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Growth characteristics of otoliths were used to determine age, and to separate known races and stocks of steelhead trout (*Salmo gairdneri*). Otoliths were the first calcified structures observed in X-ray photographs of steelhead embryos, and a continuous record of events through life was interpreted from these structures. A direct relationship was established between otolith length and fork length of the fish. Freshwater and saltwater annuli, and spawning checks on otoliths were used to describe 27 life history patterns. A significant difference in nucleus diameters of otoliths was used to separate summer and winter races. Significant differences in freshwater growth characteristics were used subjectively to separate wild from hatchery-reared stocks of steelhead. The use of otoliths represents a valid technique to supplement those now available for management of this species.

Steelhead Trout Otoliths for Age, Race, and Stock Analysis

by

John LeRoy McKern

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STEELHEAD TROUT OTOLITHS FOR AGE, RACE, AND STOCK ANALYSIS

INTRODUCTION

This is a report on an investigation of the use of otoliths for age determination and for differentiation among known races and stocks of steelhead trout (Salmo gairdneri). Three pairs of otoliths are found in the inner ear of steelhead, but only the largest pair, the sagittae, were studied. Henceforth, use of the term "otolith" refers to sagittae unless otherwise noted.

Fishery management programs are dependent upon the ability of biologists to determine age classes and to identify subpopulations of fishes. Otoliths are well suited to reveal this information because: (1) Otoliths are evident in embryos of bony fishes prior to hatching (Budd, 1940). (2) The structure of otoliths represents an accurate record of the life history of the fish (Immerman, 1908; Hickling, 1931; Rollefsen, 1935; Fitch, 1951; Irie, 1955, 1957, 1960; Kohler, 1958; Watson, 1964; Mina, 1967). (3) Relationships have been established between the size of otoliths and the size of fish (Mina, 1967; Holland, 1969). (4) Otoliths do not tend to show false annuli (Clutter and Whitesel, 1956). (5) Otoliths are protected from damage by their location in the cranial structure of the fish (Irie, 1960; Mina, 1965). (6) Variations in the zones of growth of otoliths may be due to differences between subpopulations (Einarsson, 1951; Kim, 1963; Mina, 1967).

The popularity and economic importance of steelhead as sport fish (Brown, et al., 1964) have prompted many studies on the life history and management of populations of both wild and hatchery-reared stocks (Pautzke and Meigs, 1940; Sumner, 1945; Larsen and Ward, 1954; Maher and Larkin, 1954; Shapovalov and Taft, 1954; Chapman, 1957; Wallace, 1961; Wagner, et al., 1963; Withler, 1965). Scales have been used successfully for aging and for analysis of subpopulations of salmonids (Koo, 1955; Carlander, 1956; Bali, 1958; Henry, 1961; Mosher, 1963; Anas and Murai, 1969). However, anadromous salmonids tend to lose and subsequently regenerate scales during freshwater growth and smoltification, and they tend to resorb the scale edges during spawning migrations. For these reasons, authors have used otoliths for a supplemental method of age analysis, and for the separation of subpopulations of Pacific salmon (*Oncorhynchus* sp.) (McMurrich, 1910, 1913; Clutter and Whitesel, 1956; Kim, 1963; Bilton and Jenkinson, 1968; Kim and Roberson, 1968). Except for a preliminary study on 18 fish by Koski (unpublished data, 1964, Oregon State University, Corvallis), the use of otoliths for age, race, and stock analysis of steelhead trout has not been investigated.

The objectives of the research reported here were: (1) To describe the development of otoliths in steelhead from the fertilized egg to the adult stage. (2) To determine if size of the otoliths was directly proportional to size of the steelhead. (3) To determine if characteristics of otoliths were useful as accurate indicators of age in steelhead. (4) To determine if characteristics of otoliths could be used to differentiate between summer and winter races of steelhead. (5) To determine if characteristics of otoliths could be used to differentiate between stocks of wild and hatchery-reared steelhead.

MATERIALS AND METHODS

Area of Investigation

Otoliths, scales, and pertinent data were obtained from steelhead trout from rivers in Oregon, Washington, and British Columbia. In Oregon, samples were collected from wild and hatchery-reared summer steelhead of the Rogue and Siletz Rivers, and from wild and hatchery-reared winter steelhead of the Alsea and Siletz Rivers. In Washington, samples were obtained from Washougal River summer steelhead (reared at either the Washougal River Hatchery or at the South Tacoma Hatchery on Chambers Creek), from hatchery-reared winter steelhead of the Skagit River, and from wild winter steelhead of the Hoh River and Big Beef Creek. On Vancouver Island in British Columbia, samples were obtained from wild winter steelhead of the Nanaimo and Big Qualicum Rivers (Figure 1).

Collection of Samples

Samples and data collected from steelhead caught by sport fisherman in Oregon consisted of otoliths, scales, location of capture, origin (wild or hatchery), hatchery marks if present, fork length in millimeters, sex, and date of capture. Sex was determined by external morphology or by internal examination. The first three scales above the lateral line in the diagonal row extending from the front of the dorsal fin posterio-ventrally to the lateral line were taken from each side of the fish. Otoliths were collected as described by McKern and Horton (1970).

Juvenile steelhead were obtained from the Alsea Trout Hatchery

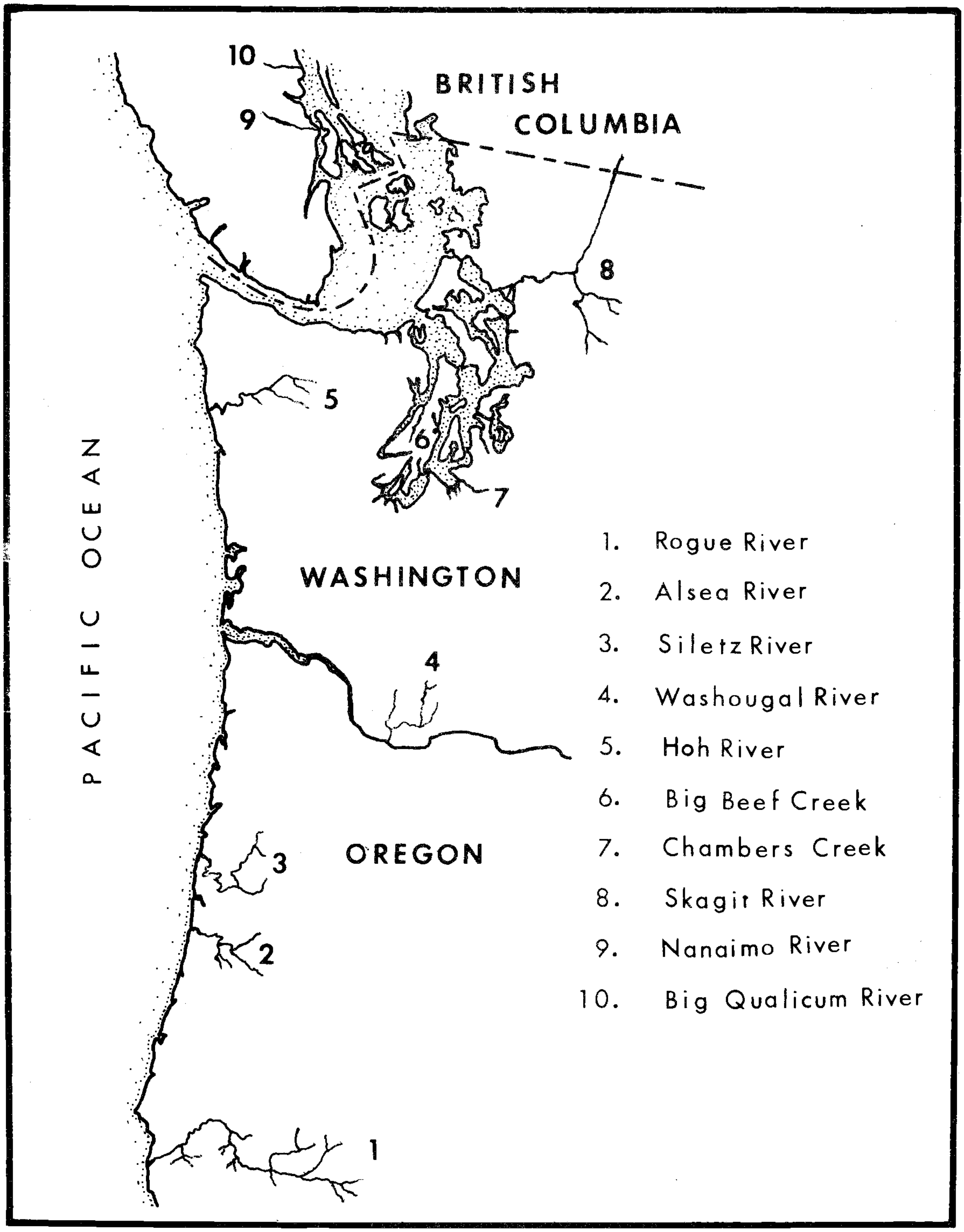

Figure 1. Rivers in Oregon, Washington, and British Columbia from which otoliths and related data from steelhead trout were obtained (1968 to 1970).

of the Oregon State Game Commission. Developing embryos and fry of Alsea River winter steelhead were obtained from the Fisheries Research Division Laboratory of the Oregon State Game Commission.

Samples contributed by Mr. K V. Koski, University of Washington, from rivers in Washington and British Columbia usually consisted of otoliths, scales, fork length, date of capture, and river of origin. In some cases, only the river of origin and the frozen heads of steelhead were available. In these cases, the otoliths were obtained by splitting the head of the fish.

Storage of Samples

Otoliths and scales of steelhead sampled in Oregon were affixed to gummed tape and inserted into coin envelopes on which other pertinent data had been recorded. Otoliths from Washington and British Columbia were either mounted dry in plastic concavity plates (Kim, 1963), stored in coin envelopes, or as previously mentioned, retained in the frozen heads of fish. Prior to examination, all otoliths were transferred to liquid filled vials. Several media including water, 50% glycerin and water, 100% glycerin, 36% isopropyl alcohol, and buffered 10% formalin were tested. With the exception of 100% glycerin, all gave satisfactory results. Isopropyl alcohol and buffered formalin were tested to determine the usability of otoliths from specimens preserved for a short period of time in these media. No undesirable effect was noted.

A minimum clearing time of two hours in water or 50% glycerin and water gave the best results. No deterioration was noted in the readability of otoliths stored as long as six months in these two media.

Scales were mounted on gummed cards, impressed on acetate cards, and read on a scale projector as described by Koo (1955).

Examination of Samples

Developing embryos and larval steelhead were fixed in buffered 10% formalin and stored for one to three weeks in 36% isopropyl alcohol. The preserved embryos and newly hatched fry were X-rayed by the Oregon State University Department of X-Ray Science. The resultant X-ray films were examined under a binocular microscope for the presence of otoliths. Otoliths from young fry were obtained by splitting their heads under a dissecting microscope and probing for the small granular otoliths.

Examination of otoliths from fry, juvenile, and adult steelhead was carried out under a binocular microscope utilizing reflected light on a black background as described by Kim (1963). To facilitate measurement, each otolith was photographed on 35 mm direct positive film (ASA 80). The photographs were made with a single lens reflex camera fitted to one eyepiece of a binocular microscope. The film was developed as directed and mounted in 35 mm slides.

The magnification used for all photographs was 10 diameters (10 X eyepiece and 1X objective). This magnification accommodated all sizes of otoliths. A double thickness concavity slide was prepared with a background of black plastic. Each otolith was immersed in 50% glycerin and water in the concavity slide with the lateral surface facing up. No cover slip was used when the photographs were made.

A magnification reference was produced by photographing a 2 mm stage micrometer disc (.01 and .001 mm divisions) at the same magnification used for the otoliths. By positioning the slide projector at a distance such that the image of the 2 mm stage micrometer was expanded to 200 mm on a screen, a magnification factor of 100 diameters was achieved. All slides were projected at a magnification of 100 diameters which was easily checked by the reference slide.

