

Evidence of Delayed Mortality on Juvenile Pacific Salmon Passing through Turbines at Columbia River Dams

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Abstract.—We evaluated the survival of juvenile salmon through turbines in Columbia River dams and found no differences between two operations but strong evidence of delayed mortality from turbine passage. After tagging with a passive integrated transponder (PIT) tag and a radio tag, yearling Chinook salmon *Oncorhynchus tshawytscha* were released at McNary Dam on the Columbia River through a turbine operating both within 1% of peak efficiency (a discharge rate of 317 m³/s) and outside the 1% range at the maximum blade angle (464 m³/s). Estimated relative survival to a detection array 15 km downstream was 0.871 at 317 m³/s and 0.856 at 464 m³/s and 0.858 and 0.814, respectively, to an array 46 km downstream. The highest point estimates of survival occurred under the lower discharge, suggesting that operating turbines within 1% of peak efficiency is a useful guideline for fish protection at McNary Dam. In a concurrent evaluation using balloon tags, estimated mean direct survival ranged from 0.930 to 0.946. Radio tag estimates were significantly lower than balloon tag estimates under both operations. Based on these differences, we estimated that delayed mortality comprised from 46% to 70% of total estimated mortality. We reviewed the literature and concluded that delayed mortality was caused by sublethal impacts to fish sensory systems, which increased vulnerability to predation in the tailrace. We recommend that future research to improve turbine designs and operations for fish passage focus on this major component of mortality.

Many stocks of Pacific salmon in the Columbia River have declined recently (Nehlsen et al. 1991; Myers et al. 1998; McClure et al. 2003), in part from high mortality associated with a series of eight dams installed from 1938 to 1975 on the river and its largest tributary, the Snake River (Raymond 1979). Survival of juvenile salmonids passing these dams during their seaward migration is

highest through spillways and lowest through turbines (Schoeneman et al. 1961; Muir et al. 2001), turbine mortality usually being caused by pressure changes, cavitation, shear stress, turbulence, strike, and grinding (Čada 2001). Relating fish injuries to specific mortality mechanisms and detecting small differences in survival between turbine operations is difficult because turbine conditions vary with discharge, head, blade angle, passage route within the turbine, and environmental conditions. Thus, there has been little improvement in fish survival through turbines (Ferguson et al. 2005).

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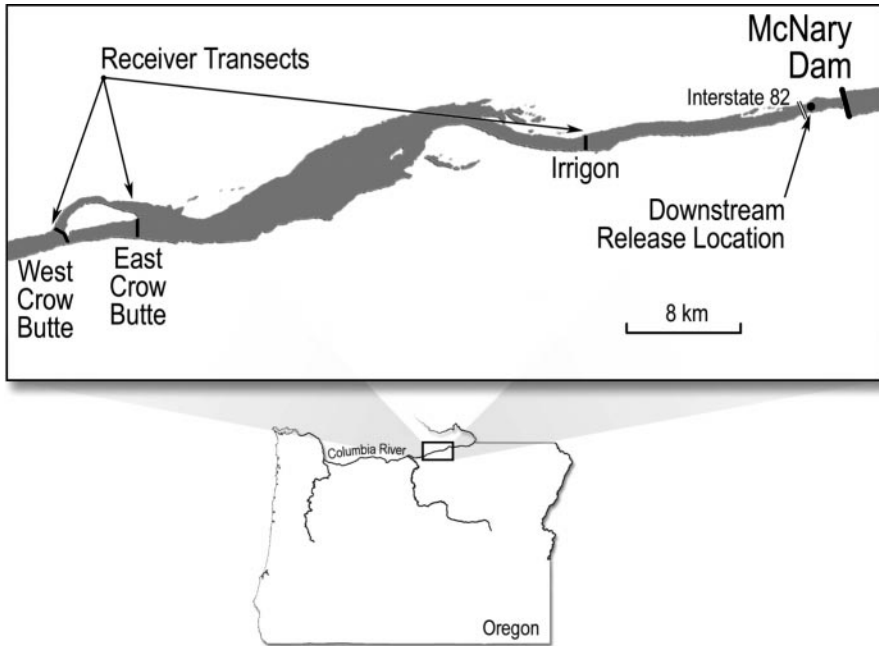


FIGURE 1.—Locations of McNary Dam on the lower Columbia River, the downstream juvenile Chinook salmon release site, and radio receiver transects at Irrigon, East Crow Butte, and West Crow Butte.

