

**Columbia River Project Water Use Plan
Columbia White Sturgeon Management Plan**

**Lower Columbia River Planning and Assessment of WSG
Turbidity**

Implementation Year 1

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Recruitment history of upper Columbia white sturgeon (*Acipenser transmontanus*) and potential causes of recruitment collapse

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Introduction

White sturgeon are part of an ancient lineage of fishes consisting of 27 living species, virtually all of which are a conservation concern (Birstien 1993; Pikitch et al. 2005). As a result of biological characteristics including longevity, late maturity, high economic value, and low population growth rates many species are endangered due to overfishing and anthropogenic habitat change. Widespread anthropogenic alteration of large river habitats occupied by sturgeon has contributed to population declines for most species (Birstien 1993; Raspopov et al. 1994; Billard and Lecointre 2001; Pikitch et al. 2005). Identified impacts include decreased connectivity (Auer 1996a), temperature change (Bevelheimer 2002; Paragamian and Wakinen 2002), pollution (Bennett and Farrel 1998; Hatfield et al. 2004; Woodland and Secor 2007), and other direct and indirect impacts of flow regulation (Votinov and Kasyanov 1978; Auer 1996b).

Limited natural recruitment (or recruitment failure) has been identified for a number of sturgeon species (e.g. Raspopov et al. 1994; Kynard 1997; Woodland and Secor 2007; Paragamian et al. 2005; McAdam et al. 2005). In the Upper Columbia River (UCR) persistent recruitment failure over the last 30-40 years indicates that extirpation could occur within 1 generation without intervention (Wood et al. 2007). While hypothesized impacts including increased predation, changes to benthic substrates, and contaminant effects have been proposed as potential causes (UCWSRI 2002; Gregory and Long 2008), recovery action continues to be limited by our limited understanding of causal mechanisms. Coutant (2004) hypothesized that the loss of riparian egg attachment sites was the likely cause of recruitment failure. In contrast, a temporal correlation between recruitment failure and substrate change in the Nechako River (McAdam et al. 2005) and the abundance of sand associated with current spawning sites in the Kootenai River (Koch 2006; Paragamian et al. 2009) both suggest the importance of substrate condition. The continued absence of clear diagnostic data in the UCR, combined with significant conservation and economic consequences of misdiagnosis, support the need for a diagnostic analysis specifically addressing this population.

Previous retrospective analyses of sturgeon recruitment failure have been based on case studies that are comparatively simpler (e.g. the presence of a single dam and no dykes in the Nechako; McAdam et al. 2005) or on readily observed impacts (e.g. sand inundation effects on eggs in the

Kootenay River; Paragamian et al. 2005, 2009; Koch et al. 2006). In contrast, white sturgeon in the upper Columbia River are potentially affected by over 15 dams within the principal influent watersheds of the Columbia, Kootenay and Pend d'Oreille rivers (Table 1). The large storage reservoirs impounded by Hugh Keenleyside Dam (completed 1968) and Libby and Mica dams (1974) have led to substantial changes in the upper Columbia River hydrograph. A variety of environmental impacts have been identified (BC Hydro 2005; Utzig and Schmidt 2011), including effects on temperature (Hamblin and McAdam 2003; Tiley 2006), hydraulic conditions (Fissel and Jiang 2007; Northwest Hydraulics 2007) dissolved gas supersaturation (or elevated total gas pressure, TGP) (R. L. & L. 1995; CRIEMP 2005, 2008). In addition, industrial activities including a pulp mill (since 1961) and a lead zinc smelter (since 1910), affect water quality due to the release of liquid effluents and historical releases of metallurgical slag (CRIEMP 2008). Due to the abundance of anthropogenic changes identifying the origin and timing of impacts and their potential relationship to white sturgeon recruitment presents a substantial challenge.

Diagnostic analysis of recruitment failure is particularly challenging in UCR due to:

- A lack of obvious candidate impacts
- Greater variety of environmental changes (especially compared to the Nechako)
- Data limitations for potentially important variables
- Uncertainty in estimated ages (little apparent effect in Nechako and not a central component of the Kootenai diagnosis)
- Population substructure (not present for Nechako or Kootenay)
- Deeper incised river channel with more limited understanding of benthic habitats
- Less severe level of impact based on greater larval captures relative to the Nechako or Kootenay rivers

Ideally diagnosis of the causes of population declines precedes restorative action, however, determining causation of historical ecosystem changes is complex due to the limited availability of historical data and the *ad hoc* nature and lack of replication in retrospective evaluations (Beyers 1998; Fabricius and De'ath 2004; Suter 2007). For sturgeon in particular the combination of biological uncertainty and the high costs of restorative action in large rivers (e.g. flow restoration) add further complexity.

In many cases recovery planning documents often contain an extensive list of potential impacts without a means to evaluate their relative importance (e.g., Williot et al. 2002; Hatfield et al. 2004; Wildhaber et al. 2011; Zhang et al. 2011) however, two previous weight-of-evidence evaluations have examined white sturgeon recruitment failure (Coutant 2004; Gregory and Long 2008). Although Coutant's (2004) analysis led to a specific hypothesis, he also readily acknowledged that his undertaking was based on relatively limited data in many cases. Subsequent evaluation based on professional judgment (Gregory and Long 2008) showed relatively limited differentiation between 5 broad hypotheses (only one was deemed unlikely). Relative to prior studies (Coutant 2004; Gregory and Long 2008) the principle difference in the present study is that population structure and temporal patterns in hindcasted recruitment are explicitly considered. Spatial and temporal contrast in recruitment patterns offer the potential for clearer differentiation of hypothesized mechanisms based on population-specific data.

Study population background

The main study area is the transboundary reach of the Columbia River between Hugh Keenleyside Dam and Lake Roosevelt (impounded by Grand Coulee Dam) (Figure 1). The small group of white sturgeon within Arrow Lakes Reservoir is also relevant to this analysis due to its genetic similarity with fish immediately downstream of Hugh Keenleyside Dam (Nelson and McAdam 2012). Both groups likely used the same spawning location historically, based on their genetic similarity (see Welsh et al. 2008), and evaluation of fin ray chemistry (Clarke et al. 2011) suggest spawning was more likely located upstream of Hugh Keenleyside Dam. The term upper Columbia River (UCR) white sturgeon will be used herein to refer to white sturgeon in both areas, whereas transboundary white sturgeon will refer only to fish in the transboundary reach.

Low juvenile white sturgeon abundance was identified in the early 1990s based on shifts in the size composition relative to sampling in the 1980s (Hildebrand et al. 1999; Irvine et al. 2007). The population estimate for the Canadian portion of the transboundary reach was 1,157 (95% confidence interval (CI) = 414-1900) in 2004 (Irvine et al. 2007), and 52 fish (95% CI = 37-92) were estimated to reside in Arrow Lakes Reservoir (Golder 2006d). The population estimate for the American portion of the transboundary reach was 2,037 (95% CI = 1093-3223) in 2005 (Howell and McLellan 2007), and those fish primarily reside between the upper section of Lake Roosevelt upstream to the international border.

The Waneta spawning site at the confluence of the Pend d'Oreille and Columbia Rivers was identified in 1993 (R. L. & L. 1994; Figure 1), and spawning has been detected in all years sampled (e.g., Golder 2005a, 2010). Spawning has since been detected in Washington State at sites near Northport and China Bend (Figure 1), and eggs, yolksac larvae and feeding larvae have all been detected (Howell and McLellan 2007, 2009, 2011). The more recent captures of yolksac larvae immediately downstream of Castlegar (Golder 2010) and downstream of Arrow Lakes Generating Station (ALGS) tailrace (Terraquatic Resource Management 2011) suggest two additional spawning locations. Egg mat sampling has also confirmed that white sturgeon residing in Arrow Lakes Reservoir spawn in the mainstem Columbia River near Revelstoke (Golder 2006d). Based on the confirmation of egg viability at multiple spawning sites, the present analysis assumes that recruitment failure results from increased mortality subsequent to fertilization. The survival of ten-month-old hatchery progeny (Golder 2006b) also indicates that mechanisms causing recruitment failure occur prior to that size/age of released fish.

Four high-use habitat areas have been identified (R. L. & L. 2001; Howell and McLellan 2007), and individuals show high fidelity to particular habitats based on analysis of growth (van Poorten and McAdam 2010), fin ray chemistry (Clarke et al. 2011) and movement and genetics (Nelson and McAdam 2012). These groups likely represent remnant population structure derived prior to river regulation (Nelson and McAdam 2012). However, due to uncertainty about contemporary genetic mixing (i.e. whether they continue to be discrete populations) and uncertainty associated with defining stocks (see Waples and Gaggiotti 2006; Kell et al. 2009), these spatially defined groups are simply referred to as groups in the present analysis.

Study goals and analytical approach

This retrospective analysis of white sturgeon recruitment failure in the UCR was intended to evaluate hypothesized causes, and provide guidance to future restoration. The selection of a weight-of-evidence approach was influenced both by the availability of historical environmental data and biological uncertainty (e.g., drift behaviour of larvae, McAdam 2011, 2012). Similar to previous analyses (McAdam et al. 2005; Paragamian et al. 2005), the present approach uses the present age structure to 'hindcast' past recruitment using virtual population analysis (Hilborn and Walters 1992). Subsequent identification of breakpoints in the recruitment time series (Anderson et al. 2008; Zeileis et al. 2002, 2003) provided a standardized approach for estimating the timing of recruitment failure. It is important to note that the present analysis focused specifically on recruitment failure rather than environmental forcing of recruitment variation (see LeBreton et al. 1999; Shaw et al. 2012).

The effects of aging inaccuracy were also evaluated to identify potential implications on the recruitment failure diagnosis. Due to potential inaccuracy (Paragamian and Beamesderfer 2003) and imprecision (Rien and Beamesderfer 1994), caution is often urged in the use of sturgeon age estimates (Rien and Beamesderfer 1994; Rossiter et al. 1995). However, despite these concerns, previous evaluations (e.g., LeBreton et al. 1999; McAdam et al. 2005; Paragamian et al. 2005; Woodland and Secor 2007; Smith et al. 2012) suggest that aging error may not be severe in all cases. Because population-specific age validation is not available for the UCR, aging accuracy scenarios (no, low and high inaccuracy) were evaluated based on age validation studies of white sturgeon and lake sturgeon (*Acipenser fulvescens*) (see Brennan and Caillet 1991; Paragamian and Beamesderfer 2003; Bruch et al. 2009).

Due to the prior development of clear hypotheses (e.g., Hatfield et al. 2004; Gregory and Long 2008) and the greater variety of environmental changes, a more structured process was utilized relative to similar prior evaluations (e.g. McAdam et al. 2005; Paragamian et al. 2005; Woodland and Secor 2007). First, the timing of recruitment failure for both individual groups and an aggregated population was estimated, including potential aging error effects. Group-specific estimates of recruitment failure timing were then compared with the timing of major anthropogenic changes in the watershed (e.g., dams, pulp mill, smelter) and available environmental monitoring data. Even though such comparison are limited to the identification of temporal correlations, they also provide important contextual information regarding the variety of anthropogenic changes in the UCR.

The final component of the study evaluated 11 recruitment failure hypotheses using a structured weight-of-evidence approach that is well established in the field of epidemiology (Forbes and Callow 2002; Suter 2007). Hypotheses were evaluated based on criteria such as the spatial and temporal similarity of expected and observed recruitment patterns, as well as experimental and group-specific monitoring information relevant to each hypothesis. Additionally, based on the concept that factors affecting recruitment should be similar for populations occupying similar habitats (Moran 1953; Koizumi et al. 2008; Manderson 2008), hypotheses were evaluated with respect to their ability to explain differences in the timing of recruitment failure among groups. The strength of use this eco-epidemiological approach lies in the ability to consider multiple disparate data sources and multiple hypotheses. While proof of historical impact causation is challenging (Fabricius and De'ath 2004; Suter 2007), the present analysis indicates poor support for all but one hypothesis. Because the ultimate goal

of identifying the causes of recruitment failure is to reverse them, results are also discussed with regard to their implications for habitat restoration.

Methods

Source data

Data for the Canadian section of the study area were extracted from the UCR white sturgeon database on February 10, 2010 (data provided by James Crossman, BC Hydro). The present analysis utilized data regarding individual identity (by PIT tag or Floy tag), capture location, date of capture and estimated age (based on fin rays and evaluated by at least two people). Age data for the U.S. section of the study area were provided for 124 fish by the Washington Department of Fish and Wildlife (Jason McLellan, 2315 Discovery Place, Spokane Valley, WA). Review of the Canadian database identified that about 30% of records had some irregularities (particularly with respect to capture location); these were corrected by cross reference within the database (using detailed site information that did not contain errors) and with previous versions of the database. Subsequent to quality control checks, the capture history of individuals was used to subdivide fish into geographic groups based on their area of most common capture.

Based on prior evaluations (Clarke et al. 2011; Nelson and McAdam 2012) the criteria for group definition were:

- HLK group- capture locations from Hugh Keenleyside Dam to 8 km downstream.
- BRL group - capture locations from the lower Kootenay River from Brilliant Dam downstream to the confluence with the Columbia River (about 3.2 km), including Kootenay Eddy.
- WAN group – capture locations from river kilometer 52-56, which includes both Fort Shephard and Waneta areas.
- ROOS group – All fish from Lake Roosevelt upstream to the international border were assigned to a fourth group.

The 22 individuals with equal numbers of captures from multiple locations were excluded due to their uncertain group designation. Ties between defined areas and locations outside defined areas were assigned to the defined area of most frequent capture. Geographic groups were then sorted to identify

fish with fin-ray based age estimates. To decrease potential aging error effects only the earlier estimate was included for fish with more than one age estimate.

Sufficient historical data are available only for some environmental variables, including river flow, reservoir elevation, water temperature, turbidity and some contaminants. Flow data were provided by BC Hydro or accessed from internet sources (<http://www.cbr.washington.edu/dart/dart.html>; accessed on March 10, 2010). Lake Roosevelt elevation data were provided by Bonneville Power Administration. Turbidity data were extracted from Van Winkle (1914), Thomas (1950), the EMS database maintained by the BC Ministry of Environment and internet sources for Northport Washington (Washington Department of Ecology site 61A070; www.ecy.wa.gov/apps/watersheds/riv/station.asp?sta=61A070, accessed May 10, 2010). Temperature (Hamblin and McAdam 2003; McAdam 2001; Tiley 2006), total gas pressure (TGP) (e.g., CRIEMP 2005) and contaminants (Kruse and Webb 2006; CRIEMP 2008) data have been summarized elsewhere and are not reproduced here.

Recruitment hindcasting

Hindcasted recruitment was calculated using the formula:

$$R_{t-a} = P_a \cdot e^{a \cdot M}$$

where P_a is the proportion of the sampled fish that were age “a” at year “t” and M is the assumed mortality rate. The assumed mortality rate of 0.04 is intermediate between the estimates of 0.108 (catch curve) and 0.027 (mark recapture), estimated by Irvine et al. (2007) for the UCR, and is similar to natural mortality estimates from the lower Fraser population (Whitlock 2007).

