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Title: SOME MORPHOLOGICAL AND BIOCHEMICAL CHANGES IN STEELHEAD TROUT DURING THE PARR-SMOLT TRANSFORMATION

Abstract approved: Redacted for Privacy
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This study was initiated to determine changes in body morphology, length-weight relationship, and chemical composition for juvenile steelhead trout from the pre-migratory through the post-migratory period, January through July. A linear discriminant analysis was run on migrants and non-migrants using coefficient of condition (K_{FL}) and nine relative growth measurements as the first discriminant, and K_{FL} and fork length as the second discriminant. Winter-run steelhead trout originating from Big Creek and the Sandy River, in Oregon, were used as experimental animals.

The parr-smolt transformation in winter steelhead is size dependent and characterized by a marked decrease in body depth, coefficient of condition, and lipid level. Changes in depth measurements and the length-weight relationship provided the most

meaningful measure of morphological change at the time of the parr-smolt transformation.

The coefficient of condition of the larger migrant-sized fish (140 to 209 mm) declined continuously from February through May but increased in June and July. The mean K_{FL} for smaller fish ($\leqslant$ 139 mm) declined from December through February, but remained relatively stable from March through June, with an upward trend in July. Juvenile steelhead migrating downstream within the first few days after stocking had a lower mean K_{FL} than the population at release. The discriminant analysis indicated that K_{FL} and fork length were nearly as powerful in separating smolts from parr as were all ten variables.

During the migratory period lipid content decreased significantly in the larger fish but remained relatively constant in small fish. Seasonal changes in protein levels occurred in the larger fish, while protein content for the smaller fish remained relatively constant throughout the period. The amount of moisture and ash did not change within a group.

Some Morphological and Biochemical Changes in Steelhead Trout During the Parr-Smolt Transformation

by

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SOME MORPHOLOGICAL AND BIOCHEMICAL CHANGES IN STEELHEAD TROUT DURING THE PARR-SMOLT TRANSFORMATION

INTRODUCTION

One of the most interesting and striking aspects of the biology of the steelhead trout, Salmo gairdneri, is its parr-smolt transformation or metamorphosis. In many anadromous salmonids the process of smolting includes profound changes in morphology, physiology, and behavior that precedes seaward migration. These changes transform the cryptic-colored, bottom-dwelling fish (parr) into a silvery pelagic animal (smolt) fitted for life in the marine environment (Hoar, 1963). In the steelhead trout the parr-smolt transformation is markedly size dependent and seasonal in occurrence (Wagner, Wallace, and Campbell, 1963; Wagner 1968). Morphological and physiological changes taking place during the parr-smolt transformation are of general biological interest for understanding the early stages of development. These changes also are of direct importance to biologists concerned with the recognition of potential steelhead migrants.

Morphological data have been used extensively in systematic, racial, and relative growth studies of fish (Martin, 1949). Evropeitseva (1957) found that Atlantic salmon (Salmo salar) smolts differed from parr in having longer and thinner caudal peduncles, less depth to the body, and relatively shorter pectoral and ventral fins. Holding Atlantic salmon in freshwater after smolting resulted in a complete loss of the silvery coloration, reduction in relative caudal peduncle length, and an increase in body and caudal peduncle depths (Evropeitseva, 1962). A decrease in the coefficient of condition (K_{FL}) at the time of parr-smolt transformation has been described for Atlantic salmon by several fishery scientists (Hoar, 1939a; Evropeitseva, 1957; Houston and Threadgold, 1963).

Differences in chemical composition have been noted between parr and smolts of juvenile sockeye salmon (Oncorhynchus nerka) by Kizevetter (1948) and Akulin (1966), in Atlantic salmon by Lovern (1934) and Malikova (1957), and in coho salmon (Oncorhynchus kisutch) by Vanstone and Markert (1968). Qualitative as well as quantitative changes in chemical constituents were observed by Lovern (1934) in the fatty acids and by Malikova (1957) in the amino acids.

Morphological and chemical changes occurring in steelhead trout during the parr-smolt transformation have not been previously described. The objective of this study was to determine changes in body morphology, length-weight relationship, and chemical composition for juvenile steelhead trout from the pre-migratory through the post-migratory period, January through July.

METHODS

General

Winter-run steelhead trout originating from Big Creek and the Sandy River were used as experimental animals. Big Creek enters the Columbia River about 10 miles from the ocean; the Sandy River enters the Columbia 80 miles from the ocean.

The eggs were incubated and the two stocks of fish reared under identical conditions at Gnat Creek Hatchery. The hatchery is located on the lower Columbia River, about 15 miles from the ocean, and is operated by the Oregon State Game Commission. The fish were fed a commercially prepared diet (J. R. Clark Co., Salt Lake City, Utah) at a rate based on fish size and water temperature. Seasonal water temperature ranged from 5^{o} to $13^{o}C$ during the sampling period.

Big Creek steelhead were reared in a single raceway; the larger number of Sandy River fish were reared in two raceways. For this study, the two groups of Sandy River fish were treated as a single population.

Sampling Technique

Fish in the hatchery, and hatchery and wild migrants were routinely sampled for length and weight. Specimens were collected for chemical analysis and morphological measurements concurrently with the length-weight samples. Individual fish were anesthetized in MS-222 (Tricane Methanesulfonate), weighed to the nearest 0.1 g, and measured to the nearest millimeter (fork length). Fish collected for morphological measurements were fixed in 10% formalin for 10 days and stored in 70% alcohol. Prior to sampling, fish in the hatchery were starved for 24-36 hours. A sample of fish in the rearing pond was obtained after lowering the water level and crowding the fish.

On May 11-13, 1964, about 82,000 juvenile steelhead of Sandy River stock were released about eight miles above Marmot Dam on the upper Sandy River. A total of 39,000 juvenile steelhead from Big Creek stock was released at the same location on May 11, 1964. Some of the hatchery fish migrating downstream were captured and sampled at the Marmot Dam trapping facility.

Morphological Measurements

The Sandy River and Big Creek stocks were examined each month for changes in length-weight relationship (coefficient of condition or K_{FL}) at the hatchery. The mean coefficient of condition ($\bar{K}_{FL}$) was calculated by using the equation

$$\frac{\Sigma \frac{100W}{L^3}}{N}$$

where,

W = weight in grams,

L = fork length in centimeters, and

N = sample size.

The population was divided into two size groups for the computation of mean K_{FL}. The first group included fish from 70-139 mm in length (non-migrants) and the second group (potential migrants) ranged from 140-209 mm in length. Fish from 140 to 159 mm appeared to be intermediate with respect to the occurrence of smolting, but for purposes of presentation they have been included in the potential migrant group.

The study of relative growth of certain external body parts was based on specimens from the Big Creek stock collected from February through July, 1964. The monthly collections consisted of 5 to 10 fish from each available 10 mm size group. Fork length, standard length, and weight were taken prior to fixation and the length-weight relationship was computed from these measurements. The following measurements were made on each preserved specimen for the relative growth of certain body parts:

Fork length	= tip of snout to fork of caudal fin;
Standard length	= tip of snout to end of hypural plate;
Head length	= tip of snout to terminal edge of opercle;
Trunk length	= terminal edge of opercle to insertion of anal fin;
Caudal fin length	= end of hypural plate to tip of caudal fin;
Dorsal fin length	= origin of dorsal fin to insertion

		of dorsal fin;
Body depth	=	maximum depth anterior to origin of dorsal fin;
Caudal peduncle depth	=	minimum depth of caudal peduncle.

All morphological measurements were made to the nearest millimeter. Linear body measurements were obtained with a measuring board contructed such that a sliding arm with an adjustable pointer could be used to make the individual projected measurements. Measurements of the dorsal fin and of depth were made with dial calipers.

The relationship of body part to fork length is best represented by a curved line which is conveniently rectified to form a straight line by use of logarithmic coordinates (Huxley, 1932; Milne, 1948). When $K = 1$, growth rate of the body part and fork length are equal and the relationship is called isometric growth. The mean values of each morphological measurement were plotted on logarithmic coordinates to show the monthly rates of change with size. These plots related the rate of change to isometric growth ($K = 1$). Actual K values were not calculated for each month. The percentage of standard length for the 130-139, 160-169, and 190-199 mm size groups was calculated for the five most important morphological characters. These characters were selected to illustrate changes in over-all body form taking place during the sampling period.

Chemical Analysis

Juvenile steelhead from the two stocks were examined for changes in chemical composition. Each month fish were selected for analysis from two categories, those which were of migrant size (167 mm and 191 mm in FL), and those which were not of migrant size (134 mm in FL). The size categories for the migrant and non-migrant groups were based on length distribution of downstream migrants captured on the Sandy River in the spring of 1963 (Wagner, n. d.). Three or more fish (minimum combined weight of 100 g) were blotted dry and then placed in a plastic bag that was collapsed by submersion in water and then sealed. The process was repeated with a second bag and the sample was frozen. Three samples were taken for each of the size groups used in the study, and the results of the three analyses were averaged.

The analyses were carried out at the Department of Agricultural Chemistry, Oregon State University, according to approved methods (Association of Official Agricultural Chemists, 1963). The frozen fish samples were thawed and autoclaved in sealed jars for 45 minutes at 15 pounds pressure to soften the bone before they were reduced to a homogeneous paste with a mortar and pestle. Samples were analyzed from one to two months after freezing.

Difficulties arise in detecting chemical changes in body composition when the data are in the form of percentage of total weight (Parker and Vanstone, 1966). In order to circumvent this difficulty, actual weights of each body component were estimated. Because the mean length of fish making up the samples varied slightly from month to month, the weight of each component was estimated for a fish of a common length, assuming no difference in relative weight or shape. The common length was selected as the most frequent mean length occurring in monthly samples.

The allometric equation,

$$W = aL^b,$$

where W = weight, L = length, and a and b are unknowns, was used to standardize samples to a common length. The exponent b is identified as the slope of the regression of log W on log L and log a is the intercept or height of the regression line where it crosses the ordinate. The equation (log adjusted length-log actual length) 3 + log actual weight = log adjusted weight, was used to standardize all samples to the common length.

Discriminant Analysis

The major objective of the linear discriminant analysis was to distinguish a parr from a smolt. An attempt at cluster analysis using the technique of principle components failed because of the evolutionary nature of the parr-smolt transformation. The cluster analysis did reveal that fork length and K_{FL} were the two variables containing most of the information. Retrospectively, I concluded that the only way to solve the problem was to obtain a sample of fish representing parr and another sample representing smolts and conduct a linear discriminant function. The smolt group was made up of Sandy River native migrants and hatchery migrants of Big Creek stock. The non-migrant or parr group included fish from the hatchery during the pre-migratory period (January, February, and March).

Two linear discriminant analyses were made on migrants and non-migrants, one using K_{FL} and nine relative growth measurements, and the other K_{FL} and fork length. A discriminant function approach combines the values of several variables to derive a statistical partition between two or more groups. It is based on a statistical procedure originally developed by Fisher (1936). Analyses were made with the BMDO5M program, as modified for the CDC 3300 computer (Yates, 1967).

RESULTS

Relative Growth Rates and Proportionate Size of Body Parts

Seasonal changes in depth measurements provided the most meaningful measure of morphological change (Figure 1). Maximum body depth approached a line with $K = 1$ for fish with a standard length up to 120 mm (Figure 2). Fish larger than 120 mm standard length decreased in body depth ($K < 1$) during the migratory period (April, May, and June). Body depth decreased from 22.8% of standard length to 20.4% from the pre-migratory to migratory periods (Figure 1).

