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[Article]

Steelhead Emigration in a Seasonal Impoundment Created by an Inflatable Rubber Dam

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Abstract.—While large, permanent dams and reservoirs are known to impede smolt movements, investigations of small, temporary impoundments are scarce. Inflatable rubber bladder dams are used to create temporary impoundments worldwide, yet downstream fish passage at these structures has not been evaluated. To examine smolt emigration in a seasonal water supply reservoir and passage at a rubber dam, we tracked 110 radio-tagged steelhead *Oncorhynchus mykiss* smolts through a 4.5-km free-flowing reach and an adjacent 5.1-km-long impoundment on the Russian River, California, during 2001, 2002, and 2004. Unlike the results of studies in other impoundments, median travel rates in the free-flowing (0.6–0.8 km/h) and reservoir (1.0–1.4 km/h) reaches did not differ significantly within or among years. Smolts slowed significantly, however, in the dam forebay. Forebay travel rates (0.02–0.1 km/h) were more than an order of magnitude lower than rates in free-flowing and reservoir reaches. Although delayed, more than 75% of the fish detected in the forebay successfully passed the dam. More than 80% of the passing fish traveled over the dam crest as opposed to through ladders and flow bypasses. To determine whether increased spill depth and velocity would reduce forebay delay, we deformed the crest of the inflatable dam into a notched configuration throughout the 2004 study year. The notched configuration increased crest depth and velocity approximately 20-fold over the normal fully inflated condition. Smolts moved significantly faster through the forebay when the dam crest was notched in 2004 (median = 2.4 h) than when the dam was fully inflated in 2001 (6.3 h). Our finding that steelhead traveled through free-flowing and impounded reaches at similar rates but slowed dramatically in the forebay should encourage others to examine forebay conditions in small reservoirs. Concentrating spill by deforming the crest of an inflatable rubber dam is a simple and effective way of reducing forebay delay.

Dams and reservoirs that impede smolt passage have contributed to the depressed status of many stocks of anadromous salmonids (NMFS 1996; Gregory and Bisson 1997). Both reservoir and dam conditions influence the proportion of fish that migrate through an impoundment (Smith et al. 2002). Smolts entering reservoirs may encounter disorienting current velocities, unfavorable water quality conditions, and higher predation rates, and may have difficulty negotiating passage routes in dam forebays (Poe et al. 1991; Berggren and Filardo 1993; Venditti et al. 2000).

Impoundments of any size have the potential to alter migratory behavior and negatively affect survival, yet most research has focused on large hydroelectric dams and reservoirs. Low summer streamflows characteristic of central California's Mediterranean climate encourage the construction of small, seasonal dams for irrigation, domestic water supply, and recreation. The operation of seasonal low-head dams is often coincident with the emigration of federally listed central California coast steelhead *Oncorhynchus mykiss* (NMFS 1997). However, the effect of these structures on smolt passage has received little attention.

The small size of seasonal impoundments may not diminish the emigration rate and survival ef-

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fects commonly attributed to large reservoirs. Declining water velocities corresponded to slower migration rates for juvenile Chinook salmon *O. tshawytscha* in a large Snake River impoundment (Venditti et al. 2000) and for brown trout *Salmo trutta* smolts in a small, permanent pond (Olsson et al. 2001). High rates of predation on emigrating salmonids have been reported in a large Columbia River reservoir (Poe et al. 1991) and a comparatively small Danish lake (Jepsen et al. 1998).

While some features of large and small permanent impoundments may impact smolts similarly, seasonal dams also present unique challenges for out-migrants. Because seasonal dams are temporary structures, they often do not contain passage routes designed specifically for smolts. The depth and flow criteria for successful smolt bypass at large dams (Ferguson et al. 1998) are unattainable at small, seasonal structures. More information about smolt responses to potential passage routes at low-head dams would improve dam management and design.

To facilitate the management of a seasonal water supply reservoir, we monitored the emigration of radio-tagged steelhead smolts through a free-flowing reach and an impounded reach of the Russian River, California. The impoundment is created by Mirabel Dam, an inflatable rubber bladder dam. Rubber dams were first developed in the 1950s, and thousands are currently in use on rivers worldwide for irrigation, water supply, power generation, flood control, navigation, and recreation (Zhang et al. 2002; Bridgestone Industrial Products America 2004). Composed of rubberized fabric and filled with air or water, the dams are crest-adjustable structures that collapse flush with the streambed when not in use (Zhang et al. 2002). More than 200 rubber dams have been installed in North America since 1984 (A.S. Parry, Bridgestone Industrial Products, personal communication), yet no investigation of fish passage at these dams appears in the literature.

Our specific objectives were to (1) determine steelhead smolt travel rates and residence times in free-flowing and impounded reaches, (2) evaluate passage routes and fish behavior in the dam forebay, and (3) compare forebay travel rate and residence time measured when the dam was fully inflated with those measured when the dam was partially deflated to concentrate spill. We hypothesized that smolts would travel through the free-flowing reach more rapidly and then slow as they approached the dam, and that forebay residence time would be reduced by increasing spill depth and velocity.

Study Site

Originating in the Coast Ranges of Mendocino and Sonoma counties, the Russian River enters the Pacific Ocean 112 km north of San Francisco, California. The 177-km-long river drains a 3,846-km^2 watershed (Florsheim and Goodwin 1993). Streamflow historically ranged from 0.02 to 2,887 m^3/s but is currently regulated by releases from two permanent reservoirs. Summer flows are typically 6–9 m^3/s.

During the low-flow season (April to November), the Sonoma County Water Agency operates a dam at river kilometer (rkm) 36 (above the river mouth) to provide drinking water for 600,000 residents. Mirabel Dam is a 45-m-wide, 4.0-m-high, air- and water-filled rubber bladder. When fully inflated, the dam creates a 5.1-km-long, 40–70-m-wide, 1–5-m-deep reservoir termed Wohler Pool. In addition to steelhead, Chinook salmon, Sacramento suckers *Catostomus occidentalis*, smallmouth bass *Micropterus dolomieu*, and hardheads *Mylopharodon conocephalus* are abundant in Wohler Pool. To facilitate upstream fish passage and minimize juvenile entrainment, the dam includes two Denil-style fishways and screened pump intakes with flow bypasses. Water not diverted through the intakes, bypasses, or ladders spills evenly across the crest of the structure (Figure 1).

We released radio-tagged steelhead smolts at rkm 47 near the town of Healdsburg and tracked them along a 9.6-km reach. The upper 4.5 km of the reach was free flowing and consisted primarily of runs, pools, and shallow glides. Mirabel Dam impounded the lower 5.1 km of the study area (Figure 1).

