REPORT ON WYOMING TROUTS:

1. Bear River Cutthroat Trout, 1984 collections
2. *Salmo letnica* diagnosis
3. Miscellaneous collections

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ABSTRACT

1. The results of examination of five samples of Bear River cutthroat trout, *Salmo clarki utah*, are presented. The sample of 18 specimens from Hobble Crk. (?) at Lake Alice Campground is judged pure (A); two samples from Smith Fork exhibit a slight lingering hybrid influence from fine-spotted Snake River cutthroat trout, and two samples from the Bear River are judged to have a slight hybrid influence. All evidence indicates strong natural selection favoring the native *S. c. utah* genotype in both the Smith Fork and Bear River samples.

2. Large specimens of *S. letnica* can generally be distinguished from *S. trutta* by spotting pattern, but there is considerable variation in spotting, especially in smaller specimens that could confuse identity as *S. letnica* or *S. trutta*. Virtual positive identification is possible based on numbers of gillrakers and pyloric caeca and also by the presence of a "pectoral appendage" in *S. letnica*.

3. Four specimens of golden trout from "Lake 65", Bull Creek drainage, Wind River Indian Reservation, collected in 1982 are discussed. The presence of a basibranchial tooth in one specimen indicates a cutthroat trout influence. Six specimens from Hidden Creek, Pacific Creek (Snake R.) drainage, collected in 1983 were examined. They represent typical "Yellowstone" cutthroat trout, *S. c. bouvieri*, but differ from Yellowstone Lake specimens in gillraker development and basibranchial teeth.

PART 1: Bear River Collections, 1984

Five samples of Bear River cutthroat trout were delivered to me by Allen Conder. These include: Smith Fork (No. 1), 9 specimens 141-271mm TL, Aug. 28, R118W, T27N, S28 SW (ca. below confluence with Hobble Creek); Smith Fork (No. 2), 11 specimens 112-203mm TL, Aug. 29, R118W, T26N, S20 SE (ca. near confluence with Howland Crk.); Bear River, two samples of 12 and 14 specimens, 51-276mm TL, both samples collected Sept. 25, at R119W, T12N, S18W (south of Evanston -- these samples are taxonomically identical and are combined); 18 specimens, 88-235mm TL, labeled "Hobble Creek at Smith Fork, Oct. 30, 1984", were mislabled according to letter from Allen Conder (Nov. 13). The corrected locality is given as "Lake Alice Campground, R117½W, T28N, S24". This sample is judged to be uncontaminated *S. c. utah*, but they differ from L. Alice *S. c. utah*. Evidently this collection site is the headwaters of Hobble Creek or one of its tributaries such as the outlet stream from Lake Alice.

Smith Fork Samples. There are differences apparent between the two samples from the Smith Fork. These differences, I believe, are real and indicate that the two samples were not drawn from a single homogeneous Smith Fork population. Sample No. 1 (upstream) contains two (of nine) specimens with erratic spotting, suggesting fine-spotted Snake River cutthroat influence. None of the 11 specimens of sample No. 2 exhibit any indication of a hybrid spotting pattern. The main suggestion of a slight hybrid influence in specimens of sample No. 2 (besides the obvious lack of isolation from mixing with hybridized fish from upstream) is the development of gillrakers and basibranchial teeth. Comparing typical fine-spotted Snake River cutthroat with grade A samples from Smith Fork drainage (Hobble Creek, this report and Howland Creek, Porcupine Creek and Coantag Creek of previous reports), reveals that, besides spotting pattern, Snake River cutthroat differ in averaging more gillrakers (ca. 20 vs. 18-19), and having the gillrakers better developed (longer, finer, fewer rudimentary rakers) and also averaging more basibranchial teeth (ca. 15 vs. 3-5). In these characters, both Smith Fork samples suggest an influence from Snake River cutthroat trout.

Mr. Conder's letter of Nov. 13, mentioned that since 1982, the Smith Fork has been stocked with Bear River cutthroat (brood stock derived from Raymond Creek and Giraffe Creek of Thomas Fork drainage). If the brood stock is representative of Raymond Creek and Giraffe Creek fish and these stocked fish survive and reproduce in the Smith Fork, the resulting impact should be a "speeding up" of the purification process (replacement on non-native genes by S. c. utah genes), but the "native" S. c. utah of the Smith Fork will be slightly different from the original Smith Fork S. c. utah.

The taxonomic characters of sample no. 2 are virtually identical with a sample from Howland Creek (also known as Coal Creek, in vicinity of sample 2) made in 1976, except the Howland Creek specimens (N = 17) averaged 3.7 basibranchial teeth (range 1-11), vs. 2-21 (8.0) teeth in sample no. 2 (Table 1).

Many fine-spotted Snake River cutthroat were stocked into the Smith Fork and lower Hobble Creek until 1973 (or 1976). Binn's (1981) mentioned specimens from the "upper Smith Fork" he caught by angling in 1979 and 1980 which distinctly reflected a fine-spotted Snake River cutthroat influence. Binns stated that these hybrid specimens "would likely grade D or F". Perhaps the hybrid influence becomes more apparent upstream from the site where sample no. 1 was made, but the two 1984 Smith Fork samples show only slight (no. 1) and very slight (no. 2) hybrid influence and I would grade these samples as B- and B+, respectively. Binns (p. 50) mentioned that: "Fine-spotted cutthroat trout are well established in the Smith's Fork River and their presence eliminates a prime S. c. utah habitat due to obvious hybridization and competition." Binn's observations made in 1979 and 1980 of fine-spotted cutthroat in the upper Smith Fork occurred only a few years after stocking of Snake River cutthroat ceased. This area should be sampled in 1985 to evaluate the progress of the "purification process" whereby natural selection favors the restoration of the native S. c. utah genotype.

Table 1. Taxonomic characters of cutthroat trout, Bear R. drainage, 1984.

Locality	Gillrakers	Scales above lat. line and in lat. series	Pyloric caeca	Basibranchial teeth	Comments
Smith Fork (no. 1) below Hobble Crk. N = 9	17-22 (18.8)	37- 44 (40.4) 156-183(170.0)	34-50 (44.4)	3-14 (7.8)	2 specimens irregular spotting, teeth and gillrakers indicate Snake R cutthroat influence B-
Smith Fork (no. 2) near Howland Crk. N = 11	16-21 (18.6)	38- 43 (39.9) 158-169(162.2)	43-54 (45.7)	2-21 (8.0)	Not same 'population' as sample 1. Lesser hybrid influence B+
Bear R. no. 1, no. 2 combined N = 26	15-20 (18.4)	38- 45 (41.1) 156-185(170.4)	29-56 (41.9)	1- 8 (3.8)	2 specimens irregular spotting, slight hybrid influence B
Hobble Crk.(?) at Alice Lake Campgroung N = 18	17-21 (18.2)	39- 44 (41.4) 163-189(173.8)	41-51 (45.1)	1- 6 (2.7)	No indication of hybrid influence A

Bear River Sample. I found the two lots of specimens from the Bear River (12 and 14 specimens) to be identical in their taxonomic characters. Later, Mr. Conder informed me that both samples were taken from the same site, on the same day (Bear R. south of Evanston). Thus, these specimens are discussed on the basis that they were drawn from a single population. The most surprising aspect of the Bear River sample is that they overwhelmingly represent S. c. utah. Two of 26 specimens have asymmetrical, irregular spotting (some very small spots, crowded together) which clearly indicates some non-native hybrid influence in this population, but this influence must be slight. All other characters are typical of the Bear River form of S. c. utah except that the gillraker development differs slightly from typical grade A populations (longer, finer, fewer rudimentary rakers). Both the spotting abberation and gillraker development could be due to a hybrid influence from either fine-spotted Snake River cutthroat trout or rainbow trout (or both). Rainbow trout were regularly stocked in this area of the Bear River in Wyoming for many years, and are still stocked in the Utah part of the drainage. Snake R. cutthroat were stocked for "4-5 years" (letter from Allen Conder).

All of my previous Wyoming Bear River system specimen evaluations, with the exception of Rock Creek, have been from the Thomas Fork and Smith Fork drainages, and all of Binn's (1981) technical bulletin on Bear River cutthroat is devoted to the Thomas Fork and Smith Fork. The presence of a viable "good" S. c. utah population in the Bear River has been considered unlikely due to badly degraded habitat and past stocking history. Also, the only direct Bear River tributary previously sampled, Rock Creek, contained obvious hybrids (erratic spotting and 2 of 7 specimens lacking basibranchial teeth). In his letter, Mr. Conder expressed doubts that trout can spawn successfully in the Bear River due to its severely degraded habitat and that recruitment must come from tributaries. It can be noted from the size composition of the 26 specimens that recruitment appears to be good, or at least adequate -- 3 specimens, 51, 61, 64mm, must represent young-of-year; 11 specimens from 98-127 (115)mm are probably I+, 3 specimens 131, 134, 154mm, may represent II+; 5 specimens from 178-195 (187)mm may be III+; and 4 specimens from 218-276 (242)mm may be IV+. These specimens were in good condition with abundant fat deposits around the pyloric caeca. Three specimens (190-220mm) were found to have consumed fish recently before capture (remains seen in esophagus). The only positive identification of a prey specimen was that of a sculpin. A 220mm specimen in the Smith Fork no. 1 sample also had eaten a sculpin.

Regarding possible sources of recruitment to the Bear River cutthroat population, in 1980 I wrote a report for the U.S. Forest Service: "Purity evaluation of Bear River cutthroat trout from Mill and Carter creeks, Wasatch National Forest, Summit County, Utah." I note on the 1978 "Stream evaluation map State of Wyoming", that Mill Creek flows from south to north joining the Bear River just over the state line in Wyoming. The Wyoming segment of Mill Creek is color-coded as class IV (lowest rating). In Utah, however, despite a long and continuous history of stocking hatchery rainbow trout, a sample of 32 specimens collected in 1980 from Mill Creek are "good" (about 90% pure or grade B) S. c. utah. Carter Creek, a small tributary of Mill Creek had no stocking record and the specimens appeared more pure (ca. 95% S. c. utah). The 1980 sample from Mill Creek, Utah is very similar to the 1984 Bear River, Wyoming, sample, but I doubt they represent the same "population". The Mill Creek specimens average more scales (179 vs. 170) and slightly more gillrakers (16-21 [19.1] vs. 15-20 [18.4]).

The finding of several age classes of cutthroat trout in good condition in the degraded Bear River (after many years of stocking non-native trouts failed to establish viable populations in both Utah and Wyoming) raises several interesting questions concerning their life history and implications for management. In my 1980 Forest Service report I urged that Utah develop a Bear River management plan emphasizing S. c. utah. The response was an embargo declared on federal agencies prohibiting the shipment of specimens out of state to me for any further "purity evaluations". The U.S. Fish and Wildlife Service has prepared a "listing package" proposing to list S. c. utah as a threatened species. In view of this, the time may be appropriate for Wyoming, Utah, and the U.S. Forest Service (and BLM) to discuss a cooperative program for the management of S. c. utah in the headwaters of the Bear River drainage, Utah-Wyoming.

Hobble (?) Creek. As mentioned above, this sample of 18 fish was collected at "Lake Alice Campground". I assume the specimens came from upper Hobble Creek (they are not from Lake Alice). I can find no evidence of any hybrid influence in these specimens and judge them pure (A). This sample is very similar to a sample collected in 1979 from Coantag Creek, a tributary to Hobble Creek. The only slight differences noted between these samples is more basibranchial teeth in the Coantag sample (5.6 vs. 2.7) and fewer pyloric caeca (42 vs. 45) in Coantag sample. They are also very similar to a grade A sample from Porcupine Creek (next tributary to Smith Fork upstream from Hobble Creek).

PART II: *Salmo letnica*

A sample of 12 relatively small (ca. 20 cm) specimens of two-year-old *S. letnica* originating from the Ten Sleep hatchery, and a sample of 11 large brood fish (ca. 40-55 cm) were examined. The aim of the taxonomic examination was to determine diagnostic characters that can reliably differentiate *S. letnica* from *S. trutta* and to note any changes that may have occurred between the hatchery stock and the parent stock in Lake Ohrid.

The most comprehensive work published on the trout endemic to Lake Ohrid, Yugoslavia-Albania, is by Stefanovic (1948). She recognized three subspecies of *Salmo letnica* distinguished by time of spawning -- *S. l. typicus* (by rules of nomenclature this must be *S. l. letnica*), spawning in January-February, *S. l. aestivalis*, spawning in June-July, and *S. l. balcanicus*, spawning mainly in December. All the subspecies spawn on shoal areas in different parts of the lake. According to the taxonomic characters recorded by Stefanovic, the three subspecies of *S. letnica* are quite similar and differ from *S. trutta* mainly by higher numbers of gillrakers and pyloric caeca. The range of gillraker counts of all three subspecies of *S. letnica* ranged from 19-25 with mean values of various samples being 21.7-22.5 for *balcanicus*, 21.5 to 22.2 for "*typicus*", and 21.5-21.6 for *aestivalis*. Pyloric caeca counts for all subspecies typically are 50-80 with subspecies means of 65.6, 66.4, and 66.6. *Salmo trutta*, as *Salmo clarki*, consists of several subspecies with great variability. All *S. trutta* imported into North America represent the north European subspecies, *S. trutta trutta*, which typically has 17-20 gillrakers and 30-50 (typically 35-45) pyloric caeca.

As discussed by Pistono (1975), when the original shipment of *S. letnica* eggs were received from Yugoslavia in 1965, it was not known which of the three subspecies produced the eggs. Subsequent observation of late January spawning in the U.S. indicates the American import represents the "*typicus*" form, (which, more correctly, is *S. l. letnica*).

I obtained the following gillraker counts on the hatchery *letnica*:

No. of gillrakers	18	19	20	21	22	23	24	$\bar{x}$
small specimens (ca. 20cm)	1	1	5	2	3			20.4
large specimens (ca.40-55cm)		1	2	4	2	1	1	21.3

I suspect this difference between the two samples is real and due to the fact that (at least under hatchery rearing) gillrakers may appear after the fish grows beyong 20 cm. This is unusual because in all instances where I have established the size when the ultimate number of gillrakers is established in rainbow and cutthroat trouts, I found it to be only 80-100 mm. In many of the small specimens I noted a space at the extremity of either the lower or upper gill arch that lacked any rudiment of a gillraker, but where I expected a gillraker should be. In the larger specimens, gillrakers were usually found to the extremities of the gill arch. The assumption of increased number of gillrakers with increased growth is supported by the data of Stefanovic (1948) who never found fewer than 19 gillrakers in hundreds of mature *letnica* from L. Ohrid. The counts of the 11 large specimens about duplicates the counts of *S. l. letnica* of L. Ohrid.

Based on the counts of the two samples (admittedly, too small to make conclusive statements), there is an indication that small specimens of *letnica* would not be consistently differentiated from *S. trutta* solely on the basis of gillraker number. If specimens with 21 or more gillrakers are classified as *letnica*, only 5 of the 12 smaller specimens have 21 or more rakers, but 8 of the 11 large specimens would qualify. However, the structure and development of the gillrakers of the two species are quite distinct.

In letnica there are virtually no rudimentary rakers, and the rakers are long and fine. This distinction becomes much more pronounced in the larger specimens.

The pyloric caeca in the specimens had turned "mushy" and accurate counts were not possible, but several "approximations" ranged from 55 to 73 -- the expected counts for letnica.

Thus, a combination of 21 or more, long, fully developed gillrakers, and/or 55 or more pyloric caeca should give good to complete separation between letnica and trutta specimens in a fishery where both might occur, depending on the characteristics of individual populations of brown trout. I have no doubt that letnica and trutta are extremely closely related and would produce fertile hybrids if crossed. Temporal (Oct.-Nov. vs. Jan.-Feb.) and spatial (stream vs. lakes) separation would be expected to insure reproductive isolation. I doubt that letnica eggs spawned during the winter would hatch in natural waters of Wyoming. Winter temperatures in L. Ohrid are about 5-7° C. Normally fall spawning salmonids (brook, brown trout, kokanee salmon), must begin egg incubation at temperatures 5-10° C above the freezing point and development must reach a certain stage before temperatures drop to or near 0° C. If newly fertilized eggs are exposed to near 0° C temperatures they will not survive to hatching. Thus, unless letnica finds areas influenced by springs of suitable temperature and water quality or adapts to fall spawning, I doubt they can successfully reproduce in Wyoming.

I discovered an external character which, I believe, can give complete separation between Ohrid trout and brown trout, in cases where spotting pattern does not show a clear-cut difference. All of the Ohrid specimens have a small, fleshy ridge or papillar-like structure on the base of the pectoral fin. This structure can be seen when the pectoral fin is pulled away from the body and the fleshy base of the fin is closely examined. I have called this structure a "pectoral appendage" (Behnke 1968) and provided an illustration in a description of a new species of trout, S. platycephalus, from Turkey. Evidently it is a primitive salmonid feature that has been lost in S. trutta (at least I have never observed it on trutta specimens).

The 9 pound 2 ounce Ohrid trout recently caught in Alcova Reservoir may be the largest authentic specimen recorded of this species (Tennessee fishery people should be contacted to find out what is the largest specimen recorded from Lake Watauga). In Lake Ohrid, according to the data of Stefanovic (1948), *S. letnica* has relatively slow growth, averaging only 800 to 1000 grams at age 5 (in 6th year) and a general maximum length of 51 cm at the maximum age of 7. The *S. l. balcanicus* exhibits slightly faster growth in L. Ohrid than do *aestivalis* or "*typicus*". The Alcova Reservoir specimen greatly exceeded the growth of the parent population in Lake Ohrid and also exceeded the maximum age (hatched 1975, age 9, completing 10th year of life). In Lake Ohrid, all three subspecies are relative generalists -- opportunists in feeding. Benthic foods include amphipods, isopods, and insects. Pelagic food includes *Daphnia* and fish. Fish is more important in the diet of larger *letnica* and the majority (ca 90%) of all fish consumed is a cyprinid, the bleak, *Alburnus albidus* -- a pelagic schooling species, morphologically and ecologically similar to smelt (*Osmerus*). Probably the North American cyprinid most closely resembling the European bleak in appearance and ecology is the lake emerald shiner, *Notropis atherinoides* (especially populations that have evolved in large lakes for past several thousand years).

It would be of interest to learn the feeding habits of Ohrid trout in Wyoming reservoirs -- what fishes are most readily preyed upon?

PART III: Miscellaneous Collections

Golden Trout from Lake 65. Dick Baldes gave me four specimens (165, 310, 315, 345 mm TL) from Lake 65, Bull Lake Creek drainage, Wind River Reservation, collected in August, 1982. The specimens resemble *S. aguabonita* except for one specimen with numerous small spots anterior on the body. One specimen has a basibranchial tooth which I assume denotes genes from cutthroat trout (I have never found basibranchial teeth in South Fork Kern golden trout (*S. a. aguabonita* -- the source of all introductions), but occasionally basibranchial teeth are found in Little Kern - Kern River trout (*S. a. gilberti*). The scale counts (193-204) are higher than expected in *S. a. aguabonita* and pyloric caeca counts (24-29) lower. These specimens were taken in August and the largest, a male, has turgid testes, the next two largest specimens are females with eggs in body cavity, and the smallest specimen shows no gonadal development. Evidently growth is good in Lake 65 but natural reproduction is not occurring based on the three sexually mature specimens.

A photograph of a golden trout was sent to me for verification by the International Game Fish Association that is of interest. The fish was only 11 inches TL but weighed 1 pound 2 ounces (shaped like a football). It was caught July 18, 1984, from "Windy Lake, Wind River Range, Wyoming". The angler made application for a "world record" golden trout caught on two pound test line. The IGFA wanted me to verify the fish in the photo as *S. aguabonita* or if I believed it to be a hybrid.

The spotting pattern and coloration of the "record" fish was approximately similar to three of the four specimens from Lake 65. I stated that I could not make positive identification of golden trout without the actual specimen, but for practical purposes, in situations where a hybrid influence is so slight to be barely detectable, the fish in the population are overwhelmingly *S. aguabonita* (90-95%) and should be classified as such.

Several years ago I examined a sample of golden trout from Surprise Lake, the source of eggs for golden trout propagation in Wyoming. Surprise L. received its golden trout from Cooks L. in 1949. I found no evidence of a hybrid influence in Surprise L. fish, but I have found slight hybrid influence in golden trout from other Wyoming lakes (basibranchial teeth, similar to specimen from Lake 65). I assumed that a slight hybrid influence occurs in those golden trout lakes that have, at least occasionally, some natural reproduction, and were stocked (probably inadvertently) at one time with cutthroat trout. The question re. purity of particular Wyoming golden trout, raised by the IGFA, is likely to come up again. The most practical advice would be: if the fish (including all fish observed in a particular population) look like golden trout, and a hybrid influence can only be detected by careful examination of several specimens, then call it golden trout, *S. aguabonita*.

Pursuing the ultimate source of the cutthroat trout genes that produced the basibranchial teeth (and erratic spotting) in the specimen from Lake 65: is there is any way that cutthroat trout influence could gain access to this lake (for example, from upstream lake where natural reproduction and hybridization is possible)?

Hidden Creek. I examined 6 specimens collected by John Erickson and Ralph Hudelson, August 10, 1983, from Hidden Creek, Pacific Creek drainage (Snake R.). These 6 specimens are virtually identical to 11 specimens from Hidden Creek, tributary to Thoroughfare River (Yellowstone River), reported on in my report IV "Evaluation of 1978 Collections", although the present specimens came from the Pacific Creek drainage. North Two Ocean Creek divides to form both Pacific Creek (Snake R.) and, Atlantic Creek (Yellowstone R.) and there is no physical barrier to free movement of trout back and forth across the Continental Divide here. Thus, only extremely limited differentiation would be expected in tributaries on both sides of the Divide. When I visited Two Ocean Pass in 1967, I noted that the trout in Atlantic Creek migrate from Yellowstone Lake for spawning, and at least some juveniles spend one or two years in the stream. All trout I observed were either large (35-40 cm) or small (12-12 cm) with no in-between sizes. In North Two Ocean Creek and in the headwaters of Pacific Creek, the trout were resident populations -- all sizes and age-classes seen. It appeared obvious to me that although there are no physical barriers isolating Atlantic Creek cutthroat trout from North Two Ocean and Pacific creeks, hereditarily based life history and behavior differences, maintained virtually complete isolation. However, this isolation is probably not absolute, nor of long duration in geological time. I found the taxonomic characters of Pacific Creek and Atlantic Creek (= Yellowstone L.) cutthroat trout to be very similar.

The characters of the 6 specimens from Hidden Creek are: gillrakers, 19-22 (20.8); scales, 40-45 (42.2) above lateral line, and 173-194 (181.2) in lateral series (all values virtually identical to Yellowstone L. cutthroat); pyloric caeca, 29-36 (32) (significantly lower than Yellowstone L. specimens -- ca. 42); and basibranchial teeth 10-20 (12.7) -- also significantly fewer than Yellowstone L. cutthroat (mean 22). Another detectable difference between Hidden Creek specimens and Yellowstone L. cutthroat is the lacustrine evolutionary influence on the development of gillrakers on the posterior side of the first gill arch in Yellowstone L. fish, which have 5 to 15 posterior gillrakers. Hidden Creek specimens have 0 (n = 2), 1 (n = 2), 2, and 4 posterior rakers. I believe the Hidden Creek specimens represent a pure population of "Yellowstone" trout, *S. c. bouvieri*, native to the Pacific Creek drainage.

I would add that I anticipated that the development of posterior gillrakers would clearly differentiate *S. letnica* from *S. trutta*. I was surprised to find that *S. letnica* has more feeble development of these rakers than is found in Yellowstone L. cutthroat trout, despite a much longer lacustrine evolutionary history.

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THE NATIVE CUTTHROAT TROUT OF WYOMING

V: Green River and Bear River Drainages

Robert J. Behnke

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This report, the fifth in a series since 1975, evaluates the relative purity of 14 samples consisting of 133 specimens. Twelve of the samples, collected in 1980, are from the Green River basin. Two samples from the Bear River drainage sent last year by Allen Binns were not evaluated in previous reports and are included here.

The Green River drainage collections are separated into "Green River westside tributaries enclave" and "Big Sandstone enclave" following Binns (1977). Several samples were not adequately labeled. A ? preceeding the site in table 1 denotes no locality data. These samples were assigned to the respective categories on the basis of spotting pattern and my categorization should be checked. A (?) following the site name in table 1 denotes that the label could not be made out and the listed name is my best approximation (or guess) of the correct name of the creeks.

As has been discussed in previous reports, the native cutthroat trout of the Little Snake drainage (Big Sandstone and North Fork enclaves of Binns 1977) have markedly larger spots than any other *Salmo clarki pleuriticus* of the Green River drainage. The Little Snake drainage cutthroat trout are identical to the greenback cutthroat, *S. c. stomias*. This form of large-spotted cutthroat trout must have given rise to *S. c. stomias* in the South Platte drainage by headwater stream transfer from the Colorado River basin.

The spotting differences between the Green River and Little Snake cutthroat trout is sufficiently diagnostic that I am relatively confident of my placement of the samples from unknown localities in table 1, even in those samples where a slight hybrid influence lessens the distinction.

Evaluation of Samples

Using Binns' (1977) rating system for S. c. pleuriticus I would suggest an A (pure, virtually pure) rating for Nylander Creek, Big Sandstone Creek, N. Fork Big Sandstone, and for the two samples of S. c. utah from Coantag Creek and Porcupine Creek (perhaps A- for Porcupine Creek). Samples of only 1 to 5 specimens from E. Branch Deep Creek, Bachelor Creek, and Beaver Creek, although of uncertain locality, so typically express the "greenback" type of spotting that it is likely they were taken from essentially pure populations of Little Snake drainage cutthroat trout. The data suggest a "B" rating for the samples from Sjhoberg (?), Ironell (?), Nameless, and Douglas Creek. A "C" rating is suggested for the Deep Creek sample.

Nylander Creek. Sample of 17 specimens. Scale counts (43.4 above lateral line, 185.6 in the lateral series) and pyloric caeca counts (39.1) are typical of Green R. S. c. pleuriticus. One of 17 specimens lacks basibranchial teeth. Three specimens from Nylander Creek were reported on in my second report (Aug. 1975). They were wholly typical of S. c. pleuriticus and Binns (1977) tentatively assigned an "A" rating to the Nylander Creek population. Including the 3 specimens from the previous report, 19 of 20 specimens (95%) have basibranchial teeth. The spotting pattern of the Nylander Creek specimens is not as uniform as

Table 1. Comparison of taxonomic characters.

