UNIVERSITY OF WYOMING

Department of Zoology and Physiology
P.O. Box 3166
Laramie, Wyoming 82071-3166
(307) 766-4207
FAX (307) 766-5625

March 26, 1996

Mr. Robert J. Behnke
Department of Fisheries and Wildlife Biology
Colorado State University
Ft. Collins, Colorado 80523

Dear Bob,

Enclosed is a copy of a manuscript I am preparing for submission to either the Great Basin Naturalist or Northwest Science. I would appreciate any comments or criticism you may have regarding the content or style of the manuscript.

The validity of meristic techniques to assess trout stock genetic integrity is an important and debatable question. This paper addresses the variation that is associated with using meristic techniques and provides insight to managers currently using this technique to assess trout genetic status.

Thank you for taking the time to review this manuscript and providing comments which might strengthen the material presented. Please respond as soon as possible; however, I realize the extra demand this request places on an already busy work schedule.

Sincerely,

Carter G. Kruse

Sources of Variation in Meristic Counts to Identify Yellowstone Cutthroat Trout

CARTER G. KRUSE AND WAYNE A. HUBERT

National Biological Service,

Wyoming Cooperative Fish and Wildlife Research Unit[1],

University of Wyoming,

Laramie, Wyoming 82071, USA

FRANK J. RAHEL

Department of Zoology and Physiology,

University of Wyoming,

Laramie, Wyoming 82071, USA

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Abstract - We determined variability in counts of meristic features (pyloric caeca, vertebrae, pelvic fin rays, gillrakers, basibranchial teeth, scales above the lateral line, and scales in the lateral series) of Yellowstone cutthroat trout Oncorhynchus clarki bouvieri made by three independent readers and the same reader on three different occasions, as well as among fish from 12 sampling sites within a 650-km^2 watershed. Meristic counts were compared to standard ranges for cutthroat trout and rainbow trout O. mykiss to determine the ability to differentiate between the two species using meristic counts. Genetic purity of the cutthroat trout was determined by electrophoretic analysis. Mean counts by individual readers were not significantly different among three occasions, but significant differences occurred among three readers and among sampling sites. Counts were similar to the standard ranges that have been suggested for Yellowstone cutthroat trout. Meristic counts identified the fish as cutthroat trout, but variation among species, sampling sites, and readers may limit their use when assessing genetic purity of cutthroat trout.

Key words: meristic counts, Yellowstone cutthroat trout, meristic variation, genetics, rainbow trout

INTRODUCTION

Hybridization of introduced rainbow trout (Oncorhynchus mykiss) with native cutthroat trout (O. clarki) has contributed to the decline of cutthroat trout in the western United States (Allendorf and Leary 1988; Gresswell 1988; Behnke 1992, Young 1995). Preservation of native cutthroat trout populations is a goal of state and federal agencies. An initial step in restoration or preservation efforts is identification of genetically pure cutthroat trout populations (Rinne 1985; Leary et al. 1989).

Comparisons of meristic features (such as fin ray or vertebrae counts) have been used to identify hybridization among species of trout. The technique assumes that hybrids are morphologically intermediate to parental taxa and have increased morphological variance (Leary et al. 1985; Marnell et al. 1987; Leary et al. 1991). Recent studies have shown that this assumption is not always valid and meristic comparisons can provide misleading genetic information (Busack and Gall 1981; Leary et al. 1984, 1985; Currens et al. 1989). Environmental influences and observer error can lead to differing meristic counts for a species among sampling sites (Barlow 1961; Rinne 1985; Currens et al. 1989; Leary et al. 1991; Hubert and Alexander 1995). However, biologists continue to use meristic features to assess genetic purity of trout populations (Loudenslager and Gall 1980; Rinne 1985; Behnke 1992), even though more definitive biochemical methods have been developed

(Leary et al. 1987, 1989).