Methods

Radio-tagging.—We surgically implanted small, microprocessor coded transmitters (Model MCFT-3HM, LOTEK Engineering, Inc., Ontario, Canada) in yearling steelhead smolts from the U.S. Army Corps of Engineers' Don Clausen Fish Hatchery. The hatchery is operated by the California Department of Fish and Game and is situated on Dry Creek, a major Russian River tributary. To minimize behavioral effects of the tags, tag weight did not exceed 2% of fish weight (Winter 1996) and we selected fish larger than 100 g. The tags transmitted on five frequencies in the 149-MHz band. The use of coded transmitters permitted the unique

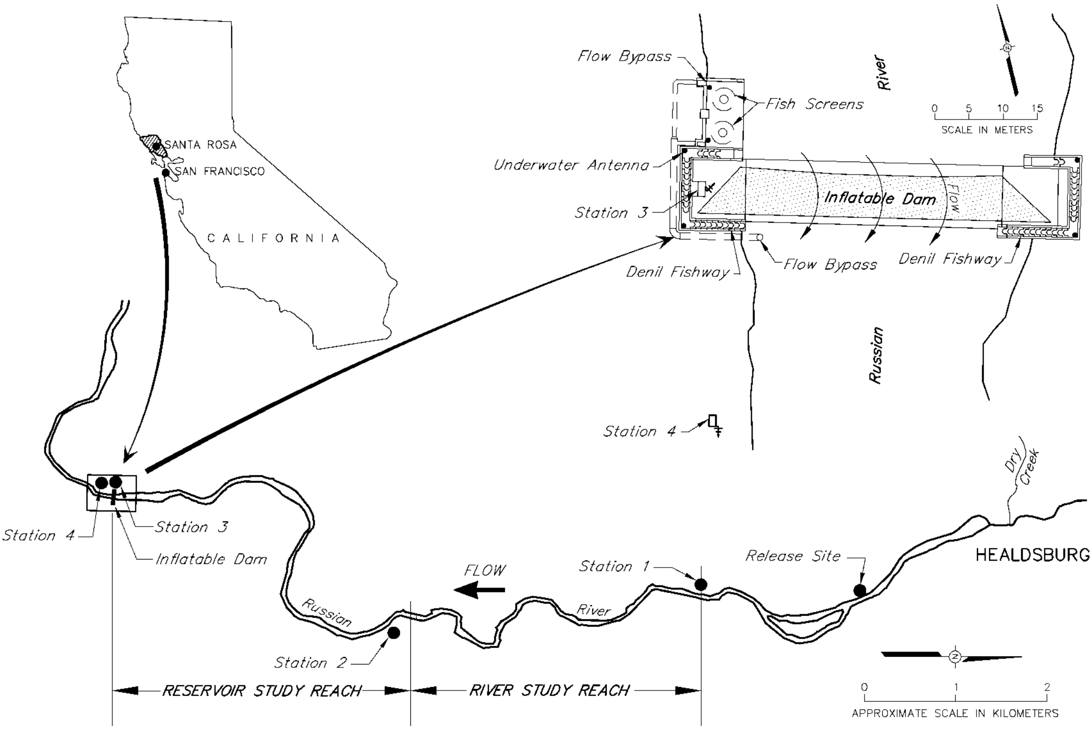

FIGURE 1.—Map of the study area showing the free-flowing (river) and impounded (reservoir) reaches of the Russian River, California, and detail of Mirabel Dam. Stations 1–4 represent data-logging radiotelemetry receiver sites. Underwater antenna locations in the dam forebay are shown as shaded circles.

identification of all fish. Minimum transmitter battery life at a 3-s pulse rate was 27 d.

Surgical procedures were performed at the hatchery and generally followed the methods of Ross and Kleiner (1982), Summerfelt and Smith (1990), and Adams et al. (1998). Prior to surgery, fish were deprived of food for 48 h. The fish were then anesthetized in a bath of tricaine methanesulfonate (MS-222) at a concentration of 50 mg per liter of water. During surgery, fish were held in a V-shaped aluminum trough lined with moistened foam rubber. To maintain fish anesthesia during the procedure, we used a dilute (20 mg/L) solution of MS-222 to continuously irrigate the gills via a tube inserted in the mouth. To maintain aseptic conditions, we disinfected all instruments with providone iodine (Swanberg et al. 1999). Infection was minimized by pipetting oxytetracycline (50 mg per kilogram of fish body weight) into the abdomen before closing the incision with sterile surgical staples. The antenna exited ventrally and was secured with a single suture to the first anal fin ray posterior to the exit site (Adams et al. 1998; Martinelli et al. 1998).

To ensure recovery, each group of tagged fish was held in an aerated 946-L circular tank for 36–48 h prior to release. At times when the water temperature was greater in the river than at the hatchery, we used submersible aquarium heaters to slowly raise the holding tank temperature by 2–3°C. Fish behavior and tag function were monitored throughout the holding period.

Seawater challenge.—Don Clausen Fish Hatchery personnel typically release smolts between January and April. Our evaluation of passage at Mirabel Dam required us to hold some fish until early June. Because smolts held beyond their normal release date may begin reverting to parr, we tested the physiological stage of smoltification over time by measuring blood plasma Na^+ concentrations in fish after 48 h of exposure to artificial seawater. Smolts have osmoregulatory mechanisms that allow them to maintain lower blood plasma Na^+ levels than parr (Clarke and Hirano 1995). Seawater challenge tests were conducted at the hatchery following the methods of Blackburn and Clarke (1987) and an unpublished protocol developed by the California–Nevada Fish Health Center (S. Foote, U.S. Fish and Wildlife Service, personal communication).

We conducted seawater challenge tests during a pilot study in 2000 and throughout the study periods in 2001 and 2002. During each test, 20 smolts were assigned to five static saltwater aquariums (four fish per aquarium). Each 75-L plastic container was filled with hatchery supply water, aerated, and partially submerged in a flow-through hatchery trough to maintain cool water temperature. We achieved salinities of 28–29‰. Salinity, temperature, dissolved oxygen, ammonia concentration, and pH were monitored daily. To reduce stress and organic loading, we did not feed the fish for 24 h prior to each experiment or during the course of each experiment. After 48 h, all fish were euthanatized in a bath of salt water and MS-222, weighed, measured, and immediately sampled for blood from the caudal artery. Blood plasma was separated by centrifugation and stored on ice. On the same day they were collected, samples were analyzed by means of an automated blood chemistry analyzer (model CX3, Beckman Instruments, Inc.).

Radio-tracking.—We transported groups of 20–40 smolts from the hatchery to the river each week between April 24 and June 5 of 2001, 2002, and 2004. Total transport times ranged from 30 to 45 min, and all fish were released at dusk between 2000 and 2200 hours. The release site was 1.5 km above the beginning of our free-flowing reference reach (Figure 1).

We recorded smolt movements with four fixed radio-tracking stations that each consisted of a three- or four-element Yagi antenna and a data-logging receiver (Model SRX 400, LOTEK Wireless, Inc., Ontario, Canada). The fixed stations were located (1) at the upstream end of the free-flowing reach, (2) at the upstream end of the reservoir, (3) in the dam forebay, and (4) 50 m below the dam (Figure 1). To evaluate passage routes at the dam, we configured station 3 to simultaneously monitor an array of one aerial and six underwater antennas. To limit signal detection range in the 100-m forebay, we oriented the aerial antenna at station 3 perpendicular to the river flow and decreased receiver gain. When the aerial antenna detected a fish in the forebay, the receiver scanned each underwater antenna in a predetermined order. The underwater antennas (200-mm sections of bare coaxial cable mounted on plastic pipes) were located inside the fish ladders on either side of the dam and at the entrance of two bypass pipes associated with the screened pump intakes. The gain on the aerial and underwater antennas differed. We set the gain on the underwater antennas to achieve a signal detection range of approximately 3 m. To verify detection ranges, we mapped signal strengths around the bypass pipes and ladders by use of a transmitter held underwater at the surface and at a depth of 1 m. The relatively short detection range was necessary to prevent overlap between antennas at the bypass entrance and ladders on the west side of the dam (Figure 1). Our observation of fish behavior near the bypass and ladder suggested that a 3-m range would detect passing fish. We routinely observed fish swimming in a circular pattern around the rotating-drum fish screens within range of the bypass antennas. To improve the likelihood of detection, the two antennas in each ladder were linked together and located in corners that we expected would serve as resting areas for the fish. Fish passing over the dam face were recorded by the aerial antenna in the forebay and at station 4 below the dam. To verify that fish passed the dam, we oriented the antenna at station 4 downstream and were able to detect signals up to 350 m below the facility. The battery-powered receivers at each station continuously scanned through five frequencies every 15 s and recorded date, time, frequency, code, and signal strength in nonvolatile memory.