	Gillrakers	Pyloric caeca	Scales above 1.1 and in lat ser.	Basibranchial teeth
		Green R. Drainage		
"Green River Westside tributaries enclave"				
Nylander Crk. N=17	17-22(19.5)	33-48(39.1)	41-48 (43.4) 177-194(185.6)	1:no teeth 16:1-20(5.5)
? Sjhoberg (?) Crk. N = 5	18-21(19.8)	32-44(39.6)	40-45 (43.8) 168-190(181.6)	1:no teeth 4:1-9(4.3)
? Ironell (?) Crk. N=9	15-22(18.8)	29-48(36.4)	34-46 (40.7) 142-184(165.3)	1:no teeth 8:1-24(5.9)
? Nameless Crk. N=7	17-22(20.3)	37-47(42.4)	32-48 (41) 132-187(167.4)	1:no teeth 6:1-12(6.7)
"Big Sandstone enclave"				
Douglas Crk. N=14	18-22(20.1)	28-33(35.8)	41-50 (44.5) 175-204(183.4)	13:1-13(6.7) 1: no teeth
Big Sandstone R87, T14, S12 el. 8840 N-11	17-22(19.8)	32-45(36.9)	45-53 (46.1) 178-213(192.8)	1-17(8.9)
N. Fk. Big Sandstone at cabin site N-6	17-21(18.7)	25-39(33.3)	45-51 (47.6) 178-200(187.5)	6-16(10.7)
Deep Creek N=11	17-21(19.2)	32-41(37.5)	38-46 (42.1) 166-190(177.2)	6:no teeth 5:1-7(3.6)
E. Br. Deep Crk. N=5	20-22(20.4)	32-38(34.4)	42-49 (46) 175-196(187.8)	4-13(9.6)
? Haskin Sta. 2 E. Branch Carbon Co. N=1	20	35	48 183	1
? Bachelor Crk. Carbon Co. N=1	21	38	45 205	3
? Beaver Crk. N=2	20,21	30,31	43,50 179,202	11,17
		Bear River Drainage		
Porcupine Crk. N=22	17-21(18.2)	38-58(42.6)	37-43 (40.1) 160-188(169)	1:no teeth 21 1-12(5.4)
Coantag Crk. N=22	16-21(18.6)	32-52(44.7)	37-45 (41.6) 156-192(176.5)	1-14(5.9)
Typical values assumed for pure Bear R. *S. c. utah*	18-19	40-50	160-175	5-10

found in the population from Lead Creek (Report III), but no indication of a hybrid influence can be detected from the spotting.

Nylander Creek is in the Cottonwood Creek drainage of the Green River westside enclave. In previous reports all samples from this drainage had some evidence of hybridization (B or C grade populations). In 1970 I caught several cutthroat trout from the North Fork of Cottonwood Creek near the Forest Service boundary and although they were predominantly cutthroat trout, they were obviously hybridized with rainbow trout and probably with Snake River cutthroat trout.

How does the Nylander Creek population maintain its high degree of purity? Are they physically isolated from contact with hybrid trout or is the population so perfectly adapted to local conditions that natural selection strongly favors the native genotype? If the latter is correct, the purity of the population would be endangered from environmental alteration.

Sjhoberg (?) Creek. Unknown locality. Five specimens; 4 typical Green River spotting, 1 with large spots. One of 5 lacks basibranchial teeth. Sample size too small for valid judgement but the population from which it was drawn would probably rate a "B" grade.

Ironell (?) Creek. Unknown locality, 9 specimens. Spotting variable in size and position; scale counts somewhat low (40.7 and 165.3). Eight of 9 specimens with basibranchial teeth. A B or B- grade could be assigned to this population.

Nameless Creek. Unknown locality. No obvious hybrid spotting influence, but scale counts reduced (41 and 167.4) and caecal counts somewhat high (42.4). One of 7 specimens lacks basibranchial teeth.

This sample appears to be very similar to a sample from Ironell (?) Creek.

Douglas Creek. Tributary to Big Sandstone Creek. If samples from the headwaters of Big Sandstone Creek were not available for comparison, I would probably suggest an "A" grade for the Douglas Creek sample. The scale counts (44.5 and 183.4) and caecal counts (35.8) are typical of the native trout and 13 of 14 specimens have basibranchial teeth (14 of 17 specimens from Douglas Creek had basibranchial teeth in earlier collection discussed in Report I). The spotting pattern of the Douglas Creek specimens is not as typically "greenback"-like as are the spots of the Big Sandstone specimens. Douglas Creek specimens tend to have smaller, more variable spots. Scale counts and average number of basibranchial teeth are fewer than in Big Sandstone samples.

In previous reports, I mentioned that obvious hybrids with rainbow trout occur in Big Sandstone Creek near the confluence with Douglas Creek. I visited Douglas Creek in 1970 and did not find any physical barrier to inhibit movement upstream from Big Sandstone Creek. I would rate the Douglas Creek sample as a B grade sample in relation to purity in the Big Sandstone enclave. It is likely that a gradient of purity exists in Douglas Creek -- least pure near confluence with Big Sandstone Creek to most pure in the headwaters.

Big Sandstone Creek. This sample of 11 specimens is a beautiful example of the "greenback"-like spotting pattern of the native cutthroat trout of Little Snake drainage. Scale counts very high (46.1 and 192.8) all specimens with basibranchial teeth (1-17 [8.9]). I would grant this sample an A grade but some questions must be raised from previous reports. The trout found in Big Sandstone Creek near the confluence with Douglas Creek are obvious rainbow x cutthroat hybrids. As I recall, there is only a few miles of habitable trout waters in Big Sandstone Creek from its confluence with Douglas Creek upstream to its headwaters. What isolates the population from which this 1980 sample was taken from the hybrids a short distance downstream?

In Report I (July 1975) I discussed a sample of 7 specimens from the "headwaters" of Big Sandstone Creek which were similar to the present sample. These were rated "A" by Binns (1977). In Report III (May 1978) I mentioned 4 obvious hybrid specimens from Big Sandstone above Douglas Creek (rated C or D by Binns). It appears that a relatively sharp break must occur in Big Sandstone Creek (a barrier falls?) between the obvious hybrid population near Douglas Creek and the essentially pure population in the headwaters.

If non-native trout stocking has ceased in Big Sandstone Creek, a sample should be made next year near the confluence with Douglas Creek to check on the degree of hybridization. Perhaps the situation is similar as with *S. c. utah* in the Thomas Fork and Smith Fork of the Bear River drainage where the native trout populations essentially were "purified" after non-native trout stocking ceased, evidently due to strong selection pressure favoring native genotypes in those particular environments.

North Fork Big Sandstone Creek. Six specimens virtually identical to Big Sandstone specimens. Both samples might be considered as drawn from a single population. Grade A.

Deep Creek. Tributary to Big Sandstone. This sample of 11 specimens is obviously hybridized with rainbow trout (grade C). Six of 11 specimens lack basibranchial teeth and the mean value of those specimens with teeth is low (3.6). Spotting pattern highly variable and erratic. Narrow, elliptical shaped spots are common on body (versus large, roundish spots on pure specimens). Scale counts and caecal counts are only slightly influenced by rainbow trout ancestry. This sample should be classified as S. c. pleuriticus because its genotyps is predominantly that of the native trout, but there is probably about a 20% or more influence from rainbow trout.

In Report III, I discussed a sample of 10 specimens from Deep Creek that were much less hybridized than the present sample (means of 42 and 182 scales, 34 caeca, and 9 of 10 specimens with basibranchial teeth in sample made in 1977). Perhaps the 1977 sample was taken further upstream than the 1980 sample, which would indicate a "purity gradient" exists in Deep Creek. The following sample discussed from the East Branch of Deep Creek, suggests a pure population exists in the headwaters.

East Branch Deep Creek. Only five specimens, but the spotting pattern and other characters are virtually identical to the grade A sample from the headwaters of Big Sandstone Creek. The samples from Deep Creek and from the East Branch of Deep Creek were obviously taken from two distinctly different populations. One is obviously hybridized, the other shows no indication of any hybrid influence. What blocks or at least strongly inhibits gene flow between trout in various segments of this small drainage?

Haskin Station 2, East Branch, Carbon County. One specimen was sent under this label. The specimen is wholly typical of the East Branch Deep Creek specimens (except that it possesses only one basibranchial tooth) and I assume that this specimen came from the East Branch of Deep Creek.

Bachelor Creek, Carbon County and Beaver Creek, Carbon County. One specimen from Bachelor Creek and two specimens from Beaver Creek (unknown localities) have the "greenback"-like spotting pattern characteristic of Little Snake native trout. Scale counts high, typical of Big Sandstone headwaters. These specimens were probably taken from pure populations in Big Sandstone drainage. Larger samples should be made to verify purity.

Bear River Collections from 1979

Porcupine Creek. Tributary to Smith Fork. This sample of 22 specimens is quite similar to the samples of S. c. utah from Raymond Creek and Upper Giraffe Creek discussed in previous reports. Basibranchial teeth occur in 21 of 22 specimens. The spotting pattern of large, roundish spots sparsely distributed over the body (not so concentrated on caudal peduncle as in S. c. pleuriticus) is typical of S. c. utah and shows no evidence of a hybrid influence. The population in Porcupine Creek appears comparable to the Raymond Creek trout in their purity. Porcupine Creek is a direct tributary to the Smith Fork and this population must have been exposed to hybridization from non-native cutthroat trout and rainbow trout in its past history. Thus, I would hesitate to judge it pure (A) and would suggest an "A-" rating, particularly in view of the fact that all 22 (25 counting previous collection) specimens from Coantag Creek have basibranchial teeth.

Coantag Creek. Tributary to Hobble Creek (Smith Fork drainage), but more isolated from influence of non-native trout introductions. A sample of 22 specimens (plus 3 specimens sent by Dr. Binns in 1978) indicates that the Coantag Creek population is perhaps the purest S. c. utah yet sampled from the Bear River drainage. This is the only large (ca. 20 or more) sample I have examined with 100% occurrence of basibranchial teeth. The spotting pattern reflects my idealized conception of what the Bear River drainage S. c. utah should be.

The scale counts (41.6 and 176.5) are higher than expected for S. c utah, but are similar to scale counts recently found in S. c. utah from the headwaters of the Bear River drainage in Utah (Behnke 1980).

I believe the higher scale counts in Coantag Creek specimens is the result of their long existence in a small stream at higher elevation. Both a direct environmental effect (non genetic) and a hereditary or selection effect probably operate to maintain slightly higher scale numbers in the Coantag Creek population. I do not believe any hybrid influence is responsible for the scale counts.

Discussion

A cooperative study with the Forest Service and perhaps the BLM in the Little Snake drainage would be a worthwhile project. More intensive sampling could document the occurrence of pure or virtually pure populations in sites such as the East Branch Deep Creek, Bachelor Creek, and Beaver Creek, represented by only a few specimens in this report. Other pure populations might be found. If ecological data could be obtained at each collection site characterizing the environment, some insight would be obtained on what factors constitute a "hybrid" environment and a "pure native trout" environment. That is, what factors favor the maintenance of pure population in certain segments of a drainage when hybridization is common in other parts of the drainage -- such as Big Sandstone and Deep

Creeks. Information on the occurrence of pure populations and quantitative data on the type of environment that favors pure populations should greatly increase the influence that the Wyoming Game and Fish Department could exert on federal agency land use decisions that would impact native trout environments.

Previously, I recommended that a diversity of sources be used to establish a brood stock propagation program for the Bear River cutthroat. This recommendation was based on the fact that the few known virtually pure populations are represented by relatively small breeding stocks in small tributaries. It would be expected that their genetic variability (heterozygosity) is low. Obtaining eggs and sperm from several populations should greatly increase heterzygosity and this would probably result in better success of the offspring stocked into new environments.

Allendorf and Phelps (1980) described the loss of genetic variability in a hatchery stock of cutthroat trout (S. c. lewisi) in Montana in less than 15 years since it was obtained from a wild population. More than half (59%) of the gene loci investigated changed from a heterozygous (two or more different genes or alleles per locus) to a homozygous (only a single gene) condition. Such a loss of genetic variability results from a small number of parent fish used to produce each generation (loss of heterozygosity due to inbreeding) and artificial selection under a hatchery environment (selection for artificial diet, growth, loss of wildness disease resistance, etc.). These authors emphasized that a brood stock program designed for native trout that has as one of its goals the maintenance of genetic diversity, should periodically infuse genes from wild populations into the hatchery brood stock.

Both of the cutthroat trout populations in Porcupine and Coantag Creeks could be used to genetically diversify a brood stock of Bear River cutthroat trout.

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RARE AND ENDANGERED SPECIES REPORT: THE NATIVE CUTTHROAT TROUT OF THE COLORADO-GREEN RIVER BASIN, *Salmo clarki pleuriticus*

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In a previous report (Progress Rept: cutthroat trout of the Rio Grande and Colorado River basins. Colo. Coop. Fish. Unit., 1968), I reviewed the systematic status of the Colorado-Green River cutthroat trout pointing out that the total information in the literature is too vague to provide a firm basis for recognition of the cutthroat trout known as *Salmo clarki pleuriticus* allowing its separation from other subspecies of *S. clarki*.

The great amount of natural isolation found between various populations of this cutthroat trout, particularly between those associated with tributaries of the Colorado River and those of the Green River (another salmonid fish, *Prosopium williamsoni*, is native only to the Green River division of the Colorado system) would suggest that great taxonomic variability exists in this subspecies and no combination of characters will serve to separate all the native cutthroat trout populations of the Colorado-Green River basin from other subspecies of other major drainages. However, as a starting point it was decided to learn more about the native cutthroat trout of the upper Green River drainage because that is the type locality for the specimen on which the name *pleuriticus* is based (near Fort Bridger, Wyoming). The plan of study consisted of examining and recording data from samples of possible pure populations of cutthroat trout from the upper Green

River basin and then compare and evaluate the data for consistency between samples which would indicate that these samples represent remnants of the cutthroat trout once inhabiting the whole upper Green River watershed.

Collections made in 1969 and 1970 by Wyoming Game and Fish Dept., U.S. Forest Service and U.S. Bureau of Sport Fisheries and Wildlife were examined and pertinent data is presented in Table 1. The amount of material is not sufficient to arrive at an absolutely authoritative opinion on the taxonomic diagnosis of _S. c. pleuriticus_, but it does indicate the range of variability and allows a basis for judgement on probably pure populations. From this data a composite, hypothetical trout can be deduced approximating a representative example of the original native cutthroat trout of the Green River drainage.

Based on these recent collections from the Green River drainage, _S. c. pleuriticus_ is characterized as follows: Large, round, pronounced black spots, typically concentrated posteriorly on the caudal peduncle and anteriorly above the lateral line with similar spots on the dorsal, adipose and caudal fins - the spotting pattern is somewhat similar to most other subspecies of interior cutthroat trout. Colors, particularly in the spawning season, are generally brilliant, almost gaudy, often with crimson suffusing the whole ventral region, a pink-red tinge on the side overlaying a bronze-gold background - typically males exhibit brighter colors than females. I noted similar coloration in the Arkansas-Platte greenback cutthroat trout (_S. c. stomias_) but it does not appear to be so highly developed in Yellowstone Lake cutthroat trout and other subspecies. Vertebral counts, 61-63, typically 62; gillrakers, typically 19-20; pyloric caeca, typically 35-40 but this can be a highly variable character within the same subspecies; scales above lateral line, typically 38-50; scales in lateral series, 170-200 - scale counts are also typically highly variable.

On the basis of these meristic characters, on uniform appearance and other characters such as number of pelvic rays and development of basibranchial teeth, the first 3 samples listed in Table 1 - Douglas Creek, Little West Fork and North Fork of Beaver Creek - are judged to most probably represent essentially pure populations of S. c. pleuriticus. The physical isolation of the populations in these streams from which the samples were drawn is not complete, however, and I suspect that a very small amount of rainbow trout and/or Yellowstone cutthroat trout introgression could have infiltrated into these populations. Although these streams are geographically remote, the three samples share strong similarities with each other, suggesting that they are good representative remnants of the once widely distributed native trout of the upper Green River area. The remaining samples indicate in one or more characters that some hybridization with rainbow trout and/or other subspecies of cutthroat trout has influenced their genotype. Trapper's Lake is a major source of cutthroat trout eggs for the state of Colorado. Large numers of Yellowstone Lake cutthroat were formerly introduced into Trapper's Lake and it is the general belief that the native genotype has been largely replaced by Yellowstone fish. My evaluations indicate that this is not true. Probably due to several thousand years of existence in Trapper's Lake, the native genotype is somewhat unique and apparently is highly adapted to conditions of Trapper's Lake so that hybridization has been resisted by negative selection against hybrids.

It is important that federal and state agencies take action to save remnant populations of S. c. pleuriticus. Pure populations are rare. The attached form was prepared for the rare and endangered species list of the International Union for the Conservation of Nature and the U.S. Department of the Interior. The major obstacle to make a valid claim for a rare status of S. c. pleuriticus is that so little was known of its taxonomy - how could they be recognized if they were found? A purpose of this paper is to provide some basis to answer that question. The introduced rainbow and brown trouts are now the major trout species in the Green River and its larger tributaries. Introduced eastern brook trout have crowded out the native cutthroat trout from many of the smaller tributaries. In the few areas where a trout occurs with predominantly cutthroat trout phenotype - critical examination reveals most of these are rainbow x cutthroat hybrids or hybrids between the native cutthroat trout and introduced Yellowstone or Snake River subspecies. Pure populations of the original S. c. pleuriticus are indeed rare. Rapid action will be necessary. The population in the Little West Fork in the Wasatch National Forest, Utah, will almost certainly be lost unless a barrier is constructed to isolate the stream from upstream migration. A dam is under construction on the Black's Fork which will back up water to the lower reaches of the Little West Fork and the new reservoir will be stocked with massive numbers of rainbow trout, a situation which inevitably leads to hybridization. The streams on BLM land are in severely overgrazed and eroded country resulting in very limited habitat - a highly precarious situation that will eventually eliminate the cutthroat trout unless better land use practices and habitat improvement are instituted soon.

It is hoped that remnant populations of S. c. pleuriticus receive the necessary protection of federal and state agencies, not only for the esthetics of preserving our biological heritage, but also to learn more about their ecological qualities and specializations with a view toward their potential in future fishery management programs.

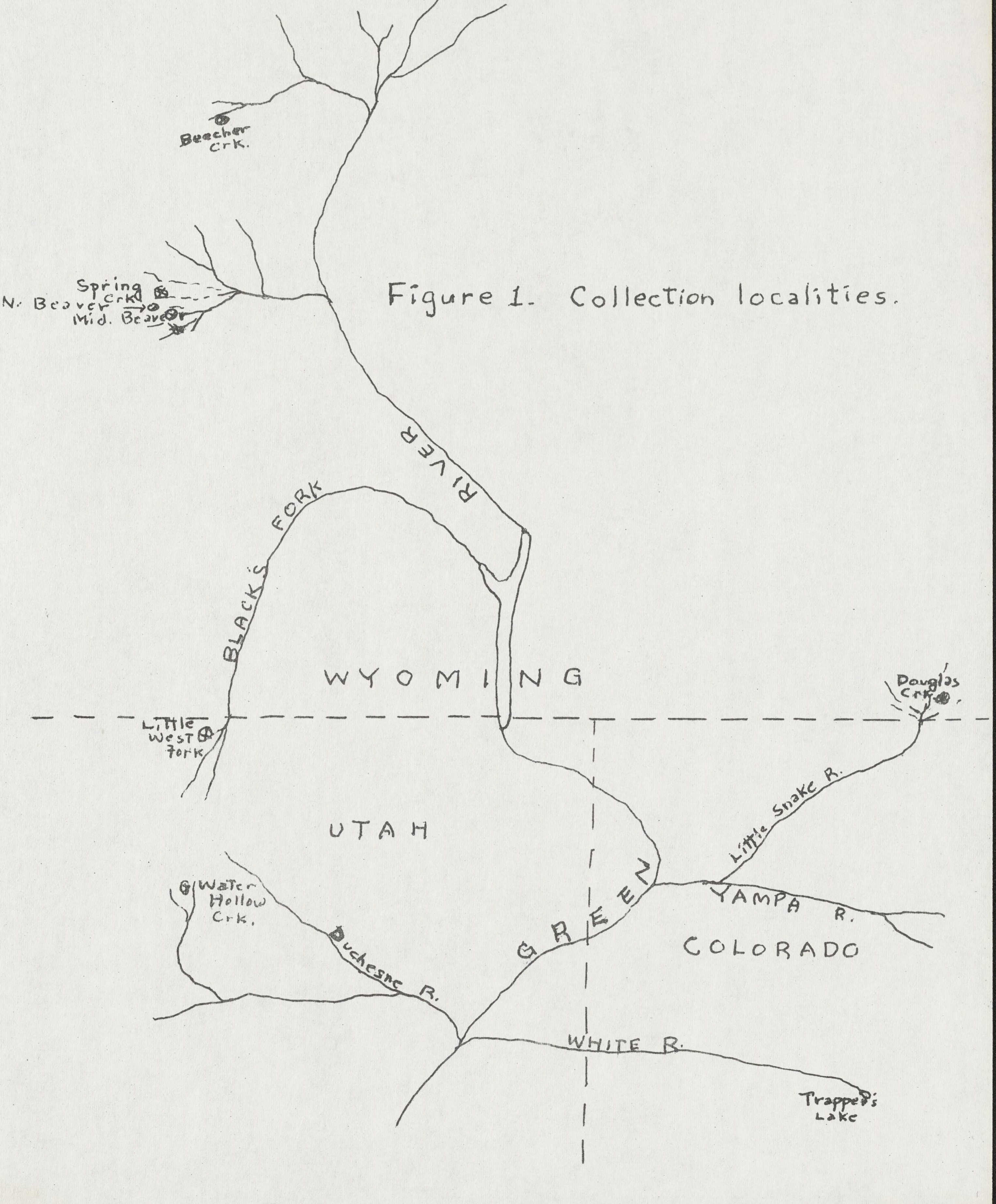

Figure 1. Collection localities.

TABLE 1. Some meristic characters of samples of Green River cutthroat trout.

Locality and Federal Agency Controlling Land	Vertebrae	Gillrakers	Pyloric caeca	Scales above lateral line	Scales, lateral series
Douglas Creek, Wyoming - U.S.F.S.	N = 41 61-63 (62.0)	N = 14 18-21 (19.4)	N = 14 31-42 (37.1)	N = 14 38-44 (41.4)	N = 14 159-197 (178.6)
Little West Fork Black Fork Utah - U.S.F.S.	N = 41 61-63 (62.2)	N = 14 18-21 (19.1)	N = 10 32-41 (37.4)	N = 10 39-47 (43.7)	N = 10 164-204 (185.4)
North Fork Beaver Creek, Wyoming - B.L.M.	N = 14 60-62 (61.4)	N = 15 18-22 (20.2)	N = 15 35-44 (39.4)	N = 15 42-52 (47.0)	N = 15 163-197 (182.3)
Middle Fork Beaver Creek, Wyoming - B.L.M.	N = 4 62-64 (62.8)	N = 5 19-20 (19.4)	N = 5 35-42 (39.2)	N = 5 38-46 (42.4)	N = 5 163-188 (173.4)
Spring Creek, Wyoming - B.L.M.	N = 8 62-64 (63.3)	N = 10 18-21 (19.4)	N = 10 34-42 (38.3)	N = 8 41-49 (44.8)	N = 8 163-190 (174.8)
Beecher Creek - B.L.M.	N = 5 60-63 (61.6)	N = 10 18-21 (19.4)	N = 10 40-52 (44.5)	N = 10 43-49 (46.0)	N = 10 136-180 (161.3)
Water Hollow Creek, Utah - U.S.F.S.	N = 22 60-64 (62.1)	N = 10 18-20 (18.7)	N = 10 29-43 (33.0)	N = 10 39-45 (41.4)	N = 10 162-182 (170.1)
Trapper's Lake, Colorado - U.S.F.S.	N = 24 59-63 (60.5)	N = 15 18-22 (20.1)	N = 10 32-41 (37.4)	N = 10 39-47 (43.7)	N = 10 162-204 (185.4)

FINAL REPORT

Effects of Brook Trout Competition on Threatened Greenback Cutthroat Trout

by

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ABSTRACT

The introduction of exotic salmonids into streams along the Front Range of Colorado has been a major reason for the decline of the federally and state threatened greenback cutthroat trout (*Salmo clarki stomias*). Effects of competition for preferred positions in Hidden Valley Creek, Rocky Mountain National Park, were evaluated by underwater observation of cutthroat trout positions before (sympatry) and after brook trout (*Salvelinus fontinalis*) were removed (allopatry). After brook trout were removed, juvenile cutthroat trout (50-150 mm) shifted to occupy more favorable stream positions that had lower focal point velocities (water velocity at the fish's snout) and were closer to cover. In contrast, when sympatric with cutthroat trout, brook trout juveniles occupied the more favorable positions with lower focal point velocities and higher water velocity differences (the difference between the focal point velocity and the fastest velocity within two body lengths of the fish). Together, this evidence indicates that brook trout juveniles were the dominant competitor, and excluded juvenile cutthroat from energetically favorable stream positions. Evidence for interactions between adult (>150 mm) cutthroat and brook trout was minimal, so these interactions were not considered a major factor in cutthroat displacement. During low water years, habitat for young-of-the-year (YOY) rapidly declines as flow decreases. These habitat constraints may force YOY cutthroat trout to occupy energetically more expensive positions in the main stream channel earlier than usual, which may result in decreased growth and lower overwinter survival for YOY cutthroat trout. Moreover, when active foraging resumes in the spring, the now age I+ cutthroat may be placed at an even greater competitive disadvantage versus juvenile brook trout, due to their smaller-than-normal size. Consequently, decreased YOY habitat during low water years may intensify competition between juvenile trout and contribute to the displacement of the greenback cutthroat trout from lotic systems in Colorado.

The greenback cutthroat trout (Salmo clarki stomias) is one of four subspecies of cutthroat trout historically found in Colorado (Behnke 1979), and is the only trout native to the South Platte River basin. With man's westward movement, the greenback cutthroat trout suffered severe declines throughout its native range, primarily due to habitat degradation, overfishing, and the introduction of exotic species. Of the introduced species, the rainbow (Salmo gairdneri) and brook trout (Salvelinus fontinalis) present the greatest threat to greenback cutthroat trout. Rainbow trout hybridize with cutthroat trout and destroy pure cutthroat populations, while the mechanism by which brook trout displace cutthroat remains unknown.

In 1976, as part of a reintroduction effort, greenback cutthroat trout were stocked into Hidden Valley Creek, Rocky Mountain National Park, Colorado. Prior to the introduction, an attempt was made to remove populations of brook trout and longnose suckers (Catostomus catostomus) from the stream using antimycin, a fish toxicant. Unfortunately, brook trout were not completely eradicated, or were reintroduced by anglers, and after several years the population began to increase. In all recorded cases, brook trout have displaced greenback cutthroat trout from streams after only a few years (Behnke 1979). The goal of our research was to determine if competition between cutthroat and brook trout was occurring, and if so, at what life stage the interaction was most intense.

Considerable controversy surrounds the role of interspecific competition in structuring natural communities (Diamond 1978; Roughgarden 1983; Schoener 1974, 1982; Simberloff 1983; Strong 1983), and what constitutes sufficient evidence for its occurrence. Problems of inappropriate experimental design have plagued field studies attempting to demonstrate interspecific competition (Connell 1980, 1983). Competition is most likely to occur between similar species which have not coevolved, and thus have a high degree of niche overlap. Therefore, we expected to find competition occurring in the unnatural sympatry between the native greenback cutthroat trout and the exotic brook trout.

We hypothesized that brook trout out-compete cutthroat for profitable positions in streams (sensu Fausch 1984), which would eventually result in decreased growth and survival of greenbacks. To test this hypothesis, we first compared characteristics of positions occupied by cutthroat trout before and after removing brook trout from a section where the two species were sympatric. Before brook trout were removed, we also compared positions of cutthroat trout with those of brook trout to determine if the species segregated by microhabitat. Third, we compared cutthroat trout positions in sympatry to those in a nearby section of cutthroat trout allopatry, where habitat was similar.

These comparisons were further complicated by changes in habitat with the natural decline in streamflow throughout the summer. Among other statistical methods we used to account for changing flows, monitoring positions of cutthroat throughout the year in allopatry served as a control for the experiment to assess position shifts related to the habitat changes, as well as shifts due to changes in fish density after brook trout removal from sympatry.

STUDY AREA

Hidden Valley Creek is located in Rocky Mountain National Park, Colorado. The stream is 7.5 km long and descends from 3456 m at its headwaters to 2597 m at its confluence with the Fall River, a tributary of the Big Thompson River. At the 3.5 km mark, Hidden Valley Creek traverses an extensive beaver pond complex, and further downstream descends falls which serve as barriers to upstream fish movement.