Terminology of Otoliths

The following terminology (adapted from Kim and Koo, 1963) was used to describe steelhead otoliths examined under reflected light on a black background (Figure 2):

Hyaline nucleus: the small oval center of the otolith which appears dark with a narrow opaque ring around the border.

Metamorphic check: a narrow hyaline ring delineating the nucleus.

Opaque rings: the uninterrupted oval opaque zones formed during summer growth in freshwater.

Hyaline rings: the uninterrupted oval hyaline zones formed during winter growth in freshwater.

Plus growth: a narrow opaque zone of freshwater growth formed after the last hyaline ring.

Metamorphic check: a narrow hyaline zone delineating plus growth.

Opaque bands: opaque zones formed during summer growth in saltwater which are interrupted by notches in the anterior and posterior regions of the otolith.

Hyaline bands: hyaline zones formed during winter growth in saltwater which are interrupted by notches in the anterior and posterior regions of the otolith.

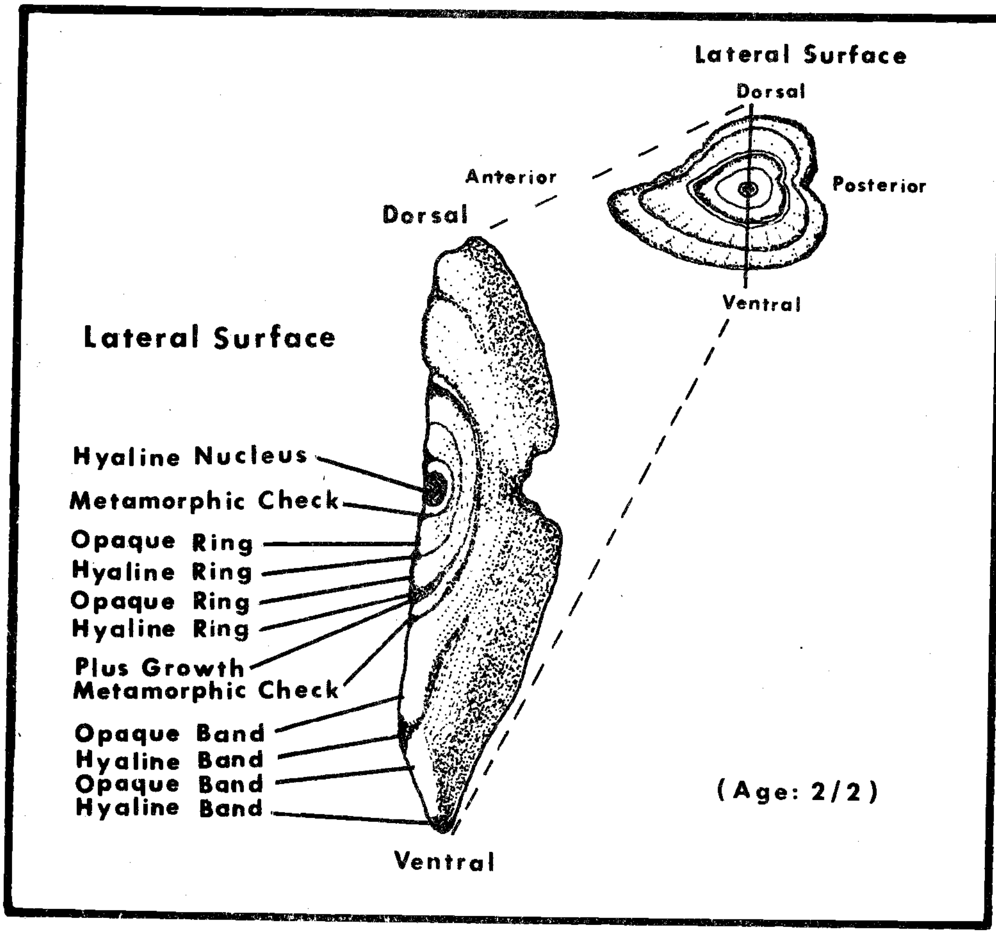

Figure 2. A posterior view of a cross section through the center of a steelhead otolith showing zones of growth at the lateral surface as they appeared in reflected light on a black background.

Measurements and Age Determination from Otoliths

Four types of measurements were taken from otoliths. Total length and total width were obtained from all otoliths showing no breakage that would effect the dimension (Figure 3A). Measurements of yearly growth were made from the center of the nucleus to the interface between a hyaline zone and the subsequent opaque zone, or to the annulus. In Figure 3B, the first year of growth was measured from the center of the nucleus to the first annulus, whereas the second year of growth was the distance from the center of the nucleus to the second annulus minus the first year of growth. Each succeeding year of growth and total freshwater growth was measured accordingly. Plus growth was total freshwater growth minus the measurement to the last freshwater annulus, and any change due to the shortening of the time spent in saltwater during the first summer was accounted for by this measurement. The fourth type of measurement, the diameter of the nucleus, was measured between the interfaces of the nucleus and the metamorphic check delineating growth of the nucleus (Figure 3C).

Age was determined from otoliths by counting the annuli present (Figure 3D), and was designated by the number of years spent in freshwater separated from the number of years spent in saltwater by a slash (/). Therefore, a 2/2 age steelhead would have spent 2 years in freshwater and 2 years in saltwater terminated by the spawning

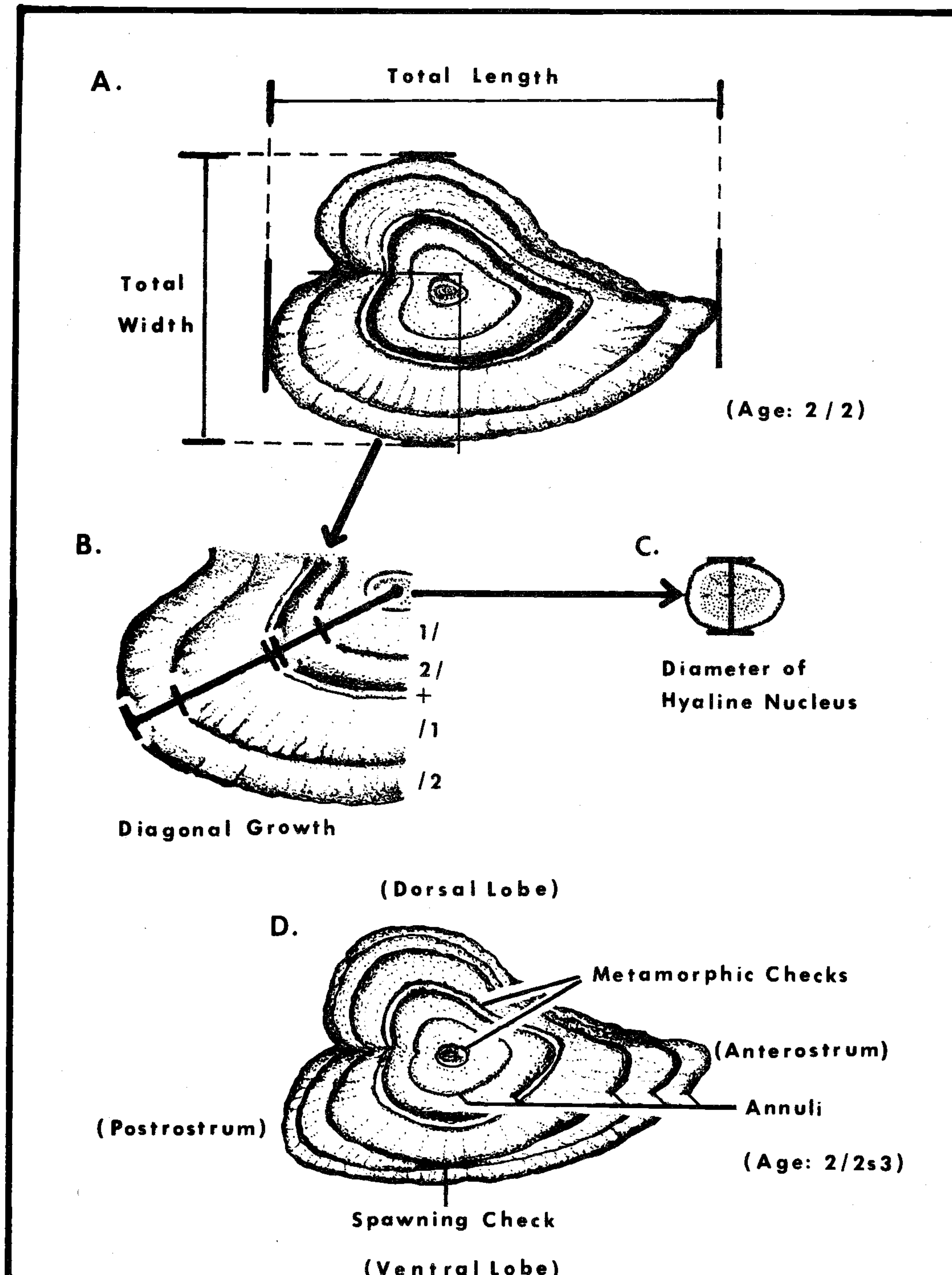

Figure 3. Graphic illustration of the measurements, (A) total length and total width, (B) diagonal growth, and (C) diameter of the hyaline nucleus, used to describe steelhead otoliths, and (D) the location of metamorphic checks, annuli and the spawning check on the otolith of a steelhead captured during its second spawning migration.

migration in which it was captured. Additional spawning migrations, designated by a small _s_, were identified by the presence of spawning checks; so a steelhead of age 2/2s3 would have spent 2 years in freshwater, 2 years in saltwater culminating in a spawning migration, and 1 year in saltwater followed by the spawning migration in which it was captured. Photomicrographs of an otolith and a scale with the principal characteristics identified are presented in Figure 4.

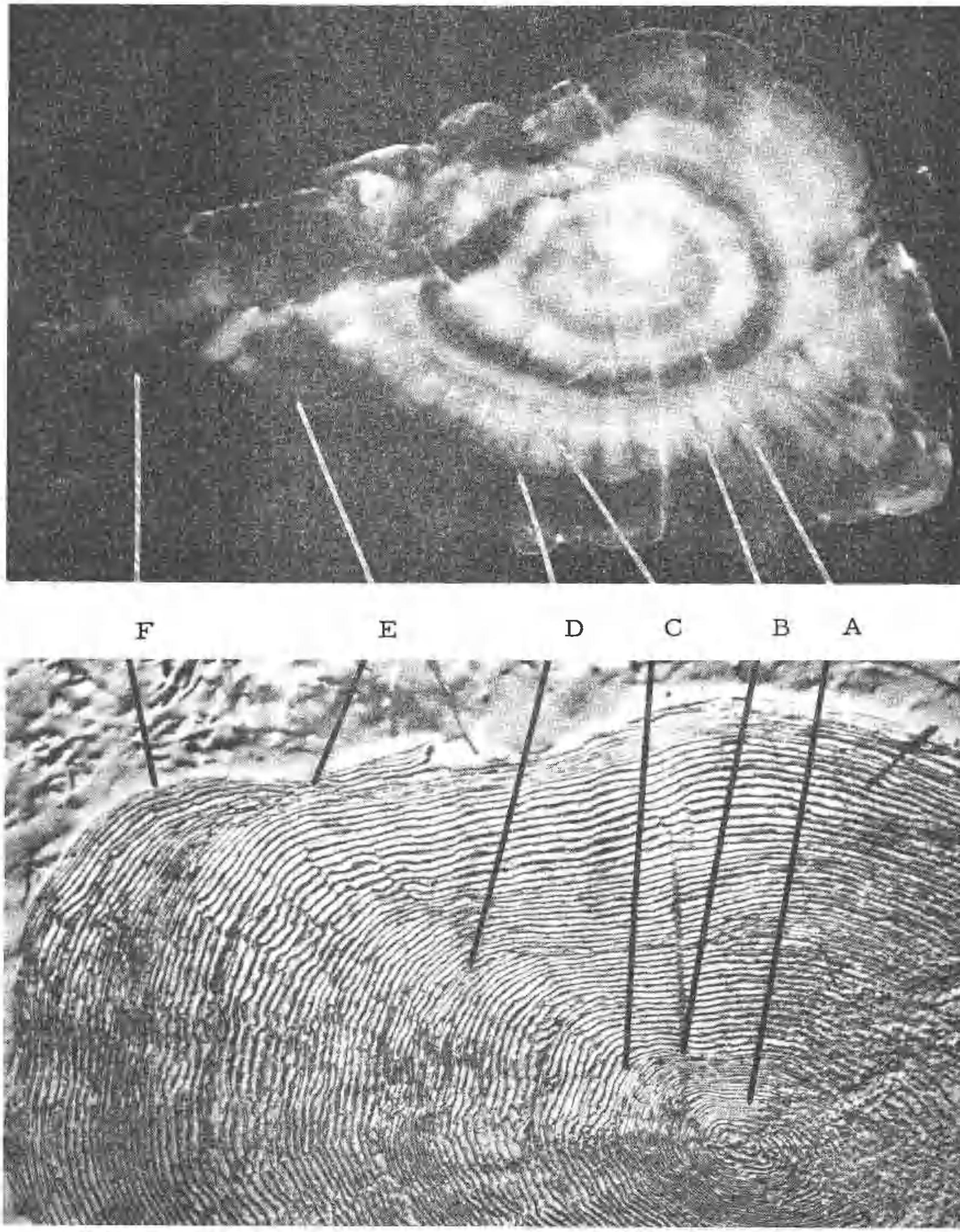

Figure 4. Photomicrographs of a steelhead trout otolith and scale showing (A) annulus 1/, (B) annulus 2/. (C) metamorphic check, (D) annulus /1, (E) spawning check /2s, and (F) spawning check /3s (magnification 20 diameters).

