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[Article]

Effects of Hydropeaking on Nearshore Habitat Use and Growth of Age-0 Rainbow Trout in a Large Regulated River

JOSH KORMAN*
Ecometric Research, Inc., and Department of Zoology, University of British Columbia,
3560 West 22nd Avenue, Vancouver, British Columbia V6S 1J3, Canada

STEVEN E. CAMPANA
Population Ecology Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography,
Post Office Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada

Abstract.—We evaluated the effects of hourly variation in flow caused by power load following at Glen Canyon Dam ("hydropeaking") on the nearshore habitat use and growth of age-0 rainbow trout *Oncorhynchus mykiss* downstream from the dam in the Colorado River, Arizona. Reduction in the extent of hydropeaking is a common element of restoration efforts in regulated rivers, but empirical support for such a practice is limited. Our assessment was based on a comparison of abundance in shoreline areas determined by electrofishing at different flows as well as analysis of otolith microstructure. The catch rates of age-0 rainbow trout in nearshore areas were at least two- to fourfold higher at the daily minimum flow than at the daily maximum, indicating that most age-0 rainbow trout do not maintain their position within immediate shoreline areas when flows are high. A striping pattern, identified by the presence of atypical daily increments formed every 7 d, was evident in over 50% of the 259 otoliths examined in 2003 but in only 6% of the 334 examined in 2004. The weekly pattern corresponded to a reduction in the extent of hourly flow fluctuations on Sundays during the growing season, which occurred in 2003 but not in 2004. The atypical increments were 25% wider than the adjacent increments and were indicative of significant ($F_{15,\ 235} = 19.2$, $P < 0.0001$) short-term increases in otolith growth. The somatic growth rate among fish with otoliths where striping was present (11.2 mm/month) was slightly greater than that among fish with otoliths without striping (10.8 mm/month), but the difference was not significant. We provide evidence suggesting that otolith growth improved on Sundays in 2003 because it was the only day of the week when most age-0 fish were found in immediate shoreline areas, where higher water temperatures and lower velocities provided better growing conditions.

Hydroelectric dams alter the magnitude and frequency of flows and can have negative effects on downstream fish communities (Cushman 1985). In some regulated rivers, power load following operations, often referred to as hydropeaking, result in considerable hourly and diel variation in flow, depth, and water velocity, creating a very unnatural and potentially harsh physical environment. This effect is of special concern for juvenile fish, which in large rivers rear almost exclusively in shallow shoreline habitats (Gaudin 2001) that are destabilized by hydropeaking operations (Freeman et al. 2001). Diel variation in flow can result in stranding and mortality of juvenile fish (Bradford 1997; Saltveit et al. 2001; Halleraker et al. 2003), and is hypothesized to limit survival rates via indirect effects from displacement out of preferred habitats, food depletion, and increases in stress, energetic costs, and predation risk (Scruton et al. 2003).

Most studies of the indirect effects of short-term flow fluctuations have focused on the behavioral and energetic responses of juvenile salmonids. Short-term variation in flow results in both negligible (Robertson et al. 2004) and extensive (Berland et al. 2004) movement in Atlantic salmon *Salmo salar* parr. Flow-dependent movement responses can be highly variable among individuals, with some parr showing strong site fidelity across a wide range of flows (Kemp et al. 2003; Scruton et al. 2003). Juvenile salmonids have been shown to use higher nose velocities with increasing water flow and not to fully compensate for increased velocity by changing microposition (Vehanen et al. 2000; Girard et al. 2004). Shirvell (1994) reported that juvenile salmonids initially responded to increased flow by moving closer to the streambed and then, if necessary, moving laterally to seek out appropriate velocity conditions. Surprisingly, there is little evidence that such responses increase stress levels or have negative bioenergetic consequences. Cardiac activity in adult brook trout *Salvelinus fontinalis* and

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* Corresponding author: jkorman@ecometric.com

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walleye *Sander vitreus* (Murchie and Smokorowksi 2004), and oxygen consumption in juvenile white sturgeon *Acipenser transmontanus* (Geist et al. 2005), did not increase under fluctuating flows. Stress responses in juvenile brown trout *Salmo trutta* caused by moderate flow fluctuations in experimental flumes subsided within a few days after the fish became habituated to the flow regime (Flodmark et al. 2002). Hourly variation in flow in experimental channels had no negative effects on the growth or survival of rainbow trout *Oncorhynchus mykiss* fry (Irvine 1987).

Overall, experimental studies document relatively little effect of hourly variation in river flows on juvenile fish, yet stabilization of regulated flows can increase the abundance of downstream fish populations (Travnichek et al. 1995; McKinney et al. 2001; Connor and Pflug 2004). However, in all these cases flow was stabilized by increasing the minimum flow and by reducing the extent of within-day variation, so the effects of the two changes are confounded. Further, the stabilized flow regimes may have benefited the spawning and incubating life stages as well as the survival of juvenile fish. Reduction in the extent of hourly variation in flow is commonly recommended as a way to improve the status of fish populations (Dejalon and Sanchez 1994; Poff et al. 1997), but empirical support for such recommendations is limited. This discrepancy leads to considerable debate, especially in large-river settings, where lost hydropower revenues resulting from flow stabilization can be substantial.

