

Estimating recruitment dynamics and movement of rainbow trout (*Oncorhynchus mykiss*) in the Colorado River in Grand Canyon using an integrated assessment model

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Abstract: We used an integrated assessment model to examine effects of flow from Glen Canyon Dam, Arizona, USA, on recruitment of nonnative rainbow trout (*Oncorhynchus mykiss*) in the Colorado River and to estimate downstream migration from Glen Canyon to Marble Canyon, a reach used by endangered native fish. Over a 20-year period, recruitment of rainbow trout in Glen Canyon increased with the annual flow volume and when hourly flow variation was reduced and after two of three controlled floods. The model predicted that approximately 16 000 trout-year⁻¹ emigrated to Marble Canyon and that the majority of trout in this reach originate from Glen Canyon. For most models that were examined, over 70% of the variation in emigration rates was explained by variation in recruitment in Glen Canyon, suggesting that flow from the dam controls in large part the extent of potential negative interactions between rainbow trout and native fish. Controlled floods and steadier flows, which were originally aimed at partially restoring conditions before the dam (greater native fish abundance and larger sand bars), appear to have been more beneficial to nonnative rainbow trout than to native fish.

Résumé : Nous avons utilisé un modèle d'évaluation intégré pour examiner les effets de l'écoulement issu du barrage du canyon Glen (Arizona, États-Unis) sur le recrutement de truites arc-en-ciel (*Oncorhynchus mykiss*) non indigènes dans le fleuve Colorado et estimer la migration vers l'aval du canyon Glen vers le canyon Marble, un tronçon utilisé par les poissons indigènes en péril. Sur une période de 20 ans, le recrutement de truites arc-en-ciel dans le canyon Glen a augmenté parallèlement aux augmentations du débit annuel et aux diminutions de la variation du débit horaire, ainsi qu'après deux des trois inondations contrôlées. Le modèle prédisait qu'environ 16 000 truites-année⁻¹ émigraient vers le canyon Marble et que la majorité des truites dans ce tronçon provenaient du canyon Glen. Pour la plupart des modèles examinés, plus de 70 % de la variation des taux d'émigration était expliquée par les variations du recrutement dans le canyon Glen, ce qui suggère que l'écoulement provenant du barrage contrôle en bonne partie l'ampleur des interactions négatives potentielles entre les truites arc-en-ciel et les poissons indigènes. Les inondations contrôlées et les débits régularisés, qui visaient à l'origine le rétablissement partiel des conditions antérieures à l'aménagement du barrage (plus grande abondance de poissons indigènes et barres de sable plus imposantes), semblent avoir été plus bénéfiques aux truites arc-en-ciel non indigènes qu'aux poissons indigènes.

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Introduction

Temporal trends in recruitment and the spatial distribution and movement of recruits are important determinants of abundance trends in fish populations. Recruitment dynamics are generally difficult to directly observe because juvenile life stages can be patchily distributed over large areas and can be hard to sample. Statistical catch-at-age or catch-at-

length models, which integrate multiple sources of data, are commonly used in assessments of commercially exploited fish populations to estimate recruitment time series from the later capture of adults of various ages (e.g., Fournier et al. 1998; Eveson et al. 2004; Deriso et al. 2007). These integrated assessment models usually treat the data as coming from a single population and ignore spatial dynamics. This can lead to incorrect conclusions about the efficacy of vari-

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ous harvest regimes and the effects of natural and anthropogenic factors on fish recruitment and abundance.

The population of rainbow trout (*Oncorhynchus mykiss*) in the Colorado River below Glen Canyon Dam, Arizona, USA, provides an excellent example to illustrate these aspects of recruitment dynamics. The central objectives of the Glen Canyon Dam Adaptive Management Program, which is tasked with evaluating the effects of flows from the dam, are to increase the abundance of the endangered humpback chub (*Gila cypha*) and other native fishes endemic to the Colorado River, to provide a high quality rainbow trout fishery immediately below the dam and to rebuild sandbars that are used by rafters as campsites and form riparian and aquatic habitats (Schmit et al. 2005). The largest population of humpback chub lives in the Colorado River just downstream of Marble Canyon near the confluence of the Little Colorado River (LCR), about 125 km downstream from the dam, while the rainbow trout population is concentrated immediately below the dam in Glen Canyon (Fig. 1; Gloss and Coggins 2005). In the early 1990s, hourly variation in flow was reduced to improve the status of humpback chub and limit sandbar erosion (Fig. 2; Bureau of Reclamation 1995). Although these objectives were not achieved over the following decade (Gloss and Coggins 2005), the abundance of nonnative rainbow trout in Glen and Marble canyons increased by three- and five-fold, respectively (Fig. 3a). While the unanticipated response in Glen Canyon was beneficial to the rainbow trout fishery, the increase in rainbow trout abundance downstream in Marble Canyon was considered detrimental to humpback chub and other native fishes because of negative effects associated with increased competition and predation (Gloss and Coggins 2005; Yard et al. 2011).

To reduce rainbow trout abundance and impacts on native fish near the LCR, flow variation from Glen Canyon Dam was increased between 2003 and 2005 during winter and spring to suppress rainbow trout recruitment (Fig. 2), and a lethal removal program targeting rainbow and brown trout (*Salmo trutta*) near the LCR was conducted between 2003 and 2006. Trout suppression flows were not severe enough to be effective (Korman et al. 2011a), but the removal effort helped reduce trout abundance near the LCR (Coggins et al. 2011). Since that time, rainbow trout abundance has rebounded to near or above the historic peak (Fig. 3a). Native American tribes have strongly objected to removal activities near the LCR because of its cultural importance (Runge et al. 2011) and lethal removal of fish in general. As a possible solution, future nonlethal removal activities are being proposed farther upstream, just downstream of Glen Canyon (Fig. 1), on the assumption that most rainbow trout in Marble Canyon originate from Glen Canyon. This assumption has not been rigorously evaluated. Furthermore, experimental flows targeted at increasing native fish abundance and sandbars, such as steady flows and controlled floods, could have unintentional negative effects by increasing the abundance of nonnative rainbow trout. A retrospective analysis of the effects of past flow experiments on rainbow trout is therefore warranted.

In this paper, we use an age-structured integrated assessment model to better understand recruitment dynamics and growth of rainbow trout in the Colorado River below Glen Canyon Dam. The objectives of the modelling are to (i) esti-

mate a 20-year time series of recruitment in Glen and Marble canyons to help understand the linkage between flow from Glen Canyon Dam and the abundance of these populations; (ii) quantitatively evaluate alternative hypotheses about the sources of recruitment for the population of rainbow trout in Marble Canyon; (iii) estimate the magnitude and dynamics of outmigration from Glen Canyon to evaluate the feasibility of controlling trout by a removal program located immediately downstream of Glen Canyon; and (iv) estimate trends in growth rates that would affect the quality of the trout fishery in Glen Canyon. Integrated assessment models are not often applied in freshwater fishery management and rarely include processes like movement or spatial distribution of recruitment. The long time series of data for rainbow trout in Grand Canyon, coupled with the modelling approach, provides a unique opportunity to gain insights about flow effects on fish populations in large regulated rivers. Our analysis is also unusual in that it applies an information-theoretic approach to a complex model to distinguish among competing hypotheses and considers the effects of process and observation error on those conclusions.

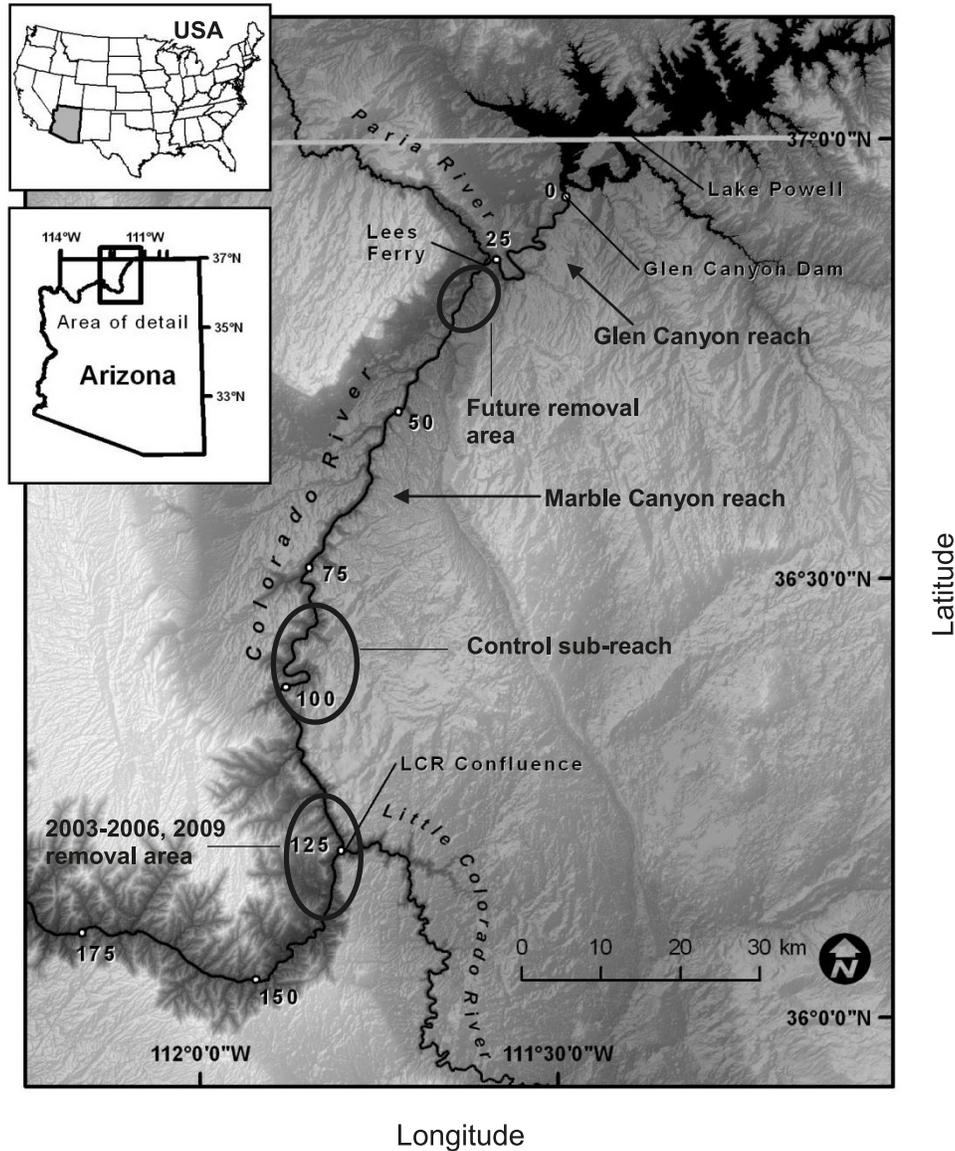
Materials and methods

Study site and hypotheses of population dynamics

The Glen Canyon reach of the Colorado River begins at Glen Canyon Dam and extends 25 km downstream to the confluence with the Paria River (Fig. 1). The reach is wide, shallow, and low-gradient. The Marble Canyon reach is 100 km long and extends from the Paria River to the confluence with the LCR (Fig. 1). This reach is steeper and more confined than Glen Canyon. Occasional large inputs of fine sediment from the Paria River result in short-term increases in turbidity and higher proportions of fines in gravel and cobble substrates relative to Glen Canyon. Average discharge over the 21-year study period (1990–2010) at the Lees Ferry gage (USGS gage 09380000) was $360 \text{ m}^3 \cdot \text{s}^{-1}$. At this flow, wetted width, average depth, and water surface gradient were 146 m, 5.5 m, and 0.025% ($0.25 \text{ m} \cdot \text{km}^{-1}$) in Glen Canyon and 79 m, 6.0 m, and 0.123% in Marble Canyon, respectively (Randle and Pemberton 1987).

The rainbow trout population in Glen Canyon supports a popular and unique blue ribbon tailwater fishery (McKinney et al. 2001). The fish fauna in Glen Canyon is almost exclusively nonnative rainbow trout, and rainbow trout are also the most abundant species in Marble Canyon. Rainbow trout were introduced below Glen Canyon Dam beginning in 1964 shortly after dam closure. Prior to 1990, less than 30% of the population was derived from natural reproduction (Maddux et al. 1987), likely because extensive hourly fluctuations in flow limited survival of early life stages (McKinney et al. 2001). This flow variation was reduced beginning in August 1990 to improve the status of native fish and restore sandbars (Bureau of Reclamation 1995), but instead led to an increase in natural reproduction of rainbow trout (McKinney et al. 2001), which in turn led to a reduction and eventual termination of stocking in 1998. The majority of rainbow trout in Glen Canyon spawn between February and April, and emergence occurs approximately 2 months after fertilization (Korman et al. 2011a). Much less information on rainbow trout spawning in Marble Canyon is available.

Fig. 1. Map of the study area within the Colorado River in Grand Canyon, Arizona. Numbers show river-kilometres (rkm) downstream from Glen Canyon Dam. Glen and Marble canyon reaches extend between rkm 0 and 25 and rkm 25 and 125, respectively. The control and removal reaches sampled in 2003–2006 and 2009 are located between rkm 96 and 109 and rkm 116 and 125, respectively. The map also shows the location of a proposed removal reach just below Lees Ferry.

