# 2005 Sawtooth Aquatic Management Indicator Species Monitoring Report 

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## Introduction

In order to evaluate the effects of management practices on fisheries and wildlife resources, the U.S. Forest Service monitors select species whose population trends are believed to reflect the effects of management activities on Forest ecosystems. These species are termed "management indicator species" (MIS) and the rationale for MIS monitoring is outlined in federal regulation 36 CFR 219.19.
"In order to estimate the effects of each alternative on fish and wildlife populations, certain vertebrate and/or invertebrate species present in the area shall be identified and selected as management indicator species and the reasons for their selection will be stated. These species shall be selected because their population changes are believed to indicate the effects of management activities."
"Population trends of the management indicator species will be monitored and relationships to habitat changes determined. "

An important criterion integral to the MIS foundation is that monitoring results must allow managers to answer questions about population trends. Historically, monitoring of habitat was used a surrogate for direct quantification of MIS populations. However, recent court cases (Sierra Club v. Martin, 168 F.3d 1 (11 ${ }^{\text {th }}$ Cir. 1999)) have ruled that assessing changes in habitat will no longer be accepted as a substitute for direct monitoring of populations. The Forest Service
has an obligation to collect and analyze quantitative population trend data at both the forest-plan and project level.

In response to issues raised by court challenges, the Sawtooth, Boise, and Payette National Forests revisited aquatic MIS species for the Draft Forest Plan EIS to determine if the population data were sufficient to determine trend at the Forest scale.

Following this reevaluation, bull trout was selected as the aquatic MIS species (For a full explanation of the MIS review, see Aquatic Management Indicator Species for the Boise, Payette, and Sawtooth Forest Plan Revision, 2003). Bull trout were selected because the species is sensitive to habitat changes, dependent upon habitat conditions that are important to many aquatic organisms, relatively well understood by Forest biologists, and widely distributed across the Ecogroup. In addition, local bull trout populations are not influenced by stocking and likely persist at relatively small spatial scales that do not extend beyond Forest boundaries. As a result, Forest bull trout populations are probably not heavily influenced by activities occurring outside Forest domains, and therefore changes in bull trout populations will more likely reflect local management activities.

## Protocol

## Objectives

- Consistent with the existing Forest Plans for the Boise, Sawtooth, and Payette National Forests, determine the status and trend in distribution of bull trout within and among patches of suitable habitat within each subbasin across the planning area.
- To the full extent practicable, use the best available peer-reviewed science to allow formal inferences about observed status and trends in the distribution of bull trout.


## Rationale

Monitoring is focused on patterns of occurrence of juvenile and small resident bull trout (<150 mm ) for two reasons. First, presence of small bull trout is an indicator of key spawning and rearing areas. These areas represent habitats that are essential for bull trout populations. Other habitats within stream networks may be important for ranging or migrating individuals, but tracking fish in these areas is much more difficult. Second, sampling patterns of occurrence requires less intense sampling than estimating abundance and is based on a peer-reviewed protocol for sampling of small bull trout (Peterson et al. 2002); similar protocols for larger, more mobile fish have not been developed. Key metrics for monitoring trends will be the proportion of habitat patches occupied in each subbasin across time and the spatial pattern of occupied patches. In the future we intend to explore indices of abundance and distribution within individual streams that may be useful to characterize linkages with local management.

## Methods

Monitoring follows procedures specified by Peterson et al. (2002) ${ }^{1}$, with the following specific procedures and modifications.

[^0]Sampling frame. The fundamental unit for inference is a patch, defined following procedures outlined in Peterson et al. (2002), and further clarified by the U.S. Fish and Wildlife Service Bull Trout Recovery Monitoring and Evaluation Group. The procedure involves delineating both down- and upstream limits to potentially suitable habitats for bull trout within stream networks, and thus the area for locating samples, and making inferences about presence.

Downstream patch boundaries were delineated by 1600 meter elevation contours in the Boise and South Fork Payette River basins, based on previous research in the basins relating the distribution of small bull trout to elevation. Outside of these basins, downstream patch boundaries correspond to stream temperature $<15^{\circ} \mathrm{C}$ (highest seven-day moving average of maximum daily temperature). Downstream limits to patches may also correspond to a confluence with a stream that is classified as too large for bull trout spawning, based on observed relationships between spawning use and stream size, as revealed by redd counts, direct observation of fish, radio telemetry, or other evidence.

