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Genetic Identification of Cutthroat Trout, *Salmo clarki*, in Glacier National Park, Montana

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Trout populations in 29 lakes in Glacier National Park were identified by meristic and electrophoretic analyses to assess the extent of introgressive hybridization between introduced nonnative trout and the indigenous cutthroat trout, *Salmo clarki lewisi*. Native cutthroat trout remain in 16 lakes draining to the North and Middle forks of the Flathead River; no native trout were found east of the Continental Divide. Introduced Yellowstone cutthroat trout, *Salmo clarki bouvieri*, occur in six headwater lakes. Hybrid populations, including both *S. c. lewisi* × *bouvieri* and *S. clarki* × *S. gairdneri*, inhabit six lakes. Hybridization between native and introduced trouts has been minimal, apparently due to strong selective pressures favoring the indigenous genotype. Close agreement was observed between the meristic and electrophoretic results.

Des populations de truites de 29 lacs du parc national Glacier ont été identifiées par analyses méristiques et électrophorétiques dans le but d'évaluer l'importance de l'hybridation introgressive entre les truites non indigènes introduites et les truites fardées indigénes (*Salmo clarki lewisi*). Les truites fardées indigènes occupent toujours 16 lacs se déversant dans les fourches North et Middle de la rivière Flathead. Aucune truite indigène n'a été décelée à l'est de la ligne de partage des eaux continentales. Des truites fardées de Yellowstone (*Salmo clarki bouvieri*) introduites occupaient six lacs d'amont. Des populations hybrides de *S. c. lewisi* × *bouvieri* et de *S. clarki* × *S. gairdneri* ont été décelées dans six lacs. Il y a eu très peu d'hybridation entre les poissons indigènes et introduits. Il semble que ce phénomène soit dû à de fortes pressions sélectives en faveur du génotype indigène. Il y avait concordance étroite entre les résultats des analyses méristiques et électrophorétiques.

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Taxonomy of the native trout of Glacier National Park has existed in a state of confusion until fairly recently. This can be traced to the belief of Jordan and Evermann (1896) that a single subspecies of cutthroat trout, *Salmo clarki clarki*, ranged from the coastal waters of the Pacific Northwest inland to the headwaters of the Columbia River system. Cutthroat trout east of the Continental Divide, including those native to the South Saskatchewan and Upper Missouri River drainages and the Yellowstone Lake basin, were classified as *S. clarki lewisi*. This scheme recognized both subspecies as part of Glacier Park's native ichthyofauna (Schultz 1941). It is now known that the coastal cutthroat trout, *S. c. clarki*, extended inland only as far as the Cascade Range and, consequently, never reached the Glacier Park area.

East of the Cascades, the "westslope" cutthroat trout, *S. c. lewisi*, historically ranged from west-central Washington across Idaho, and into western Montana, where it crossed the Continental Divide and entered portions of the South Saskatchewan and Upper Missouri River basins. Behnke (1979) attributed this distribution to headwaters crossover in the vicinity of Glacier Park. Along the western periphery of this range (e.g. St. Joe, Clark Fork, and Kootenay rivers), *S. c. lewisi* has been isolated from rainbow trout, *S. gairdneri*, by upstream barriers.

Studies of protein variation (Loudenslager and Thorgaard 1979; Loudenslager and Gall 1980) and morphomeristic character analyses (Roscoe 1974; Behnke 1979) have indicated that trout indigenous to the Snake River above Shoshone Falls and throughout the Yellowstone River drainage are distinct from *S. c. lewisi* and represent a markedly different evolutionary lineage. The name *S. clarki bouvieri* has been assigned to the Yellowstone cutthroat trout (Behnke 1979). *Salmo clarki lewisi* is, therefore, the only subspecies of cutthroat trout indigenous to Glacier Park. Although historically present in all three continental drainages that head in the park, populations in the Missouri and Saskatchewan River drainages appear to have been restricted to downstream reaches outside the existing park boundary.

A fundamental tenet of the National Park Service's Organic Act of 1916 is preservation of the indigenous biota of the national parks. However, early acceptance of sport fishing as a legitimate use of park resources created a management dilemma, particularly regarding the issue of artificial enhancement of fishery resources. Lack of a comprehensive fisheries policy prior to World War II allowed the momentum of established fish stocking practices to prevail over the Service's otherwise straightforward philosophy of nonmanipulative ecosystems management. In recent decades, attitudes have shifted back toward maintenance of self-sustaining indigenous fisheries in the Natural Area category of national parks.

Between 1912 and the post-World War II years, tens of millions of nonnative salmonid eggs, fry, and fingerlings were stocked in Glacier Park waters. The Yellowstone cutthroat trout was the principal species stocked; however, other species included the rainbow trout; brook trout, *Salvelinus fontinalis*; lake trout, *Salvelinus namaycush;* lake whitefish, *Coregonus clupeaformis*; and kokanee, *Oncorhynchus nerka*. Lake trout are native to a few park waters in the South Saskatchewan drainage, but have been introduced into several large lakes west of the Divide. Stocking diminished in Glacier Park in the 1950's and was terminated in the early 1970's.

Prior to this work, the impact of 60 yr of fish stocking on the native trout was unknown. We undertook this study to document (1) the extent of hybridization between introduced salmonids and the indigenous cutthroat trout and (2) the present distribution of native, introduced, and hybrid trout populations within the boundaries of Glacier Park.

Study Area

Glacier National Park adjoins the U.S.–Canada border in the northwest corner of Montana and encompasses approximately 410 000 ha of precipitous mountain terrain and glacial valleys. Approximately 650 lakes larger than 2 ha and 2600 km of streams drain from 2500 m MSL (elevation above mean sea level) to approximately 1000 m elevation. Lower and midelevation forests are principally composed of lodgepole pine, *Pinus contorta*. Tundra-like conditions prevail above 2400 m MSL.