The U.S. Army Corps of Engineers (USACE) operates turbines at these dams within 1% of peak electrical generating efficiency to improve fish survival, based on the assumption that survival and turbine hydraulic efficiency are positively correlated (NMFS 2000). A recent analysis found no statistical relationship between survival and turbine efficiency and differences as large as 3.2% between peak survival and survival at peak efficiency (Skalski et al. 2002). They recommended that turbine operations be based on maximum fish survival and not peak efficiency. This potential improvement in survival from operating turbines to maximize fish survival is large, and the cumulative benefits from optimized turbine operations could be substantial. For example, we estimate that 56 million juvenile salmon passed from one to nine dams in 2003 before arriving in the Columbia River estuary.

The turbines at McNary Dam on the Columbia River are nearing the end of their service life, and the USACE plans to replace all 14 with newer, high-discharge units. This presents an opportunity for redesign to improve fish survival, if mortality mechanisms can be quantified, but it also creates uncertainty regarding fish survival through the higher discharge units and how it might differ from existing conditions.

In 2002 we evaluated the survival and behavior of juvenile salmon through a turbine, the immediate tailrace, and upper reaches of the reservoir below McNary Dam under two operations to address whether operating outside the 1% efficiency range, and simulated passage through the new (high-discharge) turbines, affects survival.

Methods

Study site.—McNary Dam at river kilometer (rkm) 467 (Figure 1) was completed in 1954 and has 14, six-bladed Kaplan turbines that operate at 22 m of head. Powerhouse capacity is 6,570 m³/s in flow and 980 MW in rated generation. Each turbine has a 7.1-m diameter runner that rotates at 85.7 revolutions/min at the maximum capacity of 469 m³/s flow. During the juvenile fish passage season, turbines are operated within 1% of peak efficiency at discharges from 223 to 350 m³/s. Discharge capacity of the replacement turbines will be 501 m³/s.

Experimental design.—Based on analyses of detectable differences between treatments ranging from 3% to 5% ($\alpha = 0.05$ and $\beta = 0.2$), we planned to release, over 20 d, three groups (two turbine treatments and a reference release 2 km downstream from the dam) of 36 fish; we intended to detect a difference of 3.5% between two turbine

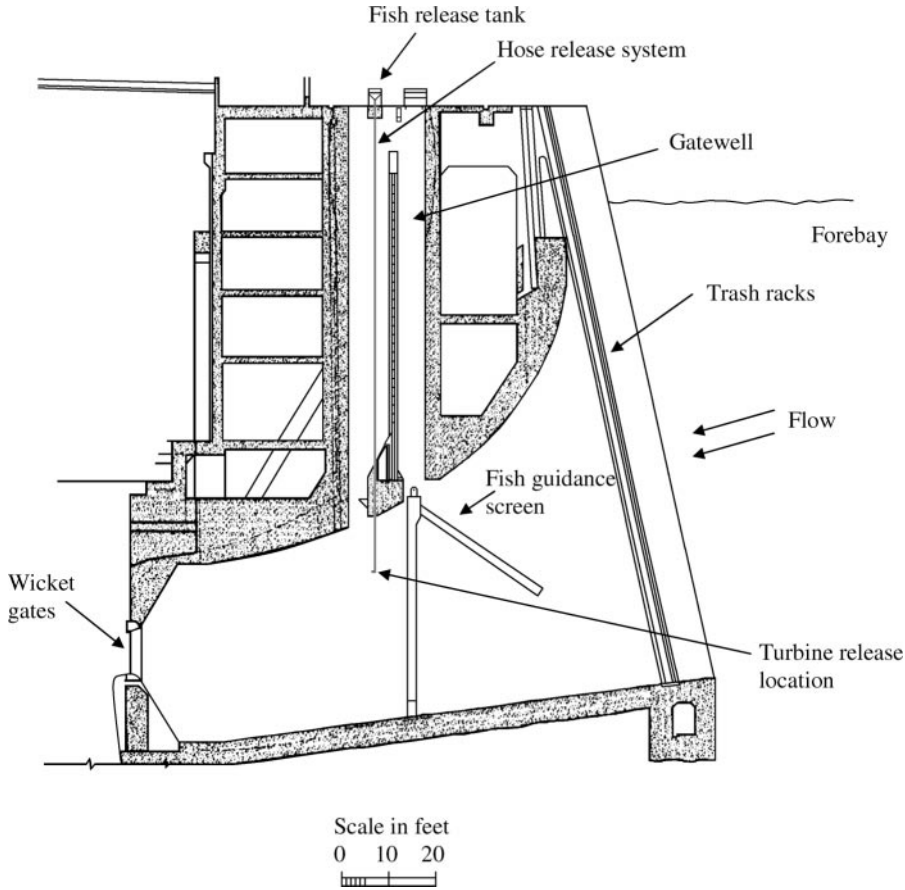


FIGURE 2.—Cross-sectional view of McNary Dam (Columbia River) turbine intakes, showing the turbine release mechanisms and locations in 2002.

operations. The 317 m³/s operation was at the upper end of a range defined as within 1% of peak turbine efficiency, and the 464 m³/s operation was outside the 1% range where turbine blades are tilted to the maximum upward angle. We evaluated survival, passage timing through a portion of the reservoir below the dam, and behavior in the immediate tailrace.

