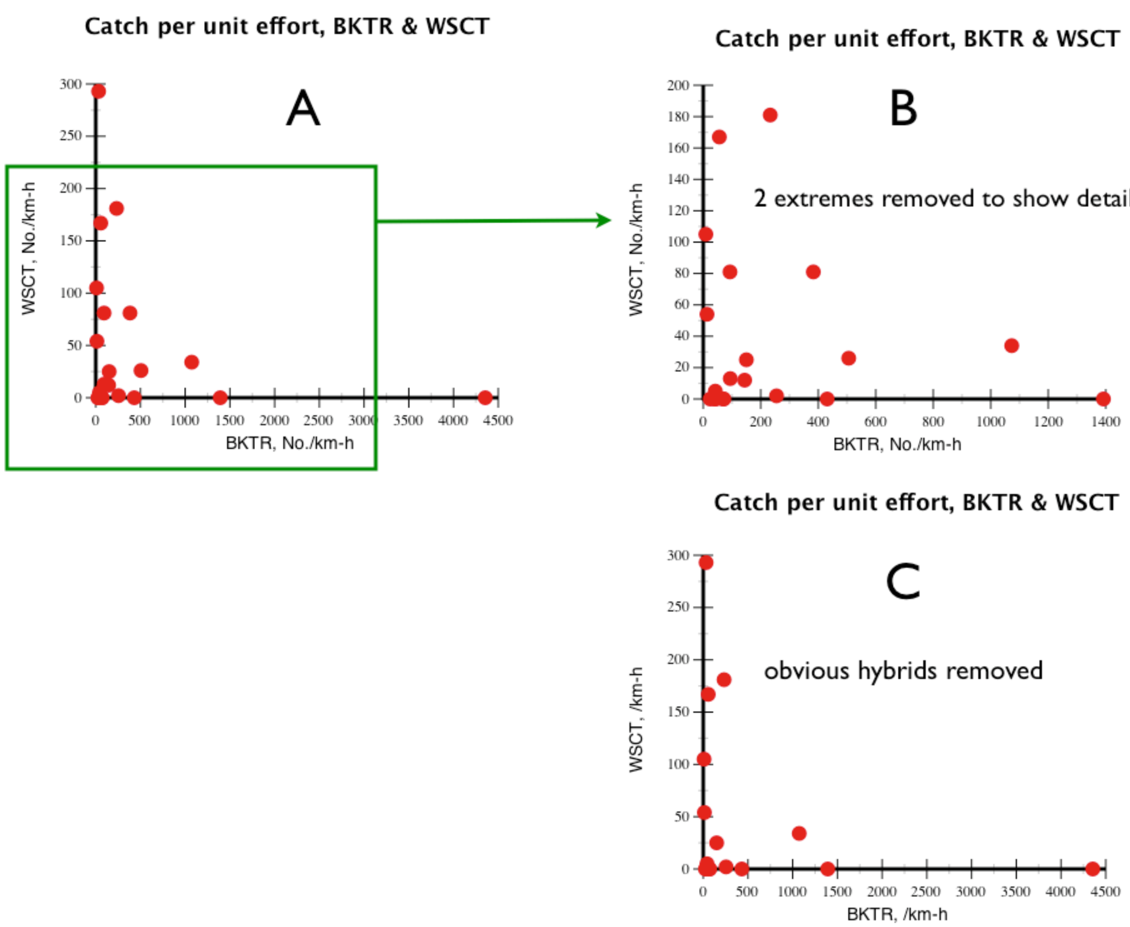
Contributions to a Recovery Plan for Westslope Cutthroat Trout (Oncorhynchus clarkii lewisi) In Alberta:

Threats and Limiting Factors

David W. Mayhood



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Prohibition of non-indigenous fish

We are of opinion (sic) *that there should be stringent prohibition against the introduction and planting of new species of fish not native to the waters of the two provinces. Great harm has resulted in many cases from the planting of foreign species of fish, which have become a nuisance.*

— Edward E. Prince, Thomas H. McGuire and Euston Sisley, Alberta and Saskatchewan Fishery Commission, 1912

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Threats and Limiting Factors

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Prepared for
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Executive Summary

Westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, is native to Montana, Idaho, small parts of Oregon and Washington, southeastern British Columbia and southwestern Alberta. It is at various degrees of risk throughout its range from a combination of historical overharvesting; habitat damage and loss; and competition, predation and introgressive hybridization with invasive non-native trouts. It faces additional future threats from current and increasing anthropogenic climate warming.

Two recent status reports prepared for the provincial and federal governments have shown the subspecies to be much reduced in abundance and distribution, and facing serious threats to its conservation status. The Alberta population of westslope cutthroat trout was identified in both reports as Threatened as of 2006. It is now being considered for listing under Canada's Species At Risk Act (SARA). Alberta has designated westslope cutthroat trout as Threatened under the provincial Wildlife Act. Alberta Fish and Wildlife is preparing a recovery plan for the subspecies.

The present report is one of a series of three resource documents prepared for the Alberta's Westslope Cutthroat Trout Recovery Team to supply supporting information and ideas for preparing a recovery plan. It reviews existing literature, and covers threats and factors limiting the subspecies in the native range in Alberta. The threats and limiting factors fall into four general categories.

Climate Change

Alberta, and the planet as a whole, is presently experiencing an increasingly warmer climate, primarily due to anthropogenic CO_2 accumulation in the atmosphere. These changes are measurable now, and are expected to persist for hundreds to thousands of years even if all further human-induced CO_2 additions were stopped immediately. The changes can be expected in turn to change the habitat and biotic interactions of remnant westslope cutthroat trout stocks, As a consequence, conditions historically experienced by westslope cutthroat trout within their native Alberta range will not apply in future. The magnitude of the problem can be summarized as follows.

Measured air temperatures across the Prairies have increased an average of 1.6°C since 1895, with more extensive regional warming over the last 50 years, particularly in certain winter and spring months. Another recent regional study has shown increases in the instrumented air temperature record of 1 to 4 °C over the past 80 to 118 years, with an accelerated rate of increase since about 1970. Over approximately the same period, moisture measures of various kinds have been declining across the prairies. In one study, nearly half of all study stations currently receive 14% to 24% less total annual precipitation than at the beginning of the period of record. There have been large contemporary decreases in Rocky Mountain glacier extent, mass and water yield over the same period. This is a serious issue because in the Bow River basin, glaciers provide a large proportion of streamflow during summer, when flows would otherwise be low and declining.

For the prairie provinces as a whole, all but one climate model scenario forecasts future combinations of mean annual precipitation and mean annual temperature that are beyond the range of natural variability. Climate projections for the native range of westslope cutthroat trout in Alberta generally mirror those for the prairie provinces as a whole, but with a some small differences. The median scenario (best estimate) forecasts temperature increases of 0 — +2 °C, +2 — +4 °C, and +4 — +6 °C for the 2020s, 2050s and 2080s, respectively. The respective projected mean annual precipitation changes are 0 — +10%, 0 — +10%, and 0 — +20%, with the higher figure in the 2080s applying to the southern part of the range (Oldman drainage). Seasonal projections for the 2050s forecast increases in mean seasonal atmospheric temperatures of +2 — +4 °C for all seasons, with zero to slight (up to +10%) increases in precipitation in winter, spring and fall, and 10 to 20% decreases in precipitation in summer in the northern part of the range (Bow drainage). In the southern part of the range (Oldman drainage), somewhat higher precipitation increases (+10 — +20%) are predicted for winter and spring, and somewhat lower decreases (0 — -10%) are projected for summer.

These climate changes within the native range of Alberta westslope cutthroats have some readily predictable consequences for trout stream habitats. Warmer fall, winter and spring temperatures combined with higher precipitation during those seasons implies that more of the precipitation will fall as rain, that fall streamflows might be somewhat higher, and that peak spring runoff may be higher and may arrive earlier. In contrast, higher summer temperatures combined with perhaps lower summer precipitation implies higher evapotranspiration, less runoff and lower summer streamflows. The higher air temperatures in all seasons will shorten winters, lengthen summers, shift spring to start earlier and shift fall to start later. Even slightly higher air temperatures will have disproportionately strong physical and ecological effects when baseline air and water temperatures ordinarily would be close to the freezing point, as they are in spring and fall. Slight increases in temperature above baseline conditions in spring and fall will cause rainfall instead of snowfall, delay freeze-up and accelerate break-up on streams and lakes and potentially will extend the runoff period on land.

Combined, these considerations suggest that in future, ice-free conditions will be longer, extending to later in the fall and beginning earlier in the spring. Spring runoff events will be larger, have higher peak flows, and will occur earlier than they do now. Streamflows will then rapidly attenuate over the summer, perhaps to recover slightly in fall. Alternatively, increased fall precipitation, if it occurs, may serve only to recharge soil moisture and groundwater drawn down over the drier summer, and may not appear as increased runoff. Higher-volume peak spring streamflows in particular can be expected to change stream channel morphology and the physical structure of the riparian zone. Because climate warming will continue for the foreseeable future, and indeed will intensify, these disturbances will be ongoing and more frequent.

The climate model scenarios above suggest that there will be substantial changes in the near future to basin hydrology, channel morphology, riparian physical structure and streamflows in westslope cutthroat trout native range in Alberta, particularly in the 2050s to at least the 2080s, and probably well beyond. In addition, because trout are poikilotherms ("cold-blooded"), higher temperatures will directly affect every biological function of remnant westslope cutthroats, including their physiology, behaviour, life history functions, interactions with invasive species, responses to habitat features, and exploitation. These changes may already have been initiated, and cannot now be avoided. These are the conditions for which the recovery team for Alberta's native westslope cutthroat trout must plan.

Land Use, Habitat Damage and Loss

The westslope cutthroat range in Alberta is heavily impacted by human land-uses. Linear disturbance density (a good measure of the intensity of land-use) within the native range in Alberta is high — among the highest observed in western North America. One consequence is that stream channels in most watersheds are at moderate (67%) to high (29%) risk of damage from the combined effects of increased peak flows and increased surface erosion as a result of forestry, oil and gas, urbanization, mining, recreation and other land-uses. There are many examples of actual damage to westslope cutthroat habitat due to linear disturbances throughout the native range, including within national parks. At-risk basins have been at risk for many decades to as much as a century. Many channels have probably been damaged for a long time, so restoration success may be both more difficult and less likely.

Higher road densities have been associated with reduced population densities of cutthroat trout, as has higher watershed surface disturbance generally. Fine sediment deposition in spawning areas, barriers to movement such as hanging culverts, cutoff side channels, channel straightening and relocation, and improved access for anglers may be the most important proximate causes of reduced cutthroat trout population densities associated with watershed surface disturbance and roads.

Roads are the principal source of fine sediments to streams in forestry operations, typically being much greater than that from all other land management activities combined. Measures of road development in watersheds commonly are correlated with the amount of fine sediment deposition in streams. Often the largest problems arise at crossings of small, intermittent and ephemeral headwater streams, because protection for such minor watercourses is considered unimportant or is simply overlooked. Unfortunately small headwater streams like these, or the headwater mainstems into which they drain, are disproportionately important ecologically, often providing critical habitat for cutthroats. It is just these small headwaters that hold the last remnant pure westslope cutthroat trout populations that this recovery plan is intended to save.

Even small increases in fine sediment loading to spawning areas can cause dramatic losses of early life-history stages of salmonids. It seems likely that there is no threshold below which fine sediment accumulation in salmonid spawning locations will be harmless. No salmonid life stage appears to require fine sediments as part of its habitat. Fine sediment levels in the substrate are a major limitation, natural or otherwise, on the carrying capacity of streams for westslope cutthroat. Fine sediment deposition is thus a major limiting factor affecting the recovery prospects of westslope cutthroat trout, and will have to be dealt with in recovery planning.

Cattle grazing is a common land-use throughout the native range outside of national parks. It has had profound effects on riparian integrity, channel form and fine sediment delivery within the native range of westslope cutthroats in Alberta.

Climate warming is both creating and interacting with other changes in watersheds in ways that will negatively impact westslope cutthroat trout habitat. Warming climate is expected to increase the frequency, intensity and extent of wildfires, increase drought frequency, and is believed to be enabling the recent outbreak of mountain pine beetle infestations in Alberta. Major effects of these changes are to greatly increase runoff and soil erosion from affected watersheds. A current policy to salvage log and preemptively remove beetle-infested or fire-killed lodgepole pine on Alberta's east slopes is likely to be seriously exacerbating the problem of increased peak runoffs and erosion from the killed forests. Higher peak runoff events, and more frequent extreme runoff events, expected as a result of climate warming-induced higher winter and spring temperatures will add to these effects. On logged, burned and beetle-killed watersheds, channel adjustment and riparian zone disturbances will be especially severe, as will increased fine-sediment deposition in westslope cutthroat trout critical habitat in those basins.

Dams are another major threat and limiting factor affecting westslope cutthroat trout recovery. Dams block movements of fish both upstream and downstream, transform upstream habitats from running water to standing water, substantially transform flow regimes in downstream habitats, and reduce downstream flows (in the case of irrigation dams and diversion weirs), among many other effects. Reservoirs are often heavily stocked with nonnative fishes to counteract the loss of native stocks and the low productivity of most of such waterbodies. All of these effects have the potential to severely disrupt fish populations, and have done so to native westslope cutthroat trout populations in Alberta.

Ten major dam projects now modify native westslope cutthroat trout habitat in the Bow River basin, and four more do so in the Oldman. Additional dams are expected to be built within the native range in response to summer streamflow reductions arising from climate warming. As well, there are many smaller dams on tributaries in the Oldman and Bow river basins, plus a very large number of impassible road culvert crossings of streams that have many of the effects of dams. All of these dams have seriously affected native westslope cutthroat trout habitat, populations, and range. All pose limitations on the possibilities for recovering the subspecies.

Invasive Nonnative Species

Four nonnative species threaten the continued existence of native westslope cutthroat trout populations in Alberta, and limit prospects for recovery of the subspecies. Three of these can be considered invasive. They impact the westslope cutthroats through hybridization, competition, predation, or possibly as vectors and reservoirs of parasites and agents of disease.

Rainbow trout are the single greatest threat to the continued existence of native westslope cutthroat stocks in Alberta. Rainbows readily hybridize with cutthroats to produce fertile offspring which can then interbreed among themselves and with either parental species. In many cases, the ultimate outcome is a fully-introgressed hybrid population called a hybrid swarm. Hybridized fish have different behaviour and physiological tolerances than either parent, and thus play a different ecological role than the native westslope cutthroat stock. Hybridization also weakens locally adapted populations, probably by disrupting coadapted gene complexes. While genetically pure cutthroats appear to be competitively superior in cooler headwaters, they appear to be inferior competitors to rainbow trout and rainbow-cutthroat hybrids in warmer waters, where rainbows and hybrids dominate. As a result, pure cutthroat stocks are almost exclusively confined now to small headwater streams. The populations are small and isolated from each other, making them susceptible to extirpation from the effects of inbreeding and stochastic events. Once lost, these populations are not replaced because, being confined to isolated headwaters, they are remote from other cutthroat populations that could move in to replace them. Rainbow trout might be considered to be the ultimate invasive species with respect to their effects on cutthroat populations because they subvert the cutthroat genome by completely and irreversibly infiltrating their own genes into the cutthroat gene pool.

Yellowstone cutthroat trout likewise introgressively hybridize with westslope cutthroat trout in a similar manner as do rainbow trout. Yellowstone cutthroats, however, appear to be less effective in competition with westslope cutthroats, which suggests that the hybrids of the two subspecies may likewise be weaker competitively than the native westslope sticks. Hybrid populations of these subspecies are primarily found in national park waters, and do not appear to be invasive.

Brown trout are an invasive species that have replaced westslope cutthroats in certain native habitats, notably the lower-gradient, larger, warmer mainstem rivers to which they seem largely to be confined. Attempts to restore native cutthroats to those habitats would likely be limited by the presence of this species, which is a predator and probably a superior competitor in such habitats.

Brook trout are an invasive species as well, although perhaps only under certain as yet undefined conditions. Certainly some populations have greatly expanded their range in certain watersheds over time, but other populations seem to have been unable to do so over many decades. The species is most successful in the smaller streams to which native cutthroat have become restricted. They can form very dense populations of small fish, becoming much more abundant than native cutthroats in many streams. Brook trout seem to outcompete cutthroats through interference at an early stage in the life histories of both fish. Brook trout appear to have displaced many native cutthroat populations from small streams in Alberta and elsewhere. They can be particularly difficult to eradicate, but successful attempts have been rewarded with greatly increased numbers of native cutthroats in some cases.