Three aging inaccuracy scenarios were evaluated, with the “no inaccuracy” (e.g., HLK-N) scenario based on Brennan and Caillet (1991). The “low inaccuracy” scenario (e.g., HLK-L) was based on estimated ages (EstAge) for lake sturgeon (Bruch et al. 2009) using the formula:

$$TrueAge = EstAge^{1.054796}$$

The “high inaccuracy” scenario (e.g., HLK-H) was based on analysis of Kootenay River white sturgeon and uses the following formula derived from Paragamian and Beamesderfer (2003):

$$TrueAge = \frac{\ln(1.74(\exp^{-0.0136(EstAge-4.06)}) + 0.078764)}{-0.0194}$$

The recruitment time series for the aggregate population was derived as the average of normalized group-specific recruitment weighted by the population estimates for each area. This approach accounts for abundance differences between areas, but assumes the current relative abundance approximates the historical condition. Departures from this assumption are not expected to have a strong effect on identification dramatic recruitment declines. Population weights were based on estimates for mature fish (corrected to 2010 using $M=0.04$), which were derived from earlier estimates in McLellan and Howell (2007) and Irvine et al. (2007). Because one population strata used by Irvine et al. (2007) encompasses both the HLK and BRL groups, the derivation of the aggregated ALL group was based on those two groups combined.

The likely timing of recruitment declines was based on evaluation of sequential F statistics (based on Chow 1960 as modified by Zeileis et al. 2002), which evaluate changes in the calculated F-statistic to identify discontinuities in data time series. This approach provides an objective method for identifying the timing of recruitment declines. Estimation of the number of breakpoints in the time series was based on techniques described by Bai and Perron (1998, 2003) and Zeileis et al. (2002, 2003). Tests of sequential F statistics and estimation of breakpoints were conducted using the *strucchange* package (Zeileis et al. 2002) in R (Version 2.9.0, R Development Core Team 2009, <http://www.rproject.org>). For breakpoint estimation the trimming parameter was set to $h=0.15$, and significance was evaluated based on the following equation from Andrews and Plober (1994) using the *scctest* function, and p values based on Hansen (1997).

$$\exp F = \log\left(\frac{1}{\bar{i} - i + 1} \sum_{i=1}^{\bar{i}} \exp(0.5 \cdot F_i)\right)$$

Initial evaluations identified the year with the highest F statistic value for each group and then normalized recruitment relative to the mean value for the previous three to 13 years (the historical reference period). This definition maximized the length of each reference period while excluding values immediately adjacent to likely decline years and highly variable values early in the time series. The analysis of recruitment time series utilized data beginning 20 years prior to the estimated decline year in order to limit the effects of high variability and missing data in the earlier portions of some time series. In cases where multiple break points were identified, only those representing declines leading to recruitment collapse are reported. If more than one breakpoint was associated with a recruitment decline then both are reported; in such cases the earlier breakpoint was used to identify the extent of historical data included. The absence of recent recruitment combined with a trimming parameter value

of $h = 0.15$ limited the identification of breakpoints near the end of the time series. In order to evaluate whether further breakpoints could be identified, four subsequent years of zero recruitment were assumed. All breakpoints identified with this modification are identified. Comparisons between groups were based on the timing of identified breakpoints and their 5% and 95% confidence intervals.

Evaluation of recruitment failure causation

A list of recruitment failure hypotheses and their inherent mechanisms (Table 2) was constructed by amalgamating information from the upper Columbia River White Sturgeon Recovery Plan (UCWSRI 2002), the draft species recovery strategy (DFO 2012), Gregory and Long (2008) and Hatfield et al. (2004). Evaluations of recruitment failure hypotheses were based on comparison of the HLK, WAN and ROOS groups, as well as the aggregate population. The BRL group was not included in the evaluation of recruitment failure hypotheses due to its small size and the resulting uncertainty in its demographic pattern (see results).

Evaluation of recruitment failure hypotheses utilized an eco-epidemiological approach based on Forbes and Callow (2002) and Suter (2007). The evaluation of temporal correlations was divided into two parts in order to identify the specific aspect of the recruitment decline being considered. Similarly, the evaluation of the biological coherence criterion was divided to identify two distinct biological questions. Scoring weights were taken from Suter (2007) and are indicated in brackets.

- 1) Temporal correlation: Is there evidence for correlation between adverse effects in white sturgeon and exposure to the causal agent in time based on:
 - a. the timing or recruitment declines? (+1/-3)
 - b. the presence of sustained recruitment failure during the collapse phase? (+1/-3)
- 2) Relative temporal difference: Is there evidence that could explain differences in the timing of recruitment failure among groups? (+1/-3, refute)
- 3) Spatial correlation: Is there evidence for correlation between adverse effects in white sturgeon and exposure to the causal agent in space? (+1/-3, refute)
- 4) Theoretical coherence: Is there theoretical evidence of potential causation? (+2/-2)
- 5) Factual coherence: Is there evidence of causation based on findings in the upper Columbia River? (+2/-3)
- 6) Biological coherence: Is there evidence of causation between adverse impacts and recruitment failure based on:

- a. controlled experiments? (+2/-2)
 - b. the expected life history stage affected? (+2/-2)
- 7) Removal: Has removal of the causal agent led to amelioration of effects on white sturgeon recruitment? (+2/-2)

For temporal comparisons, estimated recruitment decline timing was based on both the low and no aging error scenarios (see results and discussion regarding the high inaccuracy scenario). The consistency between hypothesized effects and observed recruitment patterns during the collapse phase was based on whether impacts were expected to show a binary, variable or positive impact pattern (see Table 3). For spatial comparisons, the location of the primary habitats used by each group (Figure 1; Golder 2006b; Irvine et al. 2007; Nelson and McAdam 2012) was considered relative to the expected spatial impact pattern. For the evaluation of relative temporal differences, hypotheses were considered implausible if their impact was waterborne and affected the mainstem of the transboundary reach (such impacts should affect all groups nearly simultaneously), or if location-specific impacts occurred downstream of the primary habitat of the HLK group.

Positive scores indicate that there is evidence supporting the hypothesis, and negative scores indicate contradictory evidence. For all coherence criteria scores of positive or negative two indicate strong evidence and scores of one indicate weak evidence (scores less than the maximum are referred to as partial scores). For all correlative comparisons the maximum positive score (+1) reflects the fact that correlations are not definitive indicators of causation. However, the stronger negative weighting for all correlations reflects the fact that a lack of correlation is considered a more critical indicator (Fox 1991; Forbes and Calow 2000; Suter 2007) due to the potential to refute the hypothesis (e.g. if an effect precedes the potential cause). In some cases, if the absence of either a spatial or temporal correlation was considered definitive, the hypothesis was considered to be refuted (see Suter 2007). Scores of zero were applied when no information was available. Due to the importance of transparency in the evaluation structure, a rationale for all scores is provided.

Results

Recruitment hindcasting and aging error effects

The classification of fish into groups identified 174, 46, 163 and 124 unique and aged individuals for the HLK, BRL, WAN and ROOS groups, respectively. The mean capture years were 1993, 1995, 1994 and 1994 for these same groups. All groups and the aggregate population show a similar general

pattern of variation around the historical mean followed by declines to a persistent pattern of very low or no recruitment through the duration of the collapse phase (Figures 2 to 6). Significant declines were identified for all groups ($\text{exp}F$; $p < 0.001$) except BRL ($\text{exp}F$; $p > 0.05$) (Table 4). For the BRL group quantitative analysis was limited by gaps in the recruitment time series and the small number of fish in that group. With the exception of the HLK-N scenario, which shows possible declines in 1968 and 1972, only one breakpoint was identified for all group comparisons. Two breakpoints were identified for all aging scenarios for the ALL group; however, for the ALL-N scenario these breakpoints were only evident due to extension of the recruitment time series. Breakpoints identified for the ALL group reflect its composite nature and are similar to either the declines of the HLK and ROOS groups, or the later decline of the WAN group and the smaller second step of the ROOS group decline. Hypothetical aging error scenarios led to identification of earlier declines for all groups; however, the extent of this effect differs by group. Estimated decline timing was four, one and five years earlier assuming low error, and 20, six and 14 years earlier assuming high error for the HLK, WAN and ROOS groups respectively. Based on differences between the mean capture year and the estimated decline year (i.e., 16 or 17 years for the WAN group), the lower effect of aging inaccuracy for the WAN group is apparently the result of reliance on younger fish to identify the recruitment decline of that group.

Environmental changes for which data are available

Flow

While multiple dams affect the UCR and its watershed (Table 1; Figure 1) the most substantial changes in UCR flow occurred after completion of the Hugh Keenleyside (1968) and Mica dams (1974), as well as the Duncan (1968) and Libby (1974) dams in the Kootenay River watershed (Figure 7). Winter flows have increased relative to historical conditions, with the average flow in January and February increasing from 1,100 m³/sec between 1938 and 1968 to 2,750 m³/sec for the period 1975 to 2001. Comparisons for the same years show that mean freshet flows in June and July have decreased by 48% from historical levels of 6,700 m³/sec to a contemporary average of 3,700 m³/sec. Although average contemporary freshets are diminished, high flows still occur, and freshet flows in 1997 were similar to historical average conditions (Figure 7). High flows also occurred in 2011 and 2012, but these are too recent for evaluation with current data.

Although the Pend d'Oreille River has 11 mainstem dams, all but 7-Mile Dam (1979) were constructed prior to 1967 (Table 1). The relatively low storage volume in most reservoirs on the Pend

d'Oreille River means that spring snowmelt freshets are still present; however, mean June to July flows decreased by over 30% based on comparison of the years 1958 to 1964 with 1980 to 1990 (data not shown). Notable events in the Pend d'Oreille hydrograph were a distinct decrease in total outflows from Albeni Falls Dam after 1976, as well as low summer flows in 1973 and extreme low flows in 1977 (Figure 8).

Lake Roosevelt water elevation

Prior to 1966, Lake Roosevelt was operated with a limited seasonal drawdown and rapid refill timing. From 1966 through 1980, Lake Roosevelt had deeper draw down and less variation in refill timing (Figure 9). Subsequent to 1980, drawdown was more variable and generally shallower; however, reservoir elevation still resembles 1966 to 1980 patterns in some years (Figure 10).

Turbidity

Turbidity at Castlegar prior to 1974 (n = 140) showed a maximum value of 13.0 NTU and averaged 1.5 NTU, whereas after 1974 (n = 84) data show a maximum of 2.1 NTU and a mean of 0.60 NTU (Figure 11). Turbidity at Northport shows higher values prior to 1974 (n = 62, mean = 4.2 NTU, maximum = 35 NTU) as compared to after 1974 (n = 213, mean = 1.4 NTU, maximum = 11 NTU) (Figure 12). Historically the highest turbidity was typically recorded in February and March, and neither location shows a substantial historical turbidity increase during the freshet period (all June and July values are < 7 NTU/JTU). The highest contemporary turbidity was recorded at Northport (11 NTU on June 4, 1997). At that time turbidity was also elevated in the Pend d'Oreille River (June 17, 1997 readings of 11 NTU and 13 NTU) (data not shown), but data during this period are not available for the UCR upstream of the Pend D'Oreille confluence.

Retrospective evaluation of recruitment failure hypotheses

Temporal correlation

Temporal comparisons suggest that most hypotheses were considered implausible by at least one comparison; however, data are not available for all potential comparisons (Tables 5, 6). Hypotheses also showed generally poorer temporal concordance with the timing of the WAN group decline. The flow regulation hypothesis was considered plausible due to the similar timing of the decline of the HLK (1967-1972) and ROOS (1968 - 1973) groups and the completion of Hugh Keenleyside Dam (1968). Strong correlations with flow regulation effects also suggest four other hypotheses

(connectivity, gas supersaturation, nutrient availability, and temperature) would also be considered plausible. However, all five hypotheses were considered implausible for the WAN group due to the later decline of that group (1977 - 1978). Because the smelter at Trail began operations over 55 years prior to recruitment failure, contaminant impacts from that source were considered unlikely (i.e. stronger than implausible). Partial scores were assigned for contaminant effects related to pulp mill effluent, as it only preceded recruitment failure by eight years. However, impacts related to the pulp mill contaminants were considered less plausible (-2) for the WAN group due to the more extended interval (> 10 years) until recruitment failure of that group.

Although substrates are embedded at all spawning sites (see Golder 2006a; Crossman and Hildebrand 2012), there is no clear temporal data to indicate the timing of putative changes. As a result, only the ROOS group was assigned a positive score based on the effects of flow regulation on mainstem river bed substrates (Reiser 1990; McAdam et al. 2005; Petts and Gurnell 2005). Potential effects on habitat diversity were considered implausible for the Waneta group due to its later decline, and for the ROOS group because most side channel habitat losses caused by the formation of Lake Roosevelt would have preceded recruitment failure by over 25 years. In contrast, for the HLK group the formation of Arrow Lakes Reservoir would have affected floodplain habitats near the putative historical spawning site about the time of recruitment failure. While turbidity did not decrease until after recruitment failure of the HLK and ROOS groups, partial scores were assigned due to the limited availability of historical data. Finally, changes in fish species composition were considered implausible based on the much earlier introduction of walleye in the 1960s (McMahon and Bennett 1996), particularly in comparison to the timing of the WAN group decline. In this case partial scores were assigned since populations may have required time to increase, but the timing of historical population changes is unknown.

Scoring for the aggregated population was based on the stepped decline pattern in recruitment. Because the timing of flow changes due to Hugh Keenleyside Dam (1968) and Mica Dam (1974) could conceivably lead to a stepped recruitment decline pattern, flow regulation was considered a plausible hypothesis. Similarly, for four other hypothesis which reflect impacts that would vary due to flow regulation (gas supersaturation, turbidity, nutrients and food supply, temperature) assigned scores were the same as for the HLK and ROOS groups (which were based on temporal similarity with flow regulation). Both connectivity and changes in fish species composition hypotheses were considered implausible for this group because their associated impact mechanisms are incompatible

with a two-stepped decline pattern. For both categories of contaminants, scores and logic were the same as for the HLK and ROOS groups. With regard to habitat diversity, hypothesized effects were considered implausible, but a partial score was assigned to reflect the plausibility of this hypothesis for the HLK group.

As all groups are undergoing recruitment collapse they were evaluated together with regard to consistency between hypothesized impacts and the sustained absence of recruitment during the collapse phase. Seven evaluations rated hypotheses as implausible and five were considered plausible based on their binary impact pattern. The most important criterion for identifying impacts as implausible was whether the hypothesized impact had a variable pattern that would only affect white sturgeon in some years. For example, TGP (CRIEMP 2005) and water temperature (McAdam 2001; Hamblin and McAdam 2003; CRIEMP 2008) were high in some years, but not all years. Similarly, both flows and turbidity were high in 1997, but due to the absence of full recruitment restoration (see Howell and McLellan 2011) a partial negative score was assigned. With respect to waterborne contaminants, levels have decreased (CRIEMP 2008), leading to a potentially positive effect on recruitment (which was not observed). A binary impact pattern associated with the initiation of the pulp mill in 1961 is dissimilar from the apparent timing of recruitment failure, but not sufficiently dissimilar to be rejected by this criterion. In contrast, although the smelter may have led to a binary impact when it started in 1910 (Table 1), because recruitment failure occurred over 55 year later the more relevant patterns for this analysis are the more recent declines in contaminant levels (CRIEMP 2008). Hypothesized effects of overharvest would also have been eliminated with the closure of the sport fishery in 1996 (UCWSRI 2002), but no effects on recruitment have been detected.