The headwaters of three continental drainages originate in Glacier Park. Waters west of the Continental Divide enter the North and Middle forks of the Flathead River and drain to the Pacific Ocean via the Columbia River. East of the mountains, a second divide separates the South Saskatchewan (Hudson Bay) drainage from the headwaters of the Upper Missouri Basin. Fisheries occur in at least 64 park lakes; 47 waters known or suspected to contain resident cutthroat trout were surveyed (Fig. 1). Lakes were selected for surveying on the basis of stocking records, creel census data, and recommendations by backcountry rangers.

Materials and Methods

Cutthroat trout were collected by gill nets in the lakes and by electroshocking in streams. A numbered tag was affixed to each specimen for subsequent comparison of meristic and electrophoretic data among individual trout. The right eye, a section of liver, and 1 cm^3 of muscle tissue were removed, placed in coded plastic bags, and frozen on-site for later analyses by starch–gel electrophoresis. Processed trout were preserved in 10% formalin and transported to the laboratory.

Morphomeristic and electrophoretic analyses were performed independently on the same specimens. Genetic identifications were subsequently based on a consideration of the results from both procedures.

Gillrakers were counted on the anterior and posterior sides of the first left gill arch. Basibranchial teeth were stained with alizarin-red dye and counted under a binocular microscope. scales in the lateral series (counted two rows above the lateral line) and pyloric caeca were also counted. Meristic data were compared with typical values cited for *S. c. lewisi* and *S. c. bouvieri* by Roscoe (1974) and Behnke (1979; and unpubl. data) (Table 1). Close attention was also paid to the shape, relative size, and distribution of spotting.

The protein products of 42 loci encoding 19 enzymes (Leary et al. 1984) were analyzed in the specimens. Sample preparation and electrophoresis in starch gels followed the methods of Utter et al. (1974) with the stains and buffer systems of Allendorf et al. (1977). Isozyme loci are designated with the nomenclature described by Allendorf et al. (1983).

Results and Discussion

Forty-seven waters comprising 9462 ha were surveyed during the summers from 1978 through 1985. Twenty-nine lakes encompassing 1487 ha contained cutthroat trout or hybrid trout populations; 818 specimens were collected for examination. Fourteen lakes known to have been stocked with cutthroat trout no longer contain fish or harbor species other than cutthroat trout. These include Long Bow, Pocket, Numa, and Dutch lakes (North Fork, Flathead River drainage); Flattop and Ellen Wilson lakes (Middle Fork, Flathead River drainage); and Stoney Indian, Poia, Kootenai, Cosely, Glenns, Waterton, and St. Mary lakes, and the Belly River (South Saskatchewan River drainage) (Fig. 1).

Data for McDonald, Bowman, and Kintla lakes were discarded because ecological disturbances caused by nonnative fish introductions have impacted cutthroat trout populations in these waters to the point where adequate samples could not be obtained. Also, only six specimens were collected from Rogers Lake, a 34-ha bog in an advanced stage of succession. Results for this water were similarly excluded, since the lake probably does not harbor a resident trout population.

Pure strain populations of *S. c. lewisi* were found in seven lakes draining to the North Fork, Flathead River, and in nine lakes in the Middle Fork, Flathead River. Due to close proximity of several of the lakes, the 16 lacustrine populations of *S. c. lewisi* are organized into 14 geographically distinct groups (Table 2). No populations of *S. c. lewisi* were found east of the Continental Divide.

Three North and Middle Fork lakes and three waters in the Upper Missouri drainage contained exclusively Yellowstone cutthroat trout. Six additional lakes harbored various combinations of hybrids (Table 3). Yellowstone cutthroat trout and hybrid populations occurred, with one exception, in lakes that were previously barren of fish. Typical native and Yellowstone cutthroat trout phenotypes are illustrated in Fig. 2.

Meristics

Meristic characters found most useful for separation of the two types of cutthroat trout were (1) anterior gill rakers, (2) posterior gill rakers, and (3) basibranchial teeth. The mean number of basibranchial teeth, when plotted against the mean number of posterior gill rakers, readily separated *S. c. lewisi* from *S. c. bouvieri* (Fig. 3).