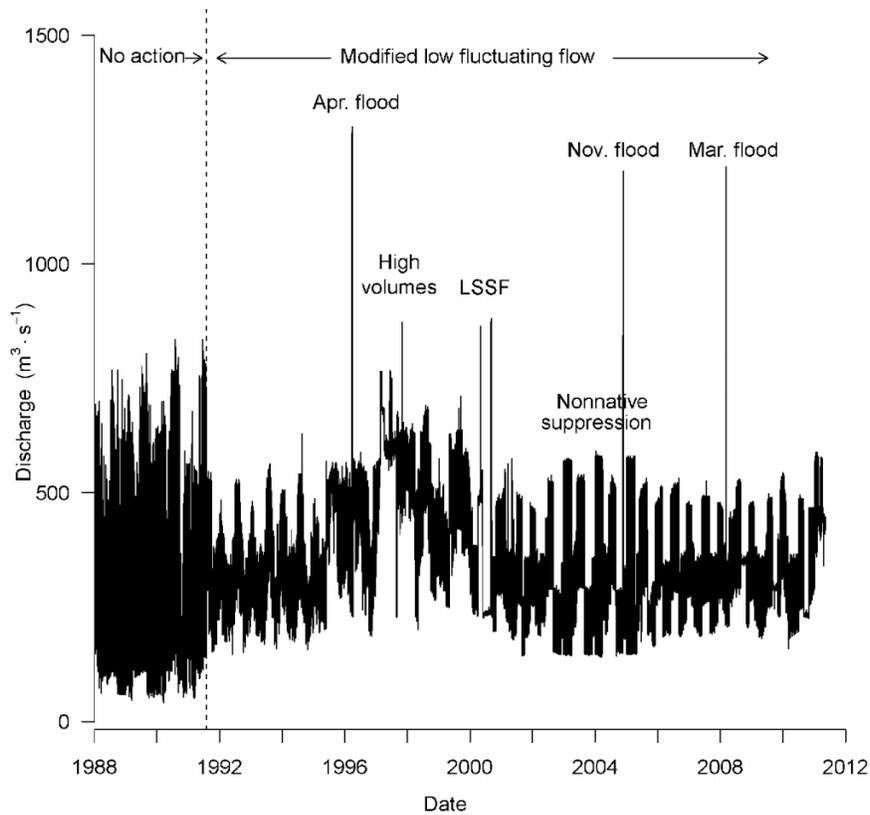


However, a limited number of surveys indicate that spawning habitat is marginal there because the reach is much more confined than Glen Canyon, thereby reducing the availability of gravel bars, and there is much more fine sediment in the substrate due to inputs from the Paria River (Korman et al. 2005).

One of the central objectives of the modelling work presented here is to evaluate hypotheses concerning movement of rainbow trout from Glen Canyon to Marble Canyon and the magnitude of local recruitment in the latter reach. Rainbow trout populations in Glen and Marble canyons were considered independent and self-sustaining, as very few marked hatchery fish released at Lees Ferry in the 1980s were recaptured downstream (Maddux et al. 1987). However,

the recapture effort for marked fish in Marble Canyon was limited, and trout densities at that time were much lower in Glen Canyon than they have been since the mid-1990s, which may have led to much lower rates of outmigration. In contrast with this conclusion, three patterns in electrofishing data between 1991 and 2010 indicate that Glen Canyon may be the primary source of rainbow trout for Marble Canyon: (i) the trend in catch per effort (CPE) in Marble Canyon lags behind the trend in Glen Canyon by a few years (Fig. 3a); (ii) there is a strong declining gradient in rainbow trout density with increasing distance from Lees Ferry (see figure 5 of Gloss and Coggins 2005); and (iii) age-0 trout sampled by electrofishing make up a large proportion of the length–frequency distribution in Glen Canyon, but are rare in Marble Canyon (Fig. 3b).

Fig. 2. Hourly hydrograph of the Colorado River at Lees Ferry, Arizona, 1988–2010. Large hourly fluctuations in flow from Glen Canyon Dam occurred during the “No action” period prior to August 1990 and were followed by reduced fluctuations called modified low fluctuating flows (MLFF). Experimental flows during MLFF include controlled floods in 1996, 2004, and 2008, a low summer steady flow experiment (LSSF) in 2000, and nonnative fish suppression flows in 2003–2005. Note that flows were higher in 1997 and 1998 because of greater inflows to the Colorado River Basin upstream of the dam.



The other key objective of the modelling work presented here is to estimate a 20-year annual recruitment trend for rainbow trout populations in the Glen and Marble canyons to evaluate hypotheses about the effects of flow from Glen Canyon Dam. Monthly water volumes released from Glen Canyon Dam depend on inflows and water management rules for the Colorado River Basin. Discharge from the dam also fluctuates on a diel cycle that is driven by power demand, but is controlled through a suite of operating rules that constrain the maximum daily flow range, minimum and maximum flows, and hourly ramping rates. The extent of daily variation in flow was reduced beginning in August 1990 (modified low fluctuation flows (MLFF); Fig. 2). A variety of experimental flows have been conducted since that time, including controlled floods in 1996, 2004, and 2008, steady low flows and smaller floods in the summer of 2000, and nonnative fish suppression flows in the winter and spring between 2003 and 2005, aimed at reducing the abundance of rainbow trout.

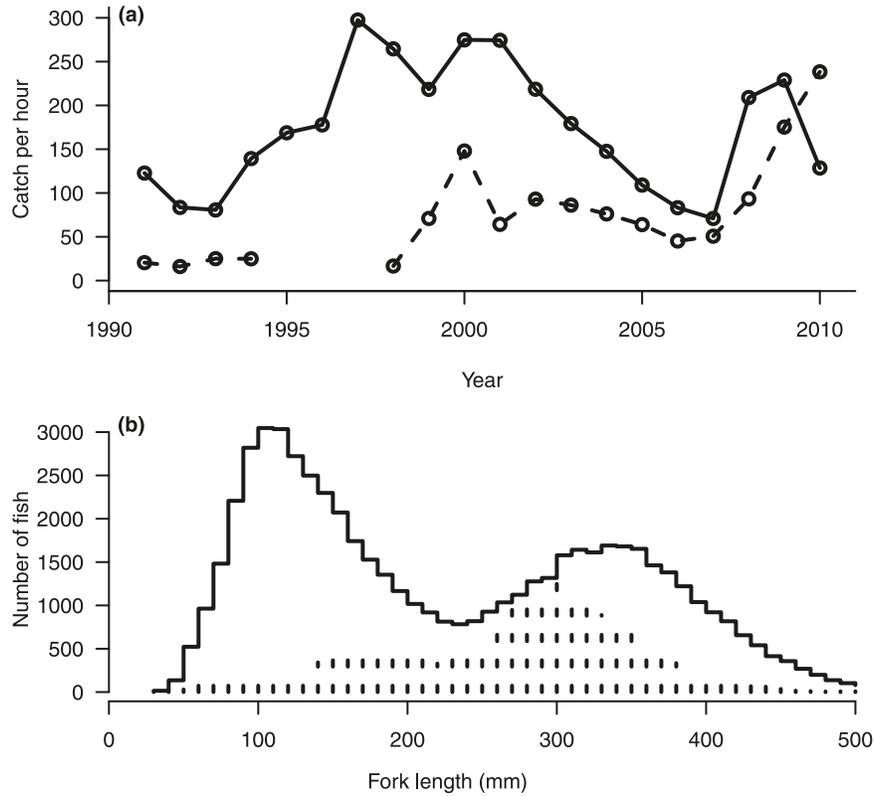
Data

We used an age-structured integrated assessment model to estimate recruitment and movement dynamics of rainbow trout by fitting the model to a variety of data sources, including (i) electrofishing catch, effort, and length–frequency data collected between 1991 and 2010 in Glen and Marble canyons; (ii) population estimates in a “control” subreach within Marble Canyon (Fig. 1), collected as part of a removal pro-

gram between 2003 and 2006 and in 2009; (iii) population estimates of age-0 rainbow trout in Glen Canyon between 2004 and 2010; and (iv) estimates of the proportion of wild fish in Glen Canyon between 1990 and 2001, when hatchery fish were still present in the system. Model-fitting also uses prior information on the ratio of mortality to growth, length-at-age of age-0 trout in Glen Canyon, and catchability of adult trout to electrofishing. We describe each of these data sets below.

Standardized monitoring of rainbow trout in Glen and Marble canyons has been conducted by single-pass boat electrofishing by the Arizona Game and Fish Department since 1991 at a combination of fixed and randomly selected sites (McKinney et al. 2001; Makinster et al. 2010). Glen Canyon has been sampled two to four times per year ($n = 60$ trips over 20 years), while sampling in Marble Canyon has been more sporadic ($n = 51$ trips), with two or more trips per year conducted prior to 1994, limited sampling between 1995 and 1999, and relatively consistent sampling (two trips per year) since 2000. All sampling has been conducted at night using pulsed direct current. In Glen Canyon, an average of approximately 5 h of electrofishing effort were completed each sampling trip, which covered approximately 6 km (10%) of the total shoreline length (50.2 km). Sampling in Marble Canyon was less thorough and based on an average of approximately 6 h of electrofishing effort per trip, covering 7 km of shoreline or 3.5% of the total shoreline length (196 km).

Fig. 3. Trends in electrofishing catch per effort of rainbow trout in Glen Canyon (solid line) and Marble Canyon (dashed line) reaches (a) and length frequencies by reach based on the total catch between 1991 and 2010 (b).



Information from the trout removal program in Marble Canyon provides additional detail on the Marble Canyon population between 2003 and 2006 (Coggins et al. 2011) and in 2009 (Makinster and Avery 2010). Trout were removed from a 15 km reach near the confluence with the LCR (Fig. 1) based on six intensive electrofishing trips per year. To evaluate how effective that program was, trends in population estimates in an unaffected “control reach”, determined by electrofishing-based mark–recapture experiments, were compared with the trend in the removal reach. As the electrofishing gear and sampling technique were identical to those used in the long-term electrofishing monitoring of Glen and Marble canyons, the average capture probability from the control reach can be used as a strong prior for the catchability of the long-term program. As six trips were conducted each year in both control and removal reaches (except in 2009, when only one trip was conducted), the removal program also provides relatively high resolution information on changes in length frequency over time, albeit for a limited period.

Estimates of abundance of age-0 trout in Glen Canyon in summer and fall are available between 2004 and 2010 from an early life stage monitoring program (Korman et al. 2011b). Otolith microstructure data from this program provide accurate estimates of daily age from hatch for fish less than 8 months old (<100 mm). Estimates of the fraction of wild trout in the population between 1990 and 2001 were based the proportion of recoveries of hatchery-origin fish, which were distinguished by an oxytetracycline mark on their otoliths (W.R. Persons, unpublished data).

Model

The age-structured integrated assessment model simulates recruitment, survival, growth, and downstream movement of rainbow trout in the Colorado River between Glen Canyon Dam and the confluence with the LCR. The process component of the model makes predictions about the state of the Glen and Marble canyon populations on a monthly time step for a 21-year period (1990–2010). The observation component of the model converts age-specific abundances to catch by length class in these reaches and the control subreach in Marble Canyon, as well as other metrics for which observations are available. The statistical component of the model computes a total log-likelihood that quantifies the difference between predictions and observations and between predictions and prior assumptions about their values. Details of these three components are described below.

Process model

Recruitment, defined as the number of fish emerging from the gravel, is computed for each monthly time step in Glen and Marble canyons ($R_{r,t}$) based on the product of the total recruitment across reaches each year (R_y), the annual proportion of recruitment from each reach ($P_{r,y}$), and the proportion of annual recruitment that emerges each month (m) of the year (product within square brackets)

$$(1) \quad R_{r,t} = R_y P_{r,y} \left[\left[\frac{m}{12} \right]^{X_y \tau - 1} \left[1 - \frac{m}{12} \right]^{(1 - X_y) \tau - 1} \right]$$

where r is the index for each reach (1 = Glen Canyon, 2 = Marble Canyon), t is the index for each cumulative month in

the time series ($t = 1 \dots 252$), y is an index for each year, and m is an index for each month within a year ($1 \dots 12$; see Table 1 for parameter definitions). Monthly variation in emergence timing (terms inside the large square brackets in eq. 1) is modelled using a beta distribution, which is defined based on estimates of the month when emergence peaks (modal month X_y , expressed on a 0–1 scale) and the precision in the proportion emerging across months within a year (τ). Annual recruitment is predicted based on a log mean recruitment level ($\bar{\epsilon}$) and annual log deviates (ϵ_y) that sum to zero across years (e.g., Schnute and Richards 1995; Maunder and Deriso 2003) from

$$(2) \quad R_y = e^{\bar{\epsilon} + \epsilon_y} \left| \sum \epsilon_y = 0 \right.$$

The proportion of recruitment from each reach is predicted from a mean proportion ($\bar{\rho}$) and annual logit-transformed deviates (ρ_y) from

$$(3) \quad P_{1,y} = \frac{e^{\bar{\rho} + \rho_y}}{1 + e^{\bar{\rho} + \rho_y}} \left| \sum \rho_y = 0, \quad P_{2,y} = 1 - P_{1,y} \right.$$

The annual modal month of emergence in eq. 1 (X_y) is calculated based on a mean modal month ($\bar{\chi}$) and annual logit-transformed deviates (χ_y) from

$$(4) \quad X_y = \frac{e^{\bar{\chi} + \chi_y}}{1 + e^{\bar{\chi} + \chi_y}} \left| \sum \chi_y = 0 \right.$$

Length-at-age ($L_{r,t,a}$) is predicted using a von Bertalanffy model where the asymptotic length ($L_{\infty,y}$) varies among years and reaches based on

$$(5) \quad L_{r,t,a} = L_{r,t-1,a-1} + (\gamma_r L_{\infty,y} - L_{r,t-1,a-1}) (1 - e^{-\frac{a}{\tau}})$$

where a is age in cumulative months from emergence, γ_r is the proportional difference in asymptotic length in Marble Canyon ($r = 2$) compared with Glen Canyon (note $\gamma_1 = 1$), and κ is the annual von Bertalanffy metabolic coefficient. We modelled changes in growth over time by varying L_{∞} by year. We varied L_{∞} rather than κ because changes in feeding rate related to competition are predicted to affect asymptotic length (Essington et al. 2001; Walters and Essington 2010; Walters and Post 1993). κ in the von Bertalanffy growth equation represents the metabolic rate, not the growth rate. Metabolic rate is expected to vary over time with temperature, but there is only a weak seasonal cycle and long-term trend in the Colorado River below Glen Canyon Dam. The same annual estimate of $L_{\infty,y}$ was applied to all 12 monthly cohorts recruiting in year y . Thus, each annual cohort can have a unique growth trajectory, with $L_{\infty,y}$ influencing length-at-age in year y and the following years (up to the terminal age). Asymptotic lengths for each annual cohort are calculated based on a log mean asymptotic length ($\bar{\lambda}$) and a vector of log annual deviates (λ_y) from

$$(6) \quad L_{\infty,y} = e^{\bar{\lambda} + \lambda_y} \left| \sum \lambda_y = 0 \right.$$

Variation in length-at-age is assumed to have a multiplicative error structure such that it is normally distributed at each age with a mean $L_{r,t,a}$ and standard deviation $G_{r,t,a}$ that depends

on the estimated coefficient of variation in length-at-age σ . The standard deviation is calculated from

$$(7) \quad G_{r,t,a} = L_{r,t,a} \sigma$$

Instantaneous monthly mortality at age ($M_{r,t,a}$) is calculated based on the estimated annual mortality at a reference length (μ) and mean length at each age ($L_{r,t,a}$) using the length-based survival function

$$(8) \quad M_{r,t,a} = \frac{\mu}{12} \left(\frac{L_{r,t,a}}{f} \right)^s, \quad S_{r,t,a} = e^{-M_{r,t,a}}$$

where $S_{r,t,a}$ is the monthly survival rate, f is the reference length where the annual mortality is μ , and s is the slope of the Lorenzen (2000) size-mortality function (fixed at -1).