Overexploitation

Overexploitation in the late 1800s and early 1900s was a major factor in the decline and extinction of perhaps hundreds of local westslope cutthroat stocks in southwestern Alberta. Massive numbers of fish were removed from streams and rivers by almost every conceivable means in the earliest years of European settlement. Brook trout and rainbow trout, then brown trout and Yellowstone cutthroat trout, all of them not native to the region, were introduced — usually repeatedly and in large numbers — on top of the decimated native cutthroat trout stocks. As a result, the remnant native fish were permanently replaced, displaced or hybridized out of existence. The loss of so many stocks in this way, and their successful replacement by nonnative species, most of them invasive, constitutes a major factor limiting the probability of success of any recovery plan.

Current angling regulations are highly restrictive, and would appear to permit very little legal harvest of native or potentially native remnant populations, in part because of high minimum size limits in many stream populations that make them effectively catch-and-release only fisheries. There is a question of whether the size limits have some undesirable selective effects that would need further research to evaluate. Unnecessarily high legal and illegal harvest is also promoted by some of the highest road densities in western North America, which make nearly all remnant populations easily accessible, quite apart from their negative effects on habitat quality in streams.

Recent simulations of angling effects on model small-stream westslope cutthroat populations under various regulatory scenarios suggest that presently depressed cutthroat trout stocks could recover under catch and release management that allows only low angler effort. Once recovered, healthy populations of westslope cutthroat trout may be maintained with catch-and-release angling if fishing effort is no more than moderate. It will be important to limit accidental hooking mortality and illegal harvest to maintain and recover these populations. Under the scenarios tested, cutthroat trout populations like those modeled would be unlikely either to maintain themselves or recover if harvested unless angler effort is controlled. Previous Alberta studies on three medium- to large-stream populations showed that cutthroats were able to maintain low to moderate population densities under a longterm regime of intermittent heavy harvest (70 — 78% of the catchable population removed every second year). Overall, these results suggest that small-stream populations may be especially vulnerable to harvest, and may therefore require a more restrictive harvesting regime than do medium- to large-stream populations.

Considerable research suggests that it is possible to keep direct mortality from catch-and-release angling to very low levels (near 3%), even in heavily fished populations. Individual fish may be caught as many as three times in one day or an average of nearly 10 times in one season, and remain vulnerable to the fishery for three years. These considerations raise the question of whether such high levels of capture can have sublethal effects with consequences for reproductive success. This question appears not to have been studied yet.

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Introduction

The westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, is native to southwestern Alberta. Recent status reports (Alberta Sustainable Resource Development and Alberta Conservation Association 2006; COSEWIC 2006) have shown the subspecies to be much reduced in abundance, and facing serious threats to its conservation status. COSEWIC assessed the Alberta population of westslope cutthroat trout as Threatened in 2006 (COSEWIC 2006), and it is now being considered for listing under Canada's Species At Risk Act (SARA). Alberta has designated westslope cutthroat trout as Threatened under the provincial Wildife Act. Accordingly, Alberta Fish and Wildlife is preparing a recovery plan for the subspecies.

This report is the second of three resource documents prepared at the request of Alberta's Westslope Cutthroat Trout Recovery Team to supply supporting information and ideas for preparing the recovery plan. It covers threats and factors limiting the subspecies in the native range in Alberta. I have interpreted threats and limiting factors to be those factors that threaten to further reduce westslope cutthroat stocks in Alberta, or that limit the recovery prospects for this fish, whether left to its own devices, or assisted by management efforts.

The recovery team may include some, all or none of the material in these reports in the final plan. I have written, formatted and arranged this report so that whole sections can be readily cut and pasted into the evolving plan and edited there as necessary.

The threats and limiting factors affecting westslope cutthroat trout stocks in Alberta are the Four Horsemen of Extinction: climate change, habitat damage and loss, invasive nonnative species, and overexploitation (Mayhood 2000; Alberta Sustainable Resource Development and Alberta Conservation Association 2006; COSEWIC 2006). Variously worded and defined, problems in these categories dominate the literature of conservation biology. Climate change has only recently been recognized as a major issue facing conservation of westslope cutthroat trout (Alberta Sustainable Resource Development and Alberta Conservation Association 2006). I give it its proper place here at the head of the line, in honour, if that is the proper word, of its now unavoidable, all-pervasive influence on the fate of this most characteristic trout of Alberta's southwest mountains and foothills.

Climate Change

Alberta, and the planet as a whole, is presently experiencing an increasingly warmer climate, primarily due to anthropogenic CO_2 accumulation in the atmosphere (IPCC 2007; Lemmen et al. 2008; Sauchyn and Kulshreshtha 2008). These changes are ongoing, and are expected to persist for hundreds to thousands of years even if all further human-induced CO_2 additions were stopped immediately (Archer et al. 2009; Solomon et al. 2009). These changes can be expected in turn to change the habitat and biotic interactions of remnant westslope cutthroat trout stocks, As a consequence, conditions historically experienced by westslope cutthroat trout within their native Alberta range will not apply in future. For this reason, it will be necessary to incorporate climate change projections into all aspects of the recovery plan (McCarty 2001).

Historical and Recent Changes in Climate

A major assessment of climate change data (current as of 2007) has recently been completed for the Government of Canada (Lemmen et al. 2008). The review presents assessments for Canada on a regional basis, providing the most recent climate change summary available for the Prairie Provinces (Sauchyn and Kulshreshtha 2008). The remarks to follow, here and in the following section, are based on these assessments unless otherwise noted. It is also possible to use online tools to model certain climate scenarios (e.g.; Canadian Climate Change Scenarios Network, http://www.cccsn.ca/index-e.html), but that exercise is well beyond the scope of this report.

Atmospheric temperatures in the Prairie Provinces are getting warmer. Measured air temperatures across the Prairies have increased an average of 1.6°C since 1895, with more extensive regional warming over the last 50 years, particularly in certain winter and spring months. Another recent regional study (Schindler and Donahue 2006) has shown increases in the instrumented air temperature record of 1 to 4 °C over the past 80 to 118 years, with an accelerated rate of increase since about 1970. Data from boreholes and tree-ring studies provide evidence that the warmest climate of the last 1000 years occurred in the twentieth century.

At the same time, moisture measures of various kinds have been declining. According to Schindler and Donahue (2006), nearly half of their study stations currently receive 14 to 24% less total annual precipitation than at the beginning of the period of record. The same authors also point to evidence of large contemporary decreases in Rocky Mountain glacier extent, mass and water yield over the same period. Water levels in most closed-basin prairie lakes that were monitored have declined since records were first kept in the 1920s to 1940s, likely due to rising temperatures, changes in snowpack and changes in rainfall intensity. Yet a variety of lines of evidence suggest that the climate of the twentieth century was relatively favourable for settlement of the Prairies because it lacked the sustained droughts observed in records of sand dune activity, the fur trade and the health of First Nations peoples.

These indications of recent climate warming on the prairies overlie a longer history of substantial natural fluctuations in climate on multidecadal to multicentennial scales that can be read in tree-ring records and lakebed cores. That is, they are thought to mark a largely anthropomorphic change that is superimposed upon those natural fluctuations.

Projected Changes in Temperature and Precipitation

Prairie Provinces as a Whole

Projections for future changes in atmospheric temperatures and precipitation for the Prairie Provinces provide a range of estimates depending on the climate model used, the season, the subregion and the number of years into the future the projection is made (Sauchyn and Kulshreshtha 2008). Sauchyn and Kulshreshtha (2008) provide a range of possible scenarios for the decadal periods 2020s, 2050s and 2080s, representing the year ranges 2010 - 2039, 2040 - 2069, and 2070 — 2089, respectively, as compared to baseline conditions (1961-1990). With a single exception (one scenario in the 2020s), all models and scenarios forecast future combinations of mean annual precipitation and mean annual temperature that are beyond the range of natural variability.

Sauchyn and Kulshreshtha (2008) provide separate analyses for the Forest subregion and the Grassland subregion of the Prairie Provinces (Table 1). Mean annual precipitation in the Grassland subregion is expected to increase slightly over baseline conditions by the 2020s, and the increases will themselves increase from the 2020s through the 2080s. Mean annual precipitation in the Forest subregion is forecast to show slightly larger increases over the same period. Accompanying increases in temperature are projected to be slightly higher in the Grasslands than in the Forest subregion, but will increase over the 2020s through the 2080s.

Table 1. Projected changes in mean annual precipitation (pptn) and mean annual temperature (°C) in the Prairie Provinces of Canada. Figures are medians of climate change scenarios derived from 7 global climate models. Data were extracted from Sauchyn and Kulshreshtha (2008:Figure 8a), and Sauchyn (personal communication).

Period	Grassland		Forest	
	Pptn, % change	°C	Pptn, % change	°C
2020s	+2	+1.6	+5	+1.4
2050s	+5	+3.1	+9	+2.4
2080s	+9	+5	+13	+4.3

Projected seasonal patterns of change in precipitation and temperature across the Prairie Provinces are available for the 2050s (Table 2). Seasonal changes in mean precipitation are expected to be identical between the Grasslands and Forest subregions from winter through summer, and differ only slightly in fall. Both subregions are expected to show small increases in precipitation in winter and spring, slight declines in summer, and very small increases in fall. Seasonal temperatures are expected to rise nearly identically in the two subregions, with the greatest increase in winter and the least in fall.

Table 2. Projected changes for the 2050s in mean seasonal precipitation (pptn) and mean seasonal temperature (°C) in the Prairie Provinces of Canada. Figures are medians of climate change scenarios derived from 7 global climate models. Data were extracted from Sauchyn and Kulshreshtha (2008:Figure 8b) and Sauchyn (personal communication).

Season	Grassland		Forest	
	Pptn, % change	°C	Pptn, % change	°C
Winter (DJF)	+13	+3.8	+13	+3.8
Spring (MAM)	+14	+3.2	+14	+3.2
Summer (JJA)	-5	+3	-5	+3
Fall (SON)	+2	+2.9	+1	+2.8

Alberta Native Range of Westslope Cutthroat Trout

Sauchyn and Kulshreshtha (2008) provide substantial regional detail in a series of maps showing the distribution and magnitude of maximum, minimum and median projections for precipitation and temperature changes for the 2020s, 2050s, and 2080s. These maps show scenarios covering the native range of westslope cutthroat trout in Alberta (hereinafter, "the native range"), which lies in a rough triangle east of the Continental Divide of the Rocky Mountains, west and northwest of Calgary (Bow River basin), and south to the Montana border (Oldman River basin), both as mean annual values and as seasonal estimates.

The weight of current climate change projections for the native range suggests that mean annual temperatures will increase steadily through the 2080s, accompanied by a slight increase in mean annual precipitation that becomes more substantial in the southern part of the range (Oldman basin) in the 2080s (Table 3, median data). The minimum scenario suggests a slight decline in precipitation in all 3 study periods, accompanied by slight increases in temperature at least by the 2080s. The maximum scenario predicts definite increases in precipitation and temperature, especially by the 2080s in the southern part of the range (Oldman River basin). All scenarios and models predict a rise in temperatures that intensifies over time, and the weight of the evidence suggests a small increase in precipitation that becomes greater in the southern part of the range by the 2080s.

The effect of the projections in Table 3 on actual annual mean air temperatures within the westslope cutthroat trout native range in Alberta is illustrated in Table 4. The mean annual air temperature in the Bow River basin part of the range (2.21 °C, n = 8) is expected to rise to 4.2 — 6.2 °C by the 2050s. The mean annual air temperature in the Oldman River basin part of the range (4.03 °C, n = 4) is expected to rise to 6.0 — 8.0 °C by the 2050s.

Table 3. Projected changes in mean annual precipitation (pptn) and mean annual temperature (°C) for the native range of westslope cutthroat trout in Alberta. Figures are medians, maxima and minima of climate change scenarios derived from 7 global climate models. Data extracted from Sauchyn and Kulshreshtha (2008: Figure 9) and Sauchyn (personal communication). Two entries in a cell indicate projections for 2 different parts of the westslope cutthroat trout range: northern above southern, roughly corresponding to the Bow and Oldman river drainages, respectively.

Period	Minimum/Driest		Median		Maximum/Wettest	
	pptn, % change	°C	pptn, % change	°C	pptn, % change	°C
2020s	0 — -10	0 — +2	0 — +10	0 — +2	+10 — +20	+2 — +4
2050s	0 — -10	0 — +2	0 — +10	+2 — +4	+10 — +20	+4 — +6
2080s	0 — -10	+2 — +4	0 — +10 +10 — +20	+4 — +6	+10 — +20 +30 — +40	+6 — +8 +8 — +10

The native range shows seasonal changes in mean temperature and mean precipitation that are more complex than the mean annual projections (Table 5). The weight of the evidence points to a rise in mean temperatures over baseline conditions in all seasons, accompanied by small increases in precipitation in winter, spring and fall, with small precipitation decreases in summer (Table 5, medians of all model predictions). There are also small differences in the precipitation projections for the northern and southern parts of the range in winter, spring and summer, but not in fall. The predicted seasonal temperature changes closely bracket the seasonal projections for the Prairie Provinces as a whole (c.f. Table 2). The precipitation projections for the southern part of the range likewise closely bracket the same projections for the Prairies as a whole, but those for the northern part of the range suggest that area will be drier in winter, spring and summer than predicted by the forecasts for the Prairie Provinces as a whole.

The minimum scenario predicts small or no increases in temperatures in all seasons (the northern part of the range may even show a slight decrease in temperature in winter), accompanied by little change in precipitation in winter and spring, and small precipitation decreases in summer and fall. The maximum scenario forecasts a temperature increase of 4 — 6 °C in all seasons (more in the south in winter), together with large increases in precipitation in winter, spring and fall, but much smaller precipitation increases in summer. The maximum scenario also predicts smaller increases in precipitation in the northern part of the range as opposed to the south in winter, spring and summer, but a distinctly larger increase in fall.

Table 4. Projected 2050s annual mean air temperatures for selected stations within the native range of Alberta westslope cutthroat trout, based on the projections in Table 3. Mean annual temperature normals are Environment Canada data (Gadd 1995). Figures in parentheses are years of record. PP, provincial park; RS, ranger station. The major river basin for each station is given.

Station	Baseline, °C	Projected 2050s, °C
Bow Valley PP (1967—1990) Bow R	3.5	5.5 — 7.5
Elbow RS (1961—1990) Bow R	1.6	3.6 — 5.6
Ghost RS (1961—1990) Bow R	2.3	4.3 — 6.3
Highwood RS (1961—1990) Bow R	1.6	3.6 — 5.6
Kananaskis (1961—1990) Bow R	3.1	5.1 — 7.1
Kananaskis RS (1962—1987) Bow R	1.3	3.3 — 5.3
Pekisko (1961—1990) Bow R	2.1	4.1 — 6.1
Sheep RS (1963—1976) Bow R	2.0	4.0 — 6.0
Turner Valley (1961—1975) Bow R	2.3	4.3 — 6.3
Beaver Mines (1961—1990) Oldman R	4.4	6.4 — 8.4
Castle RS (1961—1990) Oldman R	3.0	5.0 — 7.0
Coleman (1961—1990) Oldman R	3.5	5.5 — 7.5
Pincher Creek (1979—1990) Oldman R	5.2	7.2 — 9.2

Table 5. Projected seasonal changes in mean seasonal precipitation (pptn) and mean seasonal temperature (°C) within the native range of westslope cutthroat trout in Alberta for the 2050s. Figures are medians, maxima and minima of climate change scenarios derived from 7 global climate models. Letters in parentheses denote the months included in each season. Data were extracted from Sauchyn and Kulshreshtha (2008: Figure 10) and Sauchyn (personal communication). Two entries in a cell indicate projections for 2 different parts of the westslope cutthroat trout range: northern above southern, roughly corresponding to the Bow and Oldman river drainages, respectively.

Period	Minimum/Driest		Median		Maximum/Wettest	
	pptn, % change	°C	pptn, % change	°C	pptn, % change	°C
Winter (DJF)	0 — -10	0 — <0 0 — +2	0 — +10 +10 — +20	+2 — +4	+30 — +40 +50 — >50	+4 — +6 +6 — +8
Spring (MAM)	-10 — 0 0 — +10	0 — +2	0 — +10 +10 — +20	+2 — +4	+30 — +40 +40 — +50	+4 — +6
Summer (JJA)	-10 — -20	0 — +2	-10 — -20 0 — -10	+2 — +4	0 — +10 +10 — +20	+4 — +6
Fall (SON)	-10 — -20	0 — +2	0 — +10	+2 — +4	+30 — +40 +10 — +20	+4 — +6

For planning purposes, the best synthesis of the seasonal data for the native range of westslope cutthroats in Alberta is provided by the median projections of the 7 global climate models (Table 5, median scenario). By the 2050s, atmospheric temperatures will be higher by 2 — 4 °C in all seasons throughout the native range. In the northern part of the range (Bow River basin), precipitation will be 0 — 10 percent higher in winter, spring and fall, but 10 — 20 percent lower in summer. In the southern part of the range (Oldman River basin), precipitation will be 10 — 20 percent higher in the winter and spring, 0 — 10 percent lower in summer, and 0 — 10 percent higher in the fall.