Caudal peduncle depth followed the same growth pattern as body depth (Figure 1). However, changes in this morphological character were not as great as those in body depth.

Head length approximated a line with $K = 1$ for animals up to 100 mm standard length; for animals greater than 100 mm, head length approximated a line with $K < 1$ (Figure 3). From January through July the 130 mm group showed a gradual increase in head length, from 21.8 to 22.8% of standard length, indicating that slower growing animals had larger heads (Figure 4). Head length for the 160 mm group was more variable and inconsistent throughout the experimental period. Animals in the 190 mm group had shorter heads than the 130 and 160 mm fish.

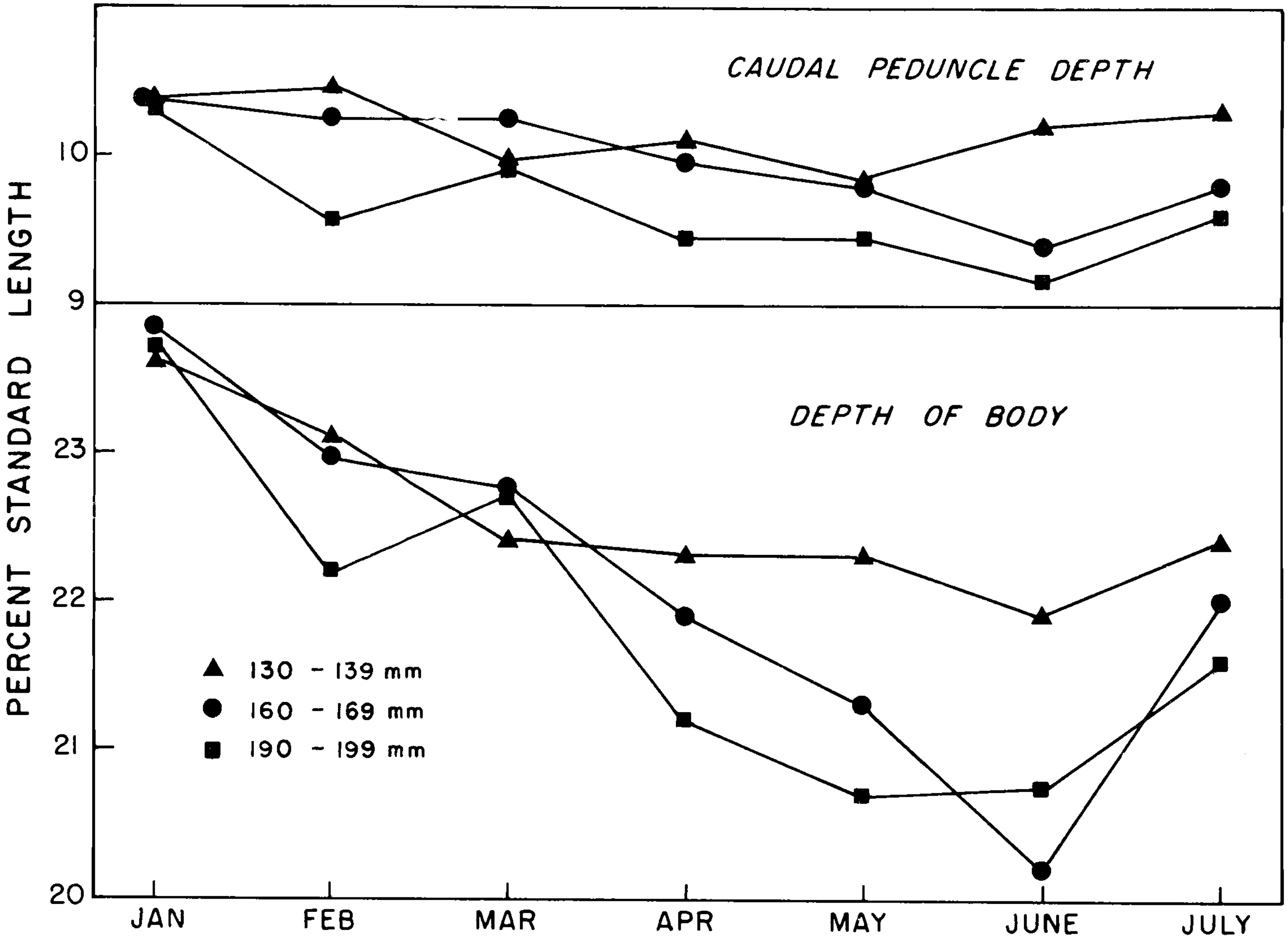

Figure 1. Body and caudal peduncle depth as a percentage of standard length for Big Creek juvenile steelhead from January through July, 1964.

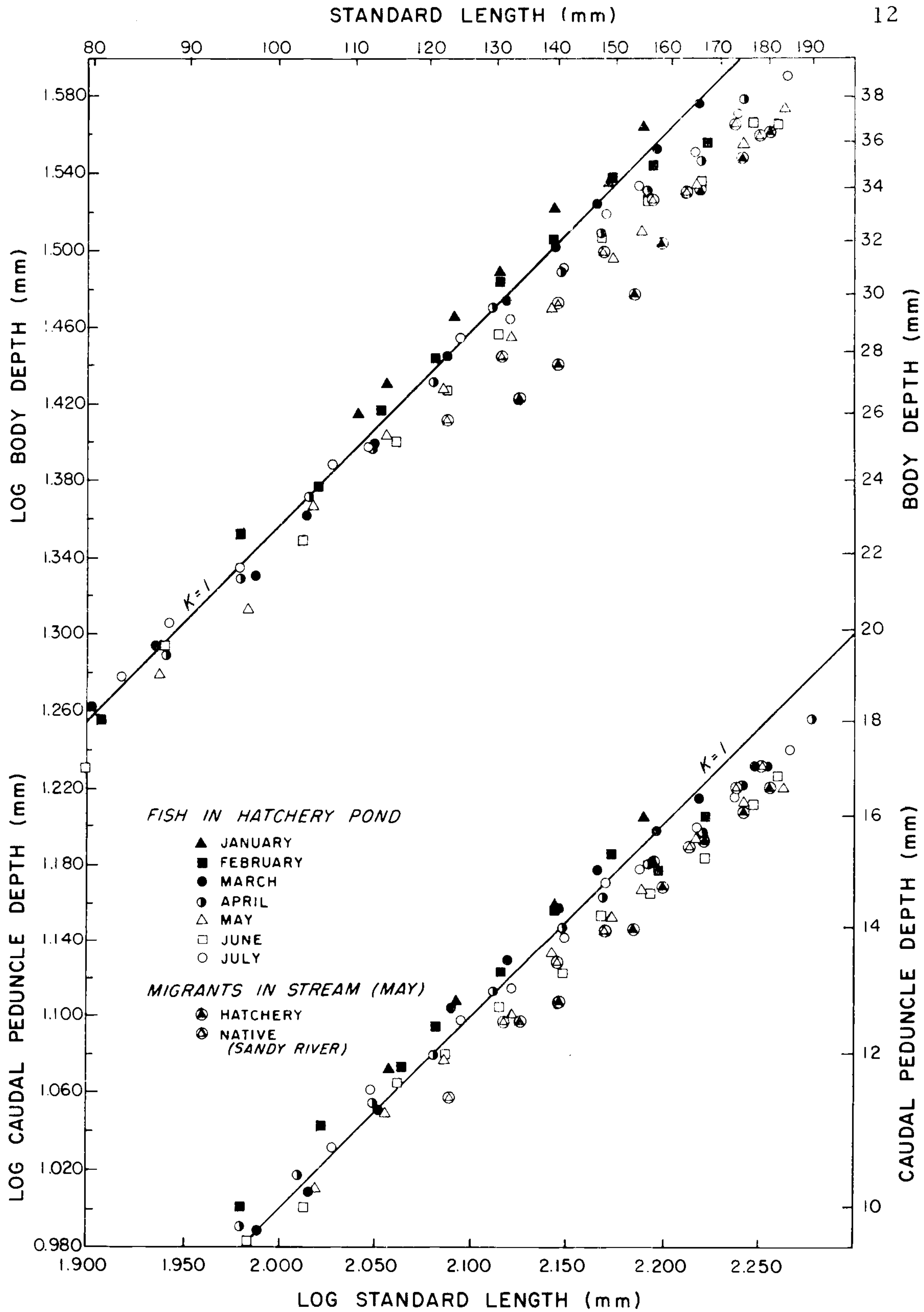

Figure 2. Relation of caudal peduncle and body depth to standard length for Big Creek juvenile steelhead in the hatchery and for migrants in the stream

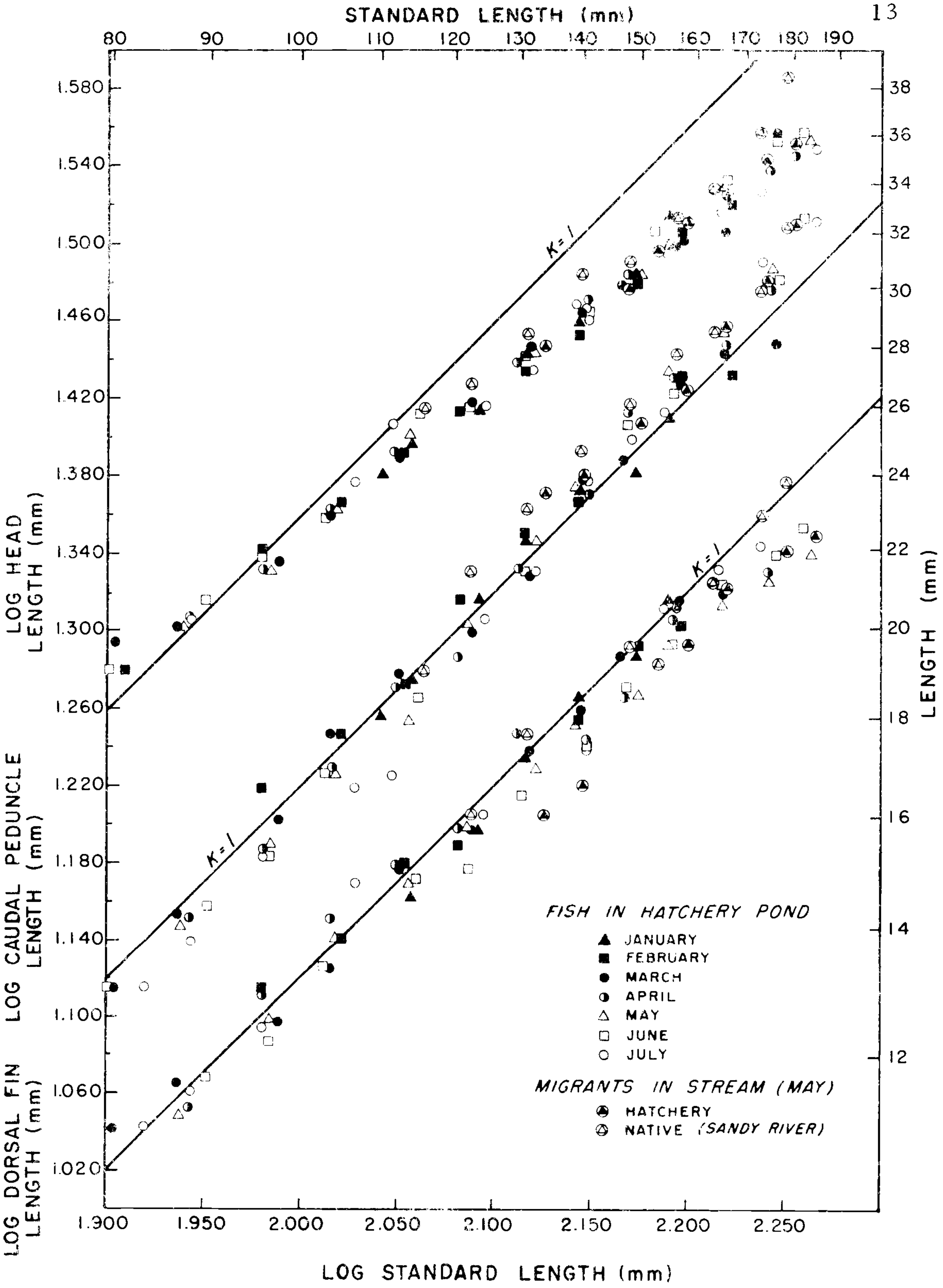

Figure 3. Relation of dorsal fin, caudal peduncle, and head length to standard length for Big Creek juvenile steelhead in the hatchery and for migrants in the stream.

