A decision analysis of flow management experiments for Columbia River mountain whitefish (*Prosopium williamsoni*) management

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Abstract: High spawning flows from Hugh Keenleyside Dam (HKD) on the Columbia River results in dewatering of eggs in mountain whitefish (*Prosopium williamsoni*) populations, but the ultimate effect on adult abundance depends on the shape of the egg-to-adult recruitment curve. Our decision analysis assessed the benefits of alternative flow experiments while accounting for uncertainties in this relationship and in flows in the Columbia and Kootenay rivers. The value of experimenting depended on the true recruitment relationship, how we quantified experimental benefits, and experimental design. With current uncertainty, the optimal HKD spawning flow (out of 11 alternative flows) was 1699.2 $m^3 \cdot s^{-1}$. Spawning flows below 1699.2 $m^3 \cdot s^{-1}$ did not improve egg survival because lower flows rendered high-quality spawning habitat unavailable and increased scour mortality. Two experimental designs, both with higher precision monitoring, had a high probability of detecting the true recruitment curve at reasonable cost. Information from these experiments suggested an optimal spawning flow of 1699.2 $m^3 \cdot s^{-1}$ if adult abundance were sensitive to egg mortality or 1982.4 $m^3 \cdot s^{-1}$ if the population were insensitive.

Résumé : Les forts débits du barrage Hugh Keenleyside (HKD) sur le Columbia pendant la période de fraye des populations du ménomini de montagne (*Prosopium williamsoni*) ont comme conséquence de laisser les oeufs à découvert; mais l'effet final sur l'abondance des adultes dépend de la forme de la courbe de recrutement de l'oeuf à l'adulte. Notre analyse décisionnelle évalue les bénéfices d'expériences de débit de rechange, tout en tenant compte des incertitudes de cette relation et des débits du Columbia et de la Kootenay. La valeur des expériences dépend de la véritable relation de recrutement, de la manière dont les bénéfices expérimentaux sont comptabilisés et du plan d'expérience. Compte tenu de l'incertitude actuelle, le débit optimal de HKD durant la fraye (de 11 débits de rechange examinés) est de 1699,2 $m^3 \cdot s^{-1}$. Les flux inférieurs à 1699,2 $m^3 \cdot s^{-1}$ n'améliorent pas la survie des oeufs parce les débits plus bas rendent inaccessibles des habitats de fraye de haute qualité et augmentent la mortalité due à l'affouillement. Deux plans d'expérience, tous deux avec une précision supérieure de surveillance, ont une probabilité de détecter la véritable courbe de recrutement à un coût raisonnable. Les informations fournies par ces expériences indiquent un débit optimal pendant la fraye de 1699,2 $m^3 \cdot s^{-1}$ si l'abondance des adultes est sensible à la mortalité des oeufs et de 1982,4 $m^3 \cdot s^{-1}$ si la populatioest pas sensible à cette mortalité.

[Traduit par la Rédaction]

Introduction

The effect of regulated rivers on downstream fish populations is a subject of considerable interest in fisheries management. These effects range from direct effects of flows and temperatures on fish migration and physiology to indirect effects of hydraulic conditions on habitat, substrate, and food supplies. Although overall qualitative effects of flows on fish populations are often apparent, precise quantitative definition of the linkages between releases from dams and fish responses is often highly uncertain. In some cases, this is because the exact mechanisms by which changes in flows affect fish are unknown. In other cases, effects of flow conditions on life-stage-specific survival rates are readily measured, but the effects on survival over the entire life cycle are obscured by nonlinear mechanisms, such as depensation and compensation.

The Hugh Keenleyside Dam (HKD) is a hydroelectric storage facility operated by BC Hydro on the Columbia River in British Columbia (Fig. 1). Mountain whitefish (*Prosopium williamsoni*) spawn at several sites downstream from the HKD, with spawning typically occurring during the first 3 weeks of January and egg hatching occurring in March (R.L. & L. Environmental Services Ltd. 1998*a*). In general, there are limited data on the population dynamics and habitat use of mountain whitefish throughout their range because

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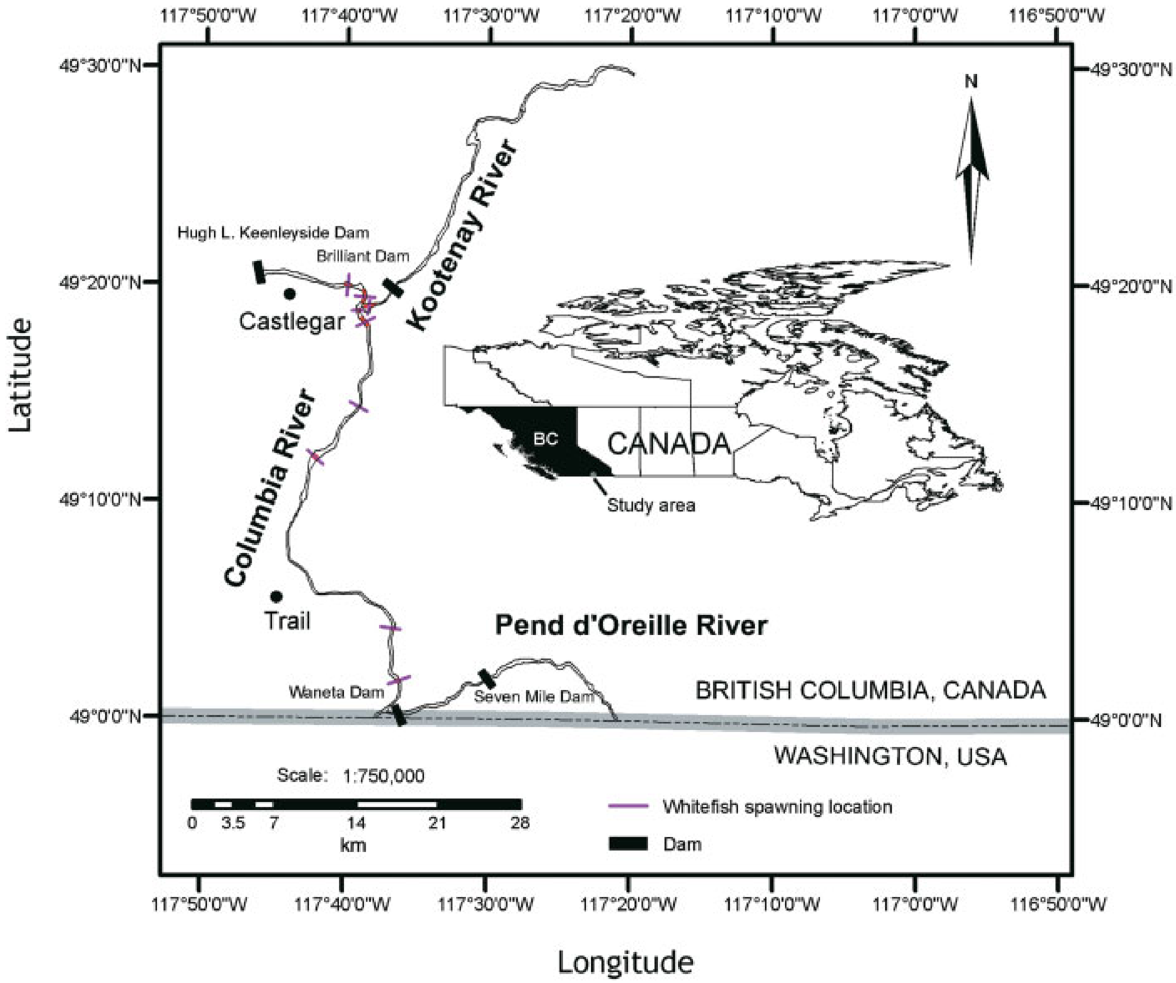
Fig. 1. Map of study area in British Columbia, Canada (inset), showing location of Hugh Keenleyside and Brilliant dams and mountain whitefish (*Prosopium williamsoni*) spawning sites.



management agencies usually regard them as a secondary sport fish (Ford et al. 1992; Northcote and Ennis 1994).

Operating HKD during the whitefish spawning period includes a trade-off between (*i*) releasing large amounts of water to increase power revenues through the peak winter demand and satisfy transborder water agreements and (*ii*) creating the potential for significant dewatering mortality of whitefish eggs if HKD flows decrease substantially between the spawning period in January and the hatching period in March. The significance of egg dewatering mortality on subsequent adult whitefish recruitment is unknown. This uncertainty makes it difficult to quantify the trade-offs between power revenues and whitefish adult abundance and thus to determine the optimal HKD releases during the whitefish spawning period. A quantitative approach that explicitly recognizes uncertainties and trade-offs generally leads to improved decision making in the long term (Von Winterfeldt and Edwards 1986; Peterman and Anderson 1999; Peters and Marmorek 2001).

The uncertainty in whitefish population dynamics could be reduced by experimentally altering HKD spawning flows and estimating adult whitefish recruitment and total egg abundance just prior to hatching. The additional evidence generated would allow an optimal action to be identified with more economic and biological certainty. During the learning period, such experiments may, however, involve both additional management costs (i.e., more extreme variations in flows to generate enough contrast to detect the relationship between egg abundance and adult recruitment, a greater investment in whitefish monitoring) and a greater biological risk (i.e., periodic and intentional increase in egg mortality). Fortunately, the relative benefits and costs of conducting management experiments can be evaluated using simulation modeling and decision analysis (Walters 1986; Walters and Green 1997; MacGregor et al. 2002).