During monitoring, efforts will be made to distinguish between "realized" and "potential" patch boundaries. The term "realized" refers to actual habitat that is used by bull trout. This may be less than potentially occupied habitat due to the influence of other factors such as nonnative brook trout, dewatering of stream channels, or habitat alterations that increase stream temperature. The term "potential" refers to the maximum extent of coldwater naturally attainable, absent of reversible human influences. This assumes the distribution of suitably cold water is the ultimate factor limiting the distribution of small bull trout.

In the upstream direction, stream networks will be truncated to include only those segments ${ }^{2}$ with valley bottom slopes of less than $20 \%$. Further, all headwater areas within catchments corresponding to a contributing area of less than 500 hectares will be removed from sampling frames, due to low probability of bull trout occurrence (Dunham and Rieman 1999; cited in Peterson et al. 2002). Information on local barriers will also be considered in truncating stream networks. For example, it may not be necessary to sample upstream of high natural waterfalls that prevent upstream passage of bull trout.

Metadata. For each patch, criteria for delineating down- and up-stream boundaries of the stream network to be sampled will be documented as metadata to accompany spatial data.

Sample allocation. Individual samples will be allocated to all patches within a Forest or subbasin. Within patches, only suitable habitat will be inventoried for informal and formal surveys. Suitable habitat is defined according to wetted width (greater than 2 meters), stream gradient (less than $20 \%$ ), water temperatures ( $15^{\circ} \mathrm{C}$ or less, 7 -day average summer maximum), and access (no natural or anthropogenic barriers). Sites within each patch will be located by dividing the suitable habitat into 100 m segments and then randomly selecting the segments.

Sampling unit. The fundamental sampling unit will be a 100 meter length of stream.
Sampling method. Daytime electrofishing will be used to capture fish, with a variable number of passes, depending on conditions. Habitat variables needed to estimate sampling efficiencies will be measured. The sequence or order of sampling within patches is assumed to be unimportant, in terms of estimating probability of presence.

[^1]Formal vs. informal sampling. Informal sampling will be used initially to determine presence of juvenile bull trout, when deemed appropriate by local biologists. If juvenile bull trout are detected the informal sampling effort can cease, unless the local biologists wants to better determine distribution within the patch. If juvenile bull trout are not detected, it will be necessary to conduct formal sampling, as prescribed to estimate probability of presence in cases where bull trout are not detected (Peterson et al. 2002; Peterson and Dunham 2003). Site level detection probabilities will be estimated as outlined in Peterson et al. (2002) or through empirical methods based on repeated sampling of occupied patches and habitat information collected throughout the monitoring effort. If juvenile bull trout are detected during formal sampling, crews may either elect to cease efforts and move to other patches or continue sampling to better determine distribution within the patch and augment the development of the empirical models.

Sampling schedule. Initially, four patch types will be recognized: 1) Known presence within last 7 years; 2) Patches that have been surveyed and baseline conditions likely will support a bull trout population, but they have not been detected or patches where bull trout have been detected, but observation are older than 7 years; 3) Likely not present due to poor habitat and bull trout not detected within last 7 years; 4) Patches without data. Patches will be defined relative to "potential" to support bull trout as defined above. Over the 2003-2018 Forest Plan timeline, targeted patches in categories 1,2 , and 4 will be sampled at least twice. Initial sampling of each patch will be completed within first and last 7 year period of the Forest Plan, preferably with as much time as possible in-between samples to determine if a change has occurred. Patches in category 3 will be sampled at least once. Additional sampling or re-sampling will be conducted if there is specific reason to do so (e.g., passage restoration, habitat improvement). Based on results following sampling, patch strata will be updated yearly (Table 1).

