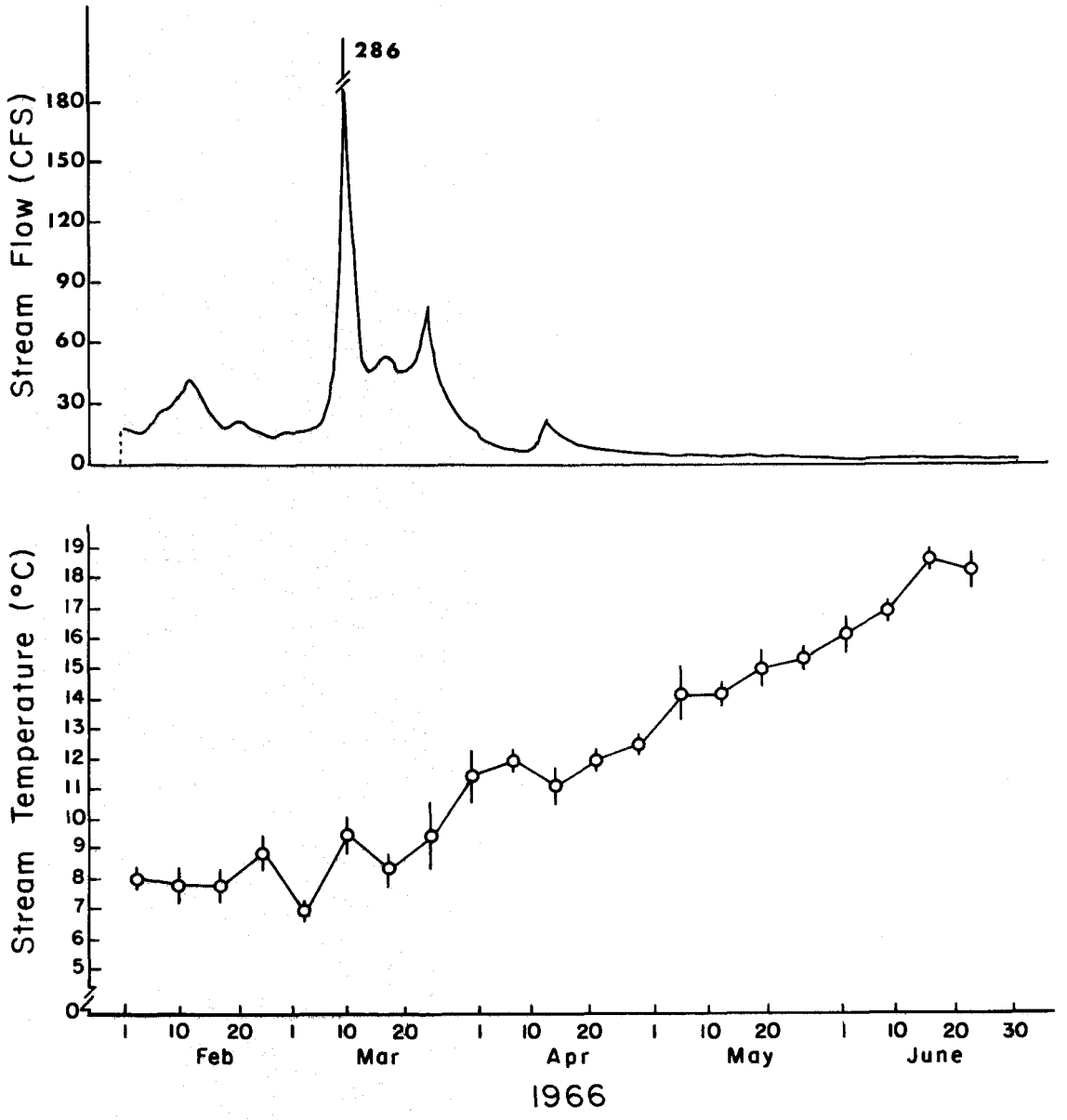
APPENDIX II.

Schedule for adjusting temperatures to simulate normal, accelerated, and decelerated cycles in Experiment II.

Mean temperature for specified period of time		Time Period		
		Normal	Accelerated	Decelerated
(°C)	(°F)			
13.6	56.5	June 1-15 (1967)	June 1-12	June 1-18
15.8	60.5	June 16-30	June 13-25	June 19-July 6
17.2	63.0	July 1-15	June 26-July 7	July 7-July 24
18.6	65.5	July 16-31	July 8-July 20	July 25-Aug. 11
18.3	65.0	Aug. 1-15	July 21-Aug. 1	Aug. 12-Aug. 29
17.8	64.0	Aug. 16-31	Aug. 2-Aug. 14	Aug. 30-Sept. 16
16.4	61.5	Sept. 1-15	Aug. 15-Aug. 26	Sept. 17-Oct. 4
15.0	59.0	Sept. 16-30	Aug. 27-Sept. 8	Oct. 5-Oct. 22
15.8	60.5	Oct. 1-15	Sept. 9-Sept. 20	Oct. 23-Nov. 9
10.8	51.5	Oct. 16-31	Sept. 21-Oct. 3	Nov. 10-Nov. 27
9.2	48.5	Nov. 1-15	Oct. 4-Oct. 15	Nov. 28-Dec. 15
8.9	48.0	Nov. 16-30	Oct. 16-Oct. 28	Dec. 16-Jan. 2
8.1	46.5	Dec. 1-15	Oct. 29-Nov. 9	Jan. 3-Jan. 20
8.1	46.5	Dec. 16-31	Nov. 10-Nov. 22	Jan. 21-Feb. 7
7.2	45.0	Jan. 1-15 (1968)	Nov. 23-Dec. 4	Feb. 8-Feb. 25
6.9	44.5	Jan. 16-31	Dec. 5-Dec. 17	Feb. 26-Mar. 15
8.6	47.5	Feb. 1-15	Dec. 18-Dec. 29	Mar. 16-Apr. 2
8.1	46.5	Feb. 16-28	Dec. 30-Jan. 11	Apr. 3-Apr. 20
7.8	46.0	Mar. 1-15	Jan. 12-Jan. 23	Apr. 21-May 8
8.9	48.0	Mar. 16-31	Jan. 24-Feb. 5	May 9-May 26
9.7	49.5	Apr. 1-15	Feb. 6-Feb. 17	May 27-June 13
9.7	49.5	Apr. 16-30	Feb. 18-Mar. 2	June 14-July 1
10.3	50.5	May 1-15	Mar. 3-Mar. 14	
12.2	54.0	May 16-31	Mar. 14-Mar. 29	
13.6	56.5	June 1-15	Mar. 30-Apr. 13	
15.8	60.5	June 16-31	Apr. 14-Apr. 28	
17.2	63.0	July 1-15	Apr. 29-May 13	
18.6	65.5	July 16-31	May 14-May 28	
18.3	65.0	Aug. 1-15	May 29-June 12	
17.8	64.0	Aug. 16-31	June 13-June 30	

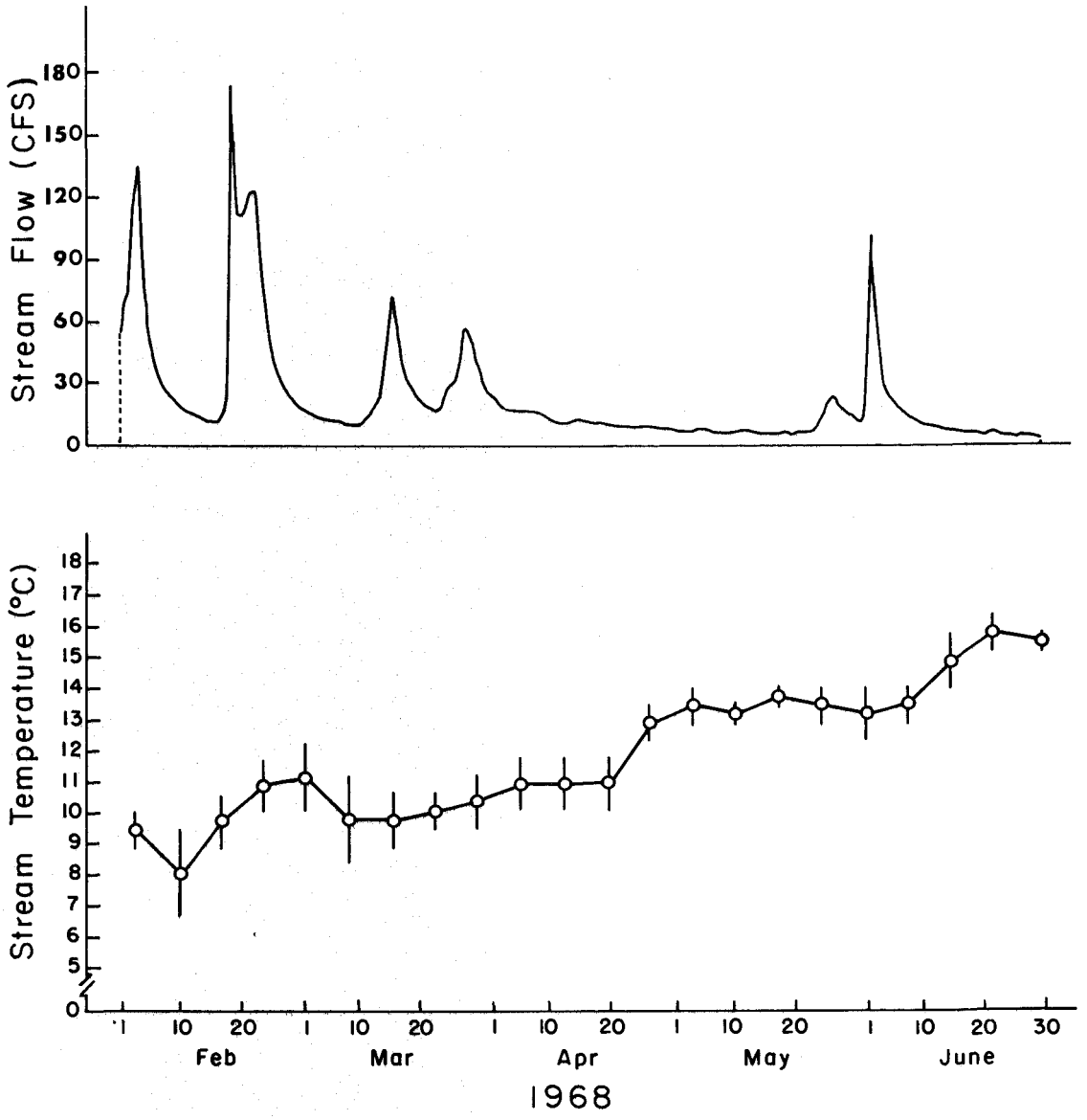
APPENDIX III.

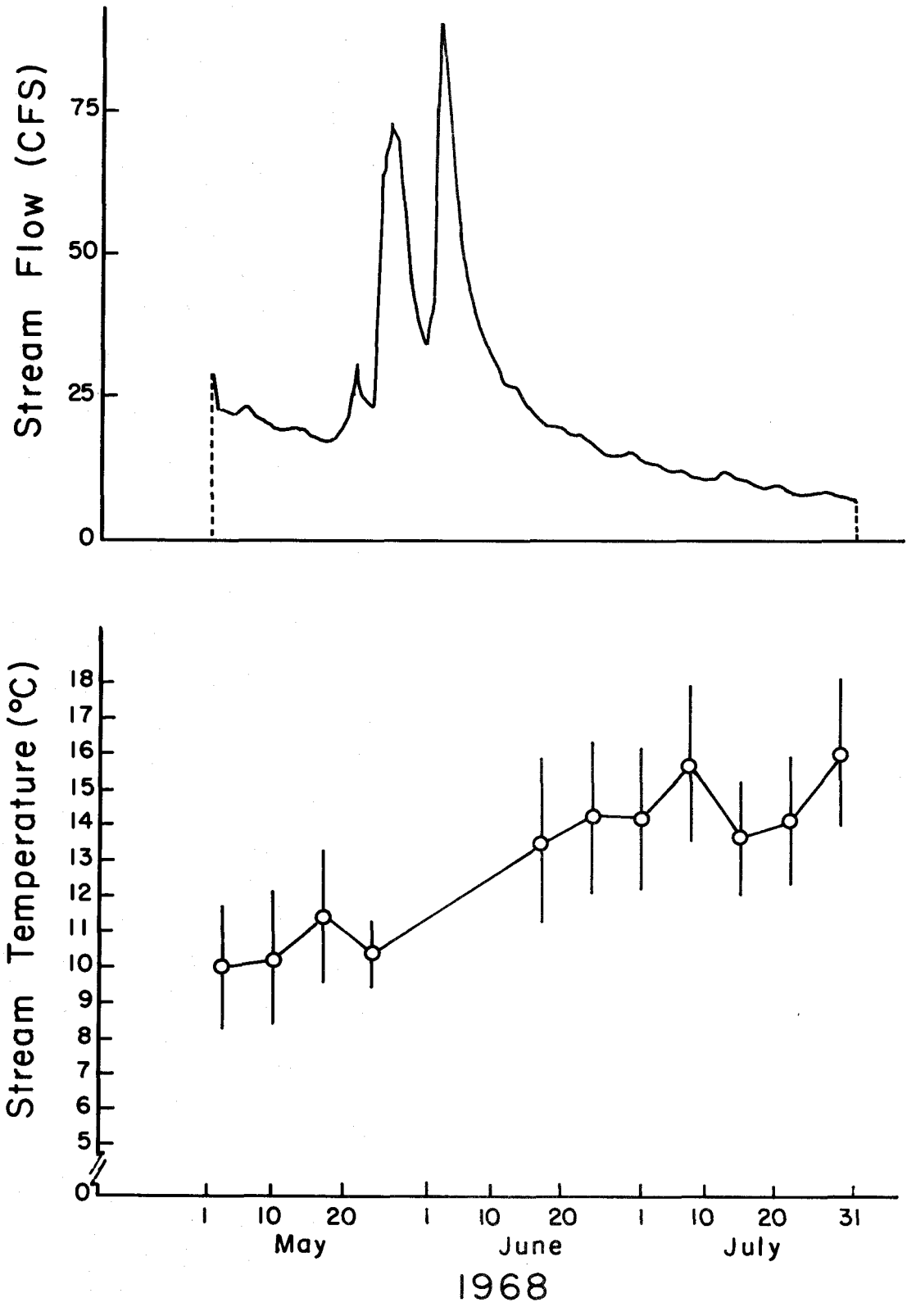
Mean weekly temperatures and daily mean flows for Lint Creek from February through June 1966. Flows are estimated and should only be used as a guide to the occurrence of freshets. Mean temperature is designated by ϕ , where the vertical bar indicates mean maximum and minimum temperature.