Hydrological Implications of Climate Change in the Native Range

The projected changes in climate within the native range of westslope cutthroat trout have important implications for the hydrology of the watersheds they occupy. Warmer fall, winter and spring temperatures combined with higher precipitation during those seasons implies that more of the precipitation will fall as rain, that fall streamflows might be somewhat higher, and that peak spring runoff may be higher and may arrive earlier. In contrast, higher summer temperatures combined with perhaps lower summer precipitation implies higher evapotranspiration, less runoff and lower summer streamflows.

The higher air temperatures in all seasons will shorten winters, lengthen summers, shift spring to start earlier and shift fall to start later. Even slightly higher air temperatures will have disproportionately strong physical and ecological effects when baseline air and water temperatures ordinarily would be close to the freezing point, as they are in spring and fall. Slight increases in temperature above baseline conditions in spring and fall will cause rainfall instead of snowfall, delay freeze-up and accelerate break-up on streams and lakes and potentially will extend the runoff period on land.

Combined, these considerations suggest that in future, ice-free conditions will be longer, extending to later in the fall and beginning earlier in the spring. Spring runoff events will be larger, have higher peak flows, and will occur earlier than they do now. Streamflows will then rapidly attenuate over the summer, perhaps to recover slightly in fall. Alternatively, increased fall precipitation, if it occurs, may serve only to recharge soil moisture and groundwater drawn down over the drier summer. Higher-volume peak spring streamflows in particular can be expected to change stream channel morphology and the physical structure of the riparian zone. Because climate warming will continue for the foreseeable future, and indeed will intensify, these disturbances will be ongoing and more frequent.

The climate model scenarios above suggest that there will be substantial changes in the near future to basin hydrology, channel morphology, riparian physical structure and streamflows in westslope cutthroat trout native range in Alberta, particularly in the 2050s to at least the 2080s, and probably well beyond. These changes may already have been initiated, and cannot now be avoided, as noted earlier in this section (Archer et al. 2009, Solomon et al. 2009). These are the conditions for which the recovery team for Alberta's native westslope cutthroat trout must plan.

Implications of Climate Change for Westslope Cutthroat Trout in Alberta

Poikilotherms ("cold-blooded" animals) such as fish cannot regulate their internal temperature to any great extent, so are highly sensitive to changes in the temperature of their environments. Effectively all physiological functions of most types of fish, including Salmonidae, are directly affected by the ambient temperature, including swimming, feeding and digestion, growth and metabolism, immune response and cardiovascular function (Moyle and Cech 1996; Evans 1998). Air temperatures are one of the important determinants of water temperatures in streams (Stoneman and Jones 1996; Sloat et al. 2005; Bates et al. 2008), so water temperatures in westslope cutthroat trout habitat can be expected to increase as the climate warms, affecting the physiology of westslope cutthroat trout. Through its effects on physiology, higher temperatures can be expected to affect, at a minimum, behaviour (Raleigh 1971; Sauter et al. 2001); competitive ability (Shepard 2004); vulnerability to predators, parasites and diseases (Materna 2001); habitat use (Mackay 2004; Mullner and Hubert 2005); and vulnerability to hybridization (Robinson 2007). Furthermore, the effects of of temperature increases on fish physiological rates will be especially great at the low ambient temperatures characteristic of Alberta native cutthroat streams, in accord with Krogh's "normal curve" (Winberg 1971). Higher temperatures will also affect the fish indirectly through their effects on habitat. The effects of warmer temperatures caused by global warming are considered in more detail as part of other threats and limiting factors discussed below. One thing is clear, however: the overall net effects of climate change on westslope cutthroat trout in Alberta are likely to be strongly negative (Williams et al. 2009).

Land Use, Habitat Damage and Loss

Climate Change Effects on Habitat

Climate warming will truncate the downstream native range of westslope cutthroat trout, permanently excluding the subspecies from reoccupying the downstream reaches of rivers that it historically occupied. Warming may be sufficient to isolate tributaries from each other by warming their lower reaches and their common mainstems. While the upstream limit may be extended by global warming effects, headwater habitat will be of lower quality, with a lower carrying capacity for trout.

The native range of westslope cutthroat trout in Alberta is restricted to the Bow and Oldman river basins from the extreme headwaters downstream in the mainstem rivers far out into the plains (Mayhood 2000). The downstream limit of the range was probably set by a combination of high summer maximum water temperatures, presence of coolwater predators such as northern pike (*Esox lucius*), and possibly by competitors. In the headwaters, westslope cutthroats historically were excluded from the highest elevations by barriers to movement such as waterfalls, chutes, and steep torrential reaches. Where passage into higher elevations was possible, cold summer water temperatures could have prevented populations from becoming permanently established (Peterson et al. 2004; Coleman and Fausch 2007).

Westslope cutthroats appear to be strongly cold-adapted, having a surprisingly low incipient lethal temperature of just 19.6 °C (Bear et al. 2007). This temperature is now approached in summer in many of the lower-elevation streams within the historical range [e.g., 18 °C, Waldron Bridge, Oldman River; 18 °C, Mountain View Weir on Belly River; 20 °C, lower Highwood and lower Sheep rivers (Longmore and Stenton 1981)]. Projected warming of mean summer air temperatures by 2 — 4 °C by the 2050s (Table 5), if maximum summer water temperatures are similarly affected, could directly truncate the downstream habitat of westslope cutthroats through warming of those waters. While westslope cutthroats apparently no longer occur anywhere near the historical downstream limit in any Alberta river at present, climate warming will permanently exclude them from reoccupying the downstream reaches of the historical range (Robins 2009). Warming may be sufficient to drive cutthroat populations into increasingly higher elevations, fragmenting populations as adequate habitat becomes separated from mainstems and becomes restricted to headwaters (Keleher and Rahel 1996).

On the other hand, climate warming may be expected to warm the presently cold headwaters within the native range. Accessible headwater habitats at or near the lower thermal limit for reproduction and recruitment in westslope cutthroat populations could become habitable as the climate warms, and could become naturally inhabited if stocks presently occur downstream. If the warmed headwaters are presently inaccessible, they could be engineered to be accessible, or they could become suitable sites to translocate and archive westslope cutthroat stocks of conservation value. Still, there are critical habitat and physical limits at the upstream end of many stream networks preventing trout populations from shifting into sufficiently cool locations, including dry stream channels; insufficient spawning, rearing or overwintering habitat; and waterfalls.

The net direct thermal effect of climate warming on habitat will be to shift suitable westslope cutthroat habitat upstream, to shrink its extent, and to leave only habitat that is, overall, of lower quality with lower carrying capacity. One estimate for the US Rocky Mountains in Wyoming places the projected loss of salmonid habitat (geographic area) from climate warming as high as 35.6 — 62.0% for increases in mean July air temperature of 2 — 4 °C (Keleher and Rahel 1996).

In the native range of westslope cutthroat trout in Alberta, the annual hydrograph typically shows rising flows from meltwater in April through May with a peak in early June, followed by a long tail-off over the summer to minimum base flows in December through February.

Hydrological changes caused by global warming will further reduce the amount and quality of trout habitat, especially in summer. In streams lacking summer meltwater contributions from remnant snowbanks or glacial ice, higher summer temperatures will produce lower seasonal flows, typically reducing near-bank rearing habitat and shrinking the number and size of pools favoured by adult cutthroats. Higher temperatures and possibly precipitation in winter and spring should produce higher base flows, which would provide better overwintering conditions.

The effect on trout habitat of warming-caused changes in peak spring runoff are not at all clear. Peak flows are expected to be earlier, higher and to recede more quickly as a result of higher air temperatures, as noted above. Higher peak flows will cause channels to adjust even more to accommodate more water, and in the alluvial beds of our region they will do this mainly by moving more sediment derived from the banks and channel bottom. The morphology of stream channels and riparian zones will change, but actual conformations are highly specific to individual runoff events, streams, their sediment sources and gradients, bedrock controls, and to antecedent disturbances in the watersheds and channels themselves. More frequent high flows will increase disturbance frequency and reduce stability of channel, bar, riparian and floodplain forms. How these changes will affect trout that must use the new habitat is unpredictable. Westslope cutthroat trout seem to be well-adapted to frequent physical changes and the resultant unstable habitats provided that local refuges or free and open corridors for movement are available to allow escape and recolonization (Liknes and Graham 1988; Brown and Mackay 1995; Prince and Morris 2003).

Land-use Impacts on Watersheds

Land-uses within the watersheds comprising the native range are important threats and limiting factors to cutthroat trout conservation and recovery. This is because fish habitats in inland waters are a product of their watersheds. What happens within the watershed will eventually influence the lakes and streams into which the basins drain (Rawson 1939c; Hynes 1975).

The westslope cutthroat range in Alberta is heavily impacted by human land-uses. Linear disturbance density (a good measure of the intensity of land-use) within the native range in Alberta is high — among the highest observed in western North America, commonly reaching 2 — 5 km• km^{-2} (Sawyer and Mayhood 1998b; see also Alberta Environment and Olson +Olson 1999). One consequence is that stream channels in most watersheds over a large portion of the native range are at moderate (67%) to high (29%) risk of damage from the combined effects of increased peak flows and increased surface erosion as measured by the British Columbia Interior Watershed Assessment Procedure (IWAP) as a result of forestry, oil and gas, urbanization, mining, recreation and other land-uses (Mayhood et al. 1997, 1998; Sawyer and Mayhood 1998a). Analyses of other native-range watersheds using the IWAP and another model have shown similar results (Alberta Environment and Olson+Olson 2000), and direct field surveys of native cutthroat watersheds (Parkstrom 2002; Paul and Boag 2003) have found damaged fish habitats resulting from roads and similar developments in native cutthroat watersheds.

Risk as measured by the IWAP is a good indicator of actual observed damage to trout habitat in these basins (Mayhood et al. 1997; Sawyer and Mayhood 1998a; Paul and Boag 2003). At-risk basins have been at risk for many decades to as much as a century (Mayhood et al. 2004), suggesting that actual channel damage is likely by now, that some channels have probably been damaged for a long time, and that restoration success therefore may be both more difficult and less likely. Higher road densities have been associated with reduced population densities of cutthroat trout (Eaglin and Hubert 1993), including westslope cutthroat trout (Dunnigan et al. 1998; Huntington 1998), as has higher watershed surface disturbance generally (Shepard 2004).

The above risk analyses did not specifically include any consideration of the impact of cattle grazing on riparian integrity, channel form and fine sediment delivery, but such effects are well-known within the Alberta native range of westslope cutthroats (Adams and Fitch 1995; Paul and Boag 2003) and elsewhere (Gresswell et al. 1989; Platts 1991; Armour et al. 1994; Wohl and Carline 1996). Cattle grazing is a common land-use throughout the native range outside of national parks, so habitat damage probably is widespread from that source within the native range of westslope cutthroats in Alberta.

Fine sediment deposition in spawning areas, barriers to movement such as hanging culverts, and improved access for anglers may be the most important proximate causes of reduced cutthroat trout population densities associated with watershed surface disturbance and roads. The latter is not really a habitat factor, so will be dealt with under Overexploitation, below. Culvert influences on fish passage are similar to the effects of dams, so those effects are discussed under Dams, below. Here I describe processes that affect the quantity and quality of critical habitat as they are influenced by human development in watersheds.

Roads are the principal source of fine sediments to streams in forestry operations, typically being much greater than that from all other land management activities combined (Furniss et al. 1991). Measures of road development in watersheds commonly are correlated with the amount of fine sediment deposition in streams (Shepard et al. 1984; Leathe and Enk 1985; McCaffery et al. 2007). Often the largest problems arise at crossings of small, intermittent and ephemeral headwater streams (Shaw and Thompson 1986; Chamberlin et al. 1991), because protection for such minor watercourses is considered unimportant or is simply overlooked. Unfortunately small headwater streams like these, or the headwater mainstems into which they drain, are disproportionately important ecologically (Chamberlin et al. 1991), and are often critical habitat for cutthroats (Rosenfeld et al. 2000, 2002; Robinson 2008). It is just these small headwaters that hold the last remnant pure westslope cutthroat trout populations that this recovery plan is intended to save.

Even small increases in fine sediment loading to spawning areas can cause dramatic losses of early life-history stages of salmonids. In one field experiment, increasing fines in westslope cutthroat trout redds from 0 percent to just 10 percent decreased egg-to-emergence survival by nearly 28 percent (Weaver and Fraley 1993). An increase in fines from 0 to 20 percent in test redds caused a decrease in fry-to-emergence survival of nearly 57 percent. Similar results have been reported in laboratory experiments (Irving and Bjornn 1984, cited by Weaver and Fraley 1993). It seems likely that there is no threshold below which fine sediment accumulation in salmonid spawning locations will be harmless (Suttle et al. 2004). No salmonid life stage appears to require fine sediments as part of its habitat. The principal benefit to salmonids of fine sediments in streams may be as a substrate promoting certain kinds of riparian plant growth that serves to stabilize banks and bars (Kellerhals and Church 1989).

Fine sediment levels in the substrate are a major limitation, natural or otherwise, on the carrying capacity of streams for westslope cutthroat. Without human development in watersheds there will still be some level of fine sediment in streambeds determined by the geology, geomorphology and vegetation cover of the watershed. This amount will help to set the natural carrying capacity of the stream. When development of a basin occurs, additional loading of fine sediments reduces the carrying capacity further. Fine sediment deposition is thus a major limiting factor affecting the recovery prospects of westslope cutthroat trout, and will have to be dealt with in recovery planning.

Climate warming is both creating and interacting with other changes in watersheds in ways that will negatively affect westslope cutthroat trout habitat. Warming climate is expected to increase the frequency, intensity and extent of wildfires, increase drought frequency, and is believed to be enabling the recent outbreak of mountain pine beetle infestations in Alberta (British Columbia Forest Practices Board 2007; Sauchyn and Kulshreshtha 2008; Williams et al. 2009). Major effects of these changes are to greatly increase runoff and soil erosion from affected watersheds (Beschta et al. 1995; Karr et al. 2004; Rhodes 2007). These effects are superimposed on standard forest management practices that already contribute to greater impacts from these two factors (Shaw and Thompson 1986; Alberta Environment and Olson +Olson 1999, 2000). More specifically, a current policy to salvage log and preemptively remove beetle-infested lodgepole pine on Alberta's east slopes is likely to be seriously exacerbating the problem of increased peak runoffs and erosion from the killed forests (Beschta et al. 1995; Karr et al. 2004; British Columbia Forest Practices Board 2007; Rhodes 2007). Higher peak runoff events, and more frequent extreme runoff events, expected as a result of climate warming-induced higher winter and spring temperatures will add to these effects. On logged, burned and beetle-killed watersheds, channel adjustment and riparian zone disturbances will be especially severe, as will increased fine-sediment deposition in westslope cutthroat trout critical habitat in those basins.

Road culverts are a second major artificial limitation on stream carrying capacity for westslope cutthroats (Furniss et al. 1991; Eaglin and Hubert 1993). Improperly placed and obstructed culverts are very common, blocking access by fish to the stream network upstream. The amount of habitat lost is potentially very large if fish must move past impassable culverts to complete their life-history. For example, a partial survey of 167 culverts in Banff National Park found that 55 percent were full barriers, 33 percent were partial barriers, and only 12 percent were passable to salmonids (Pacas 2007). On the other hand, barrier culverts in some cases may protect remnant stocks above them from nonnative rainbow, brook and brown trout. For this reason, it will be important to carefully evaluate the function of every existing barrier before a decision is made to remove it or make it passable as part of cutthroat trout restoration efforts.

Dams

Dams are another major threat and limiting factor affecting westslope cutthroat trout recovery. Dams block movements of fish both upstream and downstream, transform upstream habitats from running water to standing water, substantially transform flow regimes in downstream habitats, and reduce downstream flows (in the case of irrigation dams and diversion weirs), among many other effects (Burt and Mundie 1986; Bain et al. 1988; Allan 1995; Collier et al. 1996). Reservoirs are often heavily stocked with nonnative fishes to counteract the loss of native stocks and the low productivity of most of such waterbodies (e.g., Schindler and Pacas 1996). All of these effects have the potential to severely disrupt fish populations, and have done so to native westslope cutthroat trout populations in Alberta.