Table 1. Number of bull trout patches on the Sawtooth National Forest within each subbasin by category prior to 2005 sampling

| Category | S.F. Boise <br> Subbasin | M.F./N.F Boise <br> Subbasin | S.F. Payette <br> Subbasin | Upper Salmon <br> Subbasin | Total |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | 12 | 4 | 2 | 11 | 29 |
| 2 | 20 | 1 | 2 | 20 | 43 |
| 3 | 11 | 0 | 0 | 6 | 17 |
| 4 | 0 | 0 | 0 | 7 | 7 |
| Total | 43 | 5 | 4 | 44 | 96 |

## 2005 Results and Discussion

Monitoring for bull trout on the Sawtooth N.F. occurred in 16 patches in 2005 (Figure 1). In the Boise subbasins, eight patches were surveyed. Of these patches, bull trout were observed in N.F. Big Smoky, Bluff, Boardman, and Skeleton Creeks. In Skeleton and Boardman Cr., bull trout were also detected in 2004 and 2005. Sampling in these patches continued long term monitoring (since 2002) of these populations. Bull trout had been observed in Bluff Creek in 1993 and 2001, and the detection in 2005 indicates persistence of this population. Sampling in the mainstem of N.F. Big Smoky in 1993 and 1999 did not detect bull trout, though bull trout were detected in a side tributary (Snowslide Cr.) in 1999. During this year's sampling, bull trout were detected in all sample sites (3 of 3) in the N.F. Big Smoky patch (Table 4), indicating either previous sampling missed bull trout when present or possibly a population expansion within the patch.

Bull trout were not observed in Skunk Cr. despite six sampling locations and a probability of detection of $46 \%$. Similarly, bull trout were not observed in Elk, Bridge, or Paradise Creeks. However, these locations had relatively low probabilities of detection (mean $=25$, range $=21 \%$ $27 \%$ ). All of the locations in the Boise subbasins where bull trout were not detected had been sampled in prior years with similar results, indicating that bull trout were not present in these patches in the past, and therefore, have not been extirpated. Concomitantly, results imply that successful colonization of these patches has not occurred. Interestingly, despite a lack of observed bull trout, Bridge Cr. and Elk Cr. each have water temperatures that are preferred by bull trout, with MWMT at the lowest point of the patch recorded as $14.5^{\circ} \mathrm{C}$ and $12.6^{\circ} \mathrm{C}$, respectively (see Patch Stream Temperature Monitoring). However, accessible habitat within each patch is limited to the lower most mile because of steep gradients ( $>11 \%$ ), potential natural barriers, and small stream widths. Still, because of their cold-water temperatures and low probabilities of detection, Bridge Cr . and Elk Cr. should be closely monitored in the future.

During 2005 in the Salmon subbasin, seven patches were electrofished using formal protocols and one patch was snorkeled informally (Alturas Lake Cr.). Of the patches sampled, only two patches were determined to be occupied by bull trout (Warm Springs Cr. and Alturas Lake Cr.). Each of these patches was known to biologists as supporting relatively strong bull trout populations. A large fire (Valley Rd Fire) burned extensive portions of the Warm Springs Cr. patch several months after it had been sampled for bull trout. Large fish kills were associated with the fire and it is unknown what influence the fire might have on the long-term persistence of bull trout in locations affected by the fire.

One-pass electrofishing surveys failed to detect bull trout in the Frenchman, Gold, Boundary/Cleveland, Little Casino, Big Lake, or Crooked patches. Results appear to be influenced by water temperature with all patches without bull trout having MWMT above $15^{\circ} \mathrm{C}$. Two patches, Frenchman and Crooked, had prior records of bull trout detections, but in 2005, both of these patches were dominated by non-native brook trout. In the Crooked Cr. patch, two hybrid bull/brook trout were observed though no pure strain bull trout were noted (see Hybridization). In the Boundary/Cleveland patch wetted stream width was less than 2 m and in the Gold patch, MWMT at the mouth was $17.2^{\circ} \mathrm{C}$; both factors have been associated with a low probability of bull trout presence (Dunham et al. 2003). Big Lake Cr. had a probability of detection of $52 \%$ and only rainbow trout and sculpin were observed. It is possible that a low flow barrier exists downstream in Big Lake Cr. below the outflow of Jimmy Smith Lake. This barrier could influence bull trout colonization of the watershed. Little Casino had MWMT of 16.5 which is slightly above bull trout preferred values (Dunham et al. 2003); perhaps explaining the lack of any bull trout observations.

