Distribution and movement of domestic rainbow trout, *Oncorhynchus mykiss*, during pulsed flows in the South Fork American River, California

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Abstract We tracked the movements of ten small (SL=25.5–31.0 cm) and ten large (SL=32.0–38.5 cm) radio-tagged domestic rainbow trout (*Oncorhynchus mykiss*) in response to frequent pulsed releases of water in the South Fork American River (California) from July to October 2005. In week one all the small trout moved less than 1 km upstream or downstream of their release sites. Four small trout moved 1–3 km upstream or downstream of their release sites in the following 8 weeks. Seven out of ten large trout moved downstream after their release. In subsequent weeks most large trout showed smaller upstream and downstream movements, and were observed between 1 km upstream and 8 km downstream of their release sites. Our results suggest that domestic rainbow trout with SL>25 cm are not forced downstream by daily pulsed flow increases from 5 to over 40 m^3s^{-1}.

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Introduction

This is one of a set of papers that, collectively, use an interdisciplinary approach, including telemetry, physiology, behavior, and experimental biology, in both laboratory and field settings, to study the response of fish to pulsed flows (Klimley et al. 2005, 2007). This approach is consistent with recent suggestions that interdisciplinary research is essential to address complex fish biology processes such as movement and migration, and that telemetry is a tool that allows integration across disciplines and between the laboratory and field (Cooke et al. 2008). Our studies were prompted by the need to provide improved information on fish biology in light of the re-licensing efforts underway and anticipated for numerous California dams (Klimley et al 2005, 2007).

Human-controlled flows are common in rivers. Pulsed flows are relatively rapid increases in flows followed by relatively rapid decreases in these flows, with flow fluctuations lasting minutes, hours, or days (Hunter 1992). Reasons for pulsed flows include: (1) generating electricity, (2) flushing streambeds, (3) facilitating human recreation, (4) providing additional water for downstream diversion for irrigation, and (5) preventing reservoirs from flooding. The most common rationale for controlling the flows of rivers is the production of electrical energy. Pulsed flows provide additional electrical energy during hot summer days when electrical loads from air conditioners are highest (Hunter 1992). Flushing flows may be brief and

infrequent, but also sufficiently large that they move silt and sand downstream from the stream bed where they have settled due to slow water flow (Reiser et al. 1989). Recreational flows are water releases made to accommodate activities such as rafting and kayaking. It is well recognized that sudden flow fluctuations may cause stranding of juvenile salmonids in shallow side channels (Maciolek and Needham 1952; Hvidsten 1985) and on river bars (Bradford et al. 1995), and it is now common for dam operators to address this problem by gradually ramping flows up and down during pulses (e.g., PGE 2005a), thus allowing pulsed flow regimes to continue. Although pulsed water releases provide obvious benefits to humans, the cumulative effects of repeated and unseasonal flow pulses on aquatic communities are relatively unknown. Native Californian fish species have evolved with seasonal fluctuations (Moyle 2002), but the increased frequency of pulses (e.g., for electricity generation) and the late-summer timing (for recreational purposes such as whitewater rafting) represent significant deviations from the natural hydrograph.

These pulsed flows may impact the behavior of resident or migratory fish, particularly juvenile salmonids, by forcing them downstream (McCrimmon 1954; Erman and Leidy 1975; Ottaway and Clarke 1981; Ottaway and Forrest 1983; Heggenes and Traaen 1988; Crisp 1991; Crisp and Hurley 1991; Pearsons et al. 1992). This may result in increased mortality, decreased growth, or decreased reproduction. In contrast, the longitudinal displacement of larger fish seems less likely due to their increased

swimming performance, compared with smaller fishes (Webb 1971), unless there are velocity refugia that are more accessible to smaller-sized fish. Field studies have found no consistent effect of sudden, extreme peaking flows on area use or movements by adult trout and salmon (Bunt et al. 1999; Gido et al. 2000; Scruton et al. 2005; Heggenes et al. 2007).

In the current study our objective was to identify the longitudinal distribution of rainbow trout released into the South Fork American River, California under the influence of repeated pulsed flows. We were particularly interested in whether trout would be displaced downstream rapidly (i.e., over a period of days to weeks) by repeated pulses. The unpredictable flow releases in this system, which often occurred overnight, precluded our tracking the location of each fish before, during, and after each pulse release. However, given the prevalence of pulsed flow releases in California, management agencies have expressed interest in the general movement behavior of fish under this type of hydrological regime. For example, hatchery rainbow trout are stocked into the South Fork American River for sport fishing, but it is not known whether these fish remain in the river until they are caught by anglers, or whether they are rapidly washed downstream into Folsom Reservoir.

Study area

The hydrological regime of the South Fork American River is characterized by strong pulsed flows (Fig. 1).