Ten major dam projects now modify native westslope cutthroat trout habitat in the Bow River basin, and four more do so in the Oldman (Table 6). In addition there are many smaller dams on tributaries in the Oldman and Bow river basins, plus a very large number of impassible road crossings of streams that have many of the effects of dams. All of these dams have seriously impacted native westslope cutthroat trout habitat and populations. All pose limitations on the possibilities for recovering the subspecies.

Before European settlement, mainstem rivers, lakes and larger streams would have had migratory westslope cutthroat trout populations similar to those still found in other parts of the native range (Shepard et al. 1984; Liknes and Graham 1988; Schmetterling 2001; Prince and Morris 2003; Schmetterling 2003). Fluvial and adfluvial (river- and lake-migratory) stocks of westslope cutthroat trout have been documented in the pre-dam Spray River system (Miller and Macdonald 1949), probably occurred in the Crowsnest River drainage (McIllrie and White-Fraser 1983) (re: 1890), and are highly likely to have used several discrete reaches of the Bow, Kananaskis, Ghost, Elbow, Highwood, Oldman, Waterton, St. Mary, Belly and Castle rivers, as discussed elsewhere in this report series. Dams contributed to the loss of the Spray Lakes stocks (Miller and Macdonald 1949; Mudry and Green 1976; Schindler and Pacas 1996), very likely the Lake Minnewanka - Cascade River stock(s) (Rawson 1939a, 1942, 1945), and the Kananaskis River - Lower Kananaskis Lake stock(s) (Nelson 1962, 1965). Dams, reservoirs and the fish management activities they require almost certainly influenced westslope cutthroat declines in all of the remaining locations, and pose ongoing limitations to restoring native cutthroat stocks (Table 6).

The Government of Alberta has evaluated numerous sites for additional water storage and diversion in the Bow and Oldman basins within the native range of westslope cutthroat trout (MPE Engineering Ltd 2008). Although there is no commitment yet, at least some of these sites may be developed in future, especially in response to declining summer streamflows arising from climate warming (Schindler and Donahue 2006; Sauchyn and Kulshreshtha 2008). Future dams and diversions within the native range may well pose additional threats to the subspecies and limitations on recovery and restoration plans.

Table 6. Some major dams in the native range of westslope cutthroat trout populations in Alberta, their known or suspected effects, and limits on WSCT recovery and restoration. BNP - Banff National Park; WLNP - Waterton Lakes National Park; SLPP - Spray Lakes Provincial Park; PLPP - Peter Lougheed Provincial Park; WSCT - westslope cutthroat trout.

Dam	Location	Effects on present or former WSCT stocks Limitations on recovery & restoration
Minnewanka	BNP Cascade R. at former L. Minnewanka Bow basin	blocks movements along Cascade R; diversion dewaters lower Cascade R.; inundates former L. Minnewanka and Cascade R. habitat; diverts water from Ghost R. at Devil's Gap; exposes extensive areas of nearshore habitat seasonally; alters flow regime in Bow R. mainstem below Banff; acts as a reservoir of non-native fish stocks; WSCT probably extirpated or hybridized
		dam removal is an expensive & complex engineering/ ecological restoration project; native stock(s) no longer exist; restoration & amelioration of downstream fluvial Cascade R. habitat may be possible with expensive modified dam structure & operating regime, at a cost to electricity generation
Spray	SLPP Spray R. at former Spray Lakes Bow basin	blocks movements through Spray Canyon; enables movements over former Spray Falls; alters flow regime and reduces flow volumes in lower Spray R.; inundates former critical fluvial habitat in several creeks; severely deepens lacustrine habitat; enables connection with Kananaskis drainage via Mud L.; alters flow regime in Bow R. mainstem at Canmore and Banff; exposes extensive near-shore habitat seasonally; acts as a reservoir of non-native fish stocks; WSCT (several distinct stocks) extirpated, others hybridized.
		dam removal is an expensive & complex engineering/ ecological restoration project; native stock(s) no longer exist; restoration & amelioration of downstream fluvial Spray R. habitat may be possible with modified operating regime at Canyon Dam.

Dam	Location	Effects on present or former WSCT stocks Limitations on recovery & restoration
Pocaterra	PLPP Kananaskis R. at outlet of former Lower Kananaskis L. Bow basin	blocks movements into Lower Kananaskis L. from Kananaskis R. mainstem; enables access to Smith-Dorrien Cr. over former falls; alters flows in Kananaskis R. mainstem daily & seasonally; enables connection with Spray drainage via Mud L.; alters flow regime in Kananaskis R. daily, & Bow R. below Kananaskis R. confluence; inundates former fluvial habitat; deepens former lacustrine habitat; acts as a reservoir of non-native fish stocks; WSCT hybridized, effectively extirpated.
		dam removal is an expensive & complex engineering/ ecological restoration project; native stock(s) no longer exist; restoration & amelioration of downstream fluvial Kananaskis R. habitat may be possible with modified operating regime at Pocaterra Dam.
Barrier	Kananaskis R. mainstem Bow basin	blocks movements along Kananaskis R. mainstem; transforms good fluvial mainstem river habitat into poor lacustrine habitat; alters flow regime in Kananaskis R. below dam, and in the Bow R. below the confluence; acts as a reservoir of non-native fish stocks; WSCT extirpated
		dam removal is an expensive & complex engineering/ ecological restoration project; native stock(s) no longer exist; restoration & amelioration of downstream fluvial Kananaskis R. habitat may be possible with modified operating regime
Seebe - Horseshoe (2 dams)	Bow R. near Seebe Bow basin	run-of-river dams inundate mainstem Bow R. fluvial habitat; modifies flow regime above and below dams, but there is little storage; blockage of little consequence because of natural Horsehoe Falls barrier; WSCT extirpated
		the oldest of the Bow R. dams with the least storage, occupying a reach that had a natural barrier, Horseshoe Dam offers little opportunity for restoration. Seebe offers an opportunity to recreate a more natural channel upstream, but native stock(s) no longer exist.

Dam	Location	Effects on present or former WSCT stocks Limitations on recovery & restoration
Ghost	Bow R. at Ghost R. confluence Bow basin	blocks movements in the Bow R. mainstem; inundates formerly productive fluvial mainstem habitat in Bow and Ghost rivers; high-drawdown storage exposes large areas of habitat seasonally; downstream flows have high daily variability; WSCT extirpated.
		dam removal is an expensive & complex engineering/ ecological restoration project; native stock(s) no longer exist; restoration & amelioration of downstream fluvial Bow R. habitat may be possible with modified operating regime.
Bearspaw	Bow R. at Calgary Bow basin	blocks movements in the Bow R. mainstem; inundates formerly productive fluvial mainstem habitat in Bow R; high daily fluctuations in flow downstream; WSCT extirpated
		dam removal is an expensive & complex engineering/ ecological restoration project; with a change in operations a more natural flow regime could be restored downstream at a cost to water supply & electricity generation; native stock(s) no longer exist
Glenmore	Elbow R., south Calgary Bow basin	blocks movements along the Elbow R; floods fluvial habitat upstream; alters flow regime & reduces flows downstream (water withdrawals); WSCT extirpated
		dam removal is an expensive & complex engineering/ ecological restoration project; with a change in operations a more natural flow regime could be restored downstream at a cost to water supply; native stock(s) no longer exist
Calgary Weir	Bow R. at Calgary Bow basin	barrier or impediment to fish passage; WSCT extirpated
		presently being modified mostly to pass non-native fish species
Carseland Weir	Bow R. at Carseland Bow basin	barrier or impediment to fish passage; WSCT extirpated
		water temperatures are, or soon will be, too high to permit recovery of WSCT; native stocks no longer exist; near downstream limit of native range

Dam	Location	Effects on present or former WSCT stocks Limitations on recovery & restoration
Chain Lakes	upper Willow Cr. Oldman basin	blocks movements along Willow Cr; alters downstream flows; reservoir for non-native species; WSCT hybridized to extirpation
		dam removal is an expensive & complex engineering/ ecological restoration project; change in operation could restore more natural flows; native stocks extinct
Waterton	Waterton R. below WLNP Oldman basin	blocks movements along Waterton R.; inundates high-quality fluvial habitat; water extraction reduces downstream flows; reservoir drawdown exposes much shallow habitat; fish losses to irrigation system(?); reservoir of non-native species; WSCT probably hybridized to extirpation
		dam removal is an expensive & complex engineering/ ecological restoration project; change in operation could restore more natural flows at a cost to irrigation value; screening could prevent possible fish losses to irrigation system; near or at maximum thermal limit due to climate warming; native stocks no longer exist
Oldman	Oldman R. at Castle R. confluence Oldman basin	blocks movements along Oldman R.; inundates high-quality fluvial habitat; water extraction reduces downstream flows; reservoir drawdown exposes much shallow habitat; fish losses to irrigation system(?); reservoir of non-native species; WSCT hybridized to extirpation
		dam removal is an expensive & complex engineering/ ecological restoration project; change in operation could restore more natural flows at a cost to irrigation value; screening could prevent possible fish losses to irrigation system; native stocks no longer exist

Dam	Location	Effects on present or former WSCT stocks Limitations on recovery & restoration
St. Mary	St. Mary R. below Cardston Oldman basin	blocks movements along St. Mary R; inundates high-quality fluvial habitat; water extraction reduces downstream flows; reservoir drawdown exposes extensive shallow habitat; fish losses to irrigation system(?); reservoir of predatory and non-native species; WSCT hybridized, extirpated
		blocks movements along St. Mary R; inundates high-quality fluvial habitat; water extraction reduces downstream flows; reservoir drawdown exposes extensive shallow habitat; fish losses to irrigation system(?); reservoir of predatory and non-native species; WSCT hybridized, extirpated

Invasive & Nonnative Species

As noted long ago (Meffe 1986), managing endangered fishes should be directed toward three conservation goals:

- maintaining viable populations in the short term (i.e., avoiding imminent extinction),
- maintaining the capacity of fishes to adapt to changing environments, and
- maintaining the capacity for continued speciation (Soulé 1980).

First and most obviously, we need to maintain viable populations of species under our care. But that alone is not enough. The places that the saved populations live, their environments, frequently change; indeed, under human influence they are often changing uncontrollably and at an ever-increasing rate. We also need, therefore, to ensure that we maintain the capacity of the saved populations to adapt to changed conditions over the long term. If we don't, we will lose them anyway. Accepting this proposition, it becomes obvious that our ultimate goal is to maintain the capacity of the species we manage to evolve into new species. In the end, we cannot and should not maintain species fixed forever as they are now, or as they were before they became at risk. That is the conservation science of the fossil, the photograph, the taxidermist and the museum jar.

Species at risk by definition are comprised of small populations representing only a small fraction of the original species population. These remnant populations typically hold the remnant genetic resources of a formerly larger, more diverse genome. Near-term population viability requires that sufficient numbers of individuals with sufficient fitness are available to maintain the population in the face of environmental resistance. At the most fundamental level, that fitness is genetically determined. Environmental resistance works on whatever genetic resources remain in the population to cause the population to adapt and evolve, or to become extinct. Hence greater genetic resources, more kinds of alleles — *greater genetic diversity or variation* — should increase the probability that a population can persist, adapt and evolve against the selective forces presented by the environment. This is why the loss of genetic variation has been called the central problem in conservation genetics (Meffe 1986). This is why we need to understand the nature of genetic diversity in westslope cutthroat trout as part of the recovery plan.

This view is founded on three reasonable, partly evidence-supported, but not irrefutable assumptions (Meffe 1987):

- allelic diversity (heterozygosity — different forms of the same genes) is desirable, because it renders biota more fit, enhancing survival (Leberg 1990; Stockwell and Leberg 2002; Reed and Frankham 2003);
- genetic diversity is effectively a finite resource — once lost it will not be quickly recovered; and
- maintaining genetic diversity is required to allow adaptation and evolution to occur.

Adopting these assumptions minimizes the chance of making drastic, irrecoverable mistakes in managing species at risk: it is the precautionary principle applied to conservation genetics (Meffe 1987).

Heterozygosity in the westslope cutthroat trout subspecies is low within populations, but high among populations, each of which tends to be genetically unique, implying that conserving genetic variation in this subspecies entails retaining as many individual populations as possible (McAllister et al. 1981; Leary et al. 1985; Allendorf and Leary 1988; Potvin et al. 2003; Taylor et al. 2003). In the Alberta range, however, most westslope cutthroat trout stocks have been either extirpated or have introgressed with nonnative Yellowstone cutthroats and rainbow trout (Alberta Sustainable Resource Development and Alberta Conservation Association 2006; COSEWIC. 2006; Mayhood 2009). As a result, most of the genetic resources of the subspecies in Alberta have been lost. The only remaining genetically pure native populations are almost all tiny and isolated in small headwater streams and lakes (McAllister et al. 1981; Leary et al. 1985; Carl and Stelfox 1989; Strobeck 1994; Mayhood 2000; Potvin et al. 2003; Janowicz 2005; Robinson 2007; Taylor and Gow 2007; Robinson 2008).

A taxon that increases (rapidly or otherwise) in abundance and spreads into new habitat or expands its range is invasive (Elton 1958). Invasions may originate when native taxa expand their ranges as a result of changing habitat conditions, but most invasions originate from introductions of nonnative taxa. Among Alberta trout, three taxa in particular have become invasive: rainbow trout, brook trout and brown trout. All have been introduced into the native range of westslope cutthroat trout in this province, all have spread from their points of first introduction, and all now pose a threat to the continued existence of native westslope cutthroat trout stocks.

Let us consider the implications of these facts.

Hybridization

... interpreting the evolutionary significance of hybridization and determining the role of hybrid populations in developing conservation plans is more difficult than is usually appreciated (Allendorf et al. 2001).

Hybridization is the interbreeding of individuals from genetically distinct populations, regardless of the taxonomic status of such populations (Rhymer and Simberloff 1996). In other words, hybridization includes the successful interbreeding of genetically distinct stocks of the same taxon. This is a definition most consistent with the conservation goals just mentioned. Of the nonnative salmonids in Alberta, rainbow and Yellowstone cutthroat trout are a threat to westslope cutthroat trout largely because of their ability to freely hybridize with the native cutthroat subspecies, producing offspring that themselves can successfully interbreed with the parental taxa and among themselves. This type of hybridization is termed introgression. It eventually results in the complete mixing of the genetic material of the two distinct organisms.

Hybridization, introgressive and otherwise, has led to numerous extinctions of plants and animals, and is particularly a problem for rare taxa exposed to related species that are much more abundant (Rhymer and Simberloff 1996). In fish, hybridization between distinct species and subspecies often produces interfertile offspring, leading in many cases to complete introgression and the formation of hybrid swarms. The effect of introgressive hybridization is to create a single new taxon where once there were two, while the parental forms become extinct (Allendorf and Leary 1988; Leary et al. 1995). In practice, as in the case of westslope cutthroat trout in Alberta, hybridization often occurs only because a nonnative form (almost always a hatchery stock of effectively unlimited size) has been introduced into the habitat of native fish. In that case, the loss of the nonnative hatchery stock in any particular habitat is of no great concern, but the loss of the limited-size native stock has serious consequences.

Each individual population of westslope cutthroat trout tends to be unique, with genetic characteristics not found in other populations, even those nearby. In part this is almost certainly because these fish live in the highly subdivided habitats provided by stream networks, which at least partially isolate populations from one another, allowing them to diverge. In small populations (such as many westslope cutthroat populations are), random genetic drift, perhaps accompanied by inbreeding, may account for the differences among isolated populations (Hallerman 2003b, c). But another more important reason why each westslope cutthroat population tends to be genetically unique is that each population has become uniquely adapted to the particular environment it occupies (Allendorf and Leary 1988), perhaps evolving coadapted gene complexes to do so (Hallerman 2003a).

Genetically based local adaptation is a hallmark of salmonids (Kaya 1989; Groot and Margolis 1991; Kaya 1991; Kaya and Jeanes 1995; Hallerman 2003a), including cutthroat trout (Raleigh 1971; Raleigh and Chapman 1971; Bowler 1975), so is to be expected in westslope cutthroat populations, although there has been little research specifically on local adaptation in westslope cutthroat trout (McIntyre and Rieman 1995). As indirect evidence of local adaptation, those authors pointed to the sometime failure of other subspecies of cutthroat trout to grow and survive as well as native westslope cutthroats when planted in westslope cutthroat native waters. Repeated introductions of nonnative Yellowstone cutthroat trout into waters holding native populations of westslope cutthroat trout in Glacier National Park, Montana, consistently failed over a period of many decades (Marnell et al. 1987). This outcome was attributed to superior local adaptation of the native westslope cutthroats to enable them to coexist with predatory bull trout and an indigenous cestode parasite. In the West Kootenay area of British Columbia, westslope cutthroat trout populations above waterfalls, but not below them, possess a strong upstream swimming response as fry and young juveniles, an essential local adaptation to maintain populations above impassable barriers (Northcote and Hartman 1988).