Spatial correlation

Spatial comparisons generally led to considering hypotheses plausible for most comparisons (i.e., score = 1) due to the spatial proximity of impacts on either some or all groups; however, six hypotheses were considered implausible by at least one comparison. Because both movement patterns (Nelson and McAdam 2012) and fin ray chemistry (Clarke et al. 2011) suggest that the HLK group is the only group of fish that shows spatial overlap with the connectivity limitations due to Hugh Keenleyside Dam, this hypothesis was considered to be refuted based on a lack of spatial correlation for the WAN and ROOS groups. For the HLK group, contemporary and historical use of habitats from Castlegar upstream would lead to little or no spatial overlap with smelter-derived contaminants. Based on the assumption of historical spawning by the HLK group upstream of Hugh Keenleyside Dam and the

presence of recruitment failure for fish still residing in Arrow Lakes Reservoir, gas supersaturation and changes to fish species composition were also considered implausible because such impacts have not been identified in those areas. Based on a similar rationale, contaminant impacts related to the pulp mill at Castlegar were given a partial score due to the potential for some historical spatial overlap. For the WAN group, changes to habitat diversity were considered implausible because this group in particular occupies an exclusively riverine section of the Columbia River.

Relative differences of the WAN group

Due to the identification of later recruitment failure for the WAN group, hypotheses were evaluated based on their ability to explain the lagged response of this group (the relative difference criterion). Because all white sturgeon in the transboundary reach reside in the mainstem river from the stage of feeding larvae onward, all should be similarly exposed to waterborne impacts (unless impacts originate in tributaries). Waterborne effects to the mainstem UCR therefore should not lead to the observed relative differences in the WAN group. As a result, eight hypotheses that rely on a waterborne mechanism were considered implausible. Spatial comparisons also suggest that six hypotheses are inconsistent with the pattern of a later impact for the WAN group that resides between two groups that show earlier declines. For example, effects due to altered species composition and increased predator abundance are considered unlikely because they provide no mechanism by which upstream and downstream groups would be affected synchronously, but prior to the WAN group. Similar to the evaluation of spatial correlation (above), the location of the lead-zinc smelter at Trail should not lead to an earlier effect on the HLK group, which generally resides upstream of that location (Figure 1; Nelson and McAdam 2012; Clarke et al. 2011). While shifts in recreational fishing effort from the HLK area to the Waneta area (Westslope Fisheries 2001) suggest a possible correspondence with the later decline of the WAN group, fishing impacts are considered unlikely based on all other criteria. As a result, the hypothesis regarding geomorphological change was the only hypothesis considered plausible based on the evaluation of the relative difference between groups.

Coherence criteria

Evaluations based on theoretical coherence show no differentiation between hypotheses except overfishing (Table 5), which was considered implausible based on both the expected population at the time of recruitment failure (UCWSRI 2002) and theoretical evaluations of low population effects for white sturgeon (Jager et al. 2010) and lake sturgeon (Schueller and Hayes 2011). The life stage criterion

also led to fairly straightforward results, and suggest that overharvest and connectivity are implausible because neither impact is expected to affect early life history or early juvenile phases.

With respect to the factual coherence criterion, suitable data were unavailable for four hypotheses (Table 5), but scores were evaluated for seven hypotheses. For example, with respect to flow regulation, other than temporal correlations (which are scored separately) there are no monitoring data (e.g., sturgeon movement) for the upper Columbia River that specifically indicate a biological effect for a particular flow regime. The same is true for gas supersaturation and turbidity. The score for the overharvest hypothesis reflects the presence of a sport harvest until 1996. The low plausibility scoring for contaminants was based on Kruse and Webb (2006), who found no clear indication of contaminant effects based on tissue analysis and ambient contaminant levels, and Vardy et al. (2011), who found that ambient water quality guidelines provide sufficient protection from waterborne copper, cadmium and zinc. However, a partial score was assigned because contaminant levels were apparently higher historically (CRIEMP 2008) and because recent laboratory studies identified impacts to benthic invertebrate survival (Fairchild et al. 2012) and sub-lethal effects on white sturgeon (Little et al. 2012). Geomorphological change was considered plausible based on the presence of embedded substrates at the Waneta, Northport and Revelstoke spawning sites (Golder 2006a; Tiley 2006; Jason McLellan, Colville Confederated Tribes, pers. comm.) and based on the drift patterns of yolk sac larvae (see discussion).

Partial scores for hypotheses regarding changes to food supply, thermal regimes and fish species composition acknowledge that impacts have been observed, but are not considered severe. For example, elevated temperatures are likely responsible for some egg mortality (Golder 2005, 2006a, 2010), but sufficiently high temperatures do not occur in all years. Additionally, while growth limitations have been identified for WAN group adults (see Golder 2007; Van Poorten and McAdam 2010) it is unclear whether early life history stages would show similar effects. With regard to altered fish composition, walleye have been observed to prey upon juvenile white sturgeon (UCWSRI 2002), but gut content analysis of walleye does not indicate a strong predation effect (Howell and McLellan 2007, 2009). Changes in habitat diversity were rated implausible because the transboundary reach flows within a steep-sided intermountain river valley, and off channel habitat was very limited even prior to flow regulation (Northwest Hydraulics 2007).

Evaluation based on the biological coherence criterion was limited because laboratory studies have examined potential impact mechanisms for only six hypotheses. Positive rankings related to

geomorphological change, gas supersaturation, turbidity and temperature, respectively, were based on the identification of increased mortality in the absence of interstitial habitat (McAdam 2011, 2012), elevated larval mortality due to gas supersaturation (Counihan et al. 1998), decreased larval predation at higher turbidity (Gadomski and Parsley 2005a) and decreased early life history survival at elevated temperatures (Wang et al. 1985). A negative score was assigned with respect to heavy metal contaminants based on Vardy et al. (2011), who found that current water quality guidelines provide sufficient protection from the waterborne copper, cadmium and zinc. However, a partial negative score was assigned due to contradictory interpretations of sub-lethal effects by Little et al. (2012), the limited number of metals examined, and contaminant effects on benthic invertebrates (Fairchild et al. 2012). The partial positive score for the potential effects of altered fish community was based on the identification of relatively low predation by walleye on white sturgeon larvae (Gadomski and Parsley 2005b).

Four of eleven hypotheses received a zero score for the removal criteria because there is no indication that their associated impacts were removed or diminished at any time after they began. Over-harvest received a score of -2 because harvest impacts should have ceased with the fishery closure in 1996, but no recruitment effect has been observed. Both contaminants and gas supersaturation received low scores because the severity of both has declined (see Aspen Applied Sciences 1998; CRIEMP 2005, 2008) with no attendant recruitment effect. Temperature received a score of -2 because temperatures near the limits identified by Wang et al. (1985) do not affect all spawning sites and are not present in all years. Scores for flow and turbidity hypotheses were assigned partial positive scores due to the fact that both high flow and elevated turbidity could have contributed to the low level recruitment seen in 1997 (Howell and McLellan 2011). However, partial scores were assigned because recruitment was only partially restored, and the fact that flow could affect recruitment through a variety of indirect mechanisms means that causal links with these two hypotheses are not definitive. The positive score for the geomorphological change hypothesis was based on the effects of substrate remediation which increased larval retention at the Revelstoke spawning site (Crossman and Hildebrand 2012) and increased survival in the Nechako River (McAdam 2012).

Discussion

Identification of a single plausible hypothesis represents an important advancement in recovery efforts in the UCR, since uncertainty has hampered the identification of potential remediation

measures. The use of an eco-epidemiological approach provided a systematic and transparent means of reducing uncertainty based on criteria including temporal, spatial, and biological coherence. Using a weight-of-evidence approach all hypothesis except geomorphological changes were considered implausible. Testing the geomorphology hypothesis will depend on the results of habitat restoration, however, this study's findings are consistent with effects identified for other white sturgeon populations (McAdam et al. 2005; Paragamian et al. 2009) and other sturgeon species (Nichols et al. 2003; Du et al. 2009). In combination with the experimental laboratory (McAdam 2011) and field studies (Kerr et al. 2010; Crossman and Hildebrand 2012; McAdam 2012), the present results should increase certainty regarding historical causes of recruitment decline and help shift the focus of conservation efforts toward habitat restoration.

This analysis is subject to a number of critical assumptions, with the assumption that the same factor affects all groups being the most fundamental. The rationale for this approach is that if a single factor can be identified it presents a more parsimonious explanation than multiple factors. An approach suggesting different causal factors for each group would also necessarily have to explain why a proposed causal factor did not affect groups in other parts of the watershed (i.e. explanations for individual groups provide weaker evidence than comprehensive evaluations of all groups). The possibility of interactions between hypothesized mechanisms must also be considered, particularly due to the highly correlated nature of changes caused by river regulation. To the extent possible this challenge was addressed within the definition of hypotheses. With regard to geomorphological change specifically, evidence is presented to suggest that impacts are likely restricted to spawning habitats, and impacts to the egg and yolk sac larvae stage may be sufficient to cause recruitment failure. The outcomes of this analysis are also supported by the presence of similar effects of substrate condition in other sturgeon populations (e.g. McAdam et al. 2005; Paragamian et al. 2009; Dumont et al. 2011) and ongoing experimental restoration work (e.g. Crossman and Hildebrand 2012; McAdam 2012).

Recruitment decline patterns and potential aging error

Due to their longevity, sturgeon provide a unique opportunity for investigation of historical recruitment patterns based on current age composition. While long-term evaluations of year class strength may be subject to spurious correlations due to aging inaccuracy and autocorrelation (Bradford 1991; Rien and Beamesderfer 1994), this is not expected to affect the identification of drastic recruitment failures which are readily apparent in recruitment time series (present study; McAdam et al. 2005; Paragamian et al. 2005). The present analysis also meets the four principle assumptions

related to the use of recruitment residuals (see Catalano et al. 2009) because 1) catchability is similar for fish over 90 cm (Elliot and Beamesderfer 1990); 2) adult mortality rate has not changed dramatically due to impoundment, based on the similarity of natural mortality rates (Irvine et al. 2007) with estimates from unimpounded populations (Whitlock 2007); 3) recruitment varies around stable means before and after recruitment failure; and 4) the large number of year classes means mortality rates of fish vulnerable to sampling should be similar both before and after recruitment failure. Hindcasted recruitment showed consistent patterns for all groups (except BRL), with the recruitment index historically varying around a relatively stable running mean followed by declines to sustained low (near zero) recruitment. With regard to the effects of aging error, imprecision will smooth apparent decline patterns and is discussed below. The effects of inaccuracy are more challenging since they have a potential fundamental effect on the identification of recruitment decline timing.

Although age validation is a fundamental requirement for the evaluation of population dynamics (Beamish and McFarlane 1983), full age validation is unavailable for many species (Campana 2001). Evaluation of aging accuracy therefore addresses an important area of uncertainty (e.g., Rien and Beamesderfer 1994). As expected the high inaccuracy scenario led to the earliest estimates of recruitment failure. While the timing of impacts in tributary watersheds might be compatible with the WAN-H and ROOS-H scenarios, the estimated decline of the HLK group in 1951 is prior to major anthropogenic changes to the assumed historical habitat of this group (i.e., the UCR from Castlegar upstream). This large discrepancy suggests that the high inaccuracy scenario overestimates inaccuracy for UCR white sturgeon. Paragamian and Beamesderfer (2003) acknowledged potential overestimation if growth changed over time, but suggested that a stable Fulton's condition factor was evidence of stable growth. However, the identification of increased condition factor with length for lake sturgeon (Beamish et al. 1996) suggests that a stable condition factor may be insufficient indicator of stable growth. Due to the apparent overestimation which resulted from the high inaccuracy scenario (see also Golder 2005b) recruitment failure timing estimates based on this scenario were not included in the evaluation of recruitment failure causation.

In contrast to the high inaccuracy scenario, the low and no inaccuracy scenarios indicate relatively similar timing for recruitment declines. This effect appears to result from the fact that estimates of recruitment decline timing were primarily based on relatively young fish (i.e. 17 to 23 years old), which should limit the effects of inaccuracy. For lake sturgeon Bruch et al. (2009) indicates that ages are accurate up to age 14, which appears to be related to the fact that this is age of first

reproduction (Bruch pers. Comm.). If a similar effect occurred in white sturgeon, based on their later age of first reproduction (~25 years) then inaccuracy might be limited (and possibly absent) up to that age. If true this suggests that for analyses based on younger fish aging accuracy may be a tractable uncertainty. The fact that the apparent recruitment failure timing for the HLK-N and HLK-L scenarios also bracket the years that Hugh Keenleyside Dam was completed (1968) provides some support for the validity of these two inaccuracy scenarios. This assertion is based on the suggestion that recruitment failure would be unexpected to occur prior the first large scale impact to the presumed historical habitat for this group (based both on their current distribution and fin ray chemistry (Clarke et al. 2011) that indicates greater historical use of upstream sites; see also HLK specific analysis).

Consistent observation of relatively rapid recruitment variation (Paragamian et al. 2005) or declines (present study; McAdam et al. 2005) suggests the rate of recruitment change may also be informative, for example since longer-duration changes, such as changes to the fish community, might be less likely causes of recruitment failure. Considering the smoothing effects of imprecision, and assuming mean capture ages between 17 and 23 years and imprecision based on Rien and Beamesderfer (1994), a rapid recruitment failure within one year could be smoothed to appear as a seven to nine year decline. Although observation of recruitment declines over about three to five years for the HLK and WAN groups and in the Nechako River (McAdam et al. 2005) suggest smoothing effects are less than predicted based on Rien and Beamesderfer (1994), such observations are still not definitive. Even though most studies of hindcasted recruitment show evidence of rapid recruitment changes (i.e. smoothing effects diminish but don't eliminate changes) conclusions based on apparent decline rates may be overly speculative.

The temporal and spatial differences in the demography of the WAN group provide contrast that is fundamental to diagnosis of causation. Demographic differences over relatively small spatial scales contradict the general assumption of population homogeneity over larger spatial scales for white sturgeon (Setter and Brannon 1992; Drauch-Schrier et al. 2011). While the stepped decline pattern of the ROOS group suggests demographic links between the WAN and ROOS, such links are conceivably due to downstream drift by early life stages (see McAdam 2011, 2012), and do not affect the demographic distinction of the WAN group (i.e. based on the timing or recruitment failure). Notably, a similar relationship is not apparent with the HLK group, which may limit potential rescue effects in an upstream direction.