Three sections of Hidden Valley Creek, between the beaver ponds and the falls, were selected as study areas (Table 1). In the upstream section, which has the highest gradient, greenback cutthroat trout are sympatric with brook trout (40% cutthroat and 60% brook trout). Two low-gradient meadow sections further downstream contain populations of cutthroat-brook trout in sympatry (67% cutthroat and 33% brook trout), and cutthroat trout in allopatry. Habitat in the two meadow sections was similar in length, width, depth, and gradient, and was dominated by long runs and pools. Conversely, the upstream high-gradient section was shorter, and dominated by riffles and plunge pools.

Discharge in Hidden Valley Creek followed a typical pattern for high elevation Rocky Mountain streams (Figure 1), normally reaching a maximum in early summer then gradually declining to baseflow in late fall. During 1984, a high water year, discharge reached 0.52 m^3/sec and declined to 0.04 m^3/sec by mid-September. In 1985, a year of moderate flow, discharge reached 0.42 m^3/sec in mid-June and decreased more rapidly to 0.03 m^3/sec at baseflow. During high flows the lower-gradient meadow sections flooded, creating extensive backwater habitat. As flows decreased backwater areas were either isolated, or completely dewatered.

METHODS

During summer 1985, positions of trout were observed underwater by the research assistant using a dry suit, snorkel, and mask. Characteristics of fish positions were measured in each section from 19 June to 28 August, at which time brook trout were removed from the downstream sympatric section. After brook trout removal, observations continued from 6 September to 23 September.

On each day of diving, fish were observed 1-2 hours each morning and afternoon, contingent on water temperature and weather conditions. Water temperature measured while observing fish averaged 8.6 C (range 4-10 C). The diver began at the downstream end of each section and proceeded upstream, attempting to observe undisturbed fish. On subsequent days, snorkeling began where it had ended previously, so each section was completely traversed several times. A total of 126 hours were spent snorkeling to measure 200 fish positions.

When measuring positions of individual trout, the diver crawled along the stream bottom investigating possible hiding places for fish. When a fish was sighted, the diver remained motionless for approximately five minutes while observing the fish's behavior. He slowly approached to within 2 m of the fish, determined the species, and estimated its total length and distance above the substrate before marking the position. Trout were grouped into six size classes: 20-50 mm, 50-100 mm, 100-150mm, 150-200 mm, 200-250 mm, and >250 mm. After practice estimating the lengths of submerged objects, and then measuring them, the size of fish could be accurately determined.

After fish positions were marked, 10 more variables were measured at the focal point (the relatively fixed position of the fish's snout in the water column): 1) water depth, 2) distance to nearest cover, 3) focal point water velocity, 4) mean water velocity at 0.6 depth, 5) the maximum water velocity within two body lengths of the focal point in any direction, 6) temperature, 7) substrate (silt, sand, gravel, rubble, boulder, bedrock), 8) habitat type (run, riffle, pool), 9) light conditions (bright sun, partial shade, deep shade), and 10) distance to each stream bank.

Nearest cover was defined as the closest object which provided a refuge from current. Fish positioned beneath an undercut bank were judged to be using it in part as a velocity refuge, so the distance to cover for these fish was zero.

The maximum water velocity was measured within a distance of two body lengths from each fish, using the midpoint of the fish's size class (e.g. 250 mm for a fish of 100-150 mm). These distances approximated feeding radii (Fausch 1984), and were used to determine the water velocity difference (maximum water velocity minus focal point velocity) a measure of profitability for stream salmonid positions (Fausch and White 1981). Water velocities were measured using midget Bentzel velocity tubes (Everest 1967) that covered three different velocity ranges. Each tube was calibrated using a standardized Ott current meter in a flume with maximum flow of 0.14 m^3/sec.

After YOY cutthroat trout emerged in early August, their microhabitat in small pools at the stream margins was identified and the volume of these areas monitored through mid-September. During September, when YOY trout began occupying the main channel, their positions where measured by underwater observation in the same manner as juveniles and adults.

Available habitat (depth, velocity, and substrate) in the downstream sympatric and allopatric sections was measured at random distances from one stream bank along 172-222 transects perpendicular to flow, spaced at 2-2.5 meter intervals throughout each section. Habitat was measured on 8 August during moderately low flow (0.06 m^3/sec) and on 26 September during baseflow (0.03 m^3/sec). Habitat availability in each section was statistically compared using a G-test for independence (Sokal and Rohlf 1981).

During 1985, each section was electrofished in the spring, before the study, during mid-summer when brook trout were removed from the downstream sympatric section, and in the fall at the conclusion of the study. No brook trout were observed while snorkeling in the downstream sympatric section after their removal, but nine adults were captured during the final electrofishing on 17 October. These adults most likely emigrated downstream after snorkeling was completed, from either the upstream sympatric section or the beaver ponds.

Seventy-three fish larger than 120 mm collected during the spring sample were individually marked using cold brands. Anesthetized fish received four or fewer brands at four locations on each side of the body: predorsal, postdorsal, below the adipose fin, and above the anal fin. In addition, the adipose fin and the tips of the caudal fin lobes were clipped to identify fish from each section. Total lengths and weights of all fish were recorded.

Trout abundance in the two downstream sections was estimated using a two-pass Seber-LeCren estimator (Seber and LeCren 1967). In the upstream sympatric section, trout abundance was estimated using three removal passes and a generalized removal estimator (Otis et al. 1978; White et al. 1982). Growth of individually marked fish was estimated between each capture date. The population age structure was determined from scales collected during 1984. Diet of trout, and the incidence of predation on young-of-the-year (YOY) cutthroat trout, was determined by flushing stomach contents from fish larger than 120 mm collected during September and October, 1984.

RESULTS

Trout Population Structure

Young-of-the-year (YOY) brook trout spawned the previous fall emerge in early spring, while YOY cutthroat trout spawned in the spring do not emerge until mid-summer. Earlier spawning and emergence times give YOY brook trout a size advantage over YOY cutthroat trout. Rarely do YOY greenback cutthroat trout exceed 45 mm in length by the end of their first growing season in streams (Bulkley 1959) and many have not yet formed scales. Furthermore, as age I+ fish, they may still form scales so late that few or no circuli are deposited, hence no annuli can be formed.

Similarly, in high altitude lakes few YOY greenback cutthroat trout form annuli after their first year of life (Nelson 1972).

Of the 185 scales collected from cutthroat trout in 1984, only regenerated scales were collected from 28 fish. The remaining 157 scales were used to calculate the regression of total body length versus scale radius (Figure 2). Twenty-six of the cutthroat trout examined did not have any annuli present, and ranged from 78 mm to 146 mm. A total of 96 fish that had one annulus were tentatively aged I+, and ranged in length from 108 mm to 220 mm. Similarly, 35 fish ranging from 172 mm to 293 mm had two annuli and were assumed age II+.

We assumed that late emergence and the short growing season at high altitude prevented any of the cutthroats sampled from growing large enough to form an annulus their first year. In order to determine which fish failed to form an annulus at the end of their second year, a two-step procedure was used: 1) body lengths at each annulus were back-calculated for all fish initially aged as I+ and II+ using the standard Fraser-Lee method (Carlander 1981); 2) to objectively add a second annulus, a "critical length value" was established representing the maximum length of cutthroat trout at the time of second annulus formation. If the back-calculated length at the first annulus was greater than the "critical length value" we assumed the fish did not form an annulus after its second year of life (age I+), so an additional annulus was added.

The critical length value was defined as the upper 95% confidence limit for length of age I+ greenback cutthroat trout after their second summer of growth. This length was calculated from cutthroat less than 140 mm captured on all 1984 sampling dates (Figure 3). Age-0 fish were easily separated from age-1 by size and were not included. When scales were collected for the last time on 12 September, the smallest cutthroat aged II+ was 115 mm. Therefore, fish less than 115 mm were assumed age I+, and were used to establish a mean length for fish of this age in the fall when further growth was minimal. The upper 95% confidence limit of the fall age I+ mean length was 108.5 mm, which represented the "critical length value".

First annuli were added to all fish, and second annuli were added to 50 fish previously aged I+, making them III+. Similarly, a second annulus was added to 31 fish previously aged II+, making them IV+. No fish older than IV+ were found in the sample. Mean lengths for cutthroat in June 1984 for ages I+ through IV+ were 112.6 mm, 150.2 mm, 179.1 mm, and 219.8 mm, respectively. We defined juvenile fish as 100-150 mm and adults as larger than 150 mm, because the smallest sexually mature male cutthroat trout were about 150 mm. Thus, juveniles included age I and some age II fish, while adults were age II and older.

Abundance estimates indicate that the two low-gradient sections had similar population size and density (Table 2), although cutthroat trout biomass in the allopatric section was higher than the combined cutthroat and brook trout biomass in the downstream sympatric section. Mean lengths and weights illustrate that juvenile cutthroat in the downstream sympatric section were significantly smaller than juvenile brook trout (Table 3). Adult fish of the two species were not significantly different in mean length, although brook trout were significantly heavier than cutthroat. Cutthroat trout juveniles and adults were of similar length and weight in downstream sympatry and allopatry. Due to the inconsistent pattern of recaptures of individually marked fish throughout the study, estimates of fish growth in sympatry versus allopatry were not attempted.

Habitat Availability

Depth and velocity declined throughout the summer as flows decreased in Hidden

Valley Creek (Figures 4-7). However, the distribution of velocities was similar in the two downstream sections, hereafter called simply sympatry and allopatry, on each date measured ($p<0.50$ and 0.90 by G-test). The distribution of depths was similar between sections in early fall ($p<0.50$), but the sympatric section was shallower than the allopatric section in summer ($p<0.01$). The distribution of substrates differed in the two sections ($p<0.01$ both dates), due to a higher proportion of sand and gravel in the allopatric section.

Trout Position Shifts

Because depth and velocity declined with flow, we also expected trout position characteristics to change during the summer, even in the absence of interspecific competition. Therefore, we compared regression lines relating position variables, such as focal point velocity, to discharge between sympatry to allopatry using analysis of covariance (ANCOVA) to detect position shifts caused by ecological release from interspecific competition.

Three main comparisons were made to detect these position shifts. The strongest test of interspecific competition was comparing positions of cutthroat trout in the sympatric section before and after brook trout were removed (early vs. late season). If interspecific competition was occurring, we expected cutthroat trout to shift to more favorable positions after brook trout were removed. Two other tests providing further evidence for such a shift were: 1) comparing positions of cutthroat trout in allopatry versus those in sympatry with brook trout (allopatric vs. sympatric sections, early season), and 2) comparing positions of cutthroat versus brook trout in the sympatric section, before the latter were removed.

Because the allopatric section was unmanipulated, it served as a control for habitat changes with flow in our experiment. That is, we expected to see no change in cutthroat trout microhabitat use except those caused by declining flows. Finally, comparisons between the allopatric and sympatric sections after brook trout were removed allowed us to determine the effect of intraspecific competition at two different densities, since late in the season the sympatric section was then lower density allopatry (0.35 fish/m in the allopatric versus 0.25 fish/m in the "sympatric" section).

In the ANCOVA, the square-root transformation was used on all variables to correct for heterogeneous variance. A few water velocity readings were below the sensitivity of the Bentzel tubes and were recorded as zero. These measurements were excluded from the analysis because the square-root transformation caused a much lower value than if the true velocity were known. Comparisons of fish positions measured in the upstream high-gradient sympatric section were not analyzed further due to low sample size and substantially different habitat. Consequently, the downstream sympatric section will be referred to hereafter simply as the sympatric section.

Juvenile trout

After brook trout were removed from the sympatric section, juvenile (50-150 mm) greenback cutthroat trout shifted to occupy more favorable stream positions. Juvenile cutthroat trout focal point velocities were significantly lower in allopatry ($p<0.0005$, Figure 8 and Table 4a), after accounting for the effects of declining discharge using ANCOVA. Similarly, juvenile cutthroat trout maintained positions that were closer to cover ($p=0.036$) and had lower maximum water velocities ($p=0.001$) after brook trout were removed. There was no significant change in water velocity difference after brook trout were removed, although it did increase slightly (Table 4a).

Comparisons between juvenile cutthroat and brook trout within the sympatric section indicated that cutthroat trout held positions with significantly higher focal point velocities ($p=0.025$, Figure 9) and lower water velocity differences ($p=0.027$) than brook trout. Both comparisons indicate that before brook trout were removed, they maintained more favorable positions in sympatry than cutthroat.

Comparisons between cutthroat trout in the allopatric versus sympatric sections before brook trout were removed (early season) showed that juvenile cutthroat trout in sympatry were located closer to the nearest stream bank ($p=0.013$). Conversely, later in the summer juvenile cutthroat in lower density allopatry (late season sympatry) maintained positions farther from the nearest stream bank ($p<0.0005$) than those at higher density (late season allopatry). However, in the allopatric section juvenile cutthroat trout shifted to occupy positions closer to the nearest stream bank in late versus early season ($p=0.017$). Due to this shift in the unmanipulated allopatric section from early to late season, meaningful inferences regarding the distance to the nearest bank were impossible.

Throughout the year, juvenile greenback cutthroat trout within sympatry and allopatry occupied similar habitats in early and late season, so the data within sections were pooled. Juvenile cutthroat trout in sympatry and allopatry strongly selected runs over either pools or riffles (Figure 10). Similarly, lighting at juvenile cutthroat positions was constant during the summer, so data were also pooled within sections. Juvenile trout selected positions in partial shade in both sympatric and allopatric sections (Figure 11).

Despite differences in the distribution of substrates between sympatric and allopatric sections, juvenile cutthroat trout held positions over similar substrates in the two sections, so the data were combined within seasons. During the early part of the summer, juvenile cutthroat trout maintained positions over a wide variety of substrates, but selected sand and gravel (Figure 12a). Preference of juvenile trout was relatively constant through the season, but the range of substrates selected decreased in late summer (Figure 12b) because fewer coarse substrates were available as flows declined.

Adult trout

While adult (>150 mm) cutthroat trout exhibited significant shifts in some position variables, the evidence for direct competition with brook trout was less than for juvenile cutthroat. After brook trout were removed from the sympatric section, adult cutthroat trout shifted to occupy positions deeper in the water column ($p=0.043$) and closer to the substrate ($p=0.024$). These shifts alone do not indicate that strong competition for more profitable positions was occurring.

During the early season adult cutthroat trout in allopatry occupied positions with greater maximum water velocity ($p=0.015$) and higher water velocity differences ($p<0.0005$) than adult cutthroat in sympatry with brook trout. Allopatric cutthroat also maintained positions deeper in the water column ($p=0.004$) and farther above the stream bed ($p=0.038$) than those in sympatry. Because the sympatric section was significantly shallower than the allopatric one, these data may indicate that adult cutthroat trout select positions in deeper water when it is available.

During late summer, adult cutthroat trout in low density allopatry held positions farther away from cover ($p=0.040$) than similar sized cutthroat in higher-density allopatry. Thus, there was little apparent shift in adult cutthroat trout positions as a function of decreased density. However, further examination would be necessary to determine the strength of intraspecific competition. In summary, although adult cutthroat and brook trout segregated by depth, velocity, and distance to cover in some comparisons, a pattern of position shifts providing strong evidence for competition was not apparent.

Habitat and light conditions at positions of adult cutthroat trout were similar within allopatric and sympatric sections between early and late seasons so the data were pooled, as for juveniles. Adult cutthroat trout were similar to juveniles in that they selected positions in partial shade throughout the summer in both sections (Figures 13). However contrary to juvenile cutthroat trout, adults in both sympatry and allopatry used both runs and pools in relatively the same proportion (Figure 14).

Because adult cutthroat trout in sympatry and allopatry selected positions over similar substrates, these data were pooled within seasons, as for juveniles. Like juveniles, adult cutthroat trout also selected positions primarily over silt, sand, and gravel substrates, although fewer coarse substrates were available during late summer (Figure 15).

Early in the season, juvenile cutthroat trout segregated from adult cutthroat by focal point velocity and distance above the stream bed (Table 4a and 4b). However, during late summer juveniles and adults segregated by depth alone.

Young-of-the-year Microhabitat

Young-of-the-year greenback cutthroat trout occupied microhabitats with unmeasureable velocity and silt substrate at the margins of the stream. Nursery pool volume decreased with declining flows throughout late summer. By 14 September 1985, 79% (15 of 19) of the nursery areas marked in the sympatric section during early August, and 64% (7 of 11) of those in the allopatric section, were dry. Dewatering of nursery habitat coincided with the period when YOY cutthroat were first observed using positions in the main channel on 9 September. Moreover, YOY cutthroat microhabitat overlapped significantly with that of juvenile cutthroat when they moved into the main channel, so the possibility for niche overlap and intraspecific interaction existed (Table 5). Young-of-the-year cutthroat selected similar habitat, substrate, and light conditions in both sympatry and allopatry, so the data were pooled (Figures 16, 17, and 18). Positions chosen by YOY cutthroat in the main channel were located in runs, in partial shade over silt and sand substrate.

Diet of Cutthroat Trout

Cutthroat trout in Hidden Valley Creek fed on a wide variety of organisms and strongly selected those food items which were temporarily abundant. Of the 77 trout stomachs sampled in 1984, only one was from a brook trout and three cutthroat trout stomachs were empty. The frequency of occurrence and percent composition by number of each taxon both varied with time (Table 6), and indicate that greenback cutthroat trout fed opportunistically on available organisms. This type of feeding behavior is common among stream salmonids (Ringler 1979).

Gravimetric analysis revealed that terrestrial invertebrates comprised a relatively constant proportion of the diet throughout September, but declined rapidly in October (Table 7), concomitant with decreasing temperatures. The diet of cutthroat also reflected the availability of emerging aquatic insects. Peak emergence of baetid mayflies (Ephemeroptera) occurred in early September, while peak emergence of adult tipulids (Diptera) was in early October. None of the stomachs analyzed contained YOY greenback cutthroat trout.

DISCUSSION

The testing of interspecific competition in aquatic habitats has its foundation in lentic systems (Werner and Hall 1977, 1979; Laughlin and Werner 1980; Mittelbach 1984; Hanson and Leggett 1985; Persson 1986). These studies illuminate the critical role of habitat segregation in resource partitioning among species. This type of resource use requires coevolved species which interactively segregate (Nillson 1967), but such niche shifts would not be expected between the cutthroat and brook trout we studied, which did not coevolve.

Substantial overlap in resource use may result in resource limitation and would likely promote interspecific interactions between two such species. It is also thought that competition would be most intense in low diversity systems where the potential for encounter between species increases (Connell 1980). Therefore, the two-species assemblage of exotic brook trout and native greenback cutthroat trout in Hidden Valley Creek was a likely arena in which to search for interspecific competition.

Lotic systems present certain complications not found in lentic habitats when investigating species interactions. Differences in available habitat, changes in habitat due to declining discharge levels, and variable densities due to emigration and immigration often complicate studies in natural streams. We attempted to account for differences in available habitat by limiting our comparisons to the two downstream sections which have similar macrohabitat (Table 1) and microhabitat (Figures 4-7). Although significant differences in depth and substrate types existed between sections, both were dominated by long runs and pools with sand and gravel bottoms. We feel that these habitat differences do not invalidate the comparisons of trout positions.

Adjusting for trout position changes due to declining flow with ANCOVA addressed to problem of fluctuating habitat throughout the season. Finally, greenback cutthroat trout in Hidden Valley Creek were relatively sedentary, maintaining positions within a stream section for relatively long periods of time. This lack of emigration and immigration assured that our density estimates were valid and that the integrity of our study populations was maintained.

If, in fact, salmonid positions in streams are not random, but selected and maintained, preferred positions should be ones which maximize net energy gain. Furthermore, fish that maintain positions which maximize net energy gain should have a selective advantage over fish in sub-optimal positions. Thus, in accordance with optimal foraging theory (Schoener 1971), preferred positions for salmonids should be characterized by relatively low focal point velocity and high water velocity difference (Everest and Chapman 1972; Fausch and White 1981; Fausch 1984; Fausch and White 1986)

In testing for interspecific competition between greenback cutthroat trout and brook trout, we found strong evidence that interactions between juveniles may account for the decline of cutthroat trout in Hidden Valley Creek. Competition was tested by measuring position shifts of cutthroat and brook trout in sympatry and allopatry. If brook trout were competing with cutthroat trout for profitable stream positions, we would expected a shift in one or more of the position variables after brook trout removal. Juvenile cutthroat trout demonstrated an ecological release in the sympatric section as measured by focal point velocity and distance to cover. Juvenile cutthroat shifted to occupy positions closer to cover and with lower focal point velocities after brook trout were removed. Moreover, even with declining water velocities as discharge decreased, water velocity difference did not decrease. Overall, this set of shifts indicates that juvenile cutthroat trout shifted to use more profitable positions after brook trout were removed.

Similar shifts were not observed in the allopatric (control) section, indicating that shifts in sympatry were due to the absence of brook trout. This was the strongest test for interspecific competition between the two species.

Further evidence for competition between juveniles was provided when positions of cutthroat and brook trout in sympatry were compared. Brook trout maintained positions in slower velocity water and with higher water velocity differences. Due to their earlier emergence and size advantage juvenile brook trout may force cutthroat into less profitable positions.

Unlike the juveniles, adult cutthroat trout demonstrated fewer position shifts in comparisons between and within sections. Adult cutthroat trout occupied positions with higher water velocity differences in allopatry when compared to early season sympatry. Significant depth comparisons (e.g. distance above the substrate and distance above the focal point) indicate that adult greenbacks in sympatry were maintaining positions in shallower water than adults in allopatry. However, this may be an artifact of the shallower habitat available in the downstream sympatric section. Overall, evidence for interactions was less convincing and competition among adults probably plays at best, a small role in cutthroat trout displacement.

Brook trout domination of cutthroat in western U.S. streams has been previously documented in Idaho (Griffith 1972). Griffith found that earlier emergence gave YOY brook trout, on average, a 20 mm size advantage over YOY cutthroat. During the summer, Griffith reported that YOY cutthroat and brook trout segregated into different microhabitat, and thus minimized the possibility for interaction. However, in a stream aquarium YOY brook trout consistently dominated the smaller cutthroats.

Under laboratory conditions, Griffith found that yearling and older (age I+ to III+) brook trout were less active socially than cutthroats, initiating 40% fewer aggressive encounters, and could not displace older and larger cutthroats. In several Idaho streams, age I+ and older cutthroat occupied significantly higher focal point velocities than brook trout.

We agree that the potential for interaction between YOY cutthroat and brook trout would be low during summer. However, in Hidden Valley Creek, sympatry may occur during mid-September when YOY cutthroats leave their backwater nursery areas and occupy positions in the main channel. Therefore, the potential for encounter and interaction should increase during late summer and fall.

Results from our underwater observations in part, substantiate Griffith's work with age I+ and older cutthroat. We found that juvenile (age I+ and some age II+) cutthroat trout in early season sympatry were significantly smaller and occupied higher focal point velocities than brook trout. However, adult (some age II+ and all age III-IV+) cutthroat and brook trout in Hidden Valley Creek, overlapped considerably in size and did not segregate by velocity. Intense agonistic behavior of cutthroat trout, similar to that observed by Griffith, coupled with a reduced size advantage may limit adult brook trout dominance.

Fausch (1984) proposed that profitable positions are a limiting resource for stream salmonids. In natural systems this resource fluctuates, and during periods of low availability competition may be intensified (Wiens 1977). In stream systems, available habitat constantly changes as flows decline. Declining microhabitat may force YOY greenback cutthroat trout to occupy energetically more expensive positions in the main stream channel. Positions in zero velocity nursery areas provide protection from high velocity currents and may further allow for rapid growth in shallower, warmer locations (personal communication, Ken Bovee, Instream Flow and Aquatic Systems Group, U.S. Fish and Wildlife Service, Fort Collins, CO). We speculate that if these habitats dewater prematurely, as is the case in low water years, growth of YOY cutthroat may be reduced, which would likely cause lower overwinter survival (Hunt 1969). The following spring, when active foraging resumes, the now age I+ cutthroat trout may be placed at an even greater competitive disadvantage due to their smaller-than-normal size. Consequently, habitat constraints during low water years may cause poor overwinter survival and/or intensified competition the following spring resulting in increased juvenile mortality. This supports the observation that periodic year-class failures occur among greenback cutthroat trout in Hidden Valley Creek (personal communication, Bruce Rosenlund, U.S.Fish and Wildlife Service, Golden, CO).

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Table 1. Physical characteristics of study sections in Hidden Valley Creek, 1985.

	Section		
Characteristic	Downstream sympatry	Upstream sympatry	Allopatry
Length (m)	519	168	509
Mean width (m)	2.5	3.3	2.1
Mean depth (cm)	29	26	32
% Gradient	0.2	2.3	0.4
Riffle-Pool ratio	0.3:1.0	2.4:1.0	0.2:1.0
% Run	58	7	52
% Pool	32	27	40
% Riffle	10	66	8

Table 2. Estimates of population size, biomass, and density for all trout greater than 50 mm in three sections of Hidden Valley Creek, 1985. Estimates and 95% confidence intervals are based on mid-season electrofishing samples.

	Population Estimate	Biomass (kg)	Density (fish/m)
Allopatry	179 ± 10	8.3 ± 0.13	0.37 ± 0.02
Downstream Sympatry	194 ± 3	5.2 ± 1.01	0.35 ± 0.04
Upstream Sympatry	102 ± 10	2.7 ± 0.03	0.61 ± 0.18

Table 3. Mean weight (g) and length (mm) ± 95% confidence intervals for juvenile (50-150 mm) and adult (>150 mm) trout in the downstream sympatric and allopatric sections of Hidden Valley Creek, summer 1985.

	Downstream sympatry		Allopatry
Age group	Cutthroat	Brook	Cutthroat
Juvenile			
mean weight	11.4 ± .09	24.3 ± 1.4	11.0 ± 0.8
mean length	104.3 ± 2.8	123.1 ± 3.8	100.2 ± 2.1
Adult			
mean weight	83.6 ± 4.7	114.2 ± 23.4	71.1 ± 4.6
mean length	192.7 ± 6.0	205.7 ± 14.9	194.0 ± 2.7

Table 4a. Means and 95% confidence intervals for position variables measured at the focal point for juvenile (50-150 mm) and cutthroat and brook trout in the downstream sympatric and allopatric sections of Hidden Valley Creek, summer 1985.

	Sympatry			Allopatry	
	Early Season		Late Season	Early Season	Late Season
	Cutthroat (N=17)	Brook (N=15)	Cutthroat (N=21)	Cutthroat (N=25)	Cutthroat (N=9)
Distance above substrate (mm)	55 ± 10	45 ± 11	49 ± 9	49 ± 11	42 ± 12
Distance above focal point (mm)	266 ± 36	314 ± 47	365 ± 37	376 ± 51	381 ± 55
Distance to cover (mm)	328 ± 59	301 ± 152	202 ± 66	341 ± 68	230 ± 132
Distance to nearest bank (mm)	441 ± 105	530 ± 215	397 ± 104	515 ± 130	293 ± 127
Focal point velocity (cm/sec)	12.9 ± 2.0	11.7 ± 3.0	5.6 ± 0.7	13.1 ± 2.7	4.9 ± 2.6
High velocity (cm/sec)	17.6 ± 1.9	24.5 ± 4.9	11.2 ± 1.4	21.8 ± 4.0	11.5 ± 4.5
Water velocity difference (cm/sec)	4.7 ± 1.1	12.8 ± 3.8	5.6 ± 1.3	8.8 ± 2.5	6.6 ± 3.6

Table 4b. Means and 95% confidence intervals for position variables measured at the focal point for adult (>150mm) cutthroat and brook trout in the downstream sympatric and allopatric sections of Hidden Valley Creek, summer 1985.