Daily samples of run-of-river, injury-free, hatchery yearling Chinook salmon *Oncorhynchus tshawytscha* from the McNary Dam juvenile bypass system (121–239 mm in length; median, 145 mm) were held in 113-L containers with flow-through river water. After 24 h holding, 1.4 g (17 × 6 mm) radio tags were surgically implanted using the method of Adams et al. (1998). A 30-cm antenna trailed outside each fish, and tags were pulse-coded for unique identification (transmitted at 40 signals/min). A passive integrated transponder (PIT) tag was placed in each fish during sur-

gery to estimate survival to West Crow Butte (the lowest telemetry receiver site). After surgery, fish were held in oxygenated 19-L containers and, after recovery from anesthesia, were transferred to and held for 24 h in an insulated holding tank (1.2 × 2.1 × 0.4 m) supplied with flow-through river water.

Turbine releases were made (as described in Normandeau Associates et al. 2003) mid-bay and below the fish guidance screens in all three intakes of unit 9 (Figure 2). Each day a group was released at one turbine operation, followed shortly thereafter by a second group released at the other operation; the first operation tested was alternated daily. Treatment fish were released equally among all three turbine intakes at 5–8-min intervals. A reference group of fish was released via a barge at 2 km downstream of the dam; these were released at 15-min intervals to spread their time of release over both turbine releases. All fish were

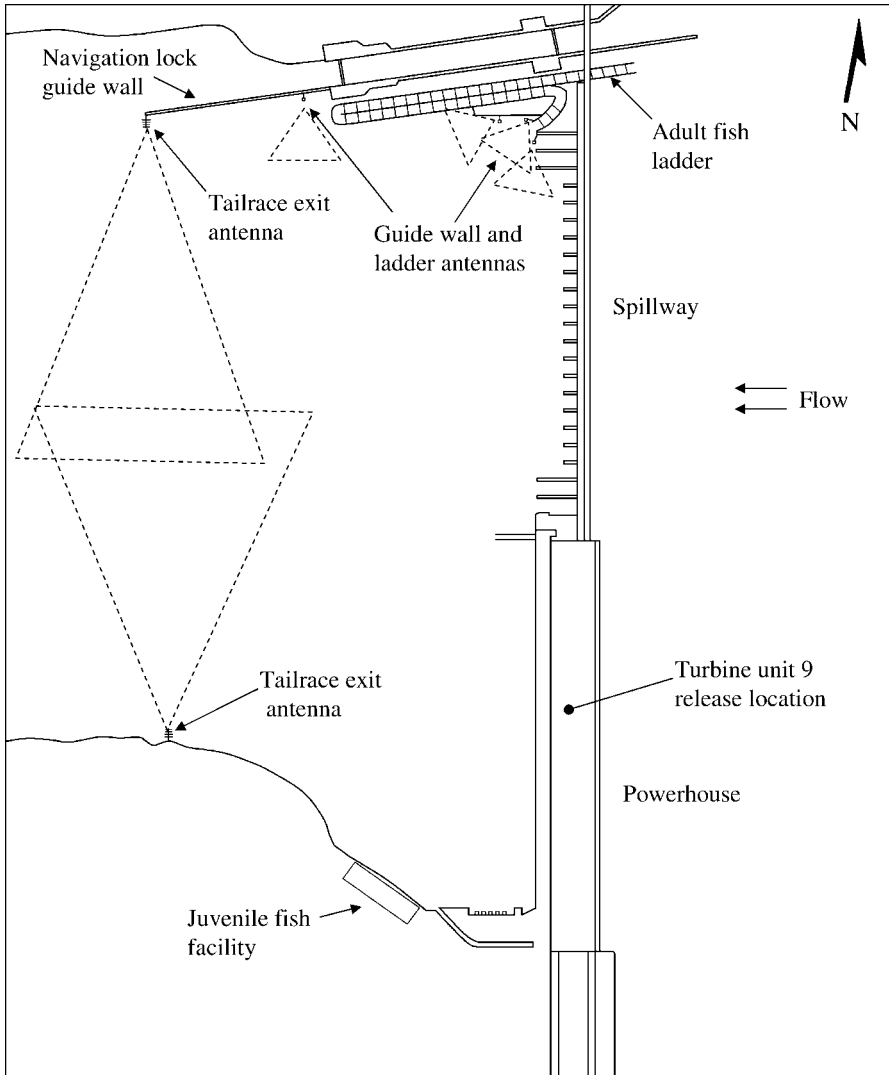


FIGURE 3.—Tailrace of McNary Dam (Columbia River), showing radio receiver locations along the navigation lock guide wall and in the immediate tailrace used to detect radio-tagged juvenile Chinook salmon. Triangles (dashed lines) indicate the approximate coverage by the antennas.

released two at a time, typically between 0930 and 1430 hours, from 14 May through 11 June.

