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[Article]

Identification and Characterization of Migratory and Nonmigratory Bull Trout Populations in the St. Mary River Drainage, Montana

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Abstract.—Populations of migratory and nonmigratory bull trout *Salvelinus confluentus* were identified in the St. Mary River drainage, Montana. Migratory fish were most conspicuous because they were caught in traps operated near creek mouths or moved between creeks. Capture of postspawning bull trout in traps during four consecutive years suggested that most migratory fish had spawned by late September. Migratory bull trout reached maturity mainly as age-5 fish that were typically 300 mm or larger in total length. Estimates based on the recapture of tagged fish in traps indicated that populations of migratory adult bull trout were significantly larger than the mean values from annual catches of trapped fish. Juvenile migratory bull trout departed natal creeks mainly as age-2 or age-3 fish. The scarcity of age-4 bull trout in trap samples indicated that most migratory age-4 fish were immature and inhabited either the downstream lakes or main-stem river. Conversely, the abundance of age-4 bull trout in electrofishing samples was primary evidence of nonmigratory populations in creeks. The occurrence of age-0 bull trout in electrofishing samples indicated recent spawning and reproduction in five creeks, and annual reproduction was indicated by multiple age-classes of young bull trout. Bull trout had growth rates similar to those of bull trout elsewhere, including marked growth of age-4 fish that ostensibly resulted from their transition to a largely piscivorous diet. Migratory bull trout in the St. Mary River drainage are more common than previously believed and may be more common than in many other regions of the species' natural range.

The bull trout *Salvelinus confluentus* is primarily a freshwater fish whose natural range extends from northern areas of California and Nevada to upstream regions of the Yukon River basin in Alaska and the Yukon, encompassing Puget Sound and major coastal river systems in Washington, British Columbia, and Southeast Alaska (Cavender 1978; Haas and McPhail 1991; Nelson and Paetz 1992). Inland, bull trout inhabit rivers and lakes of the Columbia River basin, including headwater areas in Idaho, Montana, and British Columbia, as well as the Klamath River basin in Oregon. Bull trout also occur east of the Continental Divide in the upper MacKenzie River basin (Arctic drainage) in the Northwest Territories, British Columbia, and Alberta; the upper Peace, Athabasca, North Saskatchewan, and South Saskatchewan River basins (Hudson Bay drainage) in Alberta; and the South Saskatchewan River basin in Montana.

Highly piscivorous as adults, bull trout usually mature when 5–7 years old and spawn entirely in coldwater tributaries that are primarily second- to fourth-order streams (Fraley and Shepard 1989; see Goetz 1989 and Rieman and McIntyre 1993 for reviews). Like most inland salmonids, bull trout have been broadly categorized into two life history forms on the basis of their movements (e.g., McCart 1997). Nonmigratory bull trout spend their lives entirely within their natal stream, whereas migratory bull trout spawn in small streams and return to rivers or lakes. Their young eventually move downstream to either rivers or lakes where the fish mature. Constituent life history forms of migratory bull trout and other salmonids are also recognized (e.g., Northcote 1997) but will not be considered in this report. Although bull trout have been collected from estuaries and recaptured fish have sometimes moved between coastal rivers (Cavender 1978; Haas and McPhail 1991), anadromy—characterized in part by residence of the fish in the sea for a substantial period (McDowall 1987)—has not been conclusively shown for the species.

Both migratory and nonmigratory bull trout may coexist in a single stream (McCart 1997; Jakober et al. 1998; Nelson et al. 2002). It is unknown whether these life history forms represent heritable

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(i.e., genetically based) traits, conditional behaviors whose individual expressions are partly dependent upon the variety of accessible aquatic habitats (i.e., phenotypic plasticity), or a combination of these factors (Rieman and McIntryre 1993; McCart 1997; Nelson et al. 2002; see also Northcote 1992; Jonsson and Jonsson 1993). Within the nonmigratory form, McCart (1997) distinguished the "resident" type from the "isolated" type, which occurs upstream from a natural or man-made physical barrier (e.g., waterfall or dam) that prevents the return of fish that move downstream. Such barriers do not confine the resident type.

In 1999, the bull trout was classified as a "threatened" species throughout the contiguous United States under the U.S. Endangered Species Act (USFWS 1999). Central to that classification was the belief that many migratory bull trout had been lost as a result of dam construction or other barriers to fish movement. Information on "threatened" bull trout east of the Continental Divide was especially meager, however. On the basis of interviews of elderly Alberta anglers and a review of agency reports, Fitch (1997) concluded that migratory bull trout no longer occurred in the St. Mary River (South Saskatchewan River basin) in Alberta, but the species persisted as nonmigratory fish in the river's tributaries in Alberta and Montana.

The main objective of this study was to identify the migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. Such identification required the determination of key population characteristics, in particular, population age structure, fish length at age, and the extent that bull trout move among tributary creeks. In addition, we sought to estimate the size of migratory bull trout spawning populations and broadly characterize the fish communities of the creeks.

Study Area

Aquatic Habitats

The St. Mary River begins at Gunsight Lake in Glacier National Park and flows northeast through St. Mary and Lower St. Mary lakes and across the international border to St. Mary Reservoir in Alberta. Among the 11 creeks in the St. Mary River drainage examined during this study (Figure 1), 3 were first-order streams (Jule, Middle Fork Lee, and East Fork Lee creeks), 5 were second-order streams (Rose, Wild, Divide, Canyon, and Lee creeks), and 3 were third-order streams (Boulder, Kennedy, and Otatso creeks). Except for the first-order streams, each of the creeks begins at high elevation (>1,800 m), flows mainly through coniferous forest, and has one or more natural or man-made, year-round, or seasonal barriers to fish movement somewhere along its length. Depending on flow volume, Divide, Boulder, and Kennedy creeks each become entirely subsurface in reaches up to 1.5 km long (Figure 1) as they pass through gravel–cobble alluvium during the seasonal low-flow (i.e., nonrunoff) period. Downstream from those locations, the creeks emerge as groundwater upwellings. On upper Otatso Creek, the Slide Lakes were formed by a rockslide that prehistorically swept across the creek. Creek flows are entirely subsurface when passing through the extant rubble pile during nonrunoff. Red Eagle Creek (Figure 1), the largest creek in the drainage, was not examined because it was difficult to access and too large for our sampling equipment.