Fig. 1 Water discharge from Chili Bar Dam into the South Fork American River during 13 weeks from July to October 2005 (data from Pacific Gas and Electric). *Arrow* indicates the date when pulsed flows started. Note: Flow values were sometimes missing for periods of hours to days, resulting in the jagged (pixilated) appearance of the data line
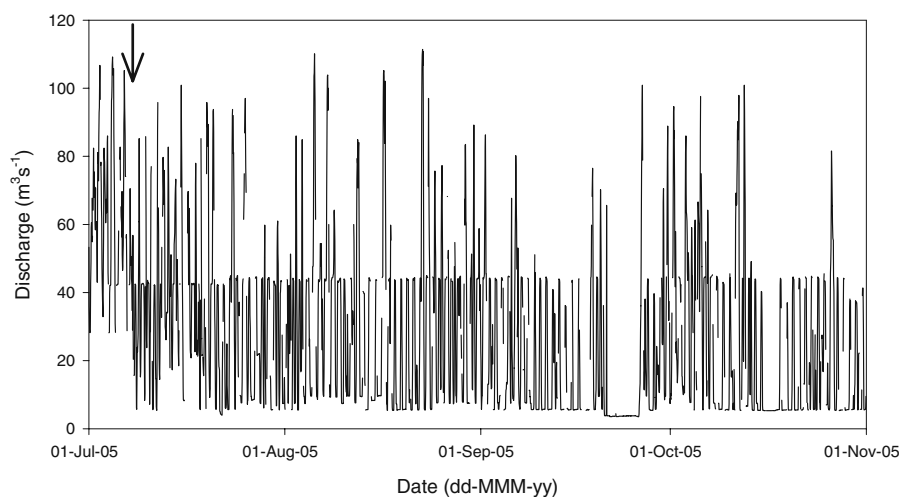
From July to September water is released in pulses from Chili Bar Dam during the day, for recreational flows, and sometimes during the night, as part of hydroelectric power generation by the chain of dams along the South Fork American River. The baseflow in the 30 km Chili Bar reach is typically 5 m^3s^{-1} and recreational pulses are usually 40 m^3s^{-1}. Pulses are ramped, last about 4–5 h, and move through the reach to Folsom Reservoir in about 6 h (PGE 2005a). The mean daily temperature of water released from Chili Bar Dam ranges from 11°C to 18°C during summer (PGE 2005b). The water warms during passage along the reach, with the daily mean ranging from 13°C to 21.7°C near the end of the reach. At the sites at which our fish were released the mean daily water temperature typically does not exceed 20°C (FERC 2008). The daily temperature range at a given point along the reach is approximately 3°C, with midday warming offset by the pulse of cooler water (PGE 2005a).

Methods

The rainbow trout used in the study were raised in the California Department of Fish and Game's American River Trout Hatchery, which is located on the American River downstream of Nimbus Dam. We obtained two groups of rainbow trout: one in mid-February 2005, and the other in late June 2005. The two groups of trout were from two different spawning events. The mid-February fish (June release) were born in November 2004 and the late-June fish (August release) were born in February 2005. Once they were transferred to the University of California, Davis, Center for Aquatic Biology and Aquaculture (CABA) both groups of fish were raised at 18°C (the ambient temperature of the well water). The fish we obtained in February had 4 months to grow at this temperature, while the second group had only 2 months. Thus, the first release group was both 3 months older, and had more time at 18°C, resulting in a larger average size prior to release (Table 1).

We used hatchery, instead of wild, rainbow trout in our studies because the sections of the Chili Bar reach in which we worked had particularly low densities of catchable trout (rainbow trout and brown trout ≥150 mm TL) (SMUD and PGE 2005). It was of value to identify the effect of pulsed flows on hatchery-reared trout because they are

periodically released into the South Fork American River by the California Department of Fish and Game to provide recreational fishing opportunities.

We placed radio transmitters of two sizes in the peritoneum of large and small trout. The individually coded transmitter (Lotek, NTC-6-2) implanted in large trout was cylindrical, 30.1 mm long with a diameter of 9.1 mm, and weighed 4.5 g in air. It emitted a pulse burst every 5 s of a radio frequency of 147 MHz and had a life span of 124 days. The coded transmitter (Lotek, NTC-4-2L) placed in small trout was also cylindrical, 18.3 mm long with a diameter of 8.3 mm, weighed 2.1 g in air. This tag emitted a pulse burst every 5 s of 149 MHz and had a life span of 85 days. The tags' masses were <2% of body masses, and thus were unlikely to hinder the swimming movements of the trout (Jepsen et al. 2002).

The fish were anesthetized with a solution of sodium bicarbonate and glacial acetic acid (Peake 1998). Each fish was anesthetized to Stage 4 anesthesia; characterized by loss of orientation and slowing of opercular movement. The fish was then removed from the anesthetic solution, weighed, and measured for its standard length (SL). A health index was calculated for each fish based on its external body condition, using a modification of the injury index developed by Swanson et al. (2004). Damage was rated from 1 (no damage) to 5 (severe damage) for the following 11 physical features: eyes, operculum, fins (anal, caudal, dorsal, pectoral, pelvic), scales, abrasions, fin blood, and presence of fungus. A fish in ideal condition would score 11, while the worst possible score was 55.

