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Integrating conservation genetic considerations into conservation planning: a case study of bull trout in the Lake Pend Oreille—lower Clark Fork River system

ABSTRACT

Bull trout (*Salvelinus confluentus*) is a species of conservation concern—listed as "threatened" under the Endangered Species Act—throughout its native range in the western United States. The authors were assembled by the Clark Fork River Aquatic Implementation Team, composed of biologists representing Montana Fish, Wildlife and Parks (MFWP); Idaho Department of Fish and Game (IDFG); and Avista Corporation, to provide a conservation genetics perspective and to assist those managers charged with stewardship of the bull trout populations occupying the Lake Pend Oreille (ID)—lower Clark Fork River (ID, MT) drainage. More specifically, we were asked to assess the risks to bull trout from alternative conservation strategies and to recommend a plan of action aimed at promoting the species' long-term viability and functional recovery. We describe here a case study of one application of the expert advisory panel approach within the context of a restoration program and of the underlying perspectives this panel brought to bear on bull trout conservation (including identifying conservation units and the actions needed to restore long-term viability to the resource). Although the panel focused specifically on bull trout in a specific basin, the general considerations and approach should have more general application elsewhere for bull trout and for other at-risk fish populations.

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Introduction and background

Integration and inclusion of population genetics perspectives and data are increasingly critical for conservation planning of at-risk living resources (Waples 1991; Nielsen 1995). This requirement, however, has not been routinely or comprehensively implemented in past conservation efforts. We discuss a generalized approach for ensuring an open and deliberative process whose aim is the long-term conservation of population-level biological diversity in bull trout (*Salvelinus confluentus*). We describe a practical application of principles for defining conservation units. Moreover, we describe the primary conservation genetic considerations

DONA HORANA

Snorkelers counting bull trout in tributaries to Lake Pend Oreille.

JASON DUNHAM

Collecting adult bull trout in tributary to Lake Pend Oreille.

JASON DUNHAM

Collecting adult bull trout at a barrier in Save Creek.

JASON DUNHAM

Collecting adult bull trout in tributary to Lake Pend Oreille.

BRUCE RIEMA

Sampling adult bull trout.

associated with management alternatives and the ultimate goal of recovery of a complex of demographically depressed populations.

The authors comprised a technical panel assembled in June 2000 at Clark Fork, Idaho by the Clark Fork Aquatic Implementation Team (AIT, charged by the Federal Energy Regulatory Commission [FERC] to ensure compliance with licensing standards affecting the aquatic ecosystem of the lower Clark Fork River). The panel's primary tasks were: (1) to deliberate population genetic, demographic, and life-history data and the processes responsible for their patterns of variation, and (2) to recommend courses of short- and long-term action necessary to conserve and restore bull trout populations in the Lake Pend Oreille—lower Clark Fork River. Our goal here is to describe this generalized approach and the most salient considerations and recommendations that emerged from our deliberations as a specific "case study" to increase the long-term population viability of bull trout. Key outcomes from this case study will also prove relevant to other species and conservation contexts.

Before the latter third of the 20th century, presumed genetic relationships within species were commonly inferred from such phenotypic traits as timings of maturity and adult migration. The complex and unknown genetic basis of these traits, coupled with an often-considerable environmental influence, provided only rough approximations of actual evolutionary relationships. Thus, there was risk of inappropriately assigning common ancestry to genetically distinct groups that shared such phenotypes via convergent evolutionary processes (Allendorf et al. 1987). Emerging in the 1960s concurrently with a heightened awareness of conservation issues (Carson 1964; Utter 1981), use of molecular genetic markers soon became an essential tool for fish conservation. A purely genetic approach—based on simple inheritance of multiple independent population markers—permits identification, monitoring, and assignment of evolutionary relationships to groups in a manner that was previously exceedingly difficult.

Increased power to identify important relationships among populations has enlivened a debate regarding appropriate biological units for management and conservation (STOCS 1981; Nielsen 1995). Basic information on population genetic structure has proven particularly useful where populations are threatened with extinction and have been targeted for remedial actions (e.g., Waples 1991;

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NRC 2002). Agencies and organizations responsible for management of threatened populations often must rely on specialists within as well as outside their organizations. Given the breadth of expertise required, groups or teams are needed to outline the foundations for suitable action. From these foundational principles, a plan for recovery can be drafted and implemented. The process of recovery may be carefully monitored, with adjustments undertaken as needed until a healthy and stable population has been restored.

Before the 1990s, bull trout largely were neglected as a focal species of recreational fisheries management or biodiversity conservation. The position of bull trout as apex predators coupled with their reputation as inferior game fish facilitated their neglect and, in some instances, their eradication in favor of other native and introduced salmonids that are preyed upon by and compete with bull trout (e.g., Blake 1997). Moreover, bull trout formerly were misidentified as the resident form of the anadromous species Dolly Varden (*S. malma*), in part because they are morphologically similar and their respective ranges overlap. More recently, bull trout have been described as a species phylogenetically distinct from Dolly Varden (Cavender 1978). Subsequent investigation further supported the two-species hypothesis indicating that bull trout and Asian white spotted char (S. *leucomanis*) are paired sister taxa distinct from the Dolly Varden and Arctic char (S. *alpinus*) taxa pair (Crane et al. 1994; Phillips et al. 1994). In spite of this taxonomic resolution, both species are still managed as a single common taxon in some areas (e.g., Leary and Allendorf 1997). Finally, like other salmonid species, bull trout are polytypic in terms of their life-history strategies, adding further complexity to management considerations. In addition to resident forms that complete their life-history within their natal streams, the migratory form grows to adulthood in large rivers or lakes (Rieman and McIntyre 1993). These migratory fish depend upon interconnected networks of streams to complete their life cycles, but unfortunately, such passages have been eliminated in many areas through stream impoundments and diversions (Rieman and McIntyre 1993).

