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STATUS AND CONSERVATION OF SALMONIDS IN RELATION TO HYDROLOGIC INTEGRITY IN THE GREATER YELLOWSTONE ECOSYSTEM

Robert W. Van Kirk[1] and Lyn Benjamin[2]

ABSTRACT.—Native salmonid status was evaluated with an index quantifying distribution and abundance of cutthroat trout (*Oncorhynchus clarki*) and grayling (*Thymallus arcticus*) in 41 watersheds comprising the Greater Yellowstone Ecosystem. We assessed hydrologic integrity with a percentile-based index measuring cumulative effects of reservoirs, surface water withdrawals, and consumptive water use. Status of native salmonids was poor in 70% of the watersheds; exceptions occurred in a north–south core extending from the Upper Yellowstone southward through the national parks to Bear Lake. Hydrologic integrity was highest in headwater areas and lowest in lower-elevation watersheds. Status of native and nonnative salmonid populations currently existing in the ecosystem was positively correlated with hydrologic integrity ($r = 0.58$), indicating that the hydrologic index performed well on a watershed scale in quantifying suitability of stream environments for salmonids. However, native trout status and hydrologic integrity were similarly correlated ($r = 0.63$) only when watersheds receiving the lowest possible native salmonid index score were removed from analysis because these watersheds were uniformly distributed across hydrologic integrity. We infer that nonphysical factors such as interactions with introduced fish species have played an important role in the disappearance of native salmonids. The highest priority for conservation is preservation of core watersheds, where both hydrologic integrity and native trout status are high. Restoration opportunities exist in the Teton, Idaho Falls, Willow Creek, Central Bear, and Bear Lake watersheds, where viable cutthroat trout populations remain but are threatened by habitat degradation.

Key words: Greater Yellowstone, cutthroat trout, Oncorhynchus clarki, *hydrologic alteration, watersheds, introduced species.*

The Greater Yellowstone Ecosystem (GYE) contains the headwaters of 3 continental-scale watersheds, those of the Missouri, Snake, and Green rivers. These rivers are primary tributaries, respectively, to the Mississippi, Columbia, and Colorado rivers, which, together, drain well over half of the conterminous United States. Average annual discharge from the GYE into these rivers totals 2.0 million ha-m. Rivers and lakes of the GYE are internationally famous for their recreational and scenic values; the GYE is arguably the most popular trout fishing destination in the world. Despite the economic and ecological importance of the rivers and watersheds of the GYE, there exists relatively little ecosystem-scale information on the status of these rivers and the species that inhabit them. Of 9 papers in a 1991 special section of *Conservation Biology* devoted to the GYE (Brussard 1991), none dealt with fish or other aquatic resources. Only the paper of Marston and Anderson (1991) mentioned the importance of watersheds in contributing to the ecological structure and function of the GYE. These authors concluded that spatial trends in watershed condition need to be quantified as a key step in developing ecosystem management for the GYE.

The need for an ecosystem-scale inventory of aquatic resources in the GYE has become even more critical over the past decade. The 1994 discovery of lake trout (*Salvelinus namaycush*), a nonnative species, in Yellowstone Lake illustrated that even in the center of the largest piece of relatively undisturbed land in the conterminous United States, persistence of native aquatic species is in jeopardy (Kaeding et al. 1996). In the past few years, conservation organizations have petitioned the U.S. Fish and Wildlife Service to protect under the federal Endangered Species Act all 4 subspecies of cutthroat trout (*Oncorhynchus clarki*) native to the GYE as well as the native Montana grayling (*Thymallus arcticus montanus*).

The goals of this study are to evaluate the ecological integrity of and provide conservation

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strategies at the watershed scale for aquatic systems in the GYE. In general, ecological integrity is determined by physical and biotic components. Indices of biotic integrity incorporate measures of aquatic organism assemblage structure and have been used as quick and accurate alternatives to more traditional physical- and chemical-based assessments of stream health (Karr 1981, Fausch et al. 1984, Hilsenhoff 1987). From a management perspective, however, an ideal assessment of ecological integrity should incorporate enough measures of both the biotic and physical components to allow testing of relationships between the two. If changes in the biotic component can be linked to changes in the physical component, and these, in turn, can be linked to natural resource management and use, then results of the assessment can be used to determine restoration, conservation, and management activities aimed at maintaining and improving ecological integrity.

Toward this end, we inventoried available data that could be used to assess ecological integrity of watersheds in the GYE (Van Kirk 1999, Van Kirk et al. 2000). Unfortunately, this effort failed to identify habitat and water-quality data of sufficient quantity, quality, and consistency at the watershed scale to allow development of a meaningful ecosystem-wide index of stream physical habitat condition. However, consistent U.S. Geological Survey (USGS) hydrologic data are available at the appropriate scale for all watersheds in the ecosystem, and review of the rapidly growing body of literature identifying the role of hydrologic regime in determining physical and biological characteristics of streams suggested that an index of hydrologic integrity might prove useful in quantifying the physical component of ecological integrity.

The natural hydrologic and sediment regimes of a given stream are determined by climate, geology, and topography (Gregory at al. 1991). In turn, hydrologic and sediment regimes play major roles in determining channel morphology, water temperature, and nutrient and energy fluxes. Lotic and riparian ecosystems have evolved in response to physical environment and to variability in the natural flow regime (Vannote et al. 1980, Resh et al. 1988, Poff and Ward 1989). Recent research has focused extensively on how the presence of dams and reservoirs has altered the timing and quantity of water and sediment delivered to a river system (Petts 1984, Williams and Wolman 1984, Hirsch et al. 1990), affecting both abiotic and biotic components of the riverine environment (Hill et al. 1991, Sparks 1992, Ligon et al. 1995, Collier et al. 1996). In the western U.S., reduction of peak flows, rapidly fluctuating hydropower discharges, and absence of sediment immediately below dams have been the most dramatic downstream effects of river impoundment.