Early in the 20th century, Swiftcurrent Creek was impounded by construction of a 33-m-high earthen dam 9 km upstream from the creek's mouth, thereby forming Lake Sherburne (Figure 1). Also constructed was the 2-m-high St. Mary Diversion Dam, a concrete structure located 1.2 km downstream from Lower St. Mary Lake. Each year between about April and October, that dam deflects water released from Lake Sherburne into a canal.

Land use practices that may impair bull trout habitat are limited in the St. Mary River drainage in Montana. Within Glacier National Park, no extant land use activities are known to adversely affect bull trout. However, the lowermost 2 km of Divide Creek is periodically channelized to protect adjacent developed facilities from major seasonal flooding. On the Blackfeet Reservation (Figure 1), livestock grazing and timber harvest occur in limited areas, although timber harvest is extensive in some parts of the Lee Creek drainage.

Fish Species

The historic distribution of native fishes in the St. Mary River drainage was delimited by natural year-round barriers to fish movement (Figure 1). Among the fishes indigenous to the drainage, bull trout, westslope cutthroat trout *Oncorhynchus clarkii lewisi*, mountain whitefish *Prosopium williamsoni*, mottled sculpin *Cottus bairdii*, and spoonhead sculpin *C. ricei* are believed to have occurred in all of the streams and lakes to which they had access, including the Slide Lakes, while lake trout *S. namaycush* inhabited St. Mary and Lower St.

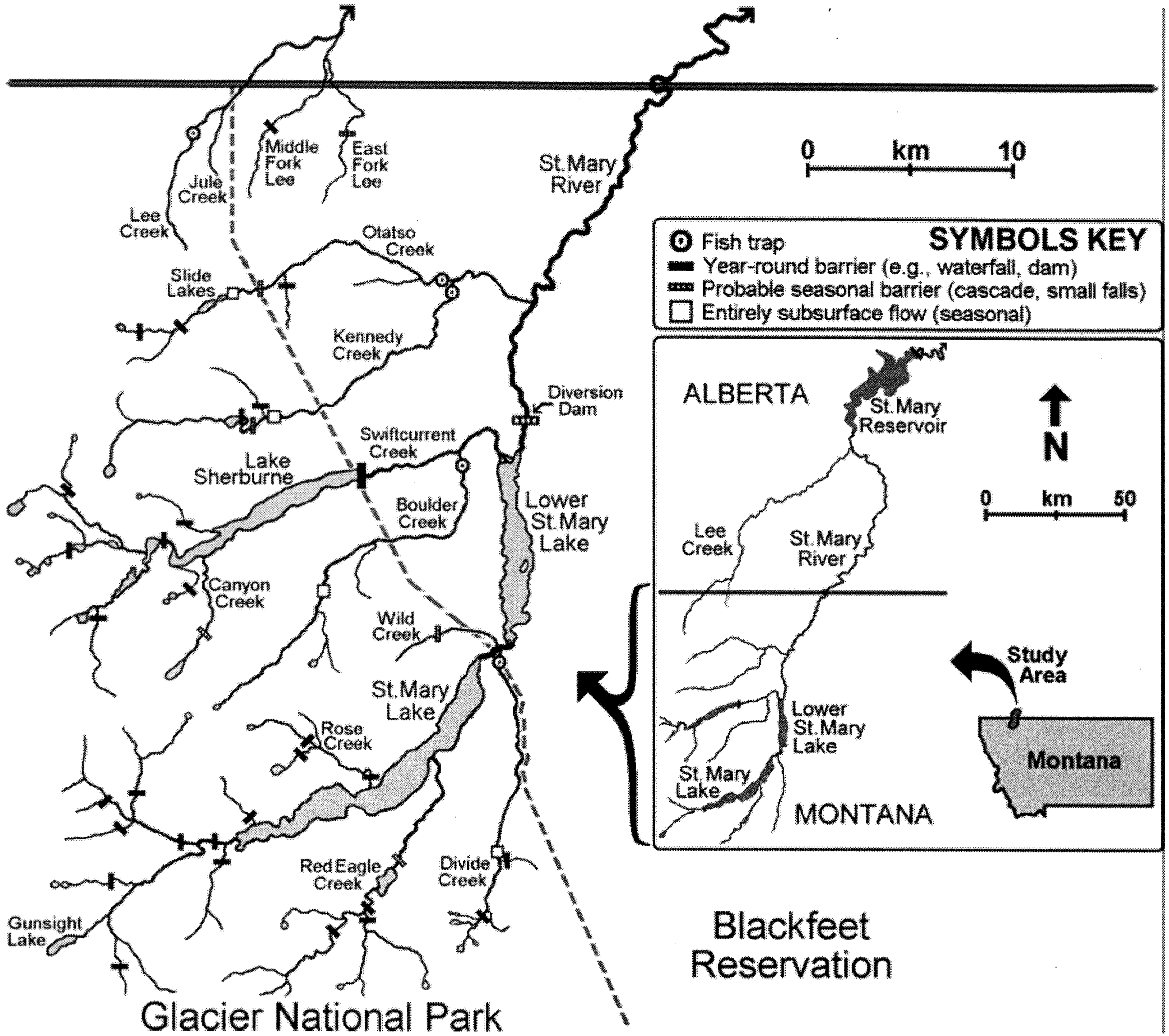

FIGURE 1.—Study area, St. Mary River drainage, Montana, where migratory and nonmigratory bull trout populations were identified between 1997 and 2003.

Mary lakes (Brown 1971). Nowhere else in the contiguous United States were bull trout naturally sympatric with lake trout (Donald and Alger 1993).

