

APPLIED ISSUES

Test of an environmental flow release in a British Columbia river: does more water mean more fish?

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SUMMARY

1. Water managers must make difficult decisions about the allocation of streamflows between out-of-channel human uses and environmental flows for aquatic resources. However, the effects environmental flows on stream ecosystems are infrequently evaluated.
2. We used a 13-year experiment in the regulated Bridge River, British Columbia, Canada, to determine whether an environmental flow release designed to increase salmonid productivity was successful. A hierarchical Bayesian model was used to compare juvenile Pacific salmon (*Oncorhynchus* spp.) abundance before and after the flow release.
3. We found that the total number of salmonids did increase after the release, but most of the gains could be attributed to the rewatering of a previously dry channel located immediately below the dam. In reaches that had flowing water during the baseline period, the response of individual salmon species to the increase in flow was variable, and there was little change in total abundance after the flow release. Our results were inconsistent with both habitat modelling, which predicted a decrease in habitat quality with increasing flow, and holistic instream flow approaches, which imply greater benefits with larger flows.
4. We question whether biotic responses to flow changes can be predicted reliably with currently available methods and suggest that adaptive management or the use of decision tools that account for the uncertainty in the biotic response is required for instream flow decisions when the competing demands for water are great.

Keywords: environmental flow release, hierarchical Bayesian modelling, instream flows, *Oncorhynchus*

Introduction

Rivers need water, but determining how much remains a challenging problem in environmental

management (Richter *et al.*, 1997). Competing demands for water force water managers to make difficult decisions between in-channel needs and human uses such as irrigation and power production. Adding to the challenge is the asymmetry in uncertainty: while the benefits of out-of-channel uses can be readily calculated based on megawatts of electricity generated or hectares of fields irrigated, the environmental benefits of in-channel flows are difficult to

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predict with accuracy or precision. Some of that uncertainty is attributed to shortcomings of the tools or models used for evaluating flows (Castleberry *et al.*, 1996; Lancaster & Downes, 2010), and much is the result of unpredictability in the response of the ecosystem to changes in flow (Sabaton *et al.*, 2008; Poff & Zimmerman, 2010).

There are perhaps two schools of thought regarding the determination of instream or environmental flows that differ in both their underlying assumptions and the management objectives they attempt to satisfy. The first, articulated by Richter *et al.* (1997) and Poff *et al.* (1997) and others, is based on the paradigm of a monotonic relation between the degree of hydraulic alteration and disturbance to the ecosystem. Flow determinations based on this paradigm attempt to minimise differences between the regulated and natural flow regime and rely heavily on hydrological statistics (Richter *et al.*, 2003), and a hypothesised or empirical relation between flow alteration and ecosystem processes that predicts that river health will tend to increase as flows more resemble the natural hydrograph (Arthington *et al.*, 2006; King & Brown, 2006; Poff *et al.*, 2010). Management goals accompanying this approach are more likely to focus on broad-based values than targets for specific components of the ecosystem.

The second approach generally begins with some relatively specific management goals for the river (e.g. the abundance of key or valued species) and uses knowledge of those species' life history and habitat requirements to build a flow regime to meet the goals. While early application of this 'bottom-up' approach focused on the minimum or base flows required to maintain game fish populations during the low flow period, newer approaches consider the full hydrological cycle in what has been termed a 'building block' process (Tharme, 2003; Enders, Scruton & Clarke, 2009; Acreman & Ferguson, 2010). Also entertained is the possibility that aspects of the natural flow regime may be limiting for some species, and with sufficient understanding of key ecological processes, management objectives can be met with a flow regime that deviates significantly from the natural or unregulated flow (Jowett & Biggs, 2008).

The two approaches are not exclusive, though, as inclusion of hydrological processes in the building block process often leads to hydrographs that resemble the natural regime. This blending has led to the

concept of river downsizing (Trush, McBain & Leopold, 2000). Recognising that out-of-channel water needs will not subside, Trush *et al.* (2000) propose that shaping the flows that are available into a naturalised flow regime will promote seasonal physical and biological processes to create a functioning, but smaller, river ecosystem. Some of the strongest support for this approach comes from studies on riparian forests, as recruitment is dependent on a recession of flows from the spring freshet (Rood *et al.*, 2005; Hall, Rood & Higgins, 2011), but can be independent of the magnitude of flows themselves.

The tools used to predict the environmental effects of instream flow recommendations often have poor or unknown reliability. Over the past 40 years, increasingly sophisticated methods have been employed, but the ecological relevance of many of the instream flow approaches has been criticised (Lancaster & Downes, 2010). Common to most procedures currently in use is a lack of testing of the assumptions of the models or predictions that they make (Souchon *et al.*, 2008). At the heart of this issue is the 'flow alteration–ecological response relationship' (Poff *et al.*, 2010), which in many cases is hypothetical or only weakly supported by empirical information. This deficiency led Castleberry *et al.* (1996) to conclude that there was no scientifically defensible method for instream flow determinations and that an adaptive management approach is needed to develop a body of evidence for the efficacy of instream flow methodologies and their recommendations, a call that has been recently repeated (Arthington *et al.*, 2010). Souchon *et al.* (2008) note the many opportunities to monitor and evaluate the biological effects of instream flows have been lost, although this situation is changing (Jowett & Biggs, 2006; Lamouroux *et al.*, 2006; Ovidio, Capra & Phillippart, 2008; Sabaton *et al.*, 2008).

Here, we present the results of a long-term flow experiment in the regulated Bridge River, located in south-western British Columbia, Canada. The Bridge River is a large glacially fed river [Mean annual discharge (MAD) = $100 \text{ m}^3 \text{ s}^{-1}$], and it has been developed as a significant producer of hydroelectricity by BC Hydro and its predecessors through the diversion of virtually all flows to an adjacent catchment. There has been no continuous flow released from the dam since its completion in 1960. To restore the river below the dam, an environmental flow release was proposed, but the benefits of those flows

on the river, and in particular highly valued salmon (*Oncorhynchus* spp.) populations, are very uncertain (Failing, Horn & Higgins, 2004). The costs, however, in terms of foregone electricity production are readily quantifiable and significant.

It made little sense to use the predevelopment hydrograph of the Bridge River as a template for developing a flow release strategy below the dam because prior to regulation summer flows of 100–900 m³ s⁻¹ of glacially turbid water within the confined channel likely did not create conditions suitable for fish production (Fig. 1). Historical records indicate that most of the best fish habitat (including spawning areas for salmon) were located upstream of the dam site and are now flooded by a reservoir, and the river below the damsite was primarily used for the passage of anadromous species to and from natal areas (O'Donnell, 1988). Thus, an environmental flow was designed that would meet stakeholder expectations and agency goals for the river below the dam as well as allowing for other uses of the water; the technical committee responsible for flow management accepted that the flow regime would be largely independent of the historical condition.