As a result of altered discharge and sediment regimes, downstream channel morphology can be changed in many ways that affect stream biota. Lack of sediment in water issuing directly from a dam results in erosion of the streambed below the dam, loss of spawning gravels, streambed armoring, and stream incision (Petts 1979, Andrews 1986, Kondolf 1995). In many rivers, for example, the Colorado River below Glen Canyon Dam, warm, silt-laden water has been replaced by clear, cold water, causing a shift in the aquatic ecosystem from heterotrophic to autotrophic (Marzolf et al. 1999). Key geomorphic factors that influence river ecology and are altered by river regulation include the following: (1) cross-sectional shape, which determines the nature of habitat features such as overhanging bank cover; (2) cross-sectional size, one determinant of frequency and duration of overbank floods, which link the floodplain with the river channel and allow terrestrial/aquatic nutrient flux (Ward and Stanford 1995); (3) pool/riffle/run ratios, which determine the proportion of various habitat types available to aquatic organisms; (4) point bar and island formation, which determines availability of a variety of fish habitat; and (5) channel substrate composition, which determines, in part, invertebrate diversity and abundance and the quality and quantity of spawning gravels for fish (Petts 1984, Stanford 1994, Ligon et al. 1995).

Aquatic insect assemblage composition, diversity, and abundance are affected by quantity and timing of discharge, current velocity, substrate, temperature, and water chemistry, all of which can be modified by river regulation (Hauer and Stanford 1982, Brittain and Saltveit 1989, Casado et al. 1989, De Jalon and Sanchez 1994, Rader and Belish 1999). Hydrologic regime also determines the amount and timing of water available to streamside plants and the disturbance regime experienced by those plants. Numerous studies have documented changes in composition and abundance of riparian vegetation throughout the western states as a result of altered hydrologic regime; these changes often consist of declines in native species and establishment of exotic species (Johnson 1990, Carothers and Brown 1991, Stromberg and Patten 1991, Stromberg et al. 1993, Everitt 1995, Scott et al. 1996, 1997, Merigliano 1997, Patten 1998). Changes in riparian area structure can have substantial impacts on stream biota because of the critical functional links between terrestrial and aquatic ecosystems provided by riparian areas. For example, the riparian canopy modifies the amount of solar radiation that reaches the stream channel, affecting primary production and stream temperature. The riparian area also supplies woody debris, an important source of structural habitat in the stream channel. Several studies have examined how patterns of discharge variability and extreme high and low flow events influence fish assemblage structure (Horwitz 1978, Meffe 1984, Coon 1987, Bain et al. 1988, Jowett and Duncan 1990, Poff and Allan 1995).

Based on the importance of native salmonids in the GYE, availability of consistent watershed-scale hydrologic data across the ecosystem, and well-documented relationships between hydrologic regime and stream physical environment, we chose to utilize the status of native salmonids as the biotic index and hydrologic integrity as the physical index in our assessment. The objectives of this study are to quantify the status of native salmonid populations in the GYE, quantify hydrologic integrity of the watersheds in the GYE, assess the relationship between native salmonid status and hydrologic integrity, and develop a general strategy for conserving watersheds in the GYE.

STUDY AREA

Watersheds of the GYE

The GYE has been defined in numerous ways, but most definitions include an area of approximately 50,000 km^2 comprising Yellowstone and Grand Teton national parks and adjacent lands at elevations above 1500 m (Anderson 1991). We define the GYE as the area bounded on the east by the western edge of the Wyoming Basin ecoregion (Omernik 1987), on the south and west by the 1500-m-elevation contour and the boundary of the Middle Rockies ecoregion (Omernik 1987), and on the north by an approximate east–west line running from the Jefferson-Madison-Gallatin confluence through the Shields-Yellowstone confluence and down the Yellowstone River to its confluence with Clarks Fork (Fig. 1). Based on this definition, the GYE consists of that portion of the Middle Rockies ecoregion that lies south of the Bridger Range, the adjoining portions of the Northern Basin and Range, Snake River Basin, and Montana Valley and Foothill Prairie ecoregions (Omernik 1987) that lie above about 1500 m in elevation, and the Yellowstone River riparian corridor upstream of the Clarks Fork confluence. A substantial amount of land in the GYE is managed by public agencies other than the National Park Service, including the U.S. Bureau of Land Management and the U.S. Forest Service. Because USGS 8-digit hydrologic units (HUCs) are used as the geographic reporting unit for most water-related data, these were chosen as the basic watershed units for this study. With the exception of a few watersheds containing only a small amount of land lying within the GYE, the study area consisted of all HUCs lying wholly or partially within the GYE as defined above. This resulted in inclusion of 41 eight-digit hydrologic units (Table 1, Fig. 1). These 41 watersheds have a combined area of 162,000 km^2, which is substantially larger than most generally accepted definitions of the GYE. However, because the condition of stream biota and habitats reflects the condition of the entire watershed upstream, inclusion of lowland watersheds lying only partially within the GYE is necessary to gain an understanding of the condition of watersheds in higher elevation areas.

Salmonid Fishes of the GYE

Six species of salmonids are native to the GYE. Cutthroat trout and mountain whitefish (*Prosopium williamsoni*) are native to nearly all GYE watersheds. The Montana graying is native to watersheds of the Upper Missouri River basin. The other 3 native salmonids are endemic to Bear Lake at the southern edge of the GYE. These are the Bear Lake whitefish (*P. abyssicola*), Bonneville cisco (*P. gemmifer*), and Bonneville whitefish (*P. spilonotus*). Four