Authorized stocking of nonnative fishes in the drainage began early in the 20th century and continued in Glacier National Park until midcentury (Marnell 1988). Such stocking continues today only in some Blackfeet Reservation waters (mainly isolated ponds and lakes). Nonnative fishes that have established self-sustaining populations at various locations in the drainage include brook trout *S. fontinalis*, rainbow trout *O. mykiss*, Yellowstone cutthroat trout *O. clarkii bouvieri*, and genetic intergrades (i.e., hybrids) among the three oncorhynchids (Marnell 1988).

Methods

This study was conducted between 1997 and 2003. However, each of the methods of fish collection was not employed in all study years.

Electrofishing (1998–2003).—Electrofishing was performed between mid-July and late August to characterize the bull trout populations and fish communities in the creeks. Because the creeks were mainly accessible only by foot, it was not possible to annually electrofish entire creeks. Therefore, in each creek we established a sampling reach that contained a variety of mesohabitats and, where present, bull trout of a broad range of size-classes.

Electrofishing occurred annually, unless otherwise noted, throughout (1) a 2-km sampling reach of Divide Creek that extended downstream from the region of entirely subsurface flow (except 2000, 2001); (2) a 6-km reach of Boulder Creek that extended downstream from the region of subsurface flow; (3) an 8-km reach of Kennedy Creek that extended downstream from the region of subsurface flow; (4) three reaches of Otatso Creek (i.e., [a] lower Otatso, a 2-km reach that extended downstream from the fall and cascades 13 km upstream from the creek's mouth (except 1998), [b] middle Otatso, from the fall and cascades upstream 2 km to the rockslide that formed the Slide Lakes (except 2001), and [c] Slide Lakes, the subsequent 2-km reach to the fall above the lakes (except 2001), except the lakes themselves were not sampled); and (5) a 4-km reach of Lee Creek that extended upstream from Jule Creek. In addition, periodic (i.e., during 2 or 3 years) electrofishing occurred in (6) the lowermost 2 km of Rose Creek; (7) a 1-km reach of Wild Creek that extended upstream from the park boundary; (8) a 3-km reach of Canyon Creek; as well as (9) Jule, (10) Middle Fork Lee, and (11) East Fork Lee creeks, each within 0.5 km upstream and downstream from their crossings by the highway.

We used a battery-powered backpack electrofisher operated at 500–800 V with pulsed DC (25–30 Hz) to capture fish. During electrofishing, a single, upstream-moving pass was made through each sampling reach, sometimes requiring multiple days. Creek flows were seasonally low and clear and we selectively netted bull trout, brook trout, and other oncorhynchids (i.e., char and trout). Age-0 fish were not specifically sought during 1998 and 1999 and often passed through our nets. However, beginning in 2000 we also caught representative samples of age-0 bull trout.

Captured char and trout were identified to species and counted, whereas the occurrences of mountain whitefish and the sculpins (species not distinguished) were only noted. Accordingly, all char and trout caught from a creek (or each Otatso Creek reach) in a single year constituted an electrofishing sample. It was not practical for us to distinguish the hybrids or genetic intergrades of cutthroat trout and rainbow trout from their parent species or subspecies on the basis of external morphological characteristics evident in the field. Consequently, all of those fishes were assigned to a single taxon (i.e., cutthroat trout × rainbow trout intergrades).

Bull trout were measured to total length (TL; mm) and weighed (g), and (through 2002) scales were taken from an area just posterior to the dorsal fin and above the lateral line of many fish longer than about 75 mm TL. We did not distinguish between sexes. Passive integrated transponder (PIT) tags, each uniquely coded, were injected into dorsal musculature (approximately parallel to the spine and about 5 mm under the skin) of bull trout 200 mm TL or larger. The adipose fin was removed from tagged fish. All bull trout were examined for previously applied tags. For analyses of data taken from recaptured bull trout, a recapture event consisted of a recapture that occurred at least one field season after the previous capture.

Trapping (1997–2000).—Annually between about late August and mid-October, fish traps were operated near the mouths of Divide Creek (except 1999, 2000), Boulder, Kennedy, and Otatso creeks, and on Lee Creek at the highway crossing (except 1997, 1998; Figure 1). Trapping was primarily intended to catch postspawning migratory bull trout as they departed the creeks.

Traps caught only fishes moving downstream and consisted of a holding box and attached weirs. Boxes (1.0 m × 1.0 m × 1.0 m) had steel-tubing frames, 1.3-cm-mesh hardware-cloth walls and bottoms, and lockable plywood lids. Weirs consisted of 1.2-m lengths of 1.7-cm-diameter steel conduit that were separated by 2.5-cm plastic spacers and tightly strung on two parallel cables to form a picket fence. Weirs were attached to the box entrance, angled upstream to opposing creek banks, and supported by steel fence posts driven into the creek bottom. A 20-cm-long, rubber-coated hardware-cloth funnel extended from the entrance into the box.

Traps were operated continuously and checked daily. Creek flows were usually clear and rarely exceeded 0.5 m^3/s, except frequent rains in 1999 and 2000 sometimes resulted in higher flows. Leaves from quaking aspen *Populus tremuloides* frequently clogged weirs, which sometimes collapsed. Creek temperatures were recorded bi-hourly during trapping by an electronic thermometer installed at each trap site.

Captured fish were processed as previously described, except that only char, trout, and mountain whitefish were counted. Also, in 1997 bull trout were tagged with uniquely coded visual implant (VI) tags injected just under the epidermis and immediately posterior to the left eye. All tallied fish caught in a trap during a single year constituted a sample. For some subsequent analyses, we used TL measurements less than 300 mm and 300 mm or larger to classify bull trout as either juveniles or adults. That delineation was supported by additional data described herein. Traps were removed for the year either when few bull trout were being caught and the postspawning migration appeared to have ended or when inclement weather precluded further trapping.