Presently, several threats to longer term bull trout viability have been implicated. These threats include loss or degradation of spawning stream habitat (associated with land use practices), fragmentation and

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DONA HORAN

Enumerating bull trout “redds” in a tributary to Lake Pend Oreille.

JASON DUNHAM

RUSS THUROW

Adult bull trout migrating upstream in Trestle Creek, a tributary to Lake Pend Oreille.

disconnection of migratory corridors (associated with the operation of hydropower dams), hybridization with or displacement by non-native brook trout (S. *fontinalis*; Kanda et al. 2002), and ecological interactions with other non-native fishes (McMaster 1999; Lohr et al. 2000 and references therein).

These factors have led directly to the decline of bull trout over so much of its historical range (Rieman and McIntyre 1993; Rieman et al. 1997) within the United States that the species is now listed as “threatened” under the U.S. Endangered Species Act (ESA; USFWS 1999). Moreover, remaining populations are characterized by sharply reduced numbers and reduced variation of life-history characteristics (Howell and Buchanan 1992; Rieman and McIntyre 1993). Formal recovery planning, required by ESA, established objectives to (1) maintain existing populations; (2) restore the distribution into some previously occupied areas; (3) maintain stable or increasing trends in abundance range-wide; (4) restore conditions for all life stages and life histories; (5) conserve genetic diversity; and (6) provide the opportunity for historical patterns genetic exchange (Lohr et al. 2000). These objectives will continue as a conservation challenge because bull trout of the Lake Pend Oreille—lower Clark Fork River system (Figure 1) present a full spectrum of challenges and possibilities. Within this system, local populations range from “abundant and stable” to “declining” to “locally extinct” (Pratt and Huston 1993; Rieman and Myers 1997). As a whole, however, individual remaining populations within the basin are experiencing a reduced complement of life-histories (Rieman and McIntyre 1993; Neraas and Spruell 2001).