Caudal peduncle length approximated a line with K = 1 for all groups, with a slight increase (K > 1) as the fish approached 120 mm standard length (Figure 3). Caudal peduncle length remained constant throughout the experimental period for the 160 and 190 mm groups, but decreased in the 130 mm group from 16.6% of standard length in April to 15.0% in July (Figure 4).

The length of the base of the dorsal fin approached a line with K = 1 for most of the groups up to a standard length of 120 mm (Figure 3). For fish ⩾120 mm, the growth pattern was characterized by K < 1.

Trunk length approximated a line with K = 1 for all groups sampled (Figure 5). As a percentage of standard length, it remained relatively constant for the 130 and 160 mm size groups (Figure 4). Measurements for the 190 mm groups increased from 62.3% of standard length to 64% during the pre-migratory period, with a decrease to 62.4% during the migratory period (Figure 4).

Caudal fin length was difficult to determine because of fin erosion, which resulted in increased variability (Figure 5). The growth pattern of the caudal fin was similar to that of the head.

No distinct pattern or trend between sexes could be detected for changes in any of the morphological characters. I concluded that no morphological difference existed between juvenile male and female steelhead during the pre-migratory, migratory, and post-migratory

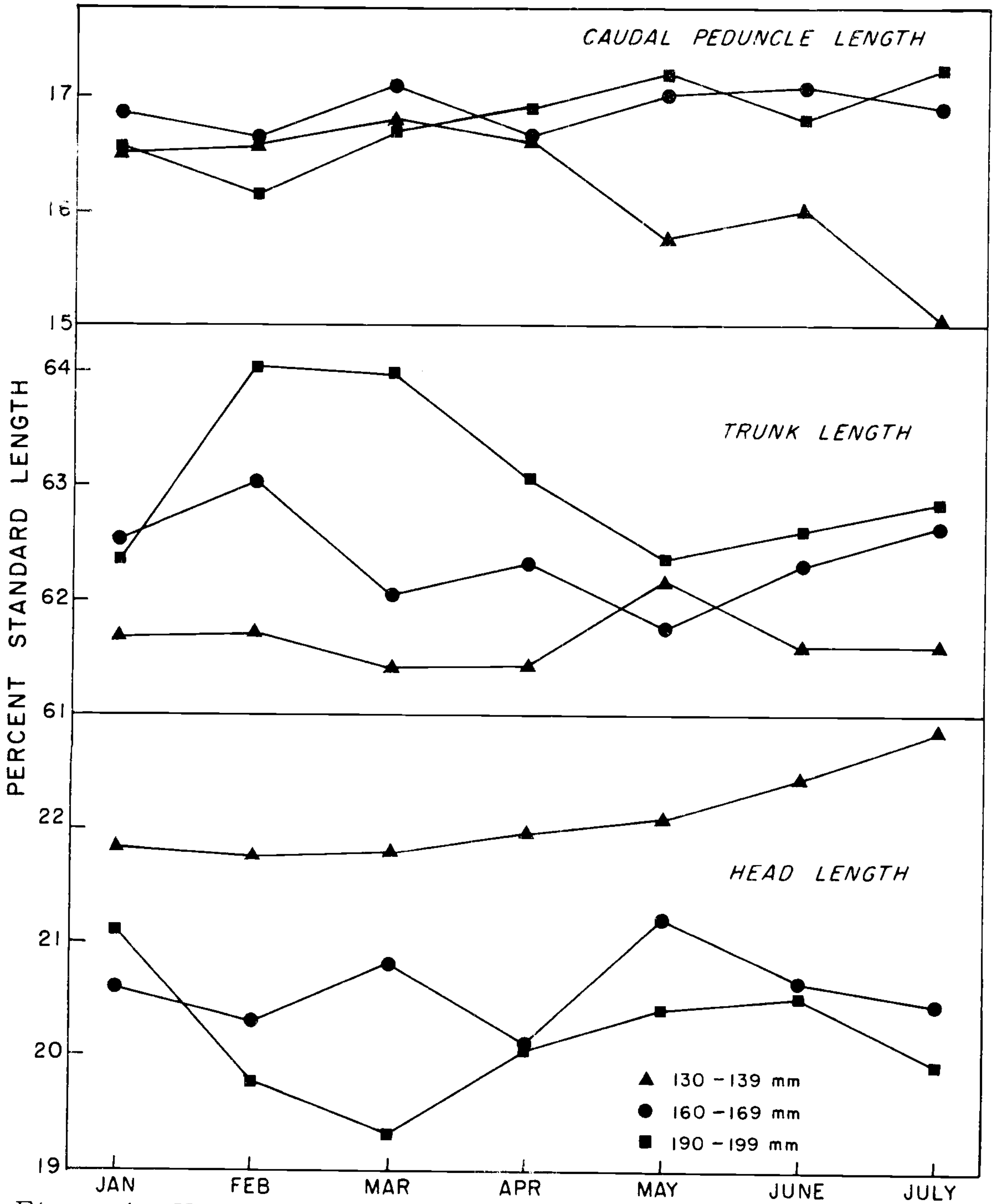

Figure 4. Head, trunk, and caudal peduncle length as a percentage of standard length for Big Creek juvenile steelhead from January through July, 1964.

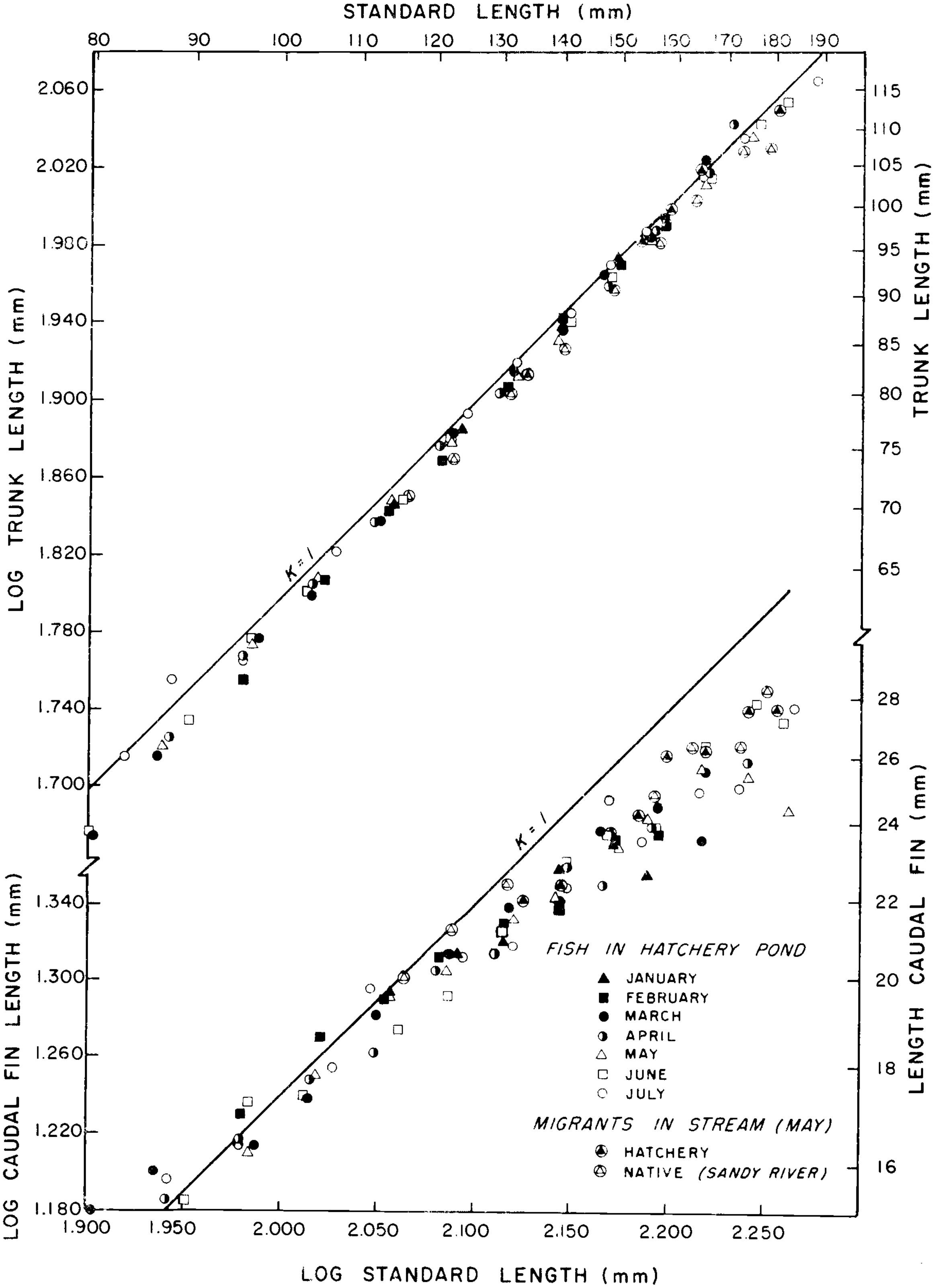

Figure 5. Relation of caudal fin and trunk length to standard length for Big Creek juvenile steelhead in the hatchery and for migrants in the stream.

period.

Coefficient of Condition

Changes in K_{FL} (Figure 6) were similar to changes in body depth (Figure 1). Coefficient of condition for the larger fish (140 to 209 mm) from the Sandy River stock paralleled that for the smaller Sandy River non-migrants initially, but was lower in April and May (Figure 6). The mean K_{FL} for both groups increased in July. Condition of fish in the larger size groups originating from Big Creek stock declined continuously from February through May and then increased in June and July. The mean K_{FL} for small fish (non-migrants) held at the hatchery declined during the December-February period for both Sandy River stock and Big Creek stock. The initial decline was followed by a more or less stable K_{FL} during the March-June period, with an upward trend noted in July.

Juvenile steelhead captured while they were migrating downstream within the first few days after stocking had a lower mean K_{FL} than the population at release (Figure 6). Big Creek fish released on May 11, 1964 had a mean K_{FL} of 0.896. In this group the mean K_{FL} for fish with a typical silvery smolt appearance was 0.876 (n = 819) as contrasted with 0.963 (n = 127) for fish with the typical parr appearance. Big Creek fish trapped eight miles below the release site from May 12-15 had a mean K_{FL} of 0.859 (Figure 6).