The fish was then placed supinely on a surgical table and the anesthetic solution was passed continuously over the gills with tubing connected to a re-circulating pump. A 1–2 cm long incision was made between the ribs and the pelvic girdle, 1–2 cm lateral to the midline. To avoid damaging internal organs, a plastic-sheathed, 16-gauge needle-tipped catheter was used to puncture the body wall, creating an exit point for the whip antenna. After removing the needle, the whip antenna was threaded into the peritoneum through the incision and out through the plastic catheter sheath. The tag was then gently pushed through the incision into the fish's peritoneum. Three to four absorbable sutures (Vicryl™, 3/0) closed the incision, and each suture was dotted with liquid topical tissue adhesive (Nexaband™) to secure the knots.

Table 1 Standard length (SL) and weight of radio-tagged rainbow trout released in the South Fork American River. The large trout (RT1-10) were released in the river on 7 July 2006 and tracked for a period of 13 weeks from 8 July to 29 September 2005, including 11 August. The small trout (RT11-20) were released in the river on 12 August 2005 and tracked for a period of 9 weeks from 13 August to 13 October 2005

Fish	SL (cm)	Weight (g)	Telemetry Error (m) mean ± se	July				August				September					October	
				8	14	21	28	4	11/13	18	25	1	8	15	22	29	6	13
RT1	38.5	1242	15.0±3.1	+	−	0	0	+	■	■	■	■	■	■	■	■		
RT2	35.0	970	14.5±2.9	■	−	+	0	0	0	−	−	■	■	■	■	■		
RT3	34.0	909	15.1±2.8	■	−	+	+	−	0	0	+	+	0	0	0	0		
RT4	36.0	1020	15.4±3.3	■	−	−	+	0	+	−	0	■	■	■	■	■		
RT5	32.0	864	15.9±2.8	■	0	−	■	−	0	0	0	0	+	+	0	+		
RT6	36.0	1050	20.3±3.7	■	0	+	■	−	0	0	X							
RT7	38.0	1205	12.6±1.9	■	−	+	■	+	−	0	0	0	0	0	−	−		
RT8	34.0	1115	18.3±4.7	■	−	−	■	−	+	■	■	■	■	■	■	■		
RT9	36.0	1235	20.8±2.7	■	−	0	■	0	+	−	0	+	0	0	0	■		
RT10	34.0	980	20.9±5.0	■	−	0	■	−	0	+	0	0	0	0	■	■		
RT11	28.0	365	11.9±2.9						+	+	+	−	+	X				
RT12	27.0	341	10.2±1.6						+	+	−	+	0	+	■	+	−	+
RT13	31.0	500	10.5±1.9						+	−	−	0	+	+	0	0	−	+
RT14	29.0	459	11.4±1.7						−	0	0	0	0	0	0	−	X	
RT15	28.0	374	10.0±1.7						−	0	0	0	0	−	0	0	−	0
RT16	27.5	335	12.8±2.3						0	−	+	−	+	+	■	+	−	+
RT17	30.5	520	15.0±1.8						−	−	+	−	+	−	0	−	+	0
RT18	30.0	474	12.5±1.3						+	0	0	−	0	−	0	+	0	−
RT19	25.5	242	10.5±1.9						−	+	0	−	+	+	0	−	−	0
RT20	31.0	479	16.0±3.8						−	+	−	+	−	+	0	+	−	+

Symbols under each date indicate the location of each fish relative to its position the previous week: same location (0), upstream (+), downstream (−), or not located (■). Upstream or downstream movement is noted only where this movement was in excess of the additive telemetry error for a given fish for the previous and current week. Three fish were captured by anglers, killed, and their tags returned, indicated by an X

We placed radio transmitters in 20 rainbow trout (Table 1). There was no mortality or illness following surgery. Ten large individuals (RT1-RT10), with SL from 32.0 to 38.5 cm, were tagged on 24 and 30 June 2005 and permitted to recover from the surgery at CABA for 1–2 weeks. On 7 July 2005, five large fish were released into the river at Site 1, 16.1 km upstream (Rkm) of Folsom Reservoir, and five were released at Site 2, 12.9 Rkm from the reservoir. Ten small individuals (RT11-RT20), with SL from 25.5 to 31.0 cm, were tagged on 4 August 2005 and allowed to recover for a week. On 12 August 2005, five small fish were released at Site 1, and five were released at Site 2. The tagged trout were released at two different sites to avoid introducing fish in high densities that might displace fish already present, and to minimize tag-code collisions while tracking. To facilitate locating the trout within the river we related transmitter signal power to distance for trout held temporarily in an enclosure in the river at the release sites.