RESULTS

Structure and Development of Otoliths

Structure

Otoliths of steelhead are composed of organic and inorganic materials. The organic material comprised 7% of the total weight of the otolith (6% lipid, .5% protein, .34% glucose, and .16% nonprotein nitrogen), while the inorganic material comprised 93% of the total weight (primarily calcium carbonate and water) (Lannon, personal communication). The organic material formed the fibrous framework of the otolith, while the calcium carbonate formed as crystals throughout the framework in varying degrees of density. Crystals formed most abundantly at the lateral surface of the otolith (Figure 2) in zones corresponding with summer growth, and because of this abundance of crystal formation these zones were white (opaque) under reflected light. Winter growth appeared dark (hyaline) because there was less crystal formation resulting in the transmission of light.

Embryonic Development

Otoliths were the first calcified structures found in the embryonic development of steelhead. Microscopic examination of X-ray films made of eyed eggs (incubated at 12°C) revealed the presence of paired structures which were identified as otoliths 14 days before the ova hatched (Figure 5A). A second pair of otoliths appeared nine days before hatching (Figure 5B), and these two pairs of otoliths were the only calcified structures evident when the eggs hatched (Figure 5C). Growth of the sagittae at the time of complete absorption of the yolk was hyaline in nature with a narrow outer ring of opaque growth (Figure 5D). Comparison of X-ray films of embryos with an X-ray of a juvenile (Figure 5E) verified that the sagittae were the first otoliths to appear.

Juvenile Development

The otoliths of most steelhead revealed the formation of a metamorphic check around the nucleus. Growth of the otolith after the metamorphic check was generally seasonal in nature.

Six patterns of juvenile development were identified from otoliths. Wild steelhead migrated to saltwater after the formation of 1 to 4 pairs of opaque and hyaline rings representing a corresponding number of years in freshwater. Freshwater growth on otoliths of hatchery-reared steelhead revealed no seasonal pattern in those individuals that migrated to saltwater after liberation, but those that remained had nonseasonal growth and seasonal growth that indicated an additional year in the river. Plus growth was not evident on otoliths of hatchery-reared steelhead, though it was found on the

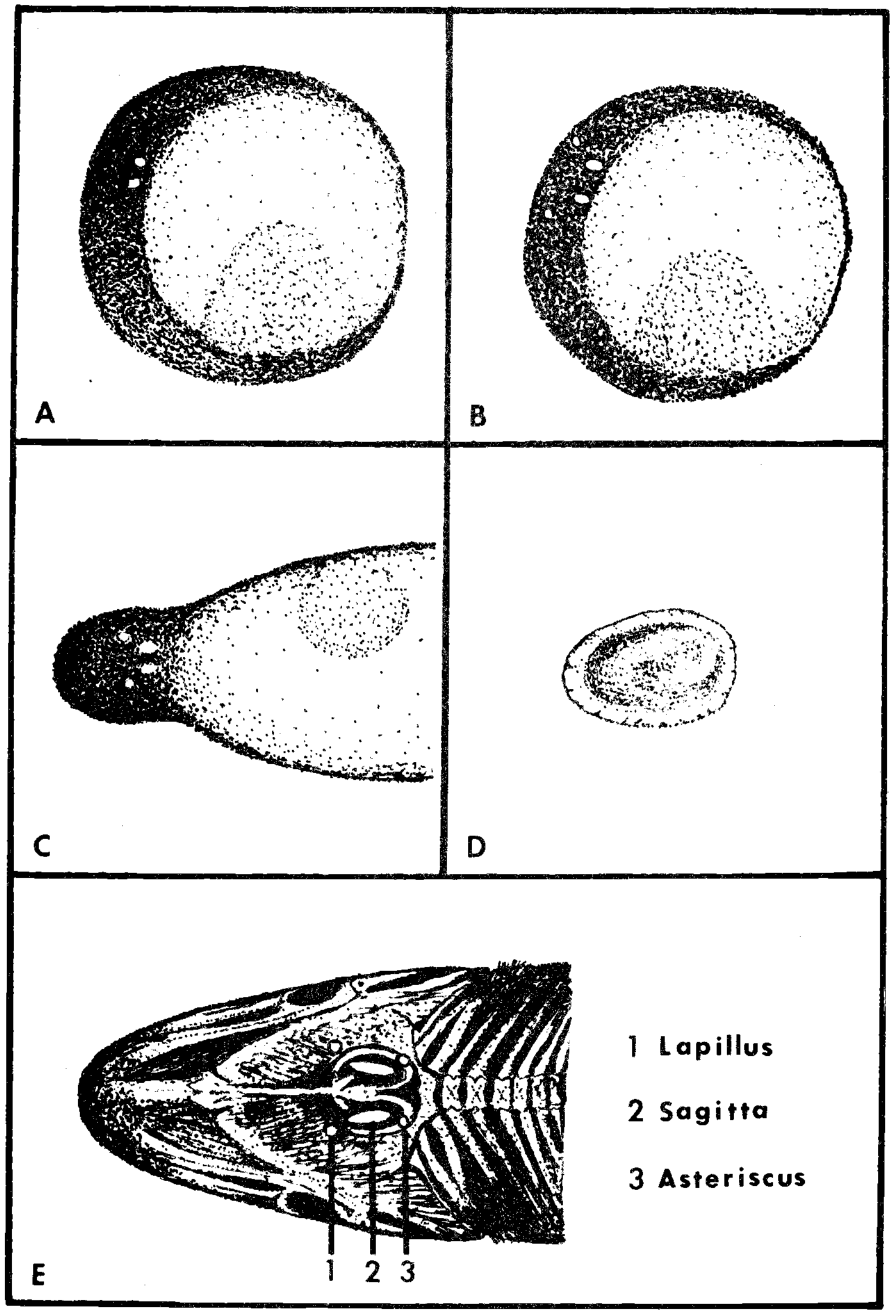

Figure 5. The development of otoliths in steelhead as reproduced from X-ray films of eyed eggs: (A) ovum 14 days before hatching with one pair of otoliths present; (B) ovum 9 days before hatching with two pairs of otoliths present; (C) a newly hatched fry with two pairs of otoliths present; and (D) the otolith from a fry that had completely used the yolk. (E) Comparison of X-rays of embryos (A, B, and C) with an X-ray of a juvenile verified that the sagittae were the first otoliths to appear.

otoliths of many wild fish. However, a metamorphic check delineated freshwater growth in each stock of fish.

Ninety-nine percent of the hatchery fish migrated at the end of one year in freshwater and over 97% of the wild fish migrated after two or three years (Table 1). Comparison of these three patterns of juvenile development by Duncan's _t_ test (Bruning and Kintz, 1968) revealed significant differences between many of the characteristics of freshwater growth on otoliths (Table 2).

Adult Development

The seasonal pattern observed in freshwater persisted in saltwater growth on the otoliths, with each year of growth represented by subsequent opaque and hyaline bands. Regardless of juvenile life history, steelhead spent one, two, or three years in saltwater prior to capture in rivers during their first spawning migration. The only relationship of significance in saltwater growth was that an increase in years spent in saltwater resulted in an increase in the size of the otolith at the time of return to freshwater.

Relationship of Otolith Length to Fish Length

Total otolith length and fork length of steelhead were used to test for a relationship between otolith size and fish size. Differences were noted between the lengths of left and right otoliths from some

Table 1. Grand means* of diagonally measured growth of otoliths from wild and hatchery-reared steelhead of rivers in Oregon, Washington, and British Columbia (1968 to 1970)

Period of Growth	Hatchery-Reared Steelhead (in mm)			Wild Steelhead (in mm)				
Freshwater Growth (smolts and adults)								
Age		(1/)			(2/)			(3/)
After 1 Year		1.291			.868			.769
After 2 Years					1.263			1.092
Annual Increase					.395			.323
After 3 Years								1.377
Annual Increase								.285
Plus Growth					.066			.059
Total Freshwater Growth		1.291			1.329			1.436
Saltwater Growth (adults)								
Age	(1/1)	(1/2)	(1/3)	(2/1)	(2/2)	(2/3)	(3/1)	(3/2)
To Last Freshwater Annulus	1.424	1.300	1.217	1.384	1.291	1.237	1.385	1.405
Plus Growth				.035	.050	.093	.010	.044
After 1 Year	2.055	1.894	1.796	2.020	1.913	1.814	1.870	2.005
Annual Increase	.631	.594	.579	.636	.622	.577	.485	.600
After 2 Years		2.411	2.287		2.415	2.218		2.386
Annual Increase		.517	.491		.502	.404		.381
After 3 Years			2.713			2.623		
Annual Increase			.426			.405		
Total Growth	2.055	2.411	2.713	2.020	2.415	2.623	1.870	2.386

* Grand means were taken from Appendices 1 and 2

Table 2. Comparison of grand means (Table 1) of diagonally measured freshwater growth of otoliths from wild and hatchery-reared steelhead of rivers in Oregon, Washington, and British Columbia (1968 to 1970).

Period of Growth	Comparisons*(in mm)		
	1/ vs 2/	1/ vs 3/	2/ vs 3/
After 1 Year	1.291 vs .868**	1.291 vs. .769**	.868 vs .769**
After 2 Years			1.263 vs 1.092**
Annual Increase			.395 vs .323^{+}
To Last Annulus	1.291 vs 1.263^{++}	1.291 vs 1.377^{++}	1.263 vs 1.377^{+}
Plus Growth			.066 vs .059^{++}
Total Freshwater Growth	1.291 vs 1.329^{++}	1.291 vs 1.436**	1.329 vs 1.436^{+}

* Grand means were compared by Duncan's t test with the following significance rating.
** Was significant at $P \leq .01$.
$^{+}$ Was significant at $P \leq .05$.
$^{++}$ Was not significant.

individuals, and female steelhead tended to be larger than males in most of the rivers represented. Based on student's t tests (Bruning and Kintz, 1968) however, these variations had no significant effect ($P \leq .05$) on the ratio of otolith length to fork length as a total sample or as individual river samples.