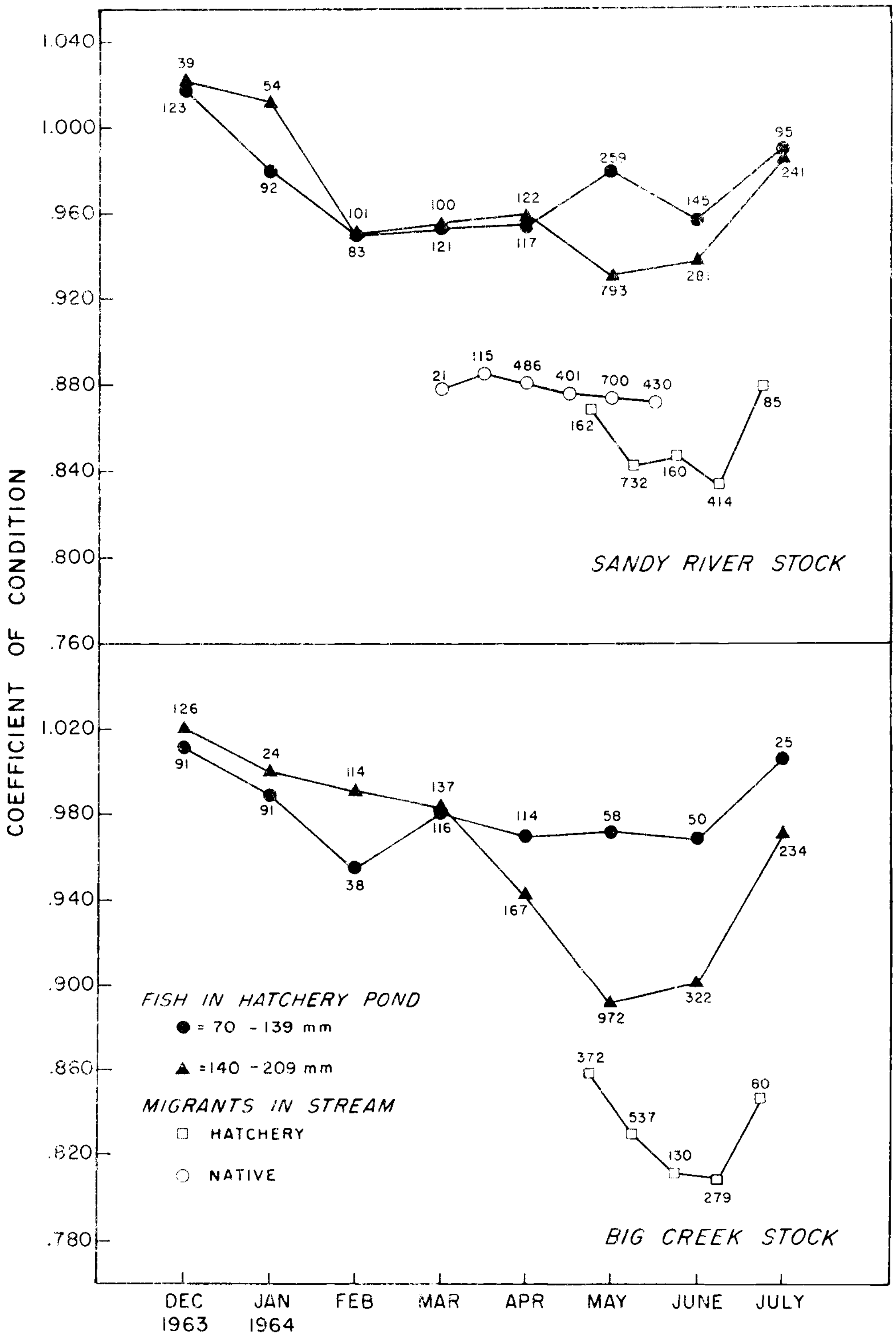

Figure 6. Coefficient of condition (K_{FL}) for Big Creek and Sandy River juvenile steelhead trout in the hatchery and for native and hatchery migrants. Sample sizes are noted at each point.

Condition of migrants captured during the ensuing days and weeks continued to decline until the latter part of June, but increased in July (Figure 6).

Steelhead of Sandy River origin released May 11-13, 1964 had a mean K_{FL} of 0.943. Fish with the silvery smolt appearance had a mean K_{FL} of 0.907 (n = 495), whereas the mean K_{FL} for those with a parr appearance was 0.970 (n = 515). The mean K_{FL} for migrants captured from May 12-15 was 0.869, considerably lower than that observed at the time of release (Figure 6). The condition of fish captured while they were moving downstream continued to decline through June and increased rapidly in the first weeks of July, as it had done for the Big Creek stock. The condition of the native migrants remained relatively constant during the March to May period (Figure 6).

Chemical Composition

There were significant changes in the chemical composition of the larger fish. In February, Big Creek steelhead in the 167 and 191 mm groups weighed more than fish of comparable length in May (Appendix A). The lower weight in May was the result of a loss of lipid and protein during the migratory period. Fish in the 134 mm size group had similar weights throughout the sampling period.

Lipid content showed the greatest changes in the 191 and 167 mm groups and the least change in the 134 mm group (Figure 7 and Appendix A, B, C, and D). Lipid constituted 2.47 g of the total adjusted body weight for fish in the 167 mm size group in February, while during May the mean weight of lipid was 0.54 g. In July lipid again made up 2.41 g of the total adjusted weight in this size group. Big Creek steelhead in the 191 mm group showed a similar pattern of variation in the amount of lipid.

Lipid content was similar for the 167 mm size groups of Big Creek and Sandy River fish during the pre-migratory period. At the time of release, fish of Sandy River origin in the 167 mm size group had a higher lipid content (1.25 g) than Big Creek fish of similar size (0.54 g). Hatchery fish from both stocks captured while they were migrating downstream shortly after release (May 12-18) were similar in chemical composition, however.

Hatchery migrants of Sandy River origin, captured while they were migrating downstream, were similar in chemical composition to the native stock in the Sandy River shortly after release (Appendix C). Hatchery migrants in the 167 mm group had a lipid content of 0.58 g in mid-May. By mid-June the lipid content of these fish had decreased to 0.32 g. Lipid content of native migrants in the 167 mm size group increased from 0.65 g in May to 0.70 g in June.

Seasonal changes in protein levels occurred in the 167 and 191 mm groups (Figure 7). In these groups protein decreased from

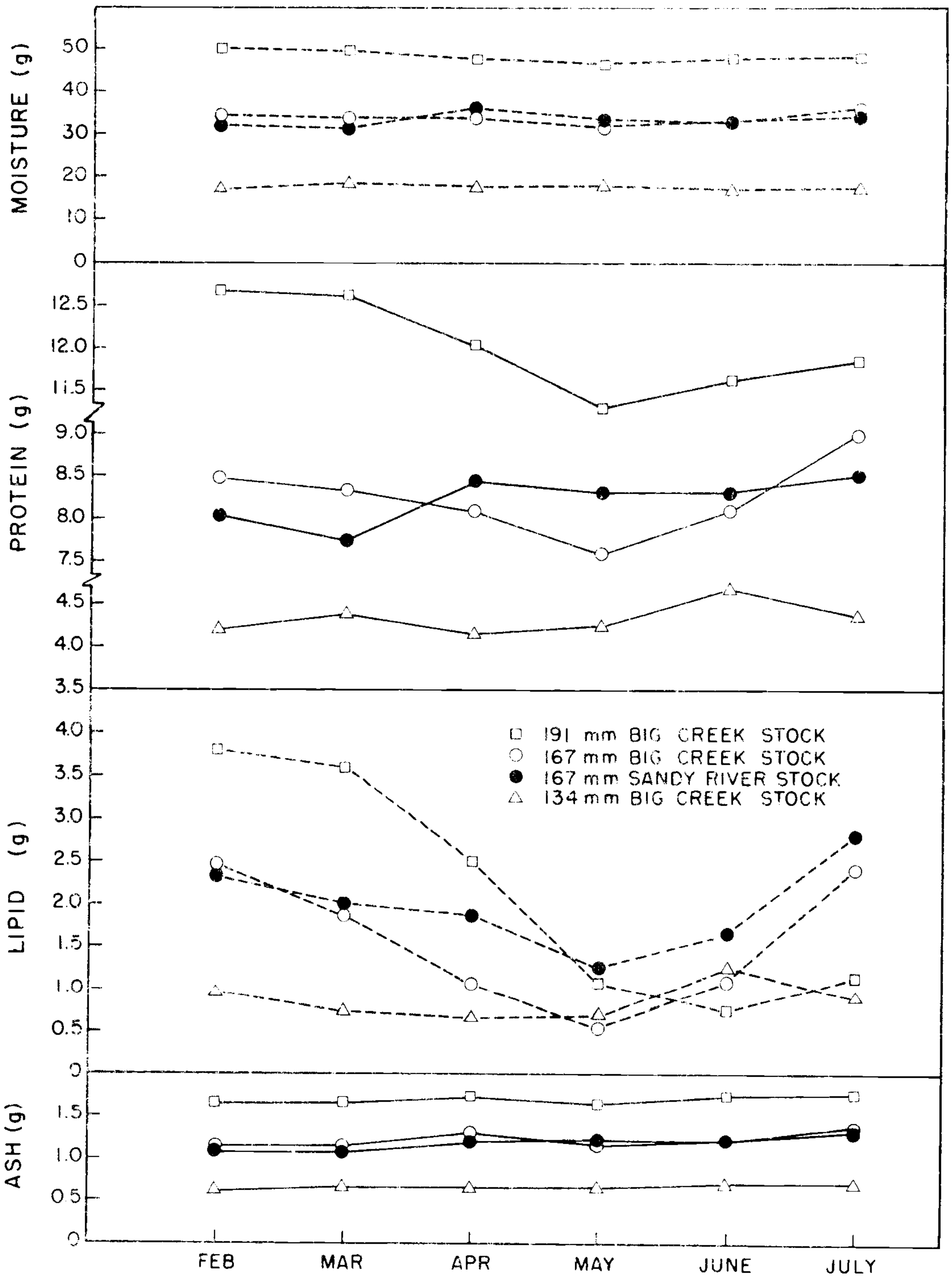

Figure 7. Body composition of Big Creek and Sandy River hatchery-reared steelhead from February through July, 1964.

February through May and then increased in June and July. This pattern was similar to that seen for lipid. Protein content for the 134 mm group remained relatively constant throughout the sampling period.

The amount of moisture and ash remained relatively constant for each size group (Figure 7). The Big Creek and Sandy River fish in the 167 mm group contained similar amounts of moisture and ash.

Fish Size and Migration

Length-frequency distributions of Sandy River steelhead differed markedly for fish in the hatchery and for hatchery migrants (Figure 8). The Sandy River fish ranged from 110-200 mm at the time of release, whereas the range of fork lengths for migrants captured was 150-200 mm. From an analysis of length frequencies, assuming little or no growth during this period, I estimated that 40 to 50% of the Sandy River fish that were stocked did not migrate downstream. In contrast, the length frequency distributions for fish released and migrants captured were almost identical for the Big Creek stock, suggesting that a large percentage of these animals migrated downstream.