The trout were located once weekly using a radio receiver and antenna, as we moved down the river in an inflatable raft during a pulsed flow. This sampling frequency was chosen to allow us to detect any net weekly displacement upstream or downstream that might occur in the presence of repeated pulsed releases. For safety reasons, track-

ing was conducted during daylight only. We recorded at least two sets of bearings from points on the riverbank for each fish, one further upstream or downstream from the other, and from the opposite side of the river, when possible. Fish location was estimated by triangulation of lines based on recorded maximum-signal-strength bearings. Fish locations were also based on transmitter signal strengths recorded as we rafted down the river. We recorded the trout's geographical coordinates using the receiver, the signal strength of the transmitter, the receiver's gain while observing the habitat of the trout (rapid, run, pool), and its location (river right, left, or middle) when the signal power of the transmitter was above 160 units. Tag calibration regressions were combined with the spatial error displayed on a GPS receiver (Garmin GPSmap 76s) to calculate the amount of error associated with each GPS-derived position, termed the telemetry error. Water temperature was measured from the raft during morning and evening periods to corroborate temperature patterns observed along the reach between Chili Bar Dam and Folsom Reservoir in prior studies.

We performed a mixed-model analysis of fish movement, using the ranked distance moved per week as the dependent variable (SAS for Windows Version 9.1®, proc mixed), using restricted maximum likelihood (REML, default), and including tests for the variance components (covtest option). The distribution of the data precluded analyzing the data using linear model theory. Fish identification number was a subject effect. Weekly distance moved was a repeated measure over time. We considered 11 fixed main effects: size, weight, health index, release location, week, habitat type, lateral location in the river, mean weekly daytime peak flow, mean weekly nighttime peak flow, mean weekly flow, and weekly flow range.

We did not include water temperature as a predictive variable because we did not know at which locations fish might have been between the weekly times that we located them, thus we did not know what temperatures fish had experienced. Furthermore, daily temperatures fluctuated over a relatively small range, compared with the large flow fluctuations that occurred once or more each day. Temperatures at the release sites were always well below the lethal limit for rainbow trout (approximately 24°C; Beschta et al. 1987), and frequently in the optimal range for rearing.

Results

During this study pulsed flows were usually discharged daily from Chili Bar Dam for approximately 4 hours, 09:00–13:00, for recreation, increasing the flow of water in the South Fork American River from $5 \text{ m}^3\text{s}^{-1}$ to $40 \text{ m}^3\text{s}^{-1}$ (Fig. 1). This pattern is absent during the first week of July because of snowmelt flows that exceeded the minimum recreational releases. In addition to the recreational releases, flows ranging from 50 to $110 \text{ m}^3\text{s}^{-1}$ were released, generally overnight, to manage water for hydroelectric power generation. There was greater variability between the baseline and maximum flows during the nighttime releases than during the day—the baseline varied from the absence of a release to $40 \text{ m}^3\text{s}^{-1}$ and maximum flows varied from the absence of a pulsed flow to a release of $110 \text{ m}^3\text{s}^{-1}$.

Water temperatures fell within the range observed in previous studies (PGE 2005a, b; FERC 2008). The afternoon temperature of the river, measured from the tracking boat, was between 16°C and 19.4°C in early July, during the week after the ten large fish were released, and was still over 16°C when the small fish were released in mid-August. Afternoon temperatures decreased to less than 15°C by mid October. The daily variation in temperature as we moved downstream was 1.0°C to 2.5°C from upstream sites in the morning to downstream sites in the afternoon.

The signal strength of transmitters in two small trout (NTC-4-2L tag) was described by the following relationship: Signal power=−3.34 Distance (m) + 226.11 (r^2=0.83, n=36). For one large trout (NTC-6-2 tag), with receiver gain set at 60, the relationship was: Signal power=−2.69 Distance (m) + 233.75 (r^2=0.85, n=8). The range of the transmitter's positional error was: large tags, 4 to 49 m; small tags, 4 to 36 m).

The location of each radio-tagged trout was determined weekly from 7 July 2005 to 13 October 2005. The large trout were detected within the river for periods ranging from 5 to 13 weeks (Table 1). RT3, RT5, and RT 7 were detected over a period of 13 weeks, until 29 September. After this they were no longer detected, and the tag batteries had likely expired. RT6 was captured by an angler and its tag returned to us; this fish was not observed in the river after week seven. Six large trout went unaccounted for at some point between weeks six and 13. The small trout were detected for periods ranging from 5

to 10 weeks, and eight out of the ten tagged trout were recorded over the entire 10-week duration of the study. RT11 and RT14 were captured by anglers and their tags returned to us; these fish were not observed in the river after weeks five and eight, respectively. We assumed that a given fish was still alive and actively swimming during a week in which upstream movement was observed. Eighteen of twenty fish showed upstream movement (greater than the additive telemetry error of the previous and current week) on at least one tracking date (Table 1), with the last upstream movement occurring between two and 12 weeks after release. RT14 and RT15 showed only downstream or no movement, but RT14 was captured by anglers after 7 weeks in the river, indicating that it survived 7 weeks in spite of showing no upstream movement during tracking.