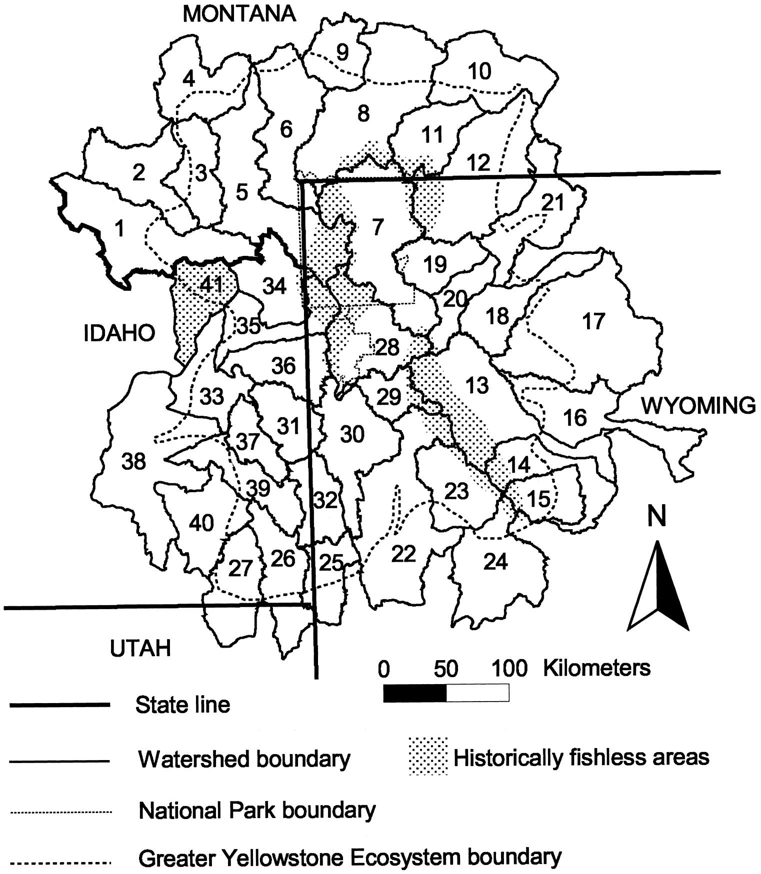

Fig. 1. Watersheds of the Greater Yellowstone Ecosystem. Shading indicates approximate location of historically fishless areas, clockwise from left: Snake River Plain sinks drainages, Yellowstone Plateau/Teton Range crest, Absaroka Range/Beartooth Plateau, and Wind River Range. Watershed identification numbers correspond to those in Table 1.

subspecies of cutthroat trout are recognized as native to the GYE. The Yellowstone cutthroat (*O. c. bouvieri*) was by far the most widely distributed of all cutthroat subspecies in the GYE, historically occupying most of the Upper Snake and Upper Yellowstone River drainages. Although the Snake River finespotted cutthroat is sometimes listed as a subspecies distinct from the Yellowstone cutthroat (Behnke 1992), this distinction has not been officially recognized taxonomically (May 1996). Westslope cutthroat (*O. c. lewisii*) are native to watersheds of the Upper Missouri basin, and Colorado River cutthroat (*O. c. pleuriticus*) are native to the Green River basin. The cutthroat subspecies inhabiting the Bear River drainage has been classified as Bonneville cutthroat trout (*O. c. utah;* Behnke 1992, Duff 1996a). However, recent genetic evidence shows that the Bear River cutthroat is more closely related to the Yellowstone subspecies than to other members of the Bonneville subspecies (Shiozawa and Evans 1995). A geomorphic explanation for this is that the Bear River became a tributary of the Great Salt Lake, the remnant of ancient Lake Bonneville, only about 30,000 years ago; prior to that time it was a tributary to the Snake River, to which the Yellowstone cutthroat is native.

The GYE contains 4 major areas that were likely barren of salmonid fish prior to Euro-American settlement: the Yellowstone Plateau/Teton Range crest, Absaroka Range/Beartooth Plateau, Wind River Range, and the entire Beaver-Camas hydrologic unit (Fig. 1). Most waters historically barren of salmonids were also barren of other fish species, with the possible exception of sculpin (*Cottus* sp.) in a few locations. Geological barriers prevented upstream migration of fish into headwater areas in the first 3 of these areas following the most recent periods of glaciation (Behnke 1992, May 1996, Varley and Schullery 1998). The Beaver-Camas watershed is part of a large region of the Snake River plain in which surface water originating in the adjacent mountains sinks into highly porous lava rock without any surface connection to the Snake River (Hackett and Bonnichsen 1994). Although it is not known with certainty whether this watershed was historically fishless, most literature (e.g., Behnke 1992, Duff 1996b) lists the watershed as historically barren of salmonids, and we will thus consider this to be the case (but see Jaeger et al. 2000).

Four species of nonnative salmonids have been introduced to the GYE. Brown (*Salmo trutta*), rainbow (*O. mykiss*), and brook (*Salvelinus fontinalis*) trout are widespread throughout the GYE. Lake trout are found in many GYE lakes and reservoirs, including Yellowstone and Jackson lakes, and golden trout (*O. m. aguabonita*) have been stocked extensively in the high mountain lakes of the Wind River and Absaroka-Beartooth ranges. Fish of all species were introduced into waters throughout the West beginning in the 1870s (U.S. Commission on Fish and Fisheries 1877), and, throughout most of the 20th century, stocking was used to provide angling opportunity in the face of increased angler numbers and decreased habitat quality. Rainbow trout have been by far the most widely utilized fish in hatchery programs, but various strains of Yellowstone cutthroat have also been stocked liberally throughout the West. Although the National Park Service ceased stocking nonnative trout in Yellowstone in 1916, it continued to stock Yellowstone cutthroat in the park until the 1950s (Varley and Schullery 1998). Hybridization with and competition from introduced salmonids have negatively affected cutthroat trout throughout the western U.S. (Krueger and May 1991). Habitat degradation associated with natural resource development and use has also been cited in the decline of native cutthroat trout (e.g., numerous papers in Gresswell 1988). Aquatic habitat in the GYE has been affected over the past 130 years by irrigated agriculture, timber harvest, livestock grazing, mining, and oil and gas exploration and extraction (Marston and Anderson 1991).

METHODS

Salmonid Status Indices

Indices of biotic integrity specific to the parameters of the GYE were developed based on concepts of naturalness proposed by Anderson (1991) and on indices utilized in the Sierra Nevada ecosystem by Moyle and Randall (1998). We assessed native salmonid status with an index based on spatial distribution and population status of native trout and grayling. We omitted the whitefish species from analysis because 3 of the species are endemic to only a single lake in the ecosystem and because consistent ecosystem-wide data on mountain whitefish populations were not available. Current and historical distribution and current population status of native trout and grayling were determined from Duff (1996b) and Varley and Schullery (1998).