The possibilities of race or stock differences and the effect of previous spawning were considered by placing wild winter steelhead, hatchery winter steelhead, hatchery summer steelhead, and repeat spawning steelhead in separate groups. Lines representing regression of otolith length (Y) on fork length (X) of smolt and adult steelhead (Figure 6) were:

Wild winter steelhead:	$Y = 2.15901 + .00564\,(X)$
Hatchery winter steelhead:	$Y = 1.77465 + .00589\,(X)$
Hatchery summer steelhead:	$Y = 2.22378 + .00559\,(X)$
Repeat spawning steelhead:	$Y = 2.18778 + .00572\,(X)$

Otoliths for Age

Interfaces between winter growth and subsequent summer growth form in late March or early April on the otoliths of steelhead. Because steelhead spawn around a peak in March, these interfaces represent the completion of a calendar year in the life of the fish.

Ages obtained from otoliths were compared to those obtained from scales and to those from known aged hatchery-marked

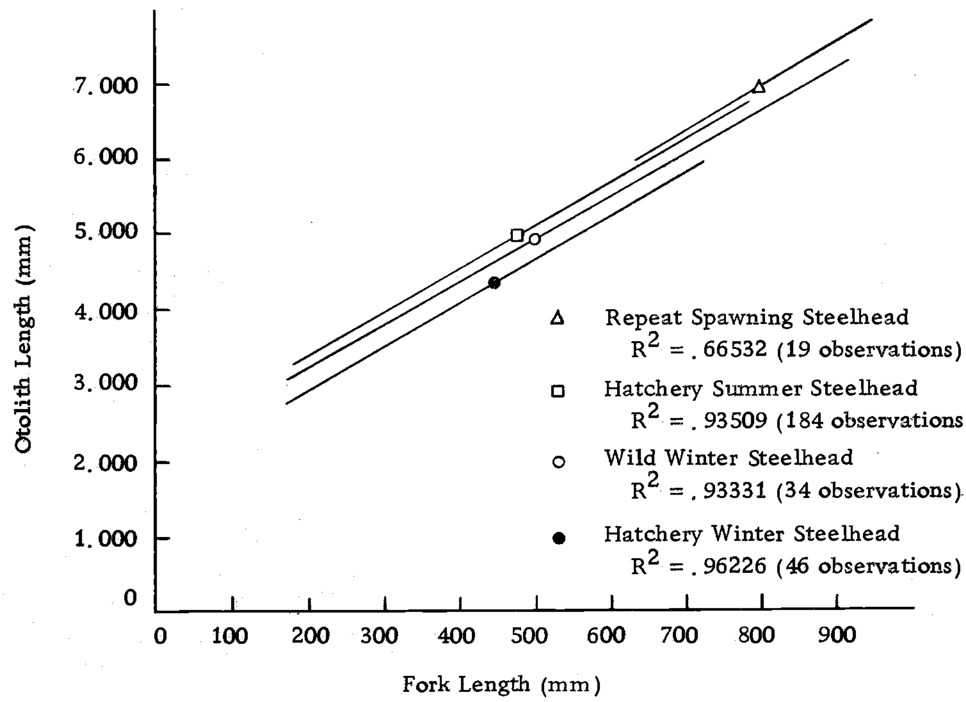

Figure 6. The lines represent the regression of otolith length on fork length of smolt and adult steelhead from rivers in Oregon, Washington, and British Columbia (1968 to 1970).

steelhead. Otoliths were usable from 28 of 31 hatchery-marked adults, and scales were usable from 23 of these fish. Ages determined from 26 otoliths (93%) and from 20 scale samples (87%) agreed with known ages. Of 466 fish from which otoliths were taken, at least one otolith was usable in 436 cases (95%). Scales were available from 290 fish, and age determinations were possible in 237 cases (82%). Comparison of 210 cases in which both otoliths and scales were used resulted in 195 agreements (93%). Disagreement generally occurred between otoliths and scales of repeat spawning steelhead, and might be attributed to differential resorption between the two structures.

Twenty-seven different age types were identified from otoliths (Table 3). Four freshwater age groups were recognized (Table 4), and 11 patterns of saltwater growth which included three patterns for fish making their first spawning migration, four patterns for fish making a second migration, and three patterns for fish making a third migration.

Race Analysis of Summer and Winter Steelhead

Characteristics of growth of otoliths provided sufficient evidence to separate summer from winter races of steelhead. The mean diameters of the nuclei of otoliths from summer steelhead were significantly smaller than those from winter steelhead (Student's _t_ test, $P \leq .01$) in the Siletz River where both races occurred, and

Table 3. Age composition of steelhead trout from rivers in Oregon, Washington, and British Columbia (1968 to 1970) as determined from analysis of otoliths.

Age Type	Rogue R. (summer, hatchery & wild)	Alsea R. (winter, wild)	Alsea R. (winter, hatchery)	Siletz R. (winter, hatchery & wild)	Siletz R. (summer, hatchery)	Siletz R. (summer & winter, wild)	Washougal R. (summer, hatchery)	Hoh R. (winter, wild)	Big Beef Cr. (winter, wild)	Chambers Cr. (summer, hatchery)	Skagit R. (winter, hatchery)	Nanaimo R. (winter, wild)	Big Qualicum R. (winter, wild)	Frequency/Age Type
1/			25				69		1*	106				201
1/1					5						1			6
1/2	1			10	24	1**			1**		53			90
1/3				5										5
1/1s2											2			2
1/2s3				3							11			14
1/2s3s4				1										1
2/									11					11
2/1	2					2		1	1					6
2/2		4		6		7		7	1		3*	4	2	34
2/3		1		4				2	1				1	9
2/1s2	2							1	1					4
2/1s3													2	2
2/1s2s3												1	3	4
2/2s3	1					1						1	1	4
2/2s4													1	1
2/2s3s4									1			1		2
2/2s4s5													2	2
3/									7					7
3/1						1		1	1					3
3/2		1		3		1		3	6			1	2	17
3/3											1**			1
3/1s2													4	4
3/1s3				1										1
3/1s2s3													1	1
3/2s3								1					2	3
4/2												1		1
Total/River	6	6	25	33	29	13	69	16	32	106	71	9	21	436

* Wild or hatchery fish showing uncommon age types.

** Wild or hatchery strays in a sample that was predominantly of the opposing stock.

Table 4. Age composition of steelhead trout from rivers in Oregon, Washington, and British Columbia (1968 to 1970) as determined from analysis of otoliths.

Age Type	Total Sample		Hatchery-Reared Steelhead		Wild Steelhead	
	Number	Percent	Number	Percent	Number	Percent
Freshwater Age (smolts and adults)						
1/	319	73.6	318	99.1	1	0.9
2/	79	18.1	3	0.9	76	66.1
3/	37	8.5			37	32.2
4/	1	0.2			1	0.9
Total	436	100	321	100	115	100
Saltwater Age (adults)						
/1	15	6.9	6	5.0	9	9.4
/2	141	64.9	93	76.9	49	51.0
/3	15	6.9	5	4.1	10	10.4
/1s2, /1s3, /2s3, /2s4	35	16.1	16	13.2	19	19.8
/1s2s3, /2s3s4, /2s4s5	10	4.6	1	0.8	9	9.4
Total	217	100	121	100	96	100

throughout the total sample (Table 5). A frequency diagram revealed no significant overlap in either case (Figure 7).

Table 5. A comparison of mean diameters of nuclei of otoliths from summer and winter races of steelhead trout from rivers in Oregon, Washington, and British Columbia (1968 to 1970).

Summer Steelhead	Mean Nucleus Diameter (mm)	Winter Steelhead	Mean Nucleus Diameter (mm)
Rogue R. (hatchery)	.368	Alsea R. (hatchery)	.427
Rogue R. (wild)	.384	Alsea R. (wild)	.431
Siletz R. (hatchery)	.356	Siletz R. (hatchery)	.435
Siletz R. (wild)	.346	Siletz R. (wild)	.444
Washougal R. (hatchery)	.342	Skagit R. (hatchery)	.463
Chambers Cr. (hatchery)	.346	Hoh R. (wild)	.432
		Big Beef Cr. (wild)	.424
		Nanaimo R. (wild)	.429
		Big Qualicum R. (wild)	.459

Comparison of Mean Diameters

		Student's t Test ($P \leq .01$) Test Value	Critical Value
Siletz Summer Steelhead	.351	10.08	2.69
Siletz Winter Steelhead	.439		
Total Sample Summer Steelhead	.346	32.46	2.58
Total Sample Winter Steelhead	.440		

Wild and Hatchery Stock Differentiation

A comparison of grand means of diagonally measured growth of otoliths from wild and hatchery-reared steelhead resulted in a highly significant difference in the amount of freshwater growth attained in

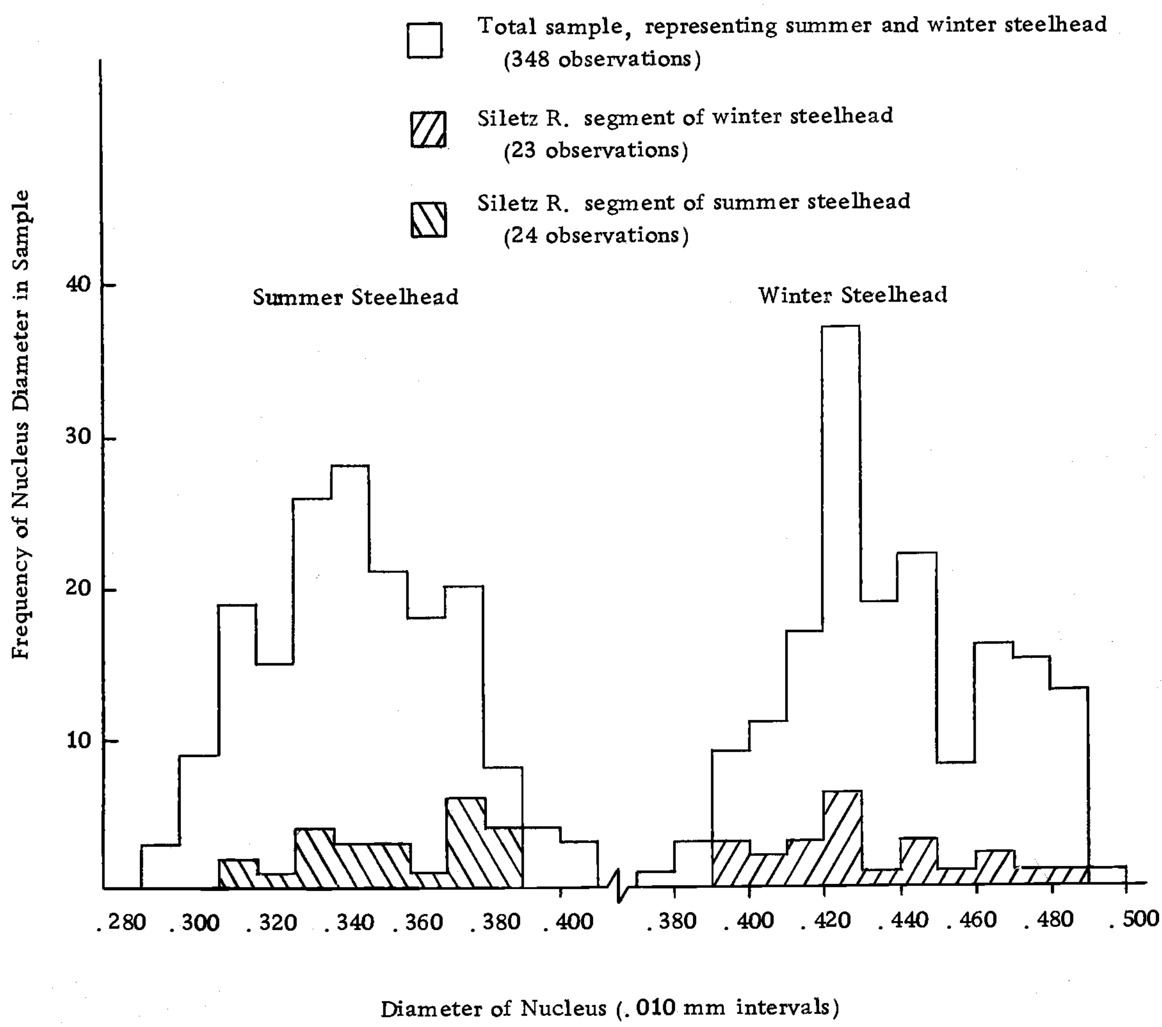

Figure 7. Frequency distributions of the diameters of nuclei of otoliths from summer and winter steelhead from the Siletz River, Oregon, and from rivers in Oregon, Washington, and British Columbia (1968 to 1970).

the first year by each stock (Table 2). This was sufficient evidence to separate these stocks; however, a visual comparison of the non-seasonal growth on otoliths of hatchery-reared fish with seasonal growth on otoliths of wild fish was just as reliable. In this study, 99% of the hatchery fish and 98% of the wild fish conformed to the pattern typical to each stock (Figure 8).