We evaluate the effects of hourly variation in flow caused by hydropeaking at Glen Canyon Dam on the nearshore habitat use and growth of age-0 rainbow trout in the Lee's Ferry reach of the Colorado River, Arizona. Maximum flows over a 24-h (diel) cycle at Glen Canyon Dam occur during the day and early evening when power demand is high, and are reduced at night when demand subsides (Figure 1a). We propose two alternate hypotheses of how age-0 fish will respond to this diel regime (Figure 2). The shoreline-tracking hypothesis assumes that trout move freely in response to hourly changes in flow so that they remain in shallow and low-velocity habitat typically used by age-0 fish (Chapman and Bjornn 1969; Everest and Chapman 1972). If this hypothesis holds in the Lee's Ferry reach, age-0 trout will need to make two lateral movements per day with the rise and fall in flow to remain within immediate nearshore areas where these depth and velocity conditions occur. The restricted-movement hypothesis assumes that age-0 trout restrict the extent to which they move in response to hourly flow variation. If this hypothesis holds in the Lee's Ferry reach, only a limited proportion of trout will be found within immediate nearshore areas at the daily maximum flow. The remainder will be found further from the bank in deeper and faster water, with some perhaps remaining in the permanently submerged zone. During the day in the Lee's Ferry reach in summer months, when daily maximum air temperatures on the surface of exposed gravel and sand bars can reach 50–60°C, a horizontal gradient in water temperature is created where temperatures in the immediate shoreline areas within 1–2 m from the waters edge are 3–5°C warmer than in the main flow further offshore (Figure 2; Korman et al. 2006). Under the shoreline-tracking hypothesis, age-0 trout will experience warmer water temperatures during the day because they maintain their position in immediate nearshore areas. In contrast, trout that behave according to the restricted-movement hypothesis would mostly be located further offshore during the day and therefore in colder water.

The shoreline-tracking hypothesis assumes that habitat use by age-0 fish in regulated rivers follows the pattern observed in natural systems (e.g., Chapman and Bjornn 1969; Everest and Chapman 1972; Bustard and Narver 1975; Sheppard and Johnson 1985), where fish limit themselves to immediate shoreline areas in which the water depths and velocities are optimal for feeding (Nislow et al. 2000, 2004), resting, and avoiding piscivorous predators (Schlosser 1987; Walters and Juanes 1993; Rosenfeld and Boss 2001). The restricted-movement hypothesis assumes that the benefits of tracking optimal depths and velocities on an hourly basis by remaining in immediate nearshore areas do not outweigh the costs associated with moving, such as increased exposure to predation while moving (Biro et al. 2003), or the competitive disadvantage of abandoning territories (Elliott 1986; Ward et al. 2007). The density of benthic invertebrates in the Lee's Ferry reach in shoreline areas exposed to air owing to hourly variation in flow, sometimes referred to as varial zones, are considerably lower than in permanently submerged zones (Blinn et al. 1995; Benenati et al. 1998). Thus, reduced food density within the varial zone could also limit the use of these areas at the daily maximum flow and, therefore, contribute to restricted movement.

We evaluate the shoreline-tracking and restricted-movement hypotheses by comparing the catch rates of age-0 rainbow trout in immediate shoreline areas sampled at daily minimum and maximum flows. If the shoreline-tracking hypothesis is correct, catch rates should be similar under both flows (Figure 2). If the restricted-movement hypothesis is correct, catch rates should be much lower at the daily maximum flow because fish will be more dispersed, with the majority