For each of the 41 watersheds, we assigned a score for distribution of native trout and grayling using the following criteria:

5 = area currently occupied within the watershed deviates from area historically occupied by ≤ 20%
3 = area currently occupied within the watershed deviates from area historically occupied by 20–40%
1 = area currently occupied in the watershed deviates from area historically occupied by >40%

A score for native trout and grayling population status was assigned based on populations currently existing within their historic range in the watershed as follows:

5 = existing populations are locally abundant, natives make up majority of current trout/grayling community, all life history forms historically present in the watershed are well represented, subpopulations remain connected in metapopulations
3 = some populations may be locally abundant but nonnatives are as abundant as natives, some life history forms are not well represented, many subpopulations are isolated from others
1 = natives are rare within the watershed, existing native populations make up only a small percentage of existing trout/grayling assemblages, little or no connectivity exists among subpopulations

The native salmonid index was computed by averaging the distribution and population status

TABLE 1. Watersheds of Greater Yellowstone, the status of their salmonid fishes, and their hydrologic integrity. Salmonid status indices are interpreted qualitatively as follows: 4–5 = good, 3 = fair, 1–2 = poor. The hydrologic integrity index is interpreted qualitatively as follows: 66.7–100 = good, 33.3– 66.6 = fair, 0–33.2 = poor.

ID no.	Watershed name	USGS cataloging no.	Hydrologic subregion (major river basin)	Area (km^2)	Perennial stream (km)	Mean annual discharge (ha-m)	Native salmonid index	Existing salmonid index	Hydrologic integrity
1	Red Rock	10020001	Missouri headwaters	6,035	2,368	39,387	1	5	45.1
2	Beaverhead	10020002	Missouri headwaters	3,781	1,288	36,771	1	5	17.3
3	Ruby	10020003	Missouri headwaters	2,559	1,132	18,879	1	5	47.9
4	Jefferson	10020005	Missouri headwaters	3,504	1,445	187,557	1	4	51.1
5	Madison	10020007	Missouri headwaters	6,656	3,407	188,865	1	5	71.0
6	Gallatin	10020008	Missouri headwaters	4,714	3,239	96,296	1	5	68.3
7	Yellowstone headwaters	10070001	Upper Yellowstone	6,734	3,541	279,485	5	5	95.0
8	Upper Yellowstone	10070002	Upper Yellowstone	7,615	4,406	336,493	3	5	82.5
9	Shields	10070003	Upper Yellowstone	2,209	1,648	27,541	1	5	61.7
10	Upper Yellowstone–Lake Basin	10070004	Upper Yellowstone	4,053	1,088	631,279	1	4	82.5
11	Stillwater	10070005	Upper Yellowstone	2,745	1,422	84,660	1	5	93.8
12	Clarks Fork Yellowstone	10070006	Upper Yellowstone	7,174	2,835	93,186	1	3	50.1
13	Upper Wind	10080001	Bighorn	6,579	2,763	72,987	1	2	57.5
14	Little Wind	10080002	Bighorn	2,823	890	51,566	1	1	78.9
15	Popo Agie	10080003	Bighorn	2,067	858	28,037	1	2	70.3
16	Lower Wind	10080005	Bighorn	4,429	454	113,744	1	2	30.5
17	Upper Bighorn	10080007	Bighorn	8,936	1,557	156,709	1	2	25.4
18	Greybull	10080009	Bighorn	2,979	1,078	43,064	1	3	50.5
19	North Fork Shoshone	10080012	Bighorn	2,209	1,546	80,033	1	5	83.3
20	South Fork Shoshone	10080013	Bighorn	1,707	1,169	34,723	1	5	67.5
21	Shoshone	10080014	Bighorn	3,859	889	82,858	1	2	33.0
22	Upper Green	14040101	Upper Green	7,589	2,924	148,318	1	3	64.2
23	New Fork	14040102	Upper Green	3,160	1,168	66,250	1	4	58.3
24	Big Sandy	14040104	Upper Green	4,688	742	6,737	1	1	6.1
25	Central Bear	16010102	Bear	2,160	920	18,926	3	4	10.8
26	Bear Lake	16010201	Bear	3,160	768	71,340	3	3	10.8
27	Middle Bear	16010202	Bear	3,134	1,026	103,132	1	2	14.5
28	Snake headwaters	17040101	Upper Snake	4,351	2,098	265,665	5	5	79.8
29	Gros Ventre	17040102	Upper Snake	1,652	836	57,284	5	5	95.0
30	Greys-Hobock	17040103	Upper Snake	4,066	2,140	409,295	5	5	84.8
31	Palisades	17040104	Upper Snake	2,370	1,245	625,726	4	5	77.0
32	Salt	17040105	Upper Snake	2,297	1,190	70,408	3	4	83.3

33	Idaho Falls	17040201	Upper Snake	2,953	519	690,137	4	4	42.8
34	Upper Henrys	17040202	Upper Snake	2,823	973	136,102	2	5	76.8
35	Lower Henrys	17040203	Upper Snake	2,694	1,019	187,557	1	3	64.9
36	Teton	17040204	Upper Snake	2,927	1,230	74,813	4	4	65.0
37	Willow	17040205	Upper Snake	1,671	1,065	10,548	4	4	40.0
38	American Falls	17040206	Upper Snake	7,659	3,158	800,697	2	3	32.4
39	Blackfoot	17040207	Upper Snake	2,797	1,221	33,032	2	2	22.4
40	Portneuf	17040208	Upper Snake	3,419	1,088	24,975	1	1	24.9
41	Beaver-Camas	17040214	Upper Snake	2,543	873	3,251	1	2	33.3