	Sympatry			Allopatry	
	Early Season		Late Season	Early Season	Late Season
	Cutthroat (N=18)	Brook (N=6)	Cutthroat (N=16)	Cutthroat (N=14)	Cutthroat (N=6)
Distance above substrate (mm)	172 ± 56	138 ± 78	76 ± 21	115 ± 41	105 ± 45
Distance above focal point (mm)	444 ± 80	315 ± 80	371 ± 53	363 ± 53	307 ± 109
Distance to cover (mm)	445 ± 110	315 ± 230	503 ± 123	464 ± 117	300 ± 196
Distance to nearest bank (mm)	621 ± 141	332 ± 272	559 ± 135	671 ± 133	385 ± 234
Focal point velocity (cm/sec)	15.6 ± 3.0	11.7 ± 5.2	6.6 ± 1.1	21.6 ± 5.7	8.5 ± 5.0
High velocity (cm/sec)	28.0 ± 4.5	19.0 ± 6.0	11.1 ± 1.1	37.8 ± 8.5	14.2 ± 5.4
Water velocity difference (cm/sec)	12.3 ± 3.5	7.3 ± 4.9	4.5 ± 1.1	16.2 ± 8.0	5.7 ± 1.0

Table 5. Late season means and 95% conficence intervals for position variables measured at the focal point for young-of-the-year cutthroat in Hidden Valley Creek (sympatric and allopatric sections combined), summer 1985.

Position Variables	Mean + 95% CI
Distance above substrate (mm)	35.8 ± 5.2
Distance above focal point (mm)	183.5 ± 20.5
Distance to cover (mm)	120.8 ± 50.5
Distance to nearest bank (mm)	410.0 ± 72.9
Focal point velocity (cm/sec)	4.2 ± 0.6
High velocity (cm/sec)	8.4 ± 1.5
Water velocity difference (cm/sec)	4.4 ± 1.3

Table 6. Frequency of occurrence (FO) and percent composition by number (PCN) of invertebrate taxa in greenback cutthroat stomach on four sampling dates during 1984 in Hidden Valley Creek.

	Sampling Date							
	2 September		7 September		29 September		5 October	
Taxon	FO	PCN	FO	PCN	FO	PCN	FO	PCN
Plecoptera	67.7	12.2	34.8	5.0	90.9	24.0	66.7	12.1
Ephemeroptera	74.2	28.8	82.6	83.1	100.0	51.2	55.6	14.0
Oligochaeta	41.9	12.8	4.4	0.4	9.1	0.8	88.9	11.4
Diptera	64.5	5.9	34.8	4.3	9.1	1.6	66.7	50.4
Coleoptera	6.5	0.6	4.4	0.2	-	-	-	
Trichoptera	25.8	2.7	8.7	0.4	45.5	6.2	44.4	1.9
Terrestrial insects	80.7	35.6	52.2	7.6	45.5	15.5	5.6	8.5

Table 7. Percent composition by weight of aquatic and terrestrial invertebrates in greenback cutthroat trout stomachs in allopatric (9/2 and 9/29) and sympatric (9/7 and 10/5) sections of Hidden Valley Creek, summer 1984.

Stream Section	Date	Aquatic	Terrestrial
Allopatry	9/2	82.6	17.4
	9/29	71.2	28.8
Sympatry	9/7	74.9	25.1
	10/5	94/5	5.5

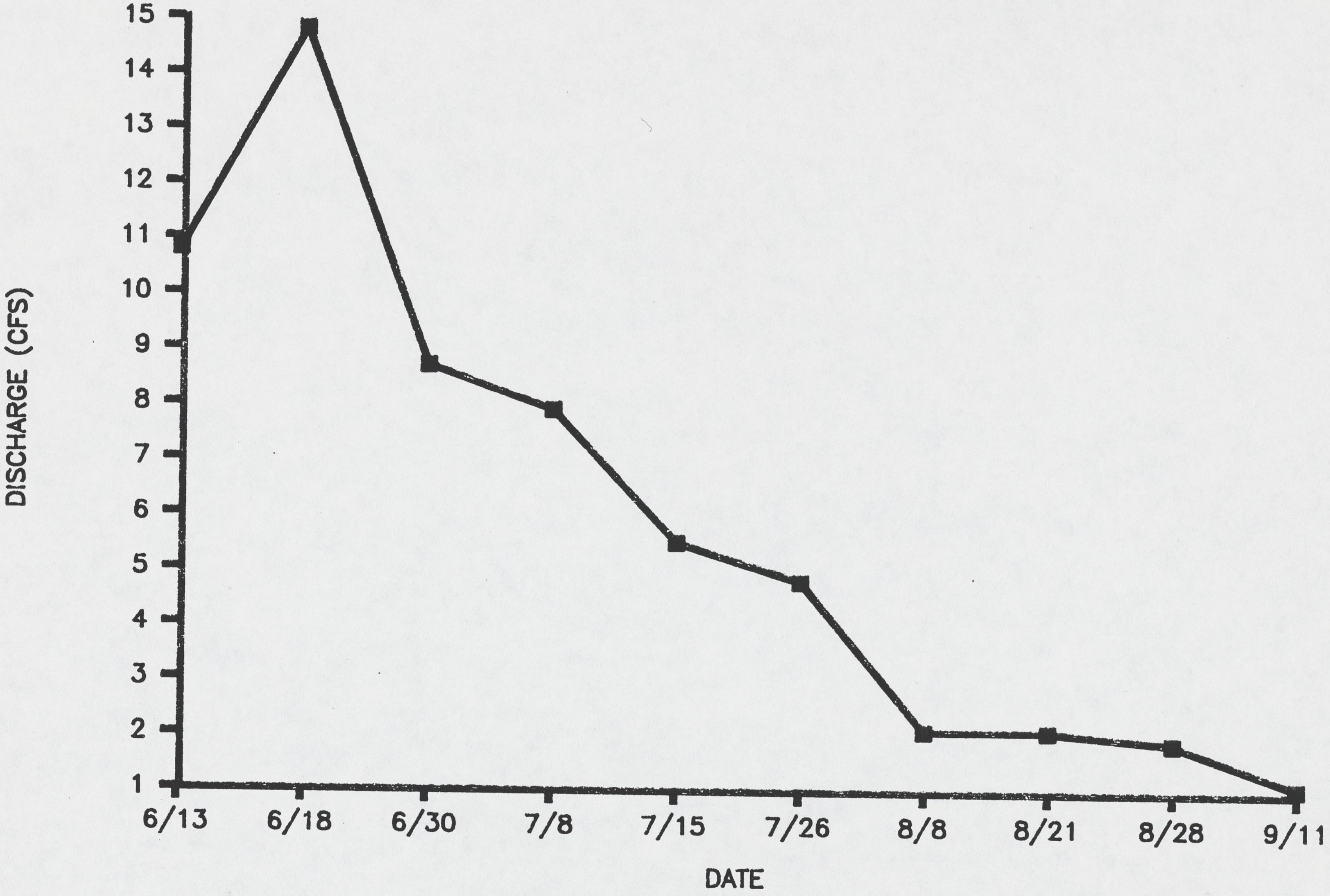

Figure 1. Discharge (m^3/sec) in Hidden Valley Creek during summer, 1985.

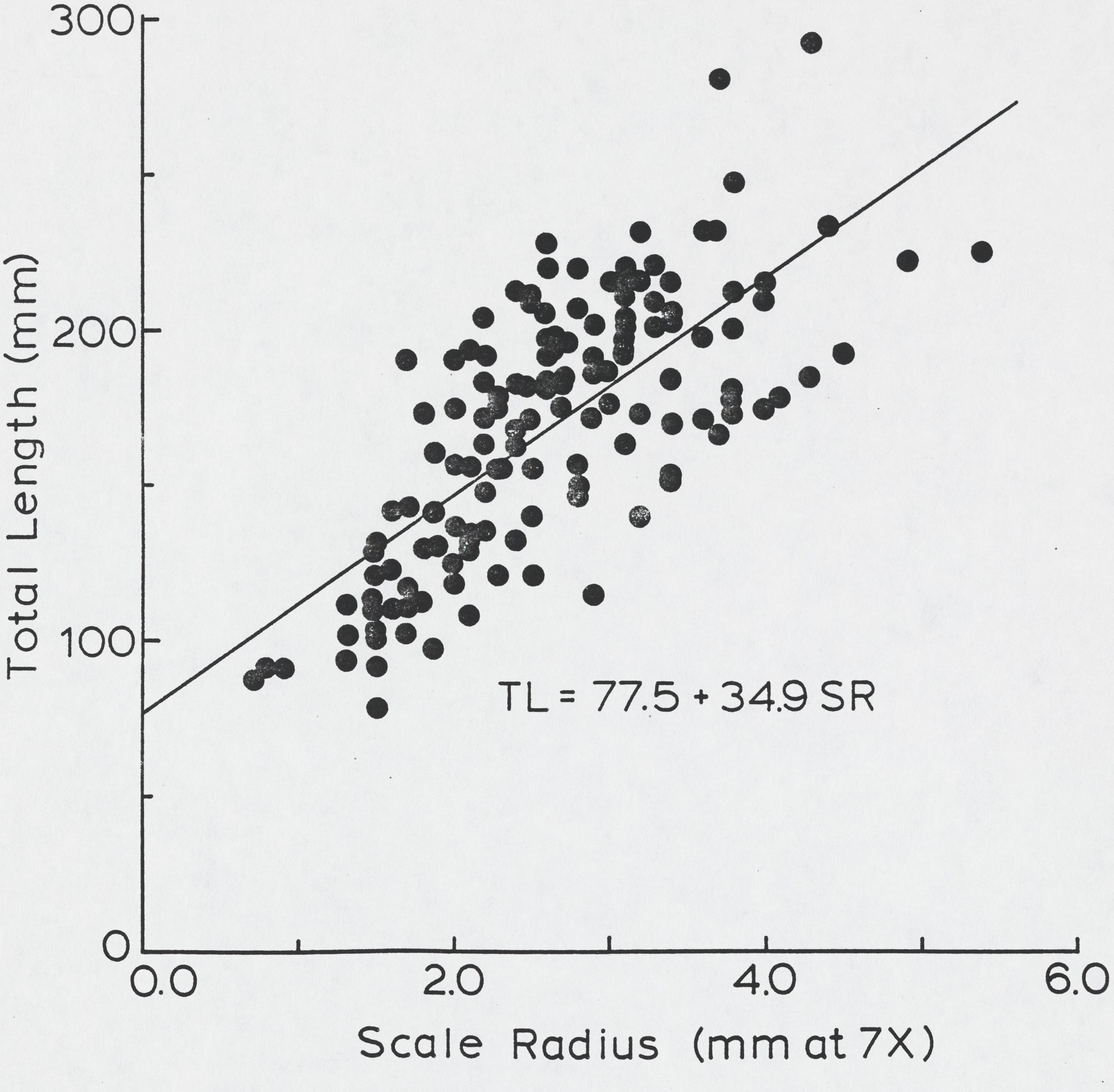

Fig. 2. Body length-scale radius relationship for greenback cutthroat trout captured in Hidden Valley Creek 13 July to 12 September 1984.

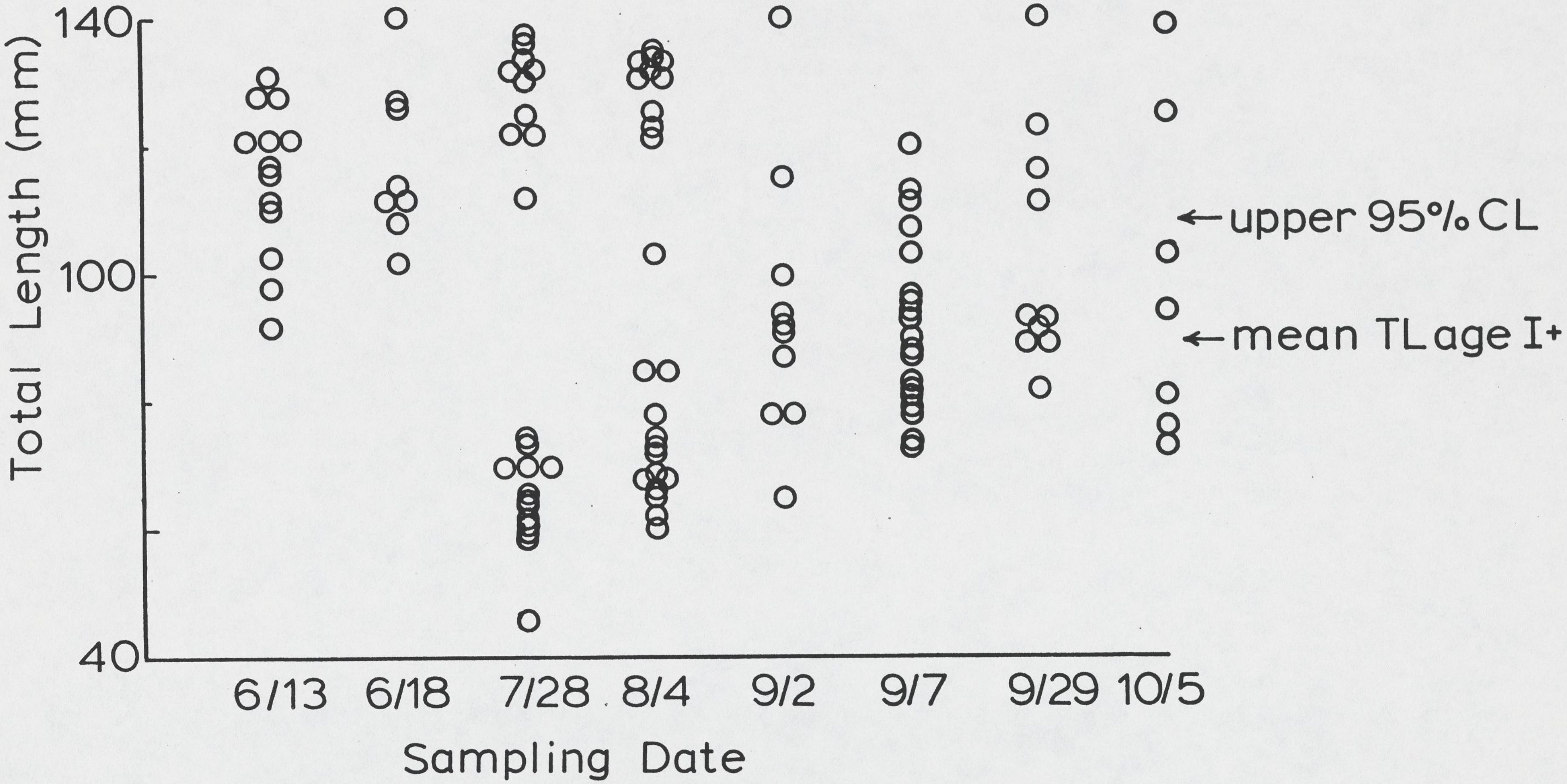

Fig. 3. Distribution of total lengths of greenback cutthroat trout captured in Hidden Valley Creek on eight dates in 1984. The mean total length for age I+ fish and the upper 95% confidence limit for this length are shown.

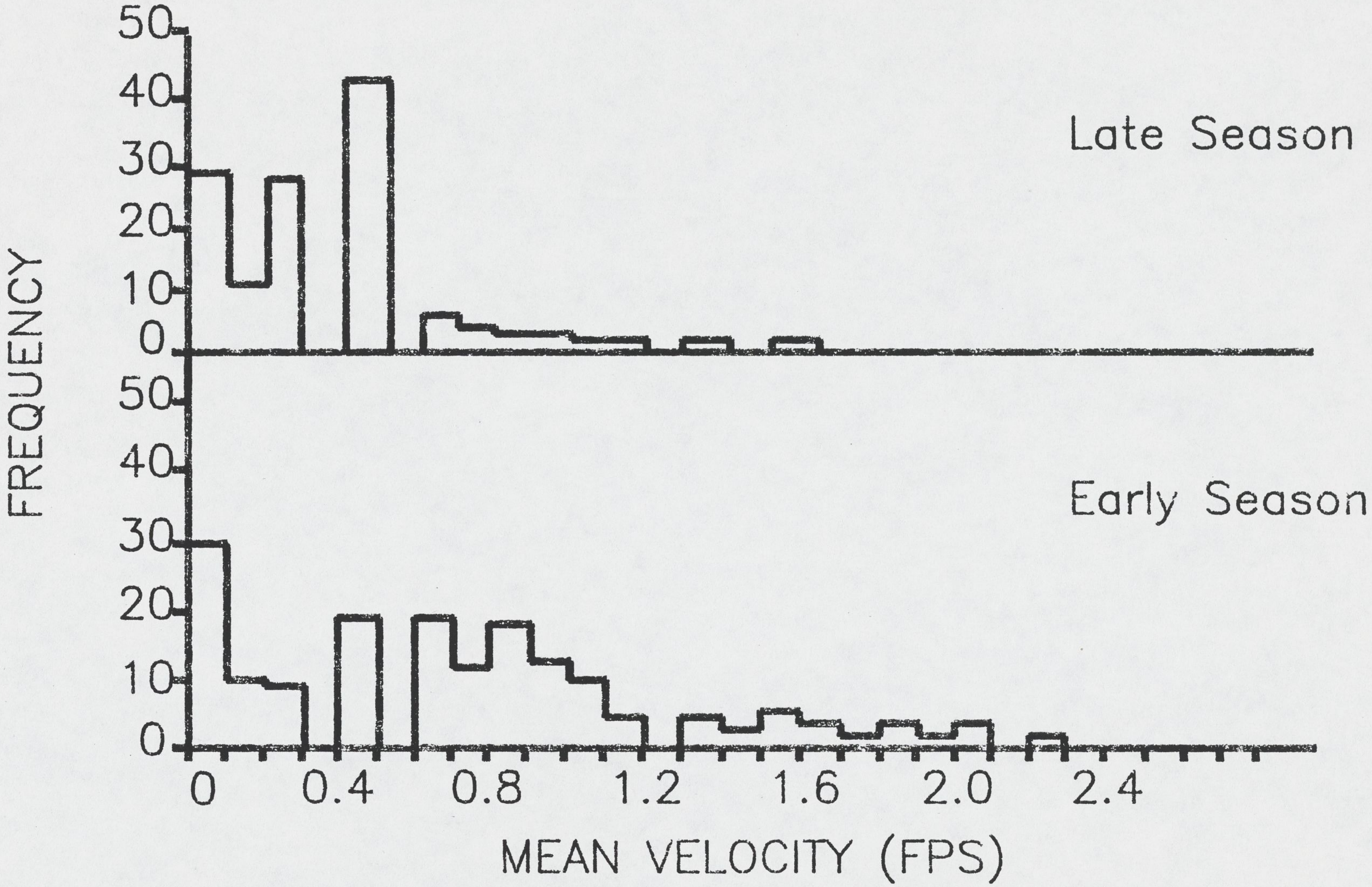

Figure 4. Available velocities (feet per second) in the sympatric section of Hidden Valley Creek on 8 August (early season) and 26 September (late season), 1985.

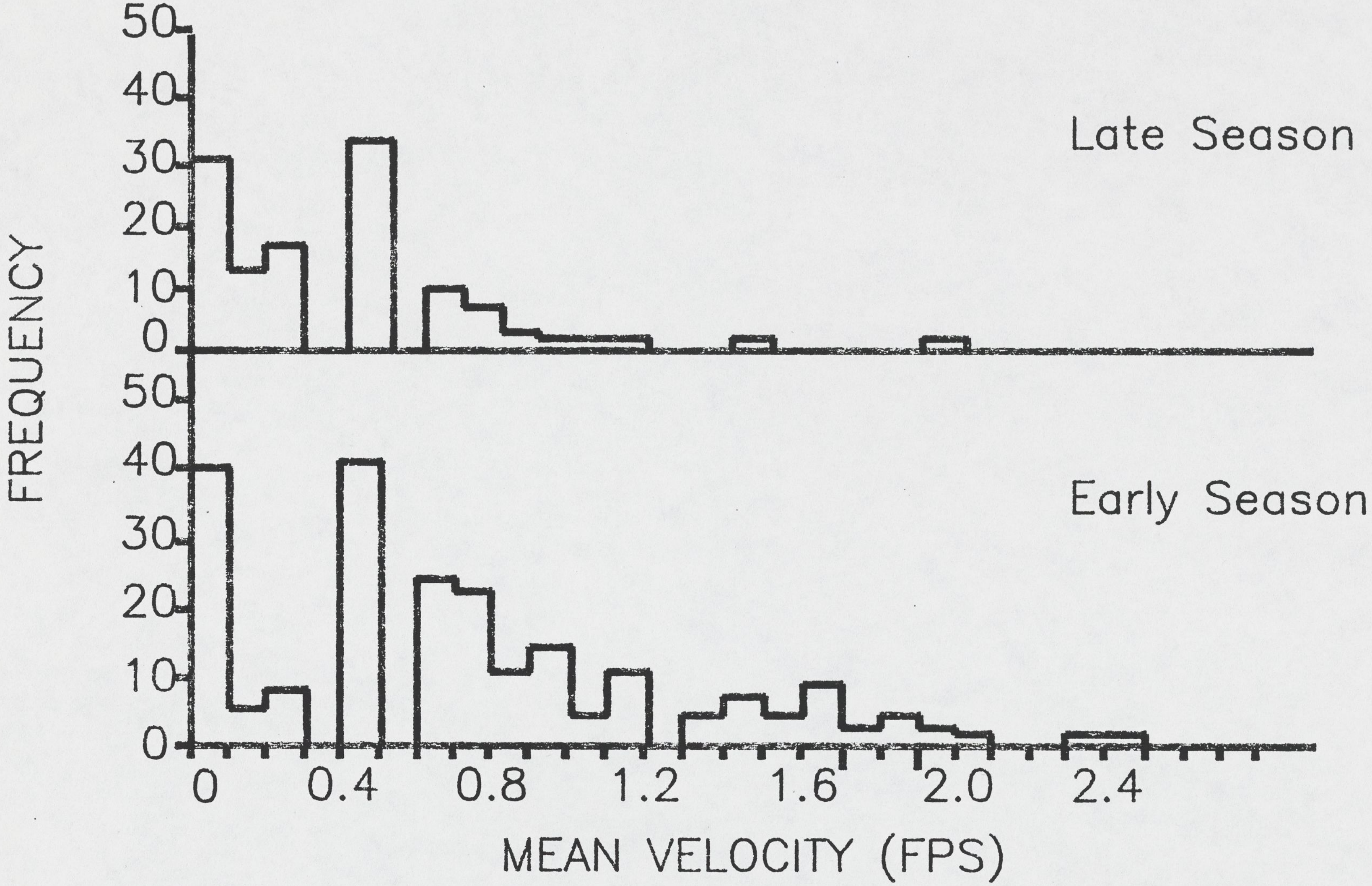

Figure 5. Available velocities (feet per second) in the allopatric section of Hidden Valley Creek on 8 August (early season) and 26 September (late season), 1985.

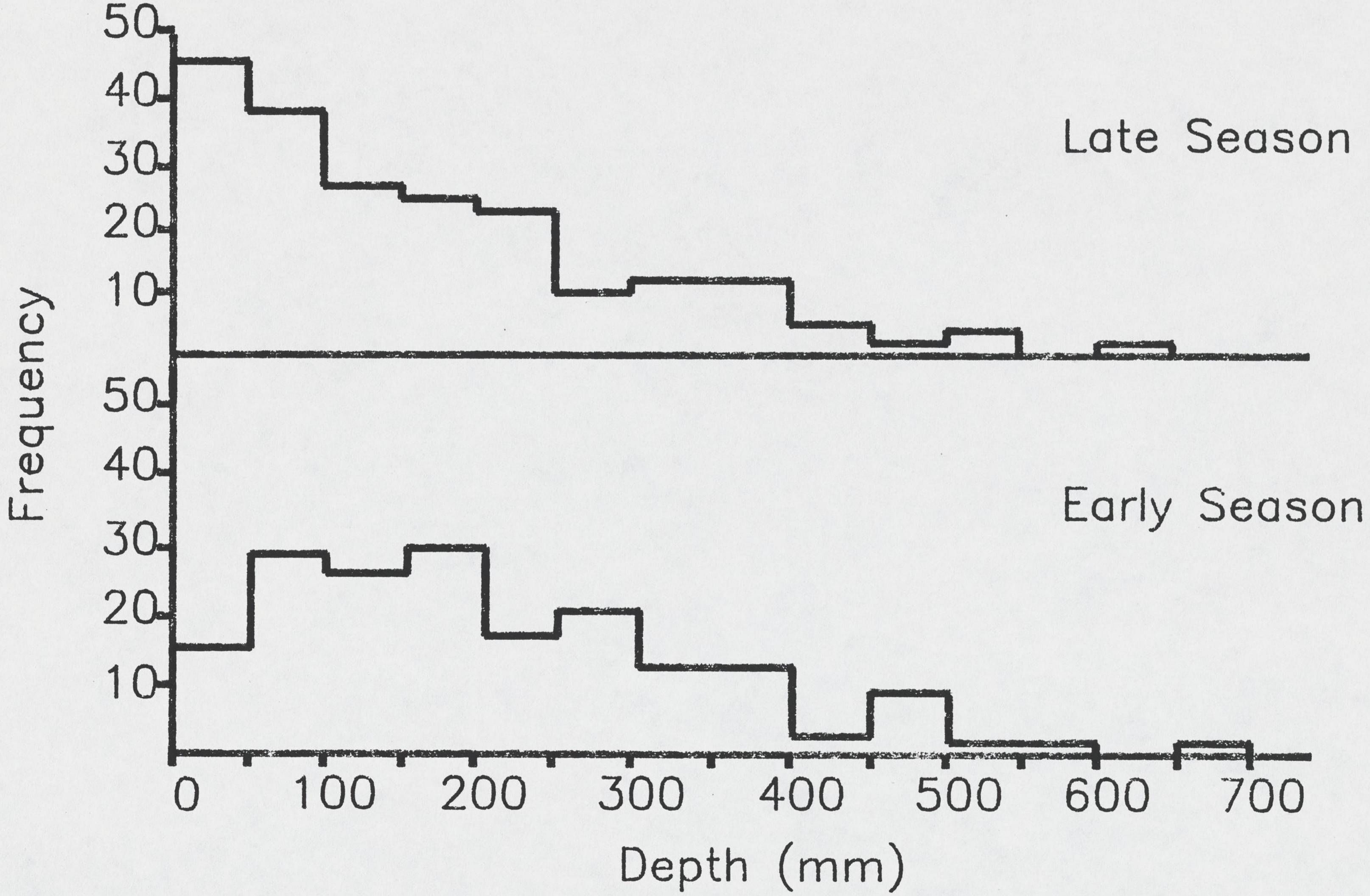

Figure 6. Available depths (mm) in the sympatric section of Hidden Valley Creek on 8 August (early season) and 26 September (late season), 1985.