Our research addressed four primary questions. First, what is the optimal HKD spawning flow given the current lack of information on the relationship between egg abundance and adult recruitment? Second, which flow experiment would generate the most information for the lowest cost? Third, is it worth conducting such experiments to reduce uncertainty in whitefish recruitment dynamics? Fourth, what factors and assumptions determine whether it is worth conducting flow experiments in this and other systems? By addressing these questions, we demonstrate a quantitative framework for evaluating flow actions and experiments and provide general guidelines on when it may be worth conducting flow experiments.

Materials and methods

Our analysis proceeded in two steps. First, we conducted a "base case" decision analysis of alternative, long-term management actions based on the current level of uncertainty in flows, whitefish recruitment dynamics, and other important factors. For each of these factors, we formulated several hypotheses about the response of whitefish recruitment to changes in egg abundance and assigned probabilities to each according to currently available evidence. Second, we simulated alternative HKD flow operations and measurement error from hypothetical mark–recapture population abundance surveys to evaluate the long-term value of collecting information on the whitefish egg-to-age-4 recruitment relationship. We used the simulated "new information" to update prior probabilities on the alternative egg-to-age-4 recruitment relationships in the base case decision analysis. We then repeated the base case decision analysis using the updated probabilities to determine the benefit of collecting that information relative to the current situation, where the shape of the recruitment relationship is unknown. These steps are described in detail below.

Data sources

In addition to acquiring data from unpublished agency and consultant reports, we facilitated model design and review workshops involving over a dozen specialists in whitefish biology and related field sampling, as well as experts in Columbia and Kootenay river hydrology, dam operations, and hydro valuation. (A list of the participating experts is available from the corresponding author). Model assumptions reflect the collective professional judgments of these workshop participants.

Base case decision analysis

We computed expected outcomes for each management action (e.g., alternative HKD spawning flows), probability-weighted over alternative hypotheses (e.g., whitefish population dynamics and Columbia and Kootenay river flows). There were five components of our decision analysis of HKD spawning flows: management objectives, alternative actions, performance measures, models, and uncertainties (including associated probabilities). Each component is described below.

Management objectives

To evaluate alternative flow release actions, we formulated the following management objective: maximize power generation opportunities (i.e., maximize HKD spawning flows) subject to maintaining the adult whitefish population at or above 45 000 individuals. If none of the actions produced an adult population of 45 000 fish or more, then the optimal action was the one that maximized the adult whitefish population. This objective was accepted by workshop participants for illustrative analyses of economic–biological trade-offs. Field mark–recapture estimates suggested that the population abundance was 40 000 – 60 000 adults (R.L. & L. Environmental Services Ltd. 1998*b*). 45 000 was chosen as the lower limit below which stakeholders did not wish to see the population fall. However, it did not necessarily reflect the specific objectives that might be proposed by stakeholders (e.g., Fisheries and Oceans Canada; British Columbia Ministry of Water, Land, and Air Protection; BC Hydro; and First Nations). As the best action generally depends on the objective, we recommend repeating our analysis for objectives formally developed by agency representatives, including objectives for other fish species.

Alternative management actions

In the base case decision analysis, we evaluated 11 different flows potentially released from the HKD during the spawning period (1–21 January) ranging from 566.4 to 2407.2 $m^3 \cdot s^{-1}$. These flows span the range of average discharge over the period of record (26 years), which in recent years has averaged 1557.6 $m^3 \cdot s^{-1}$. Except for the Kootenay River, we ignored flow variation from other small tributaries between HKD and the US border because they contribute little to the total Columbia River flow at the spawning areas of interest.

Performance measures

We used two performance measures to assess the merits of alternative spawning flows below HKD. Our biological performance measure was the expected adult (ages 4–11) whitefish population abundance in simulation year 50. The economic performance measure was based on the expected annual maximum power revenues at a particular average spawning flow. Estimates of maximum power revenues at each alternative spawning flow were probability-weighted to account for uncertainties in power demand and other factors that determine revenues (A. Woo, BC Hydro, Operations and Energy Purchases, 6911 Southpoint Drive, Burnaby, BC V3N 4X8, Canada, personal communication). Hence, these revenue estimates represent best professional judgment. Knowing that other factors affect operations beyond fisheries concerns (e.g., Columbia River Treaty obligations and flood control), we used these maximum power revenue values to estimate the incremental differences in annual revenue under different flow release experiments.

Uncertain states of nature and their probabilities

We explicitly accounted for three uncertainties in the base case decision analysis: (*i*) average Kootenay River flows during whitefish spawning, (*ii*) minimum Kootenay and Columbia river flows during whitefish egg incubation, and (*iii*) the shape of the egg-to-age-4 recruitment relationship.

The Kootenay River joins the Columbia River about 10 km downstream from the HKD and affects Columbia River water depths at several key whitefish spawning locations (Fig. 1). Kootenay River flows are regulated by the Brilliant hydroelectric facility, but because this facility is operated independently of HKD, we did not directly consider linked management policies between the Brilliant and HKD dams. Instead, we considered a range of average Kootenay spawning flows from 283.2 to 1557.6 $m^3 \cdot s^{-1}$ in 141.6 $m^3 \cdot s^{-1}$ increments, which correspond to the range of flows since 1990 (Environment Canada 1999). Probabilities for each of these Kootenay River spawning flows were assigned based on expert judgement of BC Hydro managers and hydrologists and reflected flow frequencies under normal operation of the Brilliant Dam. We explored the effects of altering this probability distribution using sensitivity analysis.

We also considered uncertainty in the average minimum flows in the Kootenay and Columbia rivers between 1 and 15 March (end of whitefish egg incubation having lowest flows). These flows are under management control, but because they are much more dependent on electricity demand and hydrologic conditions than on desired whitefish spawning flows, we chose to treat them as an uncertainty rather than a management action. We considered Kootenay River flows ranging from 283.2 to 1557.6 $m^3 \cdot s^{-1}$ and Columbia River flows ranging from 424.8 to 2407.2 $m^3 \cdot s^{-1}$, both in 141.6 $m^3 \cdot s^{-1}$ increments (total of 150 unique combinations of flows from the two rivers). The short duration of the historical record and the many nonrandom flow management considerations implicit in these data prevented empirical estimation of probabilities, so we assigned subjective weights to each of the 150 combinations of flows based on the professional judgments of participating experts. These subjective distributions were also conditional and reflected observed, weak negative correlations between spawning flows and subsequent minimum incubation flows (i.e., higher spawning flows reduced the range of minimum incubation flows just prior to hatching because of watershed storage considerations). We also used sensitivity analysis to explore the effects of altering these flow distributions.

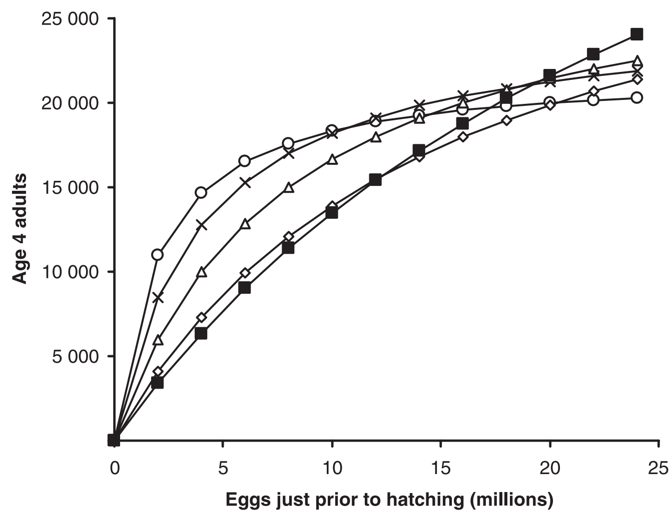
Field studies show that lower Columbia River mountain whitefish are reproductively mature at ages 3–11 years, adult spawners broadcast their eggs, and the median adult population abundance during the early 1990s was approximately 50 000 (R.L. & L. Environmental Services Ltd. 1998*b*). However, there were no reliable data on the underlying population dynamics. We used the Beverton–Holt model (Beverton and Holt 1957) to represent the assumed relationship between the abundance of eggs and the subsequent recruitment of age-4 whitefish:

$$(1) \qquad R_{\text{age4},t} = [aE_{t-4}/(b + E_{t-4})]\exp(\nu)$$

where $R_{\text{age4},t}$ is the total abundance of 4-year-old mountain whitefish produced from eggs, E (millions), that were spawned in year $t - 4$, a and b are estimated parameters, and $\exp(\nu)$ is a lognormally distributed random variable that accounts for natural variability (ν is a normally distributed random variable with a mean of 0 and standard deviation, SD_ν). For the base case decision analysis, simulations assumed $SD_\nu = 0$. We focused on 4-year-old adults because it is difficult to reliably sample individuals less than 4 years of age (D. Sneep, Fisheries and Oceans Canada, Suite 200 401 Burrard Street, Vancouver, BC, Canada V6C 3S4, personal communication).