The proportion of fish from Glen Canyon that migrate downstream into Marble Canyon can vary across months in a year (W_m) based on the cosine function

$$(9) \quad W_m = \psi + \frac{1 - \psi}{2} + \left(\frac{1 - \psi}{2} \right) \cos \left(\frac{m}{12} 2\pi + \omega \right)$$

where ψ is the lowest proportion outmigrating from Glen Canyon over 12 months within the year, and ω is the cosine function shift for monthly variation in movement. The proportion moving by year and age ($F_{t,a}$) also depends on fish length based on the double logistic function

$$(10) \quad F_{t,a} = D_y \left[1 + e^{-\left(\frac{L_{r,t,a} - \alpha}{\eta} \right)} \right]^{-1} \left(1 - \left\{ 1 + e^{-\left[\frac{L_{r,t,a} - (\alpha + \beta)}{\eta} \right]} \right\}^{-1} \right)$$

where D_y is the maximum proportion that migrate (across all size classes) each year, α is the length at which the movement rate is 50% of the maximum on the ascending limb of the double logistic function, β is an offset (>0) determining the length at 50% of the maximum rate on the descending limb, and η is the inverse of the steepness of the function for both slopes. This function has the flexibility to allow the proportion moving to be independent of fish size or for the proportion moving to be a dome-, flat-dome-, or a logistic-shaped function of fish size. As described below, the total proportion of fish emigrating from Glen Canyon is computed using the product of W_m (eq. 9) and $F_{t,a}$ (eq. 10). D_y in eq. 10 varies by year and is calculated from

$$(11) \quad D_y = \frac{e^{\bar{\delta} + \delta_y}}{1 - e^{\bar{\delta} + \delta_y}} \left| \sum \delta_y = 0 \right.$$

where $\bar{\delta}$ is the logit-transformed mean proportion, and δ_y are annual deviates.

The model predicts the number of trout stocked in Glen Canyon in wild-age equivalents ($H_{t,a}$) from

$$(12) \quad H_{t,a} = \sum_l h_{t,l} A_{l,t,a} e^{-\xi \left(\frac{h_{t,l}}{f} \right)^s}$$

where l is the index for each 10 mm length class, $h_{t,l}$ is the recorded number of stocked trout in each length class, $A_{l,t,a}$ is the predicted proportion of each age by 10 mm length class, ξ is the instantaneous mortality rate at stocking at reference length f , and b_l is the mid-point of each length class. $H_{t,a}$ is the number of hatchery fish that enter the naturally produced

Table 1. Definition of model variables.

Variable	Description	Value or transformation
Parameters		
τ	Precision in emergence (recruitment) timing across months	
$\bar{\epsilon}, \epsilon_y$	Mean number of recruits (emerging fish) and annual deviates	Log
$\bar{\rho}, \rho_y$	Mean proportion of recruitment in GC and annual deviates	Logit
$\bar{\chi}, \chi_y$	Mean month of emergence (recruitment) and annual deviates	Logit
γ	Proportional difference in asymptotic length in MC relative to GC	
κ	Annual von Bertalanffy metabolic coefficient	
$\bar{\lambda}, \lambda_y$	Mean asymptotic length and annual deviates	Log
σ	Coefficient of variation in length-at-age	
μ	Annual instantaneous mortality rate at reference length	
Ψ	Lowest proportion outmigrating from GC over 12 months in year	
ω	Cosine function shift for monthly variation in movement	
α	Length at which movement rate is 50% of maximum on ascending limb	
β	Length-movement function offset determining location of descending limb (>0)	
η	Inverse of steepness of length-movement function	
$\bar{\delta}, \delta_y$	Mean maximum proportion outmigrating and annual deviates	Logit
ζ	Instantaneous mortality rate at stocking at reference length	
θ	Proportion of fish captured in 1 km if electrofished for 1 h	Logit
ν	Relative difference in catchability in steady flow months by length	$\nu = 1$ if $L > 150$ mm
Ω	Length at which vulnerability is 50% of maximum	
ξ	Inverse of steepness of length-vulnerability function	
State variables (predicted as functions of parameters, data, and constants)		
$R_{r,t}$	Number of recruits (emerging fish)	
$P_{r,y}$	Proportion of recruits from GC and MC	
X_y	Modal month of recruitment	
$L_{\infty,y}$	Asymptotic length	
$L_{r,t,a}$	Length-at-age	
$G_{r,t,a}$	Standard deviation in length-at-age	
$M_{r,t,a}$	Monthly instantaneous mortality rate	
$S_{r,t,a}$	Monthly survival rate	
W_m	Relative difference in proportion outmigrating across months in a year	
$F_{l,a}$	Relative difference in proportion outmigrating by month and age	
D_y	Maximum proportion outmigrating from GC by year	
$A_{r,t,l,a}$	Proportion of each age class by 10 mm length class	
$H_{t,a}$	Number of trout stocked in wild age equivalents	
$K_{t,a}$	Number of trout removed from MC reach by age	
$O_{t,a}$	Number of outmigrants from LF to MC	
$N_{r,t,a}$	Number of trout alive	
V_l	Relative difference in catchability by length class	
$\widehat{C}_{r,t,l}$	Number of trout captured by electrofishing by length class and reach	
\widehat{JP}_t	Juvenile population size in Glen Canyon	
\widehat{CP}_t	Population size in control subreach of Marble Canyon	
\widehat{PW}_t	Proportion of wild fish in Glen Canyon	
Data		
$h_{t,l}$	Number of trout stocked by length class	
$k_{t,l}$	Number of trout removed from MC reach by length class	
$c_{r,t,l}$	Number of trout captured by electrofishing	
$e_{r,t}$	Number of hours of electrofishing effort	
d_r	Kilometres of shoreline in GC (d_1), MC(d_2), and control subreach (CR, d_3)	$d_1 = 50, d_2 = 196, d_3 = 26$
Indices and constants		
r	Index for reach	GC = 1, MC = 2
t	Index for cumulative month	1...252
y	Index for year	1...21

Table 1 (concluded).

Variable	Description	Value or transformation
<i>m</i>	Index for calendar month	1...12
<i>a</i>	Index for monthly age	1...84
<i>l</i>	Index for 10 mm length class	1...49
<i>b</i>	Midpoint of each 10 mm length class	20, 30, ..., 500
<i>s</i>	Slope of Lorenzen mortality function	-1
<i>f</i>	Reference length for Lorenzen mortality function	250
Likelihood Terms		
<i>Likelihood of catch data</i>		Low, High
<i>z</i>	Negative binomial exponent	1×10 ⁶ , 2
<i>Likelihood of population-level variables</i>		
jp, σ _{JP}	Juvenile population estimates in GC in Sept. and SD of estimates	Data ^a
cp, σ _{CP}	Control reach population estimates in MC and SD of estimates	Data ^b
pw, σ _{PW}	Proportion of wild recruits and CV of this proportion	Data ^c
<i>Penalty on process error deviates</i>		
σ _ε	SD for penalty on annual variation in recruitment	0.1, 0.3
σ _ρ	SD for penalty on annual variation in proportion of recruitment in GC	0.1, 0.3
σ _χ	SD for penalty on annual variation in peak month of emergence	0.1, 0.3
σ _λ	SD for penalty on annual variation in asymptotic length	0.1, 0.3
σ _δ	SD for penalty on annual variation in maximum proportion outmigrating	0.1, 0.3
<i>Priors on parameter estimates</i>		
μ _{μ/κ} , σ _{μ/κ}	Mean (and CV) for prior on ratio of mortality to Brody growth coefficient	1.5 ^d (0.01)
μ _{L6} , σ _{L6}	Mean (and CV) for prior on length at 6 months from emergence	100 (0.05 ^a)
μ _θ , σ _θ	Mean (and CV) for prior on proportion of fish captured in per kilometer per hour of effort (logit)	-1.4 ^b (0.01)

Note: Greek and capital Arabic letters denote parameters and state variables (values derived as a function of parameters and data), respectively. Lowercase Arabic letters denote data and constants. All likelihood terms were fixed at the specified values. GC, MC, and CR denote Glen Canyon and Marble Canyon reaches and the control subreach within Marble Canyon, respectively. Footnotes identify the source of information for priors.

^aKorman et al. 2011b.

^bCoggins et al. 2011; Makinster and Avery 2010; and Makinster et al. 2010.

^cMaddux et al. 1987.

^dJensen 1996.

population and depends on the number stocked and the estimated proportion that survive shortly after stocking events, which depends on their size at stocking. The number of fish removed in Marble Canyon from the mechanical removal program ($K_{t,a}$) is predicted from

$$(13) \quad K_{t,a} = \sum_l k_{t,l} A_{2,t,l,a}$$

where $k_{t,l}$ is the number of trout removed by 10 mm length class. The age-length transition matrix used in eqs. 12 and 13 depends on the predicted mean and standard deviation in length-at-age, and is calculated from

$$(14) \quad A_{r,t,l,a} = \frac{1}{G_{r,t,a} \sqrt{2\pi}} \int_{b_l-5}^{b_l+5} e^{-\frac{(l_{r,t,a}-b_l)^2}{2G_{r,t,a}^2}} dl$$

where 5 is 1/2 of the 10 mm length class bin. The number of trout migrating from Glen Canyon to Marble Canyon ($O_{t,a}$) is predicted from the numbers alive on the previous time step ($N_{1,t-1,a-1}$) and the proportion that migrate, which can vary by month, size class, and year, and is computed from

$$(15) \quad O_{t,a} = (N_{1,t-1,a-1} + H_{t-1,a-1}) W_m F_{t,a}$$

Predicted numbers of fish alive in Glen Canyon (eq. 16) and Marble Canyon (eq. 17) depend on the losses and gains due to movement and survival and are predicted from

$$(16) \quad N_{1,t,a} = (N_{1,t-1,a-1} + H_{t-1,a-1} - O_{t,a}) S_{1,t,a}$$

$$(17) \quad N_{2,t,a} = (N_{2,t-1,a-1} + O_{t,a}) S_{2,t,a} - K_{t,a}$$

The equations predicting the number of fish alive do not account for losses from angler harvest or incidental mortality from angling or scientific sampling. These losses were either negligible or would not substantively affect model predictions. Over the last 10–15 years of the study period, the vast majority of angling effort in Glen Canyon is catch-and-release (Makinster et al. 2011), and angling effort in Marble Canyon has always been very limited. Annual removals in Glen Canyon from harvest after 1991 were small (average 3750 or 3%–6% of the abundance of the vulnerable population; Makinster et al. 2011). Harvest prior to 1992 was larger, but effects of not removing it from the modelled population would be absorbed by the recruitment estimates prior to 1990, which are used for initialization but not presented here. Finally, only a small fraction of the population is

handled during scientific sampling, and mortalities from sampling are rare (Makinster et al. 2010, 2011).

At the beginning of each monthly time step, the population in Marble Canyon is composed of recent immigrants ($O_{t,a}$) and fish from Marble Canyon still alive from the previous time step ($N_{2,t-1,a-1}$). The size of fish from the previous age-time step used in the length-at-age equation for Marble Canyon (eq. 5) is thus calculated as a number-weighted average length of these two components (i.e., $L_{2,t-1,a-1} = \frac{L_{1,t-1,a-1}O_{t,a} + L_{2,t-1,a-1}N_{2,t-1,a-1}}{O_{t,a} + N_{2,t-1,a-1}}$).

Observation model

The observation model translates predictions of the size and numbers of fish alive by time step into metrics for which observations are available, such as the electrofishing catch by 10 mm length class on individual trips in each reach ($c_{r,t,l}$). Predictions are also made for auxiliary observations, such as estimates of age-0 population size in Glen Canyon in the fall (JP_t), total population size in the control subreach in Marble Canyon (CP_t), and the proportion of wild trout in Glen Canyon (PW_t) during the first half of the time series when stocked fish were still present in the system. The majority of fish in the electrofishing data set used to fit the model are larger than 80 mm. Differences in recruitment estimates among years from the model therefore reflect variation in both the number of trout emerging from the gravel (caused by differences in egg deposition and incubation survival) and their survival rates up to this minimum size at capture.