Introgressive hybridization threatens to disrupt such local adaptations and coadapted gene complexes, rendering populations less fit (Edmands and Timmerman 2003). For example, both reciprocal F_1 hybrids of inlet- and outlet-spawning genetic lines of Arctic grayling had weaker upstream swimming responses than the outlet-spawning parent line (Kaya 1989). A strong tendency for fry to swim upstream is an essential local adaptation of outlet-spawning populations that allows offspring to colonize the lake of parental origin. A weakness in this response is maladaptive, and presumably would be strongly selected against.

When genetically divergent genomes such as westslope cutthroat trout and either rainbow trout or Yellowstone cutthroat trout (Ferguson et al. 1985; Gyllensten et al. 1985; Utter 2003) hybridize, intermediate or reduced fitness (outbreeding depression) is held to be the most likely outcome (Leary et al. 1995). In one experiment, artificially produced hybrids of rainbow and westslope cutthroat trout had higher fertilization and hatching success than the pure parental westslope cutthroat strain, but ultimately the hybrids had reduced fitness in the form of poorer growth and posthatching survival (Leary et al. 1995). Similarly, a recent field study found that as little as a 20 percent admixture of rainbow trout alleles reduced reproductive success of westslope cutthroat trout males and females by about 50 percent (Muhlfeld et al. 2009a). Bear (2005, cited by Robinson 2007), reportedly found selection against westslope cutthroat X rainbow during development, with only 3% survival. One explanation for an observed lower incidence of hybrids at older life-history stages in one study (Rubidge et al. 2001) is that hybrids are less fit and die at a higher rate than do genetically pure fish. The situation is complex, and hybrids are not less fit in all respects or in all situations (Ferguson et al. 1985; Rubidge and Taylor 2004).

This sort of complexity in hybrid effects is probably common. Reviewing several hybridization studies, (Leary et al. 1995) concluded that, overall, superior performance of rainbow-cutthroat and cutthroat-cutthroat hybrids relative to the parental stocks is the exception rather than the rule. They speculated that, more likely, introgressive hybridization drives native forms to extinction, homogenizing once genetically distinct evolutionary lineages, and replaces them with less well-adapted, less productive hybrid populations.

Hybridization between introduced rainbow and native westslope cutthroat trout is spreading rapidly in the North Fork Flathead River in Montana, even though hybridization is rapidly reducing fitness in this metapopulation (Hitt et al. 2003; Boyer et al. 2008; Muhlfeld et al. 2009a).

If hybrids are less well-adapted than the parental forms, it might at first be expected that the hybrids could not outcompete and replace the parental form. But in freely interbreeding mixed stocks, hybrid swarms can form in the face of selection against hybrids (Epifanio and Philipp 2001), because the great majority of offspring of hybrid matings will themselves be hybrids (Allendorf et al. 2001)[1]. For this reason the proportion of hybrids will continue to increase over time while the proportion of non-introgressed parental types will continue to decrease, ultimately reaching zero. This process would allow less fit stocks to prevail, replacing fitter stocks. Conceivably the less fit introgressed stock, having eliminated the native stock, might then itself eventually decline to extinction.

This mechanism might explain the recent loss of westslope cutthroats from one of the Fish Lakes in Banff National Park (C. Pacas, personal communication). Although the lake may have had an indigenous population, the Spray Lakes - Marvel Lake stock was also introduced there (Ward 1974).

Hybridization between westslope cutthroats and rainbows is usually limited where the two species occur naturally in sympatry (Kozfkay et al. 2007). Hybridization with cutthroats increases when rainbow populations are supplemented with hatchery rainbows (Docker et al. 2003). Hatchery rainbows introduced into allopatric native cutthroat ranges frequently produce extensive hybridization (Allendorf and Leary 1988). It may be that hatcheries produce rainbow trout stocks that are especially prone to hybridizing with other *Oncorhynchus* as a result of any number of selective pressures that occur in hatchery environments (Weber and Fausch 2003).

Both inter- and intraspecific hybridization remain a threat to remnant westslope cutthroat trout populations within the native range in Alberta. For example, rainbow-cutthroat hybrids exist in Savanna Creek (Janowicz 2005), in direct contact with pure-strain cutthroats in the upper Livingstone River (Robinson 2007). Similarly, rainbows in lower Jumpingpound Creek (Nibourg 1985) have no impassable barrier separating them from pure native cutthroats in the extreme headwaters (Janowicz 2005). In Banff National Park, rainbow trout occur in several

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[1] These authors assert that “all the progeny of hybrid individuals will be hybrids” (Allendorf et al. 2001:618), but this is not strictly true, because recombination in theory could reconstruct some parental species individuals. When considering large numbers of loci, the probability that parental species genotypes will be reconstructed is diminishingly small, and this distinction becomes moot.

lakes with surface outlets in the Bow River drainage (Ward 1974), and hybrids occur in the upper Bow River mainstem (Potvin et al. 2003). Some fish showing Yellowstone genes occur in Luellen Lake (Strobeck 1994), a lake freely open to the Bow drainage via Johnston Creek. Finally, several headwater lakes in the Kananaskis and Highwood drainages have surface outlets and hold introduced Spray/Marvel/Job Lake westslope cutthroats, a genetically-depauperate stock (McAllister et al. 1981; Carl and Stelfox 1989; Bernatchez 1999) that could hybridize with any native pure stocks downstream.

Global warming can be expected to exacerbate hybridization problems (Muhlfeld et al. 2009c). Robinson (2007) has pointed out that rainbow trout occupy warmer habitats than do westslope cutthroats, even without barriers to upstream movement. He found in his own study that hybrids between these two species did not occur above a summer mean daily temperature of 7.25 °C. A barrierless stream that was warmer than that held hybrids throughout, while another barrierless stream lacked hybrids only in the upper reaches where temperatures in summer were lower than 7.25 °C. He hypothesized that global warming, by increasing stream temperatures, could have a devastating effect on remnant native cutthroat populations if low temperatures are presently all that is preventing hybrids from spreading into colder cutthroat-only headwaters. Should the most likely climate-warming scenario (2 — 4 °C increase in seasonal and annual mean air temperatures by the 2050s[2]) play out, these remnant stocks would seem to be in jeopardy of extirpation by hybridization.

Continuing habitat damage and loss within the native range of westslope cutthroats in Alberta can be expected to exacerbate hybridization among rainbow, Yellowstone cutthroat and westslope cutthroat trout, and among individual native stocks of westslope cutthroats. In a Montana study, hybridization between rainbow trout and westslope cutthroat trout was found to be more likely in streams with warm water and higher land surface disturbance (Muhlfeld et al. 2009c).

Habitat modification can break down isolating mechanisms between native species, allowing them to hybridize (Rhymer and Simberloff 1996).

- Habitat disruption can severely reduce a population, making its breeding members more likely to mate with a member of a less-affected population or introduced stock.
- Habitats disrupted to the extent that they permit the mixing of previously isolated native stocks effectively promote the introgression of those stocks.

Even species resistant to hybridizing, and those that exist in natural sympatry without hybridizing, will hybridize when introduced into disrupted habitats such as dammed river systems (Nelson 1962, 1965, 1966, 1973). Nelson (1966) explained a doubtful record of “blacknose dace” in Minnewanka Reservoir (Rawson 1939a) as most likely a hybrid between lake chub and longnose dace, which appear only occasionally to hybridize in natural sympatry.

Rainbow trout, and probably Yellowstone cutthroat trout, are nonnative taxa that spread their genes inexorably into the native populations primarily through matings of hybrids with the natives (Hitt et al. 2003; Boyer et al. 2008; Muhlfeld et al. 2009b), ultimately eliminating the native stock. Hybrids in effect are vectors of rainbow or Yellowstone cutthroat trout genes, infecting the native populations through indiscriminate matings because the natural mechanism isolating the distinct taxa — geography and watershed divides — has been

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[2] see Climate Change, this report

artificially removed by humans through stocking. Under the new regime, westslope cutthroats in Alberta are victims of their own innate behaviour, caught in a classic evolutionary trap (Schlaepfer et al. 2005) that is driving them toward extinction.

Other Biotic Interactions: Competitors, Predators, Parasites & Disease

Competition occurs when organisms living in the same place require a resource that is in limited supply. Competitors will eliminate, displace or exclude each other in the order of least to most able until the quantity of the resource is no longer limiting for the remaining organisms. The remaining organisms may limit or avoid competition by partitioning the resource among themselves, thereby allowing the survivors to coexist. Coexistence is at the cost of access to less-than-optimal kinds or quantities of the resource for all competitors. This implies that removing one competing type will free up resources for the other competitor type.

It has been argued that when ecologically similar species exist in natural communities, they have coevolved to limit energetically costly competitive interactions, but when introductions bring ecologically similar species together, competition is likely to be very strong (Seiler and Keeley 2009). If so, we should expect to find evidence of this competition between native westslope cutthroats and introduced salmonids in Alberta.

At least four nonnative fish, three of the invasive, occur over large parts of the native westslope cutthroat trout range, so are significant potential competitors of the native fish in Alberta: rainbow, Yellowstone cutthroat, brown, and brook trout. Two, rainbow trout and Yellowstone cutthroat trout, compete with our native cutthroats by the insidious but elegant tactic of infusing their genes into the native fish populations, thereby taking over the genome and making the native trout more like themselves. This tactic, which effectively allows the invader to take over the entire accessible range of the native fish, was discussed extensively under Hybridization, above.

Rainbow trout, Yellowstone cutthroat trout and their hybrids with native stocks may also compete with native cutthroats in other ways.

Rainbow trout

Where rainbow trout and westslope cutthroat trout occur in the same drainage, rainbows or rainbow-cutthroat hybrids favour the lower reaches while pure-strain cutthroats are often restricted to, or at least are more common in the headwaters (Paul and Post 2001; Hitt et al. 2003; Rubidge 2003; Rubidge and Taylor 2005; Robinson 2007). Remnant westslope cutthroat trout populations in the Bow, Oldman (Mayhood 2000) and Missouri drainages (Shepard et al. 1997) are now found almost exclusively in headwater reaches, where they can exist only in the absence of rainbow trout. In general, stream-resident rainbows characteristically are found in larger, lower-gradient, lower-elevation streams while cutthroats typically occupy smaller, higher-gradient, higher-elevation streams (Bozek and Hubert 1992).

Even without introgressive hybridization, westslope cutthroats may be unable to sustain populations in their warmer, lower-elevation, larger former habitats in the face of competition from rainbow trout because of the latter species' better warm-temperature performance. Rainbow trout and westslope cutthroat trout favour similar temperatures, but have markedly different temperature tolerances. In a laboratory study, rainbows and westslope cutthroats had similar growth rates over the range 8 — 20 °C, and nearly identical optimum growth temperatures (13.1 °C and 13.6 °C, respectively), but the cutthroat's upper incipient lethal temperature (19.6 °C) was 4.7 °C lower than that for rainbow trout (Bear et al. 2007). Rainbow trout had greater survival at temperatures above 20 °C, grew at higher temperatures and grew over a wider range of temperature than cutthroat trout. The authors reasoned that the rainbow trout's higher upper temperature tolerance and greater growth capacity at warmer temperatures may account for the species' displacement of westslope cutthroat trout at lower elevations.

Field observations in the Oldman-Livingstone drainage are consistent with the postulated importance of temperature in determining the relative distributions within drainages of rainbows and cutthroats (Robinson 2007). In two streams lacking dispersal barriers, rainbow trout and hybrids were restricted to downstream reaches where mean daily temperatures did not exceed 7.25 °C. Only genetically pure westslope cutthroats occupied the cooler headwaters.

Yellowstone cutthroat trout

A pure population of Yellowstone cutthroat trout is established in Taylor Lake, a previously fishless subalpine lake in Banff National Park (BNP) (McAllister et al. 1981). Westslope X Yellowstone hybrids have been found in Baker Lake, BNP; and Sofa and Dungarvan creeks, in and near Waterton Lakes National Park (WLNP) (McAllister et al. 1981; Potvin et al. 2003). Yellowstone alleles have been detected within the native westslope cutthroat trout range in specimens from the Bow River, Luellen Lake, Mummy and Scarab lakes in BNP (Strobeck 1994) and are suspected in Leman Lake trout (Potvin et al. 2003). All but the Bow River lacked native populations of trout originally. Clearly, Yellowstone cutthroats or their hybrids are established in the native range of westslope cutthroat trout in Alberta. Through dispersal, these populations are capable of contacting any remnant westslope cutthroat populations downstream in many of those drainages, so biotic interactions between the subspecies are at least theoretically possible.

Introgression of Yellowstone and westslope stocks could conceivably produce a less-competitive hybrid stock. In Glacier National Park, introduced Yellowstone cutthroat trout have been unable to replace or significantly hybridize with native westslope cutthroats in any lake in which the latter is indigenous (Marnell et al. 1987). The nonnative subspecies has successfully colonized only small, high-elevation lakes in that park that were previously barren of fish. The authors attributed this result to the lack of appropriate local adaptations in behaviour to native highly-piscivorous bull trout and an indigenous cestode parasite. Similarly, Yellowstone cutthroats have been singularly unsuccessful in colonizing waters throughout North America and elsewhere, despite 818 million eggs being shipped from Yellowstone National Park for this purpose (Varley and Gresswell 1988). Most of the successful establishments are said to have occurred when the subspecies was transplanted into small high-elevation lakes that had been fishless. Yellowstone cutthroats are less competitive in a number of respects in comparison to rainbow trout in laboratory experiments (Seiler and Keeley 2007a, b, 2009).

Predation by Yellowstone cutthroat trout on native populations of westslope cutthroat trout seems unlikely to pose a problem for the latter. Piscivory is documented in certain Yellowstone cutthroat populations, but the form in Yellowstone Lake, the most likely source of Alberta populations, is notably not piscivorous (Gresswell 1995).

Yellowstone cutthroats introduced into Alberta could have introduced their parasite fauna as well. The significance of or potential for parasite introductions from this source would require more research to resolve. This matter is discussed in more detail below (Parasites and Disease).

Brown trout

Brown trout were introduced once into the Bow River drainage: in 1925 at Carrot Creek, BNP, when a hatchery truck carrying 45,000 fingerlings to Alberta provincial waters broke down there (Nelson 1962; Ward 1974). From there the species spread at least 18 km upstream to the Vermilion Lakes above Bow Falls, and at least 212 km downstream at Carseland (Ward 1974; Culp et al. 1992). It was first recognized as having colonized the river at Banff below Bow Falls (15 km upstream), but not above, in 1938 (Rawson 1939a). It had colonized Gap Lake (large population; 26 km downstream) near the Kananaskis confluence and Ghost Reservoir (one specimen, 62 km downstream) no later than 1938, but evidently was not yet known in the Kananaskis system at that time (Rawson 1939b). Brown trout must have colonized the Kananaskis drainage before 1947, because the impassable Barrier dam and reservoir was completed then, yet brown trout had penetrated several kilometres above the dam by 1961 (Nelson 1962). The species had established a population in the Bow River at the city of Calgary, 135 km downstream from the point of release, no more than 25 years after its first introduction (Miller 1950).

The brown trout is clearly invasive in the Bow River basin as evidenced by its widespread dispersal (over 230 river kilometres, surmounting a 10-m cataract) in the Bow mainstem and into several major tributaries in 25 years or less from a single introduction of fingerlings into a small tributary. Westslope cutthroat trout are now effectively absent from all the locations now occupied by brown trout in the Bow River basin, although all the locations were part of the historical range of native westslope cutthroats (Mayhood 2000).

In the Oldman River drainage, brown trout are common in the Crowsnest River from below Lundbreck Falls to the Oldman River confluence after initial stocking in 1967, 1968 and 1969 (Fitch 1978). Brown trout were recorded in the Oldman River immediately below the Crowsnest River confluence before construction of the Oldman Dam (Allan 1985). There is a locality record for the species as far downstream as Lethbridge in the Oldman River mainstem (Nelson and Paetz 1992). In a five-year study, a total of just 8 brown trout were captured in the Oldman Reservoir, and none were taken in the Oldman or Crowsnest rivers above the dam, or in the reach downstream from the dam as far as Fort Macleod (Schwalme and Smiley 1999). Brown trout have not been reported from the Castle River drainage (Brewin 2004). There is a locality record in the Pincher Creek drainage that appears to be a small isolated lake (Paetz and Nelson 1970; Nelson and Paetz 1992). This was probably Beauvais Lake, which had been stocked with brown trout prior to 1956, but was poisoned with toxaphene in 1958 (Paetz 1967b).

