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ASSESSING THE IMPACTS OF RIVER REGULATION ON NATIVE BULL TROUT (*SALVELINUS CONFLUENTUS*) AND WESTSLOPE CUTTHROAT TROUT (*ONCORHYNCHUS CLARKII LEWISI*) HABITATS IN THE UPPER FLATHEAD RIVER, MONTANA, USA

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ABSTRACT

Hungry Horse Dam on the South Fork Flathead River, Montana, USA, has modified the natural flow regimen for power generation, flood risk management and flow augmentation for anadromous fish recovery in the Columbia River. Concern over the detrimental effects of dam operations on native resident fishes prompted research to quantify the impacts of alternative flow management strategies on threatened bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) habitats. Seasonal and life-stage specific habitat suitability criteria were combined with a two-dimensional hydrodynamic habitat model to assess discharge effects on usable habitats. Telemetry data used to construct seasonal habitat suitability curves revealed that subadult (fish that emigrated from natal streams to the river system) bull trout move to shallow, low-velocity shoreline areas at night, which are most sensitive to flow fluctuations. Habitat time series analyses comparing the natural flow regimen (predam, 1929–1952) with five postdam flow management strategies (1953–2008) show that the natural flow conditions optimize the critical bull trout habitats and that the current strategy best resembles the natural flow conditions of all postdam periods. Late summer flow augmentation for anadromous fish recovery, however, produces higher discharges than predam conditions, which reduces the availability of usable habitat during this critical growing season. Our results suggest that past flow management policies that created sporadic streamflow fluctuations were likely detrimental to resident salmonids and that natural flow management strategies will likely improve the chances of protecting key ecosystem processes and help to maintain and restore threatened bull trout and westslope cutthroat trout populations in the upper Columbia River Basin.

KEY WORDS: flow regulation; dams; bull trout; westslope cutthroat trout; IFIM; fish habitat; two-dimensional hydrodynamic habitat modelling

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INTRODUCTION

Dams are one of the greatest threats to river biodiversity worldwide (Postel *et al.*, 1996; Poff *et al.*, 2007). Nearly half of the world's large river systems have been modified by dams and diversions for water, energy and transportation (Nilsson *et al.*, 2005). Dams fragment riverine systems and modify the natural flow regimen, thereby altering fluvial dynamics, streamflow processes, and biological diversity at multiple spatial and temporal scales (Stanford *et al.*, 1996; Poff *et al.*, 1997; Richter *et al.*, 1997; Rosenberg *et al.*, 2000; Petts, 2009). The construction and operation of hydroelectric dams modify both downstream and upstream fish communities and habitats through inundation, flow modification and fragmentation (Bain *et al.*, 1988; Poff *et al.*, 1997; Murchie *et al.*, 2008). Dams block fish movements, causing genetic isolation (Heggenes and Roed, 2006) and loss of migratory populations (Gosset *et al.*, 2006; Northcote, 1997), and may produce large daily and hourly streamflow fluctuations that negatively impact fish populations and lotic community structure (Cushman, 1985; Poff and Ward, 1989), which have contributed to the decline and extinction of many populations and species of freshwater fishes and native aquatic biota (Rahel, 2000; Freeman *et al.*, 2001). Consequently, conservation of riverine ecosystems can be enhanced by understanding the impacts of alternative dam operations on critical aquatic habitats (Petts, 1984).

Dams in the Columbia River Basin of North America have contributed to severe declines in anadromous fish stocks during the latter part of the 20th century (Williams *et al.*, 1989). Most acknowledged are the declines of wild

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salmon and steelhead runs, resulting from habitat alteration and increased smolt and adult migration mortality associated with hydroelectric dams along the Columbia and Snake Rivers (Hatten *et al.*, 2009; Kareiva *et al.*, 2000). Accordingly, recovery programmes have called for late summer flow augmentation in the Columbia River intended to assist with the out-migration of salmon and steelhead smolts (ISAB, 1997; USFWS, 2000, 2006; NOAA-Fisheries, 2000, 2008). Flow augmentation is provided, in part, by releasing water from the Hungry Horse (South Fork Flathead River) and Libby (Kootenai River) reservoirs in the headwater reaches of the Columbia River in Montana. In addition, these two headwater reservoirs provide approximately 40% of the usable water storage in the US portion of the Columbia Basin power and flood control operations (B. Marotz, unpublished data). Despite these water-use demands from headwater storage areas, to our knowledge, no studies have quantified the impacts of flow management strategies on native freshwater (resident) salmonids inhabiting the headwaters of the Columbia River Basin.

The two native resident fish species affected by flow augmentation and dam operations in the Columbia River Basin are the bull trout (*Salvelinus confluentus*) and the westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Populations have declined throughout much of their native ranges in western North America, including all portions of the Columbia River Basin (Williams *et al.*, 1989; Rieman *et al.*, 1997; Shepard *et al.*, 2005), owing primarily to habitat destruction, fragmentation and non-native species. As a result, bull trout are listed as a threatened species under the US Endangered Species Act, and westslope cutthroat trout are classified as a species of special concern throughout their native range in the United States. Loss of habitat connectivity and habitat modification can be especially detrimental to migratory populations because they require large, relatively pristine and ecologically diverse connected habitats for spawning, rearing and feeding (Schmetterling, 2001; Muhlfeld and Marotz, 2005; Muhlfeld *et al.*, 2009b), which is vital for metapopulation persistence (Rieman and McIntyre, 1995; Rieman and Allendorf, 2001).

The upper Flathead River system in Montana, USA, and British Columbia, Canada, is considered a range-wide stronghold for native bull trout and westslope cutthroat trout populations (Fraley and Shepard, 1989; Muhlfeld *et al.*, 2009b). The flow-regulated portion of the Flathead River upstream of Flathead Lake (Figure 1) provides critical overwintering and rearing habitats for migratory populations (Shepard *et al.*, 1984; Fraley and Shepard, 1989; Muhlfeld *et al.*, 2003; Muhlfeld and Marotz, 2005; Muhlfeld *et al.*, 2009a). Since the construction of Hungry Horse Dam in 1952, the natural flow regimen has been modified for power generation, flood risk management and flow augmentation for anadromous fish recovery in the Columbia River downstream, by storing water derived from spring run-off and sporadically releasing it during the summer, fall and winter months when flows were historically low (Figure 2) (Marotz *et al.*, 1996). Concern over the detrimental effects of flow fluctuations on native salmonid populations prompted managers to restore and enhance critical river habitats through flow management strategies that balance human water uses and the recovery and conservation of resident and anadromous fishes.

The purpose of this study was to quantify how flow management strategies have influenced the availability of critical native salmonid habitats in the regulated portion of the main-stem Flathead River. Our objectives were as follows: (i) develop site-specific habitat suitability functions for subadult bull trout, adult bull trout and westslope cutthroat trout to characterize seasonal use of depth and velocity in the Flathead River; (ii) use a two-dimensional (2D) hydrodynamic model to simulate the microhabitat (depths and velocities) conditions in the river as a function of streamflow; (iii) combine the habitat suitability curves with the microhabitat conditions using a geographic information system (GIS)-based habitat model (Miller *et al.*, 2003) to estimate how the quantity and the quality of habitat vary spatially over a range of discharges; and (iv) evaluate the impacts of five postdam flow management regimens (1953–2008) on critical habitats and compare the results with predam natural flow conditions (1929–1952). Understanding discharge effects on critical habitats is essential to developing management programmes for recovery of resident fishes while simultaneously balancing management constraints of power, flood control and anadromous fish recovery.

STUDY AREA

The upper Flathead River drainage

The upper Flathead River drainage originates in the Rocky Mountains of north-western Montana, and British Columbia, and includes the North Fork, Middle Fork, South Fork, main-stem Flathead River and Flathead Lake. The drainage area is approximately 18 400 km^2 and is in the headwaters of the upper Columbia River Basin. Our study was conducted in the flow-regulated main stem of the Flathead River between the South Fork Flathead River and the Stillwater River (Figure 1). It was divided into two reaches based on changes in geomorphology. Reach 1 is mostly a single-thread channel (average gradient = 0.23%) that begins at the South Fork confluence and extends 17.6 km downstream. Reach 2 is a 19.2-km (average gradient = 0.03%) anastomosing channel (multiple stable channels that have a large area covered by mature vegetation) that extends downriver to the confluence with the Stillwater River.