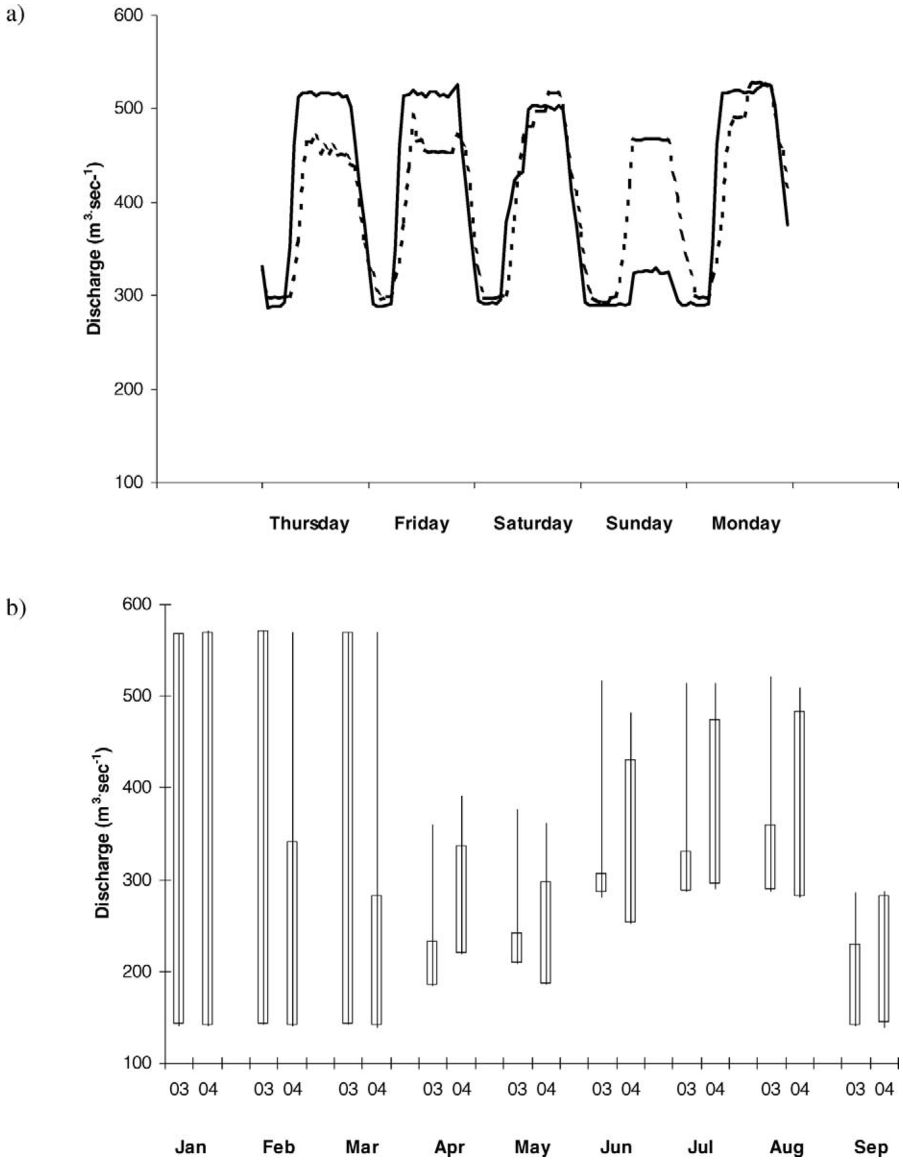

FIGURE 1.—**(a)** Hydrograph of releases from Glen Canyon Dam during a typical 5-d period in 2003 (July 10–14; solid line) and 2004 (July 8–12; dashed line) and **(b)** the average daily minimum and maximum flows during the week (lines) and on Sundays (bars) from January through September. The monthly averages of the daily minimum and maximum flows are based on 15-min automated flow measurements taken at Glen Canyon Dam.

residing outside of the immediate shorelines areas that are sampled. Both shoreline-tracking and restricted-movement hypotheses predict potential negative bioenergetic consequences associated with hourly fluctuations in flow, and that growth should improve under a more stable regime. Under the shoreline-tracking hypothesis, food availability in the varial zone occupied by fish during the day would be lower and there would be higher energetic costs associated with the additional movement required to remain within immediate nearshore areas as flows fluctuate. Under the restricted-movement hypothesis, fish would occupy areas further offshore during the day, where water velocity is higher and water temperature is colder. This would lead to higher energetic costs and reduced feeding efficiency associated with holding position at higher velocities as well as reduced growth owing to lower water temperature. In one year of our study

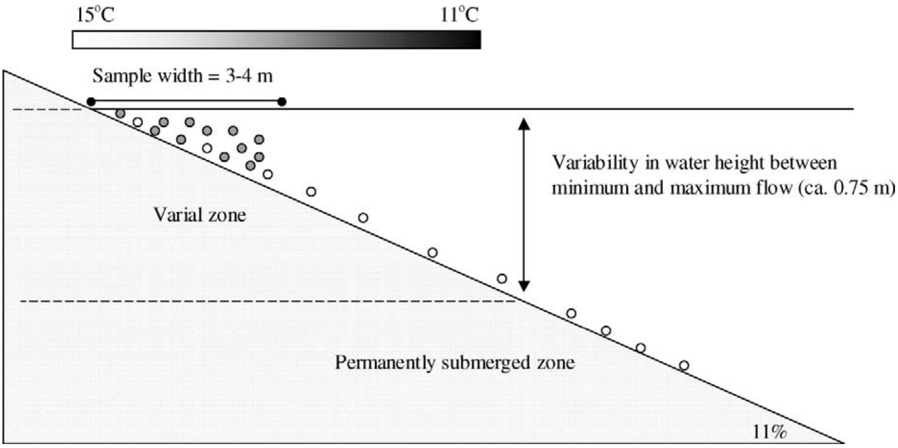

FIGURE 2.—Cross section of low-angle shoreline habitat at the maximum daily discharge showing the daytime horizontal water temperature gradient and the daily variation in water surface elevation during summer months. The shaded circles represent the hypothesized distribution of age-0 rainbow trout during the daily maximum flow on weekdays under the shoreline-tracking hypothesis. The open circles represent the distribution under the restricted-movement hypothesis, where only a small proportion of individuals remain in the immediate nearshore area close to the water's edge. The width of shoreline habitat sampled by electrofishing, which is referred to in the text as the immediate nearshore area, is also shown. The same sample width is applied when sampling at the minimum flow, and the same water temperature gradient occurs at the minimum flow elevation when flows remain low during the day (Sundays in 2003; see Figure 1).

(2003), flow remained low and steady over a 24-h period on Sundays during summer months (Figure 1). We evaluate whether growth improved under this situation by comparing otolith microstructure from samples taken in 2003, with microstructure from 2004, when flows on Sunday underwent normal hourly fluctuations. Results from the habitat use and growth analysis are interpreted in relation to existing information and current hypotheses on the effects of hourly variation in flow on the behavior and growth of juvenile fish.

Methods

Study area.—The Lee's Ferry reach of the Colorado River, Arizona, begins at Glen Canyon Dam below Lake Powell and extends 26 km downstream to the confluence with the Paria River. The average flow in 2003 and 2004, when the study was conducted, was 328 m^3/s (U.S. Geological Survey gauge 09380000). The reach is wide and shallow, with an average wetted width and depth at this flow of 144 m and 5.2 m, respectively (Randle and Pemberton 1987). Main-stem water temperatures recorded at the downstream end of the reach since 2003 have ranged from 9°C to 15°C but typically range from 9°C to 11°C (Voichick and Wright 2007). The fish fauna in the Lee's Ferry reach is almost exclusively comprised of nonnative rainbow trout that reproduce naturally (McKinney et al. 2001). Flow from Glen Canyon Dam normally fluctuates on a diel cycle driven by power demand, but controlled through regulations on the maximum daily flow range, minimum and maximum flows, and maximum downramp and upramp rates. There is little variation in flow during low- and high-flow periods within a day (e.g., Figure 1a), and because upramp and downramp periods are relatively short (total of 6 h per day) high flows occur over the majority (13 h) of the day. Hourly variation in flow during weekdays was very similar in 2003 and 2004, but variation in flow on Sundays during the summer was much lower in 2003 (Figure 1).