Brown trout quickly invaded the Waterton River drainage. Brown trout were stocked into Waterton River “recently” as of 1967 (Paetz 1967a). A single brown trout was reportedly angled from the Waterton River below Knights Lake within Waterton Lakes National Park in 1975, 41 km above Waterton Dam (Anderson et al. 1976). There were locality records for the species in that river immediately below the park by no later than 1970 (Paetz and Nelson 1970), and in the Waterton River at the Waterton Reservoir no later than 1992 (Nelson and Paetz 1992). At present brown trout “are now very common in the Waterton River downstream of Lower Waterton Lake (both inside and outside the park)” (Barb Johnston, personal communication to Shelley Humphries, 2009/03/30).

There is also a locality record in the headwaters of the Little Bow River (Nelson and Paetz 1992).

On the basis of these incomplete stocking and locality records, brown trout do appear to be invasive in the Oldman system. The extreme downstream record at Lethbridge (187 km below Lundbreck, and 182 km below Waterton Dam) and the extreme upstream record in Waterton Lakes National Park suggests that the species bears careful monitoring. Native westslope cutthroat trout are now apparently absent in all the locations from which brown trout have been reported in the Oldman River drainage, but the loss may predate the late 1960s introductions. The entire region was part of the native range of westslope cutthroats historically (Mayhood 2000).

Cutthroat trout tend to occur in high-elevation, high-gradient, small streams, whereas brown trout characteristically inhabit low-elevation, low-gradient large streams (Bozek and Hubert 1992). This distribution presently holds true in Alberta, but historically it did not. Originally, westslope cutthroats in this province occupied all fluvial habitat types from large low-elevation rivers to small, high-gradient mountain streams, not to mention some accessible lakes (Mayhood 2000). The almost complete loss of native westslope cutthroats from mainstem rivers where brown trout (together with rainbow trout) now dominate suggests that one or the other, or both, invasive species have excluded the native fish from these mainstem habitats.

The loss of mainstem habitats by whatever processes (overexploitation, dams, biotic interactions with invasive species, introgression) has been devastating to native cutthroats. The mainstem habitats once held large-bodied fluvial life-history stocks. These are now almost certainly extinct. The demographic effect was to isolate once-abundant potentially interconnected stocks in the tributaries. There, various processes have inexorably diminished native cutthroat stocks. These stocks can no longer be restored or supplemented by immigrants by way of the mainstems, so once they decline, they can only be restored by their own reproductive abilities.

The mechanism of exclusion, if it exists, is not clear, but several possibilities have been suggested in the literature. In the South Fork of the Snake River, Idaho, age 0 and age 1 cutthroats and age 0 brown trout used the identical concealment habitat along the edge of the wetted perimeter in winter (Griffith and Smith 1993). In a laboratory study, juvenile greenback cutthroat trout were consistently dominated and displaced by brown trout of similar or even much smaller sizes, being subjected to many more attacks than they initiated (Wang and White 1994). Cutthroat trout are much more susceptible to angling than are brown trout (Behnke 1992). Both brown trout and cutthroat trout abundance is positively associated with abundant, high-quality pools. In the Salt River basin of Idaho and Wyoming, cutthroat trout were able to sustain themselves in some habitats when brown trout populations were low, but were consistently at low densities when brown trout populations were high, even in high-quality habitats (Quist and Hubert 2005). In experimental manipulations of trout abundance in streams, investigators demonstrated reduced Bonneville cutthroat trout growth and movement, and changes in diet owing to the presence of brown trout (McHugh and Budy 2006). In the Logan River, Utah, survival rate and fish density of Bonneville cutthroat trout were consistently lower at sites where they were sympatric with exotic brown trout (Budy et al. 2007). Rio Grande cutthroat trout shifted diet, stored less fat and suffered fin damage due to aggression from brown trout in an experimental study (Shemai et al. 2007). Brown trout are a serious predator of at-risk Rio Grande cutthroat trout, Gila trout and Apache trout in the US Southwest (Rinne and Calamusso 2007). In the same study, the combination of introduced book trout and brown trout dramatically reduced populations of Rio Grande cutthroat and Gila trout.

The evidence of this brief survey strongly suggests that brown trout can and do exclude or seriously reduce cutthroat trout populations where the two occur together, both through competition and predation. There are nevertheless some indications that, despite these negative impacts, the two species can coexist in some circumstances. In the Blackfoot River, Montana, native fluvial and resident westslope cutthroat appear able to sustain themselves in the face of mainstem-spawning brown trout (Aitken 1997). Brown trout appear to be coexisting with Colorado River cutthroat trout in a few tributaries of the Escalante River, Utah (Hepworth et al. 2001). These examples may upon further study offer some useful ideas on how the same might be accomplished with Alberta native cutthroat populations. Still, brown trout occupancy of rivers in the Bow and Oldman drainages present a major limitation on prospects for reestablishing westslope cutthroat migratory stocks in mainstem rivers in Alberta.

Brook trout

Nonnative brook trout are often invasive when stocked outside of their native range in western North America and elsewhere (Adams et al. 2000, 2001; Peterson and Fausch 2003; Carlson et al. 2007), although the extent and success of invasion is often variable (Adams et al. 2002). If successful, brook trout may replace, and often displace, native salmonids, especially various subspecies of cutthroat trout (Behnke 1992; Stelfox et al. 2001; Peterson et al. 2004; Fausch 2007; McGrath and Lewis Jr. 2007; Peterson et al. 2008). The mechanism of replacement sometimes may be related to differential susceptibility of native cutthroats to harvest (MacPhee 1966; Stelfox et al. 2001; Paul et al. 2003), because this species is notably susceptible to anglers (MacPhee 1966; Schill et al. 1986; Varley and Gresswell 1988; Stelfox et al. 2001). Displacement mechanisms involve brook trout interference competition effects on survival of cutthroats at early life-history stages (Peterson et al. 2004; McGrath and Lewis Jr. 2007), and high immigration from a well-established brook trout population, typically downstream (Peterson et al. 2004; Benjamin et al. 2007), but sometimes from populations stocked into headwater lakes (Adams et al. 2001). Watershed-level habitat damage seems to favour takeover by brook trout (Behnke 1992; Shepard 2004). “Squeezing out” of headwater populations into high reaches that are too cold to sustain cutthroat reproduction may effect the *coup de grâce* (Peterson et al. 2004). Brook trout populations within Alberta’s westslope cutthroat trout native range therefore comprise a potentially serious threat to the continued existence of westslope cutthroat trout remnant populations.

Brook trout are not native to Alberta. The species was first introduced in the Banff area shortly after the 1883 arrival of the Canadian Pacific Railway. The railway made it possible to ship this species from its native eastern Canada, possibly sometime before 1886, but certainly by 1904 (Table 7). A large number of introductions of brook trout have been made into Alberta waters since then (Table 8). It is now widespread, and sometimes very abundant, in the native range of westslope cutthroat trout in this province (Figure 1).

It is suspected that rail workers and others made many early unrecorded trout introductions, including transplants of native species into naturally fishless waters, because there are several occurrences of trout that are otherwise difficult to explain (Ward 1974). Certainly many introductions have gone unrecorded nearly to the present day. These complications make tracking the invasions of nonnative trout a speculative exercise.

Table 7. Invasion history of brook trout in the Bow River mainstem.

Year	Observation	Reference
1886	Fish identified as *Salvelinus fontinalis* reported as occurring in what is now Banff National Park. Record plausible, but possibly based on hearsay.	Mayhood 1992
1900	Reference to brook trout appearing in anglers' catches.	Ward 1974
1904	800 adult brook trout of L. Nipigon stock introduced into the Bow R. by Canadian Pacific Railway; hints of earlier stocking	Lothian 1981
1913	L. Nipigon brook trout introduced into Banff Park waters "a few years ago"	Vick 1913
1932	Nearly 150,000 eggs of brook trout collected at Vermilion Lakes by Banff hatchery staff.	Department of Fisheries 1933
1936-38	Common below Bow Falls, also above in the beaver ponds 7 miles upstream and in lower parts of several streams; not especially numerous in Third Vermilion L.	Rawson 1939a
1938	Five specimens of brook trout were taken in the Bow River (4 near Exshaw, 1 in the Ghost Reservoir); described as "scattered and few" in the river from Banff National Park boundary to Calgary; "large numbers" at Banff	Rawson 1939b
1947	[in comparison to 1938:] slightly larger numbers of brook trout taken in 1938 (*sic*), [in the Gap Lake - Lac des Arcs area] but few in the Ghost reservoir. The context indicates that the 1947 sampling season was meant.	Rawson 1948
1975-76	brook trout common near Canmore (impt spawning area); occurs in Ghost Reservoir; no data for areas downstream to Bearspaw	Howes 1976 Longmore and Stenton 1981

Table 8. Notable stocking records for brook trout in the Bow and Oldman river basins. Source waterbodies are those that were stocked and potentially contributed fish to the invaded drainage. This list is not exhaustive; many introductions were not recorded.

Invaded Drainage	Source Waterbody	Year introduced	Reference
Bow upper Cascade	L. Minnewanka	1932, first stocking	Ward 1974
		1933-1936	Department of Fisheries 1933
Bow Jumpingpound	Sibbald Cr	1934, only known stocking	Department of Fisheries 1934
Bow River headwaters	Hector L.	1965, first stocking	Ward 1974
Bow River L. Louise area	L. Louise	1941, first stocking	Ward 1974
Bow Baker Cr	Baker L.	1965, first stocking	Ward 1974
Bow Moraine Cr	upper Consolation L.	1964, first stocking	Ward 1974
Bow Redearth Cr	Shadow L.	1964, first stocking	Ward 1974
Bow Banff area	Vermilion Lakes	1931, first stocking	Ward 1974
	Bow R,	1904	Lothian 1981
Oldman upper Waterton	Cameron L.	1922, first stocking	Ward 1974
	Kesler L.	1931, first stocking	Ward 1974
	Knights L.	1951, first stocking	Ward 1974
Oldman upper Waterton	Buffalo Cr. ponds	1955, first stocking	Ward 1974
	Waterton Lakes	1957, first stocking	Ward 1974
Oldman Castle R. (Mill Cr)	Mill Cr	1949, only recorded stocking	Fitch 1979c
Oldman upper Crowsnest R.	Allison Cr tributary	1964, 1965	Fitch 1978
	Gold Cr	1949, only recorded stocking	

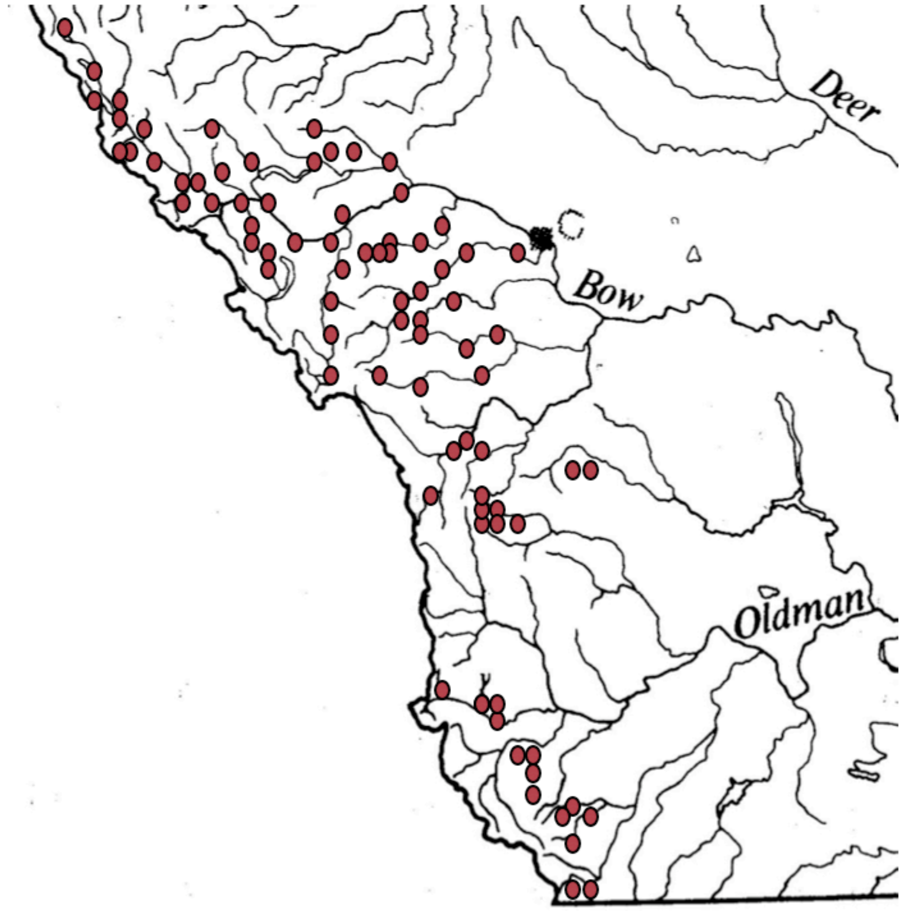

Figure 1. Distribution of brook trout within the historical range of native westslope cutthroat trout in Alberta. Data sources: Henderson and Peter (1969); Paetz and Nelson (1970); Ward (1974); Mayhood and Anderson (1976); Mayhood et al. (1976); Fitch (1978); Wiebe (1978); Fitch (1979a, c); Tripp et al. (1979); Nibourg (1985); Mayhood (1988, 1995); Nelson and Paetz (1992); Mayhood and Paczkowski (1993); Dahl-Fequet (2000); Jacques Whitford AXYS Ltd. (2008); Robinson (2008), Base map adapted from Nelson and Paetz (1992).

The Bow River introductions (Table 7) and introductions into the Jumpingpound Creek drainage (Table 9) do seem to give some reasonable indication of the rate of spread, by whatever means, of brook trout into westslope cutthroat native waters in Alberta. In the Bow River, it appears to have taken brook trout 34 — 52 years to reach downstream as far as the Ghost Reservoir, 78 km from Banff town. This is 2.6 — 4 times as long as it took brown trout to colonize the same reach. In Jumpingpound Creek it appears to have taken brook trout 29 years to establish a significant population over 15 km of small creek mainstem (Sibbald Flats to Forest Reserve boundary), with some invasion of the lower reaches of a few tributaries (Table 9, 1949 — 1978). A population estimate from just above the TransCanada Highway suggests that only small numbers had colonized much of the lower mainstem by 1981. Brook trout did not appear in my own angling catches in that reach in the early 1960s.

Table 9. Invasion history of brook trout in the Jumpingpound Creek drainage.

Year	Observation	Reference
1938	Anglers reported in 1938 "an occasional eastern brook trout" occurs in lower Jumpingpound Creek	Rawson 1939b
1947	90 trout caught in a survey of Jumpingpound (upper, mid, lower), Sibbald, Moose, Muskeg, Little Jumpingpound, Pine, unnamed & Sibbald Lake; but 0 brook trout; recommended to continue stocking with cutthroat only	Miller and Macdonald 1949
1949	brook trout stocked in Jumpingpound Cr	Nibourg 1985
1959	some brook trout tallied in a creel census on Jumpingpound Cr	Cunningham 1962
1959 to 1962	very low numbers of brook trout caught by anglers in Jumpingpound Cr. 14 (0.6% of catch); Sibbald Cr 6 (0.2%); Moose Cr 2 (0.6%); Bateman Cr 1 (0.5%);	Cunningham 1962
1961	brook trout comprised 4.7% of censused angling catch (92 brook trout)	Cunningham 1961
1963	brook trout caught by anglers: Jumpingpound Cr - 20 (1.3%); Sibbald Cr - 0; Pine Cr. 1 (0.3%); Bateman Cr. 0; Moose and Little Jumpingpound Cr - negligible effort, 0; Coxhill Cr - 0; Muskeg Cr - 0;	Cunningham 1964
1964	brook trout caught by anglers: Jumpingpound Cr - 27 (1.6%); Sibbald Cr - 5 (0.5%); Pine Cr. 0; Bateman Cr. 0; Moose Cr 0; Little Jumpingpound Cr - 0	Cunningham 1964
1978	in the Sibbald Flat Snowmobile Area, brook trout adult, juvenile and young-of-year present throughout the Jumpingpound Cr, mainstem, lower Sibbald Cr (scarce), lower Bateman Cr; adults in Coxhill Cr, adults & juveniles in Moose (scarce)	Tripp et al. 1979
1981 to 1983	brook trout ~36• km^{-1} in mainstem Jumpingpound Cr above TransCanada Hwy Bridge; ~19• km^{-1} above Sibbald Cr confluence; Bateman Cr ~103• km^{-1}, dominant; Coxhill 1 brook trout captured; lower Pine Cr ~383• km^{-1}, dominant, but much less abundant in headwaters; absent from Moose Cr, Sibbald Cr, Little Jumpingpound Cr	Nibourg 1985

Another instance may be informative on the matter of invasion rate by brook trout in Alberta streams. Mill Creek is a direct tributary of the Castle River with two major tributaries, Gladstone Creek and Whitney Creek. Brook trout were stocked into Mill Creek in 1949 (Fitch 1979c). That author reported finding a single brook trout in his 1978 Mill Creek stream survey, at a headwater station but not near the mouth, commenting that “the distribution of brook trout [in Mill Creek] is unclear but the species is probably found only in the upper portions of the stream.” He found no brook trout the next year in the upper Mill Creek tributary, Whitney Creek (Fitch 1979d). Brook trout were not found in a stream survey of Gladstone Creek in 1979 (Fitch 1979b). In an intensive 1988 survey of sample reaches representing the entire length of Whitney Creek, I captured a single brook trout in the lowest reach, one more in the reach of Mill Creek immediately below the Whitney Creek confluence, and none upstream to the headwaters of Whitney Creek (Mayhood 1988). In 2000, 1 brook trout was taken in Mill Creek above Fitch’s 1978 headwater sample site, and 1 brook trout was found in Whitney Creek immediately above the confluence with Mill Creek, but none were found in a 200 m middle section of Whitney Creek (Dahl-Fequet 2000). I captured no brook trout in an intensive survey of Whitney Creek middle reaches to the headwaters in 2002 (D. W. Mayhood, unpublished data).