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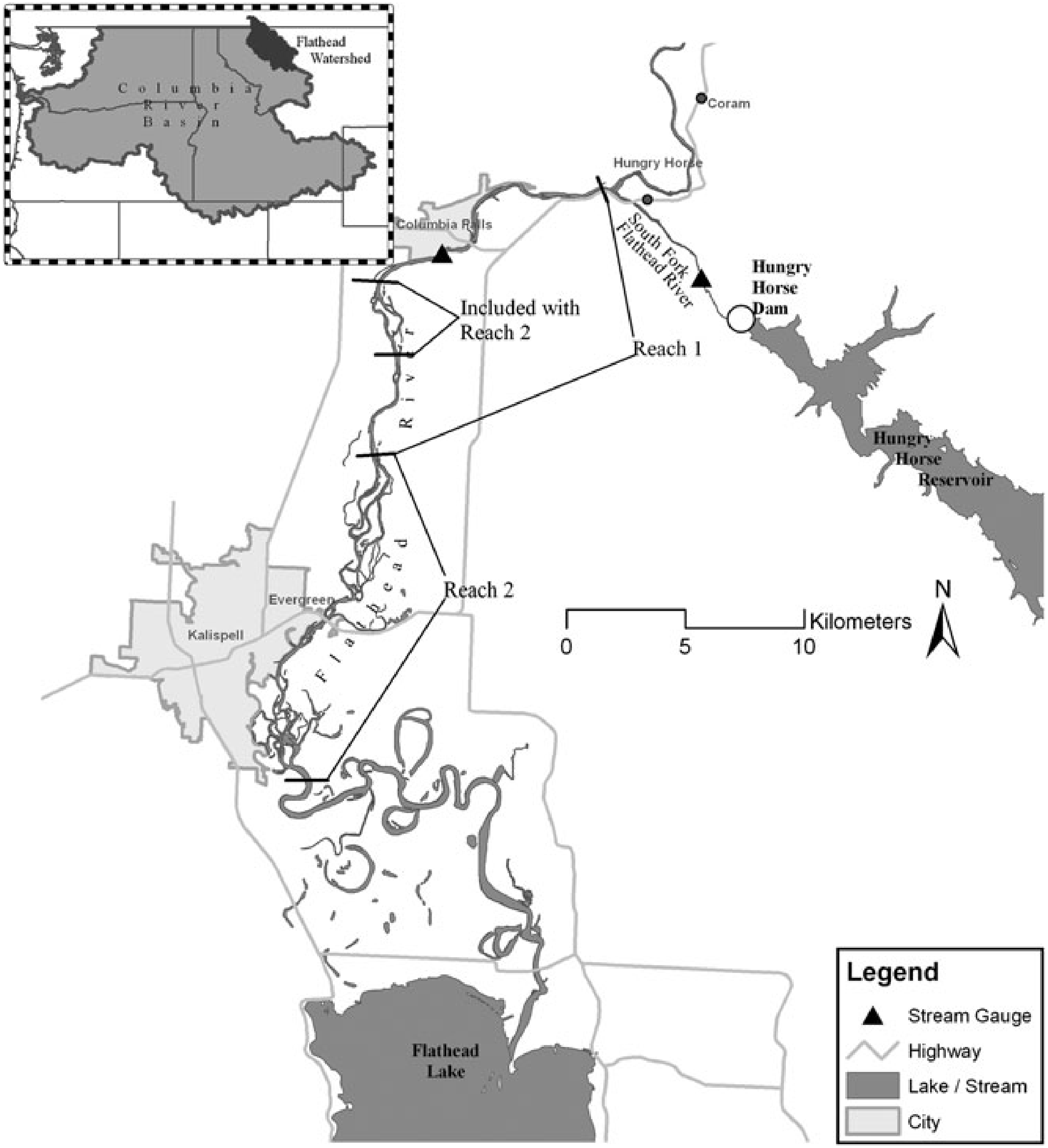

Figure 1. Study reaches in the upper Flathead River, Montana.

A representative study section was selected in each reach and was used to construct a 2D, spatially explicit habitat model (Miller *et al.*, 2003). The study section in reach 1 was 3.4 km (~500 000 m^2), and the study section in reach 2 was 3.9 km (~820 000 m^2). Native fish species found in reaches 1 and 2 include bull trout, westslope cutthroat trout, mountain whitefish (*Prosopium williamsoni*), longnose sucker (*Catostomus catostomus*), largescale sucker (*Catostomus macrocheilus*) and sculpins (*Cottus* spp.). Non-native fishes include rainbow trout (*Oncorhynchus mykiss*), lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*).

Hungry Horse Dam, South Fork Flathead River

The North, Middle and South Forks of the Flathead River drain approximately 12 000 km^2, with an average annual discharge of 275 m^3 (measured at Columbia Falls). The main stem of the Flathead River, beginning at the confluence of the South Fork, then flows through the Flathead Valley from Columbia Falls to Flathead Lake. Hungry Horse Dam, located 8.5 km upstream of the South Fork Flathead River confluence with the main-stem Flathead River, was completed in 1952. The upstream drainage area in the South Fork is 4248 km^2, contributing

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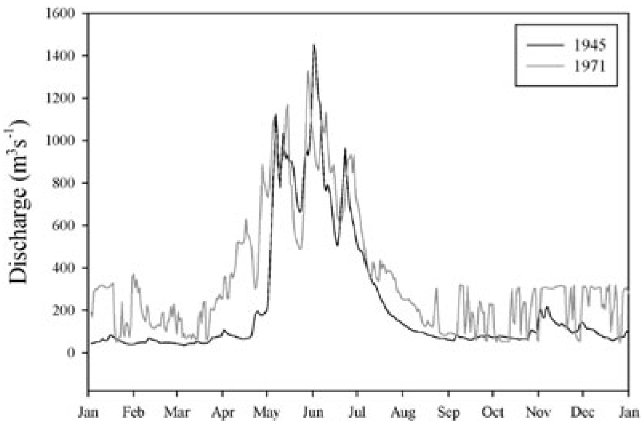

Figure 2. Typical hydrograph of the Flathead River for a 'predam' (1945) and 'postdam' (1971) year.

approximately one-third of the total discharge in the mainstem Flathead River. The dam regulates river discharge, impedes upstream fish migration, isolates fish populations upstream (Figure 1) and has modified the physical and biological characteristics of the Flathead River downstream (Appert and Graham, 1982; Fraley and Graham 1982; Fraley and Decker-Hess, 1987; Fraley *et al.*, 1989; Hauer *et al.*, 1997). Hypolimnetic releases artificially cooled the river from 1952 to 1996. In August of 1996, a selective withdrawal system was installed on four penstocks of the dam to control temperatures in the tailrace, which restored the river temperatures to near predam conditions (Christenson *et al.*, 1996; Marotz *et al.*, 1999). Power production and flood control operations, however, have reversed the annual hydrograph, storing water derived from spring run-off and releasing it during summer, fall and winter months when flows were historically low (Marotz *et al.*, 1996). Consequently, flow regulation has had a relatively minimal effect on peak spring flows and a greater effect on base flows and rates of change during base flows (Figure 2). Short-term sporadic releases in the tailwater have created an unproductive varial zone, increased substrate embeddedness, and have decreased the diversity and the productivity of macroinvertebrate communities (Ward and Stanford, 1979; Hauer *et al.*, 1994). Rapid flow reductions have also been shown to desiccate river margins and strand insects, zooplankton, fish and fish eggs (Hauer and Stanford, 1982; Perry *et al.*, 1986; Hauer *et al.*, 1994; Hauer *et al.*, 1997). Moreover, the dam has restricted the movement and the establishment of non-native species, including lake trout and rainbow trout, from downstream areas to areas upstream of the dam. Although the impacts of flow modifications on lower trophic levels are well understood, before this study, the flow impacts on native salmonid habitats were unknown.

Native bull trout and westslope cutthroat trout

The upper Flathead River and Lake system is considered one of the most biodiverse aquatic ecosystems in North America (Hauer *et al.*, 2007). Over the past century, however, native fish populations have declined because of major community changes in Flathead Lake (i.e. introduced non-native mysid shrimp and increase in the non-native lake trout population), habitat degradation and fragmentation, introduction of non-native invasive aquatic organisms and the construction and operation of Hungry Horse Dam (Liknes and Graham, 1988; Fraley and Shepard, 1989; Spencer *et al.*, 1991; Hitt *et al.*, 2003; Boyer *et al.*, 2008). These species require the coldest water temperatures of any native north-west salmonid; clean substrates for spawning and rearing; and complex habitat connections between river, lake and headwater streams that support annual spawning and feeding migrations (Liknes and Graham, 1988; Fraley and Shepard, 1989).

The bull trout populations are migratory, whereas the westslope cutthroat trout populations will either remain in their home stream for life or migrate throughout the Flathead system (Liknes and Graham 1988; Fraley and Shepard 1989; Muhlfeld and Marotz 2005; Muhlfeld *et al.*, 2009b). Juvenile bull trout and cutthroat trout will rear in natal streams for 1–4 years, and then as subadults, they will move downstream during spring or fall to overwintering areas in the dam-influenced portions of the river and Flathead Lake (Shepard *et al.*, 1984; Muhlfeld and Marotz, 2005). Migratory bull and cutthroat trout grow to maturity in the flow-regulated portion of the Flathead River or Flathead Lake and then travel up to 250 km upriver to spawn in natal streams that contain clean gravel, cold groundwater recharge and protective cover. Bull trout begin spawning migrations in the spring and summer and spawn from late August through early October when water temperatures fall below 9°C in low-gradient reaches (Fraley and Shepard, 1989). In contrast, westslope cutthroat trout migrate upstream as flows increase during spring run-off and spawn during peak spring flows and as flows decline and temperatures rise to about 9°C (Muhlfeld *et al.*, 2009b). Understanding the seasonal habitat requirements of these species and life stages in the dam-influenced portion of the Flathead River is critical for developing successful conservation and recovery programmes.

METHODS

One of the most widely applied methodologies for developing flow recommendations is the instream flow incremental methodology (IFIM) (Bovee *et al.*, 1998) and its component hydraulic model, physical habitat simulation (Milhous *et al.*, 1989). 2D hydrodynamic simulation models

DOI: 10.1002/rra

are now used in place of the original one-dimensional hydraulic simulation models (Leclerc *et al.*, 1995; Steffler and Blackburn, 2002). In the approach used here, habitat suitability functions are developed for key species to characterize the microhabitat use of water depth and velocity and are combined with the detailed depth and velocity information derived from the hydrodynamic model to estimate how habitat varies temporally and spatially over a range of discharges in two river reaches (Kondolf *et al.*, 2000).