Test fish were monitored by two tailrace exit antennas 500 m downstream from the dam, by four antennas along the guide wall and adult fish ladder entrance (Figure 3), and on receiver arrays at Irigon at 15 km, East Crow Butte at 41 km, and West Crow Butte at 46 km downstream from McNary Dam (Figure 1). Additional PIT-tag detections were obtained from fish bypass systems at John Day Dam (rkm 347) and Bonneville Dam (rkm 235). Survival estimates relied on the assumption that dead test fish were not detected

downstream; fish that died after tagging were released with live fish from each release group to test this assumption.

Statistical methods.—Receiver data files (date, time, transmitter frequency and code, antenna number, and signal strength) were downloaded daily into a database and screened. A record was excluded if it had less than 5 signal detections, date stamps before release time, less than 2 detections/min, or was from a receiver upstream of the dam. Records were examined for validity based on location, travel time, number of detections, and number of detections per minute. The final data set was

analyzed with the SURPH (survival under proportional hazards) software program for survival estimation (Lady et al. 2001). This software used the single-release model (Cormack 1964; Jolly 1965; Seber 1965; Skalski et al. 1998, 2001), where the “complete capture history” protocol of Burnham et al. (1987) is used to estimate survival and detection probabilities. The model was applied independently to daily treatment and reference groups, each day being a replicate. Relative estimates of survival (ratios) were developed by comparing treatment and reference survival estimates.

The geometric mean was used to average relative survival estimates, which are ratios of proportions, and were assumed to be lognormally distributed (Snedecor and Cochran 1980). Weighted geometric mean relative survival estimates were calculated using inverse relative variance for the weights (Zabel et al. 2001). Confidence intervals (95%) for each weighted geometric mean were made on the log scale, and the endpoints were back-transformed. Standard error estimates were based on empirical replicate variability.

Treatment means were compared using two-factor, weighted analysis of variance (ANOVA; turbine flow and release day), and normality tests were visually examined to assess the assumption that log-transformed data were normally distributed. All groups released on the same day were assumed to be mixed because they passed the downstream detection arrays in nearly 1 d and had similar detection and survival probabilities. Paired *t*-tests were used to compare relative survival estimates to Irrigon and West Crow Butte within each turbine treatment. We partitioned the test fish into four length quartiles for each turbine and reference release and used pairwise *t*-tests to look for size-dependent mortality effects.

Because medians are less sensitive to outliers than averages, median travel times from release to first detection at each downstream receiver array were calculated for each replicate in all three release groups and compared using ANOVA. Normality plots of the residuals were visually examined to ensure the model assumptions were valid. We compared our results with the findings from two concurrent studies.

One was a study of direct mortality in which balloon-tagged yearling Chinook salmon were released through structures, locations, and turbine operations identical to those of radio-tagged fish. The fish used were also run-of-river, injury-free, hatchery fish collected from the McNary Dam juvenile bypass system (Normandeau Associates et

al. 2003). Balloon-tagged fish were removed from the tailrace shortly after release and held for 48 h in tanks. Under each turbine operation, survivals at 1 and 48 h were not significantly different, and we used the lower point estimate for each operation to test the smallest differences in survival between the two methodologies. We defined delayed mortality as mortality among fish that experience low (sublethal) levels of physical stress or injury during dam passage and subsequently die from increased susceptibility to disease or predation (Čada 2001). Survival estimates based on radiotelemetry included direct and delayed mortality expressed to the downstream receiver locations, whereas those based on balloon tags include only direct mortality. Therefore, we assumed that differences between balloon tag and radio tag survival estimates provided evidence of delayed mortality. We compared survival means using *Z*-tests rather than *t*-tests because our estimates were based on temporal replication, whereas the estimates of Normandeau Associates et al. (2003) were calculated using pooled data and thus had no replicate-based degrees of freedom. We computed *Z*-test statistics as the radiotelemetry mean minus the balloon tag mean divided by the square root of the sum of the radio and balloon tag calculated variances. We then compared radio to balloon tag survival estimates using a *Z* score. Standard errors from the balloon tag study were calculated using a variance formula provided by Normandeau Associates et al. (2003). We assumed that radio tag survival estimates (direct and delayed mortality) would be lower than balloon tag estimates (direct mortality); we used a one-sided test, and calculated *P*-values as the lower tail of the *Z* score using a standard normal distribution.