Large trout dispersed both upstream and downstream from the release site at Rkm 16.1, but only downstream from the release site at Rkm 12.9 (Fig. 2). The large trout moved mainly during the first 4 weeks after their release. Eight of the trout moved 1.0–4.5 km downstream (Fig. 3a). RT10 moved the farthest during this period, quickly moving downstream 4.5 km, before moving downstream another 0.5 km. This fish moved upstream in the sixth week after release, then stayed in the same location for the next 4 weeks (Fig. 3a). While most of the others moved within 1.0–2.5 km downstream during this period, two trout (RT5 and RT6) stayed near their release sites for periods of 7 and 12 weeks respectively (Fig. 3a). Both these fish were apparently alive, since RT 5 moved upstream during the last week it was detected, and RT6 was captured by an angler. After the first 2 weeks, nine of the ten large trout moved little from one reach in the river, but all showed some upstream movement indicating that they were alive. In contrast, RT2 moved from a position 1.0 km downstream of the release site to a position 3.5 km downstream from the release site between the fifth and sixth week after its release (Fig. 2), and another 4.0 km downstream the following week (Figs. 2, 3a).

Small trout dispersed both upstream and downstream from both release sites (Fig. 2). They dispersed over a reach 1 km upstream and downstream of the release site during the first week (Fig. 3b). Eight of the small trout moved very little over the following eight weeks, although two fish were captured by

anglers, and all but one of the remaining fish showed small upstream movements during this period, indicating that they were alive. In contrast to the other small trout, RT16 moved 2.0 km upstream between the fourth and seventh weeks, and RT12 moved the same distance downstream during the fifth and seventh weeks.

The median distances moved by the fish showed little relationship to mean water discharge rates (Fig. 4). The median movement of large trout was 1.1 km downstream during the large discharge rate of 40 m^3s^{-1} during the first week after release. However, the distance moved by large trout during the second week was less than in the first, despite the rate of discharge being slightly higher, at 43 m^3s^{-1}. Furthermore, the majority of large and small trout moved little during subsequent weeks despite the discharge rate varying intermittently from 12 to 37 m^3s^{-1}.

Habitat types (pools, runs, rapids) used by trout did not change markedly between base flow and pulse flow conditions. The movement of habitat boundaries was less than the transmitter location error. The large trout spent most of their time in runs (41%), followed by pools (30%) and rapids (29%) during the 12 weeks that they were located within the river. The small trout were located in runs most often (42%), followed by rapids (30%) and pools (28%) during the 9 weeks that they were located within the river. Both large (56%) and small (51%) trout tended to inhabit the main channel slightly more often than in the river margins over the two periods, although no clear pattern of preference emerged.

No significant relationships were found between weekly trout movement and the 11 potential predictive variables in the mixed model analysis of the ranked movement data (Table 2), although the model fit was adequate (convergence criteria were met; covariance parameter estimate for compound symmetry (subject=fish-id(size)): Pr Z=0.9889, residual: Pr Z<0.0001; fit statistics: −2 res log likelihood= 1321.3, AIC=1325.3; null model likelihood ratio test: df=1, χ^2=0.00, Pr>χ^2=0.9888).

Discussion

The hatchery rainbow trout in this study did not appear to be displaced downstream by the pulsed flow

regime of the South Fork American River in the summer of 2005, in spite of over 20-fold daily flow fluctuations, or if fish were displaced they were able to regain their position prior to the next tracking event. Weekly movements of trout, either upstream or downstream, did not appear to be affected by the various metrics for flow and habitat we used in our model, nor did fish size appear to be a significant factor. Our results are similar to those of Gido et al. (2000) in which most adult rainbow trout were able to maintain position in the San Juan River during a reservoir discharge. Likewise, Klimley et al. (2005) found that radio-tagged adult rainbow trout and brown trout (*Salmo trutta*) were not displaced downstream by a one-day pulsed flow release in Silver Creek, a tributary of the South Fork American River, that experienced a greater than 35-fold increase

in flow. Salamunovich (2003) found little change in the observed species, number and sizes of fish before and after recreational pulsed flows in the Rock Creek and Cresta reaches of the North Fork Feather River. However, since observations were made on unmarked fish, via snorkel surveys, it is possible that fish were displaced downstream but were replaced by similar fish displaced from further upstream.