Evaluation of recruitment failure causation

Recruitment declines for the HLK and ROOS groups occurred about the time that substantial upstream regulation of mainstem Columbia River flow began in 1968. By comparison, the construction of Grand Coulee Dam and most dams on the lower Kootenay River and Pend d'Oreille River preceded recruitment declines by many years (over 30 years in the case of Grand Coulee Dam), which suggests that impacts caused by the creation of Lake Roosevelt and loss of tributary access were not a primary cause of recruitment failure. The completion of the Duncan, Hugh Keenleyside, Libby and Mica dams, all within a six-year period from 1968 to 1974, led to a 48% decrease in the average contemporary freshet volume, as well as multiple associated environmental changes (see Hamblin and McAdam 2003; Pieters et al. 2003; BC Hydro 2005; Matzinger et al. 2007; Utzig and Schmidt 2011). Because river flow is a fundamental driver of the structure and productivity of riverine ecosystems (Petts 1985; Bunn and Arthington 2002; Moyle and Mount 2007) it is not at all surprising that river regulation is associated with recruitment failure, however, identification of specific mechanisms is required to support restoration.

Although low-level wild recruitment in 1997 (Howell and McLellan 2011) suggests a possible effect of high flows, correlations between flow and many other variable limits the ability to identify a specific mechanism. For example, both flow and turbidity reached historical levels during the spawning period in 1997 (Figures 7, 11), but effects on other conditions are unknown. Additionally, length class abundance shows that abundance of the 1997 cohort is low relative to levels required to sustain the population, and therefore conditions in 1997 were unable to fully restore recruitment for that birth year. The absence of recruitment restoration in response to 'natural' or anthropogenic flow experiments in the Nechako and Kootenai rivers (McAdam et al. 2005; McDonald et al. 2010) also suggests that flow alone does not provide a sufficient explanation for recruitment declines.

Compared to the two prior studies of white sturgeon recruitment failure (Coutant 2004; Gregory and Long 2008) the key innovation in the present study was consideration of temporal recruitment patterns and group structure. Although correlations cannot prove causation, their utility in the present investigation is their ability to disprove hypotheses based on a lack of temporal or spatial correlation (Suter 2007). For example, the later decline of the WAN group provides very clear distinctions between hypotheses because the mechanisms implied by most hypotheses are incompatible with the presence of time lags between adjacent groups. Because demographic differences often reflect differences in

environmental factors affecting recruitment (Moran 1953; Manderson 2008), demographic differences between groups were assumed to reflect differences in habitat use. As a result, recruitment failure hypotheses that rely on a waterborne mechanism (e.g., turbidity, flow regulation, waterborne contaminants) provide no reasonable explanation for the later decline of the WAN group because all fish occupy the same river from the stage of feeding larvae onward. Similar to the use of demographic asynchrony to identify groups for other species (Myers et al. 1997; Fox et al. 2000; Koizumi et al. 2008), the demographic distinctness of the WAN group provides critical diagnostic information, and only two hypotheses (overharvest and geomorphological change) appear compatible with such a pattern (and overharvest is considered unlikely by other criteria). Two important advantages of relative comparison of demographic patterns were 1) that aging error effects should be eliminated (because all groups are assumed to be affected by the same error scenario (although inaccuracy can vary with age) and 2) limited effects due to limited environmental data availability (because expected patterns are derived from hypotheses). The identification of geomorphological change as the hypothesis with the greatest support both by methods that should not be sensitive to aging inaccuracy effects (i.e., relative differences) and by those that should be (other temporal criteria) further indicates that errors due to aging inaccuracy were sufficiently bounded by the no and low inaccuracy scenarios.

Despite identification of one hypothesis as most plausible, detailed consideration of the all hypothesis is valuable due to continued uncertainty regarding recruitment declines in sturgeon. Three hypotheses (overharvest, habitat diversity, connectivity) appear to have limited supporting evidence with regard to white sturgeon in the UCR. Hypothesized effects on habitat diversity reflect concerns regarding losses of off-channel and floodplain habitat, which are generally considered important attributes of sturgeon habitat (Bemis and Kynard 2002; Coutant 2004). However, such habitats were historically limited in the transboundary reach. Although floodplain habitat was inundated due to the creation of Lake Roosevelt (UCWSRI 2002), that habitat (Marcus Flats) was affected well before recruitment failure occurred. Decreased inundation of riparian habitat was hypothesized to provide a general explanation for recruitment failure (Coutant 2004), but the present evaluation suggests that effects to riparian channel habitat provide a poor explanation for recruitment failure of white sturgeon in the UCR (see also McAdam et al. 2005). This is particularly true for the WAN group, which principally resides in areas of the transboundary reach that never contained substantial riparian habitat.

Overharvest and connectivity effects also appear implausible. White sturgeon are particularly prone to overharvest due to their longevity and late maturation (Boreman 1997), and overharvest has

caused severe declines for multiple sturgeon species (Birstein 1993; Pikitch et al. 2005; Ruban 2005). However, the fact that harvest affects juveniles and adults suggests harvest might only affect recruitment via impacts such as Allee effects (i.e. secondary effects of small population size). Even at current population such levels impacts are considered unlikely on a theoretical basis (Jager et al. 2010; Schueller and Hayes 2011). Furthermore, continued recruitment in the upper Fraser River (population ~125 adults - Yarmish and Toth 2002) suggests very small populations can sustain themselves.

With regard to connectivity, while Jager et al. (2001a) suggest that larval mortality may result from entrainment and lost connectivity due to dams, such effects are considered unlikely in the present case. First, because downstream movements out of Arrow Lakes Reservoir by juveniles and adults (based on fin ray chemistry; Clarke et al. 2011) suggest early life history stages are not affected. Additionally, at the downstream end of the transboundary reach, the large distances upstream of Grand Coulee Reservoir and the much earlier formation of Lake Roosevelt both suggest that larval losses due to the presence of the reservoir alone are an unlikely cause of recruitment failure.

Temperature and TGP hypotheses appear to be refuted by incompatibility between continue presence of historical conditions in some years. Both temperature and TGP are elevated due to river regulation (Hamblin and McAdam 2003; R. L. & L. 1995; CRIEMP 2005) and both may decrease early life history survival (Wang et al. 1985; Counihan et al. 1998; Boucher 2012). However, elevated levels do not occur in all years (see Hamblin and McAdam 2003; CRIEMP 2005), nor do they occur at all spawning sites (see Golder 2005a, 2010; Howell and McLellan 2007, 2009; Terraquatic Resource Management 2011). Additionally, with regard to the impacts of gas supersaturation, while Counihan et al. (1998) identified that elevated TGP has a strong effect on larval survival, the fact that all white sturgeon life stages typically reside below the compensation depth suggests that larvae would rarely be affected by such impacts.¹ Additionally, TGP levels have been substantially reduced due to upgrades at all three hydroelectric plants feeding into the transboundary reach, but without any attendant recruitment effect.

Turbidity changes provide an unlikely explanation of recruitment failure for UCR white sturgeon based on both their magnitude and timing. The possibility that turbidity decreases may have caused recruitment declines is of particular interest due to the proposal to experimentally increase turbidity as a means to restore recruitment (BC Hydro 2005). Previously support for this hypothesis has been based

¹ Susceptibility to dissolved gas supersaturation decreases with depth because increased pressure prevents gases from coming out of solution to form bubbles.

on local knowledge which suggests elevated historical turbidity (UCWSRI 2002; Gregory and Long 2008) as well as the general tendency of dams and impoundments to decrease downstream turbidity (Petts 1985). A similar hypothesis has also been suggested to explain recruitment declines of pallid sturgeon (Dryer and Sandoval 1993). However, the historical data indicate no concordance with the observed patterns of recruitment failure. Historically, turbidity at Castlegar was relatively low (likely due to the settlement of fine particulates within the historical Arrow Lakes ; see Northwest Hydraulics 2007; Matzinger et al. 2007), and was much lower than the 40-60 NTU at which larval predation declined in laboratory experiments (Gadomski and Parsley 2005a) . Additionally, historical data show that the highest historical values occurred outside the spring freshet (i.e., not during the spawning period), and the relatively small decrease in turbidity occurred after the initiation of recruitment failure.

Although there are continued concerns about contaminant levels in the UCR contaminants do not provide a plausible mechanism for recruitment failure, largely due to the fact that contaminant loadings were high prior to recruitment failure. The presence of significant historical contaminant inputs (e.g., 400 MT of metallurgical slag daily from 1930 to 1994; Northwest Hydraulics 2007) has supported international interest in potential contaminant effects on in the transboundary reach (e.g. Du Bey and Sanscrainte 2004). Despite prior indications that contaminants might be a lower priority (Gregory and Long 2008) recent investigations (Vardy et al. 2011; Fairchild et al. 2012; Little et al. 2012) suggest the need for further evaluation. Upgrades to both major contributors of contaminants to the UCR (Celgar's pulp mill in 1993; Cominco's lead-zinc smelter 1980 to 1997) have led to substantial water quality improvements, including declines in ambient levels of all waterborne contaminants (including multiple metals, PCBs, dioxins, furans) except polybrominated diphenyl ethers (CRIEMP 2008). However, water quality improvements were not associated with a positive recruitment response. Additionally, while a variety of contaminants have been detected in sturgeon tissues there is no indication that contaminant loadings for juveniles and adults are at potentially lethal levels (Kruse and Webb 2006). While lethal and sub-lethal metal toxicity has been detected during early life history (Vardy et al. 2011; Little et al. 2012), considering copper levels in particular, effects were detected only at concentrations greater than ambient levels in the UCR (~0.5ug/L; CRIEMP 2008). While higher metal concentrations in substrate pore water (Cox et al. 2005) have been suggested as a potential contributor to increased larval mortality (Little et al. 2012), it is unclear whether elevated metal concentrations would be found within the relatively larger interstitial habitats occupied during the yolk sac larvae phase.

The fact that contaminant inputs were elevated well before recruitment failure occurred indicate the temporal concordance between these two changes is weak, or absent, and waterborne contaminants cannot explain the later decline timing of the WAN group. Although, increased contaminant exposure could be compatible with the recruitment failure timing of the ROOS and WAN groups in combination with geomorphological effects (see below). However, recruitment failure in other rivers (e.g. McAdam et al. 2005; Paragamian et al. 2009) in the absence of heavy metal effects, and in the HLK group which most likely spawned upstream of Trail, indicate that recruitment failure can be explained without contaminant effects. Additionally, while the identification of both lethal and sub-lethal effects on benthic invertebrates (CRIEMP 2008; Fairchild et al. 2012) suggest toxins could be ingested, monitoring of multiple populations (present study; McAdam et al. 2005; Duke et al. 1999) suggests recruitment failure is the result of impacts at the egg and yolk sac larvae stages (i.e. prior to the initiation of feeding). In summary, while contaminants may have negative effects on UCR white sturgeon, their inability to provide a general explanation for all groups (and other populations) suggests that contaminant effects are not the primary cause of recruitment failure.

Nutrients and food supply limitations have been hypothesized to affect recruitment as a result of nutrient-trapping by upstream reservoirs (Pieters et al. 2003) and the possibility of larval mortality due to food limitations (Howell and McLellan 2011), however this hypothesis appears implausible due to the apparent timing of nutrient changes and the inability to explain the unique timing of the WAN group. The effects of impoundment on downstream nutrient regimes can be complex. For example, both the conversion of large lakes to reservoirs (Matzinger 2007) and reservoir inundation (Stockner et al. 2000) would have initially increased downstream nutrient levels. As a result, the expectation of a delayed decrease in downstream nutrient levels relative to the construction of both the Hugh Keenleyside and Mica dams suggests that nutrient decreases occurred after recruitment failure. The absence of a recruitment response to the fertilization of Arrow Lakes Reservoir also suggests that nutrients levels do not provide a plausible explanation for recruitment failure. With regard to effects on food availability links between nutrient levels and food abundance suggest that such effects are implausible, however, effects may occur due to changes in habitat condition (e.g. substrate) and these are addressed in later sections.

Evaluations of the recruitment patterns of an assumed aggregate population (the ALL group) show that it has a more complex decline pattern than its four component groups, and that a stepped decline is indicated for all aging accuracy scenarios. While patterns for this group clearly reflect the

decline patterns of component groups, the diagnosis of recruitment failure causation is challenging without considering group structure. Comparison with the timing of major development projects shows the first decline step coincides with the completion of Hugh Keenleyside Dam and changes associated with the initiation of river regulation. The second decline step could also be attributed to river regulation, and conceivably could be associated with the completion of Mica and Libby dams or a more gradual decline initiated about the time of HKD completion. Unfortunately none of these possibilities identify causal mechanisms.

Retrospective evaluation of recruitment failure based on the ALL group, but without reference to groups, provides a much less confident diagnosis because it precludes comparisons based on spatial differences (i.e., the location of the HLK group upstream of smelter inputs) and temporal differences (i.e., the later timing of the WAN group decline). Sustained low recruitment during the collapse phase still leads to a negative score for some hypotheses, with the exception of the same four hypotheses identified by professional judgment (Gregory and Long 2008). However, consideration of the removal criterion indicates rates both nutrient limitations and geomorphological change as more plausible than either flow or turbidity effects.

Differences in the analytical outcomes emphasize the importance of the spatial scale of analysis, and numerous indicators support the analysis of groups rather than the aggregate population. This is due to identification of among group differences based on movement and genetics (Nelson and McAdam 2012), fin ray chemistry (Clarke et al. 2011), growth (Van Poorten and McAdam 2010) and the present identification of demographic differences. Although the similar groups were not identified using DNA microsatellites (Drauch-Schrier et al. 2011) this difference is readily explained by the fact that the indicators showing differences are considered leading indicators (i.e. earlier in time) of differentiation (Zink and Barrowclough 2009). Failure to recognize the presence of distinct groups can lead to elevated extinction risk to smaller component groups (e.g., the BRL group), and, particularly for endangered species, biological definitions of management units (i.e. as compared to dam locations) provide a more precautionary approach (Begg et al. 1999).

Apparent mechanism of geomorphological effects

Geomorphological change is the only hypothesis that is not considered implausible by any criteria. While data specific to the temporal pattern of effects in the UCR are relatively limited, this hypothesis shows consistent plausibility based on all coherence criteria. The strongest support for this hypothesis is based on the later recruitment decline of the WAN group. The tributary spawning location makes the WAN group unique relative to the other two groups, and the fact that flow and substrate are strongly influenced by tributary conditions provides an explanation for the delayed onset of recruitment failure relative to the HLK and ROOS group.

Similar to all other sites, the proposed mechanism of recruitment failure for the WAN group is the loss of interstitial habitat within substrates at spawning sites; however, the principle difference at that location is that spawning occurs within the Pend d'Oreille plume. Based on a variety of evidence I propose the following explanation for the mechanism and timing of recruitment failure related to the Waneta spawning site. Due to the upstream proximity of Waneta Dam, suspended sediment inputs would be minimal from the Pend d'Oreille River. Additionally, the location of the Pend d'Oreille plume along the southeast bank of the UCR (Figure 13) should limit the incursion of mainstem-derived fine sediment into the spawning area under most conditions (i.e., suspended sediments and bedload should not move perpendicular to the prevailing current). The exception to the protective effects of tributary flow is that flow regulation can lead to near zero flow in the Pend d'Oreille River, and under such conditions the mainstem Columbia River is the primary hydraulic influence on the Waneta spawning area (Figure 13; Fissel and Jiang 2007). During periods of low flow in the Pend d'Oreille River, fine substrates originating from the Columbia River mainstem therefore could affect conditions at the Waneta spawning site.