Effects of hourly flow variation on nearshore habitat use.—The catch rates of age-0 rainbow trout at 24 shoreline locations sampled by electrofishing at both daily minimum and maximum flows between June 30 and July 6, 2004, were compared to evaluate the effects of diel variation in flow on nearshore habitat use. Shoreline habitat was stratified into low- (cobble and vegetated sand bars and debris fans) and high-angle (talus slopes) types that could be sampled by backpack and boat electrofishing, respectively. Twelve units were randomly selected for sampling from both low- and high-angle habitat strata, and in the field, divided into four, noncontiguous, 30-m and 50-m sections, respectively. Each section was then electrofished under one of the four following light and flow conditions: (1) light (daytime) with daily maximum flow; (2) light with daily minimum flow; (3) dark (nighttime) with daily maximum flow; and (4) dark with daily minimum flow. Thus, 12 replicate samples for each habitat type (low or high angle) were obtained for each of the four alternate light level–daily flow combinations. The electrofishing sites were 3–4 m wide, not enclosed by block-nets, and fished methodically in an upstream (backpack electrofishing) or downstream (boat electrofishing) direction. After collection, fish were anesthetized and fork lengths (FL) were measured to the nearest millimeter (see Korman et al. 2009 [this issue], for additional details on sampling). We assume that the catch in nearshore zones (C) always represents a constant proportion of the total abundance in these areas (N) because capture probability (p) does not vary with abundance or flow (i.e., $C = pN$). This assumption is supported by a large number of depletion ($n = 66$) and mark–recapture ($n = 42$) experiments conducted in the Lee's Ferry reach in 2006 and 2007, respectively (Korman et al. 2009).

The statistical significance of the differences in log-transformed catch rates measured at daily minimum and maximum flows and during the day and night was determined via two-way nested analysis of variance (ANOVA), where the effects of flow and light were nested within sites. Log-transformed catch data met ANOVA assumptions of normality based on the Kolmogorov–Smirnov test (P-values = 0.397 and 0.950 for the low- and high-angle habitats, respectively), and homoscedastic variance among treatments based on Bartlett's test (P-values = 0.617 and 0.315 for the low- and high-angle habitats, respectively).

The physical characteristics at diel sampling sites were measured to evaluate the change in habitat conditions in nearshore areas at daily minimum and maximum flows. Depth and average water column velocity were measured at 10 equally spaced locations 1.5 m from shore along an axis parallel to the direction of flow at each site using a Swoffer current meter with topset wading rod (Model 2100). Measurements were taken at both the daily minimum and maximum flows. Measurements at the daily maximum flow were also taken further offshore at the edge of the permanently submerged zone (Figure 2). The cross-sectional slope at each site was measured using a laser level and survey rod to estimate the vertical and horizontal distances between elevations inundated by the daily minimum and maximum flows. Statistical differences in depth and velocity at daily maximum and minimum flows within sites were evaluated using paired t-tests.

Effects of hourly flow variation on growth.— Otoliths were extracted from a subsample of fish captured by electrofishing during multiple surveys conducted in 2003 and 2004 as part of a longer-term study of the early life history dynamics of rainbow trout in the Lee's Ferry reach (Korman 2009). Following the random-stratified design described previously, 20 units were selected from both low- and high-angle habitat strata to sample by backpack and boat electrofishing, respectively. On each sampling trip, we returned to these same 40 units, but randomly selected different 30-m and 50-m sections to sample in low- and high-angle habitat, respectively. In 2003, six sampling trips were conducted between April and October, and only low-angle shorelines were sampled (934 age-0 trout fish captured). In 2004, both shoreline types were sampled and eight trips were conducted between April and December (4,459 age-0 trout captured). On each trip, 2.5% of low-angle shorelines (600 m) were sampled in 2003 and 2004, and 4.5% of high-angle shorelines (1,000 m) were sampled in 2004. Electrofishing protocols were identical to those described for the nearshore habitat study component with two exceptions: (1) sampling was only conducted during darkness between midnight and dawn at the daily minimum flow and (2) on each trip, a subsample of five fish from each habitat type within 10-mm length categories between 20 and 100 mm were sacrificed and preserved in 95% ethanol for later analysis of otolith microstructure.

Both sagittal otoliths were removed from a sample of preserved fish to determine the daily age from hatch and otolith growth using methods described in Stevenson and Campana (1992) and Campana (1992). A total of 259 and 334 otoliths were successfully extracted and aged from fish collected in 2003 and 2004, respectively. A striped pattern in daily increments was observed on the otoliths of many individuals (see Results). This visual pattern was identified by atypical increments (different appearance, usually light in color under transmitted light) formed at regular intervals. The number of otoliths for which the striping pattern was present, absent, or ambiguous was recorded. To determine whether the striping pattern was associated with periodic growth, a random sample of otoliths ($n =$ 15) with a clear striping pattern was examined and the width of individual daily increments was measured. The significance of differences in the width of atypical and typical increments was determined using a two-level nested ANOVA, where the effect of increment type on width was nested within fish.