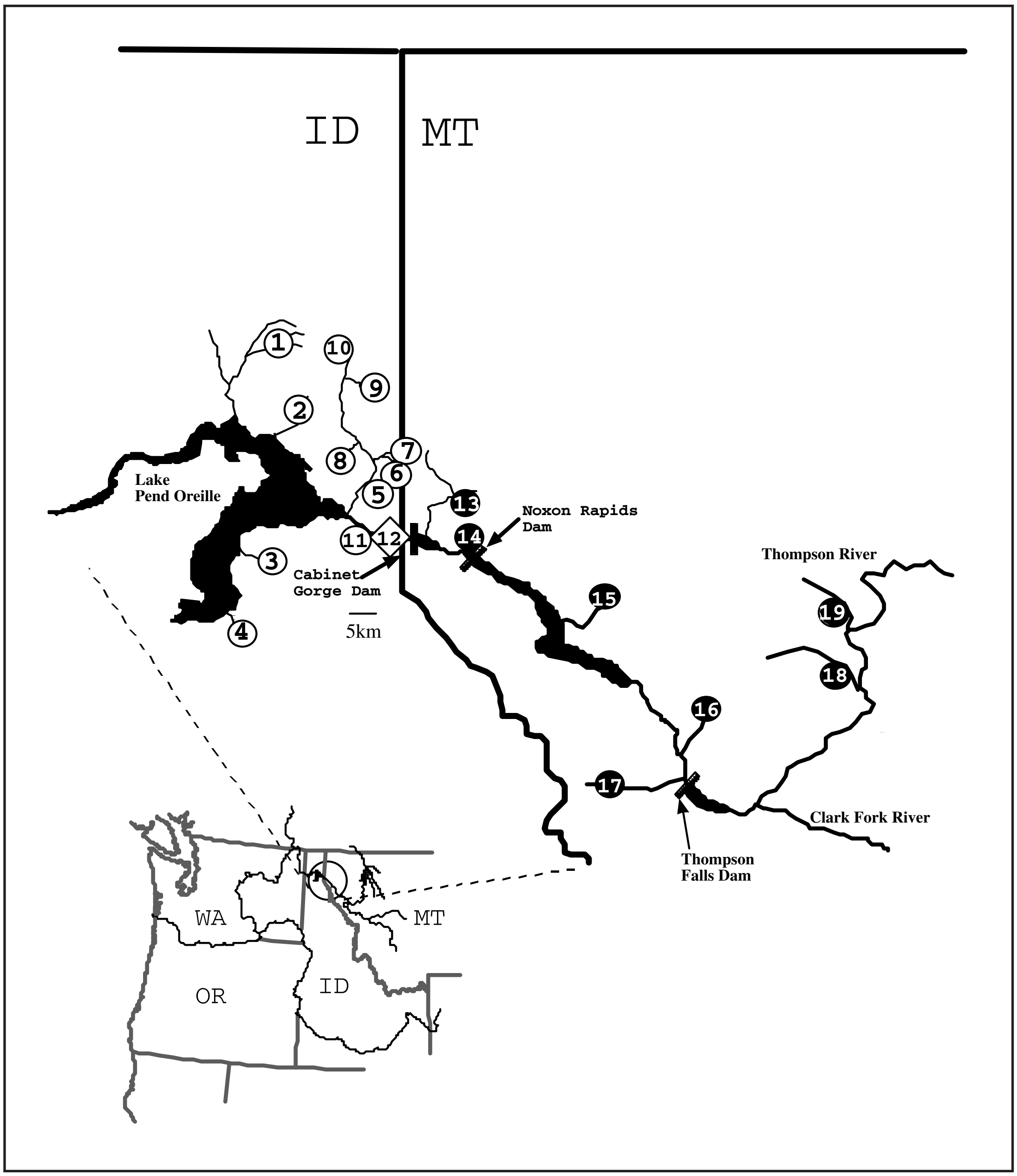


Figure 1. Approximate sample sites for bull trout from lower Clark Fork River and Lake Pend Orielle within the lower Clark Fork Recovery Subunit. White circles indicate locations below Cabinet Gorge Dam (the lower core area), black circles are locations above the dam (the upper core area), and the diamond is the sampling site at the base of the dam. Sample sites include local populations from (1) Grouse Creek, (2) Trestle Creek, (3) Granite Creek, (4) Gold Creek, (5) Morris Creek, (6) Savage Creek, (7) East Fork Lightning Creek, (8) Porcupine Creek, (9) Rattle Creek, (10) upper Lightning Creek, (11) Twin Creek, (12) Cabinet Gorge Dam sampled in 1997, 1998, and 1999, (13) East Fork Bull River, (14) Rock Creek, (15) Swamp Creek, (16) Graves Creek, (17) Prospect Creek, (18) Thompson River, and (19) Fishtrap Creek. From Neraas and Spruell (2001).

Methodology and approach

Implementation of restoration and recovery standards contained in the Clark Fork Settlement Agreement (part of the FERC licensing agreement for the Noxon and Cabinet Gorge Dams) within the lower Clark Fork—Lake Pend Oreille system is currently the responsibility of the Clark Fork River AIT. The AIT is composed of biologists representing Montana Fish, Wildlife and Parks (MFWP); Idaho Department of Fish & Game (IDFG); and Avista Corporation (which owns and operates hydropower dams at Noxon Rapids and Cabinet Gorge on the lower Clark Fork River; Figure 1). The AIT invited the authors as a panel of experts to a workshop in June 2000 at Clark Fork, Idaho, to deliberate and address the genetic and biological diversity consequences of a suite of proposed management options. Panelists were selected to represent a diversity of interests and direct experiences with bull trout and salmonid conservation.

In preparation for the workshop, panelists were provided background materials from available studies pertaining to lower Clark Fork bull trout and a series of 21 questions from the AIT (Box 1). As a result, each panelist was exposed to the range of issues confronting the AIT. Although the set of questions was developed specifically with lower Clark Fork bull trout in mind, most questions have more general relevance to all at-risk fish species.

The workshop also included biologists and managers from state and federal agencies and non-governmental organizations experienced or interested in the system. These other participants provided perspective, clarification, and additional information for the panel. Several site visits allowed the panel to witness first-hand the conditions of the Clark Fork above and below the dams, the dams themselves, and some of the tributary streams important to the bull trout in the system. The panel also visited several streams to observe the range of environmental conditions and to gain additional perspective. The panelists deliberated over and crafted responses to the issues identified in Box 1. Throughout the deliberations, the panelists employed a consensus-based approach to addressing the issues. Not surprisingly, panelists occasionally disagreed on the meaning of data provided or a resulting recommendation. Where absolute consensus was not achieved, we attempted to capture dissenting views or informational uncertainties within the formal responses.

An important consideration given to the panel were the “sideboards” placed on the deliberations regarding dam operation. Several potential options, including dam decommissioning or breaching, were precluded as viable in the near future because a the FERC operating license was renewed in 2000 and will not expire until 2044. Similarly, although construction of passive fish passage facilities has not been dismissed, it is unlikely in the near future.

Box 1. Specific questions directed to the Genetics Technical Panel by the lower Clark Fork River Bull Trout Aquatic Implementation Team (AIT). Questions have been edited for clarity.

1. What are the appropriate "conservation units" for bull trout in the lower Clark Fork River and Lake Pend Oreille?
2. How do we [the AIT] prioritize areas in which actions will be taken?
3. What are the current genetic risks faced by bull trout in the Lake Pend Oreille-lower Clark Fork River system?
4. What potential actions could be taken to reduce these risks?
5. Is there additional information to be collected allowing us to better evaluate these risks?
6. What are the potential genetic benefits and risks of fish passage at Cabinet Gorge Dam?
7. What are the potential genetic benefits and risks of fish passage at Thompson Falls and Noxon Rapids dams?
8. Should we move fish over a single dam (individually) or over several dams (sequentially)?
9. What fish should be moved and how; should we move adults, eggs, or both?
10. When might transfer of individuals among tributaries be an appropriate tool to increase population numbers?
11. When might reintroductions be an appropriate tool to found populations in currently unoccupied habitat?
12. How should donor stock(s) be identified?
13. At what life stage might acceptable transfers be made?
14. Assuming a receiving stream is functionally barren of bull trout, how many fish and at what ages should transfers be made to minimize genetic risk to the potentially established stock?
15. For how many years (potential generations) should fish be transferred to the receiving stream to maximize genetic viability and/or minimize genetic risk?
16. What is the target population size (for a tributary stock) in a stream restoration or re-introduction attempt?
17. How might we ensure that we are not damaging the donor stock?
18. When might hatchery supplementation be an appropriate tool to increase population numbers?
19. How long can fish be held in a hatchery before domestication becomes as issue?
20. What is a reasonable numeric goal at which point a population can be considered "recovered"?
21. What data should be collected to allow us to evaluate the actions we have chosen?

Outcomes and panel findings

In responding to the AIT questions, we focused our discussions and findings within the following general issue categories:

1. defining operationally the appropriate population units;
2. identifying priority areas for conservation efforts;
3. identifying risks to population structure and viability from competing management options;
4. overcoming population fragmentation associated with migratory fish passage;
5. potential for translocating or reintroducing populations into vacated habitats;
6. the potential role for hatchery supplementation; and
7. the role for monitoring and evaluation.

The following sections summarize our responses to these categories, which are reported more extensively in Spruell et al. (2000).