The second comparison was a qualitative assessment of our results to acceleration and pressure values collected within the turbine from sensor bodies (near the size and mass of juvenile yearling salmon) released through two operations: 218 and 470 m³/s (Carlson and Duncan 2004). These operations were chosen for reasons unrelated to our research, but provided data on a broad range of physical differences fish are exposed to during turbine passage. The 218 m³/s operation was at the lower end of the 1% efficiency range in the same manner that the 317 m³/s operation was near the upper end of the range; the 470 m³/s operation was nearly identical to the 464 m³/s operation we tested.

TABLE 1.—Comparison of mean survival estimated by balloon tags, radio tags, and passive integrated transponder (PIT) tags to Irrigon and West Crow Butte radio receiver arrays, and rates of mortality per kilometer of river reach for yearling Chinook salmon released into turbine unit 9 (McNary Dam, Columbia River) operated at 317 or 464 m³/s.

Method and detection site	Survival (SE)	
	Turbine at 317 m ³ /s	Turbine at 464 m ³ /s
1-h or 48-h direct survival; balloon tags	0.930 (0.021)	0.946 (0.019)
Direct and delayed survival to Irrigon; radio tags	0.871 (0.016)	0.856 (0.011)
Direct and delayed survival to East Crow Butte; radio tags	0.832 (0.023)	0.823 (0.021)
Direct and delayed survival to West Crow Butte; radio tags	0.858 (0.038)	0.814 (0.037)
Direct and delayed survival to John Day Dam; PIT tags	0.724 (0.197)	0.796 (0.227)
Mortality/km from release to Irrigon	0.0086	0.0096
Mortality/km from Irrigon to West Crow Butte	0.0031	0.0040

Results

Mean detection probabilities at the Irrigon, East Crow Butte, and West Crow Butte receiver arrays were high for fish alive at release (0.84–0.97) and similar among release groups for each array, and the combined detection probability was greater than 0.999 for each release group. Fish availability decreased at the end of the study period, and we released a total of 1,708 radio-tagged yearling Chinook salmon on 17 of the planned 20 d. Although this reduced our sample size, detection probabilities were higher than anticipated, as was the empirical variability. An estimated difference of 5.5% in survival between treatments was detectable.

Detection of radio and PIT tags at downstream sites was sufficient to estimate relative survival to Irrigon, East Crow Butte, and West Crow Butte (Table 1). Because estimates of survival to East Crow Butte were similar to West Crow Butte and the two sites were only 5 km apart, we based our analyses on survival to West Crow Butte, the farthest downstream receiver array. Estimates of survival under the two turbine operations were not significantly different to Irrigon ($P = 0.201$; Table 1) or West Crow Butte ($P = 0.696$; Table 1). There were no differences in estimated survival between detection sites within each turbine treatment ($P > 0.50$), although point estimates of survival to Irrigon and West Crow Butte were highest under the 317-m³/s operation. We estimated survival to John Day Dam based on PIT tags only (Table 1), but

due to the small sample size and low detection probabilities, they provided no statistical power and were not used in subsequent analyses. The rate of mortality based on the radio tags varied between detection sites but not within turbine treatments and was highest from release to Irrigon (Table 1). We found no differences in survival between fish length quartiles at the 464-m³/s operation, but at 317 m³/s there was a trend of higher mortality in the smallest fish.

Mean differences in median travel time between the two turbine operations were not significantly different (P -values ranged from 0.393 to 0.977), but those between turbine and tailrace releases were highly significant for all comparisons ($P < 0.001$). Median travel times from release to detection ranged from 3.35 to 22.48 h (Table 2). Travel speeds from release to Irrigon, Irrigon to East Crow Butte, and East Crow Butte to West Crow Butte ranged from 1.5 to 4.0 km/h. We did not analyze these data further because travel speed in each reach probably reflected channel morphology and, thus, river velocity (see Figure 1), and these physical factors could not be separated from other variables, such as light level and diel behavior.

Twenty-five fish (17 released at 317 m³/s and 8 released at 464 m³/s) released into turbines were detected on one or more guide wall and ladder entrance antenna and remained in an eddy from 3 min to nearly 70 h (median 2.4 h). Two were first detected on tailrace exit antennas, indicating the

TABLE 2.—Median travel time (h) from release to first detection at the Irrigon, East Crow Butte, and West Crow Butte radio receiver arrays for radio-tagged yearling Chinook salmon released into the tailrace 2 km downstream from McNary Dam (Columbia River) or into turbine unit 9 operated at 317 or 464 m³/s.