Because the true relationship is unknown, we hypothesized five alternative recruitment relationships characterized by unique combinations of a and b parameter values (Fig. 2). The relationships covered a wide range of assumptions about the degree of compensatory density dependence acting to stabilize the adult population to reductions in egg abundance. We assigned equal probabilities to each of the five alternative hypotheses in the base case decision analysis because there were no reliable data nor informed expert opinions to justify unequal probabilities. Since our analysis was centered around the ability of different flow experiments to detect compensatory recruitment (rather than providing specific population parameter estimates or forecasting expected abundance), we did not attempt to specify a continuous bivariate posterior distribution. Instead, we chose five recruitment relationships that all produced an equilibrium adult population abundance of roughly 50 000 adults in the absence of dewatering mortality but were greatly different in their sensitivity to egg dewatering mortality (steepness values, z, of 0.54–0.94).

Fig. 2. Alternative hypotheses for the relationship (eq. 1) between eggs and subsequent age-4 mountain whitefish (*Prosopium williamsoni*). In the base case decision analysis, each curve was assigned equal probability because there were no data to estimate probabilities empirically. The alternative hypotheses represent different levels of sensitivity: insensitive (open circles, H5), moderately insensitive (crosses, H4), neutral (open triangles, H3), moderately sensitive (open diamonds, H2), and sensitive (solid squares, H1); values of steepness (z) for these five recruitment curves were 0.94, 0.9, 0.82, 0.67, and 0.54, respectively.



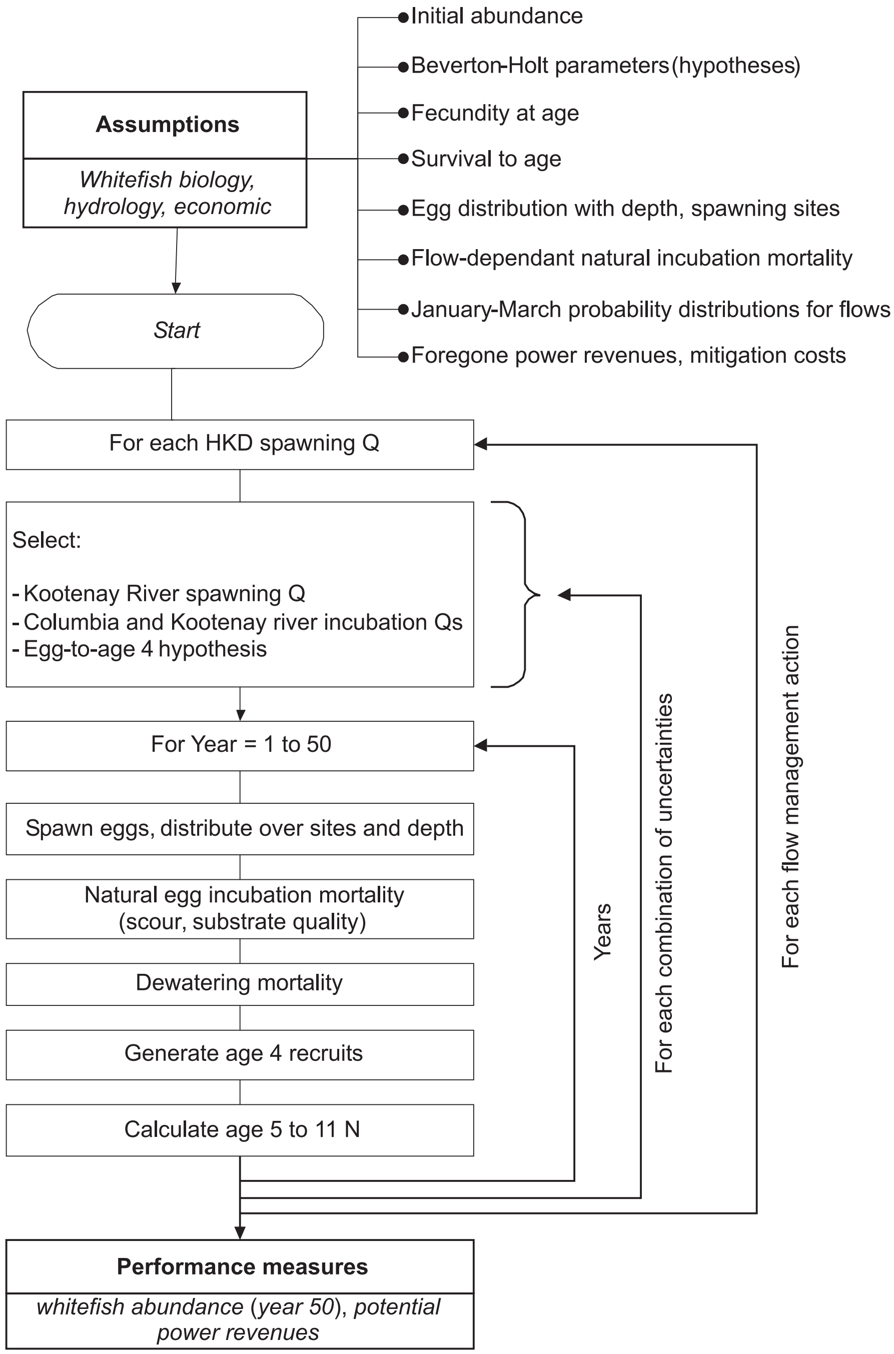
Model

We developed an age-structured population model (Hilborn and Walters 1992) for mountain whitefish to evaluate the biological and economic trade-offs of alternative spawning flows at HKD (Fig. 3). The model had five major components: (*i*) spawning and distribution of eggs; (*ii*) survival rate of eggs during incubation; (*iii*) dewatering mortality of eggs; (*iv*) egg-to-age-4 recruitment; and (*v*) survival of age-4+ adults. We ran each simulation for 50 years to ensure that the population had achieved equilibrium conditions.

Spawning site preferences and vertical distribution of eggs

Twelve major spawning sites for mountain whitefish have been identified through field observations downstream from HKD (Fig. 1). We assumed that the proportion of whitefish spawning at each site was the same in all simulation years. We calculated the total number of eggs deposited at each site from the total number of adult spawners, the proportion spawning at that site, and average fecundity-at-age values provided by field studies (R.L. & L. Environmental Services Ltd. 1998*b*). In our simulations, spawning mountain whitefish broadcast their eggs at different depths in the manner determined by a fixed egg deposition function (Fig. 4*a*), based on spawning studies at a limited number of sites (R.L. & L. Environmental Services Ltd. 1995, 1998*b*) and expert judgment. This assumed egg depth distribution was then weighted by each site's wetted area at depth in increments of 30 cm to account for cross-sectional characteristics (Fig. 4*b*). We used the US Army Corps of Engineers Hydrologic Engineering Center's River Analysis System (HEC-RAS v.2.2) (http://

Fig. 3. Flowchart of the simulation model used to calculate the outcome of each Hugh Keenleyside Dam (HKD) spawning flow option for each recruitment hypothesis and Columbia–Kootenay river flow combination. *Q*, river discharge.



www.hec.usace.army.mil/) to generate estimates of wetted area at depth increments for each spawning location and each combination of Columbia and Kootenay river incubation flows (Fig. 4*c*). We explored the effects of altering spawning site preferences and the egg deposition function using sensitivity analysis.

Natural (unrelated to dewatering) survival rate of eggs

We assumed that the natural survival rate of incubating eggs would vary with both spawning and incubation flows (Fig. 5). Survival rates were assumed to be higher with high spawning flows because these flows expose better quality spawning substrate found higher on the channel banks. However, high incubation flows led to increased scour of egg pockets and lower rates of survival. For typical Columbia and Kootenay river spawning and incubation flows, we assumed that these relationships resulted in an average survival rate of 0.1, consistent with rates suggested by field studies (D. Sneep, Fisheries and Oceans Canada, Suite 200 401 Burrard Street, Vancouver, BC V6C 3S4, Canada, personal communication).

Dewatering mortality of incubating eggs

The proportion of eggs dewatered at each spawning loca-

Fig. 4. (*a*) Vertical egg deposition function used for all 12 spawning sites. (*b*) Example of eggs at depth produced by combining the egg deposition function with wetted area at depth results from Hydrologic Engineering Center's River Analysis System (HEC-RAS) for Middle Tin Cup rapids at a particular discharge. The solid line in panel *b* represents the egg deposition function, the line with solid diamonds represents the physical wetted area at depth, and the line with shaded circles indicates the resultant eggs at depth (product of egg deposition and wetted area at depth). (*c*) Water elevation – discharge relationship from HEC-RAS for Middle Tin Cup rapids.