ISSUE 1: defining appropriate population units for bull trout conservation

Describing conservation units first required clear delineation of populations within the drainage hierarchy that were consistent with the terminology used in U.S. Fish and Wildlife Service (FWS) status reviews and recovery documents (Lohr et al. 2000). Accordingly, all populations within the lower Clark Fork River basin, including Lake Pend Oreille upriver to the Thompson River, comprised one of several bull trout recovery subunits—generally an area such as a large sub-watershed encompassing clusters of populations. Within this subunit, two core areas were defined—Lake Pend Oreille and the lower Clark Fork River (including impoundments). Each core area was further divided into local populations—spawning aggregates occupying third order streams (or above).

Defining appropriate units for conservation requires an appreciation of evolutionary origins and life-history variability as well as demographic and ecological insights pertaining to extant populations (Table 1). Bull trout from the lower Clark Fork—Lake Pend Oreille drainage display two genetically cohesive population clusters (Neraas and Spruell 2001; Figures 1 and 2), reflecting spatially-defined relationships within the basin. The first cluster (the open circles in the lower half of Figure 2) represents bull trout from tributaries below Cabinet Gorge Dam near the lake. The bull trout in these streams have been monitored regularly since 1984 (C. Downs, IDFG, Clark Fork, Idaho, unpublished data; and see Rieman and Myers 1997). These fish are considered to be derived from local populations with free access to Lake Pend Oreille and tributaries

Table 1. Population status estimated from observed number of spawning redds, densities of young in tributaries, and sizes of migratory adults for streams supporting bull trout above and below Cabinet Gorge Dam. Data are summarized from several unpublished sources (C. Downs, Idaho Fish and Game, Clark Fork, ID; L. Lockard, U.S. Fish and Wildlife Service, Creston, MT; Avista Corporation, Noxon, MT; L. Katzman, Montana Fish, Wildlife, and Parks, Noxon, MT; B. Rieman, USDA Forest Service, Boise, ID; and G. Gillin, Missoula, MT) or from reports or publications (Katzman and Tholl 2003; Lierman et al. 2003; Lockard et al. 2002a,b; Moran 2002; Dunham et al. 2001).

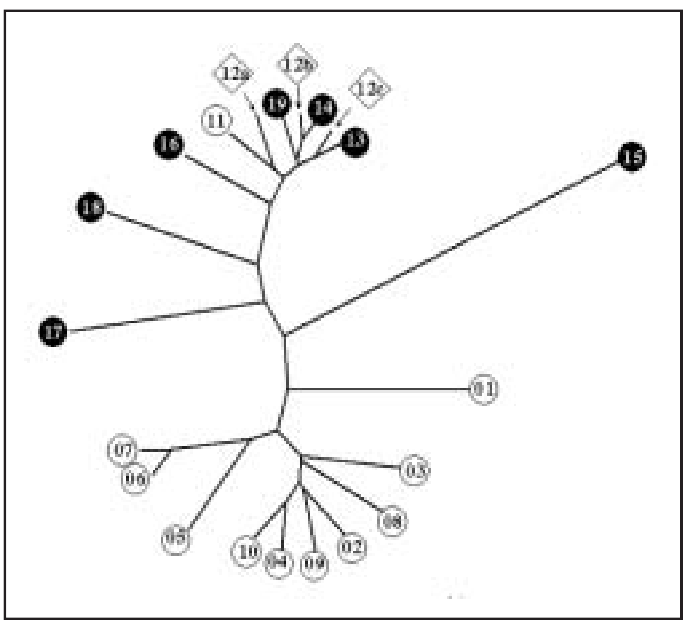
Local stream population	Annual mean redd counts 1983–2002	Redd counts 2001–2002	Adult population estimates	Sub-adult density (fish/100 m^2)	Maximum adult lengths (mm)
Core area below Cabinet Gorge					
East Fork Lightning Creek	50		283	2.50	850
Johnson Creek	20				772
Trestle Creek	253		1,383	4.30	820
Grouse Creek	37		231		703
Granite Creek	33				753
Twin Creek	9				
North Gold Creek	29				
Gold Creek	112		348		762
Clark Fork River spawning channel	8				852
Core area above Cabinet Gorge					
East Fork Bull River		21/32	15	1.43	765
South Fork Bull River		1/10			
Graves Creek		11/10		4.36	
Rock Creek		0/0		1.80	
Vermilion River		37/25	118	1.01	700
Prospect Creek				2.87	703
West Fork Thompson River		0/7		3.60	565
Fish Trap Creek				2.30	800

downstream of Cabinet Gorge (the location of the lower-most dam) and are dominated by a migratory (or adfluvial) life-history and a pattern of larger adult size (450 and 900 mm in length). These populations generally are demographically larger and considered to be more resilient than those upstream, although there is still considerable variation among them (Rieman and Myers 1997; Table 1).

The second genetic cluster (the blackened circles in the upper half of Figure 2) includes populations upstream of Cabinet Gorge Dam (completed in 1952). Densities of sub-adult or tributary-resident bull trout are comparable between the two population clusters. Unlike the downriver cluster, however, there appear to be few migratory adults in the upriver cluster (Pratt and Huston 1993). The Cabinet Gorge Dam and the Noxon Rapids Dam, 20 miles upstream (completed in 1959), appear to have suppressed or eliminated migratory life histories that occurred historically throughout the Clark Fork River up to and above Thompson Falls, an additional 60 miles upstream (Pratt and Huston 1993).