286
Stream Flow (CFS)
180
150
120
90
60
30
0
Stream Temperature (°C)
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
0
1
10
20
1
10
20
1
10
20
1
10
20
1
10
20
30
Feb
Mar
Apr
May
June
1966

APPENDIX IV.

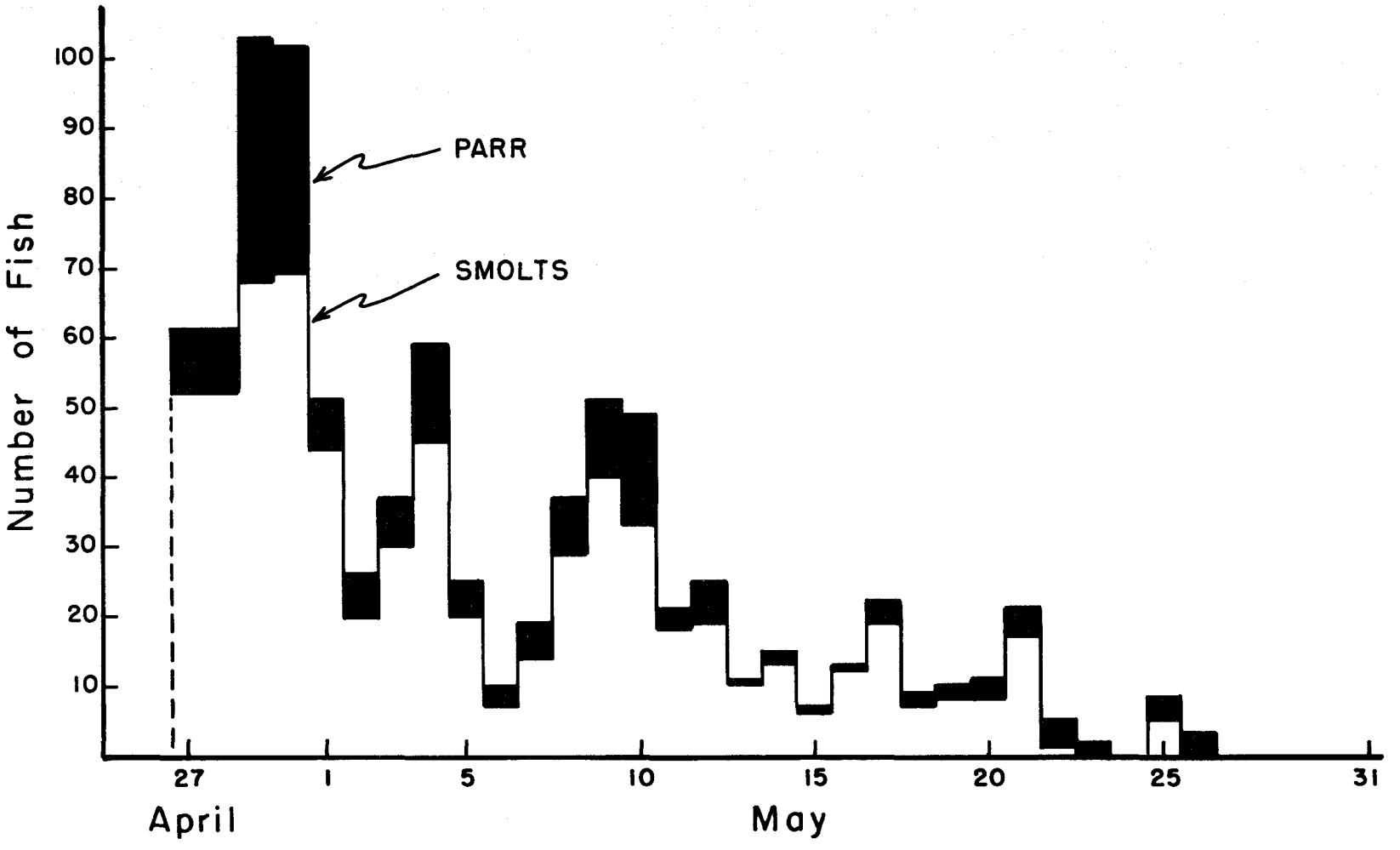
Mean weekly temperatures and daily mean flows for Lint Creek from February through June 1968. Flows are estimated and should only be used as a guide to the occurrence of freshets. Mean temperature is designated by ϕ, where the vertical bar indicates mean maximum and minimum temperature.


Stream Flow (CFS)
180
150
120
90
60
30
0
Stream Temperature (°C)
18
17
16
15
14
13
12
11
10
9
8
7
6
5
0
1
10
20
1
10
20
1
10
20
1
10
20
1
10
20
30
Feb
Mar
Apr
May
June
1968


Stream Flow (CFS)
75
50
25
0
Stream Temperature (°C)
18
17
16
15
14
13
12
11
10
9
8
7
6
5
0
1
10
20
1
10
20
1
10
20
31
May
June
July
1968

APPENDIX VI.

Pattern of downstream migration of stream-reared juvenile steelhead trout on Crooked Creek. Trapping was initiated April 26 and terminated on July 29, 1968. Fish movement by the weir from May 26 to June 12 was not monitored. No movement of stream-reared steelhead occurred from June 13 to July 29, 1968.


Number of Fish
100
90
80
70
60
50
40
30
20
10
PARR
SMOLTS
27
1
5
10
15
20
25
31
April
May

APPENDIX VII.

The mean length, weight, and coefficient of condition of experimental fish from the June 13 release captured near the release site on Crooked Creek, August 6, 1968.

Mean length (cm)	Range (cm)	Mean weight (g)	Range (g)	Mean coefficient of condition	Range	Sample size
21.4	17.6-23.7	106.3	55.0-162.0	1.052	.867-1.230	25

APPENDIX VIII.

Growth statistics of juvenile steelhead trout which were introduced into controlled photoperiods on July 11, 1965 (Lot A) in Experiment I.

Treatment[a]	Date	Age[b]	Mean Length (cm)	Mean Weight (g)	K	Sample size
SL-CT	5/26/65	41	3.03 ± 0.03[c]	0.21 ± 0.1	0.734	25
	6/10/65	56	3.44 ± 0.04	0.34 ± 0.01	0.822	25
	7/13/65	89	4.27 ± 0.08	0.79 ± 0.05	0.935	60
	8/3/65	110	5.15 ± 0.08	1.48 ± 0.07	1.000	101
	8/30/65	137	6.86 ± 0.09	3.34 ± 0.13	0.975	100
	9/30/65	168	8.20 ± 0.11	5.98 ± 0.24	1.027	100
	11/2/65	201	9.44 ± 0.15	9.29 ± 0.45	1.024	100
	11/30/65	229	10.5 ± 0.2	12.9 ± 0.6	1.022	100
	12/30/65	259	11.6 ± 0.2	18.2 ± 1.0	1.047	100
	2/10/66	301	14.6 ± 0.2	36.1 ± 1.3	1.107	100
	3/3/66	323	15.4 ± 0.2	43.8 ± 1.9	1.110	100
	4/12/66	363	17.7 ± 0.3	62.2 ± 2.5	1.071	75
	5/13/66	393	19.5 ± 0.3	83.2 ± 3.4	1.075	75
	6/17/66	428	20.6 ± 0.4	104.9 ± 6.1	1.123	50
	7/26/66	467	23.1 ± 0.4	146.5 ± 6.6	1.142	50
	8/31/66	503	25.3 ± 0.8	197.1 ± 15.6	1.146	21
NL-CT	8/3/65	110	5.39 ± 0.09	1.70 ± 0.10	1.019	70
	8/30/65	137	7.02 ± 0.02	3.60 ± 0.13	0.998	100
	9/30/65	168	8.36 ± 0.11	6.84 ± 0.26	1.036	100
	11/2/65	201	10.3 ± 0.2	12.3 ± 0.5	1.066	100
	11/30/65	229	11.2 ± 0.2	16.1 ± 0.8	1.042	100
	12/30/65	259	13.0 ± 0.2	24.9 ± 1.0	1.076	100
	2/10/66	301	14.2 ± 0.2	33.8 ± 1.4	1.101	100
	3/3/66	323	15.9 ± 0.2	46.9 ± 1.8	1.096	100
	4/12/66	363	18.1 ± 0.2	65.4 ± 2.3	1.068	75
	5/13/66	393	19.1 ± 0.3	73.4 ± 3.1	1.001	75
	6/17/66	428	19.8 ± 0.3	80.9 ± 4.1	0.994	50
	7/26/66	467	20.9 ± 0.3	103.4 ± 5.8	1.075	49
	8/31/66	503	24.0 ± 0.7	167.6 ± 12.9	1.140	24

[a] See abbreviations on pages 20-21.

[b] Age in days post-hatching.

[c] ± 1 Standard error.

Appendix VIII. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
DD-CT	7/13/65	27	3.40 ± 0.03	0.34 ± 0.01	0.861	32
	8/3/65	58	3.92 ± 0.05	0.59 ± 0.03	0.947	50
	8/30/65	85	4.69 ± 0.06	1.14 ± 0.04	1.055	70
	9/30/65	116	5.91 ± 0.08	2.14 ± 0.09	0.989	75
	11/2/65	149	6.44 ± 0.07	2.95 ± 0.10	1.058	100
	11/30/65	177	8.01 ± 0.08	5.80 ± 0.17	1.096	100
	12/30/65	207	9.83 ± 0.11	11.23 ± 0.39	1.143	75
	2/10/66	249	11.4 ± 0.1	18.1 ± 0.5	1.179	100
	3/3/66	270	12.7 ± 0.1	24.4 ± 0.8	1.150	80
	4/12/66	310	13.6 ± 0.2	29.2 ± 1.0	1.122	75
	5/13/66	341	15.0 ± 0.2	38.8 ± 1.3	1.117	75
	6/17/66	376	15.8 ± 0.2	47.2 ± 1.8	1.167	49
	7/26/66	415	16.9 ± 0.2	55.6 ± 2.1	1.128	49
	8/31/66	451	18.7 ± 0.3	77.2 ± 3.5	1.143	43
8.5L-CT	8/3/65	110	5.14 ± 0.07	1.47 ± 0.07	1.014	95
	8/30/65	137	6.57 ± 0.08	3.02 ± 0.12	1.016	100
	9/30/65	168	8.18 ± 0.10	6.00 ± 0.24	1.046	100
	11/2/65	201	9.50 ± 0.12	9.49 ± 0.41	1.044	100
	11/30/65	229	10.1 ± 0.2	11.6 ± 0.6	1.031	100
	12/30/65	259	12.4 ± 0.2	22.1 ± 1.0	1.075	100
	2/10/66	301	13.8 ± 0.2	30.8 ± 1.3	1.111	100
	3/3/66	323	14.9 ± 0.2	40.2 ± 1.6	1.157	100
	4/12/66	363	16.8 ± 0.2	55.6 ± 2.4	1.111	75
	5/13/66	393	18.2 ± 0.4	73.1 ± 4.1	1.126	65
	6/17/66	428	19.5 ± 0.4	83.9 ± 5.0	1.066	50
	7/26/66	467	20.9 ± 0.5	110.9 ± 7.4	1.130	48
	8/31/66	503	22.4 ± 0.6	135.5 ± 11.6	1.101	35
12L-CT	8/3/65	110	5.03 ± 0.08	1.40 ± 0.09	1.018	77
	8/30/65	137	6.72 ± 0.09	3.33 ± 0.14	1.035	100
	9/30/65	168	8.35 ± 0.10	6.46 ± 0.24	1.057	100
	11/2/65	201	10.2 ± 0.2	12.1 ± 0.6	1.062	100
	11/30/65	229	11.5 ± 0.2	17.1 ± 0.7	1.034	100
	12/30/65	259	11.6 ± 0.2	18.4 ± 0.9	1.083	100
	2/10/66	301	14.7 ± 0.2	36.9 ± 1.2	1.113	100
	3/3/66	323	16.4 ± 0.2	50.6 ± 1.6	1.101	100
	4/12/66	363	17.1 ± 0.3	59.6 ± 2.6	1.108	75
	5.13/66	393	19.0 ± 0.3	79.1 ± 3.4	1.101	75
	6/17/66	428	20.4 ± 0.4	93.6 ± 4.9	1.051	50
	7/26/66	467	21.8 ± 0.5	122.5 ± 7.9	1.098	50
	8/31/66	503	23.8 ± 0.8	161.4 ± 14.7	1.115	21