The presence of metallurgical slag at the Waneta spawning site (Golder 2006a), which must have originated from smelter located upstream on the mainstem Columbia River, indicates that mainstem bedload has indeed moved into the spawning area. While the exact timing of such movements has not been determined, extended periods of extreme low flow in 1977 (Figure 8) presumably allowed sustained movement of mainstem-origin fine substrates into the spawning area. Such an effect is consistent with the modelled hydraulic effects on the confluence area (Fissel and Jiang 2007), the timing of extreme low flows in the Pend d'Oreille River and the timing of the WAN group recruitment failure.

Photographic evidence and visual observation (Golder 2006a) indicate that embedded cobble is the primary substrate at the Waneta spawning area, which is indicative of degraded conditions at other spawning locations (McAdam et al. 2005; Triton 2009; Crossman and Hildebrand 2012). Similar to the Nechako River (Triton 2009), the dominance of yolksac larvae in drift samples downstream of the Waneta spawning site (e.g. Golder 2006a) also indicate a degraded substrate condition that provides limited hiding habitat. Given that embedded substrates decrease egg survival (Forsythe 2010) as well as yolksac larvae hiding, survival, growth and development (McAdam 2011; Boucher 2012; Crossman and Hildebrand 2012), drift by yolksac larvae provides additional evidence of degraded substrate conditions at the Waneta spawning site. The effects of substrate condition on sturgeon recruitment are also increasingly supported by other studies (McAdam et al. 2005; Kerr et al. 2010; Dumont et al. 2011; Crossman and Hildebrand 2012); however, further hydraulic modelling could provide a detailed understanding of the recruitment failure mechanism at this spawning site.

Given that the spawning location for the ROOS group is only about 30 km downstream from the Waneta spawning site, similar impacts would be expected to affect both sites. With regard to substrate conditions at the Northport spawning site, the high proportion of sand in that reach of the Columbia River (Besser et al. 2008) and the semi-embedded large cobble at the Northport spawning area specifically (Jason McLellan, Colville Confederated Tribes, pers. comm.) are both indicative of degraded spawning substrate (McAdam 2011). The prevalence of yolksac larvae in drift samples from some years (e.g., 2005 – 75% of larval captures were yolksac larvae; Howell and McLellan 2007), also suggests the presence of degraded substrate conditions. However, the predominance of feeding larvae in drift captures for other years (e.g., 76% and 73% in 2006 and 2007; Howell and McLellan 2009, 2011) suggests substrate conditions are less degraded than other sites in the UCR.

Potential declines in feeding larvae survival as a result of substrate change are supported by the possibility of decreased benthic food supply and cover habitat (Wood and Armitage 1997; Osmundson et al. 2002; Finstad et al. 2007). Contaminant effects on the survival of benthic invertebrates (Fairchild et al. 2012) might also contributed to food limitations. Carry-over effects (i.e., reduced growth and survival) due to habitat conditions experienced by yolksac larvae provide another potential substrate-mediated effect (Boucher 2012). Lower larval growth that has been associated with sub-optimal habitat conditions for yolksac larvae (Boucher 2012; Crossman and Hildebrand 2012) and may decrease survival due to increased predation (Werner and Gilliam 1984; Fuiman 2002). Substrate mediated effects throughout early life history, and including the feeding larvae stage, are therefore compatible

with impacts suggested for other locations (and particularly the Waneta spawning site). However, a more definitive diagnosis of the impacts to this group requires further investigation. For example, identification of whether larval mortality results from effects upon the yolk sac larvae or feeding larvae stages may have important implications for the spatial delineation of future habitat restoration.

Reservoir backwatering effects and upstream flow regulation provide a possible explanation for degraded substrate conditions at the Revelstoke spawning location including increased armouring and embeddedness (see Crossman and Hildebrand 2012). While habitats occupied by the WAN and ROOS groups each have well-studied spawning sites, both contemporary and historical spawning locations are less certain for the HLK group. A portion of this group spawns at Revelstoke, and fish within the ALR primarily spawn in that area (James Crossman unpubl.). Currently, substrates in the Revelstoke spawning reach are highly embedded (Tiley 2006) and have been experimentally shown to limit larval hiding (Crossman and Hildebrand 2012) and likely survival (based on McAdam 2012).

The recently identified spawning site in the ALGS tailrace (Terraquatic Resource Management 2011) likely represents a spawning location that is used in lieu of upstream movement to a historical spawning location. Although spawning was not detected in this reach prior to the construction of the ALGS in 2002 (R. L. & L. 1994), eggs and yolk sac larvae (but only one feeding larvae) were detected in 2010 and 2011 (Terraquatic Resource Management 2011). Based on McAdam (2011) the large cobble boulder substrate in the tailrace likely create interstitial habitats that are too large for hiding yolk sac larvae (McAdam 2011; Terraquatic Resource Management 2011). The upstream proximity of ALGS suggests that interstitial infilling may be limited at this location, and as a result modification of the available substrate at this location may provide a long-term option for habitat restoration.

Biological insights and implications for restoration

The presence of demographic differences and historical reproductive isolation (Nelson and McAdam 2012) are two principal indicators of stock/population differentiation (Waples and Gaggiotti 2006; Reiss et al. 2009); however, the recovery of UCR white sturgeon is currently based on a single population. Identification of distinct demographic and breeding units (present study; Welsh et al. 2009; Nelson and McAdam 2012) indicates that localized recruitment dynamics influence this species despite its potential for long range movement. The delayed decline of the WAN group specifically links recruitment decline to changes to spawning habitat where conditions are influenced by tributary flow (vs. mainstem conditions). Effects to spawning habitat also indicates that the egg and yolk sac larvae

stages are the primary stages at which survival declines lead to recruitment failure. Based on the earlier decline of the ROOS group (due to changes in mainstem habitats), and since feeding larvae are expected to drift into the mainstem from the Waneta spawning location, the absence of a WAN group recruitment failure at the same time as the ROOS group suggests that substrate mediated impacts on feeding larvae are not strong enough to cause recruitment failure. Although feeding larvae are readily captured downstream of ROOS group spawning sites, evidence based on the WAN group suggests that impacts causing recruitment failure manifest their effects prior to that life stage.

An additional implication of the high habitat fidelity and the long term maintenance of spatially distinct demographic patterns is that it suggests that restoration affecting one group (e.g., at one spawning site) may have limited benefit for other groups, particularly the HLK and WAN groups which show no demographic connections. Restoration at multiple spawning sites may therefore be needed in order to maintain the current distribution and biological diversity of white sturgeon in UCR.

While the present analysis identified the most plausible hypothesis for the historical recruitment failure in the UCR, it is important to note that subsequent anthropogenic effects may limit the effectiveness of restoration. For example, while geomorphological change provides a sufficient explanation for recruitment failure, the subsequent construction of Revelstoke Dam has substantially decreased summer temperatures (Tiley 2006). The effects of temperature changes leading to effects such as delayed spawning and development (Golder 2006d; Crossman and Hildebrand 2012), and possibly juvenile growth (James Crossman, BC Hydro, pers. comm.) all suggest that subsequent changes at that location make it uncertain whether substrate restoration alone will be sufficient to restore recruitment within Arrow Lakes Reservoir.

Identification of changes to spawning substrates as the apparent cause of recruitment collapse adds to other studies that identify the importance of substrate condition to sturgeon spawning (see Kerr et al. 2010; Du et al. 2011). One positive implication of this finding is that habitat restoration requirements are more spatially restricted than if large-scale larval drift is assumed (e.g., Kynard et al. 2002; Braaten et al. 2008, 2012). The delayed recruitment decline of the WAN group also emphasizes the importance of tributary effects (Moyle and Mount 2007). This observation suggests that spawning sites for which fine sediments inputs are limited by adjacent upstream dams may have a greater restoration potential (see also Kerr et al. 2010). Considering spawning areas for the three groups primarily considered here suggests that spawning sites used by the ROOS group may be comparatively

more challenging to restore relative to the ALGS and Waneta spawning sites for which upstream dams offer some protection from fine sediment inputs.

Recommendations

This analysis identifies geomorphic change as the most plausible hypothesis to explain recruitment failure, and suggests a mechanism that is consistent with data from this and other populations. The next important step is to directly test this hypothesis (Caughley 1994; Walters and Collie 1994). The following recommendations represent areas where further information would be useful to verify, modify or possibly refute proposed mechanisms. Key areas where further works is suggested include:

1. Substrate restoration at spawning sites is supported by this analysis. Further information regarding the geomorphology and substrate condition of all spawning sites is likely required in order to assist future habitat restoration.
2. Detailed modelling of sediment transport for the Waneta spawning site is recommended in order to verify the proposed mechanism of substrate change at this spawning site, and to provide a foundation for future habitat restoration.
3. Further experimental restoration of substrates in key spawning areas is supported by this analysis.
4. Evaluation of methods for identifying the hatch location of captured larvae/juveniles would be beneficial. The availability of such techniques would support evaluations of the importance of spawning habitat quality and its effects on the abundance and condition of larvae or juveniles. Such a tool could be important for the evaluation of site specific habitat restoration.
5. Although substrate changes at spawning sites are the proposed cause of recruitment failure for all groups, feeding larvae are regularly detected downstream of ROOS group spawning sites. Substrate changes may also affect that life stage, and investigation of the proximate (e.g. food availability, predation, carryover effects) and ultimate (e.g. substrate change) factors affecting feeding larvae survival is suggested to validate or refute conclusions made in this analysis. Thoroughly understanding factors affect all early life stages will likely be critical to restoration of recruitment in that area.

Table 1 Timing of major industrial projects affecting the upper Columbia River watershed. For hydroelectric dams, small (S) and large (SS) storage projects are identified to indicate the project's potential to affect seasonal flows.

Watershed / Industry	Dams / impact	Timing
Columbia mainstem / Hydroelectric dams and reservoirs	Grand Coulee (SS) Hugh Keenleyside (SS) Revelstoke Mica (SS)	1944 1968 1983 1974
Kootenay / Hydroelectric dams and reservoirs	Brilliant Canal Plant Duncan (S) Libby (SS) Lower/upper Bonnington, South Slocan/Corra Linn (S)	1944 1975 1969 1972 1907 - 1932
Pend d'Oreille / Hydroelectric dams and reservoirs	Waneta Seven Mile Boundary Box Canyon/ Albeni Falls (S) / Noxon Rapids / Cabinet Gorge / Hungry Horse (S) /Kerr (S) /Thompson Falls/Priest Lake (S)	1954 1979 1967 1915 -1960
Columbia mainstem / Lead Zinc smelter (Trail)	Contaminants release Slag release	1910-present; significant declines after 1995 1910-1994
Columbia mainstem / Pulp mill (Castlegar)	Contaminants	1961-present; declined significantly after 1993

Table 2 Description of the recruitment failure hypotheses evaluated based on the expected pattern of effect on recruitment.

Hypothesis	Description of Mechanism
Overfishing	In conjunction with low intrinsic population growth rates, recruitment failure could occur if harvest diminished populations below threshold levels, for example via Allee effects.
Flow regulation	Recruitment failure is a direct result of flow regulation via effects such as decreased spawning flows, hydraulic effects on spawning site selection or increased predation due to diminished water velocities.
Connectivity	Prior to impoundment, white sturgeon could move throughout the UCR. Recruitment failure may have occurred as a direct result of a decreased ability to move to their requisite habitats.
Contaminants	The UCR is affected by contaminants from a variety of sources (e.g., lead zinc smelter, pulp mill, municipal effluent). The presence of contaminants may have caused the recruitment failure through direct toxicological effects.
Geomorphic change	Sediment supply and river bed disruption due to flow regulation and long-term slag inputs may all contribute to geomorphic change. Recruitment failure may be caused by resultant habitat changes, particularly an increase in the proportion of fine material in river bed substrates at spawning sites.
Habitat diversity	Dams, reservoirs and flow regulation may have decreased the diversity of riverine habitats (e.g., side channels, off channel rearing areas), and the loss or alteration of such habitats may have led to recruitment failure.
Total gas pressure (TGP)	Elevated TGP in the UCR downstream of Keenleyside Dam may have caused recruitment failure by increasing mortality, particularly for larvae and juveniles.
Turbidity	Turbidity decreases downstream of large reservoirs may lead to recruitment failure via increased predation mortality due to increased water clarity.
Nutrients and food supply	Nutrient reductions due to nutrient trapping by upstream reservoirs could lead to decreased ecosystem productivity. Such changes could cause recruitment failure via effects such as decreased spawning frequency and decreased early life history survival.
Temperature	Temperature increases in the UCR have occurred due to upstream impoundment and possibly climate change.
Altered fish species composition	Changes in the community composition include the loss of anadromous salmonids and increased exotic species (e.g., walleye, northern pike smallmouth bass), and the effects of such changes are poorly understood. Recruitment failure could occur if changes in fish community composition increased predation mortality.

Table 3. Description of recruitment pattern designations during the recruitment collapse phase.

Criteria	Category – Rationale
Collapse phase pattern	Binary – an irreversible change from one state to another, with very limited range overlap expected (e.g., connectivity related to dam construction)
	Variable – the range of impact magnitude is similar, but the distribution with its range has changed (e.g., an increased frequency of high water temperature)
	Positive – the impact severity has declined and risk due to this variable has decreased relative to the time of recruitment failure (e.g., overharvest, inputs of some contaminants)

Table 4 Estimated timing of recruitment failure for three aging inaccuracy scenarios. Values in brackets are the 5% and 95% confidence intervals (i.e., 67 = 1967). AD indicates results when four additional years of zero recruitment were assumed. NS= not significant (exp *F*, *p* > 0.05).

Group	No inaccuracy	Low inaccuracy	High inaccuracy
HLK	1968 (67-72)	1967 (66- 71)	1951 (50-55)
	1972 (71-74)		
BRL	NS	NS	1949 (44-60)
WAN	1978 (77-80)	1977 (76 – 81)	1972 (71 -77)
ROOS	1973 (72- 77)	1968 (67 – 74)	1959 (57 –68)
ALL	1969 (68-74)	1967 (66-72)	1958 (57-62)
	AD=1969 (68-78)		
	AD= 1978 (77-80)	1977 (76-79)	1972 (71-74)

Table 5 Weighted comparisons for the retrospective evaluation of recruitment failure hypotheses. Criteria and scoring are described in the methods. Comparisons that refuted hypotheses are indicated by R. For evaluation of the collapse phase, expected recruitment patterns were identified as positive (P), binary (B) or variable (V) recruitment. For the relative differences between groups, whether an impact mechanism was waterborne (W) or the location of impacts (L) is indicated.