Estimation of migratory adult population size.—Tagging and recapture event data from trapping were used to estimate size of the migratory adult (i.e., ≥300 mm TL) bull trout population in each creek. Accordingly, a bull trout tagged during electrofishing but subsequently caught in the trap was treated as a "new" fish when trapped. For population estimation, we fitted the POPAN-5 parameterization of the Jolly–Seber open-population model provided in program MARK (White and Burnham 1999) to the encounter histories for bull trout caught in each trap. We considered all possible combinations of both constant and time-dependent forms for each of the three relevant parameters estimated by the model (i.e., ϕ [apparent survival between years], p_d [probability of detection], and p_e [probability of entrance into the population]). We report results only for those models that also provided estimates of population size. The logit function was used to link the linear model specified in the design matrix; however, when the model being fitted had multiple p_e parameters, the multinomial logit link function was used to constrain the real parameters. Because open-population models require data for at least three capture events (i.e., years in our study), only data from traps at Boulder, Kennedy, and Otatso creeks could be used to estimate population size.

Bull trout age estimation.—Scales taken from bull trout were impressed on cellulose-acetate cards. Magnified impressions were examined by a single analyst (J.T.M.), who counted the apparent annuli (i.e., zones of closely spaced circuli) used to estimate age. Impressions for 891 (90%) of 989 bull trout sampled for scales were readable, not indicative of regenerate scales and, thus, useful for such counts. As one means of checking our aging technique, we compared mean total lengths at capture for the scale-based age-classes of bull trout with representative length-frequency distributions for bull trout caught by electrofishing. As a second check, we compared the increase in scale-based age (year) for each recaptured bull trout with the fish's known increase in age (i.e., the year of recapture minus the year of initial capture).

Statistical analyses.—Statistical analyses, apart from those provided in program MARK (White and Burnham 1999), were performed with the Number Cruncher Statistical System (Hintze 2001)

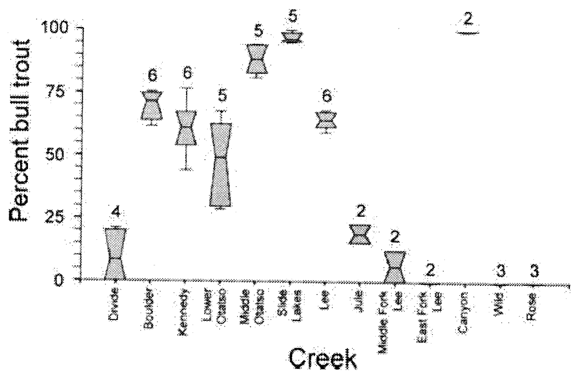

FIGURE 2.—Box plots of percent bull trout in samples caught by electrofishing in creeks of the St. Mary River drainage, Montana, 1998–2003. Plots indicate the median value at the box notch, interquartile range by the box itself, and the range of values by horizontal lines at the ends of vertical lines. Numbers are the numbers of samples (years).

after tests had been conducted to ensure that the routine assumptions of normality and equal variance in the error term had been met. When necessary, transformations of appropriate variables were performed to meet those assumptions (Neter et al. 1996). One-way analysis of variance (ANOVA) and a general linear model (GLM) ANOVA procedure were used to determine whether significant ($P < 0.05$) differences in the variable of concern occurred between or among the sampled populations.

Results

Distribution of Bull Trout and Other Fishes

Bull trout were found in 8 of the 11 creeks (i.e., all those except East Fork Lee, Wild, and Rose creeks). They constituted more than half of the fish in each electrofishing sample from Boulder, Lee, and Canyon creeks and the middle Otatso and Slide Lakes reaches, as well as many of the samples from Kennedy and lower Otatso creeks (Figure 2). Average size of the 51 electrofishing samples was 91 fish (range, 2–434 fish); samples did not exceed 48 fish for first-order creeks. Collectively, 88% of the other fishes in samples were cutthroat trout × rainbow trout intergrades. Brook trout were found only in Divide, Boulder, Kennedy, and Rose creeks, where they averaged 8% (range, 0% to 21%) of samples. Mottled or spoonhead sculpins were found in Divide, Boulder, Kennedy, and lower Otatso creeks, as were mountain whitefish, which were also found in Rose Creek.