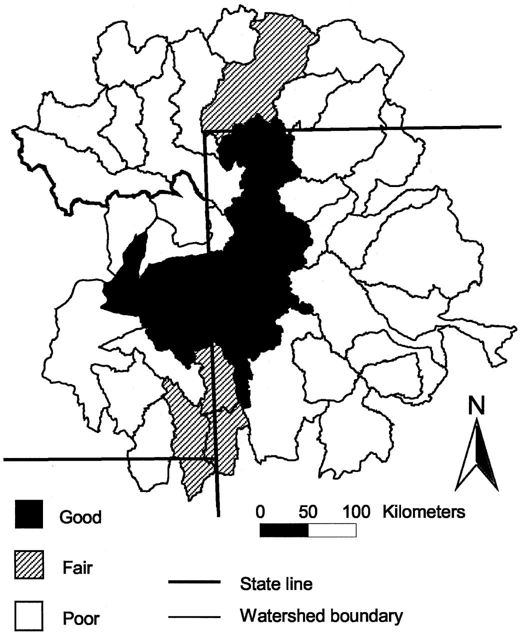

Fig. 2. Status of native trout and grayling by watershed.

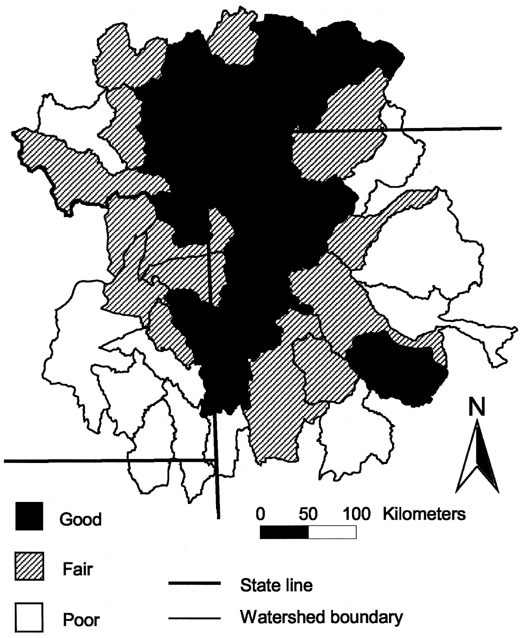

Fig. 3. Hydrologic integrity by watershed.

scores. Average scores of 4 and 5 were considered good, 3 was considered fair, and 1 and 2 were considered poor.

A 2nd index was computed to determine the status of salmonids currently existing in each watershed, whether or not the species present are native, introduced, or hybrids of native and introduced species. We refer to this index hereafter as the "existing salmonid" index. Data for determining this index came from state fish and game agencies in Idaho, Montana, Wyoming, and Utah and from federal agencies responsible for fisheries management in Yellowstone National Park and on the Wind River Indian Reservation. These data were primarily contained in unpublished agency fisheries inventory and management reports, although information gained through personal communications with fisheries biologists and managers was also used. The existing salmonid index was computed in a manner analogous to that for native species. Distribution scores were assigned exactly as for the native species, except that all presently occurring trout species were included. For example, in an area historically containing native trout and/or grayling, a score of 5 would be given if trout and grayling of any species currently occupy 80–100% of the area originally occupied by trout and grayling, even if the current occupants are nonnative species. We assigned a population status score to existing trout and grayling populations (native, nonnative, and/or hybrid) where they currently exist according to the following criteria:

5 = abundant, populations generally stable and wild
3 = moderately abundant, some populations are supplemented by stocking, population size is limited by water quality and habitat in some locations
1 = low abundance, many fisheries are supported by stocking, habitat degradation limits population abundance over large areas

The existing salmonid index was calculated by averaging these distribution and population status scores.

Hydrologic Integrity Index

An index of hydrologic integrity was computed for each watershed by determining cumulative impacts of water resource development and use in the entire drainage area upstream from the bottom of the watershed. Because all watersheds within the GYE have experienced at least some degree of hydrologic alteration and because there is no absolute scale on which to measure hydrologic integrity, the index is based on percentile rankings and thus compares each watershed to the least altered watershed in the ecosystem. We used 3 parameters reported in the U.S. Geological Survey water use database: total reservoir surface area, total surface water withdrawals, and total consumptive water use. For all but headwater HUCs, determining cumulative impacts involved totaling water use figures for the HUC in question as well as for all HUCs lying upstream, with 2 exceptions: (1) the surface area of a reservoir marking the downstream boundary of the HUC was not included in the cumulative reservoir surface area, and (2) cumulative reservoir surface area for a tributary, the confluence of which marked the downstream boundary of the HUC in question, was not included.

All cumulative totals were divided by mean annual discharge from the given HUC to obtain normalized values. Mean annual discharge was determined from USGS stream discharge data at the recording station located nearest the downstream boundary of the HUC. For normalized reservoir surface area figures, watersheds with 0 surface area were assigned a score of 0 and removed. We then assigned remaining watersheds a score based on their percentile rank. These scores were subtracted from 100 so that watersheds with 0 reservoir surface area received a score of 100, and scores decreased as relative reservoir surface area in the watershed increased. Water use figures were percentile-ranked and results subtracted from 100. Hydrologic integrity index was computed as the mean of the 3 reverse-percentile figures. Hydrologic integrity scores from 0 to 33.2 were considered poor, those from 33.3 to 66.6 were considered fair, and those of 66.7 and above were considered good. We assessed correlation between salmonid status and hydrologic integrity with Spearman's rank correlation test incorporating correction for ties.

Conservation Strategy and Priority

Conservation strategy and priority were determined based on the concepts in Moyle and Sato (1991) and Frissell (1997). These concepts state loosely that (1) existing native species should be protected where they already exist in viable populations, (2) restoration should be undertaken first in areas where it is possible to return species assemblages to historical condition without unreasonable efforts such as removing a large dam, (3) large, high-integrity watersheds can act as sources of native species to recolonize adjacent 2nd-tier watersheds as they are restored, and (4) some watersheds will never be restored to historical condition with any reasonable amount of effort and are thus better suited for appropriate management to enhance or maintain recreational, scenic, or water resource values. Such management may include stocking sport fish and maintaining popular nonnative sport fisheries. Conservation strategy and priority were assigned based on the status of native and existing salmonids and on hydrologic integrity according to the criteria in Table 2.