Our approach addresses some of the criticisms of the IFIM modelling approach (Poff *et al.*, 1997), in terms of statistical validity of physical habitat characterizations and biological assumptions, by (i) developing seasonal and life-stage specific habitat suitability criteria over multiple temporal scales (annual, seasonal, diurnal); (ii) statistically evaluating a species and life stage that is most sensitive to changes in flow; (iii) analysing how a range of flows (inter-annual and intra-annual variation) influences critical habitats, as opposed to establishing minimum flows for target species; and (iv) applying a 2D hydrodynamic habitat model, which integrates hydraulic data simulations and habitat suitability data, in a spatially explicit framework to estimate usable habitat at various flows.

Habitat use assessments

Radiotelemetry and snorkel surveys were used to investigate the habitat use by bull trout and westslope cutthroat trout from 1999 to 2002 in the main-stem Flathead River. The habitat use data were collected to develop habitat suitability functions for each species and life stage within the study reaches (Rosenfeld, 2003). For each target species, fish were classified into subadult (i.e. fish that emigrated from natal streams to the river) or adult size classes based on length frequency distributions. Bull trout <400 mm were classified as subadult fish, whereas bull trout with lengths $\geq$400 mm were classified as adults (Muhlfeld *et al.*, 2003). For westslope cutthroat trout, fish <300 mm were classified as subadults, and fish $\geq$300 mm were classified as adults (Muhlfeld *et al.*, 2009a).

Radiotelemetry was used to assess day and night habitat use during fall and winter months. Seasons were delineated based on historic temperature and flow data in the Flathead River and were classified as follows: winter (1 December–31 March), spring (1 April–30 June), summer (1 July–15 September) and fall (16 September–30 November). Fall and winter habitat use data were pooled because of some fish being implanted in late October. Fish were captured in reaches 1 and 2 primarily by boat electrofishing and a few by angling and passive traps (hoop nets). Each fish was surgically tagged with a radio transmitter (Muhlfeld *et al.*, 2003) that weighed 2.0–8.9 g (models MCFT-3HM, MCFT-3D, MCFT-3EM; Lotek Wireless Inc., Newmarket, ON, Canada), depending on the size and weight of the fish, and was released near its capture location. Transmitter life ranged from 40 to 399 days, and each tag emitted a signal every 5 s at 148.730 MHz. Fish were tracked from a jet boat equipped with a scanning receiver (Lotek model W30), a whip antenna and a directional yagi antenna. Tag location tests revealed that location accuracy was within 2 m of the transmitter (Muhlfeld *et al.*, 2003), which was sufficiently accurate for purposes of collecting habitat suitability data. At each fish location, a brightly numbered rock (labelled for species and size class) was placed at the focal point, and locations were georeferenced (±1 m) using a global positioning system (GPS) unit (TSC1 Asset Surveyor; Trimble Navigation Ltd, Sunnyvale, CA, USA). The microhabitat and macrohabitat use data were collected at each fish location, including water depth (m) and mean water column velocity (m s^{-1}). Water depth and mean velocity were measured from the jet boat using a US Geological Survey (USGS) A-55 sounding reel, a 13.6-kg sounding weight, and a Price AA current meter (Geo Scientific Ltd, Vancouver, BC, Canada). In a GIS, point locations were overlaid onto a hydrography map to assess the model results, which were highly concordant with the fish location data (Miller *et al.*, 2004). Macrohabitat units were classified as riffle, run or pool (Bisson *et al.*, 1982).

Snorkel surveys were used to collect the summer day habitat use data in 1999 and 2000. Each study reach was partitioned into 250-m river sections using a GIS. The length of each section was measured along the thalweg, and the section boundaries were positioned perpendicular to the stream bank. Divers snorkelled parallel to the stream bank along a randomly chosen transect, beginning at the upstream boundary and floating downstream noting fish locations. The habitat use data were collected at each fish location as described above.

Multivariate analysis of variance (MANOVA) was used to simultaneously test for differences in habitat use of both depth and velocity among target species and life stages. Independent comparisons of depth and velocity were conducted using analysis of variance (ANOVA) and Bonferroni *post hoc* tests (Statistica, 1995).

Habitat suitability functions

An accurate characterization of microhabitat use by native biota is crucial to developing reliable habitat suitability functions, which is an integral step in assessing flow impacts on usable habitats (Jowett, 1992). Telemetry and snorkel data were used to develop site-specific habitat suitability functions for select species and life stages in each study reach. Paired depth and velocity data were used to produce a three-dimensional bivariate histogram of habitat use. This three-dimensional histogram was then fit with an

DOI: 10.1002/rra

exponential polynomial equation by regressing depth and velocity variables onto the frequency histogram surface using a least-squares regression smoothing procedure (Bovee, 1986; Statistica, 1995; Miller Ecological Consultants, Inc., 2001; Miller *et al.*, 2003) with the following equation: $Z = \exp(\beta_0 + \beta_1 D + \beta_2 V + \beta_3 DV + \beta_4 D^2 + \beta_5 V^2 + \beta_6 D^3 + \beta_7 V^3)$, where Z = number of fish observed; D = water column depth; V = average water column velocity; and $\beta_0, \beta_1, \beta_2, \ldots$ = equation coefficients. The best fit to the three-dimensional surface was determined by selecting a final model that produced the largest coefficient of determination with the fewest terms (e.g. parsimonious model). All the exponential polynomial regression functions used third-order terms for depth and velocity and a first-order interaction term (Table I and Figure 2). The final regression equation was normalized to provide a maximum habitat suitability index (HSI) of 1; $\mathrm{HSI} = ((1/N)\exp(\beta_0 + \beta_1 D + \beta_2 V + \beta_3 DV + \beta_4 D^2 + \beta_5 V^2 + \beta_6 D^3 + \beta_7 V^3))$, where N = normalizing term; D = water column depth; V = average water column velocity; and $\beta_0, \beta_1, \beta_2, \ldots$ = equation coefficients. These curves were combined with outputs from the detailed hydrodynamic models to estimate how habitat varies over a range of discharges (Miller *et al.*, 2003).

Hydrodynamic model

A modified IFIM approach was used to quantify the availability of water depths and velocities in each study reach for various flows of interest (Miller *et al.*, 2003). This methodology uses a combination of georeferenced field data (i.e. habitat use assessments), habitat suitability criteria (i.e. habitat suitability functions) and a 2D river hydraulic simulation model in a GIS. Model outputs provide a quantitative characterization of habitat throughout the reaches and illustrate the spatial variability of habitat at various discharge rates. The Flathead River hydrodynamic model was run and calibrated for 10 discharges (105, 127, 169, 226, 246, 283, 339, 424, 597 and 849 $\mathrm{m^3\,s^{-1}}$) and field verified at multiple flows.

Two-dimensional hydraulic modelling

Hydraulic modelling was conducted to simulate the changing hydraulic characteristics of the study segments at various flow rates (Miller *et al.*, 2003). Variations in the hydraulic character were then related to the species hydraulic preferences and used to assess habitat availability. RMA2 (U.S. Army Corps of Engineers (ACOE) Vicksburg, MS, USA) (King, 1990) and Surface-water Modeling System's (SMS; U.S. Army Corps of Engineers (UCOE) Vicksburg, MS, USA) preprocessing and postprocessing software were used to model the river hydraulic characteristics in the Flathead River. Detailed measurements of depth and velocity were collected in each segment using a forward-scanning Doppler profiler, whereas survey-grade GPS (0.03 m accuracy) provided x and y locations and elevations for the digital terrain models. Other field data necessary for the hydraulic simulations included the following: bathymetry data, water discharge(s) entering the stream reach, water surface elevation throughout and at the downstream end of the reach and channel roughness estimates. With this data, RMA2 simulated the depth-averaged velocities in the x and y directions at every node within a finite element mesh.

Geographic information system model and weighted usable area

The GIS model integrates hydraulic data simulations and habitat suitability data in a spatial framework to estimate usable habitat at various flow rates (Miller Ecological Consultants, Inc., Spatial Sciences and Imaging, 2003). The habitat suitability equations (Table I) combined with the georeferenced output from the hydraulic data sets produce habitat use values, which are calculated based on the depth and the velocity predicted at each point within the site. Each spatially referenced 2-$\mathrm{m^2}$ cell has an associated HSI value, which allows for a qualitative comparison of habitat suitability within a GIS. HSI scores range from 0 to 1.0, where values equal to 0 represent unsuitable habitat and values equal to 1.0 represent the highest quality habitat. The total usable habitat area ($\mathrm{m^2}$) in each reach was quantified by the summation of the product of area and HSI value of each cell at selected discharge rates. Each reach-specific total area was standardized by reach length (km) to produce a weighted usable area (WUA) ($\mathrm{m^2\,km^{-1}}$), which is defined as usable habitat available at the select discharge rate within each reach. This process was repeated for all species and life stages in each reach at the 10 flows of interest. The evaluation of available habitat at each discharge results in a habitat–flow relationship (i.e. WUA versus discharge curve) for each species, which is then used as the data input for the habitat time series analysis.

Identifying the most sensitive species and life stage

One of the most common methods for conducting this type of instream flow analysis is to base the assessment on a single species and life stage that is most sensitive to changes in flow. We used this approach for the habitat time series analysis while attempting to minimize potential adverse impacts to other species and life stages. In many situations, improvements in the primary target's habitat can be achieved while retaining adequate habitat availability for other species and life stages. This approach is called ‘keystone’ or ‘cornerstone’ species analysis (Bovee, 1986).