Appendix VIII. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
16L-CT	8/3/65	110	5.35 ± 0.09	1.64 ± 0.09	1.008	70
	8/30/65	137	6.78 ± 0.09	3.24 ± 0.14	0.978	100
	9/30/65	168	8.26 ± 0.10	6.17 ± 0.24	1.043	100
	11/2/65	201	10.1 ± 0.1	11.1 ± 0.5	1.040	100
	11/30/65	229	11.0 ± 0.2	15.1 ± 0.7	1.047	100
	12/30/65	259	12.2 ± 0.2	21.1 ± 1.0	1.078	100
	2/10/66	301	13.9 ± 0.2	33.0 ± 1.4	1.148	100
	3/3/66	323	15.6 ± 0.2	45.0 ± 1.7	1.129	100
	4/12/66	363	16.6 ± 0.2	53.9 ± 2.4	1.126	75
	5/13/66	393	18.4 ± 0.2	73.2 ± 3.0	1.123	75
	6/17/66	428	18.9 ± 0.4	80.4 ± 5.3	1.108	50
	7/26/66	467	20.8 ± 0.3	103.6 ± 5.0	1.108	50
	8/31/66	503	22.2 ± 0.6	127.1 ± 9.7	1.115	24
LL-CT	8/3/65	110	5.12 ± 0.06	1.40 ± 0.05	1.020	50
	8/30/65	137	6.82 ± 0.08	3.35 ± 0.11	1.013	100
	9/30/65	168	8.31 ± 0.10	6.10 ± 0.24	1.012	100
	11/2/65	201	9.6 ± 0.12	9.59 ± 0.37	1.036	100
	11/30/65	229	10.8 ± 0.2	14.3 ± 0.7	1.050	100
	12/30/65	259	12.2 ± 0.2	20.9 ± 0.9	1.087	100
	2/10/66	301	13.8 ± 0.2	31.4 ± 1.3	1.118	100
	3/3/66	323	16.0 ± 0.2	48.4 ± 1.5	1.143	100
	4/12/66	363	16.6 ± 0.2	52.7 ± 2.2	1.102	75
	5/13/66	393	17.5 ± 0.2	62.4 ± 2.5	1.114	75
	6/17/66	428	18.8 ± 0.3	75.7 ± 3.5	1.096	50
	7/26/66	467	21.6 ± 0.4	115.8 ± 6.2	1.101	47
	8/31/66	503	21.3 ± 0.4	106.9 ± 7.0	1.072	25

APPENDIX IX.

Growth statistics of juvenile steelhead trout which were introduced into controlled photoperiods on December 22, 1965 (Lot B) in Experiment I.

Treatment[a]	Date	Age[b]	Mean Length (cm)	Mean Weight (g)	K	Sample size
NL-CT	2/10/66	301	14.5 ± 0.2[c]	36.6 ± 1.7	1.114	75
	3/3/66	323	15.8 ± 0.3	46.6 ± 2.9	1.097	50
	4/12/66	363	18.2 ± 0.3	65.9 ± 2.7	1.058	50
	5/13/66	393	20.3 ± 0.3	86.7 ± 3.4	1.007	50
	6/17/66	428	20.9 ± 0.4	97.2 ± 5.9	1.012	35
	7/26/66	467	22.5 ± 0.4	130.8 ± 7.2	1.103	35
	8/31/66	503	24.0 ± 0.7	167.6 ± 12.9	1.140	24
8.5L-CT	2/10/66	301	14.0 ± 0.2	32.7 ± 1.6	1.089	75
	3/3/66	323	15.6 ± 0.4	47.4 ± 3.2	1.139	50
	4/12/66	363	17.7 ± 0.4	65.8 ± 3.3	1.142	50
	5/13/66	393	19.6 ± 0.3	87.1 ± 4.1	1.112	50
	6/17/66	428	21.9 ± 0.4	116.3 ± 6.1	1.066	35
	7/26/66	467	23.2 ± 0.4	145.8 ± 8.4	1.102	49
	8/31/66	503	24.6 ± 0.4	167.7 ± 8.5	1.088	34
12L-CT	2/10/66	301	15.0 ± 0.3	40.6 ± 1.9	1.118	75
	3/3/66	323	17.9 ± 0.4	66.8 ± 3.5	1.100	50
	4/12/66	363	18.2 ± 0.4	70.4 ± 4.5	1.077	50
	5/13/66	393	20.7 ± 0.3	101.1 ± 4.9	1.100	50
	6/17/66	428	22.5 ± 0.4	125.3 ± 7.1	1.065	35
	7/26/66	467	23.6 ± 0.5	157.4 ± 9.8	1.135	34
	8/31/66	503	25.2 ± 0.7	184.5 ± 13.4	1.108	17
16L-CT	2/10/66	301	14.4 ± 0.3	34.1 ± 1.6	1.073	75
	3/3/66	323	16.3 ± 0.4	51.9 ± 2.9	1.118	50
	4/12/66	363	18.2 ± 0.4	73.0 ± 4.6	1.127	50
	5/13/66	393	19.9 ± 0.4	92.8 ± 5.0	1.122	50
	6/17/66	428	20.8 ± 0.5	105.3 ± 7.8	1.096	35
	7/26/66	467	22.7 ± 0.6	140.5 ± 11.1	1.117	32
	8/31/66	503	23.2 ± 0.6	147.4 ± 12.4	1.125	24
LL-CT	2/10/66	301	14.5 ± 0.2	35.5 ± 1.5	1.108	75
	3/3/66	323	16.6 ± 0.3	57.3 ± 3.3	1.171	50
	4/12/66	363	17.8 ± 0.4	67.0 ± 4.3	1.112	50
	5/13/66	393	18.9 ± 0.4	81.1 ± 5.3	1.121	49
	6/17/66	428	19.8 ± 0.4	88.9 ± 6.4	1.089	35
	7/26/66	467	21.1 ± 0.5	110.1 ± 8.9	1.092	35
	8/31/66	503	22.2 ± 0.6	126.5 ± 10.1	1.092	25

[a] See abbreviations on pages 20-21.

[b] Age in days post-hatching.

[c] ± 1 standard error.

APPENDIX X.

Growth statistics of juvenile steelhead trout reared under controlled photoperiod and temperature cycles in Experiment II.

Treatment[a]	Date	Age[b]	Mean Length (cm)	Mean Weight (g)	K	Sample size
SL-CT	7/6/67	126	7.2 ± 0.1[c]	3.97 ± 0.18	1.027	49
	7/20/67	140	8.1 ± 0.1	5.62 ± 0.24	1.041	49
	8/7/67	158	8.9 ± 0.1	7.67 ± 0.37	1.041	50
	8/23/67	174	9.5 ± 0.1	9.51 ± 0.45	1.056	50
	9/7/67	189	10.4 ± 0.1	12.6 ± 0.5	1.074	50
	9/25/67	207	11.3 ± 0.2	16.5 ± 0.7	1.107	50
	10/12/67	224	12.5 ± 0.2	21.3 ± 0.8	1.077	50
	10/30/67	242	13.1 ± 0.2	24.5 ± 1.1	1.041	50
	11/15/67	258	13.7 ± 0.2	28.2 ± 1.5	1.052	50
	11/30/67	273	14.8 ± 0.2	34.5 ± 1.3	1.047	50
	12/15/67	288	15.0 ± 0.2	35.9 ± 1.6	1.026	50
	1/3/68	307	16.0 ± 0.2	42.8 ± 1.6	1.020	50
	1/15/68	319	16.5 ± 0.2	47.4 ± 2.0	1.026	50
	1/31/68	335	16.7 ± 0.2	48.9 ± 2.0	1.028	50
	2/15/68	350	17.2 ± 0.2	53.7 ± 2.1	1.022	50
	2/29/68	364	17.9 ± 0.2	61.3 ± 2.6	1.029	50
	3/15/68	379	18.5 ± 0.2	66.0 ± 2.4	1.026	50
	3/29/68	393	18.5 ± 0.3	66.9 ± 3.5	1.010	50
	4/11/68	406	20.0 ± 0.3	84.5 ± 4.1	1.010	50
	4/29/68	424	20.4 ± 0.3	82.8 ± 3.4	0.953	50
	5/16/68	441	20.9 ± 0.3	89.1 ± 3.5	0.963	40
	6/17/68	473	22.2 ± 0.2	118.2 ± 3.8	1.051	78

[a] See abbreviations on pages 22-23.

[b] Age in days post-hatching.

[c] ± 1 standard error.

Appendix X. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
SL-NT	7/6/67	126	7.3 ± 0.1	4.3 ± 0.19	1.072	50
	7/20/67	140	8.6 ± 0.1	7.6 ± 0.38	1.129	49
	8/7/67	158	9.9 ± 0.1	11.4 ± 0.5	1.153	49
	8/23/67	174	10.8 ± 0.2	15.4 ± 0.8	1.153	49
	9/7/67	189	11.8 ± 0.2	19.7 ± 0.9	1.148	49
	9/25/67	207	13.1 ± 0.2	26.0 ± 0.9	1.128	49
	10/12/67	224	13.9 ± 0.2	31.7 ± 1.2	1.144	50
	10/30/67	242	14.9 ± 0.2	36.4 ± 1.5	1.070	50
	11/15/67	258	15.7 ± 0.2	42.4 ± 1.5	1.064	50
	11/30/67	273	15.9 ± 0.2	42.8 ± 1.6	1.038	50
	12/15/67	288	16.7 ± 0.2	49.5 ± 1.5	1.041	50
	1/3/68	307	17.3 ± 0.2	53.9 ± 1.8	1.022	50
	1/15/68	319	17.2 ± 0.2	51.7 ± 1.8	1.004	50
	1/31/68	335	18.0 ± 0.2	60.3 ± 1.9	1.016	50
	2/15/68	350	18.2 ± 0.2	61.3 ± 1.9	1.001	50
	2/29/68	364	18.5 ± 0.2	64.5 ± 1.8	1.004	50
	3/15/68	379	18.7 ± 0.2	66.8 ± 2.3	1.003	50
	3/29/68	393	19.1 ± 0.3	70.6 ± 2.8	0.992	50
	4/11/68	406	19.8 ± 0.3	77.0 ± 3.2	0.963	50
	4/29/68	424	20.8 ± 0.3	85.1 ± 3.2	0.928	50
	5/16/68	441	20.5 ± 0.3	80.8 ± 3.6	0.911	40
	6/17/68	473	21.9 ± 0.2	107.5 ± 3.3	0.993	85
NL-CT	6/5/67	95	4.9 ± 0.1	1.2 ± 0.06	0.986	50
	6/20/67	110	6.2 ± 0.1	2.4 ± 0.11	1.003	50
	7/6/67	126	6.8 ± 0.1	3.3 ± 0.18	1.011	50
	7/20/67	140	7.7 ± 0.1	5.1 ± 0.22	1.068	50
	8/7/67	158	9.0 ± 0.1	7.7 ± 0.33	1.031	48
	8/23/67	174	9.9 ± 0.1	10.2 ± 0.4	1.020	49
	9/7/67	189	10.8 ± 0.2	13.5 ± 0.6	1.042	50
	9/25/67	207	11.7 ± 0.2	17.4 ± 0.9	1.040	50
	10/12/67	224	12.1 ± 0.2	20.1 ± 1.0	1.089	49
	10/30/67	242	13.0 ± 0.2	24.6 ± 1.2	1.077	50
	11/15/67	258	13.7 ± 0.2	28.5 ± 1.3	1.081	50
	11/30/67	273	14.7 ± 0.2	36.2 ± 1.4	1.104	50
	12/15/67	288	15.9 ± 0.2	46.5 ± 1.9	1.133	50
	1/3/68	307	15.7 ± 0.3	44.8 ± 2.3	1.089	50
	1/15/68	319	17.2 ± 0.2	56.4 ± 2.2	1.089	50
	1/31/68	335	17.3 ± 0.2	59.1 ± 2.5	1.100	50
	2/15/68	350	18.4 ± 0.3	70.6 ± 3.0	1.101	50
	2/29/68	364	18.8 ± 0.3	75.5 ± 3.5	1.101	48
	3/15/68	379	19.0 ± 0.2	76.5 ± 2.9	1.095	50
	3/29/68	393	19.7 ± 0.3	85.6 ± 3.7	1.087	50
	4/11/68	406	20.3 ± 0.3	93.5 ± 4.0	1.089	50
	4/29/68	424	22.0 ± 0.3	112.3 ± 4.5	1.031	53
	5/16/68	441	22.0 ± 0.3	113.4 ± 5.8	1.042	40
	6/17/68	473	23.3 ± 0.2	137.4 ± 4.6	1.059	82