Detection site	Tailrace releases	Combined turbine releases	Turbine release at 317 m ³ /s	Turbine release at 464 m ³ /s
Irrigon	3.35	3.95	4.00	3.88
East Crow Butte	19.62	21.07	21.48	20.75
West Crow Butte	21.03	22.48	22.58	22.27

fish traveled 500 m downstream before moving upstream. We speculate the other 23 fish traveled directly north across turbine units 10–14 and the spillway and entered the eddy along the wing wall. Of the 25, 13 were never detected again (8 released at 317 m³/s and 5 at 464 m³/s), and the 11 detected at Irrigon had a median travel time of 6.3 h compared with 3.95 h for all turbine-released fish. None of the reference released fish were detected on the guide wall or ladder antennas.

Sixteen fish (<1%) died during the 24-h post-tagging holding period, and all were released: 5 into the tailrace, 4 into the 317-m³/s turbine, and 7 into the 464-m³/s turbine. Although this release was not large enough to test the assumption that dead fish were not detected at downstream receivers, none were detected, and we had no evidence to refute the assumption. Tagging mortality was lower than the 2–3% typically reported for surgical tagging (Hockersmith et al. 2003).

Discussion

Survival Test Results

We found no significant differences in the survival of radio-tagged yearling Chinook salmon under the two turbine operating conditions tested, and point estimates were within a range reported from other survival studies at Snake and Columbia River dams (Bickford and Skalski 2000; Muir et al. 2001; Ferguson et al. 2005). We found some evidence for size-dependent mortality at the 317-m³/s operation, smaller fish having lower survivals than larger fish. These results were somewhat counterintuitive (i.e., because larger fish have a higher risk of striking rotating blades) and may have resulted from random variability. However, they may also reflected a real, causal relationship between survival and something other than physical strike (e.g., turbulence, as discussed below).

The rate of mortality was higher from release to Irrigon than from Irrigon to West Crow Butte, indicating that most fish died within 15 km of the powerhouse. Because survival estimates to Irrigon and West Crow Butte were not significantly different, but were lower to West Crow Butte, additional mortality may have occurred below Irrigon. Hockersmith et al. (2003) compared radio-tagged and PIT-tagged fish and found that probabilities of detection at downstream dams varied by less than 5%; survival rates were similar for median travel times of less than approximately 6 d (a migration distance of 106 km). Considering the shorter migration distance we sampled (46 km,

< 1 d travel time), we believe the observed mortality resulted from delayed effects of turbine passage and not from tag effects.

Point estimates of survival were higher for the operation within 1% of peak efficiency, which supports the 1% fish protection guideline and agrees with Skalski et al. (2002), who found operations within 1% of peak efficiency most often captured the maximum fish survival estimate. However, because measurements of flow through turbines (and thus of efficiency) are inaccurate, the USACE is focusing future improvements on operating at the point of “lowest avoidable losses,” rather than turbine efficiency.

Within the turbine releases we found no differences between median travel time to downstream receivers; however, the median travel time of the combined turbine releases was significantly longer than that of the tailrace release groups. These differences were small (<1.5 h) and probably resulted from the physical location of the tailrace reference release site being 2 km closer to the downstream detection arrays than the turbine releases. Thus, we do not ascribe any biological meaning to these differences.

We concluded that test fish survived and generally behaved the same after release under both turbine operations, except in the immediate tailrace, where a small number of fish released under the 317-m³/s operation were more likely to be detected in an eddy near the navigation guide wall than were their cohorts released under the 464-m³/s operation. The small sample did not allow further analyses of these data; however, half of these fish were never detected again, and fish that entered the eddy spent twice as much time in the immediate tailrace as fish not detected in the eddy. Because project conditions (total flow, percent spill, and spill volume) were similar during testing, we believe these fine-scale tailrace behaviors probably resulted from fish reacting to physical conditions experienced during turbine passage.

Delayed Mortality

Normandeau Associates et al. (2003) also found no significant differences between turbine operation effects on balloon-tagged Chinook salmon. Estimated survival was 0.930 and 0.946 for the 317- and 464-m³/s operations, respectively, similar to the 0.933 estimate of direct survival from a meta-analysis of balloon tag data (Bickford and Skalski 2000). Our radio tag estimates of survival to Irrigon (*P*-values: 0.012 to 0.038) and West Crow Butte (*P* ≤ 0.001; Table 1) were significantly

TABLE 3.—Comparison of the physical environment to which juvenile Chinook salmon may have been exposed when passing turbine unit 9 (McNary Dam, Columbia River) operated at 218 or 470 m³/s. Atmospheric pressure is 101.3 kPa.