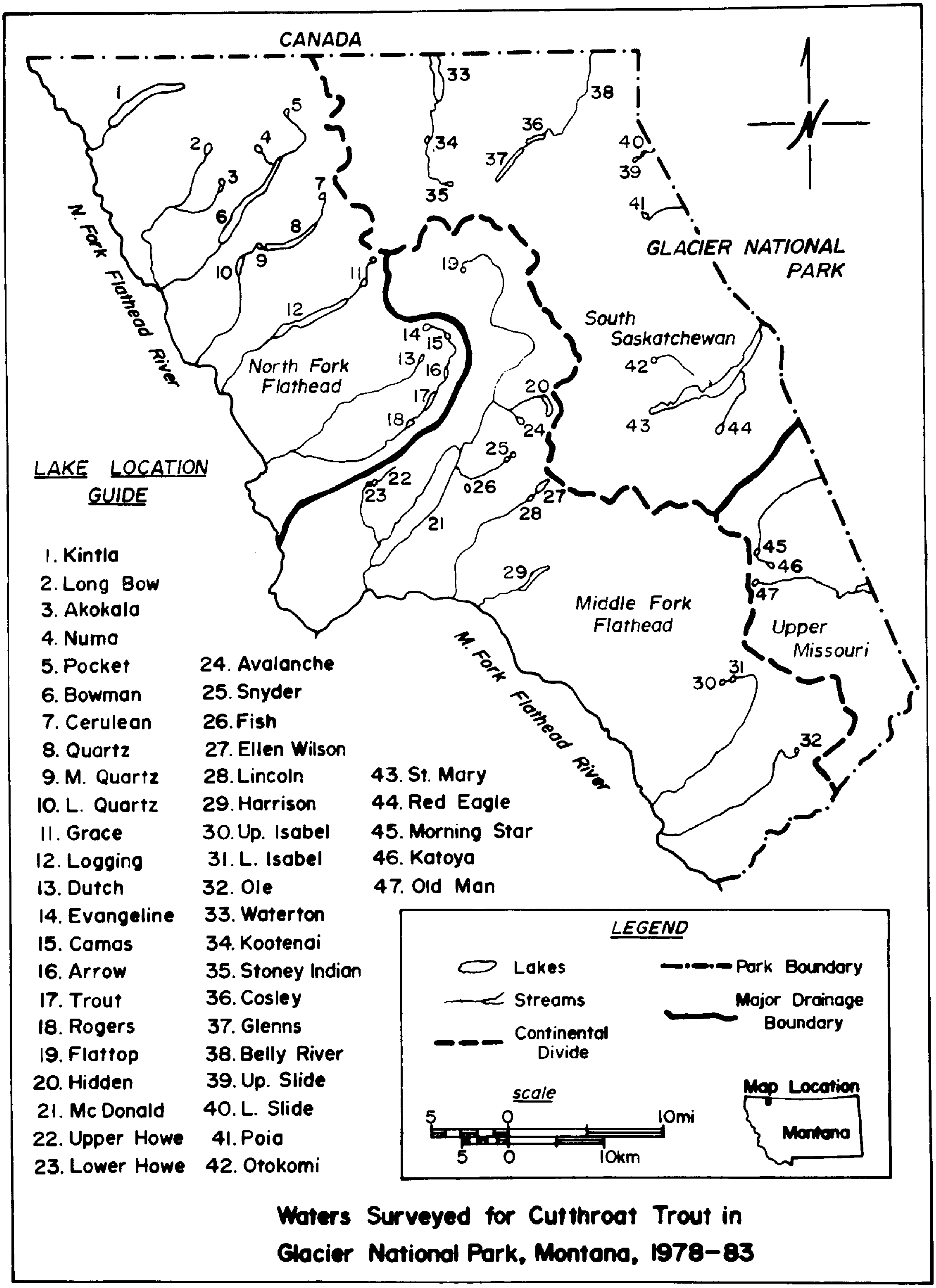

FIG. 1. Waters surveyed in Glacier National Park, Montana.

TABLE 1. Ranges of meristic character values for *S. c. lewisi*, *S. c. bouvieri*, and *S. gairdneri* used for identification of specimens from Glacier National Park, Montana. Typical mean values are given in parentheses. (Adapted from Roscoe 1974; Behnke 1979)

Character	*S. c. lewisi*	*S. c. bouvieri*	*S. gairdneri*
Gillrakers			
Anterior	16–21 (17–19)	18–24 (20–21)	16–21 (18–20)
Posterior	0–5 (1–3)	5–15 (7–10)	0
Basibranchial teeth	1–15 (4–8)	6–40 (22)	0

TABLE 2. Lakes in Glacier National Park containing native cutthroat trout, *S. c. lewisi*.

Name of water	Area (ha)	Origin of population
North Fork, Flathead River drainage		
Akokala L.	9	Indigenous
Cerulean L.	20	Indigenous
Quartz L.	349	Indigenous
Middle Quartz L.	19	Indigenous
Lower Quartz L.	67	Indigenous
Logging L.	444	Indigenous
Trout L.	86	Indigenous
Middle Fork, Flathead River drainage		
Avalanche L.	23	Introduced
Snyder L.	2	Introduced
Upper Howe L.	3	Introduced
Lower Howe L.	12	Introduced
Lincoln L.	14	Indigenous
Harrison L.	101	Indigenous
Upper Isabel L.	6	Indigenous
Lower Isabel L.	17	Indigenous
Ole L.	2	Indigenous

TABLE 3. Electrophoretic classification of nonnative and hybrid trout populations in Glacier National Park.

Name of water	Area (ha)	Type of trout[a]	Sample size
North Fork, Flathead River			
Grace L.	32	YCT × WCT	30
Evangeline L.	28	YCT	30
Camas L.	8	YCT	30
Arrow L.	23	WCT × YCT	30
Middle Fork, Flathead River			
Hidden L.	110	YCT	30
Fish L.	3	WCT × YCT	31
South Saskatchewan drainage			
Otokomi L.	9	YCT × RT	23
Upper Slide L.[b]	5	YCT × RT	12 } 30
Lower Slide L.	15	YCT × RT	18 } 30
Upper Missouri drainage			
Katoya L.	4	YCT	30
Old Man L.	17	YCT	30
Morning Star L.	4	YCT	11

[a]RT = *S. gairdneri*; WCT = *S. clarki lewisi*; YCT = *S. c. bouvieri*. Symbol of the dominant phenotype appears first in the case of hybrids.
[b]Upper and Lower Slide lakes contain the same trout population.

The meristic index represents the sum of the mean values of the three principal characters (Table 4). Usefulness of this index derives from the fact that the mean value of all three characters is higher for *S. c. bouvieri* than for *S. c. lewisi*. Thus, small differences in mean counts of individual characters within any given sample are amplified. This more clearly separates the two subspecies of cutthroat trout.