To determine whether the presence of otolith striping was related to somatic growth, we compared length-at-age relationships based on data from fish with and without otolith striping. The constant, slope, and standard deviation (SD) of linear length-at-age models were estimated assuming observation error was log-normally distributed from the equation,

$$L_{x,i} = (\alpha_x + \beta_x A_{x,i})e^{\nu_{x,i}}$$

where L is FL (mm), A is age (days from hatch), α and β are the constant (size at hatch) and slope (growth rate

TABLE 1.—Average depth (cm) and velocity (cm/s at 0.6·total depth) at 12 sites in both low- and high-angle shoreline habitats based on 10 measurements per site taken 1.5 m from shore (immediate nearshore zone) sampled at the daily minimum (Min.) and maximum (Max.) flows, June 30–July 6, 2004. Also shown are the average gradients between the elevations inundated by the daily minimum and maximum flows and the average depths and velocities taken at the edge of the permanently submerged zone at the daily maximum flow, which occurred 6.5 and 2.2 m from shore in low- and high-angle habitats, respectively (see Figure 2). Standard errors are given in parentheses and show the variation in mean conditions across sample sites.

	Low-angle habitat		High-angle habitat	
Variable	Min. flow	Max. flow	Min. flow	Max. flow
Gradient (%)	12		37	
Immediate nearshore zone				
Depth	29 (7)	39 (13)	60 (19)	75 (16)
Velocity	7 (6)	3 (6)	6 (7)	12 (13)
Edge of permanently submerged zone				
Depth		63 (8)		85 (14)
Velocity		17 (16)		12 (17)

in mm/d), respectively, ν is a random deviate from a normal distribution with a mean of 0 and a SD of σ_x, x is a classification term that denotes whether the data and parameters are based on fish where striping was present ($x = p$) or absent ($x = a$), and i denotes the index number for individual fish. Although length at age is commonly described using nonlinear models because growth rates typically decline in older fish, there was no indication of this pattern in our data (see Results).

The parameters for the length-at-age models were estimated by maximizing the lognormal likelihood using a nonlinear iterative search procedure. Four models were evaluated: (1) pooled ($\alpha_p = \alpha_a$, $\beta_p = \beta_a$, $\sigma_p = \sigma_a$); (2) individual (α_p, α_a, β_p, β_a, σ_p, σ_a); (3) individual slopes ($\alpha_p = \alpha_a$, $\sigma_p = \sigma_a$, β_p, β_a); and (4) expected striping slope ($\alpha_p = \alpha_a$, $\sigma_p = \sigma_a$, β_a, $\beta_p = \beta_a z$, where $z = og \times f$). The last model assumes that the proportional increase in the somatic growth rate of fish with otoliths where striping was present (z) can be computed based on the measured average proportional increase in the width of atypical increments (og), and the expected frequency at which such increments form (f). We evaluate the hypothesis that short-term increases in growth rate occurred only on Sundays when flows were low and steady by setting $f = 1/7$. The models were compared by means of the Akaike information criterion (AIC), where the model with the smallest AIC value is considered to have the best out-of-sample predictive power if the difference in AIC values is 2 or more (Burnham and Anderson 2002). The models were also compared by means of likelihood ratio tests to determine the probability that the improved fit of more complex models that accounted for the effects of otolith striping (models 2–4), relative to the simplest model that did not (model 1), could be due to chance alone.

Results

Effects of Hourly Flow Variation on Nearshore Habitat Use

During summer months, the difference between the daily minimum and maximum flow rates of approximately 225 m^3/s (Figure 1) resulted in an average horizontal shift in the water's edge of 6.5 m and 2.2 m in low- and high-angle shorelines, respectively. At a typical cross section, the increase in stage from the daily minimum to maximum flow was 0.75 m. In low-angle habitat at the daily maximum flow, average water velocity was over fivefold higher at the edge of the permanently submerged zone (6.5 m from shore) compared with 1.5 m from shore (Table 1). In high-angle habitat, the difference in the distance 1.5 m from shore and the edge of the permanently submerged zone (2.2 m from shore) was small owing to the higher gradient of the shoreline. As a result, average velocities at these two locations were similar (Table 1). Although daily variation in flow during the summer was substantial (Figure 1b), there were relatively minor absolute changes in depth and velocity within the immediate shoreline habitats sampled (Table 1). Average depth 1.5 m from shore was 10–15 cm greater at the daily maximum flow compared with that at the daily minimum, but the difference was only statistically significant ($P < 0.05$) in high-angle habitat (paired t-test: $P = 0.028$). Average velocity was marginally higher at the daily minimum flow compared with the daily maximum in low-angle habitats and marginally lower in high-angle habitats, but neither difference was significantly different (paired t-test: $P = 0.100$ and 0.107, respectively).

There was a very strong effect of flow on the catch rates of rainbow trout. In low-angle habitats, catches at the daily minimum flow were higher than at the daily maximum at 11 of 12 sites sampled at night, and 9 of

TABLE 2.—Catch (*n*) of age-0 rainbow trout in low- and high-angle shoreline habitats sampled at night and day at the daily minimum (Min.) and maximum (Max.) flows. The site lengths in the low- and high-angle habitats were 30 and 50 m, respectively. Cells with missing values denote cases in which no sampling was conducted.