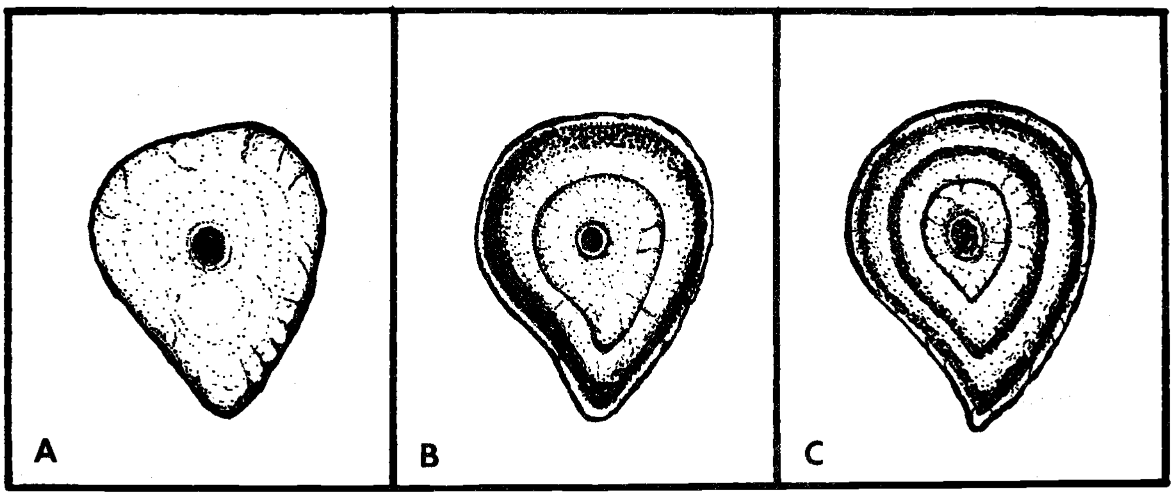

Figure 8. A visual comparison between (A) the total freshwater growth of a hatchery-reared steelhead which spent 1 year in freshwater, and (B and C) the total freshwater growth of wild steelhead which spent 2 and 3 years in freshwater, respectively.

DISCUSSION

Development of Otoliths

Although 93% of the total weight of steelhead otoliths is calcium carbonate, availability of calcium does not control the formation of opaque and hyaline zones on the otolith. This hypothesis is supported by the following facts: (1) Calcium is available in freshwater, and is ten times more abundant in saltwater (Copp, 1969). (2) Young anadromous salmonids can concentrate calcium in their blood during freshwater life (Ball and Baker, 1969). (3) During the parr-smolt transformation, juvenile steelhead commence to regulate calcium concentrations in their blood before migrating to saltwater (Conte, 1969).

In most instances, the formation of opaque and hyaline zones, or the degree of calcium carbonate crystalization, appears to be a function of food abundance (Irie, 1960). Two exceptions were found in the development of steelhead otoliths. First, because the nucleus forms during embryonic growth when nutrition is available from the yolk, it should be opaque in structure. However, that portion of the nucleus which develops before hatching is hyaline in nature. Organic components (lipids, protein, glucose, and nonprotein nitrogen) are contained in the yolk (Blaxter, 1969), and X-rays of embryos revealed that calcium was present in the otoliths. Apparently, calcium linked to protein is available in the yolk (Booke, 1964), though the availability of environmental calcium is limited prior to hatching by the semipermiability of the chorion (Holliday, 1969) and the impermiability of the yolk membrane to electrolytes (Leitritz, 1963). Therefore, limitation of calcium to that available in the yolk may prohibit formation of opaque growth. After hatching, the block to environmental calcium is evidently removed, because an opaque ring forms during the utilization of the remainder of the yolk. At this time, the fry are capable of concentrating electrolytes through their skin, and eventually through their gills, kidneys, and gut (Holliday, 1969).

The second exception was found in the formation of the metamorphic check that delineates total freshwater growth. During the parr-smolt transformation, steelhead continue to feed though their nutritional requirements are changing (Fessler, 1969), and their osmotic and ionic regulatory mechanisms are developing in preparation for migration to saltwater (Conte and Wagner, 1965). The stress of metamorphosis and the change in regulation of calcium levels in the blood possibly result in hyaline growth at this time.

With one exception, all other opaque and hyaline zones corresponded with seasonal fluctuations in food abundance. The exception was the metamorphic check that delineates growth of the nucleus. The formation of this hyaline zone coincides with a time lapse between yolk utilization and the beginning of feeding (Blaxter, 1969).

Normal seasonal growth is represented by opaque rings and bands during summer residence in freshwater and saltwater. This growth reflects food abundance which results in the formation of calcium carbonate crystals. Winter residence in freshwater and saltwater is represented by the formation of hyaline rings and bands, respectively, in which calcium carbonate crystals are less abundantly formed during seasonal food shortages.

Life History Interpretation from Otoliths

Three patterns of freshwater growth of otoliths were compared. The otoliths of hatchery fish showed nonseasonal freshwater growth because these individuals are fed a balanced diet throughout the year, whereas wild fish showed seasonal growth corresponding to two or three years in freshwater. Comparison of the three patterns revealed results similar to those found by Andrews (1959). Hatchery fish grew at a faster rate than wild fish, and 2-year wild fish grew at a faster rate than those spending three years in freshwater. By the end of the last year in freshwater, 3-year wild fish were larger than hatchery or 2-year wild fish, but no significant difference in size was found between hatchery fish and either group of wild fish. Because wild fish tended to migrate later than hatchery fish, 2-year wild fish, which were smaller than hatchery fish at the time of annulus formation or liberation, were larger at migration, and 3-year wild fish attained a size that made them significantly larger than hatchery as well as 2-year wild fish.

Regardless of juvenile life history, a seasonal pattern was found in saltwater growth of the otolith, and with two exceptions, an opaque band followed by a hyaline band was considered as one full year in saltwater.

The first exception was found in cases where considerable plus growth occurred. Because plus growth occurs during the calendar year in which the first saltwater growth occurs, it was included with saltwater growth in the full year.

The second exception occurred in the formation of checks due to spawning. Rollefsen (1935) described spawning checks as part of the pattern of continuous growth of otoliths, but in steelhead, spawning checks result from resorption of the otolith which is apparently controlled by a hormone, calcitonin (Copp, 1969). This resorption was most common along the ventral edge of the otolith (the edge used in aging), and allowance for any changes caused by it were made.

Winter steelhead normally enter freshwater during the winter, spawn in late winter or early spring, and return to saltwater immediately after spawning. In this case, the spawning check coincides with the formation of the annulus, and though resorption is easily detectable, the record of previous growth remains interpretable.

Summer steelhead, on the other hand, enter streams during the summer or early fall, remain in freshwater until late winter or early spring, spawn, then return to saltwater. The stress of formation of sexual products during this time of little or no feeding may result in resorption of the otolith over a long period of time. In that case, much of the growth record may be missing as a result of the spawning check. In either case, growth of otoliths follows the saltwater pattern after return to the sea, but new growth along the resorbed edge follows the contours as changed by resorption. This change in the pattern makes the occurrence of past spawning checks obvious.

Spawning checks and annuli formed on otoliths were used in the interpretation of 27 life history patterns, and, in aggregate, the results were comparable to those found by others (Maher and Larkin, 1954; Shapovalov and Taft, 1954; Chapman, 1957; Bali, 1958; Andrews, 1959; Withler, 1965).

Race Differentiation

The diameters of nuclei of otoliths are sufficiently different between summer and winter steelhead for the separation of these races. Summer steelhead have a significantly smaller nucleus (.346 mm) than winter steelhead (.440 mm), a trend which was true throughout the range studied. Because the nucleus represents that portion of the otolith which develops during embryonic growth when nourishment comes entirely from the yolk, this reflects a quantitative and qualitative difference in the substance available to the young of each race. Bulkley (1967) found that steelhead from the southern part of their range tended toward higher fecundity than their northern counterparts because of additional stresses from the freshwater environment. The same trend might be expected as a difference between summer and winter steelhead because summer steelhead enter streams when flows are low and water temperatures are relatively high (Rousseau, unpublished report, 1967. Oregon State Game Comm.), whereas winter steelhead enter streams when flows are higher and water temperatures are lower (Wallace, 1961). Egg counts substantiate this hypothesis. Bulkley (1967) reported an average fecundity of 3, 438 eggs per female for Alsea winter steelhead, and Rousseau (unpublished report, 1967. Oregon State Game Comm.) reported an average fecundity of 4, 150 eggs per female for Siletz summer steelhead. In addition, summer steelhead enter freshwater 6 to 10 months prior to spawning and are dependent on body reserves for life support and development of their sexual products during their stay in freshwater (Smith, 1969). The smaller diameter of the nucleus of the otolith probably reflects a stress placed on summer steelhead by the freshwater environment that is not imposed on winter steelhead which remain at sea until just before the spawning season.

Stock Differentiation

Hatchery-reared steelhead grew at a rate that was significantly faster than the rate of growth found in wild steelhead, and because the sizes of the otoliths of hatchery and wild steelhead were comparable at the time of smoltification, the stocks can be separated by the different rates of growth represented in each. In addition to quantitative separation, a qualitative separation similar to that described by Chapman (1957) and Bali (1958) for separating scales of hatchery and wild steelhead can be made on the basis of nonseasonal versus seasonal otolith growth.

SUMMARY AND CONCLUSIONS

1. Otoliths appeared in X-ray films of eyed eggs 14 days before hatching, and they were the only calcified structures evident in X-ray films of embryos at hatching. The nucleus of the otolith represents growth during embryonic development, and freshwater and saltwater growth represents a continuous record of the events in the life of the fish. With the exception of resorption at the time of spawning, growth of the otolith is continuous throughout the life of the fish.
2. Over 93% of the variability in the length of the otolith is explained by variability in the fork length of the fish for those steelhead captured during their first spawning migration, but the figure is much lower, 67%, for steelhead captured during a second or third migration.
3. Annuli formed in freshwater and saltwater, and spawning checks representing previous spawning migrations were used to describe 27 life history patterns for steelhead. Over 97% of the wild fish spent two or three years in freshwater, and over 99% of the hatchery fish spent one year in freshwater prior to smoltification. Regardless of juvenile life history, steelhead spent one, two, or three years in saltwater prior to their first spawning migration. Over 28% of the wild fish were captured during a second or third

spawning migration, whereas 14% of the hatchery-reared fish returned more than once.

4. Sufficient difference was found between the diameters of the nuclei of summer and winter steelhead otoliths to separate these races with less than 1% probability of error.

5. Significant differences between the freshwater growth of wild and hatchery-reared steelhead otoliths were used subjectively to separate these stocks.

Otoliths represent an accurate, complete, and usable record of the life history of steelhead trout. Growth characteristics of steelhead otoliths can be used with a high degree of accuracy for the separation of subpopulations of these fish. Therefore, the use of otoliths represents a valid technique to supplement those now available for management of this species.

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APPENDIX

Appendix 1. Arithmetic and grand means* of diagonally measured freshwater growth of otoliths from steelhead trout of rivers in Oregon, Washington, and British Columbia (1968 to 1970).