However, within the technical committee, there was a divergence in views about how flows would impact salmonid productivity that in many ways mirrors the diversity of current thinking about environmental flows (Failing *et al.*, 2004). One perspective was informed by the results of physical habitat modelling (Fig. 2), empirical observations along the length of the river (Bradford & Higgins, 2001) and other experiences (i.e. Jowett & Biggs, 2006) that suggest that small flow releases may be able to achieve management goals for fish production and that larger flows may be less than optimal because of a potential deterioration in fish habitat quality (Failing *et al.*, 2004). Other members were of the view that a larger release would

result in a larger, more diverse river environment that would support larger fish populations and would enhance other values associated with the river and its ecosystem. The latter perspective is consistent with holistic instream flow methodologies and the natural flow regime paradigm that postulates that impacts to aquatic ecosystems will monotonically decrease as the degree of flow alteration or diminishment is decreased (Arthington *et al.*, 2006). Because of this uncertainty and the magnitude of the potential losses in electricity production resulting from environmental flow releases, an experiment was implemented to test four different flow regimes (Failing *et al.*, 2004) to establish an empirical relationship between flow and fish production. In this report, we describe the results of the first two flow trials.

Methods

Study site

The Bridge River drains a large glaciated region of the Coast Range of British Columbia and flows eastward, eventually joining the Fraser River near the town of Lillooet (confluence: 50°45'N, 121°56'W; Fig. 3). Historically, the MAD in the study area was 100 m³ s⁻¹, with peak flows exceeding 900 m³ s⁻¹ (Hall *et al.*, 2011). The river was impounded in 1960 by the construction of the Terzaghi Dam, located in a canyon 41 km upstream from Fraser River that resulted in the creation of the Carpenter Reservoir. Other than occasional mid-summer spills caused by high inflows (Higgins & Bradford, 1996), all flows were diverted to the adjacent Seton catchment for hydroelectric power production (490 MW capacity). There are no generation facilities at Terzaghi dam, and water releases for environmental needs in the lower Bridge River result in losses to power production for the Bridge-Seton



Fig. 1 (a) Lower Bridge River in 1909, during a period of high flows; the exact location is unknown. Taken by surveyor Frank Swannell, image I-57543 courtesy of Royal BC Museum, BC Archives. (b) Low-gradient section of Reach 3, September 1999, at c. 0.5 m³ s⁻¹; (c) same location after the flow release, September 2001, at 3 m³ s⁻¹.

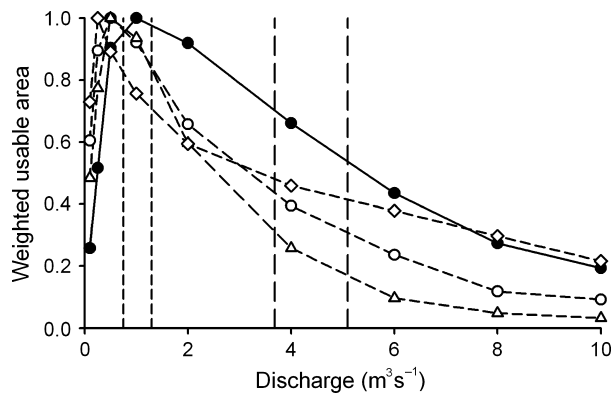


Fig. 2 Results of a physical habitat simulation for juvenile salmonids in Reach 3 of the Bridge River using the PHABSIM procedure (Bovee, 1982) based on hydraulic data from 24 transects. Habitat conditions were sampled at 0.3 and 1.9 $\text{m}^3 \text{s}^{-1}$, and those data were used to model habitat conditions across a range of flows. Habitat suitability curves for trout were based on data collected in the Bridge River; however, for the other taxa, generic habitat suitability curves developed for BC streams were used (Lewis & Tesch, 1996). Weighted usable area is scaled to the maximum value for each taxon. Shown are age-0 rainbow trout (open circles), age-1 rainbow trout (filled circles), chinook salmon (triangles) and coho salmon (diamonds). Paired vertical lines bracket the range of the mean monthly flows in Reach 3 in August and September during the baseline (left pair) and flow release (right pair) periods.

hydroelectric system. Those losses are 1.7–2.8 million C\$ for each annualised $\text{m}^3 \text{s}^{-1}$ released from the dam.

The completion of the Bridge-Seton project resulted in the complete dewatering of more than 3 km of river immediately downstream of the dam. Downstream of

the dewatered reach, the river had a low but continuous and relatively stable streamflow, with ground water and five small tributaries cumulatively providing a MAD of c. $0.7 \text{ m}^3 \text{s}^{-1}$ (<1% of the pre-impoundment MAD). Fifteen km downstream from the dam, the unregulated Yalakom River joins the Bridge River and supplies, on average, an additional $4.4 \text{ m}^3 \text{s}^{-1}$ (daily minimum $1.00 \text{ m}^3 \text{s}^{-1}$, maximum $43.0 \text{ m}^3 \text{s}^{-1}$; Water Survey of Canada (WSC) gauge 08ME025, 1996–2008) to the remaining 26 km of the lower Bridge River.

The lower Bridge River channel is confined within a canyon throughout its length and has a relatively steep gradient (0.7–3%; Fig. 1). The substratum was shaped by the high volumes of water that flowed through the canyon prior to regulation and is mainly bedrock, large boulder and cobble with isolated pockets of gravel. In a number of locations, artificial spawning areas were created in the early 1990s through the addition of clean gravel to the channel. In addition, there is recruitment of smaller material from mass wasting of the canyon walls and from debris flows associated with the tributary streams.

The fish community of the Bridge River is mainly juvenile salmonids that are progeny of adults that spawn throughout the system. Juvenile anadromous steelhead and freshwater rainbow trout (*O. mykiss* Walbaum) are most abundant, followed by coho (*O. kisutch* Walbaum) and chinook salmon (*O. tshawytscha* Walbaum) (Higgins & Bradford, 1996). We did not attempt to distinguish between

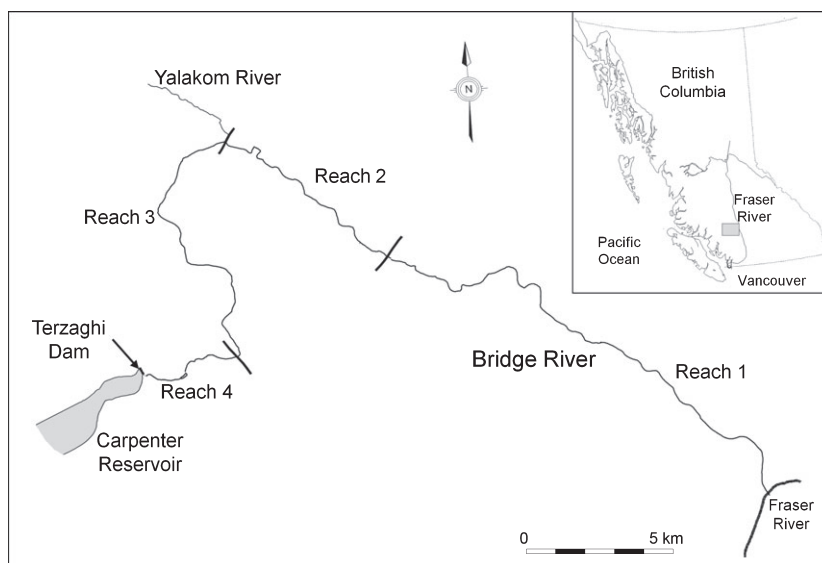


Fig. 3 Map of lower Bridge River showing the location of the dam and the four study reaches.