We did not attempt to fit to available data on angling catch rates in Glen Canyon (Makinster et al. 2011) because the electrofishing and angling CPE time series were highly correlated between 1991 and 2001 ($r^2 = 0.80$), and we did not know how to adjust effort data to account for major changes in the fishery (increase in fly fishing and guided effort) that occurred over the period of record (Wilberg and Bence 2006).

Electrofishing catch by reach, time step, and length class ($\hat{C}_{r,t,l}$) is predicted as a function of overall catchability (θ), length-dependent vulnerability to capture (V_l), proportional differences in catchability for small fish associated with steady flows during sampling ($v_{r,l}$), reach length (d_r), effort ($e_{r,t}$), and the number of fish alive by length class from

$$(18) \quad \hat{C}_{r,t,l} = \frac{\theta v_{r,l}}{d_r} V_l e_{r,t} \sum_a A_{r,t,l,a} N_{r,t,a}$$

Overall catchability (θ) represents the proportion of the population in 1 km of shoreline caught per hour of electrofishing effort for fish large enough to be fully vulnerable to electro-

fishing ($V_l = 1$). Relative vulnerability to electrofishing increases with fish size according to the logistic function

$$(19) \quad V_l = \left[1 + e^{-\left(\frac{l_r - \Omega}{\xi}\right)} \right]^{-1}$$

where Ω is the length at which vulnerability is 50% of maximum, and ξ is the inverse of steepness of length-vulnerability function. The catchability for each reach (i.e., proportion of the population caught per hour of effort) for fish of a given size is simply the product of the overall catchability and length-specific vulnerability divided by the total shoreline length for the reach (d_r). The latter adjustment is necessary, because catch from a given level of effort (time or length sampled) depends on fish density rather than reach-wide abundance. For example, given the same abundance and effort in two reaches that differ in shoreline length by twofold, the catch in the longer reach would be twofold lower than that in the shorter one because fish density in the former would be twofold lower. Thus, the product of $\frac{\theta}{d_r}$ and the number of hours of electrofishing per trip ($e_{r,t}$) determines the total proportion of fully vulnerable fish caught in the reach on a trip. Catchability of smaller fish has been shown to be considerably higher when there is no diurnal variation in flow within a day (Korman and Campana 2009). An adjustment to the base catchability for fish < 150 mm ($v_{r,l}$) is estimated and applied in months when steady flows occurred.

The abundance of the age-0 population in Glen Canyon in late fall (JP_t) is calculated as the sum of the number of fish with fork lengths less than 150 mm (see figure 7 of Korman et al. 2011a) from

$$(20) \quad \hat{JP}_t = \sum_a N_{1,a,t} | L_{1,a,t} < 150 \text{ mm}$$

The abundance of the population in the control subreach ($r = 3$) in Marble Canyon (CP_t) is the product of the estimate for all of Marble Canyon ($r = 2$) and a multiplier that represents the proportion of shoreline length in the control subreach (d_3) relative to Marble Canyon (d_2) and is predicted from

$$(21) \quad \hat{CP}_t = \frac{d_3}{d_2} \sum_a N_{2,a,t}$$

These predictions are based on the assumption that trout density in the control reach is equivalent to the average density for all of Marble Canyon. The proportion of the population in Glen Canyon that is wild in origin is computed based on the number of hatchery fish alive in each time step (based on stocking at that time step as well as those alive from previous time steps) relative to the total number of fish alive and is predicted from

$$(22) \quad \hat{PW}_t = 1 - \frac{\sum_a H_{a,t} + \sum_a H_{a,t-12} e^{-M_{1,t-12,a}} + \sum_a H_{a,t-24} e^{-\frac{24}{12}M_{1,t-24,a}} + \dots}{\sum_a N_{1,a,t}}$$

Statistical model

The statistical model computes a total log-likelihood (LL_{tot}) that quantifies the degree to which predictions match observations (LL_{catch} and LL_{pop}) or assumptions about predicted val-

ues as specified by penalty functions or prior distributions (LL_{proc} , LL_{par}). The total log-likelihood is computed from

$$(23) \quad LL_{tot} = LL_{catch} + LL_{pop} + LL_{proc} + LL_{par}$$

The first term (LL_{catch}) quantifies the discrepancy between predicted ($\hat{C}_{r,t,l}$) and observed ($c_{r,t,l}$) catch across all reaches, sampling trips, and length classes and is calculated from

$$(24) \quad LL_{\text{catch}} = \sum_r \sum_t \sum_l \text{NegBin}(c_{r,t,l}, \hat{C}_{r,t,l}, z)$$

NegBin returns the log-likelihood from a negative binomial distribution with a mean defined by the predicted catch and the term z that determines the extent of overdispersion in the data (see eq. 3.10 of Hilborn and Mangel 1997). The overdispersion term was fixed at different values to evaluate effects of the assumed level of observation error in the catch-at-length data. This error represents uncertainty in the catch data with respect to indexing actual abundance. The uncertainty will be driven by variability in catchability among sampling trips because of differences in flow and turbidity (Coggins et al. 2011; Speas et al. 2004), differences in the distribution of fish within each reach relative to the spatial distribution of sampling effort on each trip, and the extent of nonindependence among samples (Fournier et al. 1998; Schnute and Richards 1995). Note that z is inversely related to the extent of overdispersion in the data. To evaluate the case where we assume no overdispersion in the catch data, z is set to a large number (1×10^6), which results in the error model converging to a Poisson distribution.

The second term (LL_{pop}) in the total log-likelihood (eq. 23) quantifies the discrepancy between predicted and observed population-level predictions and is calculated from

$$(25) \quad LL_{\text{pop}} = \sum \text{Norm}(\hat{JP}_t - jp_t, \sigma_{JP_t}) + \sum \text{Norm}(\hat{CP}_t - cp_t, \sigma_{CP_t}) + \sum \text{Norm}(\hat{PW}_t - pw_t, \sigma_{PW_t})$$

Norm is the log-likelihood returned from a normal distribution given predicted and observed values and the standard deviation of each observation (σ_x). This includes age-0 abundance in Glen Canyon in September between 2004 and 2010 (jp_t) from juvenile surveys (no data for 2005, $n = 6$), total abundance in the control subreach (cp_t), which was estimated five to six times per year based on mark-recapture experiments between 2003 and 2006 and once in 2009 ($n = 24$), and the proportion of wild fish in the sampled population in Glen Canyon (pw_t), which was estimated in 9 years between 1991 and 2001.

The third term in the total log-likelihood (eq. 23), LL_{proc} , quantifies the discrepancy between realized process error and assumptions about the extent of process error for model parameters where annual deviations are estimated (eqs. 2, 4, 6, 11). This log-likelihood is computed from

$$(26) \quad LL_{\text{proc}} = \sum_y \text{Norm}(\varepsilon_y, \sigma_\varepsilon) + \sum_y \text{Norm}(\rho_y, \sigma_\rho) + \sum_y \text{Norm}(\chi_y, \sigma_\chi) + \sum_y \text{Norm}(\lambda_y, \sigma_\lambda) + \sum_y \text{Norm}(\delta_y, \sigma_\delta)$$

Norm is the log-likelihood returned from a normal distribution given the deviates ($\varepsilon_y, \rho_y, \dots$) and the assumed standard deviation of the process error (σ_x). All else being equal, the extent of annual deviations in terms like recruitment (ε_y) predicted by the model will be greater when the assumed standard deviation for that error type is high (e.g., $\sigma_\varepsilon = 0.3$) compared with when it is low (e.g., $\sigma_\varepsilon = 0.1$). This likelihood component is a penalty that is used to constrain the extent of process error.

As in many assessments based on statistical catch-at-age or catch-at-length models, it is necessary to use such penalties to provide stable solutions for parameter estimates (see Schnute and Richards 1995; Maunder and Deriso 2003).

The final term in the total log-likelihood (eq. 23), LL_{par} , quantifies the discrepancy between parameter estimates and prior probabilities for those estimates. This log-likelihood includes priors for the ratio of mortality to the Brody metabolic constant coefficient ($\frac{\mu}{\kappa}$), length at 6 months from emergence in Glen Canyon ($L_{1,t,6}$), and catchability (θ) and is computed from

$$(27) \quad LL_{\text{par}} = \text{Norm}\left(\frac{\mu}{\kappa} - \mu_{\frac{\mu}{\kappa}}, \sigma_{\frac{\mu}{\kappa}}\right) \sum_t \text{Norm}(L_{1,t,6} - \mu_{L6}, \sigma_{L6}) + \text{Norm}(\theta - \mu_\theta, \sigma_\theta)$$

Norm returns the log-likelihood from a normal distribution based on the difference between the predicted value and the mean (μ_x) of the prior distribution given the amount of information at that prior, as determined by its standard deviation (σ_x). The mean and standard deviation of the prior on the ratio of mortality to growth rate was set at 1.5 (Jensen 1996) and 0.05, respectively. The mean and standard deviation of length at 6 months from emergence, based on otolith data (Korman et al. 2011a), was set at 100 and 0.05 mm, respectively. The mean of the normal prior on catchability in logit space (θ) was fixed at -1.4 (equivalent to 0.19 when back-transformed). This mean was calculated based on the product of the average capture probability from one pass of electrofishing effort during 24 mark-recapture experiments in the control reach of Marble Canyon between 2003 and 2006 (Coggins et al. 2011) and the average distance of shoreline sampled per hour of electrofishing effort (1.15 km). We assumed that the standard deviation of the prior on θ was 0.01.

A range of scenarios defined the variance terms in the log-likelihood model, which in part determine the relative importance of each component to the overall fit. The extent of overdispersion in the catch-at-length data and the extent of process error are uncertain. Thus, values were fixed at low and high values (Table 1), and the sensitivity of the model to these conditions was evaluated. The amount of information associated with each LL_{pop} component depended on the standard deviations of the observations. These were defined using the standard deviations of the annual population estimates for jp_t and cp_t (Coggins et al. 2011). The value of σ_{PW} was set at the minimally informative level to produce a good fit between the predicted and observed proportion of wild fish in Glen Canyon across all model scenarios (Table 1). All standard deviation terms in LL_{par} were minimally informative values needed to achieve stable solutions for parameter estimates, as evaluated based on criteria outlined below.

The effect of the variance terms in the log-likelihood on model fit and uncertainty depends on the magnitude of relative changes in individual components. For example, the realized annual variation in process deviates may exceed the assumed extent of those deviates (σ_ε in eq. 26) if the decrease in the log-likelihood from larger deviates (as quantified through LL_{proc}) is more than offset by an improvement in the log-likelihood for other components of the total likelihood because of the greater variation in deviates. Similarly, estimates of parameters with strong priors like catchability

(θ) may vary significantly from the prior mean if the cost of reduced fit to the prior is less than the cost associated with reduced fit for other likelihood components.

Parameters of the model were estimated by minimizing the negative value of the total log-likelihood (eq. 23) using the nonlinear search procedure in the AD Model Builder (ADMB) software (Fournier et al. 2011). The model was initialized by simulating the numbers and size of fish alive for 7 years prior to the first model year (1990) by estimating one additional annual deviate for all terms that included process error. We checked that the model had reached a global minimum by ensuring that estimates were the same when the model was initialized with randomly selected starting values for each parameter. We ensured convergence had occurred based on the gradients of change in parameter values relative to changes in the log-likelihood and the condition of the Hessian matrix returned by ADMB. Asymptotic estimates of the standard error of parameter estimates at their maximum likelihood values were computed from the Hessian matrix within ADMB.

Model scenarios and model selection

All combinations of two structural models and four error scenarios were used to evaluate alternate hypotheses about recruitment and the effect of observation and process error assumptions. The global model estimated 128 parameters for the entire 21-year time series. A nested model simulated a case where there was no recruitment from Marble Canyon (NoRecMC). Under this model, $P_{1,y} = 1$, $P_{2,y} = 0$ (eq. 1), and $\bar{\rho}$ and ρ_y in eq. 3 are not estimated, reducing the model to 106 parameters. For these two models, we conducted the estimation under four error scenarios based on all four combinations of low ($z = 1 \times 10^6$) and high ($z = 2$) observation error and low ($\sigma_x = 0.1$) and high ($\sigma_x = 0.3$) process error (Table 1). The high process error value was the approximate maximum level that allowed the model to meet all the convergence criteria described above, and the low value was arbitrarily selected to provide contrast in the extent of process error. We also computed maximum likelihood estimates for the global model without any penalty on process error. Although parameter estimates from these latter models were more uncertain and the condition of the Hessian matrix was sometimes poor, they allowed us to further evaluate the effects of assumptions about the extent of process error. Within each error scenario, we used the Akaike information criterion (AIC) to evaluate which model (global or NoRecMC) achieved the best balance between bias and precision (Burnham and Anderson 2002). The AIC statistic is based on the number of parameters that are estimated and the fit of the model to the data, as measured by the total log-likelihood. Models with lower AIC are considered to have better predictive performance when applied to replicate data sets compared with models with higher values. AIC comparisons can only be made between models applied to the same information, which in our case includes catch-at-length data, the form of the likelihood model used for that data (Poisson or overdispersed), auxiliary data, prior parameter distributions, and assumptions about the extent of process error. Thus, AIC comparisons can only be made between global and NoRecMC models within each of the four observation-process error scenarios. Models with similar AIC values to