Appendix X. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
NL-NT	7/6/67	126	7.4 ± 0.1	4.5 ± 0.23	1.055	50
	7/20/67	140	8.5 ± 0.1	7.0 ± 0.38	1.093	50
	8/7/67	158	9.9 ± 0.2	11.7 ± 0.6	1.151	50
	8/23/67	174	11.2 ± 0.2	17.0 ± 0.8	1.170	50
	9/7/67	189	12.1 ± 0.2	21.3 ± 0.8	1.163	50
	9/25/67	207	13.2 ± 0.2	26.9 ± 1.2	1.140	50
	10/12/67	224	14.2 ± 0.2	33.7 ± 1.2	1.141	50
	10/30/67	242	14.8 ± 0.2	37.1 ± 1.6	1.102	50
	11/15/67	258	15.3 ± 0.2	39.1 ± 1.5	1.070	50
	11/30/67	273	15.7 ± 0.2	41.8 ± 1.5	1.049	50
	12/15/67	288	16.3 ± 0.2	46.7 ± 1.7	1.057	50
	1/3/68	307	16.8 ± 0.2	50.6 ± 1.7	1.047	50
	1/15/68	319	16.9 ± 0.2	51.2 ± 2.0	1.027	50
	1/31/68	335	17.0 ± 0.2	52.8 ± 1.8	1.059	50
	2/15/68	350	17.6 ± 0.2	58.4 ± 2.2	1.040	50
	2/29/68	364	18.4 ± 0.2	67.4 ± 2.3	1.047	49
	3/15/68	379	18.6 ± 0.2	67.1 ± 2.6	1.018	50
	3/29/68	393	18.8 ± 0.2	68.8 ± 2.4	1.018	49
	4/11/68	406	19.3 ± 0.2	72.7 ± 2.7	0.987	50
	4/29/68	424	19.3 ± 0.3	71.2 ± 2.8	0.961	50
	5/16/68	441	20.0 ± 0.3	80.1 ± 3.6	0.982	39
	6/17/68	473	21.6 ± 0.2	108.9 ± 3.2	1.061	91
NL-AT	7/6/67	126	7.3 ± 0.1	4.5 ± 0.23	1.111	50
	7/20/67	140	8.7 ± 0.1	7.5 ± 0.30	1.115	49
	8/7/67	158	10.4 ± 0.2	13.3 ± 0.6	1.156	50
	8/23/67	174	11.3 ± 0.2	17.0 ± 0.7	1.141	50
	9/7/67	189	12.5 ± 0.1	21.8 ± 0.8	1.091	50
	9/25/67	207	13.3 ± 0.2	26.5 ± 0.9	1.104	50
	10/12/67	224	13.8 ± 0.2	29.9 ± 1.2	1.103	49
	10/30/67	242	15.0 ± 0.2	36.1 ± 1.2	1.060	50
	11/15/67	258	15.1 ± 0.2	36.6 ± 1.2	1.048	50
	11/30/67	273	15.5 ± 0.2	39.5 ± 1.4	1.037	50
	12/15/67	288	16.0 ± 0.1	43.3 ± 1.1	1.039	50
	1/3/68	307	16.3 ± 0.2	46.0 ± 1.6	1.038	49
	1/15/68	319	16.7 ± 0.2	49.1 ± 1.8	1.030	50
	1/31/68	335	17.1 ± 0.2	53.5 ± 1.9	1.038	50
	2/15/68	350	17.8 ± 0.2	60.3 ± 1.9	1.049	50
	2/29/68	364	17.9 ± 0.2	61.8 ± 2.0	1.050	50
	3/15/68	379	18.5 ± 0.2	67.1 ± 2.4	1.037	50
	3/29/68	393	19.1 ± 0.2	73.0 ± 2.6	1.021	50
	4/11/68	406	19.7 ± 0.3	79.7 ± 3.1	1.016	50
	4/29/68	424	20.8 ± 0.3	91.9 ± 3.8	0.990	56
	5/16/68	441	22.0 ± 0.3	114.8 ± 4.7	1.063	40
	6/17/68	473	23.4 ± 0.2	153.1 ± 4.4	1.166	92

Appendix X. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
NL-DT	7/6/67	126	6.9 ± 0.1	3.6 ± 0.14	1.053	50
	7/20/67	140	8.1 ± 0.1	5.8 ± 0.28	1.065	50
	8/7/67	158	9.6 ± 0.1	10.7 ± 0.5	1.179	50
	8/23/67	174	10.7 ± 0.1	15.2 ± 0.6	1.196	50
	9/7/67	189	11.6 ± 0.1	19.0 ± 0.7	1.181	49
	9/25/67	207	13.0 ± 0.1	25.7 ± 0.8	1.158	50
	10/12/67	224	14.0 ± 0.2	33.0 ± 1.3	1.175	50
	10/30/67	242	14.9 ± 0.2	38.6 ± 1.6	1.129	50
	11/15/67	258	15.7 ± 0.2	44.4 ± 1.7	1.121	50
	11/30/67	273	16.9 ± 0.2	54.4 ± 1.8	1.111	49
	12/15/67	288	17.0 ± 0.2	53.5 ± 1.6	1.081	50
	1/3/68	307	17.7 ± 0.2	60.2 ± 1.7	1.072	50
	1/15/68	319	17.5 ± 0.2	57.5 ± 1.8	1.061	50
	1/31/68	335	17.6 ± 0.2	60.1 ± 2.3	1.064	50
	2/15/68	350	19.0 ± 0.2	75.8 ± 2.4	1.080	50
	2/29/68	364	19.2 ± 0.2	77.3 ± 2.6	1.059	50
	3/15/68	379	19.5 ± 0.2	77.9 ± 2.9	1.035	50
	3/29/68	393	20.0 ± 0.3	84.0 ± 3.3	1.017	50
	4/11/68	406	20.8 ± 0.2	91.6 ± 3.2	0.999	50
	4/29/68	424	21.0 ± 0.3	90.5 ± 3.5	0.952	49
	5/16/68	441	20.7 ± 0.3	89.4 ± 4.5	0.969	40
	6/17/68	473	22.2 ± 0.2	113.9 ± 3.7	1.014	89
DL-NT	7/6/67	126	7.0 ± 0.1	3.9 ± 0.20	1.077	50
	7/20/67	140	8.3 ± 0.1	6.3 ± 0.32	1.064	50
	8/7/67	158	9.4 ± 0.1	9.9 ± 0.48	1.147	50
	8/23/67	174	10.3 ± 0.2	13.2 ± 0.6	1.174	50
	9/7/67	189	11.4 ± 0.2	18.0 ± 0.9	1.157	50
	9/25/67	207	12.8 ± 0.2	24.7 ± 1.0	1.144	50
	10/12/67	224	14.3 ± 0.1	34.6 ± 1.0	1.163	50
	10/30/67	242	14.7 ± 0.2	36.1 ± 1.6	1.105	50
	11/15/67	258	15.0 ± 0.2	37.6 ± 1.6	1.082	50
	11/30/67	273	15.6 ± 0.2	43.7 ± 1.7	1.103	50
	12/15/67	288	16.2 ± 0.2	47.2 ± 1.8	1.085	50
	1/3/68	307	16.5 ± 0.2	49.0 ± 1.9	1.068	50
	1/15/68	319	16.8 ± 0.2	51.6 ± 1.7	1.071	50
	1/31/68	335	17.2 ± 0.3	55.6 ± 2.2	1.058	50
	2/15/68	350	17.0 ± 0.2	54.1 ± 2.0	1.070	50
	2/29/68	364	18.0 ± 0.2	63.6 ± 2.4	1.071	50
	3/15/68	379	18.3 ± 0.2	65.6 ± 2.4	1.049	48
	3/29/68	393	18.4 ± 0.2	67.8 ± 2.5	1.065	50
	4/11/68	406	19.1 ± 0.2	75.1 ± 2.8	1.049	50
	4/29/68	424	20.1 ± 0.3	89.0 ± 3.5	1.070	50
	5/16/68	441	20.0 ± 0.4	86.7 ± 4.2	1.049	40
	6/17/68	473	22.1 ± 0.3	117.5 ± 4.7	1.045	76

Appendix X. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
DL-DT	7/6/67	126	7.1 ± 0.11	4.1 ± 0.20	1.078	47
	7/20/67	140	8.1 ± 0.12	5.8 ± 0.26	1.048	50
	8/7/67	158	9.7 ± 0.14	10.8 ± 0.4	1.164	49
	8/23/67	174	11.0 ± 0.1	16.1 ± 0.6	1.173	50
	9/7/67	189	12.0 ± 0.1	20.6 = 0.7	1.164	50
	9/25/67	207	12.6 ± 0.1	23.8 ± 0.8	1.156	50
	10/12/67	224	13.6 ± 0.2	30.5 ± 1.3	1.173	50
	10/30/67	242	14.9 ± 0.2	37.5 ± 1.3	1.115	50
	11/15/67	258	15.6 ± 0.2	44.5 ± 1.7	1.134	50
	11/30/67	273	16.0 ± 0.2	46.0 ± 1.6	1.104	50
	12/15/67	288	16.6 ± 0.2	49.3 ± 1.7	1.067	50
	1/3/68	307	17.1 ± 0.2	55.0 ± 1.8	1.073	50
	1/15/68	319	17.5 ± 0.2	58.2 ± 1.8	1.072	50
	1/31/68	335	17.6 ± 0.2	58.3 ± 1.8	1.056	50
	2/15/68	350	17.9 ± 0.2	62.2 ± 2.4	1.065	50
	2/29/68	364	18.3 ± 0.2	65.7 ± 2.2	1.049	50
	3/15/68	379	18.6 ± 0.2	68.6 ± 2.6	1.038	50
	3/29/68	393	19.1 ± 0.3	75.1 ± 2.7	1.050	50
	4/11/68	406	19.6 ± 0.2	78.5 ± 3.0	1.016	50
	4/29/68	424	19.8 ± 0.3	81.3 ± 3.2	1.028	50
	5/16/68	441	21.1 ± 0.4	96.3 ± 4.5	0.999	40
	6/17/68	473	21.8 ± 0.2	104.7 ± 3.8	0.979	80
AL-NT	7/6/67	126	7.3 ± 0.11	4.4 ± 0.21	1.095	48
	7/20/67	140	8.3 ± 0.13	6.6 ± 0.31	1.075	50
	8/7/67	158	9.9 ± 0.11	11.3 ± 0.4	1.149	50
	8/23/67	174	10.6 ± 0.1	14.4 ± 0.6	1.168	50
	9/7/67	189	11.7 ± 0.2	18.8 ± 0.8	1.145	50
	9/25/67	207	12.9 ± 0.2	25.3 ± 0.9	1.141	50
	10/12/67	224	13.4 ± 0.2	28.5 ± 1.1	1.147	50
	10/30/67	242	14.6 ± 0.1	34.4 ± 0.8	1.103	50
	11/15/67	258	14.9 ± 0.2	36.6 ± 1.0	1.082	50
	11/30/67	273	15.7 ± 0.2	42.3 ± 1.4	1.067	50
	12/15/67	288	16.1 ± 0.1	44.8 ± 1.2	1.063	50
	1/3/68	307	16.5 ± 0.2	48.1 ± 1.7	1.058	50
	1/15/68	319	16.6 ± 0.2	50.8 ± 1.6	1.075	50
	1/31/68	335	17.3 ± 0.2	55.4 ± 1.8	1.059	50
	2/15/68	350	17.8 ± 0.2	60.7 ± 2.2	1.053	49
	2/29/68	364	18.8 ± 0.2	65.4 ± 2.2	0.969	50
	3/15/68	379	18.9 ± 0.2	66.1 ± 2.3	0.955	50
	3/29/68	393	19.0 ± 0.2	66.0 ± 2.4	0.942	50
	4/11/68	406	19.6 ± 0.2	74.8 ± 3.0	0.962	50
	4/29/68	424	20.3 ± 0.2	85.7 ± 3.4	1.004	55
	5/16/68	441	20.7 ± 0.3	97.3 ± 5.1	1.058	40
	6/17/68	473	22.0 ± 0.2	120.1 ± 3.7	1.098	75