The remaining bull trout populations were collected a relatively short distance downstream of Cabinet Gorge Dam. Large adult bull trout (>450 mm) congregate in a spring-fed area below the dam (identified as open diamond population 12 in Figure 1 and open diamond 12a, b, and c in Figure 2) as well as in Twin Creek (population 11- open circle—in Figures 1 and 2), which is the first tributary below the dam (Figure 1). Bull trout from these collections display a strong genetic affinity with populations above the dam and are distinct from other populations below (Figure 2); however, this local population displays a migratory life-history pattern similar to populations in the downstream cluster (B. Rieman, unpublished data). The exact history of the fish in these two sites is uncertain, and records of their occurrence and abundance do not pre-date the dam. Whether these are historical or recently invading populations to the site remains unresolved, however, we judged that these fish represent the remnants of the upriver migratory fish that require assistance with upriver passage.

Figure 2. Depiction of genetic relatedness among bull trout from lower Clark Fork River and Lake Pend Oreille. Shown is "relatedness tree" based on genetic distances (i.e., Cavalli-Sforza and Edwards chord distances) of allelic variants at eight microsatellite loci. Numbers and symbols are as in Figure 1. From Neraas and Spruell (2001).



***ISSUE 2:** identifying priority areas for conservation focus*

Given these evolutionary relationships and the genetic background of the populations of interest, we shifted our focus to prioritization of groups or populations needing conservation or restoration actions. Saving or restoring "every" individual in "every" population, although a laudable goal, may prove unrealistic given the current state of the science, public/private will to reach this goal, and limitations in financial and human resources (see Allendorf et al. 1997 for a discussion on the need for prioritization). Therefore, we needed to develop a conservation "triage" approach based on a few rules of prioritization (following the medical terminology for a rapid or brief clinical assessment that determines priority order in which patients receive attention or care aimed producing the greatest benefits from limited resources or capabilities).

Prioritizing for protection and restoration was based first on identifying those populations that can provide the greatest (or optimal) "return" for investment. We then identified those attributes that presently limit a population's abundance or resilience. While we believe it important to take advantage of funding opportunities and cooperation by local landowners as they arise, these do not negate the need to develop a general strategy and priority order. To do so, benefits and risks must be balanced in an optimal strategy. A contrast of several potential, but not mutually exclusive, strategies illustrates some potential conflicts in seeking such balance.

These generalized strategies allow one to prioritize populations based on attributes such as ecological or evolutionary uniqueness. For example, a "save the best" priority standard focuses on the most demographically robust or viable populations as a way of ensuring at least partial representation of interpopulational relatedness. This option contrasts directly with a "save the worst (most critical need)" priority standard. The latter scheme emphasizes stabilizing the most critically imperiled population(s) to prevent immediate extinction on an emergency basis before returning to it full health. A "save the most unique" priority standard emphasizes conserving the most rare elements of biological diversity such as morphological or life-history forms derived from a rare evolutionary lineage. A "save the most common" priority standard emphasizes preserving redundancy of apparently successful extant forms. A "save the easiest to access" priority standard takes an approach focusing on those populations for which we have considerable information or are more easily reachable as a way of securing some early successes or programmatic efficiencies. Finally, a "save the most isolated" priority standard emphasizes focusing on secured refuge populations (which may or may not be the most unique).

Within the realm of conservation, selection of the single most appropriate triage strategy (see Table 2) remains somewhat controversial. For example, populations that are simultaneously robust, common, and accessible might have high conservation prioritization because a substantial benefit would be gained with a relatively limited investment. However, such populations tend not to require direct or immediate intervention because they are presently stable. Therefore, we assert that highest priority, as well as the greatest investment, should be directed to depleted, unique, and isolated populations as the most irreplaceable elements of biological diversity. Here, we considered not only genetic irreplicability, but also ecological irreplacibility (see Crandall et al. 2000). Multiple strong self-sufficient populations with common genetic and phenotypic characteristics would warrant joint protection but with limited investment under stable conditions. Investment in populations destined for extinction, but possessing characteristics in common with stronger self-sustaining ones would have minimal effect on biological diversity and thus lowest priority. Thus, based on this triage approach, we determined that adfluvial (migratory) populations derived or descended from upstream spawning populations should be the first priority, followed by at-risk upriver resident populations. Next, depressed populations from the downriver or Lake Pend Oreille clusters would follow. Abundant resident and migratory populations downriver would be the final priority; however, we must recognize that preventing currently healthy populations from degrading into an expensive or attention-diverting status remains a high priority that requires continual attention. Continuing our medical analogy, we must not sacrifice preventative medicine for emergency care.

Beneath these broad guidelines for prioritization lie further considerations requiring attention. Effective long-term maintenance and recovery efforts require accumulation of information, that will lead to a broader understanding of the biology and dynamics of the local populations and their interactions. Addressing such information gaps will result in a more complete assessment of the status of existing populations, a more thorough understanding of the underlying causes populations decline, and a more effective prioritization of resources available for restoration. Prioritization of restoration actions, however, ultimately must move forward with whatever information is available (Holling 1978; Walters 1986). Consideration of fundamental genetic and ecological theory and principles can provide an important foundation for management faced with the uncertainty inherent in any conservation case such as this.

ISSUE 3: genetic risks of conservation alternatives

Appropriate corrective actions must be preceded by as clear an understanding as practicable of potential or realized genetic risks related to existing populations in a very formal sense. Three general categories of genetic risk (i.e., bottlenecks, outbreeding depression, and interspecific hybridization) are addressed separately below along with potential actions to minimize these risks. Although these do not represent the entirety of possible risks (see Busack and Currens 1995 for a more extensive list), we focused on them as the most pressing. We further caution, however, that it is practically impossible to simultaneously eliminate the three categories of risk; therefore, we also considered potential trade-offs (Waples 1999).

Table 2. The triage approach to conservation prioritization applied to lower Clark Fork River—Lake Pend Oreille bull trout populations. 1 = highest immediate priority, 4 = lowest immediate priority.