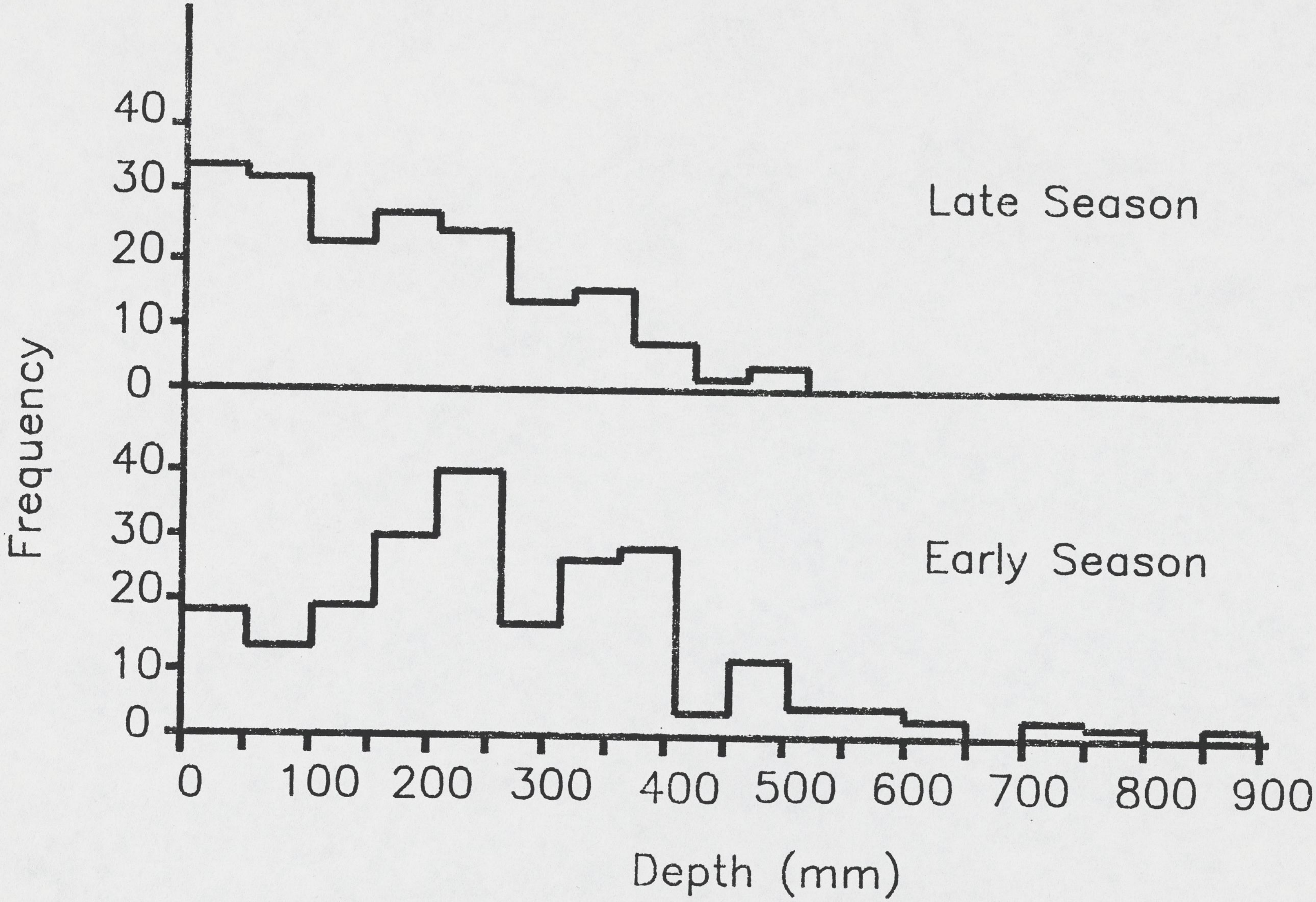

Figure 7. Available depths (mm) in the allopatric section of Hidden Valley Creek on 8 August (early season) and 26 September (late season), 1985.

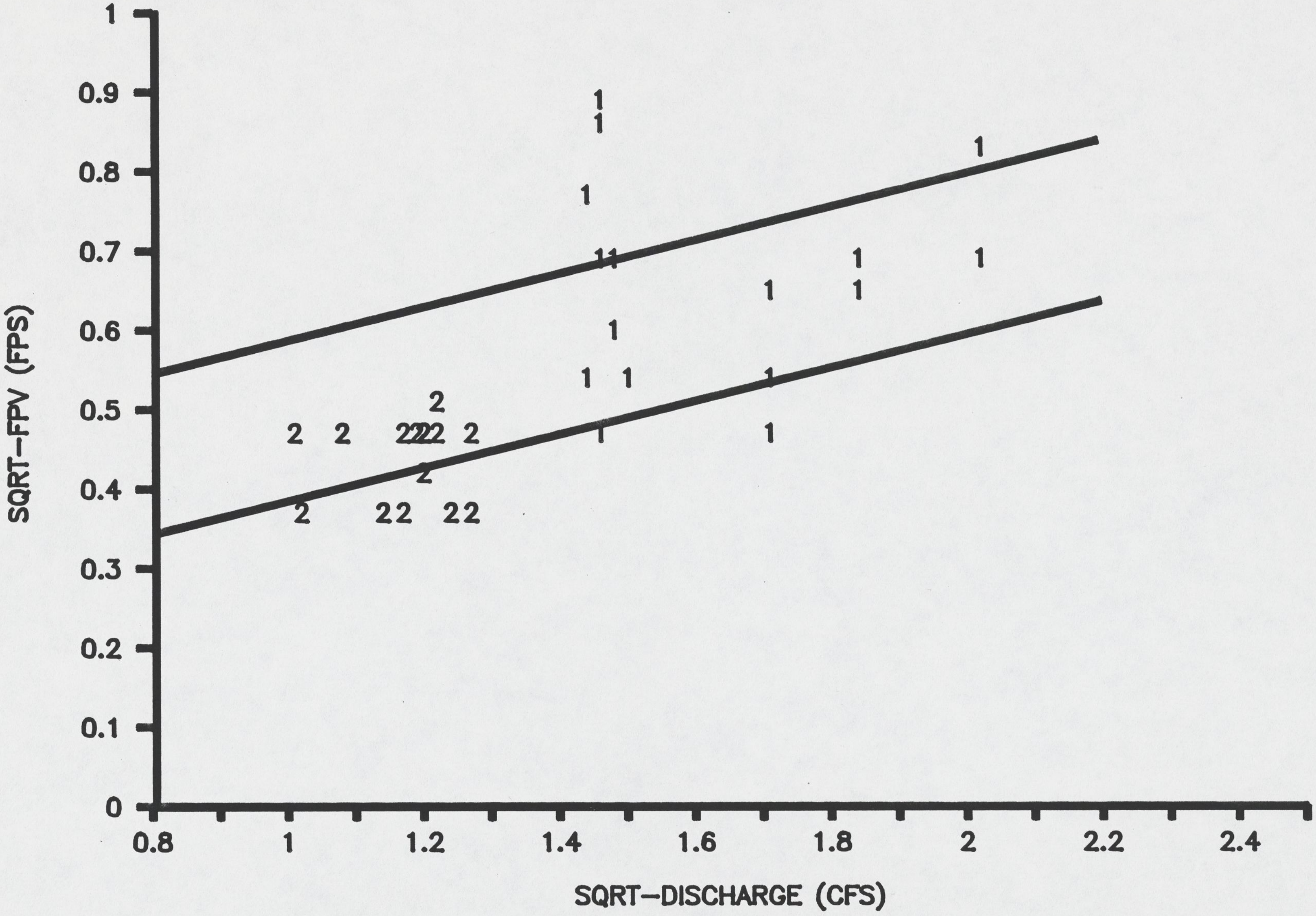

Figure 8. Analysis of covariance for focal point velocity as a function of discharge for juvenile (50-150 mm) cutthroat trout before (1) and after (2) brook trout were removed from the sympatric section of Hidden Valley Creek, 1985. Data were transformed using the square-root function to correct for heterogenous variance.

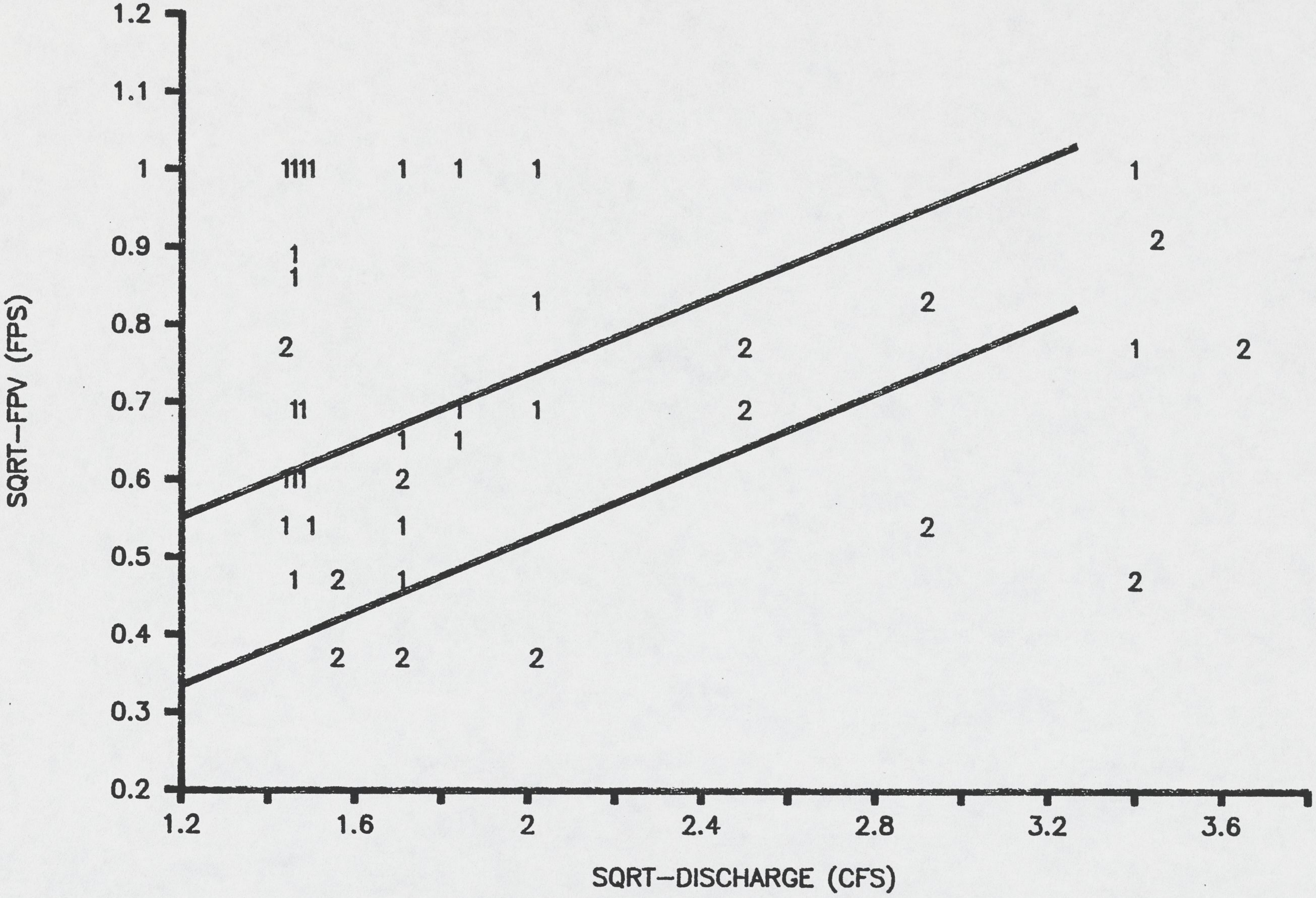

Figure 9. Analysis of covariance for focal point velocity as a function of discharge for juvenile (50-150 mm) cutthroat (1) and brook trout (2) in the sympatric section of Hidden Valley Creek, 1985. Data were transformed using the square-root function to correct for heterogenous variance.

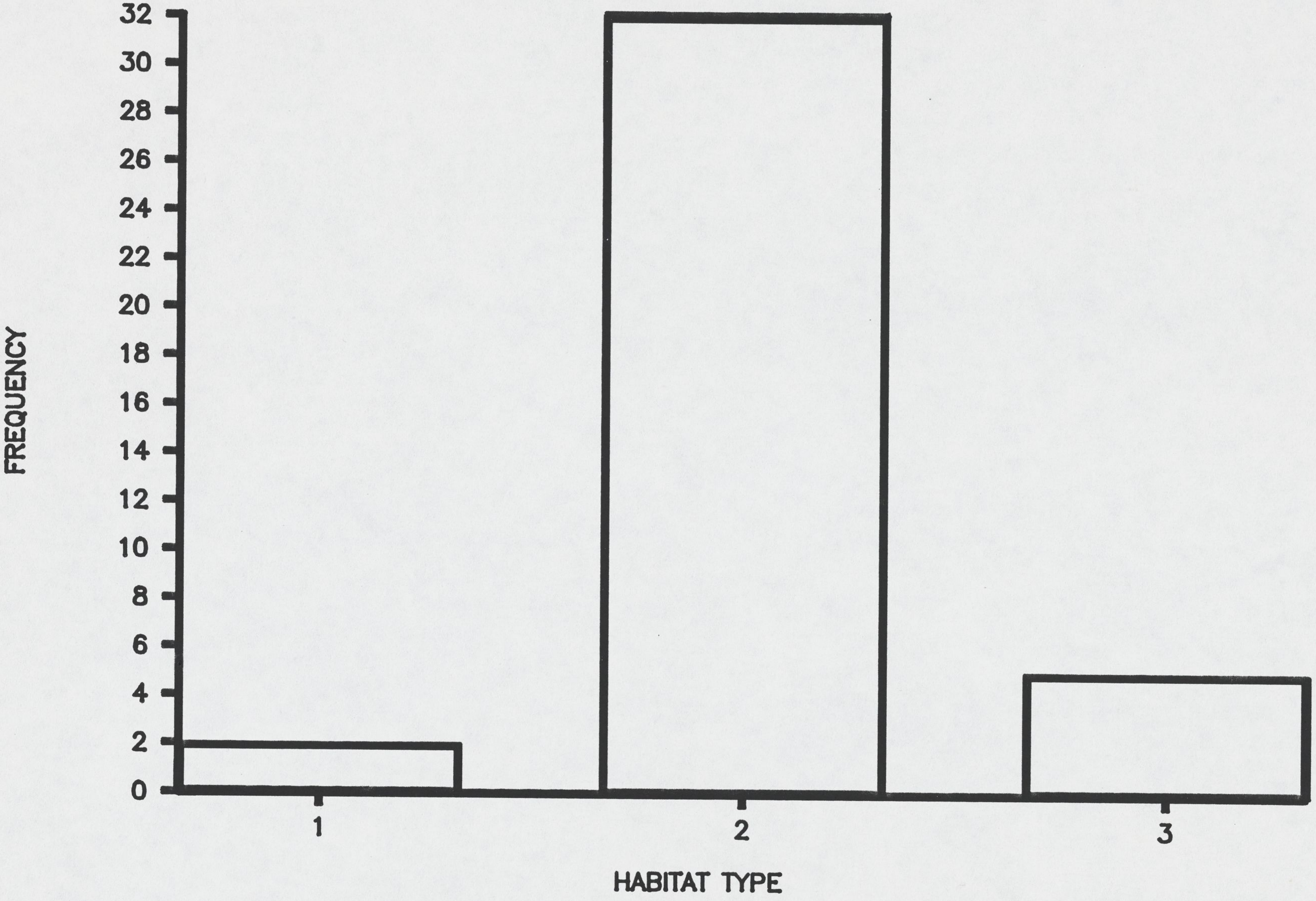

Figure 10a. Use of positions in different habitat types (1 - riffle, 2 - run, 3 - pool) by juvenile (50-150 mm) cutthroat trout in the sympatric section of Hidden Valley Creek, 1985.

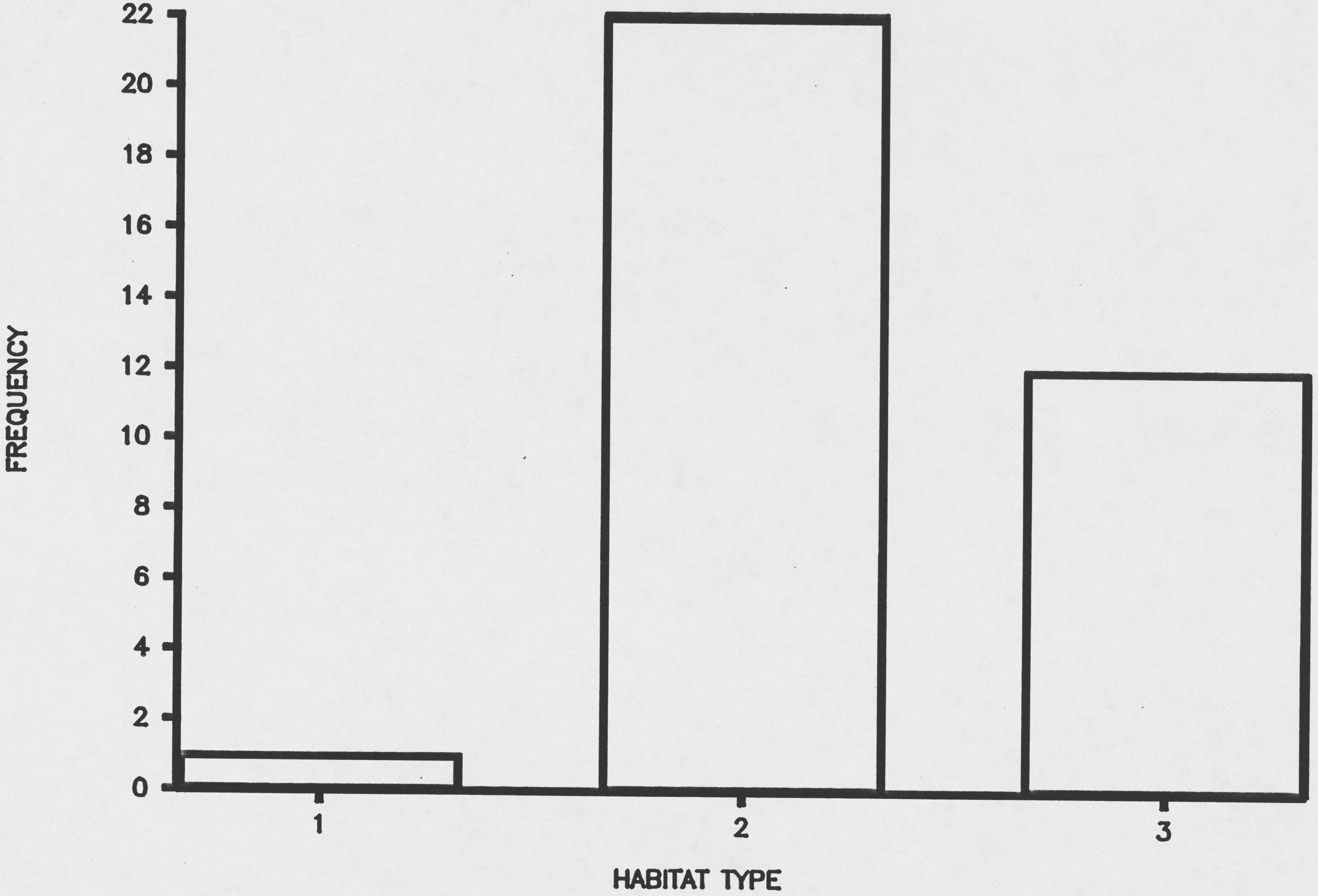

Figure 10b. Use of positions in different habitat types (1 - riffle, 2 - run, 3 - pool) by juvenile (50-150 mm) cutthroat trout in the allopatric section of Hidden Valley Creek, 1985.

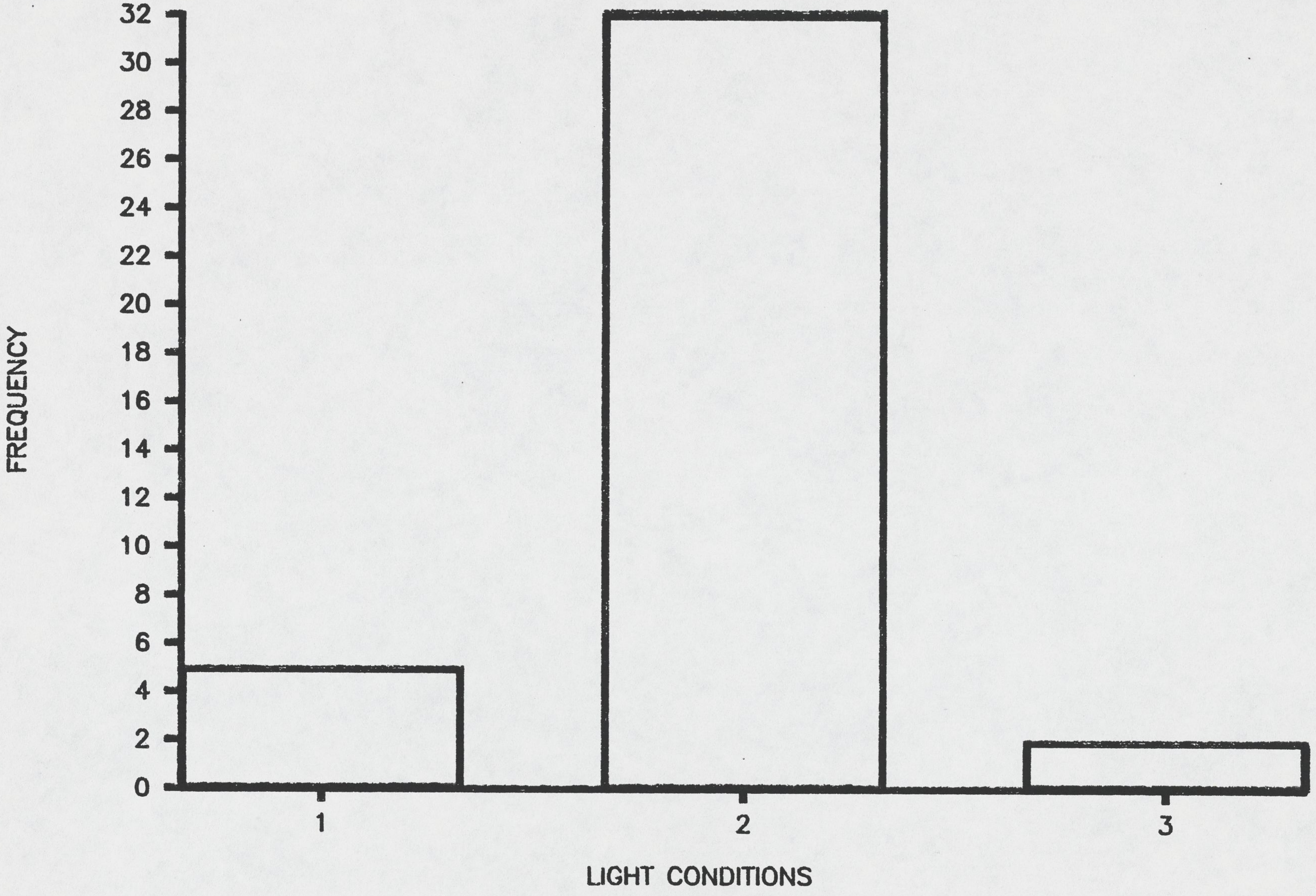

Figure 11a. Use of positions with different lighting (1 - bright sun, 2 - partial shade, 3--deep shade) by juvenile (50-150 mm) cutthroat trout in the sympatric section of Hidden Valley Creek, 1985.

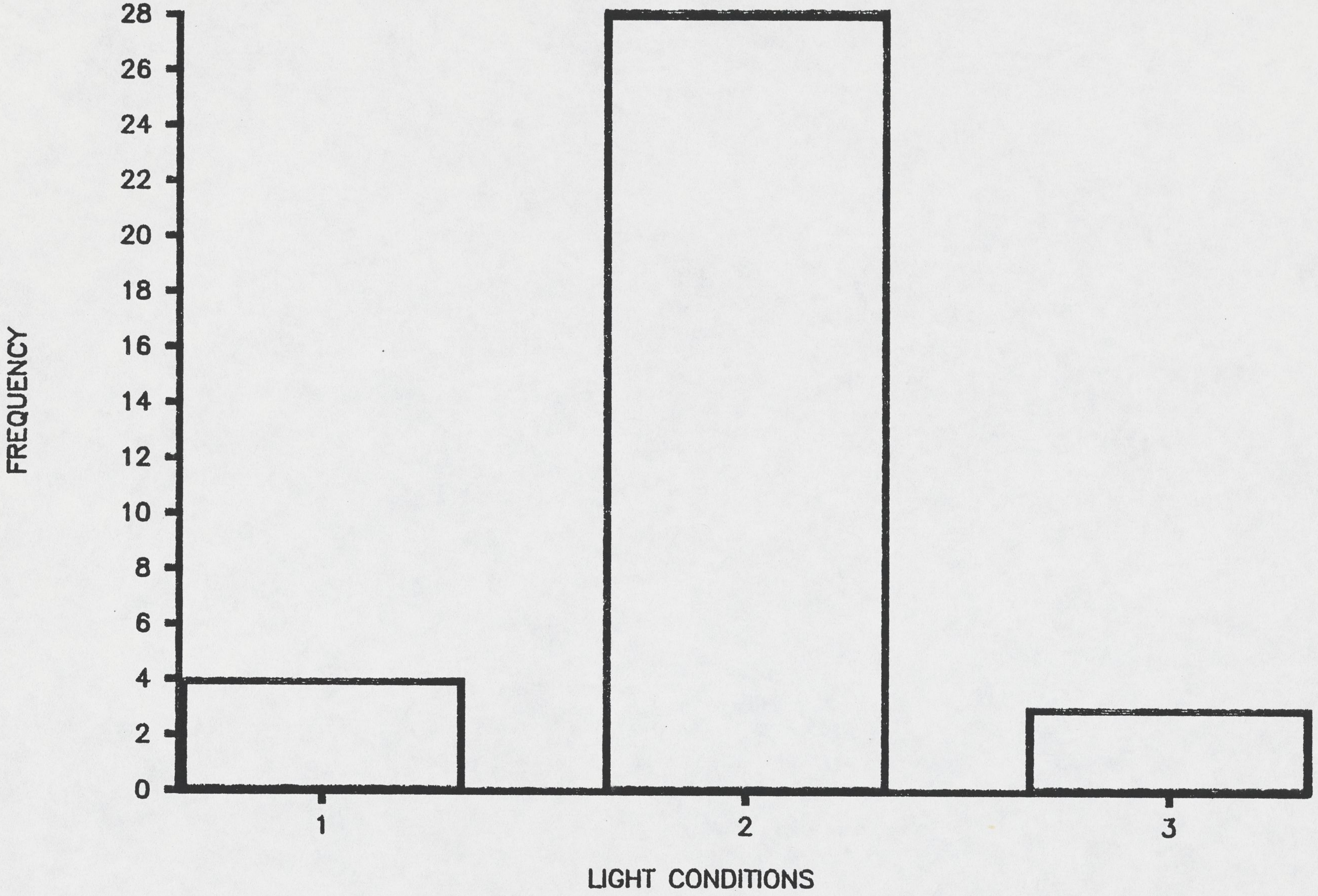

Figure 11b. Use of positions with different lighting (1 - bright sun, 2 - partial shade, 3 - deep shade) by juvenile (50-150 mm) cutthroat trout in the allopatric section of Hidden Valley Creek, 1985.