Analysis of proteins using electrophoresis is a powerful and reliable method of determining genetic status of trout populations (Leary et al. 1987, 1989; Marnell et al. 1987). Electrophoresis provides data on allelic frequencies at genetic loci for different populations (Avise 1972). Genetic composition of a sample from a population can be determined when differences in allele frequencies at several diagnostic loci occur between taxa (Ayala and Powell 1972; Leary et al. 1989). For example, Yellowstone cutthroat trout (O. c. bouvieri) can be differentiated from rainbow trout using 10 loci commonly assayed in electrophoretic analysis.

Managers may save considerable time and money using meristic features instead of biochemical analysis to assess genetic purity of cutthroat trout. However, unless variation in meristic counts is minimal among readers or sampling sites, use of meristic features to assess genetic purity will be limited. The objectives of this study were to determine the variability in counts of meristic features: (1) among independent readers, (2) among counts by a single reader, and (3) among sampling sites within a moderate-sized watershed (650 km^2). We also compared species identification determined by electrophoresis to that indicated by meristic counts.

STUDY AREA

The Greybull River drains 2900 km^2 of the eastern Absaroka Mountain Range in northwestern Wyoming. The study area included that portion of the Greybull River drainage within the Shoshone National Forest (Figure 1). A total of 56 perennial tributaries (355 km of total stream length) occur in the 650 km^2 headwater drainage.

The Greybull River and its tributaries are torrential, high-elevation mountain streams with high channel slopes, unstable substrates, and large fluctuations in discharge from spring to late summer (Hansen and Glover 1973). Elevations of streams in the study area range from 2300 to 3050 m above mean sea level. Stream gradients range from 0.5 to 25% with a mean of 8.5%, generally considered steep (Kondolf et al. 1991; Rosgen 1994). Snowmelt dominates the annual hydrograph and results in extremely high spring flows (Hansen and Glover 1973; Martner 1982; Zafft and Annear 1992).

The Greybull River was historic Yellowstone cutthroat trout range and is currently managed by the Wyoming Game and Fish Department as a native "sport" fishery for cutthroat trout and mountain whitefish (Prosopium williamsoni). Non-native brook trout (Salvelinus fontinalus) and rainbow trout have been stocked in the system.

METHODS

Fifty-six study streams in the Greybull River drainage were sampled with battery back-pack electroshockers from June to September 1994. One-pass electrofishing runs (100-m reaches), starting at the confluence of tributaries with the Wood or Greybull river and moving upstream, were performed at approximately 1-km intervals until cutthroat trout were no longer captured in each stream.

Cutthroat trout were collected from one site (12-20 fish) on each of 18 streams in the Greybull River drainage. Fish were collected from the midpoint of the length of each stream where cutthroat trout were found. A sample of head, liver, and muscle tissue were removed from each cutthroat trout, wrapped in aluminum foil, and frozen within 1 hr in liquid nitrogen. The portion of each fish not used for electrophoretic analysis was preserved in 75% ethyl alcohol. Tissue samples from each fish were individually identified.

Frozen tissue samples from seven of the 18 streams were sent to the Wild Trout and Salmon Genetics Lab (WTSGL) at the University of Montana, Missoula, for genetic analysis. The seven sites were selected to represent the distribution of fish in the drainage. Protein electrophoresis (Allendorf and Phelps 1980; Leary et al. 1984; Marnell et al. 1987; Perkins et al. 1993) was performed to detect each fish's genetic characteristics at 45 loci coding for proteins present in muscle, liver, or eye tissue. Differences in allele frequencies at diagnostic loci were

evaluated to determine hybridization with rainbow trout.

Seven meristic features were counted on the preserved cutthroat trout: (1) basibranchial teeth; (2) anterior gillrakers (upper and lower limb of the first branchial arch); (3) pelvic fin rays; (4) scales in the lateral series; (5) scales above the lateral line; (6) pyloric caeca; and (7) vertebrae (Marnell et al. 1987; Behnke 1992).

Three independent readers (all fisheries biologists with training in anatomy and taxonomy of salmonids) counted each meristic structure on 50 randomly chosen cutthroat trout (≥ 150 mm total length) three different times to assess repeatability and variation of counts within and among individual readers. Additionally, one reader counted the seven meristic features on 125 additional cutthroat trout to determine mean counts for each structure and allow comparison among sampling sites where ≥ 5 fish were collected.