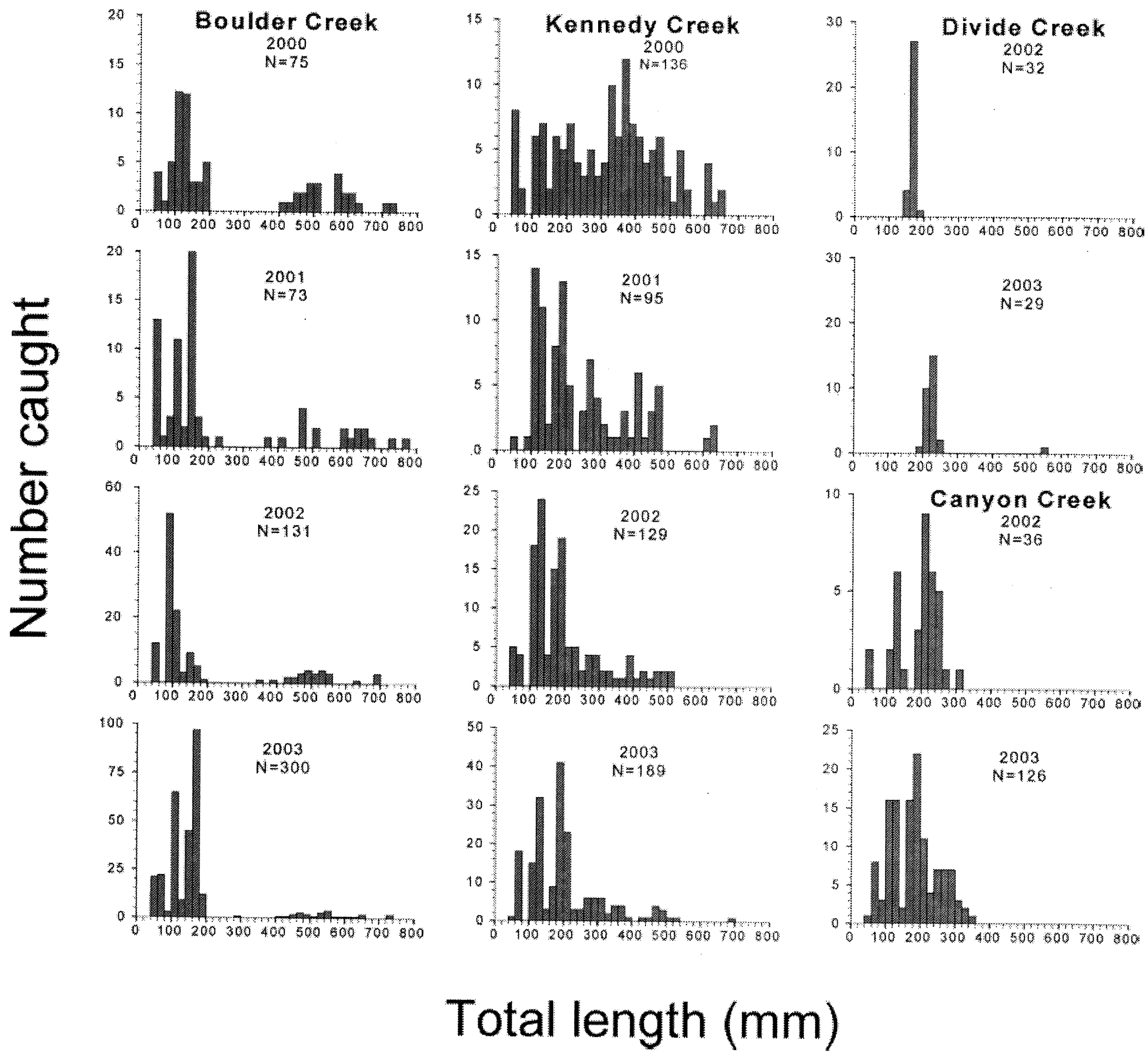

FIGURE 3.—Length-frequency distributions for bull trout caught by electrofishing in selected creeks in the St. Mary River drainage, Montana. Data are from Boulder and Kennedy creeks (third-order streams) and Divide and Canyon creeks (second-order streams) in 2000–2003, when samples of age-0 bull trout were also collected.

Length Frequency of Electrofished Bull Trout

Length-frequency distributions for bull trout caught by electrofishing revealed multiple size-classes and indicated recent reproduction in Boulder, Kennedy, Otatso (middle and Slide Lakes reaches), Lee, and Canyon creeks, as evidenced by the presence of fish less than 100 mm TL. Bull trout in Boulder, Kennedy, and Canyon creeks showed modal size-classes centered around fish about 50 mm TL, 100 mm TL, and 180 mm TL that appeared to be age 0, age 1, and age 2, respectively (Figure 3). The single bull trout size-class in Divide Creek was about 180 mm TL in 2002 and 220 mm TL in 2003 when one 547 mm TL bull trout was also caught. The largest bull trout caught during the study was 763 mm TL.

Bull Trout Age and Growth

The first scale annulus was formed during the second year of life, as evidenced by its occurrence near the margin on scales taken from nearly all bull trout considered age 1 on the basis of length frequency. The relation between bull trout TL and scale-based age at capture indicated growth at all ages, particularly as age-4 fish (Figure 4). Among study years, we found no consistent within-age differences in mean TL of bull trout, either among creeks or reaches or between bull trout caught by

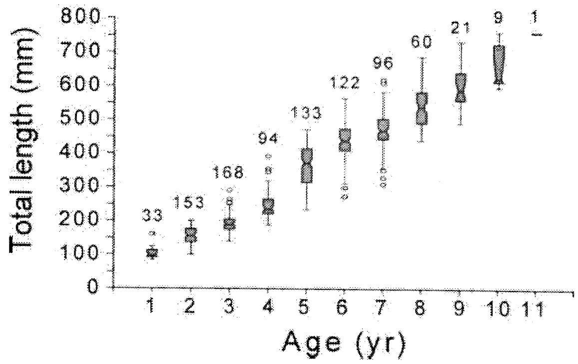

FIGURE 4.—Box plots of total length at capture by scale-based age for 890 bull trout (the single age-0 fish is not shown) caught by electrofishing and in traps in the St. Mary River drainage, Montana, 1997–2002. Plots indicate the median value at the box notch, the interquartile range (IQR) by the box itself, and the range of values by horizontal lines at the ends of the vertical lines; outliers (i.e., data values >1.5 IQR from the box) are indicated by circles. Numbers are the numbers of fish.

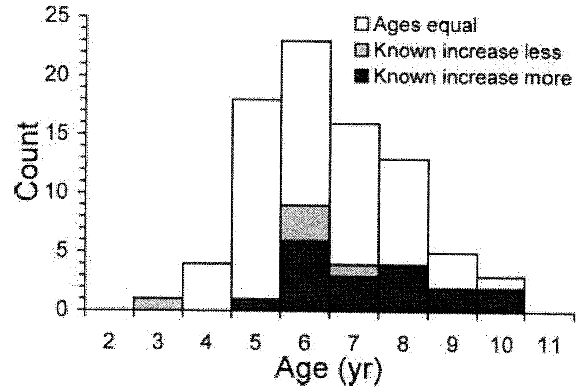

FIGURE 5.—Age frequency of 83 recaptured bull trout from the St. Mary River drainage, Montana, 1997–2002, for which increases in known age and scale-based age were compared. The horizontal axis shows scale-based age at time of initial capture. Fish were separated into three groups: those for which the increases in ages were equal, those for which the known increase was more than the scale-based increase, and those for which the known increase was less than the scale-based increase.

electrofishing or in traps in each creek where those methods were concurrently employed (GLM ANOVAs). Mean total length at capture for age-1 bull trout was 103.2 ± 5.2 mm (mean and 95% confidence interval), 155.4 ± 3.8 mm for age-2 bull trout, and 191.5 ± 3.9 mm for age-3 bull trout. Thus, the length-frequency distributions (Figure 3) revealed age-1 (and age-0) bull trout, but age-2 and age-3 fish apparently formed a single size-class. The single size-class of bull trout in Divide Creek in 2002 (Figure 3) consisted entirely of age-2 fish (scales were not collected in 2003).