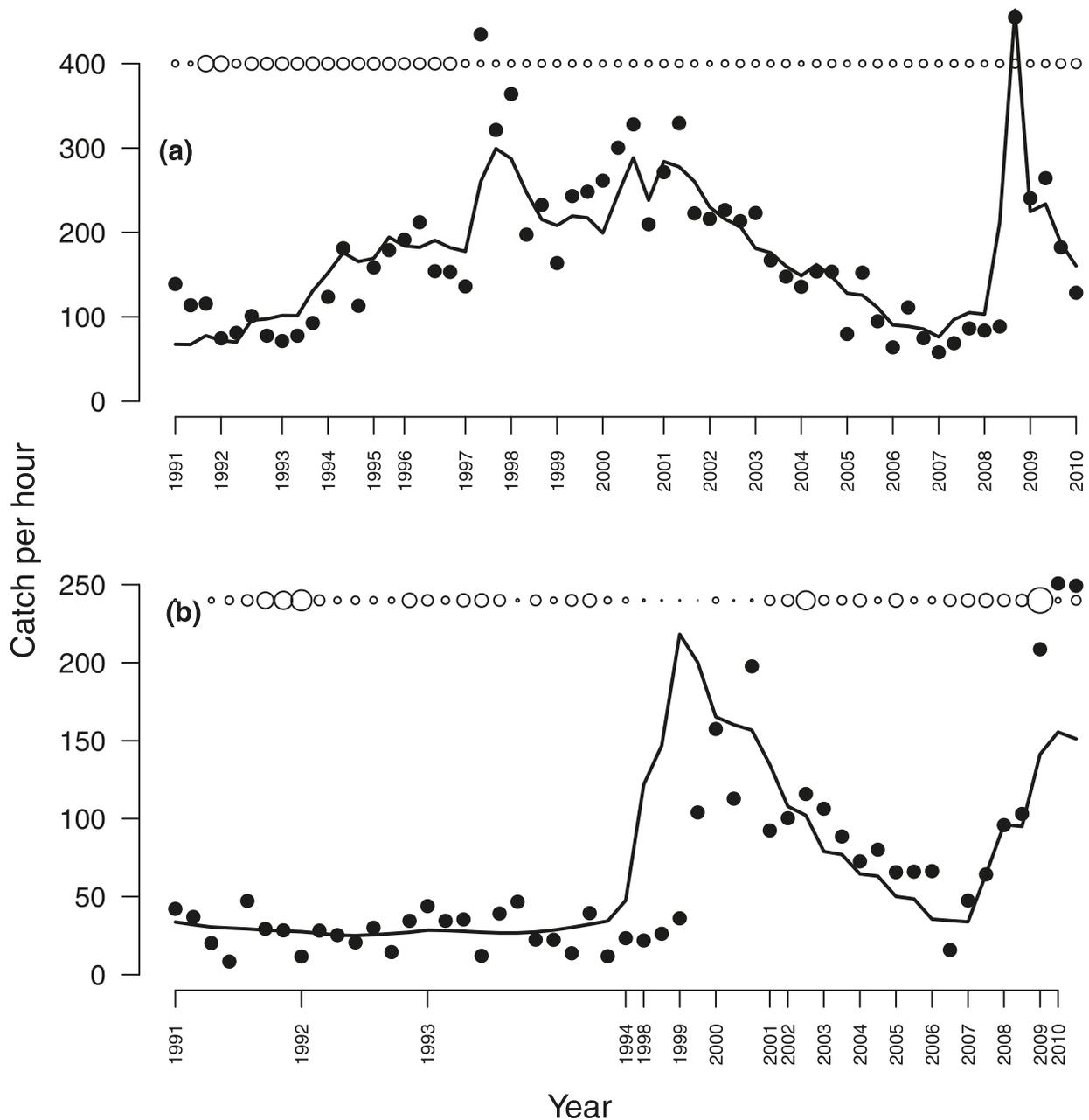
the model with the lowest AIC ($\Delta\text{AIC} < 2$) were considered to have strong support. Models with AIC values that were 4–7 or >10 units higher than the model with the lowest AIC value were considered to have moderate or essentially no support, respectively (Burnham and Anderson 2002).

We evaluated the effects of flow on recruitment based on comparisons of predicted recruitments in normal water years with those from years having flow characteristics hypothesized to increase recruitment. Based on releases from Glen Canyon Dam as measured by the discharge at Lees Ferry (Fig. 1), we computed (i) the annual release volume; (ii) the average difference in maximum and minimum discharges within a day between May and August for each year; and (iii) the maximum instantaneous flow each year. The first statistic addresses the hypothesis that greater volumes increase habitat area and therefore juvenile survival rates throughout their first year of life (McKinney et al. 2001). The second statistic addresses the hypothesis that greater within-day flow fluctuations during the critical period for young trout (0–4 months from emergence; Elliott 1994) reduces survival (Korman and Campana 2009; McKinney et al. 2001). The third statistic addresses the hypotheses that short-term high flows (e.g., experimental floods) scour the bed and increase interstitial spaces and food availability for young trout, which increases their survival after the flood has receded (Cross et al. 2011; Korman et al. 2011a, 2011b). Flow statistics were used to classify each year into normal or potentially beneficial water years. We then tested whether the mean of predicted log recruitments from potentially beneficial water years was statistically greater than the mean from normal water years using a one-sided *t* test. We also compared AICs from the global model with a modified version that estimated separate mean recruitments ($\bar{\epsilon}$ from eq. 2) for normal and potentially beneficial water years. Finally, single-variable and multiple linear regression was used to predict log recruitments estimated by the model as a function of the flow variables, and backward stepwise regression based on AIC was used to determine which variables were the most important. These statistical procedures were implemented in the R statistical package (R Development Core Team 2010).

Results

We present estimates from the global model based on low observation error and high process error to highlight key aspects of model behavior and fit to the data. The predicted CPE, aggregated across all size classes, provided a very good fit to data from Glen Canyon and to most of the data from Marble Canyon (Fig. 4). The model overpredicted abundance in the late 1990s in Marble Canyon. These patterns were also apparent in the comparison of predicted and observed catch-at-length distributions (Fig. 5). The observed catch of larger fish (~250–350 mm) in Marble Canyon increased suddenly during the last sampling trip in 1999 and was not preceded by increased numbers of smaller fish on earlier trips. As out-migration of larger fish from Glen Canyon is inconsistent with observations in most years, the best way for the model to maximize the likelihood of the catch-at-length data in this case was to increase abundance of smaller fish in the mid- to late 1990s to fit the data by the last trip in 1999 and in 2000.

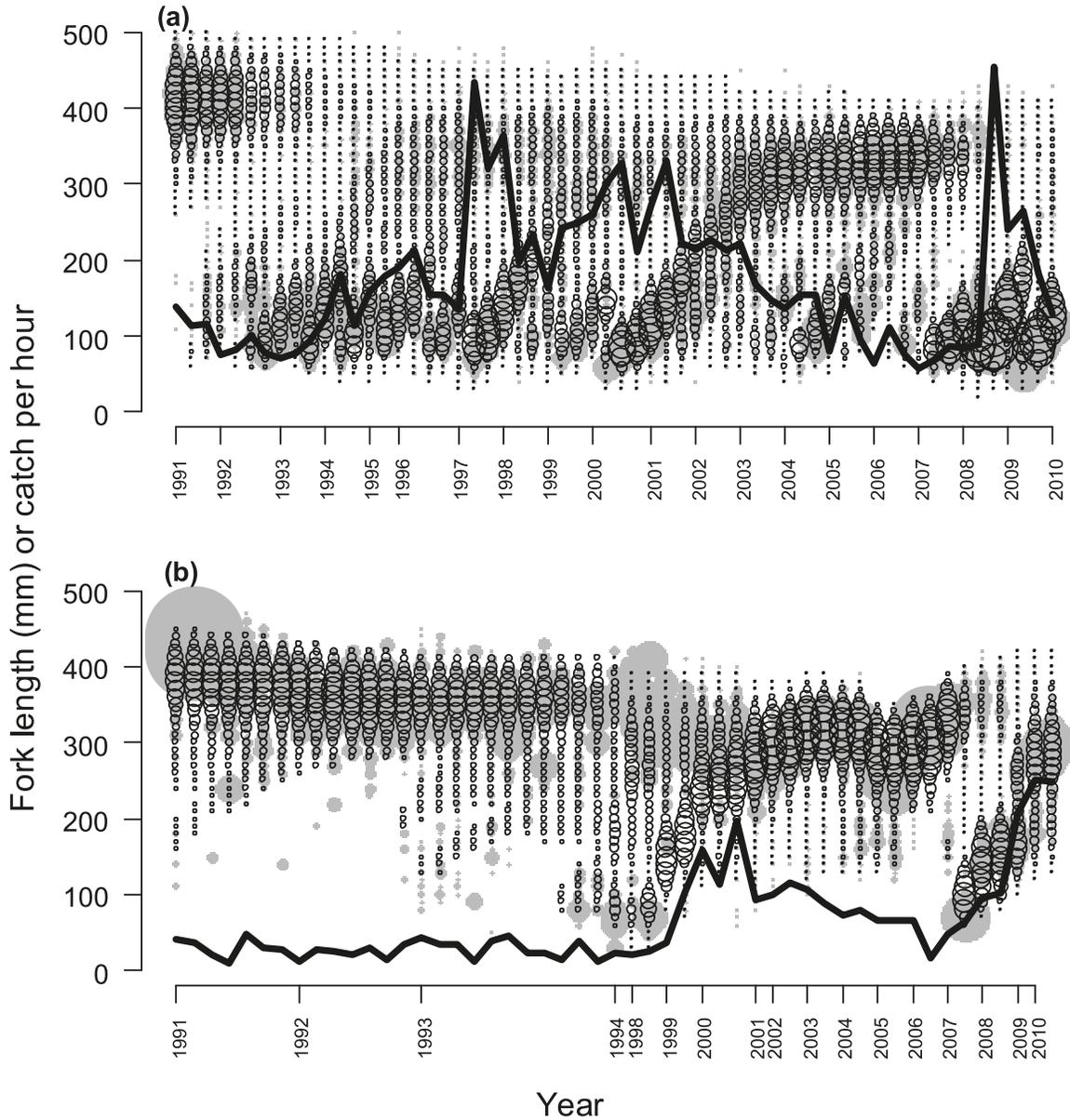
Fig. 4. Comparison of predicted (lines) and observed (filled circles) rainbow trout electrofishing catch per effort (aggregated across all sizes) in Glen (a) and Marble (b) canyons. Differences in the area of the open circles at the top of each plot are proportional to the amount of electrofishing effort and highlight differences across sampling trips and reaches. Predictions are based on the global model assuming low observation error and high process error.



There was very little penalty in doing this, as there were no sampling trips in Marble Canyon between 1995 and 1997 and very limited sampling effort in 1998 and 1999 (Fig. 4b). The model also underpredicted the sudden increase in abundance of 150–300 mm fish in Marble Canyon during the last three sampling trips (2009–2010; Fig. 5b). This increase could not be predicted adequately given the relatively low abundances during preceding trips, and we suspect the apparent sudden increase was driven in part by unusually high catchability in 2009 and 2010 (Coggins et al. 2011; Makinster et al. 2010). This effect was not captured in the model because catchability was assumed constant over time.

Both models and all error scenarios fit the auxiliary data well. The modeled recruitment trend in Glen Canyon in recent years matched the observed trend based on age-0 sampling, although the model underestimated the large 2008 cohort, perhaps indicating that there was higher mortality for younger age classes in this year due to higher density (Fig. 6a; r^2 range across all eight model–error combinations = 0.71–0.87). The predicted decline in abundance in the control reach between 2003 and 2006 was similar to the observed trend, but the model overestimated abundance in 2009, likely because catchability during those trips was higher than assumed (Fig. 6b; $r^2 = 0.51–0.68$). The model provided good

Fig. 5. Comparison of observed (gray filled circles) and predicted (open circles) rainbow trout catch per hour by 10 mm size class and sampling trip (columns) in Glen (a) and Marble (b) canyons. The size of the circles represents the relative proportion of the catch per hour across size classes within trips. Values < 0.5 fish-hour⁻¹ are not shown for clarity. The black solid lines represent the trends in the observed total catch (aggregated across all size classes) per hour of electrofishing effort. Results are based on the global model assuming low observation error and high process error.

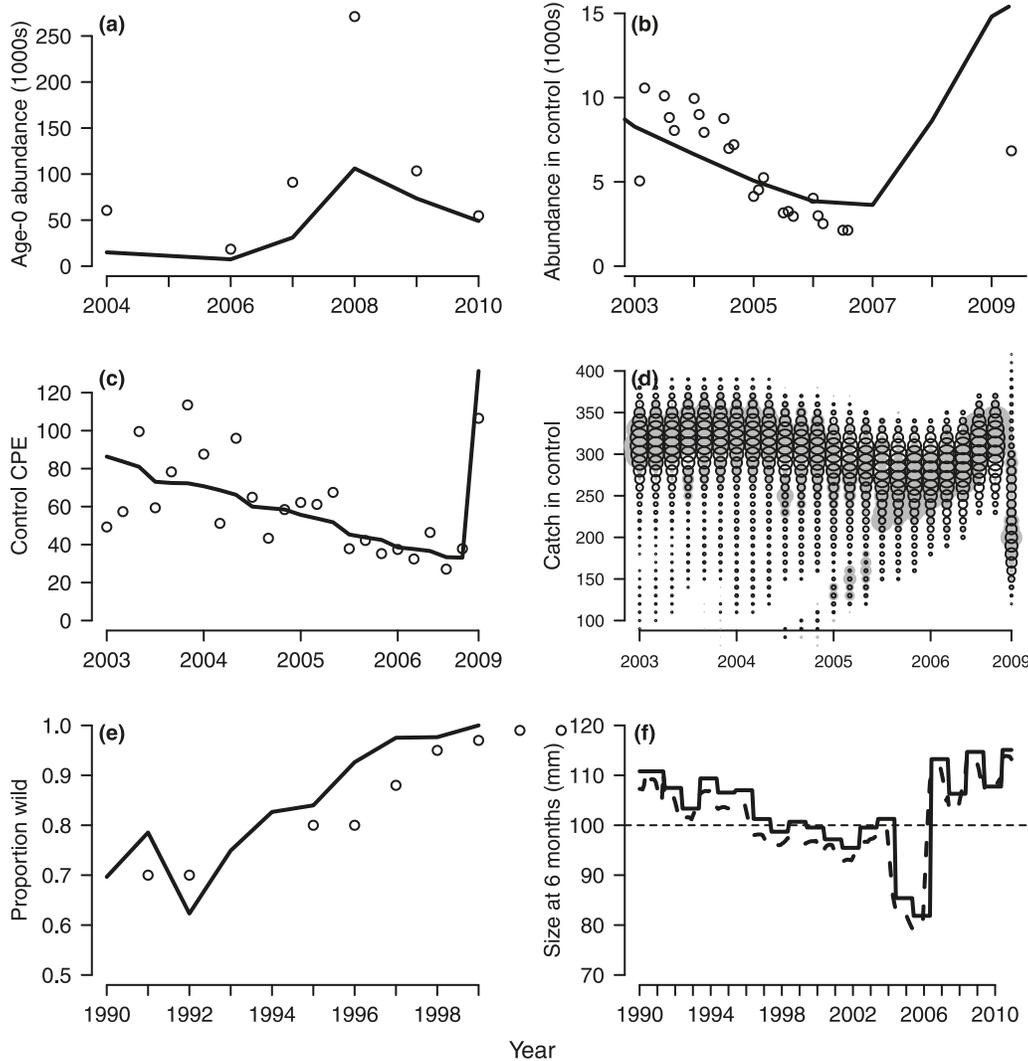


fits to CPE (Fig. 6c; $r^2 = 0.47\text{--}0.51$) and catch-at-length data (Fig. 6d; $r^2 = 0.53\text{--}0.76$) in the control reach. It also provided a good fit to the estimated proportion of wild fish in Glen Canyon during the early part of the time series when the population was stocked (Fig. 6e; $r^2 = 0.78\text{--}0.80$). Finally, predicted fork length at 6 months from emergence between 1990 and 2010 ranged from 80 to 117 mm (across all model–error combinations), which was close to the observed range of 90–110 mm based on otoliths collected between 2004 and 2010 (Fig. 6f; Korman et al. 2011a).