Appendix X, continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
AL-AT	7/6/67	126	7.3 ± 0.1	4.6 ± 0.22	1.118	49
	7/20/67	140	8.5 ± 0.1	6.8 ± 0.27	1.099	50
	8/7/67	158	9.7 ± 0.1	11.0 ± 0.5	1.179	49
	8/23/67	174	10.7 ± 0.2	15.1 ± 0.7	1.172	50
	9/7/67	189	12.1 ± 0.2	20.3 ± 0.8	1.110	50
	9/25/67	207	12.8 ± 0.1	24.0 ± 0.8	1.125	50
	10/12/67	224	13.5 ± 0.2	28.3 ± 1.1	1.111	50
	10/30/67	242	14.0 ± 0.2	30.1 ± 1.2	1.073	50
	11/15/67	258	14.2 ± 0.2	31.0 ± 1.2	1.049	50
	11/30/67	273	14.6 ± 0.2	33.4 ± 1.2	1.049	50
	12/15/67	288	15.5 ± 0.2	39.7 ± 1.2	1.057	50
	1/3/68	307	15.5 ± 0.2	40.3 ± 1.8	1.039	50
	1/15/68	319	16.0 ± 0.2	44.2 ± 1.5	1.059	50
	1/31/68	335	16.8 ± 0.2	50.6 ± 1.9	1.044	50
	2/15/68	350	17.6 ± 0.2	58.4 ± 2.3	1.051	50
	2/29/68	364	18.2 ± 0.2	59.7 ± 2.1	0.976	50
	3/15/68	379	18.1 ± 0.2	57.8 ± 2.2	0.951	50
	3/29/68	393	18.8 ± 0.3	68.2 ± 3.3	0.987	50
	4/11/68	406	19.3 ± 0.2	74.4 ± 3.1	0.1005	50
	4/29/68	424	20.1 ± 0.2	86.7 ± 3.2	1.046	55
	5/16/68	441	20.4 ± 0.4	101.4 ± 5.3	1.147	40
	6/17/68	473	22.7 ± 0.3	148.0 ± 5.5	1.216	68
NLB-CT	6/5/67	95	5.2 ± 0.1	1.4 ± 0.05	0.994	47
	6/20/67	110	6.1 ± 0.1	2.3 ± 0.08	1.013	50
	7/6/67	126	6.9 ± 0.1	3.4 ± 0.15	1.010	50
	7/20/67	140	7.7 ± 0.1	4.8 ± 0.25	1.005	50
	8/7/67	158	9.0 ± 0.1	7.7 ± 0.37	1.008	49
	8/23/67	174	9.6 ± 0.1	9.8 ± 0.48	1.054	50
	9/7/67	189	10.5 ± 0.1	12.7 ± 0.5	1.056	50
	9/25/67	207	11.7 ± 0.2	18.2 ± 0.8	1.107	50
	10/12/67	224	12.2 ± 0.2	20.7 ± 1.1	1.083	49
	10/30/67	242	13.1 ± 0.2	25.8 ± 1.3	1.099	50
	11/15/67	258	13.9 ± 0.2	32.0 ± 1.7	1.140	49
	11/30/67	273	14.2 ± 0.2	33.9 ± 1.7	1.126	50
	12/15/67	288	15.0 ± 0.2	40.0 ± 1.7	1.138	50
	1/3/68	307	15.8 ± 0.2	45.2 ± 2.0	1.113	50
	1/15/68	319	16.6 ± 0.2	54.4 ± 2.3	1.145	50
	1/31/68	335	16.9 ± 0.3	57.4 ± 2.6	1.146	50
	2/15/68	350	17.9 ± 0.3	66.8 ± 3.2	1.121	50
	2/29/68	364	18.2 ± 0.3	69.6 ± 3.2	1.123	49
	3/15/68	379	18.3 ± 0.3	71.9 ± 3.9	1.116	50
	3/29/68	393	19.0 ± 0.3	79.8 ± 4.2	1.107	50
	4/11/68	406	19.2 ± 0.3	80.2 ± 3.5	1.099	49
	4/29/68	424	20.8 ± 0.4	102.7 ± 5.7	1.090	50
	5/16/68	441	21.6 ± 0.4	116.6 ± 7.6	1.106	39
	6/17/68	473	22.4 ± 0.3	138.3 ± 6.3	1.159	87

Appendix X, continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
NLG-CT	6/5/67	95	4.9 ± 0.1	1.2 ± 0.04	0.984	50
	6/20/67	110	6.0 ± 0.1	2.3 ± 0.08	1.029	50
	7/6/67	126	7.2 ± 0.1	4.0 ± 0.16	1.031	50
	7/20/67	140	8.0 ± 0.1	5.3 ± 0.19	1.007	50
	8/7/67	158	9.3 ± 0.1	8.7 ± 0.30	1.050	50
	8/23/67	174	9.9 ± 0.1	10.6 ± 0.4	1.067	50
	9/7/67	189	10.9 ± 0.2	14.6 ± 0.6	1.085	50
	9/25/67	207	11.8 ± 0.2	18.6 ± 0.8	1.097	50
	10/12/67	224	12.0 ± 0.2	19.8 ± 1.0	1.092	50
	10/30/67	242	12.7 ± 0.2	23.1 ± 1.2	1.092	50
	11/15/67	258	13.7 ± 0.2	30.1 ± 1.2	1.133	50
	11/30/67	273	14.5 ± 0.3	35.0 ± 1.7	1.102	50
	12/15/67	288	14.8 ± 0.3	38.6 ± 1.9	1.126	50
	1/3/68	307	15.7 ± 0.2	44.0 ± 1.8	1.099	50
	1/15/68	319	16.2 ± 0.3	49.8 ± 2.3	1.127	50
	1/31/68	335	17.2 ± 0.2	59.3 ± 2.6	1.131	50
	2/15/68	350	18.0 ± 0.2	66.8 ± 2.8	1.108	50
	2/29/68	364	18.9 ± 0.4	78.7 ± 4.0	1.109	50
	3/15/68	379	18.6 ± 0.3	74.4 ± 3.8	1.107	50
	3/29/68	393	19.9 ± 0.3	87.1 ± 3.6	1.078	50
	4/11/68	406	20.4 ± 0.3	93.1 ± 4.3	1.056	49
	4/29/68	424	21.1 ± 0.3	99.2 ± 4.3	1.028	53
	5/16/68	441	21.5 ± 0.4	108.7 ± 6.0	1.038	40
	6/17/68	473	23.0 ± 0.3	144.1 ± 5.7	1.138	83
NLR-CT	6/5/67	95	5.5 ± 0.1	1.7 ± 0.08	1.030	50
	6/20/67	110	6.4 ± 0.1	2.8 ± 0.12	1.025	50
	7/6/67	126	7.2 ± 0.1	4.0 ± 0.17	1.041	50
	7/20/67	140	8.1 ± 0.1	5.9 ± 0.27	1.058	49
	8/7/67	158	9.4 ± 0.1	9.3 ± 0.37	1.093	49
	8/23/67	174	9.5 ± 0.1	9.8 ± 0.53	1.096	50
	9/7/67	189	10.8 ± 0.1	14.1 ± 0.6	1.098	50
	9/25/67	207	12.0 ± 0.2	19.9 ± 0.8	1.111	50
	10/12/67	224	12.1 ± 0.2	20.1 ± 0.9	1.110	50
	10/30/67	242	13.0 ± 0.2	25.6 ± 1.3	1.100	50
	11/15/67	258	13.9 ± 0.2	32.2 ± 1.6	1.140	50
	11/30/67	273	14.2 ± 0.3	34.3 ± 2.2	1.100	48
	12/15/67	288	14.8 ± 0.3	38.6 ± 2.0	1.124	50
	1/3/68	307	15.7 ± 0.3	45.4 ± 2.6	1.098	50
	1/15/68	319	16.0 ± 0.3	49.2 ± 2.7	1.131	50
	1/31/68	335	16.6 ± 0.3	53.9 ± 2.9	1.129	50
	2/15/68	350	17.8 ± 0.3	65.9 ± 3.1	1.116	50
	2/29/68	364	18.2 ± 0.3	70.2 ± 3.3	1.126	50
	3/15/68	379	18.1 ± 0.4	69.0 ± 4.1	1.091	50
	3/29/68	393	19.2 ± 0.3	81.1 ± 3.8	1.094	50
	4/11/68	406	20.1 ± 0.3	92.3 ± 4.6	1.089	50
	4/29/68	424	20.9 ± 0.3	99.3 ± 4.3	1.050	50
	5/16/68	441	20.5 ± 0.4	92.6 ± 6.0	1.090	40
	6/17/68	473	21.9 ± 0.3	127.3 ± 5.1	1.155	96

Appendix X. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (cm)	K	Sample size
DD-CT	5/15/67	75	3.9 ± 0.1	0.55 ± 0.04	0.862	25
	6/5/67	95	4.7 ± 0.2	1.2 ± 0.14	0.994	25
	6/20/67	110	5.9 ± 0.1	2.2 ± 0.14	1.035	25
	7/6/67	126	6.7 ± 0.1	3.1 ± 0.19	1.021	25
	7/20/67	140	7.0 ± 0.1	3.6 ± 0.24	1.039	25
	8/7/67	158	8.0 ± 0.2	5.5 ± 0.37	1.022	25
	8/23/67	174	9.1 ± 0.2	8.5 ± 0.56	1.086	24
	9/7/67	189	9.9 ± 0.2	10.8 ± 0.9	1.045	24
	9/25/67	207	10.8 ± 0.3	14.5 ± 1.1	1.078	25
	10/12/67	224	11.8 ± 0.2	18.7 ± 1.1	1.108	25
	10/30/67	242	12.8 ± 0.3	23.2 ± 1.4	1.079	25
	11/15/67	258	13.0 ± 0.4	26.8 ± 2.4	1.131	25
	11/30/67	273	14.0 ± 0.4	31.7 ± 2.5	1.105	25
	12/15/67	288	15.4 ± 0.3	42.5 ± 2.4	1.133	25
	1/3/68	307	15.7 ± 0.4	45.9 ± 2.7	1.144	25
	1/15/68	319	17.0 ± 0.3	56.3 ± 2.5	1.144	25
	1/31/68	335	16.9 ± 0.4	58.4 ± 4.6	1.150	25
	2/15/68	350	17.8 ± 0.4	64.1 ± 3.8	1.104	25
	2/29/68	364	18.2 ± 0.5	69.1 ± 5.0	1.112	25
	3/15/68	379	18.6 ± 0.5	76.8 ± 5.9	1.158	25
	3/29/68	393	18.7 ± 0.4	77.5 ± 3.8	1.180	25
	4/11/68	406	19.9 ± 0.5	90.6 ± 5.6	1.124	25
	4/29/68	424	20.9 ± 0.5	104.6 ± 6.7	1.107	30
	5/16/68	441	21.7 ± 0.5	117.8 ± 7.2	1.117	25
	6/17/68	473	22.8 ± 0.4	142.2 ± 6.6	1.144	64
DD-NT	5/15/67	75	3.9 ± 0.1	0.57 ± 0.05	0.874	24
	6/5/67	95	4.9 ± 0.1	1.2 ± 0.10	0.906	25
	6/20/67	110	5.0 ± 0.1	1.0 ± 0.09	0.803	25
	7/6/67	126	6.5 ± 0.2	3.3 ± 0.34	1.074	25
	7/20/67	140	7.1 ± 0.3	4.2 ± 0.48	1.036	25
	8/7/67	158	8.4 ± 0.2	7.0 ± 0.50	1.143	25
	8/23/67	174	9.4 ± 0.2	10.1 ± 0.7	1.164	25
	9/7/67	189	10.4 ± 0.2	13.5 ± 1.1	1.133	25
	9/25/67	207	11.2 ± 0.3	17.0 ± 1.5	1.142	25
	10/12/67	224	12.2 ± 0.4	23.0 ± 1.8	1.160	25
	10/30/67	242	12.4 ± 0.3	22.5 ± 1.8	1.123	25
	11/15/67	258	13.9 ± 0.3	32.0 ± 1.8	1.146	25
	11/30/67	273	13.7 ± 0.6	32.0 ± 3.6	1.097	23
	12/15/67	288	14.8 ± 0.4	38.7 ± 2.8	1.143	25
	1/3/68	307	16.1 ± 0.4	49.1 ± 3.6	1.144	25
	1/15/68	319	16.9 ± 0.3	54.4 ± 2.7	1.113	25
	1/31/68	335	16.6 ± 0.4	54.7 ± 3.5	1.146	25
	2/15/68	350	16.9 ± 0.3	55.6 ± 2.4	1.135	25
	2/29/68	364	17.8 ± 0.4	64.9 ± 4.1	1.114	25
	3/15/68	379	18.0 ± 0.4	66.5 ± 4.4	1.110	25
	3/29/68	393	18.6 ± 0.4	70.1 ± 4.9	1.056	25
	4/11/68	406	19.1 ± 0.5	77.6 ± 5.5	1.083	25

Appendix X. continued

Treatment	Date	Age	Mean Length (cm)	Mean Weight (g)	K	Sample size
DD-NT	4/29/68	424	19.0 ± 0.4	74.1 ± 4.1	1.045	30
(continued)	5/16/68	441	19.5 ± 0.6	78.8 ± 7.4	1.030	18
	6/17/68	473	21.3 ± 0.9	110.9 ± 14.7	1.084	13
RL-CT	7/20/67	140	7.1 ± 0.1	3.6 ± 0.08	1.000	50
	8/7/67	158	8.4 ± 0.1	6.2 ± 0.13	1.054	50
	8/23/67	174	9.6 ± 0.1	9.5 ± 0.28	1.051	49
	9/7/67	189	10.8 ± 0.1	13.9 ± 0.5	1.072	50
	9/25/67	207	11.9 ± 0.2	18.1 ± 0.7	1.052	50
	10/12/67	224	12.3 ± 0.1	20.4 ± 0.7	1.082	50
	10/30/67	242	12.8 ± 0.2	22.8 ± 0.9	1.064	50
	11/15/67	258	13.6 ± 0.2	27.9 ± 1.0	1.070	50
	11/30/67	273	15.0 ± 0.2	36.0 ± 1.6	1.040	50
	12/15/67	288	15.6 ± 0.2	38.8 ± 1.3	1.004	50
	1/3/68	307	16.3 ± 0.2	45.8 ± 1..9	1.025	49
	1/15/68	319	16.7 ± 0.2	49.9 ± 2.2	1.043	50
	1/31/68	335	17.7 ± 0.3	63.2 ± 2.6	1.110	50
	2/15/68	350	18.9 ± 0.2	75.3 ± 2.7	1.100	50
	2/29/68	364	18.8 ± 0.3	74.9 ± 3.6	1.075	49
	3/15/68	379	18.7 ± 0.3	75.0 ± 4.2	1.088	50
	3/29/68	393	19.9 ± 0.3	92.1 ± 4.8	1.114	50
	4/11/68	406	20.0 ± 0.3	95.1 ± 4.5	1.136	49
	4/29/68	424	21.1 ± 0.4	110.3 ± 5.8	1.110	50
	5/16/68	441	21.1 ± 0.4	109.5 ± 6.2	1.111	40

APPENDIX XI.