As part of the ‘keystone’ approach, seasonal and diel WUA versus discharge relationships for adult bull trout, subadult bull trout and westslope cutthroat trout were

DOI: 10.1002/rra

Table I. Telemetry and snorkel data were used to develop seasonal site-specific habitat suitability functions for each species and life stage in each study reach

Species	Life stage	Season(s)	Reach	Period	Method	Sample size	r^2
Bull trout	Subadult	Fall and winter	1 and 2	Night	Radiotelemetry	62 obs, 12 fish	0.99
HSI = (1/39.7878) exp(−((−2.944924) + (4.95138D) + (−17.72043V) + (−0.5488206DV) + (−3.746975D^2) + (39.7878V^2) + (1.056424D^3) + (6.828736V^3))							
Bull trout	Subadult	Fall and winter	1 and 2	Day	Radiotelemetry	300 obs, 33 fish	0.93
HSI = (1/30.81154) exp(−((0.689862) + (−1.87937D) + (−13.2634V) + (0.0801644DV) + (0.4020176D^2) + (30.81154V^2) + (−0.0220096D^3) + (−15.90897V^3))							
Bull trout	Adult	Fall and winter	1 and 2	Day	Radiotelemetry	373 obs, 23 fish	0.97
HSI = (1/10.2655) exp(−((1.141814) + (−4.833177D) + (−3.476033V) + (0.1908487DV) + (1.738853D^2) + (−4.079766V^2) + (−0.156164D^3) + (10.2655V^3))							
Westslope cutthroat trout	Juvenile and adult	Fall and winter	1	Day	Radiotelemetry	153 obs, 27 fish	0.9
HSI = (1/6.18764) exp(−((−1.5048) + (−1.08667D) + (−3.086353V) + (−1.248964DV) + (0.592707D^2) + (1.636417V^2) + (−0.0382413D^3) + (6.18764V^3))							
Westslope cutthroat trout	Juvenile and adult	Fall and winter	2	Day	Radiotelemetry	150 obs, 17 fish	0.88
HSI = (1/−60.0161) exp(−((3.13705) + (−2.297913D) + (20.58693V) + (−1.4665DV) + (1.00676D^2) + (−60.0161V^2) + (−0.0773899D^3) + (55.1524V^3))							
Westslope cutthroat trout	Juvenile and adult	Summer	1	Day	Snorkelling	143 obs	0.88
HSI = (1/−75.9382) exp(−((−5.0705) + (−2.152625D) + (34.20934V) + (2.34565DV) + (0.334153D^2) + (−75.9382V^2) + (0.0015202D^3) + (48.8566V^3))							
Westslope cutthroat trout	Juvenile and adult	Summer	2	Day	Snorkelling	63 obs	0.98
HSI = (1/14.84984) exp(−((4.484183) + (−5.51542D) + (−10.3783V) + (−1.85533DV) + (1.30197D^2) + (14.84984V^2) + (0.393951D^3) + (−3.985407V^3))							

Habitat suitability equations were constructed by fitting polynomial regression models to frequency distributions for paired depth and velocity observations (obs).

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evaluated for each reach at the 10 flows of interest. Exponential decay functions were fit to these data to examine the rate of change in habitat (slope), as flow increases, and strength (model fitness) of the relationship between discharge and habitat (PROC REG, SAS version 9.2; SAS Institute Inc., Cary, NC, USA). This sensitivity analysis was used in combination with site-specific data and other qualifying characteristics of ecological importance to select the 'keystone' species. After the selection was made, a generalized linear model was used to determine the effect of different reaches on habitat for the 'keystone' species, and time series model outputs for reaches 1 and 2 were aggregated based on these results (PROC GLM, SAS version 9.2).

Habitat time series

Instream flow assessments can be used to explore the potential limiting conditions for specific species and life stages through the application of habitat time series. The habitat time series extension of the IFIM simulates the temporal predictions of habitat availability, an important step when examining the long-term impacts on fish and invertebrate populations. This process is the decision point in IFIM because it allows for comparisons of flow management regimens, which can be used to inform future management decisions. The premise of habitat time series analysis is that habitat is a function of streamflow and that streamflow varies over time. Therefore, to conduct the habitat time series analysis, we obtained a baseline (predam) time series and five alternative postdam time series of flows (1953–2008) in the main-stem Flathead River. Mean daily discharge rates from 1929 to 2008 were used to interpolate daily usable habitat quantities from the habitat versus flow function (i.e. WUA versus discharge curves). We used these model outputs to investigate the temporal and spatial arrangement of available habitats under the flow management strategies used from 1929 to 2008.

Continuous mean daily discharge data from USGS gauging station 12363000, on the Flathead River at Columbia Falls, Montana, were grouped into six flow management periods, all of which varied in terms of time, magnitude, frequency and duration of flows resulting from alternative management strategies. We assumed that channel morphology and habitat suitability remained constant over all periods. Management periods were classified as follows:

Period 1 (Predam, 1929–1952)—Period 1 represents natural flow conditions in the Flathead River before the installation of Hungry Horse Dam in 1952. The natural flow regimen is characterized by high spring flows in late May or early June associated with snowmelt, followed by stable base flow conditions in the late summer, fall and winter. The number of days with flows exceeding 20% change from the previous day ranged from 9 to 33 days per year.

Period 2 (1953–1968)—Period 2 is the first postdam management period. The Hungry Horse Reservoir reached full pool for the first time in 1955, and dam discharges were adjusted experimentally during this time to fine tune dam capabilities and reservoir levels, producing erratic year-to-year changes. The number of days with flows exceeding 20% change from the previous day ranged from 40 to 113 days per year.

Period 3 (1969–1985)—Period 3 was a flow management period with sporadic and extreme hourly, daily and weekday flow peaking events for power generation and flood control. A minimum flow requirement of 99 $m^3 s^{-1}$ was implemented in 1982 (15 December through 15 April) to eliminate dewatering of resident kokanee (*Oncorhynchus nerka*) spawning areas. The number of days with flows exceeding 20% change from the previous day ranged from 58 to 160 days per year.

Period 4 (1986–1994)—In 1986, radical peaking of flow rates became more intermittent, weekly pulses became the norm and there were periods of relatively high stable flows in the fall and winter. Refill failures were common because of 4 years of drought conditions. The number of days with flows exceeding 20% change from the previous day ranged from 20 to 70 days per year.

Period 5 (1995–2000)—Late summer flow augmentation was initiated in 1995 to assist the out-migration of threatened Snake River fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River Basin (ISAB, 1997). Beginning in 1995, operational strategies attempted to fill the Hungry Horse Reservoir by 30 June and then draft 6.1 m by the end of August. The August release produced an unnatural second flow peak following the natural spring freshet. This differed substantially from the natural hydrograph, which historically had a gradual decline from peak flows in early June to basal low flows in late July. The number of days with flows exceeding 20% change from the previous day ranged from 20 to 75 days per year.

Period 6 (Mainstem Amendments, 2001–2008)—The operational strategy for summer flow augmentation changed in 2001 when the double peak was smoothed out to restore river flows closer to natural conditions. The new variable flow and system flood control strategy (Variable Flow; VARQ) (ACOE, 1999) was called for by the

DOI: 10.1002/rra

2000 Biological Opinions (BiOp) on the operation of the Federal Columbia River Power System by both the National Marine Fisheries Service (NOAA-Fisheries, 2000) and US Fish and Wildlife Service (USFWS, 2000). VARQ was intended to allow dam operators to store more water before run-off following a sliding scale based on water supply from low to high-water years. This allowed for spring flow augmentation without compromising reservoir refill probability and was intended to create a naturalized spring run-off (within flood constraints) while simultaneously protecting resident fish in the storage reservoir. In addition, a stable flow release requirement began in 2001 (15 September–15 December) to stabilize flows for spawning habitats of resident fish, requiring discharge rates to remain between 99 and 127 $m^3 s^{-1}$ for this late fall and early winter period. These operational changes coupled with prescribed flow ramping rates from the dam (USFWS, 2006; NOAA-Fisheries, 2008) are herein referred to as the 'Mainstem Amendments' or management period 6. The number of days with flows exceeding 20% change from the previous day ranged from 6 to 13 days per year.

Habitat magnitude and variability

The mean daily and mean monthly WUA values were calculated from the time series model outputs to compare predam and postdam flow management regimens. ANOVA was used to test for mean monthly differences in WUA among management periods and to identify the months with the largest variation in habitat availability due to management strategies (PROC GLM, SAS version 9.2). Welch's (1951) ANOVA was chosen for these tests because the data did not meet the assumptions of equal variance and group size across management periods required of standard ANOVA techniques. A *post hoc* multiple comparison test that assumes unequal variance (Games–Howell procedure) was used to test for mean monthly differences in WUA among postdam management periods. Period 1 was used as a baseline condition in the *post hoc* analysis and was contrasted to the five postdam flow management periods (PROC MIXED, SAS version 9.2). This allowed us to identify management regimens that best replicate natural flow conditions in the river, thereby maximizing critical habitat for the 'keystone' species.

Habitat duration

Habitat duration curves are particularly useful for assessing the impacts of alternative flow regimens and for examining habitat changes due to artificial influences. In the IFIM analytical process, habitat duration curves are used to represent the percentage of time a given habitat threshold is equalled or exceeded. We developed monthly and seasonal habitat duration curves for each management period by sorting the time series data and expressing each data point as a percentage of the total number of values. Cumulative frequencies were then ordered from minimum to maximum to create exceedance probabilities.