RESULTS

The status of native salmonids was good in 8 of 41 watersheds (20%), fair in 4 (10%), and poor in the remaining 29 (70%; Table 1). All watersheds in which native salmonid status was either good or fair occurred in the Upper Yellowstone, Upper Snake, and Bear River basins (Fig. 1). All salmonids native to these watersheds, including the endemic Bear Lake whitefishes, were present in viable populations. Yellowstone cutthroat are found throughout much of their original range in the GYE, but few viable populations exist east of the Yellowstone and Snake River headwaters areas. Viable populations of Bear River cutthroat are found in Bear Lake and a few of its tributaries and in the Smiths and Thomas Fork drainages along the Idaho-Wyoming border.

Native salmonid status was poor in all watersheds historically containing either Colorado River cutthroat or westslope cutthroat and grayling. The Montana grayling is essentially extinct in the GYE; it is found in its native range in only a few lakes in the Red Rock watershed and has been introduced in other lakes scattered throughout the GYE. A small remnant population of fluvial grayling exists in the Bighole watershed west of the GYE. Westslope cutthroat are found in a few isolated enclaves in the Red Rock, Ruby, Madison, and Gallatin drainages. Colorado cutthroat exist in numerous but generally disconnected headwater streams along the eastern slopes of the Gros Ventre and Wyoming ranges. A majority of the streams and lakes in all of the historically fishless areas now contain introduced salmonid species.

The status of all salmonid species (native, introduced, and/or hybrids) currently existing in GYE was substantially better than that of native species. Existing salmonid status was good in 24 watersheds (59%), fair in 6 (15%), and poor in only 11 (27%; Table 1). Eighteen watersheds in which native salmonid status was poor received a score of fair or good for the status of their nonnative salmonids. These watersheds are characterized by salmonid distributions that are not substantially different from those occurring historically and by viable populations of wild trout displaying varied life history patterns. However, the majority of trout populations in these watersheds comprise nonnative species rather than natives.

Because the hydrologic integrity index is a percentile-based measurement, the distribution of watersheds among the good, fair, and poor status classes was roughly uniform, as expected (Table 1). However, spatial distribution of hydrologic integrity was not uniform. All watersheds with a high degree of hydrologic integrity were located in headwater areas, and all but 2 (Little Wind and Popo Agie) occurred in a large, contiguous region in the north central part of the ecosystem centered on the national parks (Fig. 3). Those with poor scores were located at lower elevations around the perimeter of the GYE, where reservoirs, withdrawals, and consumption have resulted in substantial alteration of natural hydrologic regimes.

The population status of both native and existing salmonids was positively correlated with hydrologic integrity. With all 41 watersheds included in the analysis, native salmonid index was weakly but significantly correlated with hydrologic integrity index (Spearman's $r = 0.27$, $P = 0.041$). However, the 26 watersheds receiving a native salmonid index score of 1 (the lowest score possible) were nearly uniformly distributed across hydrologic integrity scores (Fig. 4, Table 1). With these 26 watersheds removed from analysis, the correlation between the native salmonid index and the hydrologic integrity index increased substantially

TABLE 2. Criteria for assigning conservation priority and strategy.

Native salmonid status	Existing salmonid status	Hydrologic integrity	Priority	Strategy
good/fair	good/fair	good	1 (p)	Preserve and protect
good/fair	good/fair	fair/poor	1 (r)	Rehabilitate and restore ecological processes
poor	good	good	2	Preserve and protect
poor	good	fair/poor	3	Rehabilitate and restore ecological processes
poor	fair/poor	good	4	Maintain scenic, recreational, ecological values
poor	fair/poor	fair/poor	5	Enhance scenic, recreational, ecological values

(Spearman's $r = 0.63$, $P = 0.0057$). With all 41 watersheds included, existing salmonid index was also positively correlated with hydrologic integrity (Spearman's $r = 0.58$, $P = 3.6 \times 10^{-5}$).

Based on the conservation priority and strategy criteria in Table 2, the 12 watersheds in which native trout status was either fair or good were assigned 1st priority for conservation (Table 3). The status of existing (native, nonnative, and hybrid) salmonid populations in 13 watersheds was high enough to warrant 2nd- or 3rd-tier priority for aquatic conservation in these watersheds (Table 3). The remaining 16 watersheds (39%) fell into the lowest 2 priority classifications.

DISCUSSION

The native salmonid status and hydrologic integrity indices quantify the pattern identified by Marston and Anderson (1991) of high ecological integrity in the center of the GYE and decreasing integrity with distance away from this center (Figs. 2, 3). Because the mountainous region of the GYE generally runs in a north–south orientation, the high-integrity core of the GYE consists of a central band of watersheds that extends from the Shields and upper Yellowstone watersheds on the north side of GYE southward through Yellowstone and Grand Teton national parks to the Greys and Salt rivers. Although we did not analyze our results in the context of land ownership and management, the watersheds in the high-integrity core of the GYE tend to contain large amounts of public land managed by the National Park Service and National Forest Service (Table 3). The lowest degree of ecological integrity is generally found in the nonmountainous watersheds on the west and east sides of the GYE. These watersheds generally contain large amounts of private agricultural land and rangeland managed by the Bureau of Land Management (Table 3).

The status of native salmonids across the GYE is generally poor, illustrating that even in a large, relatively undeveloped ecosystem, native fish and probably other native aquatic species are imperiled. The population status of existing native and nonnative salmonid species in the GYE is much better, indicating that in many watersheds nonnative trout species that have replaced natives are doing well. Not surprisingly, watersheds in which native species status was poor but existing species status was good support the most popular sport fisheries in the GYE for introduced brown, rainbow, brook, and cutthroat-rainbow hybrid trout. Examples include the Madison, Gallatin, Henrys Fork, Beaverhead, and North Fork Shoshone (Table 1). Habitat conditions in these watersheds are apparently good enough to support viable populations of wild trout, but the trout that currently inhabit these watersheds are nonnatives. Because our analysis was conducted on a watershed scale, it is important to note that many watersheds in which native salmonid status was poor still contain viable, but small and disconnected, populations of native trout on a local scale. Examples include Henrys Fork (Yellowstone cutthroat; Jaeger et al. 2000), Upper Green (Colorado River cutthroat; Young et al. 1996), and Greybull (Yellowstone cutthroat; Kruse et al. 2000).