Sea-water survival statistics for juvenile steelhead trout reared under controlled photoperiods from July 11, 1965 to September 10, 1966.

Treatment[a]	Date exposure started	Age[b]	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
SL-CT	7/20/65	96	4.3	0.8	40	1	0/40	0
	8/6/65	113	5.1	1.5	25	15	1/25	4 (0-8)
	9/1/65	139	7.0	3.5	30	26	1/30	3 (0-6)
	10/4/65	172	8.3	6.3	28	23	11/28	39 (35-42)
	11/6/65	205	9.6	9.8	27	20	15/27	55
	12/14/65	243	10.4	12.9	29	24	21/29	72
	1/6/66	266	11.4	17.8	30	15[25][c]	23/30[13/30][c]	76[43][c] (73-80)
	2/9/66	300	14.9	37.6	22	20	21/22	95 (91-100)
	3/12/66	332	16.0	48.4	21	20	21/21	100
	4/12/66	363	17.6	59.3	15	28	15/15	100
	5/20/66	400	20.6	98.7	15	15[28]	14/15[1/15]	93[7]
	6/24/66	435	20.8	112.5	10	28	6/10	60
	7/29/66	470	22.6	135.9	14	26	13/14	93
	9/3/66	506	22.6	140.7	10	20	9/10	90

[a] See abbreviations on pages 20-21

[b] Age in days post-hatching

[c] Mortalities that occurred over a 1 or 2 day period late in the test were believed to be artifacts and the survival for the first 15 days of the test period was used as the measure of salinity tolerance of the population. The data in brackets represents the length of the complete exposure period, the fraction of fish alive, and percent survival for that period.

Appendix XI. continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
NL-CT	8/6/65	113	5.3	1.6	30	15	1/30	3 (0-6)
	9/1/65	139	7.1	3.7	30	26	1/30	3 (0-6)
	10/4/65	172	8.8	7.3	30	23	16/30	53 (40-66)
	11/6/65	205	10.2	12.2	29	20	11/29	38
	12/14/65	243	11.7	18.5	29	24	19/29	66
	1/6/66	266	13.1	26.2	28	15[25]	25/28[13/28]	80[46] (84-93)
	2/9/66	300	14.9	38.4	21	20	20/21	95 (91-100)
	3/12/66	332	16.0	47.0	17	20	15/17	88
	4/12/66	363	19.0	77.0	15	15[28]	13/15[3/15]	87[20]
	5/20/66	400	19.8	82.3	15	28	13/15	87
	6/24/66	435	20.0	86.5	9	28	4/9	45
	7/29/66	470	21.6	114.8	15	26	13/15	87
	9/3/66	506	22.4	135.4	9	20	9/9	100

Appendix XI. continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
DD-CT	8/6/65	61	3.9	0.6	30	2	0/30	0
	9/1/65	87	4.8	1.1	30	5	0/30	0
	10/4/65	120	5.8	2.0	24	23	2/24	8
	11/19/65	166	6.4	2.9	30	7	3/30	10
	12/4/65	181	8.0	5.9	28	24	24/28	86
	1/6/66	214	9.9	11.6	50	25	41/50	82 (77-90)
	2/9/66	248	11.6	19.3	35	20	33/35	94 (90-100)
	3/12/66	279	13.1	26.2	17	20	15/17	88
	4/12/66	310	14.1	32.1	15	28	15/15	100
	5/20/66	348	14.7	36.6	15	15[28]	12/15[7/15]	80[47]
	6/24/66	383	15.8	48.8	10	28	7/10	70
	7/29/66	418	16.8	53.8	20	26	19/20	95
	9/3/66	454	18.5	74.4	20	20	20/20	100

Appendix XI continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
8. 5L-CT	8/6/65	113	5.0	1.3	30	2	0/30	0
	9/1/65	139	6.8	3.3	30	26	3/30	10 (5-13)
	10/4/65	172	8.1	5.7	30	23	7/30	23 (13-33)
	11/19/65	205	9.7	10.2	30	20	22/30	73
	12/14/65	243	10.4	12.6	30	24	17/30	57
	1/6/66	266	11.4	17.4	30	15[25]	24/30[6/30]	80[20] (66-93)
	2/9/66	300	13.4	28.9	20	20	20/20	100
	3/12/66	332	15.3	43.1	19	15[20]	19/19[8/19]	100[42]
	4/12/66	363	17.6	62.4	15	28	14/15	93
	5/20/66	400	17.6	65.2	14	15[28]	8/14[4/14]	57[29]
	6/24/66	435	20.4	98.4	10	28	9/10	90
	7/29/66	470	20.2	97.4	15	26	15/15	100
	9/3/66	506	23.6	154.3	10	20	10/10	100

Appendix XI. continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
12L-CT	8/6/65	113	5.0	1.3	30	2	0/30	0
	9/1/65	139	6.7	3.3	30	26	1/30	3 (0-6)
	10/4/65	172	8.1	5.8	30	23	15/30	50 (40-60)
	11/19/65	205	9.8	11.1	27	20	21/27	78
	12/4/65	243	11.5	16.4	29	24	23/29	79
	1/6/66	266	12.6	23.7	24	15[25]	20/24[3/24]	83[12] (81-84)
	2/9/66	300	14.7	23.6	20	20	19/20	95 (90-100)
	3/12/66	332	16.4	50.0	18	15[20]	18/18[14/18]	100[78]
	4/12/66	363	17.3	60.6	14	28	14/14	100
	5/20/66	400	19.4	84.2	15	28	13/15	87
	6/24/66	435	20.2	90.6	10	28	6/10	60
	7/29/66	470	21.7	117.8	15	26	14/15	93
	9/3/66	506	23.2	137.7	10	20	9/10	90

Appendix XI. continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
16L-CT	8/6/65	113	5.4	1.7	30	14	0/30	0
	9/1/65	139	6.7	3.2	31	26	4/31	13 (6-20)
	10/4/65	172	8.1	5.9	28	23	11/28	39 (35-42)
	11/19/65	205	10.2	12.0	27	20	17/27	63
	12/4/65	243	11.4	16.8	30	24	14/30	47
	1/6/66	266	12.7	23.5	30	15[25]	26/30[3/30]	87[27] (80-93)
	2/9/66	300	13.9	32.5	17	20	17/17	100
	3/12/66	332	15.5	45.1	19	20	16/19	84
	4/12/66	363	16.2	51.1	15	28	11/15	73
	5/20/66	400	18.5	75.0	15	15[28]	14/15[5/15]	93[33]
	6/24/66	435	19.5	85.8	10	28	5/10	50
	7/29/66	470	20.5	96.9	15	26	11/15	73
	9/3/66	506	20.8	107.5	10	20	9/10	90

Appendix XI. continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after explosure	Percent survival (range)
LL-CT	8/6/65	113	5.1	1.4	30	15	1/30	3 (0-6)
	9/1/65	139	7.0	3.6	30	5	0/30	0
	10/4/65	172	8.5	6.4	28	23	13/28	46 (35-57)
	11/19/65	205	9.6	9.9	28	20	20/28	71
	12/4/65	243	10.8	14.3	28	24	20/28	71
	1/6/66	266	12.0	19.9	29	15[25]	25/29[12/29]	86[41] (80-93)
	2/9/66	300	13.8	31.0	17	20	15/17	88 (77-100)
	3/12/66	332	16.4	51.6	20	20	16/20	80
	4/12/66	363	17.7	63.5	15	28	15/15	100
	5/20/66	400	18.1	69.3	14	28	8/14	57
	6/24/66	435	19.0	78.2	10	28	6/10	60
	7/29/66	470	20.9	102.9	15	26	14/15	93
	9/3/66	506	21.4	103.7	10	20	6/10	60

APPENDIX XII.

Sea-water survival of juvenile steelhead trout reared under controlled photoperiods from December 22, 1965 to September 10, 1966.

Treatment[a]	Date exposure started	Age[b]	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
8.5L-CT	3/12/66	332	15.4	46.9	17	15[20][c]	17/17[11/17][c]	100[65][c]
	4/12/66	363	17.0	59.1	20	28	20/20	100
	5/20/66	400	20.1	92.0	16	15[28]	13/16[7/16]	81[44]
	6/24/66	435	22.0	114.5	10	28	9/10	90
	7/29/66	470	23.4	142.6	15	15[26]	13/15[7/15]	87[47]
	9/3/66	507	25.2	174.5	10	20	10/10	100
12L-CT	3/12/66	332	18.3	69.9	17	15[20]	17/17[11/17]	100[65]
	4/12/66	363	17.7	65.8	20	28	19/20	95
	5/20/66	400	20.7	101.1	15	28	15/15	100
	6/24/66	435	22.9	135.7	10	28	9/10	90
	7/29/66	470	23.4	150.6	10	15[26]	8/10[4/10]	80[40]
	9/3/66	507	26.3	212.4	8	20	4/8	50
16L-CT	3/12/66	332	16.5	52.9	18	20	17/18	94
	4/12/66	363	17.8	71.9	20	28	15/20	75
	5/20/66	400	19.9	95.4	15	28	10/15	66
	6/24/66	435	20.4	95.8	10	28	5/10	50
	7/29/66	470	21.4	113.2	8	15[26]	6/8[4/8]	75[50]
	9/3/66	507	23.9	158.4	10	20	8/10	80

[a] See abbreviations on pages 20-21

[b] Age in days post-hatching

[c] Mortalities that occurred over a 1 or 2 day period late in the test were believed to be artifacts and the survival for the first 15 days of the test period was used as the measure of salinity tolerance of the population. The data in brackets represents the length of the complete exposure period, the fraction of fish alive, and percent survival for that period.

Appendix XII. continued

Treatment	Date exposure started	Age	Mean Length (cm)	Mean Weight (g)	Number of animals exposed	Length of exposure (days)	Fraction alive after exposure	Percent survival (range)
LL-CT	3/12/66	332	16.4	54.7	17	20	14/17	82
	4/12/66	363	18.2	72.2	19	28	17/19	89
	5/20/66	400	19.5	92.6	15	28	11/15	73
	6/24/66	435	20.9	105.0	10	28	7/10	70
	7/29/66	470	21.1	107.7	15	26	14/15	93
	9/3/66	507	22.3	122.8	10	20	8/10	80
NL-CT	3/12/66	332	16.0	48.7	18	20	15/18	83
	4/12/66	363	18.0	62.7	18	15[28]	16/18[5/18]	89[28]
	5/20/66	400	20.5	89.4	14	28	13/14	93
	6/24/66	435	21.8	107.4	9	28	8/9	88
	7/29/66	470	21.8	120.3	15	26	11/15	73
	9/3/66	507	23.2	156.4	10	20	6/10	60

APPENDIX XIII.

Plasma osmotic and electrolyte concentrations of juvenile steelhead trout reared under controlled photoperiods from July 11, 1965 that survived a 20-28 day exposure to sea water for the months of April through September, 1966.