Data from the fixed stations generally showed clear patterns of increasing, peak, and decreasing signal strengths as fish approached, reached, and passed the fixed sites. To better determine movement patterns, we augmented data from the fixed stations with mobile tracking. We used an H-antenna and scanning receiver to track smolts twice weekly in 2001 and once weekly in 2002 and 2004 from a two-person kayak. Kayak surveys were conducted over a 15-km reach from rkm 57 (4.8 km above the smolt release site) to the dam. Tag frequencies were scanned continuously, and the latitude and longitude of fish locations were recorded with a hand-held Global Positioning System receiver when signal strength was maximized. We conducted our final kayak survey 30 d after the last smolt release each year.

Dam operations and hydraulic measurements.—Because Mirabel Dam is inflatable, its height can be carefully adjusted. During 2001, the dam was operated normally and any water not diverted through the pump intakes, bypasses, or fish ladders was spilled evenly across the crest of the structure (Figure 2). During the weeks of April 25, May 1, and May 14, 2002, and for the entire study period in 2004, we partially deflated the dam and deformed the crest into a notched shape to increase spill depth and velocity (Figure 2). During normal

FIGURE 2.—Photographs of Mirabel Dam on the Russian River, California. The dam is shown in its normal inflated configuration (top panel) and in a notched configuration (bottom panel).

operation, the dam is inflated to hold a working water surface elevation of 11.6 m in the forebay. To create a concentrated flow area (the notch), we released water from the dam bladder to an elevation of approximately 11.2 m and injected air to raise the sides of the bladder near the abutments. We attempted various configurations in 2002 but maintained a consistent notch in 2004. During our 2002 dam crest manipulations, we alternated configurations weekly. However, we had difficulty comparing configurations because the number of fish detected in the forebay also varied weekly. In an attempt to increase the proportion of fish that entered the forebay by avoiding losses in the river reach, we released approximately half the fish in 2002 at the upstream end of the reservoir. The notch trials had no influence on velocity beyond the forebay and did not confound comparisons of river and reservoir travel rates.

During 2004, we measured depth and velocity at the dam crest, in the forebay, throughout the reservoir, and in the lower portion of the free-flowing reach. Depth in the notch and water level in the forebay were monitored continuously at 15-min intervals with two data-logging pressure transducers (model WL 15, Global Water Instrumentation, Inc.). Velocity and depth at the dam crest were measured directly on three occasions with a calibrated wading rod and current meter (Flo-Mate 2000, Marsh-McBirney, Inc.). To place the current meter directly in the notch, extension poles and tethers were held by persons standing on the dam bladder. Depth and velocity were also measured at six horizontal transects extending from the forebay upstream to the free-flowing reach with a broadband acoustic Doppler current profiler (ADCP; 1,200-KHz Workhorse, RD Instruments, San Diego, California). For measurements in the forebay, the ADCP was mounted on a custom-made catamaran, connected to a laptop computer via a radio modem, and tethered to a cableway located 4 m upstream of the dam crest. We used the cableway to pull the ADCP across the transect. For measurement in the reservoir, we mounted the ADCP to the bow of a motorized boat.

An ADCP uses the Doppler shift principle to measure the velocity of suspended sediment particles within discrete vertical depth cells or bins (Simpson 2001). We used a bin size of 5 cm and collected velocities every 0.3–0.6 m along 20–50-m transects. Acoustic signal interference prohibits measurements at the top and bottom of the water column. This interference and the depth of the ADCP transducer below the catamaran prohibited velocity measurements within 35 cm of the water surface. The ADCP also had a bottom tracking feature to determine the horizontal position of each velocity profile relative to the transect starting point.

On one occasion in 2004, we directly measured velocity in the notch while simultaneously releasing 50 untagged hatchery smolts into the forebay during daylight hours. This single release allowed us to observe fish responses to flow fields in the notch. However, because these fish were unable to acclimate to river conditions, we did not attempt to quantify the numbers passing downstream or their residence time.

Streamflow in the study area was estimated by summing daily flows from the U.S. Geological Survey (USGS) Dry Creek and Healdsburg gauging stations. Use of the two gauges yielded an approximate flow for a site located 3.3 km above the free-flowing study reach. We used a continuously recording thermograph to measure water temperature each year at the upstream end of the reservoir. We used this site because water quality data collected in 1999–2001 showed that the reservoir does not stratify and that temperatures vary by no more than 1°C throughout the impoundment (Chase et al. 2002).

Data analysis.—We calculated smolt residence times, travel times, and travel rates in the river and reservoir reaches by use of fixed-station and mobile tracking data. Our analysis was limited to fish that passed the dam. Residence time was defined as the total amount of time fish spent in a reach regardless of direction of movement and gaps in time. We calculated travel time as the time elapsed from the initial detection at an upstream station to the first detection at the next station downstream. Travel time approximated the time elapsed during directed downstream movement. Travel rates were determined by dividing reach length by travel time. Our travel rate is not analogous to a total migration rate (i.e., reach length divided by total residence time). We calculated travel rate to help determine whether migratory delays were associated with low water velocities through the impoundment or with conditions in the forebay. If low velocities through the reservoir slowed migration, then river and reservoir travel rates should differ. If we only analyzed total migration rates, we might not detect delays associated with passage routes in the forebay. Forebay residence time, a portion of total reservoir residence time, was calculated as the time elapsed from first detection 100 m above the dam to the fish's passage at the dam.

We hypothesized that fish would slow as they entered the reservoir and approached the dam. Because residence times and travel rates were not normally distributed, we used nonparametric Kruskal–Wallis one-way analysis of variance (ANOVA) tests ($\alpha = 0.05$) to compare these values within and among years (Siegel and Castellan 1988). The Kruskal–Wallis ANOVAs tested the null hypotheses that the median river or reservoir travel rate and residence time were equivalent in 2001, 2002, and 2004. Rejection of the null hypothesis suggested differences among at least 2 years, so we used the Kruskal–Wallis multiple comparison procedure to determine which years differed (Siegel and Castellan 1988). Likewise, we used ANOVA to compare river, reservoir, and forebay rates within 2001 and 2004. Because our dam crest manipulations in 2002 affected forebay travel rate and residence time, we compared only river and reservoir reaches by use of a two-sample Wilcoxon–Mann–Whitney test ($\alpha = 0.05$). We also used the Wilcoxon–Mann–Whitney procedure to test the null hypothesis that median forebay travel rate and residence time did not differ between 2001 (fully inflated dam) and 2004 (notched dam) against the alternative hypothesis that travel rate was lower and residence time was higher in 2001 than 2004. We used nonparametric techniques to compare plasma Na^+ concentrations from the seawater challenges. Plasma Na^+ concentrations were compared with Kruskal–Wallis ANOVA and multiple comparison procedures ($\alpha = 0.05$). Statistical analyses were performed by use of the Number Cruncher Statistical System version 2001 (Hintze 2001).

We compared the travel rate of tagged smolts with estimated travel rates of untagged hatchery smolts captured in a downstream migrant trap at the dam site in 2002. As part of a long-term juvenile Chinook salmon monitoring effort (Chase et al. 2002), one 2.4-m-diameter and two 1.5-m-diameter rotary screw traps were operated annually 50 m below the dam site. The traps operated 24 h/d and were checked once daily. Traps are typically installed in April, but during 2002 trapping began in late February. The late-February installation date allowed us to capture smolts from the March and April releases at the Don Clausen Fish Hatchery (30 km above the dam site) and the Coyote Valley Fish Facility (117 km above the dam site).