Habitat rate of change

The 2D hydrodynamic model allowed us to assess the influence of river discharge on WUA, as well as riffle habitat. We examined simulated flow scenarios between 100 and 850 $m^3 s^{-1}$ for WUA and riffle habitat. Riffle habitats are important for the production of aquatic invertebrates and are similarly affected by higher flow regimens (Brooker and Hemsworth, 1978; White *et al.*, 1981; Poff and Ward, 1991). Stable, low flows maximize habitat for macroinvertebrates and fish; therefore, maintaining the riffle and nearshore habitat through stable minimum flows will ultimately have a positive effect on fish community health and stream biodiversity. Riffle habitat was digitized using National Agriculture Imagery Program 2005 digital orthoimagery and verified by field GPS observations. The daily discharge value at the USGS Columbia Falls gauging station was 225 $m^3 s^{-1}$ during the aerial acquisition of orthoimagery, which was used in combination with velocity and depth ranges of >0.5 $m s^{-1}$ and <0.7 m, respectively, to define the riffle habitat. To further explore how increasing discharge rates influence usable and riffle habitat, we calculated the percentage change in the area at 50 $m^3 s^{-1}$ increments. This method was helpful to quantify the rate of habitat decline and to identify optimum flow scenarios, which maximize both usable habitat and riffle habitat, simultaneously.

RESULTS

Habitat use

Observed habitat use differed significantly among species and life stages of native salmonids inhabiting dam-influenced portions of the main-stem Flathead River during fall and winter (MANOVA, Wilks' lambda = 0.0221, $p < 0.0001$). Bull trout adults and subadults occupied daytime locations in deep, complex areas of the channel (i.e. runs and pools with large woody debris), whereas westslope cutthroat trout primarily used pools located along the channel margins. At night, subadult bull trout moved to shallow [mean depth = 1.0 m; standard deviation (SD), 0.7], low-velocity (mean = 0.22 $m s^{-1}$; SD, 0.16) shoreline areas of the river channel, presumably to feed (Muhlfeld *et al.*, 2003). ANOVA ($F = 9.912$, d.f. = 4,122; $p < 0.0001$) found

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that subadult bull trout used significantly deeper areas of the channel during the day and significantly shallower areas along the channel margins at night as compared with the adult bull trout and westslope cutthroat trout. No statistically significant differences ($p > 0.05$) in habitat use among reaches 1 and 2 were detected for subadult and adult bull trout; therefore, microhabitat data used in the habitat suitability models were combined for both reaches. MANOVA results also support no significant differences for subadult and adult westslope cutthroat habitat use in each reach; therefore, data were combined for these life stages (Table I). The site-specific habitat suitability functions modelled from the observed habitat use data and the associated metadata for each species and life stage are reported in Table I.

Identification of the most sensitive species and life stage

In both reaches, the available habitat is higher at lower discharge rates and lower at higher discharges (Figure 3). In addition, the WUA versus discharge relationship for subadult bull trout night-time habitat, grouping HSI values into three qualitative categories (low = $0.0 < \text{HSI} \le 0.3$, medium = $0.3 < \text{HSI} \le 0.7$ and high = $0.7 < \text{HSI} \le 1.0$.), shows a similar pattern of increased habitat availability at low flows (Figure 3). Exponential regression models fit to these data show that river discharge has a statistically significant ($p < 0.05$) negative effect on the availability of WUA, demonstrating that increased river flows rapidly reduce critical habitat for all species, seasons and life stages in both reaches (Table II). Specifically, the rate of habitat decline was greatest for night-time subadult bull trout habitat (reach 1: slope = −0.0022; reach 2: slope = −0.0025), indicating that the shoreline areas preferred by subadult bull trout at night are most sensitive to changes in river discharge, especially at lower flows. Declining exponential regressions for subadult bull trout night-time habitat in reach 1 ($y = 59\,511.7\ e^{-0.0022x}$) and reach 2 ($y = 110\,508.8\ e^{-0.0025x}$) suggest that the available habitat declines by approximately 11% with each 50 $m^3\ s^{-1}$ increase in discharge.

Aerial plan views of reach 1 (Figure 4) show that the spatial arrangement of night-time subadult bull trout habitat is more widely distributed through the channel at low flows as compared with high flows. As river discharge increases, subsequent increased velocities and depths reduce the total availability of habitat for subadult bull trout, with most of the usable night-time habitat located along the lower

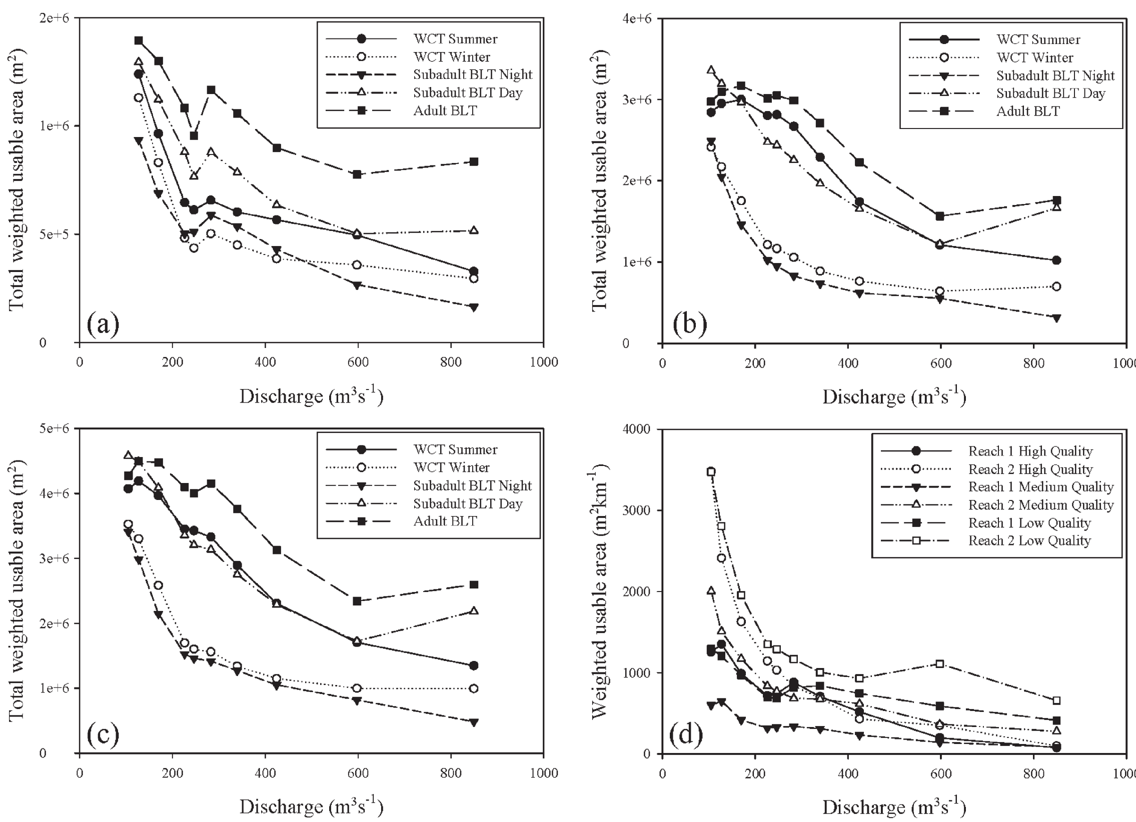

Figure 3. Weighted usable area versus discharge curves for each target species in reach 1 (a), reach 2 (b), and reaches 1 and 2 combined (c). The bottom right panel (d) summarizes the subadult bull trout night-time habitat by grouping the HSI values into three qualitative categories (low = $0.0 < \text{HSI} \le 0.3$, medium = $0.3 < \text{HSI} \le 0.7$, high = $0.7 < \text{HSI} \le 1.0$).

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Table II. Exponential regression model results including slope coefficients (b), standard errors (SE) and coefficients of determination (r^2) are estimated for all species and habitat types of interest in the main-stem Flathead River, Montana

Reach	Species	b	SE	d.f.	t-value	p-value	r^2
1	WCT summer	−0.0016	0.00027	1,8	−5.85	0.0040	0.8107
1	WCT winter	−0.0017	0.00041	1,8	−4.00	0.0040	0.6664
1	Subadult BLT night	−0.0022	0.00019	1,8	−11.77	<0.0001	0.9454
1	Subadult BLT day	−0.0013	0.00021	1,8	−6.07	0.0003	0.8216
1	Adult BLT	−0.0007	0.00016	1,8	−4.50	0.0020	0.7167
2	WCT summer	−0.0016	0.00015	1,8	−10.95	<0.0001	0.9375
2	WCT winter	−0.0017	0.00039	1,8	−4.39	0.0023	0.7068
2	Subadult BLT night	−0.0025	0.00037	1,8	−6.68	0.0002	0.8481
2	Subadult BLT day	−0.0012	0.00027	1,8	−4.36	0.0024	0.7042
2	Adult BLT	−0.0010	0.00017	1,8	−5.99	0.0003	0.8178

WCT, westslope cutthroat trout; BLT, bull trout.

velocity margins of the river channel and island complexes rather than in the main channel.

Combined, results show that the reduction in suitable nearshore habitat is especially detrimental to subadult bull trout, suggesting that this species and life stage is most sensitive to flow variability. Based on this sensitivity analysis, the site-specific movement information, the importance of night-time feeding habitat to subadults and the threatened status of the bull trout, we chose to base the time series analysis on the availability of channel margin habitat for subadult bull trout. Analysis of covariance, used to examine the effect of different reaches on usable habitat for subadult bull trout, shows that there is no significant difference in the slopes of the discharge/habitat relationship among the reaches at night ($F = 3.46$, $p = 0.0813$). Because the rate of habitat loss for subadult bull trout is equivalent among reach types, the time series analyses results were aggregated for reaches 1 and 2.