Hypothesis	Temporal Correlation					Spatial Correlation				Relative difference	Coherence				
	HLK (+1/ -3)	WAN (+1/ -3)	ROOS (+1/ -3)	ALL (+1/ -3)	Collapse phase pattern	HLK (+1/ -3)	WAN (+1/ -3)	ROOS (+1/ -3)	ALL (+1/ -3)		Theoretical (+2/ -2)	Factual (+2/ -3)	Biological (+2/ -2)	Life stage (+2 / -2)	Removal (+2/ -2)
Over-harvest	0	0	0	0	-2 (P)	0	0	0	0	1 (L)	-3	-3	0	-2	-2
Flow regulation	1	1	1	1	-1 (V)	1	1	1	1	-3 (W)	2	0	0	2	-1
Connectivity	1	-2	1	-2	1 (B)	1	R	R	-3	-3 (W,L)	2	R	0	-2	0
Contaminants:															
-Pulp mill	-1	-2	-1	-1	-1 (P)	-1	1	1	1	R (W)	2	0	-1	2	-2
-Smelter	-3	-3	-3	-3	-1 (P)	-2	1	1	-1	-3 (W,L)	2	-1	-1	2	-1
Geomorphological change	0	0	1	0	1 (B)	1	1	1	1	1	2	2	2	2	2
Habitat diversity	1	-2	-2	-1	1 (B)	1	-3	1	1	-3 (W)	2	-2	0	2	0
Gas supersaturation	1	-1	1	1	-3 (V/P)	-2	1	1	1	R (W)	2	0	2	2	-2
Turbidity	-1	-1	-1	-1	-1 (V)	1	1	1	1	-3 (W)	2	0	2	2	-1
Nutrients and food supply	1	-1	1	1	1 (B)	1	1	1	1	-2 (W,L)	2	1	0	2	0
Temperature	1	-1	1	1	-3 (V)	1	1	1	1	-3 (W,L)	2	1	2	2	-2
Fish species composition	-1	-2	-1	-1	1 (B)	-1	1	1	1	-2 (L)	2	1	1	2	0

Table 6 Summary of the scoring rationale for recruitment failure hypotheses. Signs in parentheses indicate whether evidence supports (+) or does not support (-) each hypothesis.

Hypothesis	Determination	Rationale
Overharvest	Unlikely	<ol style="list-style-type: none"> 1. Should affect juveniles and adults (-) 2. Allee effects unsupported (-)
Flow regulation	Implausible	<ol style="list-style-type: none"> 1. Mainstem flow regulation does not explain later decline of the WAN group (-) 2. Flow regulation on the Pend d'Oreille River preceded recruitment failure (-) 3. High flow in 1997 only led to low level recruitment (+)
Connectivity	Refuted	<ol style="list-style-type: none"> 1. Should primarily affect HLK group and fish in Arrow Lakes Reservoir. (-) 2. ROOS and WAN groups show limited movement to the vicinity of Hugh Keenleyside Dam (-) 3. HLK group fish are still spawning at locations upstream and downstream of Hugh Keenleyside Dam (-) 4. Cannot explain the later decline of the WAN group (-)
Contaminants	Implausible	<ol style="list-style-type: none"> 1. The two major contaminant sources preceded recruitment failure by eight years (pulp mill) or 55 years (smelter) (-) 2. Most contaminants (except slag) are waterborne and cannot explain the later recruitment failure of the WAN group (-) 3. Contaminants from the smelter are located downstream from the primary habitat of the HLK group (-) 4. Contaminant levels from both sources have decreased substantially, but with no recruitment effect (-) 5. Toxicological studies show exposure to Ca, Cu and Zn are detrimental, but only at levels above current ambient concentrations (-) 6. Tissue sampling and summary investigation found no clear evidence of contaminant mediated recruitment effects (-) 7. Contaminant levels were higher historically (+) 8. Benthic invertebrate survival diminished (+)
Geomorphic change	Plausible	<ol style="list-style-type: none"> 1. Can explain the later decline of the WAN group (+) 2. Substrates are embedded at all spawning sites (except the ALGS site which is recently created) (+) 3. Drift by yolk sac larvae at all spawning sites indicates an inability to access interstitial habitat (+) 4. Substrates that limit hiding by yolk sac larvae are linked to recruitment failure in other sturgeon (+) 5. Timing of putative mechanism agrees with recruitment failure timing (+)
Habitat diversity	Unlikely	<ol style="list-style-type: none"> 1. Off-channel habitat was historically limited in the transboundary reach and was minimally affected by flow regulation (-) 2. Off-channel habitat was reduced by the creation of Lake Roosevelt, but over 25 years prior to recruitment failure (-) 3. Losses of off-channel habitat near Revelstoke coincided with the timing of recruitment failure and the creation of Arrow Lakes Reservoir (+)

Table 6 Summary of the scoring rationale for recruitment failure hypotheses (cont.)

Hypothesis	Determination	Rationale
Total gas pressure (TGP)	Refuted	<ol style="list-style-type: none"> 1. TGP was elevated seasonally, but not in all years (-) 2. TGP levels have declined substantially (-) 3. Elevated TGP is a waterborne effect and cannot explain the later recruitment failure of the WAN group (-) 4. White sturgeon larvae typically reside below the compensation depth (-) 5. Lab studies show elevated TGP can be lethal (+)
Turbidity	Implausible	<ol style="list-style-type: none"> 1. Historical turbidity levels were not high (-) 2. Turbidity levels declined after recruitment failure (-) 3. Historically peak turbidity levels occurred during non-freshet periods (-) 4. Turbidity is a waterborne effect and cannot explain the later recruitment failure of the WAN group (-) 5. Laboratory studies show that elevated turbidity can decrease predation, but only at levels higher than ambient or historical conditions (+)
Nutrients and food supply	Implausible	<ol style="list-style-type: none"> 1. Nutrient levels show complex response to reservoir formation. 2. Initial increases followed by declines would lead to nutrient declines occurring after the initiation of recruitment failure (-) 3. Egg viability suggests adult condition is adequate (-) 4. No evidence of nutrient limitation for HLK and ROOS groups (-) 5. Lower growth of the WAN group may limit reproductive frequency (+)
Temperature	Unlikely	<ol style="list-style-type: none"> 1. Temperature is a waterborne effect and cannot explain the later recruitment failure of the WAN group (-) 2. Temperatures are higher than historically, but are not high every year (-) 3. Temperatures can exceed early life history tolerance limits and mortality at the Waneta spawning site, but effects are intermittent (+)
Altered fish species composition	Implausible	<ol style="list-style-type: none"> 1. Increased walleye abundance preceded recruitment failure (-) 2. There is no apparent mechanism by which walleye might affect both the HLK and ROOS groups prior to the WAN group (-) 3. Laboratory studies do show predation on white sturgeon, but effects on early life history stages were limited (-) 4. Field studies do not show that sturgeon are abundant in walleye stomachs (-) 5. Recruitment failure is present in Arrow Lakes Reservoir in the absence of walleye and other introduced species (-)

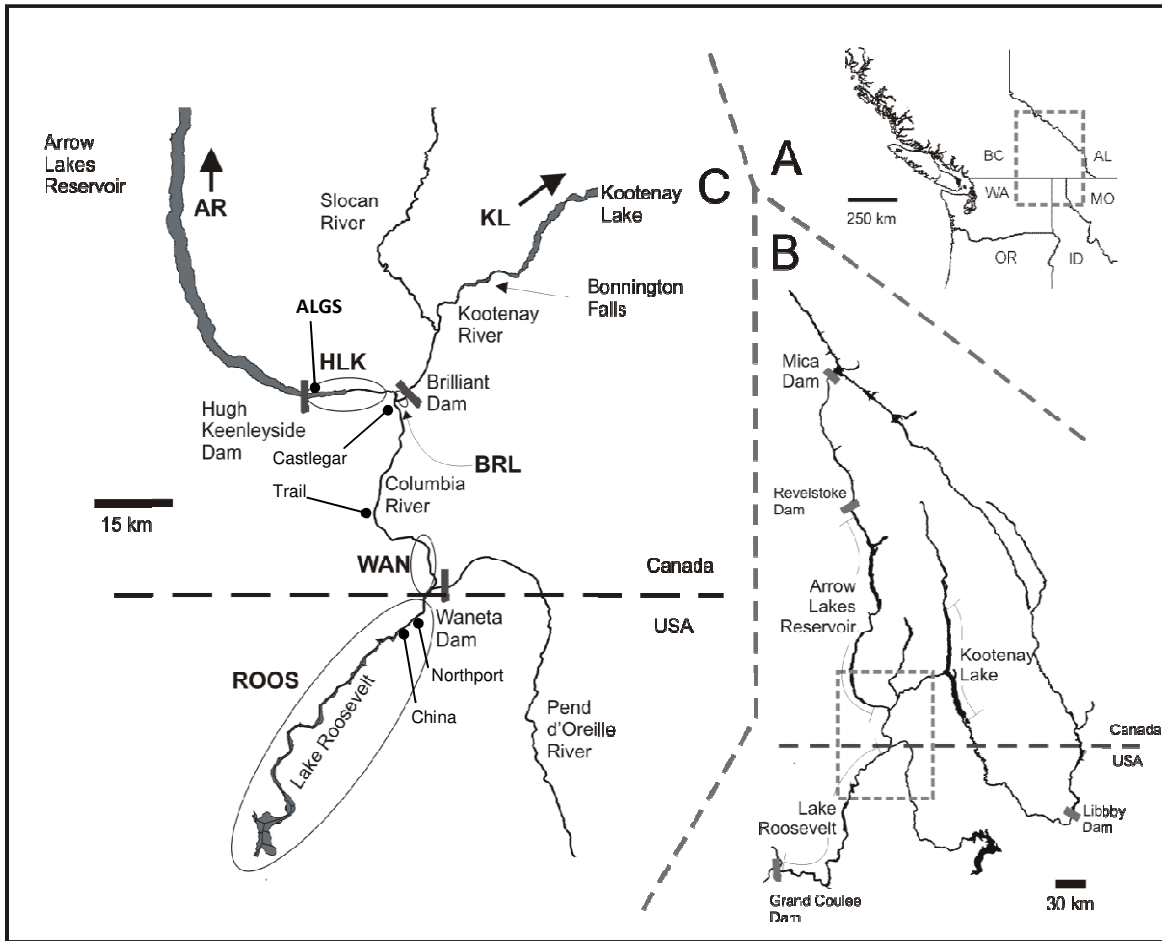


Figure 1 Map of the transboundary reach of the upper Columbia River and its relative location on the west coast of North America (A). Geographic groups defined in the text are indicated in bold adjacent to their associated river zone (C). Principal dam locations are indicated by text and curved arrows. Bold abbreviations referring to putative groups of white sturgeon are defined in the text, and include fish in Arrow Lakes Reservoir (AR), directly downstream of Keenleyside Dam (HLK), directly downstream of Brilliant Dam (BRL), the Waneta area (WAN) and Lake Roosevelt (ROOS). Kootenay Lake and the population it contains (KR) are also identified for reference.

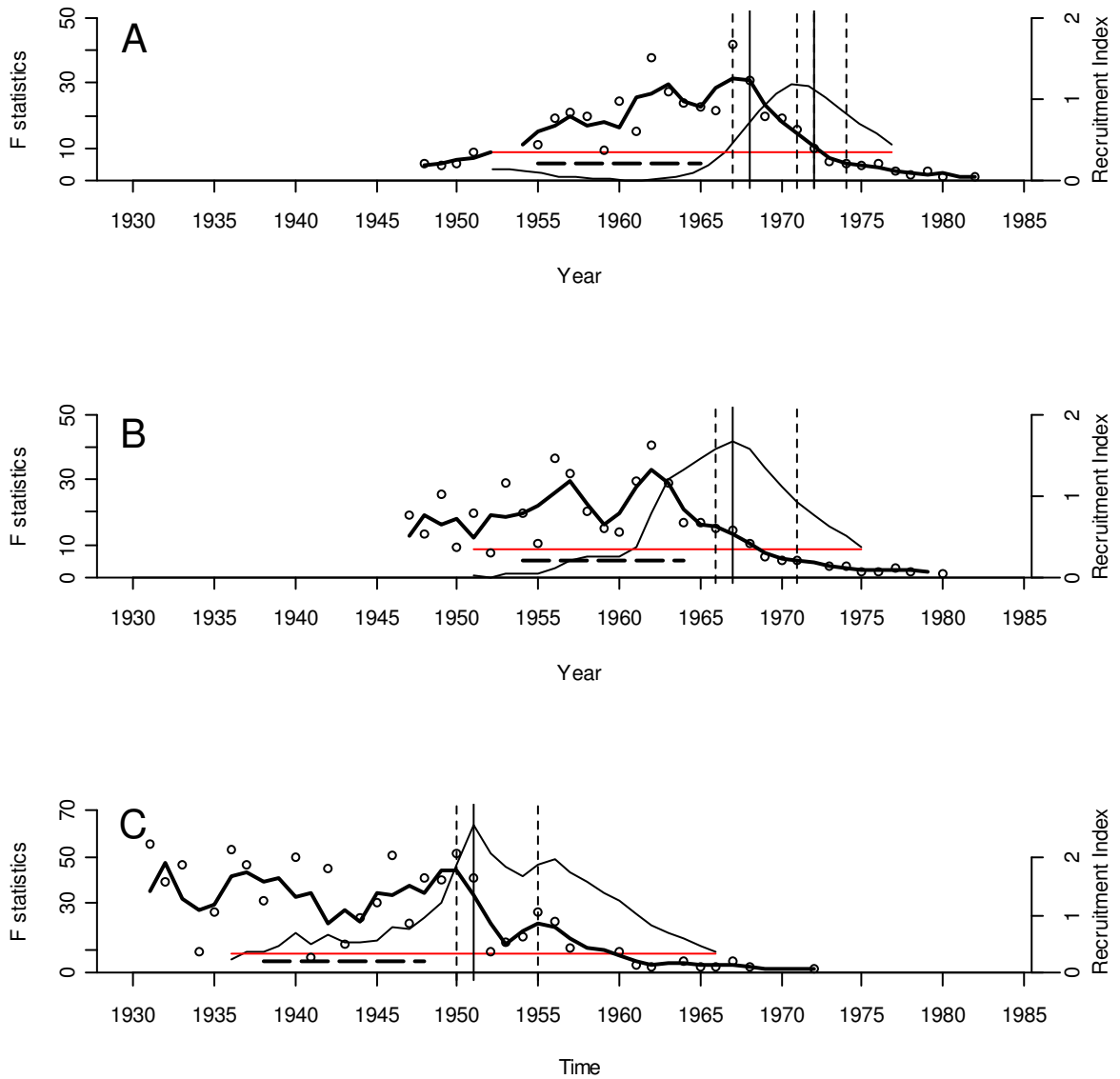


Figure 2 Hindcasted recruitment for the HLK group, including the HLK-N (A), HLK-L (B) and HLK-H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