	Low-angle habitat				High-angle habitat			
	Night		Day		Night		Day	
Site	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
1	123	23	70	25	9	11	9	2
2	55	27	12	2	64	45	56	25
3	25	0	30	1	74	33	22	4
4	21	1		5		22	31	9
5	20	2	19	2	44	14	15	13
6	5	3	6	0	47	6	65	9
7	15	0	17	0	32	14	22	8
8	7	0	4	0		15		2
9	2	0	0	1	4	0	48	5
10	29	1	11	2	18	7	10	5
11	15	3	11	2	31	10	18	19
12	3	3	5	5	9	7	49	7
Average	27	5	17	4	33	15	31	9
Average/100 m	89	18	56	13	66	31	63	18
Min./Max.	5.1		4.5		2.2		3.5	

11 sites sampled during the day (Table 2). In high-angle shorelines, catches at the daily minimum flow were higher than at the daily maximum in 9 of 10 and 10 of 11 sites sampled during night and day, respectively. On average, catch rates in low-angle habitats at the daily minimum flow were 4.5- and 5.1-fold higher than those at the daily maximum flow during day and night, respectively (Table 2). At high-angle sites, catch rates at minimum flows were 3.5- and 2.2-fold higher than at maximum flows during day and night, respectively. The increase in catch rates at the daily minimum flow compared with those at the maximum flow within sites was statistically significant in both low-angle ($F_{12,\ 12} = 4.09$, $P = 0.011$) and high-angle ($F_{11,\ 12} = 6.41$, $P = 0.003$) habitats (Figure 3).

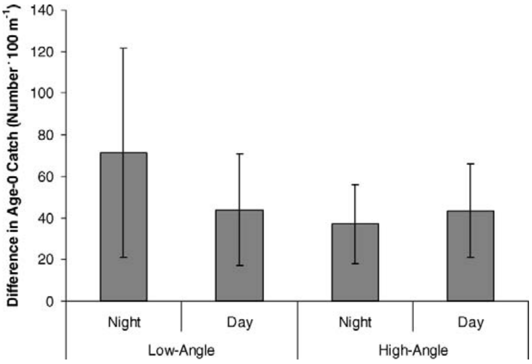

FIGURE 3.—Average differences in the catch rates of age-0 rainbow trout based on sampling at the daily minimum and maximum flow between June 30 and July 6, 2004, by time of day and habitat. The error bars denote the 95% confidence intervals of the mean differences. The raw data are presented in Table 2.

Effects of Hourly Flow Variation on Otolith and Somatic Growth

A striping pattern was evident in many of the otoliths sampled from rainbow trout in 2003 but in only a fraction of those sampled in 2004. The visual pattern was identified by the presence of atypical daily increments formed at a frequency of exactly 7 d (Figure 4). The weekly pattern was evident in at least 51% (131) of the 259 otoliths examined in 2003, but in only 6% (20) of the 334 otoliths examined in 2004 (Table 3). In general, striping was most evident in the middle and outer sections of the otolith, and in larger individuals. The dates on which atypical increments were formed were determined for 12 randomly selected otoliths where striping was present and where the edge of the otolith was clearly defined. In all cases, atypical increments were formed on Sundays, the only day of the week in 2003 when flows were low and steady during the day (Figure 1a). The frequency of otolith striping varied over time (Table 3). In 2003, striping was common in samples from all months except April, while in 2004, striping was only common in April and May and declined steadily in later months. The atypical increments tended to be 25% wider (3.12 μm) than the other increments (2.51 μm) when averaged across all striping cycles from 15 fish. Within fish, the average increment width of the atypical bands was larger than the average width of the other increments in between the atypical bands in 14 of 15 cases. The atypical increment widths were significantly wider than the

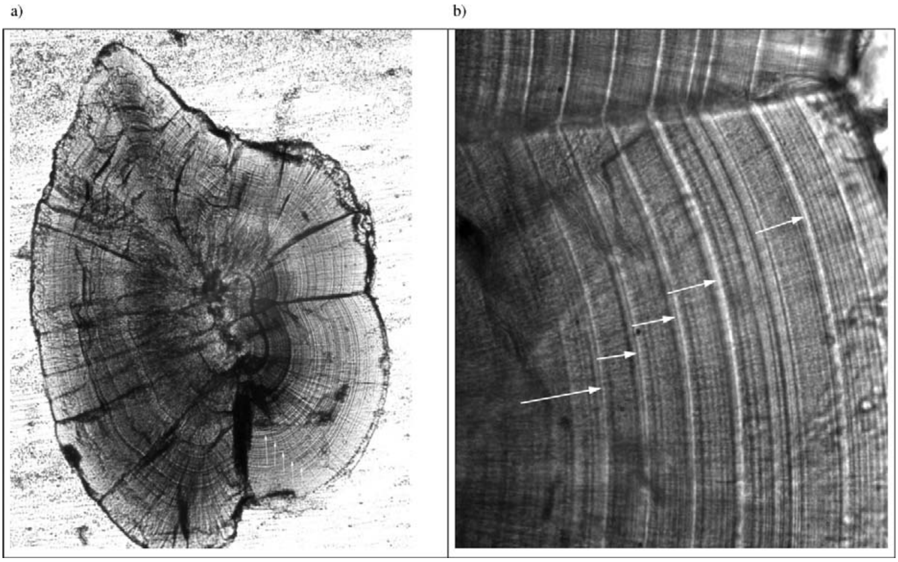

FIGURE 4.—Cross section of an otolith from a 43-mm age-0 rainbow trout that was 81 d old (from hatch) when sampled on July 30, 2003. The images show the weekly striping pattern, identified by white arrows, at magnifications of **(a)** 16× and **(b)** 400×. The stripes are indicative of increased otolith growth on Sundays in 2003, when flow was low and steady relative to normal weekday operations (see Figure 1).

typical ones based on the nested ANOVA ($F_{15,\ 235} = 19.2$, $P < 0.0001$).