All counts were done on the right side of each cutthroat trout. Scales in the lateral series were counted two scale rows above the lateral line starting at the opercle opening and continuing to the insertion of the caudal fin, while scales above the lateral line were counted from the lateral line vertically to the anterior of the dorsal fin. Vertebral counts were completed by dissecting the cutthroat trout and counting the exposed vertebrae. Pyloric caeca were enumerated by stretching the stomach and counting the number of caeca ends. Meristic features were viewed under a dissecting microscope using 30x magnification

and reflected light to aid in counting. Readers practiced the protocol and compared results to resolve procedural differences before initiation of counts. All fish were counted at similar times by each reader with several different cutthroat trout counted between subsequent counts.

Two-way analysis of variance (ANOVA) and paired t-tests were used to asses differences in counts of meristic features among readers and among readings by individual readers. One-way ANOVA was used to compare counts among sampling sites. Tukey's multiple comparison test was used to make pairwise comparisons if significant differences were found. Statistical analyses were performed using SPSS/PC+ (SPSS Inc. 1991). Significance was determined at $P \leq 0.05$ for all tests.

RESULTS AND DISCUSSION

Cutthroat trout were present in 23 of 56 study streams; but no rainbow trout were collected. Electrophoretic analysis of fish sampled from the seven streams showed no rainbow trout genes at any of the diagnostic gene loci that differentiate Yellowstone cutthroat trout and rainbow trout.

No significant differences were found among counts by the same reader for any meristic feature. All three readers had high agreement among multiple counts for each structure (RUN; Table 1). Significant differences were observed in mean counts among readers for all structures except gill rakers (Tables 1 and 2). All three readers had significantly different mean counts of

pyloric caeca, pelvic fin rays, and scales above the lateral line, while at least one reader was significantly different from the other two readers in mean counts of vertebrae, basibranchial teeth, and scales in the lateral series. Paired reader comparisons (Table 3) showed similar results. Readers 1 and 2 had significantly different counts in at least one run for all structures except gill rakers. Readers 2 and 3 agreed on counts of scales in the lateral series and gill rakers, while readers 1 and 3 agreed on gill raker and basibranchial teeth counts. This suggests, similar to table 2, that between reader counts are inconsistent for all structures except gill rakers. Readers were consistent across individual counts; however, differences were apparent when comparing among readers. Hubert and Alexander (1995) also found poor agreement among readers when counting meristic features on rainbow trout.

Significant differences in counts of meristic features were observed among fish from the 12 streams sampled (Table 4), suggesting that meristic features may be environmentally controlled within specific areas or sub-drainages within the larger drainage basin, as has been suggested previously (Barlow 1961; Rinne 1985; Currens et al. 1989). Environmental variables measured at each sampling site, including elevation, gradient, and stream size, were not correlated with meristic counts (Kruse 1995). Additionally, counts from hatchery stocks introduced into the drainage were compared to those from wild stocks, with no significant differences found in the mean meristic counts.

Due to the relatively simple methodology, meristic counts have been used to assess hybridization in trout. Marnell et al. (1987) found close agreement between meristic and electrophoretic results with Yellowstone cutthroat trout and westslope cutthroat trout (O. c. lewisi), two subspecies with a relatively large evolutionary separation (Shiozawa and Williams 1988; Behnke 1992). However, Loudenslager and Kitchen (1979) and Loudenslager and Gall (1980) were unable to find consistent differences between more closely related subspecies (Yellowstone cutthroat trout and finespotted Snake River cutthroat trout). Recent research has shown that meristic comparisons can provide potentially misleading information (Busack and Gall 1981; Leary et al. 1984, 1985). Behnke (1992) warns that meristic counts and morphological descriptions are often specific to localized populations. Leary et al. (1991) suggest that while meristic characteristics can be strongly influenced by genetic variation, fish naturally tend to have more variable meristic characteristics than most vertebrates.