rainbow and steelhead trout in our analysis. Bull trout (*Salvelinus confluentus* Suckley) and mountain whitefish (*Prosopium williamsoni* Girard) are also present, but are mostly found downstream of the Yalakom River confluence. Pink salmon (*O. gorbuscha* Walbaum) spawn in very large numbers (often in excess of 50 000 fish) in odd-numbered years, but the juveniles emigrate directly to the ocean after emergence from spawning beds. The river is closed to angling to protect the steelhead population.

We divided the river into four contiguous reaches (Fig. 3). Reach 1 extends upstream from the confluence with the Fraser River for 18.9 km and is largely inaccessible and was not sampled during the experiment. Reach 2 is 7.0 km long and the upstream limit is the confluence of the Yalakom River. Flows in Reach 2 are dominated by the inflows from the Yalakom River. Reach 3 is 11.6 km long and is the reach that was supplied by ground water and tributary inflows prior to the flow release. The 3.3 km Reach 4 extends to the dam and had been without continuous flow since 1960.

The flow experiment

Fisheries agencies initially expressed an interest in restoring the dewatered reach in 1980s, and in the late 1990s, an agreement was reached with BC Hydro to refit Terzaghi dam to allow for a continuous flow release. The initial release was based on an annual water budget equivalent to a MAD of $3 \text{ m}^3 \text{ s}^{-1}$, and the regulatory agencies and BC Hydro were directed to develop an adaptive management experiment to define the relation between flow and salmonid production (Failing *et al.*, 2004).

The experiment began with 4 years (1996–99) of baseline monitoring prior to the initiation of the flow release. In 2000, a controllable low level outlet was installed in the dam, and a seasonally variable flow regime was established. Prior to the release, the channel immediately below the dam was regraded with a pool–riffle structure, and side channels and spawning beds were added as the channel had been altered by placer mining since the closure of the dam (Decker, Bradford & Higgins, 2008). The flow regime provided a summertime peak, and a significantly enhanced winter flow. The original experimental design was for flow treatments to occur in 4-year blocks with a different flow regime in each block

(Failing *et al.*, 2004); however, for reasons unrelated to environmental issues, the $3 \text{ m}^3 \text{ s}^{-1}$ release has continued from 2000 to 2011.

The interagency fisheries technical committee that designed the flow experiment decided that juvenile salmonid abundance would be used as the primary performance measure to evaluate the effects of each flow regime on fish populations in the river. Preliminary sampling suggested that juveniles were abundant in the river and that habitats were likely fully seeded. Thus, it was assumed that populations were limited by the amount of suitable physical habitat, as is often the case for these species (i.e. Bradford, Myers & Irvine, 2000). Adult salmon abundance was not considered as an indicator because adult returns are affected by potentially confounding factors (e.g. ocean survival and fishing mortality) that would obscure the effects of the flow treatment. In addition, there are logistic difficulties in obtaining accurate estimates of spawner abundance for all species. The taxa used in our analysis were age-0 chinook and coho salmon, and age-0 and age-1 rainbow trout. Virtually, all chinook and coho salmon migrate to sea as age-1 smolts in the spring months and very few older individuals are in the river. Larger fish, mainly older trout, were caught but we did not consider our sampling gear sufficient to obtain reliable estimates of their abundance.

A before–after–control–impact (BACI) design is often used in large-scale ecological monitoring experiments, and it makes use of replicated treated and unmanipulated sites to control for variation unrelated to the experimental treatment (Bradford, Korman & Higgins, 2005; Liermann & Roni, 2008). For the Bridge River replication is not possible, nor is a comparable control stream available nearby, so we are forced to rely primarily on before–after comparisons within the Bridge River. During the growing season, inflows from the Yalakom River are much larger than the dam releases under the $3 \text{ m}^3 \text{ s}^{-1}$ water budget, and we expected that the flow release would have a smaller effect on Reach 2 compared with Reaches 3 and 4.

Sampling

Discharge estimates were derived by a variety of means. Flows in Reach 3 were estimated using depth data from pressure transducers that were converted to discharge using local rating curves. Reach 4 inflows

after 2000 were estimated directly at the dam as there are only minor tributary inputs in this reach. Reach 2 flows were the sum of the Yalalom inflows from the gauge and the estimated flows in Reach 3. Hourly stream temperatures were recorded in each reach with dataloggers. Temperature data were summarised as monthly means for the baseline and treatment periods for Reaches 2 and 3.

Surveys of hydraulic conditions were conducted during the baseline period in October 1996, and after the flow release in October 2006, to evaluate the effect of the flow release on river conditions. Wetted widths and lengths of each habitat type (cascades, runs, riffles, pools, side channels) were measured with an optical rangefinder. Water depth and velocity (at 0.6 of depth) were measured using a Swoffer flowmeter with topset wading rod at two or more locations along the thalweg in each habitat unit. Data were averaged by reach.

The abundance of juvenile salmonids was estimated with annual electrofishing campaigns. For 1996–98, sampling was conducted in late September and early October, but for the remainder of the experiment, sampling occurred in the first half of September. The selection of sampling sites was based on a habitat survey that was conducted in 1993 in Reaches 2 and 3 that inventoried all major meso-habitat types. Eighteen sampling units in each reach were randomly selected from the inventory of habitat units in proportion to their occurrence in the inventory. Although the original intent was to use these sites throughout the entire flow experiment, some sites had to be relocated slightly owing to changes in the channel morphology resulting from debris flows and spills from the dam. New sites were chosen to have the same characteristics as the altered sites to maintain the same distribution of habitat types being sampled. Two new sites were added to the upper region of Reach 3 in 1998. In 2000, an additional 12 sites were selected in the rewetted Reach 4 by the same procedure that was used for Reaches 2 and 3.

At each site, the area to be sampled was enclosed with block nets constructed of 6-mm mesh. The average size of a sampled area was 97 m² (range, 20–273 m²). Population estimates were derived using the removal method based on three or four passes of backpack electrofishing. A minimum of 30 min elapsed between passes. After each pass, captured fish were identified and fork length (nearest mm) and

weight (0.1 g) of all salmonids were recorded before they were released outside the enclosure. Length–frequency analysis was used to separate rainbow trout into age-0, age-1, and older fish.