Results

We released a total of 455 tagged smolts between April 24 and June 5 of 2001, 2002, and 2004 (Table 1). Mean fork length for each year ranged from 228 to 239 mm, and mean weight ranged from 122.8 to 143.5 g (Table 1). Smolts were significantly longer in 2002 than in 2001 and 2004, and weight differed significantly among years (Kruskal–Wallis ANOVA: $P < 0.001$).

Survival during the 36–48-h prerelease holding period was 99%. Two fish in 2001 and two fish in 2002 died within 24 h after surgery. Another four radio-tagged fish that displayed abnormal swimming behavior were sacrificed prior to release in 2002. Active transmitters removed from fish that did not survive were sterilized and re-implanted in healthy fish.

Seawater Challenge

We conducted 3, 12, and 3 seawater challenges in 2000, 2001, and 2002, respectively (Figure 3). Median plasma Na^+ levels ranged from 161 to 185 mmol/L in 2000 and from 173 to 195 mmol/L in

TABLE 1.—Release date, number (*N*), and mean (SD) fork length (mm), and weight (g) of radio-tagged steelhead smolts released 11 km above Mirabel Dam on the Russian River, California, in 2001, 2002, and 2004.

Date	*N*	Fork length (SD)	Weight (SD)
		2001	
Apr 24	20	235 (8)	145.1 (17.0)
May 1	20	231 (12)	136.0 (20.3)
May 8	20	230 (10)	135.3 (17.9)
May 15	19	228 (12)	139.8 (20.3)
May 22	20	225 (10)	128.7 (12.5)
May 30	20	224 (9)	125.2 (14.2)
Jun 5	20	234 (12)	142.0 (26.9)
All	139	230 (11)	136.0 (19.7)
		2002	
Apr 25	30	234 (9)	134.6 (17.7)
May 1	30	240 (11)	145.4 (21.2)
May 7	20	236 (9)	135.9 (19.1)
May 14	30	240 (10)	142.2 (17.4)
May 22	30	239 (13)	142.5 (20.7)
Jun 4	18	246 (10)	167.2 (20.6)
All	158	239 (11)	143.5 (21.3)
		2004	
May 4	40	229 (11)	122.1 (15.7)
May 11	40	229 (8)	116.5 (21.6)
May 18	40	231 (9)	127.7 (14.6)
May 26	38	222 (9)	119.8 (12.4)
All	158	228 (9)	122.8 (15.7)

2001, and differed significantly over the course of the study in both years (Kruskal–Wallis ANOVA: $P < 0.001$). Plasma Na^+ concentrations were higher in 2002, ranging from 202 to 205 mmol/L, and did not differ significantly between dates (Kruskal–Wallis ANOVA: $P = 0.53$). Despite elevated Na^+ levels, survival after the 48-h challenges was 100% in 2000, 99.6% in 2001, and 100% in 2002. In addition to one fish that did not survive, 3 of the 240 fish in 2001 were moribund after 48 h and 5 of the 60 fish in 2002 were lethargic and probably close to death. Variability (interquartile range) within test groups was similar among years (Figure 3).

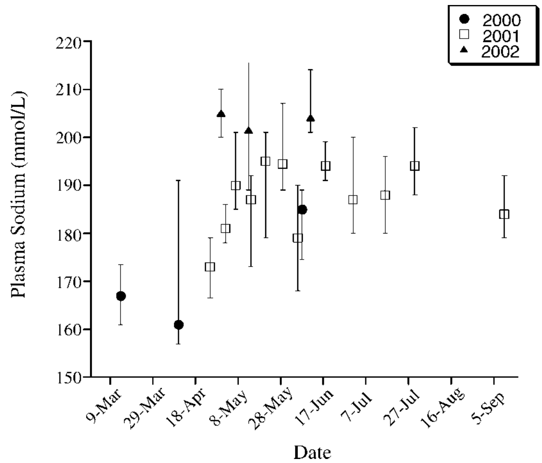

FIGURE 3.—Median blood plasma Na^+ levels in groups of steelhead smolts sampled after 48-h seawater challenge tests conducted in 2000–2002 ($N = 19$–21 fish). Error bars depict interquartile range.

Emigration Behavior

The number of smolts detected entering the reservoir at station 2 ranged from 46 in 2004 to 70 in 2002, or 29–49% of the total fish released each year (Table 2). Between 53% and 84% of the fish that entered the reservoir were also detected in the forebay, and more than 75% of fish detected in the forebay successfully passed the dam. In 2001, 44 fish passed the dam; 33 smolts passed successfully in both 2002 and 2004 (Table 2). We could not calculate river reach travel rates or residence times for 14 of the passing fish in 2002 because they were released at the downstream end of the river reach (Table 3). River and reservoir travel rate and residence time were also unavailable for 11 fish in 2004 because of a malfunction at station 2.

River and reservoir travel rates did not differ significantly among years (Table 4). Contrary to our expectations, median river reach travel rates (0.6–0.8 km/h) were lower than reservoir rates

TABLE 2.—Number and proportion of radio-tagged steelhead smolts that were detected in the reservoir and forebay and that passed Mirabel Dam on the Russian River, California, in 2001, 2002, and 2004. The number and proportion of passing fish that used three potential passage routes (dam crest, bypass pipes, and Denil fishways) are shown for 2001 and 2002. The underwater antenna array in the fishways and bypass pipes was not deployed in 2004, so passage route information is not available for that year.

	Detected					Passage route		
Year	Reservoir (*n*)	Forebay (*n*)	Reservoir/ forebay (%)	Passed dam (*n*)	Forebay/ passed (%)	Crest (*n* [%])	Bypass (*n* [%])	Fishway (*n* [%])
2001	68	57	84	44	76	37 (84)	4 (9)	3 (7)
2002	70	37	53	33	89	31 (94)	2 (6)	0 (0)
2004	46	36	78	33	92			

TABLE 3.—Travel rates and residence times for radio-tagged steelhead smolts that passed Mirabel Dam on the Russian River, California, during 2001, 2002, and 2004. The river and reservoir reaches were 4.5 and 5.1 km long, respectively. Forebay residence time, a portion of total reservoir residence time, was calculated as time elapsed from detection 100 m above the dam to passage. We could not calculate river reach travel rates or residence times for 14 of the passing fish in 2002 because they were released at the downstream end of the river reach. River and reservoir travel rate and residence time were also unavailable for 11 fish in 2004 because of a malfunction at station 2.