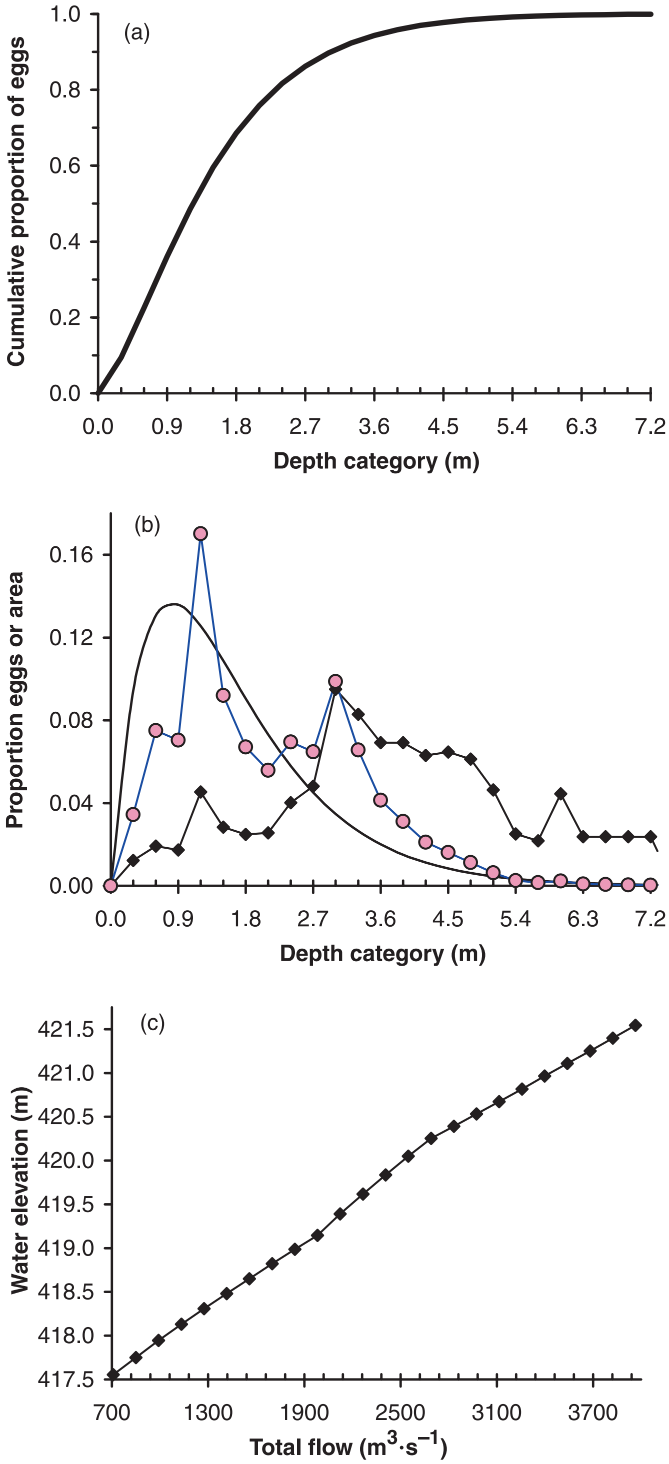
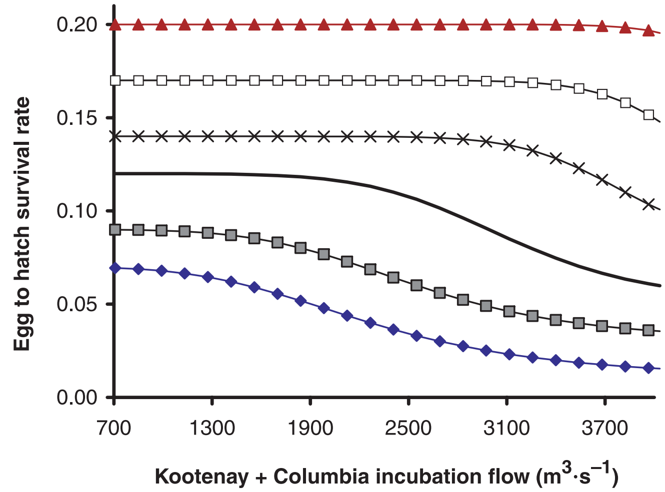


Fig. 5. Assumed family of curves used to calculate natural survival rate of incubating eggs that is unrelated to dewatering mortality. Lines represent different Columbia plus Kootenay river combined spawning flows (top to bottom): 4248 $m^3 \cdot s^{-1}$ (solid triangles); 3540 $m^3 \cdot s^{-1}$ (open squares); 2832 $m^3 \cdot s^{-1}$ (crosses); 2124 $m^3 \cdot s^{-1}$ (solid line), 1416 $m^3 \cdot s^{-1}$ (shaded squares), and 708 $m^3 \cdot s^{-1}$ (solid diamonds). Higher spawning flows increase availability of better substrate, improving egg survival. Higher incubation flows increase egg scour. Simple linear interpolation was used to obtain survival rates for flows between these curves of 708 $m^3 \cdot s^{-1}$ increments.



tion was calculated in two steps. First, we used relationships between river flow and water depth for each spawning location (described above) to determine the difference in river depth between spawning period and incubation flows. We then applied the area-weighted egg deposition function described earlier to calculate the proportion of eggs in each dewatered depth interval in 30 cm increments.

Egg-to-age-4 recruitment

We used the Beverton–Holt model (parameterized for the selected hypothesis) as described earlier in eq. 1 (and shown in Fig. 2).

Survival of age-4+ adults

We assumed constant, age-specific survival rates averaging 0.58 (0.62 for age-4 to 0.53 for age-10) to calculate the abundance of adults aged 5–11 years for each simulation year. These values were based on limited field data and professional judgment of workshop participants. With negligible dewatering mortality, this survival rate and our natural egg-survival assumptions yielded a long-term population abundance of roughly 50 000 under average flow conditions and any of our five egg-to-age-4 recruitment hypotheses.

Simulated adaptive management

Simulated experimental flow scenarios and population monitoring

In our adaptive management simulations, an experimental action consisted of a temporal pattern of HKD spawning flows, a total duration for the experiment over which that pattern was repeated, and a specified intensity of field monitoring in a hypothetical adult whitefish mark–recapture program

Table 1. Definition of alternative experiments.

Flow pattern	Experiment	Duration (years)	Survey intensity	CV Ages 4 to 11	CV Eggs	Experimental cost ($ millions)
Constant	C10L	10	Low	0.45	0.10	0.48
	C10H	10	High	0.18	0.0125	1.55
Passive	P10L	10	Low	0.45	0.10	0.63
	P10H	10	High	0.18	0.0125	1.70
	P20L	20	Low	0.45	0.10	1.24
	P20H	20	High	0.18	0.0125	3.35
	P40L	40	Low	0.45	0.10	2.46
	P40H	40	High	0.18	0.0125	6.65
Active	Ac10L	10	Low	0.45	0.10	3.48
	Ac10H	10	High	0.18	0.0125	4.55
	Ac20L	20	Low	0.45	0.10	6.94
	Ac20H	20	High	0.18	0.0125	9.05
Aggressive	Ag+10L	10	Low	0.45	0.10	19.23
	Ag+10H	10	High	0.18	0.0125	20.30

Note: Survey intensity is the level of population monitoring effort within a year gauged by the number of repeat surveys (2 or 8). CV (coefficient of variation) is the relative measurement error for these two levels of monitoring effort. Ages 4 to 11 CVs were stable from ages 4 through 7, and then slowly increased, to reflect increased sampling variability for less abundant, older age classes. Values shown are averages (slightly lower for younger ages, slightly higher for older ages) across all ages. Costs (in millions of year 2000 Canadian dollars) include foregone power revenues for experimental flows, one-time establishment costs for monitoring programs, and annual operating costs.

(number of sequential passes and removals through the study area). We formulated four alternative patterns of HKD spawning flows: (*i*) a constant approach that fixed HKD spawning flows at 1557.6 $m^3 \cdot s^{-1}$ (the average daily flow from 1985 to 2002) in each simulation year; (*ii*) a low-contrast passive pattern based on actual spawning flows since 1997 in which flows varied from 1274.4 to 1840.8 $m^3 \cdot s^{-1}$ in a 10-year sequence (average 1557.6 $m^3 \cdot s^{-1}$); (*iii*) a high-contrast active approach that alternated between flows of 991.2 and 1840.8 $m^3 \cdot s^{-1}$; and (*iv*) an aggressive active approach that alternated between flows of 566.4 and 2265.6 $m^3 \cdot s^{-1}$. Not all of these flows were necessarily practical given current HKD operational constraints, but they provided an illustrative range of contrasts in flows. We considered experimental durations ranging from 10 to 40 years. For whitefish mark–recapture surveys, we considered low (two repeat surveys per year) and high (eight surveys) levels of sampling effort. We assumed two levels of measurement error in estimates of egg and adult abundance for these surveys, consistent with the range of those estimated for large-scale biological sample surveys (Cochran 1977). Annual costs for these two levels of survey effort were based on costs of previous mark–recapture studies for the study area. We present 14 overall experimental actions composed of unique combinations of these various components (Table 1).

Model

To assess the value of alternative adaptive management experiments, we added a Monte Carlo shell around our age-structured population model for mountain whitefish to generate simulated data that included both process and observation error. The simulated data was then used to update the probabilities in, and thus the expected outcomes for, the base case decision analysis. Specifically, this required the addition of three new components to the model just described: (*i*) specification of the true underlying egg-to-age-4 recruitment dynamics and level of natural variability; (*ii*) measurement variability in field estimates of egg and age-4+ whitefish abundances; and (*iii*) an assessment model to update relative probabilities for the five alternative egg-to-age-4 recruitment hypotheses based on the new simulated data. Components (*i*) and (*ii*) were required (respectively) to simulate true population dynamics and to generate associated sample data associated with the assumed true dynamics. Component (*iii*) was used to find updated probabilities for the five uncertain states of nature and to recalculate expected outcomes in the decision analysis. We determined the value of experimenting and monitoring by comparing expected outcomes without data (base case decision analysis described previously) with the new sample data from the different experiments. We describe details of our management strategy evaluation framework (see Butterworth and Punt 1999; McAllister et al. 1999; Smith et al. 1999) and its steps along with several new performance measures for appraising the 14 experiments below.