Concentration	Photoperiod[a] NL	SL	DD	8.5L	12L	16L	LL	Freshwater Controls
				April				
Osmotic (m-osmol./ℓ)	409 ± 24 n=10	405 ± 37 n=10	415 ± 26[b] n=10	389 ± 29 n=10	366 ± 34 n=10	445 ± 32 n=10	415 ± 40 n=10	327 ± 17 n=10
Sodium (m-equiv./ℓ)	184 ± 10 n=8	189 ± 13 n=10	197 ± 14 n=10	185 ± 14 n=9	187 ± 20 n=10	220 ± 21 n=9	196 ± 15 n=10	162 ± 8 n=10
Chloride (m-equiv./ℓ)	152 ± 7 n=10	149 ± 22 n=10	153 ± 10 n=10	149 ± 11 n=9	149 ± 15 n=10	178 ± 18 n=8	161 ± 15 n=10	121 ± 10 n=10
				May-June				
Osmotic (m-osmol./ℓ)	441 ± 73 n=3	420 ± 15 n=5	409 ± 46 n=5	391 ± 18 n=5	466 ± 59 n=5	466 ± 39 n=5	404 ± 70 n=5	344 ± 20 n=11
Sodium (m-equiv./ℓ)	195 ± 17 n=5	200 n=1	199 ± 13 n=7	200 ± 8 n=4	213 ± 9 n=5	200 ± 10 n=4	200 ± 10 n=5	160 ± 2 n=10
Chloride (m-equiv./ℓ)	183 ± 16 n=4	201 n=1	176 ± 14 n=7	170 ± 4 n=4	194 ± 7 n=5	169 ± 10 n=3	179 ± 7 n=5	116 ± 6 n=10

[a] See abbreviations on pages 20-21.

[b] ± 1 standard error.

Appendix XIII. continued

Concentration	NL	SL	DD	Photoperiod 8.5L	12L	16L	LL	Freshwater Controls
				June-July				
Osmotic (m-osmol./ℓ)	412 ± 49 n=3	402 ± 26 n=4	399 ± 37 n=5	419 ± 37 n=5	385 ± 13 n=5	402 ± 42 n=5	392 ± 32 n=5	338 ± 15 n=14
Sodium (m-equiv./ℓ)	186 ± 12 n=4	207 ± 10 n=4	195 ± 13 n=5	188 ± 14 n=5	189 ± 17 n=5	193 ± 8 n=5	187 ± 12 n=6	159 ± 5 n=14
Chloride (m-equiv./ℓ)	164 ± 12 n=4	154 ± 12 n=4	159 ± 12 n=5	161 ± 15 n=5	165 ± 22 n=5	161 ± 18 n=5	149 ± 22 n=6	123 ± 13 n=14
				July-August				
Osmotic (m-osmol./ℓ)	395 ± 33 n = 5	387 ± 22 n=5	390 ± 30 n=5	345 ± 27 n=5	363 ± 22 n=5	447 ± 58 n=5	360 ± 25 n=5	346 ± 15 n=14
Sodium (m-equiv./ℓ)	178 ± 1 n=4	182 ± 12 n=5	183 ± 13 n=5	170 ± 5 n=5	182 ± 8 n=5	201 ± 23 n=5	170 ± 16 n=5	163 ± 5 n=14
Chloride (m-equiv./ℓ)	152 ± 7 n=4	141 ± 14 n=5	148 ± 10 n=5	132 ± 10 n=5	144 ± 8 n=5	175 ± 26 n=5	137 ± 15 n=5	120 ± 4 n=14
				September				
Osmotic (m-osmol./ℓ)	353 ± 20 n=5	358 ± 16 n=4	312 ± 13 n=5	322 ± 25 n=5	354 ± 36 n=5	348 ± 39 n=5	337 ± 18 n=5	302 ± 20 n=13
Sodium (m-equiv./ℓ)	182 ± 7 n=5	190 ± 15 n=4	179 ± 11 n=7	176 ± 6 n=5	177 ± 25 n=5	185 ± 14 n=6	187 ± 5 n=5	164 ± 6 n=13
Chloride (m-equiv./ℓ)	148 ± 13 n=6	153 ± 10 n=4	141 ± 9 n=7	134 ± 3 n=5	158 ± 18 n=5	154 ± 19 n=5	148 ± 5 n=5	119 ± 8 n=12

APPENDIX XIV.

Plasma osmotic and electrolyte concentrations for juvenile steelhead trout reared under controlled photoperiods from December 22, 1965 that survived a 20-28 day exposure to sea water for the months of May through September, 1966.

Concentration	Photoperiod[a] NL	8.5L	12L	16L	LL
		May-June			
Osmotic (m-osmol./ℓ)	450 ± 41 n=5	446 ± 14[b] n=5	429 ± 38 n=5	390 ± 37 n=4	419 ± 58 n=7
Sodium (m-equiv./ℓ)	193 ± 11 n=4	191 ± 12 n=6	194 ± 17 n=5	199 ± 5 n=5	221 ± 18 n=5
Chloride (m-equiv./ℓ)	167 ± 20 n=4	164 ± 18 n=6	169 ± 26 n=5	171 ± 6 n=5	199 ± 11 n=5
		June-July			
Osmotic (m-osmol./ℓ)	396 ± 31 n=5	403 ± 28 n=5	373 ± 27 n=5	376 ± 14 n=5	418 ± 16 n=5
Sodium (m-equiv./ℓ)	183 ± 13 n=5	187 ± 7 n=5	175 ± 12 n=5	183 ± 8 n=5	190 ± 14 n=6
Chloride (m-equiv./ℓ)	163 ± 18 n=5	162 ± 10 n=5	138 ± 19 n=5	154 ± 7 n=5	158 ± 7 n=6
		July-August			
Osmotic (m-osmol./ℓ)	No data	370 ± 9 n=5	368 ± 9 n=4	378 ± 24 n=5	377 ± 21 n=5
Sodium (m-equiv./ℓ)	No data	175 ± 10 n=5	176 ± 4 n=4	172 ± 5 n=4	185 ± 13 n=4
Chloride (m-equiv./ℓ)	No data	143 ± 7 n=5	132 ± 6 n=4	133 ± 14 n=4	152 ± 11 n=4
		September			
Osmotic (m-osmol./ℓ)	343 ± 26 n=3	314 ± 26 n=5	332 ± 30 n=4	333 ± 17 n=6	344 ± 22 n=5
Sodium (m-equiv./ℓ)	184 ± 7 n=4	171 ± 5 n=5	176 ± 11 n=4	175 ± 8 n=6	178 ± 10 n=4
Chloride (m-equiv./ℓ)	137 ± 11 n=4	138 ± 7 n=5	147 ± 11 n=4	142 ± 15 n=6	151 ± 9 n=4

[a] See abbreviations on pages 20-21.

[b] ± 1 standard error.

APPENDIX XV.

Analysis of variance and least significant difference calculations for the plasma osmotic concentration of sea-water survivors in Experiment I.

(a) Lot A Analysis of Variance

Source of variation	Sums of squares	Degrees of freedom	Mean squares	F	Tabular F (P = 0.01)
Month (M)	30192.171	4	7548.043	16.885	4.218
Photoperiod (P)	7595.543	6	1266.257	2.830	3.667
MP	10737.029	24	447.376		
Total	48526.743	34			

(b) Lot B Analysis of Variance

Source of variation	Sums of squares	Degrees of freedom	Mean squares	F	Tabular F (P = 0.01)
Month (M)	17227.250	3	5742.417	19.398	6.992
Photoperiod (P)	940.250	3	313.417	1.059	6.992
MP	2664.250	9	296.028		
Total	20831.750	15			

(c) Lot A and B Analysis of Variance

Source of variation	Sums of squares	Degrees of freedom	Mean squares	F	Tabular F (P = 0.01)
Month (M)	34838.094	3	11612.698	29.76	6.992
Photoperiod (P)	1105.094	3	368.365	0.94	6.992
MP	6154.281	9	683.809	1.75	5.351
Lot (L)	536.281	1	536.281	1.37	10.561
ML	33.844	3	11.281	0.03	6.992
PL	5252.844	3	1750.948	4.49	6.992
MPL	3511.531	9	390.170		
Total	51431.969	31			

Appendix XV. continued

(d) Test of Least Significant Difference[a]

Lot A (LSD 0.01 = 31)

Month	Sept.	July-Aug.	June-July	Apr.	May-June
Mean osmotic conc.	340	384	402	406	428

Lot B (LSD 0.01 = 37)

Month	Sept.	July-Aug.	June-July	May-June
Mean osmotic conc.	331	373	392	421

Lot A and B (LSD 0.01 = 32)

Month	Sept.	July-Aug.	June-July	May-June
Mean osmotic conc.	336	376	396	426

[a] Groups of means underlined by a continuous single line are not significantly different from each other.

APPENDIX XVI.

Duncan's multiple range test of differences among monthly means of thyroid follicle cell height for fish reared in various photoperiods. Means underscored with solid line in any given subset are not significantly different from first mean in that subset; conversely means underscored with broken line are significantly different.

A. Photoperiod DD

1. Shortest significant ranges ($P = 0.05$)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Rp:	7.27	7.66	7.92	8.07	8.22	8.33	8.43	8.51	8.56

2. Comparisons

Month:	9/29/65	7/14/65	12/30/65	11/30/65	11/2/65	5/13/66	3/3/66	2/1/66	9/1/66	4/6/66
Means (μ)	6.0	6.1	7.4	8.4	8.7	11.1	11.2	11.4	12.3	14.2

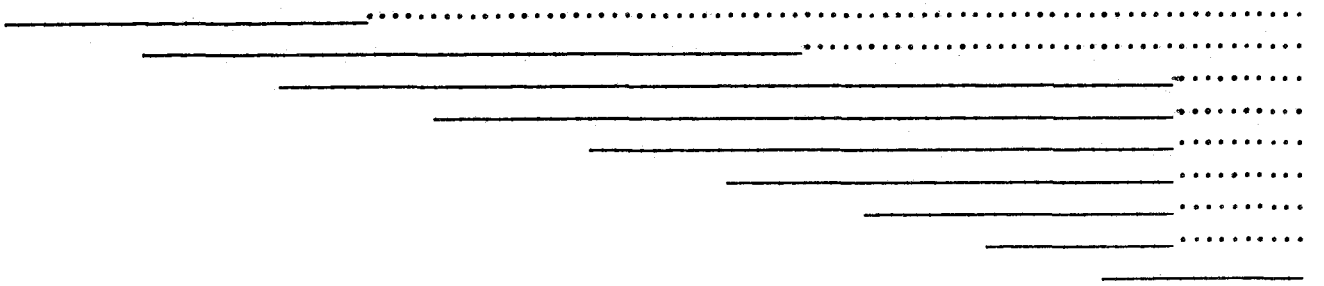
B. Photoperiod 8.5L

1. Shortest significant ranges ($P = 0.05$)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Rp:	4.39	4.62	4.76	4.87	4.94	5.02	5.07	5.11	5.14

2. Comparisons

Month:	12/30/65	11/30/65	5/13/66	4/6/66	8/30/65	2/1/66	11/2/65	9/29/65	9/1/66	3/3/66
Means (μ)	5.2	6.1	6.8	7.0	7.2	7.3	7.8	8.1	8.8	10.9



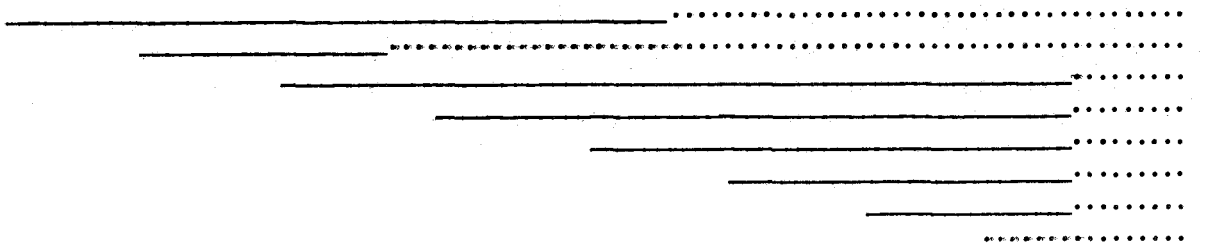
C. Photoperiod 12L

1. Shortest significant ranges ($P = 0.05$)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Rp:	5.95	6.26	6.45	6.59	6.70	6.80	6.86	6.93

2. Comparisons

Month:	8/30/65	12/30/65	11/30/65	9/29/65	2/1/66	4/6/66	3/3/66	11/2/65	9/1/66
Means (μ)	6.3	6.8	7.4	7.7	7.7	8.4	8.8	9.2	14.8



Appendix XVI. continued

D. Photoperiod 16L

1. Shortest significant ranges ($P = 0.05$)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Rp:	6.33	6.67	6.87	7.07	7.14	7.25	7.31	7.38	7.42

2. Comparisons

Month:	5/13/66	11/30/65	12/30/65	8/30/65	2/1/66	4/6/66	9/29/65	11/2/65	3/3/65	9/1/66
Means (μ)	5.9	6.2	6.4	6.8	7.1	7.3	7.6	8.0	9.1	11.7