Predictions from the global model for a range of state variables are shown (Fig. 7), with large recruitment events in Glen Canyon in 1997, 2000, and 2008 and substantial recruitment in Marble Canyon in 1996, 1998, and 2007

(Fig. 7a). The predicted trend in reach-wide abundance of fish > 150 mm was similar in Glen and Marble canyons, reaching peaks between 1998 and 2002 (Fig. 7b). Predicted asymptotic length declined slowly for annual cohorts born between 1990 and 2003 and was lowest in 2004 and 2005 (Fig. 7c). Note that some of the temporal trends in catch-at-length, such as the near absence of very large trout (450–500 mm) after the early 1990s (Fig. 5) and the very low frequency of fish larger than 350 mm in 2004 and 2005 in Marble Canyon (Fig. 5b) and the control reach (Fig. 6d), are largely captured by temporal changes in asymptotic length. The estimated size–vulnerability relationship indicates that fish are fully vulnerable to sampling by approximately 100 mm (Fig. 7d). There was considerable annual variation

Fig. 6. Fit of the global model (with low observation error and high process error) to auxiliary data, which includes (a) rainbow trout age-0 population estimates in September in Glen Canyon (open circles and solid line represent data and predictions, respectively); (b) population estimates from the control reach in Marble Canyon; (c) catch per hour of effort (CPE) in the control reach; (d) catch-at-length in the control reach (gray filled and open circles represent data and predictions, respectively, and the size of the circles represents the relative proportion of the catch per hour across size classes within trips); (e) proportion of wild-origin fish in Glen Canyon; and (f) size of fish at 6 months from emergence in Glen Canyon (solid line) and Marble Canyon (dashed line). The horizontal dotted line in panel (f) represents the mean of the prior distribution for length at 6 months.



in the predicted maximum proportion of trout outmigrating from Glen Canyon each year (~ 0.05 – 0.60), with the majority of fish moving at sizes between 125 and 225 mm (Fig. 7e) during fall and winter (Fig. 7f).

Model fit was affected by assumptions on the extent of variance in observation and process error. As expected, for a given level of observation error, the realized annual variation in deviates was always greater when the penalty on that deviation was less (i.e., when the assumed process error variance was higher; Table 2). When observation error was low (Poisson, $z = 1 \times 10^6$), the model provided good fits to the catch-at-length data ($r^2 = 0.73$ – 0.76) by increasing the extent of annual variation in process error deviates controlling recruitment, growth, emergence timing, and movement. When observation error was higher ($z = 2$), the fit to the catch-at-length data was worse ($r^2 = 0.37$ – 0.42) because there was

less relative change in the likelihood for the catch-at-length data under different parameter estimates. This led to a relative increase in the penalty for process error, which in turn led to a decrease in the realized extent of annual variation in process deviates. Put more simply, when there is less belief in the data (high observation error), there is less information to support predictions that exhibit greater annual variation in factors like recruitment, movement, and growth. The poorer fit associated with lower process error is consistent with the data when those data are assumed to be less reliable. There were negligible to modest changes in the fit of the model to the catch-at-length data when we excluded the process error penalty (LL_{proc}) from the total likelihood (eq. 23). The proportion of variation in observed catch-at-length explained by the global model with low observation error increased from 0.761 under high process error (Table 2) to 0.765 without

Fig. 7. Predictions from the global model (with low observation error and high process error) showing (a) rainbow trout recruitment in Glen (solid line) and Marble (dashed line) canyons; (b) total abundance of trout > 150 mm in Glen and Marble canyons, with Glen Canyon abundance inflated by a factor of 3 to highlight the similarity in trends between reaches; (c) asymptotic length for each annual cohort; (d) vulnerability to electrofishing as a function of fork length; (e) proportion outmigrating from Glen Canyon as a function of fork length (lines show predictions for each year); and (f) variation in the proportion outmigrating by month.

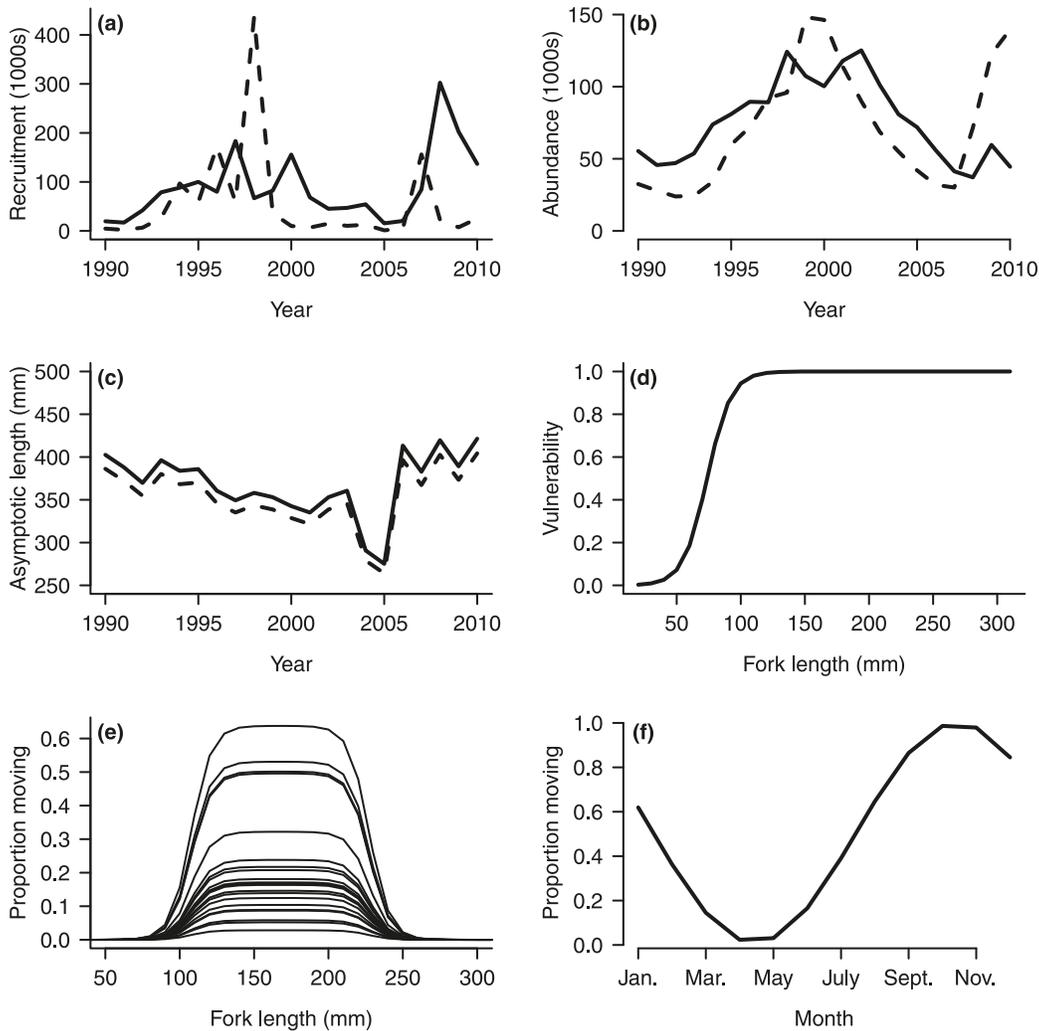
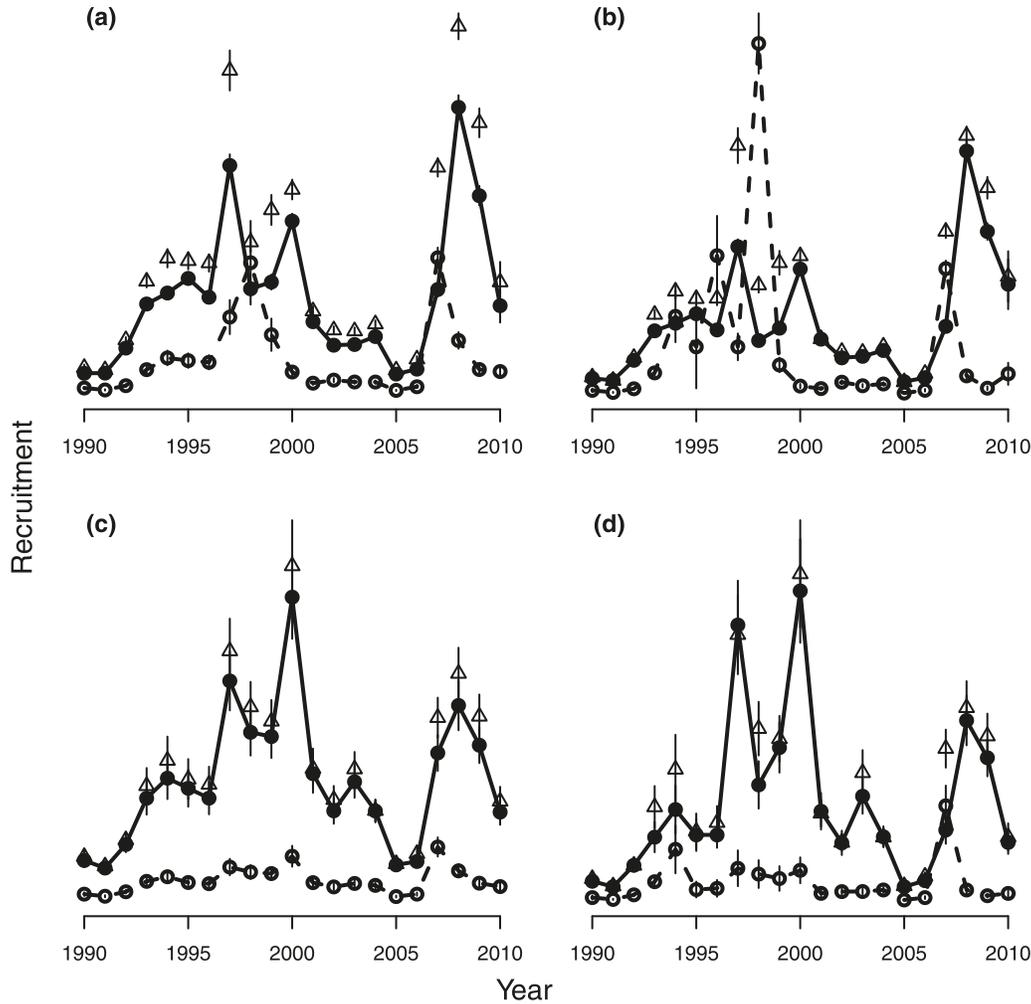


Table 2. Statistics summarizing differences in behavior of models that include all parameters (global) and a nested model that assumes no recruitment in Marble Canyon (NoRecMC) under different observation and process error scenarios.

Model structure	Error scenario		Catch (r^2)	Realized SD in process error					Recruitment vs. outmigration (r^2)
	Observation	Process		L	R	P	E	M	
Global	Low	Low	0.75	0.10	0.87	0.62	0.39	0.60	0.71
		High	0.76	0.11	1.01	1.27	0.58	1.05	0.67
	High	Low	0.39	0.04	0.63	0.22	0.25	0.21	0.46
		High	0.37	0.05	0.89	0.76	0.43	0.67	0.37
NoRecMC	Low	Low	0.73	0.10	0.87	0.00	0.38	0.60	0.87
		High	0.73	0.11	0.97	0.00	0.54	0.87	0.88
	High	Low	0.42	0.04	0.64	0.00	0.26	0.32	0.85
		High	0.39	0.05	0.90	0.00	0.48	0.72	0.68

Note: From left to right, the columns show the coefficient of determination (r^2) between observed and predicted catch by 10 mm size category across all sampling trips and reaches, the realized standard deviation (SD) in process error deviates (extent of interannual variation) for asymptotic length (L), recruitment (R), the proportion of recruitment from Marble Canyon relative to the total (P), emergence timing (E), and proportion moving from Glen Canyon to Marble Canyon (M), and the coefficient of determination between recruitment and outmigration in the same year. See Table 1 for the SDs of observation and process error levels.