True recruitment dynamics

Because the true recruitment dynamics are unknowable, we focused only on the two most extreme recruitment hypotheses, which we refer to as the insensitive and sensitive cases (defined by the *a* and *b* parameter values in eq. 1). These two cases bracketed the range of possible responses of adult whitefish abundance to egg mortality (Fig. 2) and also defined the range of effect sizes that the experiments must detect (the sensitive hypothesis should be easier to detect because a given reduction in eggs causes a much larger decline in adult abundance than with the insensitive hypothesis). We used the Beverton–Holt stock–recruitment model (eq. 1) to simulate production of age-4 adult recruits for these two separate cases of true dynamics. So that simulated data produced by the model accounted for natural variability in recruitment, the lognormally distributed random variable

$\exp(\nu)$ was set to $SD_\nu = 0.40$ for both cases of true dynamics. We conducted a sensitivity analysis with values of SD_ν of 0.55 and 0.25.

Observation model

We simulated the measured abundance of mountain whitefish ages 4 through 11 ($N_{age,o}$) from a hypothetical mark–recapture survey by adding a multiplicative normal error term to the true abundance at age (N_{age}):

$$(2) \qquad N_{age,o} = N_{age} + (N_{age} \cdot CV_{age} \cdot \omega)$$

where CV_{age} is the age-specific coefficient of variation in the adult abundance estimates associated with the two levels of monitoring intensity (Table 1), and ω is a normal random variable with a mean of 0 and SD of 1 (applied across all ages). The observation model also included adding a multiplicative normal error term to the average age-specific fecundity values to simulate measurement error in the estimated total population egg abundance, E_{brood}, as follows:

$$(3) \qquad E_{brood} = \sum_{age=4}^{age=11} N_{age,o}\,[f_{age} + (f_{age} \cdot CV^*_{age} \cdot \omega^*)]$$

where $N_{age,o}$ is the estimated mountain whitefish abundance at age from eq. 2, f_{age} is the true average fecundity at age, CV^*_{age} is the age-specific coefficient of variation in estimates of age-specific fecundity for the two levels of monitoring intensity (Table 1), and ω^* is defined as in eq. 2 (note that the value from eq. 3 is independent from the value used in eq. 2).

Next, we performed 350 Monte Carlo trials, each producing a simulated data set having *n* egg-to-age-4 observations, where *n* is the length in years of the adaptive management experiment. Tests showed that 350 Monte Carlo trials were sufficient to produce stable values for all model performance measures. Because of the 4-year lag involved in generating a single egg-to-age-4 data point, we assumed the population monitoring program continued 4 years beyond the end of a flow experiment to estimate adult abundance.

Assessment model

We assigned relative probabilities to each alternative egg-to-age-4 recruitment hypothesis by taking the average normalized likelihood estimates for each hypothesis over all simulated data sets. We used the normalized likelihoods rather than Bayesian posterior probabilities because we did not have any informative prior beliefs about whitefish recruitment dynamics to introduce into the calculations (Hilborn and Mangel 1997). The likelihood of each simulated data point for a given hypothesis was calculated from the normal probability density function after taking the logarithm of the abundance at age-4 (R_{age4}):

$$(4) \qquad L_t(R_{age4}\,\text{datum} \mid a_h, b_h) = \frac{1}{(2\pi)^{0.5}\sigma} \times \exp\left[-\frac{(\log_e R_{age4,o} - \log_e R_{age4,p})^2}{2\sigma^2}\right]$$

where *t* is brood year, *h* indicates the Beverton–Holt parameter values for a particular egg-to-age-4 recruitment hypothesis, $R_{age4,o}$ is the observed age-4 recruitment from a hypothetical population monitoring survey (i.e., value of N_{age} for age-4 whitefish obtained from eq. 2), $R_{age4,p}$ is the age-4 recruitment predicted from eq. 1 (with natural variation) for the true state of nature assumed (sensitive or insensitive curve in Fig. 2), and σ is the computed residual SD for all ($\log_e R_{age4,o} - \log_e R_{age4,p}$) values. Thus, the term $L_t(R_{age4}\,\text{datum}_t \mid a_h, b_h)$ is the likelihood of a particular simulated data point given the hypothesis *h* (datum_t refers to one $R_{age4,o}$ observation in the *n* member simulated data set). The likelihood of all the simulated data given a particular hypothesis was simply the product of the likelihoods for all data points. Post-experimental probabilities for each recruitment hypothesis were approximated by normalizing these likelihoods.

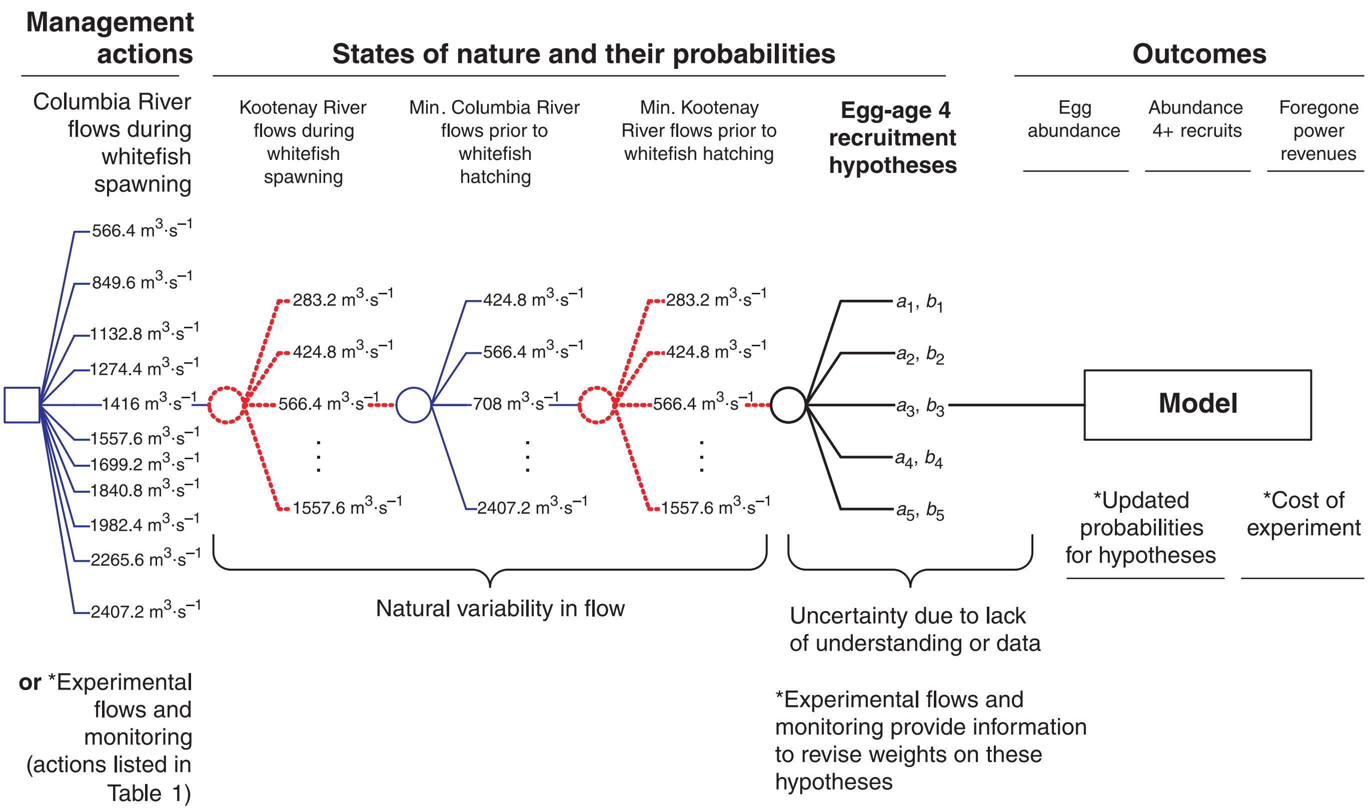
Performance measures and management objectives

We calculated the learning benefits of alternative experiments by calculating the proportion of the 350 Monte Carlo trials in which the experiment would detect either the sensitive (H1) or moderately sensitive (H2) hypotheses when the sensitive hypothesis were true, (i.e., the highest relative likelihoods among all five alternative hypotheses were under H1 or H2). Similarly, we computed the probability that the experiment would detect either the moderately insensitive (H4) or insensitive (H5) hypotheses when the insensitive hypotheses were true. This detection probability provided a measure of the experiment's ability to identify directional signals in the underlying recruitment dynamics and thus is similar (but not equivalent) to a measure of statistical power. The detection probability depended on three factors: (*i*) the schedule of experimental flows (experiments that generate greater contrast in egg mortality ought to provide better information for defining the egg-to-age-4 recruitment function); (*ii*) the magnitude of measurement error associated with different levels of monitoring effort; and (*iii*) the true underlying recruitment dynamics (magnitude of sensitivity of adult abundance to egg mortality; Fig. 2). Because the last factor was outside of the control of the experimenter, we report detection probabilities for the sensitive and insensitive cases separately.