At the time of release Big Creek steelhead were larger than the Sandy River fish (Table 1), because the adult spawning run of steelhead into Big Creek is about two months earlier than that in the

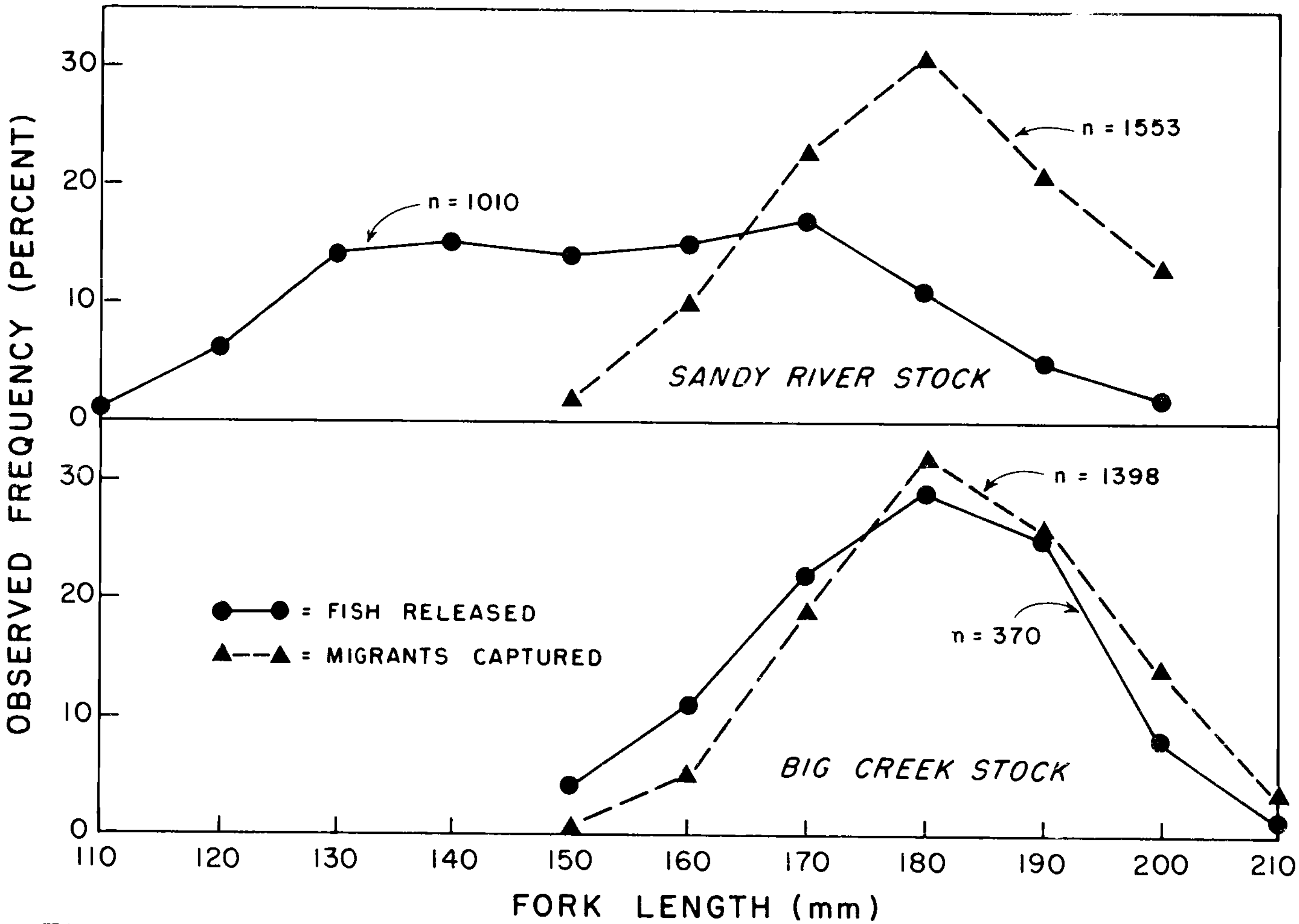

Figure 8. Length-frequency distribution for Big Creek and Sandy River steelhead for fish released from the hatchery and for migrants captured while moving downstream. The Sandy River release group was composed of fish from two ponds that had a later hatching date and wider range of hatching dates than did the Big Creek stock.

Sandy River. The earlier Big Creek spawning run resulted in an earlier hatching date for the eggs, giving the fry an additional period of growth. The length-weight relationship of Big Creek steelhead in the hatchery approached a line with a slope of 3.0 (Figure 9). The native migrants approached the same line. Hatchery migrants followed a line with a slope near 3.0 but fell into another growth stanza.

Table 1. Growth rate (weight in grams) of Big Creek and Sandy River steelhead during the experimental period, January through July, 1964.

Stock	Month						
	January	February	March	April	May	June	July
Big Creek	36.6	45.5	47.0	49.6	54.9	61.5	79.5
Sandy River	24.2	31.0	29.5	38.5	39.2	49.7	57.2

Coefficient of condition was similar for the Sandy River and Big Creek steelhead migrants regardless of length (Figure 10). However, the relationship of K_{FL} to fork length for fish released differed markedly for the two stocks of fish. The large proportion of non-migrants present in the Sandy River stock separated the K_{FL} values for steelhead released and migrants captured.

The frequency distributions of K_{FL} for the Big Creek fish at the time of release and for migrants captured (Figure 11) are almost identical, except for a downward shift for the migrants. The shift

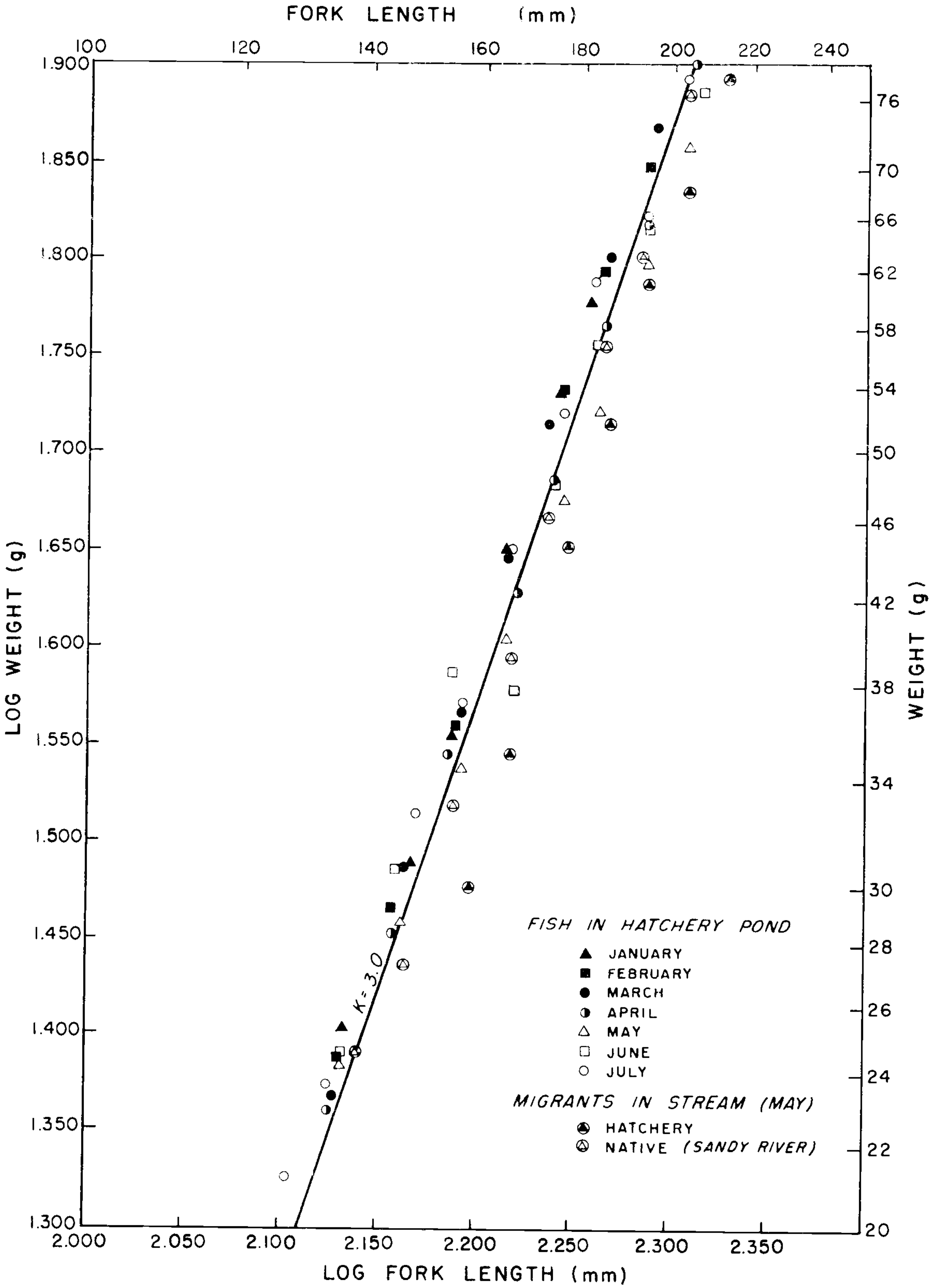

Figure 9. Relation of weight to fork length for Big Creek steelhead in the hatchery and for native and hatchery migrants.