There were six large trout that went unaccounted for after the 6th to 13th week of the study. They may have been eaten by predators such as river otters, or caught by anglers who did not return the tags; anglers may have been more likely to release the smaller trout after capture. The large trout began to go missing around the same time that known angler captures occurred (5–8 weeks after release). It is possible that the large fish moved either upstream or downstream
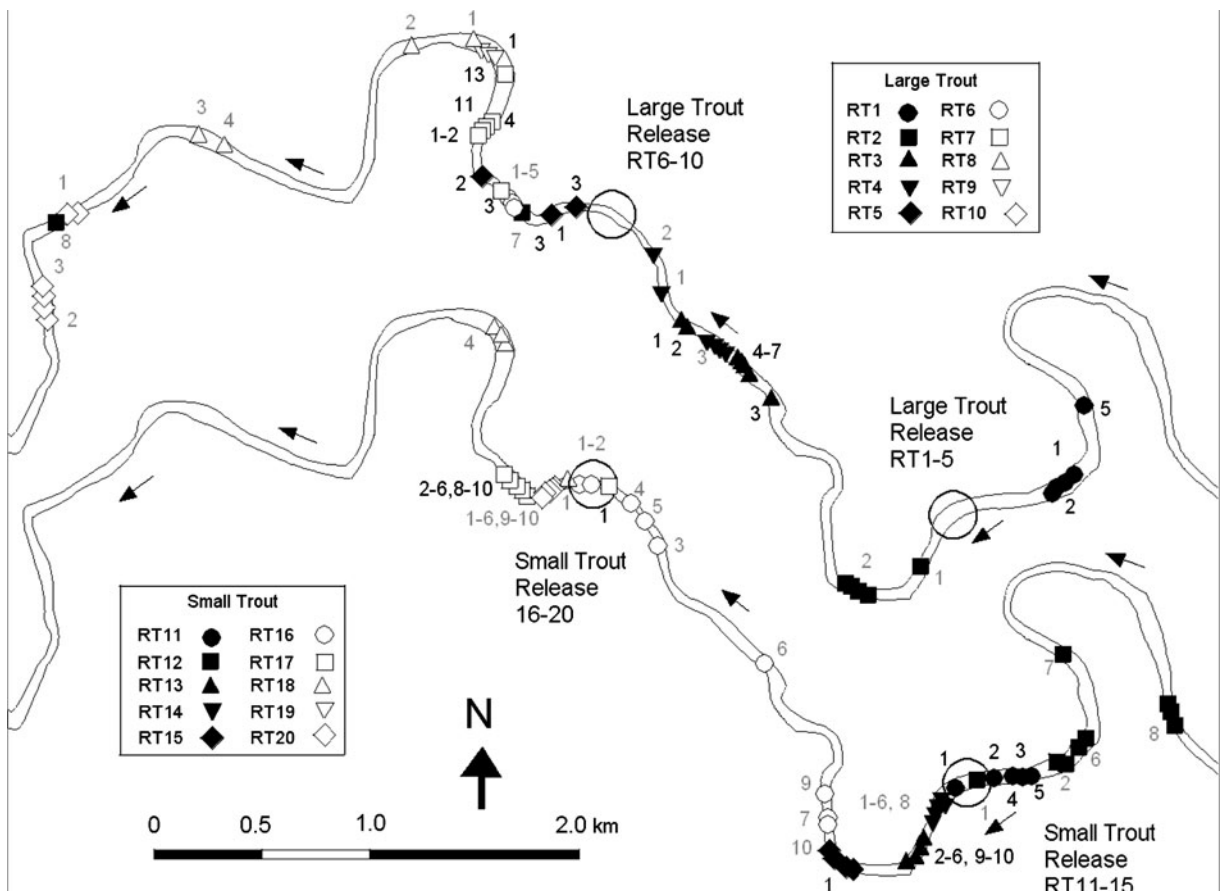
Fig. 2 Maps of the South Fork American River showing the release locations of the ten large rainbow trout (upper map) and ten small rainbow trout (lower map). Large trout were released on 7 July 2005, and small trout were released on 12 August 2005. The locations of individual fish in subsequent weeks are indicated with *symbols*, while the *associated numbers* indicate the week in which the fish was at a particular location. Fish ID codes correspond to the fish listed in Table 1