In 2004 and 2005, the MIS protocol was used to sample a significant portion of the patches on the Sawtooth N.F. (Table 2). In addition, using data from the past 7 years (since 1999) (Table 3), all of the patches in the S.F. Boise and M.F./N.F. Boise have been sampled. In the Upper Salmon $59 \%$ of the patches have been sampled, while $75 \%$ in the S.F. Payette on the Forest are sampled.


Figure 1. Bull trout patches sampled and probabilities of detection on the North Zone of the Sawtooth N.F. (2005).

Table 2. Number of bull trout patches on the Sawtooth National Forest and the number surveyed with the current MIS protocol (as conducted in 2004 and 2005) within each subbasin by category (category based on 2004 strata).

| Category | S.F. Boise Subbasin |  | N.F. and M.F. Boise Subbasin |  | S.F. Payette Subbasin |  | Upper Salmon Subbasin |  | Total |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Patches | Surveyed | Patches | Surveyed | Patches | Surveyed | Patches | Surveyed | Patches | Surveyed |
| 1 | 12 | 4 (33\%) | 4 | 0 | 2 | 2 (100\%) | 11 | 1 (9\%) | 29 | 7 (24\%) |
| 2 | 20 | 7 (35\%) | 1 | 0 | 2 | 1 (75\%) | 20 | 7 (35\%) | 43 | 28 (65\%) |
| 3 | 11 | 0 | 0 | 0 | 0 | 0 | 6 | 3 (50\%) | 17 | 3 (18\%) |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 2 (29\%) | 7 | 2 (29\%) |
| Total | 43 | 11 (25\%) | 5 | 0 | 4 | 3 (75\%) | 44 | 13 (30\%) | 96 | 27 (28\%) |

Table 3. Number of bull trout patches on the Sawtooth National Forest and the number surveyed within the past 7 years (since 1999) within each subbasin by category (category based on 2004 strata).

| Category | S.F. Boise <br> Subbasin |  | N.F. and M.F. Boise Subbasin |  | S.F. Payette Subbasin |  | Upper Salmon Subbasin |  | Total |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Patches | Surveyed | Patches | Surveyed | Patches | Surveyed | Patches | Surveyed | Patches | Surveyed |
| 1 | 12 | 12 (100\%) | 4 | 4 (100\%) | 2 | 2 (100\%) | 11 | 11 (100\%) | 29 | 29 (100\%) |
| 2 | 20 | 20 (100\%) | 1 | 1 (100\%) | 2 | 1 (50\%) | 20 | 13 (65\%) | 43 | 36 (81\%) |
| 3 | 11 | 11 (100\%) | 0 | 0 | 0 | 0 | 6 | 2 (33\%) | 17 | 13 (76\%) |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 7 | 0 (0\%) |
| Total | 43 | 43 (100\%) | 5 | 5 (100\%) | 4 | 3 (75\%) | 44 | 26 (59\%) | 96 | 78 (81\%) |

## Bull Trout Detection

At the patch scale, probability of detection of bull trout ranged from 21-53\% (Figure 1, Table 4). Interestingly, current data suggests that bull trout are detected more frequently in relatively large patches vs. smaller patches (Figure 2). This could be artifact of sampling error associated with patch delineations, or may provide further insight into the habitat requirements of bull trout on the Sawtooth N.F. For example, larger patches, due solely to their larger size, may have a higher probability of providing the habitat heterogeneity necessary for bull trout persistence.

Table 4. Summary of results from 2005 aquatic MIS sampling on the Sawtooth N.F.

| Subbasin | Patch | Strata <br> $(\mathbf{2 0 0 4})$ | Bull Trout <br> Detected | \# Sites sampled | \# Sites where <br> Bull Trout <br> < 150mm were <br> found |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Salmon | Alturas | 1 | + | 2 | 2 |
| Salmon | Crooked | 2 | - | 8 | - |
| Salmon | Warm Springs | 1 | + | 8 | 4 |
| Salmon | Little Casino | 4 | - | 7 | - |
| Salmon | Boundary/Cleveland | 4 | - | 3 | - |
| Salmon | Frenchman | 2 | - | 8 | - |
| Salmon | Gold | 2 | - | 5 | - |
| Salmon | Big Lake | 2 | - | 8 | - |
| S.F. Boise | Paradise | 2 | - | 3 | - |
| S.F. Boise | Bluff | 1 | + | 1 | 1 |
| S.F. Boise | N.F. Big Smoky | 1 | + | 3 | 3 |
| S.F. Boise | Skunk | 2 | - | 6 | - |
| S.F. Boise | Boardman | 1 | + | 16 | - |
| S.F. Boise | Elk | 2 | - | 3 | - |
| S.F. Boise | Bridge | 2 | - | 3 | - |
| S.F. Boise | Skeleton | 1 | + | 12 | 9 |