Index values for cutthroat hybrids tended to be intermediate; however, some overlap occurred between the upper values for hybrids of *S. c. lewisi* × *bouvieri* and the lower values for *S. c. bouvieri*. Thus, the meristic index is best suited for separating genetically pure populations of the two cutthroat trout subspecies. Hybridization between these forms was indicated by atypical pigmentation. Native trout typically displayed small irregularly shaped spots with very few (i.e. less than 2% of total) located below the lateral line anterior to the anal fin. The Yellowstone subspecies by contrast exhibits larger spots, essentially round in shape, with 10–15% of them lying anterior to the anal fin below the lateral line (see Fig. 2). Hybrids of *S. c. lewisi* × *bouvieri* usually revealed some deviation from the typical shape, size, and/or distribution of lateral spotting.

Hybrid influence from rainbow trout into either *S. c. lewisi* or *S. c. bouvieri* was inferred from anomalous spotting on the snout and any notable increase in the density of lateral spotting accompanied by a decrease in the relative size of spots. Examination of stocking records confirmed exposure to *S. gairdneri* in all samples where rainbow trout influence was suspected on the basis of atypical spotting patterns. Tentative identification of rainbow trout influence in cutthroat trout was consistently confirmed by the electrophoretic results.

Electrophoresis

Previous examination (Leary et al. 1984) revealed that 8 of 42 enzyme loci examined could be used to differentiate among the two cutthroat trout subspecies and rainbow trout (Table 5). Electrophoretic classifications of nonnative and hybrid trout populations are presented in Table 3. Populations listed in Table 2 were determined by electrophoresis to be *S. c. lewisi*. Slight discrepancies in sample sizes (*N*) for the meristic and electrophoretic analyses occurred because a few specimens were mutilated by the gill nets to such an extent that meristic characters could not be accurately counted and because accidental thawing destroyed a few electrophoretic samples.

Native Cutthroat Trout

Although *S. c. lewisi* is indigenous to all three continental drainages with headwaters in Glacier Park (Hanzel 1959; Roscoe 1974; Behnke 1979), the subspecies was evidently unable to gain access to the headwater lakes of the South

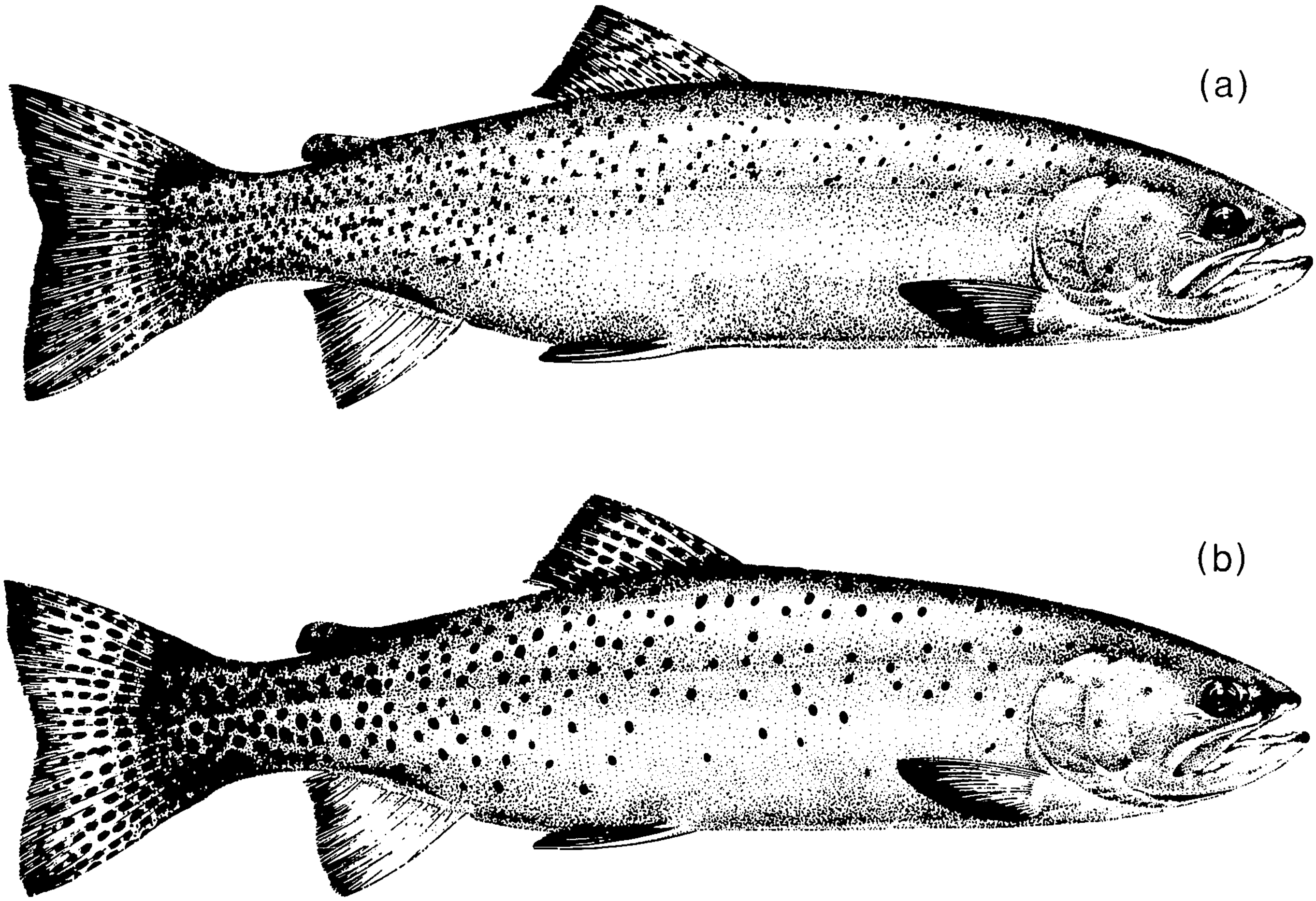

FIG. 2. Illustrations of (a) westslope (*S. c. lewisi*) and (b) Yellowstone (*S. c. bouvieri*) cutthroat trout.