River	Sample Size	Age	Race	Growth After 1 Year ($\bar{x}$ mm)	Growth After 2 Years ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)	Growth After 3 Years ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)	Plus Growth ($\bar{x}$ mm)	Total River Growth ($\bar{x}$ mm)
				Hatchery Fish						
Alsea R.	25	1/	Winter	1.128						1.128
Siletz R.	19	1/	Winter	1.208						1.208
Siletz R.	29	1/	Summer	1.338						1.338
Washougal R.	69	1/	Summer	1.359						1.359
Chambers Cr.	106	1/	Summer	1.360						1.360
Skagit R.	67	1/	Winter	1.355						1.355
Grand Means				1.291						1.291
				Wild Fish						
Alsea R.	5	2/	Winter	.907	1.289	.382			.046	1.335
Siletz R.	17	2/	Winter	.857	1.267	.410			.025	1.292
Siletz R.	4	2/	Summer	1.023	1.393	.370			.071	1.464
Hoh R.	10	2/	Winter	.852	1.233	.381			.090	1.323
Big Beef Cr.	14	2/	Winter	.845	1.237	.392			.027	1.254
Nanaimo R.	6	2/	Winter	.818	1.206	.388			.086	1.292
Big Qualicum R.	9	2/	Winter	.774	1.217	.443			.120	1.337
Grand Means				.868	1.263	.395			.066	1.329
Alsea R.	1	3/	Winter	.760	1.220	.460	1.370	.150	.020	1.390
Siletz R.	7	3/	Winter	.834	1.162	.328	1.474	.312	.028	1.502
Siletz R.	1	3/	Summer	.670	.870	.200	1.350	.480	.010	1.360
Hoh R.	5	3/	Winter	.869	1.187	.318	1.495	.308	.079	1.574
Big Beef Cr.	14	3/	Winter	.754	1.129	.375	1.354	.225	.044	1.433
Nanaimo R.	4	3/	Winter	.845	1.115	.270	1.359	.244	.066	1.425
Big Qualicum R.	9	3/	Winter	.654	.961	.307	1.234	.271	.166	1.400
Grand Means				.769	1.092	.323	1.377	.284	.059	1.436

* The grand means represent the mean value of the unweighted arithmetic means.

Appendix 2. Arithmetic and grand means* of diagonally measured saltwater growth of otoliths from steelhead of rivers in Oregon, Washington, and British Columbia (1968 to 1970)

River	Sample Size	Age	Race	Growth to Last Fresh-water Annulus ($\bar{x}$ mm)	Plus Growth ($\bar{x}$ mm)	Growth After 1 Year ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)	Growth After 2 Years ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)	Growth After 3 Years ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)
					Hatchery Fish						
Siletz R.	5	1/1	Summer	1.361		2.220	.857				
Skagit R.	1	1/1	Winter	1.485		1.890	.405				
Grand Means				1.424		2.055	.631				
Siletz R.	10	1/2	Winter	1.208		1.853	.645	2.397	.544		
Siletz R.	21	1/2	Summer	1.338		2.004	.666	2.641	.637		
Skagit R.	53	1/2	Winter	1.355		1.826	.471	2.194	.368		
Grand Means				1.300		1.894	.594	2.411	.517		
Siletz R.	5	1/3	Winter	1.217		1.796	.579	2.287	.491	2.713	.426
Grand Means				1.217		1.796	.579	2.287	.491	2.713	.426
					Wild Fish						
Siletz R.	1	2/1	Winter	1.410	.020	1.680	.270				
Siletz R.	1	2/1	Summer	1.530	.025	2.310	.780				
Hoh R.	1	2/1	Winter	1.305	.025	2.310	1.005				
Big Beef Cr.	1	2/1	Winter	1.290	.070	1.780	.390				
				1.384	.035	2.020	.636				
Siletz R.	1	3/1	Winter	1.360	.010	1.790	.430				
Hoh R.	1	3/1	Winter	1.410	.010	1.950	.540				
Grand Means				1.385	.010	1.870	.485				

Appendix 2. (continued)

River	Sample Size	Age	Race	Growth to Last Fresh-water Annulus ($\bar{x}$ mm)	Plus Growth ($\bar{x}$ mm)	Growth After 1 Year ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)	Growth After 2 Years ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)	Growth After 3 Years ($\bar{x}$ mm)	Annual Increase ($\bar{x}$ mm)
Alsea R.	4	2/2	Winter	1.318	.040	1.878	.560	2.660	.782		
Siletz R.	4	2/2	Winter	1.380	.025	2.059	.679	2.516	.457		
Siletz R.	3	2/2	Summer	1.348	.015	2.098	.750	3.553	.455		
Hoh R.	6	2/2	Winter	1.232	.063	1.912	.680	2.400	.488		
Big Beef Cr.	1	2/2	Winter	1.170	.125	1.765	.595	2.315	.550		
Nanaimo R.	4	2/2	Winter	1.319	.080	1.921	.602	2.269	.348		
Big Qualicum R.	1	2/2	Winter	1.270	.050	1.755	.485	2.190	.435		
Grand Means				1.291	.057	1.913	.662	2.415	.502		
Alsea R.	1	3/2	Winter	1.485	.060	1.875	.390	2.400	.525		
Siletz R.	1	3/2	Winter	1.610	.035	2.290	.680	2.605	.315		
Hoh R.	3	3/2	Winter	1.448	.084	2.200	.752	2.512	.312		
Big Beef Cr.	6	3/2	Winter	1.292	.021	1.843	.551	2.248	.405		
Big Qualicum R.	2	3/2	Winter	1.190	.018	1.818	.628	2.167	.349		
Grand Means				1.405	.044	2.005	.600	2.386	.381		
Alsea R.	1	2/3	Winter	1.260	.070	1.840	.580	2.485	.645	3.055	.570
Hoh R.	2	2/3	Winter	1.250	.096	1.800	.550	2.300	.500	2.680	.380
Big Beef Cr.	1	2/3	Winter	1.120	.165	1.790	.672	2.025	.235	2.540	.515
Big Qualicum R.	1	2/3	Winter	1.320	.040	1.825	.505	2.060	.235	2.215	.155
Grand Means				1.237	.093	1.814	.577	2.218	.404	2.623	.405

* The grand means represent the mean value of the unweighted arithmetic means.

Appendix 3. Raw data on steelhead and their otoliths from rivers in Oregon, Washington, and British Columbia (1968 to 1970).

Sex	Age	Nucleus Diameter (mm)	Diagonal Freshwater Growth of Otolith (mm) 1/	2/	3/	+	Diagonal Saltwater Growth of Otolith (mm) /1	/2	/3	Total Otolith Length (mm)	Fork Length of Fish (mm)
Rogue River Summer Steelhead (Wild Stock) (November 1970)											
M	2/2s3	.378	.905	1.280			1.695	1.995s		5.260	458
M	2/1s2	.362	.880	1.370			1.770s			5.365	482
M	2/1	.381	.790	1.295			1.960			4.555	370
M	2/1	.356	.930	1.400			1.920			4.515	386
Rogue River Summer Steelhead (Hatchery Stock) (November 1970)											
M	1/2	.377	1.370				1.540	2.275		4.875	483
M	1/2	.357	1.300				1.680	2.050		4.670	484
Alsea River Winter Steelhead (Wild Stock) (March 1969)											
F	2/3	.472	.800	1.260		.070	1.840	2.485	3.055	--	603
M	--	.436	--	--		--	--	--	--	--	742
F	2/2	.409	.935	1.355		.040	1.870	2.675		5.810	685
F	2/2	.449	.910	1.305		.045	1.886	2.649		5.935	610
F	2/2	.393	.975	1.250		.050	1.857	2.595		--	596
F	3/2	.440	.760	.915	1.875	.060	1.875	2.400		--	610
F	2/2	.418	.915	1.365		.025	1.899	2.727		5.860	584
Alsea River Winter Steelhead (Hatchery Stock) (April 1970)											
-	1/	--	1.160							2.960	207
-	1/	--	1.160							2.790	192
-	1/	.397	1.040							2.660	133
-	1/	.428	1.095							2.925	171
-	1/	.423	1.230							3.055	192
-	1/	.397	1.140							2.960	172
-	1/	.461	1.200							2.970	210
-	1/	--	1.160							2.800	192
-	1/	.452	1.110							2.775	164
-	1/	--	1.210							3.190	221
-	1/	.432	1.090							2.855	198
-	1/	--	1.110							2.905	183
-	1/	.404	1.130							2.820	172
-	1/	.393	1.050							2.700	185
-	1/	.403	1.185							2.810	185
-	1/	.386	1.010							2.645	163
-	1/	.393	1.020							2.890	207
-	1/	--	1.150							2.940	202
-	1/	.441	1.195							--	203
-	1/	.472	1.260							3.100	194
-	1/	.462	1.220							2.820	181
-	1/	.443	1.005							2.880	169
-	1/	.483	1.150							2.680	191
-	1/	--	1.090							2.815	184
-	1/	.456	1.035							2.880	157

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
Siletz River Summer Steelhead (Hatchery Stock) (Oct.-Nov. 1969, Oct. 1970)											
F	1/1	--	1.255				1.905			4.790	560
F	1/2	--	1.210				1.700	2.450		5.150	650
F	1/2	--	1.200				1.780	1.960		5.210	550
M	1/2	.385	1.400				1.920	2.390		5.830	775
M	---	--	1.505				1.910	2.485		5.325	580
F	---	.385	--				--			6.410	704
F	1/2	.318	1.435				1.790	2.330		6.410	617
F	1/2	.339	1.415				2.060	2.540		6.420	685
F	1/2	.346	1.320				2.120	2.920		6.370	630
F	1/2	.373	1.330				1.825	2.860		6.710	640
M	---	.371	--				--			4.720	470
M	1/2	--	1.340				2.020	2.620		6.450	700
M	1/2	.357	1.355				--			5.880	700
M	1/2	.334	1.440				2.030	2.780		5.875	710
F	1/2	.355	1.500				1.975	2.515		6.990	--
M	1/1	.336	1.330				2.230			4.930	--
M	1/2	.380	1.255				1.970	2.500		5.870	--
F	1/2	.320	1.375				2.150	2.865		6.055	--
F	1/2	.316	1.320				--			5.865	675
M	1/2	.335	1.510				2.020	2.770		6.155	745
M	1/2	.348	1.470				2.035	2.685		5.880	720
M	---	.345	1.420				2.075	2.620		5.990	735
M	1/2	--	--				--			5.870	790
M	1/1	--	1.380				2.290			--	560
M	1/2	--	1.455				1.890	2.450		6.740	710
M	1/1	.364	1.350				2.210			--	465
F	1/2	.370	1.390				2.120	2.605		--	675
F	1/2	.374	1.455				2.015	2.570		5.390	705
F	1/2	.388	1.450				2.135	2.660		6.120	635
F	1/2	.358	1.485				2.270	3.140		7.545	711
M	1/1	.370	1.400				2.360			--	--
M	1/2	--	1.550				2.010	2.800		5.710	--
M	1/2	.376	1.420				1.980	2.730		6.125	--
Siletz River Summer Steelhead (Wild Stock) (Nov. 1969 to Jan. 1970)											
M	2/1	.349	1.000	1.530		.025	2.310			5.520	595
F	2/2	.367	1.010	1.190		.085	1.885	2.360		5.600	675
F	2/2	.346	1.090	1.425		.060	2.290	2.760		6.140	690
F	2/2	.358	.990	1.430		.115	2.120	2.540		5.630	660
M	3/1	.311	.670	.870	1.350	.010	1.790			--	465
Siletz River Winter Steelhead (Wild and Hatchery Stocks) (1968 to 1969)											
-	1/2	--	1.310				1.950	2.255		5.320	--
-	1/2	.423	1.095				1.650	2.160		6.515	--
-	1/2	.395	1.200				1.595	2.050		--	--
-	1/2s3	.396	1.250				1.890	2.010s		--	--
-	1/3	.428	1.195				1.655	1.990	2.510	5.480	--
-	1/2	.428	1.055				1.625	2.310		--	--
-	1/2	.414	1.340				1.870	2.570		5.920	--
-	1/2	.463	1.235				1.745	2.250		5.990	--
-	1/2s3	.454	1.100				1.590	2.200s		--	--
-	1/3	--	1.320				1.925	2.570	2.990	--	--