Prior to the flow release, we blocked off the full width of the stream with nets in Reach 3; thus, the sampled areas included the entire channel. We were not able to do this in Reach 2 at any point during the experiment or in Reaches 3 and 4 after the flow release because of the greater depths and velocities. Instead, sampling was conducted in three-sided enclosures along shore; these enclosures averaged 5.4 m in width. Some fish may have fled the sampling areas when the nets installed; however, we note that at the water temperatures during sampling (9–12 °C), we expected many fish to be concealed within the substratum during the day (Bradford & Higgins, 2001), reducing the likelihood of flight.

When we used the three-sided sampling areas, there is potential for some fish to be located further offshore and inaccessible to our gear. We estimated the proportion of the population that was vulnerable to our sampling protocol using data collected as part of a microhabitat use study. In that study, divers located the position of juvenile salmonids during the day relative to the shoreline at two sites in Reach 2 and two sites in Reach 3 in August 1999, October 1999 and July 2000, prior to the flow release, and in August 2000, after the flow release. For Reach 2, where the flow release from the dam had little impact on habitat conditions, we combined observations from the August 1999 and August 2000 surveys to estimate the distribution of fish from shore. For Reaches 3 and 4, we used the data collected in Reach 3 in late August 2000, 1 month after the start of the flow release, to estimate the post-flow release distribution for these reaches. We could not determine the location of fish concealed in the substratum, so we made the assumption that the distribution of fish observed during the microhabitat study would be a reasonable approximation of the location of all fish in the channel (either concealed in the substratum or swimming in the water column).

Data analysis

We used a hierarchical Bayesian model (HBM) that simultaneously estimated computational parameters such as site-specific catchabilities and abundances, as

well as the estimates of interest, fish abundance by year and reach, and the change in abundance associated with the flow release. The HBM produces posterior probability distributions to allow managers to visualise the uncertainty surrounding the effects of interest.

Our HBM is similar to model I of Wyatt (2003). The model consists of two levels or hierarchies. Site-specific estimates of detection probability (also referred to as catchability) and densities at the lowest level of the hierarchy are considered random variables that come from hyper-distributions of catchability and density at the higher level (Fig. 4). The HBM jointly estimates both site- and hyper-parameters. The process component of the model assumes that variation in fish abundance across sites can be modelled using a Poisson/log-normal mixture (Royle & Dorazio, 2008). That is, abundance at a site is Poisson-distributed with a site-specific log-normally distributed mean. The observation component of the model assumes that variation in detection probability across sites can be modelled using a beta distribution and that electro-fishing catches across sites and passes vary according to a binomial distribution that depends on site-specific detection probability and abundance.

In the following description, 'fish' refers to one species-age group combination. Greek letters denote model parameters that are estimated. Capitalised

Arabic letters denote derived variables that are computed as a function of parameters. Lower-case Arabic letters are subscripts, data or prior parameter values.

We assumed that the number of fish captured, c , by electrofishing in year y at site i on pass j followed a binomial distribution (*dbin*) described by the detection probability (or catchability) θ , and the number of fish in the sampling arena, N :

$$c_{y,i,j} \sim \text{dbin}(\theta_{y,i}, N_{y,i,j}). \quad (1)$$

We assumed that detection probability was constant across passes but could vary among sites. The number of fish remaining in the sampling area after pass j was the difference between the number present prior to pass j and the catch on pass j :

$$N_{y,i,j+1} = N_{y,i,j} - c_{y,i,j}. \quad (2)$$

These two equations describe the binomial model on which removal estimators are based (Moran, 1951; Otis *et al.*, 1978). Site-specific detection probabilities ($\theta_{y,i}$) were assumed to be stochastic realisations from a beta hyper-distribution (*dbeta*):

$$\theta_{y,i} \sim \text{dbeta}(\alpha_y, \beta_y). \quad (3)$$

We use a convenient reparameterisation of the beta distribution where α_y and β_y are calculated from the estimated mean (μ_{θ_y}) and standard deviation (σ_{θ_y}) in

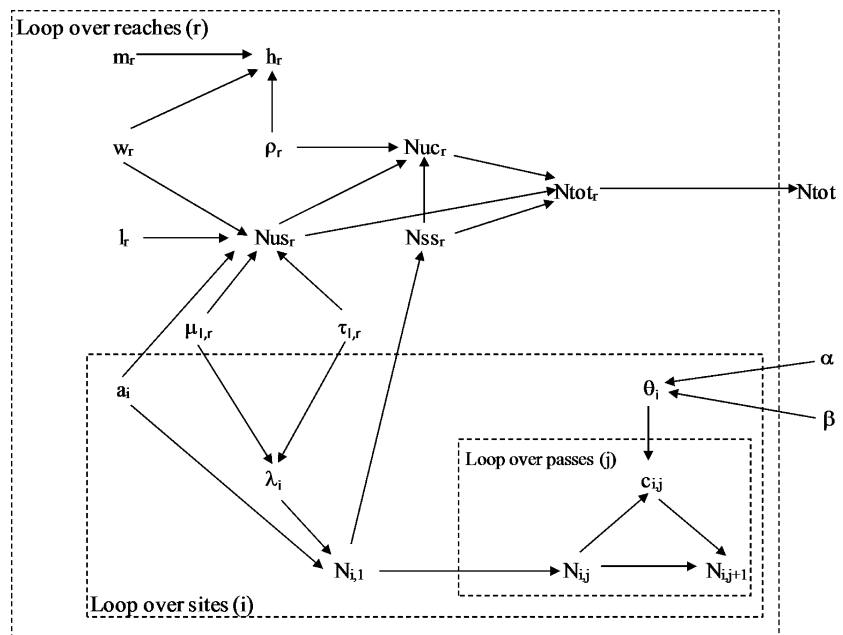


Fig. 4 Relationship among variables in the hierarchical Bayesian model used to calculate total fish abundance (N_{tot}) in the Bridge River by taxon. Lower-case letters are observed quantities, upper-case letters are calculated values, and Greek letters are model parameters as defined in the text.

detection probability across sites as $\alpha_y = \mu_{0y} \sigma_{0y}^{-2}$ and $\beta_y = \sigma_{0y}^{-2}(1 - \mu_{0y})$. Site-specific fish densities ($\lambda_{y,i}$) in log space were assumed to be stochastic realisations from a normal (*dnorm*) hyper-distribution:

$$\log(\lambda_{y,i}) \sim \text{dnorm}(\mu_{\lambda y,r}, \tau_{\lambda y,r}). \quad (4)$$