Fig. 8. Estimated rainbow trout recruitment trends based on alternate model structures and assumptions about observation and process error. Solid lines with filled circles and dashed lines with open circles represent recruitment predictions from the global model in Glen Canyon and Marble Canyon reaches, respectively. Open triangles represent recruitment predictions in Glen Canyon based on the model that assumes no recruitment in Marble Canyon (NoRecMC). Error bars represent the 95% confidence interval. (a) Low observation and low process error; (b) low observation and high process error; (c) high observation and low process error; and (d) high observation and high process error.



the process error penalty. With high observation error, the proportion of variation in catch-at-length explained by the model increased from 0.40 under high process error to 0.49 without the process error penalty.

Recruitment trends were generally consistent among alternate model structures (global vs. NoRecMC) and assumptions about observation and process errors (Fig. 8). In Glen Canyon, all model–error scenarios predicted a similar increase in recruitment during the early and mid-1990s, low recruitment from 2001 to 2006, and an increase after that. All model–error scenarios predicted significant recruitment events in Glen Canyon in 1997, 2000, and 2008, but the 2000 recruitment event was stronger when observation error was assumed to be higher. These patterns did not change appreciably when the penalty on process error (LL_{proc}) was excluded from the total log-likelihood (results not shown for brevity).

Annual release volumes were high in the mid- and late 1990s, and controlled floods occurred in 1996, 2004, and 2008 (Fig. 2; Table 3). Hourly variation in flow between

May and August, when recently emerged trout are dependent on immediate shoreline habitat (Korman et al. 2011b), was very low in 2000 because of a summer steady flow experiment and high in 1990 and 1991 during an experimental flow period. Based on these flow statistics and hypotheses outlined in the Materials and methods, we classified 1995–2000, 2004, and 2008 as years that would potentially have high recruitment because of meeting one or more beneficial flow conditions. Across all models and error scenarios examined, the ratio of average recruitment predicted in these potentially beneficial flow years was 1.9- to 2.4-fold higher than the average from normal water years. The mean of log recruitment for potentially beneficial flow years was significantly greater than the mean from other years for all model–scenario combinations ($t_{20} = 2.8\text{--}3.4$, $p = 0.002\text{--}0.006$). The AIC for the global models that estimated separate values of mean recruitment (\bar{e} in eq. 2) for normal and potentially beneficial water years ranged from 715 to 5733 units lower than the global models that estimated a single mean recruitment. Thus, there was strong support for higher recruitment during

Table 3. Discharge statistics at Lees Ferry associated with hypotheses about the effects of flow on recruitment of rainbow trout.

Year	Annual volume (ha-m, 1000s)	Avg. daily Q change May–Aug. ($m^3 \cdot s^{-1}$)	Max. Q ($m^3 \cdot s^{-1}$)
1990	974	663	835
1991	1033	584	835
1992	985	255	530
1993	1017	265	563
1994	993	299	629
1995	1265	215	569
1996	1363	281	1300
1997	1884	218	872
1998	1536	291	691
1999	1464	295	711
2000	1065	85	881
2001	998	279	575
2002	976	217	538
2003	1031	243	575
2004	1057	230	1203
2005	1040	248	580
2006	1070	225	532
2007	1032	229	527
2008	1148	223	1212
2009	1044	218	535
2010	1030	211	544

Note: Data show the annual release volume (1000s of hectares flooded to 1 m depth), the average difference in hourly discharges over a day (daily Q change) during a critical period in the early life history, and the maximum discharge over the year (Max. Q). Statistics were computed from discharge values at 15 min intervals. Shaded cells designate years that have one or more flow characteristics that potentially result in higher recruitment.

years with potentially beneficial flow conditions, consistent with the results from the t test.

Linear regressions predicting log recruitment estimates (summed across Glen and Marble canyon reaches) as a function of annual flow volume (positive slope) or the average daily flow change (negative slope) were significant ($p < 0.05$) for global and NoRecMC models under all error scenarios (Table 4; Fig. 9). There was a positive trend between the annual maximum discharge and log recruitment, but the relationship was never significant. Multiple linear regressions based on all three flow variables (AV+DQ+MQ column in Table 4) explained between 44% and 50% of the variability in log recruitment and were significant in all cases (p values ranged from 0.007 to 0.018). The stepwise multiple regression procedure consistently selected models that included annual volume and daily flow change variables, and these models explained between 42% and 49% of the variation in log recruitment. Daily flow change was a more important variable than annual flow volume in this two-variable regression for seven of the eight model structure–error scenario cases.

The global model with high observation error (Figs. 8c and 8d) predicted very limited recruitment in Marble Canyon, with the exception of a modest recruitment event in 2007. As a result, the model that assumed no recruitment in Marble Canyon produced a similar recruitment pattern to the one for Glen Canyon based on the global model. Scenarios with low observation error (Figs. 8a and 8b) could explain more variation in the data by increasing recruitment in Marble Canyon,

especially in 1998 and 2007. There was a strong relationship between recruitment in Glen Canyon and the number of outmigrants for all model scenarios (Fig. 10; Table 2). The error scenarios that fit the global model best (low observation error) predicted a median annual emigration rate of approximately 16 000 fish·year⁻¹. For most of the models examined, approximately 70% of the variation in outmigration could be explained by annual variation in recruitment in Glen Canyon. Not surprisingly, the correlation between recruitment and outmigration was higher under the NoRecMC model, which did not allow recruitment in Marble Canyon. Increasing observation error led to substantive reductions in the extent of correlation between recruitment and outmigration for the global model, but not for the NoRecMC model. These patterns did not change appreciably when we removed the penalty on process error (LL_{proc}) in the total likelihood (results not shown for brevity).

Model selection results were sensitive to the assumed levels of observation and process errors. However, in all cases, there was strong support for the global model, which allowed some recruitment in Marble Canyon (Table 5). As expected, the extent of support for the simpler NoRecMC model, as indexed by a smaller ΔAIC relative to the global model, was greater when observation error was higher. This occurred because the simpler model does not fit the data as well as the global model, but there is a lower penalty for not fitting the data as well when there is less belief in the data (higher observation error). The extent of support for the NoRecMC model declined (i.e., ΔAIC increased) for scenarios with

Table 4. Proportion of variation in log recruitment estimates explained by single-variable or multiple regressions (R^2) based on annual flow volume (AV), average maximum difference in flows within a day from May to August (DQ), and the annual maximum flow (MQ).

Model structure	Error level		Linear regression model				
	Observation	Process	AV	DQ	MQ	AV+DQ	AV+DQ+MQ
Global	Low	Low	0.27*	0.28*	0.04	0.49** (*,*)	0.50** (*,*,NS)
		High	0.24*	0.23*	0.05	0.42** (*,*)	0.44* (NS,*,NS)
	High	Low	0.19*	0.35**	0.03	0.47** (*,**)	0.49** (NS,**,NS)
		High	0.20*	0.33**	0.03	0.47** (*,**) *	0.48** (NS,**,NS)
NoRecMC	Low	Low	0.23*	0.31**	0.04	0.48** (*,**) *	0.50** (NS,**,NS)
		High	0.22*	0.30*	0.03	0.46** (*,**) *	0.47* (NS,*,NS)
	High	Low	0.20*	0.35**	0.03	0.48** (*,*)	0.50** (NS,**,NS)
		High	0.20*	0.32*	0.02	0.46** (*,**) *	0.47* (NS,**,NS)

Note: Recruitment was estimated using the global model (all parameters) and a nested model that assumes no recruitment in Marble Canyon (NoRecMC) under different observation and process error scenarios (see Table 1 for definition of error scenarios). AV+DQ was the best model based on stepwise regression. Asterisks denote the p value category of the regression (***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$), and asterisks (*) within parentheses for the multiple regression models denote the p values of individual regression coefficients. Large asterisks **in bold font** (*) within parentheses for the AV+DQ model denote the most important regression coefficient. NS, not significant.

higher process error. This occurred because there is more flexibility in annual deviations under higher process error, so the same number of parameters can explain a greater proportion of the variability in the data compared with cases with low process errors, for which parameters are more constrained.

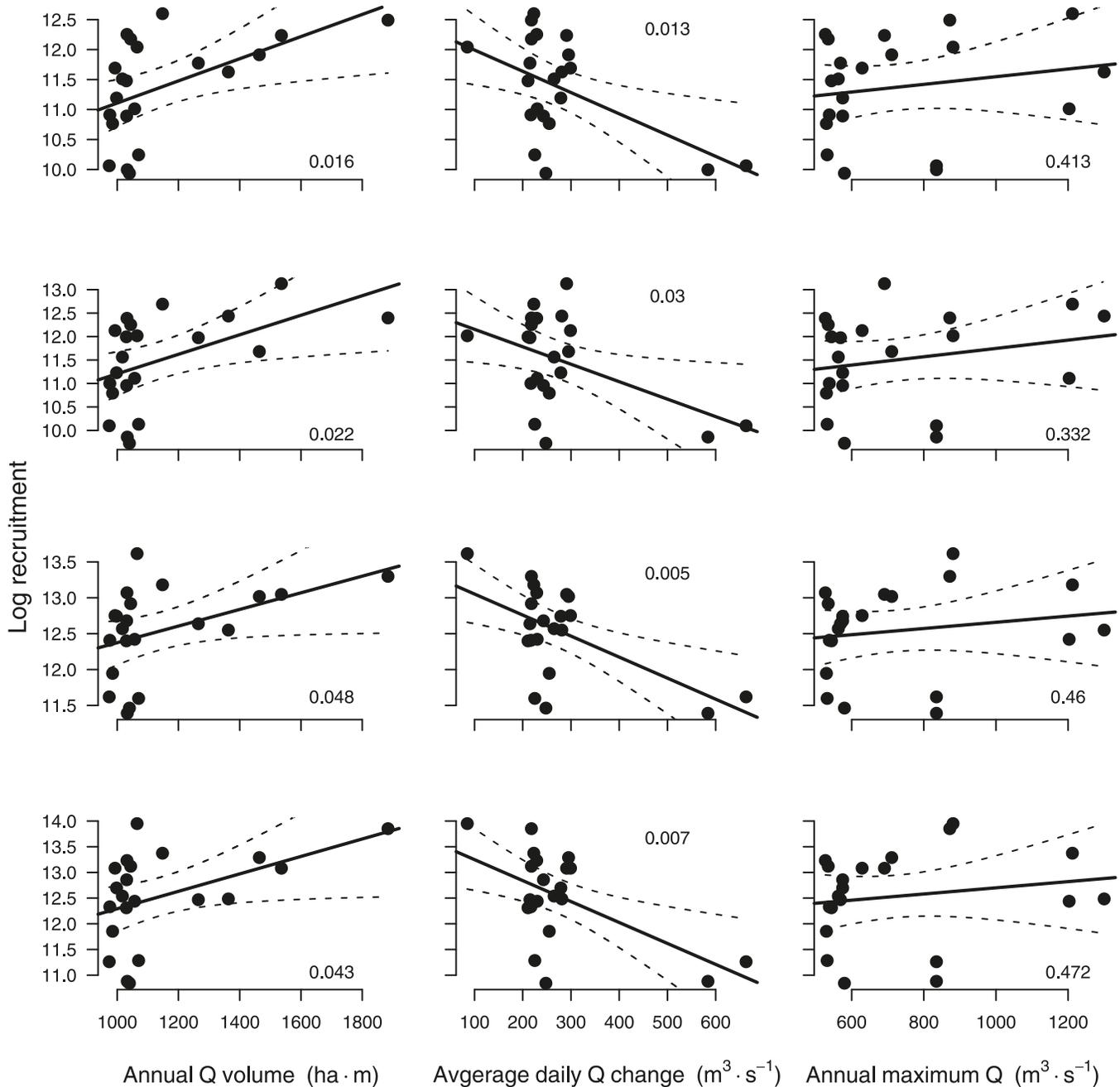
Discussion

Modelling 20 years of rainbow trout data from the Colorado River provided useful insights on temporal and spatial patterns in recruitment and movement below Glen Canyon Dam that can help manage the tailwater fishery in Glen Canyon and limit negative impacts of rainbow trout on native fish in Marble Canyon. Modelling helped formalize and sharpen interpretations of observed trends and helped identify key uncertainties, which in turn can be used to design more effective monitoring. With regard to temporal patterns in recruitment in Glen Canyon, the model predicted that (i) recruitment increased in the early and mid-1990s; (ii) there were large recruitment events in 1997, 2000, and 2008; and (iii) recruitment between 2001 and 2006 was low. McKinney et al. (2001) attributed increases in CPE between 1991 and 1997 to improvements in survival of early life stages caused by a reduction in hourly variation in flow beginning in August 1990. This hypothesis is consistent with our finding of a highly significant negative linear relationship between predicted recruitment and daily flow variation based on estimates between 1990 and 2010. The habitat stability hypothesis has been proposed and tested in other systems (Bain et al. 1988; Freeman et al. 2001; Shea and Peterson 2007) and is a likely explanation for the recruitment increase in Glen Canyon up to 1996. However, subsequent increases in CPE could also have been driven by the controlled flood in 1996, which increased food supply for rainbow trout (Shannon et al. 2001), and higher release volumes in the late 1990s, which increased habitat area. The large recruitment event in 2000, which occurred following 4 months of steady

flows during the summer when small fish are dependent on immediate shorelines that are destabilized by fluctuating flows (Korman and Campana 2009), provides additional support for the flow stability hypothesis. Increased food supply (Cross et al. 2011) and increased growth and survival of age-0 trout (Korman et al. 2011a) in Glen Canyon immediately after the 2008 controlled flood indicate that the large predicted recruitment in 2008 was caused by the controlled flood in that year. The model estimated high recruitment after the 1996 controlled flood that had not been noticed in previous analyses of the rainbow trout data. The model did not estimate high recruitment following the controlled flood in November 2004, perhaps because it occurred in the fall, well after the critical early life period (late spring and summer), or because other factors, such as unusually low dissolved oxygen in 2005 (Voichick and Wright 2007), resulted in high mortality after the flood. The cause for the limited recruitment between 2001 and 2006 is also uncertain but could be related to lower release volumes and other factors that might have limited food supply and habitat availability at that time.