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
Siletz River Winter Steelhead (Wild and Hatchery Stocks) (1968 to 1969)											
-	1/3	.428	1.120				1.765	2.435	2.695	--	--
-	1/3	.403	1.250				1.850	2.215	2.645	--	--
-	1/2s3	.426	1.160				1.695	2.155s		--	--
-	1/2	.462	1.200				1.795	2.565		5.775	
-	1/2	.439	1.390				1.920	2.435		--	--
-	1/3	.394	1.200				1.785	2.225	2.725	6.290	--
-	1/2	.413	1.170				1.770	2.395		5.420	--
-	2/3	.481	.675	1.205		.045	1.740	2.005	2.740	--	--
-	2/3	.421	.860	1.445		.020	2.020	2.495	3.040	--	--
-	3/2	.414	.795	1.280	1.610	.035	2.025	2.420		--	--
-	3/2	.402	.735	1.050	1.320	.060	1.930	2.190		--	--
-	2/2	.445	.755	1.165		.015	1.850	2.310		5.100	--
-	2/2	.450	.695	1.160		.020	2.095	2.520		--	--
-	2/2	.483	1.010	1.370		.025	2.025	2.650		--	--
-	3/1s3	.441	.810	1.185		.020	1.840s			--	--
-	2/3	.418	.745	1.400		.010	1.920	2.220	2.620	--	--
-	3/2	.445	.725	1.035	1.350	.035	1.820	2.240		5.950	--
-	2/3	--	1.060	1.415		.005	1.765	2.015	2.560	6.115	--
-	2/2	.391	.800	1.170		.050	1.810	2.240		--	--
-	2/2	.393	.855	1.250		.015	1.900	2.460		--	--
Siletz River Winter Steelhead (Hatchery Stock) (Nov. 1969 to Jan. 1970)											
F	1/2	.465	1.415				2.270	2.975		7.275	732
M	---	--	--				--			5.200	690
F	1/2	.479	1.405				2.075	2.420		5.430	660
M	1/2	.429	1.435				1.975	2.380		6.130	655
Siletz River Winter Steelhead (Wild Stock) (Nov. 1969 to Feb. 1970)											
M	1/2	.415	1.015				1.810	2.310		5.275	495
F	2/2	.449	1.100	1.410		.020	2.090	2.610		--	690
F	2/1	.420	.905	1.190		.020	1.920			3.245	365
F	3/2	.447	1.050	1.400	1.610	.035	2.290	2.605		--	660
M	2/2s3	.432	.930	1.665		.010	2.295	2.915s		7.755	825
M	2/2	.414	.920	1.330		.035	1.840	2.255		5.220	655
F	2/2	.472	.950	1.365		.020	1.900	2.315		--	675
F	2/1s2s3	.415	--	--		--	--			--	830
Washougal River Summer Steelhead (Hatchery Stock) (May 1968)											
-	1/	.326	1.550							3.600	207
-	1/	.357	1.395							2.940	158
-	1/	--	1.245							3.100	171
-	1/	.301	1.310							3.345	183
-	1/	.340	1.205							3.170	167
-	1/	.327	1.265							3.010	157
-	1/	.360	1.350							3.085	138
-	1/	--	1.440							3.130	164

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
Washougal River Summer Steelhead (Hatchery Stock) (May 1968)											
-	1/	.347	1.460							3.335	176
-	1/	.321	1.450							3.190	207
-	1/	.313	1.310							3.270	174
-	1/	.309	1.390							3.215	179
-	1/	--	1.350							1.360	155
-	1/	.362	1.350							1.500	168
-	1/	.320	1.555							3.720	212
-	1/	.341	1.310							3.160	205
-	1/	.306	1.160							2.940	162
-	1/	.319	1.355							2.745	146
-	1/	.337	1.240							3.130	164
-	1/	--	1.335							2.940	147
-	1/	.364	1.235							3.160	158
-	1/	.298	1.470							3.360	163
-	1/	.353	1.375							3.535	179
-	1/	--	1.280							3.215	174
-	1/	.391	1.505							3.235	182
-	1/	.328	1.355							3.120	172
-	1/	.365	1.260							3.475	170
-	1/	.333	1.275							3.335	186
-	1/	.401	1.220							3.125	150
-	1/	.319	1.280							3.390	168
-	1/	.389	1.270							3.310	172
-	1/	.389	1.255							3.030	164
-	1/	--	1.470							3.210	187
-	1/	.324	1.510							3.755	232
-	1/	.371	1.300							3.390	174
-	1/	.323	1.295							3.345	172
-	1/	--	1.220							3.050	159
-	1/	.346	1.220							3.065	155
-	1/	.381	1.085							3.165	186
-	1/	.370	1.315							2.100	144
-	1/	.340	1.280							2.010	107
-	1/	--	1.400							3.460	162
-	1/	.303	1.300							3.170	151
-	1/	--	1.240							2.980	182
-	1/	.372	1.280							2.925	153
-	1/	.310	1.215							2.565	147
-	1/	--	1.240							3.080	156
-	1/	.361	1.110							3.085	152
-	1/	.347	1.420							3.210	173
-	1/	.371	1.035							3.225	166
-	1/	.314	1.300							--	216
-	1/	--	1.200							2.925	171
-	1/	.389	1.310							3.420	163
-	1/	.340	1.275							3.220	175

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
		Washougal River Summer Steelhead (Hatchery Stock) (May 1968)									
-	1/	.352	1.340							3.170	169
-	1/	.357	1.240							2.980	119
-	1/	--	1.260							3.350	204
-	1/	.389	1.090							2.550	135
-	1/	--	1.430							3.125	199
-	1/	.315	1.370							3.265	187
-	1/	--	1.340							3.465	194
-	1/	.324	1.310							3.145	168
-	1/	--	1.445							3.645	188
-	1/	.349	1.485							3.330	176
-	1/	.318	1.330							3.140	188
-	1/	--	1.530							3.345	173
-	1/	.322	1.420							3.290	172
-	1/	.317	1.290							3.360	165
-	1/	.348	1.330							3.100	188
		Hoh River Winter Steelhead (Wild Stock) (1968) *Summer Steelhead									
F	2/1	.481	.880	1.305		.025	2.310			6.695	--
F	2/2	--	--	--		--	--			6.885	--
F	2/2	.462	.770	1.170		.120	1.920	2.345		5.415	--
F	3/2	.440	.810	1.320	1.420	.140	2.340	2.815		6.860	--
F	2/2	--	.760	1.150		.085	2.070	2.350		5.810	--
F	2/1s2	.422	1.005	1.255		.050	2.195s			6.135	--
F	2/2	--	.790	1.180		.065	1.640	2.285		5.540	--
F	2/2	.328*	.830	1.160		.035	1.890	2.600		6.800	--
F	2/2	.436	.775	1.100		.025	1.835	2.120		5.255	--
F	3/2s3	.440	.835	1.130	1.380	.050	1.890	2.240s		5.800	--
F	2/3	.457	.810	1.250		.085	1.840	2.200	2.580	5.750	--
M	2/2	.475	1.040	1.570		.045	2.115	2.790		6.870	--
M	2/3	.405	.860	1.185		.110	1.760	2.120	2.770	7.420	--
M	3/2	.428	.860	1.220	1.485	.070	2.050	2.460		5.930	--
M	3/1	.450	.910	1.025	1.410	.010	1.950			5.165	--
M	3/2	.387	.930	1.240	1.450	.040	2.210	2.490		6.215	--
		Big Beef Creek Winter Steelhead (Wild Stock) (May 1968)									
-	2/	.425	.805	1.305		.020				2.910	157
-	2/	.396	.895	1.260		.030				3.075	143
-	2/	.425	.895	1.215		.035				2.905	145
-	2/	--	.850	1.300		.010				--	177
-	3/	.433	.700	1.145	1.320	.085				3.390	178
-	3/	.423	.775	1.035	1.325	.060				2.765	150
-	2/	.432	.880	1.230		.030				2.965	143
-	3/	.430	.750	1.065	1.270	.045				--	155
-	3/	--	.840	1.290	1.525	.080				3.470	175
-	3/	--	.765	1.060	1.250	.095				--	142
-	2/	.421	.850	1.310		.015				--	147

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
	Big Beef Creek Winter Steelhead (Wild Stock) (May 1968)										
-	3/	.428	.630	1.070	1.285	.120				3.060	154
-	2/	.415	.765	1.040		.020				2.730	140
-	2/	.418	.895	1.400	1.625	.010				3.565	160
-	2/	.417	.940	1.350		.020				3.080	140
-	2/	.400	.800	1.320		.030				3.130	149
-	1/	.420	1.140			--				2.390	126
-	2/	.439	.815	1.220		.010				3.040	162
-	2/	.428	.730	1.080		.020				3.170	172
	Big Beef Creek Winter Steelhead (Wild Stock) (Dec. 1968 to Feb. 1969)										
M	2/3	--	.850	1.120		.165	1.790	2.025	2.540	--	720
M	1/2	--	1.335				1.835	2.320		--	648
M	3/1	.419	.775	1.390	1.605	.010	2.250			--	460
F	2/2	.445	.940	1.170		.125	1.765	2.315		--	625
F	2/1s2	--	.800	1.050		.030	1.750s			5.650	650
M	2/2s3s4	.420	.785	1.230		.010	1.960	2.550s		6.480	794
F	2/1	.435	.940	1.290		.070	1.780			4.055	457
F	3/2	.445	.850	1.100	1.330	.010	1.860	2.260		5.200	635
M	3/2	.402	.810	1.080	1.380	.005	2.030	2.450		--	724
F	3/2	.416	.790	1.065	1.380	.030	1.750	2.125		5.810	667
M	3/2	.432	.685	.990	1.180	.035	1.905	2.220		--	680
F	3/2	.446	.580	.990	1.210	.020	1.625	2.115		--	655
M	3/2	.422	.715	1.125	1.270	.025	1.885	2.315		6.220	686
	Chambers Creek Summer Steelhead (Hatchery Stock) (May 1968)										
-	1/	.325	1.425							3.460	179
-	1/	.359	1.405							3.200	177
-	1/	.391	1.190							2.925	158
-	1/	.353	1.225							2.900	145
-	1/	.364	1.410							3.430	177
-	1/	.324	1.235							3.105	132
-	1/	.331	1.210							3.020	151
-	1/	.356	1.275							3.025	177
-	1/	.337	1.390							3.160	155
-	1/	.330	1.320							2.950	136
-	1/	--	1.320							3.190	169
-	1/	.379	1.405							3.230	158
-	1/	.365	1.295							3.190	174
-	1/	.379	1.590							3.545	194
-	1/	.373	1.320							3.165	187
-	1/	--	1.350							3.005	192
-	1/	--	1.190							2.940	153
-	1/	.382	1.410							3.300	146
-	1/	.359	1.560							3.320	179
-	1/	.345	1.520							3.215	193
-	1/	.350	1.610							3.390	162