Although the core of the GYE consists of large amounts of public land, much of which is protected from development in roadless and

TABLE 3. Conservation priority and primary land ownership for the watersheds of Greater Yellowstone. Land ownership is listed in approximate decreasing order of land area owned within the watershed.

ID no.	Watershed name	Conservation priority (Table 2)	Primary land ownership[a]
1	Red Rock	3	BDNF, BLM, S
2	Beaverhead	3	BLM, P, S
3	Ruby	3	P, BDNF, BLM, S
4	Jefferson	3	P, BDNF, BLM
5	Madison	2	P, BDNF
6	Gallatin	2	GNF, P, YNP
7	Yellowstone headwaters	1(p)	YNP, SNF, GNF
8	Upper Yellowstone	1(p)	GNF, P
9	Shields	3	P, GNF
10	Upper Yellowstone—Lake Basin	2	P, GNF
11	Stillwater	2	CNF, P
12	Clarks Fork Yellowstone	5	P, BLM, CNF, YNP
13	Upper Wind	5	WR, SNF
14	Little Wind	4	WR
15	Popo Agie	4	SNF, WR, BLM
16	Lower Wind	5	WR, BLM
17	Upper Bighorn	5	BLM
18	Greybull	5	BLM, P, SNF
19	North Fork Shoshone	2	SNF, YNP
20	South Fork Shoshone	2	SNF, P
21	Shoshone	5	BLM, P
22	Upper Green	5	BLM, BTNF, P
23	New Fork	3	BLM, BTNF, P
24	Big Sandy	5	BLM, BTNF
25	Central Bear	1(r)	BLM, P, TCNF, BTN
26	Bear Lake	1(r)	WCNF, TCNF, P
27	Middle Bear	5	P, WCNF, S
28	Snake headwaters	1(p)	GTNP, BTNF, P
29	Gros Ventre	1(p)	BTNF
30	Greys-Hobock	1(p)	BTNF, P
31	Palisades	1(p)	TCNF, P
32	Salt	1(p)	BTNF, TCNF, P
33	Idaho Falls	1(r)	P, BLM
34	Upper Henrys	2	TCNF
35	Lower Henrys	5	P, BLM, TCNF, YNP
36	Teton	1(r)	P, TCNF, S
37	Willow	1(r)	P, S
38	American Falls	5	P, FH, BLM
39	Blackfoot	5	P, FH, S
40	Portneuf	5	P, TCNF, BLM
41	Beaver-Camas	5	BLM, TCNF, P, S

[a] Key to land ownership: BDNF = Beaverhead-Deerlodge National Forest, BLM = U.S. Bureau of Land Management, BTNF = Bridger-Teton National Forest, CNF = Custer National Forest, FH = Fort Hall Indian Reservation, GNF = Gallatin National Forest, GTNP = Grand Teton National Park, P = private, S = state, SNF = Shoshone National Forest, TCNF = Targhee-Caribou National Forest, WCNF = Wasatch-Cache National Forest, WR = Wind River Indian Reservation, YNP = Yellowstone National Park.

wilderness areas and in the national parks, the lower-elevation areas of the ecosystem have been extensively developed, most notably for agricultural use. Because the climate in these lower-elevation areas is arid to semiarid (Marston and Anderson 1991), most agriculture is possible only with irrigation. Thus, extensive irrigation water storage and delivery systems have been developed throughout the GYE, substantially altering hydrologic regimes in the lower-elevation watersheds of the GYE. Aquatic and riparian habitat features in these more developed watersheds are likely to be degraded by other causes such as grazing, urban development, agricultural chemical runoff, sedimentation, and flood control. Thus, we expect that aquatic habitat conditions would be correlated with our index of hydrologic integrity not only because of the direct link between hydrologic regime and ecological processes but also because other types of habitat-degrading activities are likely to occur in tandem with a high

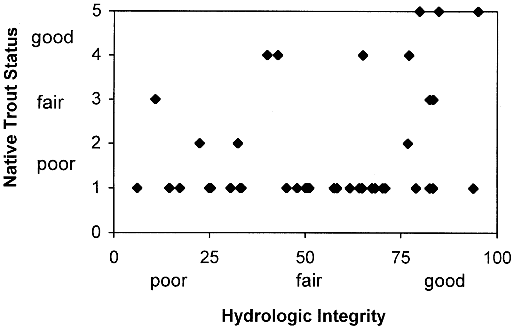

Fig. 4. Native salmonid status as a function of hydrologic integrity for 41 watersheds in Greater Yellowstone.

degree of water resource development and use.

This expectation appears to be realized in the significant positive correlation between population status of salmonid fishes and hydrologic integrity ($r = 0.58$, $P = 3.6 \times 10^{-5}$), indicating that the hydrologic integrity index performed well in quantifying the suitability of stream environments for salmonid fishes on a watershed scale. If hydrologic integrity and related environmental conditions were the only factors determining the status of native salmonids, we would expect to see an equal degree of correlation between native salmonid status and hydrologic integrity. Instead, a similar degree of correlation ($r = 0.63$) between native salmonid status and hydrologic integrity was observed only when all watersheds receiving the lowest possible native trout index score were removed from the analysis. When all 41 watersheds were included, the correlation was considerably weaker ($r = 0.27$) because the 26 watersheds receiving the lowest possible native salmonid score were nearly uniformly distributed across hydrologic integrity (Fig. 4).