Here μ_{λ} and τ_{λ} are the mean and precision of the normal probability distribution (note $\tau_{\lambda} = \sigma_{\lambda}^{-2}$) specifying the hyper-distribution of log density for each reach and year. Note that each reach contains a subset of the total number of sites that were sampled. The number of fish present at site i prior to the first electrofishing pass ($N_{y,i,1}$) was assumed to be a stochastic realisation from a Poisson distribution with an expected value determined by the product of site area, a , and fish density drawn from the hyper-distribution (eqn 4):

$$N_{y,i,1} = \text{poisson}(\lambda_{y,i} a_{y,i}). \quad (5)$$

To compute the total abundance of fish in a reach, we also needed an estimate of the number of fish in the areas of the river that we did not sample. As most of our sampling was conducted along the shorelines, we partitioned the wetted area of the river into one of three categories: the shoreline area that was sampled, the shoreline area that was not sampled and the centre of the channel that in most cases was not sampled. The total abundance in reach r and year y , $N_{tot y,r}$, was the sum of the estimates from sampled shoreline sites within the reach, N_{ss} , the estimate for the unsampled shoreline, N_{us} , and abundance in the unsampled centre channel area (N_{uc}) for that reach and year:

$$N_{tot y,r} = N_{ss y,r} + N_{us y,r} + N_{uc y,r}. \quad (6)$$

The number of fish in the sampled shoreline was the sum of abundances of all sites within the reach:

$$N_{ss y,r} = \sum_i N_{y,i,1} \mid i \text{ is a site within reach } r. \quad (7)$$

Abundance in the unsampled shoreline (N_{us}) was computed as the product of the transformed mean density from the log-normal density hyper-distribution (μ_{λ}) with log-normal bias correction ($0.5\tau_{\lambda}^{-1}$) and the area of the unsampled shoreline in the reach. The area of the unsampled shoreline is the area of the shoreline zone (the product of twice the length of the reach (l) and the average width of sampled area, w , less the total area that was sampled in the reach:

$$N_{us y,r} = \exp[\mu_{\lambda y,r} + 0.5\tau_{\lambda y,r}^{-1}](2l_r w_{y,r} - \sum_i a_{y,i}). \quad (8)$$

The number of fish in the centre of the channel (N_{uc}) was computed based on the abundance in the shoreline zone ($N_{ss} + N_{us}$) and estimates of the proportion of the total population that was in the shoreline zone (ρ).

$$N_{uc y,r} = (N_{ss y,r} + N_{us y,r})(1 - \rho_{f,r}). \quad (9)$$

The parameter ρ is calculated for each reach, r , and flow period, f , and depends on the average annual width of electrofishing sites and the distribution of fish from shore determined from the field study described earlier. We assumed that the number of fish in the microhabitat study ($h_{y,r}$) observed between the shoreline and the average annual width of electrofishing sites was a binomially distributed random variable that depended on $\rho_{y,r}$ and the total number of fish observed in the microhabitat study for that strata ($m_{f,r}$).

$$h_{y,r} \sim \text{dbin}(\rho_{y,r}, m_{f,r}). \quad (10)$$

During the baseline period, the total wetted width was sampled in Reach 3. Hence, $w_{y,r}$ in eqn 8 is the average wetted width of the reach, so the multiplier 2 in eqn 8 was not used. Also $\rho = 1$ in eqn 9, and consequently $N_{uc} = 0$.

We estimated the effect of the flow release in each reach as the difference in the estimated average abundance between the treatment and baseline years (Δ_r) for age-0 fish as:

$$\Delta_r = \frac{\sum_{y=2001}^{2008} N_{y,r}}{8} - \frac{\sum_{y=1996}^{1999} N_{y,r}}{4}. \quad (11)$$

Data for the year 2000 were not used as the change in flow occurred midway through the growing season, and it is unclear how age-0 fish would be affected. The overall effect of flow in the study area Δ , which includes the contribution from the rewetted Reach 4, is the difference in the average abundance of three Reaches (2–4) during the treatment period and the average abundance for Reaches 2 and 3 for the baseline period:

$$\Delta = \frac{\sum_{y=2001}^{2008} \sum_{r=2}^4 N_{y,r}}{8} - \frac{\sum_{y=1996}^{1999} \sum_{r=2}^3 N_{y,r}}{4}. \quad (12)$$

For age-1 trout, we considered fish sampled in September 2000 to be part of the baseline period as

they would have experienced the increased flows for only a month just before sampling, representing <10% of their life as free-swimming fish. We did not use data for 2001 for the treatment period as these fish would have experienced baseline flows during their first 2–3 months after emergence from spawning gravels, which may have affected survival during this important early life stage. The summation indices in eqns 11 & 12 were adjusted accordingly for this age group.

Posterior distributions of model parameters were estimated using WinBUGS (Spiegelhalter *et al.*, 1999) called from the R2WinBUGS (Sturtz, Legges & Gelman, 2005) library from R (R Development Core Team, 2009). Prior distributions for hyper-parameters and related transformations are given in Table 1. Posterior distributions were based on taking every second sample from a total of 5000 simulations after excluding the first 2000 to remove the effects of initial values.

The HBM was able to converge in all years using uninformative priors for both age-0 rainbow trout and age-0 chinook salmon (Table 1). For age-1 rainbow trout and age-0 coho salmon, depletion data were sparse for Reach 2 (there were small catches at many sites within the reach). In these cases, the estimated abundance and detection probability at each site were highly confounded as the model was not able to distinguish estimates of high abundance and low detection probability with the converse. This uncer-

tainty resulted in very low estimates of the precision of the hyper-distribution in log fish density across sites (τ_λ eqn 4). To avoid unrealistically low estimates of precision, which in turn would lead to overestimates of abundance in the unsampled shoreline zone because of the bias correction term (eqn 8), we used a more informative distribution for these two species-age groups (Table 1). Following recommendations by Gelman (2006), the half-Cauchy or folded *t*-distribution prior was used to constrain σ_λ and achieve convergence.

Results

Physical conditions

The flow release had a major impact on the hydrology of Reach 3 as flows increased by three- to six-fold depending on the month (Fig. 5a). The effects of the flow release on Reach 2 were less pronounced and were masked by variation in the Yalakom discharge (Fig. 5b). In the autumn and winter, the post-release flow in Reach 2 increased by 40–80%; however, in the summer months, flows in the treatment period were similar to the baseline, despite the input from the flow release. This difference is the result of a series of dry years in the region that reduced freshet volumes during the treatment period. Daily peak freshet flows $>40 \text{ m}^3 \text{ s}^{-1}$ were observed in Reach 2 in some years.

Average channel hydraulic conditions changed in a predictable manner with the increase in discharge. In Reach 3, mid-channel velocity was the most sensitive to flow as velocity more than doubled after the flow release (Table 2). There was 17.6 ha of wetted area in Reach 3 in October 1996, and after the flow release, the wetted area in October increased to 23.2 ha, a 32% change. The increase in wetted area in Reach 2 was 0.7 ha, representing a 4% change. The October wetted area of Reach 4 after the flow release was 7.2 ha.

Stream temperatures were similar after the flow release, but some important changes did occur (Fig. 5c). In particular, the hypolimnetic dam release caused the autumn temperatures in Reach 3 to increase by 2–3 °C compared with the baseline period. Temperatures were also higher in the winter months, and this reduced the occurrence of ice cover in Reach 3 (J.S. unpubl. data). Temperature changes in Reach 2 were much smaller because of the dominating influence of the Yalakom River flow (data not shown).