Year	Statistic	Travel rate (km/h)			Residence time (h)		
		River	Reservoir	Forebay	River	Reservoir	Forebay
2001	*N*	44	44	44	44	44	44
	Minimum	0.02	0.02	0.001	1.3	1.8	0.03
	First Quartile	0.2	0.6	0.004	2.9	7.8	0.8
	Median	0.8	1.2	0.02	5.8	21.5	6.3
	Third Quartile	1.5	1.8	0.1	19.1	47.8	27.0
	Maximum	3.6	3.3	3.3	225.8	337.0	147.5
	Mean	1.1	1.2	0.3	24.1	41.0	20.3
	SD	0.9	0.9	0.7	48.5	61.0	30.9
2002	*N*	19	33	33	19	33	33
	Minimum	0.03	0.1	0.001	1.3	2.2	0.02
	First Quartile	0.5	0.5	0.01	1.6	4.8	0.2
	Median	0.7	1.0	0.1	6.4	10.5	0.8
	Third Quartile	2.9	1.3	1.0	9.2	26.0	14.7
	Maximum	3.6	2.4	5.0	168.4	130.6	125.6
	Mean	1.4	1.1	0.6	18.1	23.0	12.3
	SD	1.4	0.7	1.1	38.4	28.3	24.4
2004	*N*	22	22	33	22	22	33
	Minimum	0.04	0.1	0.001	1.9	1.9	0.02
	First Quartile	0.1	0.4	0.01	3.5	4.5	0.4
	Median	0.6	1.4	0.04	7.6	13.9	2.4
	Third Quartile	1.3	2.3	0.3	37.6	31.4	9.6
	Maximum	2.4	3.3	5.0	102.8	112.7	110.6
	Mean	0.7	1.4	0.6	25.2	26.0	12.8
	SD	0.7	1.0	1.3	29.7	30.5	26.0

(1.0–1.4 km/h) each year, though not significantly (2001 and 2004 Kruskal–Wallis multiple comparison: $Z < 2.39$; 2002 Wilcoxon–Mann–Whitney test: $P = 0.96$). Smolts slowed significantly, however, in the dam forebay. During 2001 and 2004, the median forebay travel rate (0.02–0.04 km/h) was more than an order of magnitude lower than, and differed significantly from, river and reservoir rates (Table 4). As we anticipated, smolts moved significantly faster through the forebay when the

TABLE 4.—Kruskal–Wallis (three-sample) and Wilcoxon (two-sample) test results for median travel rates and residence times of radio-tagged steelhead smolts that passed Mirabel Dam on the Russian River, California, in 2001, 2002, and 2004. The Wilcoxon test was used to compare river versus reservoir travel rate and residence time in 2002, forebay travel rate in 2001 versus 2004, and forebay residence time in 2001 versus 2004. The Kruskal–Wallis test was used for all other comparisons. Sample size (*n*) and probability level (*P*) are shown for each comparison. Significance was assumed at $P < 0.05$. For three-sample comparisons, values within years having the same letter were not significantly different from each other.

Variable and reach	2001		2002		2004		
	n	Median	*n*	Median	*n*	Median	*P*
Travel rate (km/h)							
River	44	0.8 z	19	0.7	22	0.6 z	0.191
Reservoir	44	1.2 z	33	1.0	22	1.4 z	0.408
Forebay	44	0.02	33		33	0.04	0.044
P		0.000		0.955		0.000	
Residence time (h)							
River	44	5.8 z	19	6.4	22	7.6	0.192
Reservoir	44	21.5	33	10.5	22	13.9 z	0.271
Forebay	44	6.3 z	33		33	2.4	0.044
P		0.001		0.063		0.001	

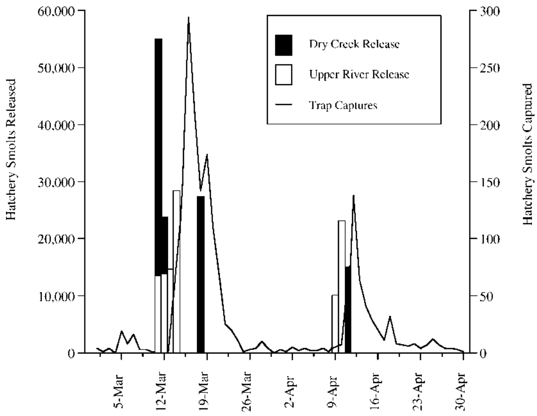

FIGURE 4.—Hatchery steelhead smolt releases into Dry Creek and the upper Russian River, California, compared with captures of hatchery steelhead in a rotary screw trap at the Mirabel Dam site during March and April 2002. The Dry Creek and upper river release locations were 30 and 117 km, respectively, above the trap site.

dam crest was notched in 2004 than when the dam was fully inflated in 2001 (Wilcoxon–Mann–Whitney test: $P = 0.04$).

The travel rate of passing fish in our free-flowing study reach was similar to the travel rate of smolts from normal hatchery releases in March and April 2002. Screw trap data from the Mirabel Dam site before the dam was inflated in 2002 showed increased captures of hatchery fish 36–120 h after large releases from Don Clausen Fish Hatchery (Figure 4). The travel rate of these normally released fish ranged from approximately 0.25 to 0.83 km/h. The median travel rate in the free-flowing reach, through which all hatchery fish must travel, was within this range during all 3 years of the study. The California Department of Fish and Game also released hatchery smolts from the Coyote Valley Fish Facility. The fish we released in May 2001, 2002, and 2004 also moved as rapidly as hatchery smolts released into the upper river in 2002.

Residence times followed the same trends as travel rates (Table 4). Median river and reservoir residence times did not differ significantly among years. As with travel rate, residence times in 2001 and 2004 suggested that the notched dam configuration accelerated smolt movement. When the dam was fully inflated in 2001, fish resided in the 0.1-km-long forebay for nearly the same amount of time that smolts spent in the 4.5-km river reach. In contrast, during 2004 smolts spent significantly less time in the forebay than in the river reach

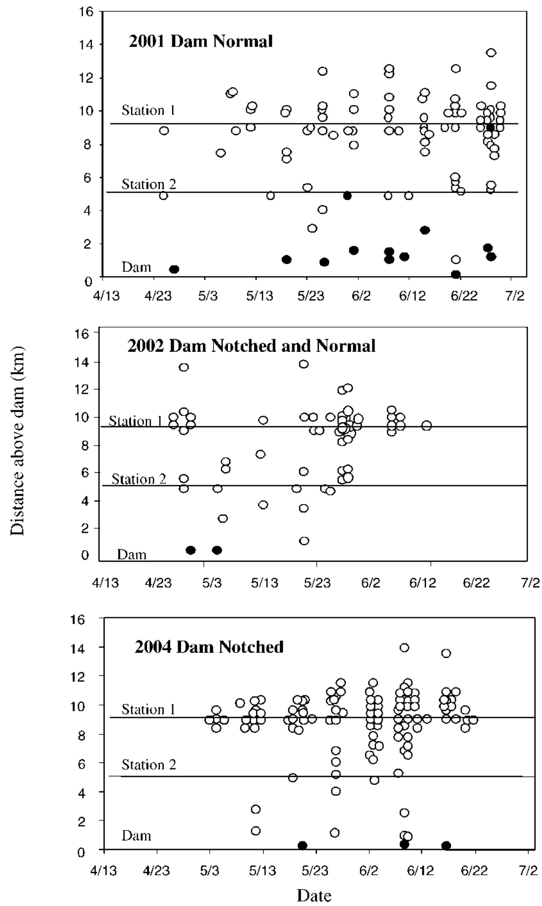

FIGURE 5.—Last recorded locations of steelhead that failed to pass Mirabel Dam on the Russian River, California, in 2001, 2002, and 2004. Shaded circles indicate fish that were detected in the dam forebay. The inflatable rubber dam was operated at normal full inflation during 2001, a variety of configurations in 2002, and a notched configuration in 2004. Station 1 was the beginning of the free-flowing reach, and station 2 was the upstream limit of the reservoir.

(Kruskal–Wallis multiple comparison: $Z > 2.39$). Median forebay residence time was reduced from 6.3 h in 2001 to 2.4 h in 2004 (Table 4). Although reservoir and forebay times decreased in 2002 and 2004, forebay residence time averaged approximately 50% of total reservoir residence time each year (Table 3).

As with travel rate and residence time, the dam configuration appeared to affect the passage success of fish that reached the forebay. More fish were detected in the forebay but failed to pass when the dam was fully inflated in 2001 than when it was notched in 2004 (Figure 5). Most smolts that successfully passed in 2001 and 2002 traveled over the dam crest (Table 2). The proportions of fish that used bypass pipes and fishways were low and nearly equivalent in 2001. Only two fish used the bypass in 2002.