We calculated the cost of each experiment (in millions of year 2000 Canadian dollars) as the sum of foregone power generation opportunities during the experimental learning period plus data collection costs (Table 1). There are no turbines at HKD. HKD operations affect power generation potential at other facilities downstream. The foregone power revenue owing to a given experimental flow was the difference between the maximum power revenues that could have been generated at the given flow less the value of power generated at 1557.6 $m^3 \cdot s^{-1}$, the historical winter flow required to meet transborder water agreements and other obligations unrelated to whitefish management (A. Woo, BC Hydro Operations and Energy Purchases, 6911 Southpoint Drive, Burnaby, BC V3N 4X8, Canada, personal communication). The costs incurred in each experimental year were summed over the duration of the experiment to give the total foregone power cost.

We computed long-term conservation and economic benefits of performing the experiments by updating the probabilities for each egg-to-age-4 recruitment hypothesis based on the new data collected for each experiment and population abundance survey and then repeating the base case decision

Fig. 6. Decision tree for calculating expected value of outcomes for alternative flow management actions involving population monitoring to reduce uncertainty about mountain whitefish (*Prosopium williamsoni*) recruitment dynamics. Management actions emerging from decision nodes (square) are evaluated first on the basis of current information and then after an experimental learning period. Uncertainties (round nodes) include time-period-specific Columbia and Kootenay river flows and whitefish population dynamics. All branches emerging from a given uncertainty node have probabilities that sum to 1. The two types of lines (solid and dotted) that span actions and hydrologic uncertainties reflect conditional probabilities between spawning (winter) and hatching (spring) flows on the Columbia and Kootenay rivers (i.e., to address presence of a weak negative correlation). Outcomes (performance measures) are calculated for all possible branches of the decision tree (7500 unique states of nature for each management action) and are weighted by their probability of occurrence. Probability-weighted values are summed for each action. An asterisk (*) indicates components related only to simulated, adaptive management experiments.



analysis using these updated probabilities. Formally, the benefit of an adaptive management experiment is the difference between the outcome of the decision chosen based on the additional sample information (using updated probabilities after each experiment) and the outcome of the decision based on current information (using prior uniform probabilities on the recruitment hypotheses). In decision theory, this benefit is known as the expected value of sample information (EVSI):

$$\text{(5)} \quad \text{EVSI} = E(\text{performance measure for optimal decision made with new sample information, after doing adaptive management and monitoring})_{\text{updated probabilities}} - E(\text{performance measure for optimal decision made with prior information, before doing adaptive management and monitoring})_{\text{prior probabilities}}$$

where $E(\ldots)$ is the expected value. We note that EVSI may be less than 0 if (*a*) the objective function is designed to minimize something (like mortality) or (*b*) the response direction of the performance measure to maximize (such as population abundance) happens to decline with improved information. In the latter case, improved information brings "bad news" that nevertheless can yield better decisions. The overall decision problem is summarized by the decision tree in Fig. 6.

Results

Base case decision analysis

Under base case assumptions (i.e., current uncertainty, equal

Table 2. Expected values for performance indicators in the base case decision analysis.

HKD spawning flow ($m^3 \cdot s^{-1}$)	Recruitment hypotheses H1 (Sens.)	H2	H3	H4	H5 (Insens.)	Expected value (adult abundance)	Maximum power revenues ($ millions)
566.4	12 954	18 542	33 555	41 927	43 970	30 190	0.02
849.6	21 812	26 524	40 298	45 955	46 128	36 143	0.50
1132.8	32 191	34 135	45 715	49 041	47 688	41 754	1.25
1274.4	36 839	37 073	47 646	50 074	48 204	43 967	1.61
1416.0	39 857	38 786	48 709	50 603	48 474	45 286	1.95
1557.6	41 390	39 429	49 045	50 737	48 534	45 827	2.15
1699.2*	41 643	39 321	48 868	50 593	48 455	45 776	2.40
1840.8	40 071	37 967	47 768	49 937	48 097	44 768	2.60
1982.4	37 361	36 067	46 230	49 070	47 642	43 274	3.00
2265.6	29 481	30 164	41 543	46 248	46 099	38 707	5.75
2407.2	25 327	27 092	39 029	44 775	45 322	36 309	9.00

Note: Equal prior probability on all recruitment hypotheses is 0.2. HKD, Hugh Keenleyside Dam; Sens., the sensitive egg-to-age-4 recruitment hypothesis; Insens., the insensitive recruitment hypothesis (see also H1 and H5 in Fig. 2). Power revenue estimates are in millions of year 2000 Canadian dollars.

*Values for spawning flow 1699.2 $m^3 \cdot s^{-1}$ indicate the expectation (i.e., probability weighted value) that best meets the management objective.

probability assigned to all hypotheses about egg-to-age-4 recruitment), a HKD spawning flow of 1699.2 $m^3 \cdot s^{-1}$ best met the management objective of maximizing power revenues while maintaining an adult whitefish population of at least 45 000 (Table 2). At this spawning flow, the expected adult population after 50 simulated years was 45 776, and potential annual power revenues were $2.4 million. Decreases in the expected abundance of adults for flows above and below 1699.2 $m^3 \cdot s^{-1}$were the result of dewatering mortality and scour at higher spawning flows and reductions in substrate quality at lower spawning flows.

The optimal spawning flow and economic benefits varied substantially depending on which recruitment hypothesis was true (Table 2). For example, if we were certain that the population was very sensitive to egg mortality (H1 in Table 2), the optimal HKD spawning flow would remain at 1699.2 $m^3 \cdot s^{-1}$. This flow would result in more adult whitefish than other flows (although the expected adult abundance would be below the stated management target of 45 000) and would still generate potential power revenues of $2.4 million. However, if we were certain that the adult population were insensitive to egg mortality (H5), HKD flows could be increased to 2407.2 $m^3 \cdot s^{-1}$. At this high flow, there would still be more than 45 000 whitefish adults, but potential annual power revenues would increase to $9 million.

The recruitment hypotheses also affected how narrowly the range of HKD spawning flows must be operated to avoid negative impacts on whitefish abundance. If the adult abundance were sensitive to egg mortality (H1), water and fish managers would have little margin for error in managing spawning flow because adult abundance dropped dramatically as flows increased or decreased away from the 1699.2 $m^3 \cdot s^{-1}$optimum (Table 2). Conversely, adult abundance remained relatively constant over spawning flows if the population were insensitive to egg mortality (H5), giving HKD operators much more flexibility in setting winter flows.

Sensitivity analyses showed that the optimal HKD spawning flow of 1699.2 $m^3 \cdot s^{-1}$was relatively robust to the other key model assumptions (joint probabilities on Columbia–Kootenay river incubation flows, Kootenay River spawning flows, spatial and vertical egg deposition), but moderately sensitive to the natural survival rate of eggs as a function of river depth and flow (Fig. 5).

Simulated adaptive management

Experiments varied in their learning value and economic implications, as measured by the probability of detecting directional signals in egg-to-adult recruitment and the total experimental costs (Table 3; Fig. 7). Detection probabilities depended on which recruitment hypothesis (sensitive or insensitive) was assumed to be true (Fig. 7*a*). The sensitive recruitment hypothesis was easier to detect than the insensitive hypothesis, because small variations in egg abundance caused larger variations in age-4 abundance over the range of experimental flows.

The most expensive experiments (e.g., 10-year aggressive experiment with high monitoring intensity (Ag + 10H), or less aggressive but much longer experiments such as Ac20 and P40) generally produced the highest detection probabilities, although a couple of the lower cost experiments (e.g., 10-year passive experiment with high monitoring intensity (P10H)) also produced high (>0.75) detection probabilities. Of the three experimental components (flow pattern, duration, and intensity of monitoring), monitoring intensity had the largest effect on detection probabilities. For example, a 10-year passive experiment with low monitoring intensity resulted in detection probabilities ranging from 0.65 to 0.81, while the same experiment with high monitoring intensity yielded detection probabilities from 0.77 to 0.86 (Table 3). The effect of monitoring intensity on detection probabilities was heightened when experimental durations were longer (e.g., P10L and P10H vs. P20L and P20H; Table 3), because of the cumulative effects of measurement errors in each sampling year.

Flow patterns that created larger contrasts in flows improved detection probabilities, but this improvement was secondary to the effect of increasing monitoring intensity (e.g., Ac10H

Table 3. Cost of various flow experiments, detection probabilities, optimal spawning flows, and expected performance of management using information from these alternative experiments.