Behnke (1992) described typical meristic counts for Yellowstone cutthroat trout and rainbow trout (Table 5). Rainbow trout have fewer scales in the lateral series, but generally, more pyloric caeca and vertebra. Rainbow trout do not have basibranchial teeth. Mean counts of meristic features of cutthroat trout in the Greybull River drainage (Table 4) were within the range of YSC (Table 5; Behnke 1992); however, many counts also fell within the ranges given for rainbow trout. The

variation and similarity in counts of meristic features for both Yellowstone cutthroat trout and rainbow trout make it difficult to determine species or hybrids based on meristic counts. Mean meristic counts for cutthroat trout in the Greybull River drainage were within ranges suggested for both pure rainbow trout and pure cutthroat trout with the exception of scales above the lateral line and presence of basibranchial teeth (Table 5). Electrophoresis determined the cutthroat trout were genetically pure Yellowstone cutthroat trout; however, use of meristic counts was inconclusive because of the variation in counts within a species. Variation among readers and sampling sites further confounds results.

Meristic counts differed significantly among samples from 12 streams in the Greybull River drainage. Behnke (1992) suggested that local influences may account for differences between sites. Environmental factors, such as temperature, elevation, and latitude (Barlow 1961) may cause differences among sites. Within the relatively small scale of the Greybull river drainage (650 km^2), it was not possible to determine environmental factors influencing meristic counts (Kruse 1995). However, in no case were the counts significantly different from the ranges described by Behnke (1992).

Meristic counts continue to be utilized to assess the genetic status of cutthroat trout populations (Remmick 1981; Hadley 1984; Behnke 1992), even though they may be inaccurate (Leary et al. 1984, 1985). However, variation among readers and

among sampling sites on streams in a small geographic area, along with relatively wide ranges in counts for YSC and rainbow trout, make it difficult to differentiate these two species with certainty using most of the commonly assessed meristic features (Table 5). Differences in scale counts and basibranchial teeth (Table 5), can differentiate genetically pure cutthroat trout from rainbow trout. However, it is unlikely that Yellowstone cutthroat trout x rainbow trout hybrids can be identified due to the extensive variation in counts, including variation associate with differences among readers, species, and sampling sites. Determining trout genetic status based solely on meristic counts may provide misleading results; more accurate information is probably provided by combining meristic counts with molecular genetic analysis and life history information.

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Table 1. Probabilities of significant differences in mean meristic counts among three readers (READER) and among three readings by individual readers (RUN).

	Main Effects		
Structure	**Reader**	**Run**	**Interaction**
Pyloric caeca	**< 0.001**	0.953	0.998
Vertebrae	**< 0.001**	0.884	0.958
Pelvic fin rays	**< 0.001**	0.990	0.745
Gillrakers	0.827	0.414	0.713
Basibranchial teeth	**0.003**	0.910	0.964
Scales in lateral series	**< 0.001**	0.980	0.987
Scales above lateral line	**< 0.001**	0.904	0.916

Table 2. Variation in mean meristic counts among three readers. Means not different significantly indicated by underline (Tukey's $P \leq 0.05$).

	Reader			
Structure	**1**	**2**	**3**	**P**
Pyloric caeca	32.7	36.9	41.0	**< 0.0001**
Vertebrae	60.5	59.5	59.3	**< 0.0001**
Pelvic Fin Rays	9.0	8.8	9.4	**< 0.0001**
Gillrakers	18.9	18.8	19.3	0.83
Basibranchial Teeth	13.7	15.3	14.2	**0.003**
Scales in Lateral Series	173.0	187.5	187.4	**< 0.0001**
Scales above Lateral Line	44	56.4	42.5	**< 0.0001**

Table 3. Paired reader comparison of meristic counts, where D = the mean paired difference between readers. Significant differences indicated by $P \leq 0.05$.