Our release of untagged fish in the forebay during 2004 provided numerous opportunities to observe smolt behavior in the notch. When fish initially approached the dam bladder, they swam laterally away from the notch as if they were testing the flow path. One or two fish at a time would allow the gradually accelerating current to carry them tail-first into the notch and over the dam. Passing fish reached a critical point at which they could not swim back upstream. Although many made brief attempts to defeat the current, those that passed more than half of the notch crest length were swept over the dam. We used the observed critical point as our measure of maximum notch velocity.

Many fish failed to move an appreciable distance from the release site and resided near or above station 1 for the duration of the study (Figure 5). During 2001, 2002, and 2004, signals were lost prematurely in 30–46% of the nonpassing fish depicted in Figure 5, or 24–37% of the total fish released each year. We defined premature signal loss as the inability to detect a signal before the minimum 27-d tag battery life had elapsed. The mean period of time to signal loss, estimated from weekly mobile tracking surveys, was 9–11 d each year. Most signals were lost prematurely in the river reach. Across all years, signal loss averaged 7% in the reach above station 1, 11% in the river reach, and 4% in the reservoir.

Hydraulic Measurements

Water velocity measured by ADCP declined downstream from the free-flowing reach through the reservoir and was lowest in the forebay when the dam was fully inflated (Figure 6). Each panel in Figure 6 shows the average water column velocity (profile or ensemble of the ADCP) across a horizontal transect. Data at the most upstream transect (Figure 6A) were collected in a deep run approximately 100 m above a riffle that marked the upstream limit of the impoundment. Velocities at that free-flowing site measured nearly 0.4 m/s for the majority of the transect width. Transects B and C (Figure 6) represent the upper and lower portions of the impoundment. Transects D and E were located 4 m upstream of the dam crest during normal and notched configurations, respectively. The notch at transect E is represented as the area of higher velocity between stations 30 and 42 (Figure 6E). Velocities were more than twice as high in the notch hydraulic zone than in adjacent portions of the transect and were nearly four times higher than the velocity measured when the dam was inflated normally (Figure 6D). The higher velocities recorded near the ends of transects D and E show some influence from the fish ladder inlets. Measurements at the dam crest showed that depth and velocity were 18–24 times greater when the dam was notched than when the dam was fully inflated (Table 5). The pressure sensor located in the dam notch, the water level recorder in the forebay, and the USGS Hacienda Bridge gauging station below the dam recorded daily cyclical changes in spill depth and flow. This daily fluctuation was due to the expansion and contraction of the dry, exposed shoulders of the dam bladder. As air temperature increased during mid-morning, and conversely cooled in the evening, the dam bladder would rise and fall, changing the cross-sectional area of the notch. Most daily depth changes were approximately 24 cm.

River flow decreased and water temperature increased over the course of the study each year (Figure 7). On average, mean flow during the week after each release was 1.5–1.6 times higher in 2002 and 2004 than in 2001. Average water temperature during the same weeks ranged from 18.1°C to 20.9°C in 2001, 15.8°C to 20.6°C in 2002, and 18.3°C to 20.6°C in 2004.

Discussion

Water velocity affects smolt migratory behavior, and studies on Chinook salmon, Atlantic salmon *Salmo salar*, and brown trout have reported decreased migration rates in impoundments (Aarestrup et al. 1999; Venditti et al. 2000; Olsson et al. 2001). We found, however, that smolts traveled through the river and reservoir reaches at approximately the same rate despite lower measured velocities in the reservoir. Olsson et al. (2001) reported that low current speed in a small, artificial pond retarded smolt out-migration and high discharge accelerated emigration rates in a free-flowing control reach. In contrast, average flow during our study was 1.5 times higher in 2004 than in 2001, yet the median travel rate was nearly equivalent between the 2 years. Declining flows over the course of the study during all three years also had no apparent influence on river or reservoir travel rates. Our inability to detect differences in travel rates among reaches and years suggests that the magnitude of velocity differences between the reaches did not alter migratory behavior.

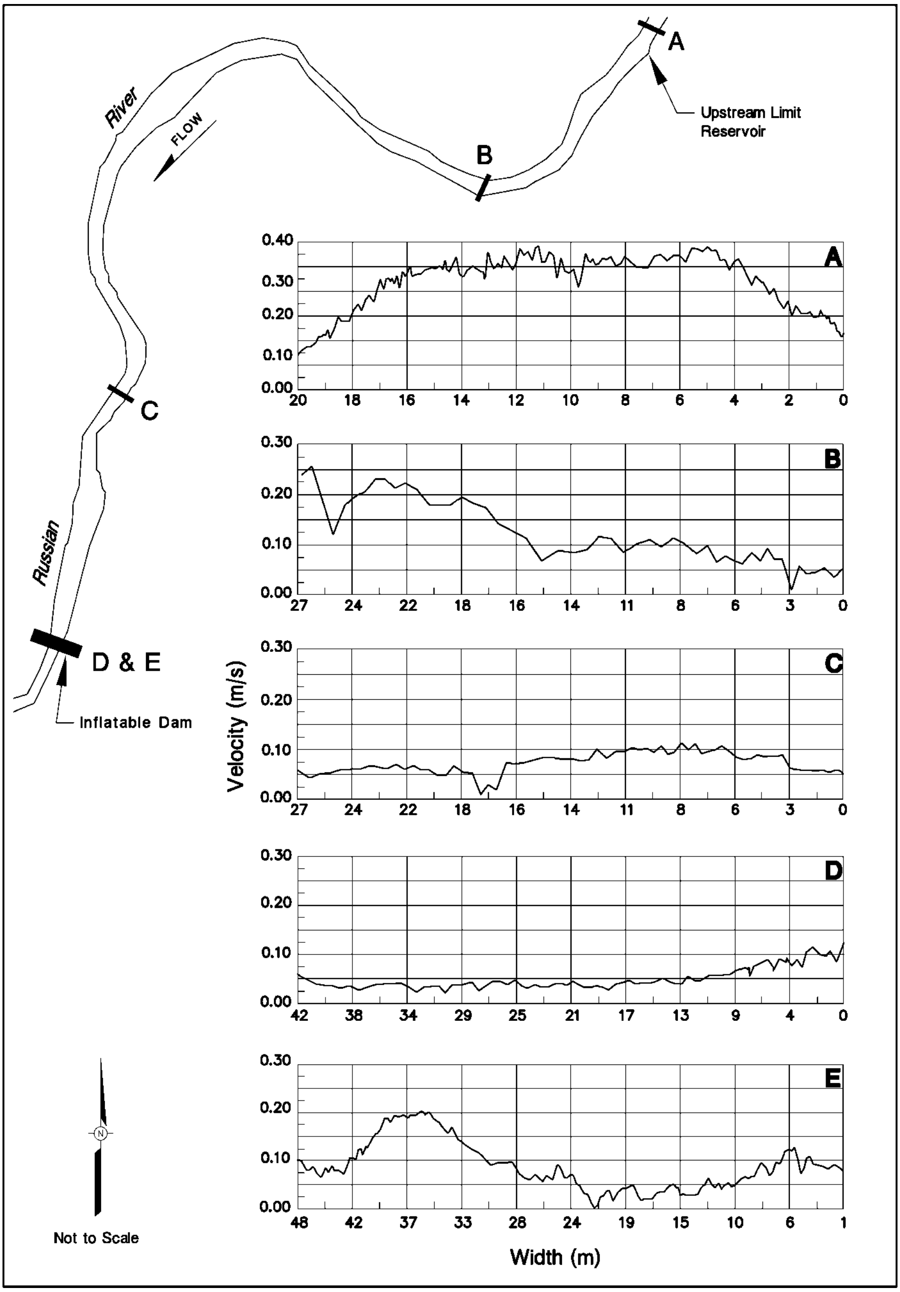

FIGURE 6.—Average water velocity measured by an acoustic Doppler current profiler at five transects in **(A)** the free-flowing reach of the Russian River, California, upstream of Mirabel Dam, **(B)** the upper portion of the reservoir above Mirabel Dam, **(C)** the lower portion of the reservoir, **(D)** the forebay when the dam was fully inflated, and **(E)** the forebay when the dam was in a notched configuration. Transects A, B, C, and E were measured on June 8, 2004, and transect D was measured on July 7, 2004.