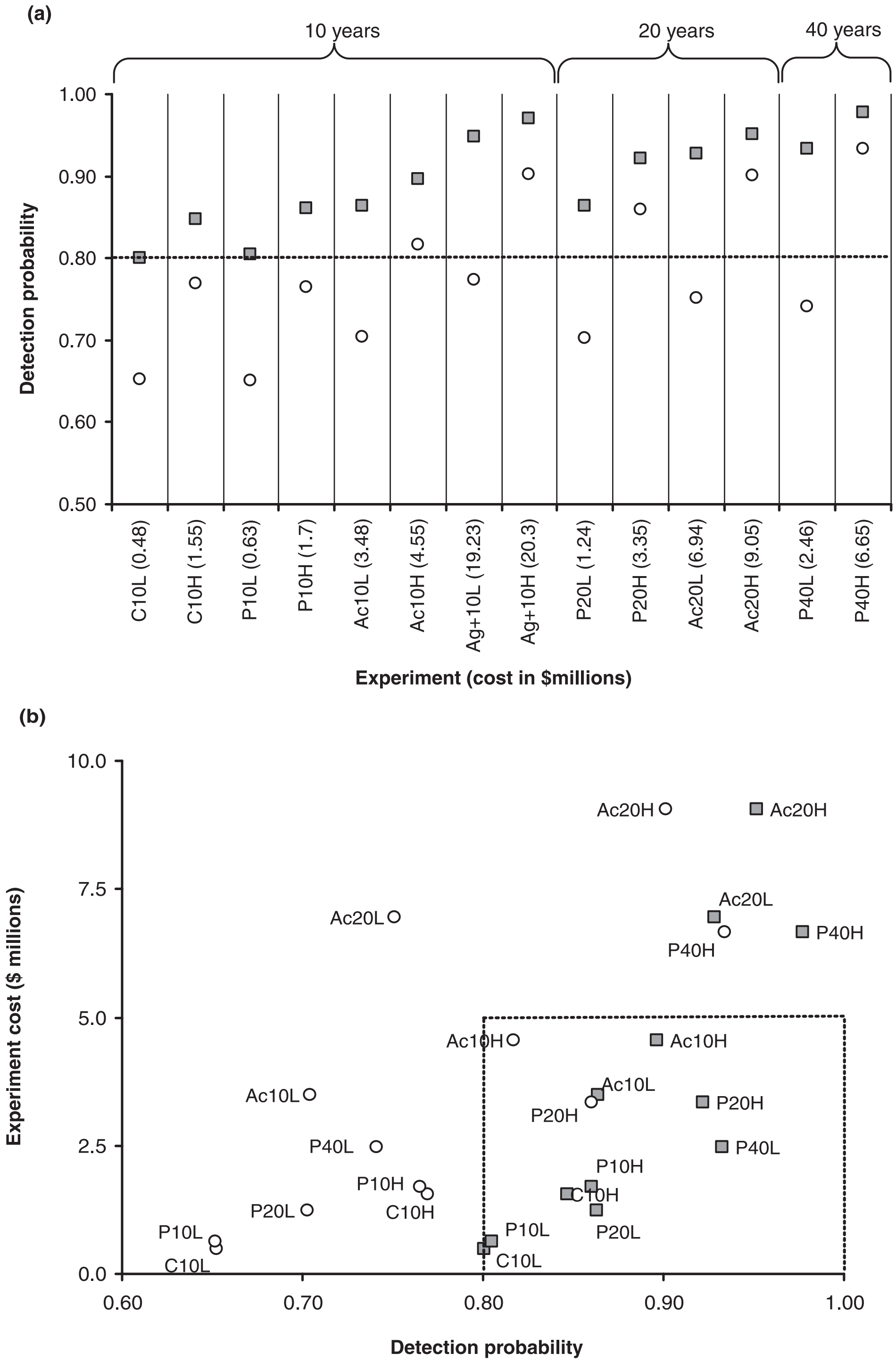
Experiment		True egg-to-age-4 recruitment dynamics									
		Sensitive (H1)					Insensitive (H5)				
Type	Cost ($ millions)	Detection probability	Optimal spawning flow ($m^3 \cdot s^{-1}$)	EV fish	EVSI fish	EVSI ($ millions)	Detection probability	Optimal spawning flow ($m^3 \cdot s^{-1}$)	EV fish	EVSI fish	EVSI ($ millions)
None	0		1699.2	45 776				1699.2	45 776		
Prior decision*			1557.6	45 827				1840.8	44 768		
								1982.4	43 274		
								2407.2	36 309		
Perfect	na	1	1699.2	41 643	–4133	0	1	2407.2	45 322	9013	6.6
C10L	0.48	0.80	1557.6	44 281	–1546	–0.25	0.65	1840.8	45 603	835	0.20
C10H	1.55	0.85	1699.2	43 539	–2237	0.00	0.77	1840.8	46 222	1454	0.20
P10L	0.63	0.81	1557.6	44 244	–1583	–0.25	0.65	1840.8	45 658	890	0.20
P10H	1.70	0.86	1699.2	43 501	–2275	0.00	0.77	1982.4	45 070	1796	0.60
Ac10L	3.48	0.86	1699.2	43 944	–1832	0.00	0.70	1840.8	45 870	1102	0.20
Ac10H†	4.55	0.90	1699.2	43 236	–2540	0.00	0.82	1982.4	45 440	2166	0.60
Ag+10L	19.23	0.95	1699.2	43 098	–2678	0.00	0.77	1982.4	45 261	1987	0.60
Ag+10H	20.30	0.97	1699.2	42 417	–3359	0.00	0.90	1982.4	46 404	3130	0.60
P20L	1.24	0.86	1699.2	43 369	–2407	0.00	0.70	1840.8	45 858	1090	0.20
P20H†	3.35	0.92	1699.2	42 872	–2904	0.00	0.86	1982.4	45 886	2612	0.60
Ac20L	6.94	0.93	1699.2	42 804	–2972	0.00	0.75	1982.4	45 000	1726	0.60
Ac20H	9.05	0.95	1699.2	42 314	–3462	0.00	0.90	1982.4	46 388	3114	0.60
P40L	2.46	0.93	1699.2	42 446	–3330	0.00	0.74	1982.4	45 064	1790	0.60
P40H	6.65	0.98	1699.2	42 120	–3656	0.00	0.93	1982.4	46 742	3468	0.60

Note: H1 and H5 refer to egg-to-age-4 recruitment hypotheses shown in Fig. 2. The expected values (EV) for adult mountain whitefish (*Prosopium williamsoni*) abundance in year 50 are given for the optimal spawning flow that would be chosen based on the information provided from each experiment. EVSI, expected value of sample information measured in units of adult whitefish and millions of year 2000 Canadian dollars; na, not applicable. Details describing each experimental type are defined in Table 1. Two main reference cases are given, the optimal action and expected performance with (*i*) no experiment (first shaded row) and (*ii*) perfect information (second shaded row).

*For comparison purposes, data are the expected values for various spawning flows based on current uncertainty (i.e., with prior uniform probabilities on recruitment hypotheses; Table 2).

†Data highlight the results for the two best adaptive management designs (see also Fig. 7).

Fig. 7. (*a*) Expected detection probabilities of all 14 alternative adaptive management experiments and (*b*) only those experiments less than CAN$10 million plotted against their respective detection probabilities. Experimental codes are defined in Table 1. Shaded squares indicate results for sensitive recruitment (hypothesis H1), open circles for insensitive recruitment (hypothesis H5).



vs. P10H). Increasing the duration of the experiment (e.g., Ac10H vs. Ac20H) caused minor improvements in detection probabilities.

Using the updated probabilities, we calculated EVSI for adult whitefish abundance and maximum power revenues for each experiment and for each assumption about the true sensitivity of adult recruitment to egg abundance (Table 3). If the population were sensitive to egg mortality (H1 in Fig. 2), we knew from the hypothetical case of perfect information that conducting experiments would not result in a change in HKD spawning flows to reduce egg mortality. This was due to the characteristics of the relationship assumed between natural egg survival rates and spawning flows; at low spawning flows, high-quality spawning habitats are unavailable (eggs deposited on armored, coarse, cobble substrate) resulting in low incubation survival rates (Fig. 5). This substrate quality effect cancelled the benefits of decreasing spawning flows to reduce dewatering mortality. In addition, EVSI measured in expected whitefish units was negative for all experiments if the population were sensitive (Table 3). This does not mean that the information had a negative value or made us worse off. Rather, EVSI reflected the directional response in expected whitefish abundance as we learned that their recruitment dynamics are more sensitive to egg losses than believed with current information.

Information generated by the experiments produced positive economic and whitefish benefits if the population were insensitive to egg mortality (Table 3). Though less than the theoretical maximum of 2407.2 $m^3 \cdot s^{-1}$, 9 of 14 experiments revealed that a 1982.4 $m^3 \cdot s^{-1}$ spawning flow would be a satisfactory management option under the insensitive hypothesis (Table 3). For these experiments, EVSI in units of increased power revenues was \$600 000·year^{-1} while still maintaining the adult whitefish population above the target of 45 000 fish (Table 3). Spawning flows greater than 1982.4 $m^3 \cdot s^{-1}$ were not selected because of the large, uncontrolled hydrological variation in the system.

Two low-contrast, low-monitoring intensity experiments (C10L and P10L) generated slightly poorer decisions than current information. These experiments led to a more conservative optimal spawning flow of 1557.6 $m^3 \cdot s^{-1}$ — a decision equivalent to committing a type I error (i.e., concluding a benefit exists when one does not). This finding presumes our management objective is strictly upheld and one made this decision assuming sensitive population dynamics. If so, the average cost of this error would be \$250 000·year^{-1} in lost power revenues. These results were not affected by the amount of natural variability in egg-to-age-4 recruitment dynamics (i.e., SD_v = 0.25 and 0.55 rather than 0.40).

Discussion

What is the optimal HKD spawning flow given the current level of information on whitefish recruitment dynamics?

Based on the current level of information on whitefish recruitment, HKD should be operated to provide spawning flows of 1699.2 $m^3 \cdot s^{-1}$. This level of spawning flow provides a balance between higher dewatering mortality at high flows and elimination of high-quality spawning habitat at lower flows. This latter factor — the effect of low spawning flow on habitat quality — proved to be an important constraint. In the absence of this effect, we would expect spawning flows to be much lower to minimize potential dewatering mortality.