Habitat magnitude and variability

Time series results in Figure 5 show the mean daily WUA (±SD) and the mean daily percentage change of WUA for subadult bull trout habitat calculated for each flow regimen period. The daily change (variation) in WUA is greatly reduced in periods 1 (predam) and 6 (Mainstem Amendments), indicating that the most recent flow regimen (period 6) stabilized flows and usable habitat on a daily, monthly and seasonal basis, better than any other postdam management regimen, and was most consistent with natural, predam flow conditions. Radical peaking of flows and high variability in usable habitat during period 3 (1969–1984) is pronounced in this plot, as habitat variability is the highest of all management periods. Because discharge and habitat are highly negatively correlated (Table II) and small increases in discharge result in significant decreases in available habitat (see Habitat rate of change), variation in flow dramatically reduces the amount of usable bull trout habitat.

Mean monthly WUA values for subadult bull trout habitat were calculated for each management regimen. Comparison of management period means for each month supports the conclusion that natural predam flow conditions (period 1) maximize the quantity of available habitat for all summer, fall and winter months. The months of April, May, June and July are subject to high spring flows from snowmelt run-off from the Middle and North Forks, and flows from Hungry Horse Dam are released relatively constantly during these months. ANOVA results indicate that monthly means are not equal across management periods ($p < 0.05$) for any months (Table III). Specifically, the months of January, February, August and September had the greatest variation in habitat availability because of flow management, as evidenced by the larger F-values in Table III.

The Games–Howell *post hoc* comparison of means shows that period 6 has the smallest mean difference in WUA of all postdam management periods for the month of January, February, March, October, November and December, as compared with period 1 baseline conditions. This supports the conclusion that the Mainstem Amendments (period 6) simulate the natural flow conditions and maximize the critical subadult bull trout habitat better than all other postdam flow management regimens. Consistent with the ANOVA results, comparison of mean monthly WUA values for periods 1 and 6 shows that the largest monthly mean differences are late summer months and winter months. Specifically, late summer discharge rates (period 1: mean = 88.62 $m^3 s^{-1}$, SD = 38.11; period 6: mean = 163.23 $m^3 s^{-1}$, SD = 63.24) and WUA values (period 1: mean = 198 695.18 $m^2 km^{-1}$, SD = 35 417.06; period 6: mean = 135 881.34 $m^2 km^{-1}$, SD = 44 579.72) are significantly different for periods 1 and 6 ($t = -24.62$, $p < 0.0001$; $t = 28.29$, $p < 0.0001$). A two-sample t-test shows that discharge rates for periods 1 and 6 (period 1: mean = 64.78 $m^3 s^{-1}$, SD = 44.10; period 6:

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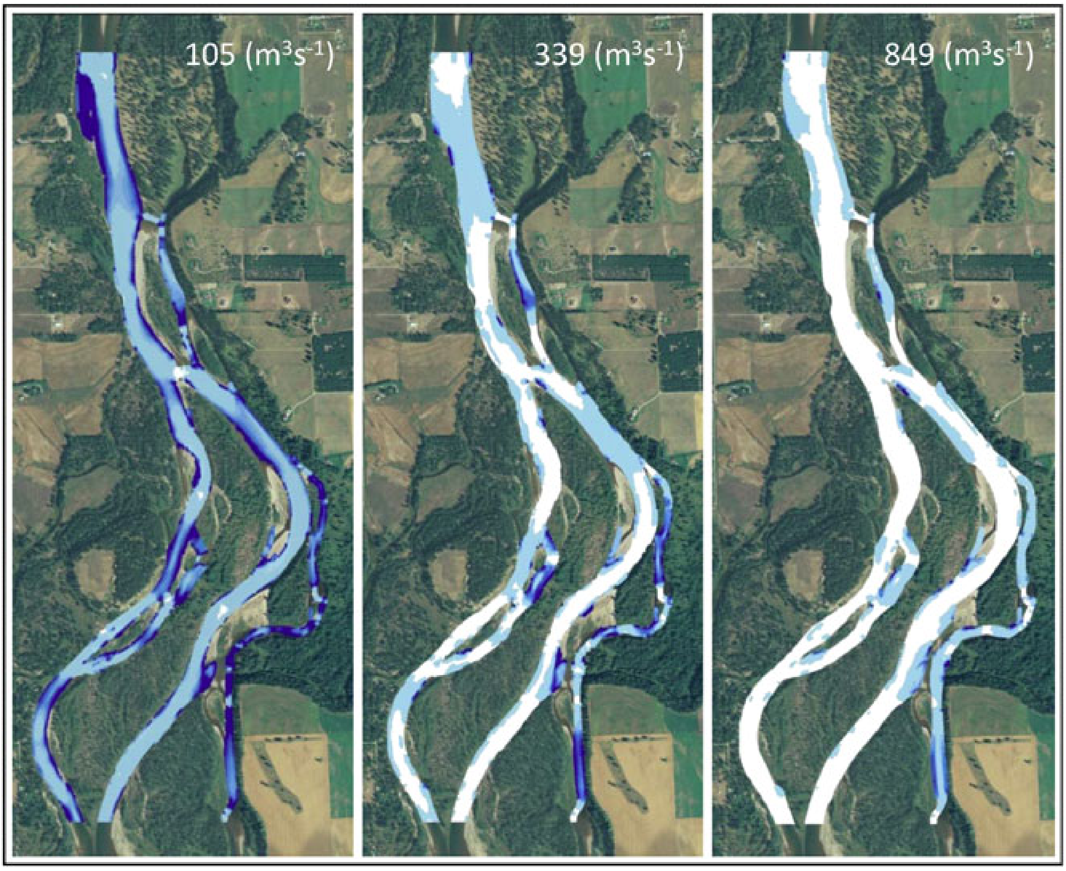

Figure 4. Reach 1 aerial views of night-time subadult bull trout habitat simulated at flows equal to 105 $m^3 s^{-1}$, 339 $m^3 s^{-1}$, and 849 $m^3 s^{-1}$. Darker blue represents higher quality habitat, and white represents unsuitable habitat.

mean = 119.87 $m^3 s^{-1}$, SD = 38.08) and WUA values (period 1: mean = 222 970.09 $m^2 km^{-1}$, SD = 36 200.35; period 6: mean = 169 813.18 $m^2 km^{-1}$, SD = 28 710.35) are significantly different for the winter months as well ($t = -26.18$, $p < 0.0001$; $t = 32.59$, $p < 0.0001$). Thus, late summer discharge rates under the Mainstem Amendments are significantly higher than natural flow conditions. Winter flows under the Mainstem Amendments are stable with low variability; however, mean discharge values are significantly higher than natural flow conditions resulting from the 99 $m^3 s^{-1}$ minimum flow requirement.

Habitat duration and rate of change

Seasonal and monthly habitat duration curves reveal that predam conditions not only maximize the quantity of habitat available but also sustain this quantity over the longest time during the summer, fall and winter periods (Figure 6). The winter habitat duration curves for each flow management regimen show that the Mainstem Amendments maintain the most consistent quantity of habitat (~3 500 000 m^2) over the longest period (~80%) compared with any other postdam management strategy. Periods 2 and 3 were able to supply more habitat than period 6 but failed to sustain this quantity over time. Winter and fall curves show that periods 1 and 6 maintain stable flow regimens that maximize habitat availability, whereas the curves for periods 2–5 demonstrate high variability in habitat caused by high variability in flows. Spring duration curves are similar among all flow regimens, which is expected because spring run-off is stored by Hungry Horse Dam, whereas natural run-off is occurring on the Middle and North Forks, producing high spring flows in the main-stem river. Summer duration curves indicate that the Mainstem Amendments do not maximize or sustain critical bull trout habitat during late summer as compared with natural flow conditions (Figure 6). Specifically, late summer drafting associated with the Mainstem Amendments produces higher discharges in the Flathead River, which decreases the amount of usable bull trout habitat.

Subadult bull trout WUA exponentially declines between 50 and 250 $m^3 s^{-1}$, with 46% of habitat loss occurring at flows from 100 to 200 $m^3 s^{-1}$ (Table IV). Riffle habitat is maximized at flows between 150 and 250 $m^3 s^{-1}$, and on average, there is a 40% loss of riffle habitat as flows increase