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
			Chambers Creek Summer Steelhead (Hatchery Stock) (May 1968)								
-	1/	.364	1.385							3.040	158
-	1/	--	1.210							3.530	188
-	1/	--	1.130							2.690	118
-	1/	.373	1.260							2.725	145
-	1/	.352	1.315							3.060	177
-	1/	.320	1.450							3.210	187
-	1/	.310	1.420							3.280	146
-	1/	.350	1.325							3.240	155
-	1/	.342	1.320							3.095	152
-	1/	.332	1.450							3.340	168
-	1/	.346	1.385							3.250	164
-	1/	.352	1.175							2.835	164
-	1/	.372	1.245							3.220	171
-	1/	.353	1.325							2.895	120
-	1/	.332	1.305							3.340	173
-	1/	.355	1.385							2.905	150
-	1/	--	1.330							3.180	182
-	1/	.342	1.270							2.885	155
-	1/	.330	1.420							2.850	140
-	1/	--	1.430							3.370	223
-	1/	.354	1.480							3.285	198
-	1/	.362	1.420							3.470	181
-	1/	.402	1.270							2.930	175
-	1/	.350	1.405							3.150	158
-	1/	.364	1.330							3.070	171
-	1/	.344	1.340							2.940	179
-	1/	.328	1.450							3.290	168
-	1/	.336	1.380							3.115	187
-	1/	.335	1.305							2.990	149
-	1/	.365	1.350							2.700	145
-	1/	.333	1.310							3.290	174
-	1/	.338	1.290							2.890	164
-	1/	.350	1.300							3.000	150
-	1/	.405	1.380							2.990	150
-	1/	.313	1.415							3.150	145
-	1/	.364	1.545							3.210	148
-	1/	.350	1.480							3.490	167
-	1/	.344	1.360							3.330	181
-	1/	.352	1.430							2.890	151
-	1/	.332	1.500							3.340	178
-	1/	.357	1.185							3.325	188
-	1/	.371	1.390							2.505	98
-	1/	.344	1.310							3.090	168
-	1/	.341	1.400							3.070	147
-	1/	.344	1.290							2.920	163
-	1/	--	1.510							3.035	157
-	1/	.325	1.305							2.840	163

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
		Chambers Creek Summer Steelhead (Hatchery Stock) (May 1968)									
-	1/	.362	1.200							3.030	178
-	1/	.373	1.460							2.775	154
-	1/	.366	1.240							3.255	183
-	1/	.341	1.500							3.120	160
-	1/	.370	1.280							3.560	177
-	1/	.364	1.670							3.030	152
-	1/	.332	1.410							3.740	188
-	1/	.311	1.295							3.065	151
-	1/	.332	1.185							3.010	140
-	1/	.298	1.450							3.150	149
-	1/	.309	1.410							3.215	168
-	1/	.355	1.370							3.280	165
-	1/	.358	1.310							3.160	198
-	1/	.398	1.400							3.140	166
-	1/	.362	1.365							3.300	183
-	1/	.343	1.425							3.135	146
-	1/	.325	1.480							3.170	194
-	1/	--	1.360							3.240	176
-	1/	.314	1.275							3.240	169
-	1/	.346	1.590							3.250	164
-	1/	.339	1.205							3.730	192
-	1/	.291	1.240							3.230	176
-	1/	.347	1.300							2.960	135
-	1/	.372	1.270							2.750	111
-	1/	.300	1.485							3.260	186
-	1/	.362	1.570							3.440	201
-	1/	.395	1.190							2.940	142
-	1/	.337	1.335							3.125	157
-	1/	.355	1.295							2.920	151
-	1/	.333	1.330							3.040	165
-	1/	.318	1.160							2.600	112
-	1/	.308	1.350							--	166
-	1/	.323	1.215							2.815	143
-	1/	.314	1.450							3.100	177
-	1/	.313	1.260							2.900	150
-	1/	.337	1.420							3.020	183
-	1/	.311	1.335							3.120	152
-	1/	.317	1.365							3.075	155
		Skagit River Winter Steelhead (Hatchery Stock) (February 1968) (* Wild)									
F	1/2	--	1.215				1.630	1.995		5.255	--
F	1/2	.473	1.480				2.150	2.395		--	--
F	1/2	.463	1.520				2.000	2.340		--	--
F	1/2	.427	--				--	--		--	--
F	1/2	.505	1.390				1.770	2.000		5.250	--
F	1/2	.473	1.195				1.700	2.155		--	--

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
Skagit River Winter Steelhead (Hatchery Stock) (February 1968) (*Wild)											
F	1/2	.485	1.330				1.795	2.150		5.940	--
F	--	--	--				--	--		6.540	--
F	1/2	.475	1.590				2.060	2.340		5.650	--
F	3/3*	.424	.660	.850	1.205		1.485	1.865	2.130	5.280	--
F	1/1	.455	1.485				1.890			4.550	--
F	1/2	.470	1.280				1.890	2.100		5.340	--
F	2/2	.463	1.010	1.250			1.815	2.305		5.550	--
F	1/2	--	1.250				1.950	2.680		5.910	--
F	2/2	--	.815	1.315			1.705	2.135		4.930	--
F	--	--	--				--	--		6.320	--
F	1/2	.477	1.315				2.220	2.510		6.405	--
F	1/2s3	.482	1.070				1.690	2.155s		6.535	--
F	1/2	.471	1.600				1.820	2.110		4.970	--
F	1/2	.462	1.295				1.840	2.045		5.385	--
F	1/2	.478	1.340				1.920	2.310		5.640	--
F	1/2	--	1.620				2.050	2.455		5.900	--
F	2/2	.443	.960	1.440			2.210	2.740		6.060	--
F	1/2	.490	1.410				1.890	2.300		6.030	--
F	--	--	--				--	--		7.030	--
F	1/2	.428	1.430				1.765	2.215		5.490	--
F	--	--	--				--	--		6.920	--
F	--	--	--				--	--		--	668
F	--	--	--				--	--		--	745
F	--	--	--				--	--		--	626
F	1/2	.421	1.220				1.885	2.310		5.345	685
F	--	--	1.235				--			--	631
F	--	--	1.215				--			--	648
F	--	.421	1.300				--			--	622
F	1/2	--	1.185				1.720	2.000		--	620
F	1/2	.442	1.210				1.695	2.155		5.280	660
F	1/2	.412	1.245				1.815	2.065		6.020	678
F	1/2	--	1.120				1.630	2.000		5.370	662
F	1/2s3	--	1.200				1.705	2.210s		5.975	719
F	1/2s3	--	1.390				1.920	2.230s		--	755
F	1/2	.407	1.175				1.900	2.290		--	647
F	1/2	--	1.615				1.905	2.190		--	597
F	1/2	.411	1.200				1.845	2.100		5.370	684
F	--	.466	--				--			5.270	633
F	1/2	.433	1.410				1.835	2.080		--	652
F	--	--	1.000				--			--	647
F	1/2	.421	1.230				1.740	2.060		--	620
F	1/2	.437	1.115				1.700	2.020		6.015	675
F	1/2s3	--	1.310				1.760	2.195s		--	766
F	1/2	.423	1.080				1.710	2.295		5.170	670

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
					Skagit River Winter Steelhead (Hatchery Stock) (February 1968)						
F	1/2	.427	1.240				1.830	2.155		--	659
F	1/1s2	.423	1.245				1.880s			--	600
F	1/2s3	--	1.415				2.120	2.460s		6.490	748
F	1/2	.448	1.235				1.760	2.300		--	--
F	--	--	--				--			--	--
F	1/2	.426	1.245				1.800	2.150		5.880	644
F	--	--	--				--			--	672
F	--	--	1.240				--			--	655
F	1/2	--	1.480				2.125	2.490		6.005	652
F	1/1s2	.468	1.410				1.610s			5.500	588
F	1/2s3	.419	1.315				1.995	2.440s		--	660
F	1/2	--	1.300				1.850	2.060		--	642
F	1/2	--	1.250				1.890	2.200		--	622
F	1/2	.451	1.300				1.870	2.060		--	692
F	1/2	.426	1.340				1.940	2.345		--	652
F	--	--	--				--	--		--	648
F	1/2s3	.471	1.150				1.890	2.190s		5.455	640
F	1/2	.485	1.340				1.765	2.065		--	645
F	1/2	--	1.130				1.640	2.130		5.330	610
F	--	--	--				--			6.040	670
F	--	--	--				--			--	716
F	1/2	.422	1.300				1.910	2.210		5.340	628
F	1/2s3	.456	1.330				1.790	2.040s		--	800
F	--	--	--				--			--	671
F	1/2	.477	1.245				1.680	1.990		--	648
F	1/2s3	.439	1.400				1.855	2.090s			652
F	1/2	.440	1.290				1.700	1.980		--	667
F	--	--	--				--	--		--	672
F	1/2	--	1.350				1.835	2.170		--	658
F	1/2	.419	1.500				1.790	2.075		--	618
F	1/2s3	.487	1.220				1.730	1.990s		--	715
F	1/2	.439	1.235				1.755	2.020		5.260	630
F	1/2	--	1.220				1.795	2.075		5.125	618
F	1/2	.446	1.335				1.880	2.110		5.225	666
F	--	--	--				--			--	--
F	1/2s3	.446	1.130				1.880	2.175s		--	710
F	1/2	.450	1.130				1.670	2.065		5.460	667
F	1/2	--	1.220				1.870	2.165		--	668
F	--	--	--				--	--		--	767
F	1/2	.433	1.310				1.780	2.000		--	689
F	1/2	.427	1.305				1.795	2.145		--	630
F	1/2	.465	1.210				1.840	2.150		--	669
F	1/2	.490	1.195				1.720	2.150		--	686
F	--	.438	--				--			--	628

Appendix 3. (continued)

Sex	Age	ND	1/	2/	3/	+	/1	/2	/3	TLO	FL
			Nanaimo River Winter Steelhead (Wild Stock) (Feb. and Mar. 1968)								
F	--	--	--				--			--	--
F	--	--	--				--			--	--
F	--	--	--				--			--	672
M	2/2s3	.473	.750	1.100		.090	1.955	2.400s		--	838
F	3/2	.421	.550	.860	1.200	.055	1.710	1.900		--	672
F	--	--	.725	1.070	1.470	.050	--			--	661
F	--	--	1.060	1.430		--	--			7.230	875
F	2/1s2s3	.433	.715	1.140		.125	1.620s			6.275	774
F	2/2	--	.990	1.270		.100	1.930	2.530		--	711
F	2/2	.490	.930	1.305		.075	1.910	2.210		--	711
M	2/2	.409	.695	1.175		.080	1.775	2.145		5.270	672
M	2/2s3s4	.379	.760	1.085		.070	1.835	2.420s		6.060	863
F	--	.443	.790	1.030	1.180	.070	--			7.090	863
F	--	.411	.895	1.200	1.490	.090	--			7.185	837
M	2/2	.427	.705	1.295		.060	1.880	2.190		--	641
F	4/2	.408	.480 .830	1.040	1.365	.015	1.835	2.230		5.900	661
			Big Qualicum River Winter Steelhead (Wild Stock) (Jan. to Apr. 1968)								
F	--	.430	--				--			--	661
M	2/2	.447	1.005	1.270		.050	1.755	2.190		--	630
M	3/2s3	--	.680	.955	1.120	.215	1.520	1.940		--	730
M	2/3	.456	.875	1.320		.040	1.825	2.060	2.215	5.980	775
F	3/1s2	.487	.780	1.065	1.475	.060	2.100s			--	640
F	3/1s2	.473	.690	1.130	1.280	.185	1.920s			--	730
M	2/1s3	.471	.760	1.100		.190	1.655s			--	838
F	3/2	.463	.700	.980	1.170	.015	1.785	2.045		--	655
M	3/2	.458	.545	.780	1.120	.020	1.785	2.100		--	680
F	2/1s2s3	--	.685	1.045		.150	1.675s			7.095	710
F	2/1s2s3	.425	.705	1.160		.135	1.530s			6.515	765
F	2/1s3	.461	.585	1.025		.100	1.735s			6.875	700
M	--	--	--				--			--	960
M	2/2s4s5	--	.710	1.330		.095	2.020	2.410s		8.500	885
F	--	.456	--				--			--	755
M	3/2s3	.461	.655	.970	1.260	.210	1.685	1.920s		6.040	695
F	2/2s4	.497	.840	1.290		.110	1.820	2.095s		6.415	810
F	2/2s4s5	.475	.780	1.230		.140	1.530	2.100s		6.500	765
F	2/1s2s3	.439	.910	1.350		.095	1.735s			6.565	720
F	3/1s2s3	.421	.570	.780	1.085	.170	1.430s			4.985	655
F	2/2s3	.489	1.015	1.260		.120	1.685	1.840s		5.575	602
F	3/1s2	.450	.525	.835	1.215	.190	1.960s			5.850	602