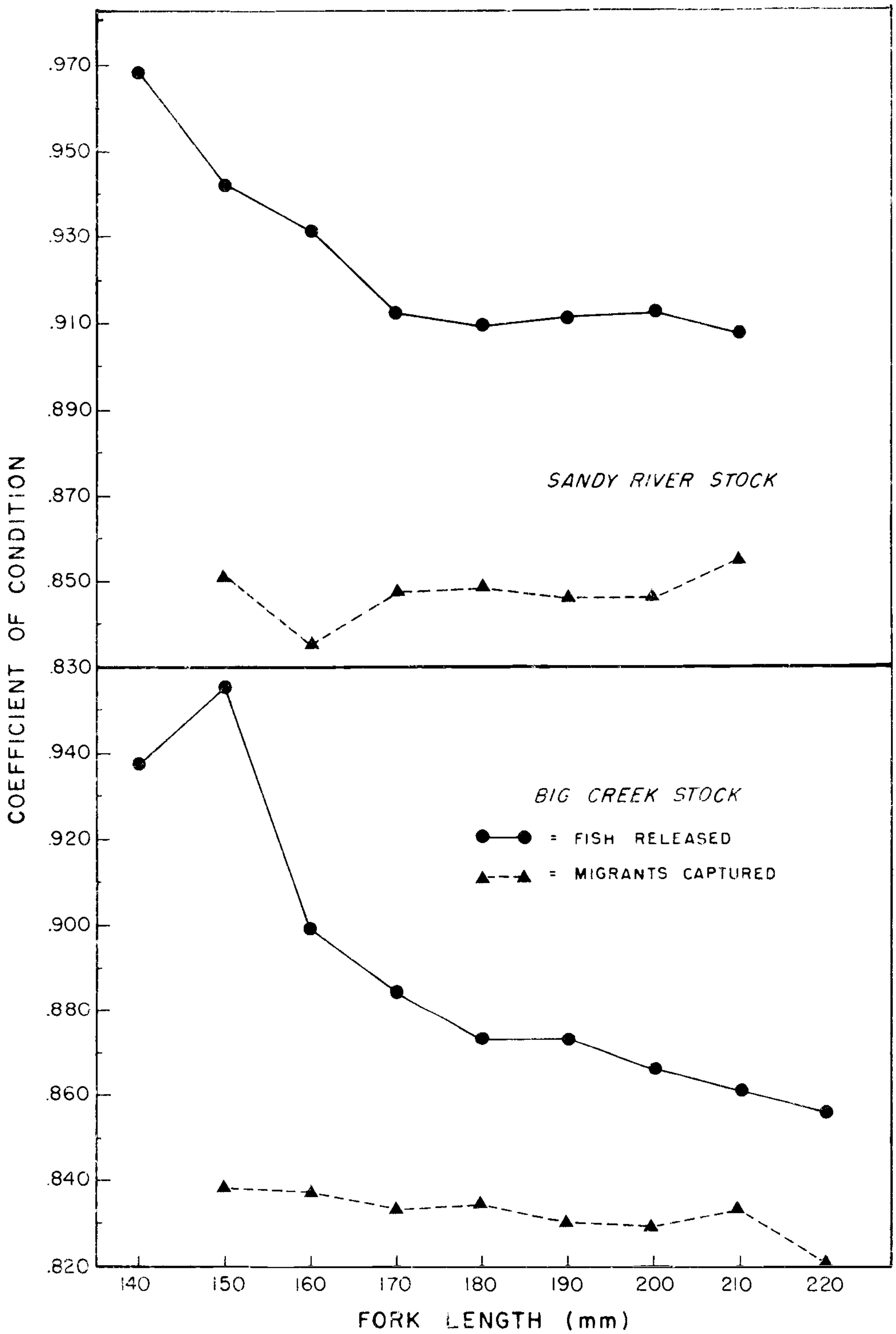

Figure 10. Relation of coefficient of condition (K_{FL}) to fork length for Big Creek and Sandy River steelhead, fish released from the hatchery and migrants captured while moving downstream.

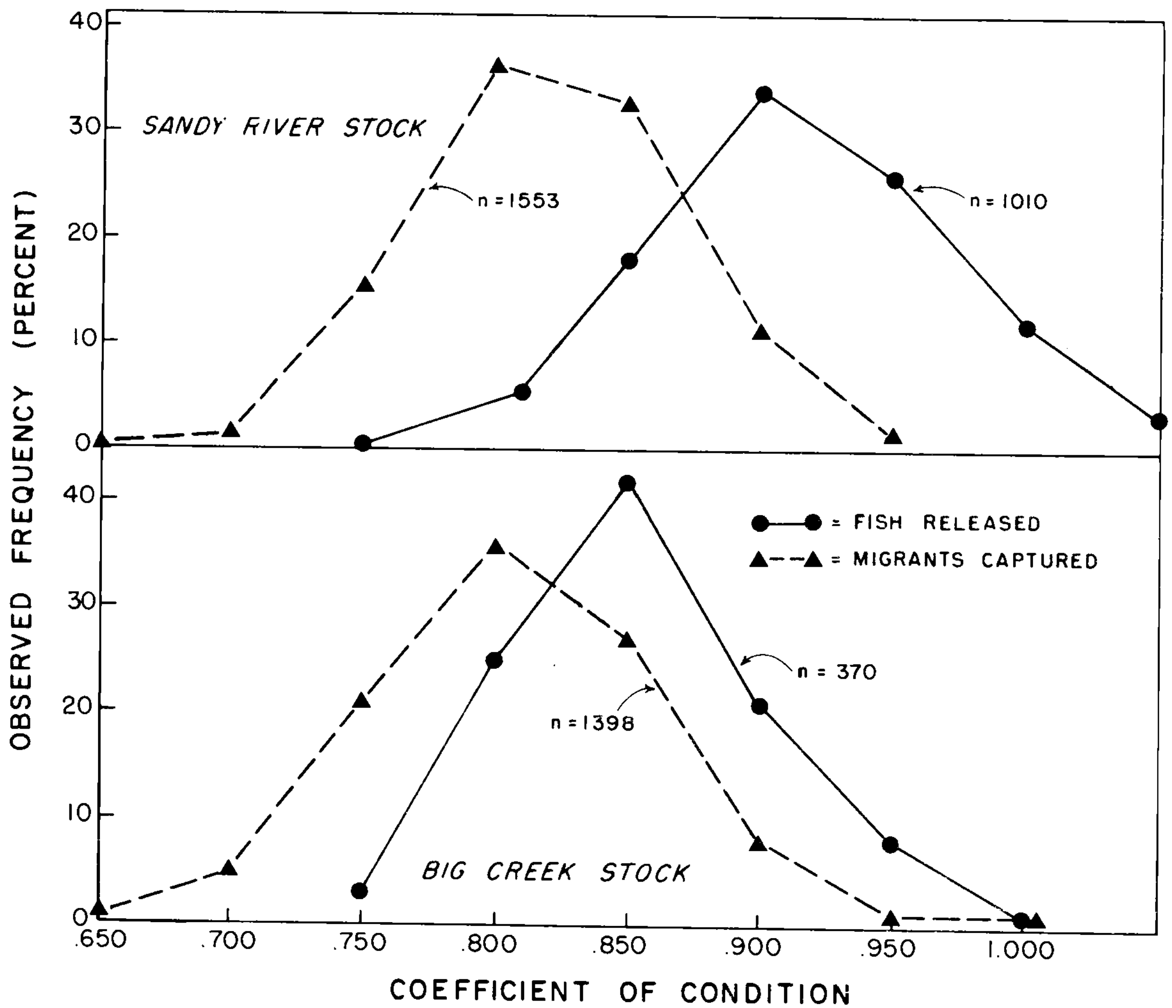

Figure 11. Frequency distribution of the coefficient of condition (K_{FL}) for Big Creek and Sandy River steelhead, fish released from the hatchery and migrants captured while moving downstream.

was greater for the Sandy River fish and again reflects the larger number of parr present in the population at the time of release.

Discriminant Analysis

A preliminary cluster analysis using the technique of principle components, showed that fork length and K_{FL} were the two most important variables. No other pair combinations of variables were used in the discriminant analysis.

A linear discriminant function was computed for a sample of fish representing parr and another sample of fish representing smolts. A summary of the discriminant analysis (Table 2) between smolts and parr indicates that the classification matrix using 10 variables was similar to the matrix resulting from K_{FL} and fork length.

Table 2. Summary of discriminant analysis between smolts and parr.

		Classification Matrix				
	Group	Smolt	Parr	Total	D^2	d.f.
10 variables	Smolt	158	4	162	1490.0**	10
	Parr	2	218	220		
		160	222	382		
2 variables	Smolt	143	19	162	773.4**	2
	Parr	5	215	220		
		148	234	382		

**Significant at .001 level.

With K_{FL} and fork length as the two variables, the equation

$$u = X_2 - .002191\ X_1$$

represents the discriminant line separating smolts and parr. In this equation X_2 and X_1 are K_{FL} and fork length respectively. If $u >$ 0.55428, the fish is classified as a parr and if $u < 0.55428$, the fish is classified as a smolt (Figure 12). The misclassified fish in Table 2 were very close to the discriminant line. If the fish are close to the discriminant line (Figure 12), the equation should be used for classification.

In the months of January, February, and March the two discriminants classified practically all of the fish into the parr group (Table 3). The number of smolts and parr does not reflect percentages of each in the population because the samples were not random. In the pre-migratory and post-migratory periods, an attempt was made to sample 5 to 10 fish from each available 10 mm size group. The number of smolts increased in April, peaked in May then decreased in June. The mean fork length ranged from 129 to 156 mm for parr for all samples. The mean K_{FL} ranged from 0.946 to 1.010 for all monthly samples of fish in the parr classification. The monthly mean K_{FL} for fish classified as smolts was lower than the mean K_{FL} for fish classified as parr.

The most important information gained by the discriminant analysis was that the first discriminant, which was calculated using

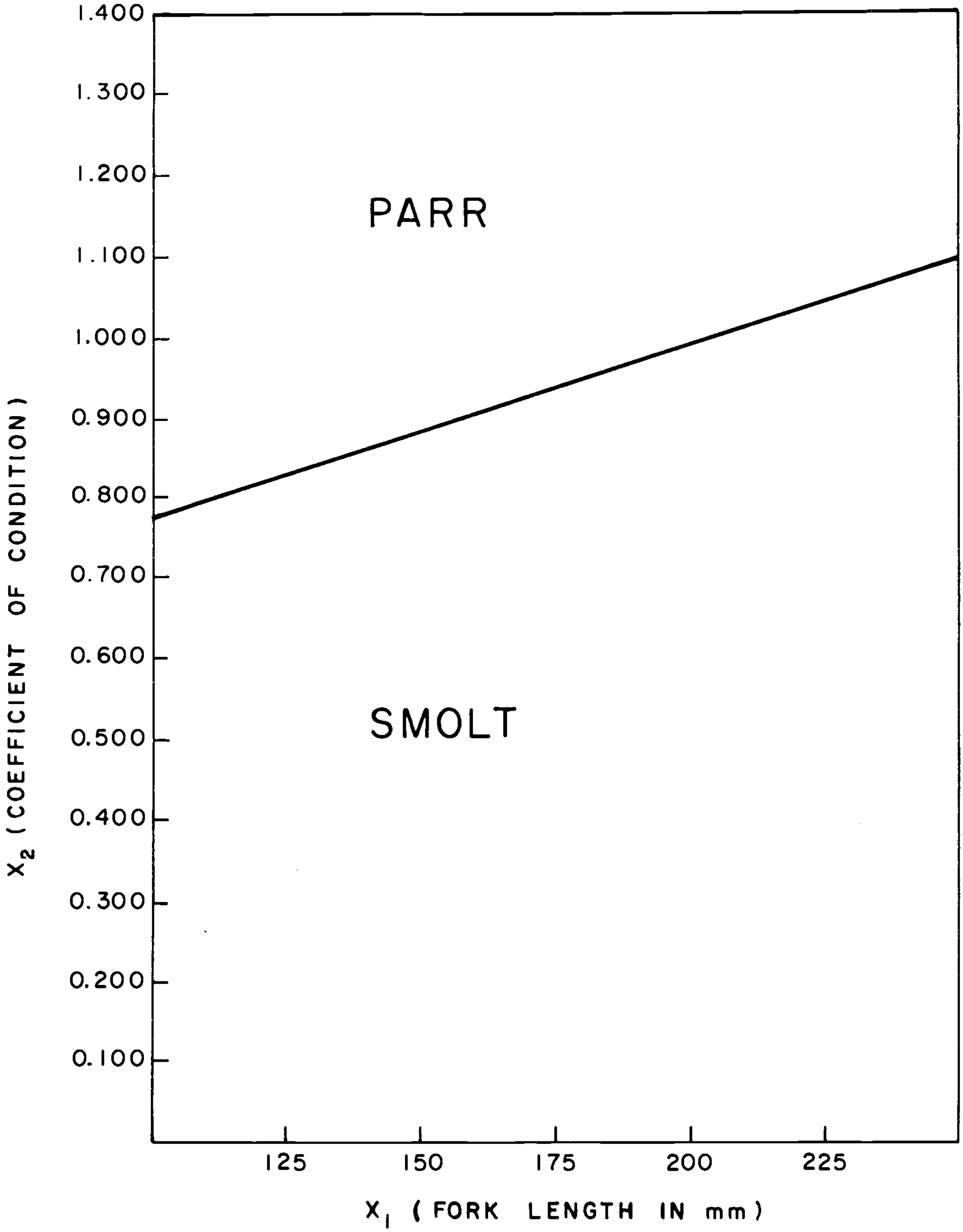

Figure 12. A discriminant function for steelhead trout, separating parr from smolts. The equation $u = X_2 - .002191X_1$ represents the discriminant line separating smolts and parr. If $u > 0.55428$, the fish is classified as a parr and if $u < 0.55428$, the fish is classified as a smolt.