Thus since their introduction in 1949, brook trout have maintained what appears to be a trace population in upper Mill Creek near and above the Whitney Creek confluence. That population has been unable to expand and dominate in that drainage over a period of 53 years. There has been no invasion of Mill and Whitney creeks by brook trout in that time.

A final example provides a sobering lesson on the consequences of a successful invasion of brook trout into Alberta native cutthroat waters. In Quirk Creek, a low-elevation tributary of the Elbow River, brook trout were introduced in 1940; did not show up in collections made in 1948; had successfully colonized the lower 3 km of the creek by 1978, forming 35% of the fish population; and occupied the entire length of the creek by 1995, when they comprised 92% of the total fish population (Stelfox et al. 2001). Perhaps significantly, the 1978 — 1995 period of the invasion was accompanied by substantial habitat deterioration, the result of vehicle use along the creek. The total time for invasion success was 55 years.

These examples leave the clear impression that brook trout may invade slowly but inexorably in Alberta streams, and may not be invasive at all in some streams. They successfully invaded the Bow River mainstem and its side channels below Banff over many decades. Brook trout in Jumpingpound Creek also seem to have successfully invaded slowly, but eventually established a significant presence over a shorter stream distance. The Quirk Creek invasion, though slow, was ultimately completely effective. However, brook trout in the Mill Creek - Whitney Creek system have been able to maintain a trace population in the headwaters, but have been unable to expand over more than half a century. These observations support the contention (Adams et al. 2002) that “although invasion may be ongoing in some streams, brook trout do not appear to be relentlessly invading every accessible stream.” When an invasion does succeed, it can be quick, dramatic and sometimes devastating (Behnke 1992; Stelfox et al. 2001; Paul et al. 2003).

Once established, brook trout can be extraordinarily tenacious in the face of concerted efforts to remove the species. Although some attempts at eradication have been successful (Shepard et al. 2002; Shepard and Nelson 2004), especially in simple habitats, others have failed despite persistent, intensive efforts (Paul et al. 2003; Earle and Lajeunesse 2007). The payoffs of a successful eradication program can be substantial in terms of increased population size of westslope cutthroats (Shepard et al. 2002).

Only two watersheds still holding genetically pure westslope cutthroats also lack brook trout populations (Figure 1). Brook trout appear so far to be absent from the Carbondale drainage above Carbondale Falls. The species also does not occur in the Oldman-Livingstone drainage, including Dutch, Racehorse and Hidden creek drainages, or any of their smaller tributaries. It is possible that some brook trout populations reported in the Sheep River drainage proper (Figure 1) are no longer extant, as (Robinson 2008) reported none were found in his extensive recent survey in the watershed. Genetically pure westslope cutthroat populations exist in the barrier-free headwaters of many watersheds in which brook trout also occur in downstream reaches, e.g., Fortymile, Waiparous, Jumpingpound, Kananaskis, and possibly North Willow. These situations pose a threat, albeit unassessed at this point, to the headwater cutthroat populations.

To see if there was any further evidence of a threat to cutthroat populations from brook trout in Alberta foothills creeks, I plotted catch-per-unit-effort (CPUE) data recently collected for Alberta Fish and Wildlife by (Robinson 2008) for 22 Alberta East Slopes stream locations in which brook trout occurred (Figure 2). Higher cutthroat trout population densities tended to occur when brook trout density was low. When brook trout density was high, cutthroat density was low, although there was substantial scatter (Figure 2, A and B). When I examined the effect of removing all populations for which Robinson noted external evidence of hybridization, the relationship seemed even more pronounced (Figure 2, C). In other words, the above relationships were even stronger for populations that had little or possibly no hybridization. Also, brook trout populations commonly reached population densities much higher than those achieved by cutthroat trout, which relative to brook trout were always low in the presence of brook trout. There are several reasonable alternative interpretations of these data, but they are at least consistent with the hypothesis that brook trout presence causes lower cutthroat trout population densities, especially for unhybridized or lightly hybridized cutthroat populations.

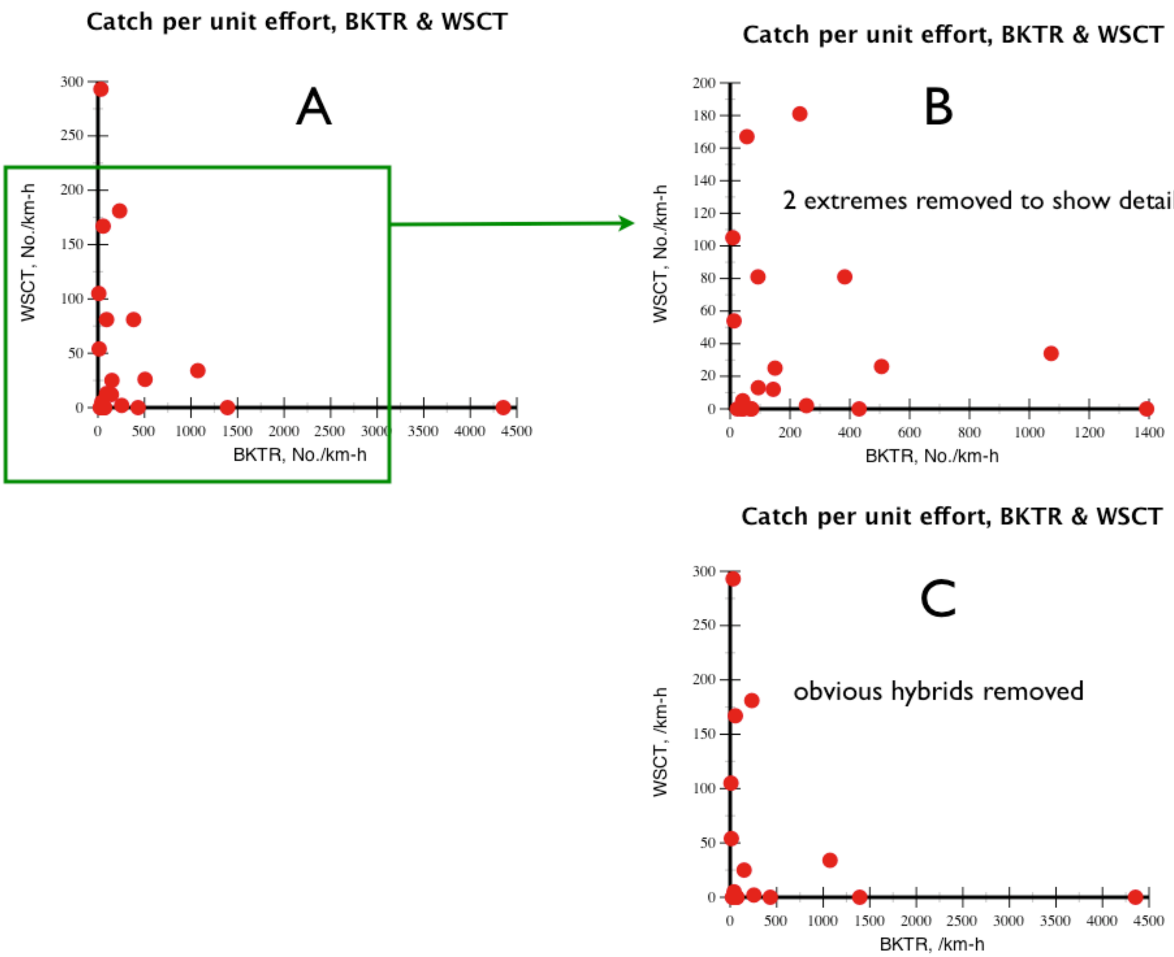

Figure 2. Catch-per-unit-effort (electrofishing kilometre-hours) of brook trout (BKTR) and westslope cutthroat trout (WSCT) from 22 Rocky Mountain eastern slopes streams in which BKTR were present with WSCT (Robinson 2008). A - all 22 samples; B - portion of the A plot magnified to show detail; C - 6 WSCT populations showing evidence of hybridization excluded.

Parasites and Disease

The only survey of parasites in Alberta cutthroat trout that I was able to find reported one nematode, one digenetic trematode and one cestode (Mudry and Anderson 1977). Infection frequencies and infection intensities were low in most of the six cutthroat populations sampled in the Alberta national parks; however only a total of 23 fish were sampled (Table 10). Of the two helminths identifiable to species, I was able to find host-effect information on only one. The digenetic trematode *Crepidostomum farionis* appears to have little effect on its host at the infection intensities found in Mudry and Anderson's survey, although it has been implicated in disease and mortalities in other studies (Klein et al. 1969).

Parasites infect all fish species at some cost to the fish, but are under adaptive and evolutionary constraints not to kill their hosts, at least until the parasite reproduces or moves on to a new host (Moyle and Cech 1996). Major problems for the host may occur when exposed to a new parasite to which it is not adapted, or which is not adapted to the new host. Thus, new parasites introduced with introduced fish species are a concern.

Table 10. Helminth parasites recorded from cutthroat trout in Alberta (Mudry and Anderson 1977). i, introduced; n, native.

Parasite	Populations affected	Infection frequency	Infection intensity, range (mean)
Rhabdocona sp.	Utopia L. (i)	1 of 5	0—1 (0.2)
Rhabdocona milleri	Crypt L. (i)	3 of 4	0—62 (35.7)
Crepidostomum farionis	Peyto L. (i), Lower Consolation L. (i, n), Babel Cr. (i, n), Lower Altrude L. (n), Boom L. (n)	0 of 2 — 5 of 5, weighted mean 60.9% of 23 fish examined from 6 waterbodies	0—307 (22.6)
Diphyllobothrium sp.	Boom L. (i, n)	2 of 5	0—7 (1.4)

Yellowstone cutthroats introduced into Alberta could have introduced their parasite fauna also, but the significance of or potential for parasite introductions from this source would require more research to resolve. Yellowstone cutthroats from Yellowstone Lake, the probable source of our introduced stocks, are notable for carrying high loads of parasites, of which a total of 18 species have been documented in the population (Gresswell 1995). Cestodes of the genus *Diphyllobothrium* are considered particularly troublesome, at least by anglers, as infection rates are high (46 — 100%) and populations are dense. Other parasites that can achieve high numbers in this population include several parasitic copepods, and a species of eye fluke, *Diplostomum baeri buccelentum*. Many of the parasites found in this stock of Yellowstone cutthroats require intermediate hosts that may not occur where these fish were stocked in Alberta; others are probably readily transferable.

Only 16 parasite taxa were found in the previously mentioned survey, which examined mainly salmonids from 32 lake and 9 stream sites in the mountain national parks of Alberta and British Columbia (Mudry and Anderson 1977). *Diphyllobothrium* pleurocercoids were found in fish from 16 of 31 lakes sampled — in five lakes and four species in the Bow River drainage, BNP, and in two lakes and two species in the Waterton River drainage, WLNP. The species could not be identified, so it is unknown whether it is the same as one of the species in Yellowstone Lake. None of the other parasites mentioned by (Gresswell 1995) appears in the list of Mudry and Anderson (1977) for populations in the mountain national parks.

The significance of or potential for microbial disease introductions from Yellowstone cutthroat trout stocking in Alberta is unknown at this point. *Aeromonas salmonicida*, the causative agent of furunculosis, is the only microbial disease organism mentioned as occurring in cutthroats that might be connected to Yellowstone Lake (Gresswell 1995). The same author mentioned proliferative kidney disease as having been found in one remote Yellowstone cutthroat population in Montana.

The Maligne River hatchery in Jasper National Park was for many years contaminated with the infectious pancreatic necrosis (IPN) virus (Mayhood 1992), thought to have been introduced there with one or more importations of infected brook trout eggs from eastern

Canada (Yamamoto 1974). This hatchery at the time was used to stock numerous national park waters with several species of trout, so the opportunity was there to spread the disease widely throughout the native range of cutthroat trout in Alberta. Although adult brook trout and rainbow trout can carry the virus with no apparent signs of disease (Yamamoto 1974, 1975; Yamamoto and Kilistoff 1979), IPN can cause acute disease with high mortalities in young salmonids. The virus is very persistent in surviving infected fish, from which it can enter the environment in water, sediment and certain invertebrates (Gregory et al. 2007). Whether these can provide longterm reservoirs for the virus is still uncertain, although there has been a suggestion that transmission in the wild in Alberta waters is less likely than once feared (Yamamoto and Kilistoff 1979). Because this latter study did not look for mortalities in very young fish, which are the most at risk, this conclusion is perhaps overly optimistic at this point.

Whirling disease, caused by the myxosporidean *Myxobolus cerebralis,* is of particular recent concern because it is strongly pathogenic to cutthroat trout (Hedrick et al. 1998), although there is some variation in the susceptibility among different stocks and subspecies (Wagner et al. 2002; DuBey et al. 2007). This pathogen is widespread in Montana waters immediately south of remnant cutthroat stocks in Alberta, and it has been feared that the organism would soon invade Alberta trout waters as well, for example, in the mud on the waders of anglers (Gates et al. 2007). *M. cerebralis* remains absent from Alberta so far (John and Derksen 2005; Alberta Fish and Wildlife. 2009). Whether it could become a major threat to Alberta remnant native cutthroat populations if it became established here is unclear. Headwater streams, where the remnant cutthroat populations now exist, are not likely to hold the obligate intermediate host, *Tubifex tubifex*, which reaches significant populations mainly in mud substrates of lower-elevation mainstem rivers. Should *M. cerebralis* enter Alberta waters, it may become a significant problem for westslope cutthroat recovery if we attempt to restore mainstem fluvial populations, in which case it could be yet one more factor tending to isolate populations in headwater reaches.

Overexploitation

Early overexploitation (also termed overkill) was a major factor in the decline and extinction of perhaps hundreds of local westslope cutthroat stocks in southwestern Alberta (Mayhood 1995, 2000, 2009). In brief, beginning with the arrival of the Canadian Pacific Railway and its construction crews in the early 1880s (Bow River basin) and early 1890s (Oldman River basin), native salmonids were taken in apparently massive numbers by almost every conceivable means, including trapping, netting, liming, explosives and angling, not to mention likely losses from industrial pollution, damming and water diversions. The resulting declines in trout populations were evidenced by numerous, almost immediate calls from the public to regulate the abuse and to restock southwestern Alberta waters with hatchery fish (Whitcher 1887; Prince et al. 1912; McIllrie and White-Fraser 1983). The destruction and depletion of stocks — not to mention the impairment and outright destruction of their habitat — in the early decades of European settlement would have greatly facilitated the establishment of the Yellowstone cutthroat, rainbow, brook and brown trout that were introduced then or shortly thereafter.

Current Alberta angling regulations for trout in lakes within the native range of westslope cutthroats are highly restrictive. Forty lakes and lake groups in the region hold, or may hold on occasion, cutthroat trout (Table 11). Only 10 of these held, or might conceivably have held, native stocks at some point. Of these, harvest is forbidden in three, while three others might conceivably allow population-effective harvest; that is, sufficient harvest that might have a detectable effect on the abundance of any remaining cutthroat population still present.

Angling regulations for streams within the native range of westslope cutthroats are even more restrictive. Thirty-six stream networks and stream segments lie within the native range under Alberta provincial jurisdiction, and 34 of these hold, or once held, native westslope cutthroat populations (Table 12). Of these, six are permanently closed to angling, while only two of the remainder are likely to permit sufficient harvest to cause detectable effects on population sizes.