For the 83 recaptured bull trout that had useful scales, known increase in age equaled the age increase determined from scales for 60 (72%) fish and was one year greater for 15 (18%) fish and one year less for 5 (6%) fish; the maximum difference was 3 years. Seventy-eight (94%) of the recaptured fish were age 5 or older when initially caught (overall mean, age 6.5); known increase in age exceeded the increase in scale-based age only for bull trout that were age 5 or older when initially caught (Figure 5).

Trapped Bull Trout

The average size of the 16 trap samples was 155 fish (range, 21–333 fish). Bull trout were annually caught in each trap (except in Divide Creek in 1998) and there was little variation in their percent occurrence among samples within individual creeks (Figure 6). Average number of bull trout in samples was 39 (range, 0–88 fish). Among the 626 bull trout caught, 317 (51%) were considered juveniles (i.e., <300 mm TL) and 309 (49%) adults (≥300 mm TL). Average number of adults in samples was 19 (range, 0–64 fish); only 2 bull trout (both adults) were caught in the Divide Creek trap in 1997. When Divide Creek was excluded, the mean number of adult bull trout per sample did not differ among creeks (ANOVA of lognormal number of adults, $F_{3,10} = 1.95$, $P = 0.19$; overall mean, 22 ± 8 adults/sample).

Although adult bull trout were often caught soon after traps were installed each year, capture of half of the total annual catch was usually not attained

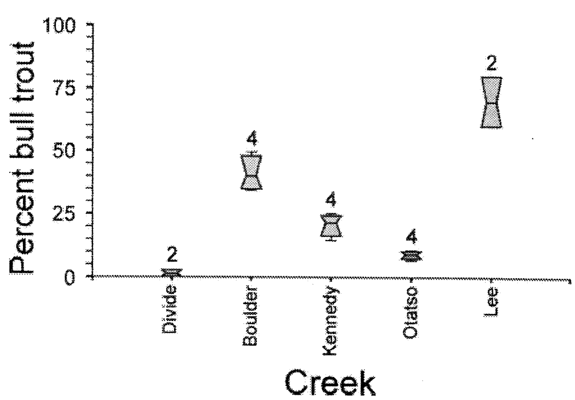

FIGURE 6.—Box plots of percent bull trout in samples caught in traps in five creeks in the St. Mary River drainage, Montana, 1997–2000. Plots indicate the median value at the box notch, the interquartile range by the box itself, and the range of values by horizontal lines at the ends of vertical lines. Numbers are the numbers of samples (years).

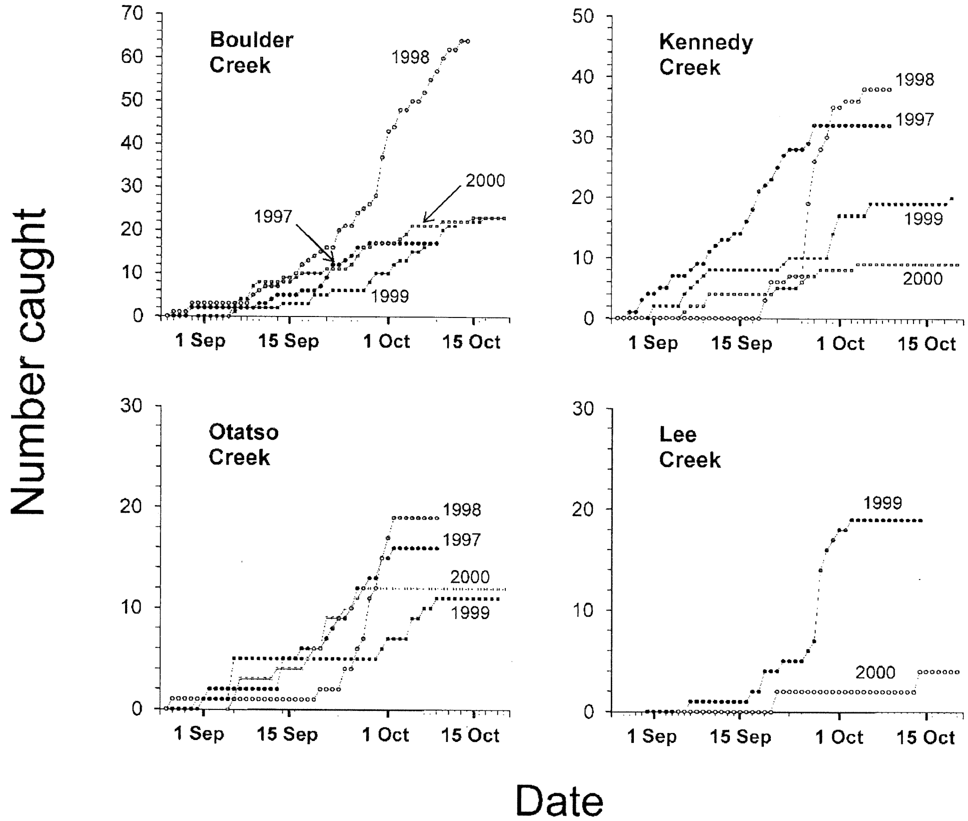

FIGURE 7.—Cumulative catches in traps of adult bull trout (≥300 mm TL) in Boulder, Kennedy, Otatso, and Lee creeks, 1997–2000, St. Mary River drainage, Montana.

until after mid-September (Figure 7). Among years, mean daily creek temperatures were usually 10–15°C on 1 September and had declined to 2–10°C by 1 October. Collectively, 85% of the other fishes in samples were mountain whitefish and 15% were cutthroat trout × rainbow trout intergrades. Four brook trout were caught—three in Boulder Creek and one in Divide Creek.