Physical data	Turbine operation: 218 m ³ /s	Turbine operation: 470 m ³ /s
Lowest pressure observed (kPa)	82.9–178.5	73.1–119.7
Mean change in pressure prior to nadir (kPa ⁻¹)	-215.3	-736.4
Maximum change in pressure prior to nadir (kPa ⁻¹)	-333.1	-990.8
Probability of striking stay vanes and wicket gates or encountering turbulence or shear upstream of the runner	High	Low
Probability of runner strike	None	None
Flow distribution between both draft tubes (turbulence)	Uneven (high)	Even (low)
Exposure summary	Strike, scraping, shear, turbulence, moderate pressure changes	Large and rapid pressure changes

lower than balloon tag estimates for both turbine operations. After comparing balloon and radio tag estimates, we concluded that direct mortality composed 30% to 54% of total estimated mortality (direct and delayed), and thus, delayed mortality accounted for 46–70% of total mortality.

We examined the sensor data for possible explanations of fine-scale tailrace behaviors and delayed mortality and found considerable variability in the lowest pressure observed and in the mean and maximum changes in pressure between the two turbine operations (Table 3). This variability was possibly due to the large number of potential sensor passage trajectories within the turbine.

At the low discharge the acceleration impulses indicated a high probability of either strike or scraping in the area of the stay vanes and wicket gates or a response to flow conditions such as turbulence or shear. The fish sensors also remained within the immediate turbine runner environment as long as 700 ms (one runner revolution) at the lower discharge. Below the runner in the draft tube, flow distribution between the two draft tubes was uneven, and turbulence varied across the three release locations (intakes) within the turbine. Under the high discharge, large and rapid pressure changes through the runner were recorded, turbulence in the draft tube was low, and flow was more uniformly distributed between draft tubes. Under both operations, no strike events were observed in the runner area, which suggested low probability of blade strike.

Our survival estimates displayed a trend of higher mortality in smaller than in larger fish at the low (317-m³/s) discharge, which may have resulted from turbulence affecting smaller fish disproportionately; however, without further information this is only speculation. Carlson and Duncan (2004) concluded that pressure-related effects

would be more severe at higher turbine discharges. Our point estimates of survival were lower at the high discharge, and if pressure effects did result in delayed mortality, then the new (high discharge) turbines scheduled for installation at McNary Dam may reduce survival compared with the existing turbines. Carlson and Duncan (2004) also found that turbulence was higher at the lower discharge, but lower than measured at Columbia River dam spillways, where survival is typically high (Ferguson et al. 2005). Thus, it is possible that turbulence may not have been responsible for the delayed mortality we observed. To summarize, we found evidence that the physical environments were different between the two operations tested, and thus, the causal mechanisms of mortality may differ among operations.

It is widely accepted that substandard prey are significantly more vulnerable to predation (Temple 1987). Mesa et al. (1994) suggest this can be caused by failure of prey to detect predators, lapses in decision-making, poor fast-start performance, the inability to shoal effectively, or increased conspicuousness of the prey. Threat recognition requires the use of many senses and a properly functioning nervous system, and there is significant evidence that prey vulnerability is increased if sensory systems or motor functions are impaired (Kruzyński and Birtwell 1994; Mesa and Warren 1997; Scholz et al. 2000). For example, Weber and Schiewe (1976) found that gas emboli can severely alter lateral line function, and Mesa and Warren (1997) observed that juvenile Chinook salmon with extensive occlusion of the lateral line and gill filaments were significantly more vulnerable to predation by northern pikeminnow *Ptychocheilus oregonensis*. Exposure to noise during passage through turbines may also affect the ability of juvenile salmon to detect predators (Popper 2003).

Therefore, we looked for relationships between sensory system impairment and exposure to physical conditions within turbines. Exposure to shear and turbulence may cause sublethal physiological effects on fish equilibrium (D. A. Neitzel and coworkers, U.S. Department of Energy, internal report on the effects of shear on fish, 2000; G. R. Guensch and coworkers, U.S. Department of Energy, internal report on fish injury mechanisms during exposure to a high-velocity jet, 2002). One mechanism for loss of equilibrium is disruption of the vestibular system, which produces body flexion, body roll, "corkscrew" swimming, and tilted body posture behaviors (von Holst 1950). Recovery from these deficits is through vestibular compensation, which occurs gradually as central brain mechanisms restore some degree of postural and locomotor control. Recovery times vary by species and can be significant. In the European river lamprey *Lampetra fluviatilis* recovery may take a month and is affected by the degree of visual input (Deliagina 1997). In goldfish *Carassius auratus* recovery from unilateral ear damage can be less than 0.5 h if normal vision is allowed, although visual-vestibular interactions may take more than 2 weeks to return to steady-state levels of bilateral symmetry (Ott and Platt 1988a, 1988b). The recovery period for salmonids is unknown.