Genotypic/Phenotypic Considerations	Population Status	
	Vulnerable	Strong
Unique	1	3
Common	2	4

Bottleneck effects—The apparent depletion of migratory adults above Cabinet Gorge Dam (Table 1) raises the risks of a genetic bottleneck (i.e., a reduction of genetic variation associated with low number of breeders) and associated inbreeding effects as well as local extirpation (the ultimate form of genetic loss). The panel concurred that re-establishing historical patterns of connectivity through upstream passage for adults returning to the base of existing dams appears to represent the single most important conservation act in the system to minimize these risks. While we do not recommend a specific method to achieve this goal (i.e., dam breaching vs. fish ladder vs. capture and transport, etc.), we judge that an effective mode of re-establishing connectivity is necessary. Moreover, whatever the action, it should be designed, undertaken, and evaluated in the context of likely historical patterns of genetic and life-history diversity. Potential benefits of a passage program include dramatic expansion of reproductive potential and population growth associated with the large adult size of migratory fish, a potential increase in effective population size (*Ne*) with larger populations, and the potential for rates of genetic and demographic exchange among populations more consistent with historical levels, thus reducing bottleneck risks.

Outbreeding effects—Concerns about outbreeding depression (i.e., a reduction in population fitness associated with interbreeding among divergent lineages; sensu Hard 1995, Gharrett et al. 1999) are based on the extent of genetic divergence observed among bull trout populations within the Lake Pend Oreille—lower Clark Fork system (Figure 2) and the potential for disrupting fine-scale local adaptations among these populations. Actions, such as purposeful crossbreeding or interbasin transfers undertaken to counteract presumed, but empirically unsupported, bottleneck effects may inadvertently promote gene flow among such historically isolated groups. Such elevated levels of gene flow among divergent gene pools have been shown to result in loss of locally adapted gene combinations and phenotypes (see Grant 1997 and references therein).

In this context, outbreeding poses a risk to bull trout populations within the system by decreasing their reproductive fitness. The panel, therefore, recommended a focus on passage of adults congregating below Cabinet Gorge dam (see comments under Issue 1 focusing on the fish sampled from site 11 and 12 in Figure 1) as having the greatest likelihood of originating from upstream populations, while acknowledging the potential isolation of these fish from those upstream for the past 50 years (7–10 bull trout generations). The clear common ancestry of these two groups, coupled with the threat of extinction of the upstream populations and the potential demographic benefits to the upstream fish, outbalances the minimal outbreeding depression arising from less than 50 years of isolation and divergence. Rapid divergence and local adaptation has been demonstrated in certain cases (e.g., Hendry et al. 2000), however, there is scant evidence available at present to suggest this is a widespread phenomenon. Moreover, the panel recommended maintaining a volitional basis for further migration following initial upstream transport into the nearest suitable cool water refuge to reduce physiological stress, maintain egg viability, and permit subsequent migratory behavior allowing the fish to select suitable or preferred spawning tributaries.

Interspecific hybridization—The final risk considered by the panel was the potential for interspecific hybridization with non-native char. There are currently no documented hybridizations with congeneric river-run and nonnative lake trout (*S. namaycush*) in these populations. However, nonnative brook trout occur throughout the system (see Pratt and Huston 1993) and have hybridized with bull trout in some streams. Unlike well-documented introgressions among native and introduced inland trout species (*Oncorhynchus* spp.), brook trout hybridization rarely proceeds beyond the first generation and introgression appears not to be a major direct threat (Kanda et al. 2002). Such hybridizations, however, may pose reproductively costly interference or waste of fitness opportunity by spawners. Ultimately, because hybridization occurs in some streams cohabited by both species, but not in others, a more detailed understanding of the invasion process and the environmental constraints of these hybridization events is necessary (but see Rich 1996; Paul and Post 2001). Regardless, the panel concurred that restoration of suitable habitat specific to bull trout preferences might decrease the risk of hybridization by producing ecological advantage for bull trout.

ISSUE 4: *general and specific requirements for fish passage*

The panel responded to fish passage questions within the context of having already acknowledged the high priority of re-establishing connectivity between adults congregating below Cabinet Gorge Dam with their upstream ancestral areas and populations. As noted above, we assert that the demographic benefits of successful upstream passage and volitional return to tributaries outweigh concerns of possible outbreeding depression within the same lower Clark Fork genetic unit. Based on a philosophy of letting a fish decide where it wants to go, fish captured just below and subsequently released just above Cabinet Gorge Dam might be again collected and released further upstream at each successive dam in a comparable manner.

ISSUE 5: *translocations and reintroductions*

The panel maintained a cautionary position regarding translocations and reintroductions among major lineages and watersheds. Given the genetic divergence apparent among bull trout populations and the existence of several population subunits, neither translocation nor supplementation were judged to be necessary or desirable restoration measures at this time. No situation or scenario was envisioned where translocation between the major lake and river core areas would be justified, except perhaps where clear physical and fitness problems were demonstrably attributed to inbreeding depression and if no suitable source populations within core areas could be identified.

Successful translocations of salmonids with complex life histories, like bull trout, are rare (Withler 1982; Allendorf and Waples 1996; but see also Unwin et al. 2000). As discussed above, the genetic distinction of population units above and below Cabinet Gorge dam increases the likelihood of outbreeding depression from potential interbreeding. Only populations containing very few spawners (e.g., *Ne*~2–5) for several years would be considered as possible candidates to receive translocated fish.

Reintroduction of individuals into vacated habitats with individuals from an outside source was also viewed as an undesirable option. The more risk-averse solution in terms of population mixing would be to restore important historical conditions and allow the system to recover on its own through more natural recolonization processes. Restoration or rehabilitation of the processes that create and maintain suitable habitats (e.g., Beechie and Bolton 1999) and support gene flow and demographic support among populations (Rieman and Allendorf 2001) is critical for the long-term persistence of these systems. Without these corrections, we assert that reintroduction has a low chance of succeeding and would not serve the real purpose in restoring biotic function to the system.