Table 3. Number, mean fork length, and mean K_{FL} of Big Creek smolts and parr in the hatchery and migrants in the stream as separated by two linear discriminant functions.

Month	Discriminant	Number		Mean F. L (mm)		Mean K_{FL}	
		Smolt	Parr	Smolt	Parr	Smolt	Parr
January	1	0	53	0	156	0	0.996
	2	0	53	0	156	0	0.996
February	1	1	68	177	151	0.959	0.983
	2	3	66	186	150	0.943	0.984
March	1	1	97	172	142	0.951	0.977
	2	2	96	197	142	0.963	0.977
April	1	26	85	188	133	0.898	0.963
	2	32	79	188	129	0.901	0.966
May	1	70	64	183	132	0.861	0.955
	2	72	62	183	131	0.859	0.961
June	1	26	34	188	137	0.876	0.985
	2	26	34	190	135	0.873	0.988
July	1	13	43	197	146	0.887	1.010
	2	11	45	201	147	0.869	1.009
Hatchery	1	73	1	192	190	0.812	0.963
Migrants	2	74	0	192	0	0.814	0
Native	1	85	3	177	179	0.884	0.956
Migrants	2	69	19	180	166	0.870	0.946

ten variables, was similar to the second discriminant, calculated from fork length and K_{FL} alone. The similarity of these two discriminants indicates that fork length and K_{FL} were a good index of smolting in this sample of steelhead trout. The single exception might be the second discriminant as used for native migrants. One would expect a high percentage of the fish sampled to be smolts, but the second discriminant classified 69 fish as smolts and 19 as parrs. The 19 migrant fish classified as parr had a higher K_{FL} than fish classified as smolts, and their fork length ranged from 140 to 191 mm. A combination of the two factors was probably responsible for classifying these fish as parr.

DISCUSSION

The transition of a parr to a smolt is associated with changes in the physico-chemical properties of the body. The parr-smolt transformation in winter steelhead is characterized by a marked reduction in lipid, and a lesser reduction in protein. At the termination of downstream migration, lipid and protein return to the normal pre-migratory levels.

The decline in lipid and protein results in gross changes in K_{FL} and body depth for migrant-sized fish ($\geqslant$ 160 mm FL). A decrease in K_{FL} at the time of the parr-smolt transformation might be the result of the individual fish remaining the same length but losing weight in the form of lipid or protein, or the individual fish growing in length, but not proportionately in weight. Both events could be taking place simultaneously and the result would be a marked decrease in K_{FL}. The design for this study and the resulting data do not distinguish between these two events. Hoar (1951) makes the assumption that during the parr-smolt transformation in Atlantic salmon, the fish become slimmer through a loss of their body fat.

There are some unpublished data on steelhead growth that may provide some insight into the question of changes in K_{FL}. In hatchery-reared steelhead trout, both length and weight increased at a constant rate prior to smoltification (Wagner, n. d.). During the parr-smolt transformation, length increased at the same constant rate as that observed prior to smoltification, while weight was decreasing. The rates of change in length and weight after smoltification were similar to the rates of change prior to smoltification. This would suggest that the decline in K_{FL} was a result of the fish losing weight in the form of lipid and protein. There is a downward shift in weight (Figure 9) of steelhead in the hatchery during the month of May. The change in weight is also apparent for hatchery migrants. The decrease in weight of migrants could be partially a result of a reduced food intake. A sudden downward shift in weight at the transition to a smolt in Atlantic salmon was observed by Hoar (1939a).

Both stocks of fish reverted to pre-migratory conditions of body morphology and chemical composition when they were held in the hatchery beyond the normal period of migration. These findings concur with those of Malikova (1957) and Evropeitseva (1962) for Atlantic salmon. The increases in head and caudal peduncle length noted for smolting Atlantic salmon by Evropeitseva (1957) were not apparent in smolting steelhead trout in my study.

At the time of release, the Sandy River fish had a higher mean K_{FL} and lipid content than the Big Creek steelhead. The higher K_{FL} and lipid content in the Sandy River fish might have been a result of the larger proportion of non-migrants in that population. This is substantiated by the fact that migrants from both stocks arriving at the trapping facility one to five days after release were similar in chemical composition and K_{FL}. Later migrants from both release groups had a lower K_{FL} and lipid content than did the early migrants. The continued decline of lipid levels in the later migrants might be attributed to reduced food consumption accompanied by increased energy demands for physical activity, growth, and completion of the transformation.

Migrants captured in late June and July had a higher K_{FL} than migrants captured in late May and early June. At the same time an increase in K_{FL} was noted for fish retained in the hatchery. One possible explanation for the increase in K_{FL} in hatchery fish is that the fish were reverting back to the non-migratory form and energy reserves were being rebuilt. Food was possibly becoming more available for fish in the stream, or these fish were adapting to the stream environment.

A comparison between Sandy River steelhead reared in the hatchery and fish resulting from natural propagation revealed some meaningful differences and similarities. Hatchery-reared fish released in May had a higher lipid content and mean K_{FL} than the native migrants in the same size group (167 mm). However, chemical composition of the hatchery fish that migrated was similar to that of native migrants. Chemical composition and K_{FL} of the native migrants remained relatively constant from April through June while that of the hatchery migrants continued to decline. A slight upward trend in lipid content was noted for later native migrants. These findings differ from those established for coho salmon by Vanstone and Markert (1968), who observed a decrease in lipid in laboratory-reared fish but an increase in the total lipid in wild fish during the period of downstream migration.

Though chemical composition and K_{FL} were similar for hatchery and native migrants, little is known about how they compare in amino and fatty acids as well as how parr differ from smolts with respect to amino and fatty acids. The process of smoltification of Atlantic salmon is accompanied by changes in the quantitative inter-relations among amino acids within the protein molecule (Malikova, 1957). The proportion of unsaturated fatty acids with 20-22 carbon atoms increases in the fat of migrating Atlantic salmon, while the proportion of fatty acids with lesser numbers of carbon atoms decreases (Lovern, 1934).

The linear discriminant analysis showed that K_{FL} and fork length were nearly as effective as all ten variables in distinguishing a smolt from a parr. The length frequency distribution (Figure 8) for fish released and migrants captured reveals that few fish under 150 mm migrated downstream. The size-dependency of the smolting phenomenon has been well demonstrated by the relationship between size at time of release and number of returning adult steelhead (Wagner et al., 1963).

The condition of Atlantic salmon, as studied through comparisons of the length-weight relationships, was found to vary considerably from place to place, from year to year, and from time to time during the same year (Hoar, 1939b). There are several variables that could affect the value of K_{FL} (Kesteven, 1947). Among these variables that are applicable to fish in the present study are a genetic capacity for growth, seasonal variations in photoperiod, temperature, pH, and turbidity as related directly or indirectly to growth, and seasonal physiological changes such as the parr-smolt transformation.

Seasonal variations in the availability of food were of minor importance because the fish in this study were fed a commercially prepared diet on a systematic feeding regime while in the hatchery. Seasonal changes in water temperature and photoperiod have a direct effect on metabolism (Brown, 1946). After the initial decline, K_{FL} remained relatively constant for the non-migrants, whereas it showed a continued sharp decline in the larger migrant-sized fish.

A decline in K_{FL} during the migratory period is not apparent in the resident form of rainbow trout (Wagner, n. d.), but the resident form displays the silvery appearance and is euryhaline prior to the migratory period. Salinity tolerance is size-dependent and both the migratory and resident form of rainbow trout are euryhaline prior to downstream migration (Conte and Wagner, 1963). This would suggest that euryhalinity and smoltification might be considered two separate phenomena.

Stocks at different hatcheries show similar patterns of change in K_{FL} but may differ in absolute values (Wagner, n. d.). The important consideration is that changes in K_{FL} can provide valuable cues to the parr-smolt transformation.

Seasonal physiological changes such as the parr-smolt transformation in the steelhead trout probably require an expenditure of energy at the cellular level. Energy might also be expended in increased activity or at the behavioral level. These changes would have a direct effect on the animal's metabolism.

There are several alternate explanations for the changes in chemical composition. First, because no obvious difference in the intensity of feeding activity has been observed during the course of the parr-smolt transformation (Hoar, 1965; Wagner, n. d.), I believe that changes in food intake contribute only slightly to the decrease in energy reserves.

Juvenile steelhead reared under natural photoperiod exhibited a bimodal activity pattern with peaks occurring in the general migratory period (April through June) and the late fall months (Lichtenheld, 1966). Brown trout (Salmo trutta) reared under natural conditions, displayed a similar annual cycle of maximum activity during May and

June (Swift, 1962). Swift (1964) further states that annual activity curves for brown trout fed on an artificial feeding regime displayed a low level of activity during the early part of the year. Activity increased during May and June, falling again in July, and rising again in August. He proposes that the second rise in activity in August might be connected with sexual maturation. When the brown trout displays maximum activity, its maintenance requirements are high (Brown, 1946). The high rate of activity displayed by steelhead trout during the spring would increase the metabolic rate. Therefore, the amount of food consumed might not be sufficient to meet the increased metabolic demands and additional energy could be obtained from lipid reserves. Another possible explanation for the uniform decrease in lipid of smolting steelhead is the growth in length during the parr-smolt transformation. An indicator of rapid growth prior to downstream migration is the wide spacing of circuli, which is strikingly different from the spacing of circuli laid down in the preceding year of freshwater life (Robertson, 1948; Chapman, 1957).

Lovern (1934) states that the fats from Atlantic salmon parr show a higher degree of unsaturation than the fats of smolts. Rapid growth taking place prior to smoltification would require a substantial amount of energy which could be obtained from the unsaturated fats stored in the body.

Increased activity and growth might be taking place simultaneously prior to downstream migration. The energy requirements to compensate for the increased activity and growth might be high and a large portion of this energy could be obtained from lipid reserves.

Changes in K_{FL} for fish larger than 140 mm appear to be a good criterion of smolting for juvenile steelhead trout reared under normal photoperiod and temperature cycles. For this index to be most useful, the pattern of change in K_{FL} should be established for each stock at each hatchery. Other needed research includes further studies on food consumption, activity, growth, and standard metabolism to determine the major site of lipid utilization during the parr-smolt transformation.