Length-at-age comparisons indicated that somatic growth was similar in fish with and without otolith striping. There was a strong linear relationship between age from hatch and FL (Figure 5), with age from hatch explaining 85% ($n = 123$), 92% ($n = 76$), and 88% ($n = 199$) of the variation in fork lengths measured in 2003 based on otoliths where striping was present, absent, and when both datasets were combined, respectively. The growth rates estimated from separate regressions for fish without striping and with striping were 0.360 (β_a) and 0.375 (β_p) mm/d, respectively (Table 4). The expected growth rate for fish with striping present, computed based on the average increase in otolith increment widths formed on Sundays (1.25-fold wider) and the expected flow-dependent frequency of such improved growth events (1 out of 7 d per week), was 0.374 mm/d ($\beta_p = \beta_a \times z$, where $z = 1.25 \times (1/7)$). The expected growth rate was almost identical to the

TABLE 3.—The number of rainbow trout otoliths sampled and the percentage with a weekly striping pattern, by sampling month in 2003 and 2004. The last two rows show the total number of otoliths sampled across all months and the average percentage that were striped.

	2003		2004	
Month	Number sampled	% Striped	Number sampled	% Striped
Apr	15	13	23	17
May	37	59	58	22
Jun	58	48	66	3
Jul	56	63	68	1
Aug			41	0
Sep	60	43	37	0
Oct	33	55		
Nov			20	0
Dec			21	0
Total Average	259	51	334	6

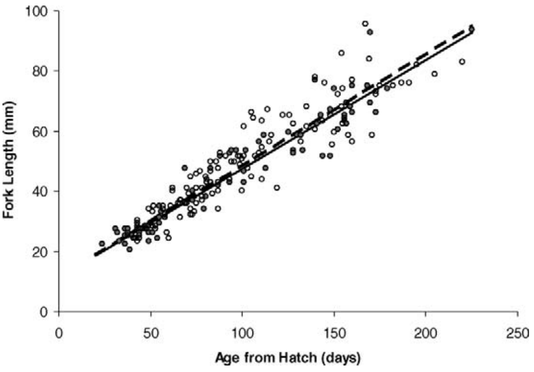

FIGURE 5.—Relationships between age from hatch and fork length in 2003 based on otoliths with (open circles; dashed line) and without (shaded circles; solid line) a weekly striping pattern. The relationships derive from the individual slope model (Table 4), in which the growth rate estimates differ for fish with and without striping but the intercept and variance estimates are common to both data sets.

TABLE 4.—Comparison of fit and predictive power of four linear models fit to the 2003 length-at-age data for rainbow trout downstream from Glen Canyon Dam. Parameters β_a and β_p are the slopes of the regressions (daily growth rates) based on otoliths without and with striping, respectively. In the case of the expected striping slope model, β_p was not estimated but computed as a function of β_a and the expected increase in somatic growth based on the increase in otolith growth seen on Sundays. The model with the lowest Akaike information criterion (AIC) has the best predictive power; ΔAIC is the difference between each model's AIC value and the lowest AIC values among the models.

Model	Number of parameters	Growth rate[a] β_a	β_p	Log likelihood	AIC	ΔAIC
Pooled	3	0.370		143.42	−280.83	1.82
Individual	6	0.360	0.375	144.86	−277.73	4.93
Individual slopes	4	0.361	0.373	144.34	−280.67	1.99
Expected striping slope	3	0.360	0.374	144.33	−282.66	

[a] Estimated slope (mm/d).

estimates from the individual ($\beta_p = 0.375$) and individual slopes models ($\beta_p = 0.373$) for fish with otolith striping present.

The AIC and likelihood-ratio tests both indicated that the differences in length at age between age-0 rainbow trout with and without otolith striping were not statistically discernable. The expected striping slope model had the best out-of-sample predictive power (lowest AIC) of all the length-at-age models considered. However, there was substantial support (Burnham and Anderson 2002) for the pooled and individual slopes models as well, indicating that there was insufficient power to determine whether the growth rates for fish with and without otolith striping were different. Likelihood ratio tests indicated that there was a high probability that the improved fit of the individual ($P = 0.409$), individual slope ($P = 0.175$), and expected striping slope ($P = 0.177$) models relative to that of the pooled model could be due to chance alone.

Discussion

Our catch data provide support for the restricted-movement hypothesis of juvenile salmonids response to hourly variation in flow. The catch rates of age-0 rainbow trout at the daily minimum flow were at least four- and twofold higher than those at the daily maximum flow in low- and high-angle habitats, respectively. The differences in catch rates reflect true differences in density in nearshore areas, and hence, habitat use, since capture probabilities at the daily minimum and maximum flows were similar (Korman et al. 2009). Limited use of immediate shoreline areas by age-0 rainbow trout may seem unusual; however, short-term variation in flow is an unnatural characteristic, and observations made under more stable conditions (e.g., Chapman and Bjornn 1969; Everest and Chapman 1972) are probably not applicable under all conditions. Our results are consistent with findings from experimental manipulations, which show that juvenile fish are reluctant to shift their lateral position in response to sudden increases in flow (Shirvell 1994; Vehenan et al. 2000; Kemp et al. 2003, Vilizzi and Copp 2005).