Saskatchewan and Missouri River drainages. Thus, trout found east of the Divide in Glacier Park today are nonnative species, subspecies, or hybrids whose origins can be traced directly to introductions dating from about 1910.

Surviving native trout populations in Glacier Park reside exclusively in waters of the North and Middle Fork drainages of the Flathead River system, including 12 lakes (1134 ha) where the subspecies is believed indigenous (Table 2). Native trout also occur in four small lakes (about 40 ha) that drain to McDonald Lake; included are Upper and Lower Howe, Snyder, and Avalanche lakes. We believe, however, that these populations were introduced, the parent stocks probably originating from McDonald Lake. All four lakes are drained by high-gradient streams containing numerous barriers.

Yellowstone Cutthroat Trout

Introduced Yellowstone cutthroat trout inhabit six park lakes (Table 3). It is noteworthy that *S. c. bouvieri* has not replaced or significantly hybridized with native trout in any water where an indigenous population was present. The Yellowstone subspecies has been able to sustain itself in Glacier Park only in small, high-elevation lakes previously barren of fish.

Hybrid Cutthroat Trout

Given the scale of fish stocking that occurred throughout Glacier Park during the first half of the century, the incidence of hybridization between native and introduced cutthroat subspecies has been minimal. Moreover, no single circumstance appears responsible. Genetic mixing of native and introduced trout has apparently resulted from circumstances unique to specific waters.

Arrow Lake

Of the three park lakes containing hybrid cutthroat trout populations, only Arrow Lake (North Fork) was inhabited by native trout prior to the introduction of *S. c. bouvieri*. The meristic index for the sample was 24.1, typical of *S. c. lewisi*, but five specimens contained no basibranchial teeth, which depressed the mean value for that character. Two specimens captured in the outlet stream possessed 13 and 15 basibranchial teeth, respectively, typical for *S. c. bouvieri*. Several specimens also displayed subtle indications of hybrid influence from Yellowstone cutthroat trout in the form of larger, more evenly distributed lateral spots.

Enzyme analysis confirmed hybridization between westslope and Yellowstone cutthroat trout in this lake; 88% of the alleles at six diagnostic loci were of westslope cutthroat trout origin (Table 6). Twenty-three of the 30 fish sampled were homozygous for the westslope allele at all six loci; five fish were heterozygous for both westslope and Yellowstone alleles at one or more loci, and the two specimens taken from the outlet were homozygous for the Yellowstone allele at all diagnostic loci. There is a significant deficiency of heterozygotes at all six diagnostic loci in this sample compared with expected (i.e. Hardy–Weinberg) proportions. Thus, this sample does not

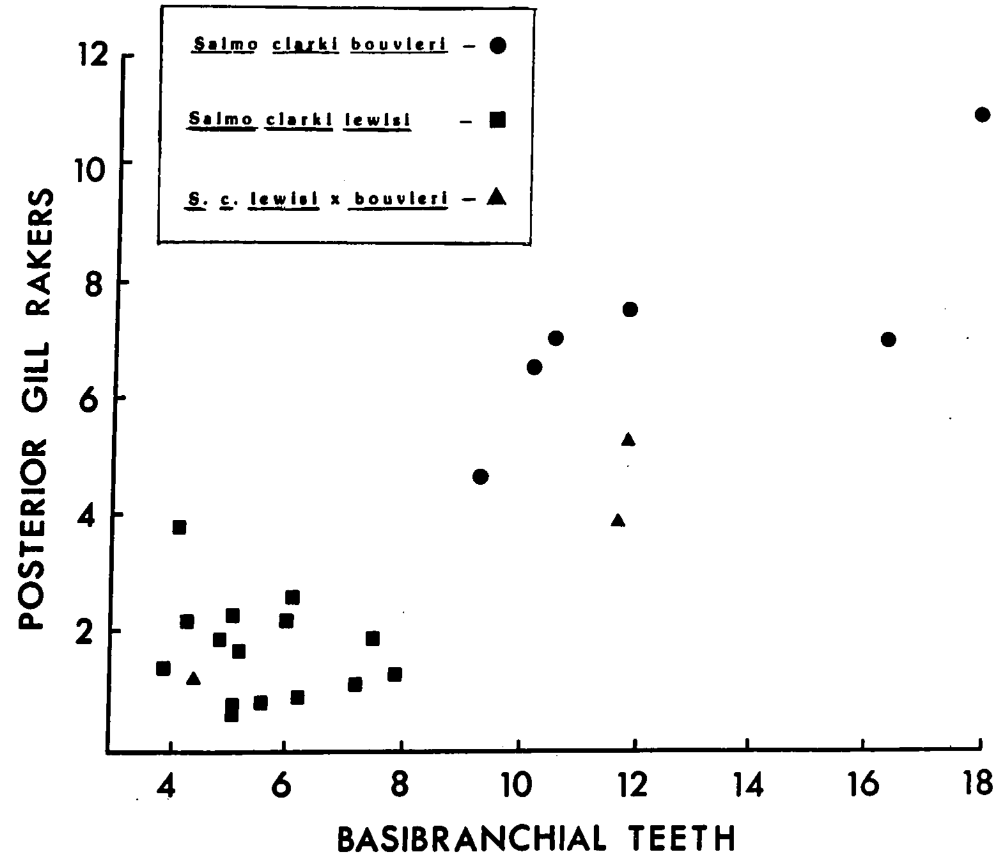

FIG. 3. Separation of *S. c. lewisi* and *S. c. bouvieri* samples by plot of mean number of posterior gill rakers against mean number of basibranchial teeth.

represent a random-mating hybrid swarm. The population is predominately westslope cutthroat trout exhibiting slight hybrid influence from the Yellowstone subspecies.