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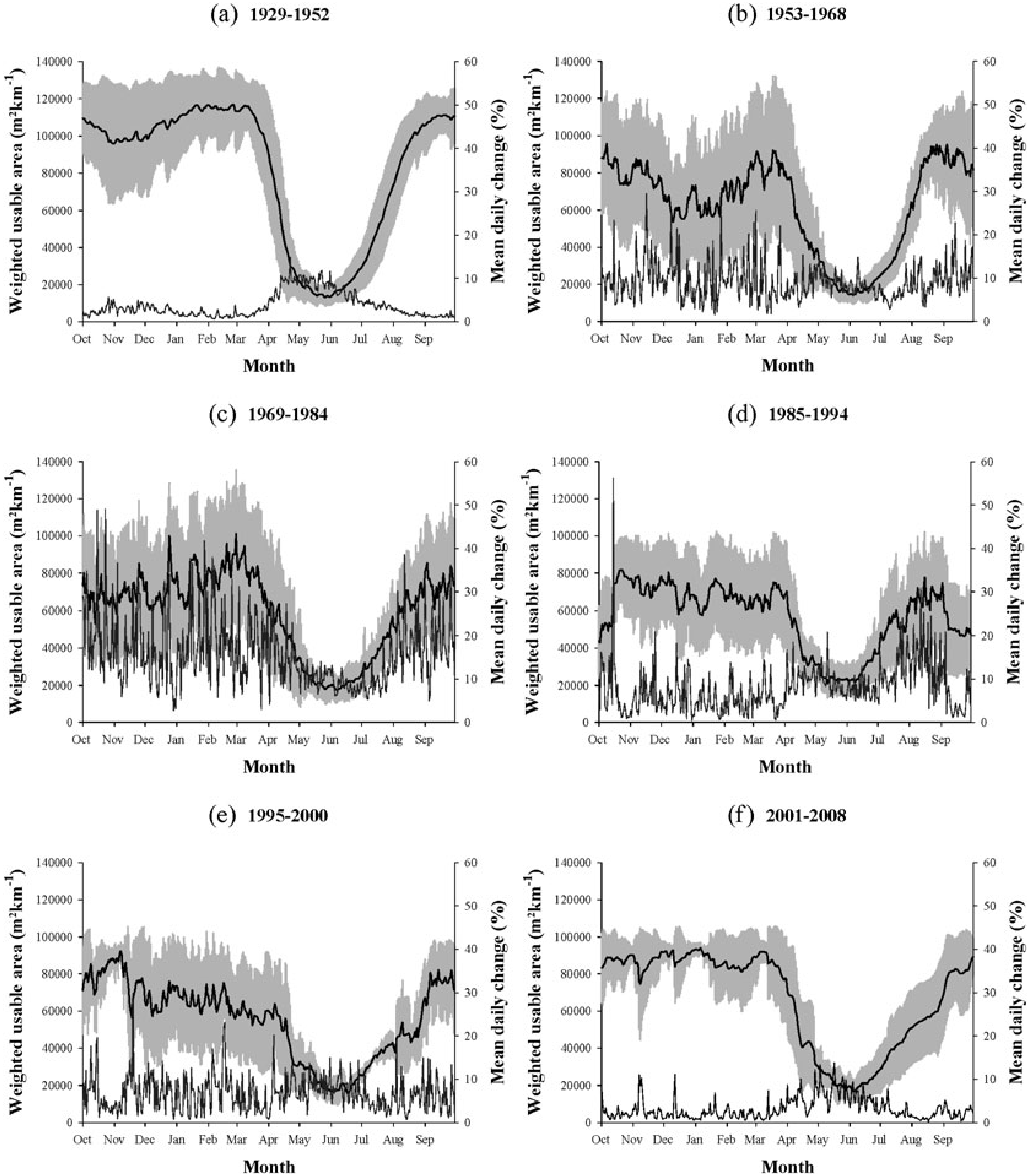

Figure 5. Mean daily weighted usable area (WUA) (±SD) time series results and mean daily percentage change (absolute values) of WUA for night-time subadult bull trout habitat calculated for each flow regimen period. The black line centred in grey is the mean daily WUA with one standard deviation (grey shading), and the single solid black line represents the mean daily WUA percentage change. Alternative flow regimens are as follows: period 1, predam, 1929–1951 (a); period 2, 1953–1968 (b); period 3, 1969–1984 (c); period 4, 1985–1994 (d); period 5, 1995–2000 (e); and period 6, Mainstem Amendments, 2001–2008 (f).

DOI: 10.1002/rra

Table III. Analysis of variance tests for differences in the mean quantity of night-time bull trout habitat available from each flow regimen management period

Month	d.f.	*F*-value	*p*-value
April	5,868	3.06	0.0095
June	5,840	42.74	<0.0001
July	5,954	59.35	<0.0001
November	5,878	73.43	<0.0001
May	5,828	88.48	<0.0001
October	5,934	154.91	<0.0001
December	5,905	227.84	<0.0001
March	5,870	246.58	<0.0001
August	5,864	314.65	<0.0001
February	5,776	358.21	<0.0001
January	5,874	383.2	<0.0001
September	5,775	516.46	<0.0001

Mean differences in management periods were tested for each month of the year.

from 200 to 400 $m^3 s^{-1}$. Thus, both riffle habitat and WUA are significantly higher at lower flows (<250 $m^3 s^{-1}$).

DISCUSSION

Conservation of river biodiversity and native biota requires understanding the impacts of flow regulation on critical habitats and populations. Several studies have shown that dam operations have profound effects on anadromous fishes, yet before this study, few studies have examined the impacts of flow management strategies on native salmonid habitats in the upper Columbia River Basin. Habitat time series analyses comparing the natural flow regimen to five postdam flow management strategies indicate that sporadic flow fluctuations were likely detrimental to native salmonid populations. Time series results show that the current management strategy simulates natural flow conditions and maximizes critical subadult bull trout habitat better than all other postdam periods. Late summer flow augmentation for anadromous fish recovery, however, produces higher discharges in the river, which reduces the amount of suitable bull trout habitat. Combined, these data indicate that unnatural flow modifications negatively impact resident fish habitats and suggest that natural flow management strategies that stabilize and maximize the availability of channel margin habitats are beneficial to the resident fishes in the upper Columbia River Basin.

Populations of bull trout and westslope cutthroat trout in the headwaters of the Columbia River Basin are of national and international conservation concern. Recovery programmes have focused on maintaining natural habitat connections, providing a diversity of complex habitats over a large spatial scale, to conserve the full expression of life history traits and metapopulation persistence. Our habitat use results from this study and companion studies (e.g. Muhlfeld *et al.*, 2000; Muhlfeld *et al.*, 2003; Muhlfeld and Marotz, 2005) illustrate the importance of the dam-influenced portion of the Flathead River to migratory bull trout and westslope cutthroat trout populations. Furthermore, our study provides a better understanding of the impacts of dam operations on critical riverine habitats, which may be used to inform recovery and management programmes and predict how water resource management decisions influence populations in the upper Columbia River Basin and other similar freshwater systems.

Habitat time series analyses comparing the natural flow regimen to five postdam flow management strategies indicate that stable flow releases during the low-flow periods provide more habitat than variable flow management regimens. These results are consistent with many studies that have shown that dam operations that produce fluctuating or abnormally high discharges disrupt fluvial processes and modify biological characteristics (Ward and Stanford, 1979; Cushman, 1985; Poff *et al.*, 1997). Our study complements other studies in the Flathead River that have shown that flow regulation has dramatically altered the physical characteristics of the riverine environment and lower trophic levels of the aquatic ecosystem (Stanford, 1975; Stanford and Hauer, 1978; Hauer and Stanford, 1982; Fraley and Graham, 1982; Fraley and Decker-Hess, 1987; Beattie *et al.*, 1988; Hauer *et al.*, 1994; Christenson *et al.*, 1996; Hauer *et al.*, 1997; Marotz *et al.*, 1999) by quantifying fish habitat changes in the river.

This study provides evidence that sporadic flow fluctuations negatively impact lateral areas of the channel and are likely detrimental to bull trout populations. In a companion study, we evaluated the diel habitat use and movements of subadult bull trout in the regulated reaches of the Flathead River (e.g. reaches 1 and 2 in this study) and found that radio-tagged fish commonly moved from deep, mid-channel areas during the day to shallow, low-velocity areas along the channel margins without overhead cover at night (Muhlfeld *et al.*, 2003). Diel shifts in habitat use have been reported for other populations of bull trout (Baxter and McPhail, 1997; Goetz, 1997; Banish *et al.*, 2008) and are common for other stream-dwelling salmonid species, including juvenile westslope cutthroat trout and mountain whitefish (C. Muhlfeld, unpublished data). Furthermore, exponential regressions fit to the discharge/habitat relationship showed that subadult bull trout habitat is the most sensitive species and life stage to changes in flow. Similarly, using life stage population modelling, Staples (2006) found that the population growth rate of the bull trout population in the upper Flathead River was most sensitive to changes in subadult survival rates. Thus, the habitat changes observed in this study may lead to potential changes in survival of