The incidence of weekly striping pattern in otoliths varied with the frequency of steady flows from Glen Canyon Dam. In 2003, when striping was common in samples collected after April, flow was much more stable on Sundays during the summer (daily flow range, 24–73 m^3/s; Figure 1) than on weekdays and Saturdays (167–262 m^3/s). In 2004, when there was little evidence for weekly striping, the hourly variation in flow on Sunday during the summer was similar to that on other days of the week and that of weekday operations in 2003. Of the 20 fish with a striping pattern in 2004, 85% were caught in April and May, while in 2003 the incidence of otolith striping was evenly distributed among monthly samples collected after April. Fish with striping in April and May 2004 were, on average, 95 and 128 d old from hatch, respectively. These fish, therefore, came from the cohort that hatched in January, which would have been exposed to Sunday flows in February, March, and April that were relatively stable compared with the variation seen on other days in these months. Thus, the conditions that created a weekly otolith striping pattern in 2004 only affected the cohort that hatched in January, and the frequency of striping for rainbow trout captured after May declined progressively as the abundance of this cohort declined over the growing season owing to mortality.

There was strong evidence of increased otolith growth on Sundays in 2003, the only day of the week when flows were low and stable. Many authors have speculated that there may be an energetic cost associated with short-term variation in flows due to hydropeaking (e.g., Scruton et al. 2003, 2005; Geist et al. 2005), and the weekly otolith striping pattern that we documented in rainbow trout supports this hypothesis. In the Introduction, we proposed that patterns of nearshore habitat use driven by flow fluctuations could influence growth. The catch data showed that most age-0 rainbow trout in the Lee's Ferry reach do not use the immediate nearshore areas during the day at the daily maximum flow and must therefore be holding further offshore. In this situation, age-0 trout may spend more time concealed in the substrate to avoid piscivorous predators and higher velocities. This strategy would probably minimize the energetic cost of holding position in faster water, but ration would decline. Alternatively, if age-0 trout do not increase the amount of time when they are concealed and do not change their foraging behavior, energetic costs would probably increase and may not be offset if feeding efficiency is reduced because of higher velocities (Nislow et al. 2000, 2004). Either way, there is probably an energetic cost associated with a restricted-movement response to fluctuating flows. We speculate that the formation of atypical increments and the increase in otolith growth on Sundays in 2003 occurred because this was the only day of the week when flows were low and stable and this cost was not incurred.

The formation of atypical increments and higher otolith growth may also have been driven by the differences in temperatures to which age-0 rainbow trout were exposed on Sundays. During the day on Sundays in 2003, age-0 trout would be holding in immediate nearshore areas and would, therefore, have experienced daytime water temperatures that were 3–5°C warmer than in the main stem and near optimal for growth (Figure 2). Given the support for the restricted-movement hypothesis, age-0 trout would be located further offshore in colder water during other days of the week. This temperature dynamic alone could have caused the increased otolith growth on Sundays in 2003. Our data are not sufficient to determine the dominant factor or combination of factors leading to increased otolith growth on Sundays. However, both energetic and temperature hypotheses describing the mechanism behind the increased otolith growth are consistent with results from Neilsen and Geen (1985), who showed that mean otolith increment width and somatic growth of Chinook salmon *O. tshawytscha* fry increased with higher ration and warmer temperature, and was reduced when fry were forced to become more active.

Differences in somatic growth rates in 2003 for age-0 rainbow trout with and without atypical increments (based on a comparison of length-at-age relationships) were not statistically discernable in this study. Effects of hourly flow fluctuation on somatic growth must, therefore, be inferred from the observed otolith growth response and results from other studies that describe the relationship between otolith and somatic growth. Over time frames of multiple weeks to months, otolith growth is strongly correlated with somatic growth (Bradford and Geen 1987). For example, in this study the length of the longitudinal axis of otoliths from age-0 rainbow trout predicted 90% and 83% of the variation in FL in 2003 ($n = 235$) and 2004 ($n = 310$), respectively. However, Bradford and Geen (1987), who measured the somatic growth of Chinook salmon fry based on changes in length and weight, showed that otolith and somatic growth decouple over time scales of days to a few weeks. In contrast, Mugiya and Oka (1991), who used more sensitive methods to measure both otolith (calcium uptake rates) and somatic (RNA : DNA ratios) growth in rainbow trout, showed that growth was coupled at a daily timescale. We conclude that the wider otolith increments of age-0 trout that were associated with low and steady flows on Sundays in 2003 was indicative of a short-term increase in somatic growth, but that this increase was not detectable because our measure of somatic growth (length at age) was not sensitive enough.

This study has shown that hourly variation in flow caused by hydropeaking alters patterns of nearshore habitat use for age-0 rainbow trout and that reducing hourly variation in flow can lead to increased otolith growth. In the Introduction, we proposed that restricted movement of age-0 trout under fluctuating flows could be caused by factors that select for strong site attachment (e.g., increased predation risk while moving or competitive disadvantages from abandoning feeding territories) or by reduced food availability in the varial zone, which limits the energetic profitability of immediate nearshore areas during the daily maximum flow. The data from this study are not sufficient to determine which of these mechanisms or combination of mechanisms caused the habitat use pattern we observed, and this would be a useful focus for future research. The effects of limited use of nearshore habitats during the day under fluctuating flows on juvenile somatic growth and survival rate remain to be determined, and will require field experiments where contrasting levels of flow stability are maintained for long intervals (e.g., months). Although the costs of such an experiment would be high owing to lost power revenues, there is no substitute for large-scale field experiments that provide contrasting conditions at the broad temporal and spatial scales needed to determine population-level responses.

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