		Paired reader comparisons					
		1 vs 2		2 vs 3		1 vs 3	
Structure	**Run**	**D**	**P**	**D**	**P**	**D**	**P**
Pyloric caeca	1	**3.84**	**0.001**	**4.32**	**0.000**	**8.16**	**0.000**
	2	**4.68**	**0.000**	**3.58**	**0.001**	**8.26**	**0.000**
	3	**4.14**	**0.001**	**4.32**	**0.000**	**8.46**	**0.000**
Vertebrae	1	**0.88**	**0.003**	0.26	0.334	**1.14**	**0.000**
	2	**1.00**	**0.000**	0.04	0.858	**1.04**	**0.000**
	3	**0.88**	**0.005**	0.40	0.213	**1.28**	**0.000**
Pelvic fin rays	1	0.22	0.200	**0.70**	**0.000**	**0.48**	**0.000**
	2	0.12	0.083	**0.54**	**0.000**	**0.42**	**0.000**
	3	**0.24**	**0.006**	**0.62**	**0.000**	**0.38**	**0.000**
Gillrakers	1	0.12	0.598	**0.48**	**0.028**	**0.60**	**0.021**
	2	0.18	0.454	2.08	0.431	1.90	0.473
	3	0.02	0.923	0.30	0.175	0.32	0.185
Basibranchial teeth	1	**1.14**	**0.018**	0.80	0.187	0.34	0.544
	2	**1.98**	**0.000**	**1.30**	**0.035**	0.68	0.187
	3	**1.88**	**0.000**	**1.24**	**0.024**	0.64	0.264
Scales in lateral series	1	**10.5**	**0.000**	0.80	0.754	**9.68**	**0.000**
	2	**8.28**	**0.001**	0.42	0.871	**8.70**	**0.000**
	3	**9.64**	**0.000**	0.12	0.963	**9.76**	**0.000**
Scales above lateral line	1	**12.4**	**0.000**	**13.8**	**0.000**	**1.40**	0.062
	2	**12.1**	**0.000**	**13.4**	**0.000**	**1.34**	**0.027**
	3	**12.8**	**0.000**	**14.6**	**0.000**	**1.80**	**0.007**

Table 4. Variation in mean meristic counts among 12 sample sites. A probability (P) of ≤ 0.05 indicates significant differences among sites.

Structure	P	Grand mean (SD)	Range in means among sites
Pyloric caeca	< **0.0001**	42.29 (10.89)	29.9 - 51.4
Vertebrae	**0.0002**	58.57 (1.39)	57.9 - 60.6
Pelvic fin rays	**0.0001**	9.23 (0.86)	9.0 - 9.9
Gillrakers	**0.0018**	18.80 (2.08)	17.8 - 19.9
Basibranchial teeth	**0.0025**	13.96 (5.45)	11.4 - 21.8
Scales in lateral series	< **0.0001**	182.7 (14.77)	175.5 - 207.3
Scales above lateral line	**0.0001**	40.39 (3.51)	37.1 - 45.5

Table 5. Variation in meristic counts among species (YSC=Yellowstone cutthroat trout and RBT=rainbow trout), readers, and sampling sites.