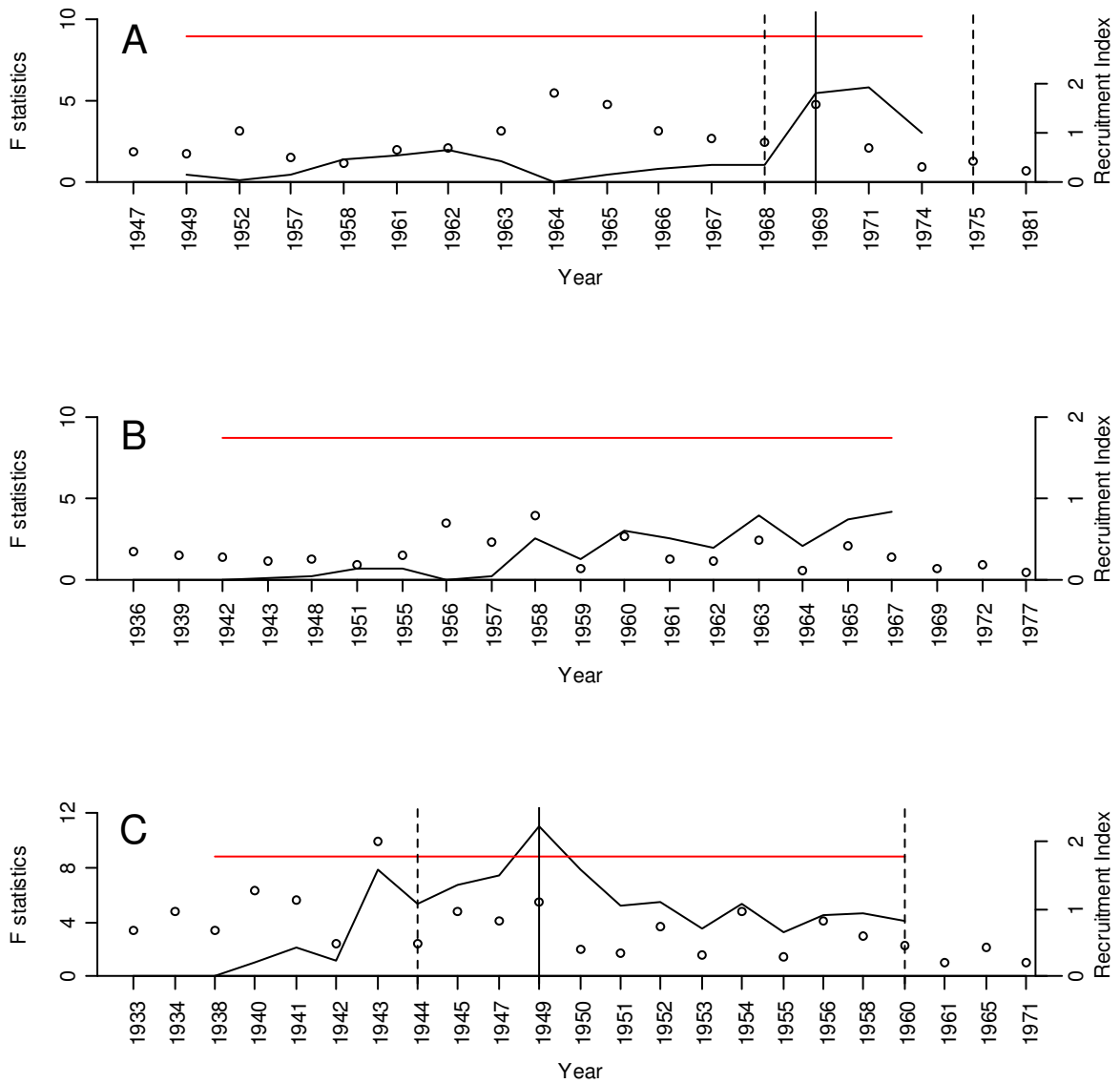


Figure 3 Hindcasted recruitment in various years for the BRL group, including the BRL-N (A), BRL-L (B) and BRL-H (C) scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line is the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. Note that the x-axis is discontinuous and only shows years for which data were available.

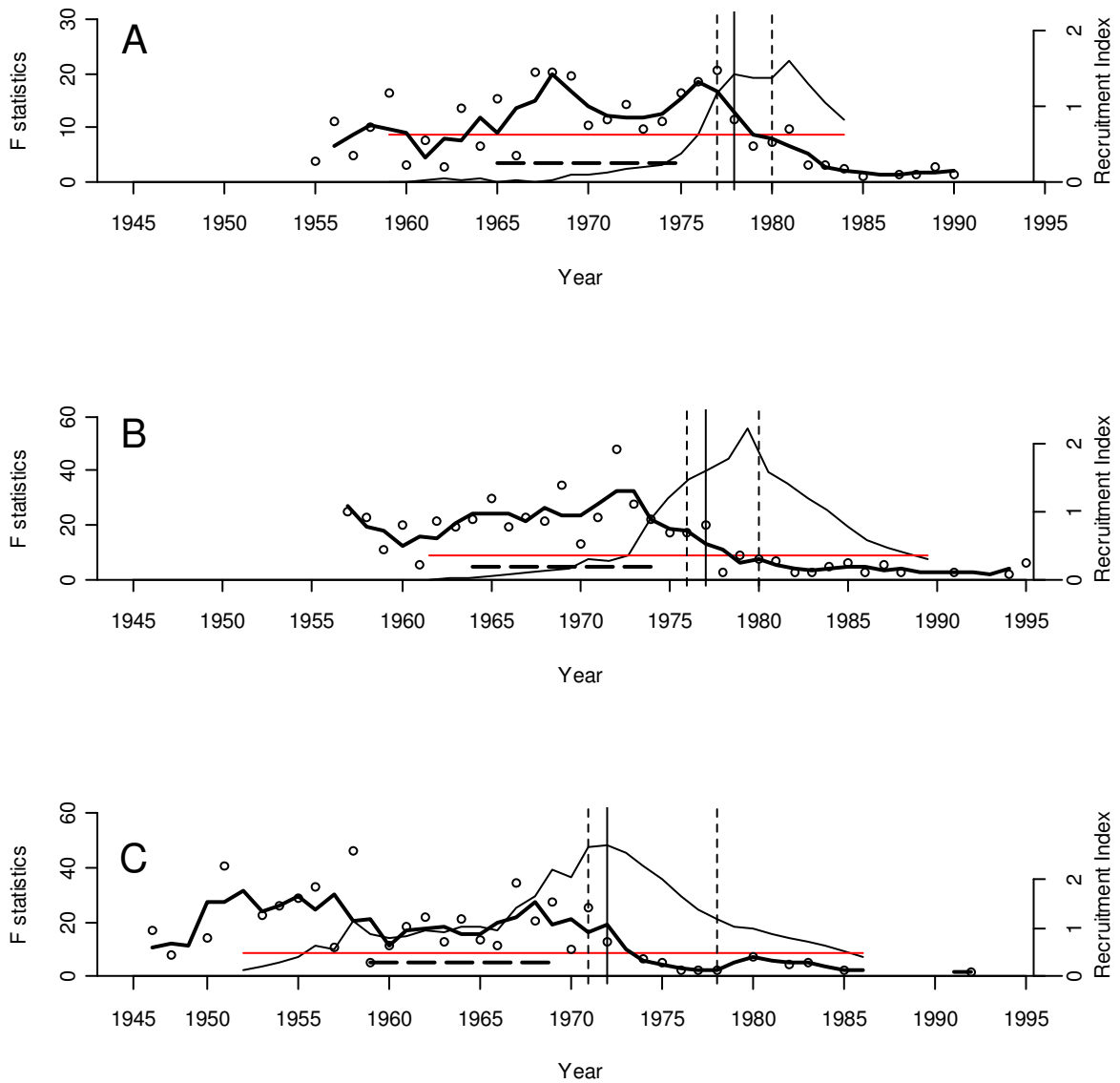


Figure 4 Hindcasted recruitment for the WAN group, including the WAN-N, (A), WAN -L (B) and WAN -H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

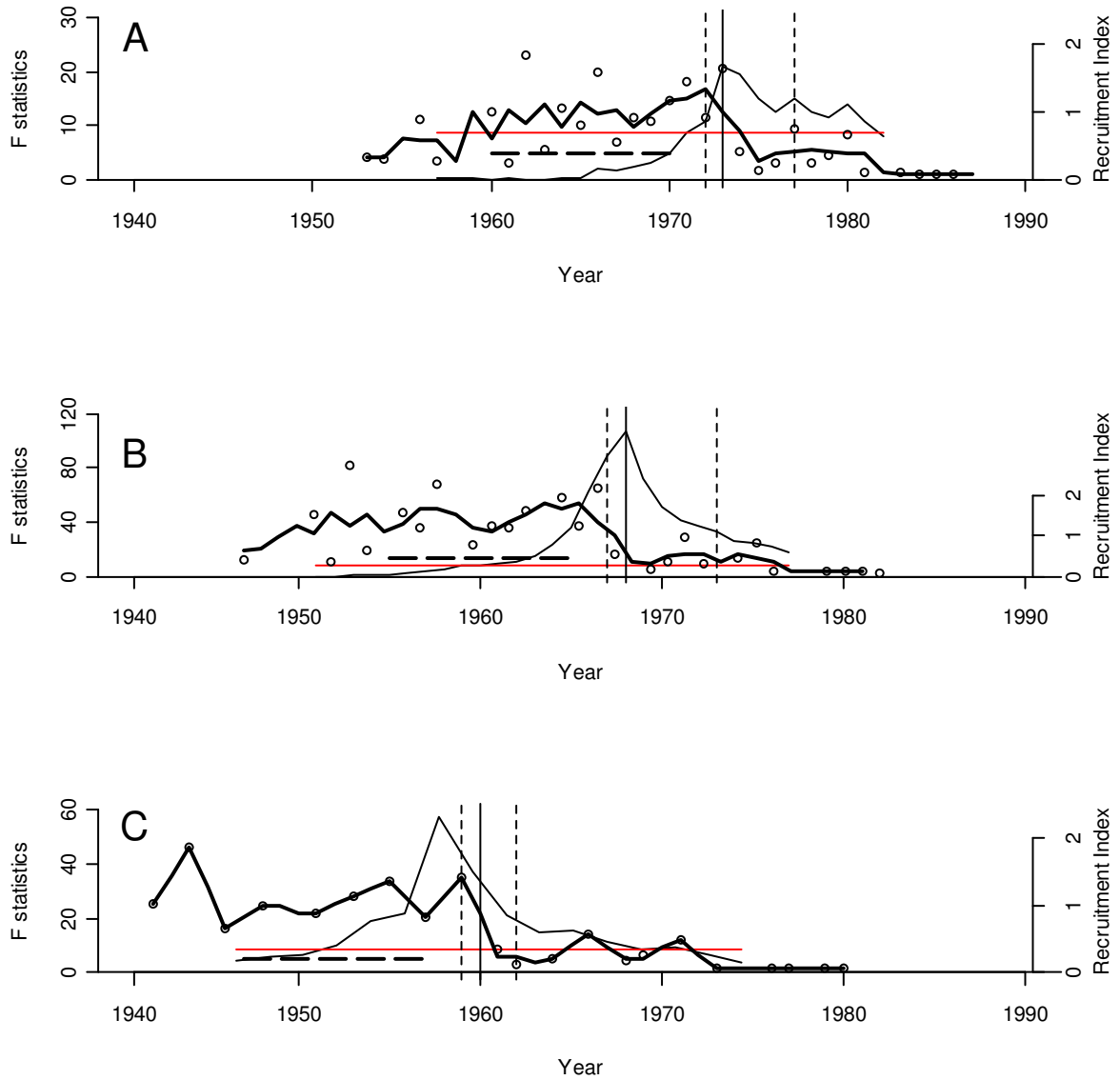


Figure 5 Hindcasted recruitment for the ROOS group, including the ROOS -N, (A), ROOS -L (B) and ROOS -H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

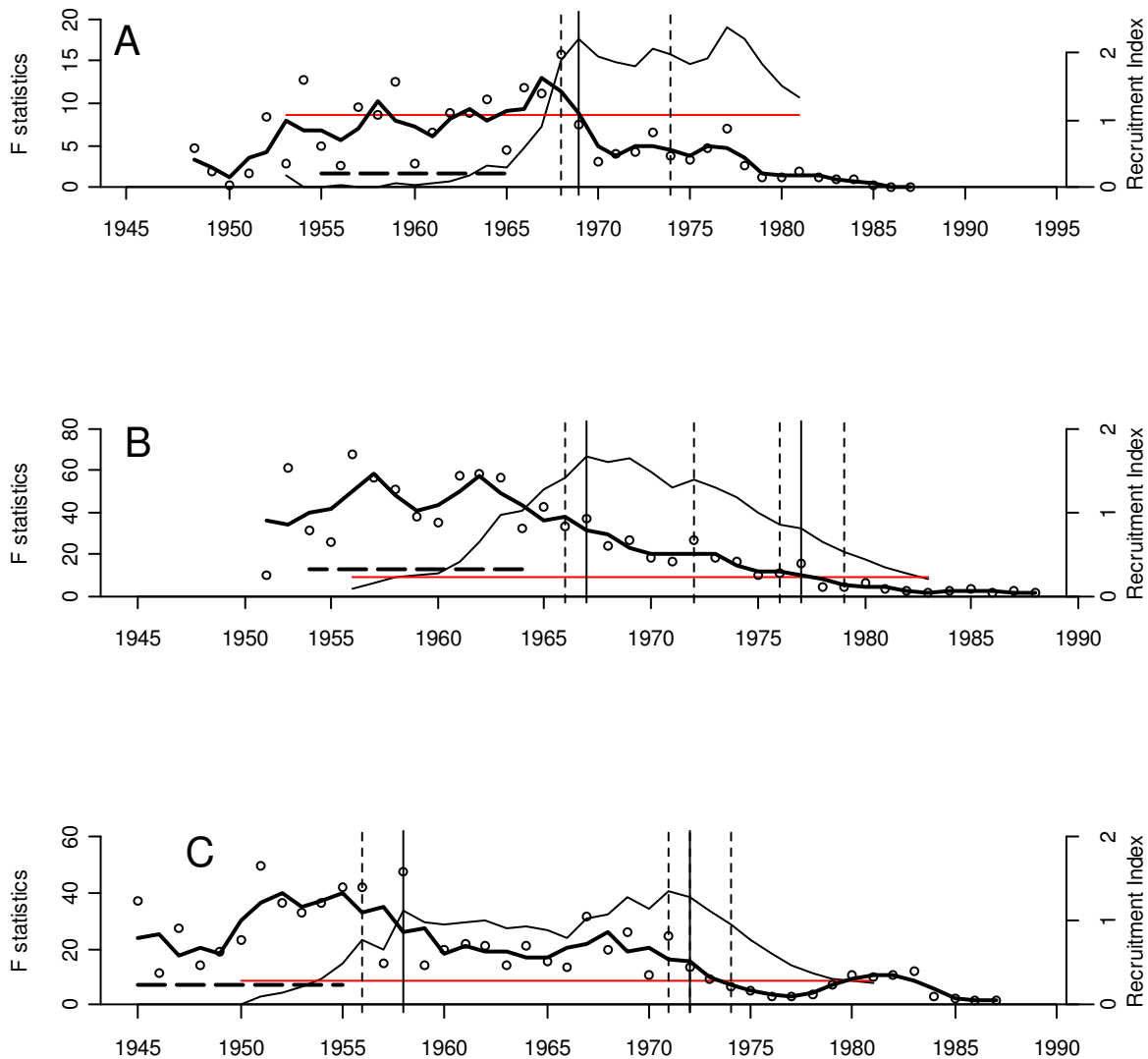


Figure 6 Hindcasted recruitment for the ALL group, including the ALL -N, (A), ALL -L (B) and ALL -H (C) aging inaccuracy scenarios (see definitions in methods). The thin black line is the F statistics (left axis) and the red horizontal line indicates the significance level. Solid vertical lines are breakpoints and dashed vertical lines are the 5% and 95% confidence intervals. The bold line is the three-year moving average of annual recruitment (points – right axis). The dashed bold horizontal line indicates the historical reference period.