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APPENDICES

APPENDIX A

Sample Statistics and Body Composition for Three Size Groups of Juvenile Steelhead Trout from February Through July, 1964

	Arithmetic means									
Month	Fork lenth (cm)	Live weight (g)	Coefficient of condition	Total weight (g)	Moisture (g)	Dry matter (g)	Crude protein (g)	Lipid (g)	Ash (g)	Un-known (g)
Big Creek Stock										
				Adjusted to standard fork length, 13.4 cm						
February	13.4	23.3	0.947	23.3	17.32	5.98	4.20	0.96	0.62	0.20
March	13.4	24.4	1.002	24.4	18.30	6.10	4.38	0.73	0.66	0.33
April	13.4	23.3	0.950	23.3	17.68	5.62	4.16	0.66	0.64	0.15
May	13.4	23.7	0.985	23.7	17.87	5.83	4.26	0.68	0.65	0.25
June	13.2	22.9	0.972	23.9	17.05	6.85	4.69	1.25	0.70	0.21
July	13.7	25.3	0.979	23.7	17.48	6.22	4.37	0.90	0.69	0.25
				Adjusted to standard fork length, 16.7 cm						
February	16.6	46.1	1.007	46.9	34.38	12.52	8.48	2.47	1.15	0.43
March	16.7	45.8	0.971	45.8	33.82	11.98	8.35	1.86	1.14	0.62
April	16.4	42.1	0.935	44.5	33.65	10.85	8.09	1.06	1.31	0.39
May	16.7	40.9	0.876	40.9	31.34	9.56	7.60	0.54	1.16	0.25
June	16.7	43.3	0.926	43.3	32.81	10.59	8.11	1.08	1.20	0.10
July	16.3	45.4	1.039	48.9	35.78	13.12	9.01	2.41	1.33	0.37
				Adjusted to standard fork length, 19.1 cm						
February	18.4	61.4	0.975	68.7	50.13	18.57	12.67	3.79	1.64	0.47
March	18.5	61.7	0.967	67.9	49.47	18.43	12.62	3.60	1.65	0.56
April	19.1	64.3	0.913	64.3	47.55	16.75	12.03	2.50	1.72	0.51
May	19.0	59.5	0.854	60.4	46.22	14.18	11.29	1.07	1.63	0.19
June	19.1	62.0	0.878	62.0	47.65	14.35	11.62	0.74	1.73	0.27
July	19.3	65.8	0.907	63.0	48.06	14.94	11.85	1.13	1.75	0.22
Sandy River Stock										
				Adjusted to standard fork length, 16.7 cm						
February	16.4	41.3	0.936	43.6	31.86	11.74	8.05	2.32	1.08	0.27
March	16.3	39.4	0.899	42.4	31.12	11.28	7.75	2.00	1.07	0,46
April	16.3	44.5	0.961	47.9	36.15	11.75	8.44	1.87	1.19	0.24
May	16.3	41.3	0.942	44.4	33.39	11.01	8.32	1.25	1.21	0.23
June	16.5	42.4	0.937	44.0	32.52	11.48	8.32	1.65	1.20	0.31
July	16.4	44.4	1.002	46.9	33.82	13.08	8.52	2.80	1.30	0.46

APPENDIX B

Sample Statistics and Percentage Body Composition for Three Size Groups of Juvenile Steelhead Trout from February Through July, 1964

Month	Mean fork length (cm)	Range of lengths (cm)	Mean live weight (g)	Range of weight (g)	Moisture (%)	Dry matter (%)	Percent of dry matter: Protein (%)	Lipid (%)	Ash (%)	Unknown (%)
				Big Creek						
February	13.4	13.0-13.9	23.3	20.4-26.6	74.34	25.66	70.18	16.01	10.38	3.43
March	13.4	13.2-13.7	24.4	21.5-27.3	75.02	24.98	71.74	12.00	10.79	5.47
April	13.4	13.0-13.9	23.3	20.4-26.2	75.88	24.12	74.01	11.82	11.44	2.73
May	13.4	13.0-13.9	23.7	21.0-25.9	75.40	24.60	73.00	11.63	11.16	4.21
June	13.2	13.0-13.8	22.9	19.9-27.2	71.34	28.66	68.47	18.28	10.22	3.03
July	13.7	12.8-14.4	25.3	19.9-28.9	73.74	26.26	70.32	14.51	11.17	4.00
February	16.6	16.0-16.9	46.1	43.0-48.5	73.31	26.69	67.72	19.69	9.16	3.43
March	16.7	16.5-16.9	45.8	41.9-49.0	73.84	26.16	69.72	14.58	9.53	5.13
April	16.4	16.1-16.9	42.1	38.6-46.6	75.61	24.39	74.55	9.78	12.08	3.59
May	16.7	16.4-16.8	40.9	37.6-44.3	76.63	23.37	79.53	5.67	12.17	2.63
June	16.7	16.3-17.0	43.3	37.8-47.1	75.78	24.22	77.30	10.26	11.45	0.99
July	16.3	16.0-16.8	45.5	39.3-51.4	73.16	26.84	68.71	18.38	10.12	2.79
February	18.4	18.1-19.0	61.4	55.1-73.0	72.97	27.03	68.21	20.43	8.85	2.51
March	18.5	18.2-19.4	61.7	53.9-78.9	72.85	27.15	68.50	19.54	8.94	3.02
April	19.1	18.5-19.7	64.3	58.3-74.1	73.95	26.05	71.81	14.91	10.25	3.03
May	19.0	18.5-19.4	59.5	53.3-69.8	76.52	23.48	79.61	7.56	11.50	1.33
June	19.1	18.4-19.9	62.0	54.0-69.8	76.86	23.14	80.95	5.14	12.05	1.86
July	19.3	19.0-19.7	65.8	59.9-76.5	76.29	23.71	79.29	7.55	11.71	1.45
				Sandy River Stock						
February	16.4	16.1-16.6	41.3	37.2-44.7	73.08	26.92	68.55	19.74	9.23	2.48
March	16.3	16.1-16.8	39.4	34.1-41.9	73.39	26.61	68.71	17.76	9.46	4.07
April	16.3	16.2-16.9	44.5	41.5-48.0	75.47	24.53	71.87	15.94	10.12	2.07
May	16.3	16.0-16.7	41.3	37.1-47.5	75.21	24.79	75.54	11.36	10.97	2.13
June	16.5	16.0-16.9	42.4	33.6-48.3	73.91	26.09	72.50	14.41	10.43	2.66
July	16.4	16.0-16.8	44.4	39.6-50.4	72.11	27.89	65.11	21.41	9.96	3.52

APPENDIX C

Sample Statistics and Body Composition for Juvenile Hatchery-reared and Native Steelhead Trout Migrating Downstream in the Sandy River, from Mid-April through Mid-June, 1964

	Arithmetic means									
Date of recovery	Fork length (cm)	Live weight (g)	Coefficient of condition	Total weight (g)	Moisture (g)	Dry matter (g)	Crude protein (g)	Lipid (g)	Ash (g)	Unknown (g)
				Sandy River Stock--Hatchery-Reared[1]						
				Adjusted to standard fork length, 16.7 cm						
Mid-May	16.6	38.4	0.828	38.9	29.50	9.40	7.60	0.58	1.13	0.10
Mid-June	16.6	36.4	0.789	37.1	29.09	8.01	6.53	0.32	1.11	0.06
				Adjusted to standard length, 19.1 cm						
Mid-May	19.3	59.4	0.820	57.5	43.40	14.10	10.97	1.22	1.63	0.28
Mid-June	19.4	58.8	0.805	56.1	43.81	12.29	10.23	0.43	1.56	0.07
				Big Creek Stock--Hatchery-Reared[2]						
				Adjusted to standard fork length, 16.7 cm						
Mid-May	16.6	40.0	0.862	40.7	31.18	9.52	7.75	0.43	1.19	0.14
Mid-June	16.5[3]	36.1	0.798	37.4	29.21	8.19	6.79	0.04	1.11	0.25
				Adjusted to standard fork length, 19.1 cm						
Mid-May	19.4	64.2	0.878	61.2	46.96	14.24	11.51	0.87	1.68	0.18
Mid-June	19.4	57.3	0.773	54.7	43.32	11.92	9.84	0.20	1.64	0.24
				Sandy River Stock--Native						
				Adjusted to standard fork length, 13.4 cm						
Mid-April	13.8	24.3	0.883	22.2	17.04	5.16	4.10	0.21	0.70	0.15
Mid-May	14.2	26.2	0.897	22.0	16.81	5.19	4.10	0.24	0.68	0.16
				Adjusted to standard fork length, 16.7 cm						
Mid-April	16.4	38.9	0.872	41.1	31.31	9.79	7.63	0.55	1.28	0.33
Mid-May	16.5	40.6	0.888	42.1	32.29	9.81	7.73	0.65	1.30	0.14
Mid-June	16.6	40.9	0.894	41.6	31.95	9.65	7.57	0.70	1.19	0.19
				Adjusted to standard fork length, 19.1 cm						
Mid-April	18.9	58.2	0.855	60.0	46.00	13.99	11.29	0.55	1.82	0.32
Mid-May	19.3	61.7	0.854	59.8	45.48	14.32	11.50	0.78	1.78	0.26
Mid-June	19.6	66.5	0.974	61.5	47.39	14.11	11.00	0.93	1.76	0.42

[1] Released May 11-13, 1964

[2] Released May 11, 1964

[3] Represents a single sample consisting of three fish

APPENDIX D

Sample Statistics and Percentage Body Composition for Juvenile Hatchery-Reared and Native Steelhead Trout Migrating Downstrean in the Sandy River from Mid-April Through Mid-June, 1964

Month	Mean fork length (cm)	Range of lengths (cm)	Mean live weight (g)	Range of weights (g)	Moisture (%)	Dry matter (%)	Percent of dry matter: Protein (%)	Lipid (%)	Ash (%)	Unknown (%)
				Sandy River Stock--Hatchery-Reared[1/]						
Mid-May	16.6	16.0-16.9	38.4	33.6-43.2	75.84	24.16	80.81	6.12	12.02	1.05
Mid-June	16.6	16.2-16.9	36.4	32.0-39.6	78.40	21.60	81.50	3.94	13.86	0.70
Mid-May	19.3	19.0-19.8	59.4	53.0-68.4	75.48	24.52	77.79	8.64	11.59	1.98
Mid-June	19.4	19.0-19.7	58.8	53.2-65.1	78.10	21.90	83.26	3.48	12.68	0.58
				Big Creek Stock--Hatchery-Reared[1/]						
Mid-May	16.6	16.3-16.9	40.0	36.5-43.4	76.61	23.39	81.45	4.56	12.54	1.45
Mid-June	16.5	16.4-16.6	36.1	35.5-36.9[2/]	68.09	21.91	82.90	0.53	13.57	3.00
Mid-May	19.4	19.0-19.9	64.2	60.1-72.6	76.73	23.27	80.81	6.12	11.80	1.27
Mid-June	19.4	19.2-19.8	57.3	54.7-63.1	79.20	20.80	82.52	1.69	13.78	2.01
				Sandy River Stock--Native						
Mid-April	13.8	12.9-14.6	24.3	18.6-27.4	76.74	23.26	79.53	4.15	13.47	2.85
Mid-May	13.4	13.7-14.8	26.2	22.3-32.9	76.43	23.57	79.04	4.68	13.19	3.08
Mid-April	16.4	16.0-16.9	38.9	33.2-43.0	76.19	23.81	77.90	5.63	13.12	3.35
Mid-May	16.5	16.1-16.9	40.6	37.1-46.4	76.69	23.31	78.76	6.59	13.27	1.38
Mid-June	16.6	16.1-16.9	40.9	37.7-45.7	76.80	23.20	78.44	7.25	12.33	1.98
Mid-April	18.9	18.4-19.7	58.2	53.3-63.9	76.69	23.31	80.71	3.95	13.02	2.32
Mid-May	19.3	19.0-19.5	61.7	58.3-66.9	76.05	23.95	80.28	5.48	12.45	1.79
Mid-June	19.6	19.3-20.0	66.5	59.7-65.1	77.04	22.95	77.96	6.60	12.48	2.96

[1/] Released May 11-13, 1964

[2/] Represents a single sample consisting of three fish