TABLE 5.—Hydraulic conditions at the crest of Mirabel Dam on the Russian River, California, during notched and normal configurations in 2004.

Date	Dam condition	Forebay water level (m)	Wetted width of spill (m)	Maximum crest depth (m)	Maximum velocity (m/s)
Jun 8	Notched	11.3	6.7	0.91	1.4
Jun 10	Notched	11.4	7.6	0.73	1.2
Jul 7	Normal	11.6	37.2	0.04	0.06

The rapid movement of smolts may also be related to the short, 5.1-km length of Wohler Pool. Studies in larger impoundments have shown that migration rates decrease downstream (Aarestrup et al. 1999; Venditti et al. 2000). Because smolt movements are guided by current direction, fish may become disoriented in low-velocity environments. Venditti et al. (2000) hypothesized that juvenile Chinook salmon were disoriented while emigrating through a 60-km-long impoundment and displayed searching behavior to relocate current. Although Wohler Pool is 5.1 km long, velocity profiles collected by ADCP in 2004 showed that current slowed most dramatically in the lower 3.5 km of the impoundment. Smolts emigrating beyond this point either detected slow currents or encountered the dam before the low-velocity environment triggered searching behavior. The lack of fisheries investigations on small impoundments makes it difficult to recommend a reservoir length that does not hinder emigration. However, the 5.1-km length of Wohler Pool had no negative influence on travel rate.

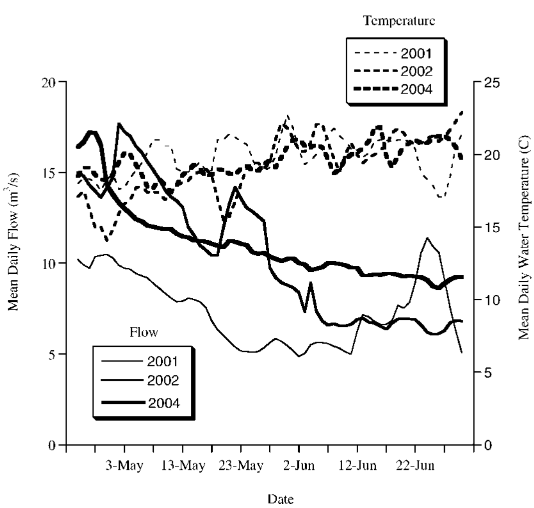

FIGURE 7.—Mean daily flow and water temperature for the reach of the Russian River from Healdsburg to Mirabel Dam, California, from April 24 to June 30 of 2001, 2002, and 2004.

The similarity in river and reservoir travel rates can be partially explained by our method of calculating travel time. Our travel rate is not analogous to a total migration rate. We calculated travel rate based on time elapsed from initial detection at an upstream station to the first detection at the next station downstream. Comparing travel rates helped us to determine whether current speed through the reservoir or forebay conditions affected total migration rate. Studies that compare total migration rates (i.e., total time elapsed from reach entry to passage) may not detect the influence of obstacles on migratory behavior. Olsson et al. (2001) used passive integrated transponder (PIT) tags to study brown trout smolt emigration through a 0.3-km-long pond. They attributed the slower migration rate in the pond to low current speeds through the small impoundment. However, their PIT tag detection system had a range of only 20 cm. Smolts may have moved through the pond rapidly and been delayed by the outlet conditions.

The dramatically reduced forebay travel rate coupled with similarities in river and reservoir travel rates suggest that Mirabel Dam, not current speed through the impoundment, slowed steelhead emigration. Forebay travel rates were more than an order of magnitude lower than river and reservoir rates. During all years, smolts traveled through the reservoir at rates higher than the average current speed measured by ADCP and then slowed when they encountered the dam. Aarestrup et al. (1999) reported that radio-tagged Atlantic salmon smolts migrating through a 12-km-long reservoir were delayed an average of 18 h in the vicinity of a narrow culvert. Venditti et al. (2000) showed that juvenile Chinook salmon had difficulty locating passage routes in the forebay of a large reservoir and experienced a delay of 14–19 h. When Mirabel Dam was fully inflated in 2001, the mean and median forebay residence times were 20.3 and 6.3 h, respectively. However, when the dam crest was notched in 2002 and 2004, mean and median forebay residence times declined to 12.3–12.8 and 0.8–2.4 h, respectively.

The travel rate data supported our hypothesis that the increased velocity and depth created by concentrating spill would accelerate smolt passage. Deforming the inflatable dam bladder into a notched configuration increased crest depth and velocity approximately 20-fold over the normal fully inflated condition. Hydraulic conditions created by the notch encouraged smolts to move twice as rapidly through the forebay and appeared to increase the proportion of fish that passed successfully after reaching the dam.

A complex set of factors enhances or discourages fish emigration past obstructions (Haro et al. 1997; Ferguson et al. 1998; Beeman and Maule 2001). Of these factors, the depth, shape, and resulting velocity gradients in the notch appeared to influence forebay residence time. The shape of a fish passage structure affects water velocity gradient, and as water falls over a sharp-crested weir it accelerates rapidly. Because smolts sense this rapid acceleration, they tend to avoid entrainment in the flow field and sharp-crested structures can hinder downstream passage. Smolts tend to pass more rapidly, however, if flow accelerates uniformly (Ferguson et al. 1998). Haro et al. (1997) found that an experimental surface bypass weir with a gently sloping upstream face gradually accelerated water velocity and passed Atlantic salmon smolts faster than a standard weir did. Our behavioral observations and velocity measurements showed that fish could sense the influence of the notch upstream and were able to maintain positive rheotaxis while being drawn gradually toward a point of critical velocity deep within the notch. When fully inflated, the rubber dam has an oval cross-sectional shape but functions more like a sharp-crested weir with a wide crest width and shallow spill depth. Our measurements of the fully inflated dam showed that smolts were unlikely to detect increased velocity within 4 m of the crest and were forced to pass through 4 cm of water that accelerated from 0.06 m/s to more than 2.0 m/s over a radial distance of approximately 1.5 m. Our travel rate data suggest that this shallow, rapidly accelerating spill is less favorable for smolt passage.

The notch configuration also improved fish entry into the pool below the dam. When the dam is fully inflated, flow adheres to the dam face until the nappe is deflected by a rubber fin that extends along the upper downstream quadrant of the bladder (Figure 2). The deflection fin is necessary to prevent vibration fatigue of the dam that would occur if the nappe continued to adhere to the entire downstream face of the bladder (Chanson 1998). Fish entrained in the nappe strike the fin before entering the receiving pool. When the dam was notched, however, the fin was deformed downward, allowing the nappe to spill directly into the receiving pool and allowing fish to pass without contacting the dam.