Patch Size vs. Bull Trout Presence


Figure 2. Patch size (hectares) in patches where bull trout were detected (1) vs. those were bull trout were not observed (0). Figure includes 2004 and 2005 data.

## Patch Stream Temperature Monitoring

Monitoring stream temperatures allows forest biologists to assess the influence of management practices on water temperatures (Meehan 1991), predict species distributions (Dunham et al. 2003), and update MIS patch strata. As such, stream temperature monitoring plays a critical role in this aquatic MIS approach. During 2005 in the Boise and Salmon sub-basins, 77 temperature loggers were deployed in 41 patches (Figure 4). Because maximum water temperatures on the Sawtooth tend to occur between mid-July and mid-September (Sawtooth NF. unpublished data), water temperature loggers are deployed in early summer (prior to July 1 ) and recovered in early fall (after Sept 1). Gamett (2002) found that mean water temperature (July 1 to September 30) appeared to be the most effective in describing bull trout abundance in the Little Lost river drainage. In addition, Dunham (2003) found that the probability of bull trout occurrence was relatively high ( $>0.50$ ) in streams with a maximum daily maximum temperature (MDMT, the warmest daily water temperature recorded during a given year or survey) $<14-16^{\circ} \mathrm{C}$.

Maximum daily maximum temperature (MDMT) and maximum weekly maximum temperature (MWMT, the mean of daily maximum water temperatures measured over the warmest consecutive seven-day period) were calculated for each patch and provide important information for managers when classifying patches into strata or assessing the presence or absence of bull trout. Even though no statistically significant relationship was observed (two sample T-test, $\alpha=$ 0.05 ), median MWMT temperatures where bull trout were observed were lower than median MWMT temperatures where bull trout were not observed $\left(16.2{ }^{\circ} \mathrm{C}\left(12-19^{\circ} \mathrm{C}\right.\right.$ range $)$ vs. $14.2^{\circ} \mathrm{C}$ ( $12-18^{\circ} \mathrm{C}$ range) as measured at patch confluence (Figure 3)).

Patch Temp at Mbuth vs. Bull Trout Presence


Figure 3. Maximum weekly maximum temperature $\left({ }^{\circ} \mathrm{C}\right)$ as measured at the confluence of patches where bull trout were detected (1) vs. those where bull trout were not observed (0). Figure includes 2004 and 2005 data.


Figure 4. Temperature Loggers Deployed on the North Zone of the Sawtooth N.F. (2005)

## Barriers

MIS results will also help managers assess the influence of fish passage barriers on bull trout populations. Passage barriers can have a strong influence upon species distributions as well as the life-history expression of fish populations. Several of the patches sampled during 2005 contained barriers that could influence the presence or persistence of bull trout. For example, in the Boundary/Cleveland patch, low flows as a result of diversions and landscape manipulations have eliminated historic connections with the mainstem Salmon, effectively isolating this patch from any fish colonization or recolonization. Current results suggest that patches must be large in order for isolated bull trout populations to persist and barriers that isolate small watersheds might prevent bull trout persistence (Figure 5). Fish passage barriers can provide positive or negative influences on bull trout populations, depending upon a variety of factors, including the presence of exotic species, the size of the isolated population, habitat conditions above and below the barrier, etc. Further MIS monitoring will assist in the evaluation of the influence of barriers on the persistence of bull trout populations on the Sawtooth N.F.

## Patch Size vs. Bull Trout Presence in Isolated Patches



Figure 5._ Isolated patch size where bull trout were detected (1) or not observed (0). Figure includes 2004 and 2005 data.