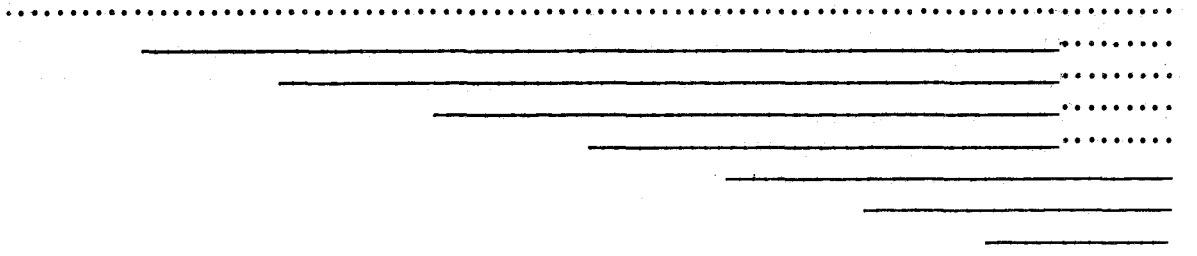
E. Photoperiod LL

1. Shortest significant ranges ($P = 0.05$)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Rp:	5.20	5.47	5.65	5.76	5.87	5.95	6.02	6.08

2. Comparisons

Month:	11/30/65	12/30/65	4/6/66	8/30/65	9/29/65	9/1/66	11/2/65	2/1/66	3/3/66
Mean (μ)	5.5	6.8	7.0	7.2	7.8	7.9	8.1	9.3	10.2



F. Photoperiod NL

1. Shortest significant ranges (P = 0.05)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Rp:	4.73	4.98	5.13	5.24	5.33	5.41	5.46	5.51

2. Comparisons

Month:	5/13/66	12/30/65	11/30/65	9/29/65	11/2/65	4/6/66	8/30/65	2/1/66	9/1/66
Mean (μ)	6.1	6.3	6.9	7.1	7.8	8.3	8.5	8.9	13.8

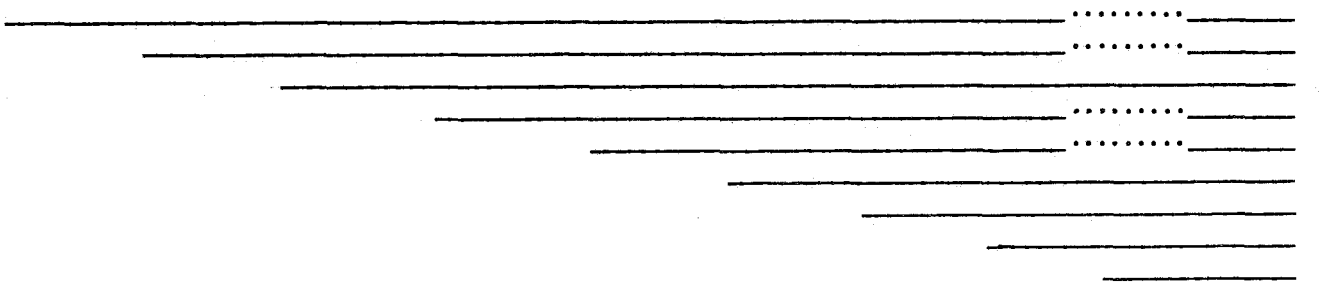
G. Photoperiod SL

1. Shortest significant ranges (P. = 0. 05)

p:	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Rp:	5. 32	5. 60	5. 77	5. 90	5. 99	6. 08	6. 14	6. 19	6. 23

2. Comparisons

Month:	5/13/66	8/30/65	12/30/65	11/2/65	9/29/65	4/6/66	11/30/65	9/1/66	2/1/66	3/3/66
Mean (μ)	6. 5	7. 0	7. 2	7. 2	7. 6	7. 8	8. 2	8. 5	8. 9	9. 0



APPENDIX XVII.

Observations on early sexual maturation of juvenile Alsea winter steelhead trout retained in freshwater beyond the normal period of downstream migration (Wagner, unpublished).

	No. fish examined			Precocial males			
					Size		
					Fork length	Weight	
Date	Males	Females	Total	Number	(cm)	(g)	GSI
10/8/61	6	6	12	2	17.2	-	unknown
					20.9	-	unknown
11/8/61	2	3	5	0	-	-	-
25/8/61	2	3	5	2	18.4	74.5	unknown
					18.4	66.2	unknown
28/8/61	3	2	5	0	-	-	-
6/9/61	6	3	9	0	-	-	-
14/9/61	4	4	8	2	19.3	91.1	11.942
					20.7	94.2	8.874
18/9/61	2	3	5	0	-	-	-
19/9/61	3	7	10	3	21.2	109.4	9.140
					32.5	382.8	7.889
					26.5	235.1	11.709
21/9/61	6	3	9	1	18.0	82.1	unknown
22/9/61	6	3	9	2	31.8	366.1	unknown
					28.8	304.3	unknown

APPENDIX XVIII.

Percentage of population maturing and the gonosomatic index for groups of fish reared under different photoperiod and temperature cycles in Experiment II.

Treatment[a]	Percent population maturing: Entire period[b]	Percent population maturing: June 1968[c]	Mean GSI and fish size: Immature Males	Mean GSI and fish size: Maturing Males	Mean GSI and fish size: Immature Females
SL-NT	0.2 (2)	2.2 (1)	0.046 ± 0.007[e] fl = 22.6 ± 2.9[f] wt = 114.4 ± 7.6[f] (16)	1.221 fl = 26.7 wt = 206.9 (1)	0.228 ± 0.042 fl = 22.6 ± 0.4 wt = 114.6 ± 6.2 (28)
SL-CT	0.8 (4)	6.1 (3)	0.034 ± 0.004 fl = 22.9 ± 0.5 wt = 125.1 ± 9.5 (21)	1.936 ± 0.004 fl = 25.0 ± 1.0 wt = 179.6 ± 18.5 (3)	0.283 ± 0.025 fl = 22.7 ± 0.04 wt = 124.4 ± 7.0 (25)
NL-NT	1.3 (6)				
NL-AT	0 (0)				
NL-DT	1.5 (7)			0.523 ± 0.114 fl = 24.1 ± 0.8 wt = 156.2 ± 7.4 (3)	
NL-CT	0.6 (3)				
NLB-CT	4.2 (21)				

[a] See abbreviations on pages 22-23.

[b] The percentage of maturing or mature males in each group is a minimal estimate based only on fish observed during routine length and weight sampling, fish killed for endocrine glands from June 1967 to June 1968, and those in selected groups killed at the termination of the experiment to determine the GSI.

[c] Percentage of maturing and mature males in population in June 1968 when fish remaining in selected groups were killed to determine GSI.

[d] Number of fish in sample.

[e] GSI ± 1 standard error.

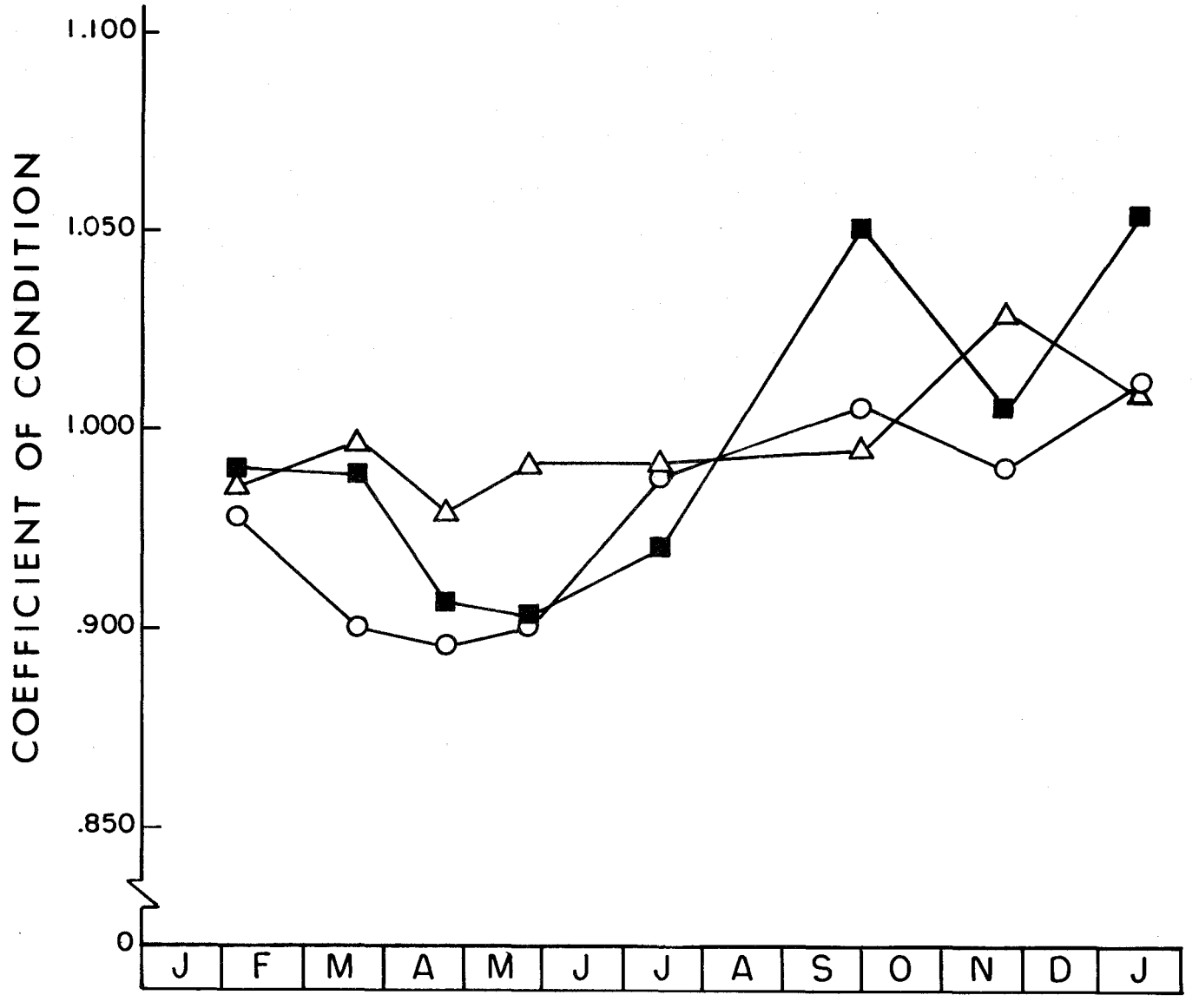
[f] fl = fork length in cm or wt = weight in grams ± 1 standard error.

Appendix XVIII. continued

Treatment	Percent population maturing: Entire period	Percent population maturing: June 1968	Mean GSI and fish size: Immature Males	Mean GSI and fish size: Maturing Males	Mean GSI and fish size: Immature Females
NLG-CT	2.8 (13)				
NLR-CT	5.2 (24)				
AL-NT	4.5 (22)	40.0 (12)	0.040 ± 0.002 fl = 21.6 ± 1.0 wt = 107.0 ± 15.3 (6)	7.693 ± 0.320 fl = 23.7 ± 0.5 wt = 162.3 ± 10.9 (12)	0.267 ± 0.024 fl = 21.0 ± 0.8 wt = 104.9 ± 8.4 (12)
AL-AT	4.8 (23)	29.7 (11)	0.033 ± 0.003 fl = 23.3 ± 0.7 wt = 144.3 ± 14.6 (8)	6.413 ± 0.487 fl = 24.1 ± 0.7 wt = 182.2 ± 16.6 (11)	0.218 ± 0.007 fl = 22.4 ± 1.4 wt = 142.6 ± 10.6 (18)
DL-NT	0.6 (3)	2.1 (1)	0.035 ± 0.015 fl = 23.4 ± 0.5 wt = 128.0 ± 8.2 (22)	0.458 fl = (?) wt = 102.2 (1)	0.238 ± 0.012 fl = 22.8 ± 0.5 wt = 125.0 ± 8.8 (25)
DL-DT	0.8 (4)	2.0 (1)	0.046 ± 0.008 fl = 23.0 ± 0.4 wt = 118.5 ± 5.7 (23)	0.418 fl = 24.7 wt = 162.0 (1)	0.245 ± 0.014 fl = 22.6 ± 0.4 wt = 114.4 ± 6.6 (26)
RL-CT	9.5 (42)	29.7 (27)	0.041 ± 0.002 fl = 20.2 ± 0.4 wt = 93.2 ± 6.0 (29)	7.020 ± 0.164 fl = 21.6 ± 0.4 wt = 131.5 ± 9.0 (27)	0.266 ± 0.010 fl = 20.9 ± 0.4 wt = 106.7 ± 5.3 (35)
DD-NT	0 (0)				
DD-CT	0.4 (2)			4.779 fl = 19.5 wt = 106.3 (1)	

APPENDIX XIX.

Seasonal changes in coefficient of condition for two-year-old steelhead. Values calculated from growth data given by Lichtenhled (1966; Table 34, p. 144).


COEFFICIENT OF CONDITION
1.100
1.050
1.000
.900
.850
0
J
F
M
A
M
J
J
A
S
O
N
D
J