Table 1 Parameters used to define prior distributions for the hyper-distribution in the hierarchical Bayesian model of abundance. Here, p_1 and p_2 refer to α and β , respectively, of the beta distribution, the scale parameters of the half-Cauchy distribution, the mean and standard deviation of the normal distribution, and the minimum and maximum of the uniform distribution. In the case of σ_λ , for age-0 coho salmon and age-1 rainbow trout, a value of 0.1 was used for p_2 to provide a more informative prior as the data for these groups were sparse. The value of 0.3 was used for the other taxa

Hyper-parameter	Distribution	Equation	Prior parameters	
			p_1	p_2
μ_0	Beta	3	1	1
σ_0	Half-Cauchy	3	0	0.3
μ_λ	Normal	4	0	1.0×10^6
σ_λ	Half-Cauchy	4	0	0.1, 0.3
ρ	Uniform	10	0	1

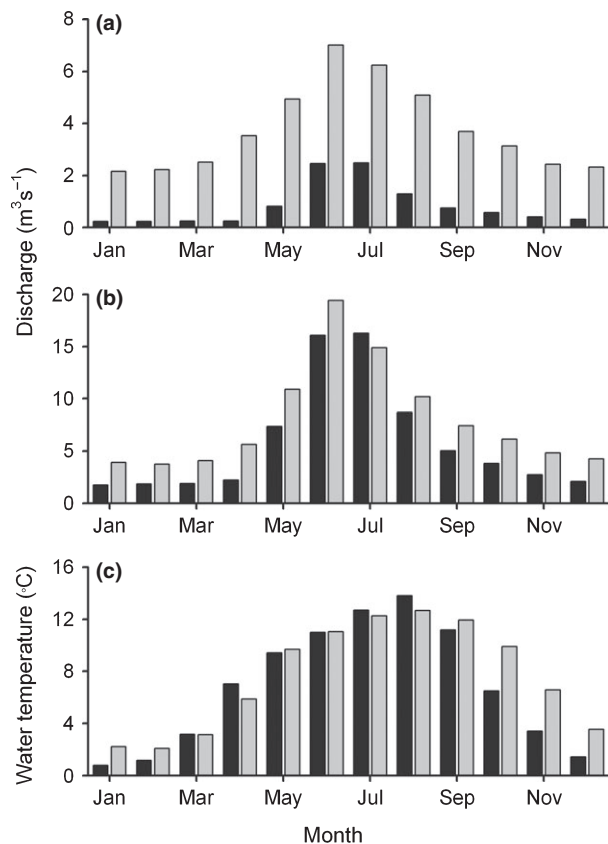


Fig. 5 (a) Average monthly discharge at the downstream boundary of Reach 3. Filled bars are the baseline period, 1996–July 2000; open bars are for the period of the flow release, August 2000–08. There were two small forced spills from the dam during this period, and data for those months are excluded from the analysis. (b) Similar figure for Reach 2. (c) Mean monthly temperatures in Reach 3 for the baseline (filled bars) and the flow release (shaded bars) periods.

Fish

After the flow release, all age-0 trout and coho salmon in Reach 3 were within 5 m of shore; however, 34–40% of age-0 chinook salmon and age-1 trout were

observed at greater distances (Fig. 6a). In Reach 2, most juveniles were within 5 m of shore and thus would be vulnerable to capture by our sampling methods (Fig. 6b). Age-1 rainbow trout were the exception as a significant proportion of observations were made at distances >5 m from shore.

The median detection probability for the whole experiment was 0.55, and population estimates for individual sampling sites were usually very similar to the total catch summed over all passes at that site. The exception was cases where catches were sparse and estimates relied more on information borrowed from other sites. The high detection probability and large number of sites sampled resulted in the annual estimates of abundance for each taxa being relatively precise (median CV = 0.19; Fig. 7).

Prior to the flow release, juvenile salmonids were very abundant in Reach 3. Median abundance was nearly 179 000 individuals in the ≈ 12 km of channel (Fig. 7), corresponding to a density summed over the four species–age groups of 1.02 m^{-2} or a lineal abundance of 15.4 m^{-1} . The average biomass was 8 g m^{-2} . In Reach 2, average abundance was 39 000; we estimated the density to be 0.22 m^{-2} or 6 m^{-1} . Over 60% of the juvenile salmonids were age-0 and age-1 rainbow trout; the remainder consisted of approximately equal proportions of age-0 chinook and coho salmon.

There was a substantial increase in the total number of juvenile salmonids in our study area after the flow release, but nearly all of this increase was attributed to the contribution of the rewetted area in Reach 4 (Fig. 8). The 95% credible interval for the change in total abundance in both Reaches 2 and 3 included zero.

The response of each taxa to the flow change varied between Reaches 2 and 3 (Fig. 8). For both age classes of rainbow trout, there was evidence for an increase in

Table 2 Average (with SE) hydraulic conditions in the Bridge River before and after the flow release. Data are from habitat surveys conducted in October 1996, during the baseline period and October 2006, after the flow release. Depth and velocity measurements were made along the channel thalweg. There was no flow in Reach 4 before the flow release

Reach	Discharge ($\text{m}^3 \text{s}^{-1}$)		Width (m)		Depth (m)		Velocity (m s^{-1})	
	Before	After	Before	After	Before	After	Before	After
4	0	2.7		20.7 (1.57)		0.90 (0.16)		0.69 (0.08)
3	0.35	3.1	15.7 (0.42)	20.1 (0.48)	0.41 (0.02)	0.75 (0.05)	0.19 (0.02)	0.62 (0.04)
2	4.5	6.1	24.3 (0.97)	25.4 (1.11)	0.58 (0.02)	0.57 (0.02)	0.55 (0.03)	0.73 (0.02)

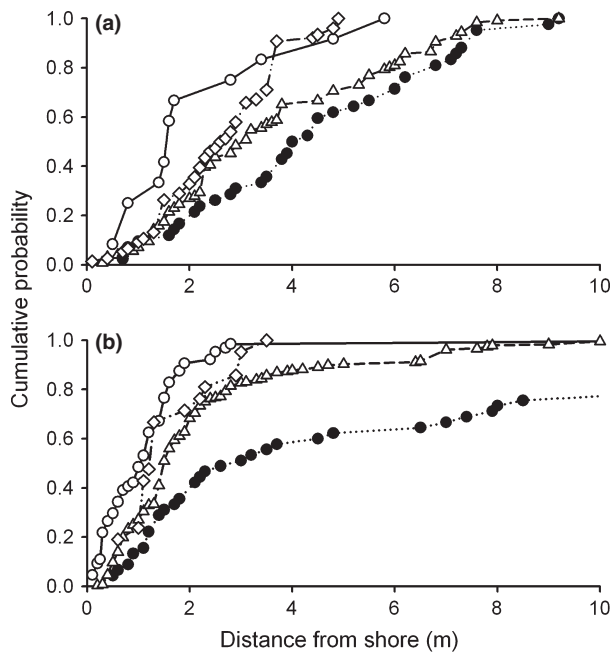


Fig. 6 The cumulative proportion of juvenile salmon observed by underwater observation as a function of their distance from shore. Shown are age-0 rainbow trout (open circles), age-1 rainbow trout (filled circles), age-0 chinook salmon (triangles) and age-0 coho salmon (diamonds). Observations in Reach 3 (a) were made in August 2000 after the flow release; in Reach 2 (b) data are combined from surveys conducted in August 1999 and August 2000. Sample sizes range from 12 to 236 (median = 45).