The likelihood that smolts will discover a passage route is related to discharge and velocity at the passage entrance (Ferguson et al. 1998). Recommended entrance velocities for surface smolt bypass systems at large dams range from 0.6 to 1.8 m/s (Johnson and Dauble 1995; Ferguson et al. 1998). While our notch velocities were within this range, velocity at the crest when the dam was fully inflated was far below these criteria. We suspect that the dam crest was the most common passage route because it was the largest structure in the forebay and passed the highest volume of flow.

The Denil fishways and bypasses, however, were less attractive to smolts. The ladder inlets are relatively small and provide a limited sphere of hydraulic influence in the forebay. Fish not emigrating along the banks may have difficultly finding the inlets. The steep fishways are also highly turbulent environments and may discourage entry. The bypass pipes are located 2 m below the water surface adjacent to rotating-drum fish screens. Although few fish apparently use the bypass pipes, signal detection was more common at these antennas than near the fishways. We routinely observed smolts swimming near the surface around the screens. The pumps have a total diversion rate of 2.83 m^3/s. This flow attracted fish to the screens, but the position of the inlets at the bottom of the collection gallery may have discouraged passage.

Although most fish that encountered the dam passed successfully, many released fish were never detected in the forebay. The distribution of fish in the study reaches, however, did not suggest that the impoundment was preventing emigration. If the reservoir was hindering emigration, then we would expect more fish to reside in the reservoir. Most fish, however, were never detected in or near the reservoir and resided in the free-flowing river close to station 1 and the release site each year. The failure of these fish to move rapidly downstream suggests that they were losing their proclivity to emigrate. Evaluating the dam and reservoir required us to hold fish for 3–7 weeks beyond their normal release date. For operational reasons, the dam could not be inflated until discharge was less than 28 m^3/s. We inflated the dam and began releasing fish when flows dropped below this threshold. However, the prolonged holding period may have induced desmolting or parr reversion (Zaugg and McLain 1972; Clarke and Hirano 1995). Our saltwater challenge results from 2000 to 2002 supported this contention and showed an increasing trend in plasma Na^+ values from early March to June.

The increasing trend we observed in Na^+ concentrations corresponds to seasonal patterns in steelhead Na^+K^+-ATPase activity reported in other studies (Zaugg and MacLain 1972; Zaugg 1981). Although published plasma Na^+ reference values for steelhead are scarce, smolts capable of adapting to seawater typically have concentrations less than or equal to 170 mmol/L (Blackburn and Clarke 1987). Median plasma Na^+ concentrations exceeded 170 mmol/L in all 2001 and 2002 test groups. The declining proportion of passing fish over time in 2001 corresponded to a general increase in plasma Na^+ values from April 25 to May 29. Higher Na^+ values in 2002 may also explain the lower percentage of fish that entered the forebay that year. While 170 mmol/L has been cited as a Na^+ threshold for successful adaptation to seawater (Blackburn and Clarke 1987), specific Na^+ levels have not been linked to smolt migratory behavior and fish that revert to parr can regain smolt characteristics (Zaugg and McLain 1970; Clarke and Hirano 1995). Zaugg (1982) found that coho salmon *O. kisutch* that had reverted to parr in a hatchery migrated seaward after release. Most smolts we detected in the forebay exhibited a strong urge to emigrate immediately after release, and it seems likely that this smaller mobile fraction of the study population was still capable of seawater adaptation.

To avoid including fish that may have lost their proclivity to emigrate, we only analyzed residence and travel time data from fish that passed the dam. The emigration behavior of these passing fish was similar to that of hatchery smolts captured in our screw traps at the dam site during March and April 2002. Moreover, downstream migrant trap data from 2000 to 2004 showed that wild steelhead smolts were emigrating during our study period (Chase et al. 2004).

Other potential factors responsible for the low percentage of migrant fish included effects related to surgery, loss due to predation, or tag failure. Prerelease survival of our radio-tagged fish was nearly 100%. Numerous studies have found minimal growth, survival, and behavioral effects from surgical tag implantation, and the technique is recommended for use in smolts (Lucas 1989; Peake et al. 1997; Adams et al. 1998; Martinelli et al. 1998). Although we collected mobile tracking data to indicate the presence or absence of fish in the study reaches, the data were not precise enough to determine subtle fish movements between surveys. We therefore could not determine whether stationary fish were alive or dead. The manufacturer of our radiotelemetry equipment reports low transmitter failure rates, and other researchers have attributed the sudden loss of signals to predation (Jepsen et al. 1998). High steelhead mortality during seaward migration is common, and the 24–37% loss rates we observed have been reported in other studies. Tipping et al. (1995) observed a hatchery smolt loss of 19.8% over 4.7 km of a small stream. Ward and Slaney (1990) found a 42% loss over 10 km of a small river, and McMichael et al. (1992) observed a 36% loss over 11 km of a large river.

Because impoundments can delay emigration, can concentrate smolts, and tend to have habitat conditions that favor predators, smolt mortality rates may be elevated in reservoirs (Poe et al. 1991; Jepsen et al. 1998). We found, however, that signal loss rates were lowest in Wohler Pool relative to the other reaches. On average, fish that disappeared before the end of the transmitter battery life were detected for more than a week before signal loss. This extended period suggests that the nonmigrant fraction of the release groups may have been more susceptible to predation.

We did not directly observe predators and cannot attribute our smolt losses to either piscivorous fish or birds. However, the disappearance of signals suggests that avian predators may have been responsible for much of the assumed mortality. Ospreys *Pandion haliaetus*, mergansers *Mergus* spp., cormorants *Phalacrocorax* spp., and herons *Ardea* spp. were routinely observed feeding in the study area. Because Wohler Pool is a seasonal reservoir, it does not provide year-round habitat conditions that would favor an unexpectedly large population of adult piscivores, such as Sacramento pikeminnow *Ptychocheilus grandis*, largemouth bass *Micropterus salmoides*, and smallmouth bass. Annual boat electrofishing surveys have found that juvenile largemouth bass and smallmouth bass are common in Wohler Pool, but Sacramento pikeminnow and basses large enough to consume steelhead smolts are not abundant (Chase et al. 2004). Permanent pools above the reservoir probably provide more habitat for adult basses than do the seasonally impounded sections of Wohler Pool. Juvenile basses appear to settle in the reservoir, but we suspect that the population crashes or is distributed downstream after the dam is deflated.

Our investigation was the first detailed examination of steelhead smolt migratory behavior in a seasonal reservoir and passage at an inflatable rubber dam. We conclude that Mirabel Dam caused delay but was not a barrier to out-migration. The National Marine Fisheries Service recently reduced the period of operation for four seasonal recreation reservoirs on the Russian River. Limiting the period of operation to times when smolts are unlikely to be emigrating is a prudent measure to protect threatened salmonids. However, water supply reservoirs must function during periods of low flow regardless of smolt movements. Although Mirabel Dam is typically inflated toward the tail portion of the steelhead smolt out-migration period, river flow dictates dam inflation date. During the past 25 years, the dam has been operated for various lengths of time during every month of the year. Dry hydrologic conditions have required water managers to inflate the structure during early spring coincident with the out-migration of most hatchery and wild smolts.

Our finding that steelhead traveled through the free-flowing and impounded reaches at similar rates but slowed dramatically in the forebay should encourage others to examine forebay passage conditions in small reservoirs. Concentrating spill by deforming the crest of an inflatable rubber dam is a simple and effective method of reducing forebay delay. If rubber dam bladders were designed with multiple independently inflatable chambers, one chamber could be partially deflated to create hydraulic conditions similar to our notch. A notched dam configuration provides better hydraulic conditions for downstream fish passage than a normal fully inflated dam bladder. We recommend the notching of inflatable dams during fish out-migration periods to increase the likelihood of safe and efficient passage.

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