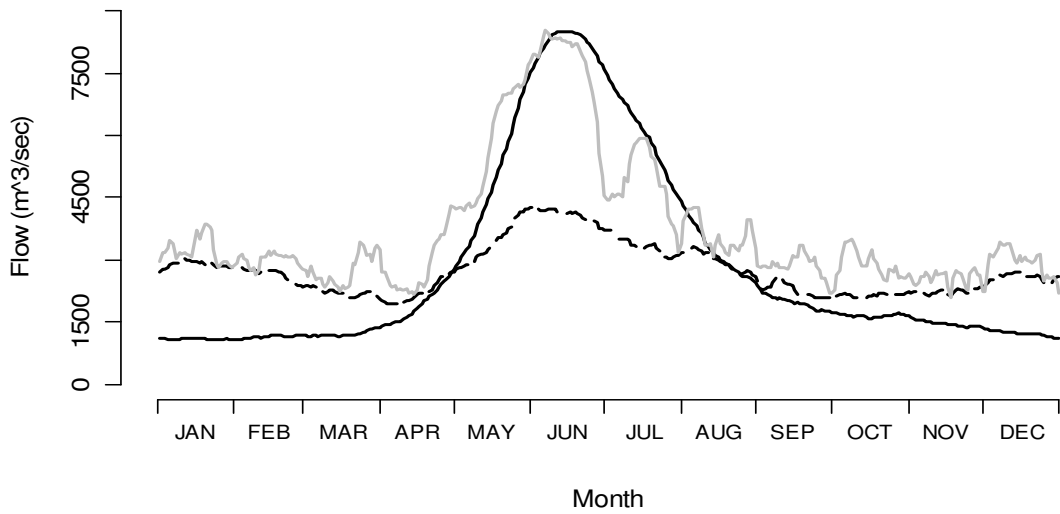


Figure 7 Historical and contemporary flow for the Columbia River at the Canada-U.S. border. Mean 1938-68 (solid), mean 1975-2001 (dashed), 1997 (grey). Data provided by BC Hydro.

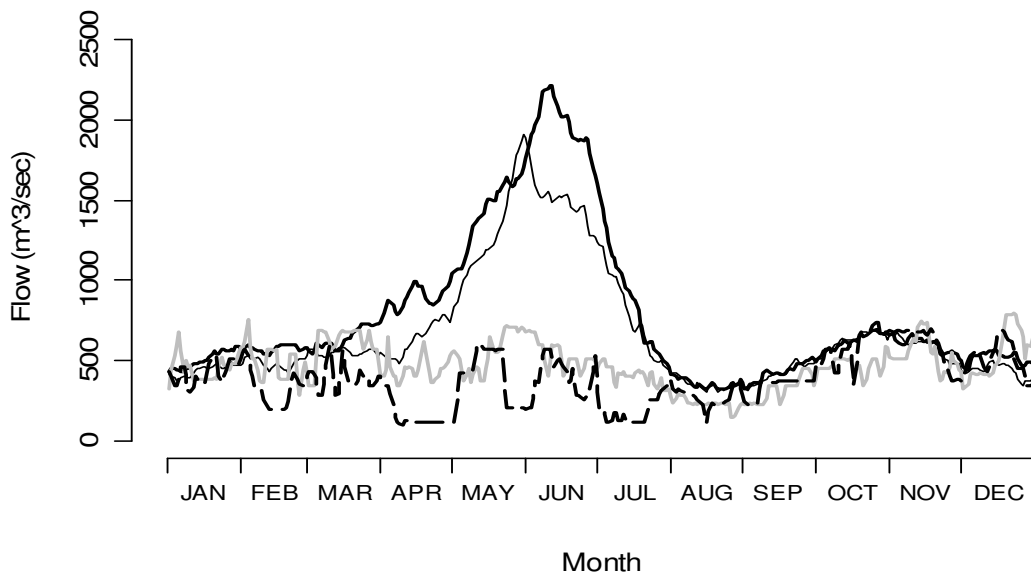


Figure 8 Mean and annual flow in the Pend d'Oreille River at Albeni Falls Dam prior to (1966-75 –black, bold) and after (1976-85 – black, thin), apparent changes in freshet volume in 1976. Two years (1973-grey, bold; 1977 -black, dashed) with uncharacteristically low flows are also shown.

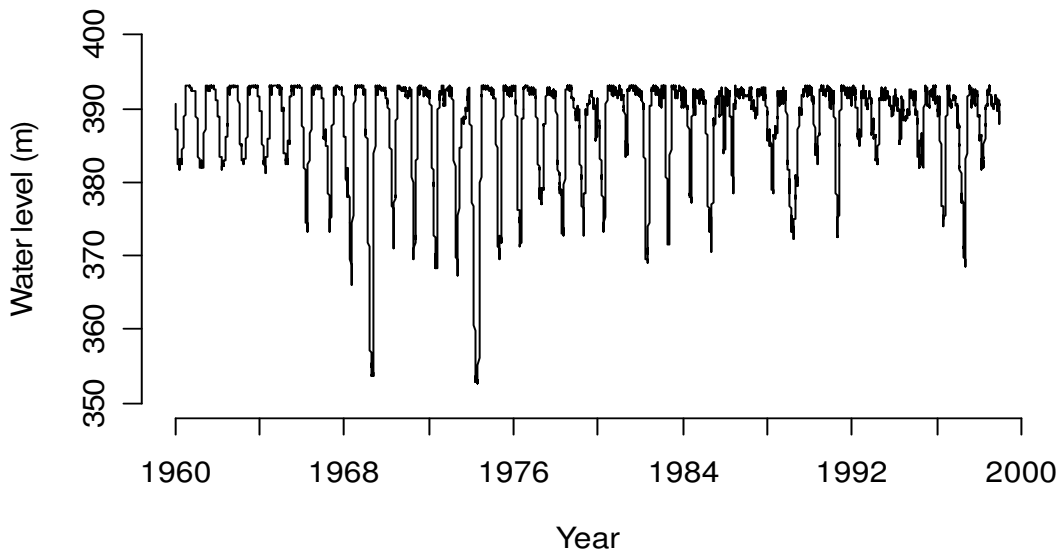


Figure 9 Daily elevation (meters above sea level) of Lake Roosevelt from 1960 to 2000.

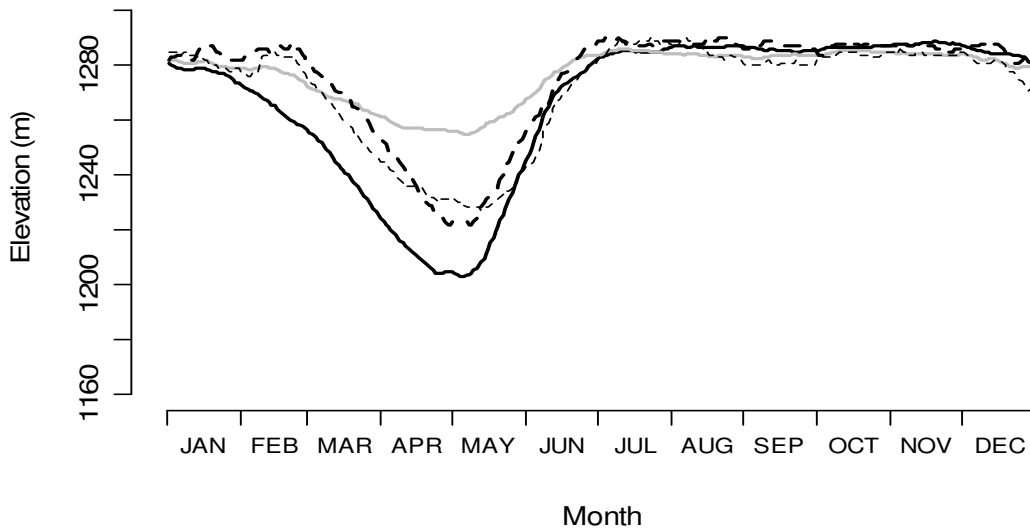


Figure 10 Daily elevation (meters above sea level) of Lake Roosevelt prior to (mean 1968-73, solid black) and after (mean 1991-96, grey) management changes about 1980. The years 1991 (bold black, dashed) and 1996 (thin black, dashed) demonstrate that variation similar to the historical conditions is still present from June to December in some years.

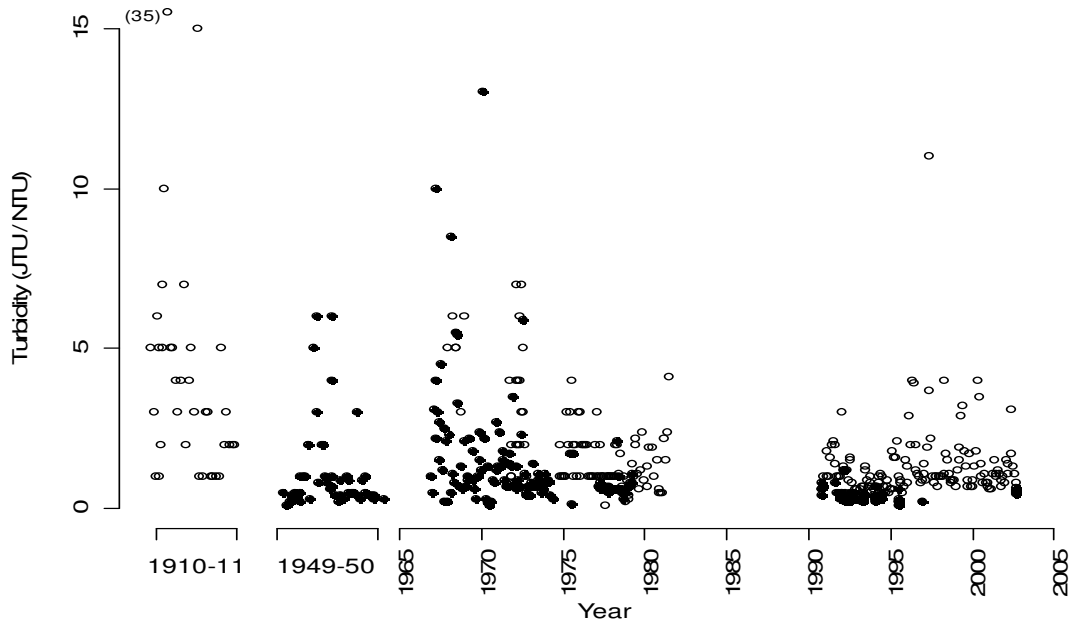


Figure 11 Turbidity at Northport (open circles) and Castlegar (filled circles) from 1967 to 2002. Note that Northport data prior to 1975 used Jackson Turbidity Units (JTU), which are roughly equivalent to Nephelometric Turbidty Units (NTU).

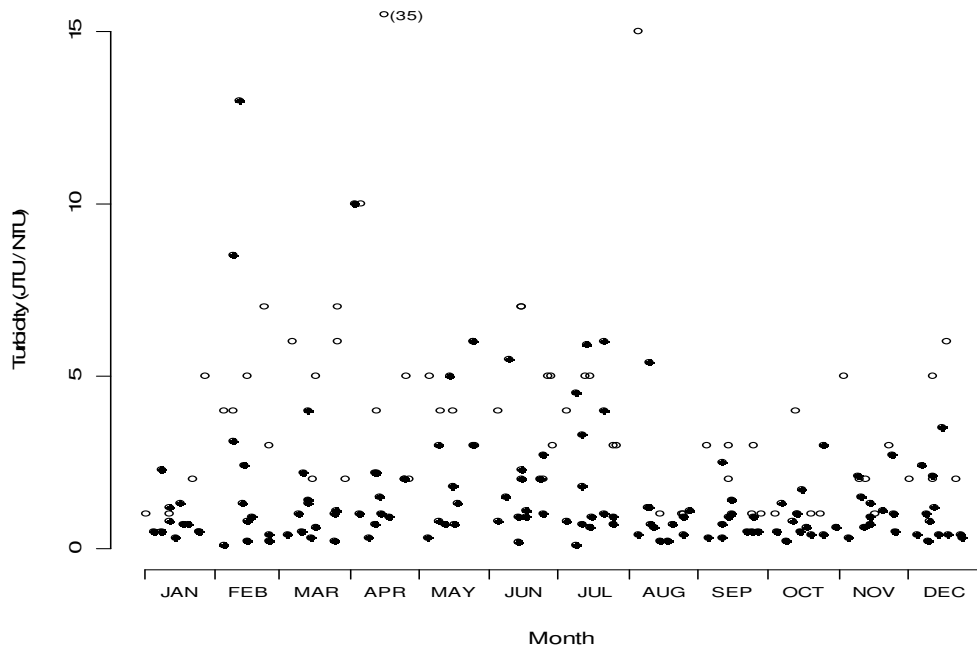


Figure 12 Seasonal pattern of turbidity prior to 1974 for Castlegar (filled circles) and Northport (open circles).

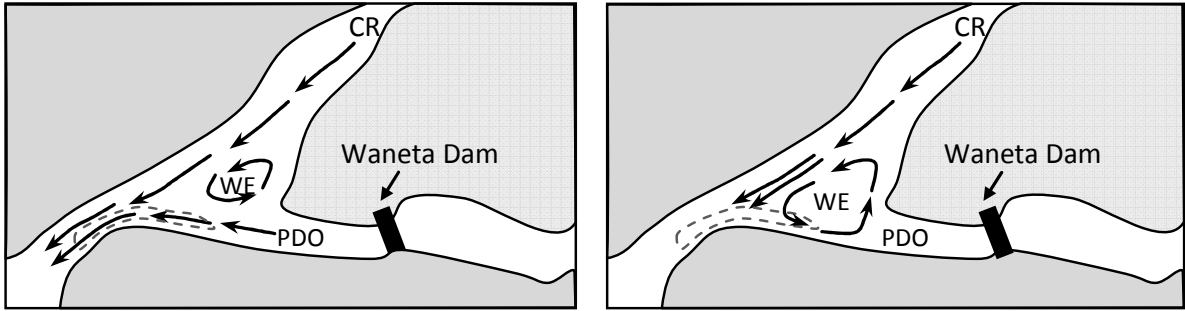


Figure 13 Schematic diagram of water circulation patterns at the confluence of the Columbia and Pend d'Oreille Rivers when Waneta Dam output is non-zero (left) and (right) when there is zero turbine or spillway flow (Fissel and Jiang 2007). WE = Waneta Eddy, CR = Columbia River, PDO = Pend d'Oreille River. Dashed grey line indicates the Waneta spawning area.

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