The stocking of Arrow Lake with 112 000 eggs and 9720 fry of *S. c. bouvieri* between 1924 and 1935 could account for the observed hybrid influence. However, a more plausible explanation is that Yellowstone cutthroat trout introduced upstream in Evangeline and Camas lakes periodically descend over a 5-m falls and enter Arrow Lake where they spawn. This interpretation is based on the low level of hybridization detected in the population and by the presence of two juvenile specimens of apparently pure *S . c. bouvieri* collected in Camas Creek below Arrow Lake; these fish could only have come from Camas or Evangeline lakes (see Fig. 1).

Fish Lake

There is no record of trout introductions into Fish Lake, but National Park Service file correspondence from the 1920's mentions stocking of this water. Although Schultz (1941) identified the population as native cutthroat trout, our data indicate that it is a hybrid swarm of *S. c. lewisi* × *bouvieri*, the most extreme example of this condition found. The meristic index for the sample was 35.9 and a wide range of coloration and spotting patterns was displayed, including phenotypes typical of both subspecies; many specimens exhibited intermediate spotting characteristics. Twenty-nine of the 31 trout examined contained electrophoretic alleles from both *S. c. lewisi* and *S. c. bouvieri*. All three electrophoretic phenotypes were detected at all marker loci, suggesting random mating within the population. Two specimens possessed only *S. c. bouvieri* alleles at the marker loci, but were probably hybrids that happened to possess exclusively Yellowstone alleles at the diagnostic loci by chance alone.

Fish Lake does not have an inlet or outlet stream suitable for trout spawning, although during high water it discharges across a bog to nearby Crystal Creek. It is possible that the lake may contain areas of suitable substrate and oxygen to permit trout spawning and egg incubation. Successful lake spawning is known for cutthroat trout and rainbow × cutthroat hybrids in several remote lakes in Rocky Mountain National Park, Colorado (Rosenlund 1980), and similar occurrences have been noted for cutthroat trout in Bigelow and Hay lakes in western Montana (J. Huston, Montana Department of Fish, Wildlife, and Parks, 490 No. Meridian Ave., Kalispell, MT 59901, pers. comm.). Penlington (1983) also reported spawning of rainbow trout in Rotoma Lake, New Zealand.

In the absence of any competitive advantage conferred upon either subspecies by a long period of prior residence, and with minimal opportunity for escapement, random mating between *S. c. lewisi* and *S. c. bouvieri* best explains the observed hybrid swarm in Fish Lake. Similar hybrid swarms involving these subspecies have been described by Gyllensten et al. (1985).

Grace Lake

Grace Lake covers approximately 32 ha and is located above a 15-m waterfall in the headwaters of the Logging Creek drainage (North Fork, Flathead River). The historically fishless water was stocked with 101 000 cutthroat trout eggs in 1925. Analysis of 30 specimens indicates a hybrid population of *S. c. bouvieri* × *lewisi* possessing predominately Yellowstone cutthroat characteristics. We believe that the 1925 plant contained a mix of eggs from both cutthroat types that gave rise to a hybrid

TABLE 4. Mean values of principal meristic characters for cutthroat trout collected from Glacier National Park. Standard deviation values are given in parentheses.

Population	N	Gill rakers		Basibranchial teeth	Meristic index
		Anterior	Posterior		
North Fork, Flathead River drainage					
Akokala L.	31	19.6 (±0.9)	1.8 (±1.8)	7.6 (±2.7)	29.0
Cerulean L.	17	18.6 (±1.4)	0.6 (±0.6)	5.1 (±3.5)	24.3
Quartz L.	30	18.1 (±0.9)	0.9 (±0.6)	6.2 (±3.8)	25.2
Middle Quartz L.	30	18.8 (±0.8)	0.7 (±0.7)	5.1 (±2.8)	24.6
Lower Quartz L.	31	18.0 (±1.2)	2.2 (±1.6)	6.0 (±3.9)	26.2
Grace L.	23	21.2 (±1.2)	5.3 (±2.9)	11.9 (±6.3)	38.4
Logging L.	35	19.0 (±1.2)	1.1 (±0.8)	7.4 (±4.2)	27.5
Evangeline L.	30	20.7 (±1.1)	11.0 (±2.8)	18.5 (±6.0)	50.2
Camas L.	15	20.3 (±1.2)	7.3 (±3.3)	10.5 (±6.1)	38.1
Arrow L.	28	18.4 (±0.9)	1.2 (±0.6)	4.5 (±3.5)	24.1
Trout L.	30	17.8 (±1.0)	2.6 (±1.3)	6.1 (±3.7)	26.5
Middle Fork, Flathead River drainage					
Hidden L.	17	19.9 (±1.4)	7.6 (±4.1)	11.4 (±4.2)	38.9
Avalanche L.	29	19.0 (±1.2)	1.3 (±0.9)	7.9 (±4.7)	28.2
Snyder L.	33	18.3 (±1.1)	2.1 (±1.1)	4.3 (±2.2)	24.7
Fish L.	29	20.3 (±1.3)	3.8 (±2.8)	11.6 (±6.2)	35.7
Upper/Lower Howe L.	24	18.3 (±1.2)	1.7 (±1.5)	4.8 (±3.4)	24.8
Lincoln L.	16	17.4 (±1.9)	3.8 (±1.7)	4.1 (±2.7)	25.3
Harrison L.	30	17.3 (±0.8)	0.8 (±0.8)	5.6 (±3.0)	23.7
Upper Isabel L.	8	19.0 (±0.8)	2.6 (±0.5)	5.1 (±4.2)	26.7
Lower Isabel L.	30	18.5 (±0.8)	1.4 (±1.3)	3.9 (±5.1)	23.8
Ole L.	30	18.9 (±1.0)	1.9 (±1.3)	5.1 (±3.3)	25.9
Upper Missouri River drainage					
Katoya L.	30	20.5 (±1.0)	7.1 (±3.0)	16.4 (±5.6)	44.0
Old Man L.	30	20.5 (±1.3)	4.6 (±1.9)	8.6 (±6.2)	33.7
Morning Star L.	11	20.0 (±1.0)	6.6 (±2.2)	10.2 (±5.1)	36.8