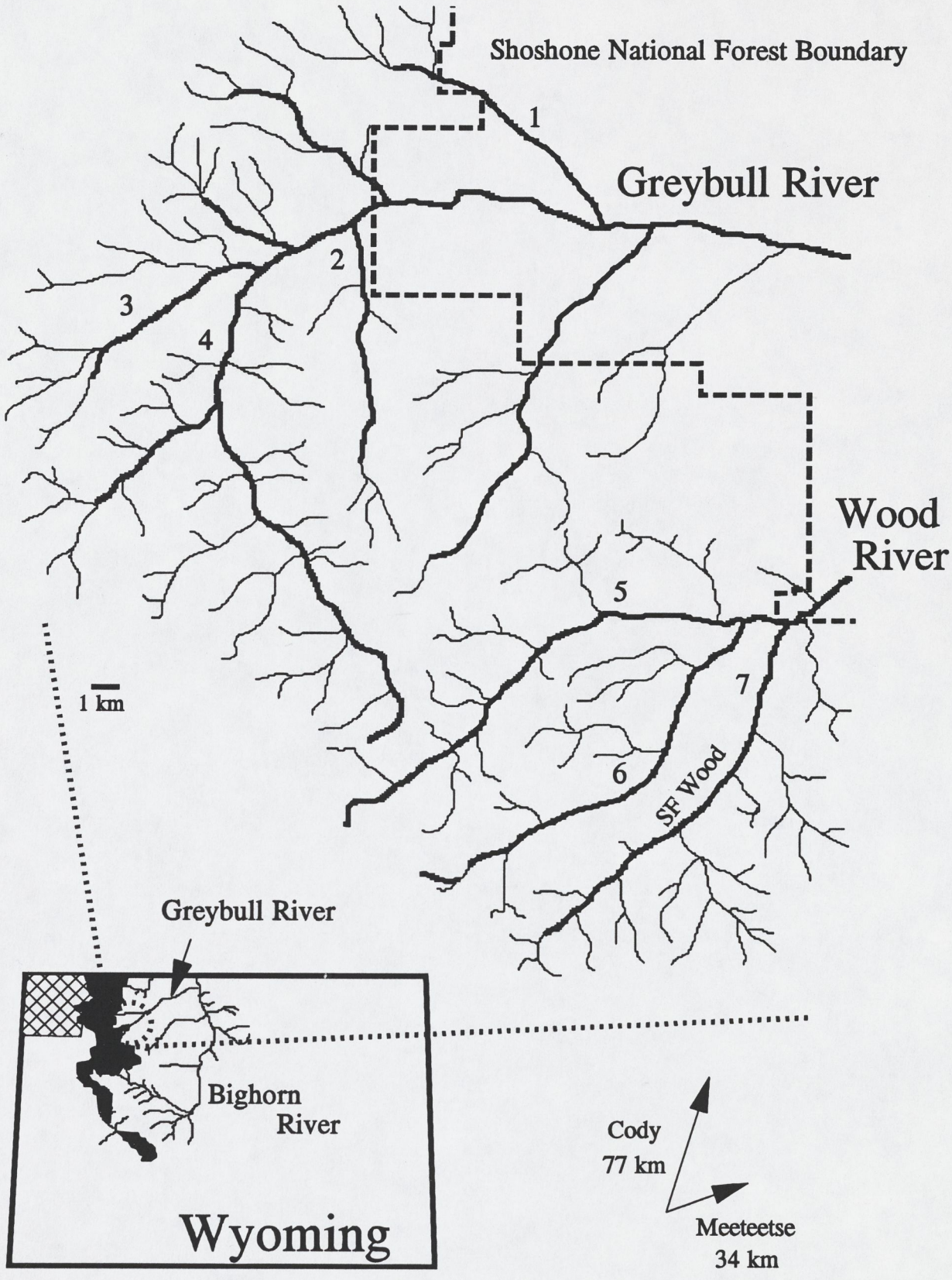
Variable	YSC[a]		RBT[a]		Variation among 3 readers[b]	Variation among sampling sites[c]
	Typical	Overall	Typical	Overall		
Pyloric caeca	35-43	25-50	37-55	30-70	33-41 (36.9)	29-51 (42.3)
Vertebrae	61-62	60-63	62-64	61-66	59-61 (59.8)	58-61 (58.6)
Pelvic fin rays	9	9-10	not reported		9 (9.0)	9-10 (9.2)
Gillrakers	19-20	17-23	19-21	17-24	18-21 (19.0)	18-20 (18.8)
Basibranchial teeth		present		absent	14-16 (14.4)	11-22 (14.0)
Scales in lateral series	165-180	150-200	125-150	120-160	179-188 (184)	176-207 (183)
Scales above lateral line	45-50	40-55	30-32	26-35	42-57 (47.6)	37-46 (40.4)

[a] - from Behnke (1992)

[b] - ranges are from the nine readings taken for each structure with means in parenthesis (3 readings by 3 readers)

[c] - ranges are from the means for the 12 sampling sites that had ≥ 5 cutthroat trout (≥ 150 mm total length) counted

List of Figures


Shoshone National Forest Boundary
1
Greybull River
2
3
4
Wood
River
5
1 km
7
6
SF Wood
Greybull River
Bighorn
River
Wyoming
Cody
77 km
Meeteetse
34 km