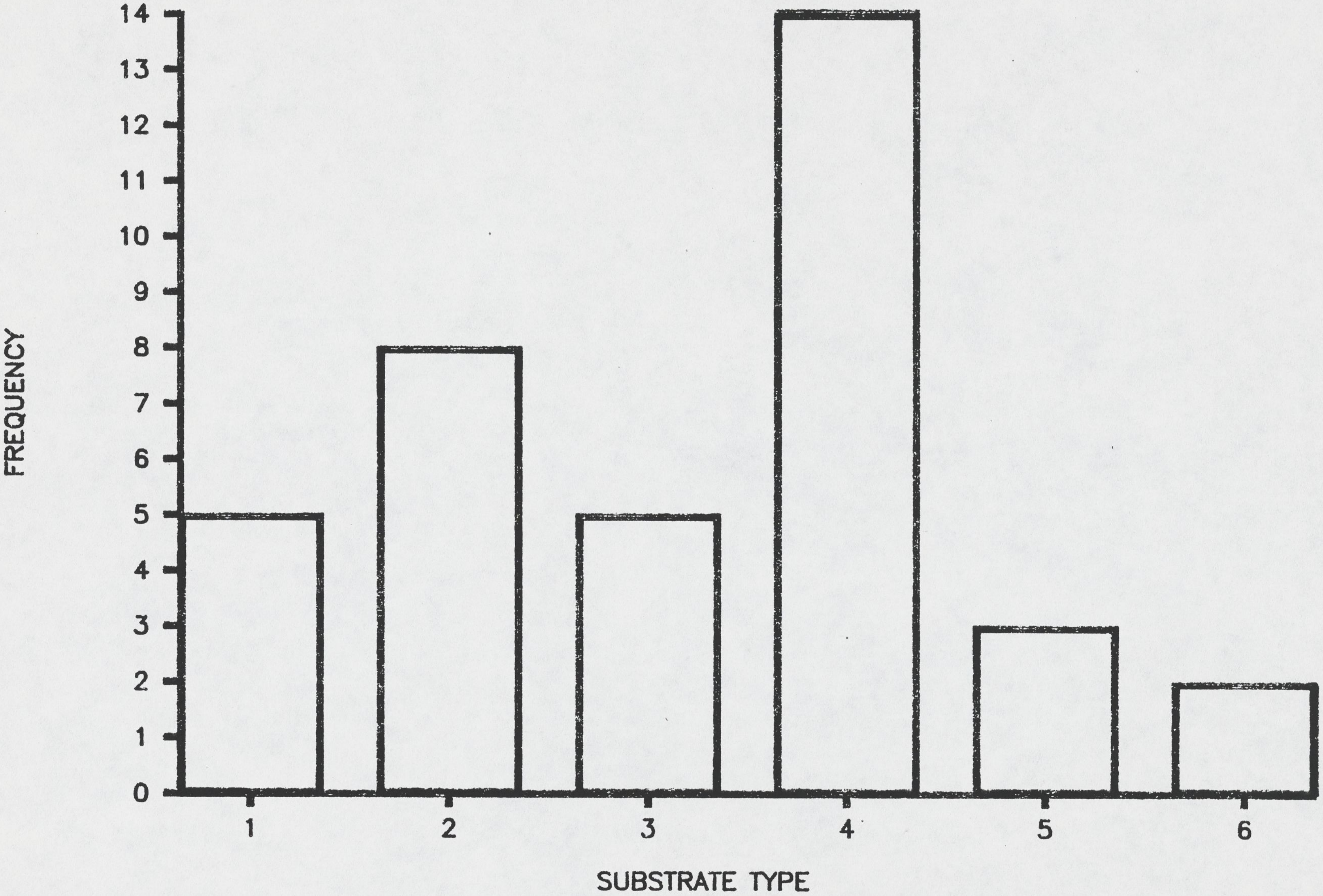

Figure 12a. Use of positions with different substrate types (1 - silt, 2 - silt and sand, 3 - sand, 4 - sand and gravel, 5 - gravel, 6 - gravel and rubble) by juvenile (50-150 mm) cutthroat trout in Hidden Valley Creek (sympatry and allopatry) in early summer, 1985.

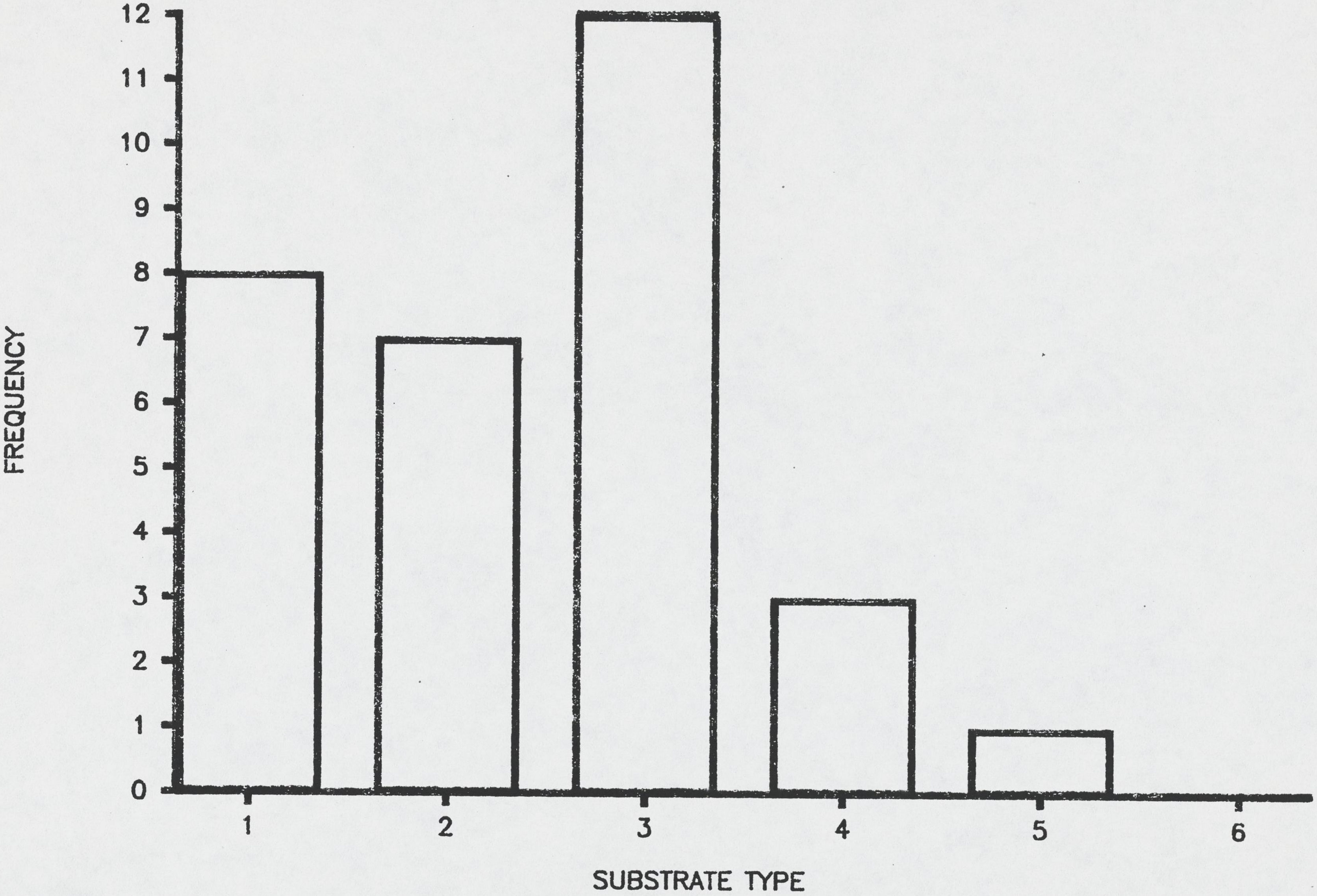

Figure 12b. Use of positions with different substrate types (1 - silt, 2 - silt and sand, 3 - sand, 4 - sand and gravel, 5 - gravel, 6 - gravel and rubble) by juvenile (50-150 mm) cutthroat trout in Hidden Valley Creek (sympatry and allopatry) in late summer, 1985.

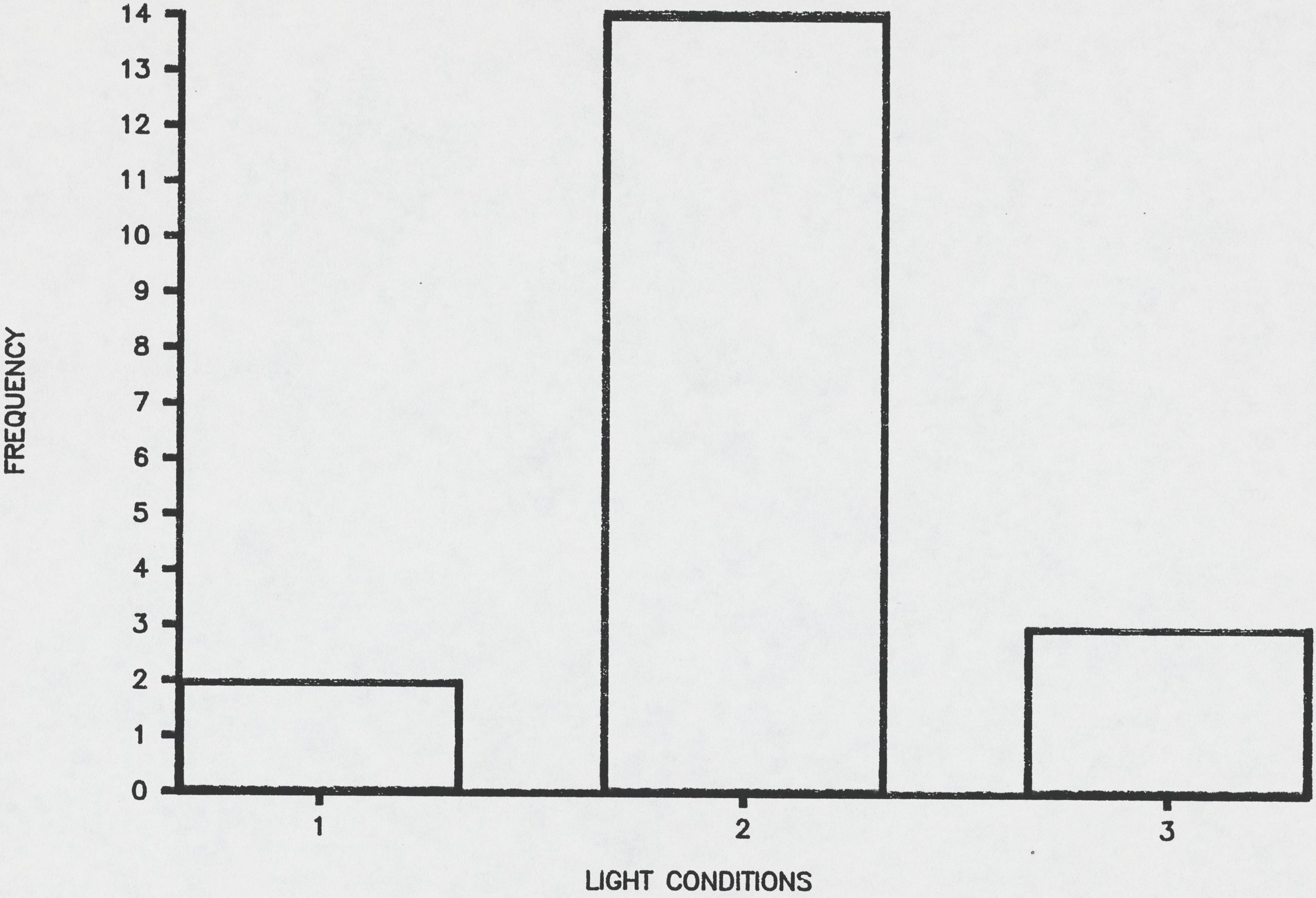

Figure 13a. Use of positions in different lighting (1 - bright sun, 2 - partial shade, 3 - deep shade) by adult (150 mm) cutthroat trout in the sympatric section of Hidden Valley Creek, 1985.

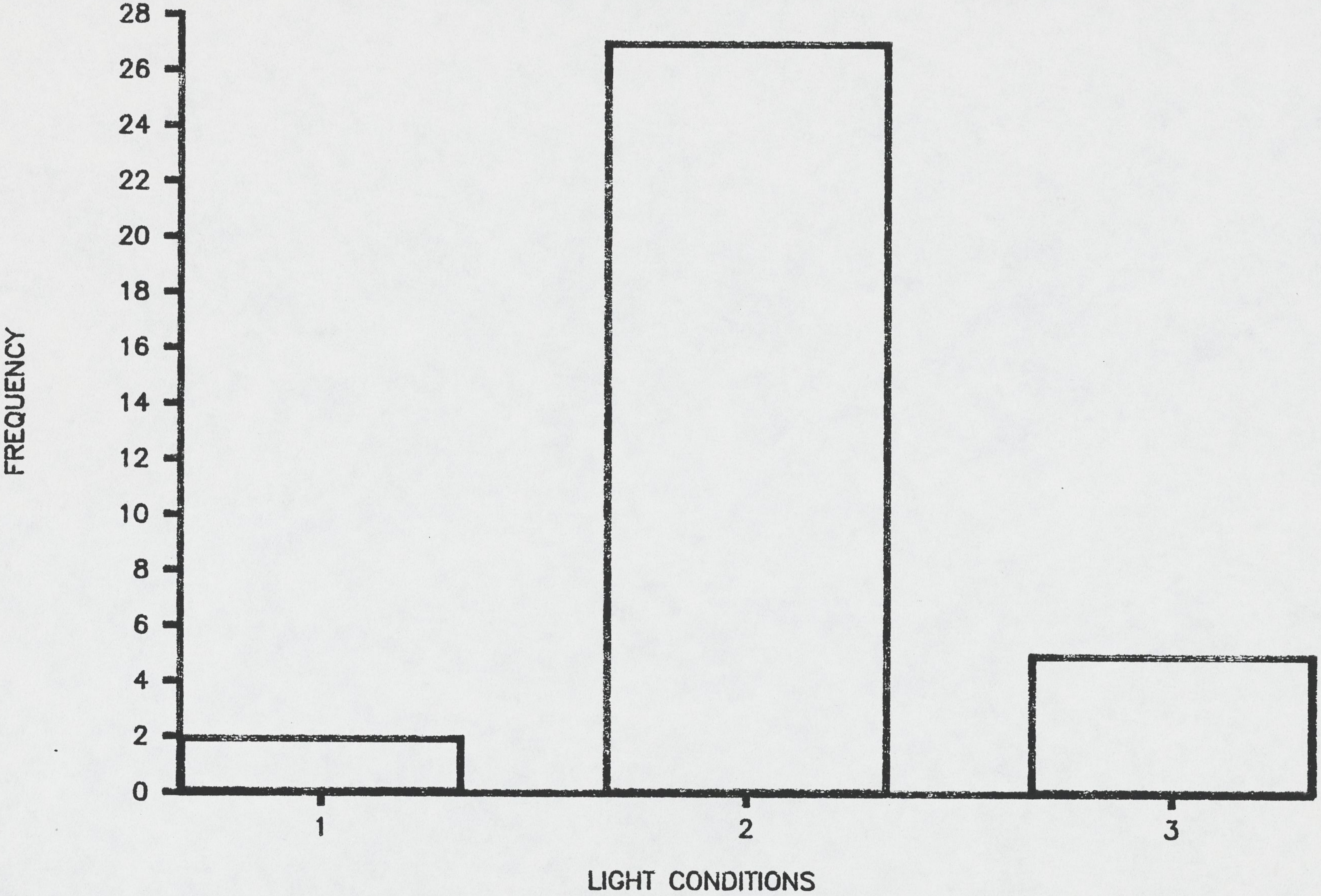

Figure 13b. Use of positions in different lighting (1 - bright sun, 2 - partial shade, 3 - deep shade) by adult (150 mm) cutthroat trout in the allopatric section of Hidden Valley Creek, 1985.

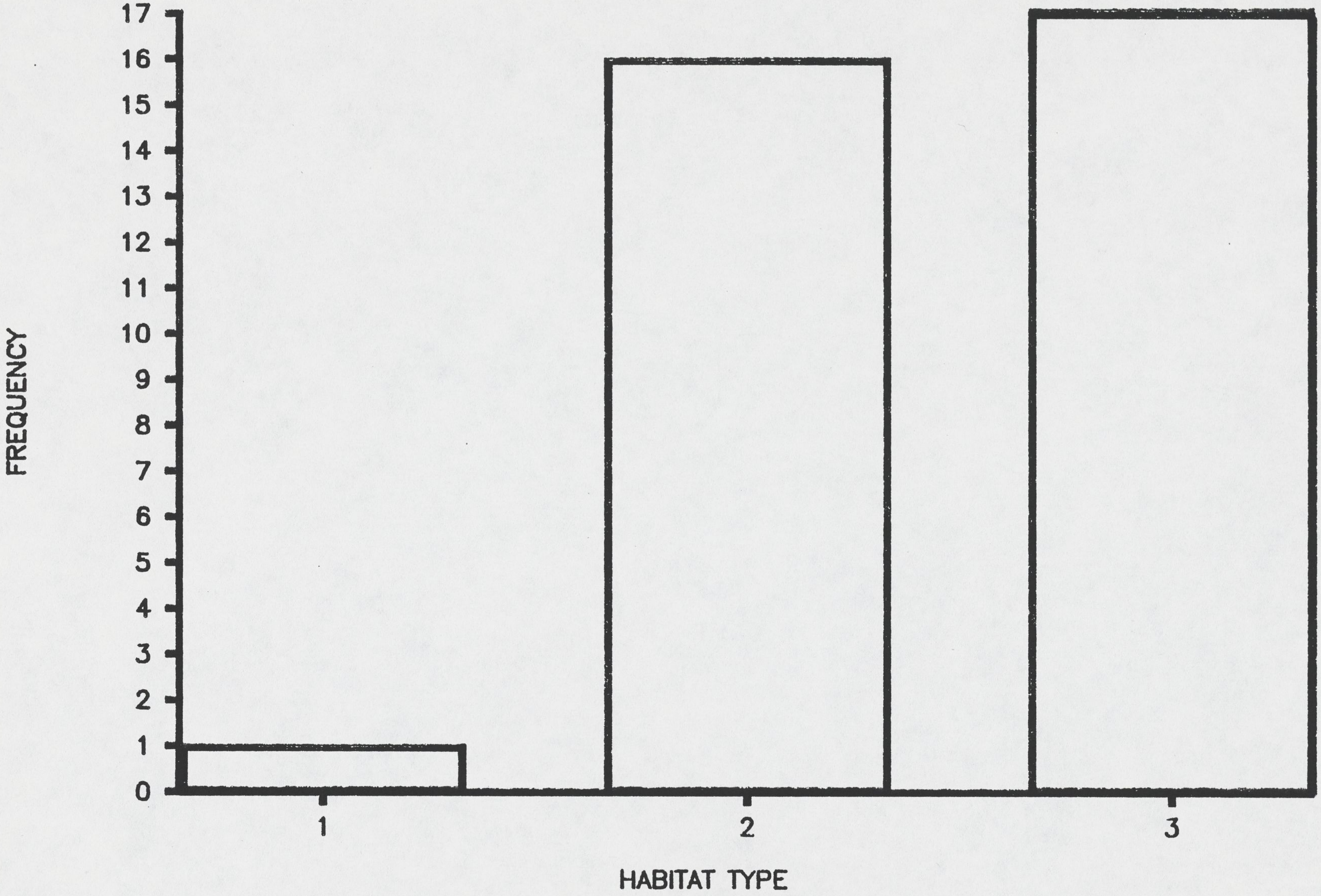

Figure 14a. Use of positions in different habitat types (1 - riffle, 2 - run, 3 - pool) by adult (150 mm) cutthroat trout in the sympatric section of Hidden Valley Creek, 1985.

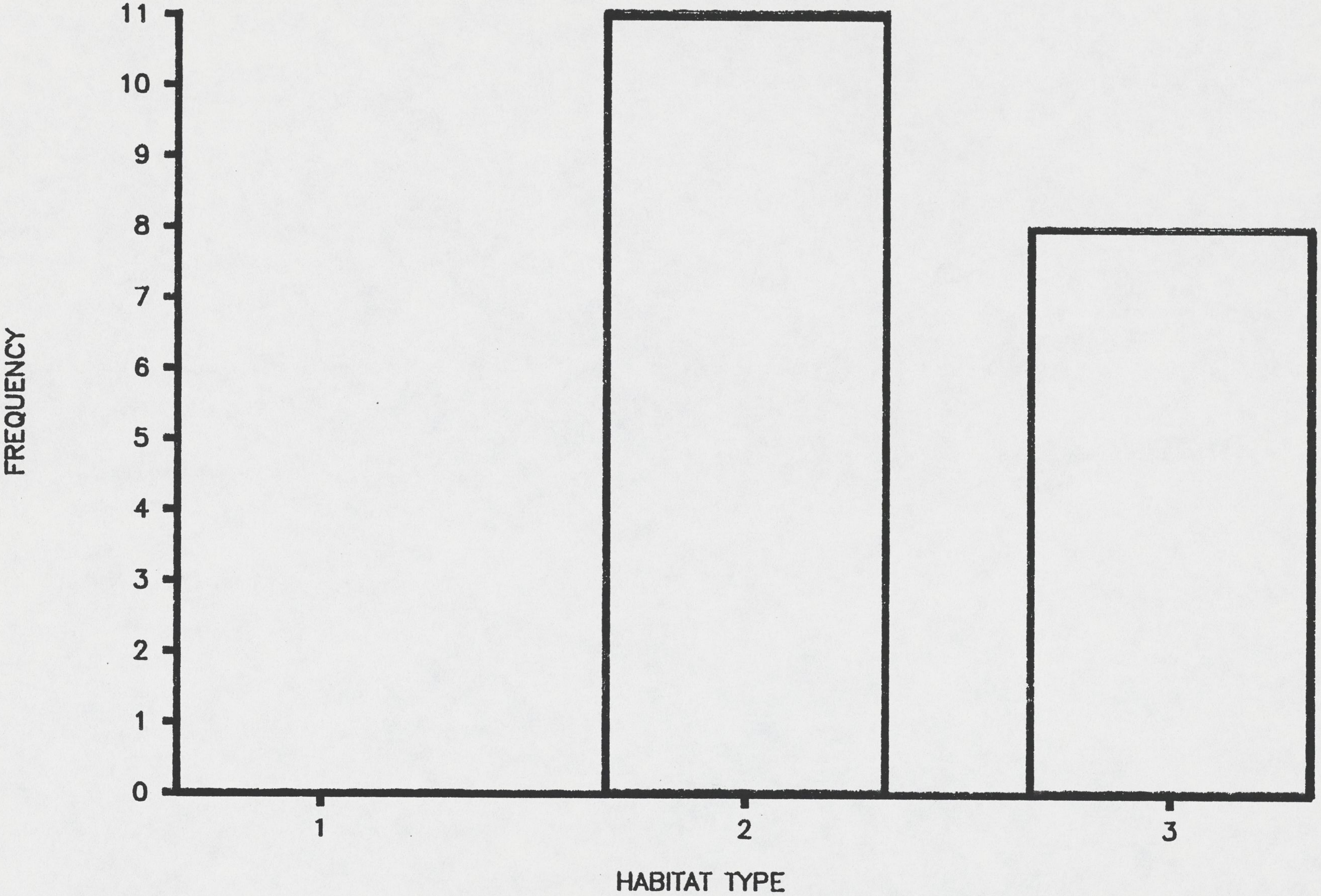

Figure 14b. Use of positions in different habitat types (1 - riffle, 2 - run, 3 - pool) by adult (150 mm) cutthroat trout in the allopatric section of Hidden Valley Creek, 1985

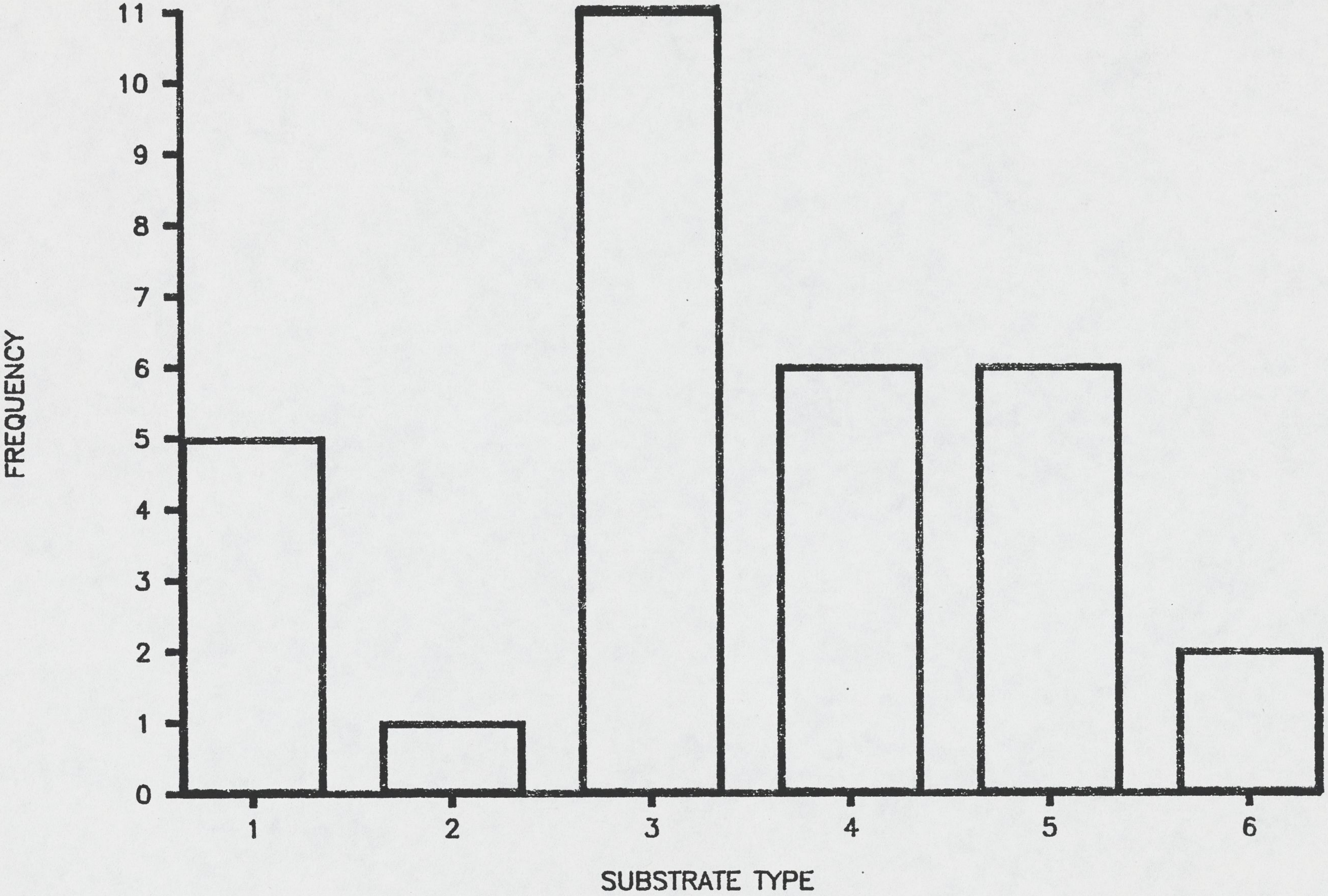

Figure 15a. Use of positions with different substrate type (1 - silt, 2 - silt and sand, 3 - sand, 4 - sand and gravel, 5 - gravel, 6 - gravel and rubble) by adult cutthroat (>150 mm) trout in Hidden Valley Creek (sympatry and allopatry) in early summer, 1985.