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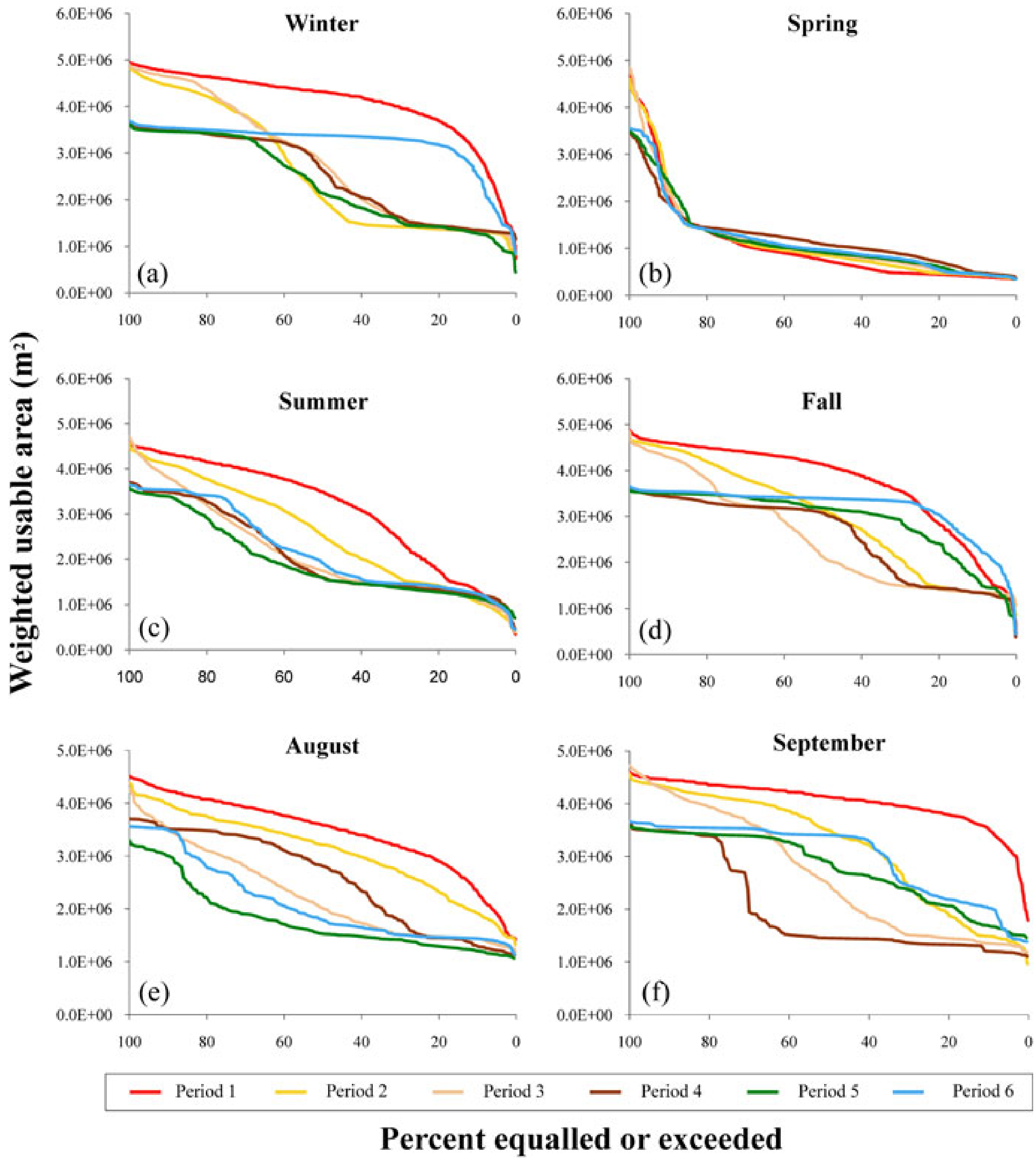

Figure 6. Seasonal habitat duration curves, winter (a), spring (b), summer (c), fall (d) and monthly duration curves, August (e) and September (f), are shown for subadult bull trout night habitat in the upper Flathead River, Montana. Alternative flow regimens are as follows: period 1, predam, 1929–1951; period 2, 1953–1968; period 3, 1969–1984; period 4, 1985–1994; period 5, 1995–2000; and period 6, Mainstem Amendments, 2001–2008.

native fishes. Future work is needed to more closely link changes in habitat conditions with population demography.

Our results suggest that dams should be operated to achieve more natural flow conditions for the recovery of native resident fishes in the headwaters of the Columbia River and may have broader implications for other bull trout and westslope cutthroat trout populations that inhabit large rivers below hydroelectric projects. For example, bull trout occupy several tailraces of the upper Clark Fork, Kootenai, Snake and Columbia Rivers (Rieman *et al.*, 1997; Swanberg, 1997; Homel and Budy, 2008; Monnot *et al.*, 2008), which are likely affected by flow fluctuations for hydropower generation and summer flow augmentation in a similar fashion to that of the Flathead River bull trout population. Our IFIM approach provides a useful tool for managers interested in balancing the needs of native resident fishes with hydropower production, flood risk management and summer flow augmentation for anadromous fish

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Table IV. Simultaneous evaluation of riffle habitat and WUA available to bull trout in the main-stem Flathead River, Montana

Discharge ($m^3 s^{-1}$)	WUA ($m^2 km^{-1}$)	Riffle habitat ($m^2 km^{-1}$)	WUA % change	Riffle habitat % change
100	186 937.59	9 452.24	—	—
150	136 120.05	12 005.21	−27.18	27.01
200	97 465.67	12 178.03	−28.40	1.44
250	78 310.36	12 179.13	−19.65	0.01
300	74 202.20	11 323.39	−5.25	−7.03
350	67 257.72	9 647.25	−9.36	−14.80
400	60 223.51	7 334.28	−10.46	−23.98
450	54 874.12	6 455.97	−8.88	−11.98
500	51 176.21	6 410.98	−6.74	−0.70
550	47 478.29	6 482.01	−7.23	1.11
600	43 787.03	6 257.81	−7.77	−3.46
650	40 230.64	5 598.96	−8.12	−10.53
700	36 674.25	4 952.65	−8.84	−11.54
750	33 117.86	4 141.10	−9.70	−16.39
800	29 561.48	3 352.27	−10.74	−19.05
850	26 034.04	2 665.97	−11.93	−20.47

Riffle habitat and WUA are compared at 50 $m^3 s^{-1}$ intervals for discharge rates ranging from 100 to 850 $m^3 s^{-1}$.
WUA, weighted usable area.

recovery. Other studies have used similar approaches to assess the impacts of flow modifications on salmon spawning, rearing and migration corridors in the lower Columbia River (Tiffan *et al.*, 2002; Dauble *et al.*, 2003; Hatten *et al.*, 2009) and in other freshwater systems throughout the world (Freeman *et al.*, 2001).

Flow ramping rates

Our IFIM approach provides empirical data for managing seasonal river flows and ramping rates because it quantifies the total availability of suitable fish and riffle habitat at various flows of interest. Ramping rates prescribed for the Flathead River (USFWS, 2006; NOAA-Fisheries, 2008) are designed to restore flood plain function and reduce the deleterious effects on biological production by minimizing the impacts of flow changes on aquatic organisms that use the varial zone (Jamieson and Braatne, 2001). Spring dam discharges are gradually ramped down following the spring freshet and stabilized, and daily and hourly maximum ramp-down rates are more gradual than ramp-up rates and are more gradual (~17 $m^3 s^{-1} h^{-1}$) at lower flows (<227 $m^3 s^{-1}$). We found that small increases in river discharge markedly reduce the availability of usable bull trout habitat, and these changes are more pronounced at lower flows. For example, a discharge increase from 100 to 150 $m^3 s^{-1}$ results in 1 870 102 m^2 of habitat loss (in reaches 1 and 2) and suggests that flow increases below 250 $m^3 s^{-1}$ affect greater proportions of available habitat for bull trout and macroinvertebrate production. Thus, these data support the current 250 $m^3 s^{-1}$ threshold and sensitivity to ramp-down rates.

Summer flow augmentation

Recovery programmes for salmon and steelhead stocks have called for late summer flow augmentation intended to assist with the out-migration of smolts in the lower Columbia River (ISAB, 1997; USFWS, 2000, 2006; NOAA-Fisheries, 2000, 2008). In an attempt to reduce adverse impacts to resident fish, the most current objective of the summer operation strategy is to mimic the natural spring run-off event, within flood constraints, gradually reducing dam discharge toward stable flows for the biologically productive summer and fall periods. Our data indicate that smoothing the discharge is beneficial to river biota because the width of the unproductive varial zone is reduced, which provides suitable habitat for native fish and invertebrate communities. However, summer flow augmentation produces higher flows during late August and early September in the Flathead River, which significantly reduces the quantity and availability of bull trout and westslope cutthroat trout habitat. Food web dynamics of the river environment are also severely affected by higher variable flows, causing significant impacts to the aquatic ecosystem (Perry *et al.*, 1986; Stanford and Hauer, 1992).

The scientific rationale for late summer flow augmentation in the main-stem Columbia River has been controversial. The BiOp (USFWS, 2000, 2006; NOAA-Fisheries, 2000, 2008) concluded that flow augmentation was necessary because slow water movement and high water temperatures at that time of year negatively impact the endangered salmon and steelhead. Biologists in the headwater areas found that the impacts of reservoir drawdowns on resident fisheries are

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substantial (Marotz *et al.*, 1996; Marotz *et al.*, 1999). Although flow augmentation is assumed to have a positive survival and migratory benefit for summer migrants, such as Snake River fall Chinook salmon, this has not been empirically shown. Any potential benefits of flow augmentation on anadromous salmon should be weighed against the deleterious effects of augmentation on resident trout habitat in the upper basin.

CONCLUSIONS

Our data demonstrate that unnatural flow management regimens (for power production, flood risk management and flow augmentation) negatively impact bull trout and westslope cutthroat trout habitats in the headwater reaches of the Columbia River Basin. Our data provide empirical support for the BiOp, which recommend that Hungry Horse Dam operate conservatively, releasing stored water gradually over the summer, fall and winter months to avoid unnatural flow fluctuations. However, summer flow augmentation for anadromous fish recovery unnaturally increases flows during August and September, thereby reducing the amount of usable fish habitat in the Flathead River. Our results suggest that the river ecosystem would benefit by stabilizing flows and restoring the natural flow regimen during late summer months.

The natural flow paradigm provides an ecological view on water management that recognizes the complex relationships between the flow regimen and ecosystem function (Poff *et al.*, 1997; Richter *et al.*, 1997; Petts, 2009). We used an instream flow model coupled with site-specific fish habitat use data to evaluate how the critical components of the natural flow regimen (e.g. magnitude, frequency, duration, timing and rate of change of hydrologic conditions) affect the availability of usable habitat among several flow management strategies. Our results suggest that past flow management policies that created sporadic flow fluctuations were likely detrimental to native salmonid habitats. Our analyses demonstrate that natural flow regimens stabilize and maximize the availability of channel margin habitats and are likely beneficial to the recovery and conservation of rare and threatened salmonids in the upper Columbia River Basin. Modification of the Hungry Horse Dam operating regimen to approach the natural flow regimen as much as possible under the current management constraints will improve the chances of protecting key ecosystem processes and help to maintain and restore the threatened bull trout and westslope cutthroat trout populations.

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