Migratory Adult Population Size

Only models with constant ϕ, p_d, and p_e parameters afforded estimates of migratory adult bull trout population size; this occurred only for Kennedy and Otatso creeks. Those estimates represent the total number of bull trout that were available for capture at any time during the study (Williams et al. 2002). Estimated populations of migratory adult bull trout in Kennedy Creek and Otatso Creek (i.e., 105 fish; asymmetric 95% confidence interval, 88–168 fish) and 49 fish (43–84 fish) were two or more times larger than the mean number (22 ± 8) of adults in trap samples.

Age Frequencies of Electrofished and Trapped Bull Trout

Scale-based age frequencies of bull trout caught by electrofishing or in traps differed consistently in the third-order creeks (i.e., Boulder, Kennedy, and Otatso) during years when both capture methods were employed (Figure 8). Although ranges in ages were similar between methods in each creek, age-4 bull trout were conspicuously scarce in trap samples (compared with adjacent age-classes), except in Lee Creek, the only second-order stream. Scarcity of age-4 fish in trap samples resulted in two modal groups that consisted mainly of ages 2 and 3 and ages 5 and 6. No age-4 or age-5 bull trout occurred in electrofishing samples from Lee Creek. In contrast, age-4 bull trout were common in electrofishing samples from Kennedy Creek and represented the most common age-class from Otatso Creek (lower and middle reaches combined).

Movements of Tagged Bull Trout

Either VI (n = 84) or PIT (n = 770) tags were placed in 854 bull trout, 628 (74%) of which had

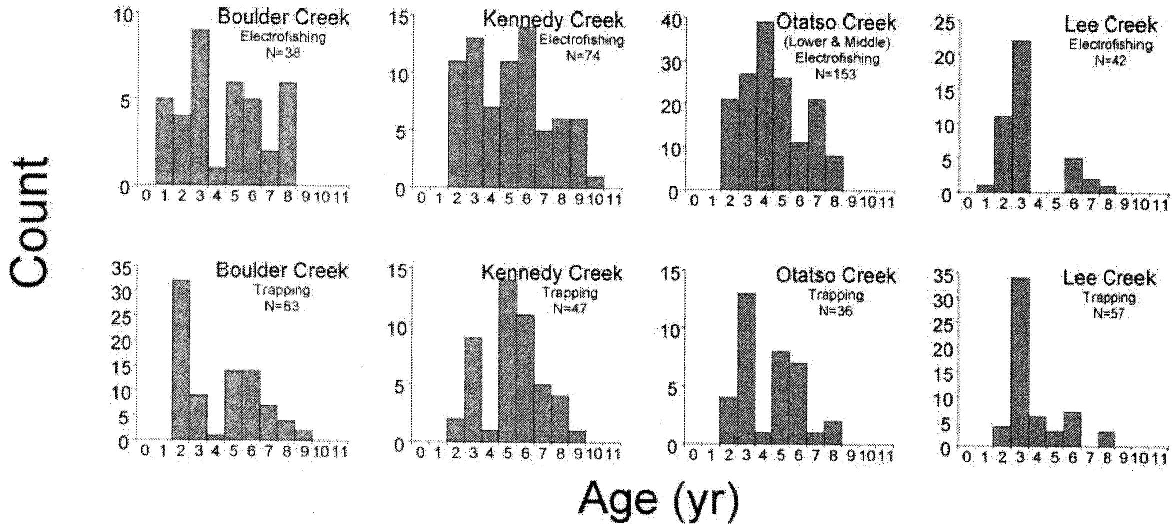

FIGURE 8.—Age-frequency distributions for bull trout caught by electrofishing or in traps in Boulder, Kennedy, Otatso (1998 and 1999 combined) and Lee (1999) creeks, St. Mary River drainage, Montana.

been caught by electrofishing and 226 (26%) in traps. On the basis of captured fish that already had excised adipose fins, 151 (18%) of the tagged bull trout were recaptured in subsequent years and tags were retained in 143 (95%) of those fish. Most (84%) recapture events occurred in the creek where the fish had been tagged, although there were 34 instances of bull trout movements between creeks (Table 1). Such movements occurred among Boulder, Kennedy, and Otatso creeks. One bull trout tagged in the Slide Lakes reach was recaptured in the middle Otatso reach. None of the bull trout tagged in Divide (2 fish) or Canyon (22 fish) creeks was recaptured.

Discussion

Catches of postspawning bull trout in traps suggested that most migratory fish had spawned by late September, although the fish continued to be caught in early October in most years. Bull trout spawning has been reported to occur when creek temperatures in the fall decline to between 9°C and 5°C (Fraley and Shepard 1989), temperatures similar to those of our study creeks in September.

The occurrence of age-0 fish indicated that bull trout recently spawned in five creeks and annual reproduction was indicated by multiple age-classes of young fish. In contrast, the single year-class of young bull trout in Divide Creek suggested only periodic reproduction there. Divide Creek's bull trout spawning population was especially small, as indicated by the capture of only two adult fish in the trap and one adult by electrofishing. We have no explanation for the scarcity of that spawning population. However, small population size and widely varying reproductive success among years

TABLE 1.—Summary of bull trout tagging and recapture events, 1997–2003 combined, St. Mary River drainage, Montana. A recapture event consisted of a recapture that occurred at least one field season after the previous capture; an individual fish may have multiple recapture events. The numbers in parentheses are percentages of tagged fish that were recaptured or recapture events for individual tagging locations or all locations together.