TABLE 5. Loci differentiating westslope cutthroat trout, Yellowstone cutthroat trout, and rainbow trout. Values represent electrophoretic mobility relative to the standard common allele of rainbow trout.

Enzyme	Locus abbreviation	Relative allelic mobility		
		Rainbow trout	Westslope cutthroat	Yellowstone cutthroat
Creatine kinase	Ck-2	100	84	84
Glucophosphate isomerase	Gpi-3	100	92	100
Isocitrate dehydrogenase	Idh-1	100	100	−75
Isocitrate dehydrogenase	Idh-3,4	100, 40 71, 114	100, 86 71, 40	100 71
Malic enzyme	Me-1	100, 57	88	100
Malic enzyme	Me-4	100, 75	100	110
Sorbitol dehydrogenase	Sdh	40, 100 200	40	100

population. This hypothesis is supported by Schultz's (1941) observation of two distinct spotting patterns among trout in Grace Lake. Specimens collected during the present study displayed intermediate pigmentation and the meristic index was 38.4. The enzyme results from Grace Lake show the presence of both westslope and Yellowstone alleles. Approximately 25% of the genes at the Me-1, Me-4, and Gpi-3 loci were of westslope origin, while the remaining 75% were of Yellowstone origin.

TABLE 6. Electrophoretic analysis of hybrids between westslope and Yellowstone cutthroat trout sampled from Glacier National Park lakes. P is the proportion of genes that are of westslope cutthroat trout origin; F is the fixation index and is the proportional deficit of heterozygotes ($F = 1 - (H_o/H_e)$), where H_o is the observed proportion of heterozygotes and H_e is the expected proportion of heterozygotes. Dashes indicate no data available. All loci could not be scored in some samples because of denaturation of some liver enzymes.

	Fish Lake		Arrow Lake		Grace Lake	
Locus	P	F	P	F^a	P	F
Gpi-3	0.290	0.076	0.900	0.636***	0.348	0.277
Idh-1	0.387	0.064	0.833	0.523**	0	—
Idh-3,4	0.242	−0.298	0.900	0.636***	—	—
Me-1	0.258	−0.160	0.900	1.000***	0.100	0.272
Me-4	0.306	0.174	0.850	0.614***	0.317	0.167
Sdh	—	—	0.900	0.636***	—	—
Mean	0.297	−0.028	0.881	0.674***	0.191	0.239

[a]Test for departure from expected genotypic distribution with $F = 0$; $**P < 0.01$; $***P < 0.001$.

There is no evidence of nonrandom mating based on phenotypes at these three loci: however, all 30 specimens were homozygous for the Yellowstone allele at Idh-1. It is unlikely that such a large difference between loci in the proportion of westslope and Yellowstone alleles could be due to chance alone. There is less than one chance in a million of sampling only Yellowstone alleles in 30 fish if the frequency of the westslope allele is 0.25. Evidence from similar hybrid swarms of these subspecies examined by Gyllensten et al. (1985) suggest that such heterogeneity may result from genetic drift.

Cutthroat × Rainbow Trout Hybrids

Three headwater lakes in the South Saskatchewan drainage contained Yellowstone × rainbow trout hybrids; Otokomi, Upper Slide, and Lower Slide, collectively encompassing 29 ha (Table 3). These lakes were stocked with cutthroat trout during the 1930's. Undocumented introductions of rainbow trout may have occurred, but it is also possible that Yellowstone cutthroats placed in these waters were mixed with rainbow trout, perhaps inadvertently at the hatchery. The Otokomi and Slide Lake populations were predominately Yellowstone cutthroat trout possessing small and variable amounts of rainbow trout characteristics, as evidenced by spotting patterns and the presence of electrophoretic alleles from rainbow trout at Ck-2, Idh-1, Idh-3, and Me-4.

Although the sample size for Red Eagle Lake was too small to allow definitive conclusions, the specimens collected appeared to represent rainbow trout possessing some hybrid influence from Yellowstone cutthroat trout. Reduced basibranchial teeth counts, anomalous spotting patterns, and electrophoresis all indicated slight contamination from *S. c. bouvieri*.

Competition

During the first half of the century, most park waters containing indigenous trout received multiple stockings of Yellowstone cutthroat trout. In view of the resulting low incidence of hybridization, it is evident that some combination of circumstances has strongly favored the indigenous subspecies.

The Yellowstone cutthroat trout evolved in a basin in which piscivorous fish species were absent. Having no evolutionary association with predatory fishes, *S. c. bouvieri* probably lacks the innate avoidance behavior necessary for coexistence. The native trout of Glacier Park, however, evolved with bull trout, *Salvelinus confluentus*, and the northern squawfish, *Ptychocheilus oregonensis*, both highly predaceous species. Therefore, *S. c. lewisi*, could be expected to possess a highly developed instinct to avoid piscivores.