## Hybridization

MIS monitoring did detect a variety of game and non-game species across the Sawtooth N.F. (Table 5) including brook trout (Salvelinus fontinalis), a species know to hybridize with bull trout (Markle 1992, Leary et al. 1993). During the 2005 sampling season, hybrid brook/bull trout were observed in Crooked Cr. and Alturas Lake Cr. (Table 5, Figure 6). Recent research indicates that bull trout/brook trout F1 generation hybrids can reproduce, though less successfully than pure crosses between parent species (Markle 1992, Leary et al. 1993, Kanda et al. 2002). Bull trout hybridization with $S$. fontinalis is recognized as a major threat to the persistence of bull trout, largely as a result of population-scale wasted reproductive effort and genetic introgression .


Figure 6. Bull trout / Brook trout hybrid observed in Crooked Cr. patch in 2005.
Information from the Sawtooth MIS program (2004-2005) reveals that bull trout and brook trout are rarely found in the same patches (Figure 7). Because brook trout are widely distributed across the Sawtooth N.F., interactions between bull trout and brook trout and the effects of hybridization and competition may play a major role in the persistence of numerous bull trout populations.

## Fish Presence



## (only patches wherebull trout and/or brooktrout were detectedare shown)

Figure 7. Pie-chart depiction of all patches where bull trout and/or brook trout were detected. Figure includes 2004 and 2005 data.

## Conclusion

A variety of factors can influence the distribution of bull trout populations. As has been reported in the literature, results from MIS sampling on the Sawtooth N.F. indicates that patch size, stream temperature, fish passage barriers, and the occurrence of brook trout can all be associated with bull trout presence and persistence. In 2005, two patches that historically contained bull trout now appear to have lost these populations (Frenchman and Crooked Cr.), possibly as a result of brook trout competition and hybridization. In contrast, one patch (N.F. Big Smoky) may contain an expanding bull trout population. Additional sampling over the life of the forest plan will help further refine the habitat requirements of bull trout on the Sawtooth N.F. and provide information for proper management.

Table 5. Fish species detected during 2005 MIS sampling on the Sawtooth N.F.

|  |  | Species Observed |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Subbasin | Patch | BLT | BKT | BLTxBKT | RBT | CCT | RBTxCCT | SCP | CHS |
| Salmon | Alturas Lake Cr | + | + | + |  | + |  |  |  |
| Salmon | Crooked | - | + | + | + | - | - | + | - |
| Salmon | Warm Springs | + | - | - | - | + | - | - | - |
| Salmon | Little Casino | - | + | - | + | + | - | + | - |
| Salmon | Boundary/Cleveland | - | - | - | - | + | - | - | - |
| Salmon | Frenchman | - | + | - | + | + | - | + | - |
| Salmon | Gold | - | + | - | + | + | - | - | + |
| Salmon | Big Lake | - | - | - | + | - | - | + | - |
| Boise | Paradise | - | + | - | + | - | - | + | - |
| Boise | Bluff | + | - | - | - | - | - | - | - |
| Boise | N.F. Big Smoky | + | - | - | + | - | - | + | - |
| Boise | Skunk | - | - | - | + | - | - | + | - |
| Boise | Boardman | + | - | - | + | - | - | + | - |
| Boise | Elk | - | - | - | + | - | - | - | - |
| Boise | Bridge | - | - | - | + | - | - | - | - |
| Boise | Skeleton | + | - | - | + | - | - | + | - |

Note: $\mathrm{BLT}=$ bull trout, $\mathrm{BKT}=$ brook trout, $\mathrm{BLTxBKT}=$ bull trout $/$ brook trout hybrid, RBT $=$ redband/rainbow trout, $\mathrm{CCT}=$ cutthroat trout, $\mathrm{RBTxCCT}=$ redband $/$ cutthroat hybrid, $\mathrm{SCP}=$ sculpin, $\mathrm{CHS}=$ Chinook salmon.

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[^0]:    ${ }^{1}$ Available at www.fisheries.org and www.fs.fed.us/rm/boise

[^1]:    ${ }^{2}$ Stream segments are defined as lengths of stream within drainage networks that are delineated on the up- and down-stream ends by tributary confluences.