Tagging location	No. of fish tagged, 1997–2002	No. of fish recaptured, 1998–2003	No. of recapture events, 1998–2003	Location and number of recapture events							
				Divide Creek	Boulder Creek	Kennedy Creek	Lower Otatso	Middle Otatso	Slide lakes	Lee Creek	Canyon Creek
Divide Creek	2	0	0	0	0	0	0	0	0	0	0
Boulder Creek	148	48 (32)	79	0	75 (95)	2 (3)	2 (3)	0	0	0	0
Kennedy Creek	230	57 (25)	79	0	8 (10)	62 (79)	9 (11)	0	0	0	0
Lower Otatso	79	27 (34)	37	0	1 (3)	10 (27)	25 (67)	1 (3)	0	0	0
Middle Otatso	101	4 (4)	5	0	0	0	0	5 (100)	0	0	0
Slide Lakes	16	1 (6)	1	0	0	0	0	1 (100)	0	0	0
Lee Creek	58	6 (10)	7	0	0	0	0	0	0	7	0
Canyon Creek	22	0	0	0	0	0	0	0	0	0	0
Total	656	143 (22)	208	0	84 (40)	74 (36)	36 (17)	7 (3)	0	7 (3)	0

probably resulted in the single year-class of young bull trout found in the creek. Moreover, bull trout in Divide Creek apparently consisted entirely of migratory fish.

Although our estimates of bull trout age could not be validated with the use of known-age fish (in the sense of Beamish and McFarlane 1983), the analyses suggested the scale annuli were broadly representative of bull trout ages in the creeks. When errors in age estimates occurred, they probably resulted most often in underestimates of actual age for bull trout age 5 or older (i.e., mature fish). Bull trout had growth rates similar to those in Montana's Flathead River drainage (Fraley and Shepard 1989) and elsewhere (Goetz 1989). The marked growth of age-4 bull trout probably resulted from their transition to a largely piscivorous diet, as has been reported for other populations of the species (Goetz 1989).

Trap samples indicated that juvenile migratory bull trout departed creeks mainly as age-2 or age-3 fish. Studies of other bull trout populations indicated that most juveniles of migratory populations remained in natal creeks 1 or, most often, 2–3 years before moving downstream to lakes or large rivers (Fraley and Shepard 1989; Goetz 1989; Riehle et al. 1997). Because our traps were operated between late August and mid-October, the entire annual period of juvenile bull trout movement from creeks could not be determined. Between late April and mid-October 1990, Riehle et al. (1997) continually operated a trap in Jack Creek, Oregon. Juvenile migratory bull trout that were emigrating from the creek were caught in all months, but were most abundant in May and June.

The scarcity of age-4 bull trout in trap samples from Boulder, Kennedy, and Otatso creeks suggested that most migratory age-4 fish were immature and inhabited either the St. Mary lakes or St. Mary River. The marked growth of age-4 bull trout supported that speculation because the lakes and river are probably more productive habitats than the creeks. Trap samples also indicated that migratory bull trout reached maturity mainly as age-5 fish, which our scale analyses indicated were typically 300 mm TL or larger. There was no conspicuous absence of age-4 bull trout in the trap sample from Lee Creek, perhaps because only one sample was available and because those fish mainly consisted of nonmigratory bull trout that were making restricted movements to nearby wintering areas (Jakober et al. 1998; Nelson et al. 2002).

Both migratory and nonmigratory bull trout occurred in the St. Mary River drainage in Montana. Migratory fish were most conspicuous because they were caught in traps or were recaptured in creeks other than those in which they had been tagged. In contrast, nonmigratory bull trout were not easily identified. For example, we found no consistent within-age differences in mean TL of bull trout caught by electrofishing or in traps in creeks where those methods were concurrently employed. However, our electrofishing samples contained both migratory and nonmigratory bull trout. Consequently, some similarity in the data from those samples and those of migratory bull trout caught subsequently in traps is anticipated. Moreover, other studies have shown that growth rates of nonmigratory salmonids may not differ from those of sympatric migratory fish of the same species (McCart 1997). On the other hand, the abundance of age-4 bull trout in electrofishing samples from Kennedy Creek and lower and middle Otatso Creek, which contrasted with Boulder Creek, strongly suggested the presence of numerous nonmigratory fish. In addition, we frequently caught bull trout less than 300 mm TL in middle Otatso, Canyon, and Lee creeks that had coloration and external morphology (e.g., kyped jaw) indicative of mature fish and suggestive of a nonmigratory population.

The estimated populations of migratory adult bull trout were larger than implied by the annual catches of trapped fish. That observation suggested that either (1) many postspawning migratory bull trout lingered in creeks before moving downstream after the traps had been removed; (2) many migratory bull trout did not spawn annually; or (3) a combination of these factors. In any case, our data indicated that mean values for the annual catches of adult bull trout in traps, which did not differ among creeks, were not by themselves indices of spawning population size.

Recapture data revealed bull trout movements among Boulder, Kennedy, and Otatso creeks. No movement was seen in bull trout tagged in Divide, Canyon, or Lee creeks, which were characterized by no recaptured fish or distinct isolation from the other study creeks. Some bull trout moved upstream or downstream over the St. Mary Diversion Dam as well as downstream over the rockslide that formed the Slide Lakes. Thus, those structures are not complete barriers to the movement of bull trout.

Although one of our tagged bull trout moved downstream from Slide Lakes into the middle Otatso reach, we saw no reciprocal movement. Nevertheless, it is unclear whether bull trout in the

Slide Lakes reach should be considered a resident or isolated nonmigratory population (in the sense of McCart 1997) because the rockslide that formed the lakes is probably only a seasonal barrier to the upstream movement of fish. Alternatively, it could be argued that these fish are migratory because they probably reside most of the year in the lakes but are also obligate stream spawners. Contemporary criteria for classification of life history forms favor detection of migratory bull trout because the fish move between streams or between lakes and streams, movements that can be objectively determined. On the other hand, nonmigratory bull trout remain within a single stream but may undertake even longer seasonal migrations than some migratory fish. The shortcomings of current convention notwithstanding, migratory bull trout in the St. Mary River drainage are more common than previously believed and may be more common than in many other regions of the species' natural range (e.g., McCart 1997; Nelson et al. 2002).

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