The optimal spawning flow of 1699.2 $m^3 \cdot s^{-1}$is similar to flows obtained in recent years from HKD operations, which are based largely on power and flood control requirements under the Columbia River Treaty and secondarily on whitefish production requirements (A. Woo, BC Hydro Operations and Energy Purchases, 6911 Southpoint Drive, Burnaby, BC V3N 4X8, Canada, personal communication). However, our analyses show that HKD could be operated at higher spawning flows (which would produce larger power revenues) without negatively affecting adult whitefish abundance if there were stronger evidence of compensatory recruitment relationships. Such information is therefore potentially valuable and provides an incentive to conduct flow management experiments and monitoring.

Which potential flow experiment generates the most information for the lowest cost?

The ability of flow experiments to detect directional signals in recruitment dynamics depends primarily on the true underlying hypothesis — experiments are better able to detect sensitive than insensitive recruitment relationships. Given that we do not yet know which of these hypotheses is true, a prudent approach to selecting a flow experiment would be to specify a target probability of correctly detecting a directional signal regardless of the true underlying dynamics. The target probability will reflect the risk preference of managers (how confident they need to be in the experiment before they will base their operating decisions on the results). Using a probability of 0.8 as our benchmark for acceptable statistical power (see Peterman 1990), five experiments met this criterion: Ac10H, Ag + 10H, P20H, Ac20H, and P40H. All of these experiments used a high-intensity monitoring program, suggesting that the intensity of monitoring is the most critical component of the experimental designs we considered. The least expensive of these experiments was a 20-year passive experiment (P20H), in which flows varied moderately between 1274.4 and 1840.8 $m^3 \cdot s^{-1}$ (cost = \$3.35 million; \$167 500·year^{-1}). If a 20-year experiment were deemed to be too long, a 10-year active experiment (Ac10H) would generate similar detection probabilities at a slightly higher cost (\$4.55 million; \$455 000·year^{-1}). The other three experiments meeting the 0.8 criterion were considerably more expensive and generated only marginal improvements in the quality of information. Thus, given a choice between conducting longer or higher contrast experiments and spending more money on sampling effort, managers in this situation should opt to invest in more precise monitoring.

All experiments generated similar and relatively modest values of EVSI, our long-term indicator of potential benefits of experimenting. If the population were sensitive to egg mortality, the feasible range of spawning flows was constrained at the lower end (1699.2 $m^3 \cdot s^{-1}$) by the effects of low flows on spawning habitat quality. The similarity of the optimal spawning flow under the most pessimistic recruitment hypothesis (H1) to current operational spawning flows suggests that water and fish managers cannot operate any more risk-aversely than they currently are. However, there are as yet no empirical studies on the survival rates of whitefish eggs at deeper depth intervals. If actual egg incubation survival rates are higher than the professional judgment of whitefish biologists involved in this study, optimal HKD spawning flows could be lower than 1699.2 $m^3 \cdot s^{-1}$. We note that with better information from future egg survival studies, it should be possible to parameterize the relationship to a point where it could be explicitly included as an uncertainty in our decision analysis and explored in a manner analogous to how we addressed recruitment.

If whitefish were insensitive to egg mortality, almost all of the experiments generated sufficient additional information to allow HKD to operate at higher spawning flows and produce greater average power revenues, without posing additional risk to the whitefish population. However, the optimal actions based on additional information were constrained to the range of 1840.8–1982.4 $m^3 \cdot s^{-1}$. This was due to the large, uncontrolled, natural variability in spawning and incubation flows, which made even the best experiments unable to completely rule out the sensitive hypothesis, even though it was false. The residual possibility that the population might be sensitive to egg mortality led to a lower optimal spawning flow than might have been possible if there were more control over natural variation (e.g., by conducting monitoring in paired reference systems).

We found that the relative detection probability and cost provided better measures of the value of alternative experiment than EVSI, which showed little variation across experiments. Using a selection rule that requires a detection probability of 0.8 within 10 years at a cost of less than \$5 million, the optimal experiment was the 10-year active experiment with a high intensity of monitoring (Ac10H). If whitefish were actually insensitive to dewatering mortality, this experiment would pay for itself in 7 or 8 years (\$4.55 million experimental cost divided by an EVSI of \$600 000·year^{-1} in increased power revenues).

What determined whether it is worth conducting flow experiments?

The value of doing adaptive management depended on four factors: the true underlying recruitment dynamics, how benefits were measured, egg incubation habitat quality at deeper depths, and experimental design. The most important factor determining whether flow experiments were worthwhile was the true underlying recruitment dynamics. Experiments will be more useful if the population is insensitive to egg mortality because this information will support higher spawning flows and power revenues. Since the true hypothesis is unknowable and outside the flow manager's control, the best approach is to use modeling and decision analysis to identify robust adaptive management experiments — those that generate information over a broad range of possible hypotheses between egg mortality and adult abundance.

The second factor that determined the value of experimenting was how we measured the benefits of conducting those experiments. We measured the most obvious benefits in terms of whitefish abundance and power revenues, but additional indicators could have been included (e.g., the economic benefits of a recreational fishery on whitefish). HKD operations may also affect the downstream rainbow trout (*Oncorhynchus mykiss*) population, which is the target of an active sport fishery, or other resident species, such as endangered white sturgeon (*Acipenser transmontanus*). Including the impacts of experimentation on reducing uncertainty in the population dynamics of rainbow trout and other species would result in additional benefits and costs that our current analysis did not consider. Other investigators (e.g., Walters and Green 1997; Parnell 2002) have found that cost and valuation procedures can have a large influence on the choice of an experimental design.

Third, our assumption that deeper depths have poorer quality egg incubation habitat provided a lower bound on the ability of flow managers to reduce dewatering mortality. If the quality of these habitats (which is available at all spawning flows) could be improved, then spawning flows could be further reduced to minimize dewatering effects. Evidence of poor mid-channel substrate could also have economic value. In recent years, BC Hydro has paid approximately \$135 000·year^{-1} to undertake required mitigation and compensation actions under an agreement with Fisheries and Oceans Canada for the impact of HKD operations on whitefish production. Research studies that provide depth-specific egg-to-fry survival estimates might permit BC Hydro to argue that lowering HKD spawning flows below the current range of 1557.6–1699.2 $m^3 \cdot s^{-1}$would not improve egg survival rates. Once some empirical information is gathered on the general form of the functional relationship between depth and the natural survival rate of eggs, then it may be possible to annually estimate and update the parameters of this relationship, concurrent with estimates of stock–recruitment parameters.

The fourth factor that determined the value of alternative flow experiments was their design. Lowering measurement error by performing more precise population abundance surveys within a year led to large increases in learning benefits for a small increase in cost. Experiments that included more extreme variations in flows or longer durations provided additional learning benefits but at a substantially higher expense. Nevertheless, where operational flexibility exists and monitoring designs are sufficiently precise, the suitable level of flow variation should be evaluated. Further improvements to our experimental designs, such as spatial replication (e.g., pairing treatment and reference sites) or more aggressive variations in flows, were constrained by the lack of a suitably similar replicate of the lower Columbia River and legal and flood control constraints on manipulating HKD flows. However, such enhancements can lead to major improvements in large-scale adaptive management experiments (Keeley and Walters 1994; MacGregor et al. 2002; Parnell 2002), and we encourage their use wherever this flexibility exists.

Is it worth conducting experiments to reduce uncertainty in whitefish dynamics?

Our results suggest that flow experiments costing \$3.5–\$4.5 million (\$167 500–\$455 000·year^{-1}) could reliably detect true underlying recruitment dynamics within the range of hypotheses we considered. For BC Hydro, the worst that could happen from conducting these experiments would be that recruitment dynamics turn out to be sensitive to egg mortality, in which case HKD operations would continue much as they have in recent years (spawning flows would remain at 1557.6–1699.2 $m^3 \cdot s^{-1}$), but with heightened resolve to avoid higher or lower flows. This would not improve whitefish abundance, but would maintain power revenues and, with additional research discussed above, might provide the basis for reducing current mitigation obligations. The best outcome for all stakeholders (including whitefish) would be that recruitment dynamics turn out to be insensitive to egg mortality, in which case BC Hydro could increase HKD spawning flows to 1982.4 $m^3 \cdot s^{-1}$ (perhaps 2124 $m^3 \cdot s^{-1}$), generating an additional \$600 000 (possibly as high as \$1.5 million) per year, without negatively affecting the whitefish population.

Is it worth spending \$167 500–\$455 000·year^{-1} for 20 or 10 years (respectively) for the possibility of increasing power revenues by \$600 000 annually thereafter? There is no clear answer. The decision on whether or not to proceed with flow experiments depends on risk and return preferences, as well as the interest rate used in determining the present value of future cash flows. We suspect that the power utility would not consider this a worthwhile investment because of the relatively low historical emphasis placed on mountain whitefish management by other stakeholders. However, new legal challenges (and their associated costs) from government agencies or other parties could tip the balance in favour of making an investment in learning to settle the issue once and for all. Also, a more informed answer to this question requires that the current analysis be extended to consider the biological and economic impacts of HKD operations on other species, such as downstream rainbow trout and sturgeon populations. These species will have a larger influence on HKD operational decisions than whitefish alone. Our analysis provides a framework for quantifying impacts on other species and the uncertainties surrounding these impacts in an a priori evaluation of alternative experimental designs.

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