Table 11. Lakes and lake groups in the native range of westslope cutthroat trout within Alberta provincial jurisdiction (Fisheries Management Area ES1), showing their trout catch limits, size limits, bait restrictions and open seasons (ASRD 2009). Lakes in boldface hold, or may once have held, native populations of westslope cutthroat trout. "Effective harvest" is my subjective assessment of whether any present population of westslope cutthroat trout is likely to be measurably altered by the level of harvest legally permitted, taking into account all restrictions and likely levels of use.

Lake	Catch limit	Size limit, cm	Bait ban	Open season	Effective harvest?
Burstall Ls.	2			all year	yes
Carnarvon	2			all year	yes
Chester	0		y	Jul1 - Oct 31	
Commonwealth	2			all year	yes
East Scarpe	2			all year	yes
Fortress	2			all year	yes
Galatea Ls.	2			all year	yes
Gap	0		y	all year	
Ghost Res.	5			all year	minimal
Headwall Ls	2			all year	yes
Hogarth Ls	1	> 40 cm		all year	minimal
Invincible	2			all year	yes
L of the Horns	2			all year	yes
Lillian	2			all year	yes
Loomis	2			all year	yes
L Kananaskis Res.	3	> 30 cm	y	all year	yes
Maude	2			all year	yes
Memorial	2			all year	yes
Mt Lorette Ponds	2			all year	yes
Mud L	2			all year	yes

Lake	Catch limit	Size limit, cm	Bait ban	Open season	Effective harvest?
Phillips	2			all year	yes
Picklejar Ls.	2			Jul 1 - Oct 31	yes
Rainy Ridge	1	> 40 cm		Jul 16 - Oct 31	minimal
Rawson	0		y	Jul 16 - Oct 31	
Ribbon	2			all year	yes
Rummel	1	> 40 cm	y	Jul 1 - Oct 31	minimal
Running Rain	1	> 40 cm	y	all year	minimal
Shark	2			all year	yes
Smuts Ls	1	> 40 cm	y	all year	minimal
Sparrows Egg	1	> 50 cm	y	Jul 1 - Oct 31	minimal
Spray Res	5		y	all year	minimal
Stenton	1	> 40 cm	y	all year	minimal
Talus	2			all year	yes
Three Isle	2			all year	yes
Tombstone	2			all year	yes
unnamed (Avalanche)	2		y	Jul 1 - Oct 31	yes
unnamed (Odlum)	2			all year	yes
Waterton Res	5			all year	minimal
Watridge	0		y	July 1 - Oct 31	
Window Mtn	2			all year	

Table 12. Streams in the native range of westslope cutthroat trout within Alberta provincial jurisdiction (Fisheries Management Area ES1), showing their trout catch limits, size limits, bait restrictions and open seasons (ASRD 2009). All but Canmore Cr. and possibly upper Sheep River hold, or may once have held, native populations of westslope cutthroat trout. "Effective harvest" is my subjective assessment of whether any present population of westslope cutthroat trout is likely to be measurably altered by the level of harvest legally permitted, taking into account all restrictions and likely levels of use.

Stream	Catch limit	Size limit, cm	Bait ban	Open season	Effective harvest?
Canmore Cr	0		y	Apr1 - Sep 30	
Canyon Cr	0		y	Jun 16 - Oct 31	
up Carbondale & tribs	2	> 30 cm	y	Jun 16 - Oct 31	minimal
Crowsnest L tribs	2	> 30 cm	y	Jun 16 - Oct 31	
Crowsnest R tribs	2	> 30 cm	y	Jun 16 - Aug 31	
	0		y	Sep 1 - Oct 31	
up Elbow R & tribs	0		y	Jun 16 - Oct 31	
Elbow R, falls - Canyon Cr	CLOSED	CLOSED	CLOSED	CLOSED	
Elbow R: Canyon Cr - Hwy 22	0		y	Jun 16 - Oct 31	
Ghost Wilderness	CLOSED	CLOSED	CLOSED	CLOSED	
Ghost R & tribs below Wilderness	2	>35 cm	y	Jun 16 - Aug 31	minimal
	0		y	Sep 1 - Oct 31	
up Highwood R	0		y	Jun 16 - Oct 31	
Jumpingpound Cr	0		y	Jun 16 - Oct 31	
up Kananaskis R	0		y	Apr 1 - Jun15	
	2	> 30 cm	y	Jun 16 - Aug 31	minimal
	0		y	Sep 1 - Oct 31	
lo Kananaskis R	0				
Livingstone R	0		y	Jun 16 - Oct 31	

Stream	Catch limit	Size limit, cm	Bait ban	Open season	Effective harvest?
Mill Cr	0		y	Jun 16 - Oct 31	
Oldman R/Racehorse Cr	2	> 30 cm	y	Jun 16 - Aug 31	y
	0		y	Sep 1 - Oct 31	
Oldman R Race-horse - Hwy 22	0		y	Jun 16 - Oct 31	
Quirk Cr	0		y	Jun 16 - Oct 31	
Rainy Ridge tribs & outlet	CLOSED	CLOSED	CLOSED	CLOSED	
Rawson L tribs & outlet	0		y	Jul 16 - Oct 31	
Rummel L tribs & outlet	1	> 40 cm	y	Jul 1 - Oct 31	minimal
Screwdriver Cr & tribs	2	> 30 cm	y	Jun 16 - Aug 31	
	0		y	Sep 1 - Oct 31	
Sheep R headwaters	0		y	Jun 16 - Oct 31	
Sheep R Indian Oil - Gorge Cr	CLOSED	CLOSED	CLOSED	CLOSED	
Sheep R Gorge Cr - Highwood	2	> 35 cm	y	Jun 16 - Aug 31	
Smith-Dorrien Cr & tribs	CLOSED	CLOSED	CLOSED	CLOSED	
S Castle R	2	> 30 cm	y	Jun 16 - Aug 31	y
	0		y	Sep 1 - Oct 31	
Spray Res tribs	2	> 30 cm	y	Jul 1 _ Aug 31	minimal
	0		y	Sep 1 - Oct 31	
Storm Cr	CLOSED	CLOSED	CLOSED	CLOSED	
Waiparous Cr	0		y	Jun 16 - Oct 31	
Waterton R above Res & tribs	2	> 35 cm	y	Jun 16 - Aug 31	
	0		y	Sep 1 - Oct 31	

Stream	Catch limit	Size limit, cm	Bait ban	Open season	Effective harvest?
Waterton R below Res	2	> 35 cm	y	Jun 16 - Aug 31	
	0			Sep 1 - Oct 31	
West Castle R & tribs	0		y	Jun 16 - Oct 31	
Whitney Cr	2	> 30 cm	y	Jun 16 - Aug 31	
	0		y	Sep 1 - Oct 31	
up Willow Cr.	2	> 30 cm	y	Jun 16 - Aug 31	
	0		y	Sep 1 - Oct 31	

Angling regulations in Banff National Park prohibit the retention of cutthroat trout from all waters at any time, but a catch and possession limit of two cutthroat trout is permitted in the open season in Waterton Lakes National Park (Parks Canada 2007).

Recent simulations of angling effects on model small-stream westslope cutthroat populations under various regulatory scenarios (Sullivan 2007) suggested that presently depressed cutthroat trout stocks could recover under catch and release management that allows only low angler effort. Once recovered, healthy populations of westslope cutthroat trout may be maintained with catch-and-release angling if fishing effort is no more than moderate. The author concluded that it will be important to limit incidental mortality (accidental hooking mortality or illegal harvest) to maintain and recover these populations. Under the scenarios tested, cutthroat trout populations like those modeled would be unlikely to either maintain themselves or recover if harvested unless angler effort is controlled.

In contrast to these model small-stream populations, three real medium- and large-stream Alberta cutthroat populations subjected to frequent though intermittent heavy exploitation maintained low- to moderately dense populations over many years. Cutthroat trout in the Oldman River above the Livingstone River confluence, and in Dutch Creek, were managed from 1952 to at least 1977[3] under a regime that allowed alternate-year harvest under the generous limitations of 10 fish per angler per day, with a 20 fish possession limit, and no size limit (Radford 1975a, b; 1977a). Anglers removed 70 — 78% of all catchable-sized fish (approximately > 12 cm in length) in years in which angling was permitted. These populations evidently maintained densities of [mean (standard error)] 153 (147-159)• km^{-1} in the Oldman below the falls, 286 (261-311)• km^{-1} above the falls, and 269 (256-282)• km^{-1} in Dutch Creek. In areal terms[4], the densities are approximately 94• ha^{-1} (lower Oldman), 447• ha^{-1} (upper Oldman) and 336• ha^{-1} (Dutch Creek). These densities are deemed to correspond to

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[3] Dutch Creek had a temporarily reduced catch limit of 5 fish per angler per day in 1974 (Radford 1977a)

[4] Estimates were calculated using stream survey mean width data (Clements and Griffith 1974; Radford 1977b). Upper Oldman width was estimated as the mean of the overall mean width and the minimum station mean width for the Oldman; similarly, lower Oldman mean width was calculated as the mean of the overall mean width and the maximum station mean width for the Oldman (Clements and Griffith 1974, Table 7).

populations at high to moderate risk of extinction (< 200 fish• ha^{-1} and 200 – 500 fish• ha^{-1}, respectively) (Sullivan 2007).

What is interesting for present purposes is that these populations appeared to be maintaining themselves, albeit undoubtedly at much lower than pristine densities, despite intermittently heavy exploitation over at least a 20-year period. This suggests that the modeling results (Sullivan 2007) may be conservative (in the precautionary sense), at least if applied to medium- and large-stream cutthroat populations managed under an alternate-year closure regime.

While the effects of direct mortality from angling on cutthroat populations presently appear to pose little threat to remnant populations under a reasonably precautionary regulatory regime, there are other potentially important effects of angling that have not yet been sufficiently considered. For example, do high intensities of catch and release angling sufficiently stress individual cutthroats so as to limit reproductive success? Do size-selective harvesting regimes now, or have they in the past, placed sufficient selective pressure on populations so as to reduce their reproductive success, or have adaptive or evolutionary effects?

In some catch and release fisheries, cutthroat trout have been caught an average of nearly 10 times, or once every five days, during the open season (Schill et al. 1986). Individual trout may be caught two and three times in a single day, and remain susceptible to the fishery for three years (Gresswell 1985). While total seasonal mortality rates due to angling capture remain as low as 3.2 percent (Schill et al. 1986), such high levels of capture of individual fish suggest that cumulative stress of repeated captures might have an effect on reproductive success, for example by using up energy that otherwise would go into egg or milt production. It has been suggested that hooking stress added to other stresses that the fish may be experiencing from adverse environmental conditions may cause delayed or indirect mortality from predators, disease or parasites (Wydoski 1977).

While a well-designed recent study has dismissed stress effects from hooking and playing salmonids (including cutthroat trout) as being largely inconsequential, these experiments were done on fish subjected to only a single capture, with handling by highly experienced professionals (Wedemeyer and Wydoski 2008). Cumulative effects of repeated hooking and handling over a short period, especially by clumsy anglers with little understanding of stress in fish (perhaps the more common situation in real life), still appears not to have been tested. Given the high frequency of broken and missing maxillaries, broken jaws, broken opercula and other severe wounds that I have seen in heavily fished cutthroat populations in Alberta, I suggest we should be disinclined to accept that cumulative stress effects from repeated hooking and handling are of no import. Further research is required on this matter, considering that threatened stocks of fish may be affected.

Selective effects on remnant cutthroat trout stocks, resulting from severely increased environmental pressures, promises to be one of the more intractable problems to be faced in conserving these fish. Under a directed harvest regime, preferential removal of larger individuals of a species has been shown to have negative effects on demography, life history and ecology (Fenberg and Roy 2008). This is in part because larger individuals often are disproportionately influential within their populations. In Atlantic cod, for example, relatively few old (large) females contribute 10.1–12.4 times more offspring surviving to age 1 than do less experienced (smaller) spawners (Carr and Kaufman 2009). Selecting large fish for harvest (the normal situation), not only places selection pressure for small size at maturity on such a population, it also stands to directly reduce population size far more than might be predicted from a traditional maximum sustainable yield analysis.

Whether similar conditions are present in remnant westslope cutthroat populations is an open question. Standard practice of anglers is to retain the largest fish caught, and that was undoubtedly so historically in past Alberta cutthroat fisheries. Even current management practice for the species is to permit harvest only of the largest individuals. Have these practices had an undesirable selective effect on these stocks?

Finally, the potential for overexploitation by both legal and illegal means is likely to be much higher in highly developed watersheds with extensive road and trail development. Such problems have long been recognized (Radford 1975a; 1977a; Radford and Wiebe 1975; Paul and Boag 2003; Parker et al. 2007), but calls to decommission roads for these and other reasons (Radford and Wiebe 1975; Sawyer and Mayhood 1998a; Mayhood et al. 2004) have gone unheeded. Roads, trails and other linear disturbances contribute not only to overexploitation but to many other classes of threat to salmonids. It is likely that many of the most serious threats and limiting factors to the continued existence of westslope cutthroat trout in Alberta — overharvest, habitat damage and loss, and their interactions with climate change and species invasions — could be significantly ameliorated by the relatively simple expedient of removing unneeded roads and restoring their rights of way to a more natural condition. This matter will be covered more thoroughly in the third report in this series.

Conclusion

History is perhaps the single greatest threat and limiting factor confronting native westslope cutthroat trout and their prospects for recovery in Alberta. Events in the past are irreversible, and their consequences have created several intractable problems for conserving this fish.

Before the coming of the Canadian Pacific Railway in the late 1800s, cutthroat trout occupied all of the accessible waters on the eastern slopes of the Rocky Mountains in the Bow and Oldman drainages, extending in the mainstem rivers far out onto the plains. Over the course of thousands of years, these fish developed hundreds of individual separate stocks, each with a unique genetic identity, home range and life history. These populations were little-used by most indigenous peoples and animal predators of the region, allowing them to maintain dense populations and become remarkably abundant. The Continental Divide protected them from invading potential salmonid competitors on the west, while 1600 kilometres of hot, dry plains to the east excluded possible coldwater competitors invading from that direction. The stocks had adapted and evolved over millennia with just two other major coldwater species, which accompanied them in their postglacial dispersal from the upper Missouri, lower Columbia, and possibly more local refugia.

With the advent of European settlement, all of that changed, dramatically and almost instantaneously. The dense, abundant standing populations were decimated by overfishing, beginning the process of fragmenting and isolating the stocks. The attempted remedy for the loss of fish, introducing — consistently, persistently and in large numbers — first brook trout, then rainbow, brown, and Yellowstone cutthroat trout, initiated the foreign invasions and a long series of competitive and predatory effects. These new species, none of which were native to the Bow or Oldman basins, readily established themselves in the now-under-occupied habitats. The brook and brown trout slowly but relentlessly spread throughout the former cutthroat stream networks where they competed with and preyed upon the native species. The rainbows and sometimes the Yellowstone cutthroats readily hybridized with the westslope cutthroats, quickly infecting the remnant native cutthroat populations with their genes, effectively taking over their range by taking over the native genome. Hybridization has permanently changed the genetic structure of the affected native cutthroat populations. Beneficial coadapted gene complexes have been disrupted, and locally adapted stocks have been lost. All the while the cutthroats, being most vulnerable to angling, were being overfished.

At the same time, large changes in the natural habitats of the native cutthroats were occurring. Massive fires swept the eastern slopes with the arrival of the railways, and later during the 1930s; river mainstems and major tributaries were being dammed; the beginnings of today's vast network of roads and other linear disturbances were being established; ranching was introducing high densities of cattle that preferentially occupied riparian areas — all of which would have contributed to large changes in channel and riparian morphology, migration blockages, stock isolation and fragmentation and reduced carrying capacity, thereby facilitating the ongoing invasion of nonnative fish. By the 1960s, native stocks had been reduced nearly to where they are today: tiny, isolated, fragmented, genetically transformed, severely weakened.

Then in the 1970s the effects of global warming began to be felt: effects that will continue to worsen, permanently changing the remaining native habitats and their hydrology. Climate change will continue the destruction of native cutthroat habitat by increasing forest fire frequency and intensity, favouring mountain pine beetle forest kill, producing more frequent extreme spring runoff and lower summer flows, increased loading of fine sediments, and warming lower reaches of streams to less favourable temperatures.

All of these changes, and more, have created permanent limitations on the remaining native cutthroat trout populations. These are the threats and limiting factors that any realistic recovery plan for Alberta's westslope cutthroat trout must address. Some ideas for doing so are presented in the final report of this series.

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