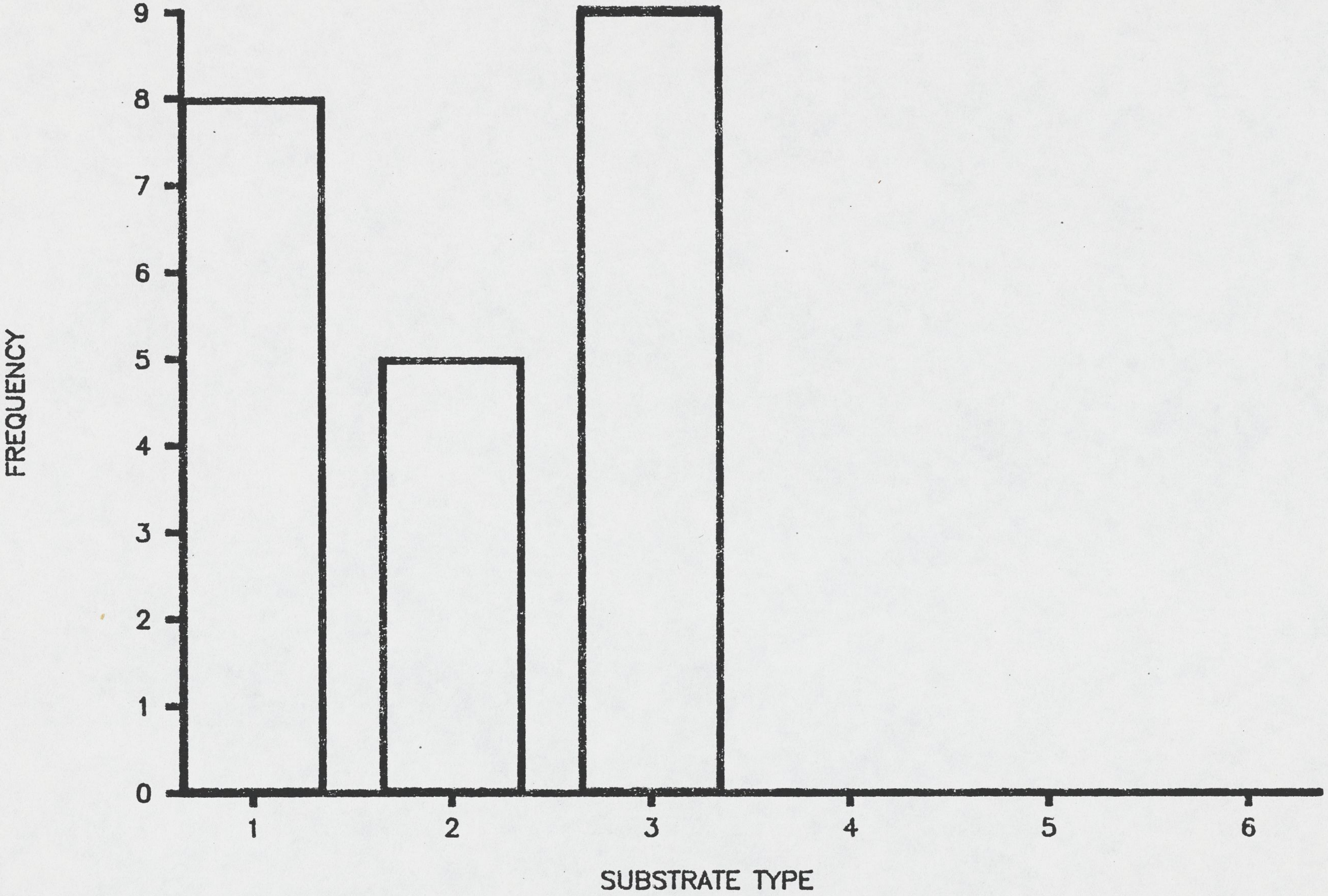

Figure 15b. Use of positions with different substrate type (1 - silt, 2 - silt and sand, 3 - sand, 4 - sand and gravel, 5 - gravel, 6-- gravel and rubble) by adult (>150 mm) cutthroat trout in Hidden Valley Creek (sympatry and allopatry) in late summer, 1985.

late

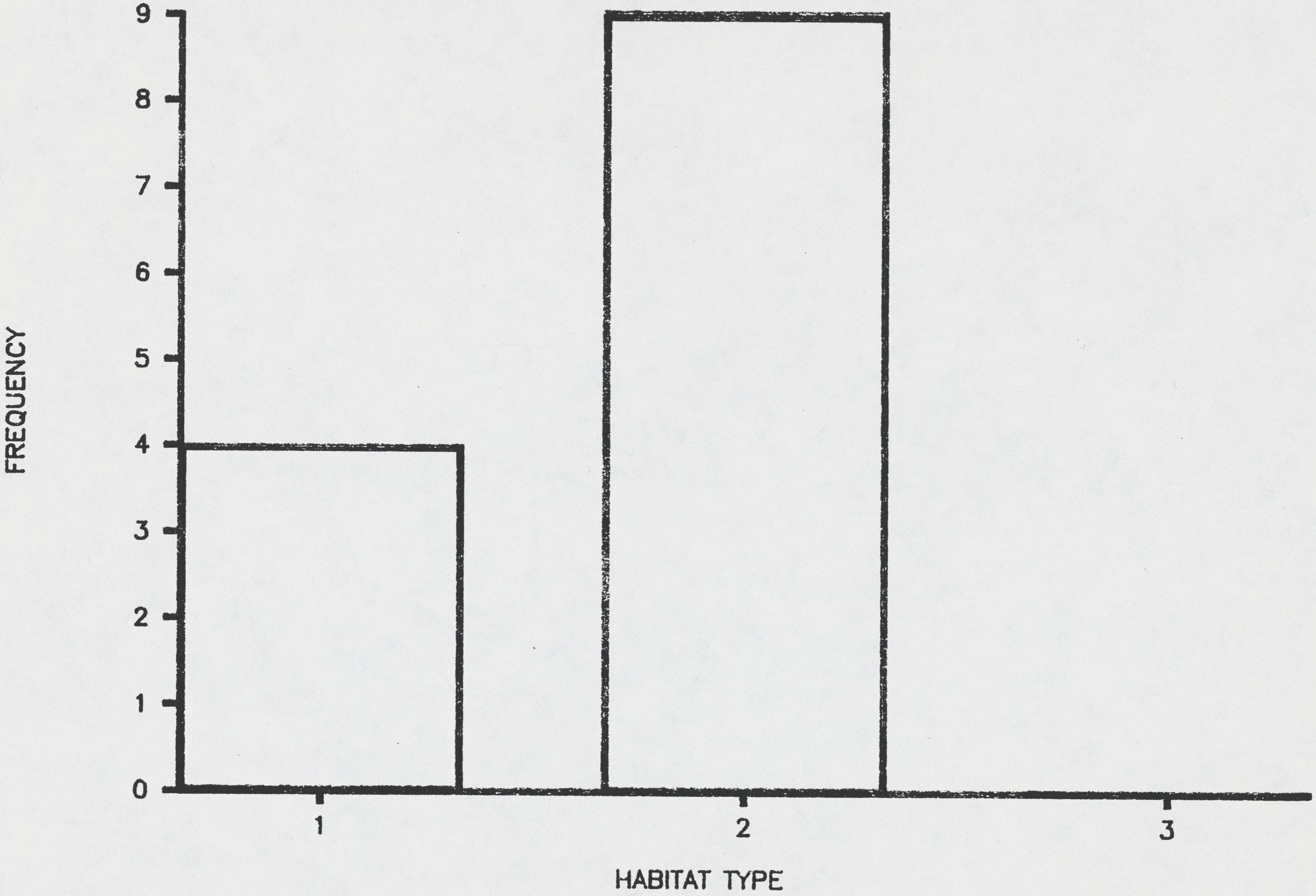

Figure 16. Use of positions by young-of-the-year cutthroat trout in different habitat types (1 - riffle 2 - run, 3 - pool) in Hidden Valley Creek (sympatric and allopatric sections) in late summer, 1985.

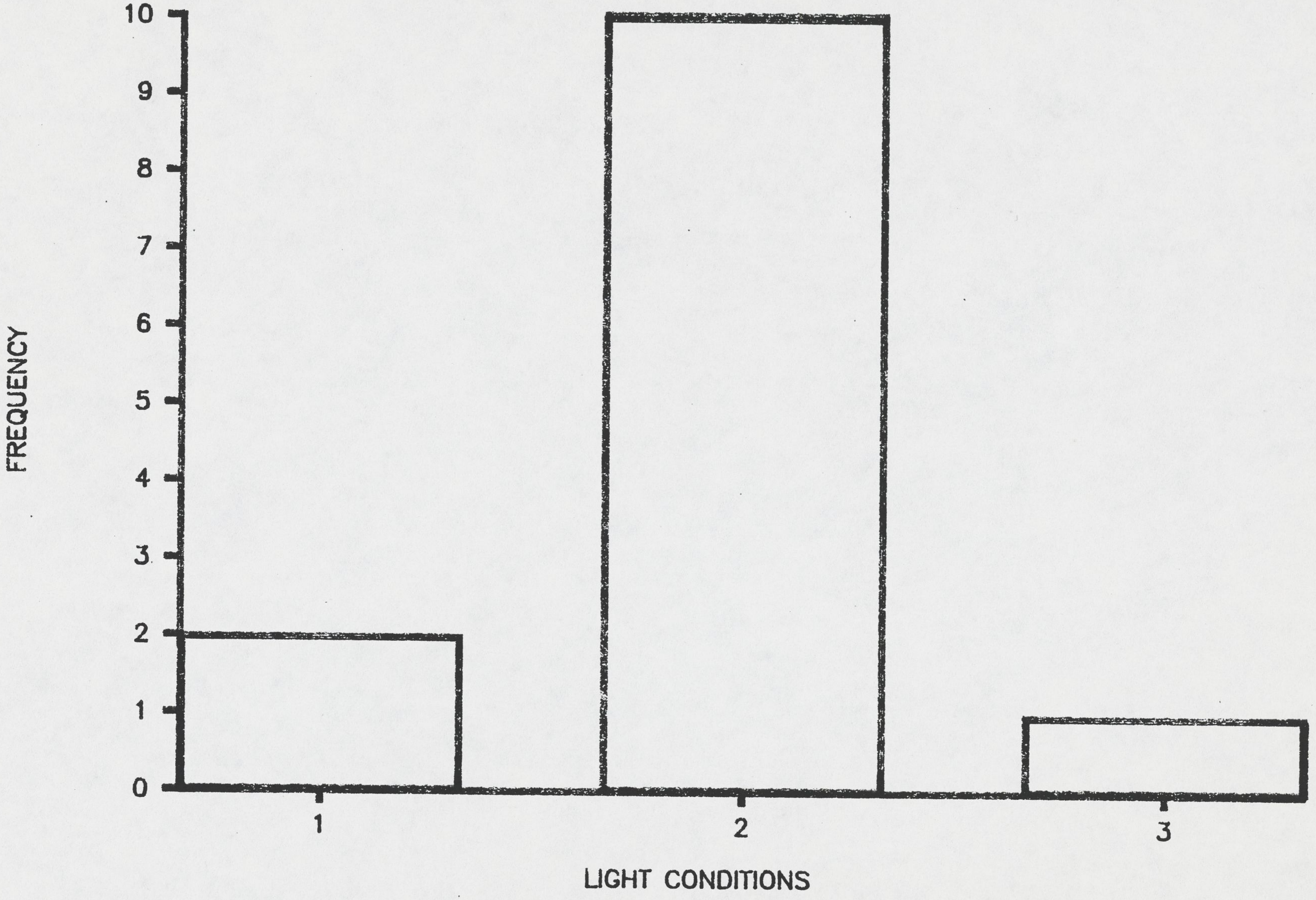

Figure 17. Use of positions by young-of-the-year cutthroat trout in different lighting (1 - bright sun, 2 - partial shade, 3 - deep shade) in Hidden Valley Creek (sympatric and allopatric sections) in late summer, 1985.

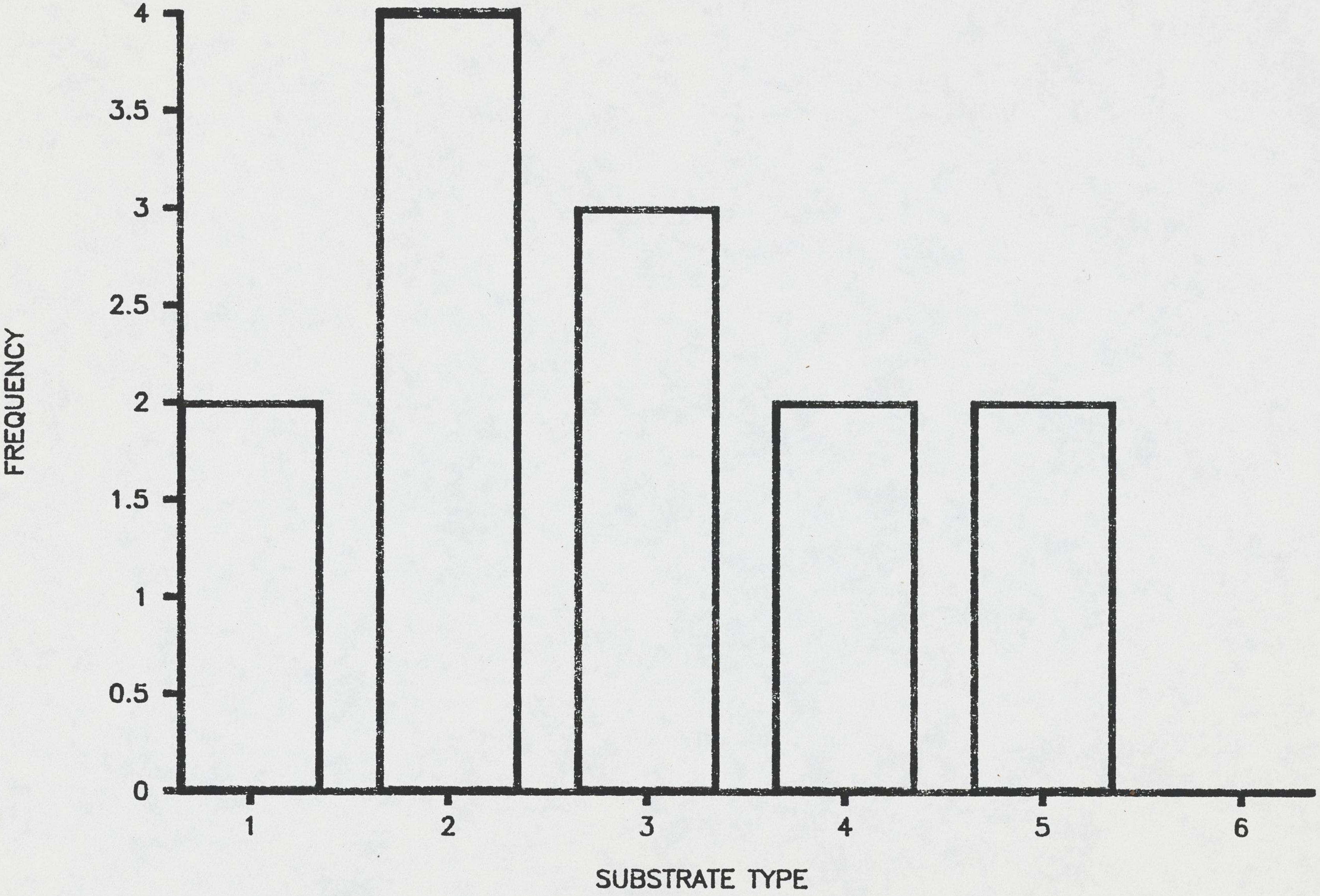

Figure 18. Use of positions by young-of-the-year cutthroat trout with different substrate types (1 - silt, 2 - silt and sand, 3 - sand, 4 - sand and gravel, 5 - gravel, 6 - gravel and rubble) in Hidden Valley Creek (sympatric and allopatric sections) in late summer, 1985.

THE NATIVE CUTTHROAT TROUTS OF WYOMING
III: Evaluation of 1977 Collections from The Green River and Bear River Drainages

Robert J. Behnke
May, 1978

In parts 1 and 2 of this series of reports written in 1975, I pointed out that six subspecies of cutthroat trout are native to Wyoming: *Salmo clarki lewisi* of the upper Missouri River (mainly restricted to the drainages above Great Falls, Montana) is native only to a small area of the northwest tip of the state forming the headwaters of the Madison and Gallatin rivers in Yellowstone National Park; *S. c. utah*, the Bonneville basin cutthroat trout, is native to the Bear River drainage in a narrow strip along the Idaho border in southwest Wyoming; the large-spotted cutthroat trout native to the upper Snake River system and to the entire Yellowstone drainage downstream to the Tongue River, I recognize as *S. c. bouvieri*; *S. c. pleuriticus* is the native trout of the Green River system; *S. c. stomias* once inhabited a small area of the South Platte River drainage south of the Laramie-Cheyenne region along the Colorado border; the only subspecies still holding its own in its native range, is the fine-spotted Snake River cutthroat trout, an undescribed subspecies.

No trout are native to the eastern half of the state in areas drained by the Powder, Belle Fourche, Cheyenne and North Platte systems. To assist in understanding the original distribution of the subspecies native to Wyoming, I have included a distribution map (figure 1).

It has been long obvious that most of the native trouts of Wyoming have suffered rapid declines and have long disappeared from most of their original range. The major factors causing the decline have been replacement by brook

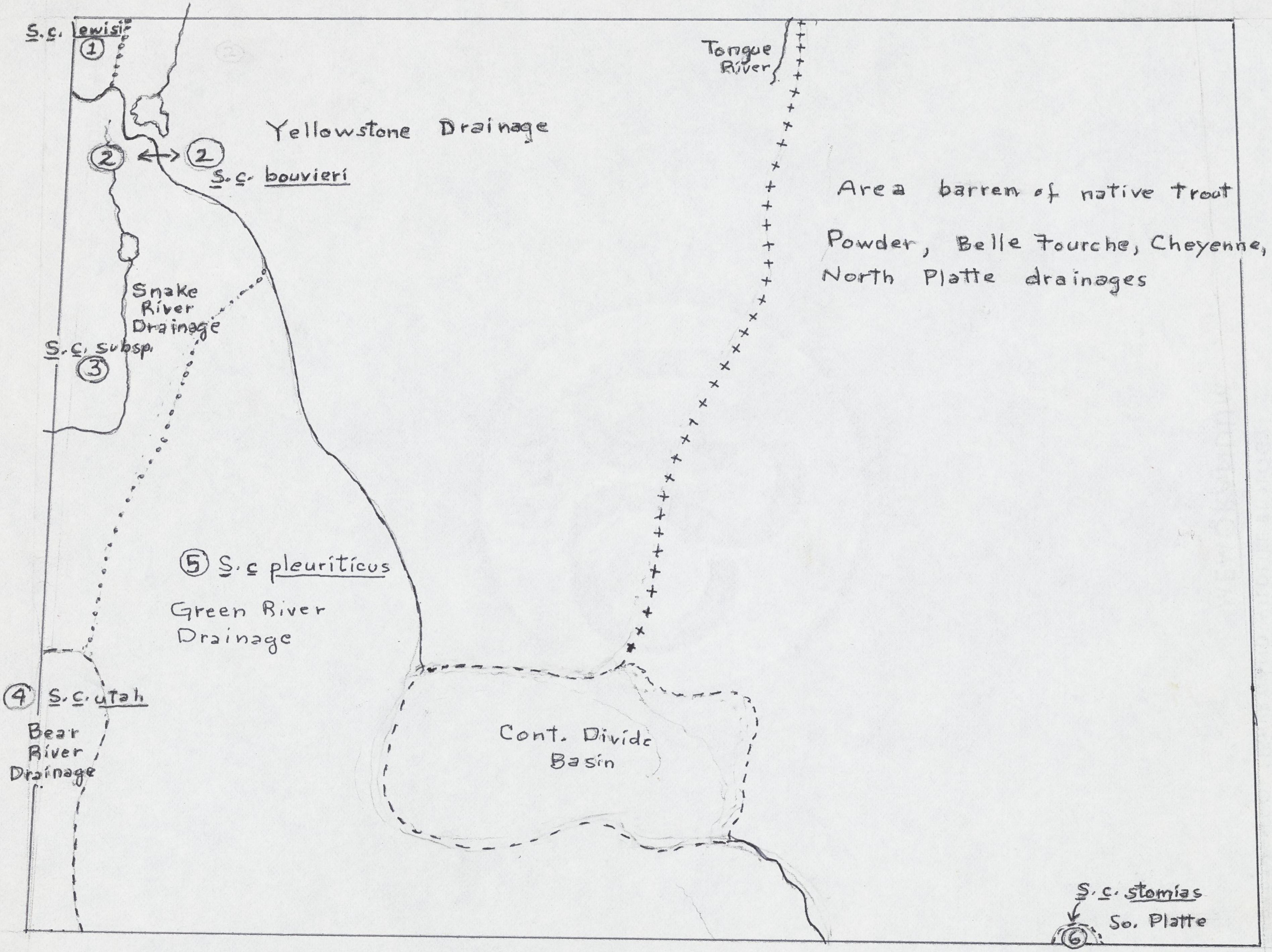

Figure 1. Distribution of native trout in Wyoming

DEPARTMENT OF FISHERY AND WILDLIFE BIOLOGY

MEMORANDUM

trout and hybridization with rainbow trout and mixing of various subspecies of cutthroat trout in fish propagation and stocking practices. Man-induced habitat alterations have a synergistic effect, greatly speeding up the process of replacement and hybridization.

The greenback cutthroat trout, *S. c. stomias*, is now extinct in Wyoming. The Madison and Gallatin rivers and their tributaries are now dominated by brown, rainbow and brook trouts. In Wyoming, I know of only one pure population of *S. c. lewisi*--in Cougar Creek, an isolated tributary of the Madison. The large-spotted cutthroat trout is still the only trout found above the falls in the Yellowstone drainage and is still a dominant trout in much of the Snake River drainage above Jackson Lake, but below the falls of the Yellowstone, I have identified only one pure population--in South Paint Rock Creek, north of Tensleep in the Bighorn drainage. The fine-spotted cutthroat trout native to the Upper Snake River, evolved in a big river environment, evolutionarily programmed by interactions with a rich native fish fauna and ecologically is very different from the other native subspecies in respect to successful competition with other fishes in diverse environments.

The Bonneville cutthroat trout and the Green River cutthroat trout are both virtually gone as pure populations from their former large ranges in several states. What is left in Wyoming can be considered as "strongholds" of these two rare subspecies.

It is apparent that the basis for any program designed for native trout management is the recognition and identification of the remnant populations of the native subspecies. This is not a simple matter as I have discussed in previous reports. The six subspecies can be correctly identified on differences in their coloration, spotting pattern and mean differences in characters such as scale counts and pyloric caecal counts. Slight hybrid influence, however, is difficult to detect and there are no absolute criteria by which a population can be "certified pure." Because of this, and because of the rareness of populations resembling rare native subspecies such as *S. c. pleuriticus* and *S. c. utah*, I previously recommended a "sliding scale" of purity recognition. I judge as "pure" those collections which approximate the "idealized" version of the spotting pattern and show no sign of hybridization in their meristic characters. For those populations showing no outward indication of hybridization but have other, more subtle indicators of hybrid influence such as reduction or loss of basibranchial teeth, I have called "virtually pure" or "good phenotypic representatives," depending on the magnitude of the hybrid influence. Binns (1977) has taken my data and further refined the purity ranking system from A (pure) to F (hybrid swarm), to provide a more quantitative basis for Wyoming's native trout program.

In this present report, I have examined 8 collections of 85 specimens (4 collections from Upper Green River and 4 from Little Snake drainage) for an evaluation of their purity as *S. c. pleuriticus*, and 51 specimens of 2 collections from the Bear River drainage for evaluation of *S. c. utah* purity.

Of particular interest is the verification of the phenomenon of spotting distinction, noted in previous reports, between the *S. c. pleuriticus* native to the Upper Green River basin and those native to the Little Snake headwaters. This unique spotting pattern, illustrated in Binns (1977), facilitates the evaluation of Little Snake drainage *pleuriticus*. As with previous studies, all of the Little Snake collections rank as virtually pure (perhaps an A-grade). Although the geographical area is small and the habitat miniscule, the occurrence of a cluster of many populations in the headwaters of the North Fork of the Little Snake (and in Deep Creek and Douglas Creek headwater tributaries to Big Sandstone Creek, just to the north), makes for the greatest known concentration of pure or virtually pure *S. c. pleuriticus* in the entire Colorado-Green River basin. The Middle Fork and South Fork of the Little Snake are in Colorado and have not yet been investigated for the occurrence of native trout.

Also of significance is the occurrence of a pure or virtually pure population of *S. c. utah* (equal in purity to the Raymond Creek population) in upper Giraffe Creek, and a probable pure population of this subspecies in Lake Alice. As discussed below, the Lake Alice trout have recognizeable differences from typical *S. c. utah*, but these differences are opposite from the direction expected from hybrid influence with rainbow trout or Yellowstone or Henry's Lake cutthroat trout and are more likely the result of long isolation and independent evolution of a population exposed to a very different environment (lacustrine vs. fluvial). Lake Alice represents the only lacustrine population of *S. c. utah* in the Bonneville basin and tremendously enlarges the area (in surface acres of water) where this subspecies is known to exist.

The collection of specimens from Lead Creek of the Upper Green River drainage represents the most consistent uniformity of the idealized *pleuriticus* spotting pattern of any sample I have yet examined. The specimens are virtual mirror images of each other.

The meristic data taken from the 1977 specimens are listed in Table 1.

Comments on Methods of Classification and Identification

In recent years it has become apparent to me that among professional biologists and administrators a naive faith has developed in the belief that the confusion surrounding trout taxonomy can be swept away by modern technology with the use of biochemical, cytogenetic and computer techniques. Much time, effort and funds can be wasted in projects which ultimately only add to the confusion. It is a matter calling for the judicious exercise of common sense.

For a better understanding of some of the limitations different techniques may have in relation to providing answers to specific evolutionary questions, it is helpful to understand the basic premises on which a classification system is based and the interpretation of the manifestations of evolutionary divergences within the phylogeny in question.

The classification of species and subspecies of a genus and of genera in a family is based on points in a network of divergent evolutionary lines. The goal of a system of natural classification is to detect unique genetic events that occur in one evolutionary line, but not another since they separated from a common ancestor. The longer the time period involved from the present to any particular branching point in a phylogeny, the more time for unique events to accumulate and the better the chance to detect these events by taxonomic methods. No matter what method is used (traditional morphological, biochemical or cytogenetic), they all depend on the detection of these unique events for their efficacy.

The branching point in time separating the ancestor of the family Salmonidae from other families in the order Salmoniformes, is perhaps of 2000 fold greater magnitude than the time since the separations leading to the present subspecies of *Salmo clarki*. With this in mind, it should be understandable why it is not likely to detect the relatively few unique genetic changes accumulated during the last 10,000 to 50,000 years in cutthroat trout subspecies by examining the products of a few gene loci (out of 100,000's) in electrophoretic studies. This is particularly true in light of the types of gene loci amenable to delineation by modern techniques--they govern protein and enzyme systems not likely to be strongly selected for under different selective pressures. That is, the small differences in gene frequencies found are more of a random nature and not of the adaptive, directional genetic change guided by natural selection (the type of change useful for taxonomy).

A recent manuscript written by Mr. Eric Loudenslager of the University of Wyoming and based on his M.S. thesis, reveals no differences in 23 gene loci between the fine-spotted Snake River cutthroat trout and the large-spotted cutthroat trout of the upper Snake River and Yellowstone Lake. Yet a small child could readily identify and accurately separate these two subspecies on the genetic based differences governing their distinctly different spotting patterns.

Mr. Loudenslager's study does verify the close genetic relationships between these subspecies and supports my previous contention that the fine-spotted Snake River cutthroat trout was derived from the large-spotted ancestor in the Upper Snake River, probably while isolated in a glacial ice-dam lake, and not from a *S. c. lewisi* ancestor transferred from the headwaters of the Salmon River drainage across the present Snake River lava plains.

Another point of great interest discovered by Mr. Loudenslager is that there is virtually no heterozygosity detectable in the 23 loci he examined in the fine-spotted Snake River cutthroat. It is a common belief that heterozygosity (more than one form of a gene *[allele]* at any one gene locus) is of predictive significance to detect inbreeding or for considering the probable success of an introduction into new waters in relation to the adaptability a particular genotype has to survive and flourish in new environments. To date, the trout with the highest heterozygosity index is the California golden trout, *Salmo aquabonita*. Considering only Wyoming experiences of use of fine-spotted Snake River cutthroat trout and of golden trout in fisheries management, it is obvious that heterozygosity indices must be viewed with some skepticism as a practical fisheries management test.