Mortality among fry and juvenile Yellowstone cutthroat trout may have been especially high in Glacier Park waters immediately after planting. Native trout typically rear in the natal stream for an extended period, perhaps 2 or more yr, prior to entering a lake where they spend most of their adult life (Graham et al. 1980; Huston et al. 1984). Yellowstone cutthroat fry, however, characteristically migrate into lacustrine habitat within a few days after emergence and are believed to rear at depths below 20 m (Varley 1979). This probably has significant adaptive value for *S. c. bouvieri* in the Yellowstone ecosystem where predaceous fishes are absent. In Glacier Park waters, however, any tendency for *S. c. bouvieri* introduced as fry or fingerlings to gravitate toward moderate lake depths for rearing would expose them to significant predation. The situation may have been compounded by the concurrent invasion of lake trout into several park lakes. While this would also have affected native cutthroat populations, introduced *S. c. bouvieri* may have been severely impacted.

Another factor that may have contributed to the demise of Yellowstone cutthroat trout stocked in Glacier Park waters was the presence of the indigenous tapeworm, *Ceratocephalus* sp., prevalent in many native trout populations. The indigenous tapeworm differs from the native cestode of the Yellowstone basin, *Diphyllobothrium* sp., in that the life cycle of *Ceratocephalus* is confined exclusively to the aquatic environment where fish represent the final host; an as yet unidentified crustacean serves as intermediate host. *Diphyllobothrium*, however, is transmitted via mammal and avian hosts, mainly pelicans and seagulls, before passing to crustaceans and subsequently to fish, the latter serving as intermediate hosts (Varley and Schullery 1983).

It can be assumed that the two cutthroat subspecies, having evolved in the presence of different parasites, developed the means to coexist with the pathogens present in their respective habitats. Glacier Park's native cestode may have presented formidable problems for *S. c. bouvieri*. Animal hosts are often highly sensitive to parasites and pathogens which infect closely related host species (Barbehenn 1969). It is noteworthy that Yellowstone cutthroat trout have been successful in Glacier Park only in waters that were previously barren of fishes (and cestode parasites). Absence of *Ceratocephalus* from these lakes is probably due to the life cycle of the parasite in which avian or mammalian hosts are not involved.

There is also the possibility that many of the Yellowstone cutthroat trout stocked in Glacier Park may have escaped downstream via tributaries draining to the Flathead River, possibly en route to Flathead Lake located approximately 100 km southwest of the park. However, the low incidence of hybridization between native trout and introduced Yellowstone cutthroat trout in Glacier Park is attributed primarily to the inability of *S. c. bouvieri* to survive in competition with native trout.

Agreement of Meristic and Electrophoretic Results

Twenty-nine population samples were subjected to both meristic and electrophoretic analyses. Since specimens were individually numbered, direct comparison between the two diagnostic procedures was possible. Very close agreement was observed.

The high degree of concordance between the two methodologies is best illustrated by the Arrow Lake sample. Of 30 specimens collected, two from the lake's outlet stream were identified as *S. c. bouvieri* by both procedures. Of the remaining 28 trout, electrophoretic and meristic character analyses identified two and five specimens, respectively, as *S. c. lewisi* possessing varying degrees of hybrid influence from *S. bouvieri*. Remaining specimens were determined to be *S. c. lewisi* by both methodologies.

Close agreement between meristic and electrophoretic results was observed in this work because the evolutionary separation between *S. c. bouvieri* and *S. c. lewisi* is relatively great (Loudenslager and Gall 1980; Gyllensten et al. 1985). That is, evolutionary distance between the lineages is sufficient for divergence to have occurred at several loci and for measurable physical differences to have occurred. Taxonomic studies comparing other subspecies of interior cutthroat trouts (i.e. *S. c. utah* and *S. c. bouvieri* (Loudenslager and Gall 1980); *S. c. bouvieri* and the undescribed fine-spotted Snake River cutthroat trout (Loudenslager and Kitchin 1979)) have been unable to demonstrate any consistent divergence in gene loci between the subspecies being compared, probably because the period of evolutionary separation between the taxa has not been as great as has been the case for *S. c. lewisi and S. c. bouvieri*. Thus, the two diagnostic procedures may or may not yield similar conclusions, depending upon the degree of evolutionary divergence between the groups being examined. We believe that application of both electrophoretic and meristic character analyses will often yield more useful information than either method used alone. A similar conclusion was reached by Reinitz (1977) and Busack and Gall (1981).

Conclusion

A noteworthy feature of the native trout of Glacier Park is the lacustrine adapted life history of populations inhabiting the park's interior lakes. Relatively small numbers of trout captured in upstream–downstream traps between 1977 and 1980 near the confluence of several park streams with the North and Middle forks, Flathead River (Graham et al. 1980: Fraley et al. 1981), suggest that most trout inhabiting these waters complete their life cycle within the confines of the natal drainage. Elsewhere throughout their remaining range, lacustrine populations of *S. c. lewisi* have been greatly reduced due largely to habitat loss and competition with introduced salmonids. Remnant populations exist mainly in small streams, often only in restricted headwater reaches (Hanzel 1959; Roscoe 1974; Reinitz 1977). Isolated populations of *S. c. lewisi* survive today in some lakes within Banff, Kootenay, and Waterton Lakes national parks, Canada (McAllister et al. 1981), and in several small lakes scattered throughout western Montana (J. Huston, pers. comm.). Thus, Glacier Park appears to represent the largest geographic province containing indigenous populations of lacustrine-adapted *S. c. lewisi* surviving today. As such, they represent potentially important gene pool reserves which could be useful for reestablishment of this unique cutthroat subspecies in portions of its former range.

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DATE DUE

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