Regardless, before undertaking any reintroduction, appropriate responses are required to four questions: (1) are we confident that bull trout are no longer present that would serve as a natural gene bank?; (2) what conditions or stressors currently prevent bull trout from occupying suitable habitats (and have these been corrected)?; (3) is a suitable habitat expected reasonably to be recolonized through natural processes if conditions are improved?; and, (4) is a suitable or compatible donor population(s) available that can itself tolerate some removal of adults? The requirements imposed by these questions tightly constrain possible reintroductions. If habitat is limiting, then the reintroduction of fish from another population will likely fail. Without addressing this issue, all other discussions and actions will surely prove a waste of resources over the long term. Even if these issues are addressed and a nearby population exists, a preferred action will be to allow natural recolonization of the vacant habitat. Ultimately, we need to answer these questions and focus effort based on evidence rather than "hope." Fortunately, there is evidence for the capacity for natural recolonization—bull trout from the East Fork of Lightning Creek have apparently recolonized Morris Creek during the past 15 years (Figure 1).

Deliberations over the numbers and ages of transferred fish as well as duration of transfer identified the embryo as the preferred life stage if transfers prove necessary. This approach presumably would allow maximum exposure to the selective forces within the system. Such transfer also would minimize variance of adult reproductive output and thus maximize the effective size of the transferred population (e.g., Gall 1987). This option did not exclude other life stages, depending on various practical matters, such as the use of kelts (spawned adults), particularly where availability of reproductively mature individuals is limited.

Presence of a self-sustaining (or viable) population was considered to be the criterion by which reintroductions should be evaluated, rather than a simple numerical goal. If necessary, the release of young across a single generation (six to seven consecutive years for bull trout) should be sufficient time to successfully establish a population with representative year classes. After that time, releases should be scheduled for termination.

ISSUE 6: *use of hatchery supplementation*

Hatchery supplementation was discussed, but ultimately dismissed as an option for this bull trout recovery subunit. Given the genetic structure (Figure 2) and the existence of multiple, divergent bull trout populations, supplementation for this system was viewed as counterproductive and risky to the remnant populations. The inevitable occurrence of domestication selection works against recovery goals. This process of adapting to an artificially regulated environment begins immediately through enhanced survival of genotypes that would otherwise perish in nature, and increases during each successive generation (Busack and Currens 1995, Waples 1999). The expressed hazards to populations from domestication selection remain widely debated in some circles and these kinds of concerns would greatly benefit from more formal risk analyses to address the extent and effects of such risks. Regardless, the Pend Oreille—Clark Fork system is still moderately robust and complex in structure in comparison to instances where conservation hatcheries have been necessary and successful (but see Utter and Epifanio 2002 for a discussion on the nuances between strategies employed for conservation and supplementation propagation programs). For example, releases of individuals from hatcheries were used to successfully recover Apache trout (*Oncorhynchus apache*) in the southwest United States (Rinne and Janisch 1995). However, at the initiation of the program, few populations remained and the only possible mechanism to recover and expand the species' range was through captive breeding and release. Founding Apache trout populations were closely monitored, cultured fish were never stocked into existing wild populations, and critical habitat questions were addressed prior to stocking. These steps both protected the wild founding populations and maximized the success of the stocking program.

> We urge that the resources that would otherwise go to intensive short-term hatchery programs be directed to advancing the protection and restoration of priority habitats.

As an alternative to propagated supplementation, we urge the protection and restoration of robust populations throughout the system to maximize the potential for natural recolonization and demographic support of depressed populations or vacant habitats. We urge that the resources that would otherwise go to intensive short-term hatchery programs be directed to advancing the protection and restoration of priority habitats. Such an approach represents a paradigm and resource shift from hatcheries treating symptoms in the short term to the creation and maintenance of natural refuges that address root causes and restore natural processes over the long term.

ISSUE 7: *monitoring and evaluation*

Continued genetic and demographic monitoring and inventory will be vital to evaluate past and present restoration efforts as well as to guide necessary adjustments as new insights are gained. We recognize the benefits of using strategies that are adaptive (in an adaptive management sense; Holling 1978; Walters 1986) as new and refined information is unveiled. For example, a more complete inventory of the system is needed to document current patterns of occurrence and evolutionary relationships and to provide a baseline for evaluating future expansions, contractions, and genetic changes. In addition to ongoing redd counts, more robust population census methods (e.g., Dunham et al. 2001) need to be used periodically throughout the system. Continued sampling of genetically characterized populations (Figure 2) is being augmented by sampling from tributary streams above and below Cabinet Gorge Dam (e.g., Vermillion River or Johnson Creek, respectively) that support bull trout to broaden our understanding of genetic relationships.

This monitoring program and the new data it provides should be incorporated into broader phenotypic and life-history characterizations for these bull trout populations. For instance, resident bull trout may occur above barriers to fish passage in many of the streams in this system. Documentation and genetic characterizations of such populations may explain or confound the existing picture of genetic structuring. Understanding the patterns and nature of phenotypic and life-history diversity can help refine conservation prioritization both within and among tributary systems. Maintenance of the physical and biological environment supporting this diversity may also be necessary to maintain the potential for evolution and adaptation in distinct environments. Representation of the full range of environments associated with distinct phenotypic variation can supplement conservation prioritization even in the absence of distinct molecular genetic differentiation.

As noted above, simple numeric goals are probably incomplete and potentially misleading measures of population status. Identifying a point of "recovery" is analogous to determining when a population is "viable." Establishing this threshold is problematic because viability depends on numerous population characteristics, which are often difficult if not impossible to define precisely (Beissinger and Westphal 1998). Any attempts to define the status and viability of populations, however, should address issues and gaps in our knowledge such as those outlined in Table 3 (Rieman and McIntyre 1993; McElhany et al. 2000). If biologists cannot ensure or otherwise document that a population is secure in the context of each issue, its status should be considered either uncertain and in need of more detailed work, or "not viable." The number of secure populations and their distribution throughout the system can be informed by further research. Without such information, setting precise "recovery" goals will be largely subjective and more a matter of policy than science.