It has also become popular in recent years to attempt to quantify relationships between subspecies of a species and species of a genus based on degree of gene loci similarity and expressed as genetic similarity or genetic identity scores. The limitations of this sort of quantification for taxonomy is apparent from the genetic similarity values showing a greater divergence between subspecies of the house mouse than between man and the chimpanzee--a tremendous amount of information incorporated by unique genetic events in the phylogenies in question was not uncovered by electrophoretic techniques.

The evolution of the races of man and of subspecies of cutthroat trout have much in common in relation to the geological time span involved, the magnitude of genetic differentiation and how we detect the manifestation of this differentiation. It would not be difficult to recognize and quantify the morphological distinctions between a pure Australian aborigine and a person typifying the Nordic race. There are, however, no consistent differences in gene loci yet examined which can do this--the races of man have recently evolved and have little genetic differences, but these differences are expressed in easily recognized characteristics.

The use of computers offers the opportunity to handle enormous amounts of data and to quantify similarities and differences by various programs in a manner not otherwise possible. My students and I have been experimenting with different computer programs to handle trout taxonomic data. Figure 2 is based on a two dimensional discriminant function analysis comparing 14 morphological and meristic characters of all the specimens of *S. c. pleuriticus* and *S. c. utah* examined for this report.

Two points must be kept in mind when considering "computer taxonomy": the computer does not create new characters and it cannot differentiate between genetic and non-genetic differences--that is three groups of trout from the same parents, raised under different conditions influencing growth rate would have morphological differences (body proportions) and be grouped as three distinct clusters in a program utilizing these morphological criteria.

Although, essentially, the computer print-outs do not tell me something I do not already know from my examination of the specimens and my familiarity with trout taxonomy, it can be a useful tool of communication to make my taxonomic conclusions more understandable to others and to attempt to place some quantifiable, but arbitrary, limits on subspecies and purity rankings of a subspecies.

In general then, the unique evolutionary changes that have accumulated in the period of relatively recent geological time to produce the six subspecies of cutthroat trout native to Wyoming, are most readily detected in genetic differences manifested in spotting pattern and coloration associated with trends in meristic characters such as number of scales, gillrakers, pyloric caeca and basibranchial teeth. My most astute advice to agencies considering taxonomic work associated with management programs for native trout is to ask the right questions and then critically consider the probability that the proposed technique will answer these questions.

Evaluation of *S. c. pleuriticus* Purity

All 38 specimens from the four streams in the Little Snake drainage are identical to previous samples of specimens from this drainage which I have judged to be virtually pure *S. c. pleuriticus*. The Little Snake native trout are, however, recognizably different from *S. c. pleuriticus* native to the upper Green River in their larger spots on the caudal peduncle area. In comparison between fish of the same size from Lead Creek (upper Green) with any of the Little Snake collections, the largest spots on the caudal peduncle of Little Snake drainage cutthroat trout are almost twice the size of those spots on upper Green River specimens. All other characters are essentially similar and I would not propose new subspecies recognition for the Little Snake (Yampa River system) cutthroat trout. It is likely that when *S. c. pleuriticus* inhabited all tributaries of the Green River, a transition in spotting size existed in tributaries upstream from the mouth of the Yampa.

The collections consist of 7 specimens from Rabbit Creek, 11 specimens from the West Branch of the North Fork, 10 specimens from Rose Creek (N. Fork Little Snake drainage) and 10 specimens from Deep Creek (tributary to Big Sandstone Creek). They are consistently uniform in appearance and show no outward sign of hybridization in any specimen. The only substantial evidence that these populations have been slightly influenced by hybridization with rainbow trout is the absence of basibranchial teeth in 10% to 27% of the three collections from the North Fork drainage (9 of 10 specimens from Deep Creek have basibranchial teeth). I have previously identified obvious rainbow-cutthroat hybrids in the lower North Fork of the Little Snake and in Big Sandstone Creek (grade D or F of Binn's ranking) and brook trout also occur in these drainages. There are no physical barriers preventing the spread of hybrid influence nor the replacement of the cutthroat trout by brook trout as has occurred throughout most of the range of the subspecies. Undoubtedly, the preservation of essentially pure *S. c. pleuriticus* genotypes in this area is due to their superiority in their particular environments resulting in negative selection against hybrid influence. This situation, however, is fragile and precarious. Any changes in the environment (flows, temperature, turbidity, etc.) may destroy the present balance and lead to the rapid spread of hybrid influence and/or replacement by brook trout.

The collection from Lead Creek of the upper Green drainage may represent a pure population of *S. c. pleuriticus*, but number of pyloric caeca are slightly higher than expected and 2 of 17 specimens lack basibranchial teeth. The 15 specimens with basibranchial teeth have from 5-18 (10.7) teeth--the greatest number of any sample examined for this report. In a sample of 12 specimens collected from Lead Creek in 1970, all specimens have basibranchial teeth (5-17 [11.1]). When combined, 27 of 29 specimens from Lead Creek (93%) have basibranchial teeth, meeting my criteria of at least 90% occurrence of these teeth in pure populations of *pleuriticus*.

As mentioned above, the spotting pattern of the Lead Creek cutthroat trout is the most consistently uniform of any sample yet examined. Hybrid influence is typically first noticeable in loss and reduction of basibranchial teeth (rainbow trout influence) and in greater variability in size, shape and position of the spots (rainbow trout and non-native cutthroat trout influence). Based on its ideal *pleuriticus* phenotype, the Lead Creek cutthroat trout might be considered for propagation and introductions into other waters.

The sample of 8 specimens from Rock Creek, a direct tributary to the Green River, below Kendall (not the Rock Creek of previous reports which is tributary to La Barge Creek) and the sample of 8 specimens from Dead Cow Creek, tributary to South Horse Creek are ranked as B in Allan Binn's rating system. All of the 8 specimens from Dead Cow Creek have basibranchial teeth, and the meristic characters are typical of *S. c. pleuriticus* but the spotting pattern, in size, shape and distribution indicates influence of probably both Yellowstone cutthroat and the fine-spotted Snake River cutthroat in this population. Two of the 8 specimens from Rock Creek lack basibranchial teeth and the spotting pattern (rough, jagged edges vs. smooth, rounded spots of *pleuriticus*) indicates rainbow trout and fine-spotted Snake River cutthroat trout influence. The meristic characters, however, indicate that both of these populations, although not pure, are overwhelmingly of the *S. c. pleuriticus* genotype. This assumption can be checked by observing the living coloration of these trout. Only *S. c. pleuriticus* genotypes can develop the brilliant red, orange and yellow hues. Rainbow trout, Snake River and Yellowstone cutthroat trout lack the genetic basis to express these bright colors on the body.

The collection from August Lake, comprising 14 specimens, is certainly predominantly *S. c. pleuriticus*, but may have been influenced by introductions of Yellowstone Lake cutthroat. All specimens have basibranchial teeth, scale counts and caecal counts are typical of *pleuriticus*, the spots are smooth and rounded in outline, but the distribution of spots is highly variable. Some specimens have only a few spots on the caudal peduncle while others have them all over the sides of the body.

I cannot find August Lake on my Forest Service map but from the geographic locality I note it is in the Boulder Creek watershed, east of Pinedale, and most of that quadrant is drained by North Boulder Creek. I point this out because of my previous identification of the cutthroat trout in lakes of North Boulder Creek drainage (Lakes Victor, Lower Pipestone Lake) as introduced Yellowstone Lake cutthroat trout. In 1969 it was believed that only pure *S. c. pleuriticus* occurred in the North Boulder Creek drainage above a lower barrier falls. After my determination of specimens as Yellowstone Lake cutthroat, Galen Boyer found Forest Service records of stocking these formerly barren waters with Yellowstone cutthroat trout in 1937.

August Lake cutthroat are definitely not Yellowstone Lake cutthroat trout (but they may have been slightly influenced by introductions from Yellowstone Lake). Is the population in August Lake natural or originally introduced by man? Are there any records of stocking? There is no way to decide if the variability in spotting pattern is a completely natural phenomenon (as it does not correlate with any of the other characters, which are typical of *pleuriticus*) or if it is caused by a slight influence from Yellowstone Lake cutthroat trout. The August Lake cutthroat trout can be considered as good, possibly pure *pleuriticus*; my reservations concern the variability in spotting pattern and an extreme gillraker count of 23. The living colors of these trout should be noted. Yellowstone trout influence would act to subdue the brilliant *pleuriticus* colors.

Evaluation of *S. c. utah* Purity

Since my last reports written in 1975 concerning the Bonneville basin native trout, *S. c. utah*, I have obtained considerably more information on this trout through a 1976 collecting trip and report written on the Thomas Fork drainage for the Rock Springs BLM office and through a study on *S. c. utah* funded by the BLM Utah State office, leading to a M.S. thesis on *S. c. utah* by my graduate student, Mr. Terry Hickman.

Previously, I had assumed that the higher number of pyloric caeca consistently associated with cutthroat trout of the Bear River drainage when compared to values of *S. c. utah* from the rest of the Bonneville basin, was a result of rainbow trout influence. I now realize that the Bear River was always a large fluvial environment, even when tributary to Lake Bonneville, and as such it would be expected that selective pressures would favor the evolution of a fluvial adapted cutthroat trout for the populations native to the Bear River (that is, they were not exposed to lacustrine selection in Lake Bonneville). This same phenomenon also occurred in the Lahontan basin to a greater degree where the cutthroat trout native to the Humboldt River drainage is distinctly different from the native trout of the rest of the Lahontan basin.

Much of both the Humboldt drainage of the Lahontan basin and the Bear River drainage of the Bonneville basin are in semiarid foothill regions characterized by highly fluctuating and unstable environments in respect to flows and temperatures. Evidently the selective pressures and evolutionary adaptations of Humboldt and Bear River cutthroat trout are similar. Both are found in habitat that would be considered completely unfit for cutthroat trout. Yet, in badly degraded habitat, in streams subjected to great extremes of flood and drought, I found the native cutthroat trout of the Thomas Fork and Smith Fork drainages of the Bear River to completely dominate the introduced brook trout and brown trout. Also the native *S. c. utah*, even along roadside areas, had resisted hybridization from past introductions of Yellowstone cutthroat and the fine-spotted Snake River cutthroat trout to an amazing degree. It appears obvious that Bear River system *S. c. utah* have adaptations superior to any other trout for the degraded conditions of the Thomas Fork and Smith Fork drainages, and as such, have a real potential for fisheries management.

In my report to the BLM I mentioned that in 1969, I sampled 30 specimens from the Smith Fork near the mouth of Hobble Creek and 22 of the 30 fish were hatchery raised fine-spotted Snake River cutthroat trout. In 1976 we sampled this same area (stocking had ceased in 1972) and all 16 trout I observed were typical of *S. c. utah*. Of 91 specimens examined from the Thomas Fork drainage in 1976, only one showed a small patch of irregular spots to indicate a lingering influence of past introductions of the fine-spotted Snake River cutthroat. Although Wyoming Game and Fish records show no introductions of rainbow trout into the Thomas Fork drainage, the absence of basibranchial teeth in several specimens, definitely indicates a slight influence of past hybridization with rainbow trout.

In my previous reports to the Wyoming Game and Fish Department and to the BLM, I rated the collections of *S. c. utah* from the Thomas Fork and Smith Fork drainages as good phenotypic representatives (B rating of Binns) and selected the more isolated population in Raymond Creek of the Thomas Fork as the purest *S. c. utah* population known from the Bear River system. In 1976, I suggested to Wyoming Game and Fish biologist Don Miller that a collection should be made from upper Giraffe Creek, which led to the 1977 collection.

In Table 1, a comparison is presented between the 34 specimens collected from upper Giraffe Creek in 1977 and 15 specimens from lower Giraffe Creek made in 1973. There are some genetic based differences in these two samples with the population in upper Giraffe Creek representing a pure or virtually pure population of the *S. c. utah* native to the Bear River system. I would now assign an "A" *S. c. utah* rating to both Raymond Creek and upper Giraffe Creek. Basibranchial teeth were found in 33 of 34 (97%). The spotting pattern is consistent and uniform, with relatively large, round spots sparsely distributed over the sides of the body.

It is not known if the trout in upper Giraffe Creek are physically isolated from the slightly hybridized population occurring near the mouth, or if, the absence of detectable hybrid influence is due to strong negative selection against non-native genes. In any event, upper Giraffe Creek (in both Idaho and Wyoming) assumes a special significance in relation to the preservation of pure *S. c. utah*.

The spotting pattern and particularly the coloration of *S. c. utah* is quite distinct from *S. c. pleuriticus* (but not very different from their closest relatives, the large-spotted cutthroat trout native to the upper Snake and Yellowstone drainages). *S. c. utah* does not develop brilliant coloration. The colors are dull and subdued. Faint traces of pink and yellow may appear on some specimens, but I have never observed the bright red, orange, or brilliant gold-yellow colors characteristic of *pleuriticus*.

Lake Alice, a lake of about 237 surface acres, was formed at some unknown time by a landslide across Hobble Creek isolating the area and converting the headwaters of the drainage into a mountain lake. The original trout population isolated above the slide gave rise to the present lacustrine population. Lake Alice cutthroat trout were formerly used for egg taking and propagation. Existing records list past introductions of non-native cutthroat trout (probably of Yellowstone Lake or Henry's Lake origin) into Lake Alice. It is also probable that, officially listed or not, rainbow trout were stocked into Lake Alice.

The 17 Lake Alice specimens are recognizably differentiated from other *S. c. utah*. They have fewer spots on the body (typically 25-30 vs. 40-50). Yellowstone or Henry's Lake cutthroat trout influence or rainbow trout hybrid influence in a *S. c. utah* population would result in more, not fewer spots. The lateral series scale count averages about 10 less in Lake Alice specimens than in collections from Raymond Creek and upper Giraffe Creek, but either Yellowstone Lake or Henry's Lake cutthroat influence would increase, not decrease, scale numbers. Basibranchial teeth are well developed and occur in 16 of 17 (95%) of the specimens.

The Lake Alice collection averages two fewer gillrakers than Yellowstone Lake or Henry's Lake cutthroat. There is no detectable evidence of non-native cutthroat trout or rainbow trout hybrid influence in the Lake Alice specimens. The differences noted between the Raymond Creek and upper Giraffe Creek *S. c. utah* and Lake Alice specimens are more likely the result of long isolation under quite different selective pressures between the populations. At least the recent evolutionary history of the Lake Alice population has been associated with a more typical pristine mountain environment and in the absence of any other native fishes (generalized type of cutthroat environment) rather than the harsh and unstable environment guiding the selection of the populations in the foothills and lowland areas. With this in mind, the Lake Alice genotype might perform quite differently from the Raymond Creek genotype when introduced into different environments. For introductions where the establishment of new populations is not intended, some creative propagation techniques might be tried, such as crosses between Lake Alice and Raymond Creek trout to broaden the base of genetic diversity.

The Bear River drainage in Wyoming has suffered enormous loss of trout habitat quality from water diversions and livestock grazing (accelerated by herbicide spraying) and is presently under the threat of energy exploration.

There is a great potential to restore quality habitat by better range management practices and livestock exclosures. The result should be a great increase in abundance of the native trout in the Thomas Fork and Smith Fork drainages, which in turn, would attract greater fishing pressure. Because of the vulnerability to angling of cutthroat trout in streams, it is likely that about 50 hrs./acre/yr. of angling pressure will remove 50% of catchable size fish. When angling pressure reaches this point, special protective regulations should be seriously considered for main-stem, easily accessible areas to maintain a quality fishery.

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Table 1. Character analysis of 1977 collections of cutthroat trout from the Green River and Bear River basins.

Locality	Gillrakers	Pyloric caeca	Scales above lat. line & lat. series	Basibranchial Teeth
Green R. Tributaries				
Rock Crk. N=8 R106W, T34N	18-22 (20.1)	28-38 (33.5)	41-46 (43.8) 168-196 (186.5)	2 no teeth 6 with 1-7 (3.2)
Dead Cow Crk. N=8 Trib. to So. Horse Crk.	18-22 (19.6)	32-46 (40.4)	39-45 (42.7) 159-192 (180.7)	2-10 (5.9)
August Lake N=14 R106W T34N	16-23 (19.1)	32-48 (39.6)	38-46 (43.3) 172-200 (186.2)	2-16 (9.3)
Lead Crk. N=17 Trib. to Horse Crk.	17-21 (19.8)	36-48 (42.1)	39-47 (42.6) 158-202 (180.2)	2 no teeth 15 with 5-18 (10.7)
Little Snake drainage				
Upper W. Br. N. Fork N=11	17-21 (19.3)	24-44 (33.2)	38-48 (42.5) 166-201 (181.3)	3 no teeth 8 with 2-8 (4.1)
Rabbit Crk. N=17	17-21 (19.1)	34-40 (36.4)	40-46 (43.0) 183-193 (187.3)	2 no teeth 5 with 3-8 (5.4)
Rose Crk. N=10	18-20 (19.0)	32-47 (38.4)	39-44 (41.7) 162-181 (174.1)	1 no teeth 9 with 2-11 (6.7)
Deep Crk. N=10 Trib. Big Sandstone	18-21 (19.6)	31-36 (33.7)	39-45 (41.9) 168-192 (181.6)	1 no teeth 9 with 1-11 (5.6)

Table 1 Continued

Locality	Gillrakers	Pyloric caeca	Scales above lat. line & lat. series	Basibranchial Teeth
Bear River drainge of Bonneville basin				
Upper Giraffe Crk. N=34	16-21 (18.5)	35-49 (41.0)	34-44 (38.9) 149-181 (168.5)	1 no teeth 33 with 1-30 (9.4)
Lower Giraffe Crk. 1973 N=15	18-21 (18.5)	34-64 (48.3)	33-44 (38.1) 141-176 (159.1)	2 no teeth 13 with 1-26 (6.9)
Raymond Crk. 1976 N=31	16-20 (17.6)	39-54 (44.8)	36-44 (39.2) 156-183 (168.6)	1 no teeth 30 with 1-21(5.1)
Lake Alice N=17	17-20 (18.7)	41-57 (47.1)	34-42 (37.7) 145-171 (157.0)	1 no teeth 16 with 1-17 (8.6)

Identification of a Sample of Cutthroat Trout from Hell Canyon Creek, Carbon County, Wyoming, with Comments on the Native Trout of the Little Snake River Drainage.

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March, 1982

Abstract

Examination of 8 specimens of cutthroat trout from Hell Canyon, tributary to Savery Creek of the Little Snake River drainage, and their comparison with numerous other collections from the Little Snake drainage, identifies the Hell Canyon trout as *Salmo clarki pleuriticus*. Variability in the size of the spots on the body suggests a slight hybrid influence, but other characters lead to the conclusion that if non-native trout genes occur in the specimens in this sample, the hybrid influence is extremely slight. In view of the spotting variability and the small sample size I provisionally assign a rank or grade of "B" to this sample. A summary of the results of collections from the Little Snake drainage is included in an attempt to delineate the distribution pattern of pure populations and of hybrids to emphasize the need to better document the occurrence of pure populations and the factors that act to maintain their purity.

Introduction

From 1974 through 1981 I examined hundreds of trout specimens for the Wyoming Game and Fish Department. The results of the examinations were prepared as 6 reports on: "The native cutthroat trouts of Wyoming." In the early reports it became obvious that pure populations of the Colorado River cutthroat trout were rare and the greatest concentration of pure or essentially pure populations occurred in a group of small headwater tributaries to the North Fork of the Little Snake River. It also became obvious that pure populations of native populations of Little Snake River drainage cutthroat trout are distinctly different from other populations of *S. c. pleuriticus* by having much larger spots on the body. In this respect, the Little Snake cutthroat trout are phenotypically identical to the greenback cutthroat trout, *S. c. stomias*, native to the South Platte and Arkansas drainages of the Missouri River basin. The tributaries with pure *S. c. pleuriticus* are extremely small (1-3 cfs low flows) and subjected to dewatering by a transbasin diversion of the City of Cheyenne and threatened by increased diversions (Binns 1977a, Jespersen 1979).

Binns (1977b) summarized the data on the trout collections from the Little Snake drainage up to that time. In the Savery Creek section of the drainage, the population in Douglas Creek was rated "B", the headwater population in Big Sandstone Creek was rated "A" and the downstream population (sampled near confluence with Douglas Creek) was rated "C" or "D" (an obvious hybrid influence). Obvious hybrids were found in the lower section of the North Fork of the Little Snake (R85W, T12N) and a hybrid influence was noted in specimens from the West Branch of the North Fork, Harrison Creek and Deadman Creek. Specimens identified as pure pleuriticus were recorded from the Middle North Fork, Solomon Creek and Ted Creek (grade "A"). Collections made in 1977 were discussed in my report III to the Wyoming Game and Fish Department. Samples from North Fork tributaries included specimens from the upper West Branch, Rabbit Creek, and Deep Creek. All of these specimens had the typical phenotypic appearance of the native trout with uniformly large spots. However, all samples had specimens lacking basibranchial teeth. Although I did not assign a "letter grade" to the 1977 samples, it would be "B" for all of them. In addition, a 1977 sample from Deep Creek, tributary to Big Sandstone Creek was examined. The Deep Creek specimens also were typical of the native trout but 1 of 10 specimens lacked basibranchial teeth.

Additional collections made in 1980 from the Big Sandstone drainage were disussed in report V. Comparing the 1980 specimens from Douglas Creek, the headwaters of Big Sandstone Creek, the North Fork of Big Sandstone, Deep Creek, East Branch of Deep Creek, Bachelor Creek, and Beaver Creek, with previous collections raised some interesting questions on the factors governing the maintenance of pure populations of native trout.

The headwaters of Big Sandstone Creek and its North Fork have pure native trout, while only a few miles downstream at the confluence with Douglas Creek, the trout are obviouslly hybridized with rainbow trout. It is not known if a physical barrier to upstream movement separates the pure population from the hybrids. In Douglas Creek there is no barrier to upstream movement and a purity gradient exists. Samples from the headwaters of Douglas Creek appear to be essentially pure, but a hybrid influence (increase in absence of basibranchial teeth, smaller spots, lower scale counts) becomes apparent downstream toward the confluence with Big Sandstone Creek. The Deep Creek sample taken in 1980 showed a greater hybrid influence than the 1977 Deep Creek sample (6 of 11 specimens lacking basibranchial teeth vs. 1 of 10), but the specimens from the East Branch of Deep Creek appear to be pure. It is not known if a barrier protects the East Branch population or if a purity gradient exists. In any event, like the Big Sandstone Creek phenomenon, the trout in the Deep Creek watershed are not homogenous. A similar situation exists in the headwaters of the North Fork of the Little Snake. Historically, there were no absolute physical barriers to movement throughout the connecting tributaries, but the distribution of hybrids, pure pleuriticus, and brook trout in various sections of the North Fork and in the tributaries exhibit striking differences. Evidently certain environments strongly favor the native genotype.

Hell Canyon Specimens

From previous collections, a characterization of pure, native Little Snake drainage cutthroat can be given. The most diagnostic feature is the size of the spots. The largest spots are concentrated on the caudal peduncle region and are larger than the pupil of the eye. The spotting pattern should be relatively uniform among the specimens of a sample. Great variation in the size and distribution of spots reflect a hybrid influence.

Pure populations can be expected to have lateral series scale counts ranging from about 170 to 210 with mean values of about 185 to 195. Scale counts above the lateral line range from about 41 to 52 with mean values of about 44 to 48. Pyloric caeca typically range from 25 to 40 with mean values of about 32 to 36. All pure pleuriticus should have basibranchial teeth, but occasionally a rare specimen may not develop these teeth or they are lost (they are tiny and fragile), thus, I have arbitrarily set a level of at least 90% occurrence of basibranchial teeth for a sample to be considered pure (grade A)--if all other characters are in agreement with purity. Typically, pure populations from the Little Snake drainage, have relative high counts of basibranchial teeth with mean values of about 8 to 10 teeth.

In the 8 specimens in the Hell Canyon sample, from 125 to 216 mm TL, 3 have the "pure" spotting pattern and 5 have smaller spots (similar to Douglas Creek specimens). Seven of the 8 specimens have basibranchial teeth, ranging from 2 to 7 (4.1) in number. The single specimen lacking teeth has a base or root on the basibranchial plate where a tooth may have once been present. The scale counts are typical of a pure population--172-209 (189.5) in the lateral series, and 42-48 (44.5) above the lateral line. Gillraker counts range from 19-21 (20.2), similar to the pure sample from the E. Branch Deep Creek.

Pyloric caeca counts could not be made accurately. Due to preservation in alcohol not completely suitable for fish preservation (odor similar to lacquer thinner), the specimens were "mushy" and partially decomposed internally. I was able to make approximate counts of caeca, which I believe are close to reality. These counts range from 28 to 35 with an average of about 30--perhaps slightly lower than the true mean of the population.

The variation in spot size, the absence of basibranchial teeth in one specimen and the low mean number of these teeth leads me to suspect a very slight influence from rainbow trout occurs in the population from which this sample was drawn.

In 1981, 10 specimens from nearby Dirtyman Creek were examined. The values for the Dirtyman Creek sample are: gillrakers, 17-21 (19.3); scales in lateral series, 166-192 (182.1); scales above the lateral line, 41-50 (44.7); pyloric caeca 31-38 (35); 2 of 10 specimens lacking basibranchial teeth, with 1-5 (3.2) teeth in the 8 specimens with teeth. The scale counts and basibranchial teeth counts would indicate a slightly greater hybrid influence in the Dirtyman Creek sample. Due to small sample size, I would provisionally assign a "B" rating to both the Hell Canyon and Dirtyman Creek samples.

Discussion

Based on previous collection results, it would be useful to know if the trout in Hell Canyon and Dirtyman creeks form homogenous populations or if purity gradients exist between upstream and downstream areas. It would also be useful to document the type of isolation of pure populations in the headwaters of Big Sandstone Creek and in the East Fork of Deep Creek. Do physical barriers prevent movement of hybrids occurring downstream? If not, what is different about the environment where pure populations exist in comparison to environments with hybrids? In situations with "purity gradients," it seems obvious that certain environments strongly favor the native genotype by natural selection and exerts negative selection against non-native genes infiltrating from downstream. It can also be assumed that environmental alterations will likely act to break down the resistance of pure populations to the effects of hybridization.

The situation in the Little Snake drainage with the varying degrees of hybrid influence in different neighboring tributaries and in different sections of the same stream denoting very different rates of gene flow among contiguous populations, seems comparable to studies on guppies by Endler (1982) and Reznick and Endler (1982) where samples of guppies from the same drainage are quite distinct in spotting and coloration in response to degrees of predation pressure (predators differentially eliminate genes for large dorsal spots and bright coloration). Similar situations are found in threespine stickleback where distinct differences in coloration, number of scutes and size of spines are associated with predation pressure. Distinctly different populations of sticklebacks may occur in close proximity to each other in the same drainage or even in a single lake (Bell 1982). A direct cause and effect relationship between the maintenance of native genotypes and a single environmental factor such as predation is not likely to be discovered in the Little Snake drainage. The genotype-enviornment interactions are probably much more subtle here with the native genotypes physiologically functioning at optimal levels in certain environments and less so in others. In environments that supply less than the optimum for all aspects of life history (or where non-native genotypes have a functional advantage), non-native genes are accepted in the native population and may even be favored by natural selection. Thus, it would be interesting to correlate the occurrence of pure or essentially pure populations with a characterization of their environments. Would any common denominator, cause-and-effect relationship become apparent that would have general applicability for management and planning?

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