Two conclusions can be deduced from these results: (1) disappearance of native salmonids from watersheds of the GYE was not due to changes in the physical environment alone, and (2) continued viability of populations of all species of salmonids (native or otherwise) is dependent on maintaining or enhancing the hydrologic integrity of watersheds in the GYE. Although habitat degradation has been an important factor leading to the decline of native cutthroat trout species throughout the West (e.g., Gresswell 1988), equally important have been the negative impacts of nonnative trout species, which include competition and hybridization (e.g., Griffith 1988, Gregory and Griffith 2000, Henderson et al. 2000). Harvest of large numbers of native fish is another factor that probably acted in concert with the spread of nonnatives to reduce native trout numbers (e.g., Gresswell and Varley 1988). However, where natives still persist, their status is positively correlated with hydrologic integrity, which, in turn, is likely to be positively correlated with aquatic habitat quality. Moyle and Randall (1998) drew similar conclusions from their study of ecologic integrity of watersheds in the Sierra Nevada. They identified introduced fish species and large dams as the 2 most important factors contributing to decline of ecological integrity. Similarly, Richter et al. (1997) reported that the 2 most important factors in the disappearance of native fish in the western U.S. are introduced species and hydrologic alteration.

Given that large-scale eradication of nonnative fish is unfeasible and that state agencies have already ceased most nonnative stocking programs in waters containing viable populations of natives, the most pragmatic approach to native trout conservation is to preserve existing populations. Thus, the 1st priority should be preventing further degradation of the GYE core watersheds that scored high in both native trout and hydrologic indices. These 7 watersheds are identified as priority 1(p) (priority = 1, strategy = preserve and protect) in Table 3, from which it is apparent that land management responsibility in these watersheds lies primarily with the National Park Service (both parks) and the Bridger-Teton, Targhee-Caribou, and Gallatin national forests. Threats from introduced trout in these watersheds (e.g., lake trout in Yellowstone Lake) should be addressed aggressively, and hydrologic integrity and habitat quality should be at least maintained, if not restored where possible. Identified in Table 3 as priority 1(r) (priority = 1, strategy = rehabilitate and restore) are the 5 watersheds that scored good or fair in the native trout index but low in hydrologic integrity. These watersheds will provide the greatest return for investment in on-the-ground restoration because they are areas where native fish are still present but suffer more greatly from habitat degradation than from nonnative species threats. These watersheds contain more private and Bureau of Land Management land than the 1(p) watersheds, although portions of the Targhee-Caribou and Wasatch-Cache national forests lie in these watersheds (Table 3). Habitat restoration in these areas is likely to involve reducing the impacts of irrigated agriculture, grazing, and flood control activities.

The watersheds in the 2nd and 3rd tiers of conservation priority are those such as the Madison, Gallatin, and Upper Henrys that provide popular nonnative angling opportunities. Preservation and restoration activities applied to both fish populations and habitat in these watersheds will provide both ecological and economic benefits. Even though these watersheds are in the 2nd- and 3rd-priority categories, they have large conservation constituencies because of the popularity of their fisheries. Generating interest in and resources for conservation work from watershed-specific recreational user groups in these drainages should be fairly easy, allowing regional and national resources to benefit the 1st-priority watersheds. Nonnative trout fisheries may be the primary beneficiaries of conservation activities in these 2nd- and 3rd-priority watersheds, but the opportunity to contribute to conservation of remnant native populations should not be overlooked. Some subbasins could be managed to maintain and/or expand the range of native trout. Land management varies widely across these watersheds (Table 3), and habitat restoration will need to address any number of issues related to agriculture, grazing, timber harvest, road construction, housing development, mining, and water management.

Watersheds in the low- and lowest-priority categories are placed there not because conservation work is not needed but because resources expended there may do little to restore native species and ecological function. However, a few like the Upper Green contain isolated remnant populations of native trout, and very specific conservation efforts have the potential to increase viability of these populations. In general, these watersheds are the most highly impacted in the GYE, and many have experienced alterations due to water resource development that may not be restored without major expenditure of resources and impacts to local communities. Conservation efforts in these watersheds should be directed toward maintaining and enhancing recreational, scenic, and water quality values, particularly those that benefit nearby cities such as Billings, Riverton, Lander, Idaho Falls, and Pocatello. Development of urban greenbelts, put-and-take fisheries in artificial ponds, and riparian protection zones are examples of cost-effective conservation measures in these watersheds. However, where possible, opportunities to restore native fish should be pursued.

An exception to this general approach to the lower-priority watersheds is restoration of what Frissell (1997) terms “grubstake habitats,” low-elevation wetland and riparian areas that are high centers of biodiversity. Large-scale restoration and preservation of these areas may be costly, but payoffs in terms of increased fish and wildlife habitat and water quality are potentially very large. Riparian areas along the lower portions of GYE’s large rivers, including the Snake, Yellowstone, Wind, Green, and Jefferson, are good examples of grubstake habitats, and large-scale watershed conservation efforts there should be implemented. Land management responsibility in the lowest-priority watersheds generally lies with private landowners, states, Native American tribes, and the Bureau of Land Management (Table 3).

CONCLUSION

The generally poor status of native salmonids in the GYE illustrates that even in an ecosystem considered to be among the most pristine and unaltered in the conterminous United States, introduced species have had detrimental impacts on native species despite the presence of high-quality habitat. Watersheds of highest ecological integrity, both in terms of native salmonid populations and hydrologic integrity, are found in the mountainous center of the ecosystem, where most of the land area and natural resources are managed by federal agencies. A practical approach to conserving watersheds and aquatic resources of the GYE is based on the observation that it is easier to maintain populations of native fish species where they currently exist than to introduce them into areas currently dominated by nonnatives. Such an approach assigns highest priority to central core watersheds, where native trout status is either good or fair. Habitat preservation and restoration in these watersheds will benefit native species without involving large-scale eradication of nonnatives. The positive correlation between the status of existing (native and nonnative) salmonid populations and hydrologic integrity in the GYE illustrates the importance of natural hydrologic function in maintaining salmonid habitat. The success of our crude hydrologic integrity index in predicting population status of salmonid fishes suggests that further development and refinement of measures of hydrologic integrity may be of great use in assessing and preserving stream biota.

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