Because the two distinct ancestral groups are currently in very different conditions, the panel actions needed for bull trout conservation in the lower Clark Fork River. First, successful passage of adults over the dams must be assessed. We believe that passage is the most genetically beneficial of all proposed actions because it reestablishes connectivity among historically connected populations without elevating risks associated with forced outbreeding. There is some promise that morphological differences among populations may permit more precise identification of the stream of origin of adults returning to Cabinet Gorge Dam (Haas and McPhail 2001). Molecular genetic markers (Neraas and Spruell 2001) might also be used to identify offspring of specific matings and to track the success of those juveniles. We avoid offering advice on the specific tools to be used for these measures. Rather, we advocate choosing appropriate methods with robust experimental designs to answer specific questions.

For example, estimates of breeding adult abundance are based presently and primarily on redd counts (Table 1). These are useful for identifying coarse trends in populations, but there remain important sampling issues to resolve (Dunham et al. 2001). More precise and less biased estimates are essential to long-term conservation efforts, but will require considerably more refinement than existing redd count methods (discussed in Dunham et al. 2001). A monitoring program implemented throughout the system that focuses on robust estimates of adults from redd counts (indexed to true population estimates conducted periodically as has been done in some locations summarized in Table 1) may prove a more accurate alternative to the approach currently used.

Generality of model for other projects

The panel's deliberations and recommendations illustrate principles that have general applicability to a range of aquatic restoration and conservation programs. However, this panel worked in the context of specific constraints. For instance, we assumed that Noxon Rapids and Cabinet Gorge dams would be relicensed and continue operation for another 45 years. Consequently, the issue of dam removal or breaching was not on the table for discussion. To resolve whether or not these obstructions are considered "permanent" changes to the watershed will require continued assessment and deliberations.

Early in our deliberations, the panel agreed to the fundamental importance for establishing favorable ecological conditions (to bull trout), where enhancement of natural processes would take precedence over technical or intensive approaches. This perspective is not unique to this case, but has precedence in others, such as salmon in the Columbia River (Williams et al. 1999). Despite the necessity of capture for upstream passage, further opportunities to increase volitional movement were identified as preferred measures to restore historical connectivity among populations and between the species and its critical habitats. Permitting voluntary formation and maintenance of populations through reconnection and habitat restoration promotes natural genetic and phenotypic diversity (e.g., Utter 2001). This model warrants general application in cases where aquatic restoration and conservation activities are preferred to captive breeding and release programs. Fish culture's proven value to commercial and recreational fishing is not an issue here. However, the uniformity of captive progeny and reduction in volitional responses imposed by captive breeding and release limit its potential for successful general application in conservation and restoration programs (NRC 1996).

Finally, it is important to consider the context that expert panels operate. In the case study outlined, we were convened at the invitation of the Aquatic Implementation Team, which is tasked to address issues outlined in Native Salmonid Restoration Plan for this area (Ault and Pratt 1998; McMaster 1999). This plan outlined several adaptive management principles including the monitoring and evaluation of management actions based on well-designed and coordinated baseline data collection. Moreover, the AIT is expected focus on activities that most effectively enhance and restore bull trout populations both in terms of demographic abundance as well as overall population viability. This structure and the general context serve as a potential model for other groups faced with restoring native fish populations.

In conclusion, we offer the following general recommendations for empanelling technical advisors to provide advice for conservation or restoration planning:

1) Identify an appropriate panel of experts. We suggest the criteria for selecting the panel should be similar to those outlined in the "Independent Scientific Review" policy adopted by the Society for Conservation Biology (Meffe et al. 1998) to avoid conflicts of interest and to ensure independence of findings.
2) As new data are rarely generated from this kind of process, the availability of a body of basic information will be critical. Solicit, compile, and distribute relevant biological data well in advance of any meeting(s). Published and peer-reviewed data and interpreted results ultimately will carry greater weight. However, important data in gray literature sources, as well as relevant unpublished data, should be included.
3) Include local experts and stakeholders on-site during a portion of the panel discussions. Personal briefings will permit a rapid, but comprehensive presentation of important and controversial issues. Moreover, having those experts on hand to address questions from the panel will allow the panel to offer more specific suggestions than would be possible otherwise.
4) Clearly articulate the goals and objectives for the panel, but recognize they also may bring experiences or expertise crucial to a broader consideration of the issue. Recognize that deliberations and recommendations may be focused on a relatively narrow set of technical issues that do not integrate other kinds of technical (and even non-technical) information. Such narrowness does not diminish the value of advice if subsequently viewed in larger contexts.
5) Develop a list of basic or fundamental questions to be addressed by the panel to help establish a set of realistic guidelines for the panel's deliberations.
6) Sequester the panel in a retreat format to minimize distractions.
7) Recognize that technical panels of any kind operate in an iterative manner. Issues may be discussed and then revisited multiple times within other contexts. Ultimately, this approach leads to refinement of ideas, conclusions, and recommendations. Depending on the complexity of the issues, multiple working meetings beyond the initially allocated time frame may prove necessary.
8) There is no single "school of thought" regarding conservation or population genetics. Recognize dissenting viewpoints as a strength, not a weakness, of the expert advisory process. Therefore, it is desirable to ensure presentation of cogent dissenting views.
9) Establish a workable timeline for the panel to provide a written report. A first draft may be distributed for public, stakeholder, or expert review to identify gaps, inconsistencies, or factual errors.

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