The related "escape-startle" reflex is mediated by signals from the inner ear and lateral line sensory organs that project into a large bilateral pair of cells in the medulla (Eaton and Popper 1995). Disruption of the vestibular system could impact this reflex and, thus, increase the susceptibility of prey to attacks from predators.

Abernethy et al. (2001) found that changes in pressure levels caused almost 100% of juvenile salmon to expel air from their swim bladder and that subsequently fish were negatively buoyant when they entered a tailrace. To regain neutral buoyancy, fish must return to the surface and gulp air to reflate the bladder, potentially increasing their exposure to surface predators.

Coutant and Whitney (2000) suggest that fish sense the water rotation downstream from the turbine blades and react through normal behavioral responses, moving to the periphery of the turbine draft tube. Fish in the tailrace eddy may have moved in this manner and, subsequently, may have been transported into the eddy by tailrace flow patterns. Alternately, they may have entered the eddy to recover from one or more of the sensory disruptions discussed above. Although the cause of fish entering the tailrace eddy is unclear, the

delay and mortality rates of these fish further implicate predation as the primary mechanism of delayed mortality associated with turbine passage.

Predators must be present to link potential sensory impairment to increased mortality from predation. Ward et al. (1995) reported that consumption of salmonids by northern pikeminnows was high in the McNary Dam tailrace compared with other dams on the Snake and Columbia rivers, and Fahler et al. (1988) showed that northern pikeminnows in the McNary Dam tailrace responded quickly to changes in project operations. Thus, it is highly likely that predators were present during our tests and predation was the actual mortality mechanism.

Muir et al. (2001) also compared estimates of survival from balloon-tagged and PIT-tagged yearling Chinook salmon released through identical mechanisms at Lower Granite Dam on the Snake River. In contrast to our findings, they did not find a significant difference between mean survival estimates based on PIT (0.927) and balloon tags (0.948). Radio and PIT tag methodologies both incorporate delayed effects in the survival estimates and would have produced lower estimates of survival than balloon tags if delayed mortality from turbine passage had been occurring. Ward et al. (1995) reported catches in 1991 of approximately 10 northern pikeminnows (>250 mm) per 15 min of effort with angling gear in the immediate tailrace of McNary Dam in 1990, but zero in the Lower Granite Dam tailrace. Muir et al. (2001) probably saw no evidence of delayed turbine mortality because of low northern pikeminnow abundance, and our results were consistent with these findings. We concluded that delayed mortality is a main component of poor survival and probably resulted from tailrace predation caused by sublethal impacts to fish sensory systems that occurred during passage through the turbine environment.

Future Research

Our integrated approach to evaluating the passage of juvenile fish through turbines was a major departure from previous, single-study approaches. However, the results were not definitive. They show the difficulty in relating fish passage survival and postturbine tailrace behavior to mechanisms of mortality and suggest that broad-scale estimates of passage metrics provide generalized information of limited value to improving turbine design and operation for fish passage survival. Studies relating survival to turbine operation lack the rigor needed to provide mechanistic linkages between

specific conditions with the turbine (e.g., magnitudes and rates of change in shear, turbulence, and pressure) and their effects on small fish.

A more effective approach would be to conduct laboratory assessments that explicitly test hypotheses of how physical conditions within the turbines affect fish sensory systems. Test fish could be exposed to specific levels of shear, turbulence, or pressure drop based on ranges, magnitudes, and durations observed during various turbine operations. Their mechano-sensory systems could then be examined, and any physiological and neurobiological effects and associated recovery periods could be quantified. By exposing test fish to predators, functional outcomes from sensory system impairment, loss of equilibrium, and other sublethal effects could be quantified. For additional insights, future investigations should also focus on differences in fine-scale tailrace behavior and relate these to physical conditions experienced within the turbine.

Our study addressed the survival of downstream-migrating juvenile Pacific salmon through relatively low-head Kaplan turbines. However, our conclusion—that delayed mortality is a major component of total mortality, which should be incorporated into survival estimates—applies broadly to many species and life stages of fish that migrate through a variety of types of turbines and barriers in regulated rivers. Recent investigations highlight the growing importance of sublethal effects on animals from anthropogenic stressors. For example, Peterson et al. (2003) found evidence in an Alaskan coastal ecosystem of an unexpected persistence of toxic subsurface oil and that chronic exposures, even at sublethal levels, continued to affect wildlife. Springman et al. (2005) used a vitality model to evaluate how a contaminant exerting sublethal, indirect effects on individual rainbow trout *O. mykiss* can affect the population. These findings and approaches challenge the conventional assumption that impacts to populations derive almost exclusively from direct mortality. Understanding sublethal effects from turbine passage will lead to improved turbine operation and design and will benefit efforts to conserve and recover the many populations of fish that must pass power generating facilities to complete their life cycle.

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