abundance in Reach 2 but not for Reach 3. Age-0 chinook salmon abundance did not change in Reach 2 after the flow release, but there was a large decrease in Reach 3. There were relatively few chinook salmon juveniles in Reach 4. There was little change in the abundance of age-0 coho salmon in Reach 2, although this species was not common at this site. Coho salmon abundance increased in Reach 3, but the credible interval for this taxon extended just beyond the zero, indicating a small probability of no change in abundance.

Discussion

The Bridge River flow experiment was designed to evaluate the effect of the flow release on salmon populations and to arbitrate between two hypotheses about the effects of flow on fish production that were rooted in competing views about the flow change–ecological response function (Failing *et al.*, 2004). For the reaches of the Bridge River that were wetted prior to the flow release, the large augmentation in flow did

not result in a change in total salmonid abundance, and consequently the hypothesis that fish production would increase with flow was not supported by the results. The greatest impact of the flow release was the sustained production of salmonids in the rewetted reach; however, since we have data on only one discharge regime, we do not know whether the current regime is optimal for fish production, or whether a different flow release could achieve similar or greater benefits.

After the completion of the dam, the residual flow in the relic channel in Reach 3 created good conditions for fish production. The 1996–99 average biomass of age-0 and age-1 salmonids in Reach 3 was more than double typical values for trout and salmon in western North America that are in the range of $1\text{--}4\text{ g m}^{-2}$ (Burns, 1971; Platts & McHenry, 1988). Juvenile productivity was likely enhanced by the complexity of the streambed that provided cover (Venter *et al.*, 2008) and substratum for invertebrate production. Fine sediment in the streambed was flushed by spills from the dam (varying from $10\text{ to }250\text{ m}^3\text{ s}^{-1}$; Higgins & Bradford, 1996; Hall *et al.*, 2011) that occurred at approximately decadal intervals. Physical habitat modelling showed that the pre-release flows in Reach 3 produced optimal depths and velocities throughout the growing season (Fig. 2), and we observed that juveniles used the full width of the channel in many areas. There was no apparent impact of the low flows on the propensity for returning anadromous adults to migrate throughout the system; spawners were able to reach the upper limits of the flowing water, and rearing juveniles were distributed throughout the system. Autumn flows in the baseline period (c. 1% of MAD) would normally be considered very low for autumn-spawning salmon; however, over 1000 chinook salmon adults were observed in Reach 3 in some years, along with smaller numbers of coho salmon and large runs of pink salmon.

We realised that conditions that led to good salmonid production during the baseline period could be disrupted by the flow release if higher flows caused a deterioration in the quality of habitat from its previously productive state (Failing *et al.*, 2004). The flow release increased the wetted area in Reach 3 by 30%, but there was little change in the total abundance of juvenile salmonids, confirming that a loss in average habitat quality had occurred. Thus, our results do not support the simplistic notion of ‘more

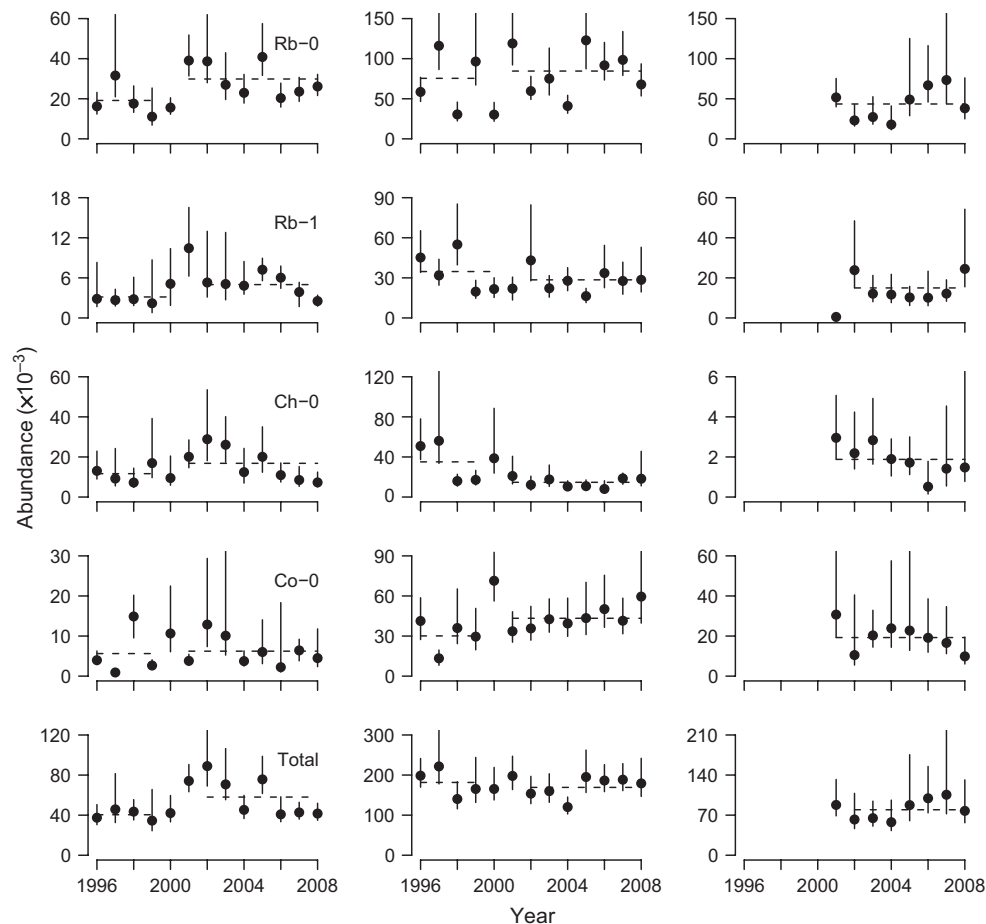


Fig. 7 Annual estimates of abundance of four salmon taxa and their total for three reaches of the Bridge River. From left to right, data are for Reaches 2, 3 and 4. Vertical lines are 95% credible intervals from the hierarchical Bayesian model. Dashed lines are the median abundance before and after the flow release.

water equals more fish'. Our findings are more consistent with the alternative hypothesis that there may be an optimal, intermediate flow that creates good habitat conditions for juvenile salmonids (Failing *et al.*, 2004; Jowett & Biggs, 2006).