Fig. 3 Distance from release site plotted for **a** large and **b** small rainbow trout released in the South Fork American River and tracked for periods of 13 and 9 weeks, respectively, while subjected to pulsed releases of water from Chili Bar Dam from 7 July to 29 September 2005. Trout released at the upstream site are indicated by *black symbols*, while trout released at the lower site are indicated by *white symbols*. Fish ID codes correspond to the fish listed in Table 1
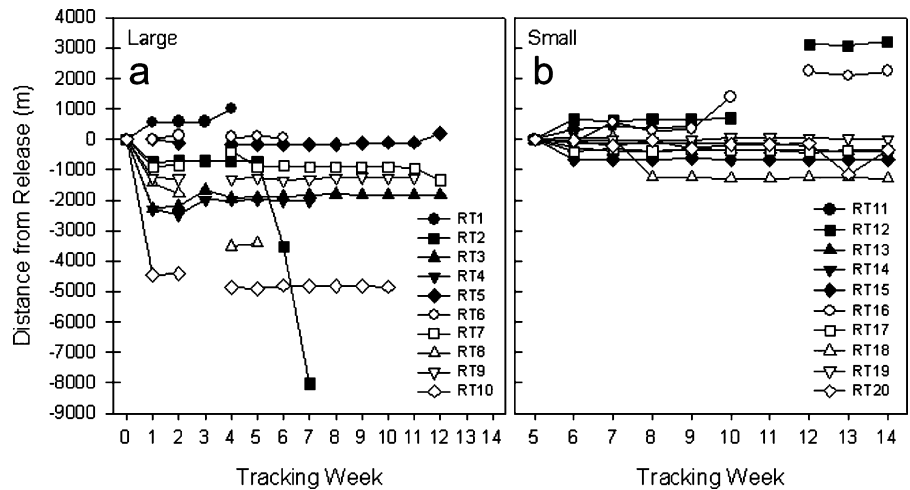

out of the study area. We did not use fixed antenna stations at the boundaries of our study area due to the very high levels of public foot and boat traffic, and consequent concerns for damage to or theft of unattended equipment. Fixed antennas would have permitted the detection of fish that left the study area. However, every fish that eventually went unaccounted for had shown both upstream or downstream movement in previous weeks of tracking (Table 1), and would have experienced a minimum of over 40 pulses before disappearing, indicating that they were not being steadily washed further and further downstream with successive pulsed flow releases. Our study

would have been improved by having a larger starting sample size, in order to compensate for losses to angling and natural predation, and to provide a greater chance of observing all the possible variation that exists in movement.

Given the repeated pulsed flows occurring in the study area both day and night, it is not possible to determine what distribution and amount of movement these trout would have displayed in the absence of pulsed flows. This is a limitation of studying a reach where frequent pulsed flows are both mandated for recreation, and permitted for hydropower generation and flood control. In order to address this limitation

Fig. 4 Movement (median ± 75th semi-quartile percentile) of trout and river discharge (mean±SE) during radio tracking studies in the American River. The large trout were released 5 weeks before the small trout. During tracks for week 13 and 14 none of the large radio-tagged trout were detected, presumably due to tag-battery senescence
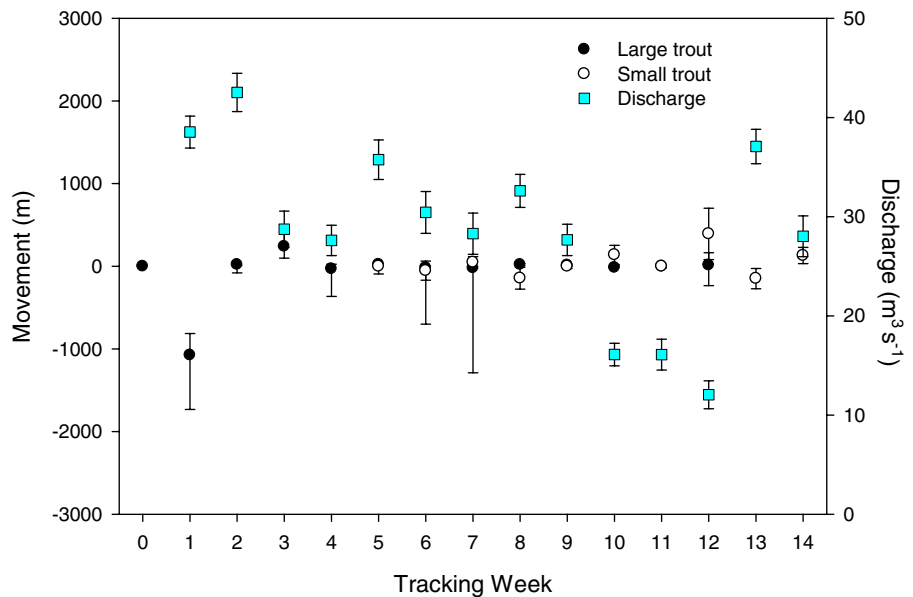
we conducted a separate study of a single-day pulse in a system where flows are rarely pulsed (Klimley et al. 2005). All the radio-tagged trout stayed within the 500-m study reach during a 35-fold increase in flow, and there was no pattern of upstream or downstream movement.