We estimated that recruitment was generally twofold higher in years with greater annual volumes, reduced hourly fluctuations in flow between May and August, or when controlled floods occurred. Log recruitment estimates increased with annual release volumes and decreased with the magnitude of within-day changes in flow, and these relationships were significant across all models and error scenarios examined. A significant relationship between log recruitment and maximum flows was not found, but sample size for high flow events was limited ($n = 3$), and conditions following the 2004 event may have negated a recruitment response. Multiple regressions including annual volume and daily flow change variables explained close to 50% of the variability in log recruitment. Daily flow variation predicted more of the variation in recruitment than annual flow volume for the majority of models examined, but the relative importance of flow variables is uncertain because of low replication and the presence of multiple flow treatments in some years.

Fig. 9. Relationships between annual estimates of log recruitment from the global model and annual discharge (Q) characteristics. Rows represent error scenarios: low observation and low process error (top row); low observation and high process error (second row); high observation and low process error (third row); and high observation and high process error (bottom row). Columns represent the annual release volume (1000s of hectares flooded to 1 m depth, left), the average difference in hourly discharges over a day during a critical period in the early life history (middle), and the maximum discharge over the year (right). Solid and dashed lines represent the best-fit relationship and the 95% confidence intervals, respectively. Text on each plot is the p value of the regression slope.



The predicted recruitment time series for rainbow trout in Glen Canyon indicates that the population is sensitive to flow from Glen Canyon Dam. This is not surprising given that (i) flows and water quality in Glen Canyon are dominated by dam releases because there are no major tributaries in this reach; (ii) the reach is wide and shallow, likely making juvenile habitat sensitive to flow variation (Bain et al. 1988; Freeman et al. 2001; Shea and Peterson 2007); and

(iii) the fish community is essentially a monoculture of rainbow trout, so there are no interspecific competitive or predation effects to complicate or confound population response to flow. It is ironic that controlled floods and steadier flows, which were originally aimed at partially restoring conditions before the dam (greater native fish abundance and larger sandbars), appear to be more beneficial to nonnative rainbow trout. A natural system model (e.g., Poff et al. 1997) was at

Fig. 10. Relationship between annual rainbow trout recruitment in Glen Canyon and the number of fish emigrating to Marble Canyon in the same year. Labels beside the points denote the year of recruitment and outmigration. Solid and dashed lines represent the best-fit relationship and the 95% confidence intervals, respectively. Results are based on the global model with low observation error and high process error.

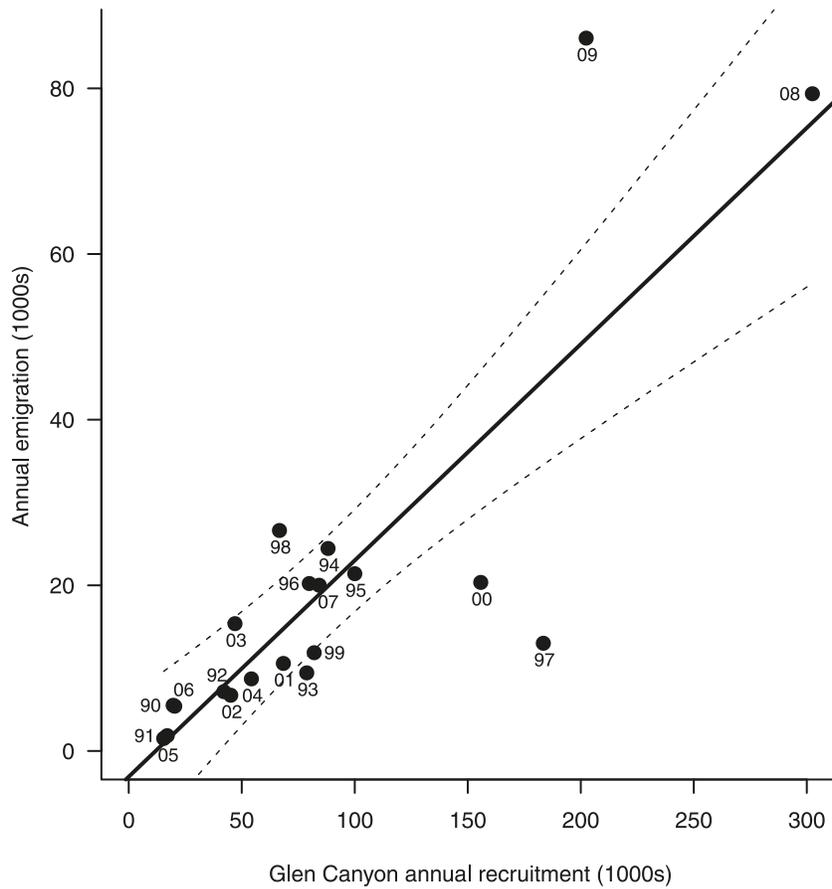


Table 5. Statistics comparing a model that includes all parameters (global) with a nested model that assumes no recruitment in Marble Canyon (NoRecMC), under different observation and process error scenarios.

Error scenario		Model	<i>K</i>	LL	AIC	Δ AIC
Observation	Process					
Low	Low	Global	128	-33 363	66 982	
		NoRecMC	106	-33 753	67 717	735
Low	High	Global	128	-31 275	62 806	
		NoRecMC	106	-32 445	65 103	2296
High	Low	Global	128	-19 874	40 004	
		NoRecMC	106	-20 057	40 326	322
High	High	Global	128	-19 135	38 525	
		NoRecMC	106	-19 341	38 894	368

Note: *K*, LL, AIC, and Δ AIC denote the number of parameters for each model, the log-likelihood (model fit), the Akaike information criteria (AIC), and the difference in AIC scores between models (for each unique error combination). See Table 1 for the standard deviation values associated with different error levels. AIC comparisons are only made across models within error scenarios.

the heart of the development of reductions in flow variation from Glen Canyon Dam in the early 1990s, implementation of controlled floods, and low and steady flows over the summer (US Fish and Wildlife Service 1994). The response of the Glen Canyon rainbow trout population to these flows indicates that natural system flows can produce undesirable results when applied in systems that are no longer biologically natural, because they have been invaded by exotic species.

The model predicts that the vast majority of rainbow trout in Marble Canyon and near the LCR come from Glen Canyon. Predictions of local recruitment in Marble Canyon in the 1990s were likely overestimated under some models. When observation error was low, large predicted recruitments in Marble Canyon helped explain CPE trends after 1998, which in part could have been driven by across-trip variation in catchability, which was assumed to be minimal when ob-

ervation error was low. There were limited data to refute these large recruitments because of gaps in the time series between 1995 and 1997. The predicted recruitment event in 2007 in Marble Canyon was not a fitting artefact, but was instead driven by age-0 trout captured in the upper 15 km during one trip that had a unique fall timing. As we did not model movement at a finer spatial scale within Marble Canyon owing to limitations in the data, these fish could easily have migrated from Glen Canyon. Given the main result of limited Marble Canyon recruitment and these caveats, a removal program targeting fish just below Glen Canyon could be effective at reducing trout abundance in Marble Canyon. However, such a program would require a much larger effort than conducted between 2003 and 2006 and would be very difficult to implement. Increasing daily variation in flow or implementing other flows that suppress rainbow trout recruitment in Glen Canyon or conducting mechanical removal near the LCR are likely better long-term options for reducing trout densities near the LCR.

We modelled interannual variation in growth, which is not commonly done in statistical catch-at-length assessments. Increasing the size of trout in the Glen Canyon fishery is an important objective, and the model quantified changes in size-at-age over time that can be related to long-term changes in the food base and other factors. Asymptotic length declined gradually for annual cohorts produced over the 1990s, dropped significantly for cohorts produced in 2004 and 2005, and then recovered to levels similar to the early 1990s by the final years of the assessment. The invertebrate community in Glen and Marble canyons changed from one dominated by large amphipods (*Gammarus lacustris*) in the late 1980s to one dominated by smaller midges (Chironomidae), simuliids (Simuliidae), and indigestible New Zealand mud snail (*Potamopyrgus antipodarum*) by the mid-1990s, decreasing the amount of energy available for rainbow trout growth (Shannon et al. 2001). The proportion of large fish captured in the fishery declined dramatically over this period (Makinster et al. 2011), likely because of these changes in the food base and higher trout densities. There were unusually high water temperatures and low dissolved oxygen concentrations in 2004 and 2005 because of very low reservoir elevations associated with a long-term drought in the southwest (Voichick and Wright 2007). These conditions may have had a severe impact on growth of adult trout as evidenced by virtually no growth of tagged individuals recaptured over this period (A. Makinster, unpublished data). Finally, the 2008 flood resulted in a large increase in digestible invertebrate drift that persisted for 2 years (Cross et al. 2011), which was the likely cause for the improved growth of tagged rainbow trout recaptured after the flood. Predicted trends in growth from the model are consistent with these observations. As well, the AIC for a version of the global model without interannual variation in growth (low observation error, high process error) was over 11 000 units higher than the global model with interannual variation (results not shown for brevity), indicating that including variation in growth greatly increased the predictive power of the model. However, the basic trend in recruitment over time predicted by the global model was very similar to one predicted by that model without annual variation in asymptotic length, so including this variation was not essential for understanding effects of flow on recruitment.

Alternate model structures could provide equally plausible explanations to some patterns in the length–frequency data. For example, the decline in the proportion of larger trout in Marble Canyon in 2004–2006 may have been caused by higher apparent mortality due to increased sediment inputs from the Paria River. Our model allowed mortality to vary over time and across reaches solely as a function of fish size. It fitted the observed patterns in Marble Canyon over this period by reducing the asymptotic size. However, a better fit could have been obtained if size-specific mortality was allowed to vary over time and between reaches. The available data are not sufficient to fit this more complex model, so it is not possible to determine which of these alternate hypotheses are more likely. Determining the cause for these types of patterns in the data should be possible in the future using data from a large-scale, multiyear tagging program in Glen and Marble canyons, which was initiated in 2011. In the long term, this program will provide much more robust estimates of movement, mortality, and growth than calculated from the model presented here.

Information-theoretic approaches, which are used to compare predictive ability of alternate models (Burnham and Anderson 2002), have not been routinely applied to complex fisheries models and are sensitive to assumptions about observation and process error. In our AIC analysis, the degree of support for the global model that allowed local recruitment in Marble Canyon was reduced when there was less belief in the data (higher observation error), and support was greater when underlying population dynamics, like interannual variation in recruitment or movement, was allowed to be more complex (higher process error). This result is intuitive, but few analyses that use information-theoretic approaches to compare models investigate effects of observation and process error (Maunder and Watters 2003). Information-theoretic approaches may have less utility when applied to integrated assessment models, such as the one presented here and those used in most stock assessments, where there can be large uncertainty about the extent of observation and process error (Punt and Butterworth 1993; Hulson et al. 2012) and the weightings assigned to various likelihood components (Deriso et al. 2007). However, this may not be a problem depending on the decision context. In our example, the global model had strong support under all error cases even though the predicted recruitment from Marble Canyon was low in most years, suggesting a high-effort removal program just below Glen Canyon with limited removal near the LCR could be effective at reducing rainbow trout in the long term (Runge et al. 2011). Recruitment trends and conclusions about the effects of flow based on all models and error scenarios were also quite similar.

Modern stock assessment models often estimate large numbers of parameters, and there is a wide range of opinions about the value of this additional complexity (Walters and Martell 2004). In our view, decisions on model complexity should consider the following: (1) evidence supporting the inclusion of a process based on data from within or outside of the system (e.g., does growth vary in other tailwater systems?); (2) the policy-relevance of the predictions provided by the more complex model (e.g., do managers care about changes in fish size over time?); (3) the potential for the more complex model to affect predictions of key policy

variables (e.g., recruitment variation by year); and (4) results from information-theoretic analyses. Information-theoretic approaches provide consistent measures to grade alternate models, but results should be viewed with caution as they are conditional on assumed error levels and will be biased towards selecting more complex models when the amount of information in the data is overestimated. Any model structure that meets criteria 1–3 should be considered, at least in preliminary evaluations.

Solutions needed to achieve unique fits of our integrated assessment model (i.e., convergence of the nonlinear estimation procedure) highlight limitations in existing information and provide useful guidance for future monitoring in Grand Canyon. Our model estimated a large number of parameters from a data set with substantial temporal data gaps (e.g., Marble Canyon between 1994 and 1997) and modelled movement in the absence of tagging information. This was accomplished by using auxiliary data (e.g., juvenile abundance), penalties on the extent of process error, and some restrictive structural assumptions (e.g., logistic length-vulnerability function, constant catchability, one-way movement). Even with the auxiliary information, the model would sometimes not converge or yielded very unrealistic results in the absence of these constraints. Discontinuities in monitoring data can have serious consequences. For example, the 3- to 4-year gap in the Marble Canyon electrofishing time series made it impossible to identify the source of recruitment leading to the increase in abundance in the late 1990s. An intensive tagging program recently implemented in Glen and Marble canyons will provide direct estimates of trout abundance and growth as well as estimates of movement within and between these reaches. Historical sampling has been sparse (~4% of shoreline) and not always evenly distributed throughout the canyon, likely leading to variation in reach-wide catchability among trips and potentially misleading conclusions about recruitment trends. Models are excellent heuristic tools and can provide useful information for fish management, but their reliability ultimately depends on robust monitoring programs that provide data at the appropriate resolution.

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