Our results also continue to cast doubt on the reliability of our tools for predicting the response of fish populations to flow. Physical habitat modelling predicted that the flow release would cause a 30–60% decrease in suitable juvenile habitat (Fig. 2) during the late summer prior compared with the baseline period. The decrease was largely due to the habitat suitability curves for water velocity, which indicated that habitat suitability declined at velocities greater than 0.20 m s^{-1} for age-0 fish and 0.4 m s^{-1} for age-1 juveniles; this was confirmed by our observations that fish tended to be distributed closer to shore in Reach 2, where discharges are higher than in Reach 3 (Fig. 6).

Underlying the use of habitat models for flow assessments is the assumption that fish populations are limited by physical habitat, particularly during the low flow season, so a decrease in fish abundance would normally be inferred from a modelled decrease in habitat suitability during low flow periods. In contrast, under many hydrologically based instream flow methods, the substantial increase in river discharge in Reach 3 would be expected to yield environmental benefits (Failing *et al.*, 2004; Arthington *et al.*, 2006). Ultimately, we observed little change in total fish abundance in Reach 3, contrary to predictions of either approach. In Reach 2, a small increase in wetted area occurred during the low flow season, and there may have been a slight decrease in habitat suitability if the modelling results from Reach 3 are extrapolated to Reach 2. Our sampling data indicated that little overall change in juvenile abundance occurred there either.

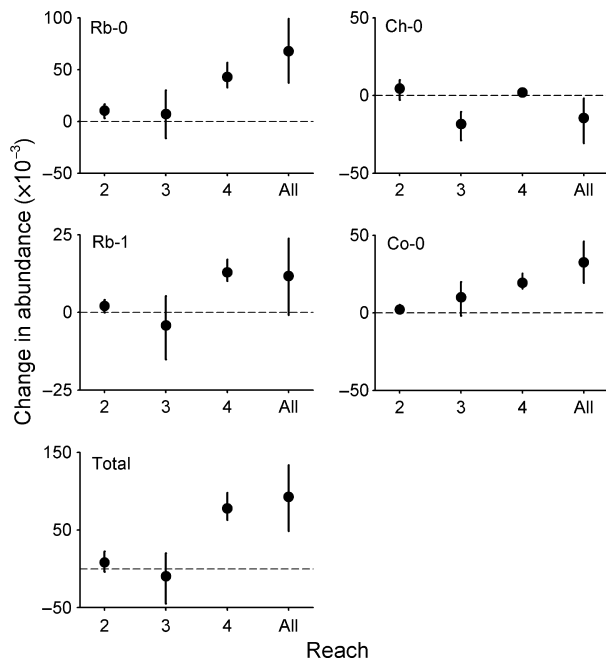


Fig. 8 Estimated change in the total abundance of juvenile salmonids after the flow release for each reach and all three reaches combined. Data are shown for each salmonid taxa individually, and the total for all groups combined. Dots indicate the median, and vertical bars are 95% credible intervals. There were no fish in Reach 4 prior to the release, so the change is the estimated abundance in the post-release period.

Only for chinook salmon did juvenile density decrease as predicted by habitat modelling. While the change in physical habitat may have contributed to decreasing chinook salmon abundance, we believe that the change in the thermal regime could be a contributing factor. As has been observed in other regulated streams in temperate environments (Bradford, 1994; Angilletta *et al.*, 2008), the hypolimnetic release caused water temperatures in the autumn months to be elevated. In the Bridge River, chinook salmon spawning occurs in early September, and increased autumn temperatures will accelerate the development of eggs and alevins. After the flow release, field crews began to observe newly emerged fry in December during electrofishing surveys conducted in Reaches 3 and 4, whereas prior to 2000, the first fry were observed in March (J.S., unpubl. data). Survival of fry that emerge in mid-winter may be poor and could be a contributing factor to the low abundance of juveniles in our surveys. While changes in stream temperatures after the flow release were predicted for the Bridge River (Failing *et al.*, 2004),

the impact on emergence timing was not considered in the design of the winter flow regime. The temperature effect can be mitigated by reducing autumn flows, as low air temperatures will cool the river at this time of year. A variety of engineering solutions are also potentially available (Olden & Naiman, 2010).

Our results add to a growing body of evidence which suggests that the response of specific components of a stream ecosystem to a change in flow regime may not be very predictable, because the dynamics of individual populations can be dominated by factors other than flow (Anderson *et al.*, 2006; Lancaster & Downes, 2010; Poff & Zimmerman, 2010). Bradford & Heinonen (2008) summarise a number of studies that found a wide range in the response of resident trout populations to relatively large changes in flow. Snelder & Lamouroux (2010) noted the relatively minor role that flow played in the diversity and abundance of fishes across a large suite of French streams. In the Électricité de France flow experiment, trout populations in some rivers were influenced more by angling or the effects of spring floods than the magnitude of base flows released from dams (Sabaton *et al.*, 2008). Bunn & Arthington (2002) posit that 'flow is a major determinant of physical habitat in streams', and while this may be true, the available evidence suggests obtaining a predictable response in key species to a change in the flow regime is far from certain. Indeed, both Arthington *et al.* (2010) and Poff & Zimmerman (2010) highlight the need for more studies of the type we report here to determine whether hydro-ecological relationships of sufficient precision for management use can be developed.

The use of the natural flow regime as a template for environmental flows has an intuitive appeal and certainly has merit where a precautionary approach is warranted owing to a lack of site-specific information (Arthington *et al.*, 2006). However, situations where there are intense competing demands for water, and there is a priority placed on key species in the river, the premise that 'increasing degrees of flow alteration from baseline conditions are associated with increasing ecological change' (Poff *et al.*, 2010) will need to be supported with empirical evidence. For the Bridge River, our 13-year monitoring programme failed to demonstrate a significant benefit to fish populations in the reach where flows were enhanced, although rewetting the channel immediately below the dam was successful in increasing fish

production (Decker *et al.*, 2008) and stimulating riparian development (Hall *et al.*, 2011). We had sufficient understanding of the system during the baseline period to realise that there would be risks to trying to further improve fish populations from its already productive state (Failing *et al.*, 2004). The unpredictability of biotic responses to habitat changes that we and others have observed (Sabaton *et al.*, 2008; Pine *et al.*, 2009) suggests that either a detailed understanding of population processes will be required to refine the predictions of standard instream flow models (e.g. Gouraud *et al.*, 2008) or site-specific monitoring in an adaptive management context will be needed for effective water management decision-making when the costs of errors are significant (Failing *et al.*, 2004). If neither is feasible, then the real limitations of instream flow science need to be made explicit in the decision-making process (Failing, Gregory & Harstone, 2007) so that those uncertainties can become part of the process for weighing the merits of alternative water management strategies.

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