Radio-tracking studies of rainbow trout, brown trout, bulltrout (*Salvelinus confluentus*), and cutthroat trout (*Oncorhynchus clarki*) under natural flow regimes are consistent in their findings that individual trout tend to remain in a small home area, generally <1 km, during non-spawning periods (Clapp et al. 1990; Young 1996, 1998; Knouft and Spotila 2002; Ovidio et al. 2002; Schrank et al. 2003; Aarestrup et al. 2005; Popoff and Neumann 2005; Hojesjo et al. 2007), but that they may move longer distances (e.g., 3–63 km) during migrations to spawning habitat (Bailey et al. 1978; Meyers et al. 1992; Brown and Mackay 1995; Swanberg 1997; Ovidio et al. 1998; Burrell et al. 2000; Hilderbrand and Kershner 2000; Meka et al. 2003; Arnekleiv and Roenning 2004; Bahr and Shrimpton 2004; Bettinger and Bettoli 2004; Muhlfeld and Marotz 2005; Venman and Dedual 2005). In the South Fork American River rainbow trout would be expected to spawn in spring, as high winter flows recede. Because our study was conducted in summer, well after the spawning period, we expected the trout to remain near their release locations unless they were affected by pulsed flows. The majority (17/20) of the trout in this study stayed in a small home area throughout the time they were observed, following an initial movement upstream or

downstream directly after release, consistent with the behavior of trout in a non-pulsed system. Notably, three of the four large trout that disappeared part way through the study had maintained their position along the river for over a month prior to their disappearance.

The largest upstream movements of trout were accomplished during weeks of lower pulsed flows (weeks 11 and 12), which may indicate that fish may move upstream more readily when pulsed flow peaks are less extreme, and that high pulsed flows may limit the degree to which trout will move upstream. In a related laboratory study using a longitudinal flume juvenile rainbow trout (mean SL=5.0 cm±0.2 SE; mean wet weight=2.6 g±0.4 SE) showed no significant net movement, upstream or downstream (longitudinal displacement) from their mid-flume starting point, and were capable of maintaining swimming speed and position during short flow pulses up to 0.46 ms^{-1} velocity (Klimley et al. 2005).

The tendency of trout in this study to stay in the main channel, as opposed to the river margins may be related to feeding behavior, as food may be more abundant in the main channel where a greater volume of water (and drifting food) would pass by a fish swimming to maintain position in the current. The assessment of swimming speed was outside the scope of the current study, but given the high potential for the influence of food supplies and energetic constraints on the movement of trout in response to pulsed flow releases, we conducted a companion study of the energetic output of trout during pulsed

Table 2 Repeated-measures analysis of variance for the ranks of weekly distance moved (m) by 15 radio-tracked rainbow trout, with fish as subjects, repeated measures over time, and 11 fixed main effects (*n*=136)

Variables	Units	Class levels	DF	F	P
Size		2 (large, small)	1	0.01	0.9289
Weight	g		1	0.02	0.8944
Health index	Score from 11 to 55		1	0.00	0.9907
Release location		2 (Rkm 16.1,Rkm 12.9)	1	0.22	0.6535
Week		12 (week 1–12)	11	0.99	0.4581
Habitat type		3 (rapid, run, pool)	2	1.57	0.2166
Lateral river location		2 (main channel, margin)	1	1.85	0.1774
Mean weekly daytime peak flow	m^{3}s^{-1}		1	1.74	0.1903
Mean weekly nighttime peak flow	m^{3}s^{-1}		1	1.82	0.1807
Mean weekly flow	m^{3}s^{-1}		1	2.60	0.1096
Weekly flow range	m^{3}s^{-1}		1	0.03	0.8554

DF degrees of freedom, *F* variance ratio, *P* probability ($\alpha \leq 0.05$)

flow events, through the use of implanted electro-myogram radio transmitters (Klimley et al. 2007).

The overall distribution of large trout in our study is similar to that observed for adult Sacramento sucker in the Mokelumne River (Jeffres et al. 2006) in which most fish moved relatively short distances upstream or downstream from the release site in response to pulsed flows, but a few individuals moved large distances downstream. Initially after their release the large trout in our study moved downstream but in subsequent weeks they tended to remain in approximately the same location. The smaller trout did not show this same initial downstream displacement. The larger fish would have had higher caloric requirements relative to the smaller trout. If the larger trout were unable to find habitat with an adequate food supply they may have traveled in search of areas with greater food abundance, with downstream movement being less costly than upstream, thus spacing themselves out relative to the locally available food supply. The study reach had very few large rainbow trout (SMUD and PGE 2005), suggesting that it may not be suitable habitat, potentially due to the cumulative effects of repeated pulsed releases. However, we would not expect the habitat upstream or downstream of our study reach to have better habitat, since the flow regime is the same, and water temperatures downstream tended to increase above the optimal rearing range.

Our results suggest that the majority of hatchery rainbow trout released into the South Fork American River will not be washed downstream by repeated pulsed flows, and that most fish will remain in a home area within 3 km of their release site for several months, similar to trout in un-pulsed systems, unless captured by anglers or predators. We caution, however, that the ability of adult fish to maintain their position in the river does not necessarily imply that juvenile fish would have the same capability. Furthermore, the ability of trout to complete their life cycle, particularly spawning, egg incubation, and juvenile rearing, under the influence of repeated pulsed flows, was outside the scope of this study.

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